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Review

Importance of the riparian zone to the conservation and management of freshwater fish: a review

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Abstract. The relationship between freshwater fish and the integrity of the riparian zone is reviewed with special emphasis on the fauna of northern Australia. Linkages between freshwater fish and riparian zone processes are diverse and important. The riparian zone occurs at the interface between terrestrial and aquatic ecosystems and it may, therefore, regulate the transfer of energy and material between these systems, as well as regulating the transmission of solar energy into the aquatic ecosystem. Riparian influences on light quantity, quality and shade in streams are discussed and predictions are made about the likely impacts associated with changes in light quality. Increased rates of transfer of thermal energy between the atmosphere and the aquatic environment in the absence of an intact riparian zone may potentially disrupt reproduction by desynchronizing the thermal regimen from regional factors, such as the flow regimen, as well as having direct effects on mortality rates, body morphology, disease resistance and metabolic rates. Impacts associated with changes in light quality range from increased egg and larval mortality due to increased ultraviolet (UV) B irradiation and a decreased ability to discriminate between potential mates to increased conspicuousness to predators. Increased insolation and proliferation of exotic pasture grasses, an increasing threat in northern Australia, are shown to have a range of impacts, including changes in habitat structure, food-web structure and the facilitation of invasion by exotic fish species. The interception of terrestrial sediments and nutrients by the riparian zone has important consequences for stream fish, maintaining habitat structure, water clarity and food-web structure. Coarse organic matter donated to the aquatic environment by the riparian zones has a large range of influences on stream habitat, which, in turn, affect biodiversity and a range of process, such as fish reproduction and predation. Terrestrial matter is also consumed directly by fish and may be a very important source of energy in some Australian systems and under certain circumstances. Attention to the linkages between fish and riparian systems is essential in efforts to rehabilitate degraded stream environments and to prevent further deterioration in freshwater fish populations in northern Australia.

Extra keywords: foodwebs, habitat diversity, habitat structure, riparian subsidy, sexual selection.

Introduction

[Naiman and Decamps \(1997\)](#) define the riparian zone as encompassing ‘... the stream channel between the low and high water marks and that portion of the terrestrial landscape from the high water mark toward the uplands where vegetation may be influenced by elevated water tables or flooding and by the ability of the soils to hold water’. Whereas the width of the riparian zone and the extent to which it exerts an influence on the aquatic environment will vary greatly according stream size, landscape context and hydrologic regime ([Naiman and Decamps 1997](#)), riparian zones are recognized as areas of biological, physical and chemical interaction between terrestrial and aquatic ecosystems ([Gregory *et al.* 1991](#)) and, consequently, are typified by unusually high biodiversity and diversity of environmental processes.

The importance of riparian zones to aquatic ecosystems is well recognized ([Welcomme 1979](#); [Bunn 1993](#); [Naiman and Decamps 1997](#)). Terrestrial primary production derived from the riparian zone and floodplains is acknowledged as a vital source of energy in riverine food webs ([Vannote *et al.* 1980](#); [Junk *et al.* 1989](#); [Bunn 1993](#); [Thorpe and DeLong 1994](#)). Terrestrial secondary production may also be a significant contributor of energy to riverine food webs ([Chloe and Garman 1996](#); [Nakano *et al.* 1999](#)). Other important influences include thermal buffering ([Lynch *et al.* 1984](#)), the provision of shade and its influence on in-stream primary production ([Bunn *et al.* 1999a, 1999b](#)), nutrient interception, storage and release ([Omernik *et al.* 1981](#); [Smith 1992](#); [Osborne and Kovacic 1993](#); [Arthington *et al.* 1997](#)), enhancement of bank stability ([Beeson and Doyle 1995](#); [Prosser *et al.*](#)

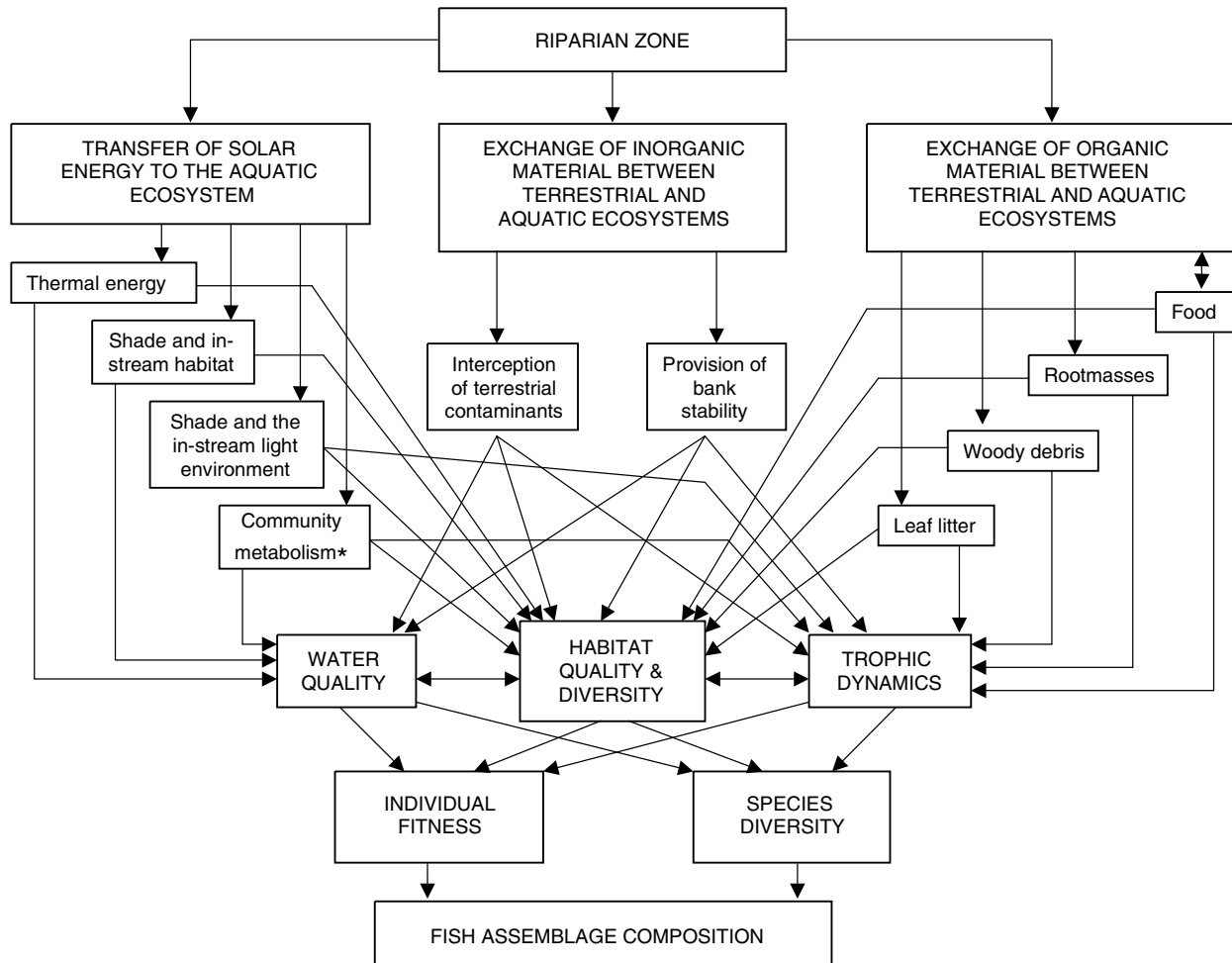


Fig. 1. Conceptual model depicting the mechanisms by which riparian regulation of energy and material transfer to the riverine ecosystem impacts on riverine fish communities. *This component will not be dealt with in detail here.

2001), the provision of coarse woody material as habitat and substrate for fish, invertebrates and microalgae (Everett and Ruiz 1993; Sheldon and Walker 1998; Crook and Robertson 1999), mediation of changes in channel morphology and habitat diversity (Nakamura and Swanson 1993; Beechie and Sibley 1997) and refuge from disturbance at a variety of scales from that of the particle (i.e. individual pieces of wood) to that of the watershed (Sedell *et al.* 1990).

Given the number and importance of links between riparian and lotic ecosystems, it is not surprising that spatial and temporal variation in fish assemblage composition and characteristics (i.e. species richness, abundance, biomass) have been linked to variation in riparian cover (Angermeier and Karr 1983; Davies 1989; Pusey *et al.* 1993, 1995a, 2000a; Amour *et al.* 1994; Penczak *et al.* 1994; Marsh-Matthews and Matthews 2000) or that fish communities are adversely affected by riparian destruction and recover

only when riparian integrity is re-established (Penczak 1997). Penczak *et al.* (1994) stressed that the mechanisms by which such relationships arise are difficult to ascertain due to the multifactorial and highly interrelated nature of the linkages between freshwater fish and riparian zones.

The present paper reviews the many linkages between the aquatic ecosystem and the riparian zone and the mechanisms by which such linkages may affect lotic fish. We consider the various pathways by which changes in these linkages may lead to alterations in stream fish assemblages and the potential for their mitigation or reversal if riparian zones are reforested. We develop a model (Fig. 1) in which the capacity of the riparian zone to regulate the transfer of energy (solar radiation) and material (both inorganic and organic) to the aquatic ecosystem influences fish assemblage composition via impacts on individual fitness and species diversity mediated by changes in water quality, habitat quality and

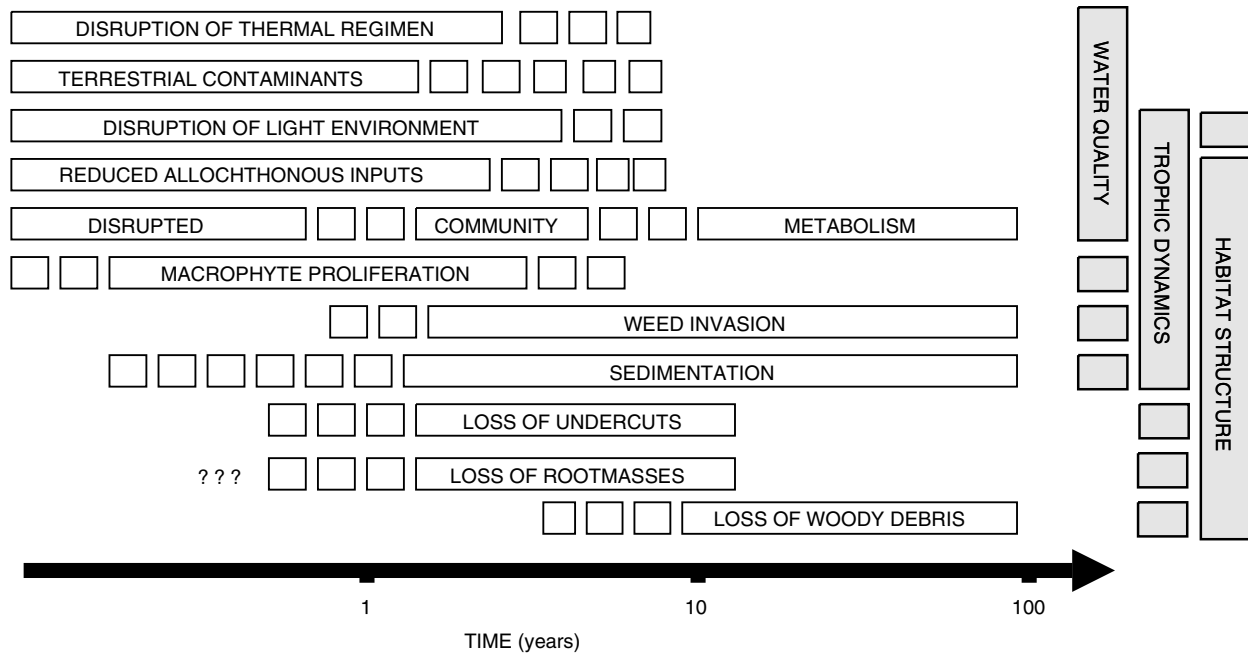


Fig. 2. Temporal scale for the imposition of impacts on fish associated with riparian degradation. Broken boxes indicate that impacts are gradually imposed or gradually decrease in importance with time.

diversity, and trophic dynamics. (The interception of light and its influence on in-stream primary and secondary production and the influence that this may have on freshwater fish (and other biota), has been reviewed by Bunn *et al.* (1999b) and will not be dealt with here in detail.) The model allows a time sequence for impacts associated with reduced riparian integrity to be developed (Fig. 2), which may then be used to identify and compare effective rehabilitation measures. Although the present review draws on examples of linkages between riparian systems and riverine fish from the world literature, emphasis will be placed on the freshwater fish of northern Australia, where streams are typically fringed by gallery forest vegetation comprised largely of rainforest tree and shrub species. Clearing and development has removed this vegetation from many streams during the past 100–150 years, replacing it with pasture grasses or sugar cane croplands, and these practices threaten the maintenance of the region’s fauna. However, we see little reason why many of the linkages proposed for northern Australia should not also be important in temperate Australia.

Transfer of solar energy to the aquatic ecosystem

Shade and its influence on the in-stream thermal regime

Riparian canopy plays a large role in regulating the transfer of thermal energy to stream ecosystems and is important in determining the thermal aspect of water quality in lotic environments. Reduced riparian cover has been shown

to result in increased average summer water temperatures (Lynch *et al.* 1984; Pearson and Penridge 1992; Quinn *et al.* 1992), decreased winter water temperatures (Lynch *et al.* 1984; Amour *et al.* 1994) and an increase in the extent and rate of change of diel fluctuations of water temperature (Lynch *et al.* 1984; Quinn *et al.* 1992). Seasonal patterns of temperature change may be obscured or modified and variability at shorter time scales may be increased (Lynch *et al.* 1984). Changes to the in-stream thermal regimen may be spatially persistent and extend well into reaches with intact riparian zones downstream of degraded riparian conditions and, thus, affect downstream habitat quality. For example, Storey and Cowley (1997) found that the thermal regimen of a stream disrupted by riparian removal returned to normal only after passing through 300 m of intact forest. Obviously, riparian rehabilitation measures will have limited large-scale effect with respect to water temperature if such measures are spatially patchy in implementation.

Environmental temperature directly controls basal metabolic rate in poikilothermic organisms such as fish and, therefore, influences growth and the allocation of resources for reproduction, both of which have fitness consequences and, ultimately, determine population size (Jobling 1995). Growth rates in fish may increase when ambient temperatures are elevated if thermal growth optima are not exceeded and provided that food availability is sufficient to provide energy in excess of that required for maintenance (McCauley and Casselman 1981). However, increased insolation also

increases the rate of photon flux, which may shift primary production away from unicellular microalgae to filamentous green algae unpalatable to invertebrate secondary producers (Bunn *et al.* 1999a). Negative growth may occur in such a circumstance if invertebrate abundances are suppressed greatly and metabolic demands remain high. In a landscape where the integrity or extent of riparian canopy cover varies in a patchy manner, but the net effect is one of elevated water temperatures, a mosaic of growth responses may arise. Many species of fish show marked preference for certain temperatures closely corresponding to their temperature optimum for growth (McCauley and Casselman 1981) and patterns of microhabitat use in fish are influenced by water temperature (Brett 1971; McCauley and Huggins 1979; Matthews 1998). Differential selection of thermal microhabitats may allow the coexistence of closely related species (Hloloowskyj and Wissing 1987). Pusey *et al.* (1997) suggested that the distribution of different species of rainbowfish (Melanotaeniidae) in streams of the Australian Wet Tropics is related to spatial variation in winter water temperatures. Changes in thermal regimen have the potential to alter the distribution of fish at both small and large spatial scales.

Extremes in temperature may have direct and lethal effects on fish arising from fluid electrolyte imbalance, alteration to rates of gaseous exchange, impaired osmoregulatory ability, hypoxia of the central nervous system and inactivation of enzyme systems (Cherry and Cairns 1982). In addition, elevated temperatures can alter the tolerance of fish to other toxicants, such as ammonia (Linton *et al.* 1997), and environmental stresses such as low concentrations of dissolved oxygen (Llewellyn 1973; Pearson and Penridge 1992). Fish species adapted to cool stream water with high oxygen concentrations are intolerant of elevated temperatures and reduced dissolved oxygen levels (Koehn and O'Connor 1990; Pearson and Penridge 1992).

Disease resistance in poikilotherms is also related to temperature. Langdon *et al.* (1985) reported massive winter mortality due to severe infection by the ciliate protozoan *Chilodonella hexasticha* in the clupeid *Nematolosa erebi* (bony bream) and, to a lesser extent, in other species in the Finke River, central Australia. These authors suggested that low winter water temperatures decreased the ability of these fish to withstand infection by inhibiting immune ability. Similarly, rates of fungal infection among populations of the Lake Eacham rainbowfish *Melanotaenia eachamensis* and the gudgeon *Mogurnda adspersa* on the Atherton Tablelands, north Queensland, are greatest when dry season water temperatures are at their lowest (B. J. Pusey and A. H. Arthington, unpublished data).

Seasonal variation in water temperature is an important cue for gonad development or spawning in many freshwater fish (Lowe-McConnell 1979; Bye 1984), including those of southern, subtropical and northern Australia (Milton and Arthington 1983, 1984, 1985; Koehn and O'Connor 1990;

Pusey *et al.* 2001a). Fish may simply not breed if critical temperatures are not reached. More importantly, changes in thermal regimen can disrupt fish reproduction if seasonal changes in stream water temperature are decoupled from other seasonal factors, such as flow regimen, and the availability of habitat and food.

Embryonic development, hatching time and larval development in fish are also significantly influenced by water temperature (Llewellyn 1973). Long development times at low temperatures may increase the potential for eggs and larvae to be consumed by predators and rapid changes in water temperature may disrupt reproduction (Graham and Orth 1986). Water temperature during embryonic development may even influence sex ratio in fish (see Holmgren 1996) and variation in temperature during early development can affect adult morphology (Taning 1952). Seasonal variation in water temperature may also provide the necessary cue to stimulate movement of adult fish for spawning or of juveniles recruiting into adult habitat (Sloane 1984; Martin 1995).

Most of the literature examples used above have been drawn from overseas studies. Although studies on the temperature tolerance of a few Australian species have been undertaken (e.g. Beumer 1979), little investigation of the influence of temperature on fish ecology has occurred. Impacts associated with changes in thermal regimen are likely to be experienced very shortly after disruption to the riparian zone and may initially be severe (i.e. exceedance of thermal tolerance levels) and categorized as a pulse disturbance. Secondary effects associated with changes in growth, fitness and habitat selection are likely to be more gradual in manifestation, more press-like with respect to disturbance regimen and to persist in importance for a longer time as fish assemblage structure adjusts to reflect changed habitat conditions (Fig. 2).

Shade and its influence on in-stream habitat

The growth and proliferation of submersed macrophytes is limited, *inter alia*, by riparian canopy cover and its effect on light availability (Canfield and Hoyer 1988; Gregory *et al.* 1991). Macrophytes provide important habitat for many fish and spatial variation in fish distributions in several Queensland rivers has been correlated with spatial variation in macrophyte abundance (Pusey *et al.* 1993, 1995a, 1998, 2000a). Macrophytes are also an important spawning substrate for many tropical fish species (Merrick and Schmida 1984; Pusey *et al.* 2001a), as well as habitat for larval and adult fish (Bishop and Forbes 1991; Kennard 1995; Pusey *et al.* 2001b). Macrophytes function as refuges from both high water velocity and predators (Losee and Wetzel 1993; Werner *et al.* 1983; Mittelbach 1986). Furthermore, many northern Australian fish consume aquatic macrophytes as part of their diet (Bishop *et al.* 1984; Arthington *et al.* 1994; Kennard 1995; Pusey *et al.* 1995b, 2000b; Kennard *et al.* 2001). Macrophytes also provide the structural matrix for the production of epiphytes that may then form the basis of

grazing food webs (Wetzel 1990). Whereas these examples illustrate the general importance of submersed macrophytes to stream fish, the proliferation of macrophytes under conditions of high light intensity (and where nutrients are not limiting) may negatively impact on fish by reducing habitat diversity and depressing secondary production (Mackay *et al.* 2001). In addition, diel fluctuations of dissolved oxygen may become so severe in dense macrophyte beds as to cause the death of fish (Townsend *et al.* 1992). It is proposed here that these impacts are likely to be felt gradually as macrophyte density gradually increases to the point where it exerts greatest influence (i.e. a press disturbance) and to decrease in importance over a number of years (e.g. a decade) as fish assemblages adjust to the altered habitat structure and water quality regimen and until the proliferation of submersed grasses (see below) results in habitat condition unsuitable for macrophytes (Fig. 2).

Light availability also limits the proliferation of weed species, such as para grass (*Urochloa mutica*), an exotic ponded-pasture species introduced into Australia as cattle fodder and to stabilize stream banks (presumably after the native riparian zone had been destroyed). The proliferation of such grasses under conditions of reduced canopy cover (Sattler 1993; Tait 1994) greatly influences in-stream habitat value by trapping sediment and channelizing flows, leading ultimately to channel contraction until low-frequency, high-intensity flood events re-establish normal channel dimensions (Bunn *et al.* 1998). The proliferation of pasture grasses leads to a suite of changes in habitat structure (Arthington *et al.* 1983), water quality and food-web structure (Bunn *et al.* 1997, 1998), all of which impact on fish. The growth of pasture grasses in streams reduces the diversity of flow environments present by confining discharge to a central flow path of uniformly high velocity. Flow diversity is an important determinant of the diversity of fish within stream reaches (Schlosser 1982, 1987; Pusey *et al.* 1993). In addition, reduced flows within the littoral grass fringe lead to conditions of poor water quality, particularly depressed dissolved oxygen due to high rates of plant respiration and reduced recharge (B. J. Pusey and A. H. Arthington, unpublished data). Stream fish are sensitive to reduced oxygen availability (Cech *et al.* 1990) and typically avoid such areas (Matthews 1998).

Finally, the living tissue of submersed C₄ grasses (i.e. those that fix carbon from carbon dioxide via the Hatch-Slack photosynthetic pathway, such as para grass) contributes very little to aquatic food webs (Bunn *et al.* 1997). Moreover, senescent leaf material collects on the stream bed, where it remains unprocessed by secondary consumers, forming a thick anoxic layer of organic ooze inimical to both fish and invertebrates. Few Australasian fish species consume large amounts of detritus (Coates 1993) and, in many cases, apparent detritivory is better characterized as the consumption of microalgae (Kennard *et al.* 2001). Thus, the

freshwater fish of northern Australia, like stream invertebrates, do not directly consume this pool of organic matter. The loss of habitat suitable for periphyton and macroinvertebrates, the absence of riparian inputs and the failure of carbon derived from the submersed grasses to enter aquatic food chains result in substantial alteration of the aquatic food-web (Bunn *et al.* 1997), with consequences for those stream fish still able to persist in the abiotic conditions of such a modified habitat. The diversity of invertebrate prey is much reduced and fish are forced to alter foraging behavior or consume prey items not normally found in the diet (Arthington 1992; Pusey *et al.* 1995b; Bunn *et al.* 1997).

Arthington *et al.* (1983) found that the proliferation of littoral grasses altered the composition of stream fish assemblages in streams of south-east Queensland and favoured the establishment of exotic fish species, particularly members of the family Poeciliidae (e.g. *Gambusi holbrooki* and species of *Xiphophorus*). A similar association between exotic poeciliid fish (*Poecilia reticulata* and the platy *Xiphophorus maculatus*) and reduced canopy cover and abundant invasive grasses occurs in streams of the Australian Wet Tropics area (Pusey *et al.* 2000a). Many members of the Poeciliidae are tolerant of hypoxia because their upturned mouths allow them to access the thin, well-oxygenated layer of surface water and they can thus make use of areas of degraded water quality (Arthington and Lloyd 1989). Tilapia (*Oreochromis mossambicus*), a noxious pest species in Australia, is similarly tolerant of low dissolved oxygen (Job 1969) and is also frequently associated with submersed littoral grasses (i.e. in tributary streams of the Barron River on the Atherton Tablelands in northern Queensland (B. J. Pusey, unpublished data). Pondered pasture grasses have a range of direct and indirect influences on stream environments and their biota and, accordingly, pose a significant threat to the maintenance of aquatic biodiversity in northern Australia (Clarkson 1995).

Weed invasion is a gradually incipient press disturbance with impacts due to changes in habitat structure, trophic dynamics and food-web structure slowly increasing in intensity as weed encroachment progresses. These impacts are likely to be very long lived because further weed encroachment favours the establishment of exotic fish species and changes in sediment deposition and channel dimensions become ever more unlikely to be returned to the natural state by natural processes such as floods (Bunn *et al.* 1998; Fig. 2).

Finally, it should be noted that shade *per se* is a feature of the habitat structure and diversity of habitats in stream and riverine environments. Fish make use of shade both as a refuge from predation and as areas of cover from which to launch predatory attacks (Helfman 1981).

Shade and its influence on the in-stream light environment

In addition to the regulation of light intensity (Hill 1996; Bunn *et al.* 1999a), riparian vegetation (or its absence) influences the spectral qualities of the light entering the stream/river

environment. Riparian vegetation intercepts light in the non-visual end of the spectrum (i.e. ultraviolet (UV) radiation). Increased exposure to UVB light (280–320 nm) has been shown to be lethal or detrimental to the eggs, embryos and larvae of some fish (Gutierrez-Rodriguez and Williamson 1999). In northern Australia, impacts due to UV exposure are most likely to be experienced by open shallow water-spawning species such as the catfish *Tandanus* sp., the grunter *Hephaestus fuliginosus* and the blue-eye *Pseudomugil signifer*. However, the larvae of many species of stream fish in the Wet Tropics region occur in the top layers of the water column (Pusey *et al.* 2001b) and, therefore, may be at risk of greater exposure to UV radiation under conditions of reduced canopy cover.

Light quality (i.e. the combination of light intensity over the wavelength spectrum of visible light) varies depending on the time of day (i.e. declination of the sun), the degree of cloudiness and the selective interception of different wavelength bands by foliage (Endler 1993). Irrespective of changes to the light spectra occurring after light penetration of the water column, streams and rivers will contain a variety of different light habitats (i.e. patches of differing spectral composition) depending on stream size and integrity of the riparian zone. Small streams with intact riparian canopy should be dominated by yellow/green light with small patches of yellow/orange light, whereas large streams should be dominated by large gap whitish light. Medium-sized streams should contain a diversity of light habitats. Destruction of, or damage to, the riparian zone causes the diversity of light habitats to decrease and, generally, to become dominated by large gap light. Fish species with different color patterns will be conspicuous under different spectral regimens (i.e. yellow or red/orange pigmentation should be most efficient as a signal color in small shaded streams, whereas blue should provide a better signal color in medium-sized streams). In addition, the juxtaposition of different light habitats within a stream may be critical to the ability of fish to attract mates while simultaneously avoiding detection by predators, as has been shown for lekking tropical forest birds (Endler and Thery 1996). For example, both Pacific blue-eye (*P. signifer*) and Empire gudgeon (*Hypseleotris compressa*) alternately display in sunlit patches, where they are conspicuous to both con- and heterospecifics, and then retreat to shade, where they are conspicuous to neither (B. J. Pusey, unpublished data). Conspicuousness increases the ability to attract mates in species that use visual cues to do so, but also increases exposure to predation and, thus, has substantial fitness consequences (Endler 1991). The efficiency of communication between visually communicating species, which includes many riverine fish, depends strongly on spatial and temporal variation in the light regimen (Endler 1993). A change in the ambient light spectrum resulting in a change in the efficiency of a color pattern to attract potential mates or to allow differentiation between potential mates, or ensure

cryptic, will impact on fitness and, ultimately, on organismal abundance and local assemblage composition (Endler 1997; Sleenhausen *et al.* 1997).

A disrupted light environment is likely to behave as both a pulse and a press disturbance first as predator/prey dynamics are shifted in favour of predator species and second as changes in mate recognition and larval survival gradually influence fish assemblage structure (Fig. 2).

Interception of potential inorganic contaminants: nutrients and sediment

Nutrients and sediment enter the lotic environment through hill slope, stream bank and gully erosion and via groundwater (Prosser *et al.* 1999). Riparian vegetation mediates their input by armoring stream banks against erosion, storing runoff, trapping sediment and transforming nutrients (Omernik *et al.* 1981; Smith 1992; Osborne and Kovacic 1993; Arthington *et al.* 1997; Prosser *et al.* 1999, 2001 Townsend and Douglas 2000). Increased nutrient availability, when combined with increased insolation, may stimulate the growth of plants to the point where they impact negatively on stream fish (see above for a discussion of the effects of prolific macrophyte and weed growth). Filamentous algae are favoured under regimens of high nutrient and light availability, but are not readily incorporated into aquatic food-webs by invertebrate consumers (Bunn *et al.* 1999b; Prosser *et al.* 1999); consequently, fish may find their food base drastically altered in composition and abundance. Exotic species (e.g. poeciliid topminnows) consume filamentous algae (Arthington 1992; Pusey *et al.* 1995b). Some native fish, particularly adult age classes of rainbowfish and grunters (Therapontidae), consume appreciable quantities of filamentous algae (Pusey *et al.* 1995b, 2000b) and, although these fish may be favoured over more insectivorous species under conditions of high algal abundance, their juvenile forms are highly reliant on insect prey and are likely to be disadvantaged by these conditions. Notably, the consumption of filamentous alga is very uncommon in fish of temperate Australia (Kennard *et al.* 2001). Irrespective of changes in trophic ecology, few fish of northern Australia use filamentous algae as a microhabitat (B. J. Pusey, M. J. Kennard and A. H. Arthington, unpublished data). Eutrophication, due to increased nutrient availability and consequent proliferation of planktonic algae, has been shown to impact on cichlid fish diversity in lakes by changing light penetration and curbing sexual selection (Sleenhausen *et al.* 1997).

Increased sedimentation has several direct and indirect consequences for stream fish (Rabeni and Smale 1995). Increased turbidity and sedimentation impact on fish by altering food availability (e.g. benthic invertebrates and algae; Berkman *et al.* 1986; Berkman and Rabeni 1987), reducing foraging behavior and efficiency (Berg and Northcote 1985; Berkman and Rabeni 1987; Breitberg 1988; Miner and Stein

1993; Bergstedt and Bergersen 1997; Boubée *et al.* 1997) and altering intraspecific interactions (Berg and Northcote 1985). Other effects include a reduction in habitat suitability (e.g. smothering of coarse gravel beds) for spawning, foraging and refuge (Balon 1975; Walser and Bart 1999), increasing physiological stress (Bergstedt and Bergersen 1997) and increasing egg mortality, as well as reducing rates of larval development and survival (Morgan *et al.* 1983). Thus, the transfer of fine sediments to the stream environment is expected to impact heavily on stream fish, but impacts will be felt only gradually, and as a press disturbance as habitat quality slowly decreases. Such impacts are expected to persist for a very long time (i.e. many decades; Detenbeck *et al.* 1992; Harding *et al.* 1998).

Restoration of water quality is frequently an implicit, desired outcome of riparian revegetation programs (Prosser *et al.* 1999). However, in the short-to-medium term, a reduction in water quality may occur due to the liberation of entrapped sediment (e.g. Bunn *et al.* 1998) following the senescence of ponded-pasture grasses as a result of increasing shade provided by the developing canopy. Increased turbidity and siltation may impact on intact downstream reaches and retard rehabilitation of fish communities.

Exchange of organic material between terrestrial and aquatic ecosystems

Terrestrial organic matter as in-stream habitat: leaf litter

Riparian forests are a large source of organic carbon, in the form of leaf litter and fine woody debris, to stream environments where, in addition to its role as a food source and habitat for macroinvertebrates, it forms habitat for fish. In streams of the Wet Tropics region, many fish species, such as juvenile eels (*Anguilla reinhardtii*), swamp eels (*Synbranchus bengalense*), gudgeons (*Mogurnda adspersa*) and even rainbowfish (*Cairnsichthys rhombosomoides*), use leaf litter as a habitat, particularly when other habitat elements, such as macrophytes and undercut banks, are in short supply (B. J. Pusey, M. J. Kennard and A. H. Arthington, unpublished data). However, leaf litter beds are not optimum habitats for many fish. Sustained microbial respiration may render the interior of leaf litter beds hypoxic and the small size of the interstices within leaf litter accumulations may render them unsuitable for all but the smallest individuals or those with anguilliform body shape. In addition, invertebrate processing, seasonal patterns of litter input and removal or redistribution during high-flow events ensure that litter beds are a transient microhabitat feature of the meso- and macrohabitat (B. J. Pusey and A. H. Arthington, unpublished data). Nonetheless, some species are known to be highly dependent on litter beds as habitat, such as the goby *Mugilogobius notospilus* in lowland streams of the Wet Tropics region (Pusey; cited in Larson 2001), and the cobitid *Pangio mariarum* of south-east Asia (Martin-Smith 1998).

Terrestrial organic matter as in-stream habitat: woody debris

Woody debris plays a multidimensional role in the structure and functioning of stream ecosystems (Angermeier and Karr 1984). It increases the retention and processing of organic matter, thus limiting nutrient spiralling distances and increasing the efficiency of energy retention in streams (Minshall *et al.* 1985), thereby supporting increased invertebrate abundance (Cummins and Klug 1979; Angermeier and Karr 1984) available to fish as food. Wood itself may be an important source of carbon when leaf litter is in short supply (Hall *et al.* 2000), its decomposition contributing significantly to supplies of dissolved organic matter and fine particulate organic matter (Ward and Aumen 1986). The complex surface structure of wood provides an important substrate for colonization by a range of microbes, including fungi, bacteria and algae, commonly referred to as 'biofilm' (Scholz and Boon 1993). Biofilm activity is essential to the generation of organic carbon and nutrients in aquatic environments. In river systems with sandy, unstable substrates, woody debris provides the only stable substrate for biofilm and macroinvertebrates (Wallace and Benke 1984; Thorpe and Delong 1994; Sheldon and Walker 1998), which constitute important components of food chains and sources of food for fish.

Woody debris is of direct consequence to fish in many ways (see the extensive review by Crook and Robertson (1999)). Woody debris provides protection from fish piscivores (Angermeier and Karr 1984; Everett and Ruiz 1993; Persson and Eklov 1995; Kennard 1995) and avian predators (Crook and Robertson 1999) and refuge from elevated water velocities (Angermeier and Karr 1984). The presence of woody debris in rivers may determine the extent to which assemblage composition is altered by flooding (Pearsons *et al.* 1992). The structural complexity of woody debris itself may be important in determining the degree to which it ameliorates high water velocity (McMahon and Hartman 1989), the extent to which it provides protection from predators (Kennard 1995) and is an important determinant of the diversity of fish it supports (Probst *et al.* 1984; Monzyk *et al.* 1997). Woody debris may be used as cover for ambush predators (Koehn *et al.* 1994) and may be an important determinant of the growth rates of piscivorous fish (Persson and Eklov 1995). Woody debris may act as a landmark to aid navigation (see Crook and Robertson 1999) and fish may move through reaches with little woody debris at higher rates than through reaches with abundant debris (Hansen 1971).

Woody debris adds structural complexity to stream habitats, as well as influencing patterns of scour and deposition sufficiently to increase physical complexity (i.e. scour pools, riffle/pool spacing; Angermeier and Karr 1984; Nakamura and Swanson 1993). Habitat complexity is an important determinant of lotic fish diversity at the meso- (i.e. reach) and macrohabitat scale (i.e. basin; Schlosser 1982, 1991, 1995;

Bishop and Forbes 1991; Pusey *et al.* 1993, 1998, 2000a; Matthews 1998).

Given the degree to which woody debris may influence freshwater fish, it is not surprising that many studies have shown that spatial variation in fish abundance, biomass, average fish size or assemblage composition is correlated with the abundance of woody debris (Congdon 1971; Hortle and Lake 1983; Angermeier and Karr 1984; Everett and Ruiz 1993; Kennard 1995) or that the addition of woody material increases fish abundance and alters assemblage composition (House and Boehne 1986; Kennard 1995). In southern Australia, species of iconic recreational and conservation significance, such as the blackfish *Gadopsis marmoratus* and *Maccullochella peeli*, *Maccullochella macquariensis* and *Macquaria ambigua*, are highly dependent on woody debris (Koehn and O'Connor 1990). Northern Australian fish with a high dependency on woody debris as resting or spawning habitat include the barramundi *Lates calcarifer*, mangrove jack *Lutjanus argentimaculatus*, catfish of the genus *Neosilurus*, the gudgeon *Oxyeleotris lineolatus*, *Hephaestus* spp., *A. reinhardtii* and many others (Bishop *et al.* 1984; Merrick and Schmida 1984; Bishop and Forbes 1991; Kennard 1995; Pusey *et al.* 1995a, 1998, 2000a). Kennard (1995) showed experimentally that the addition of woody debris to floodplain lagoons of the Normanby River altered trophic and reproductive dynamics of the resident fish fauna sufficiently to significantly affect overall assemblage composition and that this effect arose because of the refuge from predation by barramundi and fork-tailed catfish provided by woody debris.

Woody debris is a persistent feature of the lotic environment and, for this reason, impacts associated with riparian clearing and its effects on the availability of woody debris are unlikely to be felt in the short term (Fig. 2). Nonetheless, weed invasion, sedimentation and changes in channel dimensions gradually reduce the availability of woody debris to fish (although it may still be retained buried in the stream channel). In contrast with the persistence of woody debris reported for temperate Australia (see Gippel *et al.* 1992), woody debris in rainforest rivers tends not to be so refractory (B. J. Pusey and A. H. Arthington, unpublished data), possibly due to greater processing once in the water, significant decomposition while in the vertical position prior to entering the lotic environment or greater lability in high gradient rivers: the onset of impacts associated with the loss of woody debris may occur earlier in tropical environments. The loss of woody debris from the stream environment is likely to have consequences for many decades.

Terrestrial organic matter as in-stream habitat: in situ root masses and undercuts

The intact *in situ* root structures of riparian trees are important in the formation and maintenance of habitat for fish. Exposed roots (particularly the fine root tips) may be used as

spawning substrate and larval habitat by stream fish (Pusey *et al.* 2001a, 2001b), as well as habitat for adult fish (Pusey *et al.* 1998). In the Burdekin River, the relative abundance of many adult fish species is correlated with rootmass abundance (and other bank-associated structures, such as woody debris and undercutting; Pusey *et al.* 1998). The gudgeons (Eleotridinae) are notable denizens of root masses: species such as *Eleotris melanosoma*, *Eleotris fusca* and *Bunaka gyrinoides* are very infrequently collected from microhabitats other than root masses (B. J. Pusey, M. J. Kennard and A. H. Arthington, unpublished data).

It is difficult to separate the habitat provided by root masses *per se* from that provided by undercut banks, with which they are usually associated. Riparian trees provide enormous additional stability to stream banks by increasing resistance to erosion (Smith 1976; Beeson and Doyle 1995) and are critical in the formation of undercuts (Rutherford *et al.* 1999). Undercuts provide daytime resting habitat for a large array of fish of northern Australia, such as gudgeons (Eleotridinae), catfish (Plotosidae), grunthers (Terapontidae) and eels (Anguillidae; Merrick and Schmida 1984; B. J. Pusey, M. J. Kennard and A. H. Arthington, unpublished data) and of southern Australia (Davies 1989; Koehn and O'Connor 1990). Spatial variation in the abundance of such species has been correlated with spatial variation in the availability of root masses and undercuts (Pusey *et al.* 1995a, 2000a). Flood-associated mortality in the Burdekin River was noted to be much reduced in species normally associated with undercut banks and root masses compared with open water species infrequently associated with such structures (B. J. Pusey and A. H. Arthington, unpublished data). Impacts associated with the loss of undercut banks and rootmasses are likely to be felt, as a pulse-type disturbance, shortly after riparian damage occurs (<1 year), extend into the medium term (1–10 years) as a press-type disturbance, but not persist in importance longer as other changes associated with weed invasion take effect (Fig. 2).

Terrestrial organic matter as food

In their discussion of the sources of carbon in Australian floodplain rivers, Robertson *et al.* (1999) did not examine the direct consumption of terrestrial material (i.e. prior to processing by bacteria, fungi and macroinvertebrates) by aquatic organisms such as fish, yet such items are consumed by an enormous array of fish species (Garman 1991; Kennard *et al.* 2001) and other vertebrates, such as turtles and crocodiles (Georges 1982; Kennett and Tory 1996; Tucker *et al.* 1996). Riparian zones have been shown to support greater densities and diversity of invertebrates compared with adjacent non-riparian forests (Jackson and Resh 1989; Malanson 1993; Catterall *et al.* 2001) and are among the most productive ecosystems on earth (Lynch and Catterall 1999). Riparian production may substantially subsidize aquatic food webs

(Chloe and Garman 1996; Nakano *et al.* 1999), although the reverse also occurs (Sabo and Power 2002).

Lowe-McConnell (1975) believed that a pronounced dependency on terrestrial invertebrates as food was a feature of tropical freshwater fish food-webs and many studies of the ecology of tropical freshwater fish have, indeed, noted the importance of allochthonous food sources (terrestrial invertebrates, fruits and leaves). Moyle and Senanyake (1984) found that nine of 20 species in a Sri Lankan stream fish assemblage consumed terrestrial insects and this source of food comprised an average of 44% of the diet of these species. Angermeier and Karr (1983) found that two-thirds of the 30 taxa present in Panamanian streams consumed terrestrial invertebrates and this source contributed more than 20% of the diet in eight species. A similar proportion consumed terrestrial plant matter (>20% in six species). Terrestrial insects were also found to be important in the diets of stream fish in Borneo (Choy *et al.* 1996).

Terrestrially derived prey is important in the diet of fish of the wet/dry tropics of Australia, but not to the extent noted above. Twenty-one of 32 fish species in the Alligator Rivers region of northern Australia consumed terrestrial invertebrates and this food source comprised 5.6% of the diet of those species in which terrestrial invertebrates were present (Bishop *et al.* 1984). A similar pattern has been observed for riverine fish of Cape York Peninsula, where terrestrial invertebrates were present in the dry season diet of eight of 23 species and formed 6.5% of the diet of those species in which terrestrial invertebrate prey were observed (Pusey *et al.* 2000b). Greater reliance on terrestrial prey was noted in floodplain lagoon habitats of Cape York Peninsula; 13 of 17 species consumed terrestrial invertebrates and this prey source comprised an average of 13.5% of the diet in those species that contained terrestrial invertebrates (Kennard 1995).

Even greater reliance on terrestrially derived prey has been noted for rainforest stream fish of the Wet Tropics region of northern Queensland. Terrestrial prey were present in the diet of 12 of 27 species examined by Pusey *et al.* (1995b) and this prey type comprised 12.7% of the average diet for these species. It is of note that rainforest stream species of high conservation significance, such as the Cairns rainbowfish (*Cairnsichthys rhombosomoides*) and jungle perch (*Kuhlia rupestris*), are highly dependent on terrestrial prey (Pusey *et al.* 1995b; Kennard *et al.* 2001) and the maintenance of riparian integrity is critical to their continued survival.

Terrestrial plant material is also consumed by freshwater fish. Leaves formed a considerable proportion of the diet of three species of ariid catfish in the Northern Territory (17–36%; Bishop *et al.* 1984) and the consumption of pollen by fish feeding at the water's surface has been reported in Queensland dune lakes (Bayly *et al.* 1975). However, the consumption of terrestrial vegetation appears to be uncommon in Australian freshwater fish, comprising just over 1% of the total average diet (Kennard *et al.* 2001). Elsewhere,

frugivory occurs in many species of fish and may be important in seed dispersal (Goulding 1980; Kibutzki and Ziburski 1994; Sabino and Sazima 1999). It has not been detailed in the Australian scientific literature to any extent, yet, according to anecdotal accounts, the consumption of fruit by Australian freshwater fish is common (e.g. Merrick and Schmida 1984). In the Wet Tropics, many large fish, such as *Hephaestus fuliginosus*, *Hephaestus tulliensis*, *K. rupestris* and *Megalops cyprinoides* (tarpon), consume the fruits of many riparian species during the wet season (A. H. Arthington, unpublished data; B. J. Pusey, unpublished data). The extent to which frugivory contributes to the overall diets of these species or to the dispersal of riparian tree species is, unfortunately, unknown.

Terrestrially derived material may provide an important source of food for stream fish when in-stream sources are at short supply. Garman (1991) noted that the consumption of terrestrial insects by a stream-dwelling cyprinid was greatest when alternative aquatic prey were least abundant (and terrestrial prey were least abundant also) and suggested that terrestrial prey were an important additional food source at times of low in-stream secondary production. Similarly, the abnormally high reliance on terrestrial prey noted for stream fish in the Brisbane area (average consumption of 19% by volume for 11 species; Arthington 1992) may be associated with the negative impacts on primary and secondary production and, hence, the availability of aquatic prey types that are typical of urbanization. Harris (1985) noted that consumption of terrestrial prey by the bass *Macquaria novemaculeata* in the Hawkesbury River, New South Wales, was greatest in a gorge site that contained little riparian cover. Minshall *et al.* (1985) suggested that canyons should have low levels of riparian inputs and one may reasonably expect such prey to be absent or uncommon in the diet of fish in such habitats. However, light penetration and availability and, hence, primary production are likely to be limited by canyon geometry (Minshall *et al.* 1985). The transportation of terrestrially derived material into such habitats of low primary and secondary productivity may attain great significance. In an analysis of spatial and temporal variation in the structure of tropical fish trophic networks, Winemiller (1990) found that the relative importance of autochthonous and allochthonous food sources varied both seasonally and spatially. Allochthonous production was most important during the dry season in swamps and during the wet season in streams, when autochthonous production was at its lowest.

Differences in catchment lithography (e.g. nutrient-rich basalts compared with nutrient-poor granites) are known to influence primary and secondary production in tropical stream systems (Pringle *et al.* 1990) and a greater dependency on terrestrially derived prey in nutrient-poor streams is probable, as has been shown in nutrient-poor lakes (Bayly *et al.* 1975; Arthington *et al.* 1986). Thus, we may predict that changes in riparian integrity would have greater impact on fish, with respect to the supply of terrestrial invertebrate prey,

in streams draining granitic or largely siliceous sandy catchments with nutrient-poor soils. Pusey and Kennard (1995) suggested that large spatial-scale (i.e. continental) variations in the dependency on terrestrially derived prey by Australian freshwater fish reflected large-scale variation in primary and secondary productivity within streams, with a pronounced reliance on terrestrially derived prey being evident in streams supporting low levels of primary production.

Riparian forests subsidise aquatic food-webs through the donation of terrestrially derived food, such as insects or fruit, and this may lead to substantial changes in food-web structure and stability (Polis and Hurd 1996; Jefferies 2000). Low levels of allochthonous donation may stabilize food-webs when consumers preferentially feed on autochthonous primary and secondary production (Jefferies 2000). Terrestrial inputs may stabilize food-webs by buffering against short-term changes in the supply of autochthonous food. High levels of allochthonous inputs may result in instability and loss of species (Jefferies 2000) due to increases in population size of some consumers beyond that able to be supported by *in situ* production (Polis and Hurd 1996). Fish are of enormous consequence in riverine food webs (Power 1990, 1992) and changes in the extent to which fish forage inside or outside the aquatic ecosystem, and in fish population size or density, may have substantial impacts on other fauna (i.e. through changes in the intensity of predation on non-target taxa and resultant trophic cascades etc.).

Single factor or multifactor effects?

The riparian zone is clearly of great significance to riverine fish (Fig. 1), as it is to most other aquatic animals. The examples discussed above indicate that direct riparian-stream fish linkages are numerous. Moreover, indirect secondary effects are also numerous (Fig. 1) and may potentially be realized at many different levels, ranging from individual reproductive success via effects on mate recognition, egg and larval survivorship, predator avoidance or desynchronization of reproductive cues from regional factors, such as seasonal variation in flow regimen, through to assemblage-level effects due to riparian influences on habitat structure and diversity and trophic dynamics. Furthermore, an array of tertiary impacts, mediated by direct and indirect impacts of fish, on other organisms are also possible (i.e. trophic cascades; Nakano *et al.* 1999). As such, it is difficult to identify what may be the most important linkages or whether the effects of riparian removal or degradation are felt in an additive or synergistic fashion. However, the model developed here allows some assessment of the time-scale over which impacts may be felt (Fig. 2).

Community and individual responses to water quality perturbations are expected to impact first, followed by changes in trophic dynamics and, ultimately, by changes in habitat structure (Fig. 2). Although the initial impact of some of

these effects could be likened to pulse-type disturbances (e.g. altered thermal regimen and light environment), the majority of effects are persistent in time and more akin to press-type disturbance. Fish communities recover more slowly from press-type disturbance (Detenbeck *et al.* 1992) and little recovery can be expected while the riverine environment continues to be subject to the multiple insult posed by riparian degradation. Indeed, there is evidence to suggest that the recovery of stream communities, including fish, may take many decades (Harding *et al.* 1998). Nonetheless, revegetation efforts do have positive conservation outcomes (Penczak 1997).

Implications for management and stream rehabilitation

Given the importance of fish in the ecology of streams and rivers (Power 1990, 1992), the maintenance of healthy fish communities is vital for the general ecological health of streams and rivers. Many human activities and types of land use, including vegetation clearing (Arthington *et al.* 1997), grazing (Amour *et al.* 1994), fire regimen (Naiman and Decamps 1997; Askey-Doran and Pettit 1999; Townsend and Douglas 2000) and flow manipulation (Auble *et al.* 1994; Mackay *et al.* 2001; Werren and Arthington 2002), threaten the integrity of riparian vegetation in Australian catchments and such diverse impacts are highly evident in tropical rivers of northern Australia (Sattler 1993; Werren and Arthington 2002).

Large-scale revegetation works are underway in many parts of northern Australia, particularly in areas surrounding the Wet Tropics World Heritage Area of northern Queensland. The intent of such works is varied and includes re-establishment of the connectivity between forest remnants, farm forestry, repair and stabilization of degraded pasture lands, the provision of a buffer between pasture land and areas of high conservation value (i.e. World Heritage forest), the stabilization of river banks and a reduction in the transfer of sediment and agricultural chemicals to streams. Rarely are such restoration schemes specifically intended to rehabilitate stream ecosystems other than improving water quality and, even more rarely, are stream fish, lacking the charismatic profile of vertebrate taxa such as cassowaries or tree kangaroos, the target taxa. Nonetheless, the many linkages between riparian systems and stream fish clearly indicate the potential for revegetation projects incorporating consideration of stream ecosystems to help conserve the freshwater biodiversity of northern Australia.

Such revegetation projects offer great potential as experiments examining the linkages between fish and riparian forests and as a means of comparing different rehabilitation scenarios. The disturbance time-scale proposed here (Fig. 2) could be used to design experiments to assess whether restoration of the riparian zone is, in itself, sufficient to result in

restoration of degraded fish communities. For example, if biological communities, including fish, are slow to recover from disturbance wrought by poor land use, is greatest conservation benefit achieved by 'seeding' upstream areas with fish from downstream reaches or nearby streams (while acknowledging that care must be taken with respect to minimizing inappropriate impacts on population genetic structure), concomitant with restoration of the riparian zone? Similarly, seeding of newly rehabilitated streams with coarse woody debris may improve conservation outcomes given that it is unlikely that re-established vegetation will be able to contribute suitably sized woody debris for many years. Research aimed at determining which plant species are most likely to lead to a rapid re-establishment of the many and varied linkages between riparian zones and freshwater fish is also needed. Experiments could be designed to assess whether the choice of plant species used in restoring riparian zones should be governed solely by pragmatic decisions, such as which species are easiest to access and plant or grow quickest or suffer the least mortality (although these are important factors), or whether particular ecological factors need to be considered also. For example, the relative palatability to stream macroinvertebrates of the leaves of riparian plant species is likely to be an important factor governing the capacity of the food-web to support an abundant and diverse macroinvertebrate community that, in turn, is able to support a rich and abundant fish fauna. Likewise, riparian species that provide fruit consumed by fish and other aquatic vertebrates, such as turtles, should be included in the species matrix of revegetated zones.

Stream size, landscape context and hydrologic regimen all contribute to determining the role and extent of influence of the riparian zone on aquatic systems (Naiman and Decamps 1997). Spatial variation in the relative and combined importance of the three main riparian functions depicted in Fig. 1 (i.e. regulating the transfer of solar energy, inorganic material and organic material into the aquatic ecosystem) across diverse scales (i.e. within river, between rivers of different hydrology or nutrient status or between regions of differing climate) is to be expected, yet is quantitatively unknown. Research aimed at addressing this issue should yield considerable ecological insight and will also provide a sound scientific basis for the allocation of rehabilitation resources and effort.

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