Connolly, Niall Michael (2016) ***Bottom-up effects via heterotrophic pathways in invertebrate assemblages of tropical streams: nutrients, leaf litter and the relationship between productivity and diversity*****. PhD thesis, James Cook University.**

Bottom-up effects via heterotrophic pathways in invertebrate assemblages of tropical streams: nutrients, leaf litter and the relationship between productivity and diversity.

Thesis submitted by

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February 2016

For Brenda, Josie, Eloise and Cobi

Statement on the contributions of others

Intellectual input and editorial assistance were provided by my supervisor, Emeritus Professor Richard Pearson. Field assistance during my project was provided by a number of people outlined in the acknowledgements section of this thesis. Water quality and other analyses were undertaken by specialist laboratories as detailed in the methods section of relevant chapters within the thesis. Other specific input for the thesis chapters was provided as follows:

Chapter 2

Chapter 2 provides an introduction to the patterns and processes determining freshwater invertebrate diversity in streams in the Wet Tropics, drawing on the research of many people, largely undertaken at James Cook University (JCU). Faye Christidis provided information on distributions of Ephemeroptera in the Wet Tropics and Brendan McKie provided information on the distributions of Chironomidae. A large part of this information has previously been published in the review by Connolly *et al*. (2008), with co-authors – see below:

Connolly N**.**, Pearson R., Christidis F., McKie B. & Boyero L. (2008) Diversity of invertebrates in Wet Tropics streams: Patterns and Processes. Pages 161-177 ***In*** Stork, N. & Turton, S. (eds.) *Living in a dynamic tropical environment.* Blackwell Publishing, UK pp 652.

Chapter 6

The stream surveys described in Chapter 6 were undertaken as part of Task 3 of the Catchment to Reef Program, a joint initiative between the Cooperative Research Centre for Tropical Rainforest Ecology and Management and the Cooperative Research Centre for the Great Barrier Reef World Heritage Area. Water quality sampling was undertaken in collaboration with Dominique Loong (JCU). Spatial GIS analysis was undertaken in collaboration with Mirjam Maughan (JCU). Geomorphological analysis was undertaken in collaboration with Ben Pearson (JCU). Data on riparian vegetation cover was provided by Stephen Mackay (Griffith University). I was responsible for survey design and selection of sample sites and undertook all invertebrate and water quality sampling. I undertook statistical analyses with input from my supervisor, Professor Richard Pearson. Two journal articles have been published from this work with co-authors as follows:

Connolly N.M., Pearson R.G., Loong D., Maughan M. & Brodie J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture, Ecosystems and Environment* **213**: 11-20.

Connolly N.M., Pearson R.G. & Pearson B. (2016) Riparian vegetation and sediment gradients determine invertebrate diversity in streams draining an agricultural landscape. *Agriculture, Ecosystems and Environment **221**: 163–173.*

During my PhD project funding was provided by:

Chapters 1 -5 The College of Marine and Environmental Sciences, the Cooperative Research Centre for Tropical Rainforest Management, and the Australian Research Council.

Chapter 6 - The Catchment to Reef Program of the Rainforest and Reef CRCs (see above).

Acknowledgements

This thesis is the culmination of several projects involving many diverse individual tasks that would not have been possible without the advice and assistance of a large number of colleagues and friends.

Foremost, I would like to thank my supervisor Emeritus Professor Richard Pearson. Throughout this project Richard has provided enormous support and encouragement, advice, expertise and inspiration. Working with and being supervised by Richard has being an outstanding opportunity that I am very grateful for. Through his research program and the development and growth of the Australian Centre of Tropical Freshwater Research he has enabled me, and many others, to build a career in freshwater ecology and make substantial contributions to the protection, conservation and management of our tropical freshwater ecosystems throughout northern Australia and to freshwater ecology globally. Richard has been a true mentor that willingly shares his vast experience and knowledge of ecology and has demonstrated inspirational leadership and true friendship.

I would also like to thank the many colleagues that have studied and worked in the "Freshwater Lab", especially Ant Backer, Joanne Burden, Andi Cairns, Faye Christidis, Linda Davis, Tony Dell, Annika Felton, Jennifer Holt, Linda Hope, Gordon Kovacs, Michelle Reilly and Zoe Rosser for their many hours of assistance in the laboratory and in the field. The "Freshwater Lab" was a very special and fun workplace thanks to all these great people. Ben Pearson and Dominique Loong provided much appreciated assistance in the surveys of streams in the Russell and Mulgrave catchments, including being co-pilots canoeing down these streams to take longitudinal water quality samples. Mirjam Maughan also provided GIS support throughout this and many other projects.

I have much gratitude to Faye Christidis for identification of Ephemeroptera and Trichoptera and Brendan McKie and Matthew Krosch for assistance with Chironomidae identifications. Dale Dixon and Betsy Jackes also assisted with choosing and identification of plants used for leaf litter experiments.

My project was also greatly helped by the Biological Sciences technical staff including Savita Francis, and especially Rob Gegg, who although always busy, took the time to teach me how to bend and weld PVC plastic to construct the artificial stream channels and many other skills in the department's workshop. Thanks also to our very own "IT Crowd", especially Gordon Bailey, who similarly was incredibly helpful in keeping the computers up to date and running.

Special thanks also go to Rita Foster for lots of friendly chats while I waited, and waited, and waited outside Richard's office and who is now a family friend.

I wish to thank my parents, Bill and Nance, for taking myself and my brothers to great places along the west coast of Victoria where we developed a love for nature. They have provided unwavering support and encouragement and enabled us to have opportunities that they never had themselves.

Finally, I want to thank Brenda and our three beautiful children Josie, Eloise and Cobi for greatly enriching my life and being patient and understanding while I was writing this thesis.

Abstract

This project was instigated by the need to understand anthropogenic impacts on streams in the Queensland Wet Tropics bioregion, in particular the clearing of riparian vegetation and the increased flux of nutrients entering streams due to altered land use. Chapter 2 provides an introduction to the patterns and processes determining invertebrate diversity in streams in the Wet Tropics, and subsequent chapters describe how land-use change has altered the basal resources of these streams and how these changes influenced biological processes and their productivity and diversity. Nutrient enrichment interacts with the availability of organic matter and can reduce constraints on material flow and lead to increased productivity of invertebrates in these heterotrophic ecosystems. To understand these bottom-up influences I measured the response of invertebrate assemblages to two key basal resources – nutrients and terrestrial leaf litter – in manipulative experiments and *in situ* in streams subject to the impacts of agriculture.

I used artificial stream channels to investigate the effects of nutrient supplements on primary production, the decomposition of leaf litter, and the abundance and composition of the benthic invertebrate assemblage. In the first series of experiments the rates of decomposition were measured for leaves of four rainforest species with and without a broad nutrient supplement and with and without the presence of the shredder *Anisocentropus kirramus*. The decomposition of some leaf species was enhanced, but levels of chlorophyll *a* and fine particulate organic matter did not differ between treatment and control channels. Treatment channels contained 75% more invertebrates than control channels but only five of the total of 109 invertebrate species showed significant change (all positive), and there was no change in species richness or evenness. I also tested the effect of nitrogen and phosphorus nutrient enrichment separately. I measured the amount of leaf material consumed or decomposed and the microbial biomass colonising the leaves. Supplements of phosphorus, but not nitrogen, enhanced leaf breakdown, microbial growth and growth of *A. kirramus* larvae. Microbial biomass and dry mass of larvae increased with nutrient enrichment and they were significantly correlated. Thus the phosphorus supplement was transmitted through the detrital food web via the microbial pathway, resulting in higher nutritional quality of leaves and enhanced physiological condition of the shredder.

The lack of a response in the assemblage composition to nutrient enrichment was surprising given the magnitude of the nutrient enhancement and because it was clearly entering trophic pathways. To investigate the relationship between productivity and diversity, and how it might apply in these heterotrophic stream assemblages, I tested how the availability of a major resource (the abundance of leaf litter) affected invertebrate productivity and diversity at two scales (individual cobble/leaf packs in artificial stream channels, and whole-channel scales) and investigated the mechanisms by which different patterns, positive or negative, and particularly a hump-shaped relationship between productivity and diversity, could be explained. At the channel scale, macroinvertebrate diversity increased monotonically with the number of leaf packs present in the channels. However, at the cobble/leaf-pack scale, diversity had a hump-shaped relationship with % leaf pack cover.

The divergence between channel-scale and cobble/leaf-pack-scale richness at high % leaf-pack cover suggested that there were new species occurring in cobble/leaf packs in the treatment with higher % leaf-pack cover. In contrast with prevailing theory, β diversity was consistently

high and the monotonic increase in invertebrate richness was attributed to the increasing number of individual cobble/leaf packs in the higher-cover treatments. That is, despite a unimodal pattern at the smaller scale, the monotonic pattern at the larger scale was due to high β diversity ensuring a strong species-area effect.

I measured the rates of colonisation and dispersal of invertebrates on leaf litter packs to confirm the duration of experiments and test the concept that immigration limitation was responsible for the hump-shaped productivity-diversity relationship at small scales. I tracked the composition of the invertebrates colonising leaf packs through time and fitted an equilibrium model to the data to provide estimates of immigration and emigration rates. Emigration rates were also independently determined using drift nets. Both the mean number of individuals and mean number of taxa systematically approached an upper limit by day 24 although turnover of taxa on leaf packs continued to occur. A few taxa had very high mobility, with 50% or more individuals moving each day. Many other taxa had a pattern of slower, more sustained colonisation with less than 10% of individuals leaving a site each day. Ordination indicated a progressive shift in assemblage composition through the colonisation period and a convergence of the compositions on days 24 and 38. These results suggest that the invertebrate assemblage inhabiting the leaf packs approximated equilibrium and was in a dynamic flux at small (leaf pack) scales.

The numbers of potential invertebrate immigrants entering the artificial stream channels through drift was determined by the stream flow into the channels. Thus, differences in the number of leaf packs within the channels in the productivity gradient experiments altered the immigration probabilities at the cobble/leaf pack scale, and it was concluded that constrained immigration dynamics at high litter pack levels was responsible for the declining limb in the hump- shaped productivity-diversity pattern. These results are particularly interesting in that a hump-shaped pattern was nested within a monotonic pattern at the larger scale, even within a confined system, and provide new insight in to how a productivity gradient might affect diversity in biological communities and be scale-dependent.

To generalise the results of these experiments and test them in a large-scale environment, I investigated patterns of water quality and macroinvertebrate distributions in streams affected by agricultural land use. There was a strong negative relationship between invertebrate richness and distance downstream, driven by a gradient of reducing substratum particle size. The abundance of invertebrates was most strongly influenced by mean sediment size, while invertebrate richness was influenced by a combination of sediment size and the availability of coarse particulate organic matter (CPOM), mainly terrestrial leaf litter. When substratum particle size was accounted for, richness was reduced by ~24% in streams with limited availability of CPOM, resulting from lower riparian forest cover upstream. High concentrations of fertilizer-derived nitrate may have boosted invertebrate abundances, but only in upper-mid sections of streams, where coarse substrata (> 100 mm) and high insolation were available. My results indicated only a modest effect of the riparian zone on NO_x–stripping compared with the large input from agricultural land use, and suggest that with current inputs, the NO_x concentrations in these streams are largely independent of the riparian zone. The consistent pattern of downstream increase in NO_x concentrations, and the short residence times of water in these streams, also suggests there is no major in-stream uptake of NO_x. Therefore, it appears that the majority of inorganic nitrogen entering these streams from surrounding agriculture is not being utilised within the stream, but is exported.

Concentrations of different species of phosphorus showed little change or a decline in concentration with distance downstream. However, particulate and dissolved nitrogen and phosphorus concentrations did increase significantly following rainfall, indicating that both are exported from the catchment. The total phosphorus concentrations in these streams were similar to, or above, the response concentrations observed in the enrichment experiments (~20 µgP L^{-1}), but concentrations of filterable reactive phosphorus (FRP) were generally lower than those that induced a response in the experiments. The low concentrations of FRP and the decline in concentration with distance downstream suggest that phosphorus was being assimilated and, particularly given the abundance of NO_x, it appears likely that phosphorus is limiting in these streams. This concurs with the findings of the enrichment experiments, and may explain the weak response of the invertebrate assemblage to the greatly increased NO_x concentrations in the streams.

The components of this thesis enhance understanding of how selected human impacts affect the ecology of the invertebrate assemblages of low-order streams in the Wet Tropics bioregion. I have demonstrated how organic matter and nutrient availability play a central role in the ecology of these streams and how the strong linkages between nutrient and carbon cycles influence decomposer activity, consumer nutrition and energy flow through their food webs. I have also demonstrated responses of invertebrate assemblages to land-use impacts and, more importantly, I have explained the mechanisms by which the ecology and biodiversity of these systems have been modified by shifts in the basal resources, productivity and transfer of energy and nutrients. It is important to understand the processes that determine the hump-shaped productivity-diversity relationship because productivity is increasingly being affected by anthropogenic fertilisation in both terrestrial and aquatic environments. Therefore, an understanding of the processes that produce the hump-shaped relationship will help us to predict when a decline in diversity might occur and to develop the necessary measures to predict a decline in diversity.

Table of Contents

List of Figures

List of Tables

List of Plates

Chapter 1
General Introduction

1.1 Introduction

Streams are the receiving environment for materials transported by processes within their catchments, making them vulnerable to land-use change (Carpenter *et al*., 1998). As a consequence, the protection of their productivity, biodiversity and ecosystem values is particularly challenging because the influences that they depend on, and that can impact their integrity, operate across the landscape and through complex drainage networks, including the ground waters beneath the surrounding land. Riparian forests occur at the interface of the aquatic and terrestrial biomes and play an important role in regulating the transfer of energy and materials between these systems (Gregory *et al*., 1991; Naiman & Décamps, 1997; Décamps *et al*. 2004), but are themselves vulnerable to disturbance and degradation, disrupting these functions (Bunn, 1993; Bunn *et al*., 1998, 1999; Broadmeadow & Nisbet, 2004). Sala *et al*. (2000), in their review of scenarios of biodiversity change over the next century, predicted that land-use change would continue to have disproportionately large effects on freshwater ecosystems because human activity is aggregated around waterways, even in sparsely populated regions, causing increased inputs of sediments, fertilizer nutrients and other contaminants as well as disturbance to their riparian zones, affecting their biological productivity and diversity (Likens *et al*., 1970; Webster *et al*., 1990; Allan 2004; Dudgeon 1992, 2000; Dudgeon *et al*., 2006).

In their natural state forested streams typically have low concentrations of dissolved nutrients and are heterotrophic, because in-stream primary productivity is usually light-limited (Fisher & Likens, 1972; Hill *et al*., 1995; Mulholland *et al*., 2001; Bernhardt & Likens, 2004; Greenwood & Rosemond, 2005). Productivity in these systems relies on allochthonous leaf litter entering the stream from the riparian zone and being gradually broken down and modified, fuelling a detrital food web (Kaushik & Hynes, 1971; Fisher & Likens, 1973; Fittkau & Kling, 1973; Anderson & Sedell, 1979; Benfield & Webster, 1985; Wetzel, 1995; Cheshire *et al*., 2005). However, increased inputs of inorganic nutrients to streams and disturbance to their riparian vegetation are the two features of streams most commonly affected by land-use change and the development of stream catchments (Sala *et al*., 2000).

Riparian vegetation has long been recognised for its role in sustaining habit integrity, biodiversity, stream bank stability and water quality (e.g., Naiman *et al*., 1993; Decamps *et al*., 2004; de Souza *et al*., 2013; Fernandes *et al*., 2014) and providing organic subsidies in the form of organic litter input (Nakano & Murakami, 2001). The reliance of many aquatic ecosystems on the loading of terrestrial organic matter to support productivity and food web structure has long been recognised (Vannote *et al*., 1980; Wetzel, 1995; Wallace *et al*., 1999). Experiments adding or removing sources of riparian leaf litter have shown that the quantity and type of organic matter entering the stream can control productivity of the stream food webs (Richardson, 1991; Wallace *et al*., 1999). However, until recently it has not been fully appreciated how land-use change is fundamentally altering these detritus-based ecosystems (Kominoski & Rosemond, 2012; Woodward *et al*., 2012; Rosemond *et al*., 2015). For example, Rosemond *et al*. (2002, 2015) have described how the standing stock, decay rate and quality of detritus in the detrital food web of an otherwise intact stream are affected by the input of exogenous nutrients, increasing mineralization of the detritus and reducing the residence time of terrestrial carbon storage by ~50% with consequences to food webs and ecosystem services.

1.2 Nutrient enrichment of heterotrophic streams

Detrital decomposition is a key ecosystem-level process that is generally accelerated with nutrient enrichment. The input of inorganic nutrients will stimulate microbial activity on particulate organic matter (Abelho & Graca, 2006), affecting the availability and quality of detrital carbon to detritivore consumers (Melillo *et al*., 1984; Rosemond *et al*., 2002; Connolly & Pearson, 2013) and the rate of terrestrial carbon mineralization and loss from the stream ecosystem (Rosemond *et al*., 2002, 2015). Thus exogenous nutrient concentrations will interact with the availability of allochthonous organic material to determine the productivity within these streams. The integrity of the riparian canopy will also affect shading and the growth of primary producers (Feminella *et al*., 1989; Bunn *et al*., 1998, 1999). Thus, disturbance of riparian vegetation and shifts in the nutrient flux to streams will alter the basal resources and instream productivity (Likens *et al*., 1970; Webster *et al*., 1990; Williams *et al*., 1997; England & Rosemond, 2004; Kominoski & Rosemond, 2012). Algal production will increase relatively predictably when released from light and nutrient limitation (Elser *et al*., 2007), but is expected to remain low in forested streams (Greenwood & Rosemond, 2005). However, the decomposition and mineralization of particulate organic matter in streams is a complex process involving multiple trophic levels consisting of bacteria, fungi and invertebrate detritivores (Wallace *et al*., 1997), all of which can be affected by nutrient enrichment (Elwood *et al*., 1981; Suberkropp, 1998b; Pearson & Connolly, 2000; Ferreira & Chauvet, 2011).

Decomposition of particulate organic matter in streams begins with leaching and colonisation by bacteria and aquatic hyphomycetes (Suberkropp & Klug, 1976; Suberkropp, 1998a; Gessner & Chauvet, 1994; Heiber & Gessner, 2002) followed by fragmentation and consumption by invertebrate shredders (e.g., Petersen & Cummins, 1974; Anderson & Grafius, 1975; Graca, 2001; Heiber & Gessner, 2002). The rate of microbial growth and activity depends on the availability of nutrients and can be nutrient-limited (Elwood *et al*., 1981; Suberkropp, 1998b; Pearson & Connolly, 2000; Ferreira & Chauvet, 2011) and microbes colonising leaf material may utilise dissolved nutrients in preference to nutrients within the leaf material (Melillo *et al*., 1984; White & Howes, 1994). There is also evidence of control of detritivore populations by food quality (Groome & Hildrew, 1989), detritivores preferring litter that has been conditioned by some decay and colonisation by microbes (Anderson & Sedell, 1979; Arsuffi & Suberkropp, 1985, 1989). Consequently, nutrient enrichment of a stream can lead to increased microbial biomass (Gulis & Suberkropp, 2003a, b), higher nutritional quality of detrital litter and enhanced physiological condition and production of consumer invertebrates (e.g., Pearson & Connolly, 2000; Greenwood *et al*., 2007; Gulis *et al*., 2006).

1.3 The relationship between productivity and diversity

Nutrient enrichment reduces the constraints on material flows of detrital-based food webs in streams (Cross *et al*., 2007) increasing secondary production (Cross *et al*., 2006). However, the extent to which these effects propagate through food webs and determine emergent properties, such as the composition and diversity of the stream community, is not well known. Conventional theory predicts that productivity determines the number of possible trophic levels (Fretwell, 1977; Oksanen *et al*., 1981) and consumers at all trophic levels should respond positively to increased system productivity, including in detritus based systems (Moore & de Ruiter, 2000, Moore *et al*., 2004). Although considerable effort has focused on predicting the effects of enrichment and productivity on community composition of living plants and animals (e.g., Tilman, 1993; Tilman & Pacala, 1993), much less is known about how the assemblage structure of detritus-based communities are affected, prompting Moore *et al*. (2004) to ask the following key questions: (1) what factors determine species richness in detrital communities and (2) how does the diversity of detritivores affect the rates of detritus processing?

Understanding the relationship between productivity and diversity is of particular importance in aquatic environments given that they are undergoing both enrichment and species losses (Carpenter *et al*., 1998; Ricciardi & Rasmussen, 1999; Sala *et al*., 2000; Bennett *et al*., 2001; Malmqvist & Rundle, 2002; Galloway *et al*., 2003; Dudgeon *et al*., 2006). Productivity and diversity are fundamental characteristics of a biotic community and unravelling the mechanisms that determine them and the relationship between them is of importance in understanding biodiversity and how to conserve it (Huston, 1979; Pierce, 2014). However, the effects of productivity on the composition of biotic communities (including aquatic communities) are not yet fully understood (Grace *et al*., 2016; Gross, 2016), except perhaps under extreme oligotrophic or eutrophic conditions (Smith *et al*., 1999; Dodds, 2007; Smith & Schindler, 2009). Some suggest that with increasing resources, more individuals and species can be sustained in an ecosystem, so diversity increases monotonically with productivity (Wright, 1983; Currie & Paquin, 1987; Currie, 1991; Gaston, 2000). More controversial is the view that the relationship is unimodal, or "hump-shaped", in which diversity peaks at intermediate productivity (e.g., Adler *et al*., 2011; Fridley *et al*., 2012; Grace *et al*., 2012; Pan *et al*., 2012; Pierce, 2014; Fraser *et al*., 2015). Others suggest that the form of the relationship is dependent on the relative levels of productivity and disturbance (Kondoh, 2001, Kadmon & Benjamani, 2006; Tonkin & Death, 2012, 2013; Tonkin *et al*., 2013) or scale (Chase & Leibold, 2002).

Experimental work has shown that detrital carbon can limit stream detritivore biomass and production (Johnson *et al*., 2003). Increased coarse particulate organic matter (CPOM) resulted in greater masses and densities of several invertebrate species (Richardson, 1991) and exclusion of leaf litter from a headwater stream resulted in greatly reduced biomass of stream invertebrates, with the loss of several invertebrate species, including shredders, collectors and predators (Wallace *et al*., 1997). In heterotrophic streams, nutrient enrichment generally has a positive effect on the magnitude of carbon and nutrient flows to consumers with positive effects on invertebrate production (Pearson & Connolly, 2000; Cross *et al*., 2006; Greenwood *et al*., 2007; Gulis *et al*., 2006). However, the reported effects on community structure and composition are mixed, including no change (Pearson & Connolly, 2000; Ferreira *et al*., 2006; Cross *et al*., 2006), increased dominance of some species (Cross *et al*., 2007), increased richness (Gulis *et al*., 2006) and a decline in community-based benthic macroinvertebrate parameters (Lacerf *et al*., 2006). Therefore, although the effects of enrichment on streams may seem straightforward, the overall, long-term outcome on community composition and diversity is less so.

Changes to the composition of a community subject to nutrient enrichment will be determined by complex combinations of nutrient-induced changes in material flows, consumer energetics and consumer-resources stoichiometry (Cross *et al*., 2007). It will also be affected by the complexities of how productivity and diversity are related and the ecological mechanisms that determine this relationship, which are not yet fully resolved (e.g., Abrams, 1995; Waide *et al*., 1999; Mittlebach *et al*., 2001; McBride *et al*., 2014). A hump-shaped productivity-diversity relationship has profound implications for the conservation of biodiversity given the increasing fertilization of aquatic ecosystems and the implication that at higher productivity species richness will decline. Therefore, the delineation of factors that control the trophic state and energy and nutrient flow, and their relationships with community properties such as the number of species, is important for the effective management of stream ecosystem integrity.

1.4 Study aims and objectives

This project was primarily instigated by the need to understand anthropogenic impacts on streams in the Queensland Wet Tropics bioregion, in particular the clearing of riparian vegetation and the increased flux of nutrients entering streams due to altered land use. In the Wet Tropics the uplands are protected in an extensive network of national parks that make up the Queensland Wet Tropics World Heritage Area. However, most of the accessible land in the lowlands and tablelands has been cleared for agriculture and most waterways on the floodplains are modified through loss of riparian vegetation and contamination by agricultural chemicals, particularly large quantities of nutrient from fertilizer use (Connolly *et al*., 2007, 2015; Bainbridge *et al*., 2009; Pearson *et al*., 2013, 2015).

I was particularly interested in how land-use change had altered the basal resources of these streams and how these changes influenced the productivity and diversity of invertebrate assemblages, as they account for a major component of the biodiversity in these streams and are critical components of food webs, connecting basal resources to higher consumers (Petersen & Cummins, 1974; Anderson & Sedell, 1979; Cheshire *et al*., 2005). They are therefore a key determinant of how stream ecosystems respond to changes in inorganic and organic subsidies from the riparian vegetation and basal energy resources. I measured the response of macroinvertebrate assemblages to two key resources – nutrients and terrestrial leaf litter – in manipulative experiments and *in situ* in streams subject to the impacts of agriculture.

To develop a more general understanding of the relationship between productivity and diversity, I investigated the mechanisms by which different patterns, positive or negative, and particularly a hump-shaped relationship between productivity and diversity, could be explained. Whereas most studies investigating the relationship between productivity and diversity have focussed on gradients of nutrients and primary production, I investigated these relationships in a detrital food web, using leaf litter as the resource. Leaf litter, as well as being an energy source, also creates habitat patches in streams, so the manipulation of leaf litter provides for greater productivity but also alters habitat patchiness and heterogeneity. This feature enabled me to not only manipulate quantities of resources, but also to investigate the relationship between productivity and patch dynamics in an attempt to understand the effect of scale.

1.5 The structure of the thesis

The thesis is structured as seven chapters, including this General Introduction (Chapter 1) and a Synthesis & Conclusions (Chapter 7), selected from a broader body of research (Appendix 1), as follows. Chapters 2, 3 and 6 have been published, as indicated in each chapter. For convenience I present references at the end of each chapter, but appendices are presented at the end of the thesis.

Chapter 2: Diversity of invertebrates in Wet Tropics streams: Patterns and Processes.

Chapter 2 reviews current knowledge of stream invertebrate biodiversity in the Queensland Wet Tropics. I provide an introduction to the patterns and processes determining freshwater invertebrate diversity in streams in the Wet Tropics.

Chapter 3: Nutrient enrichment alters leaf litter decomposition, food quality and invertebrate production, but not diversity, in a heterotrophic rainforest stream.

Chapter 3 describes the effects of nutrient supplements on, and linkages between, (1) primary productivity, (2) microbial biomass, (3) decomposition of leaf litter and the production of fine particulate organic matter, (4) the growth and condition of a detritivore consumer, (5) the standing crop of benthic invertebrates, and (6) invertebrate assemblage composition and diversity in a low order heterotrophic stream.

Chapter 4: Colonisation and emigration of stream invertebrates inhabiting leaf litter packs in a tropical stream.

Chapter 4 measured the rates of colonisation of and dispersal from leaf litter packs – a key resource in streams – to help understand the relationships between the amount of resource, productivity and community composition and diversity, and scale, described in Chapter 5.

Chapter 5: Hump-shaped and monotonic productivity-diversity relationships at different scales in stream invertebrates inhabiting leaf litter: due to high β diversity and constrained immigration.

Chapter 5 investigated the theory around the relationship between productivity and diversity. I measured the response of the invertebrate community (abundance and diversity) to a gradient in leaf litter availability, in artificial stream channels. I investigated this relationship at the leaf-patch and whole-channel scales to determine whether it was scale-dependent and positive, negative or hump-shaped.

Chapter 6: Influence of riparian vegetation on water quality and invertebrate assemblages in streams in an agricultural landscape.

Chapter 6 investigated patterns of water quality and macroinvertebrate distributions in lowland Wet Tropics streams in a comparison of catchments with contrasting condition of the riparian zone. I aimed to determine the influence of nutrient supplements and detrital inputs at a large scale.

Chapter 7: Synthesis & Conclusions.

In Chapter 7 I synthesise the outcomes of the previous chapters, and assess their contribution to our current understanding of the ecology of stream invertebrates in the Wet Tropics and globally.

1.6 References

Abelho M. & Graca M.A.S. (2006) Effects of nutrient enrichment on decomposition and fungal colonization of sweet chestnut leaves in an Iberian stream (Central Portugal). *Hydrobiologia* **560**: 239-247.

Abrams P. A. (1995) Monotonic or unimodal diversity productivity gradients – What does competition theory predict. *Ecology* **76**: 2019-2027.

Adler P.B., Seabloom E.W., Borer E.T., Hillebrand H., Hautler Y., Hector A., Harpole W.S., O"Halloran L.R., Grace J.B., Anderson T.M., Bakker J.D., Biederman L.A., Brown C.S., Buckley Y.M., Calabrese L.B., Chu C.J., Cleland E.E., Collins S.L., Cottingham K.L., Crawley M.J., Damschen E.I., Davies K.F., DeCrappeo N.M., Fay P.A., Firn J., Frater P., Gasarch E.I., Gruner D.S., Hagenah N., Hille Ris Lambers J., Humphries H., Jin V.L., Kay A.D., Kirkman K.P., Klein J.A., Knops J.M., La Pierre K.J., Lambrinos J.G., Li W., MacDougall A.S., McCulley R.L., Melbourne B.A., Mitchell C.E., Moore J.L., Morgan J.W., Mortensen B., Orrock J.L., Prober S.M., Pyke D.A., Risch A.C., Schuetz M., Smith M.D., Stevens C.J., Sullivan L.L., Wang G., Wragg P.D., Wright J.P. & Yang L.H. (2011) Productivity is a poor predictor of plant species richness. *Science* **333**: 1750-1752.

Allan J.D. (2004) Landscapes and Riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics* **35**: 257-284.

Anderson N.H. & Grafius E. (1975) Utilisation and processing of allochthonous material by stream Trichoptera. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **19**: 3083-3088.

Anderson, N.H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* **24**: 351-377.

Arsuffi, T.L. & Suberkropp K. (1985) Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. *Oikos* **45**: 50-58.

Arsuffi T.L. & Suberkropp K. (1989) Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. *Oecologia* **79**: 30-37.

Bainbridge Z.T., Brodie J.E., Faithful J.W., Sydes D.A. & Lewis S.E. (2009) Identifying the land-based sources of suspended sediments, nutrients and pesticides discharged to the Great Barrier Reef from the Tully-Murray Basin, Queensland, Australia. *Marine and Freshwater Research* **60**: 1081-1090.

Benfield, E.F. & Webster J.R. (1985) Shredder abundance and leaf breakdown in an Appalachian Mountain stream. *Freshwater Biology* **15**: 113-120.

Bennett E.M., Carpenter S.R. & Caraco N.F. (2001) Human impact on erodible phosphorus and eutrophication: a global perspective. *BioScience* **51**: 227-234.

Bernhardt E.S. & Likens G.E. (2004) Controls on periphyton biomass in heterotrophic streams. *Freshwater Biology* **49**: 14-27.

Broadmeadows S. & Nisbet T.R. (2004) The effect of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences* **8**(3): 286-305.

Bunn S.E. (1993) Riparian-stream linkages: research needs for the protection of in-stream values. *Australian Biologist* **6**: 46-51.

Bunn S.E., Davies P.M., Kellaway, D.M. & Prosser I.P. (1998) Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* **37**: 171-178.

Bunn S.E., Davies P.M. & Mosisch T.D. (1999) Ecosystem measures of river health and their response to riparian and catchment clearing. *Freshwater Biology* **41**: 333-346.

Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecology and Evolution* **8**: 51-54.

Chase J.M. & Leibold M.A. (2002) Spatial scale dictates the productivity-diversity relationship. *Nature* **416**: 427-430.

Cheshire K., Boyero L. & Pearson R.G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Connolly N., Pearson R., Christidis F., McKie B. & Boyero, L. (2008) Diversity of invertebrates in Wet Tropics streams: Patterns and Processes. Pages 161-177 ***In*** Stork, N. & Turton, S. (eds.) *Living in a dynamic tropical environment.* Blackwell Publishing, UK.

Connolly N.M., Pearson B., Loong D., Maughan M. & Pearson R.G. (2007) Hydrology, geomorphology and water quality of four Wet Tropics streams with contrasting land-use management. Pages 15-78 **In** Arthington A.H. & Pearson R.G. (eds.) *Biological Indicators of Ecosystem Health in Wet Tropics Streams*. Final Report Task 3 Catchment to Reef Research Program. Cooperative Centre for the Great Barrier Reef World Heritage Area.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Connolly N.M., Pearson, R.G., Loong, D., Maughan, M. & Brodie, J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture, Ecosystems and Environment* **213**: 11-20.

Cross W.F., Wallace J.B., Rosemond A.D. & Eggert S.L. (2006) Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. *Ecology* **87**: 1556-1565.

Cross W.F., Wallace J.B. & Rosemond A.D. (2007) Nutrient enrichment reduces constraints on material flows in detritus-based food web. *Ecology* **88**: 2563-2575.

Currie D.J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist* **137**: 27-49.

Currie D.J. & Paquin V. (1987) Large-scale biogeographic patterns of species richness of trees. *Nature* **329**: 326-327.

Decamps H., Pinay G., Naiman R.J., Petts G.E., McClain M.E., Hillbricht-Ilkowska A., Hanley T.A., Holmes R.M., Quinn J., Gibert J., Planty Tabacchi A.-M., Schiemer F., Tabacchi E. & Zalewski M. (2004) Riparian zones: where biogeochemistry meets biodiversity in management practice. *Polish Journal of Ecology* **52**: 3-18.

de Souza A.L.T., Fonseca D.G., Libório R.A. & Tanaka M.O. (2013) Influence of riparian vegetation and forest structure on the water quality of rural low-order streams in SE Brazil. *Forest Ecology and Management* **298**: 12-18.

Dodds W.K. (2007) Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology & Evolution* **22**: 669-676.

Dudgeon D. (1992) Endangered ecosystems: a review of the conservation status of tropical Asian rivers. *Hydrobiologia* **248**: 167-191.

Dudgeon D. (2000) The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Reviews of Ecology and Systematics* **31**: 239-263.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z., Knowler D.J., Lévéque C., Naiman R.J., Prieur-Richard A., Soto D., Stiassny L.J. & Sullivan C.A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**: 163-182.

Elser J.J., Bracken M.E.S., Cleland E.E., Gruner D.S., Harpole W.S., Hillebrand H., Ngai J.T., Seabloom E.W., Shurin J.B. & Smith J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater marine and terrestrial ecosystems. *Ecology Letters* **10**: 1135-1142.

Elwood J.W., Newbold J.D., Trimble A.F. & Stark R.W. (1981) The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. *Ecology* **62**: 146-158.

England L.E. & Rosemond A.D. (2004) Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. *Freshwater Biology* **49**: 721-734.

Feminella J.W., Power M.E. & Resh V.H. (1989) Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology* **22**: 445-457.

Fernandes J.F., de Souza A.L.T. & Tanaka, M.O. (2014) Can the structure of a riparian forest remnant influence stream water quality? A tropical case study. *Hydrobiologia* **724**: 175-185.

Ferreira V., Gulis V. & Graça M.A.S. (2006) Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* **149**: 718-729.

Ferreira V. & Chauvet E. (2011) Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* **17**: 551-564.

Fisher S.G. & Likens G.E. (1972) Stream ecosystem: organic energy budget. *BioScience* **22**: 33-35.

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**: 421-439.

Fittkau E.J. & Klinge H. (1973) On biomass and trophic structure of the Central Amazon rain forest ecosystem. *Biotropica* **5**: 2-14.

Fraser L.H., Pither J., Jentsch A., Sternberg M., Zobel M., Askarizadeh D., Bartha S., Beierkuhnlein C., Bennett J.A., Bittel A., Boldgiv B., Boldrini I.I., Bork E., Brown L., Cabido M., Cahill J., Carlyle C.N., Campetella G., Chelli S., Cohen O., Csergo A.M., Díaz S., Enrico L., Ensing D., Fidelis A., Fridley J.D., Foster B., Garris H., Goheen J.R., Henry H.A.L., Hohn M., Jouri M.H., Klironomos J., Koorem K., Lawrence-Lodge R., Long R., Manning P., Mitchell R., Moora M., Müller S.C., Nabinger C., Naseri K., Overbeck G.E., Palmer T.M., Parsons S., Pesek M., Pillar V.D., Pringle R.M., Roccaforte K., Schmidt A., Shang Z., Stahlmann R., Stotz G.C., Sugiyama S.I., Szentes S., Thompson D., Tungalag R., Undrakhbold S., Van Rooyen M., Wellstein C., Wilson J.B. & Zupo T. (2015) Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* **349**: 302-305.

Fretwell S.D. (1977) The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* **20**:169-185.

Fridley J.D., Grime J.P., Huston M.A., Pierce S., Smart S.M., Thompson K., Börger L., Brooker R.W., Cerabolini B.E., Gross N., Liancourt P., Michalet R. & Le Bagousse-Pinguet Y. (2012) Comment on “Productivity is a poor predictor of plant species richness”. *Science* **335**: 1441.

Galloway J.N., Aber J.D., Erisman J.W., Seitzinger S.P., Howarth R.W., Cowling E.B. & Cosby B.J. (2003) The nitrogen cascade. *BioScience* **53**: 341-356.

Gaston K.J. (2000) Global patterns in biodiversity. *Nature* **405**: 220-227.

Gessner M.O. & Chauvet E. (1994) Importance of microfungi in controlling breakdown rates of leaf litter. *Ecology* **75**: 1807-1817.

Graca M.A.S. (2001) The role of invertebrates on leaf litter decomposition in streams – a review. *International Review of Hydrobiology* **86**: 383-393.

Grace J.B., Adler P.B., Seabloom E.W., Borer E.T., Hillebrand H., Hautier Y., Hector A., Harpole W.S., O”Halloran L.R., Anderson T.M., Bakker J.D., Brown C.S., Buckley Y.M., Collins S.L., Cottingham K.L., Crawley M.J., Damschen E.I., Davies K.F., DeCrappeo N.M., Fay P.A., Firn J., Gruner D.S., Hagenah N., Jin V.L., Kirkman K.P., Knops J.M.H., La Pierre K.J., Lambrinos J.G., Melbourne B.A., Mitchell C.E., Moore J L.,Morgan J.W., Orrock J.L., Prober S.M., Stevens C.J., Wragg P.D. & Yang, L.H. (2012) Response to comments on “Productivity is a poor predictor of plant species richness”. *Science* **335**: 1441.

Grace J.B., Anderson T.M., Seabloom E.W., Borer E.T., Adler P.B., Harpole W.S., Hautier Y., Hillebrand H., Lind E.M., Pärtel M., Bakker J.D., Buckley Y.M., Crawley M.J., Damschen E.I., Davies K.F., Fay P.A., Firn J., Gruner D.S., Hector A., Knops J.M.H., MacDougall A.S., Melbourne B.A., Morgan J.W., Orrock J.L., Prober S.M. & Smith M.D. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature: doi:10.1038/nature16524.

Greenwood J.L. & Rosemond A.D. (2005) Periphyton response to long-term nutrient enrichment in a shaded headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 2033-2045.

Greenwood J.L., Rosemond A.D., Wallace J.B., Cross W.F. & Weyers H.S. (2007) Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effect via heterotrophic pathway. *Oecologia* **151**: 637-649

Gregory S.V., Swanson F.J., McKee W.A. & Cummins K.W. (1991) An ecosystem perspective of riparian zones. *Bioscience* **41**: 540-551.

Groome A.P. & Hildrew A.G. (1989) Food quality for detritivores in streams of contrasting pH. *Journal of Animal Ecology* **58**: 863-881.

Gross K. (2016) Biodiversity and productivity entwined. *Nature*: doi:10.1038/nature16867.

Gulis V., Ferreira V., & Graça M.A.S. (2006) Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream *assessment. Freshwater Biology* **51***:* 1655-1669.

Gulis V. & Suberkropp K. (2003a) Effect of inorganic nutrients on relative contributions of fungi and bacteria to carbon flow from submerged decomposing leaf litter. *Microbial Ecology* **45**: 11-19.

Gulis V. & Suberkropp K. (2003b) Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* **48**: 123-134.

Hieber M. & Gessner M.O. (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* **83**: 1026-1038.

Hill W.R., Ryon M.G. & Schilling E.M. (1995) Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* **76**: 1297-1309.

Huston M. (1979) A general hypothesis of species diversity. *The American Naturalist* **113**: 81-101.

Johnson B.R., Cross W.F. & Wallace J.B. (2003) Long-term resource limitation reduces insect detritivore growth in a headwater stream. *Journal of the North American Benthological Society* **22**: 565-574.

Kadmon R & Benjamini Y. (2006) Effects of productivity and disturbance on species richness: A neutral model. *The American Naturalist* **167**: 939-946.

Kaushik N.K. & Hynes H.B.N. (1971) The fate of dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**: 465-515.

Kominoski J.S. & Rosemond A.D. (2012) Conservation from the bottom up: forecasting effect of global change on dynamics of organic matter and management needs for river networks. *Freshwater Science* **31**: 51-68.

Kondoh M. (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**: 269-271.

Lacerf A., Usseglio-Polatera P., Charcosset J.Y., Lambrigot D., Bracht B. & Chauvet E. (2006) Assessment of functional integrity of eutrophic stream using litter breakdown and benthic invertebrates. *Achiv für Hydrobiologie* **165**: 105-126.

Likens G.E., Borman F.H., Johnson N.M., Fisher D.W. & Pierce R.S. (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monographs* **40**: 23-47.

Nakano S. & Murakami M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Science, USA* **98**: 166-170.

Malmqvist B. & Rundle S. (2002) Threats to the running water ecosystems of the world. *Environmental Conservation* **29**: 134-153.

Melillo J.M., Naiman R.J., Aber J.D. & Linkins A.E. (1984) Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bulletin of Marine Science* **35**: 341-356.

McBride P.D., Cusens J. & Gillman L.N (2014) Revisiting spatial scale in the productivity-species richness relationship: fundamental issues and global change implications. *AoB Plants* **6**: olu057; doi:10.1093/aobpla/plus057.

Mittlebach G.G., Steiner S.F., Scheiner S.M., Gross K.L., Reynolds H.L., Waide R.B., Willig M.R., Dodson S.I. & Gough L. (2001) What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381-2396.

Moore J.C. & de Ruiter P.C. (2000) Invertebrates in detrital food webs along gradients of productivity. Pages 161-184 **In.** Coleman D.C. & Hendrix P.F. (eds.) *Invertebrates as webmasters in ecosystems.* CAB International, New York, USA.

Moore J.C., Berlow E.L., Coleman D.C., de Reuter P.C., Dong Q., Hastings A., Collins-Johnson N., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.D., Post D.M., Sabo J.L., Scow J.L., Vanni M.J. & Wall D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**: 584-600.

Mulholland P.J., Fellows C.S., Tank J.L., Grimm N.B., Webster J.R., Hamilton S.K., Marti E., Ashken L., Bowden W.B., Dodds W.K., McDowell W.H., Paul M.J. & Peterson B.J. (2001) Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* **46**: 1503-1517.

Nakano S. & Murakami M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* **98**: 166-170.

Naiman R.J. & Décamps H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**: 621-658.

Naiman R.J., Décamps H. & Pollock M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**: 209-212.

Oksanen L.S., Fretwell S.D., Arruda J. & Niemel A.P. (1981) Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**: 240-261.

Pan X., Liu F. & Zhang M. (2012) Comment on “Productivity is a poor predictor of plant species richness”. *Science* **335**: 1441.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G., Connolly N.M. & Boyero L. (2015) Ecology of streams in a biogeographic isolate – the Queensland Wet Tropics, Australia. *Freshwater Science* **34**: 797-819.

Pearson R.G., Godfrey P.C., Arthington A.H., Wallace J., Karim F. & Ellison M., (2013) Biophysical status of remnant freshwater floodplain lagoons in the Great Barrier Reef catchment: a challenge for assessment and monitoring. *Marine and Freshwater Research* **64**: 208-222.

Petersen R.C. & Cummins K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology* **4**: 343-368.

Pierce S. (2014) Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. *Functional Ecology* **28**: 253-257.

Ricciardi A. & Rasmussen J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology* **13**: 1220-1222.

Richardson J.S. (1991) Seasonal food limitation of detritivores in a montane: An experimental test. *Ecology* **72**: 873-887.

Rosemond A.D., Pringle C.M., Ramírez A., Paul M.J. & Meyer J.L. (2002) Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. *Limnology and Oceanography* **47**: 278-289.

Rosemond A.D., Benstead J.P., Bumpers P.M., Gulis V., Kominoski J.S., Manning D.W.P., Suberkropp K. & Wallace J.M. (2015) Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**: 1142-1145.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., LeRoy Poff N., Sykes M.T., Walker B.H., Walker M., & Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.

Smith V.H. & Schindler D.W. (2009). Eutrophication science: where do we go from here? *Trends in Ecology and Evolution* **24**: 201-207.

Smith V.H., Tilman G.D. & Nekola J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**: 179-196.

Suberkropp K. (1998a) Microorganisms and organic matter processing. Pages 120-143 **In.** Naiman R.J. & Bilby R.E. (eds.) *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*. Springer Verlag, New York.

Suberkropp K. (1998b) Effect of dissolved nutrients on two aquatic hyphomycetes growing on leaf litter. *Mycological Research* **102**: 998-1002.

Tilman D. (1993) Species richness of experimental productivity gradients: how important is colonisation limitation? *Ecology* **74**: 2179-2191.

Tilman D. & Pacala S. (1993) The maintenance of species richness in plant communities. Pages 13-25 **In** R.E. Ricklefs & Schluter D. (eds.) *Species diversity in ecological communities: historical and geographical perspectives.* University of Chicago Press, Chicago, Illinois, USA.

Tonkin J.D. & Death R.G. (2012) Consistent effects of productivity and disturbance on diversity between landscapes. *Ecospher* **3**: art108.

Tonkin J.D. & Death R.G. (2013) Scale dependent effects of productivity and disturbance on diversity in streams. *Fundamentals of Applied Limnology* **182**: 283-295.

Tonkin J.D., Death R.G. & Collier K.J (2013) Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams? *Hydrobiologia* **701**: 159-172.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.

Waide R.B., Willig M.R., Steiner S.F., Mittlebach G., Gough L., Dodson S.I., Juday G.P., & Parmenter R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* **30**: 257-300.

Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**: 102-104.

Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1999) Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* **69**: 409-442.

Webster J.R., Golladay S.W., Benfield E.F., D"Angelo D.J. & Peters G.T. (1990) Effects of forest disturbance on particulate organic matter budgets of small streams. *Journal of the North American Benthological Society* **9**: 120-140.

Wetzel R.G. (1995) Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology* **33**: 83-89.

White D.S. & Howes B.L. (1994) Nitrogen incorporation into decomposing litter of *Spartina alterniflora. Limnology and Oceanography* **39**: 133-140.

Williams M.R., Fisher T.R & Melack J.M. (1997) Solute dynamics in soil water and groundwater in a central Amazon catchment undergoing deforestation. *Biogeochemistry* **38**: 303-335.

Woodward, G., Gessner M.O., Giller P.S., Gulis V., Hladyz S., Lecerf A., Malmqvist B., McKie B.G., Tiegs S.D., Cariss H., Dobson M., Elosegi A., Ferreira V., Graca M.A.S., Fleituch T., Lacoursière J.O., Nistorescu M., Pozo J., Risnoveanu G., Schindler M., Vadineanu A., Vought L.B-M. & Chauvet E. (2012) Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* **336**: 1438-1440.

Wright D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos* **41**: 496-506.

Chapter 2

Diversity of invertebrates in Wet Tropics streams: patterns and processes[1]

2.1 Introduction

The development of ecological research in tropical freshwater ecosystems has a long history and has generally tracked global trends. However, although research capacity has intensified in recent decades, it has historically lagged behind temperate regions. The main characteristic of the tropics – consistent insolation (day length, high temperature) through the year – has a major influence on biological processes (e.g., life cycles, productivity) and emergent properties (e.g., diversity) in fresh waters. The tropical realm is a vast area with various climates (dry–wet, seasonal–aseasonal), biogeographic and evolutionary histories, landforms and fresh waters, but available information is geographically limited (Connolly & Pearson, 2004; Jacobsen *et al*., 2008; Boyero *et al*., 2009; Pearson *et al*., 2015). Research in streams of the Queensland Wet Tropics bioregion has included descriptive studies of systematics and phylogenetics, populations and communities; tests of theory regarding habitats, competition, predation, trophic dynamics, disturbance and productivity; investigations of landscape processes, human effects and impacts from water quality degradation; and the development of tools for monitoring ecosystem health and conservation planning. This research has been aimed at testing general ecological principles in a tropical setting to elucidate whether ecological patterns and processes fit accepted paradigms or are distinctive and how any differences are determined by the tropical biophysical characteristics. This has in turn been applied to develop general models of stream ecology in humid tropical environments and to inform conservation management in the Wet Tropics, by contributing to water resource planning and catchment management in the region (e.g., Davis, 2006; Kroon, 2008; Godfrey & Pearson, 2012; DEHP, 2014; DNRM, 2014, 2015; Terrain NRM, 2015), as threats to environmental values, including the receiving waters of the Great Barrier Reef ecosystems, become more apparent at the same time as agricultural and other development pressures intensify.

In this chapter I provide an introduction to the patterns and processes determining freshwater invertebrate diversity in streams in the Wet Tropics, drawing on the research of

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[1] This chapter contributed substantially to Connolly *et al*. (2008) and Pearson *et al*. (2015)

many people, largely undertaken at James Cook University. A large part of this information was published in the review by Connolly *et al*. (2008). Research undertaken in the Queensland Wet Tropics is also reviewed in Connolly and Pearson (2004), which describes anthropogenic impacts on streams in the humid tropics, and in Pearson *et al*. (2015), which describes Wet Tropics stream ecology more generally, including other biotic components such as fish and amphibians. This research highlights how the ecology of these ecosystems is complex and maintained by a diverse array of physical and biotic processes that interact at various temporal and spatial scales in relation to the region's biogeographic history and present-day environment.

2.2 The biophysical environment

The Queensland Wet Tropics (here abbreviated to "Wet Tropics") is a unique bioregion within Australia, characterised by high rainfall and temperature. It is a discrete area of humid tropical landscape, occupying 18,497 km^2, set on the edge of the otherwise semi-arid, wet-dry landscape of northern Australia (Figure 2.1). Despite its relatively small area, representing only 0.26% of the Australian continent, the Wet Tropics is one of Australia's most biodiverse regions and supports a high proportion of the continent's plant and animal species, including aquatic plants (Mackay *et al*., 2010, Ramsay & Cairns, 2004), stream invertebrates (Pearson *et al*., 1986, Lake *et al*., 1994, Connolly *et al*., 2008) and freshwater fishes (Pusey *et al*., 2008). It is remarkable for its ancient rainforests, high biodiversity and strong indigenous cultural history, all underpinning its listing as the Wet Tropics of Queensland World Heritage Area (WTMA, 2013).

The Wet Tropics has a varied landscape with a chain of high mountain ranges, rising sharply from a relatively flat and narrow coastal floodplain, providing steep escarpments, deep valleys and extensive uplands and tablelands. The ranges include the highest peaks in Queensland, rising to 1660 m at Mt Bartle Frere, and catch the easterly winds that carry moisture-laden air from the warm waters of the Coral Sea. This produces a climate that is warm and humid, dominated by seasonal patterns of rainfall, with a summer wet season and winter drier season. Summer mean daily temperatures are 23-31˚C on the coast and 17-28˚C in the uplands; with winter temperatures 18-26˚C and 9-22˚C respectively. But temperature ranges throughout the region can be extreme, dropping to 0˚C on the mountains and reaching greater than 40˚C in the lowlands. Annual rainfall is also extreme, in excess of 4000 mm in the lowlands (e.g., mean 4286 mm at Babinda) and up to 12,461 mm at the summit of Mt

Bellenden Ker (Australia Bureau of Meteorology data). Over 60% of this rainfall occurs in the December–March wet season, and is driven by equatorial monsoonal systems, including cyclones, that dump huge quantities of water on the landscape over short periods of time; daily rainfall totals in the hundreds of millimetres are common across the region.

The vegetation is dominated by rainforest (Webb & Tracey, 1981; Tracey, 1982). However, contributing to the complexity of this region, there are other regional ecosystems including wet-sclerophyll forests, open woodlands, lowland *Melaleuca* forests, and extensive palustrine wetlands and grasslands on the larger floodplains of the Herbert and Murray-Tully Rivers (Kemp *et al*., 2007). The coastline vegetation includes narrow forested/shrubby dune ridges and mangrove fringes. Most of the lowland forest has been cleared for agriculture, mostly sugar cane, but also bananas and other horticultural crops. On the Atherton Tablelands there is dairy farming, and cattle grazing occurs on coastal flats, with several introduced pasture grasses displacing native grass and herb species (Kemp *et al*., 2007). Plantation forestry (mostly of exotic pines) is also a common land use in the region.

Streams and wetlands are numerous and conspicuous features in the landscape. There are eleven major easterly flowing streams, from the Annan River in the north to the Herbert River in the south. The easterly flowing rivers are generally short, with the exception of the Barron and Herbert Rivers. Their floodplains are limited in area, the most extensive being the Tully/Murray and Herbert River floodplains. Estuaries are also generally small, but extensive estuarine habitat and mangrove forests occurs in the Hinchinbrook Channel, between Hinchinbrook Island and the mainland, and in Trinity Inlet near Cairns. The streams draining to the west have shallower gradients and are much longer, flowing outside the Wet Tropics bioregion, north-west through the Einasleigh Uplands bioregion to join the Mitchell River discharging in the Gulf of Carpentaria, or west into the Northern Brigalow bioregion to join the Burdekin River that meanders eastwards again to discharge into the Great Barrier Reef lagoon south of the township of Ayr.

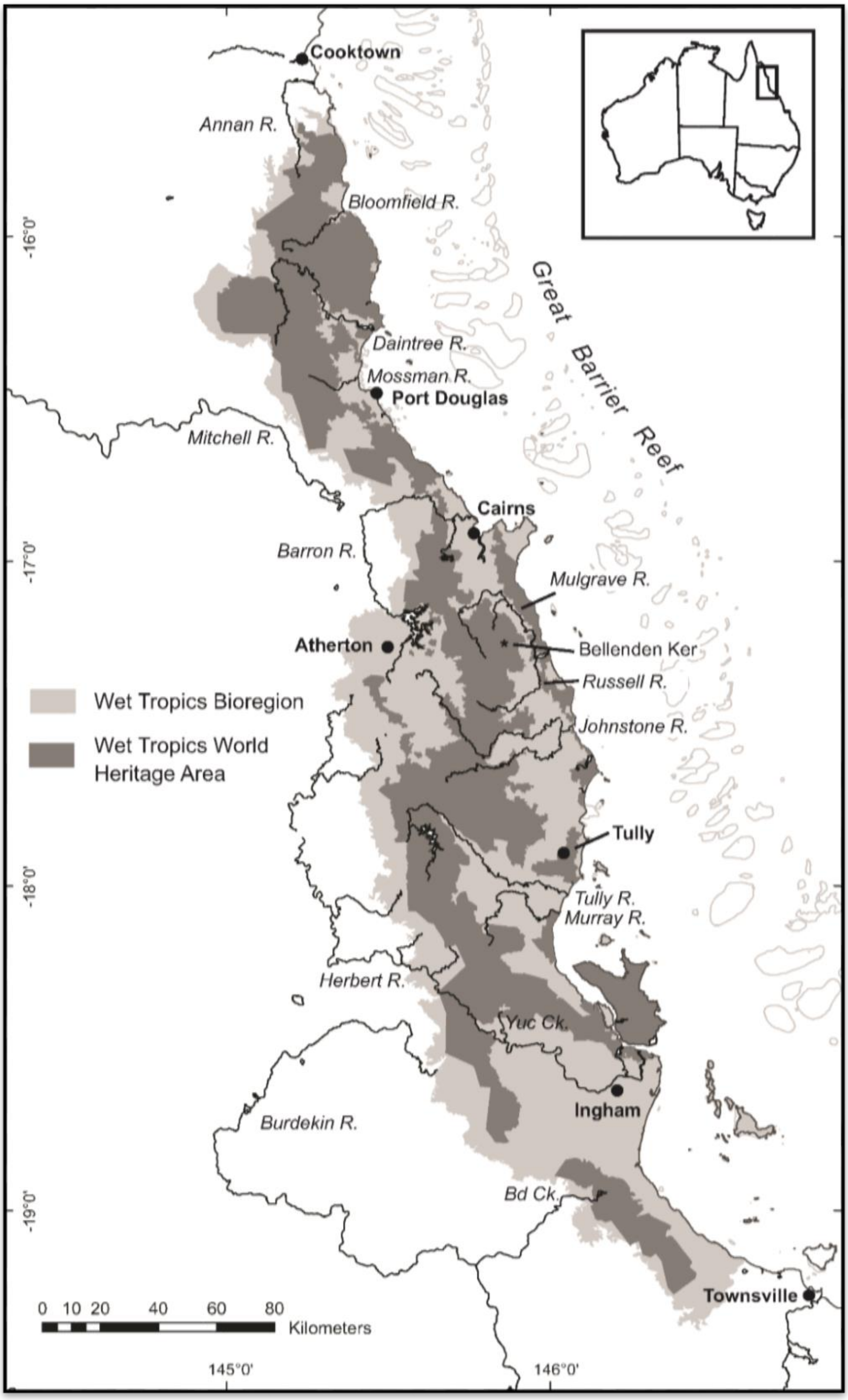

Figure 2.1 Map of the Australian Wet Tropics biogeographic region showing locations of the Wet Tropics World Heritage Area, major rivers and towns, two small study streams referred to in the text (Yuccabine Creek [Yuc Ck] and Birthday Creek [Bd Ck]) and Mount Bellenden Ker, site of Australia's maximum annual rainfall.

Stream flow is seasonal and with spates and flooding common through the wet season, inundating the floodplains and replenishing wetlands (Karim *et al*., 2011). But unlike flood-pulse rivers (Junk *et al*., 1989), many of the major rivers have natural levies and the distributary channels do not drain back to the main river channels, but enter coastal wetlands and drain to other coastal streams. The drainage of much of the floodplains has also been modified to facilitate sugar cane agriculture. Although stream discharge peaks in the wet season, base flow does contribute a high proportion of total annual discharge within the Wet Tropics. Most streams, although seasonal in flow, are perennial and during the dry season flow is sustained by fractured rock aquifers, orographic rainfall and forest cloud capture associated with the mountain massifs (McJannet *et al*., 2007), as well as floodplain alluvial aquifers and lesser rainfall events that occur through the dry season (Connolly *et al*., 2007a). This contrasts with the seasonally intermittent and ephemeral hydrology of streams in many other parts of Australia, including most of the tropical region. Queensland's Wet Tropics streams are ancient, and probably have remained perennial over millions of years (Nott, 2005). Gondwanan origins of many species and high levels of endemism also suggest that the Wet Tropics stream have been significant refugia through Pleistocene climatic change (McKie, 2002; Pearson, 2005; Krosch, 2006). In an Australian context, therefore, Wet Tropics streams are exceptional and sustain a unique and diverse freshwater fauna, including species-rich invertebrate communities (e.g., Pearson *et al*., 1986; Walker *et al*., 1995; Pearson & Boyero, 2009), distinctive fish fauna with many endemic species (Pusey & Kennard, 1996; Pusey *et al*., 2008) and a diverse frog fauna (e.g., Williams *et al*., 1996).

2.3 Wet tropics stream invertebrates

Research within the Wet Tropics, including experiments examining small-scale processes and interactions (e.g., Pearson & Connolly, 2000; Connolly *et al*., 2004; Cheshire *et al*., 2005; McKie & Pearson, 2006; Connolly & Pearson, 2007; Connolly & Pearson, 2013) and large-scale surveys crossing broad latitudinal and/or altitudinal gradients (e.g., Christidis, 2003; McKie *et al.*, 2005; Connolly *et al*., 2016), has provided a good basis for commenting on small- and large-scale diversity patterns of tropical stream invertebrates. However, most ecological studies of freshwater invertebrates in the Wet Tropics have been limited to crustaceans and insects, and the ecology of numerous non-arthropods, such as Oligochaeta, is largely unknown.

Decapod crustaceans are common in most Wet Tropics streams and include 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 (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 spiny crayfish *Euastacus* (Parastacidae) occur on different mountain tops as a result of vicariant speciation (Morgan, 1988; Short & Davie, 1993; Ponniah & Hughes, 2006). Patterns of diversity vary among taxa according to their dispersal abilities and biogeographic history. For example, endemic species of Ephemeroptera have restricted distributions, limited dispersal abilities and require cool streams (Christidis, 2003; Christidis & Dean, 2005), whereas species of Trichoptera and Chironomidae are more widely distributed (McKie *et al*., 2005). High levels of genetic differentiation in populations of the shrimp *Caridina zebra* in the Tully catchment, indicate that movement is locally limited, whereas less differentiation of animals between the Herbert and adjacent Tully streams suggests past stream capture (Hughes *et al*., 1996). Crayfish are generally resident in stream reaches (e.g., Coughlan, 1990), whereas several shrimp species undergo cyclic short or long migrations (Kneipp, 1979; Smith, 1987).

The Ephemeroptera, Trichoptera and Chironomidae typically dominate invertebrate assemblages in Wet Tropics streams, both in abundance and numbers of species (e.g., Pearson *et al.*, 1986; Pearson & Connolly, 2000; Connolly *et al*., 2007b, 2016) and are the taxa best described in the region (Walker *et al*., 1995; Cranston, 2000; Christidis, 2003; Christidis & Dean, 2005; McKie *et al*., 2005; Krosch, 2006). Their varied life histories, dispersal abilities and feeding ecologies facilitate assessment of the factors causing or sustaining current patterns of distribution.

The Ephemeroptera of the Wet Tropics comprises 28 genera and 58 species from five families (Christidis, 2003; Christidis & Dean, 2005). Despite the smaller size of the Wet Tropics region, species richness appears to be comparable to that of other Australian regions: about 70 species of mayfly are known from Victoria (Dean & Suter, 1996), 30 from Tasmania, 12 from south-western Australia (Dean & Suter 1996), 14 from South Australia (Suter 1986; Alba-Tercedor & Suter, 1990), 9 from Cape York Peninsula (Wells & Cartwright, 1993) and 24 from the Alligator Rivers region of the Northern Territory (Suter, 1992). The majority of mayflies in the Wet Tropics have Gondwanan affinities, but there are two major components of the Wet Tropics fauna: (i) a Gondwanan element, including the family Amelotopsidae and almost all of the Leptophlebiidae, which have phylogenetic affinities with taxa present on other Gondwanan landmasses, particularly southern South America and New Zealand; and (ii) an oriental element, including the family Prosopistomatidae, the leptophlebiid genus *Thraulus* and some Baetidae, which are restricted to northern Australia. A striking feature of the mayfly fauna of the Wet Tropics is the high level of endemism: 21 of the 29 species of Leptophlebiidae recorded from the Wet Tropics are endemic to the region, and some of these species are also subregional endemics (Christidis, 2003).

Walker *et al*. (1995) provided a detailed examination of the species records of Trichoptera from a large number of sites in the Wet Tropics. They found high species richness at site and regional scales, confirming previous reports (Pearson *et al*., 1986; Vinson & Hawkins, 1998, 2003). They found that species richness of Trichoptera in the Wet Tropics was greater than in the Tasmanian World Heritage Area (Neboiss *et al*., 1989). The highest diversity recorded at any Wet Tropics site was 78 species at Yuccabine Creek (Pearson *et al*., 1986), exceeding the richest sites in Tasmania (Franklin River, Roaring Creek Junction, 45 species; Walker *et al*., 1995), Victoria (O'Shannassy River, 44 species; Dean & Cartwright, 1987) and Cape York Peninsula (Gunshot Creek, 47 species; Wells & Cartwright, 1993). The species lists for Yuccabine Creek and O'Shannassy River resulted from extensive collecting, and lower diversity at other sites may reflect a smaller collecting effort. However, there is strong evidence that species richness of Trichoptera is greater in the Wet Tropics than in other areas of Australia at site and regional scales.

McKie *et al*. (2005) identified 87 chironomid species in 49 genera in a survey of small streams across the Wet Tropics. Estimation of the total Australian species pool is difficult, since new species are frequently discovered, but the Wet Tropics count evidently represents a substantial proportion of the currently recognized pool of 160–200 species. On the basis of appropriate extrapolations, Cranston (2000) estimates the number of species in the Wet Tropics to be approximately 110–158; however, he points out that this total is much lower than for tropical regions of Asia and the Americas and that the chironomid fauna is relatively depauperate compared to that of other continents. For example, 216 species were recorded from two sites 3 km apart in Costa Rica, and 174 species were collected from only one drift net deployed for 12 hours in Guinea (Cranston, 2000). However, endemism in the Wet Tropics is high, with 15 of the genera being novel, and several novel species within previously recognized genera. Over half the genera occur worldwide and about 25% of the fauna has Gondwanan affinities, while some species are clearly of Asian origin. Recent molecular studies of *Echinocladius martini* have found that dispersal of chironomids may be much more restricted than previously thought, and that the presupposed extensive distribution of *E. martini* along the east coast of Australia may actually constitute a broader species complex (Krosch, 2006).

2.4 Comparisons with other latitudes

The diversity of stream invertebrates in the Wet Tropics has been reported to be high in comparison with similar streams elsewhere in Australia (Lake *et al*., 1994; Walker *et al.,* 1995) and globally (Pearson *et al.*, 1986; Vinson & Hawkins, 2003; Pearson & Boyero, 2009; Pearson, 2014). However, Cranston (2000), in a broad review of the Chironomidae along the Australian eastern states, reports no compelling evidence for a larger regional species pool in the tropics than in south-eastern Australian streams. These contrasting observations are interesting because there are conflicting accounts of the latitudinal patterns of lotic invertebrates. Stout and Vandermeer (1975) and Boyero (2002) found greater diversity of stream invertebrates at lower latitudes in the Americas. However, other authors have suggested that lotic invertebrates are an exception to the rule that biodiversity decreases with latitude (Patrick, 1966; Coffman, 1989; Coffman & De La Rosa, 1998; Flowers, 1991).

Most studies of lotic invertebrates rely on small-scale samples taken at a limited number of sites, and data on regional species pools are consequently deficient. The lack of comprehensive descriptions of lotic faunas at regional scales, particularly in the tropics, means that broad comparisons along latitudinal gradients are problematic. For example, Lake *et al.* (1994) estimated the regional species pool of benthic invertebrates from within-site samples from two Victorian and two Wet Tropics sites, following procedures used by Stout and Vandermeer (1975) in a similar latitudinal comparison. These sites had been studied over long periods of time and so the species pools were well described. However, their estimates of species richness were actually at the site rather than the regional scale, raising the question of how well the assemblages at two sites (per region) could represent the regional species pool even if all species were recorded for each site.

Nevertheless, the comparisons by Lake *et al.* (1994) and Stout and Vandermeer (1975) highlight some interesting differences between sites at different latitudes, with both concluding that species richness on stones was greater at tropical sites than in temperate sites. In both studies, stone samples accumulated species more gradually in tropical than in temperate sites, but continued to accumulate for longer in the tropics as additional stone samples were added to the data. This observation reflects the distribution of species amongst the stones sampled. If the assemblages on individual stones are randomly assembled then a lower slope could occur if there were fewer individuals found per stone at tropical sites, or if the distribution of species amongst stones were more heterogeneous. Stout and Vandermeer (1975) concluded that tropical invertebrates were more spatially heterogeneous than their higher latitude counterparts and observed lower densities on stones in the tropics. It is not clear if the same was observed by Lake *et al.* (1994), although Pearson (1994) does comment that fauna at Yuccabine Creek, one of the sites used in the comparison by Lake *et al.* (1994), *"was not abundant compared to streams elsewhere"*. Thus, because the curves at tropical sites rise more gradually but plateau at a higher level, there appear to be more species in the site species pool in the tropics and a greater number of rare species with spatially patchy distributions. Interestingly, these within-site patterns may be mirrored in multi-site studies from the Wet Tropics, in which the rate of Trichoptera and Chironomidae species accumulation showed little sign of declining over samples collected from 20 and 33 sites respectively (McKie, 2002; Pearson, 2005). Marchant et al. (2006) observed similar patterns in Victoria, with the total numbers of species (of all macroinvertebrates) at a series of reference sites in 25 drainage basins still increasing after examination of 38-45 samples in each basin..

The differences in distribution of aquatic invertebrate diversity with latitude has implications for comparisons of species richness, with greater effort required at tropical sites to avoid underestimating species richness. Both Stout and Vandermeer (1975) and Lake *et al.* (1994) recognise that differences between sites at different latitudes were not detectable until a large number of stone samples were collected, because of the relatively slower rate of occurrence of taxa at the tropical sites. Stout and Vandermeer (1975) suggest that the lack of difference detected in other studies (e.g., Patrick, 1966) was due to inadequate sampling, with further problems arising from inconsistent methodology.

Our best estimates of regional species pools currently are usually not derived from quantitative surveys but from accumulated knowledge of species records by taxonomists and systematists with intimate knowledge of their particular group (e.g., Walker *et al.*, 1995; Cranston, 2000; Christidis, 2003; Christidis & Dean, 2005). The review by Walker *et al.* (1995), which compared the diversity of Trichoptera in the Wet Tropics with that of the temperate Tasmanian World Heritage Area, is rare in considering the full suite of species records at a large number of sites. This study was not limited by taxonomy, as it was undertaken by recognised Australian Trichoptera systematists and sampling effort appears to have been high, including sampling of some sites at multiple times. They found that although richness at the family and genus levels does not appear to differ between the Wet Tropics and the Tasmanian WHA, species richness diverges markedly. The average number of species for the ten most diverse sites in the two World Heritage Areas was 41.8 species for the Wet Tropics and 37.0 species for the Tasmanian World Heritage Area. This is not a large difference and given the higher regional difference, suggests that regional richness is greater but local richness is constrained in the Wet Tropics.

Cranston (2000) has similarly suggested that individual stream richness is constrained for the chironomid fauna, and argued there was no overall difference in regional species pools between tropical and temperate regions. This contrasts with observations for Trichoptera and some vertebrates (especially fishes and frogs) and may relate to differences in the degree of ecological specialisation characteristic of these different groups (McKie *et al*., 2004). More generally, recent assessment of regional diversity patterns of stream faunas, based on published species lists, suggests that those taxa that have a significant terrestrial phase (e.g., Odonata) are more species-rich in the tropics (Boulton *et al.*, 2008; Pearson & Boyero, 2009). Inconsistency in the responses of different invertebrate groups may explain Hillebrand's (2004) observation that while a latitudinal gradient in species richness seems apparent for freshwater systems, it appears weaker than in marine or terrestrial environments, and differs between continents and habitat types.

2.5 Biogeographic history

Large-scale patterns of distribution of fauna and flora are typically associated with regional or subregional differences in environmental conditions. However, as conditions are not constant in time, current distributions may reflect past rather than present climate and geology. The distribution of rainforest within the Wet Tropics has fluctuated with climate during the Quaternary (Quilty, 1994). During the late Pleistocene (13,000 to 8,000 years ago), drier sclerophyll forests displaced most rainforest, with only isolated moist upland refugia remaining (Nix, 1991). Subsequently, increased rainfall allowed rainforest to expand to its current extent (Hopkins *et al.*, 1996), but current diversity and distributional patterns of several groups of terrestrial organisms bear the signature of the past rainforest contractions: for example, diversity and endemism of terrestrial vertebrates are greatest in the largest refugial areas (Williams & Pearson, 1997; Winter, 1997). In contrast, current diversity patterns of the Wet Tropics freshwater fish, Chironomidae and Trichoptera seem little affected by the Pleistocene contractions, with most species homogeneously distributed throughout the region's latitudinal range (Walker *et al.*, 1995; Pusey & Kennard, 1996; McKie *et al*., 2005; Pearson, 2005), although there is some indication of loss of lowland species of Trichoptera, as seen for the terrestrial vertebrates (Pearson, 2005), and some invertebrate species appear to have restricted distributions – for example, some mayflies (Christidis, 2003) and *Euastacus* crayfish species restricted to mountain tops in the Wet Tropics (Morgan, 1988, Short & Davie, 1993).

McKie *et al*. (2005) found no evidence for an enduring effect of historical rainforest contractions on current distribution patterns for Chironomidae, with most species present at all latitudes within the Wet Tropics. Further, their surveys showed no "hotspots" of species richness associated with rainforest persistence during dry glacial periods, although abundance (but not richness) of some Gondwanan species tended to increase with altitude. They suggest that stream habitats may have been buffered from the effects of climate change where stream flow and shade were maintained. Mountain ranges may have continued to capture enough precipitation to maintain flows and narrow riparian strips of rainforest vegetation, or even drier sclerophyllous vegetation, may have maintained shade and kept water temperatures cool. In locations where streams became ephemeral or dried completely, they suggested that the vagility of the adult chironomids would have allowed recolonisation as the climate ameliorated and flow returned, obscuring any effects on contemporary distributional patterns. The widespread distribution across broad latitudinal and altitudinal bands of Australian lotic chironomids show their relatively unconstrained ecology (Brundin, 1966), substantiated by ecophysiological studies demonstrating broad temperature tolerances, even for cool-Gondwanan species (McKie *et al*., 2004). However, molecular research highlighted substantial genetic differentiation among populations of one chironomid species, *Echinocladius martini*, inhabiting different rainforest blocks, and even adjacent streams (Krosch, 2006). This indicates that the forest environment may constitute a substantial barrier to dispersal between streams for adults of weakly flying taxa such as the Chironomidae, and demonstrates that the biogeography of the Wet Tropics can have a substantial influence on the distribution of freshwater diversity at the genetic level.

The Trichoptera appear to be homogeneously distributed throughout the latitudinal extent of the Wet Tropics, with no subregional species distribution patterns (Walker *et al.*, 1995; Pearson, 2005). In contrast, distributional patterns among leptophlebiid mayflies within the Wet Tropics suggest that the biogeographic history of the region has influenced the present-day distributions of species (Christidis, 2003). Although some leptophlebiid species occur throughout the Wet Tropics (e.g., *Jappa serrata*, *Atalophlebia* sp. AV13, *Nousia* sp.NQ1), others appear to have far more restricted distributions. For example, WT sp. 4, an undescribed species of a new genus, is presently known only from the Daintree region, whereas its sister species WT sp. 2 occurs in the Daintree as well as the Cardwell / Ingham area north of the Herbert River, but is absent from the Paluma Range to the south of the Herbert River. Molecular data may show whether the presence of WT sp. 2 in the Cardwell / Ingham area represents recent dispersal into the area from populations further north. The absence of several species from the Paluma Range suggests that the Herbert River may be an effective barrier to the dispersal of some mayfly species. Interestingly, the distributions of a number of the endemic rainforest vertebrates also do not extend south of the Herbert River (Nix, 1991, Williams *et al.*, 1996). A new genus of leptophlebiid, WT sp. 6, was also collected from only two downstream lowland sites, in Babinda Creek and the adjacent Behana Creek, in the central Wet Tropics (Connolly *et al*., 2007b, Connolly *et al*., 2016; Chapter 6).

The restricted geographic distribution of many of the leptophlebiid species is not surprising given the limited dispersal abilities of mayflies. The nymphs of many species are confined to cool forest streams and the potentially dispersive adults are short lived (two to three days) and prone to desiccation. It is noteworthy that widely distributed species tend to have broader ecological tolerances and occur in a range of flow regimes including pools with reduced flow, whereas species with more restricted distributions are found predominantly in fast-flowing waters (Christidis, 2003).

Overall, past climatic fluctuations in the region appear to have had an enduring effect on the present-day distributions of leptophlebiid species, probably because of their limited dispersal abilities and narrow ecological tolerances. In contrast, the possibly more vagile and tolerant Chironomidae and Trichoptera have long since overcome any restrictions imposed in the past and are now widespread in suitable habitats across the Wet Tropics.

2.6 Environmental gradients

Within-stream gradients are also important determinants of aquatic invertebrate distributions and need to be accounted for in any intra- or inter-regional comparisons of stream sites. Wet Tropics streams descend quickly from the ranges, passing over tablelands and through steep gorges, before flowing across a narrow coastal floodplain to wetlands and estuaries. The rapid changes in altitude coupled with a narrow floodplain have resulted in a sharp geomorphic gradient in these systems (Connolly *et al*., 2007a). Such gradients are usually reflected in the distributions of invertebrates (e.g., Allan, 1975; Vannote *et al.*, 1980; Bapista *et al.*, 2001), which follow the physical changes that occur along the stream continuum, including gradients of temperature, stream size, slope, discharge, current velocity and substratum.

2.6.1 Altitudinal gradient

McKie *et al.* (2005) found consistent trends in chironomid distributions in Wet Tropics streams with altitude, with cool Gondwanan taxa (originating in cooler regions of the former Gondwanan supercontinent and with distributions now centred on Australia's southeast) occurring predominantly in cooler upland streams (e.g., *Echinocladius martini, Botryocladius grapeth*), while species from tropical and cosmopolitan genera were more typical of lowland sites (e.g., *Rheocricotopus* sp. and *Nanocladius* sp.). However, cool Gondwanan species were also found in well-shaded lowland streams (e.g., Gap Creek, north of Bloomfield) characterised by cooler conditions arising from the mountain mass effect (Nix, 1991), whereby streams drop rapidly down steep escarpments, limiting the scope for warming. Conversely, poorly shaded upland streams (e.g., Yuccabine Creek), that can be two to three degrees warmer than predicted for their altitude, may support no cool Gondwanan species. Thus, the complexity of the Wet Tropics environment precludes strict zonation of chironomid faunas with altitude, as observed elsewhere in both tropical (e.g., Jacobsen *et al*., 1997) and temperate regions (e.g., Rossaro, 1991) of the world, and any systematic relationship with species diversity. Nevertheless, cool upland streams appear to have favoured the persistence of a cool-temperate chironomid fauna in the otherwise warm Wet Tropics region, as the Australian continent drifted northwards. Furthermore, altitude is likely to prove an important determinant for distributions of other taxa: for example, distributions of Trichoptera are correlated with altitude, with more species in upland than lowland streams and with a greater number of exclusive trichopteran species at more than 700 m above sea level than at lower altitudes (Pearson, 2005).

Wet Tropics streams crossing abrupt escarpments create waterfalls, which have specialised faunas that are essentially isolated from each other by the lack of suitable intervening habitat (Clayton 1995). Special characteristics included high-velocity regions, dominated by species of Simuliidae, moderate velocity regions with Hydropsychidae and Blephariciidae, and low velocity and splash zones with Pyralidae and various beetles. As waterfalls often create a gap in the canopy, algal growth is possible and several of the specialist species are algal grazers (e.g., Blephariciidae and Pyralidae); others are filter feeders, benefiting from the food supplied in the strong currents (e.g., Simuliidae and Hydropsychidae).

2.6.2 Lowland longitudinal gradient

In lowland streams, the chemical and physical character of the streams changes gradually along their length and invertebrate distributions reflect this longitudinal gradient (Connolly *et al.*, 2007a, b, 2015, 2016). Species richness strongly correlates with mean sediment size, with more species present in riffles dominated by cobbles than in sandy stretches, and there is a consistent longitudinal pattern of species turnover with different assemblages in the upper, middle and lower parts of the stream. These patterns are described in detail in Chapter 6.

2.7 Local patterns of α diversity

While large-scale patterns of diversity are predominantly structured by biogeographic and climatological histories and through broad environmental gradients, the composition of the invertebrate assemblage at any given location is further influenced by ecological interactions and processes, immigration, emigration and disturbance.

2.7.1 Disturbance

Physical disturbance is a characteristic of Wet Tropics stream environments, caused by high flows that shift substrata and abrade objects in their path. High flows can cause catastrophic local mortality, but also promote diversity by providing continually renewed habitat heterogeneity and preventing dominant species from displacing others. Flooding creates a somewhat unpredictable stream environment, but is inevitable, so resistance to disturbance and recolonisation capacity are necessary characteristics of stream faunas world-wide (Gore & Milner, 1990; Mackay, 1992). The occurrence of spates, associated with widespread density-independent mortality, may dilute the importance of factors such as predation and competition as structuring forces in streams, at least in the wet season, although these factors may be important during the dry season, when habitats are reduced in extent and animal densities are higher (e.g., Dudgeon, 1993; Pearson, 2005).

Rosser and Pearson (1995) showed that riffle faunas in the Wet Tropics were generally well adapted to unpredictable high-flow events, such that recolonisation of denuded areas of stream bed took place remarkably rapidly. On smaller scales, two chironomid species showed great resistance to physical disturbance in the laboratory, though sublethal effects of the disturbance on growth and fecundity were apparent (McKie, 2004). Recolonisation of denuded substrata following disturbance may be from several sources and depends on the scale of the disturbance and the source of colonists – local movements from nearby undisturbed patches, immigration from other sections of the stream or aerial immigration and egg-laying by adults of aquatic insects. Typically, many aquatic invertebrates drift with the current over short distances and this gives them the ability to quickly recolonise available space. For example, Benson and Pearson (1987a, b) demonstrated the capacity of the stream fauna to recolonise denuded substrata in experiments in Yuccabine Creek, particularly by drifting, but also by means of upstream movements.

Experiments in Birthday Creek (Chapter 4) showed that at small scales (individual leaf litter packs) the assemblage of invertebrates approximate equilibrium dynamics involving the immigration and emigration of individuals from the drift or surrounding substrata, with ~10% turnover of individuals on a leaf pack per day. Therefore, these animals not only have a strong capacity for recolonisation after disturbance, they are also continually dispersing within the riffle substrata, and with around 10% of the riffle fauna available to colonise available substrata every day, it is not surprising that small areas of experimentally denuded substrata were rapidly reoccupied.

2.7.2 Biotic interactions

Effects of competition and predation have been demonstrated in streams (Kohler, 1992; Peckarsky *et al.*, 1993), and succession was apparent in the colonisation of the small units of substratum used in the experiments described above, suggesting that biotic interactions have some role at these small scales. However, it is difficult to demonstrate that changes in habitat use and distribution are the consequences of such interactions (Giller & Malmqvist, 1998).

Some small-scale biotic interactions may be specific and subtle. For example, McKie and Pearson (2006) revealed remarkably specific developmental and behavioural responses by chironomid prey to different predator species. Boyero *et al.* (2008) showed that fish predators had substantial indirect effects on detritus-based food webs in streams, mediated by changes in consumer behaviour. Sublethal effects of predation on the behaviour and development of individuals have potential to influence individual fitness and habitat use at small scales, but even at larger scales these effects could influence the demographics of prey populations, and hence patterns of species distribution, especially where responses of prey to predators are well differentiated (McPeek & Peckarsky, 1998; McKie & Pearson, 2006).

Boyero & Pearson (2006) also demonstrated interactions between detritivores (shredders) in Wet Tropics streams. For example, per-capita leaf processing by individual shredders decreased exponentially when other individuals of the same species were present, although overall breakdown increased with greater density of shredders. Further, shredders were able to detect chemical cues from conspecifics and responded to them by reducing their immediate activity (Allan *et al*., 2009). However, this reduction in activity was not reflected in individual rates of shredding, so it is probable that visual or physical interactions are more important, or that individuals get used to the presence of the chemical cues.

2.7.3 Habitat partitioning

It has long been accepted that species-specific responses to current velocity, substratum characteristics and food sources affect diversity and distribution of invertebrates at the riffle scale through partitioning of microhabitats (Cummins & Lauff, 1969; Rabeni & Minshall, 1977; Minshall, 1984), even with continuous movement of individuals. McKie (2002) found clear patterns in the microdistribution of chironomids across five habitats in Birthday Creek. Even within a single genus, *Polypedilum*, that is otherwise morphologically uniform, there were distinct differences between pools and riffles, and between leaf litter and stones: thus, *P. australotropicus* was found in pool leaf packs, *P. vespertinus* was found only on pool rocks, *P*. "alpha", was found in all leaf and rock riffle habitats, while *P. oresitrophuus* was found only in riffle leaf packs.

Likewise, fine divisions of habitat by mayflies were evident in Yuccabine Creek and were confirmed by manipulative experiments in the stream (Hearnden & Pearson, 1991). Twelve species occurred in all the microhabitats examined, but each species had significant peaks in abundance in particular microhabitats, and where two species preferred the same habitat, they were very different in size. Like the chironomids, the mayfly species showed distinct preferences for either pools or riffles, and further discriminated among habitats on the basis of substratum size (sand to large rock) and presence of leaf litter. Such habitat preferences have been shown for entire assemblages in Birthday Creek (Benson, 1999). Habitat partitioning is also a characteristic of odonates, again relating to the same habitat variables (Charlton, 1989), but neither the mayflies (mostly detritivores) nor the odonates (predators) showed much partitioning of food resources, except perhaps by particle size. However, there is partitioning of food resources elsewhere in the aquatic food web (Cheshire *et al.*, 2005), and within some invertebrate groups. For example, trichopteran shredders apparently have distinct preferences for different resources: some eat leaves in riffles, some eat leaves in pools and others eat mostly woody material (Boyero *et al.*, 2007).

2.7.4 Phylogenic influence on patterns of habitat use

Many studies on stream fauna have emphasised the importance of physical factors in structuring communities and in determining the distribution of species among local habitats (e.g., Cummins & Lauff, 1969; Hynes, 1970; Rabeni & Minshall, 1977; Hart & Finelli, 1999), and it has often been assumed or inferred that this is due to competitive or other ecological pressures. There has been little consideration of the influence of evolutionary history in determining the distribution of species amongst the substrata in stream habitats. However, Christidis (2003) showed that substratum and habitat use by leptophlebiid mayflies in the Wet Tropics reflected phylogenetic relationships, with closely related species tending to occur on similar substrata (e.g., *Austrophlebioides* species on stones), and in some instances in similar habitats (e.g., *Koorrnonga* species in pools). High levels of partitioning based on substratum type resulted from differences among phylogenetic lineages in the use of substrata: the litter fauna was dominated by species of the *Nousia* lineage, whereas the stone fauna was dominated by species of the *Meridialaris* lineage. Likewise, association with a particular habitat type of species within some lineages contributed to the distinctiveness of mayfly assemblages of pool, run and riffle habitats. Thus phylogenetic history is important in determining some ecological traits and present-day species' distributions among substratum and habitat types. It is unknown how broadly such conclusions might apply, but it is likely that other elements of the fauna are similarly influenced by their phylogenetic history.

2.8 Influence of biodiversity on ecological processes

While attention has been paid to the historical and current factors that influence biodiversity patterns, there is increasing interest in how biodiversity influences ecosystem function because of concerns about the potential consequences of species loss (Loreau, 2000; Loreau *et al.*, 2001). Jonsson & Malmqvist (2003) focussed on the influence of biodiversity on the decomposition of terrestrially derived leaf litter, which drives the food web in forest streams (Vannote *et al.*, 1980), including tropical rainforest streams (Benson & Pearson, 1993; Dobson *et al.*, 2002; Cheshire *et al.*, 2005). Temperate streams harbour a numerically important shredder guild but shredders are reported to be scarce in the tropics (Dudgeon & Wu, 1999; Dobson *et al.*, 2002; Mathuriau & Chauvet, 2002). This is not true for Wet Tropics streams where insect shredders constitute around 20% of the total species richness (*cf*. world average of 11%) (Cheshire *et al.*, 2005). Previous research has demonstrated the importance of shredders in the community (Pearson & Tobin, 1989; Pearson *et al.*, 1989, Coughlan, 1990; Nolen & Pearson, 1992; Coughlan *et al.,* 2010) and experiments, outlined below, have investigated the relationship between the diversity of shredders and the decomposition process.

Activity of shredders (including several species of Parastacidae, Trichoptera, Leptophlebiidae, Chironomidae and Coleoptera) is high in Birthday and Camp Creeks (Cheshire *et al*., 2005; Coughlan *et al*., 2010). Colonisation of leaf litter packs occurs within two weeks (Chapter 4) and competitive interactions are likely to take place mostly among individuals of the most abundant species. Intraspecific interactions in these species also occur in laboratory conditions, as individual leaf breakdown activity decreases as density increases over a wide range (from two to twelve individuals per leaf) (Boyero & Pearson, 2006). Although abundance of leaves is not usually a limiting factor, shredders show strong preferences for particular leaf species, which are patchily distributed (Bastian *et al*., 2007).

The number of shredder species, their individual patterns of behaviour and their intraspecific and interspecific interactions all influence breakdown rates. It is possible that there is redundancy in the species complement, but the nature of the redundancy cannot be assumed and must be determined at the species level. For example, Boyero *et al.* (2006, 2007) showed that species identity was the main factor governing leaf breakdown rates in Wet Tropics streams, but species richness also had some effect. Leaf breakdown rates were higher than expected when the three most common shredder species were present together, suggesting the existence of at least one of three mechanisms (niche complementarity, interspecific facilitation or release from intraspecific interference). However, there is no evidence of different feeding abilities of the different species or facilitation, while release from intraspecific interference has been previously found in these species (Boyero & Pearson, 2006) and other shredders (Jonsson & Malmqvist, 2003).

Bastian *et al*. (2008) manipulated species richness and composition simultaneously across two trophic levels (leaves and shredders) and found that breakdown of leaf litter was affected by temperature, the composition of shredder communities and the diversity and identity of leaf species present, due largely to a so-called sampling effect. Different shredder species had different processing capabilities, but leaf preferences were similar for all shredder species. Increasing shredder diversity had no effect on leaf breakdown rates, but the identity of shredder species present was significant in determining those rates, as the different insect species process litter at different rates. These results corroborate findings from other studies that have shown the important role that taxonomic identity can play in the dynamics and functioning of ecosystems (Vanni *et al.*, 2002; Huston, 1997).

2.9 Conclusion

Our understanding of Wet Tropics streams is important at a regional scale for their inherent water resource, water quality and biodiversity values, and at a national scale because of their high biodiversity compared with the rest of the continent (Pearson *et al.*, 1986; Lake *et al.*, 1994; Connolly *et al*., 2008; Pearson *et al*., 2015). At a global scale, there are few other tropical regions where extensive stream research is being undertaken (some examples are: Latin America (Pringle, 2000; Pringle *et al.*, 2000; Ramirez *et al*., 2008); Hong Kong (Dudgeon, 1995, 1999, 2006, 2008; Dudgeon *et al*., 2010); and Kenya (Dobson *et al.*, 2002)). The research in the Wet Tropics, therefore, can make a substantial contribution to understanding of stream ecology generally, and to appropriate management of tropical streams, which are among the most threatened of ecosystems globally (Dudgeon, 1992, 2002, 2012; Boyero 2000; Connolly & Pearson 2004).

As for any regional biota, the diversity of invertebrates in Wet Tropics streams is influenced by a range of interlinked biogeographic, evolutionary, ecological and behavioural processes, operating at a range of scales. Thus the species assemblage on a particular unit of habitat (e.g., a cobble or leaf pack) is determined by the species pool, individual species' requirements, colonisation dynamics, small-scale interactions and chance. Understanding of such influences on the generation and maintenance of species diversity underpins further studies and, especially, appropriate management activities of ecosystems.

The invertebrate fauna of Wet Tropics streams is largely Gondwanan in origin, including several cool-adapted elements, which might otherwise struggle to persist in the region, but also includes some Asian-derived elements. The overlap between major biogeographic regions contributes to the diversity of Wet Tropics streams, like other regions (Willig *et al*., 2003). Diversity has also been increased by speciation in the region, or by the region acting as a refuge for particular species, as there is a high level of endemism for some groups (e.g., Trichoptera, Leptophlebiidae, Odonata), and subregional endemism for non-vagile taxa such as Leptophlebiidae and Parastacidae. Consequently, species richness for some taxa is higher than elsewhere in Australia and most other places that have been studied in detail globally (Vinson & Hawkins, 2003; Boulton *et al.*, 2008; Pearson & Boyero, 2009). At subregional scales, there are clear patterns of distribution of some taxa according to altitude and position along the stream continuum, relating to physical factors such as temperature, current and substratum. At local scales there are differences in assemblages between pools and riffles, and between stone and leaf pack habitats, reflecting species' habitat preferences that stem from their phylogenetic origins or subsequent evolution. At a fine scale, interactions may determine which species immediately cohabit, and impacts of biotic interactions on individuals are of significance for population demographic parameters (growth, fecundity) and have potential to influence larger-scale patterns of diversity and distribution, though the importance of such effects in the frequently disturbed streams of the Wet Tropics is presently difficult to assess. Between-latitude differences in spatial distribution, relative abundances and rarity are interesting and warrant further investigation by means of standardised studies across regions and continents. Understanding the links between diversity and ecosystem function is becoming particularly important in the face of rapid global change and species loss, and more extensive research is required to understand the processes and to apply that understanding to management responses. Research in the Wet Tropics can play a major role because of its research base, and its special place in terms of Australian and global biodiversity.

2.10 References

Alba-Tercedor J. & Suter P.J. (1990) A new species of Caenidae from Australia: *Tasmanocoensis arcuata* sp. n (Insecta, Ephemeroptera). *Aquatic Insects* **12**: 85-94.

Allan J.D. (1975) Faunal replacement and longitudinal zonation in an alpine stream. Verhandlungen des Internatiionalen Verein Limnologie **19**: 1646-1652.

Allan K., Boyero L. & Pearson R.G. (2009) Chemical communication in competitive interactions among tropical stream detritivores. *Tropical Zoology* **22**: 195-204.

Arthington A.H. (1992) Diets and trophic guild structure of freshwater fishes in Brisbane streams. *Proceedings of the Royal Society of Queensland* **102**: 31-47.

Bapista D.F., Dorville L.F.M., Buss D.F. & Nessiamian J.L. (2001) Spatial and temporal organisation of aquatic insect assemblages in the longitudinal gradient of a tropical river. *Revista. Brasileira de Biologia* **61**: 295-304.

Bastian M., Pearson R. G. & Boyero L. (2008) Effects of diversity loss on ecosystem function across trophic levels and ecosystems: a test in a detritus-based tropical food web. *Austral Ecology* **33**: 301-306.

Bastian M., Boyero L., Jackes B. R. & Pearson R. G. (2007) Leaf litter diversity and shredder preferences in an Australian tropical rainforest stream. *Journal of Tropical Ecology* **23**: 219-29.

Benson L.J. (1999) Allochthonous input and dynamics in and upland tropical stream. PhD thesis, James Cook University, Townsville, Australia.

Benson L.J. & Pearson R.G. (1987a) Drift and upstream movements of macro invertebrates in a tropical Australian stream. *Hydrobiologia* **153**: 225-239.

Benson L.J. & Pearson R.G. (1987b) The role of drift and effect of season in colonization of implanted substrata in a tropical Australian stream. *Freshwater Biology* **18**: 109-116.

Benson L.J. & Pearson R.G. (1988) Diversity and seasonality of adult Trichoptera captured in a light-trap at Yuccabine Creek, a tropical Australian rainforest stream. *Australian Journal of Ecology* **13**: 337-344.

Benson L.J. & Pearson R.G. (1993) Litter inputs to a tropical Australian upland rainforest stream. *Australian Journal of Ecology* **18**: 377-383.

Boulton A.J., Boyero L., Covich A.P., Dobson M., Lake P.S. & Pearson R.G. (2008) Are tropical streams ecologically different from temperate streams? Pages 257-284 **In** D. Dudgeon (ed.) *Tropical Stream Ecology.* Academic Press, London, UK.

Boyero L. (2000) Towards a global stream ecology. *Trends in Ecology and Evolution* **15**: 390-391.

Boyero L. (2002) Insect biodiversity in freshwater ecosystems: is there any latitudinal gradient? *Marine and Freshwater Research* **53**: 753-755.

Boyero L. & Pearson R.G. (2006) Intraspecific interference in a tropical stream shredder guild. *Marine and Freshwater Research* **57**: 201-206.

Boyero L., Pearson R.G. & Camacho R. (2006) Leaf processing in Australian tropical streams: the role of different species in ecosystem functioning. *Archiv für Hydrobiologie* **166**: 453-466.

Boyero L., Pearson R.G. & Bastian M. (2007) How biological diversity influences ecosystem function: the separate role of species richness and evenness. *Ecological Research* **22**: 551-558.

Brundin L. (1966) *Transantarctic relationships and their significance as evidenced by chironomid midges*. Gleneagles Publishing, Glen Osmond, South Australia.

Camacho R., Boyero L., Cornejo A., Ibáñez A. & Pearson, R.G. (2009) Local variation in shredder distribution can explain their oversight in tropical streams. *Biotropica* **41**: 625-632.

Charlton L. (1989) The ecology of dragonflies (Odonata) in a tropical Australian stream. Honours thesis, James Cook University, Townsville, Australia.

Cheshire K., Boyero L. & Pearson R.G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Christidis F. (2003) Sytematics, phylogeny and ecology of Australian Leptophlebiidae (Ephemeroptera). PhD Thesis, James Cook University, Townsville, Australia.

Clayton P.D. (1995) The ecology of waterfalls in the Australian Wet Tropics. PhD Thesis, James Cook University, Townsville, Australia.

Coffman W.P. (1989) Factors that determine the species richness of lotic communities of Chironomidae. *Acta Biologica Debrecina Oecologica Hungarica* **3**: 95-100.

Coffman W.P. & De La Rosa C. (1998) Taxonomic composition and temporal organization of tropical and temperate assemblages of lotic communities. *Journal of Kansas Entomological Society* **71**: 388-406.

Connolly N.M., Crossland M.R. & Pearson R.G. (2004) Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. *Journal of the North American Benthological Society* **23**: 251-270.

Connolly N.M. & Pearson R.G. (2004) Impacts of forest conversion on the ecology of streams in the humid tropics. Pages 811-835 **In** Bonnell M. & Bruijnzeel L.A. (eds.) *Forests, Water and People in the Humid Tropics: Past, Present and Future Hydrological Research for Integrated Land and Water Management.* Cambridge University Press, Cambridge, UK.

Connolly N.M. & Pearson R.G. (2007) The effect of fine sedimentation on a tropical stream macroinvertebrate assemblage: A comparison using flow-through artificial stream channels and recirculating mesocosms. *Hydrobiologia* **592**: 423-438.

Connolly N.M., Pearson B.A., Loong D., Maughan M. & Pearson R.G. (2007a) Study area and sites: geographic setting, hydrology, geomorphology and water quality of four Wet Tropics streams with contrasting land-use management. Pages 15-78 **In** Arthington, A. & Pearson, R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 247.

Connolly N.M., Pearson R.G. & Pearson B. (2007b) Macroinvertebrates as monitors of river health in Wet Tropics streams. Pages 129-176 **In** Arthington, A. & Pearson, R.G. (eds.)

Biological Indicators of Health in Wet Tropics Streams. Catchment to Reef CRC technical publication. pp 247.

Connolly N., Pearson R., Christidis, F., McKie B. & Boyero L. (2008) Diversity of invertebrates in Wet Tropics streams: Patterns and Processes. Pages 161-177 ***In*** Stork, N. and Turton, S. (eds.) *Living in a dynamic tropical environment.* Blackwell Publishing, UK. pp 652.

Connolly N.M., Pearson R.G., Loong D., Maughan M. & Brodie J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture, Ecosystems and Environment* **213**: 11-20.

Connolly N.M., Pearson R.G. & Pearson, B. (2016) Riparian vegetation and sediment gradients determine invertebrate diversity in streams draining an agricultural landscape. *Agriculture, Ecosystems and Environment* **221**: 163-173.

Cornell H.V. & Lawton J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**: 1-12.

Coughlan J.F. (1990) Population and trophic ecology of the freshwater crayfish *Cherax depressus* (Crustacea: Parastacidae) in a North Queensland tropical rainforest stream. Honours Thesis, James Cook University, Townsville, Australia.

Coughlan J.F., Pearson R.G. & Boyero, L. (2010) Crayfish process leaf litter in tropical streams even when shredding insects are common. *Marine and Freshwater Research* **61**: 1-8.

Cranston P.S. (2000) August Thienemann"s influence on modern chironomidology – an Australian perspective. *Verhandlungen Internationale Vereinigung der Limnologie* **27**: 278-283.

Cummins K.W. & Lauff G.F. (1969) The influence of substratum particle size on the distribution of stream benthos. *Hydrobiologia* **34**: 145-181.

Davis R. (2005) Douglas Shire Water Quality Improvement Plan. Douglas Shire Council. pp 176.

Dean J. & Cartwright D. (1987) Trichoptera of a Victorian forest stream: species composition and life histories. *Australian Journal of Marine and Freshwater Research* **38**: 845-860.

Dean J.C. & Suter P.J. (1996) Mayfly nymphs of Australia. A guide to genera. CRC Freshwater Research Identification Guide No. 7.

DEHP (2014) Scheduled Environmental Values (EVs) and Water Quality Objectives (WQOs) for all Wet Tropics region surface and ground waters under the Environmental Protection Policy (Water) 2009. Department of Environment & Heritage Protection, Queensland Government, Brisbane. http://www.ehp.qld.gov.au/water/policy/schedule1/wet_tropics_waters_scheduled_evs__wqos.html

DNRM (2014) Water Act 2000: Water Resource (Wet Tropics) Plan 2013. Department of Natural Resources and Mines, Queensland Government, Brisbane. pp 65.

DNRM (2015) Water Act 2000: Water Resource (Barron) Plan 2013. Department of Natural Resources and Mines, Queensland Government, Brisbane. pp 71.

Dobson M., Mathooko J.M., Magana A. & Ndegwa F.K. (2002) Macroinvertebrate assemblages and detritus processing in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshwater Biology* **47**: 909-919.

Dudgeon D. (1992) Endangered ecosystems: a review of the conservation status of tropical Asian rivers. *Hydrobiologia* **248**: 167-191.

Dudgeon D. (1993) The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshwater Biology* **30**: 189-197.

Dudgeon D. (1995) The ecology of rivers and streams in tropical Asia. Pages 615-657 **In** Cushing C.E., Cummins K.W. & Minshall G.W. (eds.) *Ecosystems of the world 22. River and stream ecosystems*. Elsevier, Amsterdam.

Dudgeon D. (1999) *Tropical Asian Streams*. Hong Kong University Press. Hong Kong.

Dudgeon D. (2002) Fisheries: pollution and habitat degradation in tropical Asian rivers. Pages 316-323 **In** Douglas I. (ed.) *Encyclopaedia of Global Environmental Change*, Volume 3. John Wiley & Sons, Chichester, UK.

Dudgeon D. (2006) The ecology of rivers and streams in tropical Asia. Pages 615-657 **In** Cushing C.E., Cummins K.W. & Minshall G.W. (eds.) *River and Stream Ecosystems of the World.* The University of California Press, Berkeley, USA.

Dudgeon D. (2008) *Tropical Stream Ecology*. Academic Press, London. pp 316.

Dudgeon D. (2012) Threats to biodiversity globally and in the Indo-Burma Biodiversity Hotspot. Pages 1-28 **In** Allen D.J., Smith K.G. & Darwall W.R.T. (eds.) The Status and Distribution of Freshwater Biodiversity in Indo-Burma. IUCN, Cambridge, U.K. & Gland, Switzerland.

Dudgeon D. & Wu K.K.Y. (1999) Leaf litter in a tropical stream: food or substratum for macroinvertebrates? *Archiv fü Hydrobiologie* **146**: 65-82.

Dudgeon D., Cheung F.K.W. & Mantel S.K. (2010) Food-web structure in small streams: do we need different models for the tropics? *Journal of the North American Benthological Society* **29**: 395-412.

Faragher R. A., Grant T.R. & Carrick F.N. (1979) Food of the platypus (*Ornithorhynchus anatinus*) with notes on the food of Brown Trout (*Salmo trutta*) in the Shoalhaven River, NSW. *Australian Journal of Ecology* **4**: 171-179.

Flowers R.W. (1991) Diversity of stream-living insects in north western panama. *Journal of the North American Benthological Society* **10**: 322-334.

Giller P.S. & Malmqvist B. 1998. *The biology of streams and rivers*. Oxford University Press Inc., New York. 296 pp.

Godfrey P.C. & Pearson R.G. (2012) *Wet Tropics Waterways Condition Assessment: Mulgrave, Russell, Johnstone and Herbert Rivers*. Report to Terrain Natural Resource Management and the Department of Environment and Heritage Protection. ACTFR Report No. 12/03, James Cook University.

Gore J.A. & Milner A.M (1990) Island biogeography theory: Can it be used to predict lotic recovery rates. *Environmental Management* **14**: 737-753.

Gray L.J. (1993) Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tall grass prairie stream. *American Midland Naturalist* **129**: 288-300.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* **30**: 363-395.

Hearnden M.N. & Pearson R.G. (1991) Habitat partitioning among the mayfly species (Ephemereoptera) of Yuccabine Creek, a tropical Australian stream. *Oecologia* **87**: 91-101.

Hillebrand H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**: 192-211.

Hopkins M., Head J., Ash J., Hewett R., & Graham A. (1996) Evidence of a Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. *Journal of Biogeography* **23**: 737-45.

Hughes J.M., Bunn S.E., Hurwood D.A., Choy S., & Pearson R.G. (1996) Genetic differentiation among populations of *Caridina zebra* (Decapoda: Atyidae) in tropical rainforest streams, northern Australia. *Freshwater Biology* **36**: 289-296.

Huston M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449-460.

Hynes H.B.N. (1970) *The ecology of running waters*. University of Toronto Press.

Iwai N., Pearson R.G. & Alford, R.A. (2009) Shredder–tadpole facilitation of leaf litter decomposition in a tropical stream. *Freshwater Biology* **54**: 2573-2580.

Jackson J.K. & Fisher S.G. (1986) Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology* **67**: 629-638.

Jacobsen D., Schultz R. & Encalada A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* **38**: 247–61.

Januchowski-Hartley S.R., Pearson R.G., Puschendorf R. & Rayner T. (2011) Fresh waters and fish diversity: distribution, protection and disturbance in tropical Australia. *PLoS One* **6**:0025846.

Jonsson M. & Malmqvist B. (2003) Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypothesis. *Oecologia* **134**: 554-559.

Karim F., Kinsey-Henderson A., Wallace J., Arthington A.H. & Pearson R.G. (2011) Modelling wetland connectivity during overbank flooding in a tropical floodplain in north Queensland, Australia. *Hydrological Processes* **26**: 2710-2723.

Kemp J.E., Lovatt R.J., Bahr J.C., Kahler C.P. & Appleman C.N. (2007) Pre-clearing vegetation of the coastal lowlands of the Wet Tropics Bioregion, North Queensland. *Cunninghamia* **10**: 285-329 including Appendices.

Kennard M.J., Pusey B.J. & Arthington A.H. (2001) *Trophic ecology of freshwater fishes in Australia.* Summary Report, CRC for Freshwater Ecology Scoping Study ScD6. Centre for Catchment and In-stream Research, Griffith University, Brisbane.

Kneipp, S.D. (1979) The ecology of *Macrobrachium* species (Decapoda, Palaemonidae) in a coastal stream in north Queensland. PhD Thesis, James Cook University, Townsville, Australia.

Kohler S.L. (1992) Competition and the structure of a benthic stream community. *Ecological Monographs* **62**: 165-188.

Kroon F.J. (2008) *Draft Tully Water Quality Improvement Plan*. Report to Terrain Natural Resource Management. CSIRO Sustainable Ecosystems, Atherton, Qld.

Krosch M.N. (2006) Phylogeography of *Echinocladius martini* (Chironomidae: Orthocladiinae) in the Australian Wet Tropics. Honours Thesis, Queensland University of Technology, Brisbane.

Lake P.S., Schreiber E.S.G., Milne B.J. & Pearson, R.G. (1994) Species richness in streams: Patterns over time, with stream size and with latitude. *Verhandlungen des Internatiionalen Verein Limnologie* **25**: 1822-1826.

Likens G.E. & Bormann F.H. (1974) Linkages between terrestrial and aquatic ecosystems. *Bioscience* **24**: 447-456.

Loreau M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**: 3-17.

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J.P., Hector A., Hooper D.U., Huston M.A., Rafaelli D., Schmid B., Tilman D. & Wardle D.A, (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* **294**: 804-808.

Mackay R.J. (1992) Colonisation by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Science* **49**: 617-628.

Marchant R., Ryan D. & Metzeling L. (2006) Regional and local species diversity patterns for lotic invertebrates across multiple drainage basins in Victoria. *Marine and Freshwater Research* **57**: 675-684.

Mathuriau C. & Chauvet E. (2002) Breakdown of leaf litter in a neotropical stream. *Journal of the North American Benthological Society* **21**: 384-396.

McKie B.G.L. (2002) Multiscale abiotic, biotic and biogeographic influences on the ecology and distribution of lotic Chironomidae (Diptera) in the Australian Wet Tropics. PhD Thesis, School of Tropical Biology, James Cook University, Townsville, Australia.

McKie B.G. (2004) Disturbance and investment: developmental responses of tropical lotic midges to repeated tube destruction in the juvenile stages. *Ecological Entomology* **29**:457-466.

McKie B.G., Cranston P.S. & Pearson R.G. (2004) Gondwanan mesotherms and cosmopolitan eurytherms: effect of temperature on the development and survival of Australian Chironomidae (Diptera) from tropical and temperate populations. *Marine and Freshwater Research* **55**: 759-768.

McKie B.G., Pearson R.G. & Cranston P.S. (2005) Does biogeographical history matter? Diversity and distribution of lotic midges (Diptera: Chironomidae) in the Australian Wet Tropics. *Austral Ecology* **30**: 1-13.

McKie B.G. & Pearson R.G. (2006) Environmental variation and the predator-specific responses of tropical stream insects: effects of temperature and predation on survival and development of Australian Chironomidae (Diptera). *Oecologia* **149**: 328-339.

McPeek M.A. & Peckarsky B.L. (1998) Life histories and the strengths of species interactions: combining mortality, growth and fecundity effects. *Ecology* **79**: 867-879.

Minshall G.W. (1984) Aquatic insect-substratum relationships. Pages 358-400 **In** Resh V.H. & Rosenberg D.M. (eds.) *The ecology of aquatic insects*. Praeger, New York.

Morgan, G.J. (1988) Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Paratacidae) from Queensland. *Memoirs of the Museum of Victoria* **49**: 1-49.

Neboiss A., Jackson J. & Walker K. (1989) Caddis-flies (Insecta: Trichoptera) of the World Heritage Area in Tasmania – species composition and distribution. *Occasional Papers of the Museum of Victoria* **4**: 1-41.

Nix H.A. (1991) Biogeography: pattern and process. Pages 10-39 **In** Nix H.A. and Switzer M.A. (eds.) *Rainforest Animals: Atlas of Vertebrates Endemic to Australia"s Wet Tropics* (Kowari 1) Australian National Parks and Wildlife Service, Canberra.

Nolen J.A. & Pearson R.G. (1992) Life History Studies of *Anisocentropus kirramus*, Neboiss (Trichoptera: Calamoceratidae) in a Tropical Australian Rainforest Stream. *Aquatic Insects* **14**: 213-221.

Patrick R. (1966) The Catherwood Foundation Peruvian Amazon Expedition: Limnological and systematic studies. *Monograph of Academy National Science of Philadelphia* **14**: 1-495.

Pearson R.G. (1994) Limnology in the northeastern tropics of Australia, the wettest part of the driest continent. *Verhandlungen des Internationalen Verein Limnologie*. **24**: 155-163.

Pearson R.G. (2005) Biodiversity of the freshwater fauna of the Wet Tropics region of north-eastern Australia: patterns and possible determinants. Pages 470-485 **In** Bermingham E., Dick C. W. & Moritz C. (eds). *Tropical Rain Forests: Past, Present and Future*. University of Chicago Press, Chicago and London. 1004 pp.

Pearson R.G., Benson L.J. & Smith R.E.W. (1986) Diversity and Abundance of the Fauna in Yuccabine Creek, a Tropical Rainforest Stream. Pages 329-342 **In** deDecker, P. & Williams, W.D. (eds.), *Limnology in Australia*. CSIRO, Melbourne.

Pearson R.G. & Boyero L. (2009) Gradients in regional diversity of freshwater taxa. *J. North American Benthological Society* **28**: 504–514.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G., Connolly N.M. & Boyero L. (2015) Ecology of streams in a biogeographic isolate – the Queensland Wet Tropics, Australia. *Freshwater Science* **34**: 797-819.

Pearson R.G., Godfrey R.C., Arthington A.H., Wallace J., Karin F. & Ellison M. (2013) Biophysical status of remnant freshwater floodplain lagoons in the Great Barrier Reef catchment: a challenge for assessment and monitoring. *Marine and Freshwater Research* **64**: 208-222.

Pearson R.G. & Tobin R.K. (1989) Litter consumption by invertebrates from an Australian tropical rainforest stream. *Archiv für Hydrobiologie* **116**: 71 80.

Pearson R.G., Tobin R.K., Benson L.J. & Smith R.E.W. (1989) Standing crop and processing of rainforest litter in a tropical Australian stream. *Archiv für Hydrobiologie* **115**: 481-498.

Peckarsky B.L., Cowan C.A., Penton M.A. & Anderson C. (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* **74**: 1836-1846.

Pringle C.M. (2000) Riverine conservation in tropical versus temperate regions: Ecological and socioeconomic considerations, Chapter 15, Pages 367-378. **In** Boon P.J. and Davies B. (eds.) *Global perspectives on river conservation: Science, policy and practice.* John Wiley and Sons.

Pringle C.M., Scatena F., Paaby P., & Nunez M. (2000) Conservation of riverine ecosystems of Latin America and the Caribbean, Chapter 2, Pages 39-75. **In** Boon P.J. and Davies B. (eds.) *Global perspectives on river conservation: Science, policy and practice.* John Wiley and Sons.

Pusey B.J. & Kennard M.J. (1996) Species richness and geographical variation in assemblage structure of the freshwater fish fauna of the Wet Tropics Region of north Queensland. *Marine and Freshwater Research* **47**: 563-573.

Pusey B.J., Read M.G. & Arthington, A.H. (1995) The feeding ecology of freshwater fishes in two rivers of the Australian Wet Tropics. *Environmental Biology of Fishes* **43**: 85-318.

Pusey, B.J., Kennard, M.J. & Arthington A.H. (2008) Origins and maintenance of freshwater fish biodiversity in the Wet Tropics region. Pages 150-160 **In** Stork N.E. and Turton S. (eds.) *Living in a dynamic tropical forest landscape*. Blackwell Publishing, Oxford, UK.

Quilty P.G. (1994) The background: 144 million years of Australian palaeoclimate and palaeogeography. Pages 14-43 **In** Hill R.S. (ed.) *History of the Australian Vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge, UK.

Rabeni C.F. & Minshall G.W. (1977) Factors affecting the microdistribution of stream benthic insects. *Oikos* **29**: 33-43.

Ramirez A., Pringle C.M., & Wantzen K.M. (2008) Chapter 10: Tropical River Conservation, pp. 285-304. **In** Dudgeon D. and Cressa C. *Tropical Stream Ecology*. Academic Press, 316 pp.

Rosenberg D.M. & Resh V.H. (eds.) (1993) *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall, London and New York. 488 pp.

Rossaro B. (1991) Chironomids and water temperature. *Aquatic Insects* **13**: 87-98.

Rosser Z.C. & Pearson R.G. (1995) Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. *Journal of the North American Benthological Society* **14**: 183-196.

Short J.W. & Davie P.J.F. (1993) Two new species of freshwater crayfish (Crustacea: Decapoda: Parastacidae) from northeastern Queensland rainforest. *Memoirs of the Queensland Museum* **34**: 69-80.

Stout J. & Vandermeer J. (1975) Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. *The American Naturalist* **109**: 263-280.

Suter P.J. (1986) The Ephemeroptera (Mayflies) of South Australia. *Records of the South Australian Museum* **19**: 339-397.

Suter P.J. (1992) Taxonomic key to the Ephemeroptera (mayflies) of the Alligator Rivers Region, Northern Territory. Open File Record No. 96, Supervising Scientist for the Alligator Rivers Region.

Terrain NRM (2015) Wet Tropics Water Quality Improvement Plan 2015-2020. http://www.terrain.org.au/Projects/Water-Quality-Improvement-Plan

Tracey J. G. (1982) *The Vegetation of the Humid Tropical Region of North Queensland*. (CSIRO: Melbourne).

Vanni M.J., Flecker A.S., Hood J.M. & Headworth J.L. (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* **5**: 285-93.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E., (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.

Vinson M.R. & Hawkins C.P. (1998) Biodiversity of stream insects: Variation at local, basin, and regional scales. *Annual Review Entomology* **43**: 271-93.

Vinson M.R. & Hawkins C.P. (2003) Broad-scale geographical patterns in local stream insect genera richness. *Ecography* **26**: 751-767.

Walker K., Neboiss A., Dean J. & Cartwright D. (1995) A preliminary investigation of the caddis-flies (Insecta: Trichoptera) of the Queensland Wet Tropics. *Australian Entomology* **22**: 19-31.

Wells A. & Cartwright D.I. (1993) Trichoptera, Ephemeroptera, Plecoptera and Odonata of the Jardine River area, Cape York Peninsula, North Queensland. Pages 221-230 **In** *Cape York Scientific Expedition Wet Season 1992*. The Royal Geographic Society of Queensland Inc..

Williams S.E. (1997) Patterns of mammalian species richness in the Australian tropical rainforests: are extinctions during historical contractions of the rainforest the primary determinant of current regional patterns in biodiversity. *Wildlife Research* **59**: 1211-29.

Williams S.E. & Pearson R.G. (1997) Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia"s wet tropics. *Proceedings of the Royal Society London B* **264**: 709-16.

Williams S.E., Pearson R.G. & Walsh P.J. (1996) Distributions and biodiversity of the terrestrial vertebrates of Australia"s Wet Tropics: a review of current knowledge. *Pacific Conservation Biology* **2**: 327-362.

Willig M.R., Kaufman D.M. & Stevens R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics* **34**: 273–309.

Winter J.W. (1997) Responses of non-volant mammals to the late Quarternary climatic changes in the Wet Tropics region of north-eastern Australia. *Wildlife Research* **24**: 493-511.

Chapter 3

Nutrient enrichment alters leaf litter decomposition, food quality and invertebrate production, but not diversity, in a heterotrophic rainforest stream.[2]

3.1 Introduction

Probably the most ubiquitous ecological change that is occurring in aquatic systems throughout the world is the increased input of nutrients and, consequently, the fertilisation of fresh waters, with concentrations of exogenous nutrients generally proportional to the area of developed land in their catchments (Connolly *et al.*, 2015; Chapter 6). The effects of nutrient enrichment in streams are generally predictable: if adequate light is available, enrichment enhances plant growth (Hill *et al.*, 1995; Tank & Dodds, 2003; Hill & Knight, 2008); and if appropriate substrates and carbon sources are available, exogenous nutrients will increase microbial activity and biomass (Mellillo *et al.*, 1984) with knock-on effects to decomposition of organic material and secondary productivity (Elwood *et al.*, 1981; Gulis & Suberkropp, 2003; Ferreira *et al.*, 2006a; Ferriera & Graca, 2007; Encalada *et al.*, 2010; Ferreira & Chauvet, 2011; Ferreira *et al.*, 2014). However, the effects on community composition and diversity are less predictable, because these are indirect and involve complex biotic interactions (e.g., Abrams, 1995; Waide *et al.*, 1999; Middlebach *et al.*, 2001; Chapter 5).

Low-order forest streams in the humid tropics are generally nutrient-limited (Perakis & Hedlin, 2002) and heterotrophic because instream primary productivity is light-limited (e.g., Fisher & Likens, 1972; Vannote *et al.*, 1980; Hill *et al.*, 1995). Low nutrient concentrations limit primary production, but also detrital processing (Stockner & Shortreed 1978; Elwood *et al.*, 1981; Winterbourne, 1990), and potentially nutrition and productivity of detritivores. Productivity in these systems relies mainly on allochthonous leaf litter entering the stream and being gradually broken down and modified, fuelling a detrital food web (Kaushik & Hynes, 1971; Fisher & Likens, 1973; Fittkau & Kling, 1973; Anderson & Sedell, 1979; Benfield & Webster, 1985; Heiber & Gessner 2002; Cheshire *et al.*, 2005). The process of leaf litter decomposition in streams typically involves leaching, colonisation by bacteria and aquatic hyphomycetes (Suberkropp & Klug, 1976), and fragmentation and consumption by

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[2] This chapter is based on material presented in Pearson & Connolly (2000) and Connolly & Pearson (2013).

invertebrate detritivores (“shredders”) (Ferreira *et al*., 2006b). This process in turn makes fine particulate organic matter, including faecal pellets, available for other detritivores (“collectors”) (Petersen & Cummins, 1974; Anderson & Grafius, 1975, Cheshire *et al*., 2005). Thus decomposition of allochthonous organic matter is a major pathway of energy transfer in forest stream communities, in which microbes and shredders play a major role (Winterbourn & Davis, 1976; Graca, 2001).

Shredders can discriminate between leaf species and their stages of decomposition to select more nutritional leaves or patches on leaves (Arsuffi & Suberkropp, 1985, 1989; Chung & Suberkropp, 2009; Cornut *et al*., 2015) or to avoid unpalatable compounds (Stout, 1980). Typically, shredders feed and grow more on leaf litter that has been conditioned by leaching and microbial colonisation, with concomitant reduction in leaf “toughness” and the carbon: nitrogen ratio (i.e., relative increase in nitrogen) (Kaushik & Hynes, 1971; Iversen, 1974; Anderson & Sedell, 1979) and detritivore populations may be controlled by food quality (Groome & Hildrew, 1989, Danger *et al*., 2013). The rate of microbial growth and activity depends on the availability of nutrients and is, at least in some instances, nutrient-limited (Elwood *et al*., 1981; Ferreira & Chauvet, 2011; Cornut *et al*., 2015). Microbes colonising leaf material may utilise dissolved nutrients in preference to nutrients within the leaf material (Melillo *et al*., 1984; White & Howes, 1994). Consequently, nutrient enrichment of a stream can reduce constraints on material flow (Cross *et al*., 2007) and lead to increased microbial biomass, higher nutritional quality of leaf litter and enhanced physiological condition and productivity of invertebrates (e.g., Elwood *et al*., 1981; Graca, 2001; Gulis *et al*., 2006).

The forested upland streams in the Wet Tropics have very low concentrations of dissolved nutrients and have high species richness of macroinvertebrates (Pearson *et al*., 1986; Lake *et al*., 1994; Connolly *et al*., 2008). These streams provide an opportunity to test the effects of increased nutrient status on invertebrate nutrition, abundance and assemblage composition. I used artificial stream channels to investigate the effects of nutrient supplements on primary production, the decomposition of allochthonous leaf litter, and the abundance and composition of the benthic invertebrate assemblage over a seven-month period. During this study the rates of decomposition were measured for leaves of four rainforest species with and without nutrient supplements and with and without the presence of the shredder *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae) larvae, which is a major contributor to leaf litter breakdown and detritus production in Wet Tropics streams (Pearson & Tobin, 1989; Nolen & Pearson, 1993). The influence of nutrient supplements and leaf species on the condition of *A. kirramus* was also assessed.

3.2 Materials and Methods

Four experiments were undertaken in artificial stream channels positioned beside a second-order section of Birthday Creek, an upland stream, located in tropical Queensland, Australia (19° 0′ S, 146° 11′ E; altitude 840 m). The natural stream bed comprised granite bedrock, boulders, cobbles, gravel and leaf litter, in a pool-riffle sequence. The site was situated in a dense simple notophyll vine forest (Tracey, 1982) with complete canopy cover. The climate at the site is seasonal, typically with warm wet summers (December to April) and drier winters (May to November). Birthday Creek typically had a pH of 6.8 and a conductivity of 33 μS cm^{-1}.

Experiments 3.1 to 3.3 were conducted in artificial stream channels constructed from 300-mm diameter PVC pipe, cut lengthways into two halves, each 3.6 m long. V-notched weirs were installed to maintain water depth. Eight channels were fixed to a steel frame on the bank (Plate 3.1). Experiment 3.4 was conducted in reconstructed artificial stream channels that replaced the older version. These consisted of twenty channels, each 240 cm long, 14 cm wide and 10 cm deep, constructed from PVC (Plate 3.2). Stream water was supplied to the channels from a small weir above a waterfall via a polyethylene pipe and a header tank, from which 20-mm pipes supplied each channel, controlled using plastic taps, and maintained at 6.0 L min^{-1}. A coarse filter (20-mm mesh) on the inlet of the pipe prevented clogging by leaf litter, but allowed passage of most other suspended material, including animals.

3.2.1 Experiment 3.1 – Mixed nutrient enrichment

The eight channels were each filled with the same quantities of cobbles and gravel collected from the stream and natural litter fall was allowed to enter the channels. Macroinvertebrates were added to the channels attached to substrata, and were allowed to colonise naturally. Loss via drift and emergence was allowed. Small (22 cm^2) ceramic tiles were placed randomly through the channels to measure chlorophyll *a* concentrations of colonised algae as an indicator of primary productivity. Air and water temperatures during this experiment ranged from 5 to 24 °C and 11 to 21 °C respectively.

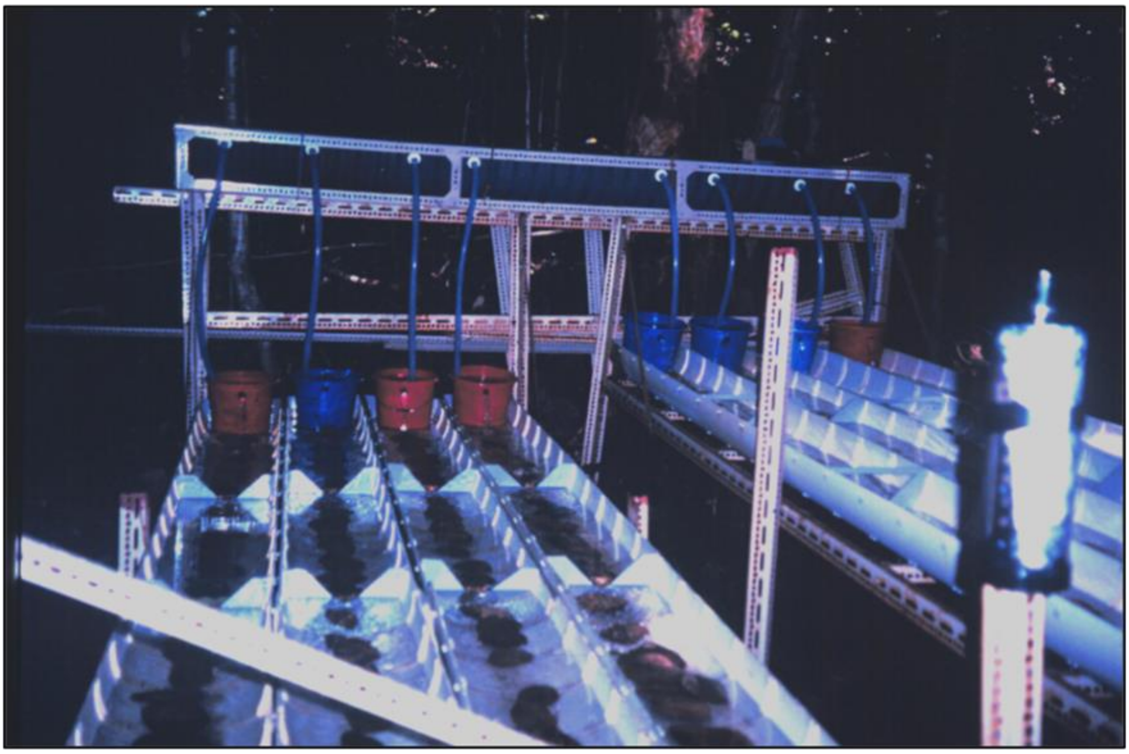


Plate 3.1. Artificial stream channels used in Experiments 3.1 to 3.3.

Plate 3.2. Artificial stream channels used in Experiment 3.4.

Channels were randomly designated as controls or treatments. Nutrients were added to the four treatment channels by placing 10 Agriform™ slow release fertilizer pellets in a 1 mm mesh bag in a plastic bucket though which water entered each channel. The fertilizer pellets were intended to give a large, broad spectrum nutrient boost, without precise control of nutrient levels. Pellets were replaced weekly. N and P concentrations were monitored throughout the experiment. At the commencement of the experiment, water samples were taken after 30 minutes, 1 hour, 1 day and then every day for another six days and were analysed in the laboratory for N and P to determine the pattern of nutrient release over a one-week period. Subsequently, water samples were taken weekly, one hour after changing nutrient pellets and again after seven days, prior to changing the pellets. Water samples were collected directly in flow injection sample tubes, immediately placed on ice and then frozen. They were analysed in the Australian Centre for Freshwater Research (now TropWater) laboratory using an Alpchem™ flow injection analyser.

The experiment was continued for seven months through the dry season between March and October, providing time for establishment of biota via drift (normally a few weeks would be sufficient – Benson & Pearson, 1987; Chapter 4). At the end of the seven-month period, ceramic tiles were removed for chlorophyll *a* levels to be measured, following Wintermans & De Mot (1965). Invertebrates and particulate organic material were collected by washing the contents of each channel section separately into a receiving net (63 µm mesh size) at the downstream end of each channel. All rocks and submerged channel surfaces were scrubbed clean, with the removed material also being washed into the net. Material was preserved in 70% ethanol and returned to the laboratory for processing. Material from the central section (1.0 m long) of each channel was processed in the laboratory; each sample was therefore derived from an area of stream bed of 1 m x 0.3 m, so densities reported here are as number of individuals per 0.3 m^2. In the laboratory, samples were washed through 1.0-mm, 210-µm and 63-µm sieves and the resultant material was sorted under a stereo microscope. Invertebrates were identified to the lowest level possible or allocated to “morpho-species” when morphological differences were clear. Particulate organic matter from each sieved fraction were dried and weighed.

3.2.2 Experiment 3.2 – Leaf decomposition

During Experiment 1, the effect of nutrient supplements on microbial leaf decomposition was examined in the downstream section of each channel. Fresh leaves of three rainforest tree species – *Cryptocaria densiflora* Blume, *C. leucaphylla* Bittyland (Lauraceae), and *Macaranga subdentata* Benth. (Euphorbaceae), and one vine – *Freycinetia scandens* Gaudich (Pandanaceae) – were taken from plants near the stream and dried. For each species, five bundles of five leaves were weighed and randomly placed in one of four compartments in a 1.0-mm mesh cage, which prevented entry of large shredders. After 44 days the leaves were collected, dried and re-weighed to record the amount of decomposition.

Toughness of the leaves was measured by using a simple penetrometer (Plate 3.3; Pearson & Connolly, 2000; Boyero *et al*., 2011), which measured the mass required to force a steel rod (0.6 mm diameter) through each leaf. Five measurements were taken from different sections of each leaf, avoiding major leaf veins.

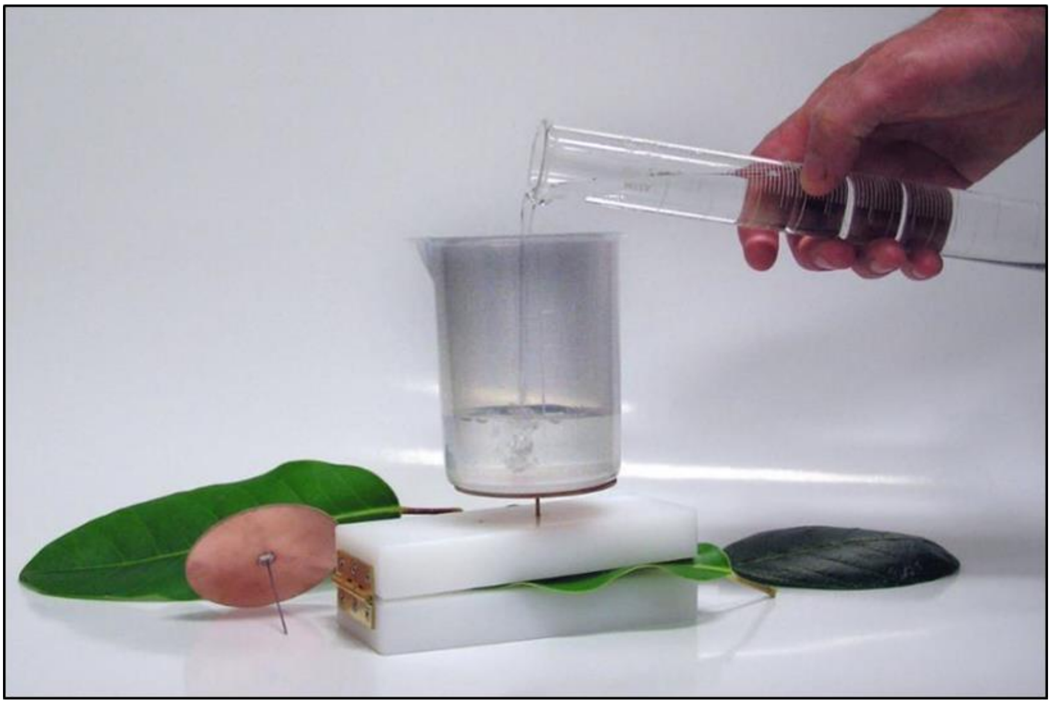


Plate 3.3. Penetrometer used to measure leaf toughness.

3.2.3 Experiment 3.3 – Nutrition of the shredder Anisocentropus kirramus

The influence of leaf species and nutrient enrichment on nutrition of the shredder *Anisocentropus kirramus* was tested using leaves from three of the above species – *C. densiflora*, *F. scandens* and *M. subdentata* – and *Apodytes brachistylus* F. Muell. (Icacinaceae), which replaced *C. leucophylla* because neither *Cryptocaria* species is readily digested by *A. kirramus* (Nolen & Pearson, 1993). This experiment was conducted in the dry season between May and July and air temperature during the this experiment ranged between 5°C and 24°C and water temperature between 11°C and 21°C.

Leaves were collected from trees close to the stream, dried and made into bundles of approximately 2.5 g. The exact weight of each bundle was recorded and the bundles were secured and labelled using plastic tags. Three bundles of a single species were loosely placed in a 1.0-mm mesh cage. Two cages of each leaf species were then placed in the downstream section of two of the eight stream channels, chosen randomly, with a single cage in each channel. The leaves were then allowed to condition for 21 days prior to addition of ten larvae of *A. kirramus* to one cage of each leaf species.

The leaves were left another 28 days before being gently removed and rinsed, air dried and weighed. Leaf cases discarded by *A. kirramus* were collected and included in the dry weight. Leaves were checked for the presence of other macroinvertebrates that might have colonized the cages. The ten *A. kirramus* larvae were collected from the mesh cages, removed from their cases and frozen in nitrogen-filled vials at –80°C. The larvae were then ground using a mortar and pestle and analysed for protein, carbohydrate and lipid composition to assess their physiological condition, using methods based on Mann & Gallager (1985) by the Department of Molecular Biology at James Cook University.

3.2.4 Experiment 3.4 – P and N enrichment: leaf decomposition, microbial biomass and growth of A. kirramus

Experiment 3.4 investigated the influence of the separate and combined effects of phosphate (P) and nitrate (N) enrichment on microbial biomass and on the nutrition of *A. kirramus*.

The experiment was run for 7 weeks in the early part of the winter dry season between June and July. Water temperature during the study ranged from 15 to 19 °C. Channels were randomly designated as controls or treatments (Figure 3.1). Treatments involved adding nutrients to each channel: N, as sodium nitrate solution; P, as disodium hydrogen orthophosphate solution; or N and P combinations. The four intended treatments were: N (300 µg N L^{-1} total N), P (30 µg P L^{-1} total P), N+P (300 µg N L^{-1} total N plus 30 µg P L^{-1} total P), and 2N+2P (600 µg N L^{-1} total N plus 60 µg P L^{-1} total P). These concentrations had similar N:P ratios but were several-fold higher than typical ambient levels in Birthday Creek (N < 100 and P < 10 µg L^{-1} – Experiment 1). The control channels were supplied with stream water without nutrient supplements.

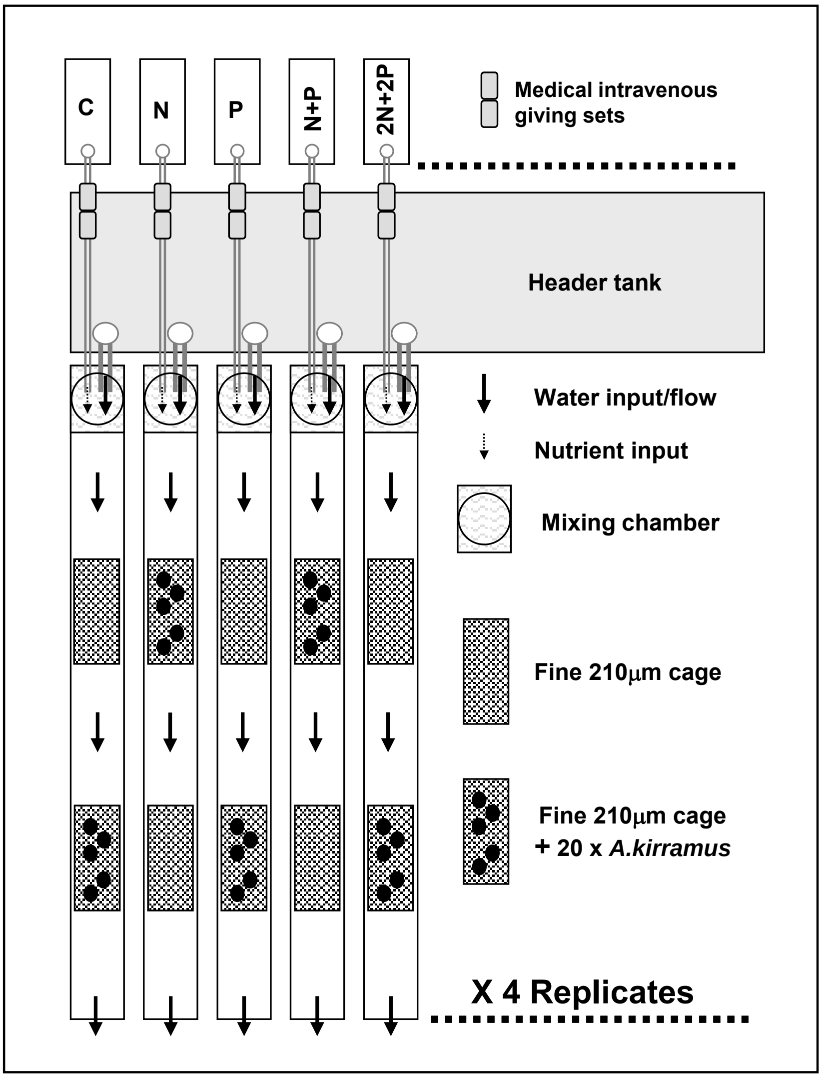


Figure 3.1. Layout of Experiment 3.4, indicating the five treatments.

Nutrient stock solutions were made using stream water, filtered through 5.0 µm and 1.0 µm cartridge filters, and contained in individual 20-L plastic carboys (one for each channel) (Plate 3.4), positioned on a stand above the channels. The carboys were covered with black plastic film and stock solutions were replaced weekly. Nutrients were supplied to individual channels through gravity feed by dripping a controlled volume into a mixing chamber (with inflowing stream water from the header tank) using Braun™ medical intravenous giving sets (Plate 3.5a, b). The volume of an individual drip was set by the manufacturer at 0.058 ml, and drip rate was controlled by the adjustment of a pressure cam. I used a rate of 30 drips per minute, resulting in 1.74 ml min.$^{-1}$ nutrient solution entering channels. From this rate I determined the concentrations required in the stock solutions to deliver the target concentrations in each channel.

Plate 3.4. Plastic 20-L carboys used in Experiment 3.4 to hold stock solutions of nutrient supplements.

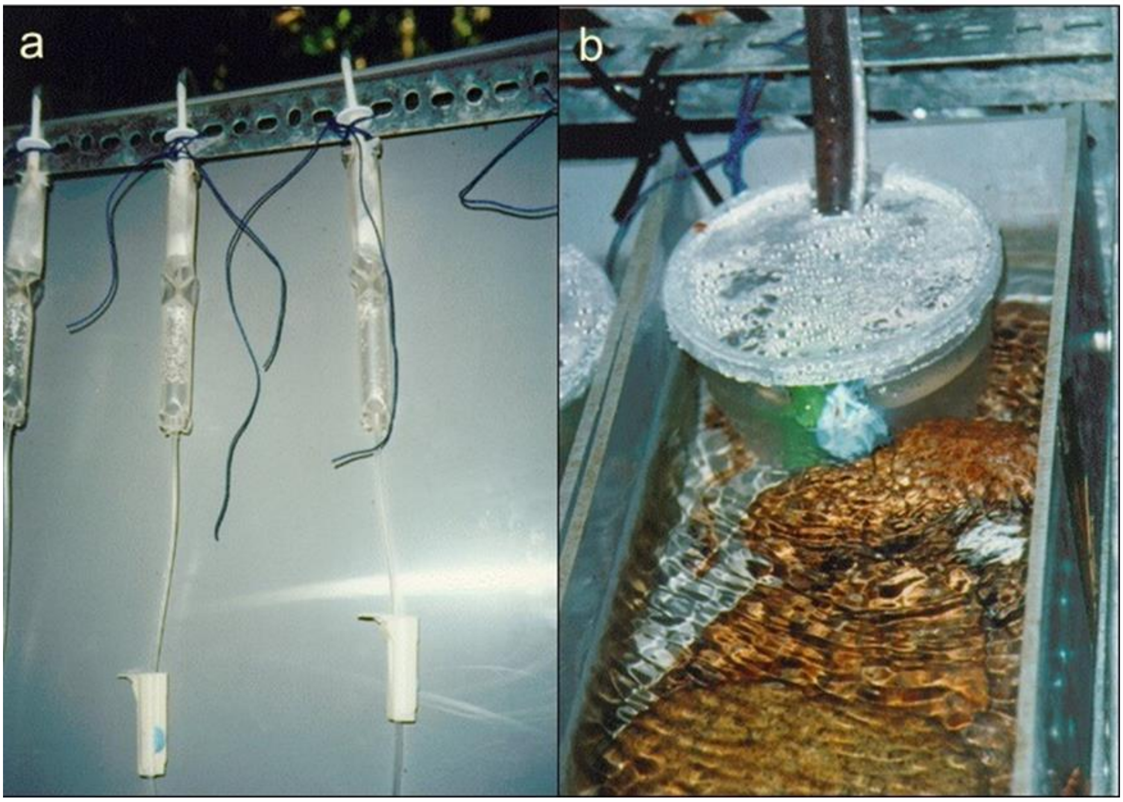


Plate 3.5. Nutrient supplement supply method: (a) Braun™ medical intravenous giving sets used to supply individual artificial streams channels a controlled volume of nutrient treatment solution (or filtered water in the case of control channels); (b) mixing chamber (with inflowing stream water from the header tank).

A series of water samples was collected from each channel mid-way through the experiment to test whether target concentrations were achieved. These samples were analysed as in Experiment 3.1.

Leaves of *Apodytes brachystylus* F. Muell. (Icacinaceae) were collected from a single tree at Birthday Creek. Leaves of this species are colonised by a diverse community of invertebrates in the stream and are readily consumed by *Anisocentropus kirramus* (Nolen & Pearson, 1993; Bastian *et al*., 2007; Experiment 3.3). Leaves were air dried and made into ~ 3.0-g bundles using plastic tags and labels. The exact weight of each bundle was recorded. Leaf bundles were placed in the channels within fine-mesh cages (one bundle per cage, two cages per channel: Plate 3.6). Cages were made from 10-mm polyethylene mesh covered with 210-µm screen to exclude macroinvertebrates. Twenty-one days after commencement of the experiment, 20 *A. kirramus* larvae, collected from Birthday Creek, were introduced into one cage in each of the 20 channels. The larvae were then allowed to consume *A. brachystylus* leaf material for 28 days. After this time (49 d total) all cages were removed from the channels, placed in sealed plastic bags and transported to the laboratory.

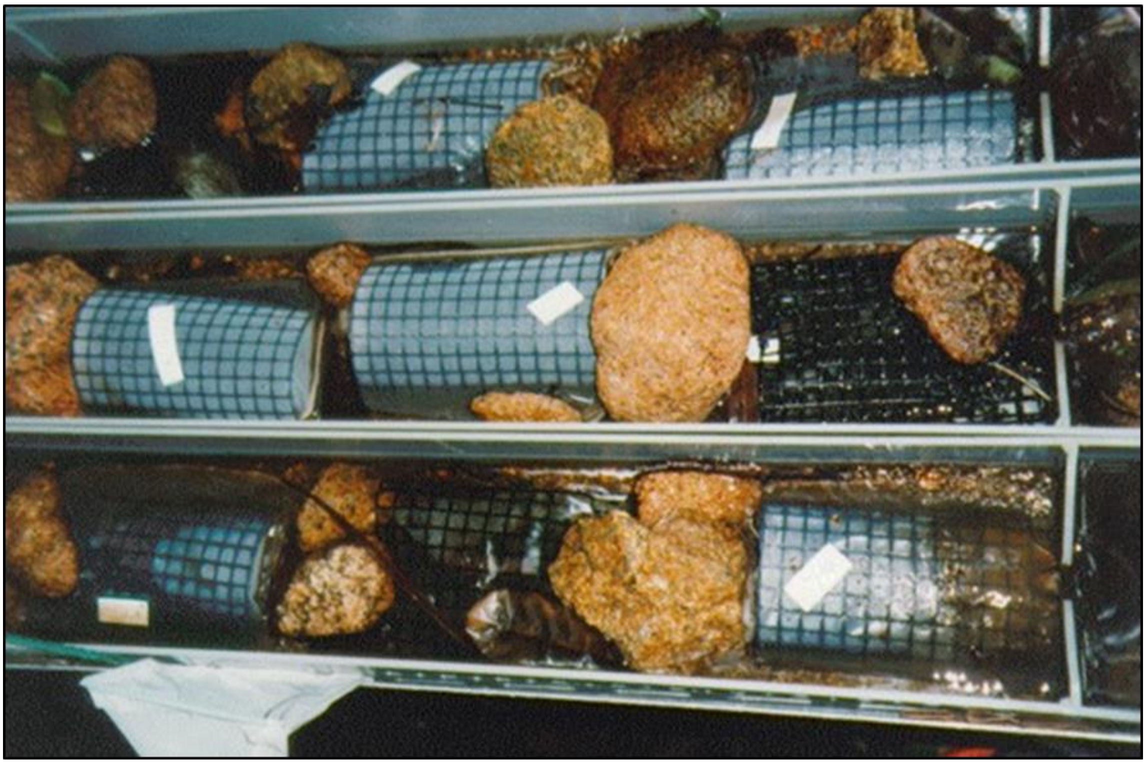


Plate 3.6. Fine mesh cages used to contain *Apodytes brachystylus* leaf bundles and *A. brachystylus* leaves plus *Anisocentropus kirramus* larvae.

It was not possible to weigh or measure individual *A. kirramus* larvae prior to the experiment as removing them from their leaf cases can cause mortality. Instead, larvae allocated to each channel were standardised by similar lengths of the ventral leaf case, as this correlates well with larval size and instar (Nolen & Pearson, 1992). All animals used in this experiment had a ventral case length of approximately 16 mm, corresponding to fourth-instar larvae: they metamorphose at the sixth instar (Nolen and Pearson 1992). In the laboratory, *A. kirramus* individuals were extracted from litter bags, removed from their cases and frozen in nitrogen at –80 °C before being freeze-dried. The larvae were processed as in Experiment 3.3 (above).

Microbial biomass (bacteria and fungi) on leaf bundles from each cage was determined using the fluorescein diacetate (FDA) hydrolysis method, in which 4 ml of FDA and 200 ml of buffer are added to each sample (Swisher & Carroll, 1980; Schnurer & Rosswall, 1982). Samples were incubated at 25 °C for 55 minutes with the shaking rate of the incubator set at 70 rpm. After FDA hydrolysis, leaf material was washed in tap water, dried at 60 °C for 48 h and weighed.

Leaf-litter mass loss in cages without *A. kirramus* larvae was used to estimate the effects of leaching, fragmentation and microbial processing in each channel over 49 days. The difference between initial and final mass of leaf material remaining in cages with *A. kirramus* was used to calculate combined losses due to leaching, fragmentation and microbial activity (over 49 days) and feeding by *A. kirramus* larvae (over 28 days) for each channel. The daily per-capita feeding rate of *A. kirramus* larvae was estimated by dividing the difference in leaf loss from cages with and without larvae for each channel by the number of larvae.

3.2.5 Statistical analyses

Experiment 3.1.

Principal component analysis, run in PC-ORD (McCune & Mefford, 2011) was used to compare community composition in the eight channels.

Experiment 3.2.

Analysis of variance (ANOVA) was used to determine if there was an effect of nutrient supplementation on leaf decomposition and leaf toughness, with $\alpha = 0.05$.

Experiment 3.3.

An analysis of covariance (ANCOVA), using the dry weight of the leaf bundles before treatment as a covariate, was used to determine the effect of nutrient supplement, leaf species and presence of *A. kirramus* on leaf breakdown. ANOVA was used to detect differences in biochemical composition of the *A. kirramus* larvae that fed on different leaf species and with or without nutrient supplements. $\alpha = 0.05$ was used in all analyses.

Experiment 3.4.

Analysis of data was by ANOVA or ANCOVA on untransformed data followed, where appropriate, by post-hoc Tukey tests, with $\alpha = 0.05$, using Statistix 7 software. One-way ANOVA was used to compare nutrient concentrations among treatments and to determine the effects of nutrient treatments on microbial biomass, mass of *Anisocentropus kirramus*, and protein, lipid and carbohydrate content of *A. kirramus*. Two-way ANCOVA was used to determine the effects of nutrient treatments, presence or absence of shredders, and interactions between them, with channel position as the covariate; and one-way ANCOVA was used to test the effect of number of individuals of *A. kirramus* on the results.

3.3 Results

3.3.1 Experiment 3.1 – Mixed nutrient enrichment

Ambient concentrations of dissolved N and P in the control channels were very low (Figure 3.2). Addition of the nutrient pellets in the treatment channels caused an initial high pulse of both N and P which quickly stabilised during day 1 to provide continuing substantial N and P enhancement (Figure 3.2). This pattern was repeated throughout the experiment as nutrient supplements were replaced weekly.

The change in nutrient status had no significant effect on chlorophyll *a* concentrations and there was no difference in standing crop of particulate organic matter in fine and coarse fractions in control and treatment channels (Figure 3.3a and 3.3b, respectively; Table 3.1).

There was a 75% increase in overall abundance of invertebrates in the treatment channels at the end of the seven-month experiment (Figure 3.4). However, only five of the 109 taxa, plus the juvenile chironomids, showed significant change, all increasing in abundance (Table 3.2). Many species were too rare for any difference to be demonstrated, but many abundant species showed no change. The taxa that increased in abundance were all detritivorous collectors apart from *Plectrocnemia* sp. (Polycentropodidae), which is a predator (McKie & Pearson, 2006). A comparison of the ranked abundance of the 25 most abundant taxa in control and treatment channels (representing 96.0 and 97.6% of the fauna, respectively) indicated only two significant changes in rank: *Aphroteniella filicornis* (Chironomidae) dropped from rank 9 to rank 16 in the treatment channels (d.f. = 6, t = 3.94, *P* = 0.012) and the Copepoda rose from rank 25 to rank 18 (d.f. = 6, t = 3.04, *P* = 0.023). These changes in rank were not associated with significant changes in abundance. Overall, therefore, the effect was that ranks maintained stability between control and treatment channels – that is, there was little change in proportional composition of the community.

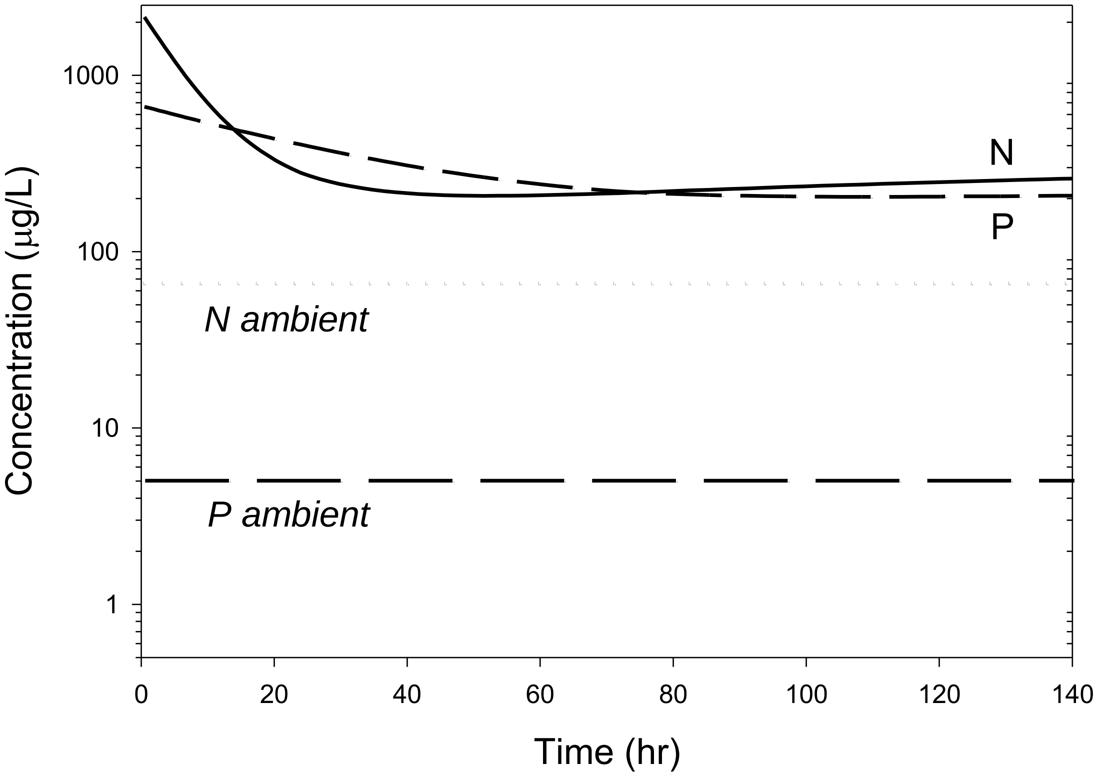


Figure 3.2. Total dissolved nitrogen and phosphorus concentrations in treatment channels following addition of nutrient supplement and through to replacement of supplement. Nutrient levels in control channels were the ambient concentrations over the whole study: ambient N = 66.37 ± 11.40 μg l^{-1}, ambient P = 5.00 ± 0.92 μg l^{-1}.

Species richness and evenness did not differ between treatment and control channels (Table 3.2). The number of rare species recorded in one but not the other of the treatments and controls was similar (21 vs. 26). Principal component analysis was used to compare community composition in the eight channels (Figure 3.5). There was substantial overlap between control and treatment channels on Axis 1, which explained 45% of the variance, indicating that the major single cause of variance was similar in treatment and controls, and therefore not due to nutrient supplement. However, there was separation of the two groups on Axis 2, which explained 21% of the variance, indicating a distinct but not major difference between the communities. A similar analysis of presence/absence data produced no pattern that could be ascribed to the effects of the treatment (i.e., treatment and control samples were not separated on any axis), so differences between samples were simply due to shifts in densities of the most abundant species.

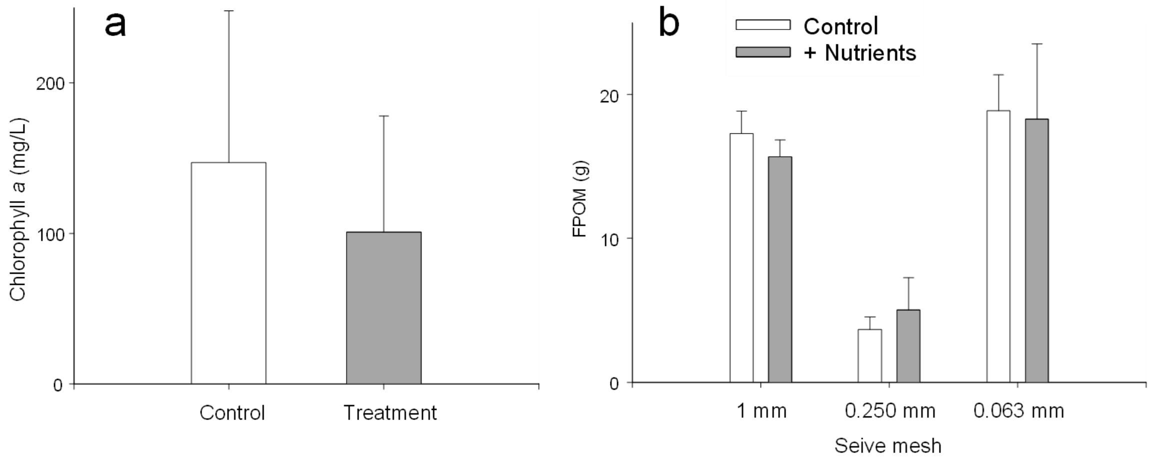


Figure 3.3. (a) Chlorophyll *a* concentrations on tiles in treatment and control channels after seven months of nutrient supplement. (b) Standing crop (dry weight) of particulate organic matter in control and nutrient supplement channels after seven months. There was no significant difference between treatments in (a) or (b) (Table 3.1).

Table 3.1. (a) Chlorophyll *a* concentrations (mg/L ± s.e), and (b) standing crop of three fractions of particulate organic matter in control and nutrient-supplemented channels after seven months; (a) compared by t-test, (b) by ANOVA.

	Control	+ Nutrient	F/t	d.f.	*P*
(a) Chlorophyll a (mg/L)	147.07 ± 101.21	101.07 ± 77.00	t = 1.43	70	0.156
(b) Particulate Organic Matter (g dry weight)					
>1.000 mm	17.28 ± 1.57	15.67 ± 1.18	F = 2.693	1	0.152
>0.250 mm	3.66 ± 0.87	5.04 ± 2.22	F = 1.361	1	0.288
>0.063 mm	18.87 ± 2.48	18.28 ± 5.21	F = 0.041	1	0.846

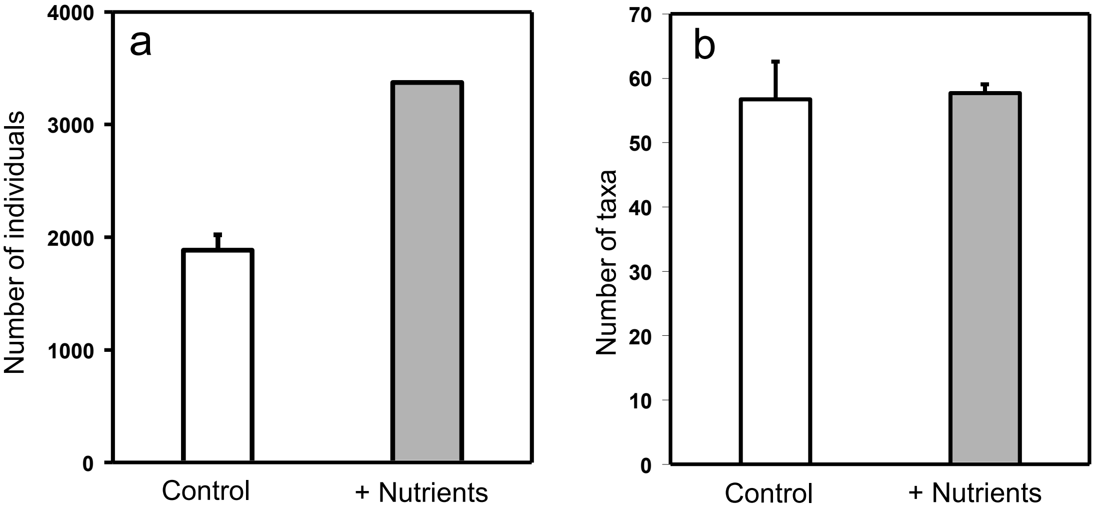


Figure 3.4. (a) Mean number of individuals and (b) mean number of taxa collected on 0.3 m^2 of the substratum in artificial stream channels with and without nutrient supplements. See Table 3.2 for statistics.

Table 3.2. Summary of major effects of enhanced nutrient levels on the macroinvertebrate community in experimental stream channels (mean counts ± s.e.). *P* is probability based on one-way ANOVA (run as part of MANOVA); only species for which $P < 0.05$ are included. Experiment 3.1.

	Control			**+ Nutrients**			***P***
Diptera: Chironomidae:							
Pentaneura+Peramerina spp.	205.5	±	50.2	420.3	±	68.7	0.048
Tanytarsus sp.	645.5	±	29.4	1085.6	±	142.8	0.017
Polypedilum sp.	48.8	±	19.7	170.0	±	36.7	0.026
Indeterminate juveniles	59.3	±	39.5	355.0	±	47.0	0.005
Ephemeroptera: Leptophlebiidae							
Atalophlebia sp.	28.3	±	5.7	50.3	±	4.9	0.038
Trichoptera: Polycentropodidae							
Plectrocnemia sp.	3.8	±	2.2	14.7	±	3.2	0.032
Total number of animals	1886.8	±	134.1	3373.0	±	241.3	0.002
Total number of taxa (grand total = 109)	56.8	±	5.0	57.7	±	1.3	0.886
Evenness, E (= H/H_{max})	0.62	±	0.01	0.61	±	0.02	0.560
Shannon Weaver diversity, H	2.29	±	0.06	2.23	±	0.06	0.485

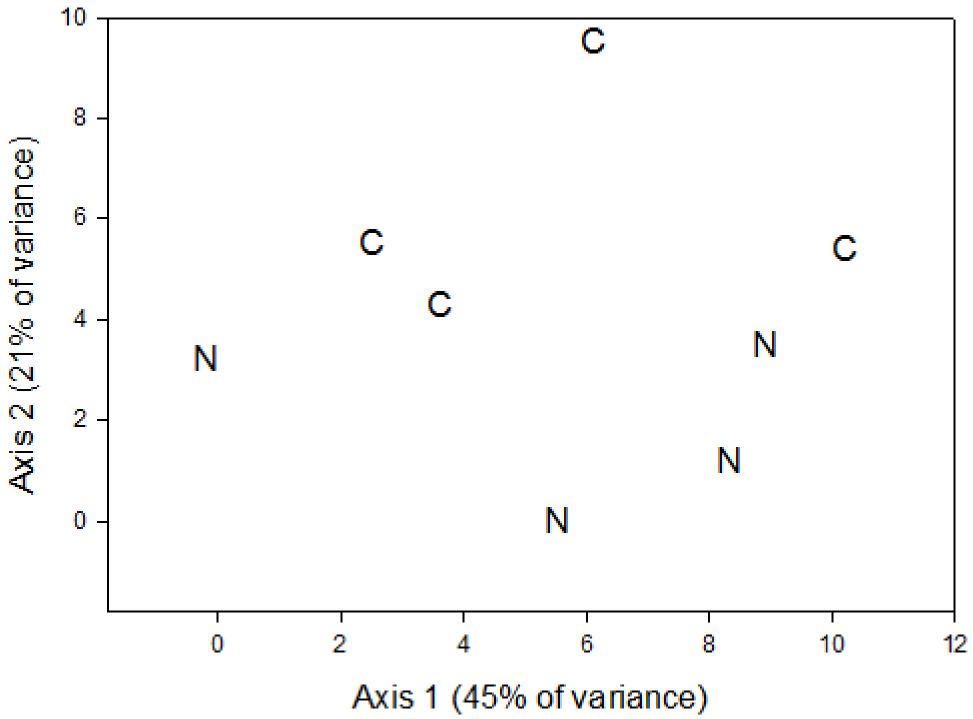


Figure 3.5. Principle components ordination of invertebrate samples from control (C) and nutrient (N) treatment channels.

3.3.2 Experiment 3.2 – Leaf decomposition

The rate of leaf breakdown increased in the nutrient-enriched channels for *Freycenetia scandens* and *Macaranga subdentata*, but not for *Cryptocarya densiflora* or *C. leucophylla* (Figure 3.6a; Table 3.3). Leaf toughness was significantly reduced for *Freycinetia scandens* in the nutrient treatment channels, but for other species there was no significant difference (Figure 3.6b; Table 3.3).

3.3.3 Experiment 3.3 – Nutrition of the shredder *Anisocentropus kirramus*

Leaf species, nutrient supplement and shredder presence all had a significant effect on dry weight of leaf material remaining in cages after 49 days (Figure 3.7, Table 3.4). There was no interaction between the nutrient treatment and the leaf species, indicating that all leaf species were affected similarly by the presence of nutrient supplements. There was an interaction between leaf species and presence of shredders, so the rate at which *A. kirramus* was able to shred the leaf material depended on the leaf species. However, there was no significant interaction between shredder presence and nutrient supplement, except for *Cryptocarya densiflora*, indicating that, although varying across species, *A. kirramus* did not alter its shredding rate in the presence of nutrient supplements for three of the four leaf species tested. The interaction between shredder presence and nutrient supplements observed for *C. densiflora* was because the nutrient supplements alone did not increase the rate of dry weight loss of *Cryptocarya densiflora* leaves, as in the other species. But the combined effect of shredder and nutrient supplement caused them to break down more rapidly (Figure 3.7b).

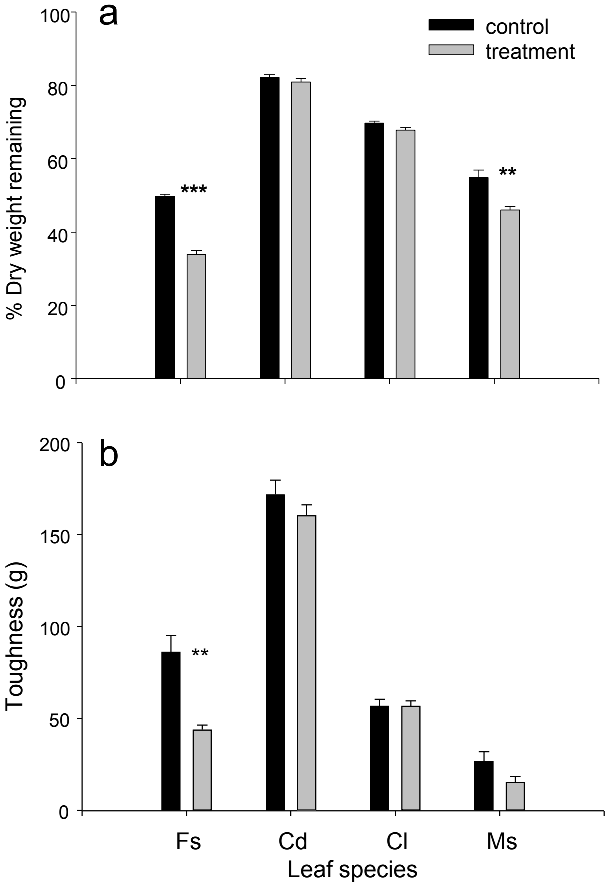


Figure 3.6. (a) Breakdown (% dry weight remaining) of four species of leaves in nutrient enriched and control channels over 44 d. (b) Toughness of leaves in control and nutrient enhanced channels after 44 days, measured as mass required (g) for penetrometer to penetrate leaf. Abbreviations of leaf species' names: Fs, *Freycinetia scandens*; Cd, *Cryptocaria densiflora*; Cl, *Cryptocaria leucaphylla*; Ms, *Macaranga subdentata*. *** = $P < 0.001$; ** = $P < 0.005$. See Table 3.3 for statistics.

Table 3.3. a) Breakdown (% dry weight remaining ± s.e.) and b) toughness (g required to penetrate in penetrometer ± s.e.) of four species of leaves in nutrient-enriched and control channels over 44 days. Comparisons are by ANOVA ($\alpha = 0.05$).

	Control	+ Nutrient	$F_{d.f. = 1}$	*P*
a) % Dry Weight Remaining				
Freycenetia scandens	49.71 ± 0.57	33.91 ± 0.98	193.54	<0.001
Cryptocarya densiflora	82.19 ± 0.73	80.94 ± 0.97	1.08	0.340
Cryptocarya leucophylla	69.67 ± 0.48	67.80 ± 0.79	4.05	0.091
Macaranga subdentata	54.81 ± 2.07	46.00 ± 1.04	14.51	0.009
b) Toughness				
Freycenetia scandens	86.85 ± 8.33	43.85 ± 2.54	21.07	0.004
Cryptocarya densiflora	171.73 ± 7.85	162.00 ± 4.41	1.34	0.291
Cryptocarya leucophylla	56.72 ± 3.63	56.65 ± 2.78	0.00	0.988
Macaranga subdentata	26.79 ± 5.07	15.21 ± 3.09	3.80	0.099

Biochemical analyses of the shredder biomass showed that the nutrient supplements had a significant effect on the ability of *A. kirramus* to accumulate metabolic tissue (i.e., combined % mass of protein, lipid and carbohydrate) (Figure 3.8a). Two-way ANOVA (Table 3.5) showed that there was no difference in the biochemical condition of individuals feeding on different leaf species in the absence of nutrient supplements. The addition of nutrients resulted in a significant increase in the biochemical condition of *A. kirramus* overall. Therefore, nutrient supplements had a greater influence on shredder condition than did leaf species, even though leaf species had been shown to be a significant factor in processing rate. Enhanced condition was mainly due to increases in the amount of carbohydrate in the tissue of *A. kirramus* (Figure 3.8b). The amount of lipid in the tissue also showed an increasing trend with nutrient supplement but the differences were not significant (Figure 3.8c). The amount of protein in the tissue was not affected significantly (Figure 3.8d).

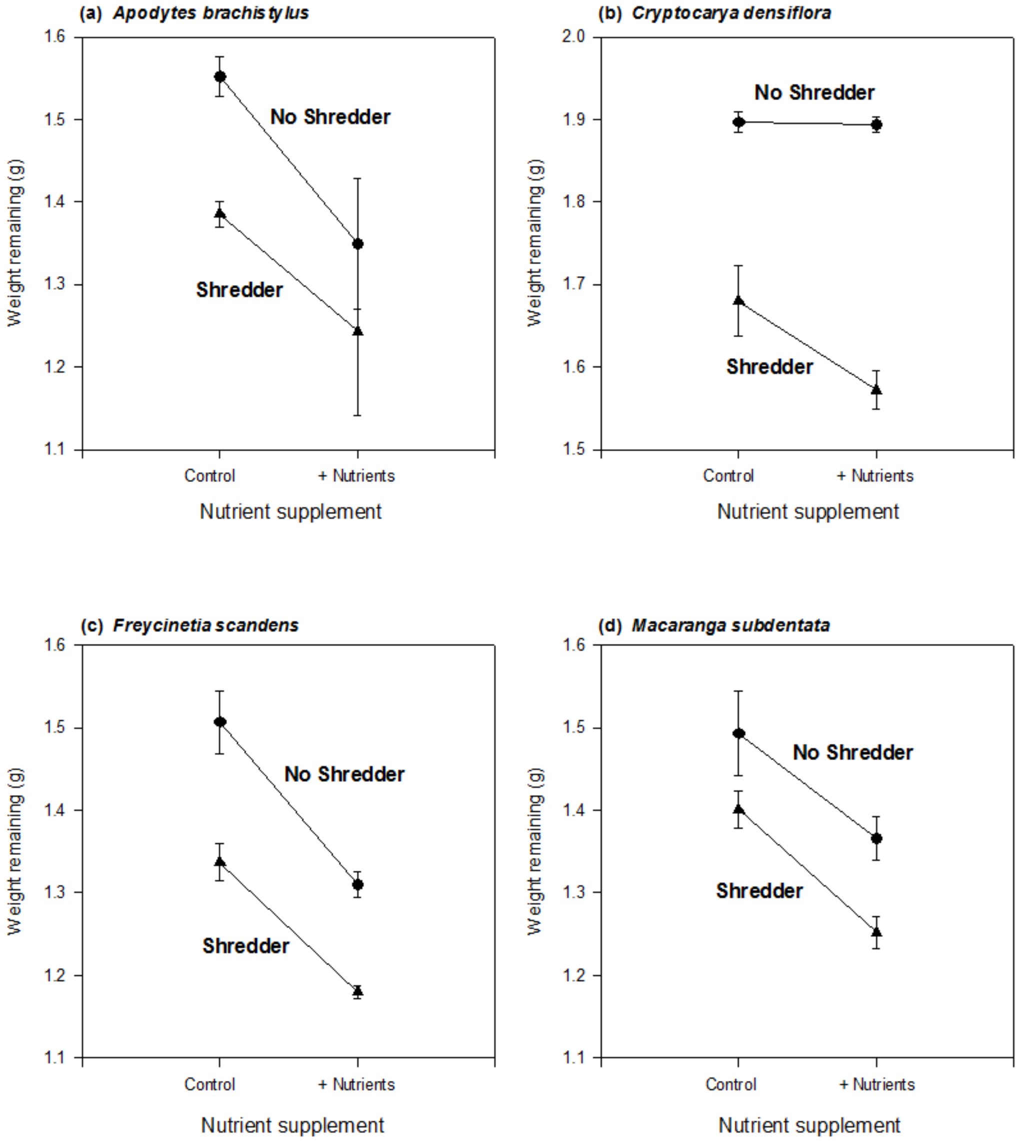


Figure 3.7. Weight remaining of four leaf species – a) *Apodytes brachistylus* b) *Cryptocarya densiflora* c) *Freycenetia scandens* d) *Macaranga subdentata* – with and without nutrient supplements and with and without the shredder, *Anisocentropus kirramus* present. See Table 3.4 for statistics.

Table 3.4. Summary of ANCOVA comparing dry weight of leaf packs between treatments in Experiment 3. (α = 0.05)

Source	Sums of Squares	d.f.	Mean Square	F	*P*
Dry weight before	1.791E-02	1	1.791E-03	0.077	0.782
Nutrient treatment	0.957	1	0.957	41.156	0.000
Shredder treatment	1.195	1	1.195	51.375	0.000
Leaf species	5.914	3	1.971	84.778	0.000
Nutrient*Shredder	7.742E-04	1	7.742E-04	0.033	0.855
Nutrient*Leaf species	0.146	3	4.853E-02	2.087	0.104
Shredder*Leaf species	0.204	3	6.811E-02	2.929	0.035
Nutrient*Shredder*Leaf sp.	7.026E-02	3	2.342E-02	1.007	0.391
Error	4.070	175	2.325E-02		
Total	421.915	192			

Table 3.5. Summary of ANOVA comparing biochemical composition of *Anisocentropus kirramus* larvae between treatments in Experiment 3.3.

Source	Sums of Squares	df	Mean Square	F	*P*
Leaf species	652.338	3	217.446	1.117	0.367
Nutrient treatment	1069.603	1	1069.603	5.496	0.030
Leaf species*Nutrient	351.513	3	117.171	0.602	0.622
Error	3697.973	19	194.630		
Total	58139.826	27			

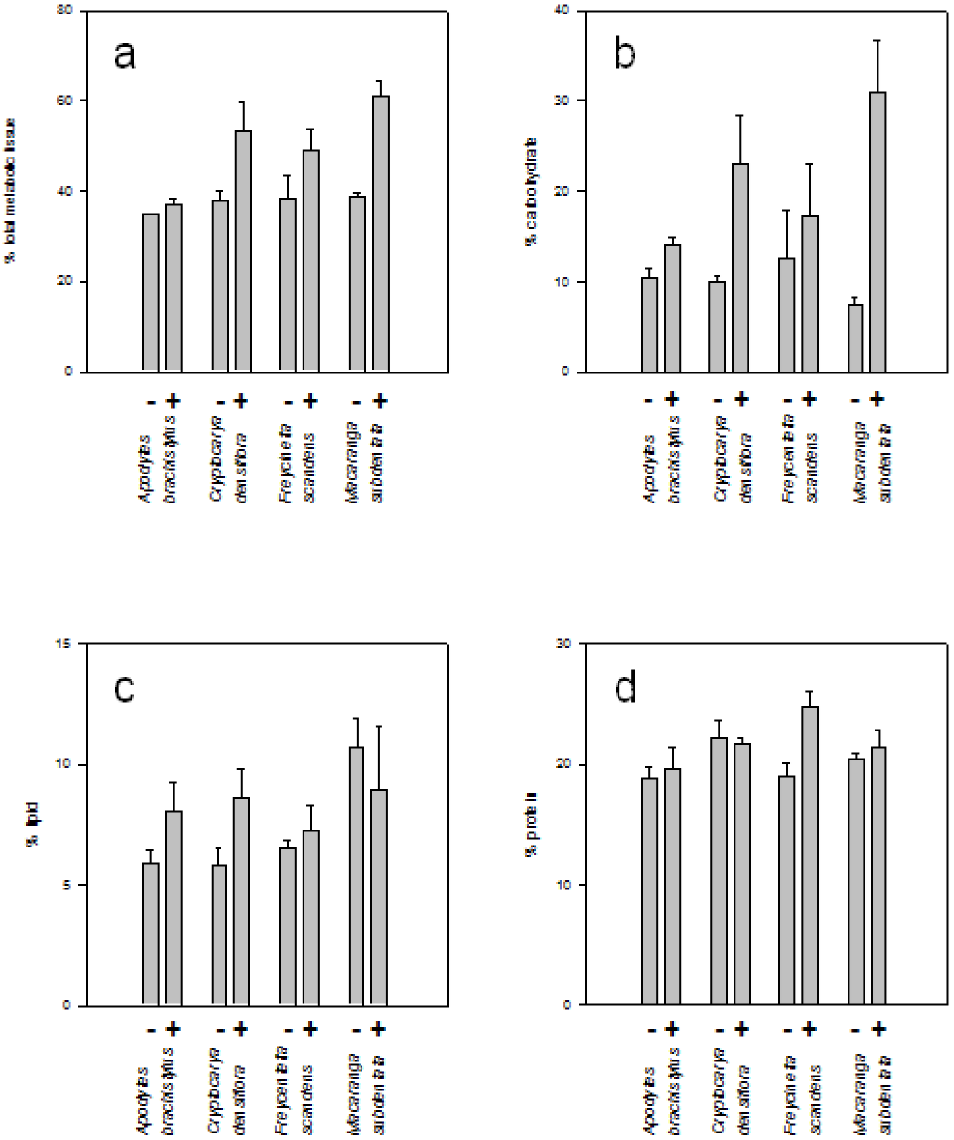


Figure 3.8. Comparison of metabolic tissue content of *Anisocentropus kirramus* fed on four leaf species – *Apodytes brachistylus*, *Cryptocarya densiflora*, *Freycenetia scandens* and *Macaranga subdentata* – with (+) and without (–) nutrient supplements: a) total metabolic tissue, b) carbohydrate, c) lipid and d) protein. See Table 3.5 for statistics.

3.3.4 Experiment 3.4 – P and N enrichment: leaf decomposition, microbial biomass and growth of *A. kirramus*

In Experiment 3.4 the nutrient concentrations in treated channels were generally elevated well above controls, although target concentrations were not always achieved (Table 3.6). Although the mean nitrogen concentrations recorded for the N and N+P treatments were near the 300 µg N L^{-1} target, the 2N+2P treatment total nitrogen concentration was lower than the 600 µg N L^{-1} target. The majority of the nitrogen was in the form of nitrate. The mean total phosphorus concentrations in the P and N+P treatments were lower than the targets but were approximately ten times higher than ambient concentration. The phosphorus concentrations in the 2N+2P treatment were also lower than the target and not significantly higher than in the P and N+P treatments. Nevertheless, gradients in both N and P reflected the treatments.

Table 3.6. Nutrient treatments, target nutrient concentrations, recorded concentrations and comparisons between treatments in water samples from experimental channels (mean ± s.e., µgL^{-1}, of 4 channels per treatment). Results of ANOVA across treatments are shown for each variable; where *P* < 0.05, results of Tukey post-hoc tests are shown, with letters a-c identifying groups of treatments for which the means are not significantly different (α = 0.05). N = nitrogen, NO_3 = nitrate, NO_2 = nitrite, P = phosphorus, FRP = filterable reactive phosphorus.

	ANOVA		**Treatment**				
	$F_{4,15}$	**P**	**Control**	**+N**	**+P**	**+N +P**	**+2N +2P**
Target values							
N			ambient	300	ambient	300	600
FRP			ambient	ambient	30	30	60
Recorded values							
Total N	46.95	<0.001	45.7 ±1.6 a	257.0 ±34.6 b	57.8 ±10.4 a	332.0 ±37.5 ab	483.7 ±17.2 b
NO_3	63.23	<0.001	26.3 ±1.0 a	220.3 ±1.0 b	22.6 ±1.9 a	295.5 ±41.9 bc	447.7 ±13.9 c
NO_2	1.13	0.379	1.00 ±0.1	0.9 ±0.1	0.7 ±0.1	1.0 ±0.1	0.9 ±0.1
Total P	9.15	<0.001	2.4 ±0.5 a	4.1 ±1.1 ab	24.2 ±2.0 c	20.9 ±3.5 bc	30.3 ±7.9 c
FRP	9.12	<0.001	1.4 ±0.5 a	1.4 ±0.5 a	10.2 ±4.4 b	16.7 ±2.9 b	21.6 ±2.6 b

P supplements, both alone and with N, and the presence of *Anisocentropus kirramus* had significant effects on the dry weight of *Apodytes brachystylus* leaf material remaining in the cages after 49 days (Figure 3.9; Table 3.7). Enrichment with N alone had no effect on the amount of leaf material remaining. The effect of N + P enrichment did not differ significantly from the P-only treatment. There was no interaction between the nutrient treatments and the presence of *A. kirramus* (as in Experiment 3.3), indicating that although less leaf material remained, the shredding rate and the amounts consumed by *A. kirramus* were similar in all nutrient treatments. Thus, the mean per-capita feeding rates did not differ among treatments ($F_{1,18}$ = 1.984, $P = 0.176$). Additionally, across all treatments the mean leaf mass losses were 51.0 ± 2.3 % due to leaching and microbial processing and 22.6 ± 1.6 % due to shredding by *A. kirramus*; this difference of about 28 % was the same across treatments ($F_{4,15}$ = 0.26, P = 0.897), confirming the consistency of the feeding rate of *A. kirramus*. The results were not influenced by channel position ($F_{1,29}$ = 0.80, $P = 0.378$) or loss of individuals of *A. kirramus* ($F_{1,14}$ = 0.68, $P = 0.18$).

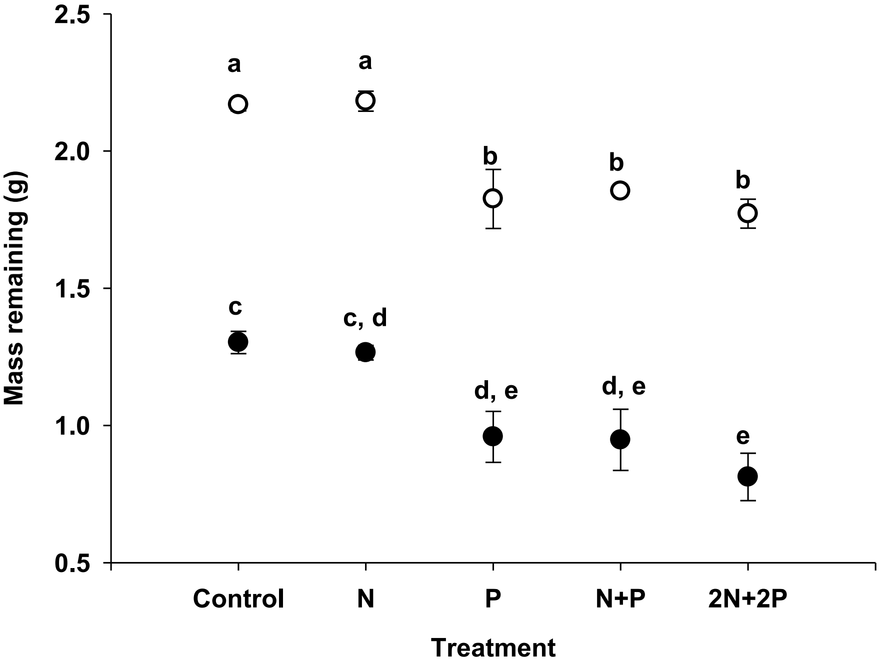


Figure 3.9. Mean dry mass (± s.e.) of *Apodytes brachystylus* leaf material remaining after 49 days under different nutrient enrichment treatments, with (•) and without (○) the presence of the shredder *Anisocentropus kirramus*. ANOVA results: for shredder presence/absence, $F_{2,53}$ = 93.43, $P < 0.001$; for nutrient treatment, $F_{4,53}$ = 18.96, $P < 0.001$; there was no interaction between them ($F_{8,45}$ = 1.570, $P = 0.167$). Different letters indicate pairwise difference between means (Tukey test, α = 0.05). See Table 3.7 for full statistics.

Microbial biomass and dry mass of *A. kirramus* larvae increased with nutrient enrichment (Figure 3.10) and there was a significant correlation between them ($r^2 = 0.3018$, $P = 0.012$). Tukey tests show that the main effect on microbial mass was due to enrichment with P, but this was not enhanced in the 2N+2P treatment. The mean rate of leaf material loss attributed to microbial activity was significantly different between treatments ($F_{1,18} = 23.557$, $P < 0.001$). Overall microbial activity (plus leaching and any fragmentation) (treatment means between 35.8 and 44.0 mg day^{-1}) accounted for a greater proportion of the leaf loss, particularly with nutrient enrichment, than shredder activity (treatment means between 29.7 and 34.6 mg day^{-1}).

Biochemical analysis showed that, despite their increase in tissue weight with nutrient enrichment, *A. kirramus* larvae did not increase storage of carbohydrate or lipid, as the proportions of protein, lipid and carbohydrate in larvae were consistent across nutrient treatments (Figure 3.11). Therefore, the increased weight of larvae in the nutrient treatments is attributed to general growth rather than storage of any particular metabolite.

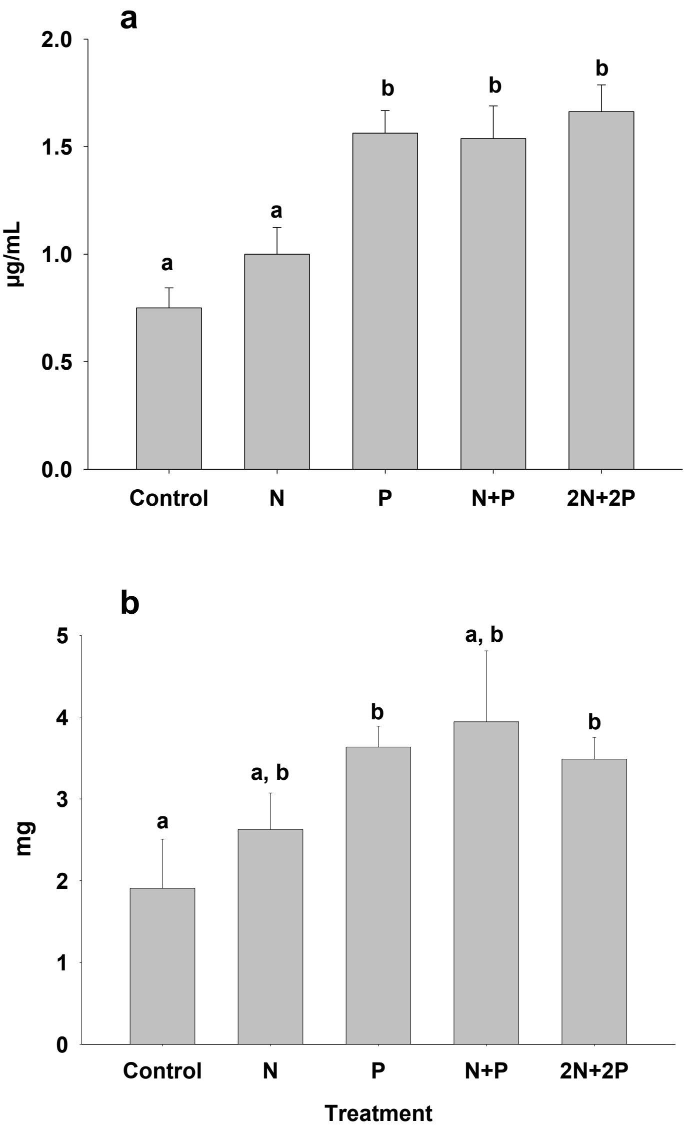


Figure 3.10. Mean (± s.e.) of (a) microbial biomass (fluorescein *µ*g ml^{-1}) on *Apodytes brachystylus* leaf material; and (b) dry mass (mg) of *Anisocentropus kirramus* larvae from different nutrient-enrichment treatments. ANOVA results for (a) $F_{1,18} = 32.154$, $P < 0.001$; for (b) $F_{1,18} = 7.040$, $P = 0.016$. Different letters indicate pairwise difference between means (Tukey test, $\alpha = 0.05$).

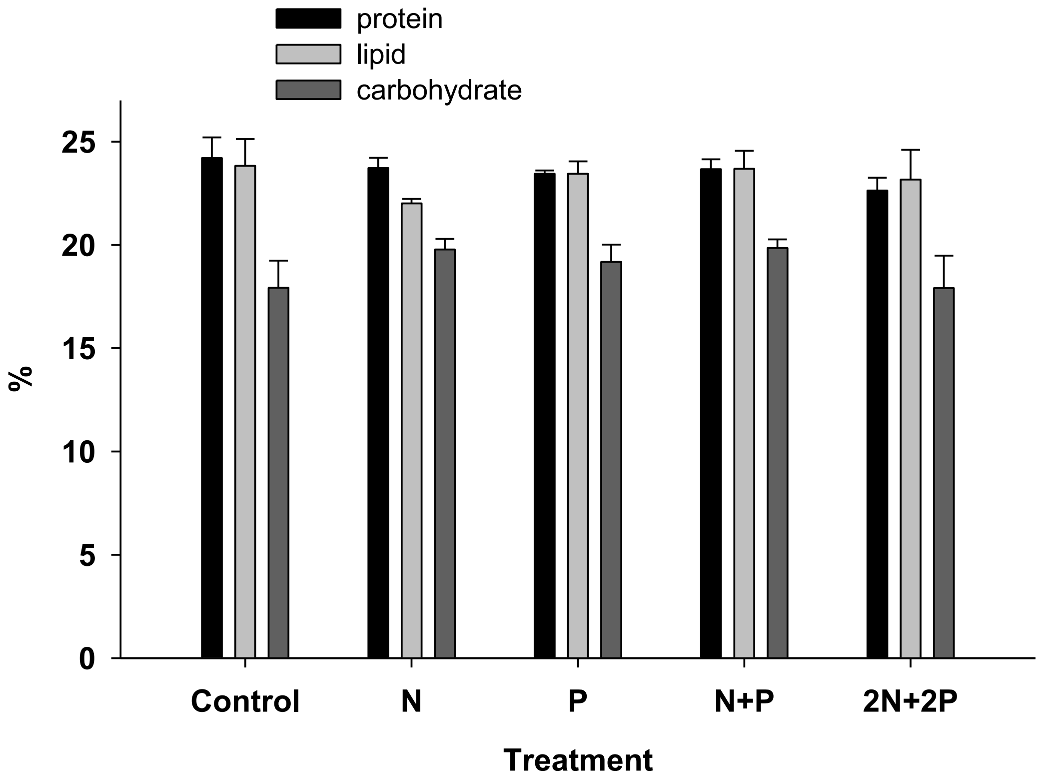


Figure 3.11. Protein, lipid and carbohydrate content of *Anisocentropus kirramus* tissue (% ± s.e.). Proportions of each component did not differ among treatments (protein $F_{1,15}$ = 0.89, P = 0.492; lipid $F_{1,15}$ = 0.53, P = 0.713; carbohydrate $F_{1,15}$ = 0.86, P = 0.508).

3.4 Discussion

The overall abundance and composition of the invertebrate assemblage in the artificial stream channels was similar to that in the stream (unpublished data) and to other similar streams (Pearson *et al.*, 1986) in its high species richness, low number of common taxa and the high relative abundance of Chironomidae. The increase in abundance of invertebrates in the nutrient-enhanced channels concurs with results of other studies (e.g., Winterbourn, 1990; Mundie *et al.*, 1991; Perrin & Richardson, 1997; Scrimgeour & Chambers, 1997; Cross *et al.*, 2006). However, the low number of species contributing to this increase was surprising and suggested that only a few taxa were able to take advantage of the enhanced decomposition rate of organic matter. As in the study by Perrin and Richardson (1997), chironomids and mayflies were the predominant taxa responding to nutrient enhancement, which may reflect rapid life cycles and/or high colonisation ability (Benson & Pearson, 1987; Rosser & Pearson, 1995; Chapter 4). Using mesocosms, Perrin and Richardson (1997) found a near doubling of invertebrate abundance, much as I report here.

Because ambient nutrient levels in Birthday Creek were very low, it might be expected that sustained supplementation of nutrients would enhance primary production (e.g., Elwood *et al.*, 1981; Hart & Robinson, 1990; Johnston *et al.*, 1990; Perrin & Richardson, 1997; Scrimgeour & Chambers, 1997). However, there was no measured increase in chlorophyll *a* levels with nutrient supplements. While this could be because of extra grazing response (Elwood *et al.*, 1981), the lack of increase in abundance of grazers suggests that light or other variables are the major factors limiting autotrophy in much of the stream. But increases in leaf decomposition, microbial biomass and invertebrate condition and abundance indicate that the heterotrophic pathway was boosted by nutrient enrichment.

Nutrient supplements and the presence of *Anisocentropus kirramus* both affected the rate of leaf decomposition. In Experiment 3.4 the breakdown of *Apodytes brachystylus* leaf material was clearly accelerated by supplements of P, but was not significantly affected by supplements of N. The microbial biomass on *A. brachystylus* leaves and growth of *A. kirramus* larvae was also greater with supplements of P, but not N. This suggests that in the Wet Tropics P is a limiting nutrient in upland rainforest steams like Birthday Creek.

The lack of interaction between nutrients and shredder presence in the breakdown of leaf material, observed in both Experiments 3.3 and 3.4, was unexpected. It was predicted that enhanced nutrient levels would facilitate the conditioning process, reducing the toughness and making the leaves more palatable for *A. kirramus*. But toughness was only significantly reduced for *Freycenetia scandens*, and it appears that, although shredding rates varied between species, *A. kirramus* was shredding at a consistent rate, with or without nutrient supplements. Only in *Cryptocarya densiflora* was there an interaction between nutrients and presence of shredders, because nutrient supplements had no effect on leaf breakdown in the absence of *A. kirramus*. *C. densiflora* has a tough leaf that has previously been found to resist decomposition and be avoided by *A. kirramus* if other leaf species are present (Nolen & Pearson, 1993). It appears that in the case of *C. densiflora*, shredding facilitated microbial decomposition, rather than vice versa, as is generally reported. Shredding by *A. kirramus* may have enabled microbes to colonise the leaves more easily, breaching an otherwise impenetrable outer layer, and caused *C. densiflora* leaves to react to nutrient supplements like the other three leaf species.

A. kirramus benefited nutritionally from nutrient supplements, by increasing its proportion of metabolic tissue (Experiment 3.3) and growth (Experiment 3.4). The biochemical analyses in Experiment 3.3 showed that there was little variation in the overall condition of individuals of *A. kirramus* feeding on different leaf species in the absence of nutrient supplements. This is interesting because leaf species did have a significant effect on dry weight loss of leaf material and did have a significant interaction with shredder presence. Nolen and Pearson (1993) and Bastian *et al*. (2007) also showed that *A. kirramus* has distinct preferences for particular leaf species. Li and Dudgeon (2008) recorded similar effects for *A. maculates*, indicating that shredding by *Anisocentropus* species is affected by specific leaf properties. However, shredder condition was more influenced by the nutrient supplements than by the leaf species. The lack of interaction between nutrient supplements and shredder presence shows that the increased condition of *A. kirramus* was not due to increased ingestion of leaf material, so must have been due to its food quality. The correlation between the growth rate of *A. kirramus* larvae and microbial biomass on the leaves (Experiment 3.4) indicates that *A. kirramus* received a nutritional benefit from the nutrient supplements via the microbial biomass on the leaves, which is generally the principal pathway from allochthonous organic material to higher consumers (Cargill *et al*., 1985; France, 2011).

Fungal lipids provide polyunsaturated fatty acids (Brett & Mueller-Navarra, 1997; Arce-Funck *et al*. 2015) and important cues for food selection for several stream invertebrates (Chung & Suberkropp, 2009). For example, late-instar caddisfly larvae choose leaves treated with crude lipid and the neutral lipid fraction from aquatic hyphomycetes fungal over naturally conditioned leaves (Cargill *et al.*, 1985). These caddisflies accumulated large stores of triglycerides and free fatty acids necessary for successful reproduction. The effect on lipid storage due to nutrient supplements was not significant in our experiments, possibly because the *A. kirramus* larvae used were not in their last instar, or because the digested leaf material was initially stored as carbohydrate. *A. kirramus* may convert carbohydrate into lipid reserves over time but, if so, our experiment was not long enough to show significant conversion.

It was not determined if the nutritional benefit resulted in increased survival, reproductive success and population size of *A. kirramus*, but the increase in overall invertebrate abundance (Experiment 3.1) suggests that nutrient status has a direct role in the productivity of the stream, by enhancing the biomass and nutritional status of detritus microbes and the animals that feed on them. It is noteworthy that the enhanced growth of *A. kirramus* and, therefore, assimilation of supplemented nutrients, occurred within ~ 1 m of the nutrient release in the experimental channels. It was apparent that the effects of nutrient enhancement were confined to a rather tight relationship between the breakdown of a few leaf species, the consumption of the resultant particulate organic matter by a few detritivorous collector species, and increased predation on them by the single predator species *Plectronemia* sp. However, it is possible that an effect on a broader range of collector and predator species was masked by their rapid consumption by predators, and/or by their low abundance and patchy distribution. It is interesting to note that the greatest effect was an increase in abundance of juvenile chironomids, indicating that their survival was enhanced by the nutrient supplements, reflecting the suggestion that adequate nutrition is a bottleneck for early instars which, in turn, limits the size of stream insect populations (Cummins & Klug, 1979).

The lack of major change in community composition was surprising given the magnitude of the nutrient enhancement (Experiment 3.1). While a drop in species richness would have been straightforward to observe, any potential increase in richness is limited by the available pool of species. However, the consistency of the evenness suggests that the enhanced nutrient levels had no effect on overall diversity. Given the increase in abundance of the fauna, this result is unexpected. The ordination of samples showed no shift in community structure, with differences between samples from control and treatment channels being due to changes in abundance of the fauna.

Studies elsewhere have demonstrated similar effects of nutrient supplement on litter breakdown largely through microbial processes, but with different nutrients being important. For example, Gulis *et al*. (2006) found positive effects of dissolved inorganic N and P on litter decomposition rates in Portugal; Meyer and Johnson (1983) found that high nitrate concentrations accelerated microbial processing of leaf litter in streams in North Carolina; Howarth and Fisher (1976) found that enrichment with N + P in laboratory streams accelerated leaf decomposition but enrichment with P did not; Ferreira *et al*. (2006a) found that N enrichment of a Portuguese stream enhanced fungal activity and litter decomposition; Danger *et al*. (2013) found that the growth and survival of *Gammarus fossarum* was greater when fed P enriched leaf litter; Ramirez *et al*. (2003) found that P was the major variable driving inter-stream differences in microbial respiration rates and growth of chironomids in Costa Rican streams; and Elwood *et al*. (1981) demonstrated that P limitation of detrital processing is a significant factor in Tennessee streams. Thus, nutrient concentrations are important in determining the course of basic biological processes in streams, including autotrophic production (e.g., Newbold *et al*., 1982; Peterson *et al*., 1983) and detrital processing and heterotrophic production, discussed here. However, the identity of the important nutrient (N or P in this case) differs with the local environment – that is, presumably, the lithology and soil characteristics of the catchment. Additionally, there is local or regional variation in impacts through the food web: for example, Elwood *et al*. (1981) and Gulis *et al*. (2006) demonstrated that nutrient supplements boost invertebrate abundance, whereas Ferreira *et al*. (2006a) did not. The pathways in the food web are quite clear – for example, Cheshire *et al*. (2005) demonstrated the importance of shredders in processing leaf litter, the principal heterotrophic source of organic material in the food web of Birthday Creek, and of the fine particulate feeders which benefit from shredder activity. Thus, nutrient supplements can be transmitted through the food web. However, success of animals (e.g., recruitment of viable individuals) depends not only on population numbers, but especially on the physiological condition of the parent generation, so it is surprising that so little on this topic is reported for stream invertebrates, except for an extensive literature on physiological responses for monitoring of environmental stressors (e.g., Maltby *et al*., 1990; Feltena, 2008; Koop *et al*., 2011).

Descriptions of fundamental small-scale relationships are important to the understanding of the links between basic ecosystem processes and species' tolerances and needs (Attrill & Depledge, 1997; Baird *et al*., 2007). The latter are important in predicting the effects of future environmental change, and may be important in monitoring ecosystems. Woodward *et al*. (2012) point out that nutrient loading is a major threat to aquatic ecosystems worldwide, leading to major changes in biodiversity and biophysical processes, and they highlight the need to complement established monitoring approaches (e.g., measures of water quality and biological diversity) with functional measures (such as litter-breakdown rate) for assessing ecosystem health. I agree: it is clear that, as nutrient supplements have different effects in different systems, these effects can only be identified and gauged by direct measurement of ecosystem processes rather than simple monitoring of nutrient concentrations.

My results and others show that the response of detrital food webs to nutrient supplements is fundamentally different from that of food webs based on living plants and can have as significant effects on food web dynamics. The fate of most plant production is to enter the detrital pool (Cebrian, 1999; Moore *et al*., 2004) and, therefore, increasing the rate of detrital processing through nutrient enrichment also has the potential to alter large-scale ecosystem functions. Whereas nutrient enrichment may increase carbon sequestration and storage of autotrophic organic material (Elser *et al*., 2007), it is now recognized that nutrient enrichment will reduce the basal carbon storage in detritus-based systems (Mack *et al*., 2004; Cleveland *et al*., 2006; Benstead *et al*., 2009; Rosemond *et al*., 2001, 2015). For example, long-term nitrogen and phosphorus additions to a first-order stream had only minor effects on primary production, the storage of non-leaf CPOM and dissolved carbon inputs, but caused a 69% decrease in leaf litter standing stock during the two years of nutrient addition (Benstead *et al*., 2009). The consumption of leaf litter by invertebrates and fungi, and the export of fine particulate organic matter (FPOM) increased dramatically following nutrient addition as did heterotrophic respiration on leaf litter, wood and FPOM, increasing losses of CO_2 to the atmosphere. The increased FPOM exports could not be accounted for by increased processing of recent inputs of organic matter alone, and they concluded that deeply buried stores of detritus were also mobilized, paralleling the effect of enrichment on terrestrial soils (e.g., Pregitzer *et al*., 2004; Mack *et al*., 2004; Cleveland & Townsend 2006). Rosemond *et al*. (2015) found that the average rates of terrestrial organic carbon loss increased by 1.65 times and residence time was reduced by ~50% in streams as a result of long-term moderate nitrogen and phosphorus additions through nutrient stimulation of microbial decomposition and detritivore feeding. Litter quantity in the benthos was predicted to be 2.8 and 7.7 times higher in reference streams compared to the nutrient-enriched streams after 6 and 12 months respectively. They suggested that, although not as obvious as increased algal biomass, this magnitude of carbon loss could exceed predicted algal carbon gains with nutrient enrichment across river networks, diminishing associated ecosystem services. This net loss of detrital carbon through biological processes is only recently being appreciated and may contribute to substantial deficits in the stream organic matter budgets and long-term shifts in organic matter storage as a result of even mild nutrient addition, potentially altering the stability that detrital resources afford to their food webs (DeAngelis & Mulholland, 2004; Moore *et al*., 2004; Rosemond *et al*., 2015).

3.5 References

Abrams P.A. (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology* **76**: 2019-2027.

Anderson N.H. & Grafius E. (1975) Utilisation and processing of allochthonous material by stream Trichoptera. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **19**: 3083-3088.

Anderson N.H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* **24**: 351-377.

Arce Funck J., Bec A., Perriere F., Felten V. & Danger M. (2015) Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* **13**: 205-210.

Arsuffi T.L. & Suberkropp K. (1985) Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. *Oikos* **45**: 50-58.

Arsuffi T.L. & Suberkropp K. (1989) Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. *Oecologia* **79**: 30-37.

Attrill M.J. & Depledge M.H. (1997) Community and population indicators of ecosystem health: targeting links between levels of biological organisation. *Aquatic Toxicology* **38**: 183-197.

Baird D.J., Brown S.S., Lagadic L., Liess M., Maltby L., Moreira-Santos M., Schulz R. & Scott G.I. (2007) In situ–based effects measures: determining the ecological relevance of measured responses. *Integrated Environmental Assessment and Management* **3**: 259-267.

Bastian M., Boyero L., Jackes B.R., & Pearson R.G. (2007) Leaf litter diversity and shredder preferences in an Australian tropical rain-forest stream. *Journal of Tropical Ecology* **23**: 219-229.

Benfield E.F. & Webster J.R. (1985) Shredder abundance and leaf breakdown in an Appalachian Mountain stream. *Freshwater Biology* **15**: 113-120.

Benson, L.J. & Pearson R.G. (1987) The role of drift and effect of season in colonization of implanted substrata in a tropical Australian stream. *Freshwater Biology* **18**: 109-116.

Benstead J.P., Rosemond A.D., Cross W.F., Wallace J.B., Eggert S.L., Suberkropp K., Gulis V., Greeenwood J.L. and Tant C.J. (2009) Nutrient enrichment alters storage and fluxes of detritus in a headwater stream ecosystem. *Ecology* **90**: 2556-2566.

Boyero L., Pearson R.G., Dudgeon D., Graça M.A.S., Gessner M.O., Albariño R.J., Ferreira V., Yule C.M., Boulton A.J., Arunachalam M., Callisto M., Chauvet E., Ramírez A., Chará J., Moretti M.S., Gonçalves J.F. Jr., Helson J.E., Chará A.M., Encalada A., Davies J.N., Lamothe S., Cornejo A., Castela J, Li A.O.Y., Buria L.M., Villanueva V.D., Zúñiga M.C., & Bruder A. (2011) Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology* **92**: 1839-1848.

Brett M.T. & Mueller-Navarra D.C. (1997) The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biology* **38**: 483-499.

Cargill A.S., Cummins K.W., Hanson B.J., & Lowry R.R. (1985) The role of lipids as feeding stimulants for shredding aquatic insects. *Freshwater Biology* **15**: 455-464.

Cebrian J. (1999) Patterns in the fate of production in plant communities. American *Naturalist* **154**: 449-468.

Cheshire K., Boyero L. & Pearson R.G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Chung N. & Suberkropp K. (2009) Effects of aquatic fungi on feeding preferences and bioenergetics of *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Hydrobiologia* **630**: 257-269.

Cleveland C.C., Reed S.C., & Townsend A.R. (2006) Nutrient regulation of organic matter decomposition in a tropical rainforest. *Ecology* **87**: 492-503.

Connolly N.M., Christidis F., McKie B., Boyero L. & Pearson R. (2008) Diversity of invertebrates in Wet Tropics streams: patterns and processes. Pages 161-177 **In** Stork, N. E. & Turton, S. M. (eds.) *Living in a Dynamic Tropical Forest Landscape*. Wiley-Blackwell, Oxford UK.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Cornut J., Ferreira V., Goncalves A.L., Chauvet E. & Canhoto C. (2015) Fungal alteration of the elemental composition of leaf litter affects shredder feeding activity. *Freshwater Biology* doi:10.1111/fwb.12606.

Cross W.F., Wallace J.B., Rosemond A.D. & Eggert S.L. (2006) Whole-system nutrient enrichment increases secondary production in a detrital based ecosystem. *Ecology* **87**: 1556-1565.

Cross W.F., Wallace J.B. & Rosemond A.D. (2007) Nutrient enrichment reduces constraints on material flow in a detrital-based food web. *Ecology* **88**: 2563-2575.

Cummins K.W. & Klug M.J. (1979) Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* **19**: 147-172.

Danger M., Arce Funck J., Devin S., Heberle J. & Felten V. (2013) Phosphorus content in detritus controls life-history traits of a detritivore. *Functional Ecology* **27**: 807-815.

DeAngelis D.L. & Mulholland P.J. (2004) Dynamic consequences of allochthonous nutrient inputs to freshwater systems. Pages 12-24 **In** Polis G.A., Power M.E. & Huxel G.R. (eds.) *Food webs at the landscape level.* University of Chicago Press, Chicago, Illinois, USA.

Elser J.J., Bracken M.E.S., Cleland E.E., Gruner D.S., Harpole W.S., Hillebrand H., Ngai J.T., Seabloom E.W., Shurin J.B. & Smith J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**: 1135-1142.

Elwood J.W., Newbold J.D., Trimble A.F. & Stark R.W. (1981) The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. *Ecology* **62**: 146-158.

Encalada A.C., Calles J., Ferreira V., Canhoto C.M. & Graca M.A.S. (2010) Riparian land use and the relationship between the benthos and litter decomposition in tropical mountain streams. *Freshwater Biology* **55**(8): 1719-1733.

Feltena V., Charmantier G., Charmantier-Daures M., Aujoulat F., Garrica J. & Geffard O. (2008) Physiological and behavioural responses of *Gammarus pulex* exposed to acid stress. *Comparative Biochemistry and Physiology C* **147**: 189-197.

Ferreira V., Castagneyrol B., Koricheva J., Gulis V., Chauvet E. & Graca M.A.S. (2014) A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. *Biological Review* **90**: 669-688.

Ferreira V. & Chauvet E. (2011) Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* **17**: 551-564.

Ferreira V. & Graca M.A.S. (2007) Fungal activity associated with decomposing wood is affected by nitrogen concentration in water. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*. **92**: 1-8.

Ferreira V., Gulis V. & Graça M.A.S. (2006a). Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* **149**: 718-729.

Ferreira V., Graca M.A.S., de Lima J.L.M.P. & Gomes R. (2006b) Role of physical fragmentation and invertebrate activity in the breakdown of leaves. *Archiv für Hydrobiologie* **165**: 493-513.

Fisher S.G. & Likens G.E. (1972) Stream ecosystem: organic energy budget. *BioScience* **22**: 33-35.

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**: 421-439.

Fittkau E.J. & Klinge H. (1973) On biomass and trophic structure of the Central Amazon rain forest ecosystem. *Biotropica* **5**: 2-14.

France R.L. (2011) Leaves as “crackers”, biofilm as “peanut butter”: Exploratory use of stable isotopes as evidence for microbial pathways in detrital food webs. *Oceanological and Hydrobiological Studies (International Journal of Oceanography and Hydrobiology)* **40**: 110-115.

Graca M.A.S. (2001) The role of invertebrates on leaf litter decomposition in streams: a review. *International Review Hydrobiology* **86**: 383-393.

Groome A.P. & Hildrew A.G. (1989) Food quality for detritivores in streams of contrasting pH. *Journal of Animal Ecology* **58**: 863-881.

Gulis V. & Suberkropp K. (2003) Effect of inorganic nutrients on relative contribution of fungi and bacteria to carbon flow from submerged decomposing leaf litter. *Microbial Ecology* **45**: 11-19.

Gulis V., Ferreira V., & Graça M.A.S. (2006) Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream assessment. *Freshwater Biology* **51**: 1655-1669.

Hart D.D. & Robinson C.J. (1990) Resource limitation in a stream community: phosphorus enrichment effects on periphyton and grazers. *Ecology* **71**: 1494-1502.

Hieber M. & Gessner M.O. (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* **83**: 1026-1038.

Hill W.R. & Knight A.W (2008) Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology* **24**:125-132.

Hill W.R., Ryon M.G. & Schilling E.M. (1995) Light limitation in a stream ecosystem: response by primary producers and consumers. *Ecology* **76**: 1297-1309.

Howarth R.W. & Fisher S.G. (1976) Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient-enriched stream microecosystems. *Freshwater Biology* **6**: 221-228.

Johnston N.T., Perrin C.J., Slaney P.A., & Ward B.R. (1990) Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 862-872.

Iversen T.M. (1974) Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of digested leaves. *Oikos* **25**: 278-282.

Kaushik N.K. & Hynes H.B.N. (1971) The fate of dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**: 465-515.

Koop J.H.E., Winkelmann C., Becker J., Hellmann C. & Ortmann C. (2011) Physiological indicators of fitness in benthic invertebrates: a useful measure for ecological health assessment and experimental ecology. *Aquatic Ecology* **45**: 547-559.

Lake P.S., Schreiber E.S.G., Milne B.J. & Pearson R.G. (1994) Species richness in streams: Patterns over time, with stream size and with latitude. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **25**: 1822-1826.

Li, A.O.Y. & Dudgeon D. (2008) The effects of leaf litter characteristics on feeding and fitness of a tropical stream shredder, *Anisocentropus maculatus* (Trichoptera: Calamoceratidae). *Marine and Freshwater Research* **59**: 897-901.

Mack M.C., Schuur E.A.G., Bret-Harte M.S., Shaver G.R. & Chapin F.S. (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**: 440-443.

Maltby L., Naylor C. & Calow P. (1990) Field deployment of a scope for growth assay involving *Gammarus pulex*, a freshwater benthic invertebrate. *Ecotoxicology and Environmental Safety* **19**: 292-300.

Mann R. & Gallager S. (1985) Physiological and biochemical energetics of larvae of *Terido navalis* L. and *Bankia gouldi* (Bartsch) (Bivalvia: Teredinidae). *Journal of Experimental Marine Biology and Ecology* **85**: 211-228.

McCune B., & Mefford M.J. (2011) PC-ORD. Multivariate Analysis of Ecological Data. Version 6.20. MjM Software: Gleneden Beach, Oregon, USA.

McKie B.G. & Pearson R.G. (2006) Environmental variation and the predator-specific responses of tropical stream insects: effects of temperature and predation on survival and development of Australian Chironomidae (Diptera). *Oecologia* **149**: 328-339.

Melillo J.M., Naiman R.J., Aber J.D. & Linkins A.E. (1984) Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bulletin of Marine Science* **35**: 341-356.

Meyer J.L. & Johnson C. (1983) The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. *Freshwater Biology* **13**: 177-183.

Mittlebach G.G., Steiner S.F., Scheiner S.M., Gross K.L., Reynolds H.L., Waide R.B., Willig M.R., Dodson S.I. & Gough L. (2001) What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381-2396.

Moore J.C., Berlow E.L., Coleman D.C., deRuiter P.C., Dong Q., Hastings A., Collins-Johnson N., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.M., Post D.M., Sabo J.L., Scow K.M., Vanni M.J. & Wall D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**: 584-600.

Mundie J.H., Simpson K.S. & Perrin C.J. (1991) Responses of stream periphyton and benthic insects to increases in dissolved inorganic phosphorus in a mesocosm. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 2061-2072.

Newbold J. D., O"Neill R.V., Elwood J.W. & Van Winkle W. (1982) Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *The American Naturalist* **120**: 628-652.

Nolen J.A. & Pearson R.G. (1992) Life history studies of *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae) in a tropical Australian rainforest stream. *Aquatic Insects* **14**: 213-221.

Nolen J.A. & Pearson R.G. (1993) Processing of litter from an Australian tropical stream by *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae). *Freshwater Biology* **29**: 469-479.

Pearson R.G., Benson L. J., & Smith R.E.W. (1986) Diversity and Abundance of the Fauna in Yuccabine Creek, a Tropical Rainforest Stream. Pages 329-342 **In** deDeckker P. & Williams W.D. (eds.) *Limnology in Australia*. CSIRO, Melbourne.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G. & Tobin R.K. (1989) Litter consumption by invertebrates from an Australian tropical rainforest stream. *Archiv für Hydrobiologie* **116**: 71-80.

Perakis S.S. & Hedlin L.O. (2002) Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* **415**: 416-419.

Perrin C.J. & Richardson J.S. (1997) N and P limitation of benthos abundance in the Nechako River, British Columbia. *Canadian Journal of Fisheries and Aquatic Science* **54**: 2574-2583

Petersen R.C. & Cummins K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology* **4**: 343-368.

Peterson B.J., Hobbie J.E. & Corliss T.L. (1983) A continuous-flow periphyton bioassay: tests of nutrient limitation in a tundra stream. *Limnology and Oceanography* **28**: 583-591.

Pregitzer K.S., Zak D.R., Burton A.J., Ashby J.A. & MacDonald N.W. (2004) Chronic nitrate additions dramatically increase the export of carbon and nitrogen from northern hardwood ecosystems. *Biogeochemistry* **8**: 179-197.

Ramirez A., Pringle C.M. & Molina L. (2003) Effects of stream phosphorus levels on microbial respiration. *Freshwater Biology* **48**: 88-97.

Rosemond A.D., Pringle C.M., Ramirez A. & Paul M.J. (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology* **82**: 2279-2293.

Rosemond A.D., Benstead J.P., Bumpers P.M., Gulis V., Kominoski J.S., Manning D.W.P., Suberkropp K. & Wallace J.B. (2015) Experimental nutrient editions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**: 1142-1145.

Rosser Z.C. & Pearson R.G. (1995) Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. *Journal of the North American Benthological Society* **14**: 183-196.

Schnurer J. & Rosswall T. (1982) Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. *Applied and Environmental Microbiology* **43**: 1256-1261.

Scrimgeour G.J. & Chambers P.A. (1997) Development and application of a nutrient-diffusing bioassay on large rivers. *Freshwater Biology* **38**: 221-231.

Stockner J.G. & Shortreed K.R.S. (1978) Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. *Journal of the Fisheries Research Board of Canada* **35**: 28-34.

Stout J. (1980) Leaf decomposition rates in a Costa Rican lowland tropical rainforest stream. *Biotropica* **12**: 264-272.

Suberkropp K. & Klug M.J. (1976) Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* **57**: 707-719.

Swisher R. & Carroll G.C. (1980) Fluorescein diacetate hydrolysis as an estimator of microbial biomass on coniferous needle surfaces. *Microbial Ecology* **6**: 217-226.

Tank J.L. & Dodds W.K. (2003) Nutrient limitation of epilithic and epixylic biofilm in ten North American streams. *Freshwater Biology* **48**: 1031-1049.

Tracey J. G. (1982) The Vegetation of the Humid Tropical Region of North Queensland. (CSIRO: Melbourne).

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.

Waide R. B., Willig M.R., Steiner C.F., Mittleback G., Gough L., Dodson S.I. Juday G.P & Parmenter R. (1999) The relationship between primary productivity and species richness. *Annual Review of Ecology & Systematics* **30**: 257-300.

White D.S. & Howes B.L. (1994) Nitrogen incorporation into decomposing litter of *Spartina alterniflora. Limnology and Oceanography* **39**: 133-140.

Winterbourn M.J. (1990) Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology* **23**: 463-474.

Winterbourn M.J. & Davis S.F. (1976) Ecological role of *Zealonopsyche ingens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. *Australian Journal of Marine and Freshwater Research* **27**: 197-216.

Wintermans I.F.G.M. & De Mot A. (1965) Spectrophotometric characteristics of chlorophylls *a* and *b* and their phaeophytins in ethanol. *Biochemica et Physica Acta* **109**: 448-453.

Woodward G., Gessner M.O., Giller P.S., Gulis V., Hladyz S., Lecerf A., Malmqvist B., McKie B.G., Tiegs S.D., Cariss H., Dobson M., Elosegi A., Ferreira V., Graça M.A.S., Fleituch T., Lacoursière J.O., Nistorescu M., Pozo J., Risnoveanu G., Schindler M., Vadineanu A.,. Vought L.B.-M, & Chauvet E. (2012) Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* **336**: 1438-1440.

Chapter 4

Colonisation and emigration of stream invertebrates inhabiting leaf litter packs approximate equilibrium dynamics.

4.1 Introduction

Colonisation and emigration occur continually in stream habitats at small temporal and spatial scales, and are important factors in maintaining coexistence and biodiversity of stream faunas, enabling them to recover from frequent hydrological disturbance (Downes, 1990). The study of colonisation in streams has its origins in developing predictions about how lotic assemblages recover from disturbances (Sheldon, 1984; Gore & Milner, 1990; Wallace, 1990; Mackay, 1992). Stream environments are frequently disturbed by flow events, with hydraulic forces scouring and moving the substratum, flushing resources downstream and dislodging the benthic biota. Stream environments are also subject to drought and anthropogenic disturbances, so the process of re-colonising disturbed habitat is a critical factor in the persistence of lotic populations at a number of scales: small-scale units of the substratum such as cobbles or leaf litter; stream reach scales following hydrologic or anthropogenic disturbances; or whole rivers recovering from pollution or drought.

Observed rates of colonisation and drift imply substantial turnover of individuals in stream benthic habitats (Doeg *et al*., 1989a; Downes, 1990; Rosser & Pearson, 1995; Downes *et al*., 2005), and these processes play a major role in determining the fate of stream invertebrates. Benthic invertebrates move in all directions (Elliot, 1971; Williams & Hynes, 1976; Pearson & Jones, 1987; Lancaster, 1999), including vertically through the sediments (Boulton *et al*., 1998; Gayraud *et al*., 2000; Stubbington, 2012). However, downstream drift, in which individuals enter the stream flow on mass, is typically the most important pathway for redistribution of lotic invertebrates due to the diversity and abundance of individuals and the distances involved (Waters, 1972; Townsend & Hildrew, 1976; Williams & Hynes, 1976; Benson & Pearson, 1987a, b; Lancaster *et al*., 1996). The numbers of invertebrates drifting over a unit area of stream bed has been shown to be several times greater than the standing stock of an area (Waters, 1972) and distances travelled by invertebrates in the drift is typically several meters at a time (Benson & Pearson, 1987a; Elliot, 1971b; Allan & Feifarek, 1989; Elliot, 2002, 2003).

Drift is a ubiquitous phenomenon in streams, across species and geographically, and so the frequent dispersal of large numbers of invertebrates through drift, and other mechanisms, is undoubtedly a key feature of stream ecology (Brittain & Eikland, 1988). The dynamic redistribution of the stream benthic fauna affects a number of ecological processes. There is a continuous selection and colonisation of unoccupied habitat (e.g., newly fallen leaf litter or upturned stones) (e.g., Pearson & Jones, 1987; Doeg *et al*., 1989a, b; Rosser & Pearson, 1995) and the residence time occupying habitat patches may be short, influencing the frequency and intensity of encounters with competitors or predators (McLay, 1968; Glass & Bovbjerg, 1969; Charnov *et al*., 1976; Allan, 1978). Much of the movement is in order to find resources, so foraging behaviour and the utilisation of resources (food and shelter) (Townsend & Hildrew, 1976; Hart & Resh, 1980), and energy flow and nutrient transfer (Elmes, 1991) are also affected by high rates of dispersal. There are also shifts in habitat use: for example, to find specific pupation sites (Hultin *et al*., 1969; Otto, 1971), or refugia during spates (Lancaster & Belyea, 1997; Lancaster, 1999, 2000; Stubbington, 2012). Thus, the dispersal of large numbers of invertebrates at small scales will affect local species distributions, productivity and strengths of species interactions, and in turn, this will affect persistence and population and community dynamics (Downes & Lancaster, 2010; Lancaster & Downes, 2014). However, an understanding of how dispersal affects community organisation is difficult to measure due to the difficulty in quantifying the high mobility and colonisation rates operating at small scales in the heterogeneous stream environment (Lancaster, 2008).

In this project I investigated invertebrate colonisation and emigration dynamics on leaf litter packs. Leaf litter is an important habitat and energy source in low-order forested streams (Fisher & Likens, 1972; Andersen & Sedell, 1979; Vannote *et al*., 1980; Cheshire *et al*., 2005). Leaf material enters the stream from the surrounding forest and is transported by flow before being trapped by protruding substrate or pools, accumulating into discrete packs of various sizes (Brookshire & Dwire, 2003; Li & Dudgeon, 2011; Koljonen *et al*., 2012). Leaf litter packs are transient, they are easily remobilised by spates and are consumed and decompose, but continually reform, at least in the tropics with year-round litterfall (Benson & Pearson, 1993). The patchy retention of litter on the streambed thus creates spatial heterogeneity in the distribution of organic matter necessary to support secondary productivity (Benfield & Webster, 1985; Pearson & Connolly, 2000; Connolly & Pearson 2013; Chapter 3) and, therefore, attract aggregations of benthic animals (Murphy & Giller, 1998; Kobayashi & Kagaya, 2004, 2005) that are adapted to colonise them rapidly (Pearson *et al*., 1989; Benstead, 1996; Gjerløv & Richardson, 2004) and use them as a source of food and shelter (Richardson, 1992; Dudgeon & Wu, 1999; Gjerløv & Richardson, 2004). The characteristics of the leaf material also vary with the time of exposure in the water through leaching, microbial activity and invertebrate scraping, burrowing and shredding (Abelho, 2001; Graca *et al*., 2001; Chapter 3), as well as scouring by water flow and sediment (Webster *et al*., 1990). Thus, litter packs represent a productive mosaic of patchily distributed microhabitats that are frequently changing, so the invertebrate assemblage using them must be able to find and colonise this leaf material as it enters the stream.

The dynamic nature of the invertebrate fauna is thus an important characteristic that underpins understanding of invertebrate assemblage composition and function. Therefore, the aims of this project were firstly to quantify the immigration and emigration rates of the invertebrates; secondly, by determining the length of time required for the invertebrate assemblage on the leaf packs to reach a stable or equilibrium state, confirm the necessary duration of other experiments (Chapters 3 and 5); and thirdly, inform the interpretation of the scale-dependent productivity-diversity patterns observed in Chapter 5, particularly the assembly and equilibrium dynamics of the invertebrates inhabiting leaf packs.

I used the artificial streams described in Chapter 3 to measure the rates that invertebrates colonised leaf packs and tracked the composition of the invertebrates colonising the leaf packs through time. To quantify the dynamic nature of the invertebrate assemblage I fitted a simple equilibrium model to the data to provide estimates of immigration and emigration rates (Sheldon, 1977). Emigration rates were also independently determined using drift nets to compare with model estimates.

4.2 Methods

Colonisation and dispersal of invertebrates inhabiting leaf packs were measured using twenty artificial stream channels located beside Birthday Creek (Connolly & Pearson, 2013; see Chapter 3). The experiments were conducted in the late dry season months of October and November. Water temperature during the study ranged from 17 to 21 °C.

Leaf packs were made from *Apodytes brachystylus* leaves collected fresh from a single tree on the bank of Birthday Creek. Individual packs consisted of 2.5 g air-dried leaves attached to individual fist-sized cobble (~100 mm diameter) using plastic tags and a rubber band. Leaves of this species are colonised by a diverse community of invertebrates in the stream and are readily consumed (Nolen & Pearson, 1993; Pearson & Connolly, 2000; Connolly & Pearson 2013; Chapter 3). The exact weight of each bundle was recorded.

Two experiments were run in parallel: Experiment 4.1 measured the rate of colonisation of litter packs and was conducted in the downstream section (c) of the artificial stream channels (Figure 4.1). Experiment 4.2 measured the rate of invertebrates drifting into the channels and compared the abundances on leaf packs open to immigration with those where immigration of invertebrates was excluded (Figure 4.2). Three leaf packs were located in the upstream (a) and middle sections (b) of each channel at the commencement of the experiments, and in the downstream section (c) during the colonisation periods in Experiment 4.1.

4.2.1 Experiment 4.1 – Colonisation of leaf packs

The leaf packs in the downstream section (c) of four randomly chosen channels were colonised for periods of 3, 7, 12, 24 and 38 days. To avoid variation due to time of sampling this series was run in reverse so that all samples were collected on the same day.

As invertebrates prefer conditioned leaf material (Kaushik & Hynes, 1971; Iversen, 1974; Anderson & Sedell, 1979; Nolen & Pearson, 1993), leaf packs were conditioned prior to use. At the commencement of the experiment and at the same time as the 38-day colonisation treatment commenced, another 48 leaf packs were placed in 63-μm mesh cages in flowing stream water in a 1000-L tank positioned next to the stream channels, and were transferred to the channels as required for each of the subsequent time treatments. The mesh cages excluded invertebrates but allowed leaching and microbial colonisation to occur.

At 38 days all leaf packs were removed from the downstream section (c) of each channel. Each pack was removed from its cobble and placed into a plastic container, and material adhering to the cobble surface was washed into the container. The contents were filtered through a 63-μm mesh screen and the material was preserved in 80% ethanol for processing. In the laboratory, invertebrates were identified and counted under a stereo and high-power microscope and the remaining leaf material was air dried and weighed. Invertebrates were identified to family, or to genus or species when reference voucher specimens were available (confirmed by taxonomists, including Dean, 1999; Christidis, 2003; Dean *et al*., 2004; Christidis & Dean, 2008).

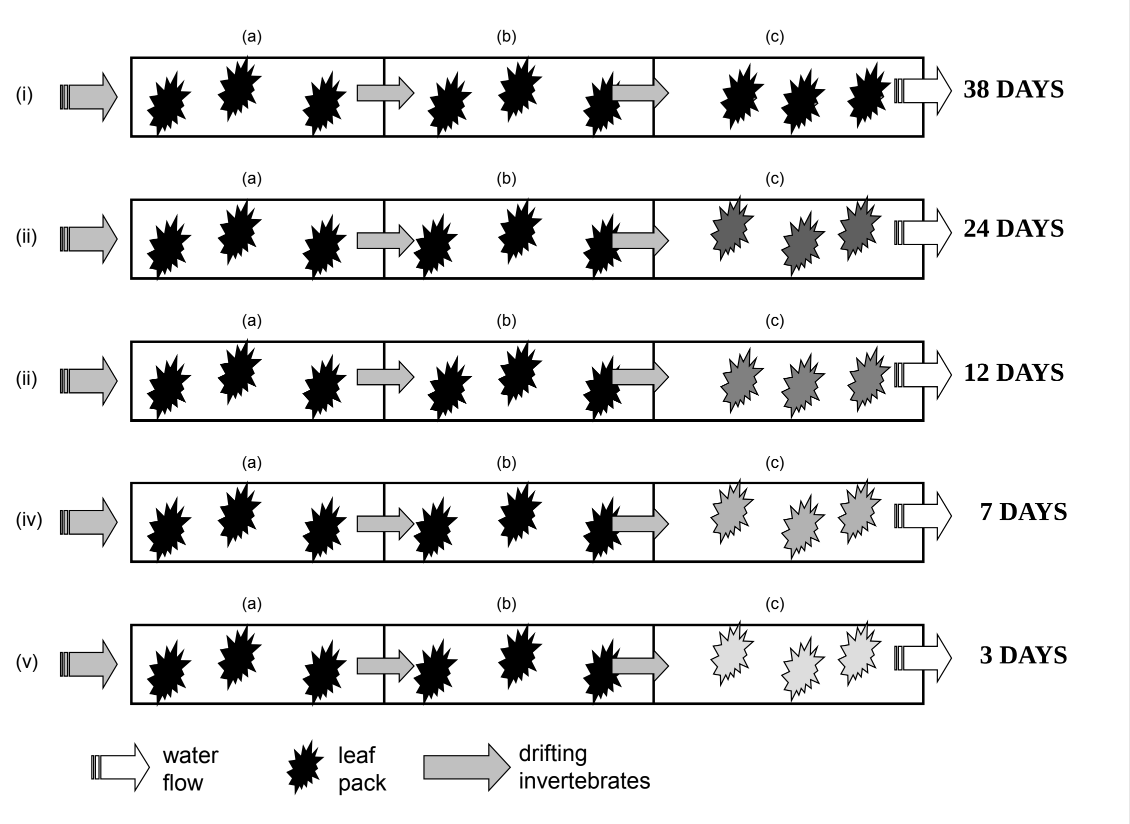


Figure 4.1. Design of Experiment 4.1, showing layout of five artificial stream channels (each of which was replicated four times). Colonisation of leaf packs over various time periods (3 to 38 days, as indicated) was monitored in section c of each channel. Leaf pack shading indicates different colonisation periods.

The individuals collected were pooled for the three packs per channel (as the channels were the replicates) and then the mean total number of individuals, mean total number of taxa and the number of individuals of several taxa were plotted over time to describe the rate of colonisation.

To determine if the invertebrate assemblage inhabiting the leaf packs was approaching equilibrium and estimate rate of immigration and proportion emigrating per unit time, an equilibrium model (McArthur & Wilson, 1967) was fitted to the data using the function for nonlinear least square curve fitting in MATLAB © V5.3, following Sheldon (1977, 1984). This model assumes that a constant number (I) of individuals arrive on to the habitat per unit time while a constant proportion (m) of those present leave that habitat. The habitat will be in equilibrium when I equals the proportion leaving and the density (N) equals I/m. The form of the model used was

$$Nt = I/m(1 - e^{-mt})$$

where Nt is the number present at time t, I/m is the asymptotic number present after infinite time and e is the base of natural logarithms.

This model was chosen over the power function also given in Sheldon (1977, 1984) because it includes a biological mechanism, which the empirical power function lacks (Sheldon, 1977), and because it gave a better fit to the data. It also enables the equilibrium density (I/m) and the rates of immigration and emigration to be estimated directly from colonisation data (Sheldon, 1977).

4.2.2 Experiment 4.2 – Drift into and dispersal from leaf packs

On day 38, at the end of the colonisation period, 63-μm-mesh drift nets were placed at the upstream entrance and downstream exit of the middle section (b) of 3 randomly selected channels. The upstream nets measured the potential immigration of invertebrates into the leaf packs in these channels and the downstream nets measured the emigration from the leaf packs. These channels were referred to as "closed" as they were closed to drift entering from upstream. Another three randomly selected channels were "open" channels for which no drift nets were installed so that drifting invertebrates could enter and exit freely. Drift nets were cleared at 8-hour intervals for 5 days, and at the end of the 5 days the leaf packs from the three “open” and three “closed” channels were removed. All samples were preserved in 80% ethanol then processes in the laboratory, as in Experiment 4.1.

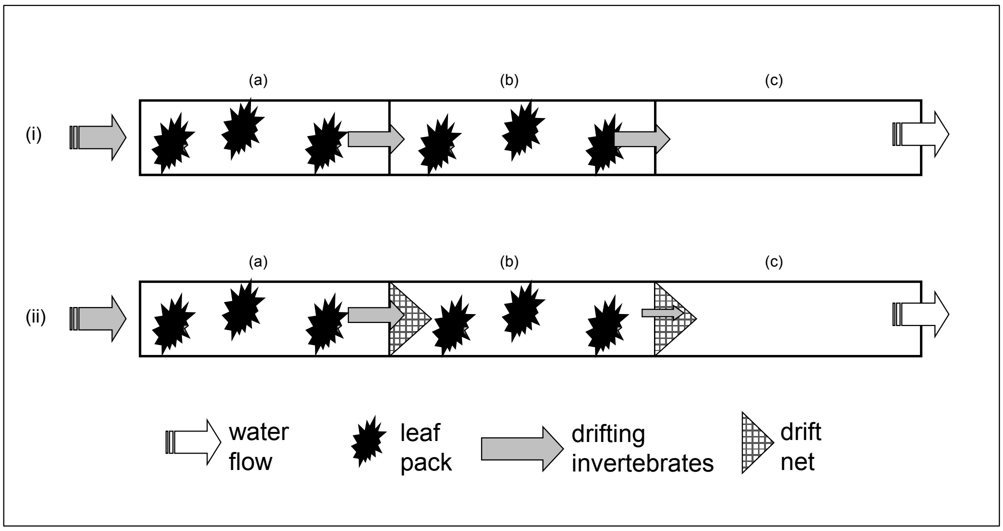


Figure 4.2. Design of Experiment 4.2, showing layout of two artificial stream channels (each of which was replicated three times). In channel (i) (“open”) there are no drift nets and immigration

and emigration are unimpaired; in channel (ii) ("closed") drift nets capture immigrants to and emigrants from section b of the channel.

The proportion of individuals present on the leaf packs that emigrated per unit time was estimated using the equation $m_{drift} = 1 - e^{-k}$, analogous to the colonisation model, where

m_{drift} = the proportion present that emigrate per unit time

and $k = \{-\ln(A_5/A_0)\}/5$

A_5=benthic abundance at day 5, and

A_0= benthic abundance at day 5 + drift abundance

Like the colonisation model, this equation assumes that the proportion emigrating (m_{drift}) is constant through time. This value was then compared to the emigration rate calculated in the colonisation experiment.

4.2.3 Statistical analyses

Assemblage data were analysed and plotted using nonmetric multidimensional scaling (NMDS) using PC-ORD (McCune & Mefford, 2011), which allowed visualisation of the position of assemblages in ordination space, followed by multi-response permutation procedures (MRPP, in PC-ORD) to test for differences between colonisation treatments.

Analysis of variance was used to test for differences in total abundance, richness, evenness and abundance of individual taxa between leaf packs open to immigration and those isolated from immigration for five days.

4.3 Results

4.3.1 Experiment 4.1 – Colonisation of leaf packs

The leaf packs were rapidly colonised by a diverse assemblage of invertebrates, with a total of 9249 animals collected. The abundances of invertebrates on leaf packs increased rapidly to day 12 and then plateaued at approximately 550 individuals (Figure 4.3 a). Richness also increased rapidly, but did not plateau until day 24, at approximately 21 taxa (Figure 4.3 b).

Richness pooled across replicates stabilised at 32 taxa by day 12, and had almost reached this level by day 7 (Figure 4.4). However, increasing cumulative richness indicates that new taxa continued to colonise the leaf packs for the remaining 26 days at a rate of approximately one new taxon every three days, with a total of 50 taxa when the experiment was terminated. Therefore, although 50 taxa were available, the number of taxa inhabiting leaf packs at any point in time was much lower (32 taxa across replicates, 21 within) and was stable through time.

Despite the apparent equilibrium, colonisation rates and patterns varied among taxa (Figure 4.5; Appendices – Table A4.1). The pattern of total abundance was largely driven by the Chironomidae, representing nearly 90% of the abundance at any time, with the mean abundance of chironomids approaching 500 individuals by day 12 (Figure 4.5 a(i)). However, many taxa occurred sporadically and in low abundance or as single individuals within replicates or time periods. Only seven taxa were common to all replicates and time periods. By far the most abundant were the chironomids, *Echinocladius martini*, *Thienemaniella* sp., *Corynoneura* sp., *Dicrotendipes* sp., *Nilotanypus* sp. and *Tanytarsus* sp. The Cyclopoda (Copepoda), *Oxyethira* sp. (Hydroptilidae), and juvenile Leptophlebiidae were also common. The Empididae, and the chironomid, Orthoclad “beta”, were found in most time periods and replicates but were always in low abundance.

The rate of colonisation by Chironomidae was initially very rapid but then quickly plateaued (Figure 4.5 a(i)). The Cyclopoda colonised rapidly, peaking in abundance on day 12, but then declined (Figure 4.5 b(i)). The rate of increase in abundance was steady for the Leptophlebiidae, mean abundance peaking on day 24 (Figure 4.5 c(i)). The Hydroptilidae, Leptoceridae and Hydracarina all began colonisation of the leaf packs relatively slowly but continued to increase though to day 38 (Figure 4.5 d(i), e(i), f(i) respectively).

The patterns of colonisation of individual chironomid species also varied considerably. *E. martini*, *Nilotanypus* sp. and *Dicrotendipes* sp. did not peak in abundance until day 24 but their abundance was also lower on day 38 (Figure 4.6 a(i), b(i), c(i)). *Thienemaniella* sp. (and *Corynoneura* sp.) were faster colonisers and peaked in abundance by day 12, but declined thereafter (Figure 4.6 d(i)), similar to the Cylopoda. *Tanytarsus* sp. and Orthoclad “beta” (Figure 4.6 e(i), f(i)) continued to increase in abundance throughout the colonisation period but slowed towards day 38.

The NMDS plots and MRPP pairwise comparisons show that the variations in colonisation patterns of individual taxa, shown in Figures 4.5 and 4.6, resulted in distinct shifts in the assemblage composition through the colonisation period on individual leaf packs, leaf packs grouped within replicates and whether abundance or presence absence data was used in the analysis (Figure 4.7, Appendices – Table A4.2).

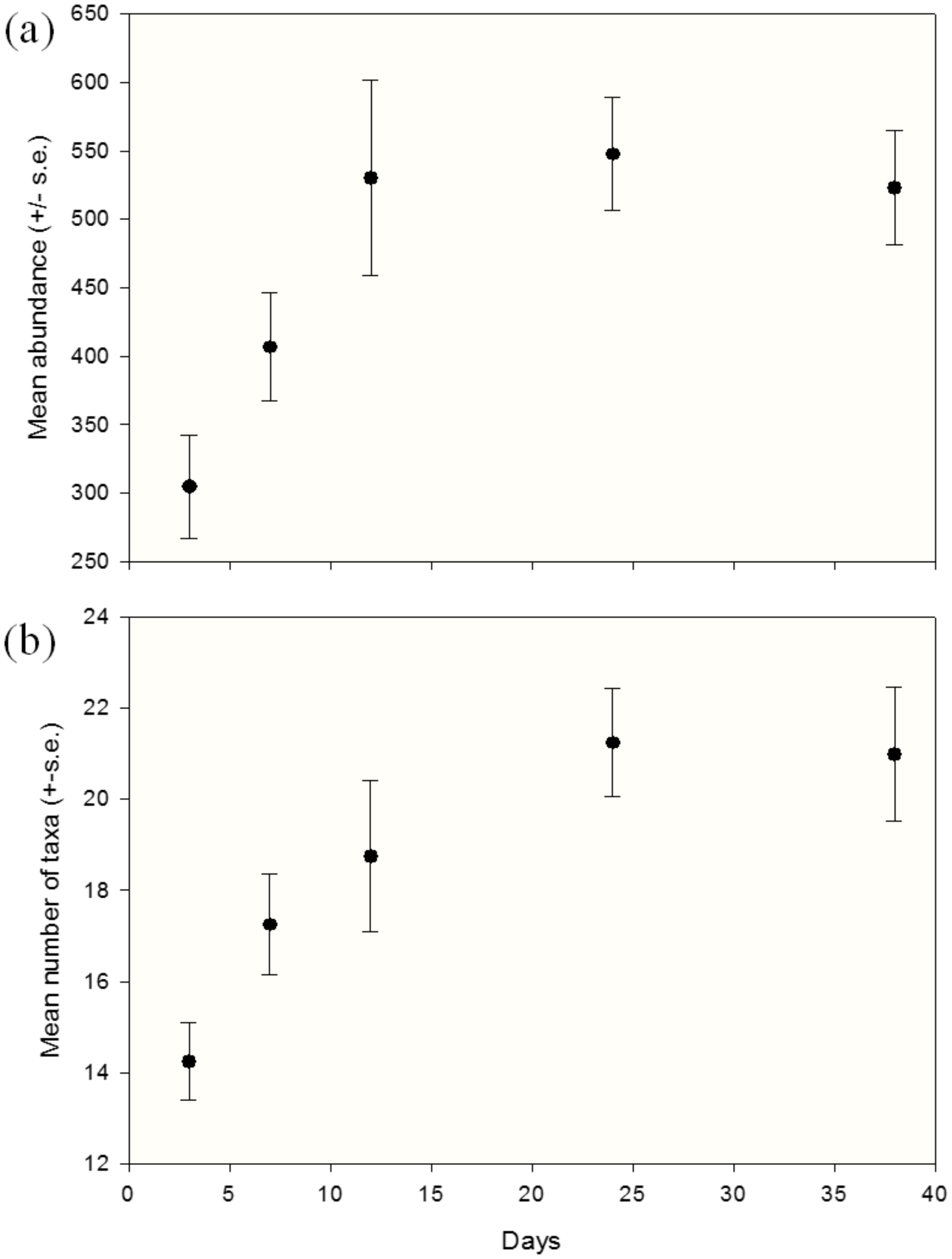


Figure 4.3. Colonisation patterns of invertebrates in artificial stream channels over 3 to 38 days in Experiment 4.1: (a) mean total number of individuals; (b) mean number of taxa.

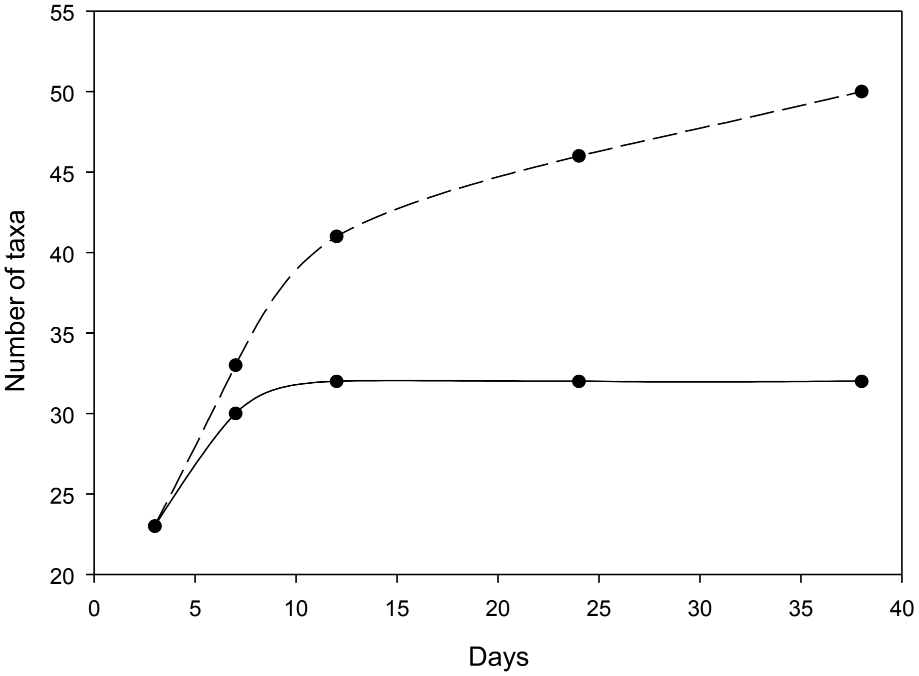


Figure 4.4. Comparison of the instantaneous total number of taxa (solid line) and the cumulative number of taxa (dashed line) colonising leaf packs over 3 to 38 days in Experiment 4.1.

4.3.2 Fitting the equilibrium model

The equilibrium model was fitted to the data for the number of taxa, total abundance, and abundances of several individual taxa (in some cases pooled across species) (Table 4.1). Overall, the colonisation of the litter packs by invertebrates was adequately described by the model, with the coefficient of determination (r^2) values for the total number of taxa and total abundance being 0.599 and 0.587, respectively, and as high as 0.730 for Orthoclad “beta”. The model infers substantial turnover of individuals and taxa through time. It estimated that, each day, ~134 individuals colonised the leaf packs and ~25% of individuals present on each leaf pack at any time emigrated. It estimated that, each day, ~7 taxa colonised the leaf packs and ~35% of the taxa present on a leaf pack emigrated. The high rate of turnover of individuals was strongly influenced by the Chironomidae with ~121 individuals estimated to immigrate to the leaf packs and ~26% emigrate from the leaf packs per day. The model fitted the Chironomidae data well (r^2 = 0.514). The model also described the colonisation patterns of the chironomids, *Echinocladius martini*, *Nilotanypus* sp., *Tanytarsus* and Orthoclad “beta” reasonably well, albeit with estimates of m being lower than for the pooled Chironomidae. However, the model did not fit the pattern of colonisation by the other chironomid species, *Dicrotendipes* sp., *Thienemaniella* sp. or the Cyclopoda. Their patterns of colonisation clearly show that these taxa did not have a constant rate of individuals arriving on the leaf packs, with a rapid initial immigration but then a decline in abundance, indicating that either the rate of immigration declined or rate of emigration increased substantially (or both) after day 12 (Figures 4.6 c(i), d(i), and 4.5 c(i)).

4.3.3 Experiment 4.2 – Drift and dispersal from leaf packs

Isolating litter packs from the input of invertebrate immigration for five days reduced the number of individuals and taxa present (Figure 4.8, Table 4.2), although the difference in the number of taxa was not significant. The mean total abundance of invertebrates on “closed” litter packs plus the mean total abundance collected in the downstream drift nets was very close to the abundance on the “open” leaf packs (725.7 vs. 732.7) (Table 4.2). The abundance collected entering the channels from upstream was over four times the numbers emigrating from the leaf packs in section (b) of the artificial stream channels (1031.3 vs. 228.7). Although channel surfaces were not sampled, visual observation indicated that there was no significant colonisation of these surfaces throughout the experiments.

Forty-six taxa were collected on “open” leaf packs, 45 on “closed” leaf packs, and 49 in the upstream drift nets. Abundances of several taxa were clearly affected by isolating the leaf pack habitat from immigration by drift (Figures 4.5, Table 4.2). For example, the mean number of Cyclopoda was about half in the “closed” channels compared to the “open” channels, and the Chironomidae were reduced by about a third in the “closed” channels of that in the “open” channels, indicating immigration is important in maintaining their populations (Figures 4.5 a(ii) & b(ii)). The mean numbers of Leptophlebiidae were also reduced in the “closed” channels but not significantly (Figure 4.5 c(ii)). However, the Hydroptilidae, Leptoceridae and Hydracarina, all of which had a convex upward colonisation curve, had very similar mean abundances in the “open” and “closed” channels (Figures 4.5 d(ii), e(ii) & f(ii)).

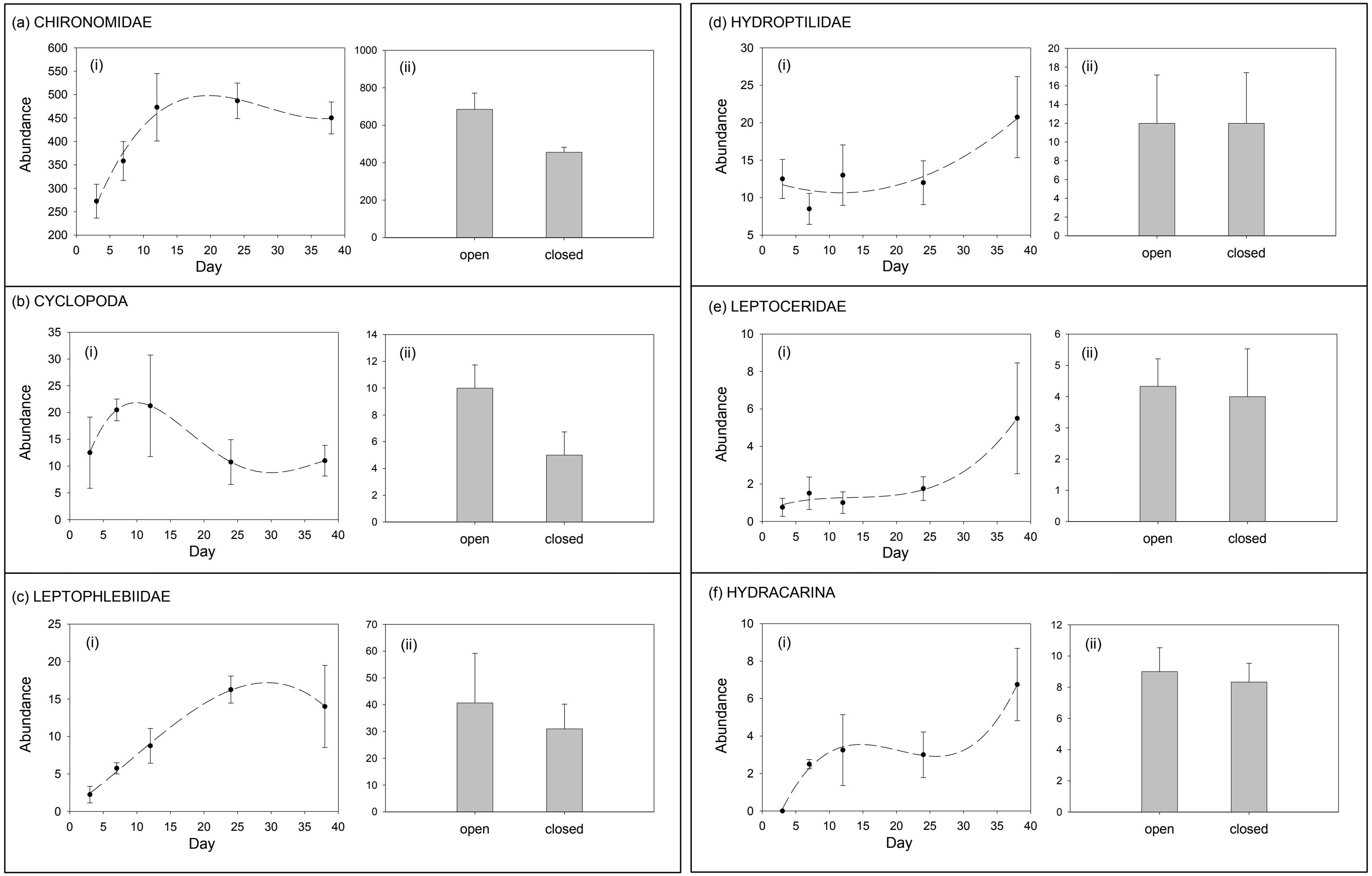


Figure 4.5. Mean abundances (± s.e.) of higher order taxa on leaf packs. (i) Experiment 4.1: Pattern of colonisation over a 38 day period. (ii) Experiment 4.2: Mean abundance remaining on leaf packs open to immigration and closed to immigration for 5 days. Dashed lines represent 3rd order polynomial least-squares regressions.

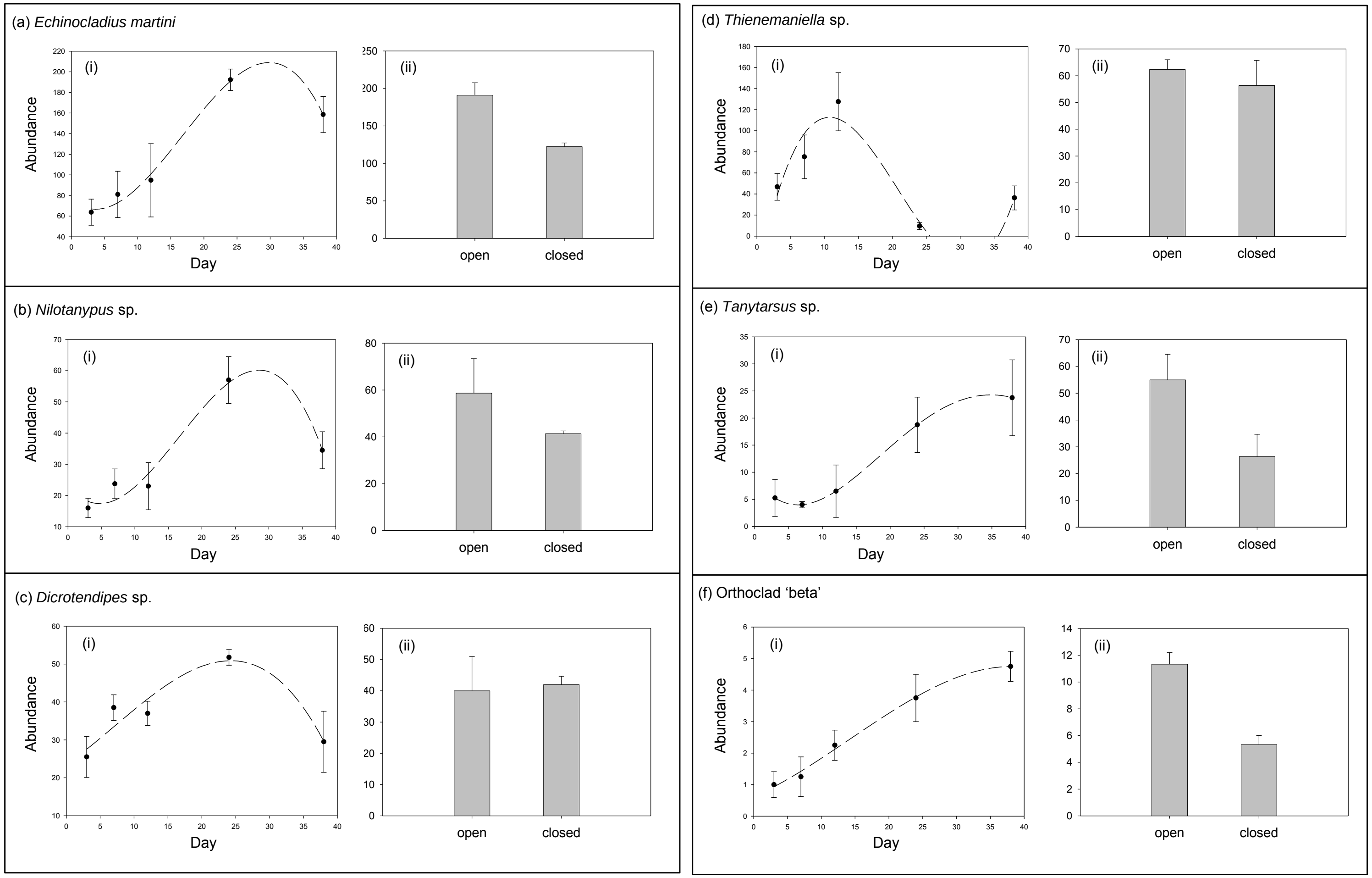


Figure 4.6. Mean abundance (± s.e.) of Chironomidae species on leaf packs. (i) Experiments 4.1: Pattern of colonisation over a 38 day period. (ii) Experiment 4.2: Mean abundance remaining on leaf packs open to immigration and closed to immigration for 5 days. Dashed lines represent 3rd order polynomial least-squares regressions.

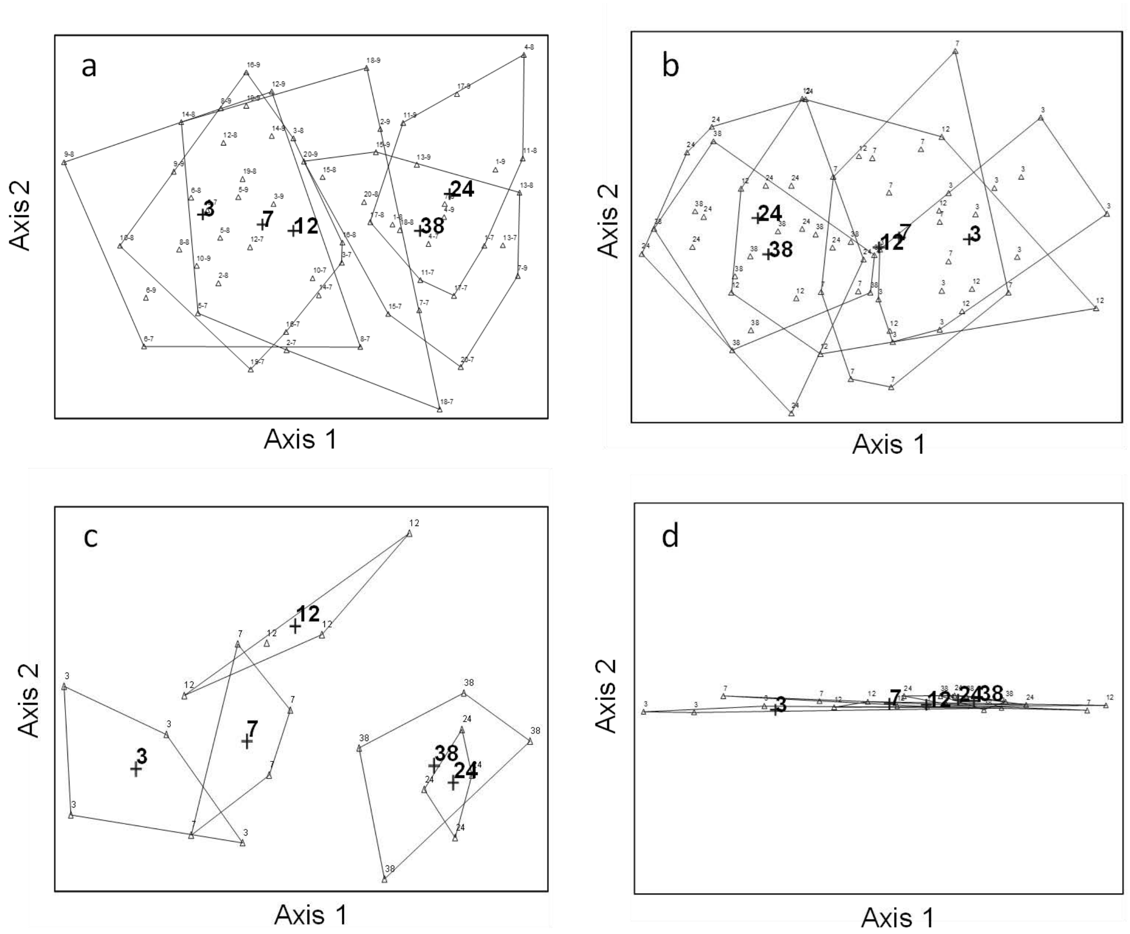


Figure 4.7. Plots of NMDS analyses of invertebrate colonisation of leaf packs in Experiment 4.1: (a) log (x+1) abundance for individual leaf packs; (b) presence/absence for individual leaf packs; (c) log (x+1) abundance in pooled replicate leaf packs; (d) presence/absence in pooled replicate leaf packs. Centroids are labelled by days of colonisation period.

Table 4.1. Immigration and emigration parameters estimated by fitting equilibrium model $N_t = I/m(1 - e^{-mt})$ to colonisation data from experiment 4.1. I = number of arrivals per day, m = proportion emigrating each day. The model is in equilibrium when I = proportion leaving at a density of I/m.

	I	m	I/m	r^2
Total taxa	7.25	0.358	20.23	0.599
Total abundance	133.71	0.249	536.75	0.587
Leptophlebiidae	1.15	0.068	16.80	0.407
Empididae	0.23	0.029	7.98	0.348
Chironomidae	121.19	0.257	470.81	0.514
Echinocladius martini	16.46	0.092	179.64	0.609
Nilotanypus sp.	4.84	0.109	44.31	0.421
Dicrotendipes sp.	14.17	0.354	40.03	0.183
Tanytarsus sp.	0.78	0.011	73.12	0.493
Orthoclad “beta”	0.23	0.037	6.27	0.7300
Thienemaniella sp.	36.65	0.597	61.39	0.006
Cyclopoda	10.14	0.646	15.70	0.007

The difference in abundance in Chironomidae between “closed” and “open” channels was mainly driven by *Echinocladius martini* (Figure 4.6 a(ii)), but also *Nilotanypus* sp. and *Tanytarsus* sp. (Figures 4.6 b(ii) & e(ii), respectively), as well as *Corynoneura* sp. The mean abundance of Orthoclad “beta” was much lower than these other chironomids, but also was clearly affected in the “closed” channels (Figure 4.6 f(ii)). However, like some higher order taxa described above, some chironomids had similar mean abundances in both “open” and “closed” channels; for example *Dicrodentipes* sp. (Figures 4.6 d (ii)). Surprisingly though, *Thienemaniella* sp., which colonised the leaf packs very rapidly but then declined, maintained its population on leaf packs in the “closed” channels, but at about half the peak abundance observed in the colonisation Experiment 4.1.

Several taxa, such as the Cyclopoda and Hydracarina, were more numerous in the drift than the benthic samples. Ceratopogonidae were also abundant in the upstream drift but rare elsewhere. In contrast, some taxa occurred in the benthic samples but not the drift. Chironominae were abundant in the benthic samples but very rare or absent in drift samples. Their abundance was also very similar in “open” and “closed” channels. The benthic abundances of *Koorrnonga* sp. were also similar in both “open” and “closed” channels but only one individual occurred in the upstream drift and none in the downstream drift.

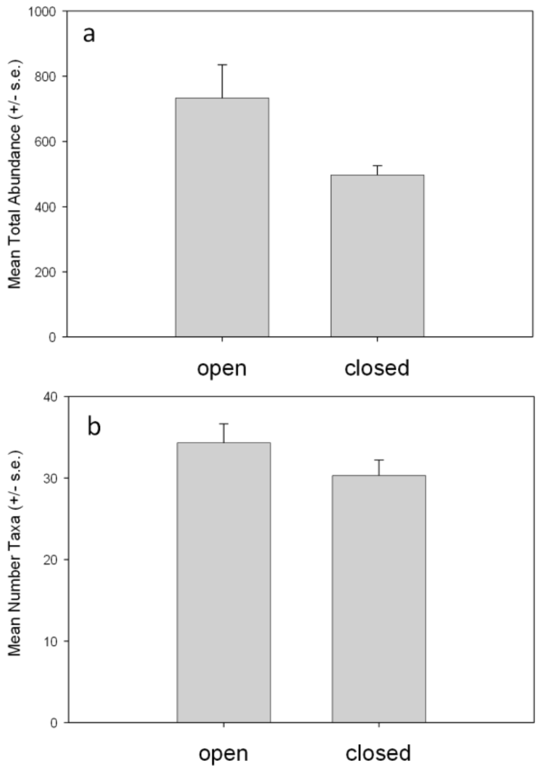


Figure 4.8. (a) Mean abundance; and (b) mean number of taxa remaining on leaf packs open to immigration and closed to immigration in Experiment 4.2.

4.3.4 Rate of emigration

The equation $m_{drift} = 1 - e^{-k}$ estimated the proportion of invertebrate individuals that emigrated per day from the densities of invertebrates remaining on the leaf packs in the channel sections (b) closed to drift and the densities collected in drift nets downstream. The emigration rates estimated this way were generally much lower than those estimated using the colonisation model (Table 4.3). For example, the equilibrium model predicted that ~25% of all individuals emigrated every day, whereas the numbers collected in the drift nets suggest that ~7% of total individuals emigrated from the leaf packs each day. Similarly the model estimated that ~36% of species emigrated, whereas the drift samples suggested that ~ 10% emigrated. The equilibrium model predicted much higher emigration rates for the Chironomidae than were collected in the drift nets, but the estimates for individual chironomid species were more similar between the two methods: for example ~11% vs. ~ 7% for *Nilotanypus* sp. The two methods also estimated very similar emigration rates for the Leptophlebiidae, both estimating ~6% emigrate each day. Both methods predicted that Cyclopoda emigrate at very high rates relative to other taxa, but the estimates varied considerably – ~65% vs. ~21%.

Table 4.2. Comparison of mean abundances (and s.e.) of invertebrate taxa collected over 5 days: (i) from leaf packs open to immigration and closed to immigration; and (ii) immigrating to and emigrating from leaf packs in section (b) of the artificial stream channels.

	(i) On leaf packs		**(ii) Collected in drift**	
Taxon	**Open (s.e)**	**Closed (s.e)**	**Upstr.drift in (s.e)**	**Emigrating (s.e)**
HYDRA	0.33 (0.33)	--	0.33 (0.33)	--
NEMATODA	1.33 (0.88)	11.67 (11.67)	0.33 (0.33)	2.00 (0.58)
OLIGOCHAETA	6.33 (2.33)	5.00 (2.08)	4.00 (0.58)	1.00 (0.58)
CRUSTACEA,				
Cladocera	1.00 (0.58)	0.67 (0.67)	2.33 (1.86)	1.00 (0.58)
Cyclopoda	10.00 (1.73)	5.00 (1.73)	34.33 (13.45)	11.00 (4.58)
Harpacticoida	2.00 (2.00)	0.67 (0.67)	18.67 (1.20)	2.33 (1.45)
Copepoda indet.			0.33 (0.33)	3.33 (2.03)
HYDRACARINA	9.00 (1.53)	8.33 (1.20)	112.33 (40.60)	40.67 (9.56)
PLECOPTERA, Gripopterygidae	0.67 (0.33)	0.33 (0.33)	4.33 (1.20)	7.67 (4.70)
EPHEMEROPTERA				
Baetidae	--	0.33 (0.33)	12.00 (4.36)	0.67 (0.33)
Caenidae	--	0.67 (0.67)	--	--
Leptophlebiidae				
Atalophlebia sp.	0.67 (0.67)	0.33 (0.33)	--	--
Genus K	--	0.33 (0.33)	--	--
Koorrnonga sp.	5.33 (4.84)	5.67 (1.76)	0.33 (0.33)	--
Neboissophlebia sp.	--	--	0.33 (0.33)	--
Nousia sp.	5.33 (2.67)	0.67 (0.67)	2.33 (0.67)	0.33 (0.33)
Indet. small instars	29.33 (10.33)	24.00 (6.11)	39.33 (5.78)	9.67 (6.17)
TRICHOPTERA				
Calamoceratidae				
Anisocentropus sp.	2.00 (0..58)	1.33 (0.67)	1.00 (1.00)	0.33 (0.33)
Ecnomidae			0.33 (0.33)	--
Helicopsychidae	0.33 (0.33)	4.00 (2.52)		
Hydrobiosidae	0.67 (0.33)	0.67 (0.67)	3.00 (0.00)	0.33 (0.33)
Hydroptilidae				
Hellyethira sp.	2.33 (0.33)	2.00 (1.00)	1.00 (0.58)	1.33 (0.88)
Orthotrichia sp.	1.33 (0.88)	--	2.00 (0.58)	
Oxyethira sp.	5.67 (2.73)	5.33 (3.53)	3.67 (1.20)	19.67 (7.80)
Indet. small instars	2.67 (1.20)	4.67 (0.88)	13.67 (6.17)	21.00 (8.66)
Hydropsychidae	0.33 (0.33)	--	0.33 (0.33)	
Leptoceridae	4.33 (0.88)	4.00 (1.53)	6.67 (2.40)	8.33 (1.76)
Philopotamidae	--	0.67 (0.33)	21.33 (7.13)	2.00 (1.15)
Polycentropodidae	1.00 (0.58)	1.00 (0.58)	2.00 (2.00)	
Indet. small instars	0.67 (0.33)	0.33 (0.33)	11.33 (7.31)	0.33 (0.33)
DIPTERA				
Ceratopogonidae	0.67 (0.33)	--	11.67 (6.17)	2.00 (1.53)
Chironomidae				
Chironominae	20.00 (2.65)	20.67 (0.88)	0.33 (0.33)	--
Corynoneura sp.	127.67 (19.98)	60.67 (13.22)	41.33 (10.99)	11.67 (1.20)
Cricotopus sp.	4.33 (2.40)	1.00 (1.00)	1.33 (0.67)	--
Dicrotendipes sp.	40.00 (10.97)	42.00 (2.65)	79.00 (56.89)	4.33 (1.45)
Echinocladius martini	191.00 (16.52)	122.33 (4.91)	66.67 (1.86)	8.33 (1.33)
Nilotanypus sp.	58.67 (14.72)	41.33 (1.20)	50.33 (13.91)	19.67 (11.22)
Orthoclad "beta"	11.33 (0.88)	5.33 (0.67)	31.67 (4.10)	1.33 (0.33)
Rheotanytarsus sp.	6.00 (2.08)	0.33 (0.33)	1.33 (0.67)	1.00 (0.58)
Stemp/Stemp	8.00 (6.11)	4.00 (2.08)	7.67 (4.63)	1.00 (0.58)
Tanytarsus sp.	55.00 (9.54)	26.33 (8.35)	79.67 (14.67)	16.00 (8.08)
Thienemanniella sp.	62.33 (3.67)	56.33 (9.40)	238.67 (53.22)	16.33 (6.01)
Indet. small instars	28.00 (7.02)	19.00 (5.29)	31.67 (21.73)	11.67 (6.23)
Culicidae	--	0.33 (0.33)		
Dixidae	--	--	18.00 (4.62)	3.00 (1.15)
Empididae	10.33 (1.20)	5.33 (1.67)	7.00 (1.53)	2.00 (0.58)
Psychodidae		0.33 (0.33)		
Simuliidae	0.33 (0.33)	0.33 (0.33)	33.67 (15.90)	5.67 (5.17)
Austrosimulium sp.			22.33 (18.94)	
Tabanidae	0.33 (0.33)	--		
Indet. small instars	0.33 (0.33)	--	0.67 (0.33)	0.67 (0.67)
COLEOPTERA				
Dytiscidae				
Elmidae	3.67 (1.33)	2.00 (0.58)	0.33 (0.33)	
Austrolimnius sp.	1.00 (1.00)	0.33 (0.33)	2.33 (1.33)	0.67 (0.33)
Kingolus sp.	0.33 (0.33)	--	0.67 (0.33)	
Hydraenidae			0.67 (0.67)	
Scirtidae	--	0.33 (0.33)		
HEMIPTERA indet.				1.33 (0.67)
UNKNOWN	0.67 (0.67)	1.00 (1.00)	6.33 (4.10)	9.67 (2.91)
Total abundance	**732.67 (102.25)**	**497.00 (28.31)**	**1031.33(120.89)**	**228.67 (83.31)**
Number of taxa	**33.67 (2.73)**	**30.33 (1.86)**	**38.67 (0.67)**	**28.33 (2.03)**

Table 4.3. Comparison of estimates of the proportion of invertebrate individuals present that migrate per day using the colonisation model $N_t = I/m(1 - e^{-mt})$ using data from Experiment 4.1 and the equation $m_{drift} = 1 - e^{-k}$ using data from Experiment 4.2.

	Colonisation model	**Closed to immigration**
	m_{model}	**mean $m_{drift\ data}$ (±s.e.)**
Total taxa	0.358	0.094 (± 0.002)
Total abundance	0.250	0.069 (± 0.017)
Leptophlebiidae	0.068	0.064 (± 0.044)
Empididae	0.029	0.075 (± 0.030)
Chironomidae	0.257	0.034 (± 0.010)
Echinocladius martini	0.092	0.013 (± 0.001)
Nilotanypus sp.	0.109	0.067 (± 0.033)
Dicrotendipes sp.	0.354	0.019 (± 0.005)
Tanytarsus sp.	0.011	0.082 (± 0.013)
Thienemaniella sp.	0.597	0.047 (± 0.009)
Cyclopoda	0.646	0.209 (± 0.043)

4.4 Discussion

4.4.1 General patterns

The overall pattern of colonisation of the leaf packs was a rapid and predictable process and followed a classic curvilinear pattern for both the total number of individuals and total number of taxa, where the rate of colonisation was initially very rapid but gradually declined towards an asymptote (e.g., Simberloff & Wilson, 1999). Although a total of 50 taxa were available, the number of taxa inhabiting leaf packs at any point in time was lower and was stable through time, suggesting leaf pack species richness was saturated and, overall, the invertebrate assemblage inhabiting the leaf packs appeared to reach an equilibrium. However, the colonisation rates and patterns of colonisation varied among taxa, with three general patterns of colonisation: the classical concave curvilinear pattern, where the rate of increase in abundance gradually slowed; a peak in abundance followed by decline, producing a definite humped pattern; and increasing colonisation, producing a convex upwards curve with no asymptote. The NMDS and MRPP analyses confirmed a temporal sequence in the invertebrate assemblage colonising the leaf packs, but because interspecific interactions could not be observed, it is not clear if this was due to interactions between taxa or due to changes that occurred to the leaf pack substrate.

The pattern of total abundance was largely driven by the abundances of the chironomids, representing nearly 90% of the number of individuals on the leaf packs at any time. However, the patterns of colonisation of chironomid species varied considerably and this affected the shape of the abundance curve due to the very abundant early colonisers – *Thienemaniella* sp. and *Corynoneura* sp. Therefore, the plateau in total abundance at day 12 was due not to the invertebrate assemblage approaching equilibrium at that time, but to a successional shift in assemblage composition. These patterns were only discernible for relatively abundant taxa, and although the abundances of these taxa peaked and declined they did not become extinct on the leaf packs and were, therefore, represented in species counts through the entire sequence.

4.4.2 Comparisons with other studies

Although this experiment was undertaken in artificial streams rather than the stream bed, the patterns of colonisation and the time elapsed for richness to stabilise on the leaf packs was comparable to other small-scale studies. Mackay (1992) concluded that the usual period for colonisation of bare stream patches is between 10 and 25 days (citing: Wise & Molles, 1979; Lake & Doeg, 1985; Minshall & Petersen, 1985; Peckarsky, 1986), but can be as short as a few days in some experiments (Townsend & Hildrew, 1976; Lake & Doeg, 1985; Pearson & Jones, 1987). There is a large and diverse literature describing the colonisation of leaf litter patches in low order streams, many investigating the process of leaf litter decomposition and how the arrival of different organisms affects that process (e.g., Parkyn & Winterbourn, 1997; Tonkin *et al*., 2015) and several testing the effect of litter species on invertebrate colonisation and decomposition (Janke & Trivinho-Strxino, 2007; Abelho, 2008; Ligeiro *et al*., 2010; Abelho, 2014). Others have used natural and artificial leaves to investigate the role of the leaf litter as food or shelter (Quinn *et al*., 2000; Richardson, 1992; Hofer & Richardson, 2007; Li & Dudgeon 2011), or have compared colonisation of benthic organisms on native and exotic leaves as part of investigations into the effect of introduced species and riparian vegetation degradation (Parkyn & Winterbourn, 1997; Quinn *et al*., 2000; Boyero *et al*., 2012). Differences in methodologies confound direct comparisons, but the time taken to colonise reported in these studies (sometimes taken as time to reach maximum species richness) ranged between 28 and 60 days, so the colonisation time in Experiment 4.1 sits approximately in the middle of this range.

4.4.3 Dispersal experiment

The abundances of a number of taxa were clearly affected by isolating the leaf pack habitat from immigration. Because the majority of invertebrates collected on the leaf packs were insect larvae, with terrestrial adult phases, and there were no indications of mass egg hatching in the samples (e.g., masses of small instars of single taxa), it was assumed that most of the animals on the leaf packs came through dispersal rather than reproduction. The structure of the artificial streams prevented dispersal from within substrata, laterally from adjacent habitat or from downstream. Therefore, immigration was from upstream, and the comparison of “open” and “closed” litter packs, in Experiment 4.2, indicated that populations were maintained through the input of invertebrates from upstream compensating for the loss of individuals through emergence, emigration or mortality.

The abundance of invertebrates drifting into the channels was over four times greater than the numbers emigrating from the leaf packs in section (b) of the channels, indicating an ample supply of potential immigrants to replace individuals lost. However, the total numbers entering the channels over the five-day period were only about 40% greater than the standing stock of invertebrates, in contrast to the observation of Waters (1972) that numbers drifting over a unit area of stream bed were several times greater than the standing stock. Several species were more numerous in the drift than the benthos. For example, the Philopotamidae, Ceratopogonidae, Simuliidae and Baetidae were much more numerous in the drift and did not choose to settle on the leaf pack habitat but passed through the channels. Other taxa, such as the Chironominae and *Koorrnoonga* sp., occurred in the benthic samples but not in the drift, with similar abundances in “open” and “closed” channels. Like the Chironominae, *Koornoonga* sp. occurred only in small numbers in the colonisation experiment in section (c) of the channels, suggesting that these species do not enter the drift freely. Similarly, Helicopsychidae were only found in the benthic samples but not the drift samples, probably because their gravel cases prevented them from entering the drift (Pringle & Ramírez, 1998). Early instars of other Trichoptera and Ephemeroptera were numerous in both the colonisation and dispersal experiments, including the drift. However, their mean abundance was lower in leaf packs isolated from drift and the abundance in the drift downstream of closed section (b) was equivalent to the difference in abundance between the open and closed channels. This suggests that these early instars readily enter the drift, possibly because they have greater propensity to disperse than later instars, but early instars are also likely to be relatively more abundant.

4.4.4 Equilibrium model results

A recurring theme in the study of colonisation dynamics in streams has been the application of equilibrium models based on those from island biogeography (MacArthur and Wilson, 1967), enabling exploration of the relative importance of stochastic and deterministic processes in shaping community structure, and estimation of immigration and extinction (emigration) rates (Sheldon, 1977, 1984). The equilibrium model used in this study is a simple version of the island biogeography models, as used by Sheldon (1977). It is essentially a neutral model, but differs from formal neutral models (e.g., Hubbell, 2001) in that the latter operate at the level of individuals rather than species, and can predict species abundances within an assemblage, rather than just presence/absence (Rosindell & Harmon, 2013), although the MacArthur and Wilson (1967) models have been applied to density of individuals, as in my experiment, (e.g., Azovsky, 1988). However, neutral models have not been applied to predict immigration and extinction rates (Rosindell & Harmon, 2013) and have only rarely been applied to stream benthic invertebrates (e.g., Thompson & Townsend, 2006).

Gore and Milner (1990) suggested that island biogeographical models, such as the equilibrium model used in our analysis, are suitable for modelling small-scale patches in streams, particularly if they have already developed an organic base that can support trophic pathways. They describe this as secondary succession as opposed to primary succession, which involves the development of biofilm on sterilised cobbles or the conditioning of leaf litter by bacteria and fungi prior to invertebrate colonisation. Sheldon (1984) applied a more complex version of his earlier model (Sheldon 1977) to allow for resource tracking as resources are likely to develop and influence the establishment of arriving colonisers, accounting for the primary succession referred to by Gore and Milner (1990). As the leaf material used in my colonisation experiment was pre-conditioned, the colonisation curve was considered to represent secondary succession, so it was unnecessary to add resource tracking into the model.

The overall colonisation pattern of the invertebrates followed the predictions of the asymptotic model, being initially high but then declining, and the equilibrium model fitted the data for total numbers of individuals and total number of taxa well. But it was clear that the assumption of a constant rate of immigration was not true for all taxa. Alternative functions could have been fitted to these taxa, for example the power function (also applied by Sheldon 1977) could accommodate cases in which the rate of colonisation increases with time (Ulfstrand *et al*., 1974), as I observed for Hydroptilidae and Leptoceridae. The model estimated that, each day, approximately seven new taxa colonised the litter packs and approximately 35% of taxa were lost (by emigration or mortality). The overall immigration rate (total abundance) on to the three litter packs was approximately 134 individuals per day and approximately 25% of individuals present on the three leaf packs were lost each day. The high rate of turnover of taxa was largely due to the high number of taxa that occurred in low abundance or as single individuals, and probably represents a negligible effect on community functioning. Most of the immigration and dispersal can be attributed to the Chironomidae, making up almost 90% of the total abundance at every time period with approximately 121 individuals arriving each day and approximately 25% of individuals present leaving each day. These high figures include both rapid early colonists and late colonists that persisted and built up large populations.

The model predicted that a few taxa (*Thienemaniella* sp., *Corynoneura* sp. and Cyclopoda) have very high mobility, with perhaps more than 50% of individuals moving each day, and consequently are fast colonisers, but do not continue to immigrate at this high rate during the later stages of the colonisation process. Consequently, the equilibrium model did not fit the data for these taxa because it assumes a constant rate of immigration. It did, however, fit many of the other taxa that had a pattern of slower, but more sustained colonisation. The model indicated that the majority of taxa had much lower mobility than the Chironomidae, with fewer than 10% of individuals leaving a site each day.

However, the emigration rates estimated from the colonisation model had variable success in matching the drift at the downstream section of section (b) of the channels. The estimates for Leptophlebiidae and *Nilotanypus* sp. were comparable, but others differed markedly, with the equilibrium model estimating much higher emigration rates. Reasons for this could include the dispersal measurements being collected after the 38 day period. The populations of several taxa had declined in the colonisation experiment by day 38 and so it is expected there would have been reduced densities on the leaf packs during the dispersal experiment, which may have altered their dispersal rates. Similarly, removing immigration into the leaf pack habitats may also have affected emigration rates, as immigration would have otherwise maintained densities, and in doing so maintained density-dependent emigration pressures. However, the equilibrium model would also have been affected by the very rapid colonisation by a few taxa that did then not persist, such as the Cyclopoda and chironomids *Thienemaniella* sp. and *Corynoneura* sp. Their pattern of colonisation steepened the face of the overall colonisation curve. Essentially, because of the contribution of these early colonisers the model predicted that the community would be in equilibrium within the time-scale where the total abundance curve plateaued (day 12), whereas equilibrium was more likely reached later (day 24), as indicated by the NMDS results, in which the assemblage composition on days 24 and 38 overlap. Thus, because the equilibrium model assumed constant rates of immigration and emigration, it assumed that this high rate of immigration was maintained throughout, causing the model to estimate much higher rates of emigration (see Sheldon 1984).

Nevertheless, both methods provided a useful estimate of the overall rates of turnover on the leaf packs, and with the comparison of “open” and “closed” leaf packs, indicate that the assemblage occupying the litter packs was maintained by immigration and emigration and that the rates of these processes influence the abundance and richness of the assemblage on the leaf packs.

4.5 References

Abelho M. (2001) From litterfall to breakdown instreams: A review. *The Scientific World* **1**: 656-680.

Abelho M. (2008) Effects of leaf litter species on macroinvertebrate colonization during decomposition in a Portuguese stream. *International Review of Hydrobiology* **93**: 358-371.

Abelho M. (2014) The effect of mixtures on colonisation of leaf litter decomposing in a stream and at its riparian zone. *Web Ecology* **14**: 13-22.

Allan J. D. (1978) Trout predation and size composition of stream drift. *Limnology and Oceanography* **23**: 1231-1237.

Allan J.D. & Feifarek B.P (1989) Distances travelled by drifting mayfly nymphs: factors influencing return to substrate. *Journal of the North American Benthological Society* **8**: 322-330.

Anderson N. H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* **24**: 351-377.

Azovsky A.I. (1988) Colonization of sand “islands” by psammophilous ciliates: the effect of microhabitat size and stage of succession. *Oikos* **51**: 48-56.

Benfield E. F. & Webster J. R. (1985) Shredder abundance and leaf breakdown in an Appalachian Mountain stream. *Freshwater Biology* **15**: 113-120.

Benson L.J. & Pearson R.G. (1987a) Drift and upstream movements of macro- invertebrates in a tropical Australian stream. *Hydrobiologia* **153**: 225- 239.

Benson L.J. & Pearson R.G. (1987b) The role of drift and effect of season in colonization of implanted substrata in a tropical Australian stream. *Freshwater Biology* **18**: 109-116.

Benson L.J. & Pearson R.G. (1993) Litter inputs to a tropical Australian upland rainforest stream. *Australian Journal of Ecology* **18**: 377-383.

Benstead J.P (1996) Macroinvertebrates and the processing of leaf litter in a tropical stream. *Biotropica* **28**: 367-375.

Boulton A. J., Findlay S., Marmonier P., Stanley E. H., & Valett, H. M. (1998). The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* **29**: 59–81.

Boyero L., Barmuta L.A., Ratnarajah L., Schmidt K. & Pearson R.G. (2012) Effects of exotic riparian vegetation on leaf breakdown by shredders: a tropical–temperate comparison. *Freshwater Science* **31**: 296–303.

Brittain J.E. & Eikland T.J. (1988) Invertebrate drift – a review. *Hydrobiologia* **166**: 77-93.

Brookshire E.N.J. & Dwire K.A. (2003) Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society* **51**: 545-553.

Charnov E.L., Orians G.H. & Hyatt K. (1976) Ecological implications of resource depression. *The American Naturalist* **110**: 247-259.

Cheshire K., Boyero L. & Pearson R. G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Christidis F. (2003) Sytematics, phylogeny and ecology of Australian Leptophlebiidae (Ephemeroptera). PhD Thesis, James Cook University, Townsville, Australia.

Christidis F. & Dean J.C. (2008) Phylogeny and distribution of the mayfly genus *Austrophlebioides* Campbell & Suter (Ephemeroptera: Leptophlebiidae). *Invertebrate Systematics* **22**: 29-36.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Dean J.C. 1999. *Preliminary Keys for the Identification of Australian Mayfly Nymphs of the Family Leptophlebiidae.* Identification Guide No. 20, Cooperative Research Centre for Freshwater Ecology, Murray-Darling Freshwater Research Centre, Albury, Australia

Dean J., St Clair R. & Cartwright D. (2004) Identification keys to Australian families and genera of caddis-fly larvae (Trichoptera). Identification Guide No. 50, Cooperative Research Centre for Freshwater Ecology, Murray-Darling Freshwater Research Centre, Albury, Australia.

Doeg T.J., Lake P.S. & Marchant R. (1989a) Colonisation of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Australian *Journal of Ecology* **14**: 207-220.

Doeg T. J., Marchant R., Douglas M. & Lake P. S. (1989b) Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. *Freshwater Biology* **22**: 57–64.

Downes B.J. (1990) Patch dynamics and mobility of fauna in streams and other habitats. *Oikos* **59**: 411-413.

Downes B.J., Bellgrove A. & Street J.L. (2005) Drifting or walking? Colonisation routes used by different instars and species of lotic, macroinvertebrate filter feeders. *Marine and Freshwater Research* **56**: 815-824.

Downes B.J. & Lancaster J. (2010) Does dispersal control population densities in advection-dominated systems? A fresh look at critical assumptions and a direct test. *Journal of Animal Ecology* **79**: 235-248.

Dudgeon D. & Wu K.K.Y. (1999) Leaf litter in a tropical stream: food or substrate for macroinvertebrates? *Archiv für Hydrobiologie* **146**: 65-82.

Elliot J.M. (1971a) Upstream movements of benthic invertebrates in a Lake District stream. *Journal of Animal Ecology* **40**: 235-252.

Elliot J.M. (1971b) The distances travelled by drifting invertebrates in a Lake District stream. *Oecologia* **6**: 350-379.

Elliot J.M. (2002) The drift distances, and time spent in the drift by freshwater shrimps, Gammarus pulex, in a small stony stream, and their implications for the interpretation of downstream dispersal. *Freshwater Biology* **47**: 1407-1417.

Elliot J.M. (2003) A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology* **48**: 1652-1668.

Elmes G.W. (1991) Ant colonies and environmental disturbance. *Symposium of the Zoological Society of London* **63**: 15-32.

Fisher S. G. & Likens G. E. (1972) Stream ecosystem: organic energy budget. *BioScience* **22**: 33-35.

Gayraud S., Philippe M., & Maridet L. (2000) The response of benthic macroinvertebrates to artificial disturbance: drift or vertical movement in the gravel bed of two sub-alpine streams? *Archiv für Hydrobiologie* **147**: 431-446.

Gjerløv C. & Richardson J.S. (2004) Patchy resources in a heterogeneous environment: effects of leaf litter and forest cover on colonisation patterns of invertebrates in a British Columbian stream. *Archiv für Hydrobiologie* **161**: 307-327.

Glass L.W. & Bovbjerg R.V. (1969) Density and dispersion in laboratory populations of caddisfly larvae (Cheumatopsyche, Hydropsychidae). *Ecology* **50**: 1082-1084.

Gore J.A. & Milner A.M. (1990) Island biogeographical theory: can it be used to predict lotic recovery rates? *Environmental Management* **14**(5): 737-753.

Graca M.A.S., Cressa C., Gessner T.M.O., Feio M.J., Callies K.A. & Barrios C. (2001) Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology* **46**: 947-957.

Hart D.D. & Resh V.H. (1980) Movement patterns and foraging ecology of a stream caddisfly larva. *Canadian Journal of Zoology* **58**: 1174-1185.

Hofer N. & Richardson J.S. (2007) Comparisons of colonisation by invertebrates of three species of wood, alder leaves, and plastic “leaves” in a temperate stream. *International Review of Hydrobiology* **92**: 647-655.

Hubbel S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Hulton L., Svensson B. & Ulfstrand S. (1969) Upstream movements of insects in s South Swedish small stream. *Oikos* **20**: 553-557.

Iversen T.M. (1974) Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of digested leaves. *Oikos* **25**: 278-282.

Janke H. & Trivinho-Strxino S. (2007) Colonization of leaf litter by aquatic macroinvertebrates: a study in a low order tropical stream. *Acta Limnologica. Brasiliensis* **19**: 109-115.

Kaushik N. K. & Hynes H. B. N. (1971) The fate of dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**: 465-515.

Kobayashi S. & Kagaya T. (2004) Litter patch types determine macroinvertebrate assemblages in pools of a Japanese headwater stream. *Journal of the North American Benthological Society* **23**: 78-89.

Kobayashi S. & Kagaya T. (2005) Hot spots of leaf breakdown within a headwater stream reach: comparing breakdown rates among litter patch types with different macroinvertebrate assemblages *Freshwater Biology* **50**: 921-929.

Koljonen S., Louhi P., Mäki-Petäys A., Huusko A. & Muotka T. (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science* **31**: 1121-1130.

Lake P.S. & Doeg T.J. (1985) Macroinvertebrate colonization of stones in two upland southern Australian streams. Hydrobiologia **126**: 199-212.

Lancaster J., Hildrew A.G. & Gjerlov C. (1996) Invertebrate drift and longitudinal transport processes in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 572-582.

Lancaster J. (1999) Small scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology* **41**: 605-619.

Lancaster J. & Belyea L.R. (1997) Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society* **16**: 221-238.

Lancaster J. (2000) Geometric scaling of microhabitat patches and their efficacy as refugia during disturbance. *Journal of Animal Ecology* **69**: 442-457.

Lancaster J. (2008) Movement and dispersion of insects in stream channels: The role of flow. pp 139-157 **In** Lancaster J. & Briers R.A. (Eds) *Aquatic Insects: Challenges to Populations*. CAB International, Wallingford, UK.

Lancaster J. & Downes B.J. (2014) population densities and density-area realtionships in a community with advective dispersal and variable mosaics of resource patches. *Oecologia* **176**: 985-996.

Li A.O.Y. & Dudgeon D. (2011). Leaf litter retention in tropical streams in Hong Kong. *Fundamental and Applied Limnology* (formerly Archiv für Hydrobiologie) **178**: 159-170.

Ligeiro R., Moretti, M.S., Goncalves J.F. & Callisto M. (2010) What is more important for invertebrate colonization in a stream with low-quality litter inputs: exposure time or leaf species? *Hydrobiologia* **654**: 125-136.

MacArthur R. H. & E. O. Wilson (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Mackay R.J. (1992) Colonisation by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Science* **49**: 617-628.

McCune B. & Mefford M.J. (2010) PC-ORD. Multivariate Analysis of Ecological Data. Version 6.20. MjM Software: Gleneden Beach, Oregon, USA.

McLay C.L. (1968) A study of drift in the Kakanui River, New Zealand. *Australian Journal of Marine and Freshwater Research* **19**: 139-149.

Minshall E. L. & Petersen R. C. (1985) Towards a theory of macroinvertebrate community structure in stream ecosystems. Archiv für Hydrobiologie **104**: 49-76.

Murphy J.F. & Giller P.S. (1998) Seasonal dynamics of macroinvertebrate assemblages in the benthos and associated with detritus packs in two low-order streams with different riparian vegetation. *Freshwater Biology* **43**: 617-631.

Nolen J.A. & Pearson R.G. (1993) Factors affecting litter processing by Anisocentropus kirramus (Trichoptera: Calamoceratidae) from an Australian tropical rainforest stream. *Freshwater Biology* **29**: 469-479.

Otto C. (1971) Growth and population movements of Potamophylax cingulatus (Trichoptera) larvae in a South Swedish stream. *Oikos* **22**: 292-301.

Parkyn S.M. & Winterbourne M.J. (1997) Leaf breakdown and colonisation by invertebrates in a headwater stream: comparisons of native and introduced tree species. *New Zealand Journal of Marine and Freshwater Research* **31**: 301-312.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G. & Jones N.V. (1987) Short-term movements of chalk stream invertebrates. *Freshwater Biology* **18**: 559-568.

Pearson R.G., Tobin R.L., Benson L.J. & Smith R.E.W. (1989) Standing crop and processing of rainforest litter in a tropical Australian stream. *Archiv für Hydrobiologie* **115**: 481-498.

Peckarsky B. L. (1986) Colonization of natural substrates by stream benthos. *Canadian Journal of Fisheries and Aquatic Sciences* **43**: 700-709.

Pringle, C.M. & Ramίrez, A. (1998) Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshwater Biology* **39**: 359-373.

Quinn J.M., Smith B.J., Burrell G.P. & Parkyn S.M. (2000) Leaf litter characteristics affect colonisation by stream invertebrates and growth of *Olinga feredayi* (Trichoptera: Conoesucidae). *New Zealand Journal of Marine and Freshwater Research* **34**: 273-287.

Richardson, J.S. (1992) Food, microhabitats, or both? Macroinvertebrates use of leaf accumulations in a mountain stream. *Freshwater Biology* **27**: 169-176.

Rosindell J. & Harmon L.J. (2013) A unified model of species immigration, extinction and abundance on islands. *Journal of Biogeography* **40**: 1107-1118.

Rosser Z. & Pearson R.G. (1995) Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. *Journal of the North American Benthological Society* **14**: 183-196.

Sheldon A.L (1977) Colonisation curves: application to stream insects on semi-natural substrates. *Oikos* **28**: 256-261.

Sheldon A.L (1984) Colonisation dynamics of aquatic insects. Pages 401-429 **In** V.H. Resh & D.M. Rosenberg (eds.) *The Ecology of Aquatic Insects*. Praeger Publishers, New York.

Simberloff D.S. & Wilson E.O. (1999) Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**: 278-296.

Stubbington R. (2012) The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research* **63**: 293-311.

Thompson R. & Townsend C. (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* **75**: 476-484.

Tonkin J. D., Brown A. & Chappell E. M. (2015) Small-scale patch complexity, benthic invertebrate colonisation and leaf breakdown in three headwater streams in Bay of Plenty, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **49**: 159-172.

Townsend C.R. & Hildrew A.G. (1976) Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* **45**: 759-772.

Ulfstrand S., Nilsson L.M. & Stergar A. (1974) Composition and diversity of benthic species collectives colonizing implanted substrates in a South Swedish stream. *Entomologia Scandinavica* **5**: 115-122.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.

Wallace J.B. (1990) Recovery of lotic macroinvertebrate communities from disturbance. *Environmental Management* **14**: 605-620.

Waters T.F. (1972) Drift of stream insects. *Annual Review of Entomology* **17**: 253-272.

Webster J.R., Golladay S.W., Benfield E.F., D”Angelo D.J. & Peters G.T. (1990) Effects of forest disturbance on particulate organic matter budgets of small streams. *Journal of the North American Benthological Society* **9**: 120-140.

Williams D.D. & Hynes H.B.N. (1976) The recolonization mechanisms of stream benthos. *Oikos* **27**: 265-272.

Wise D.H. & Molles M.C. (1979) Colonization of artificial substrates by stream insects: influence of substrate size and diversity. *Hydrobiologia* **65**: 69-74.

Chapter 5

A humped and monotonic productivity–diversity relationship at different scales in stream invertebrates inhabiting leaf litter packs: due to high β diversity and constrained immigration.

5.1 Introduction

The experiments described in Chapter 3 demonstrated that exogenous nutrient supplements increased the food quality of leaf litter to an invertebrate detrivore, through enrichment of the microbial biomass on the leaf material. Supplements also resulted in a 75% increase in the density the invertebrate assemblage without affecting diversity. The lack of a response in the community composition was surprising given the magnitude of the nutrient enhancement and because it was clearly entering trophic pathways, demonstrated through feeding trials and the increase in abundance of the invertebrate fauna. This was contrary to the commonly held view that nutrient enrichments can profoundly affect aquatic ecosystems (Carpenter *et al*., 1998; Smith *et al*., 1999) and prompted me to investigate the relationship between productivity and diversity and how it might apply in these heterotrophic stream assemblages.

There has been an enduring interest in the relationship between the productivity of an ecosystem and the number of species within it (e.g., Grime, 1973, 1979; Al-Mufti *et al*., 1977; Abrams, 1995; Waide *et al*., 1999; Mittlebach *et al*., 2001; Whittaker, 2010; Alder *et al*., 2011; Fraser *et al*., 2015; Grace *et al*., 2016). Productivity and diversity (here meaning species richness) are fundamental characteristics of a biotic community and unravelling the mechanisms that determine them and the relationship between them is of importance in understanding biodiversity and how to conserve it (Huston, 1979; Pierce, 2014; Gross, 2016). However, the effects of productivity on the composition of biotic communities (including aquatic communities) are as yet not predictable, except perhaps under extreme oligotrophic or eutrophic conditions (Vitousek *et al*., 1997; Smith *et al*., 1999; Nijboer & Verdonschot, 2004). Some suggest that with increasing resources, more individuals and species can be sustained in an ecosystem, so diversity increases monotonically with productivity (Wright, 1983; Currie & Paquin, 1987; Currie, 1991; Gaston, 2000; Cardinale *et al*., 2009). More controversial is the view that the relationship is unimodal, or “hump-shaped”, in which diversity peaks at intermediate productivity (e.g., Adler *et al*., 2011; Fridley *et al*., 2012; Grace *et al*., 2012; Pan *et al*., 2012; Pierce, 2014; Fraser *et al*., 2015). Others suggest that the form of the relationship is dependent on the relative levels of productivity and disturbance (Kondoh, 2001, Kadmon & Benjamani, 2006; Tonkin & Death, 2012, 2013; Tonkin *et al*., 2013).

The productivity-diversity debate has focussed largely on determining what the true relationship is and, if humped, on finding a mechanism to explain the descending limb of the “hump” (Abramsky & Rosenzweig, 1984; Tilman & Pacala, 1993; Rosenzweig, 1995; Leibold, 1999; Dodson *et al*., 2000). As the debate progressed, the significance of scale (Oksanen, 1996; Chase & Ryberg, 2004; Chase, 2007; Tonkin & Death, 2013) and β diversity (Chase & Leibold, 2002; Chalcraft *et al*., 2004; Harrison *et al*., 2006; Chase, 2010) were recognised, with observations that monotonic and humped realtionships can be found in the same community but at different scales (Wright *et al*., 1993; Waide *et al*., 1999; Gross *et al*., 2000; Mittlebach *et al*., 2001; Chase & Leibold, 2002; Korhonen *et al*., 2011). For example, Chase and Leibold (2002) described how the diversity of invertebrates inhabiting ponds increased monotonically with productivity at regional scales (among watersheds) but the relationship was humped at local scales (among ponds). The mechanisms underlying these differences remain uncertain, although many have been hypothesised and they, too, are likely to vary with scale (Waide *et al*., 1999; McBride *et al*., 2014).

I investigated the effect of resource enrichment on the invertebrate assemblage in Birthday Creek (see Chapter 3). This stream, like many headwater streams in the region, has very low concentrations of dissolved nutrients and is heterotrophic, because in-stream primary productivity is usually light-limited (sensu Fisher & Likens, 1972), but has high diversity of invertebrates (Lake *et al*., 1994, Walker *et al*., 1995; Connolly *et al*., 2008; Pearson *et al*., 2015). Productivity in these systems relies mainly on allochthonous leaf litter entering the stream and being gradually broken down and modified, fuelling a detrital food web (Kaushik & Hynes, 1971; Fisher & Likens, 1973; Fittkau & Kling, 1973; Anderson & Sedell, 1979; Benfield & Webster, 1985; Rosemond *et al*., 2001; Cheshire *et al*., 2005). Whereas many studies investigating the relationship between productivity and diversity have focussed on gradients of nutrients (e.g., Tilman, 1993; Tilman & Pacala, 1993; Leibold, 1999) and primary production (Minshall, 1978; Bott, 1983; Lamberti & Steinman, 1997), this project investigates these relationships in a largely detrital food web, dependent on input of an exogenous carbon source (mainly riparian leaf litter) and the biomass of microbial communities (Suberkropp & Klug, 1976; Arsuffi & Suberkropp, 1985; Gulis *et al*., 2006; Ferreira & Chauvet, 2011; Connolly & Pearson, 2013). I manipulated terrestrial leaf litter to establish a gradient of enrichment and productivity, and measured the response of the macroinvertebrate assemblage.

Leaf litter, as well as being a source of food, provides habitat patches (Richardson, 1992), so the manipulation of leaf litter allows control of both productivity and habitat heterogeneity. I was therefore able to investigate the relationship between productivity and patch dynamics in order to understand the effect of scale. I aimed to test whether invertebrate species diversity responded to the resource-productivity gradient and whether this response was positive, negative, or hump-shaped. I measured the response at two scales: individual leaf litter packs within artificial stream channels; and at the channel scale across multiple leaf litter packs. Thus, I aimed to investigate if the relationship was scale dependent as observed by Chase and Leibold (2002) in ponds: that is, whether at local scales diversity has a hump-shaped relationship with productivity, but at a regional scale diversity increases linearly with productivity.

5.2 Methods

A resource gradient in leaf litter cover was established in artificial stream channels on the bank of Birthday Creek (Connolly & Pearson 2013; Chapter 3) (Plate 5.1). The channels are rapidly colonised by a diverse assemblage of macroinvertebrates and simulate stream conditions well (Pearson & Connolly 2000; Connolly & Pearson 2007, 2013; Chapters 3 & 4). In this experiment the channels were open to colonisation via downstream drift or aerially and water flow to each channel was controlled at 6.0 L min^{-1}. A coarse filter (20-mm mesh) on the inlet of the header tank prevented clogging by leaf litter, but allowed the passage of most other suspended material, including macroinvertebrates. Each channel comprised three sections, separated by v-notch weirs to maintain water depths at approximately 70 mm.

Plate 5.1. Artificial stream channels located beside Birthday Creek. Inset shows *Apodytes brachistylus* leaf packs attached to cobbles.

The experiment was undertaken in the late dry season – early wet season (December 3 – January 12) before any major storms had occurred. Water temperature during the study ranged from 17 to 21 ˚C.

The productivity resource manipulated in this experiment consisted of *Apodytes brachystylus* F. Muell. (Icacinaceae) leaves collected fresh from a single tree on the bank of Birthday Creek. Individual leaf packs consisted of 2.5 g air-dried leaves attached to individual granite cobbles (diam. ~ 70 mm, phi = -6) using plastic tags and a rubber band (Plate 5.2). Leaves of this species are colonised by a diverse community of macroinvertebrates in the stream and are readily consumed (Nolen & Pearson 1993; Pearson & Connolly, 2000; Connolly & Pearson, 2013; Chapter 4). The exact weight of each bundle was recorded.

Plate 5.2. *Apodytes brachystylus* F. Muell. (Icacinaceae) leaf pack attached to cobble as used in the experiment.

Thirty cobbles were collected from Birthday Creek, scrubbed and distributed along each channel. A leaf litter resource gradient was established by varying the amount of leaf litter cover (the proportion of cobbles with a leaf pack attached) in each channel: 0%, 10%, 20%, 40%, 60%, 80% and 100% leaf litter cover (Figure 5.1). For example, 10% leaf litter cover was achieved by attaching leaf packs to 3 randomly chosen cobbles of the 30 available in the channel. Positions for leaf packs were determined using a random number generator (MS Excel). Cobbles were positioned so that the adjacent leaf litter packs touched but did not overlap. Treatments were distributed randomly amongst channels.

The experiment ran for 40 days to allow for adequate colonisation, but not long enough for litter packs to degrade. The colonisation experiments (Chapter 4) showed that colonisation plateaued around 24 days, and then remained largely stable up to the 38-day duration of those experiments. Previous experiments also showed that these leaf litter packs provided adequate habitat for a 40-day period (Pearson & Connolly, 2000; Connolly & Pearson, 2013; Chapter 3).

At the end of the experiment all cobbles, with or without leaf packs, were removed in sequence from downstream to upstream, placed in plastic containers, and labelled with the channel number, treatment, and cobble number to record the position within the channel. Leaf packs, when present, were removed from the cobbles. The cobbles were then washed vigorously into the container and discarded. The contents of each container were then sieved through a 63-μm-mesh screen and preserved in 80% ethanol for processing in the laboratory. In samples that included leaf packs, individual leaves of the leaf packs were rinsed with freshwater and carefully searched to remove animals. The remaining leaf material was air dried and weighed in the laboratory. Macroinvertebrates were identified to genus or species where possible (see Chapter 3 or 4), or to family.

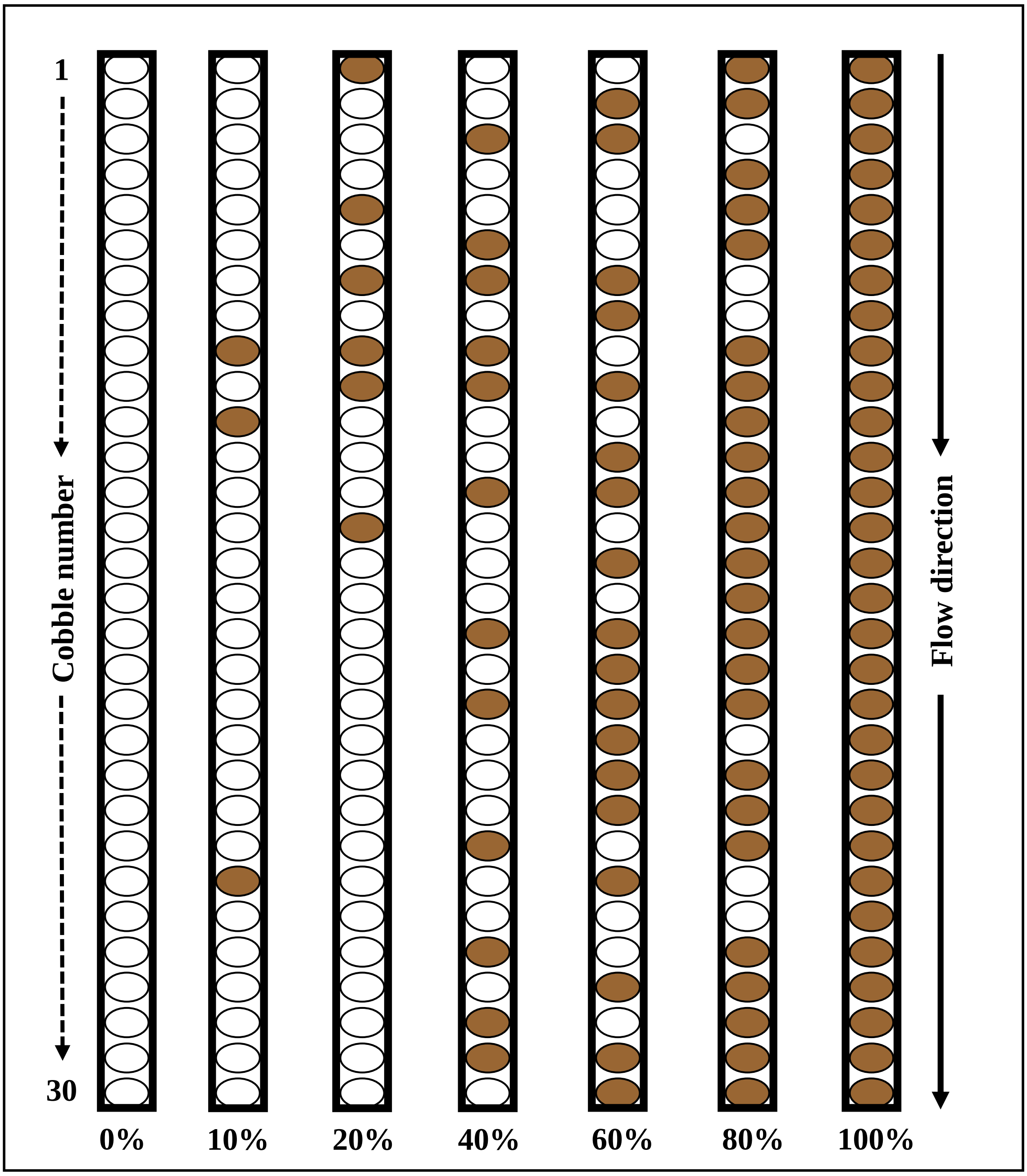


Figure 5.1. Layout of artificial stream channels showing leaf litter patch resource gradient. Circles represent cobbles. Filled circles represent cobbles with leaf packs attached as per Plate 5.2. (Actual order of channels was randomised).

Abundance and diversity of invertebrates were plotted against % leaf pack cover to describe patterns of community structure and resource availability. These were investigated at two scales: the whole of channel (the sum of invertebrates from all 30 cobbles, and the sum of invertebrates on only the cobbles plus leaf packs); and individual cobble samples within channels (number of invertebrates from each cobble or cobble plus leaf pack). All invertebrates contributed to total abundance counts, but individuals that could not be identified to genus or species did not contribute to the count of taxa within families (where other individuals were identified to species or genus).

Linear and 2nd-order polynomial regressions were fitted to plots of log abundance of individual taxa versus % leaf pack cover in SigmaPlot© 12.5. Linear, 2nd and 3rd order polynomial regressions were also fitted to plots of the number of individuals and the number of taxa versus the proportion of leaf litter pack cover at both the channel and leaf pack scales. I have presented the statistics for these regressions to indicate the strength of the patterns, but acknowledge that gradients occur in the number of individuals and number of taxa occupying individual cobble/leaf packs within channels, and so individual leaf packs within channels are not truly independent. However, it is the processes within channels that I am investigating to explain different patterns nested at different scales. The lack of independence does increase the possibility of a Type I error in these statistics. However, because the patterns are striking, and there are seven independent treatment levels, I expect significant patterns to be robust.

To test for unimodal relationships in these plots two methods were used. Firstly, the Gaussian function of the form $f(x) = a*\exp\{-0.5((x-b)^2/c^2)\}$, where a is the height of the curve's peak, b is the position of the centre of the peak and c the standard deviation (which controls the width of the curve), was fitted using SigmaPlot© 12.5 to test if the curvilinear form of these relationships approximated a concave quadratic function. A test developed by Mitchell-Olds and Shaw (1987) (MOS test), and used by several authors to test for "hump-shaped" productivity-diversity relationships (Leibold, 1999; Mittleback *et al.*, 2001; Chase & Leibold, 2002), was used to verify a unimodal relationship. This method determines whether a curvilinear relationship reaches a maximum (or minimum) within the range of observed values (as opposed to an asymptotic change) and uses quadratic regression to estimate the value associated with the peak of the relationship, as well as the 95% confidence intervals around that peak. The method then uses a t-test to determine if the estimated peak of the data is significantly greater than at the minimum and maximum values. Following Mittlebach *et al.*

(2001), curvilinear relationships that showed an internal maximum via the MOS test were classified as “hump-shaped”. The MOS test was performed in the program R 3.2.2 (R Core Team, 2015) using generalised linear models (glim) with link function. With logarithmic link function, the quadratic response defines the Gaussian response model of ecological gradients (ter Braak & Looman, 1986), locating the Gaussian optimum within the range of the gradient. The function fits a quadratic curve $\mu = b_0 + b_1x + b_2x^2$. If $b_2 < 0$, this defines a unimodal curve with highest point at $\mu = -b_1/(2b_2)$ (ter Braak & Looman, 1986). Residuals were plotted and checked for heteroscedacity and indicated a close to normal distribution.

Chase and Leibold (2002) concluded that the productivity–diversity relationship in ponds differed at different scales because dissimilarity in local species composition within regions (as an index of β diversity) increased with productivity. To test this the mean pairwise dissimilarities between leaf packs within each channel were plotted against the % leaf pack cover gradient. Presence/absence data was used to calculate dissimilarity amongst leaf packs within channels as 1 – C, where C is Jaccard’s index (following Chase & Leibold, 2002, Chase & Ryberg, 2004, Chase, 2010) using PCORD (McCune & Mefford, 2011). Bray-Curtis dissimilarity was also calculated using log abundance. Non-metric multidimensional scaling ordination (NMDS, using PC-ORD) was performed on log-transformed invertebrate data to assess if cobble/leaf pack sample composition varied across the % leaf pack cover treatments. Plots of community composition in two-dimensional space were used to compare the distance between cobble-leaf pack samples within and between treatments and multiple-response permutation procedures tests (MRPP, using PC-ORD) were performed to test for between-group differences.

Linear regression analysis in SigmaPlot© 12.5 was used to describe the relationship between abundance and diversity within channels and analysis of covariance (ANCOVA, in Statistix© 7) was used to compare channels using channel position (rock number) as the covariate. Because longitudinal gradients in litter distribution potentially confounded the regression analysis, I also analysed diversity in relation to the residuals of these gradients.

5.3 Results

A total of 31,685 animals and 76 unique taxa were collected in the seven channels (Appendices – Tables A5.1 & A5.2). The assemblage composition was similar to that collected in the colonisation and dispersal experiments (Chapter 4). Overall abundance was largely determined by a few very abundant taxa, notably: Oligochaeta; microcrustaceans including Cladocera and Cyclopoda; Hydracarina; and numerous Chironomidae, particularly *Tanytarsus* sp., *Corynoneura* sp. and *Thienemanniella* sp. Other abundant taxa included Harpacticoida (Copepoda), Gripopterigidae (Plecoptera); a number of Ephemeroptera, particularly *Atalophlebia* AV13, *Koorrnonga* AV4 and *Nousia* NQ2; dipterans Ceratopogonidae and *Austrosimulium* sp. (Simuliidae); and *Austrolimnius* sp. (Coleoptera: Elmidae). Seventeen Trichoptera taxa were collected but were never abundant.

Total abundance of invertebrates in each channel increased monotonically with % leaf pack cover (Figure 5.2 a). The shape of the relationship was sigmoid, approaching an asymptote above 80% cover. The total number of taxa from all 30 cobbles and leaf packs also increased monotonically (apart from an outlier) with % leaf pack cover at the channel scale (Figure 5.2 b). The shape of the relationship was curvilinear, with the rate of increase in the number of taxa declining towards 100% leaf pack cover. The relationships of invertebrate abundance and diversity to leaf pack cover were essentially the same when only the cobbles with leaf packs attached were considered as when all cobbles were included (Figures 5.2 c & d).

In contrast to the patterns observed at the channel scale, the average abundance per individual cobble/leaf pack was unimodal or hump-shaped (Figure 5.2 e & g). Similarly, the pattern of average number of taxa on individual leaf packs across the resource gradient was hump-shaped (Figure 5.2 f & h). Regression analysis fitting the Gaussian function indicated that the relationships in Figures 5.2 (e) and (f) were in the form of a concave curve (unimodal) (respectively, $r^2 = 0.111$, $F_{2,92} = 5.604$, $P = 0.0051$; $r^2 = 0.172$, $F_{2,92} = 9.348$, $P = 0.0002$) and the MOS test confirmed this (Table 5.1).

The number of macroinvertebrates on cobbles with leaf packs was much greater than the number on bare cobbles and there was no relationship between the total abundance of macroinvertebrates inhabiting bare cobbles and leaf pack cover (Figure 5.3 a). Similarly, the number of taxa on bare cobbles was much lower than on cobbles with leaf packs and was not affected by the leaf pack cover in the channel (Figure 5.3 b). Only a few taxa, occurring as single individuals, were found only on bare cobbles (Appendices – Table A5.1).

The relationship between % leaf pack cover and mean dissimilarity between paired leaf packs within each channel treatment increased initially but then remained constant (Figure 5.4). At 100% leaf litter cover, Jaccard dissimilarity declined.

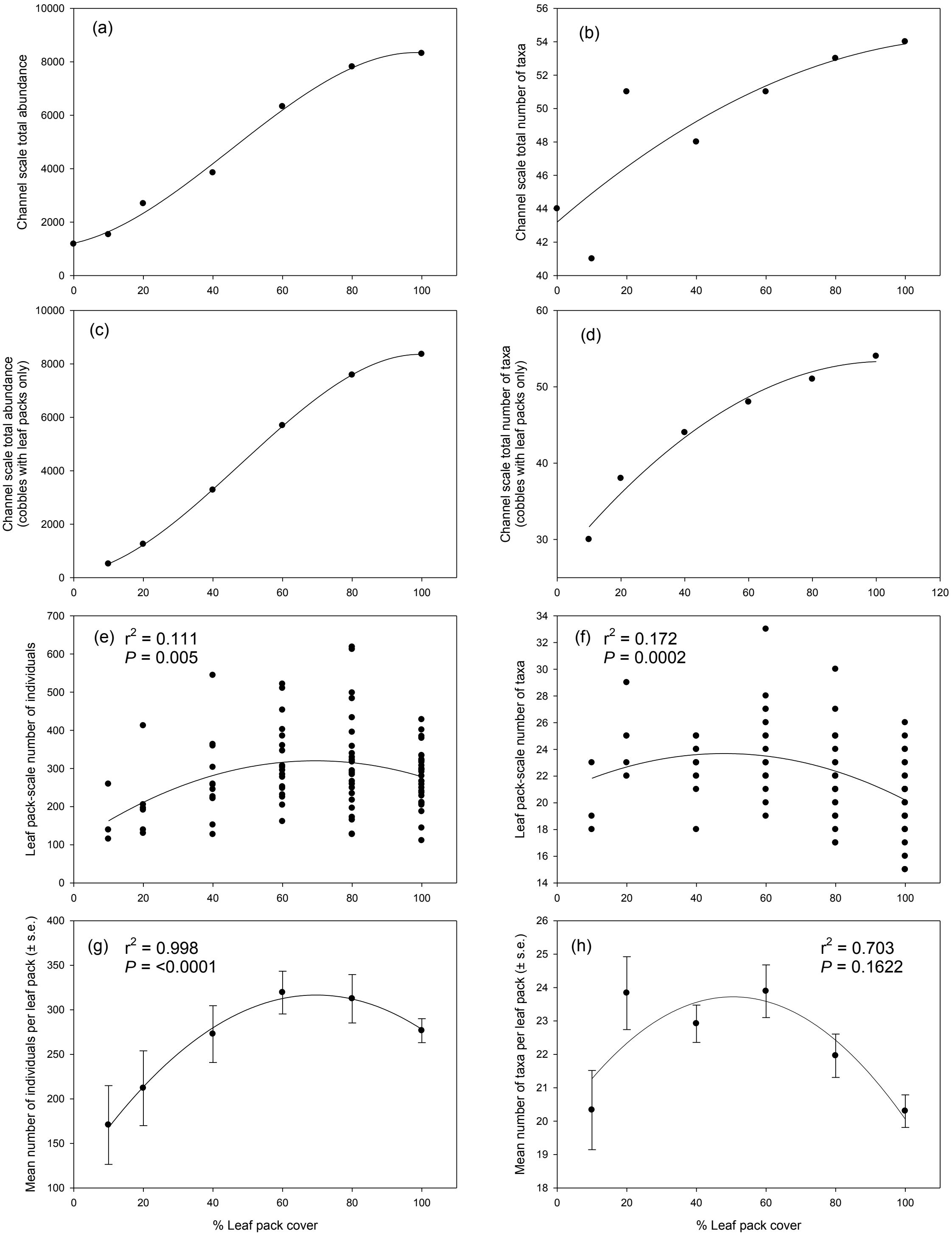


Figure 5.2. The relationship between % leaf pack cover in artificial stream channels and (a) total abundance of macroinvertebrates at the channel scale; (b) total number of taxa at the channel scale; (c) total abundance of macroinvertebrates on cobbles with leaf packs at the channel scale; (d) total number of taxa on cobbles with leaf packs at the channel scale; (e) number of macroinvertebrates on individual cobbles with leaf packs; (f) number of taxa on cobbles with leaf packs; (g) mean number of individual macroinvertebrates on cobbles with leaf packs; and (h) mean number of taxa on cobbles with leaf packs. Solid lines represent 3rd order ((a) and (c)) and 2nd order ((b), (d), and (e) – (h)) least square regressions.

Table 5.1. Results of Mitchell-Olds and Shaw (MOS) test of whether the hump of a quadratic linear predictor in the relationships between: (a) the number of individuals and % leaf pack cover (Figure 2 (e)); and (b) the number of taxa and % leaf pack cover in cobble/leaf pack samples (Figure 2 (f)) are at a minimum or maximum.

(a) Number of individuals vs % leaf pack cover (Figure 2 e)

minimum	**hump**	**maximum**	
10.0000	69.39679	100.0000	
	Min/max	**F**	***P***
Hump at minimum	10	10.531	0.0016
Hump at maximum	100	5.254	0.0242
Combined			0.0258
Is Hump = TRUE	Is Bracketed = TRUE		

(b) Number of taxa vs % leaf pack cover (Figure 2 f)

minimum	**hump**	**maximum**	
10.0000	48.07375	100.0000	
	Min/max	**F**	***P***
Hump at minimum	10	1.705	0.1916
Hump at maximum	100	5.806	0.0160
Combined			0.2045
Is Hump = TRUE	Is Bracketed = TRUE		

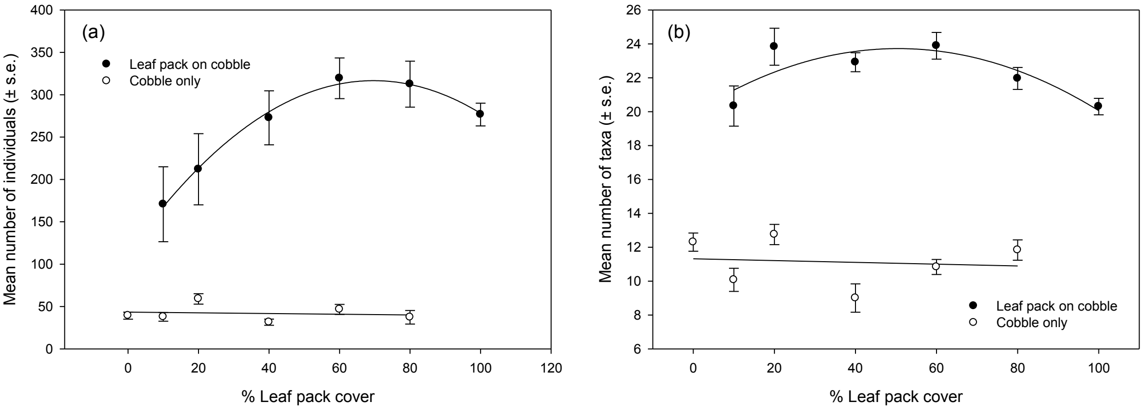


Figure 5.3. A comparison of the (a) mean number of individual macroinvertebrates and (b) number of taxa collected on cobbles with leaf pack attached (●) and on cobbles without leaf packs (○) along the % leaf pack cover resource gradient. Solid lines represent ordinary least square regressions.

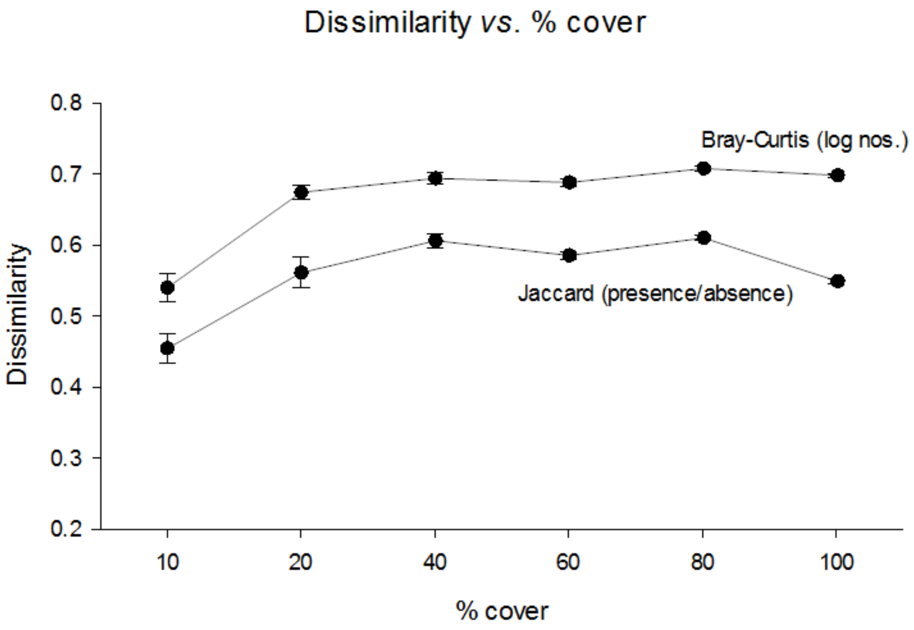


Figure 5.4. The relationship between mean species dissimilarity between leaf packs within channel treatments and the % leaf pack cover gradient. If dissimilarity = zero, then all taxa are shared among leaf pack assemblages; if dissimilarity = 1, then no taxa are shared amongst leaf packs.

NMDS and MRPP results show clear grouping of leaf packs assemblages within treatments and a shift in assemblage composition with % leaf pack cover (Figure 5.5; Table 5.2). However, the spread of variation in composition amongst leaf packs within channel treatments did not increase across this gradient. NMDS axis 1 scores had a significant positive correlation with % leaf pack cover (Figure 5.6a), whereas axis 2 scores followed a parabolic relationship with % leaf pack cover (Figure 5.6b).

The abundance of several taxa on the cobble/leaf packs varied with % leaf pack cover, with some occurring in higher abundance with lower % leaf pack cover, and others occurring in higher abundances in the higher % leaf pack cover treatments (Figure 5.7).

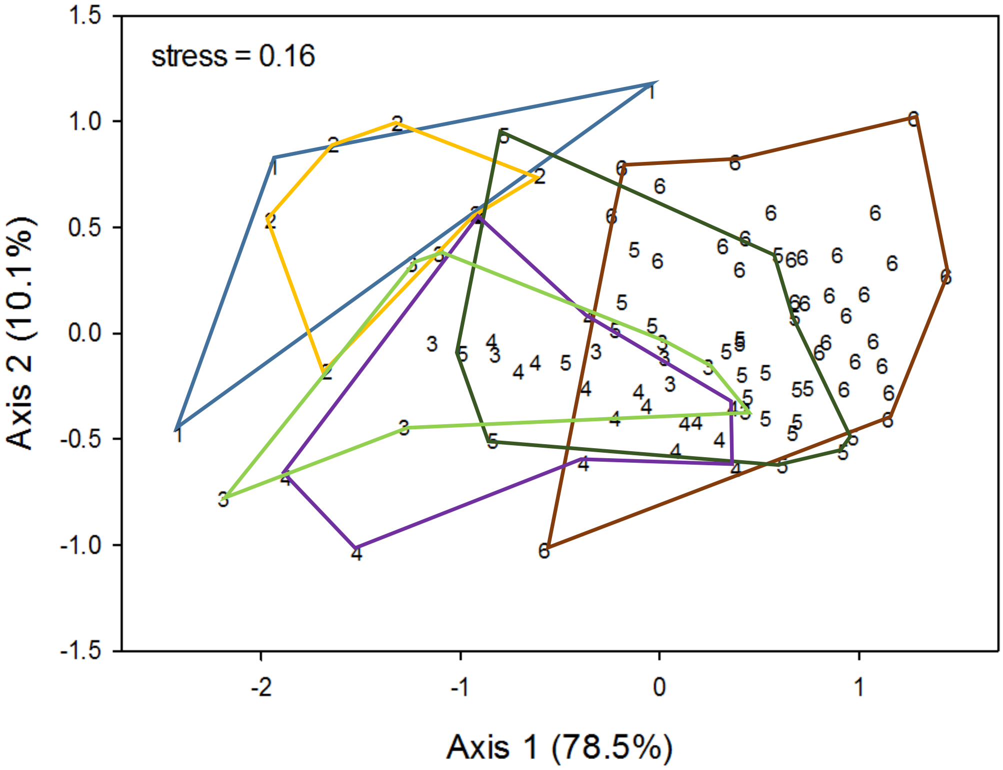


Figure 5.5. Plot of NMDS analysis of assemblage composition (log-transformed abundances of taxa). Hulls enclose samples labelled 1-6, representing treatments of 10, 20, 40, 60, 80 and 100% cover, respectively.

Table 5.2. MRPP (test for between-group differences) Test statistic: T = -20.559739, Chance-corrected within-group agreement, A = 0.15217463, Probability of a smaller or equal delta, *P* < 0.00001.

	T	A	*P*		T	A	*P*
6 vs. 5	-12.63	0.056	<0.0001	4 vs. 3	-0.67	0.007	0.1925
6 vs. 4	-20.02	0.117	<0.0001	4 vs. 2	-8.61	0.113	<0.0001
6 vs. 3	-16.02	0.110	<0.0001	4 vs. 1	-3.54	0.061	0.0056
6 vs. 2	-16.65	0.156	<0.0001	3 vs. 2	-5.41	0.091	0.0009
6 vs. 1	-8.97	0.081	<0.0001	3 vs. 1	-1.61	0.043	0.0727
5 vs. 4	-9.34	0.063	<0.0001	2 vs. 1	-2.58	0.081	0.0111
5 vs. 3	-6.77	0.058	0.0004				
5 vs. 2	-11.95	0.145	<0.0001				
5 vs. 1	-5.60	0.076	0.0005				

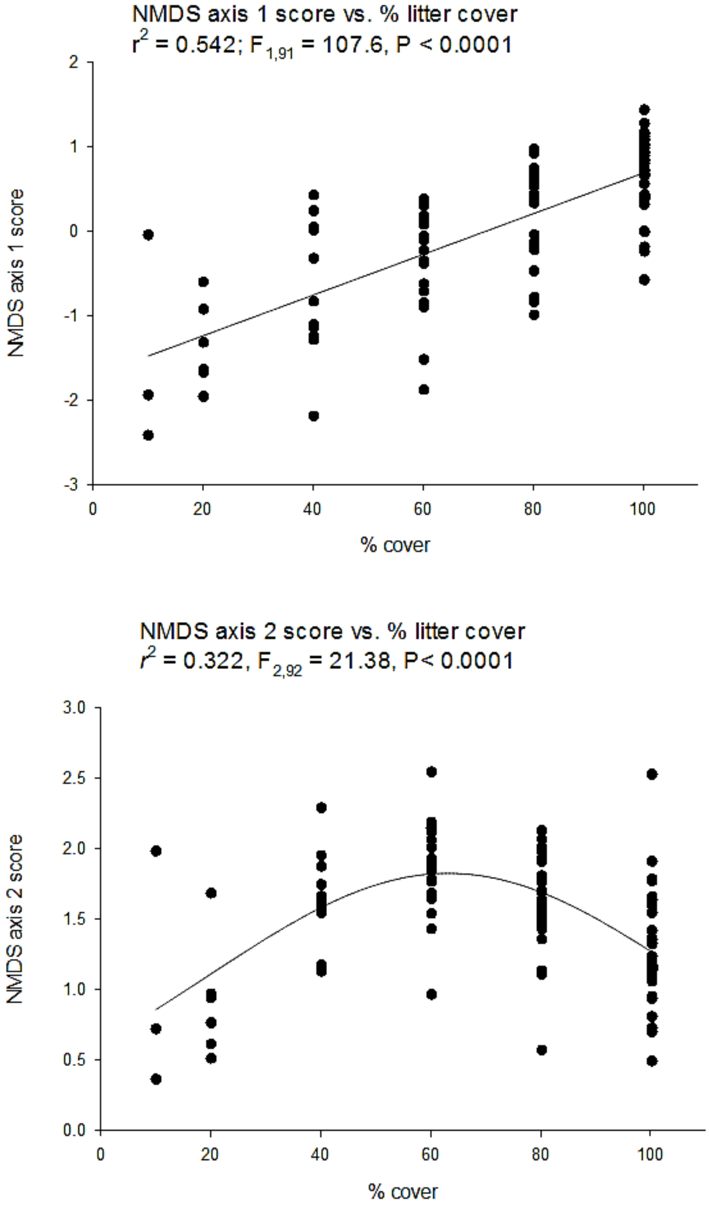


Figure 5.6. NMDS axis scores vs % leaf pack cover: (a) axis 1, (b) axis 2.

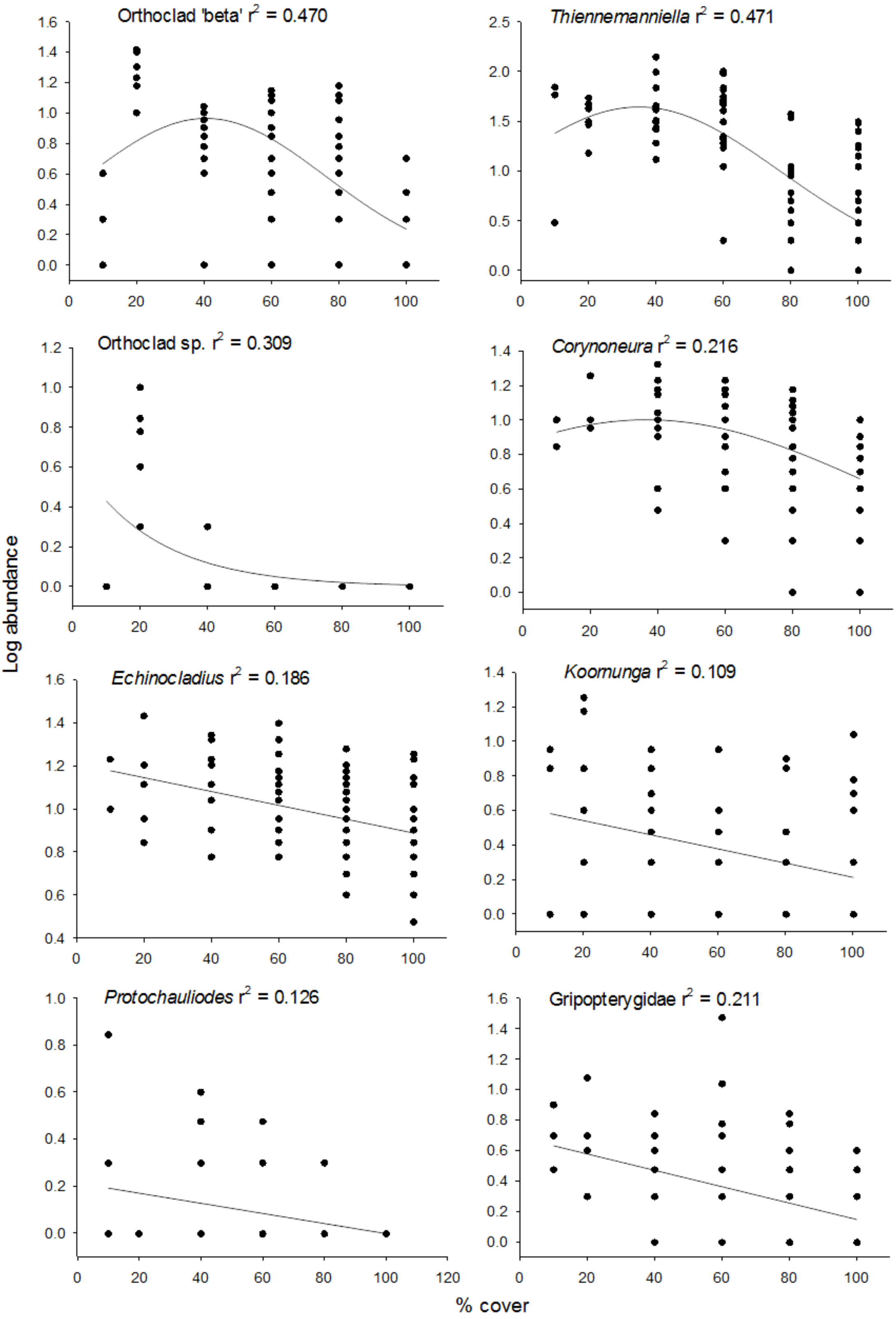
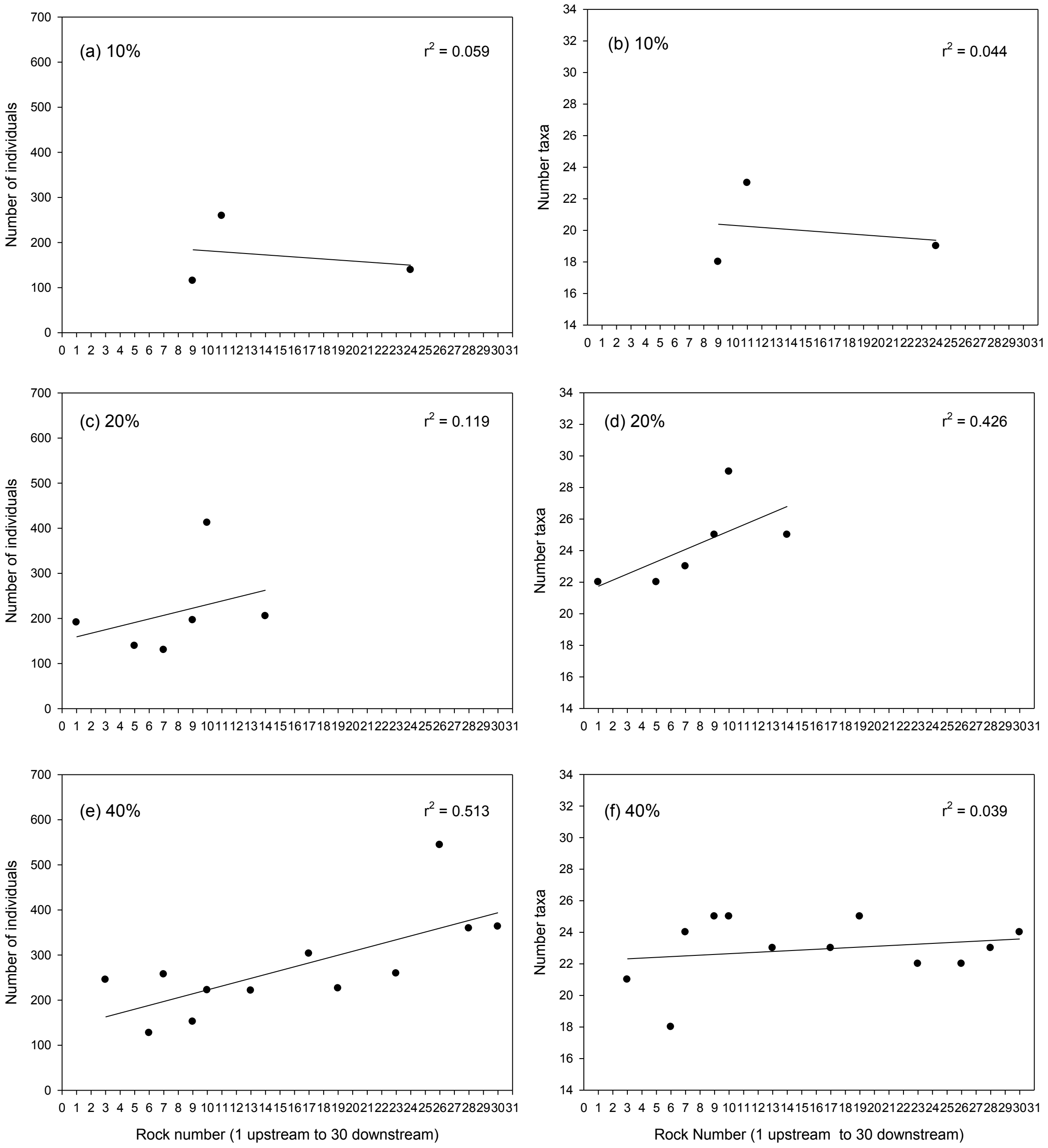


Figure 5.7. Abundance of selected invertebrate taxa on cobble/leaf packs vs. % leaf pack cover.

There were also significant longitudinal gradients in the number of individuals and number of taxa on cobble/leaf packs within the channels, but the slope of the relationships varied along the leaf pack resource gradient (Figure 5.8). Abundance generally increased with distance downstream in the channels, except at 10% leaf pack cover where there was no pattern (Figure 5.8, left panels), whereas richness increased with distance downstream in the channel at 20% leaf pack cover, but then gradually shifted with increasing % cover to a distinct negative relationship at 80% and 100% cover (Figure 5.8, right panels).

There was a strong relationship between the number of taxa and abundance at the channel scale (Figure 5.9). The relationship between the number of taxa and abundance at the cobble/leaf pack scale (Figure 5.10 a) was obscured by the opposing longitudinal gradients within the channels (Figure 5.10 b & c). Plots of residuals of abundance and richness across the longitudinal channel gradient were positive (Figure 5.10 d - f), indicating that the number of individuals on individual cobble/leaf packs influenced the number of taxa at this scale. The relationship between abundance and the number of taxa on individual leaf packs was positive in the 10 and 20% leaf pack treatments, but then broke down at high % leaf pack cover (Figure 5.11), corresponding with the shifts in gradients shown in Figure 5.8.


(a) 10%
r^2 = 0.059
Number of individuals
(b) 10%
r^2 = 0.044
Number taxa
(c) 20%
r^2 = 0.119
Number of individuals
(d) 20%
r^2 = 0.426
Number taxa
(e) 40%
r^2 = 0.513
Number of individuals
(f) 40%
r^2 = 0.039
Number taxa
0 100 200 300 400 500 600 700
14 16 18 20 22 24 26 28 30 32 34
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
Rock number (1 upstream to 30 downstream)
Rock Number (1 upstream to 30 downstream)

continued…

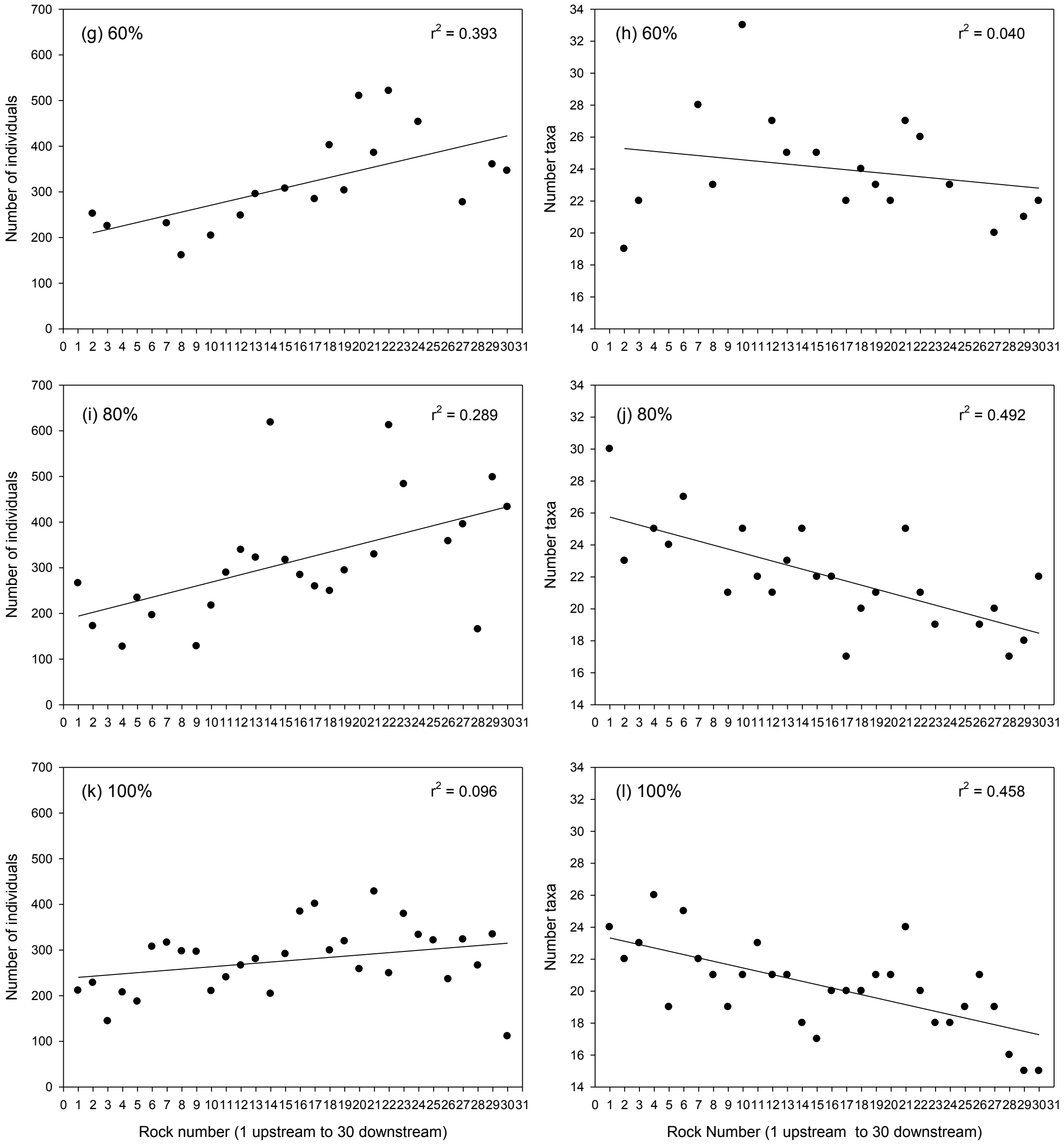


Figure 5.8. Abundance (left panels) and number of taxa (right panels) per leaf pack vs. rock number (1 upstream to 30 downstream) in artificial stream channels.

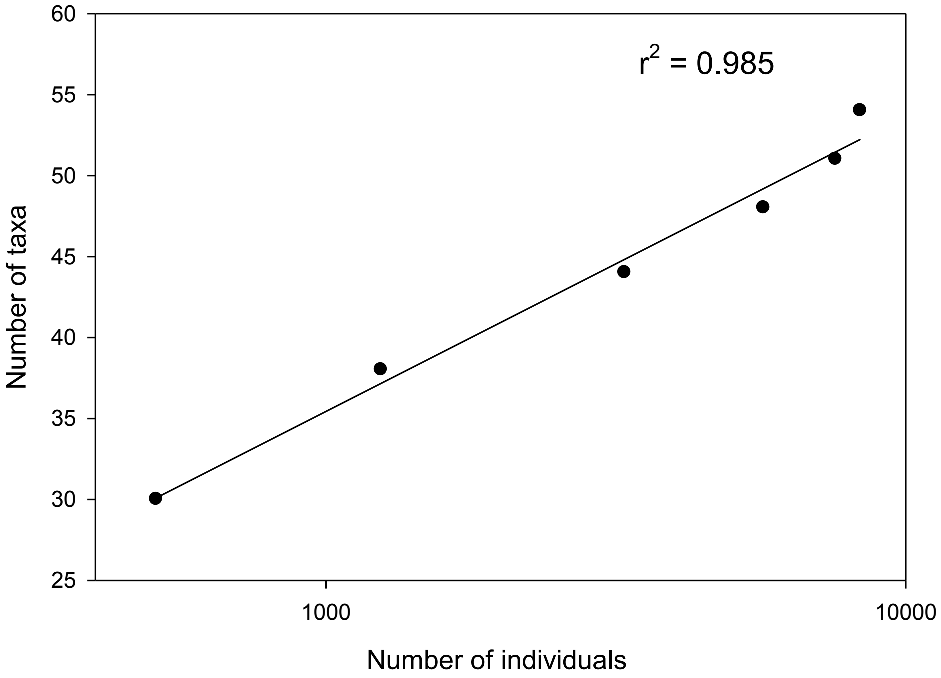


Figure 5.9. The relationship between the total number of individuals and total number of taxa summed across cobbles with leaf packs within each treatment channel. Note $\log_{10}$ scale used on the x axis.

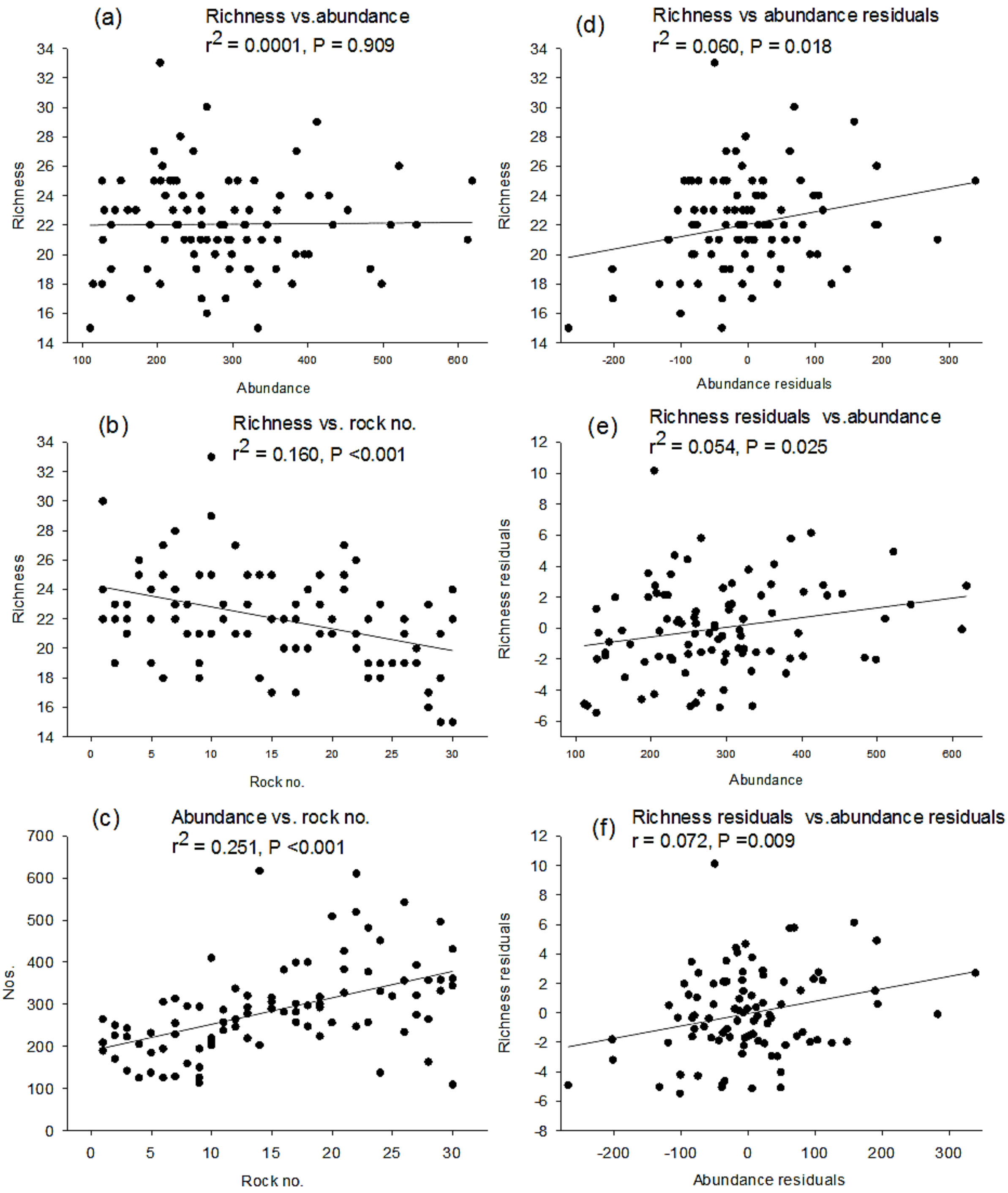


Figure 5.10. Relationships between the number of individuals, number of taxa and the residuals of these when plotted with position within the channel (Rock number) measured on individual cobble/leaf packs samples from % leaf pack cover treatments. (a) Number of taxa vs. abundance, (b) No. of taxa vs. rock number, (c) Abundance vs. rock number, (d) No. of taxa vs. residuals of (abundance vs. rock number), (e) Residuals of (No. of taxa vs. rock number) vs. abundance, and (f) Residuals of (No. of taxa vs rock number) vs. residuals of (abundance vs. rock number).

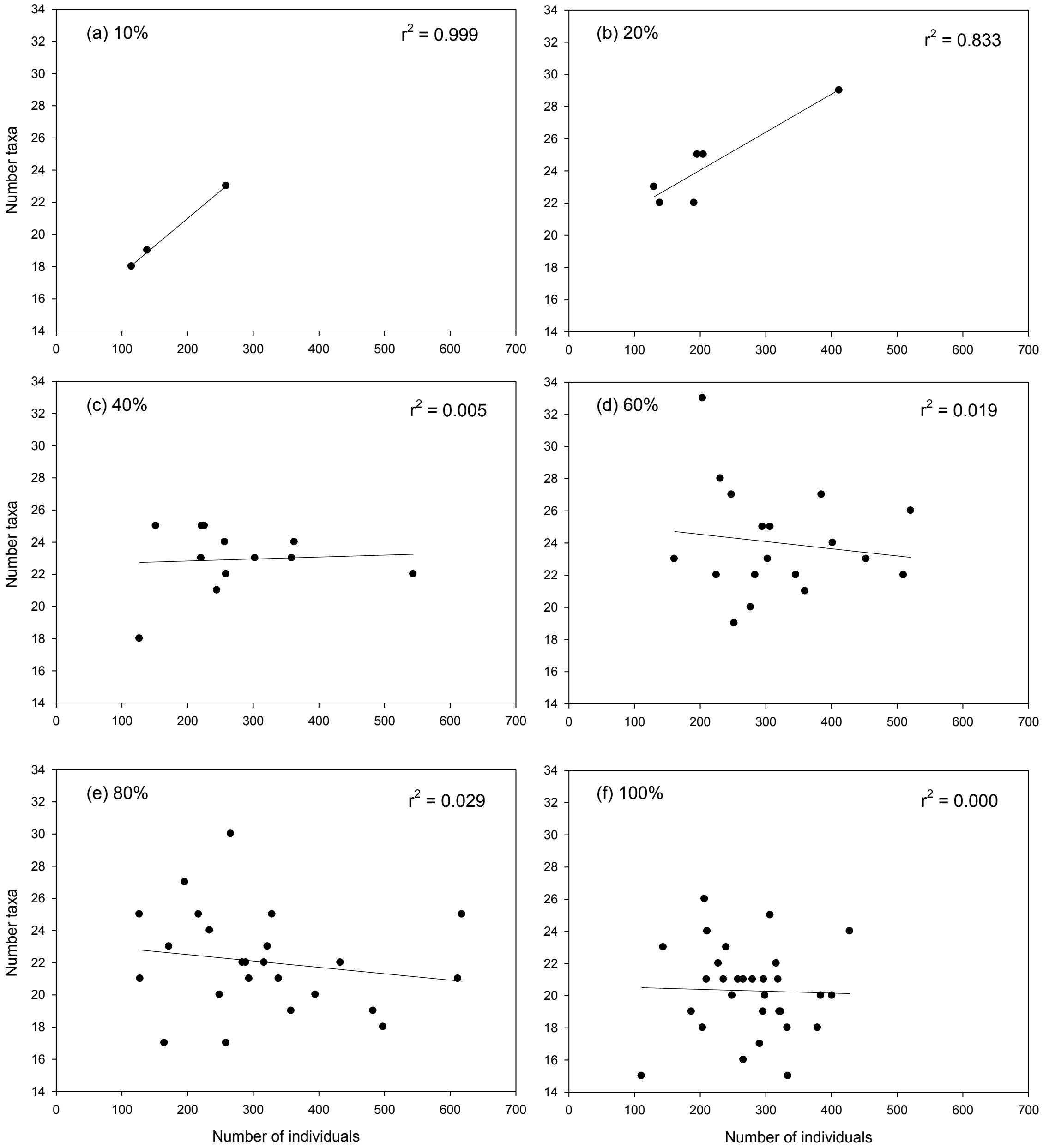


Figure 5.11. The relationship between the number of individuals and number of taxa on individual cobble/leaf packs samples from artificial stream channels for (a) 10%, (b) 20%, (c) 40%, (d) 60%, (e) 80% and (f) 100% leaf pack cover treatments.

5.4 Discussion

The abundance of litter packs, as a proportion of 100% cover, was used as a resource gradient (food and habitat) and as a surrogate for a productivity gradient for the macroinvertebrate assemblage in the artificial stream channels. For the purpose of comparisons to other studies, and to explore the concept that the productivity–diversity relationship differs between larger and smaller scales, we treated individual leaf litter patches as equivalent to a local scale and individual stream channels as equivalent to a regional scale. The number of litter packs had a strong, scale-dependent effect on the abundance and richness of macroinvertebrates in the artificial stream channels. At the channel scale macroinvertebrate diversity increased with the number of leaf packs present in the channels. This is consistent with a number of studies reporting the relationship between productivity and diversity at larger scales (e.g., Wright, 1983; Currie & Paquin, 1987; Currie, 1991; Gaston, 2000). The rate of increase in diversity in our experiment declined towards 100% leaf pack cover. Chase and Leibold (2002) reported that the relationship between productivity and diversity in ponds increased linearly at the regional scale, but inspection of their data suggests that the relationship is curvilinear, similar to the pattern we observed. Abrams (1995) also infers that a monotonic relationship between productivity and diversity may level off as productivity increases and all available species are represented. In contrast, at the cobble/leaf pack scale diversity had a hump-shaped relationship with % leaf pack cover, a pattern also reported in a number of studies (e.g., Grime, 1973; Al Mufti *et al*., 1977; Tilman, 1982; Rosenzweig & Abramsky, 1993; Fraser *et al*., 2015). These results, like Chase and Leibold (2002), indicate that the form of the productivity–diversity relationship can vary with scale in the same community. It is particularly interesting that that a hump-shaped pattern was nested within a monotonic pattern at the larger scale, even within a confined system.

5.4.1 Mechanisms

The debate about the general pattern of the productivity–diversity relationship is likely to continue while the underlying mechanisms remain uncertain. A number of possible mechanisms have been suggested (e.g., Tilman, 1993, Tilman & Pacala, 1993; Abrams, 1995; Chase, 2010; Kadmon & Benjamani, 2006; Xiao *et al*., 2010), but they do not reconcile how the relationship is unimodal in some case but monotonic in others and, in particular, how both patterns could emerge in the same community but at different scales (Chase & Leibold, 2002; Chase & Ryberg, 2004).

Mechanisms explaining monotonic pattern

Except in very harsh environments, facilitative effects at low and intermediate productivity are expected to promote coexistence (Mitchalet *et al*., 2006; Xiao *et al*., 2009) and so biodiversity should increase with productivity. Abrams (1995) suggested that (i) increased productivity may raise the abundance of rare species, thus reducing their extinction rates; (ii) increased productivity might increase the abundance of rare resources that are required by specialist species; and (iii) intraspecific density-dependent processes, such as interference behaviour or species-specific predation, increase with productivity, allowing species to coexist rather than be competitively excluded.

In my experiment the correlation between abundance and diversity at the channel scale supports Abrams' (1995) first (and simplest) explanation, that greater abundances sampled more rare taxa, thereby increasing overall richness. As a monotonic relationship at the channel scale resulted from manipulation of a uniform and common resource, it is unlikely that an increase in diversity resulted from specialist niches, Abram's second suggested mechanism. I have no evidence either way for his suggested third mechanism.

Mechanisms explaining unimodal pattern

From early on in the debate (e.g., Grime, 1973; Al Mufti *et al*., 1977) to recently (Fraser *et al*., 2015) competitive exclusion has been suggested as the cause of the decline in diversity at high productivity to explain the hump-shaped pattern. Abrams (1995) proposed two hypotheses that predict a hump-shaped productivity diversity relationship based on competition theory: (i) spatial heterogeneity in the relative supplies of resources changes with productivity and thus decreases diversity through competitive exclusion (Tilman, 1982; Tilman & Pacala, 1993); and (ii) higher productivity increases extinction rates and decrease colonisation rates in a system in which coexistence is a trade-off between colonisation ability and competitive ability. Tilman (1993) suggested that this mechanism produced a unimodal relationship in grasslands. Huston and DeAngelis (1994) also reasoned that competition for light causes competitive exclusion at high productivities, but through a different mechanism that does not assume spatial heterogeneity in resource supply rates, apart from what is produced from the growth of the plants themselves. They suggested that at low resource productivity, large zones of depleted nutrients around individual plants and a low level of nutrients causes competitive exclusion, whereas at high productivity, competition for light results in exclusion; the highest diversity therefore occurs at intermediate levels of productivity. Liebold (1999) also considered “resource heterogeneity” and “resource-ratio” hypotheses, and offered two additional hypotheses, also based on the dynamics of biotic interactions: the “paradox of enrichment” (Rosenzweig, 1971); and the “keystone-predator” hypotheses. He concluded that the patterns of distribution of planktonic organisms in pond communities were consistent with the hypothesis of productivity-dependent “keystone-predation” causing the unimodal relationship between productivity and diversity.

The idea that resource heterogeneity would change along a resource gradient was addressed in my experiment. I hypothesised that initially (0% litter) the artificial stream channels would be homogeneously depauperate, but spatial heterogeneity and invertebrate diversity would increase as resource patches (leaf packs) were added. As resource enrichment approached saturation, the point where productivity is no longer limited by the resource, spatial heterogeneity would decrease (as leaf packs filled the channels) and competitive interactions would cause diversity to decline. These processes could produce a hump-shaped relationship at the channel scale, but we observed a monotonic pattern. Where we did observe a hump-shaped pattern was at the cobble/leaf pack scale, where habitat heterogeneity was uniform. Likewise, other hypotheses that invoke biotic interactions as the cause of a decline in diversity at higher productivity would predict a hump-shaped relationship between productivity and diversity at the channel scale rather than the leaf pack scale.

Using simulations, Xiao *et al*. (2010) also found unimodal productivity-diversity patterns in neutral communities, although in most cases the diversity-productivity relationships diverged between competing and neutral communities at high productivity, with stronger declines in richness in competing communities.

Dispersal / colonization mechanism

Island biogeography theory predicts that local diversity will depend on the interplay of colonisation and extinction rates (McArthur & Wilson, 1967). The second of Abrams’ (1995) hypotheses invokes the trade-off in colonisation and extinction rates as a contributing factor in explaining a unimodal productivity-diversity relationship. Pärtel and Zobel (2007) hypothesized that in a community with a unimodal productivity-diversity relationship, species from intermediate productivity sites have higher dispersal probabilities (determined by the number of propagules and traits aiding dispersal) than species from low or high productivity sites. They found the dispersal probability due to seed number decreased significantly along the productivity gradient, whereas the probability due to dispersal syndrome (traits associated with aiding dispersal by animals, wind or water) increased along the productivity gradient. At low productivity, species without dispersal syndromes predominated, but at high productivity species with a low number of seed were common. Therefore, the total relative dispersal probability had a unimodal relationship with habitat productivity, correlating with the unimodal diversity-productivity pattern. They concluded that in conditions where species pool size and biotic interactions do not vary along productivity gradients, the variation in dispersal probabilities with productivity alone could produce the unimodal relationship.

Using a neutral model to investigate the productivity-diversity relationship Kadmon and Benjamani (2006) found increasing abundance and a decrease in stochastic extinctions from low to moderate levels of productivity. However, at higher levels of productivity, diversity decreased due to a change in the balance between reproduction and immigration, with an increase in reproduction, correlated to productivity, reducing the relative frequency of immigrants in the pool of potential colonisers (the "dilution effect"). Since only new immigrants have the potential to increase local species richness, increasing productivity was associated with a decrease in the rate by which new species were added to the local community. Likewise, Tilman (1993) concluded that decreased diversity in more productive plots in grassland fields was caused by inhibition of seedling establishment or survival (due to build-up of litter mass) resulting in reduced rates of recruitment of new species to replace those lost. He proposed colonisation limitation through litter build-up as an explanation of the hump-shaped productivity-diversity relationships observed by Al-Mufti *et al*. (1977) and Grime (1979) in preference to the "heterogeneity-diversity" hypothesis.

5.4.2 Scale: Monotonic at large scale vs. unimodal at small scale

My results concurred with those of Chase and Leibold (2002), who also found a scale-dependent productivity–diversity relationship, with a hump-shaped relationship at a local scale (among ponds), and a monotonic relationship at a regional scale (among watersheds). Geographic scale is increasingly recognised as an important influence on the drivers of biodiversity (Chase & Knight, 2013; Chase, 2014), including the patterns of productivity-diversity relationship (Oksanen, 1996; Mittlebach *et al*., 2001, Chase & Leibold, 2002; Chalcraft *et al*., 2004; Chase & Ryberg, 2004; Chase, 2007; Tonkin & Death, 2013). However, again the mechanisms that can generate different patterns at different scales have not been fully elucidated. But the fact that monotonic and unimodal patterns occur in the same assemblage under similar conditions, but at different scales, is strongly suggestive of a mechanism beyond simply competitive exclusion or alternative biotic interactions. Competitive exclusion could operate at the smaller scale to reduce richness at high productivity, but an additional explanation is required to understand how richness could concurrently continue to increase at the large scale.

ϒ diversity monotonic vs α diversity unimodal – β diversity increasing with productivity

Chase and Leibold (2002) propose that for a community to have a monotonic productivity-diversity relationship at the regional scale, but a unimodal relationship at the local scale, β diversity (compositional variation among local sites) would have to increase with productivity. β diversity is influenced by community assembly mechanisms including: deterministic processes where habitat heterogeneity leads to niche diversification across localities; stochastic process such as ecological drift, dispersal limitation, and differential colonisation and extinction dynamics across localities; or the interaction between deterministic and stochastic variation leading to more deterministic priority effects that vary across localities (Chase, 2003; Fukami & Morin, 2003; Chase, 2010). For β diversity to increase with productivity and influence regional (ϒ) diversity, then the influence of one or more of these mechanisms would have to increase with increasing productivity. Chase (2010) suggested that it was more likely that the variation in the importance of stochastic processes increased β diversity with productivity in pond communities. The hypothesis was that deterministic processes will be more prevalent in harsh environments, which filter out unsuitable taxa, but in productive environments stochastic processes due to differential colonisation history and priority effects will have a greater influence, leading to multiple stable equilibria and allowing for a greater representation of the regional pool (Chase, 2007). Chase (2003) suggests that single equilibrium outcomes are more likely in systems with small regional pools, high rates of connectance, low productivity and high disturbance; whereas, multiple stable equilibria are more likely in systems with large regional species pools, low rates of connectance, high productivity and low disturbance.

In the artificial stream channels, rapid rates of colonisation and dispersal (Chapter 4) suggest that the invertebrate assemblage inhabiting the leaf packs is in a dynamic flux at small (leaf pack) scales, but also are stable at these scales, as the assemblage fully colonised the cobble/leaf pack habitats within 24 days and remained stable through the 38 day duration of the experiment. It was not possible to track the history of individual leaf packs to test for priority effects, but ordination of the data indicated a progressive shift in assemblage composition through the colonisation period and a convergence of the compositions on days 24 and 38 (Chapter 4). These results do not support a case for multiple stable equilibria as an explanation for a scale-dependent productivity-diversity relationship that I found in this experiment, as proposed by Fukami & Morin (2003) and Chase (2010).

The high rates of colonisation and dispersal in the stream channels suggest a high temporal variance, which might give rise to the same effect as multiple stable equilibria, by resulting in spatial variation in community composition, at any point in time. Fukami (2004) refers to this as “mosaic cycles”, where particular species compositions replace one another over time, resulting in local community dissimilarity. However, my results did not detect increasing dissimilarity at higher % leaf pack cover. Similarly, while Chase (2010) found a nested ordination pattern, with increased variation with productivity, my results showed a shift in assemblage composition with % leaf pack cover, with the degree of variation in composition amongst leaf packs within channel treatments remaining the same across this gradient.

The divergence between channel-scale and cobble/leaf-pack-scale richness at high % leaf pack cover does suggest that there were new species occurring in cobble/leaf packs in higher % leaf pack cover treatments and it is intriguing why this divergence did not correspond to an increase in dissimilarity amongst cobble/leaf pack samples (β diversity). The longitudinal variation in abundance and richness may have affected the estimates of dissimilarity in our experiment as may the unequal number of leaf packs. But the ordination would counter this to some degree. The observed dissimilarity values were generally high throughout, and it may also have been that the observed differences in the number of taxa giving rise to the hump-shaped richness versus % leaf pack cover pattern were small (the range in richness of invertebrates on leaf packs being 15 to 33) relative to the species pool and number of rare taxa that could be dispersed across cobble/leaf pack habitat units (76 taxa were collected in total in the artificial channels – with many more expected in the stream proper). That is, a high regional species pool (ϒ), but a relatively low α diversity, increases the likelihood of high β diversity and compositional variation across local sites.

In this experiment the leaf packs represented habitat units, as well as a potential food source. Therefore, if dissimilarity is consistently high, maintained by a large species pool relative to the number of taxa on individual leaf packs, then by adding more leaf packs the channel scale (ϒ) diversity would be expected to increase. Therefore, at the channel scale, the monotonic pattern in the number of taxa versus % leaf pack cover was probably due to increased habitat area and a species-area effect, essentially a sampling effect, agreeing with Abrams’ (1995) first explanation for a monotonic productivity-diversity relationship. But this does not explain why the number of taxa on individual leaf packs (α diversity) declined at greater % leaf pack cover.

5.4.3 Constrained immigration an explanation for decline in α diversity at high productivity

The numbers of potential macroinvertebrate immigrants entering the artificial stream channels through drift was determined by the stream flow into the channels. The differences in the number of leaf packs within these channels then altered the immigration probabilities at the cobble/leaf pack scale, because there were a greater number of leaf pack units to colonise within more productive channels (greater % leaf pack cover) but a similar number of drifting macroinvertebrates entering each channel.

The colonisation and dispersal experiments (Chapter 4) demonstrated that the invertebrate assemblage inhabiting these leaf packs approximated an equilibrium model of immigration-emigration (MacArthur & Wilson, 1967). Therefore, the immigration-emigration dynamics, specifically a constrained immigration rate, could explain the decline in α diversity on leaf packs in the high % leaf pack cover channels, thereby explaining the discrepancy between the patterns at the larger and smaller scales. That is, as the rate of invertebrate immigration to the channels is constant, then the number of immigrants (individuals and species) is increasingly divided within the channel by the increasing number of leaf litter habitat units. At the same time, when there are few leaf litter packs in the channels, individuals are more easily lost from the channels, leading to a relatively high extinction (emigration) rate, so diversity remains low. At intermediate levels of litter pack cover the habitats become more available to drifting invertebrates, the cobble/leaf pack assemblages become more established, extinction (emigration) rates decline and diversity rises accordingly. However, at high levels of litter pack cover the channels can support greater numbers of macroinvertebrates, but the number of drifting immigrants is increasingly divided amongst greater numbers of leaf packs, compared to the number available at lower leaf pack cover, so there is a reduction in new immigrants colonising individual leaf packs and their diversity declines (Figure 5.12).

This proposed explanation is analogous to Pärtel & Zobel's (2007) hypothesis that in a community with a unimodal productivity-diversity relationship, species from intermediate productivity sites have higher dispersal probabilities than species from low or high productivity sites. A mechanism invoking a constrained immigration also agrees with the conclusions of Xiao *et al*. (2010) that when dispersal rate was low unimodal patterns develop in both neutral and competing communities. However, my results are most analogous to the process that Kadmon and Benjamani (2006) have called the “dilution effect”, albeit dilution of immigrants rather than within-patch reproduction.

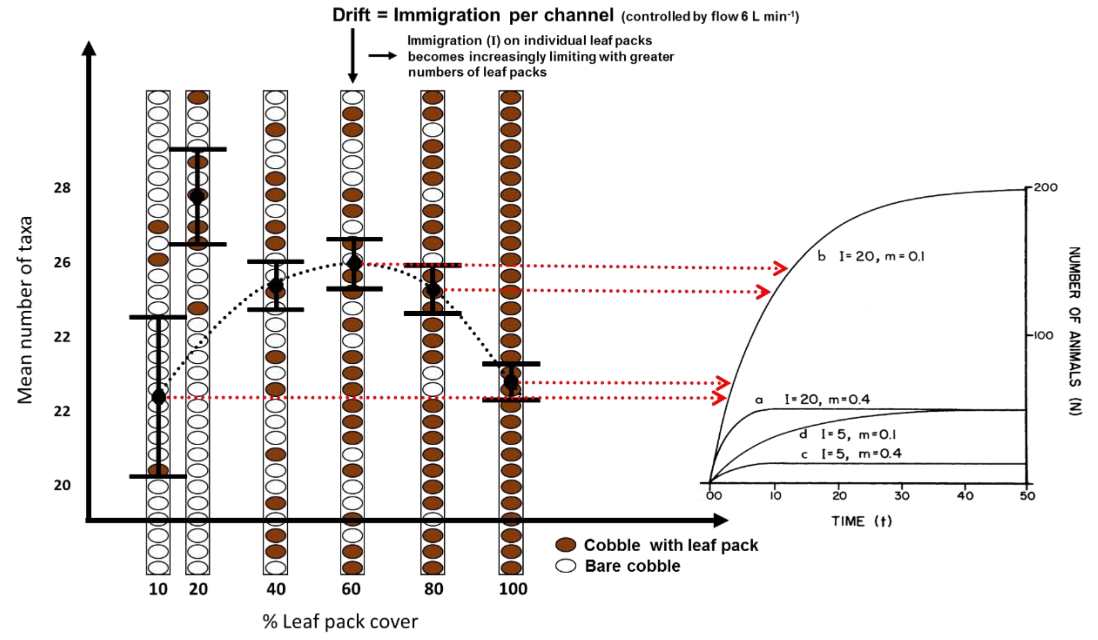


Figure 5.12. Schematic representation of the concept that a constrained immigration rate led to a hump-shaped relationship between diversity and % leaf pack cover at the cobble/leaf pack scale. The experimental treatments and observed pattern of mean diversity are shown on the left. On the right is a graphical representation of the Wilson and McArthur (1967) equilibrium model (redrawn from Sheldon 1984) as applied in Chapter 4, showing how densities will be affected by immigration rates (I) or emigration (extinction) rates (m).

However, the neutral models used by Kadmon and Benajmini (2006) and Xiao *et al*. (2010) did not consider scale or β diversity and how they might increase with productivity, producing a hump-shaped relationship for α diversity but a monotonic pattern for ϒ diversity.

A similar scale-dependent pattern was observed for abundance and diversity, which were correlated, suggesting that a sampling effect was driving diversity. The longitudinal gradients observed within the channels were also likely to be caused by differences in immigration rates across cobble/leaf pack units. It is notable that the slope of the within-channel gradient in diversity changed to negative at the peak of the “hump” in the relationship with % leaf pack cover. It appears at this point in the gradient that the number of immigrants entering the channels through drift became limiting and the leaf packs in the upstream positions received a greater complement of immigrants than downstream leaf packs (as immigrants were drawn out of the drift). This factor may also explain why the cobble/leaf pack units in the 20% leaf pack treatment tended to have slightly higher diversity, as leaf packs, although randomly positioned, happened to be located mostly in the upstream section in that channel. The patterns for abundance and diversity differed, as the downstream gradient for abundance on cobble/leaf packs was positive across the leaf pack gradient. The different slopes of the gradients in abundance and diversity could indicate that competitive exclusion was operating within cobble/leaf packs, which would likely produce a stronger hump-shaped relationship (Xiao *et al*., 2010). However, the density of individuals, although greater downstream where richness declined within the channels, was lower in the higher % leaf pack treatments, particularly the 100% treatment, and runs counter to that argument. Therefore, I conclude that the effect through constrained immigration is a more likely mechanism producing the patterns observed.

5.4.3 Conclusions

It may be that the scale-dependent pattern in the productivity-diversity relationship only arises where β diversity is high, and where β diversity is low a hump-shaped productivity-diversity relationship may be expected at both local and regional scales. Differences in β diversity may therefore explain some of the contrasting patterns in the productivity–diversity relationship reported in the literature, which have made this relationship so controversial. Hump-shaped productivity–diversity has often been referred to as a local-scale pattern, but has also been reported at large (even global) scales (e.g., Fraser *et al.*, 2015). It is not clear if most of these patterns have been derived using samples of α diversity, but it would be interesting to review this data comparing patterns of α and ϒ diversity.

Pärtel & Zobel (2007) found that positive productivity-diversity relationships have been reported more frequently in the tropics. Similarly, Pärtel *et al*. (2007) report that the proportion of unimodal relationship increases significantly with distance from the equator and were dominant in the temperate zone, but positive relationships were significantly more common in the tropics. They concluded this was due to evolutionary history resulting in larger species pools in the tropics. The likelihood of a high β diversity and compositional variation across local sites may be greater where there is a large regional species pool (ϒ). I suspect that the relationship between productivity and α diversity may generally be hump-shaped, through a decrease in the rate by which new species are added to the local community to replace species lost though stochastic extinctions at high productivity, resulting in a reduction in the steady state number of species. But a large species pool may increase the probability of high β diversity and this will result in the large-scale relationship between productivity and ϒ diversity being monotonic. Conversely, a lower regional species pool may result in lower β diversity and so the pattern is unimodal at local and regional scales.

Finally, a hump-shaped productivity diversity relationship has very significant implications for the conservation of species richness because it predicts a decline in diversity at high productivity (Pierce 2014). It is important to understand the processes that determine a hump-shaped relationship because productivity is increasingly being affected by anthropogenic fertilisation in both terrestrial and aquatic environments. Therefore, an understanding of the processes that produce a hump-shaped productivity–diversity relationship will help us to develop the necessary measures to predict when a decline in diversity may be likely.

5.5 References

Abrams P. A. (1995) Monotonic or unimodal diversity productivity gradients – What does competition theory predict. *Ecology* **76**: 2019-2027.

Abramsky Z. & Rosenzweig M.L. (1984) Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature* **309**: 150-151.

Adler P.B., Seabloom E.W., Borer E.T., Hillebrand H., Hautlier Y., Hector A., Harpole W.S., O'Halloran L.R., Grace J.B., Anderson T.M., Bakker J.D., Biederman L.A., Brown C.S., Buckley Y.M., Calabrese L.B., Chu C.J., Cleland E.E., Collins S.L., Cottingham K.L., Crawley M.J., Damschen E.I., Davies K.F., DeCrappeo N.M., Fay P.A., Firn J., Frater P., Gasarch E.I., Gruner D.S., Hagenah N., Hille Ris Lanbers J., Humphries H., Jin V.L., Kay A.D., Kirkman K.P., Lein J.A., Knops J.M., La Pierre K.J., Lambrinos J.G., Li W., McDougall A.S., McCulley R.L., Melbourne B.A., Mitchell C.E., Morre J.L., Morgan J.W., Mortensen B., Orrock J.L., Prober S.M., Pyke D.A., Risch A.C., Schuetz M., Smith M.D., Stevens C.J., Sullivan L.L., Wang G., Wragg P.D., Wright P.D. & Yang L.H. (2011) Productivity is a poor predictor of plant species richness. *Science* **333**: 1750-1752.

Al-Mufti M.M., Sydes C.L., Furness S.B., Grime J.P. & Band S.R. (1977) A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* **65**: 759-791.

Anderson N.H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **19**: 3083-3088.

Arsuffi T.L. & Suberkropp K. 1985. Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. *Oikos* **45**: 50-58.

Benfield E.F. & Webster J.R. (1985) Shredder abundance and leaf breakdown in an Appalachian Mountain stream. *Freshwater Biology* **15**: 113-120.

Bott T.L. (1983) Primary productivity in streams. Pages 29-53 **In** Barnes, J.R. and Minshall, G.W. (eds.) *Stream Ecology. Application and Testing of General Ecological Theory.* Plenum Press, New York.

Cardinale B. J., Hillebrand H., Harpole W. S., Gross K., & Ptacnik R. (2009) Separating the influence of resource '"availability" from resource "imbalance"' on productivity-diversity relationships. *Ecology Letters* **12**: 475-487.

Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* **8**: 559-568.

Chalcraft D.R., Williams J.W., Smith M.D. & Willig M.R. (2004) Scale dependence in the species-richness-productivity relationship: The role of species turnover. *Ecology* **85**: 2701-2708.

Chase J. M. (2003) Community assembly: when should history matter? *Oecologia* **136**: 489-498.

Chase J. M. (2007) Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* **104**: 17430-17434.

Chase J. M. (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**: 1388-1391.

Chase J.M. (2014) Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science* **25**: 319-322.

Chase J.M. & Knight T.M. (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters* **16**(suppl. 1): 17-26.

Chase J.M. & Leibold M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**: 427-430.

Chase J. M. & Ryberg W. A. (2004) Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecology Letters* **7**: 676-683.

Cheshire K., Boyero L. & Pearson R.G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Connolly N.M., Christidis F., McKie B., Boyero L. & Pearson R. (2008) Diversity of invertebrates in Wet Tropics streams: patterns and processes. Pages 161-177 **In** Stork, N. E. & Turton, S. M. (eds.) *Living in a Dynamic Tropical Forest Landscape*. Wiley-Blackwell, Oxford UK.

Connolly N.M. & Pearson R.G. (2007) The effect of fine sediment on tropical stream macroinvertebrate assemblages: a comparison using flow-through artificial stream channels and recirculating mesocosms. *Hydrobiologia* **592**: 423-438.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Currie D.J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist* **137**: 27-49.

Currie D.J. & Paquin V. (1987) Large-scale biogeographic patterns of species richness of trees. *Nature* **329**: 326-327.

Dodson S.I., Arnott, S.E. & Cottingham K.L. (2000) The relationship in lake communities between primary productivity and species richness. *Ecology* **81**: 2662-2679.

Ferreira V. & Chauvet E. (2011) Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* **17**: 551-564.

Fisher S.G. & Likens G.E. (1972) Stream ecosystem: organic energy budget. *BioScience* **22**: 33-35.

Fittkau E.J. & Klinge H. (1973) On biomass and trophic structure of the Central Amazon rain forest ecosystem. *Biotropica* **5**: 2-14.

Fraser L.H., Pither J., Jentsch A., Sternberg M., Zobel M., Askarizadeh D., Bartha S., Beierkuhnlein C., Bennett J.A., Bittel A., Boldgiv B., Boldrini I.I., Bork E., Brown L., Cabido M., Cahill J., Carlyle C.N., Campetella G., Chelli S., Cohen O., Csergo A-M., Díaz S., Enrico L., Ensing D., Fidelis A., Fridley J.D., Foster B., Garris H., Goheen J.R., Henry H.A.L., Hohn M., Hassan Jouri M., Klironomos J., Koorem K., Lawrence-Lodge R., Long R., Manning P., Mitchell R., Moora M., Müller S.C., Nabinger C., Naseri K., Overbeck G.E., Palmer T.M., Parsons S., Pesek M., Pillar V.D., Pringle R.M., Roccaforte K., Schmidt A., Shang Z., Stahlmann R., Stotz G.C., Sugiyama S., Szentes A., Thonpson D., Tungalag R., Undrakhbold S., van Rooyen M., Wellstein C., Wilson J.B. & Zupo T. (2015) Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* **349**: 302-305.

Fridley J.D., Grime J.P., Huston M.A., Pierce S., Smart S.M, Thompson K., Börger L., Brooker R.W., Cerabolini B.E., Gross N., Liancourt P., Michalet R. & Le Bagousse-Pinquet Y. (2012) Comment on “Productivity is a poor predictor of plant species richness”. Science **335**: 1441.

Fukami T. (2004) Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. *Population Ecology* **46**: 137-147.

Fukami T. & Morin P. J. (2003) Productivity-biodiversity relationships depend on the history of community assembly. *Nature* **424**: 423-426.

Gaston K.J. 2000 Global patterns in biodiversity. *Nature* **405**: 220-227.

Grace J.B., Adler P.B., Seabloom E.W., Borer E.T., Hillebrand H., Hautier Y., Hector A., Harpole W.S., O’Halloran W.S., Anderson T.M., Bakker J.D., Brown C.S., Buckley Y.M., Collins S.L., Cottingham K.L., Crawley M.J., Damschen E.I., Davies K.F., De Crappeo N.M., Fay P.A., Firn J., Gruner D.S., Hagenah N., Jin V.L., Kirkman K.P., Knops J.M.H., La Pierre K.J., Lambrinos J.G., Melbourne B.A., Mitchell C.E., Moore J.L., Morgan J.W., Orrock J.L., Prober S.M., Stevens C.J., Wragg P.D. & Yang L.H. (2012) Response to comments on “Productivity is a poor predictor of plant species richness”. *Science* **335**: 1441.

Grace J.B., Anderson T.M., Seabloom E.W., Borer E.T., Adler P.B., Harpole W.S., Hautier, Y., Hillebrand H., Lind E.M., Pärtel M., Bakker J.D., Buckley Y.M., Crawley M.J., Damschen E.I., Davies K.F., Fay P.A., Firn J., Gruner D.S., Hector A., Knops J.M.H., MacDougall A.S., Melbourne B.A., Morgan J.W., Orrock J.L., Prober S.M. & Smith M.D. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* doi:10.1038/nature16524.

Grime J.P. (1973) Control of species density in herbaceous vegetation. *Journal of Environmental Management* **1**: 151-167.

Grime J.P. (1979) *Plant strategies and vegetation processes*. Wiley, Chichester, UK.

Gross K. (2016) Biodiversity and productivity entwined. *Nature* doi:10.1038/nature16867.

Gross K.L., Willig M.R., Gough L., Inouye R. & Cox S.B. (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* **89**: 417-427.

Gulis V., Ferreira V. & Graça M.A.S. (2006) Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream assessment. *Freshwater Biology* **51**: 1655-1669.

Harrison S., Davies K.F., Safford H.D. & Viers J.H. (2006) Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology* **94**: 110-117.

Huston M. (1979) A general hypothesis of species diversity. *The American Naturalist* **113**: 81-100.

Huston M.A. & De Angelis D.L. (1994) Competition and coexistence – the effects of resource transport and supply. *The American Naturalist* **144**: 954-977.

Kadmon R. & Benjamini Y. (2006) Effects of productivity and disturbance on species richness: A neutral model. *The American Naturalist* **167**: 939-946.

Kaushik N.K. & Hynes H.B.N. (1971) The fate of the dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**: 465-515.

Kondoh M. (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**: 269-271.

Korhonen J.J., Wang J. and Soininen J. (2011) Productivity-Diversity relationship in lake plankton communities. *PLoS One* **6**(8): e22041. Doi:10.1371/journal.pone.0022041.

Lake P.S., Schreiber E.S.G., Milne B.J. & Pearson R.G. (1994) Species richness in streams: patterns over time, with stream size and with latitude. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie.* **25**: 1822-1826.

Lamberti G.A. & Steinman A.D. (1997) A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society* **16**: 95-104.

Leibold M.A. (1999) Biodiversity and nutrient enrichment in pond plankton communities. *Evolutionary Ecology Research* **1**: 73-95.

MacArthur R. H. & Wilson E. O. (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McBride P.D., Cusens J. & Gillman L.N (2014) Revisiting spatial scale in the productivity-species richness relationship: fundamental issues and global change implications. *AoB Plants* **6**: olu057; doi:10.1093/aobpla/plus057.

McCune B. & Mefford M.J. (2011) PC-ORD. Multivariate Analysis of Ecological Data. Version 6.20. MjM Software: Gleneden Beach, Oregon, USA.

Michalet R., Brooker R.W., Cavieres L.A., Kikvidze Z., Lortie C.J., Pugnaire F.I., Valiente-Banuet A. & Callaway R.M. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* **9**: 767-773.

Minshall G.W (1978) Autotrophy in stream ecosystems. *BioScience* **28**: 767-771.

Mitchell-Olds T. & Shaw R.G. (1997) Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* **41**: 1149-1161.

Mittlebach G.G., Steiner S.F., Scheiner S.M., Gross K.L., Reynolds H.L., Waide R.B., Willig M.R., Dodson S.I. & Gough L. (2001) What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381-2396.

Nijboer R.C. & Verdonschot P.F.M. (2004) Variable selection for modelling effects of eutrophication on stream and river ecosystems. *Ecological Modelling* **177**: 17-39.

Nolen J. A. & Pearson R.G. (1993) Processing of litter from an Australian tropical stream by *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae). *Freshwater Biology* **29**: 469-479.

Oksanen J. (1996) Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology* **84**: 293-295.

Pan X., Liu F. & Zhang M. (2012) Comment on “Productivity is a poor predictor of plant species richness”. *Science* **335**: 1441.

Pärtel M. & Zobel M. (2007) Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. *Journal of Ecology* **95**: 90-94.

Pärtel M., Laanisto L. & Zobel M. (2007) Contrasting plant productivity-diversity realtionships across latitude: the role of evolutionary history. *Ecology* **88**: 1091-1097.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G., Connolly N.M. & Boyero L. (2015) Ecology of streams in a biogeographic isolate—the Queensland Wet Tropics, Australia. *Freshwater Science* **34**: 797-819

Pierce S. (2014) Implications for biodiversity conservation of a lack of consensus regarding the humped-back model of species richness and biomass production. *Functional Ecology* **28**: 253-257.

R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Richardson J.S. (1992) Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology* **27**: 169-176.

Rosemond A.D., Pringle C.M., Ramirez A. & Paul. M.J. (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology* **82**: 2279-2293.

Rosenzweig M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**: 385-387.

Rosenzweig M.L. (1995) *Species Diversity in Space and Time.* Cambridge University Press.

Rosenzweig M.L. & Abramsky Z. (1993) How are diversity and productivity related? Pages 52-65 **In** Ricklefs R. & Schluter D. (eds.) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives.* University of Chicago Press.

Sheldon A.L (1984) Colonisation dynamics of aquatic insects. Pages 401-429 **In** Resh V.H. & Rosenberg D.M. (eds.) *The Ecology of Aquatic Insects*. Praeger Publishers, New York.

Smith V.H., Tilman G.D. & Nekola J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**: 179-196.

Suberkropp K. & Klug M.J. (1976) Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* **57**: 707-719.

ter Braak C.J.F. & Loomin C.W.N. (1986) Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* **65**: 3-11.

Tilman D. (1982) Resource *Competition and Community Structure.* Princeton University Press.

Tilman D. (1993) Species richness of experimental productivity gradients: how important is colonisation limitation? *Ecology* **74**: 2179-2191.

Tilman D. & Pacala S. (1993) The maintenance of species richness in plant communities. Pages 13-25 **In** R.E. Ricklefs & D. Schluter (eds.) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.

Tonkin J.D. & Death R.G. (2012) Consistent effects of productivity and disturbance on diversity between landscapes. *Ecosphere* **3**: art108.

Tonkin J.D. & Death R.G. (2013) Scale dependent effects of productivity and disturbance on diversity in streams. *Fundamentals of Applied Limnology* **182**: 283-295.

Tonkin J.D., Death R.G. & Collier K.J (2013) Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams? *Hydrobiologia* **701**:159-172.

Vitousek P.M., Aber J.D., Howarth R.W., Likens G.E., Matson P.A., Schindler D.W., Schlesinger W.H. & Tilman D.G. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**: 737-750.

Waide R.B., Willig M.R., Steiner S.F., Mittlebach G., Gough L., Dodson S.I., Juday G.P., & Parmenter R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* **30**: 257-300.

Walker K., Neboiss A., Dean J. & Cartwright D. (1995) A preliminary investigation of the caddis-flies (Insecta: Trichoptera) of the Queensland Wet Tropics. *Australian Entomology* **22**: 19-31.

Whitaker R.J. (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness-productivity relationship. *Ecology* **91**: 2522-2533.

Wright D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos* **41**: 496-506.

Wright D.H., Currie D.J. & Maurer B.A. (1993) Energy supply and patterns of species richness on local and regional scales. Pages 66-74 **In** Ricklefs R. & Schluter D. (eds.) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago, University Chicago Press.

Xiao S., Michalet R., Wang G. & Chen S.Y. (2009) The interplay between species' positive and negative interactions shapes the community biomass-species richness relationship. *Oikos* **118**: 1343-1348.

Xiao S., Zobel M., Szava-Kovats R. & Partel, M (2010) The effects of species pool, dispersal and competition on the diversity-productivity relationship. *Global Ecology and Biogeography* **19**: 343-351.

Chapter 6

Influence of riparian vegetation on water quality and invertebrate assemblages in streams in an agricultural landscape.[3]

6.1 Introduction

Declines in stream health associated with land clearing and agricultural development are well-documented (e.g., Richards *et al.*, 1996; Wang *et al.*, 1997; Maloney & Weller, 2011). Streams draining agricultural lands frequently have high concentrations of fertilizer-derived nutrients and other agrichemicals (Bainbridge *et al.*, 2009; Connolly *et al.*, 2015), altered geomorphology and instream habitats (Bunn *et al.*, 1998; Mazeika *et al.*, 2004; Connolly *et al.* 2007a; Dahm *et al.*, 2013) and disturbed riparian zones (Pusey & Arthington, 2003; Waite, 2014), and they support fewer species of invertebrates and fish than streams draining forested catchments (Lenat & Crawford, 1994; Wang *et al.*, 1997). However, land-use impacts are varied and complex, because of variation in hydrogeomorphic settings and composition of biotic assemblages, and because streams can be affected by multiple disturbances (Connolly & Pearson, 2004; Maloney & Weller; 2011, Clapcott *et al.*, 2012; Clements *et al.*, 2015).

Riparian forests influence the physical, chemical and biological components of steams and mediate linkages between the terrestrial and aquatic environments (Karr & Schlosser, 1978; Gregory *et al.*, 1991; Sweeney, 1992; England & Rosemond, 2004). They have long been recognised for their roles in sustaining habit integrity, biodiversity, stream bank stability and water quality (e.g., Naiman *et al.*, 1993; Decamps *et al.*, 2004; de Souza *et al.*, 2013; Fernandes *et al.*, 2014) and providing organic subsidies in the form or organic litter input (Nakano & Murakami, 2001). In agricultural areas, riparian zones have been extensively reported to be major filters and/or processors of sediments and inorganic nutrients, providing a buffer to the stream ecosystem (e.g., Lowrance *et al.*, 1984; Fail *et al.*, 1987; Osborne & Kovacic, 1993; Hill, 1996; Goss *et al.*, 2014). Connections between riparian vegetation and stream invertebrate assemblages have been reported over several decades, particularly with reference to the detrital trophic pathway, but also in relation to shade and habitat (Kaushik & Hynes, 1971;

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[3] This chapter contributed substantially to Connolly *et al*. (2015) and Connolly *et al*. (2016).

Cummins & Lauff, 1969; Dudgeon, 1989, 1994; Cheshire *et al.*, 2005). Riparian zones are therefore vital to normal ecosystem function and stream health, but the links are variable and may be difficult to demonstrate and apply to riparian management to achieve ecological objectives (Greenwood *et al.*, 2012; Hansen *et al.*, 2015).

The clearing of riparian vegetation is a major factor affecting the integrity of streams (Osborne & Kovacic, 1993; Lorion & Kennedy, 2009), diminishing the stream's resilience to changes in land use and increasing the export of sediments and agricultural chemicals (Decamps *et al*., 2004; de Souza *et al*., 2013; Fernandes *et al*., 2014; Goss *et al*., 2014). Impacts within streams include shifts in benthic community structure and declines in invertebrate diversity (Benstead *et al*., 2003; Bojsen & Jacobsen 2003; Iwata *et al*., 2003; Lorion & Kennedy, 2009). Waite (2014) reported that the nature of the riparian zone was one of the most important variables influencing invertebrate assemblages in eastern US streams. Lorion and Kennedy (2009) found few studies on the effectiveness of riparian buffers on tropical stream ecosystems, but reported that buffers reduced the effects of deforestation on benthic communities. Likewise, Dudgeon (1994) demonstrated a positive influence of riparian shade and detritus on invertebrates in New Guinea streams, but found no such clear relationship in Hong Kong (Dudgeon, 1989). In south-eastern Australian streams, standing stocks of benthic detritus, an important resource for invertebrates, were very low where riparian canopy cover was < 35%, indicating the need for restoration of canopy cover (Reid *et al.*, 2008). Rosemond *et al*. (2002; 2015) have also described how the standing stock, decay rate and quality of detritus in the detrital food web in streams is further affected by the input of exogenous nutrients (through mechanisms described in Chapter 3).

Catchment landform dictates patterns in human land use, and so anthropogenic impacts are commonly superimposed on natural gradients. Understanding these interactions is a key challenge in assessing the ecological integrity of streams (Allan, 2004). Natural longitudinal gradients of physical conditions (e.g., slope, current velocity, substratum) are characteristic of streams and are typically accompanied by changes in composition of biotic assemblages (Vannote *et al*., 1980; Grubaugh *et al*., 1996; Marchant *et al*., 1999). The linear nature of streams results in the accumulation of anthropogenic influences along them, as increasing areas of the catchment are used for agriculture or other human land uses, covarying with natural gradients in the stream. For example, in the Australian Wet Tropics bioregion, the lowland floodplains are largely developed for intensive sugar cane production, and stream water quality and riparian condition both negatively correlate with area of agricultural land use

(Bainbridge *et al.*, 2009; Mackay *et al.*, 2010; Connolly *et al.*, 2015). Therefore, in determining the influence of land use and riparian vegetation clearing on stream ecology it is necessary to account for both natural and anthropogenic gradients. However, there are few studies that investigate the influence of anthropogenic impacts on the natural longitudinal patterns in benthic community composition (exceptions are Grubaugh *et al.*, 1996; Delongi & Brusven, 1998; Niyogi *et al.*, 2007).

In the Wet Tropics, the floodplain waterways that connect the Queensland Wet Tropics World Heritage Area and the Great Barrier Reef World Heritage Area are affected by widespread degradation and loss of native riparian vegetation and contamination by agricultural chemicals as a result of extensive agricultural development (Bainbridge *et al*., 2009; Pearson *et al*., 2013). However, riparian restoration has been undertaken in some Wet Tropics catchments in order to buffer agricultural impacts (Werren, 1998; Erskine, 2002). I investigated the impacts of riparian clearing on water quality and invertebrate distributions in lowland reaches of four streams in two adjacent Wet Tropics catchments (Mulgrave River and Russell River) with the aim of identifying the causes of any differences in invertebrate assemblages along and between streams. Both catchments have extensive areas of their floodplains used for sugarcane production, but there is contrasting stream management between them: on the Mulgrave floodplain, riparian forest has been maintained and improved through replanting schemes, while on the Russell floodplain, the riparian zone is severely degraded, with sugarcane grown up to the stream banks, as in much of the Wet Tropics region (Werren, 1998; Mackay *et al.*, 2010; Connolly *et al.*, 2015) (Appendices – Figure A6.1).

My approach was to sample water quality and benthic invertebrates along the floodplain reach of each stream and separate the confounding effects of natural gradients and land use, so that I could compare streams with different degrees of anthropogenic disturbance, especially loss of riparian forest. The null hypotheses were that invertebrate assemblages would be unaffected by gradients in hydraulic habitat, water quality characteristics and condition of the riparian vegetation.

6.2 Methods

6.2.1. Study streams

Four streams were sampled in the central section of the Wet Tropics (Figure 6.1): two in the Mulgrave catchment (Little Mulgrave R. and Behana Ck.), where native riparian forest is largely intact, and two in the adjacent Russell catchment (Woopen Ck. and Babinda Ck.), where riparian vegetation has been extensively degraded. The Russell and Mulgrave rivers are located approximately centrally in the Wet Tropics bioregion, in the wettest part of Australia. The streams descend through pristine montane rainforest (gradient 6 – 16%), then meet and cross narrow coastal floodplains (gradient 0.4 – 1%). The coastal mountains are mainly granitic, but with extensive flows of basalt, especially in the upper Mulgrave catchment. Granitic soils predominate on the alluvial floodplains. The region is warm and humid, with annual rainfall in excess of 4000-mm in the lowlands (e.g., mean 4,286 mm at Babinda) and up to 12,461-mm at the summit of Mt Bellenden Ker (7 km north-east of Babinda township, Figure 6.1) (Australian Bureau of Meteorology data). Stream flows are perennial and reflect the pattern of rainfall, 60% of which occurs in the summer (December to March), although heavy rainfall can occur in any month. Sub-surface water discharges to surface drains and streams, and can cause rapid water-level rise and recession in response to rainfall (Hunter, 2012). The upper parts of the catchments are covered in dense rainforest and are protected as national parks within the Wet Tropics World Heritage Area, while the coastal floodplains have been largely cleared for agriculture and are mostly outside protected areas (Januchowski-Hartley *et al*., 2011). Fertilizer application practices were similar in the two catchments (approximately 160–170 kg N/ha—Rayment, 2003).

The study was restricted to the floodplain sections of the four study streams. It was expected that anthropogenic influence on water quality would increase with distance downstream as the area of agriculture in the catchment increased (Bainbridge *et al*., 2009) as the streams are all "gaining" streams (Hunter, 2012), so sampling sites were distributed at regular (~1 to 1.5 km) intervals along each stream, from just within national park boundaries near the base of the mountains, then across the developed floodplain to the confluence with the Mulgrave or Russell Rivers (Figure 6.1; Appendices – Table A6.1). Samples were collected in June and July 2005 during a period of stable base flow.

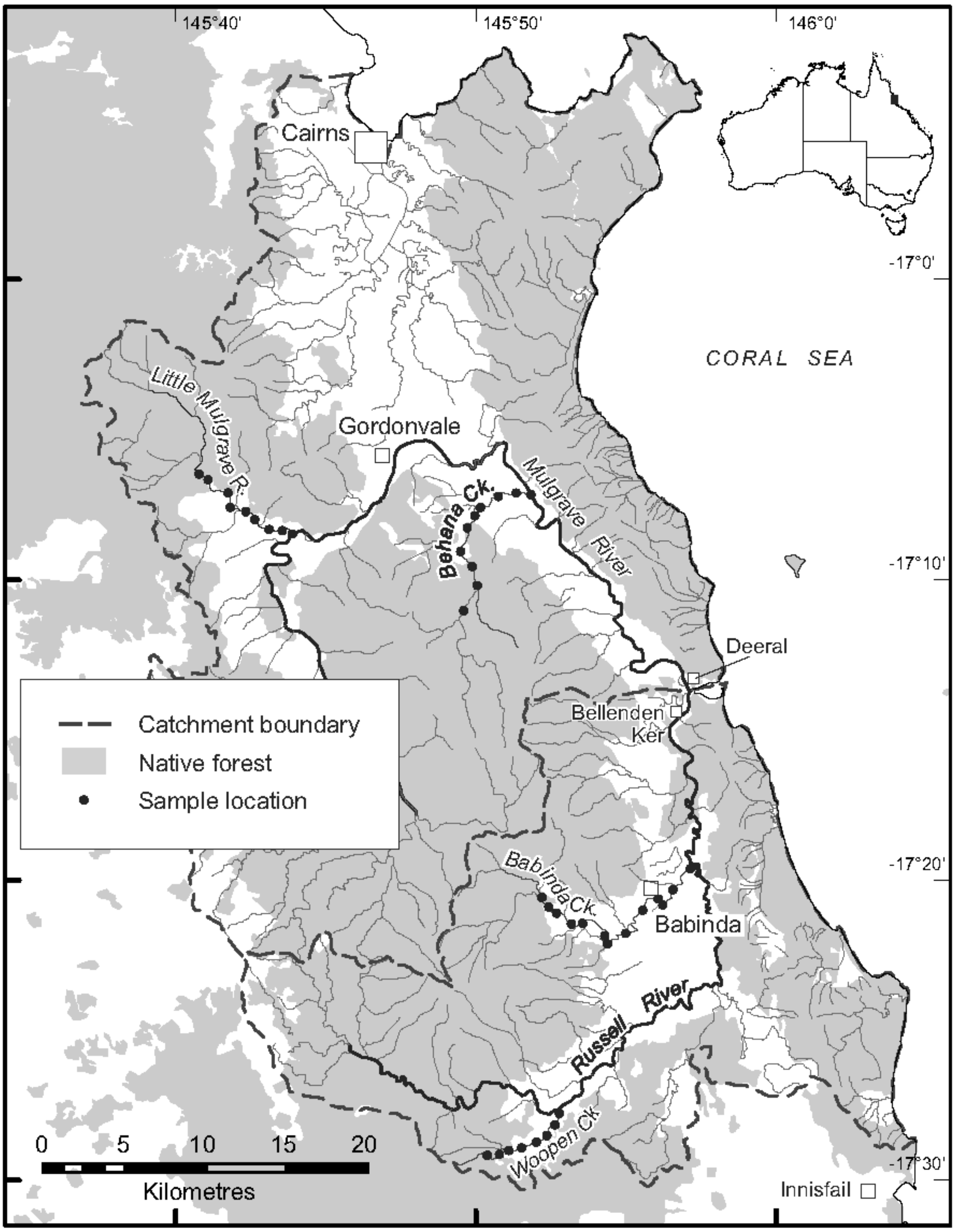

Figure 6.1. The Russell and Mulgrave River catchments and locations of the main study streams. Sample sites (●) were located at intervals of approximately 1 to 1.5 km along each stream from the base of the mountain range to the confluence with either the Russell or Mulgrave Rivers.

6.2.1 Landscape and riparian vegetation data collection

The catchment area for each site was determined using ArcMap 9.1, a 25-m digital elevation model from the Queensland Government and 1:50 000 drainage line data from the Wet Tropics Management Authority. All data were in a GDA94 geographic coordinate system. We used the Queensland Government's Land Use Mapping Program with data from 2005 to calculate the surface area of seven land-use categories in the catchment of each sample site. Categories were conservation, sugar cane, other cropping, grazing, residential/rural-residential, industrial and water storage.

Percentage cover of riparian forest was estimated at each site from measurements of 10 positions along 100-m of stream using a spherical densitometer (Lemmon, 1956). Overall riparian condition was assessed following Werren and Arthington (2002) by rating riparian-zone width, linear continuity, canopy vigor/crown health, proportion of native and alien species, and extent of native species regeneration, each on a 1 (poor) to 5 (good) scale for each stream bank (Mackay *et al.*, 2010). The scores were summed to give a score of 10 – 50 for each transect and then averaged to give a bank score. Mean upstream width of riparian forest was measured at 200-m intervals for each site using Google Earth©. The ratio of mean riparian width to mean width of agriculture (i.e., area/distance downstream) upstream of each site was used as a predictor of possible riparian performance.

6.2.2 Hydraulic variables and substratum particle size

At each site stream discharge and power were estimated from measurements of hydraulic variables following Brookes (1983, 1990). Only riffle habitat was sampled at each site. Cross-sectional area was calculated using wetted width × mean depth at 10 equidistant points across the stream using a staff and dumpy level. Site current velocity was estimated as the mean of velocity measured at 0.6 times the stream depth at the same 10 points using a Swoffer model 2100 flow meter (Mackay *et al.*, 2010). The stream gradient was measured as the change in height of the water surface from 50 m upstream to 50 m downstream of the study riffle, using a staff and dumpy level. Reynolds number and Froude number were calculated following Gordon *et al*. (2004). Residency of water in the study reach was estimated from reach length (between the most upstream and each downstream site) and mean current velocity across sites.

Sediment particle size of the target riffle was sampled using a zig-zag method (Bunte & Abt, 2001) and classified using the Wentworth Scale (Wentworth, 1922). A systematic bank-to-bank path was chosen to pick up and measure the intermediate axis of 100 clasts (substratum particles) spaced regularly across the stream bed. Fine-particle size distributions were determined by dry-sieving samples in the laboratory using mesh sizes from 4 ϕ (0.0625 mm) to -6 ϕ (64 mm). Finer material was separated hydrometrically, while particles larger than -6 ϕ were measured with vernier callipers (Rowell, 1994; Gordon *et al.*, 2004). Particle-size statistics were calculated using *GRADISTAT* Version 4.0 (Blott & Pye, 2001).

6.2.3 Water quality measurements

Water samples were collected during periods of base flow. Single surveys were undertaken by canoe in the Little Mulgrave River, Behana Creek and Babinda Creek, allowing multiple sites to be sampled over a short period of time. Woopen Creek was too shallow to canoe, so samples were collected at accessible sites along the stream.

Temperature, pH, electrical conductivity and dissolved oxygen were measured at each site using a Hydrolab H20 multi-parameter instrument, which was calibrated daily. Water samples were collected in acid-washed polyethylene bottles. Filterable nutrients were filtered on-site through pre-rinsed filter modules (MiniSart 0.45µm cellulose acetate, Sartorius, Germany), and all samples were stored temporarily on ice and frozen within two hours of collection. Samples were analysed by the Australian Centre for Tropical Freshwater Research (now TropWater) at James Cook University, Townsville, for total dissolved solids, total nitrogen (TN), total filterable nitrogen (TFN), ammonia, oxidised nitrogen (NO_x – i.e., nitrate + nitrite), total phosphorus (TP), total filterable phosphorus (TFP) and filterable reactive phosphorus (FRP – essentially phosphate) (Bainbridge *et al.*, 2009). Samples for TN, TP, TFN and TFP were digested in an autoclave using an alkaline persulfate technique (modified from Hosomi & Sudo, 1986) and the resulting solution was analysed for NO_x-N and FRP by segmented flow auto-analysis using an ALPKEM (Texas, USA) Flow Solution II following standard methods (APHA, 2005). Particulate nutrient concentrations were estimated by the subtraction of the total filterable nutrient concentrations from the total nutrient concentrations. Similarly, dissolved (filterable) organic nitrogen (DON) and phosphorus (DOP) were estimated by the subtraction of NO_x-N and ammonia and FRP from the TFN and TFP concentrations, respectively.

6.2.4 Benthic invertebrate and CPOM sampling

Invertebrates were collected from the stream bed using a triangular dip net with a 210-µm mesh, following a rapid bioassessment protocol (Metzeling & Miller, 2001), but with a composite sample. I commenced sampling at the downstream end of the riffle and progressed upstream in a zig-zag pattern, across the full width of the stream. The flat base of the net was pressed into the substratum facing into the flow and the substratum upstream of the net (approximately 0.25 x 0.25 m) was vigorously brushed and turned by hand, causing dislodged material to be washed into the net. The net was relocated at multiple positions in the riffle for a total period of 10 minutes, resulting in a composite sample from about 12 positions the full extent of the riffle. This approach may have affected our estimates of the abundance of the material collected per unit area, but was consistent across streams and the effect on our subsequent analyses was minimal (see Results section).

The material collected was fixed in 80% ethanol. In the laboratory, samples were washed through 1.0-mm, 210-µm and 63-µm sieves then sorted under a stereo microscope, and invertebrates were identified and counted. Coarse particulate organic matter (CPOM, > 1.0 mm) was dried and weighed to provide an estimate of standing stock of CPOM for each sample/site. Individuals of Ephemeroptera and Trichoptera were identified to species using available keys (e.g., Dean, 1999; Christidis, 2003; Dean *et al.*, 2004; Christidis & Dean, 2008). Other taxa were identified to the highest level possible or allocated to “morphospecies” when morphological differences were clear. Counts were recorded as catch per unit effort.

6.2.5 Statistical analysis

Water quality

I used Pearson correlation and multiple linear regression in Statistix© 7 and linear regression in SigmaPlot© 13 to determine explicit relationships among variables. Linear regression was used to examine the relationship between water quality variables and location (distance downstream from uppermost site on each floodplain), and proportion of agriculture in the catchment, upstream of each site. As distance downstream and the proportion of agriculture are likely confounding variables in comparisons of NO_x with measures of riparian condition, regressions were done using the residuals of regressions between NO_x and distance downstream, and between NO_x and % agricultural area in the catchment. The multiple linear regression analysis determined the “best” models that explained the data, indicated by

Mallow's C_p and r^2 statistics. As model variables for each site I used discharge, proportional area of agriculture, riparian cover, mean riparian width upstream and riparian score. I did two analyses, again using NO_x residuals to remove distance and % agriculture effects; in the second analysis, therefore, % agriculture was not included as a variable. Analysis of covariance (ANCOVA) in Statistix© 7 was used to compare riparian condition, in-situ water quality measures and NO_x concentrations and loads between streams, using the distance downstream as the covariate.

Benthic invertebrates

Classification and ordination were used to describe patterns of invertebrate assemblage similarity across study sites. An agglomerative hierarchical classification was generated by means of Flexible pair-Group Method using arithmetic Averages (UPGMA) and range-standardized data with β = -1 using PATN (Belbin, 1995). Ordinations of normalized environmental data by principal component analysis (PCA), and of log-transformed invertebrate data by non-metric multidimensional scaling (NMDS), using the Bray-Curtis dissimilarity measure, were performed in Primer-E© (Anderson *et al.*, 2008).

Relationships between the invertebrate matrix and environmental variables were investigated using regressions between NMDS axes and environmental variables in SigmaPlot© and by multiple regression analysis, as above, which identified the suite of variables that best explained the distribution of invertebrate richness and abundance. A reduced set of environmental variables was used in the regression models to avoid over-fitting, selected on the basis of (i) their likely relevance to benthic species, (ii) the PCA, to select representatives of closely correlated variables (Appendices – Table A6.2), and (iii) their individual correlations with the invertebrate data. Variables used were: mean substratum size, stream gradient, current velocity, Reynolds number and Froude number, representing hydrogeomorphic habitat characteristics; amount of CPOM in sample, riparian cover, riparian score, and aquatic vegetation cover, representing vegetation-related habitat features; and NO_X concentrations, representing the major upstream-downstream gradient in water quality (Connolly *et al.*, 2015). Analysis of covariance (ANCOVA, in Statistix© 7), with mean sediment particle size as the covariate, was used to identify differences in species richness between streams, effects of different levels of taxonomic resolution (species- *vs*. family-level), and effects of different sample sizes (50 – 1000 individuals, randomly resampled from the data set, using 1000 iterations).

6.3 Results

6.3.1 Landscape and riparian vegetation

The major proportion of the Russell and Mulgrave catchments was in the "conservation" category, representing the extensive forested mountain slopes and uplands (Appendices – Table A6.1). The proportion of land used for agriculture increased with distance downstream on the floodplain. Sugar cane production represented 77% of developed land use overall. Only the relationship between water quality and the area of agricultural land (i.e., summed areas of sugar cane, other cropping and grazing) is presented here as no other clear relationships were identified.

Riparian cover and condition differed between the Mulgrave and Russell catchments, but not between streams within catchments (Table 6.1; Figure 6.2), although cover declined with distance downstream in all streams (Figure 6.3 – right panels). For streams on the Mulgrave floodplain (Behana Ck. and the Little Mulgrave R.) riparian cover was mostly > 50% whereas for those on the Russell floodplain (Babinda and Woopen creeks) it was < 50% and frequently < 20%, in which case riparian vegetation consisted almost entirely of introduced weeds, especially Singapore daisy, *Sphagneticola trilobata*, and para grass, *Urochloa mutica* (Appendices – Figure A6.2).

The amount of coarse particulate organic matter (CPOM) collected with each invertebrate sample correlated strongly with associated riparian cover and score (respectively, $r = 0.513$, $P = 0.002$; and $r = 0.481$, $P = 0.003$) and with substratum particle size ($r = 0.522$, $P = 0.002$).

6.3.2. Hydraulic variables and substratum particle size

All streams experience high annual rainfall in their catchments, and low residency times of water (Table 6.2). Discharge increased with distance downstream in all streams, although the correlation was low for the short study reach of the Little Mulgrave R. (Babinda Ck., $r = 0.691$, $P = 0.039$; Behana Ck., $r = 0.851$, $P = 0.015$; Woopen Ck., $r = 0.887$, $P = 0.003$; Little Mulgrave R., $r = 0.135$, $P = 0.772$). However, stream velocity and power declined with distance, resulting in diminishing sediment particle size, from boulders in the uppermost sites, through cobbles in mid reaches, to gravel and sand in the lower reaches of Behana and Babinda creeks (Figure 6.3 – left panels; Appendices – Table A6.3).

6.3.3 Water quality

Water quality data are presented in relation to distance of sites downstream from the most upstream site (just within the national park). Distance downstream strongly correlated with the area and proportion of agriculture in each catchment (for both measures and all sites $r > 0.850$, $P < 0.005$). In-situ measures of water quality variables show that there were strong longitudinal gradients and consistent, though modest, differences between streams (Figure 6.4, Table 6.3): (i) temperature increased with distance downstream as the streams became more open; temperatures differed between all stream pairs except the little Mulgrave River and Woopen Creek; (ii) conductivity increased marginally with distance downstream, was highest in the Little Mulgrave River and Woopen Creek, and differed between all stream pairs; (iii) pH was generally lower in Babinda and Behana creeks than in the Little Mulgrave River and Woopen Creek (by 0.9 to 1.6 units), and there were pairwise differences between all streams except the Little Mulgrave River and Woopen Creek; and (iv) dissolved oxygen concentrations in all streams were close to saturation (overall mean range 94 – 104%), but there were differences between Behana and Babinda Creeks, and Behana and Woopen creeks.

Table 6.1. Pair-wise comparisons of riparian condition (cover and score) between streams and catchments using ANCOVA, with distance downstream as the covariate.

Comparisons			Riparian cover		Riparian width		Riparian score	
Streams and catchments		d.f.	F	*P*	F	*P*	F	*P*
Babinda–Behana	R–M	1, 14	25.57	<0.001	7.96	0.014	18.64	<0.001
Babinda-L Mulgrave	R–M	1, 15	64.97	<0.001	9.84	0.007	22.98	<0.001
Woopen-Behana	R–M	1, 13	11.26	0.005	9.11	0.010	19.15	<0.001
Woopen-L. Mulgrave	R–M	1, 14	23.39	<0.001	9.64	0.008	25.24	<0.001
Babinda-Woopen	R–R	1, 14	0.27	0.614	0.05	0.826	0.03	0.855
Behana-L Mulgrave	M–M	1, 14	0.64	0.438	0.01	0.922	0.02	0.882

Table 6.2. Summary of physical data for the study streams. Discharge range represents upstream– downstream gradient.

		Babinda Ck.	Woopen Ck.	Behana Ck.	Little Mulgrave R.
Floodplain rainfall 2005		3789	3230	2126	2100
Study reach length (km)		14.3	6.3	9.0	7.9
Discharge ($m^3 s^{-1}$)		2.02 – 3.61	0.05 – 1.08	0.38 – 1.16	0.55 – 1.12
Current ($m s^{-1}$)		0.98 ± 0.13	0.46 ± 0.15	0.81 ± 0.12	0.87 ± 0.12
Water residency in reach (hr)		4.05 ± 0.54	3.80 ± 1.24	3.09 ± 0.46	1.85 ± 0.26
Correlation discharge vs. distance	r	0.691	0.887	0.851	0.135
	P	0.039	0.003	0.015	0.772

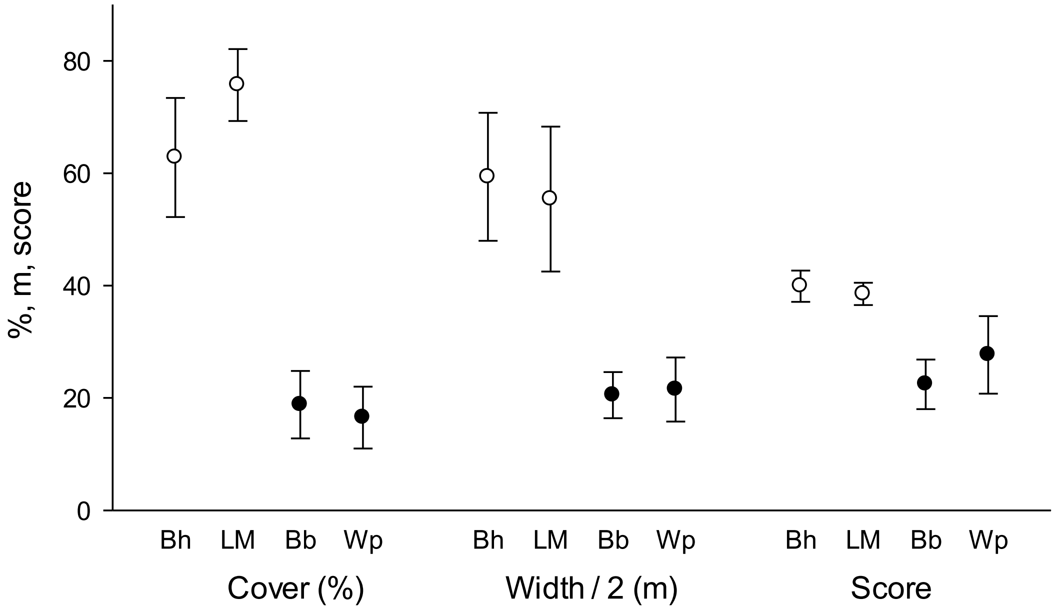

Figure 6.2. Comparison of riparian vegetation characteristics (mean ± s.e.) of each stream. ○, Mulgrave River streams; ●, Russell River streams. Streams are: Bh, Behana Ck.; LM, Little Mulgrave River; Bb, Babinda Ck.; Wp, Woopen Ck. Cover, width and score estimates explained in text. Y-axis labels represent Cover (%), width (m) or Riparian score (score), using the same 0-80 scale. Statistical comparisons are provided in Table 6.1.

Concentrations of N species showed different patterns along the streams, the most consistent being in NO_x concentrations, which increased as streams crossed the developed floodplains (Figure 6.5). Concentrations of Particulate N, Filterable organic N and NH_3 showed no clear patterns (Appendices – Figure A6.2). NO_x concentrations were greater in the Russell than the Mulgrave streams (ANOVA: $F_{1,46} = 9.57$, $P = 0.003$), with ANCOVA indicating strong contrasts between stream pairs, except Behana Ck. and the Little Mulgrave R. (Table 6.4). Contrasts were also evident when data were expressed as NO_x loads (Figure 6.5, Table 6.4), again except for Behana Ck. and the Little Mulgrave R. Babinda Ck. had higher loads than the other streams because of higher discharge (Table 6.2). The NO_x/DON ratio (inorganic/organic N) increased with distance downstream, representing a major change from organic N species to inorganic N species (linear regression: $F_{1,44} = 17.49$, $P < 0.001$).

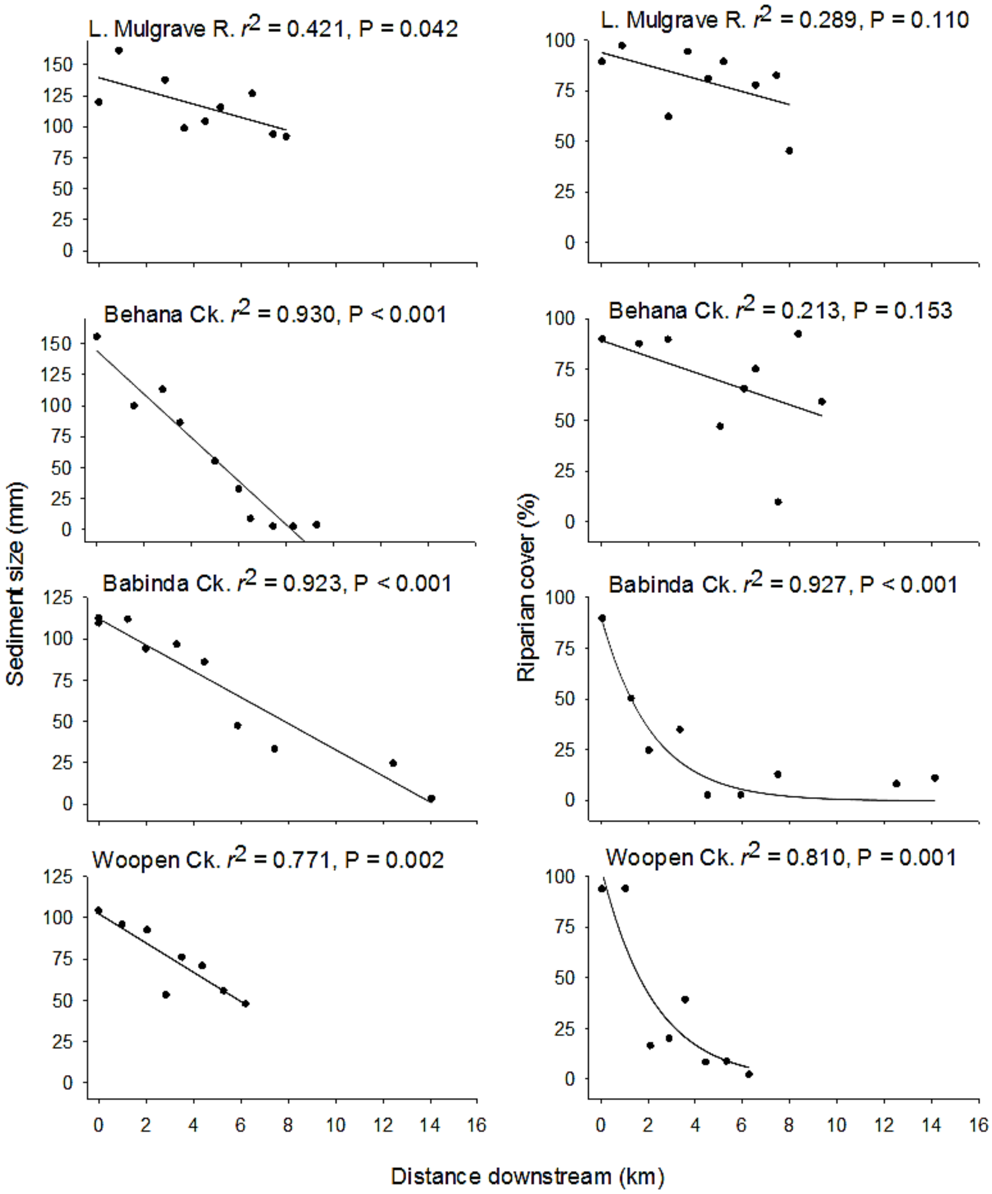

Figure 6.3. Substratum particle size (left panels) and riparian vegetation cover (right panels) in relation to distance from the uppermost floodplain site, for the four study streams. Regression lines based on linear or exponential decay models, as appropriate; r^2 and P values are shown for each regression.

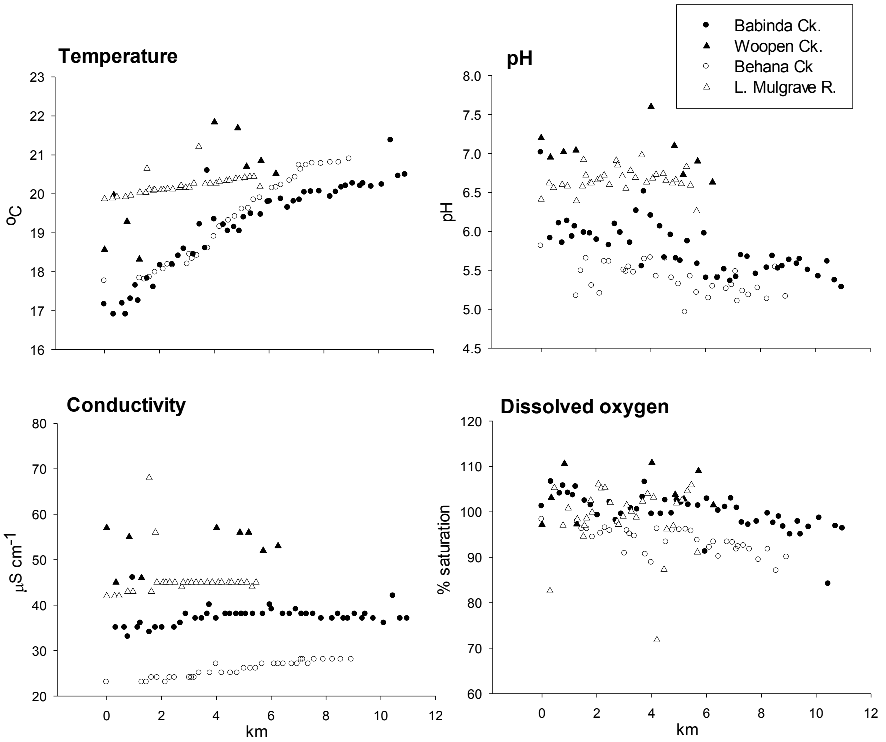

Figure 6.4. In-situ water quality variables (temperature, pH, conductivity and dissolved oxygen) measured in the four study streams. X axis shows distance downstream (km) from first site, close to national park boundary

Regression analyses showed that NO_x was strongly related to distance downstream, % agriculture in the catchment and the riparian/agriculture width ratio (Table 6.5). Analysis of residuals of NO_x vs. distance and % agriculture demonstrated strong relationships between riparian measures and the NO_x-distance residuals, and weaker realtionships with the NO_x-% agriculture residuals (Figure 6.6, Table 6.5). Multiple regression analysis for the combined streams, using NO_x-distance residuals, confirmed a strong relationship between NO_x and % agriculture in the catchment, with mean riparian width upstream also being important in the model (Table 6.6). For the individual streams, % agriculture, discharge, riparian score and mean riparian area upstream were variously important. Multiple regression results using NO_x–% agriculture residuals were generally weaker than for the NO_x–distance residuals, with discharge and riparian width or score important in the models.

Concentrations of different species of P showed inconsistent patterns along the streams, but with a tendency for little change or a decline in concentrations with distance downstream. The only significant relationship was for FRP in Woopen Ck, in which it declined with distance downstream (Appendices – Figure A6.3).

Table 6.3. ANCOVA pairwise comparisons of *in situ* water quality data between streams, with distance as the covariate.

Stream comparisons	Catchments	d.f.	F	*P*
Temperature				
Babinda-Behana	R-M	1, 78	4.39	0.039
Babinda-L. Mulgrave	R-M	1, 77	43.86	<0.001
Woopen-Behana	R-M	1, 41	41.76	<0.001
Woopen-L. Mulgrave	R-M	1, 40	0.47	0.498
Babinda-Woopen	R-R	1, 53	14.26	<0.001
Behana-L. Mulgrave	M-M	1, 65	133.31	<0.001
Conductivity				
Babinda-Behana	R-M	1, 78	127.89	<0.001
Babinda-L. Mulgrave	R-M	1, 77	17.07	0.001
Woopen-Behana	R-M	1, 41	875.94	<0.001
Woopen-L. Mulgrave	R-M	1, 40	10.97	0.002
Babinda-Woopen	R-R	1, 53	78.01	<0.001
Behana-L. Mulgrave	M-M	1, 65	130.14	<0.001
pH				
Babinda-Behana	R-M	1, 78	9.55	0.003
Babinda-L. Mulgrave	R-M	1, 77	14.45	<0.001
Woopen-Behana	R-M	1, 41	10.23	0.003
Woopen-L. Mulgrave	R-M	1, 40	0.01	0.931
Babinda-Woopen	R-R	1, 53	7.66	0.008
Behana-L. Mulgrave	M-M	1, 65	25.93	<0.001
Dissolved oxygen				
Babinda-Behana	R-M	1, 78	7.05	0.010
Babinda-L. Mulgrave	R-M	1, 77	2.56	0.114
Woopen-Behana	R-M	1, 41	7.95	0.007
Woopen-L. Mulgrave	R-M	1, 40	2.64	0.112
Babinda-Woopen	R-R	1, 53	0.13	0.719
Behana-L. Mulgrave	M-M	1, 65	0	0.961

Table 6.4. ANCOVA comparison of values of NO_x concentration and NO_x load between streams and catchments (R = Russell, M = Mulgrave) with distance downstream as the covariate.

Streams and catchments		d.f.	F	*P*
Comparisons of NO_x concentrations				
Babinda-Behana	R-M	1, 12	8.60	0.013
Babinda-L. Mulgrave	R-M	1, 12	24.89	<0.001
Woopen-Behana	R-M	1, 12	65.77	<0.001
Woopen-L. Mulgrave	R-M	1, 12	68.19	<0.001
Babinda-Woopen	R-R	1, 11	21.66	<0.001
Behana-L. Mulgrave	M-M	1, 13	1.06	0.322
Comparisons of NO_x loads				
Babinda-Behana	R-M	1, 12	42.71	<0.001
Babinda-L. Mulgrave	R-M	1, 12	36.66	0.001
Woopen-Behana	R-M	1, 12	19.10	<0.001
Woopen-L. Mulgrave	R-M	1, 12	9.57	0.009
Babinda-Woopen	R-R	1, 11	11.61	0.006
Behana-L. Mulgrave	M-M	1, 13	0.10	0.759

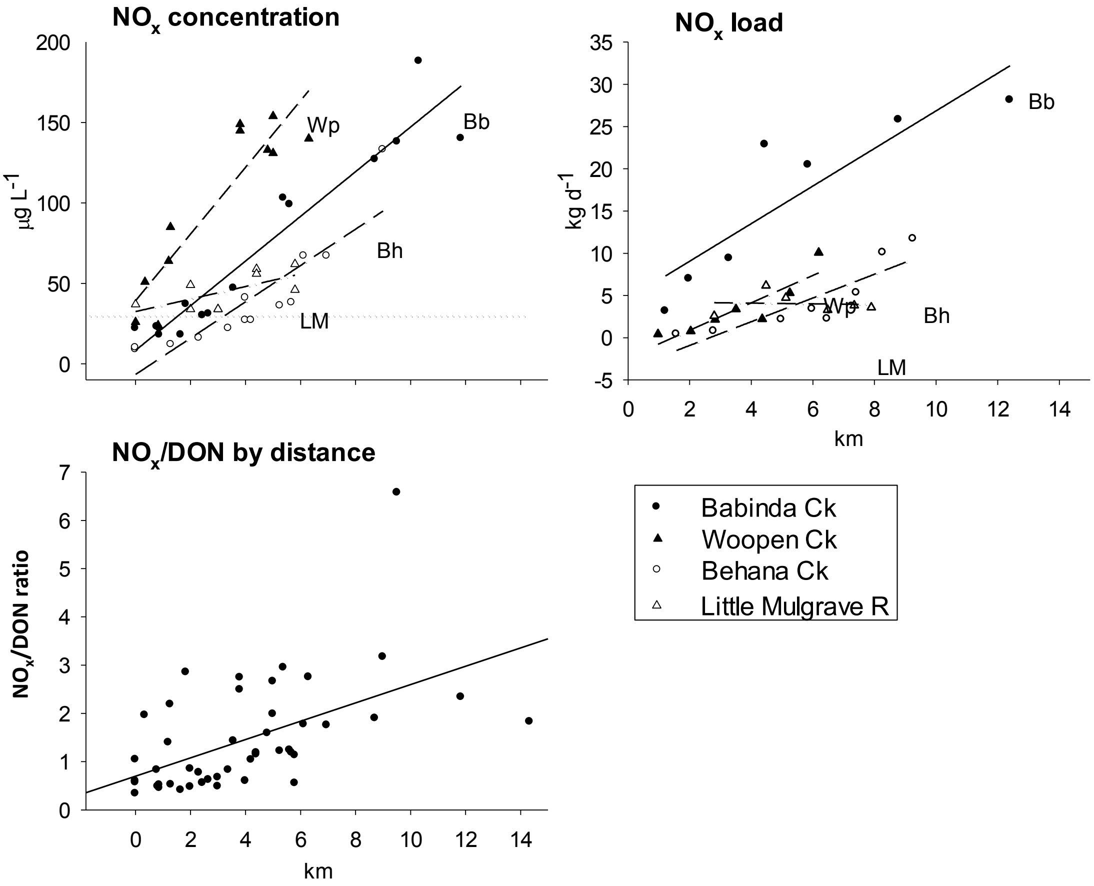

Figure 6.5 Concentrations of species of N and ratio of NO$_x$ to DON in the four study streams, in relation to distance downstream. Dashed horizontal lines indicate Queensland Water Quality Guideline concentrations (filterable organic N [=DON], 200 µg L^{-1}; NH$_3$-N, 10 µg L^{-1}; and NO$_x$-N, 30 µg L^{-1}). Only linear regression lines where $P < 0.05$ are shown – for NO$_x$ concentration and load *vs*. distance for each stream. Adjusted r^2 for each line for NO$_x$ concentration and load, respectively: Bb (Babinda), 0.909, 0.749; Bh (Behana), 0.756, 0.726; LM (Little Mulgrave), 0.343, -0.245; Wp (Woopen), 0.809, 0.745; and for the NO$_x$-DON-distance regression, 0.284. Table 4 provides further statistical details, including comparisons between streams of NO$_x$ concentrations and loads.

Table 6.5. Results of linear regression analyses of (i) NO_x and distance downstream, % of agriculture in the catchment and ratio between riparian width and width of agriculture; (ii) NO_x–distance downstream residuals and riparian measures; and (iii) NO_x–% agriculture in the catchment residuals and riparian measures. All slopes were negative (see Figure 6.6).

Regression	r^2	$F_{1,28}$	*P*
NO_x *vs.*			
Distance downstream	0.200	7.01	0.013
% agriculture in catchment	0.844	151.58	<0.001
Riparian/agriculture width ratio	0.699	65.13	<0.001
Residuals of NO_x – distance downstream *vs.*:			
Mean riparian area	0.526	31.08	<0.001
Riparian cover	0.341	14.50	<0.001
Riparian score	0.466	24.47	<0.001
Riparian width	0.386	17.63	<0.001
Riparian/agriculture width ratio	0.545	33.59	<0.001
Residuals of NO_x – % agriculture *vs.*:			
Mean riparian area	0.082	2.49	0.126
Riparian cover	0.033	0.95	0.339
Riparian score	0.142	4.63	0.040
Riparian width	0.166	5.58	0.025
Riparian/agriculture width ratio	0.218	7.80	0.009

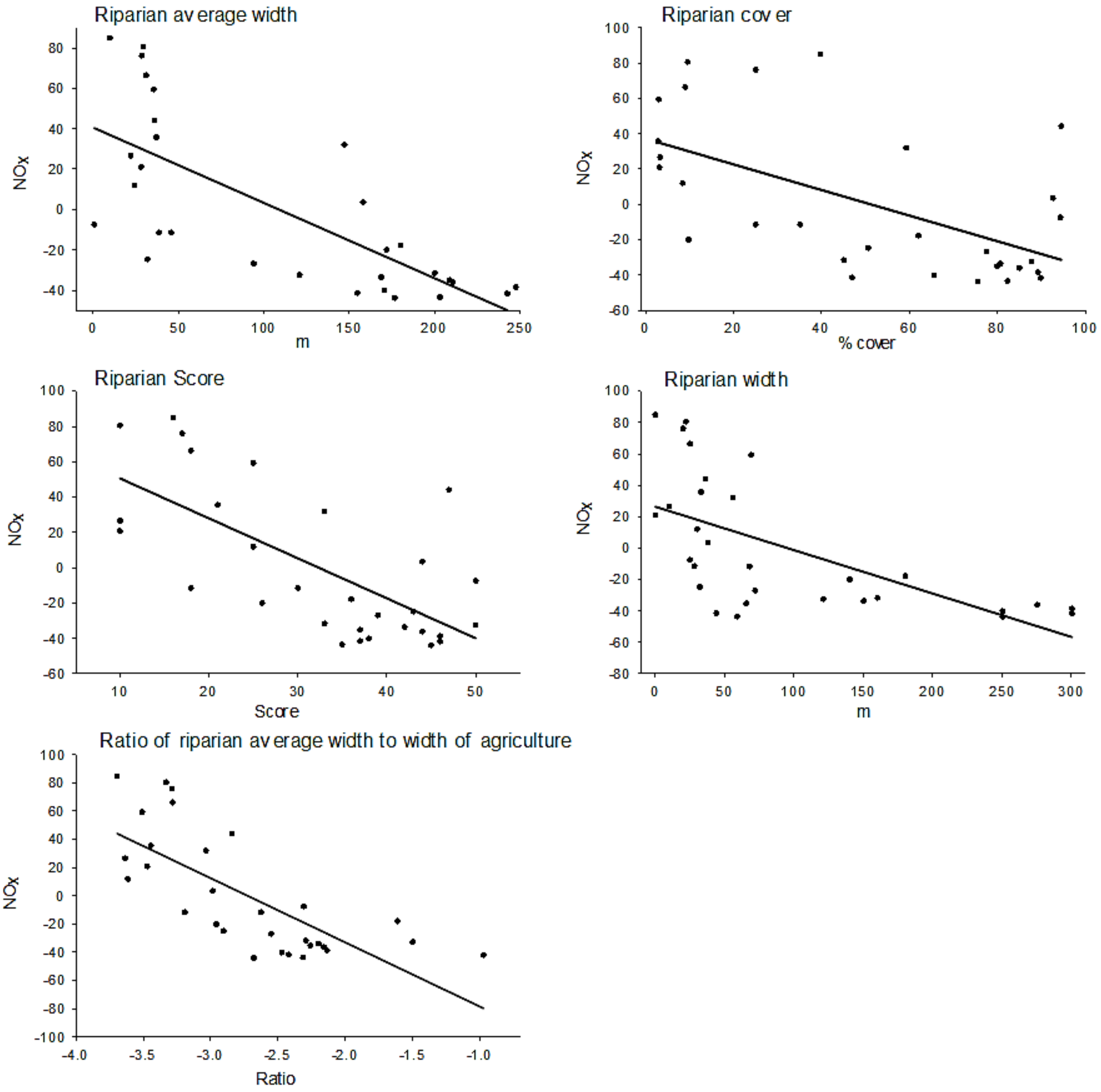

Figure 6.6 Linear regressions of NO_x–distance residuals against five measures of riparian condition: average riparian width on floodplain upstream of each site; % canopy cover; riparian score (scale 0-50, see text); riparian width at site; and ratio of riparian to agricultural width (log scale). Statistics for regressions are given in Table 6.5.

Table 6.6. “Best” linear regression models for residuals of NO_x–distance and NO_x–% agriculture vs. stream characteristics, determined from Mallow’s C_p statistic and r^2 value, for all streams together and each separate stream; “best” models are those where Mallow’s C_p is similar to the number of variables in the model. r^2 % increment shows proportional improvement in model by including second variable. Variables are: Ag, proportional area of agriculture in catchment; D, discharge; RipA, average riparian width upstream; RipSc, riparian score; and RipW, riparian width at site.

	N	No. of variables	Mallow's Cp	r^2	*P*	Variables in model	r^2 % increment
A. Stream variables vs. NO_x–distance residuals							
All streams	30	2	25.1	0.709	<0.001	Ag	
		3	3.5	0.843	<0.001	Ag, RipA	18.9
Babinda Ck.	7	2	1.4	0.801	0.003	D	
		3	1.1	0.908	<0.001	D, RipA	13.3
Behana Ck.	8	2	-0.4	0.689	0.006	Ag	
		3	1.2	0.726	0.004	Ag, RipSc	5.3
L. Mulgrave R.	8	2	6.3	0.477	0.039	D	
		3	1.8	0.807	0.001	D, RipSc	69.1
Woopen Ck.	7	2	1.3	0.799	0.003	RipSc	
		3	2	0.860	<0.001	RipSc, RipA	7.6
B. Stream variables vs. residuals of NO_x–% agriculture in catchment							
All streams	30	2	2.1	0.179	0.018	D	
		3	2.4	0.230	0.006	D, RipSc	28.2
Babinda Ck.	7	2	0.5	0.689	0.011	D	
		3	2.1	0.725	0.007	D, RipSc	5.2
Behana Ck.	8	2	0.8	0.235	0.186	D	
		3	2.2	0.33	0.106	D, RipW	40.5
L. Mulgrave R.	8	2	0.2	0.526	0.027	RipSc	
		3	2	0.539	0.024	RipSc, D	2.5
Woopen Ck.	7	2	1.2	0.650	0.016	RipW	
		3	2.4	0.716	0.008	RipW, RipSc	10.2

6.4.3 Invertebrates

A total of 119 invertebrate taxa were identified from the four streams (Appendices – Table A6.4), including 13 species of Leptophlebiidae (Ephemeroptera); 11 species of Hydropsychidae, 5 species of Philopotamidae and 5 species of Leptoceridae (Trichoptera); and at least 20 species of Elmidae (Coleoptera). A few taxa predominated: the ephemeropterans Baetidae and *Austrophlebioides* sp. (Leptophlebiidae), the Chironomidae and Simuliidae (Diptera) and several trichopterans, including species of *Cheumatopsyche* (Hydropsychidae) and *Chimarra* (Philopotamidae). These taxa were especially abundant in the mid reaches of each stream, while the Elmidae were very abundant in the lower reaches of Behana and Babinda creeks.

Hierarchical classification grouped sites into sequential upstream to downstream groups both within and among streams (Figure 6.7). Three major clusters reflected the change in substratum particle size from upstream to downstream, and sub-clusters differentiated streams of the Russell and Mulgrave catchments. There was a decline in richness downstream from the uppermost site, up to four-fold in Behana and Babinda creeks (Figure 6.8). In the Little Mulgrave R. and Woopen Ck. the upstream-downstream gradient was truncated, making these streams comparable with only the upper reaches of Behana and Babinda creeks. Sample total abundance ranged from 428 to 1959 individuals with a peak abundances 2 to 6 km from the base of the hills (Figure 6.8).

The NMDS analysis of invertebrate data indicated a spread of samples across two axes (Figure 6.9a), with strong correlations of the axes with environmental variables, especially sediment particle size and CPOM (Axis 1 – Figure 6.9b, c), and riparian score (Axis 2 – Figure 6.9d). Abundances of individual taxa varied with mean sediment particle size (Figure 6.10). Many taxa, such as Gripopterygidae, *Nousia* NQ1 and NQ2 (Leptophlebiidae), and Ptilodactylidae, were abundant in the upper reaches and absent from the most downstream sites, where the mean sediment size was ≤ 30 mm (~ -5 ϕ). *Cheumatopsyche* 16 (Cheumatopsychidae) was absent at downstream sites but *Cheumatopsyche* 5 and 15 occurred at both upstream and downstream sites. However, the abundance of Trichoptera overall was low at sites where the mean sediment particle size was < 40 mm (~ -4 ϕ) and only *Oecetis* spp. were present at sites with mean sediment particle sizes < 30 mm (~ -5 ϕ). In contrast, *Austrolimnius* Type A, Tipulidae 10, Caenidae and Baetidae were most abundant in the downstream sites where mean sediment size was < -4 ϕ. Some taxa, such as Ceratopogonidae, *Graphelmis* sp. (Elmidae), and Belostomatidae, were abundant only at the most downstream sites.

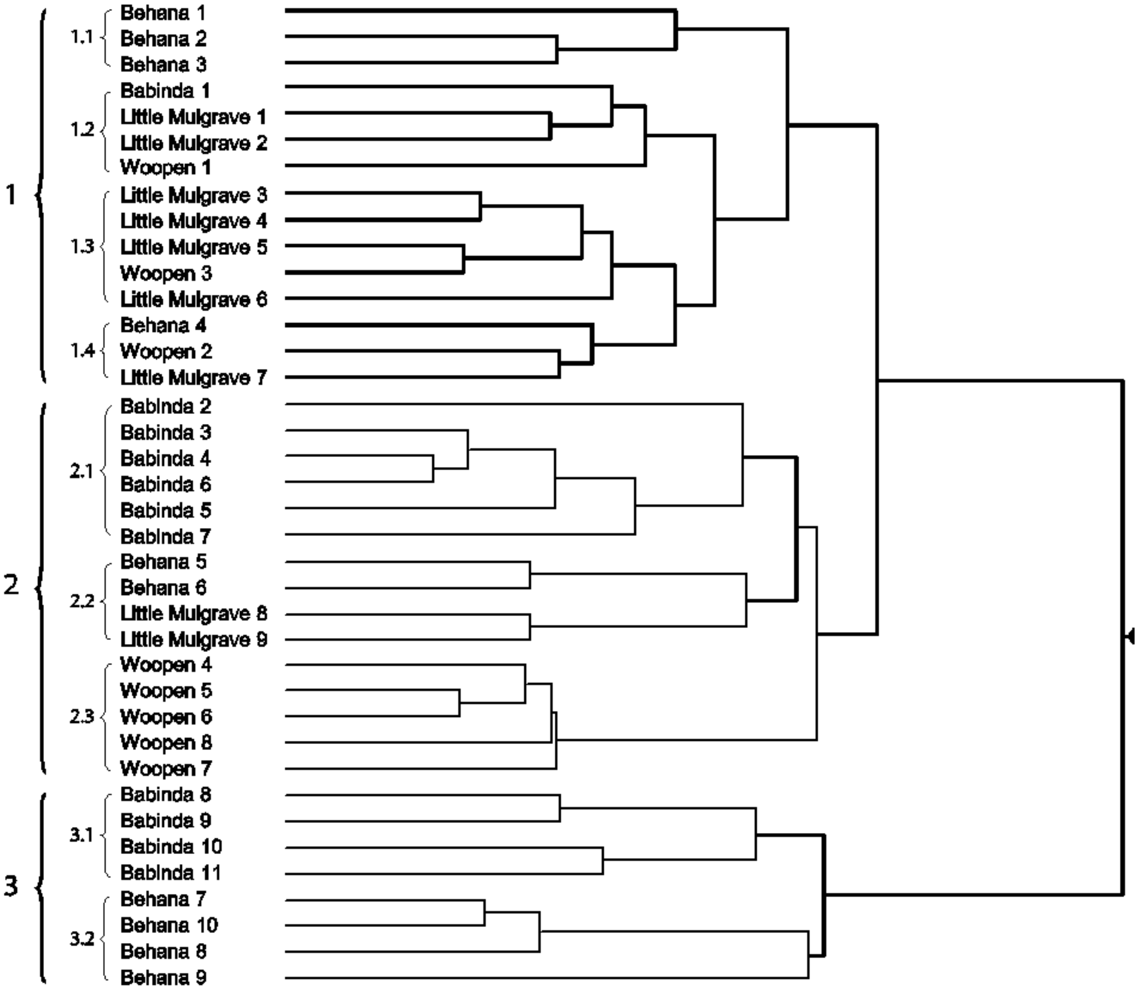

Figure 6.7. Hierarchical classification of sites in the four study streams based on macroinvertebrate assemblage data. Generated using range-standardised data and Flexible Pair-Group Method using arithmetic averages (UPGMA) with β = -1. The major clusters (1, 2 and 3) represent upstream, midstream and downstream reaches, correlating with substrate size (mean phi sizes: Group 1, -6.84 ± 0.07; Group 2, -6.15 ± 0.14; Group 3, -3.25 ± 0.65; ANOVA, $F_{2,35} = 34.71$, $P < 0.0001$); the subgroups largely contrast streams of the Russell and Mulgrave catchments (Babinda and Woopen creeks *vs.* Behana Ck. and the Little Mulgrave R.). There were no Group 3 sites in the smaller streams (Woopen Ck. and Little Mulgrave R.).

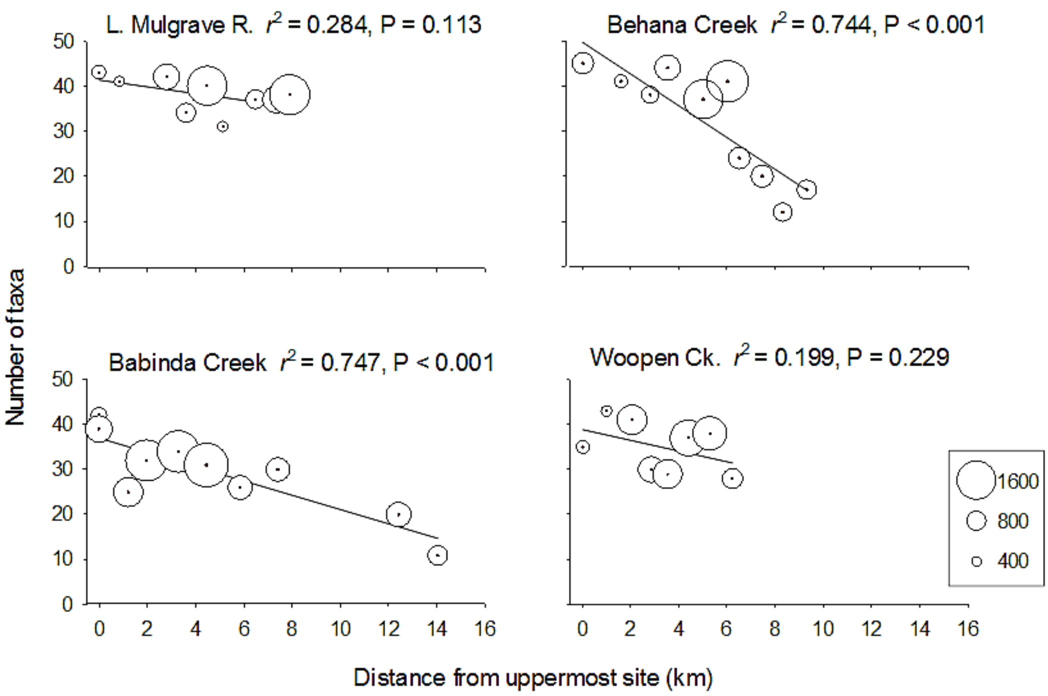

Figure 6.8. Number of macroinvertebrate taxa (bubble centres) recorded at sites in relation to the distance from the uppermost floodplain site, for each of the four study streams. Linear regression line, r^2 and P value for number of taxa are shown; bubble size represents abundance of macroinvertebrates collected at each site.

Despite the similarities in longitudinal richness gradients among streams, when the sediment gradient was accounted for, the number of taxa differed between the longer streams by ~24% (Behana Ck., 92 taxa *vs.* Babinda Ck., 74 taxa) (Figure 6.11). Re-analysis of the data for Behana and Babinda creeks with taxa grouped at the level of family and above showed little effect of resolution on the contrast (for family level, ANCOVA, $F_{1,17} = 17.02$, $P < 0.001$; for higher resolution, $F_{1,17} = 17.22$, $P < 0.001$). Analysis of resampled data, representing different sample sizes, reduced F values but P values were all < 0.05, right down to a sample size of 50 individuals: for 1000, 500, 250, 100 and 50 individuals, respectively, ANCOVA $F_{1,17}$ values were 15.71, 14.60, 12.95, 8.32 and 7.91; and P values were 0.001, 0.001, 0.002, 0.010 and 0.012 (further detail are provided in Connolly *et al*. 2007b).

Multiple regression analysis (Table 6.7) indicated that (i) taxonomic richness was strongly driven by mean substratum size and amount of CPOM in samples; (ii) total abundance of invertebrates was driven by stream gradient and riparian cover (greater abundance with less cover); and (iii) abundance of individual taxa was driven primarily by substratum size, and secondarily by several variables: for example, for taxa that normally favour high currents, Reynolds number was important. For the Chironomidae and Simuliidae, there was no significant model, probably because both taxa included several species and occurred in all samples.

There were strong relationships between the amount of CPOM in samples and invertebrate richness (Figure 6.12a). When sediment size was accounted for, there was (i) a significant difference in invertebrate richness at sites with > 50% riparian cover than at sites with < 50 % riparian cover (ANCOVA, $F_{1,32} = 4.90$, $P = 0.034$); and (ii) significantly higher richness at sites with > 5 g of CPOM in the sample (approximately the median quantity across samples) than at sites with < 5 g of CPOM (ANCOVA, $F_{1,32} = 11.67$, $P = 0.002$) (Figure 6.12b).

Table 6.7. "Best" multiple regression models for number of taxa, total abundance and abundance of 16 most abundant taxa (each ≥ 1.0% and cumulatively 90.0% of the total fauna). Best models determined by Mallows' Cp statistic (Cp) relative to number of variables (N; includes intercept as a variable) and model r^2; r^2 values are also given for variables selected by the model, "–" = $r^2 \leq 0.01$. Variables are: Phi, mean substrate size; Grad, stream gradient; Vel, current velocity; Reyn, Reynolds number; Frd, Froude number; CPOM, amount of coarse particulate organic matter in sample; RCov, Riparian cover; RipSco, Riparian score; Veg, aquatic vegetation cover; NO_X, nitrate + nitrite; FRP, filterable reactive phosphorus.

	Model statistics				r^2 for each variable in selected model										
	N	Cp	r^2	*P*	Phi	Grad	Vel	Reyn	Frd	CPOM	Rcov	Rsco	Veg	NO_X	FRP
No. of taxa	4	2.3	0.684	<0.0001	0.52	0.06				0.33					
Log abundance	4	4.8	0.496	<0.0001	0.01	0.31					0.18				
Austrophlebioides sp.	5	5.6	0.925	<0.0001	0.73	–				0.01					0.02
Asmicridea AV3	4	3.5	0.645	<0.0001	0.28							0.13		0.04	
Austrolimnius A	4	2.7	0.759	<0.0001	0.55								0.19		0.47
Baetidae	7	9.1	0.862	<0.0001	0.01	0.23	–	0.03	–						0.13
Cheumatopsyche AV15	6	6	0.853	<0.0001	0.66	0.03	0.03	–		0.12					
Cheumatopsyche AV16	7	6.9	0.813	<0.0001	0.50		–		0.11		0.16		0.16	0.30	
Cheumatopsyche AV8	5	10.6	0.535	<0.0001	0.11	–		–						0.18	
Chimara AV5	4	4.7	0.691	<0.0001	0.42							0.07		–	
Chironomidae	8	4	0.258	0.010		0.05	0.04	0.02	–	0.17	0.03		0.05		
Elmidae adults	6	1.8	0.639	<0.0001	0.31		0.05	0.23				0.28		0.10	
Gripopterygidae	5	4.4	0.876	<0.0001	0.45			–				0.19	0.27	0.45	
Pyralidae	4	4.3	0.474	<0.0001	0.15	0.07									0.02
Sclerocyphon sp.	3	2.8	0.685	<0.0001	0.60									–	
Simsonia sp. larvae	8	4.2	0.700	<0.0001	0.58		0.07		0.09		0.02	–	0.02		0.15
Simuliidae	8	4.2	0.257	0.010	0.03	0.07			–	0.01	–	0.04	–		
Smicrophylax sp.	8	4.8	0.482	<0.0001	0.21	0.04	0.07	0.07			0.25			0.25	0.13

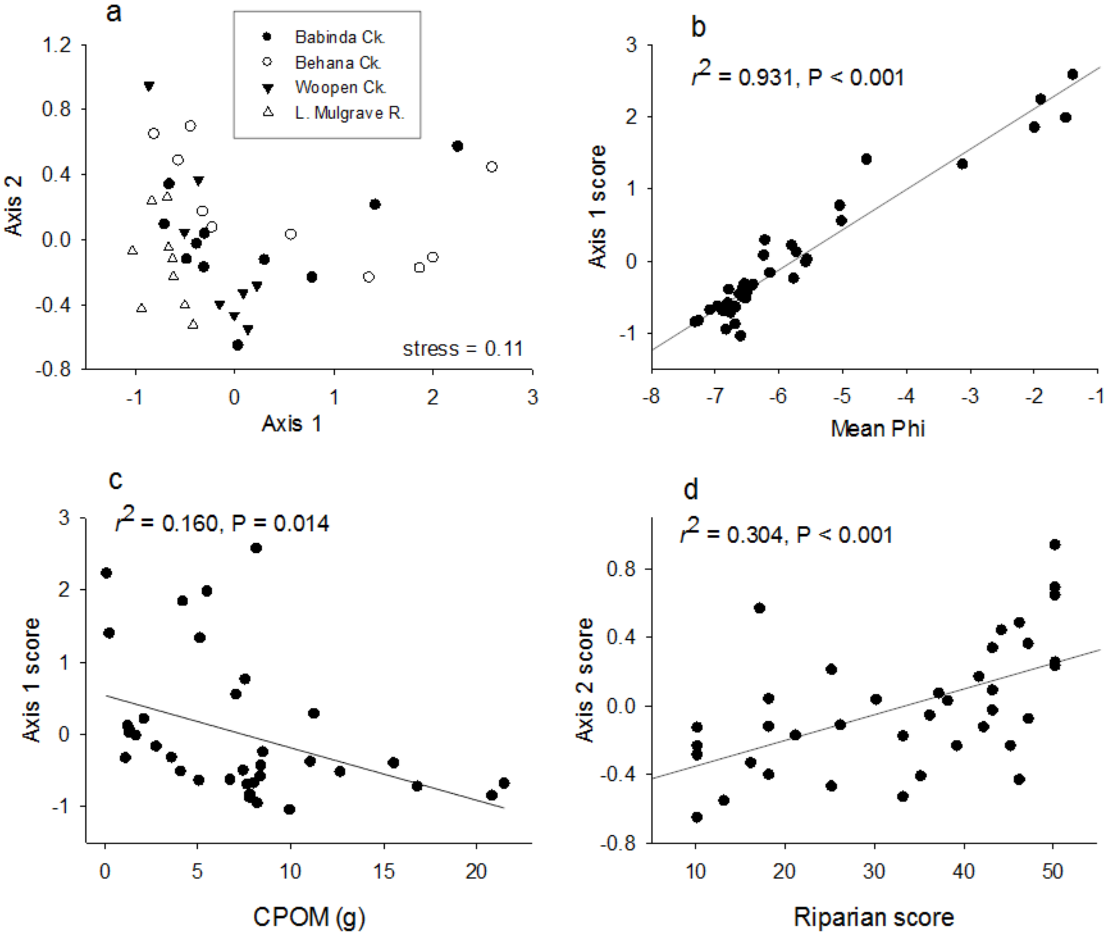

Figure 6.9. a) 2-dimensional NMDS ordination of invertebrate data showing distribution of sites from each study stream; b) regression between NMDS axis 1 scores and mean sediment size; c) Regression between NMDS axis 1 scores and CPOM; d) regression between NMDS axis 2 scores and riparian scores. r^2 and *P* values are shown for each regression. (b), (c) and (d) include all streams.

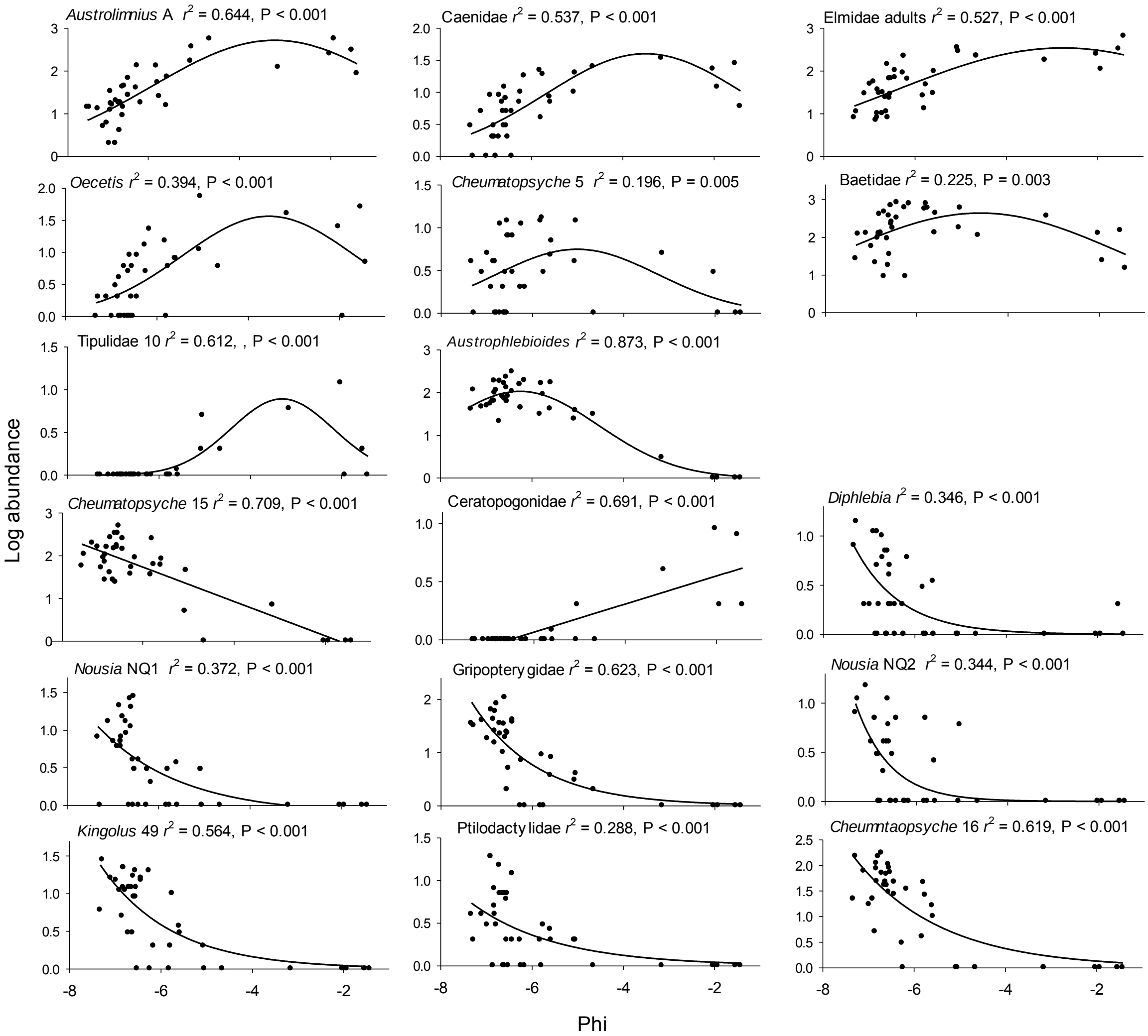

Figure 6.10. Relationship between abundance of selected invertebrate taxa with sediment particle size. Regressions use peak, linear or exponential models, as appropriate; r^2 and P values for each regression are shown. Particle size ranges from largest (upstream, left) to smallest (downstream, right).

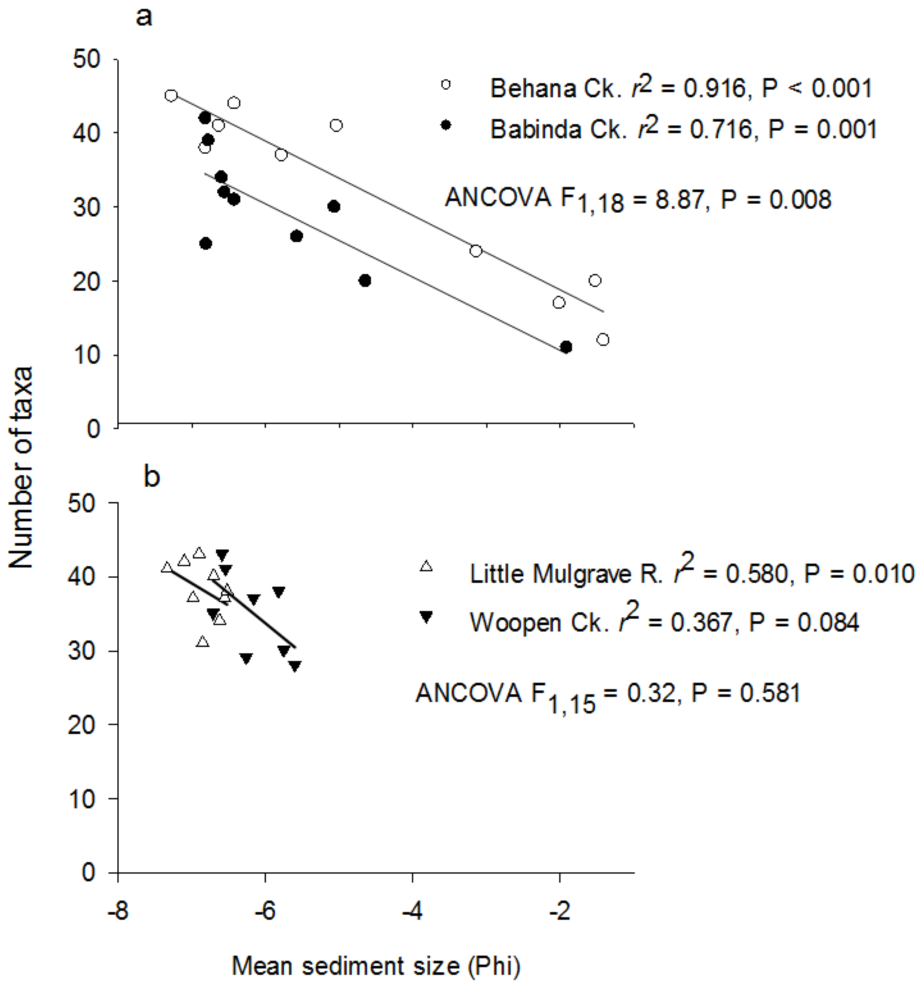

Figure 6.11. Comparisons between number of macroinvertebrate taxa and mean sediment size in (a) the two longer streams, Behana and Babinda creeks, and (b) the two shorter streams, Little Mulgrave River and Woopen Creek. Linear regression lines, associated r^2 values and results of ANCOVAs using sediment particle size as a covariate are shown.

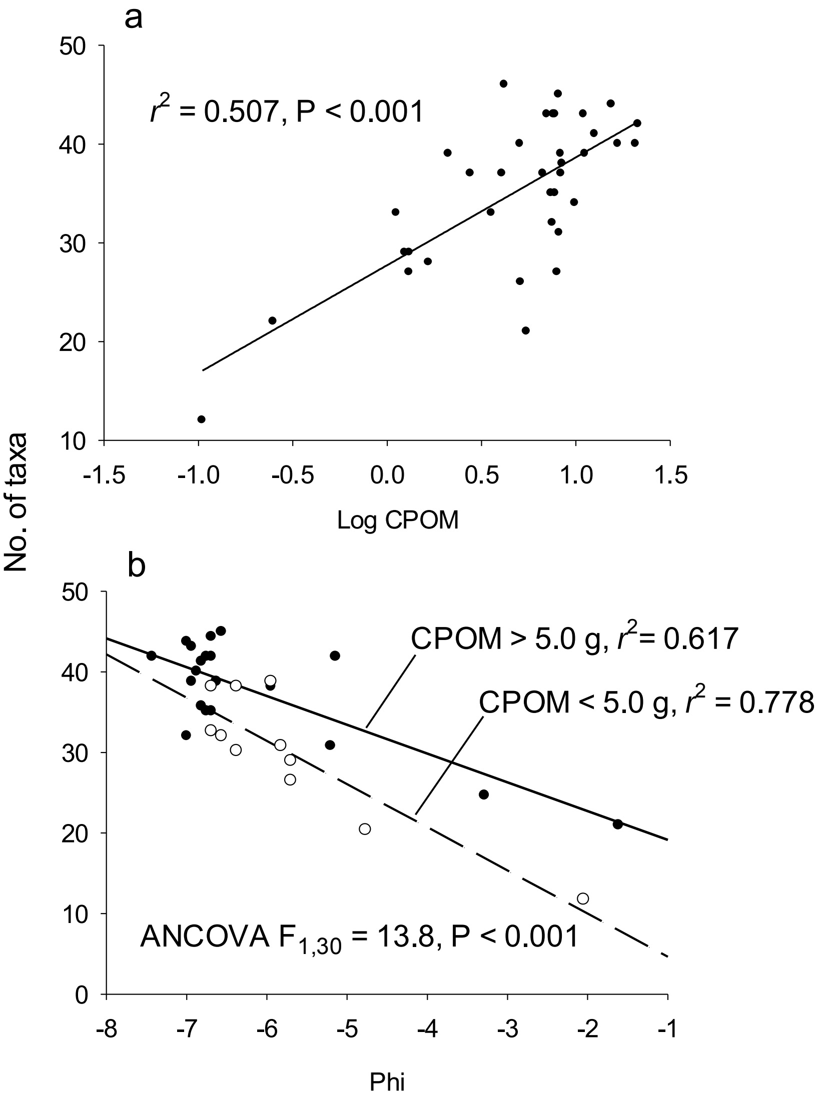

Figure 6.12. Relationship between invertebrate taxonomic richness and (a) CPOM across all sites, and (b) mean sediment size at sites with > 5 g and < 5 g of CPOM in invertebrate samples. r^2 and P values are shown for each regression, and the result of an ANCOVA comparing CPOM groups, using mean sediment size as the covariate, is shown.

6.3 Discussion

6.3.1 Water Quality

The study streams had distinct longitudinal water quality gradients. Differences between streams in temperature, pH and dissolved oxygen concentration were probably due to greater photosynthetic activity in the more open streams (Babinda and Woopen creeks). The downstream gradient in temperature is probably due to increasing insolation as streams become more open. The downstream decline in dissolved oxygen concentrations observed in all streams may be attributed to groundwater entering the streams, but is also affected by temperature, turbulence and photosynthetic activity, although standing stock of autotrophs was never high (Mackay *et al*., 2010). Differences in conductivity probably relate to minor differences in upper catchment characteristics, including lithology.

The strong gradients and concentrations of NO_x reflected inputs of nitrogenous fertilisers from the catchment and exceeded Queensland water-quality guideline concentrations (DERM, 2009) only a short distance downstream from the first appearance of agriculture in the catchment. FRP concentrations declined downstream during base flow, probably because of photosynthetic uptake as insolation reaching the stream increased, and reflecting the negligible use of phosphorus fertilisers in north Queensland sugarcane production and absence of leaching of phosphorus in Wet Tropics soils (Hunter, 2012).

The NO_x concentrations in our study streams were at levels that would be expected to induce a biological response (Pearson & Connolly, 2000; Connolly & Pearson, 2013), but were at the lower end of those reported in other streams draining sugarcane landscapes (e.g., Pearson *et al*., 2003; Faithful *et al*., 2007). However, this is due to the Russell and Mulgrave streams having smaller proportions of their catchments used for agriculture and greater dilution from upstream, rather than differences in fertiliser export rates. The differences in NO_x concentrations between streams, and regression analyses across and within streams, indicate that NO_x input to streams was variously influenced by riparian condition, discharge and proportion of agriculture in the catchment and varied considerably between streams. Our results indicate only a modest effect of the riparian zone on NO_x –stripping compared with the large input from agricultural land use. Additionally, the pattern of downstream increase in NO_x concentrations, observed at base flow and following the spate (see Connolly *et al*., 2015), and the short residence times of water in the streams (a few hours), suggest no major in-stream stripping of NO_x, in contrast to much larger river systems (Seitzinger *et al*., 2002).

6.3.2 Benthic invertebrates

The invertebrate assemblages were variously affected by longitudinal gradients in hydraulic habitat and water quality, and by the condition of the riparian vegetation. The taxa collected in this single survey represent a substantial proportion of the regional invertebrate biodiversity: for example, I collected 45 % of the Leptophlebiidae and 52% of the Hydropsychidae species currently known from the Wet Tropics (F. Christidis pers. comm.; Dean, 1999; Connolly *et al.*, 2008). The physical gradient was a strong determinant of the distributions of invertebrates, with a consistent longitudinal pattern of species turnover leading to different assemblages in the upper, middle and lower parts of the study reaches. High densities of a few grazing or filter-feeding taxa (mayflies, hydropsychid and philopotamid caddisflies, chironomids and simuliids) were responsible for the peak in abundance midway across the floodplain, probably reflecting a combination of stable cobble substratum and high productivity resulting from more open canopies and agricultural nutrient supplements.

Longitudinal gradients in streams and the effect of sediment particle size have long been recognized (e.g., Percival & Whitehead, 1929; Allan, 1975; Erman & Erman, 1984; Quinn & Hickey, 1990; Marchant *et al*., 1994, 1999; Bapista *et al.*, 2001) and can be regarded as a common denominator in the ecology of stream benthos (Cummins, 1964). In Wet Tropics streams, the strength of the longitudinal substratum gradient and its association with invertebrate assemblage composition provided predictability that facilitated comparisons between streams. The use of the mean sediment particle size as a covariate was a robust way of aligning samples and detecting differences between streams, such as the difference in number of taxa between Babinda and Behana creeks. Despite strong correlations with substratum particle size, the assemblage composition did not correlate with hydraulic variables (Froude and Reynolds numbers). Similarly, in streams in New Zealand and Missouri, change in composition was related more to sediment particle size than to hydraulic variables (Quinn & Hickey, 1994; Doisy & Rabeni, 2001).

Assemblage composition was strongly related to riparian cover and CPOM in the NMDS analysis, but not water quality. Richness was more strongly related to CPOM than immediate riparian cover, and CPOM was a strong influence on richness in the multiple regression analysis. The differences in the invertebrate assemblages between the two longer streams, Behana and Babinda creeks, therefore, are attributable to difference in CPOM availability resulting from contrasting riparian vegetation. The differences were similarly clear using smaller sample sizes and coarser taxonomic resolution typical of rapid assessment protocols (e.g., 100 individuals – Plafkin *et al.*, 1989; Metzeling

& Miller, 2001; and family-level identifications – Lenat & Resh, 2001), as has been reported elsewhere (e.g., Marchant *et al*., 1995).

The correlation between CPOM and riparian cover was strongest at the stream scale, indicating that quantities are determined by cumulative upstream conditions. Thus, contrasts were greater among streams rather than among sites. The relationship between the number of taxa and the amount of CPOM in the samples suggests that a threshold quantity of organic material (~ 5 g dry mass in our samples) is required to support the full invertebrate assemblage, whether as habitat or food. Retention of leaves by rocks and woody material is also important (Pearson *et al.*, 1989; Brookshire & Dwire, 2003; Li & Dudgeon, 2011; Koljonen *et al*., 2012) but such obstacles are much scarcer in the lower reaches of Babinda Ck., in the absence of riparian forest, than in Behana Ck., and probably contributed to the lower diversity in the former stream. Similarly, in south-eastern Australian streams, standing stocks of benthic detritus were very low where riparian canopy cover was <35% (Reid *et al.*, 2008).

The only water quality impact that was evident was due to elevated NO_X concentrations (Connolly *et al.*, 2015), which may have boosted the abundance of invertebrates in the upper-mid reaches, where stable substratum was available; in the lower reaches finer sediments did not appear to be stable enough to support production of autotrophs or large populations of invertebrates. The boost effect in the upper-mid reaches was evident in all streams and was consistent with the finding that moderate nutrient enhancement increases invertebrate abundance and condition, but not richness, in experimental Wet Tropics streams (Pearson & Connolly, 2000; Connolly & Pearson, 2013; Chapter 3). Although there were detectable differences in NO_x concentrations between streams, all streams had elevated concentrations that increased downstream with cumulative inputs from the floodplain. Otherwise, water quality was generally well within regional guidelines (DERM, 2009), so it was not surprising that water quality did not contribute to differences in invertebrate assemblages between streams. However, nutrients influence the processing of CPOM, as shown in Chapter 3, and reduce the residence time and standing stock of CPOM in the stream environment (Rosemond *et al*., 2002; Tant *et al*., 2013; Kominoski *et al*., 2015; Rosemont *et al*., 2015), and so may have interacted with CPOM standing stock in these streams with knock-on effects to the benthic invertebrate fauna. There are no comparable lowland streams lacking nutrient inputs in the Wet Tropics to test this effect.

6.3.3 Conclusions

This case study demonstrates that understanding longitudinal gradients is important in comparing the effects of agriculture and riparian vegetation on water quality and invertebrate fauna among streams. The native riparian vegetation had variable, but modest influence on NO_x concentrations in these Wet Tropics streams draining agricultural land. Even good-condition riparian zones was insufficient to bring NO_x concentrations close to recommended water quality guidelines. Given the absence of an effective riparian nutrient filter, the major pathway to reduction of N in waterways is reduction in fertiliser application (Thorburn *et al.*, 2013). The strong correlation between NO_x concentrations and the area of catchment used for fertilized agriculture indicates that discharge is important in predicting NO_x concentrations (as also indicated in regression models). Clearly, future research should quantify groundwater nutrient concentrations, rates of groundwater discharge into streams, and rates of dilution from upstream if unequivocal catchment-scale cause-effect relationships are to be determined.

My results provide strong evidence of the importance of riparian vegetation and CPOM input to the maintenance of invertebrate richness, concurring with previous experimental results in the Wet Tropics (Hearnden & Pearson, 1991) and elsewhere (Rabeni & Minshall, 1977; Hawkins *et al.*, 1982; Culp *et al.*, 1983; Richards *et al.*, 1993). They also demonstrate the need for multiple samples, strategically located, to disentangle catchment-scale influences on the ecological integrity of streams, in contrast with the more straightforward detection of point-source pollution (e.g., sugar-mill effluent in Babinda Ck. – Pearson & Penridge, 1987). A dearth of appropriate reference sites in floodplain systems can cause problems in model development (Pearson *et al.*, 2013); however, comparing streams by sampling along natural gradients facilitates partitioning of the natural gradient and impacts. Thus, what is not possible to differentiate site by site may become possible stream by stream.

The finding that riparian vegetation is a key determinant of invertebrate diversity is encouraging from a management perspective, as it confirms that remediation of riparian vegetation, often applied in the Wet Tropics, is beneficial for maintaining stream biodiversity. Even in the presence of intense agricultural development, invertebrate assemblages indicated that some streams (e.g., Behana Ck.) could be “healthy” (i.e., have diverse assemblages that we might expect from samples of pristine streams – e.g., Pearson, 2005), as long as riparian vegetation remained in good condition. However, strong flows from pristine headwaters in the study streams probably minimized adverse water quality impacts in these streams. Proper riparian management is judged as the best approach to ameliorate the impacts of deforestation on benthic communities in tropical streams (Lorion &

Kennedy, 2009), but objectives in riparian management need to be clearly espoused if the approach and its evaluation are to succeed (Hansen *et al.*, 2015). Site-scale restoration measures are unlikely to be effective if the physical habitat upstream is degraded (Lorenz & Feld, 2013), as suggested by our data. Therefore, maintenance of entire riparian zones is indicated as the soundest way to maintain the diverse assemblages in Wet Tropics streams (Pearson *et al.*, 2015).

6.4 References

Allan J.D. (1975) Faunal replacement and longitudinal zonation in an alpine stream. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **19**: 1646-1652.

Allan J.D. (2004) Landscapes and riverscapes: The influence of land use on river ecosystems. *Annual Review of Ecology and Systematics* **35**: 257-284.

Anderson M.J., Gorley R.N. & Clarke K.R. (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

APHA (2005) Standard Methods for the Examination of Water and Wastewaters. 21st edition. (American Public Health Association, American Water Works Association and Water Environment Federation: Washington).

Bainbridge Z.T., Brodie J.E., Faithful J.W., Sydes D.A. & Lewis S.E. (2009) Identifying the land-based sources of suspended sediments, nutrients and pesticides discharged to the Great Barrier Reef from the Tully-Murray Basin, Queensland, Australia. *Marine and Freshwater Research* **60**: 1081-1090.

Bapista D.F., Dorville L.F.M., Buss D.F. & Nessiamian J.L. (2001) Spatial and temporal organisation of aquatic insects assemblages in the longitudinal gradient of a tropical river. *Revista Brasileira de Biologia* **61**: 295-304.

Becker A. & Robson B.J. (2009) Riverine macroinvertebrate assemblages up to 8 years after riparian restoration in a semi-rural catchment in Victoria, Australia. *Marine and Freshwater Research* **60**: 1309-1316.

Belbin L. (1995) PATN: Pattern Analysis Package Technical Reference. CSIRO Division of Wildlife and Ecology, Australia.

Benstead J.P., Douglas M.M. & Pringle C.M. (2003) Relationships of stream invertebrate communities to deforestation in eastern Madagascar. *Ecological Applications* **13**: 1473-1490.

Blanchette M.L. & Pearson R.G. (2012) Macroinvertebrate assemblages in rivers of the Australian dry tropics are highly variable. *Freshwater Science* **31**: 865-881.

Blott S.J. & Pye K. (2001) GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Process. *Landforms* **26**: 1237-1248.

Bojsen B.H. & Jacobsen D. (2003) Effects of deforestation on macroinvertebrate diversity and assemblage structure in Ecuadorian streams. *Archiv für Hydrobiologie* **158**: 317-342.

Brookes A. (1983) River Channelisation in England and Wales: Downstream Consequences for Channel Morphology and Aquatic Vegetation. PhD Thesis. University of Southampton, UK.

Brookes A. (1990) Restoration and enhancement of engineered river channels: Some European experiences. *Regulated Rivers: Research and Management* **5**: 45-56.

Brookshire E.N.J. & Dwire K.A. (2003) Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society* **51**: 545-553.

Bunn S.E., Davies P.M. & Kellaway D.M. (1997) Contributions of sugar cane and invasive pasture grasses to the aquatic food web of a tropical lowland stream. *Marine and Freshwater Research* **48**: 173-179.

Bunn S.E., Davies P.M., Kellaway D.M. & Prosser I.P. (1998) Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* **37**: 171-178.

Bunte K. & Abt S.R. (2001) Sampling surface and subsurface particle-size distributions in wadeable gravel- and cobble-bed streams for analyses in sediment transport, hydraulics, and stream monitoring. Technical Report RMRS – GTR – 74. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 428p.

Cheshire K., Boyero L. & Pearson R.G. (2005) Food webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology* **50**: 748-769.

Christidis F. (2003) Systematics, phylogeny and ecology of Australian Leptophlebiidae (Ephemeroptera). PhD Thesis, James Cook University, Townsville, Australia.

Christidis F. & Dean J.C. (2008) Phylogeny and distribution of the mayfly genus *Austrophlebioides* Campbell and Suter (Ephemeroptera: Leptophlebiidae). *Invertebrate Systematics* **22**: 29-36.

Clapcott J.E., Collier K.J., Death R.G., Goodwin E.O., Harding J.S., Kelly D., Leathwick J.R. & Young R.G. (2012) Quantifying relationships between land-use gradients and structural and functional indicators of stream ecological integrity. *Freshwater Biology* **57**: 74–90.

Clements W.H., Kashian D.R., Kiffney P.M. & Zuellig R.E. (2015) Perspectives on the context-dependency of stream community responses to contaminants. *Freshwater Biology* doi:10.1111/fwb.12599

Connolly N.M., Christidis F., McKie B., Boyero L. & Pearson R.G. (2008) Diversity of invertebrates in Wet Tropics streams: patterns and processes. Pages 161-177 **In** Stork, N.E., Turton, S.M. (Eds.), *Living in a Dynamic Tropical Forest Landscape*. Blackwells Publishing, Oxford.

Connolly N.M., Pearson B.A., Loong D., Maughan M. & Pearson R.G. (2007a) Hydrology, Geomorphology and Water Quality of Four Wet Tropics Streams with Contrasting Land-use Management. Pages 15-78 **In** Arthington, A.H., Pearson, R.G. (eds.) *Biological Indicators of Ecosystem health in Wet Tropics Streams*. Report to the Catchment to Reef Research Program, Rainforest CRC and CRC for the Great Barrier Reef. James Cook University, Townsville, Australia.

Connolly N.M., Pearson B.A., Loong D., Maughan M. & Pearson R.G. (2007b) Macroinvertebrates as indicators of ecosystem health in Wet Tropics streams. Pages 129-176 **In** Arthington, A.H., Pearson, R.G. (eds.) *Biological Indicators of Ecosystem health in Wet Tropics Streams*. Report to the Catchment to Reef Research Program, Rainforest CRC and CRC for the Great Barrier Reef. James Cook University, Townsville, Australia.

Connolly N.M. & Pearson R.G. (2004) Impacts of forest conversion on the ecology of streams in the humid tropics. Pages 811-835 **In** Bonnell, M., Bruijnzeel, L.A. (Eds.), *Forests, Water and People in the Humid Tropics: Past, Present and Future*. Cambridge University Press, Cambridge, UK.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf-litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Connolly N.M., Pearson R.G., Loong D., Maughan M. & Brodie J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture Ecosystems and the Environment* **213**: 11-20.

Connolly N.M., Pearson R.G. & Pearson B. (2016) Riparian vegetation and sediment gradients determine invertebrate diversity in streams draining an agricultural landscape. *Agriculture, Ecosystems and Environment* **221**: 163-173.

Culp J.M., Walde S. & Davies R.W. (1983) Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1568- 1574.

Cummins K.W. (1964) Factors limiting the microdistribution of larvae of the caddisflies *Pycnopsyche lepida* (Hagen) and Pycnopsyche guttifer (Walker) in a Michigan stream. *Ecological Monographs* **34**: 271-295.

Cummins K.W. & Lauff G.H. (1969) The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* **34**: 145-181.

Dahm V., Hering D., Nemitz D., Graf W., Schmidt-Kloiber A., Leitner P.K., Melcher A. & Feld C.K. (2013) Effects of physico-chemistry, land use and hydromorphology on three riverine organism groups: a comparative analysis with monitoring data from Germany and Austria. *Hydrobiologia* **704**: 389-415.

Dean J.C. (1999) Preliminary keys for the identification of Australian Trichoptera larvae of the family Hydropsychidae. Cooperative Research Centre for Freshwater Ecology Identification Guide No. 22. The Murray-Darling Freshwater Research Centre. 40pp.

Dean J.C., St Clair R. & Cartwright D.I. (2004) Identification keys to Australian families and genera of caddis-fly larvae (Trichoptera). Cooperative Research Centre for Freshwater Ecology and Murray Darling Basin Commission Identification Guide No. 50. The Murray-Darling Freshwater Research Centre. 40pp.

Decamps H., Pinay G., Naiman R.J., Petts G.E., McClain M.E., Hillbricht-Ilkowska A., Hanley T.A., Holmes R.M., Quinn J., Gibert J., Planty Tabacch, A.-M., Schiemer F., Tabacchi E. & Zalewski M. (2004) Riparian zones: where biogeochemistry meets biodiversity in management practice. *Polish Journal of Ecology* **52**: 3-18.

DERM (2009) Queensland Water Quality Guidelines. Version 3. Department of Environment and Resource Management, Queensland Government, Brisbane. ISBN 978 0 9806986 0 2.

de Souza A.L.T., Fonseca D.G., Libório R.A. & Tanaka M.O. (2013) Influence of riparian vegetation and forest structure on the water quality of rural low-order streams in SE Brazil. *Forest Ecology and Management* **298**: 12-18.

Delongi M.D. & Brusven M.A. (1998) Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. *Environmental Management* **22**: 445-457.

Doisy K.E. & Rabeni C.F. (2001) Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society* **20**: 17-32.

Dudgeon D. (1989) The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. *Hydrobiologia* **179**: 183-194.

Dudgeon D. (1994) The influence of riparian vegetation on macroinvertebrate community structure and functional organization in six New Guinea streams. *Hydrobiologia* **294**: 65-85.

England L.E. & Rosemond A.D. (2004) Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. *Freshwater Biology* **49**: 721-734.

Erman D.C. & Erman N.A. (1984) The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia* **108**: 75-82.

Erskine P.D. (2002) Land clearing and forest rehabilitation in the Wet Tropics of north Queensland, Australia. *Ecological Management and Restoration* **3**: 135-137

Fail J.L. Jr., Haines B.L. & Todd R.L. (1987) Riparian forest communities and their role in nutrient conservation in an agricultural watershed. *American Journal of Alternative Agriculture* **2**: 114-121.

Faithful J. W., Brodie J., Hooper A., Leahy P., Henry G., Finlayson W. & Green D. (2007) Plot-scale runoff of nutrients and sediments under varying management regimes on banana and cane farms in the wet tropics, Queensland, Australia. A Report to Task 1, Catchment to Reef Project. ACTFR Report No. 05/03. Australian Centre for Tropical Freshwater Research, James Cook University, Townsville, Qld.

Fernandes J.F., de Souza, A.L.T. & Tanaka M.O. (2014) Can the structure of a riparian forest remnant influence stream water quality? A tropical case study. *Hydrobiologia* **724**: 175-185.

Gordon N.D., McMahon T.A. & Finlayson B.L. (2004) Stream Hydrology: an Introduction for Ecologists. John Wiley and Sons, Chichester, UK. 429pp.

Goss C.W., Goebel P.C. & Sullivan S.M.P. (2014) Shifts in attributes along agriculture-forest transitions of two streams in central Ohio, USA. *Agriculture Ecosystems and Environment* **197**: 106-117.

Greenwood M.J., Harding J.S., Niyogi D.K. & McIntosh A.R. (2012) Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology* **49**: 213–222.

Gregory S.V., Swanson F.J., McKee W.A. & Cummins K.W. (1991) An ecosystem perspective of riparian zones. *BioScience* **41**:540-551.

Grubaugh J.W., Wallace J.B. & Houston E.S. (1996) Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries Aquatic Sciences* **53**: 896–909.

Hansen B.D., Reich P., Cavagnaro T.R. & Lake P.S. (2015) Challenges in applying scientific evidence to width recommendations for riparian management in agricultural Australia. *Ecological Management and Restoration* DOI 2015.10.1111/emr.12149

Hawkins C.P., Murphy M.L. & Anderson N.H. (1982) Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* **63**: 1840-1856.

Hearnden M.R. & Pearson R.G. (1991) Habitat partitioning among mayflies (Insecta: Ephemeroptera) in an Australian tropical stream. *Oecologia* **87**: 91-101.

Hill A.R. (1996) Nitrate removal in stream riparian zones. *Journal Environmental Quality* **25**: 743-755.

Hosomi M. & Sudo R. (1986) Simultaneous determination of total nitrogen and total phosphorus in freshwater samples using persulfate digestion. *International Journal of Environmental Studies* **27**: 267-275.

Hunter H.M. (2012). Nutrients and herbicides in groundwater flows to the Great Barrier Reef lagoon: processes, fluxes and links to on-farm management. ISBN: 978-1-7423-0969.

Iwata T., Nakano S. & Inoue M. (2003) Impacts of past riparian deforestation on stream communities in a tropical rainforest in Borneo. *Ecological Applications* **13**: 461-473.

Januchowski-Hartley S.R., Pearson R.G., Puschendorf R. & Rayner T. (2011) Fresh waters and fish diversity, distribution, protection and disturbance in tropical Australia. *PLoS ONE* **6**: e25846. doi:10.1371/journal.pone.0025846

Karr J.R. & Schlosser I.J. (1978) Water resources and the land-water interface. *Science* **201**: 229-234.

Kaushik N.K. & Hynes H.B.N. (1971) The fate of dead leaves that fall into streams. *Archiv Für Hydrobiologie* **68**: 465-515.

Koljonen S., Louhi P., Mäki-Petäys A., Huusko A. & Muotka T. (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science* **31**: 1121-1130.

Kominoski J.S., Rosemond A.D., Benstead J.P., Gulis V., Maerz J.C. & Manning D.W.P. (2015) Low-to-moderate nitrogen and phosphorus concentrations accelerate microbially driven litter breakdown rates. *Ecological Applications* **25**: 856-865.

Lemmon P.E. (1956) A spherical densiometer for estimating forest overstorey density. *Forest Science* **2**: 314-320.

Lenat D.R. & Crawford J.K. (1994) Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. *Hydrobiologia* **294**: 185-199.

Lenat D.R. & Resh V.H. (2001) Taxonomy and stream ecology: the benefits of genus- and species-level identifications. *Journal of the North American Benthological Society* **20**: 287-298.

Li A.O.Y. & Dudgeon D. (2011). Leaf litter retention in tropical streams in Hong Kong. *Fundamental and Applied Limnology* (formerly Archiv für Hydrobiologie) **178**: 159-170.

Lorenz A.W. & Feld C.K. (2013) Upstream river morphology and riparian land use overrule local restoration effects on ecological status assessment. *Hydrobiologia* **704**: 489-501.

Lorion C.M. & Kennedy B.P. (2009) Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. *Freshwater Biology* **54**: 165-180.

Lowrance R., Todd R, Fail J., Hendrickson O., Leonard R. & Asmussen L. (1984) Riparian forests as nutrient filters in agricultural watersheds. *Bioscience* **34**: 374-377.

Mackay S.J., James C.S. & Arthington A.H. (2010) Macrophytes as indicators of stream condition in the wet tropics region, North Queensland, Australia. *Ecological Indicators* **10**: 330-340.

Maloney K.O. & Weller D.E. (2011) Anthropogenic disturbance and streams: land use and land-use change affect stream ecosystems via multiple pathways. *Freshwater Biology* **56**: 611-626.

Marchant R., Barmuta L. A. & Chessman B.C. (1995) Influence of sample quantification and taxonomic resolution on the ordination of macroinvertebrate communities from running waters in Victoria, Australia. *Marine and Freshwater Research* **46**: 501-506.

Marchant R., Barmuta L.A. & Chessman B.C. (1994) Preliminary study of the ordination and classification of macroinvertebrate communities from running waters in Victoria, Australia. *Marine and Freshwater Research* **45**: 945-962.

Marchant R., Hirst A., Norris R. & Metzeling L. (1999) Classification of macroinvertebrate communities across drainage basins in Victoria, Australia: consequences of sampling on a broad spatial scale for predictive modelling. *Freshwater Biology* **41**: 253-261.

Mazeika S., Sullivan P., Watzin M.C. & Hession W.C. (2004) Understanding stream geomorphic state in relation to ecological integrity: evidence using habitat assessments and macroinvertebrates. Environmental Management **34**: 669-683.

Metzeling L. & Miller J. (2001) Evaluation of sample size used for rapid bioassessment of rivers using macroinvertebrates. *Hydrobiologia* **444**: 159-170.

Naiman R.J., Decamps H. & Pollock M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Application* **3**: 209-212.

Nakano S. & Murakami M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* **98**: 166-170.

Niyogi D.K., Koren M., Arbuckle C.J. & Townsend C.R. (2007) Longitudinal changes in biota along four New Zealand streams: declines and improvements in stream health related to land use. New Zealand Journal of Marine Freshwater Research **41**: 63-75.

Osborne L.L. & Kovacic D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology* **29**: 243-258.

Pearson R.G. (2005) Biodiversity of the freshwater fauna of the Wet Tropics region of north-eastern Australia: patterns and possible determinants. Pages 470-485 **In** Bermingham E., Dick C. W. & Moritz C. (eds.) *Tropical Rain Forests: Past, Present and Future*. University of Chicago Press, Chicago and London.

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* **43**: 31-42.

Pearson R.G., Connolly N.M. & Boyero L. (2015) Ecology of streams in a biogeographic isolate – the Queensland Wet Tropics, Australia. *Freshwater Science* **34**: 797-819.

Pearson R.G., Crossland M., Butler B. & Manwaring S. (2003) Effects of cane-field drainage on the ecology of tropical waterways. Australian Centre for Tropical Freshwater Research Report No. 3/04-1-3, James Cook University, Townsville, Australia. 39+76+81pp.

Pearson R.G., Godfrey P.C., Arthington A.H., Wallace J., Karim F. & Ellison M. (2013) Biophysical status of remnant freshwater floodplain lagoons in the Great Barrier Reef catchment: a challenge for assessment and monitoring. *Marine and Freshwater Research* **64**: 208-222.

Pearson R.G. & Penridge L.K. (1987) The effects of pollution by organic sugar mill effluent on the macro-invertebrates of a stream in tropical Queensland, Australia. *Journal of Environmental Management* **24**: 205-215.

Pearson R.G., Tobin R.K., Benson L.J. & Smith R.E.W. (1989) Standing crop and processing of rainforest litter in a tropical Australian stream. *Archiv Für Hydrobiologie* **115**: 481-498.

Percival E. & Whitehead H. (1929) A quantitative study of the fauna of some types of stream bed. *Journal of Ecology* **17**: 283-314.

Plafkin J.L., Barbour M.T., Porter K.D., Gross S.K. & Hughes R.M. (1989) Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. EPA4 40-4- 001. Office of Water Regulations and Standards, US Environmental Protection Agency, Washington, DC, USA.

Pusey B.J. & Arthington A.H. (2003) Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine Freshwater Research* **54**: 1-16.

Quinn J.M. (2000) Effects of pastoral development. Pages 208-229 **In** Collier K.J., Winterbourn M.J. (eds.) *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society, Auckland.

Quinn J.M. & Hickey C.W. (1990) Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **24**: 411-427.

Quinn J.M. & Hickey C.W. (1994) Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. *Freshwater Biology* **32**: 489-500.

Rabeni C.F. & Minshall G.W. (1977) Factors affecting microdistribution of stream benthic insects. *Oikos* **29**: 33-43.

Reid D.J., Lake P.S., Quinn G.P. & Reich P. (2008) Association of reduced riparian vegetation cover in agricultural landscapes with coarse detritus dynamics in lowland streams. *Marine & Freshwater Research* **59**: 998-1014.

Richards C., Host G.E. & Arthur J.W. (1993) Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. *Freshwater Biology* **29**: 285-294.

Richards C., Johnson L.B. & Host G.E. (1996) Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 295-311.

Rosemond A.D., Pringle C.M., Ramírez A., Paul M.J. & Meyer J.L. (2002) Landscape variation in phosphorus concentration and effect on detritus-based tropical streams. *Limnology and Oceanography* **47**: 278-289.

Rosemond A.D., Benstead J.P., Bumpers P.M., Gulis, V., Kominoski J.S., Manning D.W., Superkropp K. & Wallace J.B. (2015) Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**: 1142-1145.

Rowell D.L. (1994) Soil science: methods and applications. Longman Scientific and Technical. Harlow, England.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfoeld J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science* **287**:1770-1774.

Seitzinger S.P., Styles R.V., Boyer E.W., Alexander R.B., Billen G., Howarth R.W., Mayer B. & Van Breemen, N. (2002) Nitrogen retention in rivers: model development andapplication to watersheds in the northeastern U.S.A. *Biogeochemistry* **57/58**: 199–237.

Stork N.E., Goosem S. & Turton S.M. (2008) Australian rainforests in a global context. Pages 4-20 **In** Stork, N.E. & Turton, S.M. (eds.), *Living in a Dynamic Tropical Forest Landscape*. Blackwells Publishing, Oxford.

Sweeney B.W. (1993) Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* **144**: 291-340.

Tant C.J. & Rosemond A.D. (2013) Stream nutrient enrichment has a greater effect on coarse than on fine benthic matter. *Freshwater Science* **32**: 1111-1121.

Thorburn P.J., Wilkinson S.N. & Silburn D.M. (2013) Water quality in agricultural lands draining to the Great Barrier Reef: A review of causes, management and priorities. *Agriculture Ecosystems and Environment* **180**: 4-20.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.
Waite I.R. (2014) Agricultural disturbance response models for invertebrate and algal metrics from streams at two spatial scales within the U.S. *Hydrobiologia* **726**: 285–303

Wang L., Lyonsa J., Kanehla P. & Gattia R. (1997) Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* **22**: 6-12.

Wentworth C.K. (1922) A scale of grade and class terms for clastic sediments. Journal of Geology **30**: 377-392.

Werren G. (1998) Russell-Mulgrave Catchment Rehabilitation Plan. Summary Report on rehabilitation needs. A report prepared by the NQ Joint Board to facilitate catchment management in the Russell-Mulgrave System. Cairns, Australia.

Werren G.L. & Arthington A.H. (2002) The assessment of riparian vegetation as an indicator of stream condition, with particular emphasis on the rapid assessment of flow-related impacts. Pages 194-

222 **In** Franks, A., Playford, J. & Shapcott, A. (eds.) Landscape Health of Queensland. Royal Society of Queensland, Brisbane, Australia.

Chapter 7

Synthesis and conclusions.

7.1 Outline of findings

This thesis has presented several diverse chapters that involved different approaches to understanding invertebrate community dynamics in streams of the Wet Tropics bioregion, an Australian biodiversity hotspot. Chapter 2 provided a detailed review of the patterns of invertebrate diversity in Wet Tropics streams, describing the research and current state of knowledge in the region. Much of the research that informed this review was based in the uplands and mountain slopes of the Wet Tropics, where extensive areas of montane rainforest have been protected in national park estates that form the greater part of the Queensland Wet Tropics World Heritage Area. Unfortunately, the streams in the lowland areas of the Wet Tropics are afforded much less protection and are variously impacted by anthropogenic disturbance (Januchowski-Hartley *et al.*, 2011). I have described the influences of anthropogenic impacts on these tropical stream ecosystems in Connolly and Pearson (2004) and Pearson *et al*. (2015) based on our understanding of impacts on streams in north Queensland (e.g., Pearson & Penridge, 1987; Pearson & Connolly, 1998; Pearson *et al*., 1998, 2003, 2013; Connolly *et al*., 2007a,b,c, 2011) and experimental work testing the tolerance of stream benthic invertebrates to specific stressors, including elevated nutrients (Pearson & Connolly, 2000), depressed dissolved oxygen concentrations (Connolly *et al*., 2004) and sedimentation (Connolly & Pearson, 2007). It is the research on nutrient enrichment that I have developed in this thesis. In particular I was interested in how nutrient enrichment interacts with allochthonous organic matter to determine productivity in these detritus-based ecosystems and how they, together, influence the diversity of the stream invertebrate assemblage.

The experiments described in Chapter 3 demonstrated that exogenous nutrient supplements increased the food quality of leaf litter to an invertebrate detrivore, through enrichment of the microbial biomass on the leaf material. Supplements also resulted in a 75% increase in the density the invertebrate assemblage without affecting diversity. The lack of a response in the community composition was surprising given the magnitude of the nutrient enhancement and because it was clearly entering trophic pathways, demonstrated through feeding trials and the increase in abundance of the invertebrate fauna. This was contrary to the commonly held view that nutrient enrichments can profoundly affect aquatic ecosystems (Carpenter *et al*., 1998; Smith *et al*., 1999) and prompted me to investigate the relationship between productivity and diversity and how it might apply in these heterotrophic stream assemblages.

In Chapters 3, 4 and 5 I used artificial stream channels to simulate natural stream conditions and manipulate nutrient and leaf-litter input. Chapter 3 investigated how nutrient enrichment influenced physiological processes and invertebrate production, while Chapter 5 explored the ecological mechanisms by which productivity and diversity are related, using the understanding of the invertebrate assemblage's colonisation and equilibrium dynamics elucidated in Chapter 4. To generalise the results of this experimental work to real environmental conditions, Chapter 6 described the results of a field survey of stream invertebrates in the lowlands of the Wet Tropics, where I measured how the input of agricultural nutrients and the clearing of riparian vegetation have altered the invertebrate assemblage in these streams. Collectively this work has enabled me to better understand the mechanisms by which nutrients and organic matter affect the ecology of the invertebrate assemblage and how the influence of these basal resources propagate through the stream food web and determine emergent properties, such as the productivity and diversity of the stream community.

Here I briefly summarise the main findings, before concluding with a brief synthesis and consideration of the utility of my approach and of my findings to improved management of streams.

7.1.1 Nutrient enrichment in streams in the Wet Tropics

In Chapter 6 I described strong longitudinal patterns in water quality in streams in the Russell and Mulgrave River catchments, particularly increasing NO_x concentrations downstream as nutrients derived from agricultural fertilisers accumulated along the streams. My results indicate only a modest effect of the riparian zone on NO_x–stripping compared with the large input from agricultural land use, and suggest that with current inputs, the NO_x concentrations in these streams are largely independent of the riparian zone. The consistent pattern of downstream increase in NO_x concentrations, and the short residence times of water in these streams, also suggests there is no major in-stream uptake of NO_x. Therefore, it appears that the majority of inorganic nitrogen entering these streams from surrounding agriculture is not being utilised within the stream, but is exported (to the detriment of the Great Barrier Reef – e.g., Brodie *et al*., 2012; Schaffelke *et al*., 2013).

In contrast to NO_x, concentrations of different species of phosphorus showed little change or a decline in concentration with distance downstream. Phosphorus concentrations were generally low, reflecting the negligible use of phosphorus fertilisers in north Queensland sugarcane production

(Hunter, 2012). However, particulate and dissolved nitrogen and phosphorus concentrations did increase significantly following rainfall (Connolly *et al.*, 2015), indicating that both are exported from the catchment. The total phosphorus concentrations in these streams were similar to, or above, the response concentrations observed in the enrichment experiments (~20 µgP L^{-1}) (Chapter 3), but concentrations of filterable reactive phosphorus (FRP) were generally lower than those that induced a response in the experiments. The low concentrations of FRP and the decline in concentration with distance downstream suggest that phosphorus was being assimilated and, particularly given the abundance of NO_x, it appears likely that phosphorus is limiting in these streams. This concurs with the findings of the enrichment experiments (Chapter 3), which found that litter breakdown, microbial biomass and growth of the shredder *Anisocentropus kirramus* all responded to supplements of phosphorus but not nitrogen, and may explain the weak response of the invertebrate assemblage to the greatly increased NO_x concentrations in the streams in the Russell and Mulgrave River catchments (Chapter 6).

7.1.2 The effects of nutrients on detrital food webs

The response of detrital food webs to nutrient supplements is fundamentally different from that of food webs based on living plants because the standing stock of detrital resources is typically expected to decrease rather than increase with nutrient enrichment (Rosemond *et al.*, 2001; 2015). Whereas nutrient enrichment may increase carbon sequestration and storage of autotophic organic material (Elser *et al.*, 2007), the fate of most plant production is to enter the detrital pool (Cebrian, 1999; Moore *et al.*, 2004) and it is now recognized that nutrient enrichment will reduce the basal carbon storage in detritus-based systems (Mack *et al.*, 2004; Cleveland *et al.*, 2006; Benstead *et al.*, 2009; Rosemond *et al.*, 2001; 2015). I showed that phosphorus enrichment greatly accelerated the rate that leaf litter was processed in the stream, resulting in greater loss of CPOM, whilst increasing the standing stock of invertebrates (Chapter 3). The rate of CPOM processing was not measured in the Russell and Mulgrave streams, but may also have been accelerated whilst still maintaining or even boosting the invertebrate populations that use it (Pearson & Connolly, 2000; Connolly & Pearson, 2013; Chapter 3). The larger-scale effects of biological consumption of detrital carbon are only recently being appreciated and may contribute to substantial deficits in the stream organic matter budgets and long-term shifts in organic matter storage as a result of even mild nutrient addition, potentially altering the stability that detrital resources afford to their food webs (DeAngelis & Mulholland, 2004; Moore *et al.*, 2004; Rosemond *et al.*, 2015).

7.1.3 Effect on macroinvertebrate assemblage

There were differences in NO_x concentrations between streams in the Russell-Mulgrave catchments, but as concentrations were elevated in all streams, it was not possible to determine the effect, if any, of elevated NO_x on the benthic invertebrate assemblages. My results showed that the abundance of invertebrates in these streams was most strongly influenced by mean substratum sediment size, while invertebrate richness was influenced by sediment size and the amount of available coarse particulate organic matter (CPOM). Within streams the abundances of benthic invertebrates were highest at sites a few kilometres downstream from the foothills, where coarse substrata (> 100 mm) and high insolation were available. However, in the longer streams, Behana and Babinda Creeks, abundances then declined downstream as sediment particle size reduced to gravels and sands, creating a roughly unimodal pattern of invertebrate density. An increase in density of benthic invertebrates may be expected to occur naturally as the streams widen and more light is available to support the growth of primary producers on the substratum surfaces. But it appears that there is an interaction between sufficient light for primary production and the availability of sediment particle sizes large enough to provide a stable substratum for the primary producers to attach and grow, and this may also influence any boost afforded by nutrient enrichment.

The standing stocks of CPOM in Babinda and Woopen Creeks were greatly depleted by the clearing of riparian vegetation and the loss of input from riparian litter fall. The loss of woody debris, which forms instream obstacles that trap and accumulate leaf litter, may also have reduced the retention of leaf litter input from upstream (Díez *et al*., 2000; Brookshire & Dwire, 2003; Li & Dudgeon, 2011; Koljonen *et al*., 2012). Invertebrate assemblages differed substantially between streams with intact riparian vegetation and streams where natural riparian vegetation was replaced by invasive weeds. This difference could have been due to physical changes to the stream habitats, a shift in the trophic state of the stream food web from heterotrophy to autotrophy or other changes to the basal resources and ecology of these streams. I found that the difference in invertebrate composition across streams was most strongly related to the amount of coarse particulate matter (CPOM) associated with riparian vegetation cover. The relationship between CPOM and riparian cover was clearest at the stream scale, indicating that quantities are determined by cumulative upstream conditions. The relationship between the number of taxa and the amount of CPOM suggested that there was a threshold quantity of organic material required to support the full invertebrate assemblage, whether as habitat or food.

7.1.5 Shift in vegetation and organic carbon

The difference in sample CPOM between streams with or without riparian vegetation also indicated that the introduced weed species, dominated by dense stands of para grass, *Urochloa mutica*, despite its vigorous growth, did not provide CPOM to the stream. Stable-isotope data from Bamboo Creek in the Wet Tropics indicated that little of the primary production from para grass and sugarcane (both C4 plants) was being transferred to the aquatic food web (Bunn *et al*., 1997; Hamilton *et al*., 1992; Forsberg *et al*., 1993). In laboratory feeding trials, *Anisocentropus kirramus* larvae (the species that I used in experiments described in Chapter 3) showed a distinct preference for *Eucalyptus* leaf material over both para grass and sugarcane leaf material (Clapcott & Bunn, 2003). Their data suggested that shredders avoided the consumption of C4 plants in favour of native C3 species, even though the latter had lower food quality (based on C:N ratios). Lower rates of consumption and lack of assimilation of C4 carbon also suggest that *A. kirramus* may have limited ability to process this material, even in the absence of alternative litter sources.

The reasons for this have not been determined, but could be associated with shifts in the type of microbial activity, particularly fungi associated with the shift in organic matter. Stream shredders discriminate between leaf species and their stages of decomposition, and to select specific fungal-colonised patches on leaves (Arsuffi & Suberkropp, 1985, 1989; Cornut *et al*., 2015). The role of fungi in decomposition arises largely from their ability to degrade the structural polymer lignin (Dix & Webster, 1995). C4 grass cell walls are very different from the cells of other angiosperms, and even other monocots (Carpita, 1996), especially in their lignin (Hatfield *et al*., 1999), and there is some evidence that fungi that decay wood have not been found to decay grasses and, therefore, are not likely to be optimal for deconstruction of grass cell walls (Shrestha *et al*., 2011).

It is clear that the invertebrate communities of these low-order streams depend on the terrestrial subsidy of CPOM from the riparian leaf litter fall and this is facilitated through the activities of aquatic hyphomycetes that colonise the organic material once it enters the stream. As demonstrated in Chapter 3, the aquatic hyphomycetes will respond to nutrient enrichment, particularly phosphorus addition in these streams. Enrichment of detrital leaf litter may occur in streams that have retained riparian tree leaf litter input, and this may provide for greater invertebrate production while at the same time accelerate the loss of carbon from the system. How these processes and trade-offs have equilibrated in streams that are receiving exogenous nutrient from agricultural fertilisers is unknown. But in streams where riparian vegetation has been displaced by aquatic weeds, particularly para grass, there is a clear loss of the CPOM input to the stream food web and the riparian weed species do not appear to be providing an equivalent subsidy. Clearly it would be worth investigating if the facilitation provided by hyphomycete fungi is disrupted by the shift in the origin of organic matter entering the stream caused by riparian disturbance.

7.1.6 Productivity – Diversity relationship

In the experiments described in Chapter 5 I demonstrated that the density of leaf litter packs had a strong effect on the abundance and richness of invertebrates. At the channel scale, macroinvertebrate diversity increased with the number of leaf packs present in the channels. However, at the cobble/leaf-pack scale, diversity had a hump-shaped relationship with % leaf pack cover. These results, like those of Chase and Leibold (2002), are particularly interesting in that that a hump-shaped pattern was nested within a monotonic pattern at the larger scale, even within a confined system, and provide new insight in to how a productivity gradient might affect diversity in biological communities.

The divergence between channel-scale and cobble/leaf-pack-scale richness at high % leaf-pack cover suggested that there were new species occurring in cobble/leaf packs in the treatment with higher % leaf-pack cover. Chase and Leibold (2002) proposed that for a community to have a monotonic productivity-diversity relationship at the regional scale, but a unimodal relationship at the local scale, β diversity (compositional variation among local sites) would have to increase with productivity. However, in my experiment β diversity did not change or increase with the level of productivity. Instead, β diversity was consistently high between cobble/leaf packs and the monotonic increase in invertebrate richness was attributed to the increasing number of individual cobble/leaf packs in the higher-cover treatments. That is, despite a unimodal pattern at the smaller scale, the monotonic pattern in the number of taxa versus % leaf pack cover at the larger scale was due to increased habitat area and a species-area effect, essentially a sampling effect.

It may be that the scale-dependent pattern in the productivity-diversity relationship only arises where β diversity is high, and where β diversity is low a hump-shaped productivity-diversity relationship may be expected at both local and regional scales. Differences in β diversity may therefore explain some of the contrasting patterns in the productivity–diversity relationship reported in the literature, which have made this relationship so controversial. Hump-shaped productivity–diversity has often been referred to as a local-scale pattern, but has also been reported at large (even global) scales (e.g., Fraser *et al*., 2015). It is not clear if most of these patterns have been derived using samples of α diversity, but it would be interesting to review this data comparing patterns of α and ϒ diversity.

A hump-shaped productivity diversity relationship has very significant implications for the conservation of species richness because it predicts a decline in diversity at high productivity (Pierce 2014). It is important to understand the processes that determine a hump-shaped relationship because productivity is increasingly being affected by anthropogenic fertilisation in both terrestrial and aquatic environments. An understanding of the processes that produce a hump-shaped productivity–diversity relationship will thus help us to predict when a decline in diversity may result and to develop the necessary measures to know when a decline in diversity may be likely.

The streams sampled in the Russell and Mulgrave catchments did not appear to have been enriched by exogenous agricultural nutrients. The productivity of the invertebrate community was probably impeded through the loss of CPOM – essentially the lower end of the productivity-diversity hump-shaped pattern. However, there are numerous cases where cultural eutrophication has resulted in loss of species richness. So, while stream ecosystems are vulnerable to eutrophication, major declines in invertebrate or fish diversity tend only to occur in extreme cases, with dramatic shifts in physical and chemical conditions. In these systems plant productivity is very high and it is likely that competitive exclusion and an inability of new species to colonise occurs, causing a decline in diversity, as the model I describe in Chapter 5 predicts. My results suggest that maintaining the ability of rare taxa to immigrate is important in sustaining species diversity at high productivity. To manage biodiversity under enriched conditions will require us to develop ways to understand and measure immigration and recruitment processes to identify when immigration will be impeded, resulting in declines in species richness. However, instigating this strategy through management will be a significant challenge.

7.2 Conclusions

Description of fundamental small-scale relationships is important to the understanding of the links between basic ecosystem processes and species' tolerances and needs (Attrill & Depledge, 1997; Baird *et al*., 2007)). The latter are important in predicting the effects of future environmental change, and may be important in monitoring ecosystems. Woodward *et al*. (2012) point out that nutrient loading is a major threat to aquatic ecosystems worldwide, leading to major changes in biodiversity and biophysical processes, and they highlight the need to complement established monitoring approaches (e.g., measures of water quality and biological diversity) with functional measures (such as litter-breakdown rate) for assessing ecosystem health. I agree: it is clear that, as nutrient supplements have different effects in different systems, these effects can only be identified and gauged by direct measurement of ecosystem processes rather than simple monitoring of nutrient concentrations.

The components of this thesis enhance understanding of how selected human impacts affect the ecology of the invertebrate assemblages of low-order streams in the Wet Tropics bioregion. I have described how organic matter and nutrient availability play a central role in the ecology of these streams and how the strong linkages between nutrient and carbon cycles influence decomposer activity, consumer nutrition and energy flow through their food webs. I have also described structural responses of invertebrate assemblages to land use impacts and, more importantly, I have aimed to understand the mechanisms by which the ecology and biodiversity of these systems have been modified by shifts in the basal resources, productivity and transfer of energy and nutrients.

From an applied perspective there is an imperative to understand how the widespread clearing of riparian vegetation and large increases in nutrient availability have affected the structure and function of stream ecosystems. In particular, we need to determine what controls the influence of these changes so that management frameworks and actions can be developed to maintain ecosystem values (Vitousek *et al.*, 1997; Elser *et al.*, 2007). From a theoretical perspective these streams also offer an opportunity to manipulate basal carbon and nutrient resources, and thereby investigate relationships between energy transfer, resource availability, productivity and diversity of a consumer assemblage dependent on those resources. Combined, a greater applied and theoretical understanding of the mechanisms by which these changes affect the basal resources and control species diversity in these streams can inform the development of effective management and remediation to conserve biodiversity and ecosystem functions and build resilience in these important, but vulnerable ecosystems.

Previous and parallel research has demonstrated the high diversity of invertebrates in Wet Tropics streams, the influence of many factors on invertebrate life cycles and assemblages, and responses of invertebrates to those influences, including climate, flow regime, natural disturbance and colonisation, allochthonous leaf litter composition and seasonality, pollution and other human impacts (Connolly & Pearson, 2004; Pearson, 2005; Connolly *et al.*, 2008; Pearson *et al.*, 2015). Our understanding of the composition and dynamics of stream invertebrate assemblages in the Australian Wet Tropics, to which the current project has substantially contributed, is equivalent to or better than for most comparable regions in the tropics. The major challenge for the future is translating this knowledge into improved policy and management that will sustain high biodiversity and normal ecosystem processes into perpetuity. With continuing interest and investment in managing the Great Barrier Reef and its catchments, this is a distinct possibility for this region, which could serve as a model for similar tropical regions elsewhere, although the wherewithal to adopt the model is likely to be very limited in much of the developing tropics.

7.3 References

Arsuffi T.L. & Suberkropp K. (1985) Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. *Oikos* **45**: 50-58.

Arsuffi T.L. & Suberkropp K. (1989) Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. *Oecologia* **79**: 30-37.

Attrill M.J. & Depledge M.H. (1997) Community and population indicators of ecosystem health: targeting links between levels of biological organisation. *Aquatic Toxicology* **38**: 183-197.

Baird D.J., Brown S.S., Lagadic L., Liess M., Maltby L., Moreira-Santos M., Schulz R. & Scott G.I. (2007) In situ–based effects measures: determining the ecological relevance of measured responses. *Integrated Environmental Assessment and Management* **3**: 259-267.

Benstead J.P., Rosemond A.D., Cross W.F., Wallace J.B., Eggert S.L., Suberkropp K., Gulis V., Greeenwood J.L. & Tant C.J. (2009) Nutrient enrichment alters storage and fluxes of detritus in a headwater stream ecosystem. *Ecology* **90**: 2556-2566.

Brodie J.E., Kroon F.J., Schaffelke B., Wolanski E.C., Lewis S.E., Devlin M.J., Bohnet I.C., Bainbridge Z.T., Waterhouse J. & Davis A.M. (2012) Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. *Marine Pollution Bulletin* **65**: 81-100.

Brookshire E. N. J. & Dwire K. A. (2003) Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society* **22**: 17-34.

Bunn S.E., Davies P.M. & Kellaway D.M. (1997) Contributions of sugar cane and invasive pasture grasses to the aquatic food web of a tropical lowland stream. *Marine and Freshwater Research* **48**: 173-179.

Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* **8**: 559-568.

Carpita N.C. (1996) Structure and biogenesis of the cell walls of grasses. *Annual Review of Plant Physiology and Plant Molecular Biology* **47**: 445-476.

Cebrian J. (1999) Patterns in the fate of production in plant communities. *The American Naturalist* **154**: 449-468.

Chase J.M. & Leibold M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**: 427-430.

Clapcott J.E. & Bunn S.E. (2003) Can C4 plants contribute to the aquatic food webs of subtropical streams? *Freshwater Biology* **48**: 1105-1116.

Cleveland C.C., Reed S.C., & Townsend A.R. (2006) Nutrient regulation of organic matter decomposition in a tropical rainforest. *Ecology* **87**: 492-503.

Connolly N.M., Crossland M.R., & Pearson R.G. (2004) Effect of low dissolved oxygen on survival, emergence and drift of tropical stream macroinvertebrates. *Journal of North American Benthological Society* **22**: 251-270**.**

Connolly N.M. & Pearson R.G. (2004) Impacts of forest conversion on the ecology of streams in the humid tropics. Pages 811-835 **In** Bonnell M. & Bruijnzeel L.A. (eds.), *Forests, Water and People in the Humid Tropics: Past, Present and Future*. Cambridge University Press, Cambridge, UK.

Connolly N.M. & Pearson R.G. (2007) The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: A comparison using flow-through artificial streams and recirculating mesocosms. *Hydrobiologia* **592**: 423-438.

Connolly N.M., Butler B., Pearson R.G. & Arthington A. (2007a) *Status and Trends of Water Quality and Ecosystem Health of Freshwaters in the Wet Tropics.* Draft Report for MTSRF Project 3.7.3, Milestone March 18th. Marine and Tropical Science Research Facility (MTSRF) technical publication. pp 45.

Connolly N.M., Pearson B.A., Loong D., Maughan M. & Pearson R.G. (2007b) Study area and sites: geographic setting, hydrology, geomorphology and water quality of four Wet Tropics streams with contrasting land-use management. Chapter 2 **In** Arthington A. & Pearson R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 63.

Connolly N.M., Pearson R.G. & Pearson B.A (2007c) Macroinvertebrates as monitors of river health in Wet Tropics streams. Chapter 4 **In** Arthington A. & Pearson R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 44.

Connolly N.M., Christidis F., McKie B., Boyero L. & Pearson R. (2008) Diversity of invertebrates in Wet Tropics streams: patterns and processes. Pages 161-177 **In** Stork N. E. & Turton S. M. (eds.) *Living in a Dynamic Tropical Forest Landscape*. Wiley-Blackwell, Oxford UK.

Connolly N., Moulton D., Tudman P., Pettit R. & Barron F. (2011) *Wet Tropics Healthy Waters Management Plan: Aquatic ecosystems Condition and Level of Protection. Technical Panel Workshop Report. The Hotel Cairns 6th December 2010.* Report prepared by Terrain NRM Pty. Ltd. and Queensland Department of Environment and Resource Management. pp. 51.

Connolly N.M. & Pearson R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Connolly N.M., Pearson R.G., Loong D., Maughan M. & Brodie J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture Ecosystems and the Environment* **213**: 11-20.

Cornut J., Ferreira V., Goncalves A.L., Chauvet E. & Canhoto C. (2015) Fungal alteration of the elemental composition of leaf litter affects shredder feeding activity. *Freshwater Biology* doi:10.1111/fwb.12606.

DeAngelis D.L. & Mulholland P.J. (2004) Dynamic consequences of allochthonous nutrient inputs to freshwater systems. Pages 12-24 **In** Polis G.A., Power M.E. & Huxel G.R. (eds.) *Food webs at the landscape level.* University of Chicago Press, Chicago, Illinois, USA.

Díez J. R., Larrañaga S., Elosegi A., & Pozo J. (2000) Effect of removal of wood on streambed stability and retention of organic matter. *Journal of the North American Benthological Society* **19**: 621-632.

Dix N.J. & Webster J. (1995) Fungal ecology. Chapman & Hall, London.

Elser J.J., Bracken M.E.S., Cleland E.E., Gruner D.S., Harpole W.S., Hillebrand H., Ngai J.T., Seabloom E.W., Shurin J.B. & Smith J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**: 1135-1142.

Forsberg B.R., Araujo-Lima C.A.R.M., Martinelli L.A., Victoria R.L. & Bonassi J.A. (1993) Autotrophic carbon sources for fish of the Central Amazon. *Ecology* **74**: 643-652.

Fraser L.H., Pither J., Jentsch A., Sternberg M., Zobel M., Askarizadeh D., Bartha S., Beierkuhnlein C., Bennett J.A., Bittel A., Boldgiv B., Boldrini I.I., Bork E., Brown L., Cabido M., Cahill J., Carlyle C.N., Campetella G., Chelli S., Cohen O., Csergo A-M., Dίaz S., Enrico L., Ensing D., Fidelis A., Fridley J.D., Foster B., Garris H., Goheen J.R., Henry H.A.L., Hohn M., Hassan Jouri M., Klironomos J., Koorem K., Lawrence-Lodge R., Long R., Manning P., Mitchell R., Moora M., Müller S.C., Nabinger C., Naseri K., Overbeck G.E., Palmer T.M., Parsons S., Pesek M., Pillar V.D., Pringle R.M., Roccaforte K., Schmidt A., Shang Z., Stahlmann R., Stotz G.C., Sugiyama S., Szentes A., Thonpson D., Tungalag R., Undrakhbold S., van Rooyen M., Wellstein C., Wilson J.B. & Zupo T. (2015) Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* **349**: 302-305.

Hamilton S.K., Lewis W.M. & Sippel S.J. (1992) Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia* **89**: 324-330.

Hatfield R.D., Wilson J.R. & Mertens D.R. (1999) Composition of cell walls isolated from cell types of grain sorghum stems. *Journal of the Science of Food and Agriculture* **79**: 891-899.

Hunter H.M. (2012). Nutrients and herbicides in groundwater flows to the Great Barrier Reef lagoon: processes, fluxes and links to on-farm management. ISBN: 978-1-7423-0969.

Januchowski-Hartley S.R., Pearson R.G., Puschendorf R. & Rayner T. (2011) Fresh waters and fish diversity: distribution, protection and disturbance in tropical Australia. *PLoS One* **6**:0025846.

Koljonen S., Louhi P., Mäki-Petäys A., Huusko A. & Muotka T. (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science* **31**: 1121-1130.

Li A.O.Y. & Dudgeon D. (2011). Leaf litter retention in tropical streams in Hong Kong. *Fundamental and Applied Limnology* (formerly *Archiv für Hydrobiologie*) **178**: 159-170.

Mack M.C., Schuur E.A.G., Bret-Harte M.S., Shaver G.R. & Chapin F.S. (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**: 440-443.

Moore J.C., Berlow E.L., Coleman D.C., deRuiter P.C., Dong Q., Hastings A., Collins-Johnson N., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.M., Post D.M., Sabo J.L., Scow K.M., Vanni M.J. & Wall D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**: 584-600.

Pearson R.G. & Penridge L.K. (1987) The effects of pollution by organic sugar mill effluent on the macroinvertebrates of a stream in tropical Queensland, Australia. *Journal of Environmental Management* **24**: 205-215.

Pearson R., Butler B., Nolen J., Christidis F., Connolly N., Cairns A., & Davis L. (1998) *Stream ecosystems as monitors of tropical forest catchments*. ACTFR Report No. 98/26

Pearson R.G. & Connolly N.M. (eds.) (1998) *Macroinvertebrates as monitors of river health in the tropics.* ACTFR Report No. 98/20

Pearson R.G. & Connolly N.M. (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology.* **43**: 31-42.

Pearson R.G., Crossland M., Butler B. & Manwaring S. (2003) *Effects of cane-field drainage on the ecology of tropical waterways*. Australian Centre for Tropical Freshwater Research Report No. 3/04-1-3. James Cook University, Townsville, Australia.

Pearson R.G., Godfrey P.C., Arthington A.H., Wallace J., Karim F. & Ellison M. (2013) Biophysical status of remnant freshwater floodplain lagoons in the Great Barrier Reef catchment: a challenge for assessment and monitoring. *Marine and Freshwater Research* **64**: 208-222.

Pearson R.G. (2005) Biodiversity of the freshwater fauna of the Wet Tropics region of north-eastern Australia: patterns and possible determinants. Pages 470-485 **In** Birmingham E., Dick C.W. and Moritz (eds.) *Tropical rain forest: past, present and future*. University of Chicago Press, Chicago, Illinois.

Pearson R.G., Connolly N.M. & Boyero L. (2015) Ecology of streams in a biogeographic isolate—the Queensland Wet Tropics, Australia. *Freshwater Science* **34**: 797-819

Pierce S. (2014) Implications for biodiversity conservation of a lack of consensus regarding the humped-back model of species richness and biomass production. *Functional Ecology* **28**: 253-257.

Rosemond A.D., Pringle C.M., Ramirez A. & Paul M.J. (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology* **82**: 2279-2293.

Rosemond A.D., Benstead J.P., Bumpers P.M., Gulis V., Kominoski J.S., Manning D.W.P., Suberkropp K. & Wallace J.B. (2015) Experimental nutrient editions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**: 1142-1145.

Schaffelke B., Anthony K., Blake J., Brodie J., Collier C., Devlin M., Fabricius K., Martin K., McKenzie L., Negri A., Ronan M., Thompson A. & Warne M. (2013) *2013 Scientific Consensus Statement: Chapter 1 Marine and coastal ecosystem impacts.* Published by the Reef Water Quality Protection Plan Secretariat, State of Queensland.

Shrestha P., Szaro T.M., Bruns T.D. & Taylor J.W. (2011) Systematic search for cultivatable fungi that best deconstruct cell walls of Miscanthus and sugarcane in the field. *Applied and Environmental Microbiology* **77**: 5490-5504.

Smith V.H., Tilman G.D. & Nekola J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**: 179-196.

Vitousek P.M., Mooney H.A., Lubchenco J. & Melillo J.M. (1997) Human domination of Earth"s ecosystems. *Science* **277**: 494-499.

Woodward G., Gessner M.O., Giller P.S., Gulis V., Hladyz S., Lecerf A., Malmqvist B., McKie B.G., Tiegs S.D., Cariss H., Dobson M., Elosegi A., Ferreira V., Graça M.A.S., Fleituch T., Lacoursière J.O., Nistorescu M., Pozo J., Risnoveanu G., Schindler M., Vadineanu A.,. Vought L.B.-M, & Chauvet E. (2012) Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* **336**: 1438-1440.

APPENDICES

Appendix 1

Professional publications, technical reports and presentations by Niall Connolly

Peer reviewed papers:

Connolly, N.M., Pearson, R.G. and Pearson, B. (*2016*) Riparian vegetation and sediment gradients determine invertebrate diversity in streams draining an agricultural landscape. *Agriculture, Ecosystems and Environment* **221**: 163-173.

Connolly, N.M., Pearson, R.G., Loong, D., Maughan, M. and Brodie, J. (2015) Water quality variation along streams with similar agricultural development but contrasting riparian vegetation. *Agriculture, Ecosystems and Environment* **213**: 11-20.

Pearson, R.G., **Connolly, N.M.** and Boyero, L. (2015) Ecology of streams in a biogeographic isolate—the Queensland Wet Tropics, Australia. *Freshwater Science* **34(2)**: 797-819

Connolly, N.M. and Pearson, R.G. (2013) Nutrient enrichment of a heterotrophic stream alters leaf litter nutritional quality and shredder physiological condition via the microbial pathway. *Hydrobiologia* **718**: 85-92.

Connolly, N., Pearson, R., Christidis, F., McKie, B. and Boyero, L. (2008) Diversity of invertebrates in Wet Tropics streams: Patterns and Processes. ***In*** Stork, N. and Turton, S. (eds) *Living in a dynamic tropical environment.* Blackwell Publishing, UK pp 652.

Connolly, N.M. and Pearson, R.G. (2007) The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: A comparison using flow-through artificial streams and recirculating mesocosms. *Hydrobiologia* **592**: 423-438.

Connolly, N.M. Crossland, M.R., and Pearson, R.G. (2004) Effect of low dissolved oxygen on survival, emergence and drift of tropical stream macroinvertebrates. *Journal of North American Benthological Society* **22**(3): 251-270**.**

Connolly, N.M. and Pearson, R.G. (2004) The impact of forest conversion on the ecology of humid tropical streams. ***In***. Bonnel, M. and Bruijzneel, L.A (eds) *Forest-Water-People in the humid tropics: Past, Present and Future Hydrological Research for Integrated Land and Water Management.* Cambridge University Press, UK.

Pearson, R.G. and **Connolly, N.M.** (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology.* **43**: 31-42.

Articles currently in preparation:

Connolly, N.M., Pearson, R.G. (*in prep*) Rates of colonisation and emigration of stream invertebrates inhabiting leaf litter packs in a tropical rainforest stream. *Freshwater Biology*

Connolly, N.M., Pearson, R.G. (*in prep*) Hump-shaped and monotonic productivity-diversity relationships at different scales in stream invertebrates inhabiting leaf litter due to high β diversity and constrained immigration.

Connolly, N.M., Kahler, C., Mackay, S., Fry, S. and Cameron, R. (*in prep*) Variation in wetland condition across geomorphic land zones in an intensive agricultural area: determined by underlying differences in hydrology and salinity regimes. *Wetlands*

Refereed conference proceedings:

Pearson R.G. and **Connolly, N.M.** (2002) Biological processing of materials in tropical freshwater ecosystems. Proceeding of 2nd National Conference on Aquatic Environments: Sustaining our aquatic environments – implementing solutions. 20-23rd November, Jupiters Townsville Hotel and Casino, Townsville, Queensland, Australia.

Technical Reports:

Connolly, N., Kahler, C., Mackay, S., Fry, S. and Cameron, R. (2012) *Variations in wetland condition across Land Zones in the lower Burdekin. Aquatic weed distributions determined by underlying differences in water and salinity regimes.* A report prepared for the NQ Dry Tropics NRM. Department of Environment and Heritage Protection, Queensland Government. pp. 50.

Connolly, N., Moulton, D., Tudman, P., Pettit, R. and Barron, F. (2011) *Wet Tropics Healthy Waters Management Plan: Aquatic ecosystems Condition and Level of Protection. Technical Panel Workshop Report. The Hotel Cairns 6th December 2010.* Report prepared by Terrain NRM Pty. Ltd. and Queensland Department of Environment and Resource Management. pp. 51.

Connolly, N., Moulton, D., Kelton, M. and Watson, F. (2011) *Broad-scale waterway condition assessments using categories in the Environmental Protection (Water) Policy 2009. A trial in the Burdekin and Black Ross basins undertaken as part of the Burdekin and Black-Ross Water Quality Improvement Plans*. Internal report prepared for the State of the Environment report. Department of Environment and Resource Management, Townsville. pp. 101.

Connolly, N., Moulton, D., Watson, F., and Kelton, M. (2008) *Description of areas containing High Ecological Value (HEV) fresh/estuarine waters in the Burdekin Water Quality Improvement Plan Area.* Prepared for the Burdekin Dry Tropics Regional NRM as input to the Burdekin Dry Tropics Water Quality Improvement Plan. Queensland Environmental Protection Agency, Townsville. pp. 47.

Connolly, N.M., Butler, B., Pearson, R.G. and Arthington, A. (2007) *Status and Trends of Water Quality and Ecosystem Health of Freshwaters in the Wet Tropics.* Draft Report for MTSRF Project 3.7.3, Milestone March 18th. Marine and Tropical Science Research Facility (MTSRF) technical publication. pp 45.

Arthington, A., **Connolly, N.M.** and Pearson, R.G. (2007) Introduction: the *Catchment to Reef* Program and Stream Health Monitoring. Chapter 1 *in* Arthington, A. and Pearson, R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 13.

Connolly, N.M., Pearson, B.A., Loong, D., Maughan, M. and Pearson, R.G. (2007) Study area and sites: geographic setting, hydrology, geomorphology and water quality of four Wet Tropics streams with contrasting land-use management. Chapter 2 *in* Arthington, A. and Pearson, R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 63.

Connolly, N.M., Pearson, R.G. and Pearson, B.A (2007) Macroinvertebrates as monitors of river health in Wet Tropics streams. Chapter 4 *in* Arthington, A. and Pearson, R.G. (eds.) *Biological Indicators of Health in Wet Tropics Streams.* Catchment to Reef CRC technical publication. pp 44.

Connolly, N.M. (2004) Mary River Basin Water Resource Plan – Macroinvertebrates: Preliminary Condition Assessment. Report prepared for the Queensland Department of Natural Resources and Mines as contribution to the Technical Advisory Panel (TAP) to the Mary River Water Resource Plan.

Connolly, N.M. (2004) Maroochy River Basin Water Resource Plan – Macroinvertebrates: Preliminary Condition Assessment. Report prepared for the Queensland Department of Natural Resources and Mines as contribution to the Technical Advisory Panel (TAP) to the Maroochy River Water Resource Plan.

Connolly, N.M. (2003) Burdekin Basin Water Resource Plan – Macroinvertebrates: Preliminary Condition Assessment. Report prepared for the Queensland Department of Natural Resources and Mines as contribution to the Technical Advisory Panel (TAP) to the Burdekin River Water Resource Plan.

Connolly, N.M. and McKie, B. (2001) An investigation into nuisance midges at The Lakes Stage 1. A report prepared for the Townsville City Council. ACTFR Report No. 01/06.

Connolly, N.M. (1998) The ACTFR macroinvertebrate and water quality data base and sensitivity index. Pages B1 –B20 *In* Pearson, R.G. and **Connolly, N.M.** (eds.) (1998*) Macroinvertebrates as monitors of river health in the tropics*. ACTFR Report No. 98/20

Connolly, N.M. (1998) Response of a stream invertebrate community to nutrient enhancement. Pages C1 – C9 *In* Pearson, R.G. and **Connolly, N.M.** (eds.) (1998) *Macroinvertebrates as monitors of river health in the tropics*. ACTFR Report No. 98/20

Connolly, N.M. (1998) The effect of sedimentation on benthic invertebrates in tropical streams. Pages D1 –D16 *In* Pearson, R.G. and **Connolly, N.M.** (eds.) (1998) *Macroinvertebrates as monitors of river health in the tropics*. ACTFR Report No. 98/20

Connolly, N.M. (1998) The effect of dissolved oxygen concentration on benthic invertebrates in tropical streams. Pages E1 – E11 *In* Pearson, R.G. and **Connolly, N.M.** (eds.) (1998) *Macroinvertebrates as monitors of river health in the tropics*. ACTFR Report No. 98/20

Pearson, R., Butler, B., Nolen, J., Christidis, F., **Connolly, N.**, Cairns, A., & Davis, L. (1998) Stream ecosystems as monitors of tropical forest catchments. ACTFR Report No. 98/26

Pearson, R.G. and **Connolly, N.M.** (eds.) **(**1998) Macroinvertebrates as monitors of river health in the tropics. ACTFR Report No. 98/20

Connolly, N.M., Doak, N. and Pearson, R.G. (1996) Environmental literature scan of Barron River catchment. ACTFR Report 96/20

Connolly, N.M. (1995) Fisheries. Pages 77 – 97 *In* Kutt, A., **Connolly, N.M.**, Clayton, P., Skull, S., and Pearson, R. (1995) *Cairns International Airport Baseline Environment surveys: Flora, Fauna and Fisheries*. Australian Centre for Tropical Freshwater Research, James Cook University of North Queensland Report No. 95/07

Connolly, N.M., Coles, R.G., and Lee Long, W. (1990), *Artificial reefs - a literature review and research recommendations.* Addendum to "An Assessment of the likely effects of the proposed Trinity Point

Project on the marine ecology of the Cairns Harbour and foreshore". Queensland Department of Primary Industries Report, 14pp.

Conference and workshop presentations

Connolly, N.M. (2011) Land use influences and river health in the Wet Tropics. Russell/Mulgrave case study. Tropical Rivers and Coastal Knowledge (TRaCK), Griffith University, Brisbane.

Connolly, N.M. and Pearson, R.G. (2006) Can equilibrium dynamics explain the humped relationship between productivity and diversity? A test using stream macroinvertebrates inhabiting leaf litter patches. North American Benthological Society, 4-9th June, Anchorage, Alaska, USA.

Connolly, N.M. and Pearson, R.G. (2006) Invertebrates as indicators in Wet Tropics streams. International Society of Wetland Scientists, July, Cairns, Queensland.

Connolly, N.M. and Pearson, R.G. (2005) Colonisation and mobility of stream invertebrates inhabiting leaf litter packs. Australian Society of Limnology, 29thNov.–2ndDec., University of Tasmania, Hobart, Tasmania.

Connolly, N.M., Pearson, B. and Pearson, R.G. (2005) Diversity in Adversity. Catchment to Reef – Joint Rainforest and Reef CRC Annual Conference, 21-23rd Nov., Southbank Convention Centre, Townsville, Queensland.

Arthington, A, **Connolly, N.**, James, C., Kennard, M., Loong, D., Mackay, S., Pearson, B. and Pearson, R. (2005) Sentinels of change: a test of biological monitoring in wet tropics streams. Joint rainforest and Reef CRCs conference, 21-23rd November, Southbank Convention Centre, Townsville.

Connolly, N.M. and Pearson, R.G. (2005) Nutrient enrichment of a detrital foodweb in a tropical rainforest stream. Plant Litter Processing in Freshwaters (PLPF) IV, 25-28th July, Laboratoire Dynamique de la Biodiversite, Toulouse, France.

Connolly, N.M. and Pearson, R.G. (2005) Nutrient enrichment of a detrital foodweb in a tropical rainforest stream. BZoNQ 6th Annual Conference, Townsville, 14-15th November, School of Tropical Biology, James Cook University.

Connolly, N.M. (2004) Riverine classification: The need for capacity building and strategy. Wetland Classification, Inventory and Geographic Information Systems Workshop. Joint Program Catchment to Reef CRC with Environmental Protection Agency Queensland, 9th August 2004, Queensland EPA Fl 15 Auditorium, 160 Ann Street, Brisbane.

Connolly, N.M. (2003) Colonisation and mobility of stream invertebrates inhabiting leaf litter packs. BZoNQ 4th Annual Conference, Townsville, 20-21st September, School of Tropical Biology, James Cook University.

Connolly, N.M. and Pearson, R.G. (2001) The effects of nitrogen and phosphorus enrichment on microbial biomass and nutrition of *Anisocentropus kirramus* (TRICHOPTERA) in a tropical rainforest stream. International Society of Limnology, SIL2001, Monash University, Melbourne.

Connolly, N.M. and Pearson, R.G. (2001) Too much of a good thing: The productivity diversity paradox. BZoNQ 2nd Annual Conference, Townsville, 11-12th August, School of Tropical Biology, James Cook University.

Pearson, R.G. and **Connolly, N.M.** (2001) Sustaining biodiversity in Wet Tropics streams. Fenner Conference on Biodiversity, Canberra.

Connolly, N.M. and Pearson, R.G. (2000) Impacts of forest conversion on freshwater ecosystems. Symposium and Workshop. *Forest-Water-People in the humid tropics: Past, Present and Future Hydrological Research for Integrated Land and Water Management.* 30th July-4th August, Hotel Equatorial, Kuala Lumpur, Malaysia.

Connolly, N.M. and Pearson, R.G. (1998) The role of resource dynamics in controlling species diversity in tropical rainforest streams. Rainforest: Past and Future Conference. CRC Tropical Rainforest Ecology and Management and Smithsonian Tropical Research Institute Conference, Cairns, North Queensland.

Connolly, N.M. and Pearson, R.G. (1998) The effect of nutrient enrichment on food quality in a detrital food web. Rainforest: Past and Future Conference. CRC Tropical Rainforest Ecology and Management and Smithsonian Tropical Research Institute Conference, Cairns, North Queensland.

Pearson, R.G. and **Connolly, N.M.** (1998) Resistance of rainforest stream invertebrate community to nutrient enrichment. Rainforest: Past and Future Conference. CRC Tropical Rainforest Ecology and Management and Smithsonian Tropical Research Institute Conference, Cairns, North Queensland.

Connolly, N.M. and Pearson, R.G. (1995) The role of nutrients in determining species diversity in tropical rainforest streams. CRC Tropical Rainforest Ecology and Management Annual Meeting, Kuranda, North Queensland.

Guest University Lectures

Connolly, Niall (2011) *Wetlands. Conservation Planning and Assessment in Queenslan*d. Wildlife Ecology, James Cook University, Townsville.

Connolly, Niall (2011) *Ecology of running waters: Streams and Rivers*. BZ3212/5212 Tropical Wetlands Ecology and Management, James Cook University, Townsville t.

Connolly, Niall (2011) *Russell/Mulgrave catchment case study*. BZ3212/5212 Tropical Wetlands Ecology and Management, James Cook University, Townsville.

Connolly, Niall (2011) *Introduction to the Queensland Wetland Program*. BZ3212/5212 Tropical Wetlands Ecology and Management, James Cook University, Townsville.

Connolly, Niall (2012) *Introduction to the Queensland Wetland Program*. BZ3212/5212 Tropical Wetlands Ecology and Management, James Cook University, Townsville.

Community education material:

Connolly, N., Kelley, R., Pearson, R. and Prior, T. (2005) Are *you connected? A guide to the processes linking Land, Sea and Reef.* A publication from the Catchment to Reef Program, a joint initiative of Rainforest CRC and CRC Reef Research Centre. ISBN 1 876054 60 3

Connolly, N., Christidis, F. and Pearson, R.G. (prototype) Atlas of the aquatic macroinvertebrates of the Wet Tropics. A multimedia interactive atlas of the distributions and taxonomy of aquatic macroinvertebrates of the Wet Tropics Bioregion.

Appendices referred to in Chapter 4.

Table A4.1. Mean densities (and s.e.) of invertebrates colonising leaf litter packs over 3 to 38 days in Experiment 4.1.

Taxon	Days				
	3	**7**	**12**	**24**	**38**
HYDRA				1.75 (0.48)	
NEMATODA	0.50 (0.29)	0.25 (0.25)	0.75 (0.48)	0.25 (0.25)	0.25 (0.25)
TURBELLARIA					
Dugesiidae			0.50 (0.50)	1.25 (0.48)	0.25 (0.25)
OLIGOCHAETA	0.50 (0.29)	0.25 (0.25)		0.25 (0.25)	2.25 (0.85)
CRUSTACEA,					
Cladocera		1.50 (0.29)	1.75 (1.11)	2.00 (0.41)	0.50 (0.29)
Cyclopoda	12.50 (6.65)	20.50 (2.02)	21.25 (9.48)	10.75 (4.19)	11.00 (2.86)
Ostracoda	0.25 (0.25)				
HYDRACARINA		2.50 (0.87)	3.25 (1.70)	3.00 (1.22)	6.75 (1.93)
PLECOPTERA, Gripopterygidae	0.75 (0.25)	0.50 (0.29)	0.25 (0.25)		0.50 (0.50)
EPHEMEROPTERA					
Baetidae			0.25 (0.25)		
Leptophlebiidae					
Atalophlebia sp.		0.75 (0.48)	0.25 (0.25)	0.25 (0.25)	
Koorrnonga sp.	0.25 (0.25)	0.75 (0.48)	1.50 (0.96)	2.25 (0.48)	1.00 (0.71)
Neboissophlebia sp.		0.25 (0.25)			
Nousia sp.					0.25 (0.25)
Indet. small instars	2.0 (1.22)	4.00 (1.08)	7.00 (2.12)	13.75 (1.93)	12.75 (4.71)
ODONATA					
Synlestidae					0.25 (0.25)
LEPIDOPTERA					0.25 (0.25)
TRICHOPTERA					
Antipodoeciidae		0.25 (0.25)			
Calamoceratidae	0.25 (0.25)		0.50 (0.29)	1.75 (0.75)	1.50 (0.87)
Helicopsychidae			0.50 (0.50)	0.25 (0.25)	
Hydrobiosidae		0.25 (0.25)	1.25 (0.25)	0.75 (0.48)	1.00 (0.41)
Hydroptilidae					
Hellyethira sp.	4.00 (2.04)	1.50 (0.96)	1.75 (1.18)	0.50 (0.50)	
Orthotrichia sp.					0.25 (0.25)
Oxyethira sp.	6.75 (1.11)	9.00 (2.27)	10.25 (4.21)	9.25 (2.66)	16.5 (5.42)
Indet. small instars	1.75 (1.18)	0.75 (0.75)	1.00 (1.00)	2.25 (0.85)	4.25 (1.11)
Leptoceridae	0.75 (0.48)	1.50 (0.87)	1.00 (0.58)	1.75 (0.63)	5.50 (2.96)
Odontoceridae				0.25 (0.25)	
Philopotamidae		0.25 (0.25)			
Polycentropodidae			0.25 (0.25)		
Indet. small instars		0.50 (0.29)			0.50 (0.50)
DIPTERA					
Ceratopogonidae			0.25 (0.25)		0.25 (0.25)
Forcimyiinae				0.25 (0.25)	
Chironomidae					
Chironominae		0.75 (0.48)		3.00 (1.08)	4.00 (1.47)
Corynoneura sp.	25.50 (7.68)	22.75 (4.99)	34.00 (3.37)	30.50 (7.58)	26.25 (3.94)
Cricotopus sp.			2.00 (2.00)		0.25 (0.25)
Dicrotendipes sp.	25.50 (5.42)	38.50 (3.38)	37.00 (3.19)	51.75 (2.06)	29.50 (8.06)
Echinocladius martini	63.75 (12.69)	81.00 (22.49)	94.75 (35.54)	192.25 (10.38)	158.50 (17.46)
Nilotanypus sp.	16.00 (3.11)	23.75 (4.75)	23.00 (7.56)	57.00 (7.49)	34.50 (5.92)
Orthoclad "beta"	1.00 (0.41)	1.25 (0.63)	2.25 (0.48)	3.75 (0.75)	4.75 (0.48)
Rheotanytarsus sp.	0.50 (0.29)	0.25 (0.25)	2.50 (2.50)	2.00 (1.22)	4.50 (2.63)
Stemp/Stemp	0.25 (0.25)	0.50 (0.29)		0.75 (0.75)	1.00 (0.58)
Tanytarsus sp.	5.25 (3.42)	4.00 (0.58)	6.50 (4.84)	18.75 (5.11)	23.75 (7.00)
Thienemanniella sp.	46.75 (12.66)	75.25 (20.73)	127.50 (27.52)	9.50 (3.30)	36.25 (11.36)
"oblong head"	83.50 (9.79)	100.25 (14.75)	125.75 (13.52)	97.25 (11.92)	101.00 (9.32)
Indet. small instars	4.50 (1.32)	10.00 (1.78)	17.75 (4.13)	20.25 (3.45)	26.00 (2.27)
Dixidae				0.25 (0.25)	
Empididae	1.00 (0.71)	0.75 (0.48)	1.50 (0.29)	5.50 (0.65)	4.75 (2.43)
Simuliidae					
Austrosimulium sp.		0.25 (0.25)	0.25 (0.25)		
Tabanidae	0.25 (0.25)	0.25 (0.25)		0.25 (0.25)	
Tipulidae				0.25 (0.25)	
Indet. small instars		1.50 (0.96)	0.25 (0.25)	0.25 (0.25)	
COLEOPTERA					
Dytiscidae	0.25 (0.25)		0.50 (0.50)		0.25 (0.25)
Elmidae					
Austrolimnius sp.	0.25 (0.25)	0.25 (0.25)	0.25 (0.25)	1.75 (0.25)	1.75 (0.25)
Psephenidae		0.25 (0.25)			
Scirtidae			0.25 (0.25)		
Staphylinidae			0.25 (0.25)		0.50 (0.29)

Table A4.2. Results of MRRPP pairwise comparisons for plots displayed in Figure 4.7a-d.

(a) All leaf packs abundance log (x+1) MRPP

```
Test statistic: T =      -12.340346
Chance-corrected within-group agreement, A =    0.10976506
Probability of a smaller or equal delta, p =    0.00000000
----------------------------------------------------------------
MRPP PAIRWISE COMPARISONS
Note: p values not corrected for multiple comparisons.

   Groups (identifiers)
    Compared          T               A                p
    3  vs.    7   -2.59534112   0.02730004   0.01742742
    3  vs.   12    -3.33193558   0.03433609   0.00546285
    3  vs.   24   -12.71301250   0.17642661   0.00000056
    3  vs.   38   -10.57547405   0.13679656   0.00000266
    7  vs.   12     0.33155550  -0.00333504   0.57498983
    7  vs.   24    -9.50707630   0.10207687   0.00000071
    7  vs.   38    -7.81017809   0.08039237   0.00000718
   12  vs.    24    -7.54034419   0.07841865   0.00001380
   12  vs.    38    -5.67065538   0.05873808   0.00027027
   24  vs.    38    -2.36597961   0.01984352   0.01843178
----------------------------------------------------------------
```

(b) All leaf packs presence absence MRPP

```
Test statistic: T =      -8.9474958
Chance-corrected within-group agreement, A =    0.09110288
Probability of a smaller or equal delta, p =    0.00000000
----------------------------------------------------------------
MRPP PAIRWISE COMPARISONS
Note: p values not corrected for multiple comparisons.

   Groups (identifiers)
    Compared          T                  A               p
    3  vs.    7   -2.96872958   0.03875331   0.00824024
    3  vs.   12    -1.86354006   0.02447817   0.05000450
    3  vs.   24    -9.70889666   0.14828680   0.00000133
    3  vs.   38    -9.16181193   0.14214138   0.00000437
    7  vs.   12     0.41984675  -0.00482906   0.63247376
    7  vs.   24    -5.38976864   0.06296957   0.00004429
    7  vs.   38    -6.25271149   0.07295948   0.00001103
   12  vs.    24    -3.86236052   0.04579897   0.00135720
   12  vs.    38    -4.43244757   0.05402113   0.00077230
   24  vs.    38    -0.70157783   0.00855984   0.22176915
```

(c) 3 leaf packs pooled within replicated abundance log (x+1) MRPP

```
 Test statistic: T =     -5.3413101
 Chance-corrected within-group agreement, A =    0.17111226
 Probability of a smaller or equal delta, p =    0.00008093
----------------------------------------------------------------
PAIRWISE COMPARISONS
Note: p values not corrected for multiple comparisons.

    Groups (identifiers)
     Compared          T               A               p
     3  vs.    7   -1.70803723   0.04851981   0.03775012
     3  vs.    12   -2.04136129   0.06506723   0.02207817
     3  vs.    24   -4.15749577   0.25940088   0.00514437
     3  vs.    38   -3.87507610   0.20573611   0.00561907
     7  vs.    12    0.45976022  -0.00921993   0.64341722
     7  vs.    24   -3.92059737   0.17438295   0.00602217
     7  vs.    38   -3.58982578   0.13944817   0.00831172
    12  vs.    24    -3.37897624   0.14578573   0.00842589
    12  vs.    38    -2.60603047   0.09998379   0.02127631
    24  vs.    38    -1.64349614   0.04953517   0.05570979
----------------------------------------------------------------
```

(d) leaf packs pooled within replicated presence absence MRPP

```
Test statistic: T =     -4.1245671
Chance-corrected within-group agreement, A =    0.12655945
Probability of a smaller or equal delta, p =    0.00032499
----------------------------------------------------------------
PAIRWISE COMPARISONS
Note: p values not corrected for multiple comparisons.

    Groups (identifiers)
     Compared          T               A               p
     3  vs.    7   -1.40821620   0.04970497   0.07820509
     3  vs.    12   -1.83753784   0.07178599   0.03216604
     3  vs.    24   -3.46246707   0.21364719   0.00811980
     3  vs.    38   -3.19142348   0.14775820   0.00625519
     7  vs.    12    0.01730709  -0.00058707   0.49128886
     7  vs.    24   -2.12146606   0.08750009   0.03343698
     7  vs.    38   -2.10255414   0.06520920   0.02811685
    12  vs.    24    -2.28460472   0.10924766   0.02954002
    12  vs.    38    -1.96901076   0.07553119   0.02289962
    24  vs.    38    -1.64903085   0.06377699   0.06612867
```

Table A4.3. Comparison of mean abundances (and s.e.) of invertebrate taxa collected over 5 days: (i) from leaf packs open to immigration and closed to immigration; and (ii) immigrating to and emigrating from leaf packs in section (b) of the artificial stream channels.

	On leaf packs		**Collected in drift**	
Taxon	**Open (s.e)**	**Closed (s.e)**	**Upstr.drift in (s.e)**	**Emigrating (s.e)**
HYDRA	0.33 (0.33)	--	0.33 (0.33)	--
NEMATODA	1.33 (0.88)	11.67 (11.67)	0.33 (0.33)	2.00 (0.58)
OLIGOCHAETA	6.33 (2.33)	5.00 (2.08)	4.00 (0.58)	1.00 (0.58)
CRUSTACEA,				
Cladocera	1.00 (0.58)	0.67 (0.67)	2.33 (1.86)	1.00 (0.58)
Cyclopoda	10.00 (1.73)	5.00 (1.73)	34.33 (13.45)	11.00 (4.58)
Harpacticoida	2.00 (2.00)	0.67 (0.67)	18.67 (1.20)	2.33 (1.45)
Copepoda indet.			0.33 (0.33)	3.33 (2.03)
HYDRACARINA	9.00 (1.53)	8.33 (1.20)	112.33 (40.60)	40.67 (9.56)
PLECOPTERA, Gripopterygidae	0.67 (0.33)	0.33 (0.33)	4.33 (1.20)	7.67 (4.70)
EPHEMEROPTERA				
Baetidae	--	0.33 (0.33)	12.00 (4.36)	0.67 (0.33)
Caenidae	--	0.67 (0.67)	--	--
Leptophlebiidae				
Atalophlebia sp.	0.67 (0.67)	0.33 (0.33)	--	--
Genus K	--	0.33 (0.33)	--	--
Koorrnonga sp.	5.33 (4.84)	5.67 (1.76)	0.33 (0.33)	--
Neboissophlebia sp.	--	--	0.33 (0.33)	--
Nousia sp.	5.33 (2.67)	0.67 (0.67)	2.33 (0.67)	0.33 (0.33)
Indet. small instars	29.33 (10.33)	24.00 (6.11)	39.33 (5.78)	9.67 (6.17)
TRICHOPTERA				
Calamoceratidae				
Anisocentropus sp.	2.00 (0..58)	1.33 (0.67)	1.00 (1.00)	0.33 (0.33)
Ecnomidae			0.33 (0.33)	--
Helicopsychidae	0.33 (0.33)	4.00 (2.52)		
Hydrobiosidae	0.67 (0.33)	0.67 (0.67)	3.00 (0.00)	0.33 (0.33)
Hydroptilidae				
Hellyethira sp.	2.33 (0.33)	2.00 (1.00)	1.00 (0.58)	1.33 (0.88)
Orthotrichia sp.	1.33 (0.88)	--	2.00 (0.58)	
Oxyethira sp.	5.67 (2.73)	5.33 (3.53)	3.67 (1.20)	19.67 (7.80)
Indet. small instars	2.67 (1.20)	4.67 (0.88)	13.67 (6.17)	21.00 (8.66)
Hydropsychidae	0.33 (0.33)	--	0.33 (0.33)	
Leptoceridae	4.33 (0.88)	4.00 (1.53)	6.67 (2.40)	8.33 (1.76)
Philopotamidae	--	0.67 (0.33)	21.33 (7.13)	2.00 (1.15)
Polycentropodidae	1.00 (0.58)	1.00 (0.58)	2.00 (2.00)	
Indet. small instars	0.67 (0.33)	0.33 (0.33)	11.33 (7.31)	0.33 (0.33)
DIPTERA				
Ceratopogonidae	0.67 (0.33)	--	11.67 (6.17)	2.00 (1.53)
Chironomidae				
Chironominae	20.00 (2.65)	20.67 (0.88)	0.33 (0.33)	--
Corynoneura sp.	127.67 (19.98)	60.67 (13.22)	41.33 (10.99)	11.67 (1.20)
Cricotopus sp.	4.33 (2.40)	1.00 (1.00)	1.33 (0.67)	--
Dicrotendipes sp.	40.00 (10.97)	42.00 (2.65)	79.00 (56.89)	4.33 (1.45)
Echinocladius martini	191.00 (16.52)	122.33 (4.91)	66.67 (1.86)	8.33 (1.33)
Nilotanypus sp.	58.67 (14.72)	41.33 (1.20)	50.33 (13.91)	19.67 (11.22)
Orthoclad “beta”	11.33 (0.88)	5.33 (0.67)	31.67 (4.10)	1.33 (0.33)
Rheotanytarsus sp.	6.00 (2.08)	0.33 (0.33)	1.33 (0.67)	1.00 (0.58)
Stemp/Stemp	8.00 (6.11)	4.00 (2.08)	7.67 (4.63)	1.00 (0.58)
Tanytarsus sp.	55.00 (9.54)	26.33 (8.35)	79.67 (14.67)	16.00 (8.08)
Thienemanniella sp.	62.33 (3.67)	56.33 (9.40)	238.67 (53.22)	16.33 (6.01)
Indet. small instars	28.00 (7.02)	19.00 (5.29)	31.67 (21.73)	11.67 (6.23)
Culicidae	--	0.33 (0.33)		
Dixidae	--	--	18.00 (4.62)	3.00 (1.15)
Empididae	10.33 (1.20)	5.33 (1.67)	7.00 (1.53)	2.00 (0.58)
Psychodidae		0.33 (0.33)		
Simuliidae	0.33 (0.33)	0.33 (0.33)	33.67 (15.90)	5.67 (5.17)
Austrosimulium sp.			22.33 (18.94)	
Tabanidae	0.33 (0.33)	--		
Indet. small instars	0.33 (0.33)	--	0.67 (0.33)	0.67 (0.67)
COLEOPTERA				
Dytiscidae				
Elmidae	3.67 (1.33)	2.00 (0.58)	0.33 (0.33)	
Austrolimnius sp.	1.00 (1.00)	0.33 (0.33)	2.33 (1.33)	0.67 (0.33)
Kingolus sp.	0.33 (0.33)	--	0.67 (0.33)	
Hydraenidae			0.67 (0.67)	
Scirtidae	--	0.33 (0.33)		
HEMIPTERA indet.				1.33 (0.67)
UNKNOWN	0.67 (0.67)	1.00 (1.00)	6.33 (4.10)	9.67 (2.91)
Total abundance	**732.67 (102.25)**	**497.00 (28.31)**	**1031.33 (120.89)**	**228.67 (83.31)**
Number of taxa	**33.67 (2.73)**	**30.33 (1.86)**	**38.67 (0.67)**	**28.33 (2.03)**

Appendices referred to in Chapter 5.

Table A5.1. Artificial stream % leaf cover experiment: densities of macroinvertebrates at the whole of channel scale (sum of 30 cobble/leaf pack samples). Taxa that contributed to the determination of the total number of unique taxa are indicated by bold text. Underlined text indicates taxa that were collected from bare cobble samples but did not occur in cobbles with leaf packs.

Taxon	% leaf pack cover – total abundance Channel scale						
	0%	**10%**	**20%**	**40%**	**60%**	**80%**	**100%**
HYDRA	52	--	72	47	80	90	24
PORIFERA	--	--	--	--	--	1	--
NEMATODA	2	--	2	43	41	42	22
PLATYHELMINTHES							
Turbellaria							
Dugesiidae	2	5	26	14	32	3	4
Temnocephalida							
Temnocephalidae	--	39	5	--	--	--	**1**
OLIGOCHAETA	117	59	581	498	1675	1082	1037
CRUSTACEA							
Amphipoda	--	--	--	--	--	--	1
Cladocera	57	55	131	692	762	2209	2671
Copepoda							
Cyclopoda	16	13	68	134	384	1188	1296
Harpacticoida	10	12	21	43	47	162	63
Copepoda indet.	--	--	3	1	--	--	28
Ostracoda	1	4	5	--	9	6	5
HYDRACARINA	76	64	84	86	126	302	243
PLECOPTERA							
Eustheniidae	--	--	--	1	--	--	--
Gripopterygidae							
Eunoptoperla kershawi	12	28	30	33	60	25	20
Indet. PLECOPTERA	--	--	4	--	--	--	3
EPHEMEROPTERA							
Baetidae	72	71	34	52	42	11	9
Caenidae	--	--	1	--	--	--	--
Ameletopsidae	--	--	--	1	--	--	--
Mirawarra sp	--	--	--	2	--	--	2
Leptophlebiidae							
Atalophlebia AV13	4	11	11	27	37	48	45
Atalomicria Sp.1	--	--	--	--	1	--	--
Koorrnonga AV4	25	23	50	37	24	27	47
Loamaggalangta AV2	1	--	--	--	1	1	3
Loamaggalangta sp.	--	--	--	--	2	--	--
Neboissophlebia NQ1	5	5	2	2	3	6	17
Neboissophlebia NQ2	--	--	--	--	--	--	3
Neboissophlebia sp.	--	--	--	--	--	--	1
Nousia NQ1	--	2	2	--	2	1	--
Nousia NQ2	14	30	51	39	54	50	30
Ulmerophlebia AV3	1	--	--	--	--	--	--
Indet. Leptophlebiidae	92	57	138	147	188	316	259
Indet. EPHEMEROPTERA		4					
ODONATA							
Aeshnidae	3	--	8	4	1	8	4
Aeshna sp.							
Cordulidae/Libellulidae	--	4	--	2	--	--	--
Synlestidae							
Episynlestes sp.	--	--	--	--	--	2	--
Synlestes sp.	--	--	1	--	--	1	18
Indet. Synlestidae	--	--	--	5	3	7	2
Chorismagrionidae	--	--	1	--	--	--	--
ZYGOPTERA	--	2	--	1	1	--	1
Indet. ODONATA	--	--	1	--	--	2	--
MEGALOPTERA							
Corydalidae			2				10
Protochauliodes sp.	--	7	4	9	7	3	--
LEPIDOPTERA							

Pyralidae	--	--	1	--	--	--	--
TRICHOPTERA							
Antipodoeciidae	1	--	--	1	--	--	--
Calamoceratidae							
Anisocentropus sp.	1	--	--	1	1	4	2
Ecnomidae							
Ecnomia sp.	--	--	1	1	--	2	--
Indet. Ecnomidae						1	1
Glossosomatidae	--	--	--	--	--	--	1
Helicopsychidae	1	8	--	--	--	3	1
Hydrobiosidae							
Apsilochorema sp.	--	--	--	--	--	1	1
Ethochorema sp.	--	--	--	--	--	--	1
Ulmerochorema sp.	--	--	--	--	--	1	--
Indet. Hydrobiosidae	--	1	1	2	2	1	1
Hydroptilidae							
Orthotrichia sp.	4	9	4	5	3	1	1
Oxyethira sp.	3	--	1	1	3	4	5
Indet. Hydroptilidae	--	1	1	1	2	--	--
Leptoceridae							
Oecitis Sp.1	--	--	7	4	2	2	6
Oecitis Sp.2	1	1	1	1	12	--	2
Oecitis sp.	--	--	--	--	--	--	1
Triplectides sp.	1	1	2	2	2	3	2
Indet. Leptoceridae	2	2	4	--	12	1	1
Philopotamidae	--	--	3	--	--	--	--
Chimara sp.	--	--	--	1	--	--	--
Philorheithridae	--	--	--	--	--	3	--
Polycentropodidae							
Genus I AV7	6	3	--	--	1	1	2
Plectrocnemia sp.	--	--	1	1	1	1	2
Indet. Polycentropidae	--	--	--	2	2	1	3
Indet. TRICHOPTERA	6	3	5	5	4	1	--
DIPTERA							
Ceratopogonidae	--	3	5	12	20	21	24
Forcimyiinae							
Chironomidae							
Chironominae	2	14	16	37	86	58	83
Corynoneura sp.	101	85	123	188	219	194	128
Cricotopus sp.	15	3	21	5	25	40	228
Dicrotendipes sp.	8	2	70	97	170	140	157
Echinocladius martini	7	63	84	146	213	203	222
Nilotanypus sp.	23	31	52	81	145	117	115
Orthoclad “beta”	34	17	53	75	129	122	13
Orthoclad Sp. ?	--	--	--	1	--	--	--
Rheotanytarsus sp.	8	38	9	48	74	303	126
Stemp/Stemp	2	--	--	--	1	3	--
Tanytarsus sp.	30	13	60	114	133	233	639
Tanytarsus/Rheotanytarsus	--	--	5	--	--	17	--
Tanytarsini	3	--	--	--	--	--	--
Thienemanniella sp.	200	537	450	737	915	223	183
Thienem./Corynoneura	12	--	56	131	133	226	215
Indet. Chironomidae	11	13	38	59	90	101	155
Dixidae	--	1	1	--	--	--	--
Empididae	5	5	11	18	31	83	15
Psychodidae	--	--	--	--	3	--	--
Simuliidae							
Austrosimulium sp.	31	36	116	104	188	23	7
Simulium sp.	--	--	1	--	--	--	--
Indet. Simulidae	49	107	87	27	64	47	11
Tanyderidae	--	--	--	--	--	--	2
Tipulidae	--	--	--	--	1	--	--
Indet. DIPTERA	--	1	8	2	3	4	3
COLEOPTERA	--	--	--	--	1	--	--
Dytiscidae	--	--	1	--	3	1	--
Elmidae							
Austrolimnius sp.	42	29	40	16	44	21	90
Coxelmis sp.	--	--	1	--	--	--	--
Kingolus sp.	4	9	2	--	--	--	1

Indet. Elmidae			2				
Psephenidae							
Sclerocyphon sp.	1	--	--	--	--	--	--
Scirtidae	1	1	1	2	1	3	1
Staphylinidae	--	--	--	--	--	1	--
Unkown	--	--	--	--	--	--	2
Number of unique taxa	**44**	**42**	**53**	**51**	**52**	**53**	**56**
Total number individuals	**1177**	**1530**	**2690**	**3845**	**6321**	**7809**	**8313**

Table A5.2. Artificial stream % leaf cover experiment: mean densities (± s.e.) of invertebrate taxa in leaf litter at the cobble/leaf pack scale. Taxa that contributed to determination of the total number of taxa are indicated by bold text. Grey text indicates taxa that were present in channels but were not collected from cobbles with leaf packs.

	% leaf pack cover – mean (s.e.) density leaf pack scale					
Taxon	10% n=3	20% n=6	40% n=12	60% n=18	80% n=24	100% n=30
HYDRA	--	1.00 (1.15)	1.50 (0.51)	2.72 (0.74)	2.38 (0.64)	0.80 (0.23)
PORIFERA	--	--	--	--	0.04 (0.04)	--
NEMATODA	--	0.33 (0.30)	1.92 (0.63)	2.28 (0.65)	1.75 (0.30)	0.73 (0.19)
PLATYHELMINTHES						
Turbellaria						
Dugesiidae	--	2.17 (1.39)	1.00 (0.39)	1.50 (0.64)	0.08 (0.06)	0.13 (0.09)
Temnocephalida						
Temnocephalidae	--	--	--	--	--	0.03 (0.03)
OLIGOCHAETA	2.00 (1.53)	17.83 (3.53)	38.08 (8.92)	85.89(12.51)	43.63 (7.48)	34.57 (5.92)
CRUSTACEA						
Amphipoda	--	--	--	--	--	0.03 (0.03)
Cladocera	9.00 (8.50)	9.33 (5.56)	55.17(23.28)	41.44 (9.78)	91.29(16.20)	89.03(10.98)
Copepoda						
Cyclopoda	2.00 (0.58)	9.67 (2.77)	10.75 (2.60)	20.72 (4.00)	48.96 (4.38)	43.20 (4.20)
Harpacticoida	0.67 (0.33)	2.67 (2.12)	3.00 (0.82)	2.56 (0.54)	6.71 (1.06)	2.17 (0.52)
Indet. Copepoda	--	0.50 (0.71)	0.08 (0.08)	--	--	0.93 (0.42)
Ostracoda	--	0.17 (0.24)	--	0.50 (0.35)	0.21 (0.08)	0.17 (0.10)
HYDRACARINA	5.33 (3.38)	4.83 (1.84)	6.17 (1.52)	6.22 (0.82)	12.29 (1.65)	8.10 (0.90)
PLECOPTERA						
Eusthenidae	--	--	--	--	--	--
Gripopterygidae						
Eunoptoperla kershawi	--	0.33 (0.47)	--	--	--	--
Indet. Gripopterygidae	4.33 (1.45)	3.50 (1.70)	2.50 (0.60)	3.22 (1.63)	1.00 (0.32)	0.67 (0.19)
Indet. PLECTOPTERA	--	--	--	--	--	0.10 (0.06)
EPHEMEROPTERA						
Baetidae	2.33 (2.33)	0.67 (0.70)	1.75 (1.41)	1.61 (0.65)	0.13 (0.09)	0.30 (0.15)
Caenidae	--	--	--	--	--	--
Ameletopsidae						
Mirrawarra sp.	--	--	--	--	--	0.07 (0.07)
Leptophlebiidae						
Atalophlebia AV13	1.00 (0.58)	1.33 (0.47)	1.92 (0.38)	1.72 (0.33)	1.96 (0.58)	1.50 (0.28)
Atalomicria Sp.1	--	--	--	--	--	--
Koorrnonga AV2	--	--	--	--	--	--
Koorrnonga AV4	4.67 (2.40)	6.83 (4.09)	3.00 (0.70)	1.33 (0.46)	1.08 (0.37)	1.57 (0.42)
Lomaggalangta AV2	--	--	--	0.17 (0.12)	0.04 (0.04)	0.10 (0.07)
Neboissophlebia NQ1	--	--	--	0.11 (0.08)	0.25 (0.15)	0.57 (0.18)
Neboissophlebia NQ2	--	--	--	--	--	0.10 (0.10)
Neboissophlebia sp.	--	--	--	--	--	0.03 (0.03)
Nousia NQ1	--	0.17 (0.24)	0.17 (0.11)	0.11 (0.08)	0.04 (0.04)	
Nousia NQ2	4.33 (2.19)	7.17 (2.95)	2.58 (1.13)	2.44 (0.62)	2.04 (0.63)	1.00 (0.43)
Ulmerophlebia AV3	--	--	--	--	--	--
Indet. Leptophlebiidae	7.00 (3.21)	12.50 (4.60)	9.50 (1.06)	8.61 (0.92)	12.33 (1.44)	8.63 (0.97)
ODONATA						
Aeshnidae	--	0.67 (0.30)	0.25 (0.25)	0.06 (0.06)	0.21 (0.12)	0.13 (0.08)
Aeshna sp.					0.08 (0.08)	
Cordulidae/Libellulidae	0.67 (0.33)	--	0.17 (0.17)	--	--	--
Synlestidae						
Episynlestes sp.	--	--	--	--	0.08 (0.08)	--
Synlestes sp.	--	--	--	--	0.04 (0.04)	0.60 (0.26)
Indet. Synlestidae	--	**0.17 (0.24)**	0.42 (0.26)	0.11 (0.08)	0.25 (0.12)	0.07 (0.05)
Chorismagrionidae	--	0.17 (0.24)	--	--	--	--
ZYGOPERA	--	--	0.08 (0.08)	0.06 (0.06)	--	0.03 (0.03)
Indet. ODONATA	--	--	--	---	0.08 (0.08)	--
MEGALOPTERA						
Corydalidae						
Protochauliodes sp.	2.33 (1.86)	0.67 (0.47)	0.75 (0.35)	0.39 (0.16)	0.13 (0.07)	--
Indet. Corydalidae	--	0.33 (0.47)	--	--	--	0.33 (0.15)
LEPIDOPTERA						
Pyralidae	--	--	--	--	--	--
TRICHOPTERA						
Antipodoeciidae	--	--	--	--	--	--
Calamoceratidae						
Anisocentropus sp.	--	--	0.08 (0.08)	0.06 (0.06)	0.13 (0.07)	0.07 (0.07)
Ecnomidae						
Ecnomia sp.	--	--	0.08 (0.08)	--	0.08 (0.06)	--
Indep. Ecnomidae	--	--	--	--	0.04 (0.04)	0.03 (0.03)
Glossosomatidae						0.03 (0.03)
Helicopsychidae	0.33 (0.33)	--	--	--	0.13 (0.07)	0.03 (0.03)
Hydrobiosidae						
Apsilochorema sp.	--	--	--	--	0.04 (0.04)	0.03 (0.03)

Ethoehorema sp.	--	--	--	--	--	0.03 (0.03)
Ulmerochorema sp.	--	--	--	--	0.04 (0.04)	--
Indep. Hydrobiosidae	0.33 (0.33)	0.17 (0.24)	0.08 (0.08)	0.06 (0.06)	0.04 (0.04)	--
Hydroptilidae						
Orthotrichia sp.	0.33 (0.33)	0.17 (0.24)	0.17 (0.11)	--	0.04 (0.04)	0.03 (0.03)
Oxyethira sp.	--	--	0.08 (0.08)	0.17 (0.09)	0.17 (0.10)	0.17 (0.10)
Indet. Hydroptilidae	0.33 (0.33)	--	--	--	--	0.10 (0.06)
Leptoceridae						
Oecitis Sp. 1	--	0.67 (0.30)	0.33 (0.33)	0.11 (0.08)	0.08 (0.06)	0.20 (0.10)
Oecitis Sp. 2	--	--	0.08 (0.08)	0.50 (0.20)	--	0.07 (0.05)
Oecitis sp.	--	--	--	--	--	0.03 (0.03)
Triplectides sp.	--	0.17 (0.24)	0.08 (0.08)	0.06 (0.06)	0.13 (0.09)	0.07 (0.05)
Indet. Leptoceridae	--	0.17 (0.24)	--	0.56 (0.22)	0.04 (0.04)	0.03 (0.03)
Philopotamidae		0.50 (0.71)				
Chimara sp.	--		0.08 (0.08)	--	--	--
Philorheithridae	--	--	--	--	0.08 (0.08)	--
Polycentropodidae						
Genus I AV7	0.33 (0.33)	--	--	0.06 (0.06)	0.04 (0.04)	0.10 (0.06)
Plectrocnemia sp.	--	0.17 (0.24)	0.08 (0.08)	0.06 (0.06)	0.04 (0.04)	0.07 (0.05)
Indet. Polycentropodidae -	--	--	0.17 (0.17)	0.11 (0.08)	0.04 (0.04)	0.07 (0.05)
Indet. Trichoptera	--	0.67 (0.47)	0.33 (0.19)	0.11 (0.08)	0.04 (0.04)	
DIPTERA						
Ceratopogonidae			0.92 (0.26)	1.11 (0.29)	0.88 (0.22)	0.80 (0.19)
Forcimyiinae	1.00 (1.00)	--				
Chironomidae						
Chironominae	4.67 (1.86)	2.67 (1.07)	3.08 (0.82)	4.78 (0.64)	2.42 (0.31)	2.77 (0.38)
Corynoneura sp.	7.00 (1.00)	9.67 (2.09)	9.83 (1.50)	9.33 (1.08)	7.17 (0.84)	4.27 (0.46)
Cricotopus sp.	0.33 (0.33)	1.33 (1.25)	0.33 (0.26)	1.28 (0.38)	1.58 (0.45)	7.60 (0.91)
Dicrotendipes sp.	--	7.67 (2.44)	7.83 (1.09)	9.33 (0.91)	5.83 (0.70)	5.23 (0.86)
Echinocladius martini	13.67 (2.33)	12.50 (4.25)	12.08 (1.46)	11.78 (1.15)	8.46 (0.84)	7.40 (0.73)
Nilotanypus sp.	5.67 (3.18)	4.50 (2.12)	6.17 (0.64)	7.50 (0.94)	4.63 (0.39)	3.83 (0.49)
Orthoclad "beta"	1.33 (0.88)	5.00 (1.59)	5.67 (0.78)	7.28 (1.20)	4.92 (0.71)	0.43 (0.17)
Orthoclad sp.	--	--	0.08 (0.08)	--	--	--
Rheotanytarsus sp.	8.33 (3.84)	0.67 (0.70)	3.92 (1.25)	3.61 (0.85)	12.29 (1.94)	4.20 (1.02)
Stemp/Stemp	--	--	--	0.06 (0.06)	0.13 (0.09)	--
Tanytarsus sp.	1.67 (0.88)	--	8.67 (1.70)	6.39 (1.11)	9.29 (1.27)	21.30 (1.79)
Thienemanniella	42.33(20.42)	35.33 (8.15)	47.58(10.58)	43.00 (6.37)	8.79 (2.43)	6.10 (1.58)
Thienem./Corynoneura	--	7.17 (1.88)	10.67 (1.29)	--	9.25 (0.70)	7.17 (0.56)
Tanytarsus/_Rheotanytarsus	--	0.50 (0.48)	--	--	0.71 (0.27)	--
Indet. Chiro - pupa	--	5.00 (2.39)	--	--	--	--
Indet. Chironomidae	--	0.08 (0.08	4.33 (1.09)	4.83 (0.71)	4.21 (0.59)	5.17 (1.07)
Dixidae	0.33 (0.33)	--	--	--	--	--
Empididae	1.00 (1.00)	1.33 (0.70)	1.33 (0.26)	1.72 (0.45)	3.29 (0.60)	0.50 (0.12)
Psychodidae	--	--	--	0.17 (0.17)	--	--
Simuliidae						
Austrosimulium sp.	12.00(12.00)	16.17(22.30)	6.92 (4.91)	10.22 (5.11)	0.71 (0.42)	0.23 (0.15)
Simulium sp.	--	--	--	--	--	--
Indet. Simulidae	22.00(22.00)	10.67(14.80)	0.08 (0.08)	3.44 (2.18)	1.96 (1.25)	0.37 (0.16)
Tanyderidae	--	--	--	--	--	0.07 (0.05)
Tipulidae	--	--	--	0.06 (0.06)	--	--
Indet. DIPTERA	0.33 (0.33)	1.00 (0.73)	0.17 (0.11)	0.17 (0.09)	0.17 (0.10)	0.10 (0.06)
COLEOPTERA						
Dytiscidae	--	--	--	0.17 (0.17)	0.04 (0.04)	--
Elmidae						
Austrolimnius sp.	1.00 (1.00)	0.50 (0.32)	0.92 (0.66)	1.39 (0.42)	0.79 (0.26)	3.00 (0.95)
Coxelmis sp.	--	--	--	--	--	--
Kingolus sp.	--	0.17 (0.24)	--	--	--	0.03 (0.03)
Psephenidae						
Sclerocyphon sp.	--	--	--	--	--	--
Scirtidae	--		0.08 (0.08)	0.06 (0.06)	0.13 (0.09)	0.03 (0.03)
Staphylinidae	--	--	--	--	--	--
Indet. COLEOPERA	--	--	--	0.06 (0.06)	--	--
UNKNOWN	--	--	--	--	--	0.07 (0.07)
Number unique taxa	30	38	44	48	51	54

Appendices referred to in Chapter 6.

Table A6.1. Locations of main sampling sites, distance downstream from first site, area of catchment upstream of each site, and land use (percentage of catchment area under conservation (Cons), agricultural (Agric) and other management).

	Location (°, “)		Distance	Area	Land use (%)		
Stream (catchment)	Latitude	Longitude	km	km^2	Cons	Agric	Other
Babinda (Russell)	17 20.377	145 52.054	0	14.9	100	0	0
	17 20.767	145 52.258	0.9	37.3	99.1	0.8	0.1
	17 21.085	145 52.543	1.8	39.3	99.0	1.0	0.1
	17 21.413	145 53.033	2.7	50.5	97.1	2.9	0
	17 21.450	145 53.563	4.6	60.1	95.0	5.0	0
	17 21.679	145 54.211	5.4	62.6	92.1	7.6	0.3
	17 21.858	145 54.929	8.7	70.8	87.9	11.8	0.3
	17 20.926	145 55.579	11.8	80.6	84.0	15.5	0.6
	17 20.764	145 56.257	12.8	83.9	82.0	16.0	2.0
	17 20.334	145 56.579	14.3	87.9	78.4	19.8	1.9
Woopen (Russell)	17 29.255	145 50.349	0	1.0	100	0	0
	17 29.156	145 50.842	0.3	3.0	92.0	2.0	0
	17 29.096	145 51.282	0.8	9.8	95.8	5.0	0
	17 28.917	145 51.683	1.2	10.1	94.2	7.0	0
	17 28.762	145 52.012	3.8	11.5	83.8	16.2	0
	17 28.543	145 52.416	4.5	11.8	82.0	18.0	0
	17 28.175	145 52.643	5.0	14.0	76.2	23.8	0
	17 27.715	145 52.765	6.3	26.8	73.2	26.4	0.5
Behana (Mulgrave)	17 09.315	145 49.651	0	63.1	100	0	0
	17 08.930	145 49.550	2.3	66.8	98.2	1.8	0
	17 08.184	145 49.829	4.0	69.1	97.1	2.9	0
	17 07.804	145 49.983	5.3	70.5	95.7	4.3	0
	17 07.569	145 50.372	5.7	85.5	93.5	6.3	0.2
	17 07.213	145 50.755	7.0	94.8	87.6	12.1	0.3
	17 07.234	145 51.782	9.0	98.3	84.7	15.0	0.4
L. Mulgrave (Mulgrave)	17 07.180	145 41.835	0	73.0	99.7	0.3	0.1
	17 07.743	145 42.312	2.0	99.2	97.9	1.2	0.9
	17 07.846	145 42.667	3.0	101.0	97.4	1.7	0.9
	17 08.380	145 43.123	4.4	104.2	97.0	2.1	0.9
	17 08.405	145 43.865	5.8	107.0	96.2	2.9	1.0

Table A6.2. Results of PCA of biophysical variables, showing first two eigenvectors scaled by their standard deviation (equivalent of correlation coefficient, *r*), and % of the variance explained by each eigenvector.

Variable	Eigenvector 1 (41%)	Variable	Eigenvector 2 (20.2%)
Phi mean	0.9274	Phi -5.5	0.7016
Phi -0.5	0.7382	Aquatic vegetation	0.6578
Phi -2.5	0.7258	Velocity	0.6137
Phi -1.5	0.7141	NO_X	0.6073
Phi -4.5	0.5271	Froude no.	0.523
NO_X	0.5047	Reynolds no.	0.466
Phi SD	0.4737	Phi -6.5	0.1467
Phi -3.5	0.4619	Phi -4.5	0.1353
Aquatic vegetation	0.3723	FRP	-0.1406
Reynolds no.	0.262	Gradient	-0.1614
Catchment area	0.1811	Phi -7.5	-0.21
Phi -5.5	0.1117	Phi -8.5	-0.2556
Velocity	0.087	Phi mean	-0.335
Froude no.	-0.1972	CPOM	-0.3995
Riparian Score	-0.4873	Catchment area	-0.4289
CPOM	-0.5816	Phi -1.5	-0.4366
Riparian cover	-0.605	Phi -3.5	-0.4646
FRP	-0.6377	Phi -2.5	-0.486
Gradient	-0.6755	Phi -0.5	-0.5326
Phi -8.5	-0.7939	Phi SD	-0.5475
Phi -6.5	-0.8434	Riparian cover	-0.6516
Phi -7.5	-0.85	Riparian Score	-0.7111

Figure A6.1. Views of sites located in lower reaches of Babinda Ck. (site 12, left) and Behana Ck. (site 9, right) showing contrasting stream and riparian condition. Photos by N.M. Connolly.

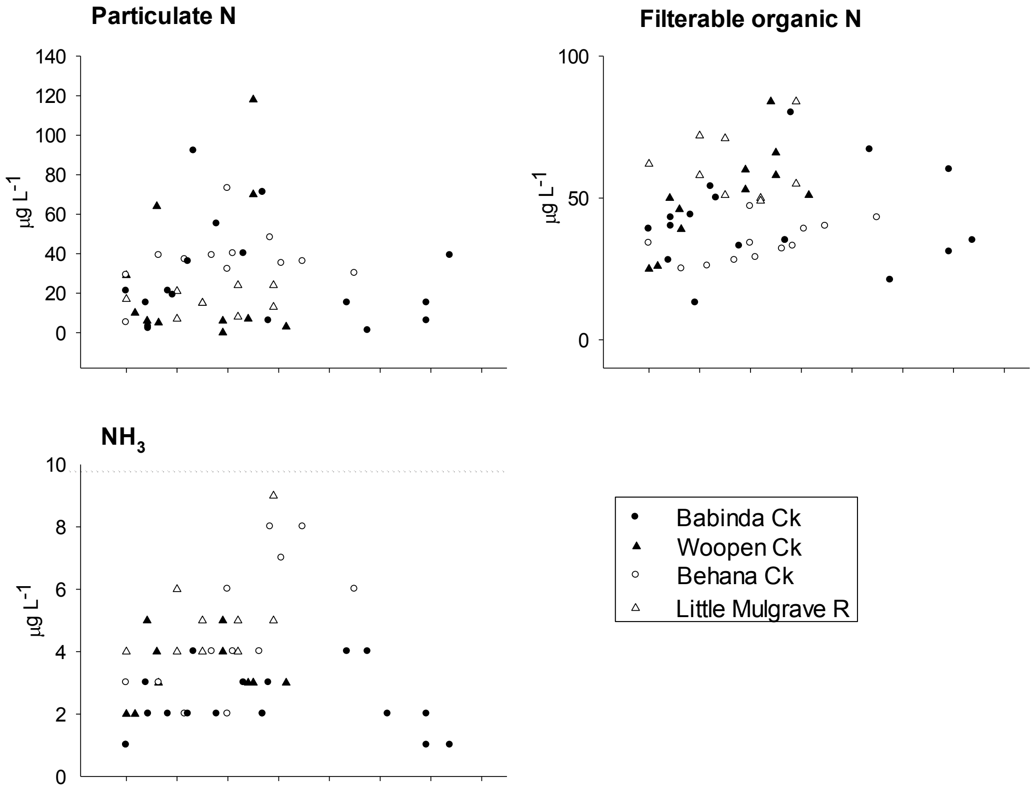

Figure A6.2. Concentrations of Particulate N, Filterable organic N and NH_3 in the four study streams, in relation to distance downstream. Dotted horizontal line indicates Queensland Water Quality Guideline concentration for NH_3 (10 µg L^{-1}).

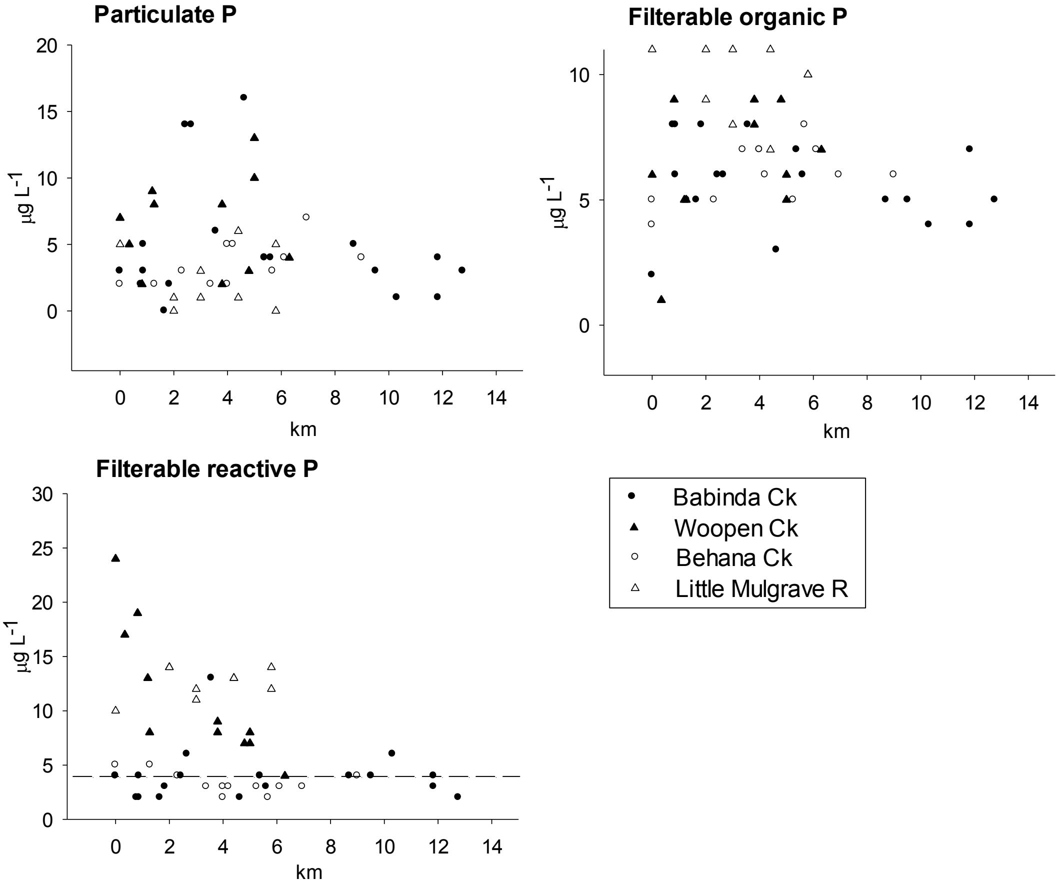

Figure A6.3. Concentrations of species of P measured in the four study streams, in relation to distance downstream. Dashed line indicates Queensland Water Quality Guideline concentration for FRP (4 µg L^{-1}). Single significant regression line shown for FRP at Woopen Ck: *r* = 0.854, P <0.001

Table A6.3. Characteristics of representative sites in each stream (Ba, Babinda Ck.; W, Woopen Ck.; Bh, Behana Ck.; and LM, Little Mulgrave R.). Variables are: Km, distance downstream from uppermost site (km); Ag, % of land area upstream that is used for agriculture; Wid, mean width (m); Dep, mean depth (m); Grd, % gradient of study reach; Vel, mean velocity (ms^{-1}); Pow, stream power (Wm^{-2}); Phi, mean sediment particle size, phi scale; RCov, % riparian cover; RSc, riparian score; Temp, temperature (°C); Turb, turbidity (NTU); Cond, conductivity (µScm^{-1}); ph; DO, % oxygen saturation; NO$_x$, nitrate + nitrite, (µgL^{-1}); FRP, filterable reactive phosphate (µgL^{-1}); Mac, macrophyte over (0-5 scale).

Site	**Km**	**Ag**	**Wid**	**Dep**	**Grd**	**Vel**	**Pow**	**Phi**	**RCov**	**RSc**	**Temp**	**Turb**	**Cond**	**pH**	**DO**	**NO$_x$**	**FRP**	**Mac**
Ba3	0.9	0.8	22.8	0.5	0.9	0.23	80	-6.8	50.5	43	19.0	0.16	20.8	6.4	100.2	18	2	3
Ba4	0.8	0.2	19.0	0.4	0.3	0.33	110	-6.6	25.0	30	18.1	0.15	25.3	6.4	102.7	37	3	4
Ba5	3.6	3.9	11.2	0.4	0.3	0.54	169	-6.6	35.1	18	18.6	0.22	26.6	6.2	116.6	47	13	2
Ba6	4.6	5	16.1	0.4	0.4	0.46	249	-6.4	2.7	21	19.2	0.20	28.2	5.5	112.6	103	4	2
Ba7	5.6	7.8	13.5	0.5	0.2	0.42	53	-5.6	3.1	10	19.8	0.09	25.5	5.9	105.2	99	3	4
Ba8	8.7	9.8	12.9	0.6	0.1	0.27	-	-5.1	13.2	10	20.8	0.15	28.4	5.7	115.1	113	3.5	5
Ba9	10.1	11.8	8.8	0.9	0.1	0.43	-	-6.2	3.2	10	21.8	0.18	31.2	5.9	104.8	127	4	4
Ba10	11.8	15.5	17.7	0.6	0.4	0.23	223	-4.7	8.4	25	20.3	0.20	29.9	5.6	105.1	140	4	4
Ba11	12.8	16	18.2	0.6	0.4	0.34	287	-1.9	11.4	17	20.9	0.56	31.2	5.6	87.4	133	2	4
W1	0	0	2.9	0.2	1.7	0.24	1144	-6.7	94.2	50	18.7	0.27	55.5	7.2	104	26	24	2
W2	1.3	8	5.8	0.1	0.9	0.19	559	-6.6	94.4	47	20.0	2.22	54.0	7.1	101.2	85	8	1
W3	2.1	10.1	7.9	0.2	0.9	0.33	482	-6.5	17.2	18	20.7	0.13	53.6	7.0	74.7	115	8	4
W4	2.9	12.3	11.9	0.2	0.2	0.17	36	-5.8	20.6	13	21.7	0.16	52.5	6.7	72.8	124	7.5	3
W5	3.8	15	13.0	0.3	0.4	0.18	202	-6.3	39.7	16	22.4	3.85	53.3	6.7	88.7	145	8	5
W6	4.8	22	7.3	0.3	0.3	0.23	42	-6.2	9.0	18	22.0	0.68	53.1	6.6	104.1	133	7	4
W7	5	23.8	6.5	0.4	0.6	0.33	208	-5.8	9.5	10	21.4	0.34	56.4	6.5	89.3	154	8	4
W8	6.3	26.4	13.5	0.2	0.7	0.36	337	-5.6	2.9	25	23.5	1.99	52.2	6.5	97.7	140	4	4
Bh2	0	0	19.3	0.5	0.2	0.06	928	-6.6	87.7	50	20.7	0.12	25.1	6.3	90.3	11	4	2
Bh3	1.3	0.5	9.7	0.3	1.0	0.25	568	-6.8	89.7	46	19.8	0.12	27.2	6.2	108.4	13	5	2
Bh4	3.4	2.4	10.8	0.4	0.6	0.22	598	-6.4	68.3	42	20.5	0.14	28.7	6.1	111.1	20	4	4
Bh5	4	2.9	11.9	0.4	0.1	0.19	519	-5.8	46.9	37	21.2	0.17	30.2	5.9	113.7	30	3	2
Bh6	5.3	4.3	23.3	0.5	0.1	0.21	501	-5.0	65.5	38	19.8	0.14	20.6	6.0	92	39	3	4
Bh7	6.1	8.5	12.2	0.3	0.1	0.18	500	-3.1	75.4	45	21.0	0.13	32.3	6.0	95.3	39	2	2
Bh8	7	12.1	9.5	0.5	0.0	0.22	152	-1.5	9.7	26	19.6	0.17	27.7	5.7	92.7	70	3	1
Bh9	8.1	13.6	13.2	0.5	0.0	0.19	185	-1.4	92.5	44	20.0	0.29	30.0	5.8	106.7	103	3.5	1.5
Bh10	9	15	15.3	0.4	0.1	0.18	261	-2.0	59.2	33	19.6	0.23	31.7	5.8	111.2	136	4	2
LM2	0	0	17.9	0.4	0.5	0.13	881	-7.3	97.0	50	17.1	0.18	46.4	6.9	118.3	37	10	2
LM3	0.9	0.28	13.9	0.3	1.3	0.25	296	-7.1	61.9	36	19.9	0.09	52.9	7.3	99.9	37	10	1
LM4	1.3	0.4	12.9	0.2	1.3	0.25	704	-6.6	94.0	47	20.2	0.12	52.9	7.2	89.4	35.5	12	2
LM5	2	1.2	22.0	0.4	0.0	0.07	130	-6.7	80.6	42	20.0	0.16	55.7	6.9	99	34	14	2
LM6	2.7	1.7	13.3	0.4	0.9	0.30	-	-6.9	89.1	46	20.9	0.74	57.2	7.0	91.8	34	12	2
LM7	3.3	2.1	14.3	0.4	1.0	0.18	803	-7.0	77.5	39	20.7	1.16	58.1	7.1	94.8	56	13	2
LM8	4.8	2.6	14.3	0.3	0.6	0.25	-	-6.6	82.2	35	20.4	0.21	59.3	7.2	84.3	59	12.5	2
LM9	5.1	2.9	13.1	0.3	0.8	0.34	458	-6.5	45.0	33	21.0	0.16	60.2	6.8	85.2	62	12	3

Table A6.4. List of taxa collected from four study streams, presence in each stream (x), % of total count (N = 40,666) and abundance rank (of 119). Bab = Babinda Ck., Wp = Woopen Ck., Beh = Behana Ck., LM = Little Mulgrave R.).

Phylum etc.	**Order etc.**	**Family**	**Genus/species or morphospecies**	**Bab**	**Wp**	**Beh**	**LM**	**%**	**Rank**
Platyhelminthes	Turbellaria			x				0.005	92
Mollusca	Bivalvia					x		0.002	104
	Gastropoda	Hydrobiidae		x	x		x	0.111	39
		Thiaridae			x			0.002	105
Annelida	Oligochaeta			x	x	x	x	0.015	73
Acarina	Hydracarina			x	x	x	x	0.042	54
Crustacea	Decapoda	Atyidae		x				0.012	78
		Penaeidae	*Macrobrachium* sp.	x		x	x	0.017	69
	Ostracoda				x	x		0.052	52
Insecta	Coleoptera	Elmidae	*Austrolimnius* A	x	x	x	x	8.084	5
			Austrolimnius B	x	x	x	x	0.612	22
			Austrolimnius C	x	x	x		0.138	37
			Austrolimnius D	x		x		0.096	41
			Austrolimnius E			x		0.002	106
			Austrolimnius F	x	x	x	x	0.482	24
			Austrolimnius G			x		0.020	66
			Austrolimnius H			x		0.032	59
			Austrolimnius J			x		0.002	107
			Austrolimnius K			x		0.002	108
			Austrolimnius L			x		0.005	93
			Austrolimnius M			x		0.002	109
			Austrolimnius N		x			0.002	110
			Austrolimnius O			x	x	0.007	85
			Elmidae adults	x	x	x	x	9.148	3
			Elmidae 2	x				0.015	74
			Elmidae 3			x	x	0.012	79
			Elmidae 4				x	0.002	111
			Graphelmis sp.	x	x	x		0.020	67
			Kingolus L49E	x	x	x	x	0.708	19
			Kingolus metallicus	x	x	x		0.037	57
			Kingolus 1		x			0.002	112
			Notriolus galstonius	x	x		x	0.015	75
			Notriolus sp.	x	x		x	0.012	80
			Ovolara leai	x	x		x	0.293	26
			Ovolara sp. 2				x	0.005	94
			Simsonia ?brooksi	x		x		0.020	68
			Simsonia leai			x		0.005	95
			Simsonia longipes	x				0.017	70
			Simsonia L2E	x				0.010	82
			Simsonia L3E	x	x	x	x	1.561	13
			Stetholus sp.	x	x	x	x	0.101	40

	Hydrophilidae	*Berosus* sp.	x	x	x	x	0.096	42
	Psephenidae	*Sclerocyphon* 1	x	x	x	x	2.422	10
		Sclerocyphon 2	x				0.002	113
	Ptilodactylidae	*Byrrocryptus* sp.	x	x	x	x	0.261	27
	Scirtidae		x	x	x	x	0.172	33
Collembola				x			0.005	96
Diptera	Athericidae		x	x	x	x	0.037	58
	Ceratopogonidae		x		x		0.052	53
	Chironomidae		x	x	x	x	6.262	6
	Empididae		x	x	x	x	0.064	46
	Psychodidae				x		0.002	114
	Simuliidae		x	x	x	x	5.266	7
	Tabanidae		x	x	x		0.032	60
	Tipulidae	Tipulidae 1	x	x	x	x	0.027	62
		Tipulidae 7	x	x	x	x	0.236	30
		Tipulidae 10	x		x		0.057	49
Ephemeroptera	Baetidae		x	x	x	x	25.250	1
	Caenidae		x	x	x	x	0.745	18
	Leptophlebiidae	*Atalomicria sexfasciatus*		x	x	x	0.079	44
		Atalomicria sp.	x		x		0.025	63
		Atalophlebia sp.		x			0.007	86
		Austrophlebioides porphyrobranchus	x		x		0.010	83
		A. wooroonooran			x		0.015	76
		Austrophlebioides sp.	x	x	x	x	8.153	4
		Jappa edmundsi	x	x	x	x	0.030	61
		Kalbaybaria sp.				x	0.005	97
		Leptophlebiidae WT6	x		x		0.074	45
		Loamaggalangta AV2	x		x		0.005	98
		Nousia NQ1	x	x	x	x	0.489	23
		Nousia NQ2	x	x	x	x	0.216	32
		Nousia NQ3	x	x	x	x	0.671	20
Hemiptera	Belostomatidae		x		x		0.012	81
	Naucoridae	*Naucoris* sp.	x		x		0.025	64
	Veliidae					x	0.007	87
Lepidoptera	Pyralidae		x	x	x	x	1.084	14
Megaloptera	Corydalidae	*Archichauliodes guttiferus*	x	x	x	x	0.061	48
Odonata	Corduliidae/Libellulidae		x		x	x	0.156	35
	Gomphidae		x	x	x	x	0.123	38
	Lestoideidae	*Diphlebia* sp.	x	x	x	x	0.226	31
	Telephlebiidae		x	x	x	x	0.022	65
Plecoptera	Eustheniidae	*Cosmioperla* sp.			x		0.005	99
	Gripopterygidae		x	x	x	x	1.905	12
Trichoptera	Calamoceratidae	*Anisocentropus* sp.	x	x	x	x	0.064	47
	Calocidae	Calocidae AV3	x				0.002	116

Conoesucidae AV1		x				0.007	88
Ecnomidae	*Ecnomina* AV3			x	x	0.007	89
	Ecnomus sp.			x		0.002	117
Glossosomatidae	*Agapetus* sp.			x		0.042	55
Helicopsychidae	*Helicopsyche* sp.	x	x	x	x	0.172	34
Hydrobiosidae	*Apsilochorema obliquum*			x		0.002	118
Hydrobiosidae	*Ethochorema brunneum*	x	x	x	x	0.042	56
	Hydrobiosidae sp			x	x	0.005	100
Hydropsychidae	*Aethaloptera sexpunctata*			x		0.002	119
	Asmicridea AV3	x	x	x	x	1.959	11
	Asmicridea AV4	x	x	x	x	0.140	36
	Baliomorpha banksi		x	x	x	0.007	90
	Cheumatopsyche AV14		x			0.017	71
	Cheumatopsyche AV15	x	x	x	x	10.142	2
	Cheumatopsyche AV16	x	x	x	x	3.897	8
	Cheumatopsyche AV5	x	x	x	x	0.352	25
	Cheumatopsyche AV8	x	x	x	x	1.003	15
	Diplectrona AV7	x				0.007	91
	Smicrophylax AV5	x	x	x	x	0.956	16
Hydroptilidae		x	x	x	x	0.057	50
Leptoceridae	*Notalina* AV12				x	0.005	101
	Notalina AV18			x		0.005	102
	Notalina sp.				x	0.010	84
	Oecetis spp.	x	x	x	x	0.797	17
	Triplectides parvus	x	x	x	x	0.054	51
	Triplectides AV12	x		x	x	0.015	77
Odontoceridae	*Barynema* AV1		x	x		0.017	72
Philopotamidae	*Chimara* AV19		x	x		0.086	43
	Chimara AV5	x	x	x	x	2.842	9
	Chimara AV6	x	x	x	x	0.654	21
	Chimara AV7	x		x	x	0.238	29
	Chimara uranka	x	x		x	0.248	28
Polycentropodidae	*Paranyctiophylax* AV4			x		0.005	103