

Patterns and determinants of macroinvertebrate diversity in headwater stream networks

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Caenota plicata (Trichoptera: Calocidae, Australia) collected from the study area.

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Dedication

for

mum and dad

*without your love and support over the past 29 years
this never would have been possible.....thank you*

Summary

Headwater streams dominate stream channel length in catchments. They are important sources of water, sediment and biota for downstream reaches and critical sites for organic matter and nutrient processing. Aquatic biodiversity in headwater streams has been overlooked in comparison to higher-order rivers, and few studies have considered spatial biodiversity patterns in headwater streams, or streams in general.

I reviewed studies of macroinvertebrate diversity in headwater streams and found equivocal evidence to support the view that headwater streams harbour high biodiversity. Headwater streams might still make an important contribution to γ (regional) diversity at the landscape (catchment) scale by virtue of high β (among-assembly) diversity. I studied eight headwater streams from three forested, upland catchments along the Great Dividing Range, Victoria, Australia to test my hypothesis of high β diversity and to understand the spatial patterns and determinants of macroinvertebrate diversity in headwater stream networks.

Diversity partitioning showed that reaches each had high α (within-assembly) diversity, while β diversity made only a small contribution to γ diversity at both the reach and catchment scales. β diversity may have been lower than hypothesized due to relatively small distances between sites and high levels of dispersal among reaches and catchments in the study area. Contrary to other studies that have found environmental factors to be important for explaining variation in macroinvertebrate assemblage structure in headwater streams, I found a limited role for environmental factors structuring macroinvertebrate assemblages in the study area.

In one year (2008), spatial factors (independent of environmental factors) were the dominant factor structuring macroinvertebrate assemblages. Therefore, metacommunity structure in the study area aligns most closely with the neutral/patch dynamic metacommunity model. This pattern of spatial structuring, coupled with low β diversity, suggests that high neighbourhood dispersal might be the main factor structuring macroinvertebrate assemblages in the study area. Flow permanence had only a seasonal effect on macroinvertebrate diversity and so there is a temporal component to the spatial diversity patterns in this system.

The explicit recognition of stream ecosystems as spatially structured networks has increased our understanding of ecological patterns and processes, and provided the impetus for this research. Recent advances in the study of networks, particularly in the fields of physics and network theory, offer an opportunity to considerably extend the current application of the network concept in stream ecology.

Determining the relative contributions of α and β diversity to γ diversity, and the scale dependence of α and β components, provides vital information for conservation planning because optimal reserve designs will differ depending on the relative contributions of α and β diversity. My finding of high α and low β diversity indicates that each stream in the study area can be considered to have low irreplaceability and the capacity to contribute a large portion of species to regional conservation targets.

Information on spatial patterns of diversity is urgently required for systematic conservation planning for freshwater reserves if we are to halt the rapid decline in global freshwater biodiversity.

General Declaration

In accordance with Monash University Doctorate Regulation 17/ Doctor of Philosophy and Master of Philosophy (MPhil) regulations the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes two published papers, one paper accepted for publication and two papers submitted for publication, all in international peer-reviewed journals. The core theme of the thesis is an investigation of the spatial patterns and determinants of macroinvertebrate diversity in headwater streams. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences under the supervision of Professor P.S. Lake, Dr Nick Bond and Professor Ralph Mac Nally.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of Chapters 1 – 5 my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status	Nature and extent of candidate's contribution
1	Macroinvertebrate diversity in headwater streams: a review	Published	80%
2	Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment	Accepted	70%
3	Conserving macroinvertebrate diversity in headwater streams: The importance of knowing the relative contributions of α and β diversity	Published	80%
4	Metacommunity structure of macroinvertebrate assemblages in headwater streams	Submitted	80%
5	River basins as complex networks: extending the 'rivers as networks' paradigm in stream ecology	Submitted	100%

I have not renumbered pages or figures for the submitted and published papers within the thesis.

Signed:

Date: 10th September 2010

Acknowledgements

To my parents, Peter and Donna, for their unwavering love and support. Without their countless hours of assistance in the field and continual encouragement from the home front, this research never would have been completed.

Dad, your four-wheel drive skills, engineer's ingenuity and ability to boil the billy in any conditions saved us many times. Those days in the field are a fantastic memory of time shared that I will always cherish, I hope you enjoyed our time out bush together as much as I did. I suspect the poor old Jeep did not appreciate it so much!

Mum, your endurance of rain, leeches, bogged cars and snakes are a testament to the fact that you would do anything for your daughters. You've always supported us and throughout this long four and a half years could always be counted on to know when times were tough and nothing but a mother's hug would suffice. Thanks for everything mum.

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To my supervisors who made this research possible:

Sam, as a young Honours student of yours I knew that if I ever did a PhD it had to be with you. I deeply admire your long and distinguished research career and always enjoy having a good debate with you about how we can improve the management of Victoria's rivers!

Nick, thanks for coming out into the field with me to understand the study sites and helping me get through a mountain of practical and statistical issues.

Ralph, your editing suggestions could always be counted on to make me go back and consider what the real message was. This whole thesis is more coherent and integrated as a result. Thanks for helping keep my spirits up when my enthusiasm started to wane, sometimes I just really needed that extra push to sit down and write something better.

Cath, you always put things back into perspective when the going got tough. Your constant reminder that, "if it was easy, everyone would have one" always gave me the strength to keep going. I cannot wait to finally celebrate with you, as we have discussed so many times over the past four and a half years!

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Thanks to the Kinglake National Park staff, especially Ion Maher, who always made my trip up to Wallaby Creek a pleasant (and safe!) one. You always provided up-to-date advice on field conditions and made time for a quick chat. I cannot even begin to imagine the devastation you felt when those fires swept through your workplace and community, my thoughts were with you all.

Big thanks to the friends I have made in office G32 over the past four and a half years; Sarina, Karen, Gillis, Elissa, Beth, Elise, Val, Greg, Nev, Darren, Megan and Jo. You could always be counted on for help with R code, solving EndNote disasters, cake celebrations for accepted papers and general commiserations about the life of being a PhD student. Good luck to everyone who is still on the journey. You will make it.

Thank you Sheila for answering my endless questions about the lab and equipment and putting up with my thousands of vials slowly covering every inch of bench space that I could possibly lay claim to.

Jim, thanks for answering all my questions about R. I got there in the end.

Thank you Richard for giving me access to museum specimens and your vast knowledge of the macroinvertebrate fauna of Victoria and, indeed, the world! I always looked forward to coming to visit you at the museum and listen to you talk in such fantastic detail about the taxonomy and ecology of macroinvertebrates in Victoria.

Big thanks to everyone in SWEID for your awesome support....best work family ever.

Introduction

Headwater stream networks are the source areas of water in river basins (Gomi *et al.* 2002) and these small, but numerous, streams make up the majority of stream channel length in catchments (Leopold *et al.* 1964; Hansen 2001; Benda *et al.* 2005). Studies over the past half century have provided important knowledge regarding geomorphology (Morisawa 1957; Strahler 1957; Leopold *et al.* 1964; Montgomery and Dietrich 1989; Benda *et al.* 2005), ecological function (Vannote *et al.* 1980; Smock *et al.* 1989; Wallace *et al.* 1997; Alexander *et al.* 2000; Peterson *et al.* 2001) and hydrology (Sidle *et al.* 2000) of headwater streams. More recently, there has been widespread recognition of the systemic importance of headwater streams in maintaining the function and health of whole river networks (Meyer and Wallace 2001; Gomi *et al.* 2002; Bernhardt *et al.* 2005; Lowe and Likens 2005; Freeman *et al.* 2007; Meyer *et al.* 2007).

There is still relatively little known about biological diversity in these systems, although several authors have suggested that headwater streams generally are ‘important’ areas for biodiversity (Cole *et al.* 2003; Lowe and Likens 2005; Meyer *et al.* 2007). Previous studies have reported the presence of undescribed, rare and specialist aquatic macroinvertebrates in headwater streams and springs (Erman and Erman 1995; Dieterich and Anderson 2000; Cole *et al.* 2003), but few studies have considered how macroinvertebrate diversity in headwater streams is distributed spatially and temporally across landscapes and the processes that drive these ecological patterns. Such information is also necessary for systematic conservation planning for freshwater reserves because the distribution of biodiversity in dendritic riverine networks differs from most terrestrial ecosystems and requires modification of traditional reserve design models (Linke *et al.*

2008; Linke *et al.* 2010). This information is required immediately because the loss of biodiversity in riverine ecosystems is more rapid than that of terrestrial systems (Abell 2002; Dudgeon *et al.* 2006). Headwater streams, in particular, are highly vulnerable to the effects of future climate change, altered flow regimes and land use change (Moore and Palmer 2005; Durance and Ormerod 2007; Freeman *et al.* 2007).

Defining ‘headwater streams’

There is no single, accepted definition of a ‘headwater stream’, although some general features such as low stream order (1st and 2nd) and small catchment (i.e. watershed) area appear to be defining criteria (Clarke *et al.* 2008). Stream order is a scale-dependent measure (Benda *et al.* 2004) and any definition of a headwater stream based on stream order should also state the map scale at which the observation is made. Hansen (2001) found that in the Chattooga River basin (Blue Ridge Mountains, southeast USA), 1:100,000 scale maps identified just 14% of the entire stream network with most of the ‘missing streams’ being orders one to three, and suggested that 1:24,000 scale maps provide a preferable base for stream ordering. It follows that many headwater streams are not represented on maps that are used to guide the management of natural resources (Lowe and Likens 2005) and that these systems have generally been overlooked in comparison to larger, lowland rivers (Cole *et al.* 2003).

Headwater streams dominate channel networks in total stream length and catchment area compared to higher order streams (Freeman *et al.* 2007; Wipfli *et al.* 2007). Headwater streams are closely coupled to hillslope processes (Gomi *et al.* 2002) and have critically important terrestrial-aquatic linkages as a function of their small size and consequent high edge to area ratio. These small streams are also structurally complex because their low

stream power means they are diverted around or under boulders, tree roots and other obstructions and this has characteristic impacts on their physical structure, dynamics and ecology (Gooderham *et al.* 2007). Physical disturbances caused by debris flows, forest fires, floods and droughts are another important driver of ecological dynamics in headwater streams (Gomi *et al.* 2002; Richardson and Danehy 2007). The periodic absence of surface flow has been identified as the characteristic disturbance regime in headwater streams and has consequent effects on local assemblages (Richardson and Danehy 2007). Drought and drying have previously been identified as an important form of disturbance structuring macroinvertebrate assemblages in streams (Boulton and Lake 1992; Boulton 2003; Humphries and Baldwin 2003; Lake 2003). Drying is likely to be particularly important for assemblages in headwater streams because these systems are prone to drying given their small size and limited tributary inputs.

Macroinvertebrate diversity in headwater streams

Irrespective of rising interest in the biodiversity of headwater streams (Meyer *et al.* 2007), surprisingly little is known about patterns of aquatic macroinvertebrate diversity (Cole *et al.* 2003; Heino *et al.* 2003). Relatively few studies have directly examined diversity patterns of macroinvertebrates in headwater streams (but see Monaghan *et al.* 2002; Heino *et al.* 2003; Brown and Swan 2010), even though understanding the patterns and underlying mechanisms that regulate diversity is essential to inform systematic conservation planning (Arponen *et al.* 2008; Ferrier and Drielsma 2010) and to prevent further losses of biodiversity (Vinson and Hawkins 1998). While there are few explicit studies of diversity patterns in headwater streams, some studies addressing the relationship between environmental variables and macroinvertebrate assemblage composition in headwater

streams have incidentally revealed information about macroinvertebrate assemblages in these systems (Cole *et al.* 2003; Heino 2005; Herlihy *et al.* 2005). In general, local environmental factors appear to be important for explaining variation in macroinvertebrate assemblage composition in headwater streams (Heino *et al.* 2002; Cole *et al.* 2003; Arscott *et al.* 2005; Stendera and Johnson 2005; Johnson *et al.* 2007; Brown and Swan 2010).

Non-local or regional processes (e.g. dispersal) also play a role in structuring macroinvertebrate assemblages in headwater streams. The branching geometry of river basins has characteristic effects on the distribution and abundance of species in these systems (Fagan 2002; Grant *et al.* 2009). Being at the very tips of the stream network, headwater streams are small patches of aquatic habitat in a broader landscape matrix that may be largely inhospitable for many aquatic species. One consequence of the structural architecture of river basins is that headwater streams form the most isolated components of a river network (Gomi *et al.* 2002). This isolation may result in high β (among-assemblage) diversity due to limited dispersal of aquatic macroinvertebrates among headwater streams within catchments or across catchment boundaries (Hughes 2007). The geographic isolation of headwater streams also may facilitate high rates of genetic differentiation within species, particularly for those taxa with poor dispersal abilities (Hughes *et al.* 1999; Finn *et al.* 2007) such as aquatic macroinvertebrates without an aerial dispersal stage.

To effectively manage diversity in headwater streams, it is vital that we understand the spatial and temporal patterns of diversity and their determinants. Different approaches to systematic conservation planning for headwater streams may be required depending on the relative importance of α (within-assemblage) and β (among-assemblage) diversity, both within and among catchments. The relative importance of local environmental factors and

regional factors in structuring macroinvertebrates assemblages in headwater streams is likely to drive these spatial patterns and will also provide crucial knowledge for future management of biodiversity and systematic conservation planning in headwater streams.

Thesis outline

The aim of my work was to investigate the patterns and determinants of macroinvertebrate diversity in headwater stream networks to understand the nature and relative importance of the relationships outlined in Fig. 1. This study was undertaken in eight headwater streams from three upland catchments in a closed water supply area; the Wallaby Creek Designated Water Supply Catchment Area (Plate 1). The study area is located on the ridge of the Great Dividing Range, Victoria, Australia (Fig. 2).

The particular objectives of the research were to:

- 1) Review the global literature on macroinvertebrate diversity in headwater streams and critically analyse the common statement that headwaters streams are ‘important’ for biodiversity in river networks (Chapter 1).
- 2) Investigate seasonal differences in the diversity and assemblage composition of aquatic macroinvertebrates in three headwater streams with a gradient of flow permanence (Chapter 2).
- 3) Use diversity partitioning to determine the relative contributions of α (within-assemblage) and β (among-assemblage) diversity to γ (regional) diversity for macroinvertebrate assemblages, and the scale dependence of α and β components (Chapter 3).
- 4) Determine the relative importance of environmental (local) factors and spatial (regional) factors on variation in macroinvertebrate assemblage composition and

search for evidence of metacommunity structure of assemblages matching any of the four main metacommunity models (Chapter 4).

- 5) Extend the current ‘rivers as networks’ paradigm by explicitly recognizing river basins as complex networks and describe how, irrespective of the local properties of river basins, their large-scale behaviour may be best understood by considering some common features of complex networks and how these might apply to river basins (Chapter 5).

My work will also inform systematic conservation planning by providing a detailed understanding of spatial diversity patterns of macroinvertebrate assemblages in headwater streams and the processes that are important in driving these patterns. The headwater streams in the study area are largely undisturbed due to their location in the closed water supply area, and provide an opportunity to study diversity patterns in a largely intact system. The ‘Big Ash’ forest of mature *Eucalyptus regnans* in the Wallaby Creek Designated Water Supply Catchment Area is an important remnant of a once extensive tall forest in central southern Victoria and home to some of the tallest hardwood trees in the world (Ashton 2000). Fire is intrinsically linked to the ecology of many Australian plant species and is essential for the germination and long-term survival of *Eucalyptus regnans*, and to prevent change of the remnant ‘Big Ash’ forest to a rainforest climax community (Ashton 2000). Sadly though, fire that swept through this area in the catastrophic February 2009 bushfires destroyed about 98% of the catchment (Cai *et al.* 2009) and 173 lost their lives on what is now referred to as ‘Black Saturday’.

Determinants/processes

Ecological patterns

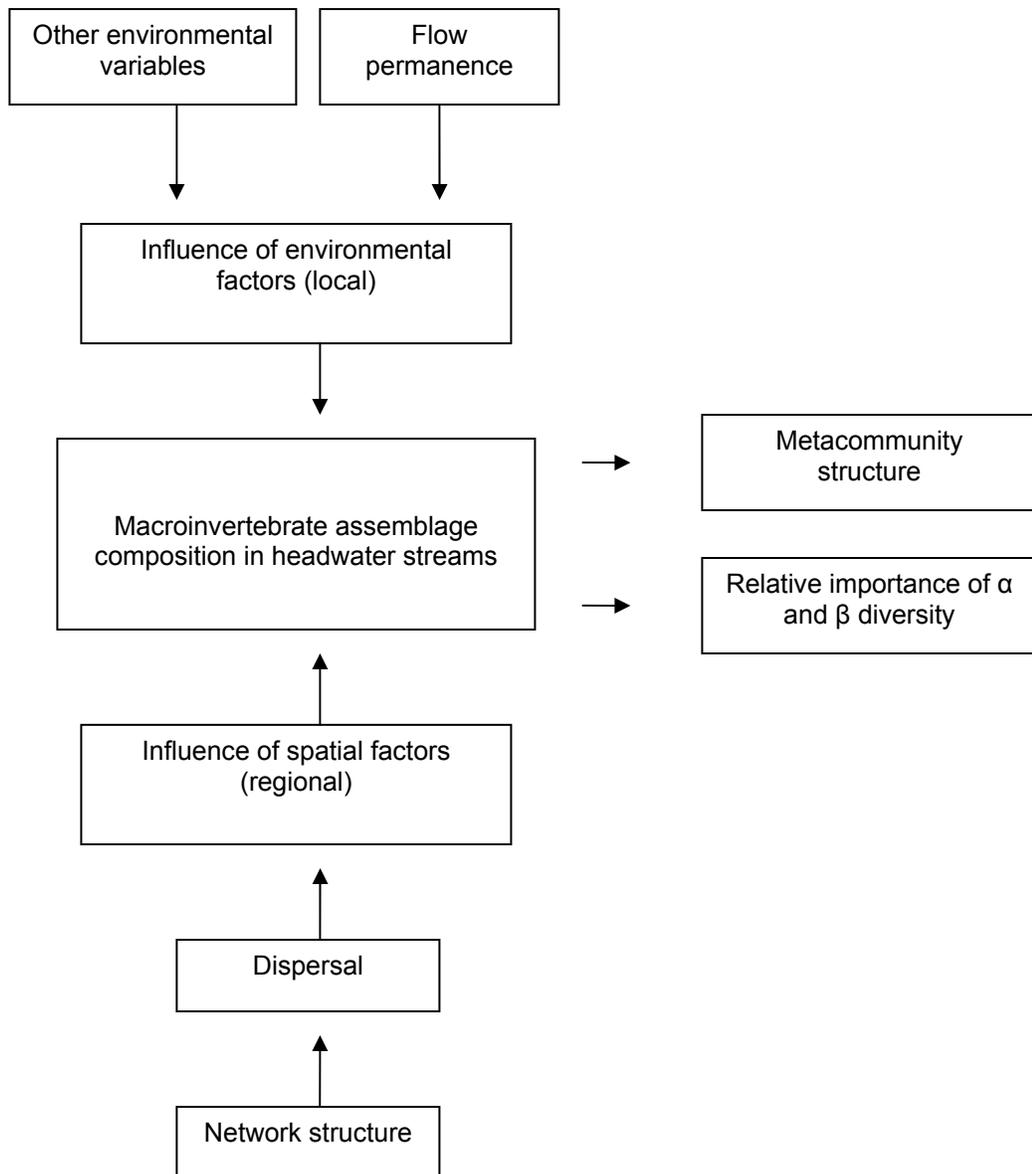


Figure 1. Conceptual model of potential factors that determine spatial patterns of macroinvertebrate diversity in headwater streams.



Plate 1. Mature *Eucalyptus regnans* in the ‘Big Ash’ forest (upper) and study stream W2 (lower) in the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia.

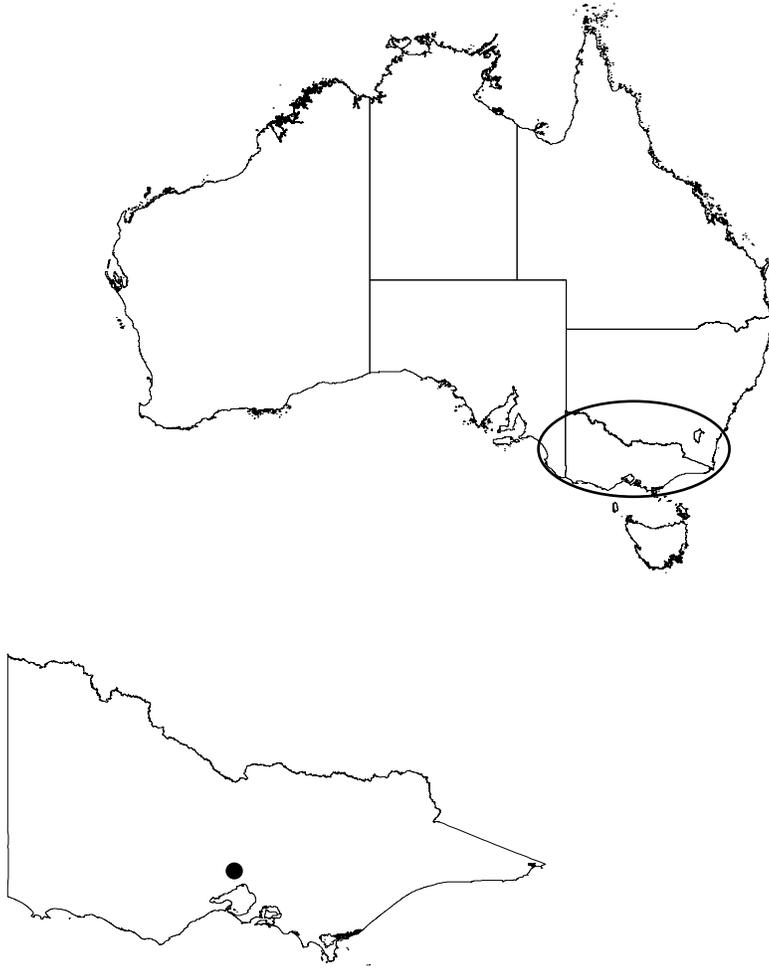


Figure 2. Location of study sites in Victoria, Australia.

Declaration for Thesis Chapter 1

This thesis chapter (Clarke *et al.* 2008) is in the same form as the final manuscript published in the peer-reviewed journal *Freshwater Biology*. The full reference for the published paper is:

Clarke A, Mac Nally R, Bond N & Lake, PS (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, **53**, 1707-1721.

Declaration by the candidate

In the case of Chapter 1, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution
I developed the conceptual models and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Nick Bond	Nick Bond contributed ideas to the work and co-authored the manuscript.
PS Lake	PS Lake contributed ideas to the work and co-authored the manuscript.

Candidate's
signature

	Date
--	------

Declaration by co-authors

The undersigned hereby certify that:

- (1) the above declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria;
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor of publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (6) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

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School of Biological Sciences, Monash University

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Signature 1		
Signature 2		
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SPECIAL REVIEW

Macroinvertebrate diversity in headwater streams: a review

AMBER CLARKE*[†], RALPH MAC NALLY*, NICK BOND*[†] AND P. S. LAKE*

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SUMMARY

1. Headwater streams are ubiquitous in the landscape and are important sources of water, sediments and biota for downstream reaches. They are critical sites for organic matter processing and nutrient cycling, and may be vital for maintaining the 'health' of whole river networks.
2. Macroinvertebrates are an important component of biodiversity in stream ecosystems and studies of macroinvertebrate diversity in headwater streams have mostly viewed stream systems as linear reaches rather than as networks, although the latter may be more appropriate to the study of diversity patterns in headwater systems.
3. Studies of macroinvertebrate diversity in headwater streams from around the world illustrated that taxonomic richness is highly variable among continents and regions, and studies addressing longitudinal changes in taxonomic richness of macroinvertebrates generally found highest richness in mid-order streams.
4. When stream systems are viewed as networks at the landscape-scale, α -diversity may be low in individual headwater streams but high β -diversity among headwater streams within catchments and among catchments may generate high γ -diversity.
5. Differing ability and opportunity for dispersal of macroinvertebrates, great physical habitat heterogeneity in headwater streams, and a wide range in local environmental conditions may all contribute to high β -diversity among headwater streams both within and among catchments.
6. Moving beyond linear conceptual models of stream ecosystems to consider the role that spatial structure of river networks might play in determining diversity patterns at the landscape scale is a promising avenue for future research.

Keywords: headwater streams, landscape, macroinvertebrate diversity, networks, β -diversity

Introduction

Headwater streams are a major component of river networks because they may contribute more than three-quarters of stream channel length in drainage basins (Leopold, Wolman & Miller, 1964; Hansen, 2001; Benda *et al.*, 2005). Their small catchments have

coupled terrestrial–aquatic linkages (Lowe & Likens, 2005) and are important sources of water, sediments and biota (Sidle *et al.*, 2000). Headwater streams are critical sites for organic matter processing (Bilby & Likens, 1980; Smock, Metzler & Gladden, 1989; Wallace *et al.*, 1997) and for nutrient cycling (Peterson *et al.*, 2001; Bernhardt *et al.*, 2005). Several authors have suggested that headwaters may be vital for maintaining the function and 'health' of whole river networks (Meyer & Wallace, 2001; Gomi, Sidle & Richardson, 2002; Bernhardt *et al.*, 2005; Lowe &

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Likens, 2005; Wipfli, Richardson & Naiman, 2007) and that they are important areas for maintaining biodiversity (Meyer & Wallace, 2001; Gomi *et al.*, 2002; Heino *et al.*, 2005a; Lowe & Likens, 2005; Meyer *et al.*, 2007; Richardson & Danehy, 2007). Meyer *et al.* (2007) gave an overview of the diversity of taxa that inhabit headwater streams and outlined the important role that headwaters might play in catchments as refugia from extremes of temperature and flow, from predation and from introduced species.

While many taxa contribute to biodiversity in headwater streams, aquatic macroinvertebrates play a central ecological role in many stream ecosystems (Boulton, 2003) and are among the most ubiquitous (Voelz & Mearns, 2000) and diverse (Strayer, 2006) organisms in fresh waters. Many studies of macroinvertebrates in headwater streams are concerned with α -diversity and appear to have been influenced by the strongly linear perspective of the River Continuum Concept (RCC) (Cole, Russell & Mabee, 2003; Eyre *et al.*, 2005; Megan *et al.*, 2007). This linear view of riverine systems has been common in many areas of stream ecology, especially material dynamics, ecological functioning and nutrient processing (Gomi *et al.*, 2002). Such a linear view has not always been the dominant paradigm. Leonardo da Vinci discussed the idea of network composition in drainage basins, comprising a main stem with ramifications, over 400 years ago (Shepherd & Ellis, 1997; Turcotte & Rundle, 2002). Nevertheless, most stream ecologists have studied drainage basins using linear conceptual models (Fisher, 1997), with little consideration of the importance of system architecture.

In this review we synthesize, from two different perspectives, quantitative studies that have examined macroinvertebrate diversity in headwater streams. First, we draw together a range of studies that have been shaped by a linear view of stream ecosystems that provide information on the local taxonomic richness of aquatic macroinvertebrates in headwater streams and the taxonomic richness of headwater streams relative to higher-order streams. Secondly, we suggest that the way forward for studies addressing macroinvertebrate diversity in headwater streams is likely to require a shift in the way we conceptualize rivers, from linear channels to networks. This idea is explored by examining the role of β -diversity in generating diversity patterns in headwater streams at the landscape

scale. Implications for conservation planning are discussed briefly.

Exactly what constitutes a headwater stream has not been well defined in the literature and, while some general principles such as 'reasonably' low stream order and 'relatively' small stream width and catchment area seem universal, a diverse range of stream types are encompassed within this general term. For the purposes of this review, we initially attempted to constrain our interest to 'zero-order basins (channel-less hollows above first-order streams) and first- and second-order streams at a map scale of 1 : 24 000 or smaller' or, where a map scale is not given, 'streams with drainage basins <100 ha'. However, we found very few (three) studies of macroinvertebrate diversity that met this definition and thus had to begin by synthesizing a range of studies that stated they were undertaken in 'headwater' streams. Developing a viable definition of what constitutes a 'headwater' stream is a topic that deserves a separate review. The focus here is on the compositional diversity of assemblages of aquatic macroinvertebrates, but we note that functional diversity is also an important component of biodiversity in any system (Ward *et al.*, 2002; Heino, 2005a) and that many other taxonomic groups contribute to biodiversity in headwater streams.

Taxonomic richness of aquatic macroinvertebrates in headwater streams

That headwater streams are important areas for biodiversity has recently gained much support (Dieterich & Anderson, 2000; Meyer & Wallace, 2001; Gomi *et al.*, 2002; Heino *et al.*, 2005a; Lowe & Likens, 2005; Meyer *et al.*, 2007). However, the oft-used adjective 'important' is ambiguous and it is uncertain whether headwater streams are considered important because they contain species that are headwater specialists (i.e. restricted to such systems), or because they may harbour undescribed species, or because they have high taxonomic richness. While there is some evidence to support the first two of these arguments (Dieterich & Anderson, 2000; Liljaniemi *et al.*, 2002; Cole *et al.*, 2003; Hauer, Stanford & Lorang, 2007; Richardson & Danehy, 2007), the latter is more difficult to answer because of a paucity of studies on diversity patterns of macroinvertebrates in headwater streams.

Whilst several studies claim high levels of taxonomic richness in headwater streams (Dieterich & Anderson, 2000; Cole *et al.*, 2003; Herlihy *et al.*, 2005) a review of 24 studies from a range of regions and continents (see Appendix S1) suggests that taxonomic richness of headwater streams is highly variable (Table 1a). The range in reported figures for taxonomic richness in individual streams is 3–125 and the range for total taxonomic richness per study (where reported) is 35–900. At least 14 different sampling methods were used, catchment area ranged from 12 to 6000 ha and the number of study streams ranged from 1 to 176. To answer whether headwater streams are taxonomically rich without these confounding factors is difficult and a more detailed discussion of these issues is given later (see 'Sampling and analytical issues'). There are insufficient individual studies that have been reported within one area or within streams of a clearly-specified size. Variability of taxonomic richness within single studies also is high. Herlihy *et al.* (2005) examined 167 sites in western Oregon (U.S.A.) that were predominantly forested and focused mostly on one habitat type (riffles). They found that taxonomic richness per stream ranged from 7 to 71.

With study streams spanning such a wide range of catchment areas, it is likely that many of the streams in these studies are mid-order streams. If a stricter definition of headwater streams is adopted, including only streams that either drain zero-order basins, are first- or second-order on a map scale of 1 : 24 000 or with catchment areas <100 ha, only three of the 24 studies remain. The lower bounds of local taxonomic richness and total taxonomic richness remained the

same but the higher values for these variables were reduced (Table 1b). There was high variability in these variables regardless of definition. Thus, whether a loose or a more strict definition of headwater streams is applied, the studies do not unequivocally support headwater streams having high taxonomic richness. Some studies showed high taxonomic richness, but there was large variability among different regions and continents and even within individual studies.

Longitudinal changes in taxonomic richness of aquatic macroinvertebrates

While the evidence for high taxonomic richness of macroinvertebrates in individual headwater streams is ambiguous, such streams still may make an important contribution to aquatic biodiversity at the catchment scale if together they have a higher taxonomic richness than mid- or high-order streams. In 1980, Vannote *et al.* (1980) suggested that species richness increases with stream size and reaches a maximum in mid-order streams. However, diversity patterns of macroinvertebrates along longitudinal gradients is still a contentious topic (Vinson & Hawkins, 1998). Arscott, Tockner & Ward (2005) tested this idea by investigating the relationship between species richness and stream size. Spanning a range of stream sizes from second- to eighth-order, they found low richness in headwater streams, an increase in mid-order streams and a decrease in richness in high-order streams. Several other studies have tested this prediction and, of the 11 studies examined here (Table 2), nine found evidence to support the hump-shaped

Table 1 Range of reported values for catchment area, number of study streams, taxonomic richness per stream and total taxonomic richness per study for (a) and (b)

Variable	Range of reported values
(a) 24 studies of aquatic macroinvertebrates in 'headwater streams' across a range of regions and continents	
Catchment area (ha)	12 (Grubaugh, Wallace & Houston, 1996)–6000 (Heino <i>et al.</i> , 2003)
Number of study streams	1 (Boyero & Bailey, 2001)–167 (Herlihy <i>et al.</i> , 2005)
Taxon richness per stream	3.5 (Haggerty <i>et al.</i> , 2002)–125 (Dieterich & Anderson, 2000)
Total taxon richness per study	35 (Haggerty <i>et al.</i> , 2002)–900 (Megan <i>et al.</i> , 2007)
(b) Studies of aquatic macroinvertebrates in headwater streams that fit the stricter definition (as described in the Introduction) of what constitutes a 'headwater stream'	
Catchment area (ha)	12.4–97.8 (Frady <i>et al.</i> , 2007)
Number of study streams	6 (Feminella, 1996; Frady <i>et al.</i> , 2007)–15 (Haggerty <i>et al.</i> , 2002)
Taxon richness per stream	3.5 (Haggerty <i>et al.</i> , 2002)–93 (Feminella, 1996)
Total taxon richness per study	35 (Haggerty <i>et al.</i> , 2002)–171 (Feminella, 1996)

Study	Stream orders	Maximum richness	Supports River Continuum Concept (Y/N)
Minshall <i>et al.</i> (1985)	Orders 2–8	46 (order 5)	Y
Melo & Froehlich (2001)	Orders 1–5	67 (order 1)	N
Grubaugh <i>et al.</i> (1996)	Orders 1–7	106 (order 5)	Y
Arscott <i>et al.</i> (2005)	Orders (not given)–7	61 (order 7)	N
Brussock & Brown (1991)	Orders 1–5	c. 59 (order 4)	Y
Lake <i>et al.</i> (1994)	Orders 2–5	42 (order 4)	Y
Growns & Davis (1994)	Orders 2–5	c. 24 (order 3)	Y
Malmqvist & Hoffsten (2000)	(orders not given)	77 (order not given)	Y [†]
Ward (1986)	Orders 1–5	106 (order 5)	Y
Malmqvist & Maki (1994)	Orders 1–5	43 (order 4*)	Y
Heino <i>et al.</i> (2005a)	Orders 1–5	Not given	Y

*B. Malmqvist, pers. comm.

[†]While stream orders are not given in the paper the authors note that, 'the most taxa rich sites were found in streams of intermediate size'.

pattern of taxonomic richness. Only one study found the highest taxonomic richness to occur in the smallest streams. Half of the studies did not include streams larger than fifth-order, so they can only provide partial tests of the hump-shaped pattern because they do not provide data for streams that Vannote *et al.* (1980) considered high-order streams. It appears that there is little evidence to support the general statement that headwater streams have higher taxonomic richness than downstream reaches. However, studies are needed that span a larger range of stream orders to elucidate further longitudinal patterns in taxonomic richness of aquatic macroinvertebrates.

Sampling and analytical issues

For a given habitat, a greater area or greater number of individuals sampled will yield a greater number of different species (Preston, 1962). Therefore, many published comparisons of species richness are not valid because they do not account for this sampling phenomenon (Gotelli & Colwell, 2001). For example, assessments of the taxonomic richness of headwater streams compared with higher-order streams may be confounded by a longitudinal increase in macroinvertebrate abundance (as a function of increasing stream size) or macroinvertebrate density as one moves from low- to high-order streams. Arscott *et al.* (2005) found that mean macroinvertebrate density increased from 7484 ± 2480 (± 1 SE) individuals m^{-2} in headwaters to $98\,811 \pm 18\,037$ individuals m^{-2} downstream on a lowland floodplain. Haggerty, Batzer &

Table 2 Summary of studies of longitudinal change in taxonomic richness of aquatic macroinvertebrates

Jackson (2002) pointed out that macroinvertebrate densities in headwater streams from several studies in the U.S.A. ranged from a mean density of 134–110 083 individuals m^{-2} . Further problems in the comparison of species richness among sites arise when the number of samples taken has been inadequate to represent the assemblage. Species richness counts can be compared rigorously only when species-accumulation curves have reached an asymptote (Gotelli & Colwell, 2001), although many studies comparing species richness do not show, or have not gathered, these data. Future studies quantifying species richness of macroinvertebrates in headwater streams should include species-accumulation curves and perhaps rarefaction procedures (Heck, Van Belle & Simberloff, 1975; Gotelli & Colwell, 2001).

Another issue is the wide range of sampling methods used to collect macroinvertebrates in headwater streams (Cole *et al.*, 2003). While most mid- to high-order streams are amenable to standard sampling techniques (e.g. Surber samplers), high heterogeneity of the physical habitat in headwater streams may mean that more than a single technique is required for these systems. It may be more important for researchers to focus on how well they have represented the assemblage in their sampling (e.g. by using nonparametric diversity estimators) than on applying one or two consistent sampling techniques to such naturally variable streams. Rarefaction procedures may be useful to standardize results where studies have taken a varied number of samples or used different sampling techniques. Differing levels of

taxonomic resolution also make it difficult to compare taxonomic richness among studies, and even among different taxonomic groups within studies. Family-level identification may drastically underestimate true diversity in many headwater streams. For example, chironomid midges have high levels of within-family and within-genus diversity (Heino *et al.*, 2005a) that may not be well represented in studies using a low taxonomic resolution. However, Heino & Soininen (2007) found that for macroinvertebrates (excluding chironomids) in headwater streams in Finland, species richness was strongly correlated with genus and family richness. Taxonomic richness, at any resolution, may not even be the most appropriate index with which to measure biodiversity, though it is undoubtedly the most popular. Heino *et al.* (2005b) highlighted the importance of considering several different measures in the assessment of assemblage-level biodiversity.

Our current inventory of macroinvertebrate diversity in headwater streams may significantly underestimate actual diversity because the majority of studies are undertaken only in stony, riffle habitats (Eyre *et al.*, 2005) and most streams, not just headwater streams, have not yet been sampled adequately (Voelz & McArthur, 2000). The common practice of excluding rare species from analyses is also problematic. Fore, Karr & Wisseman (1996) criticized this practice because it places more emphasis on requirements for statistical analysis than on biological relevance. Rare species may constitute a large component of species richness, especially in relatively unaffected sites (Cao, Williams & Williams, 1998), but there has been some debate on the importance of rare species in aquatic community ecology and their effect on various forms of multivariate analysis (Cao *et al.*, 1998; Cao & Williams, 1999; Marchant, 1999). Notwithstanding these arguments, headwater streams often contain regionally rare species (Heino *et al.*, 2005a), which may make a significant contribution to high β -diversity among headwater streams both within and among catchments.

'Losing the linear perspective': rivers as networks and the role of β -diversity

Fisher (1997) noted that, while every stream ecologist actually knows streams are branched, research in stream ecology often has little connection with stream

geometry and regards catchments as objects with only one or two dimensions. Many conceptual advances in stream ecology, such as the RCC (Vannote *et al.*, 1980) and the nutrient spiraling concept (Newbold *et al.*, 1982), invoked linear conceptual models to describe and predict a range of processes in stream ecosystems. Consideration of stream network architecture rarely has been explicitly considered in formulating hypotheses about species distributions or in designing sampling strategies. For example, among the numerous studies conducted within our own research group, examining both spatial variation and longitudinal patterns in invertebrate assemblage composition in the Acheron River and neighbouring tributaries (Lake & Schreiber, 1991; Downes, Lake & Schreiber, 1993; Lake *et al.*, 1994; Downes, Hindell & Bond, 2000), none has explicitly treated the system as a network and explored its properties as such. More recently, ecologists have taken a broader perspective of riverine systems and have begun to describe and predict processes at the landscape scale, applying concepts from landscape ecology to stream environments (Ward *et al.*, 2002; Wiens, 2002; Benda *et al.*, 2004).

This broader ecological perspective of riverine systems has seen increased recognition of the importance of system architecture on many ecological processes. Several authors have argued that considerable conceptual advances might be made by considering how the branching pattern of river networks influences ecological function (Fisher, 1997; Fisher, Sponseller & Heffernan, 2004; Lake, 2007). Benda *et al.* (2004) stated that conceiving rivers as networks is fundamental to the 'new' landscape view of rivers. However, it is worth noting that drainage basins have long been considered as networks in the field of fluvial geomorphology, leading to conceptual advances in understanding fractal scaling laws, emergent patterns of ecological organization and modelling optimal channel networks and quantitative river system structure (Nikora & Sapozhnikov, 1993; Rinaldo *et al.*, 1993; Maritan *et al.*, 1999; Brown *et al.*, 2002; Turcotte & Rundle, 2002; Newman, 2003). Advances from network (graph) theory are beginning to influence stream ecology, as shown by the recent exploration of how network structure of stream systems may influence population dynamics of individual species and ensuing patterns in species diversity (Fagan,

2002; Grant, Lowe & Fagan, 2007; Muneeppeerakul et al., 2007).

Components of diversity

The total taxonomic richness in a region (γ -diversity) consists of two components, a within-assemblage component (α -diversity) and an among-assemblage component (β -diversity) (Whittaker, 1972). β -diversity measures the difference in species composition among two or more local assemblages and captures a fundamental aspect of the spatial pattern of biodiversity (Koleff, Gaston & Lennon, 2003). High rates of turnover in species composition can occur where taxa are poor dispersers or environmental gradients (both spatial and temporal) are strong (Harrison, Ross & Lawton, 1992).

Exploring the contribution of β -diversity at the landscape scale

While the evidence presented does not support any general statement for headwater streams having high local diversity, or higher diversity than mid- to high-order reaches, we believe it is necessary to examine patterns of macroinvertebrate diversity in headwater streams from a different perspective. While taxonomic richness at a given point (e.g. α -diversity) may not always be high in headwater streams compared to mid-order streams, this does not mean that headwater streams make a small contribution to aquatic biodiversity at larger spatial scales. The importance of headwater streams to landscape-scale diversity (e.g. γ -diversity) may emerge from their unique architectural characteristics and only become apparent when the catchment is examined as a system, and not just as point estimates of diversity.

Freeman, Pringle & Jackson (2007) argued that productivity generally increases from headwaters to downstream reaches, although the large total length of headwater streams means that headwaters may contribute a large proportion of total system productivity. A similar effect may arise when comparing the taxonomic richness of headwater streams with downstream reaches. While a comparison of one headwater stream with one mid-order stream and with one high-order stream (the traditional linear approach, Fig. 1a) may reveal a higher taxonomic richness in the high-order stream, a comparison of total taxonomic

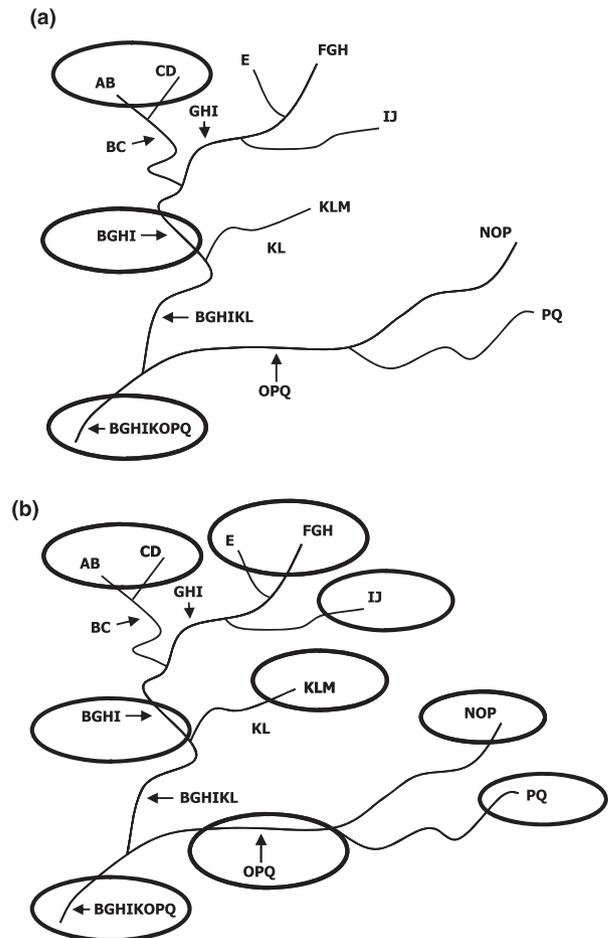


Fig. 1 Contrasting sampling designs for investigating longitudinal changes in taxonomic richness of macroinvertebrates: (a) a traditional 'linear' sampling approach to studying longitudinal patterns in taxonomic richness. Circles represent sampling sites. This sampling approach assumes that by sampling one part of the headwater network inferences can be made about diversity patterns across all headwaters in the network; (b) a 'network' sampling approach to studying longitudinal patterns in species richness. Circles represent sampling sites. This sampling approach ensures that empirical data is gathered on diversity patterns across the headwater network and illustrates how taxonomic richness in headwater networks may be drastically underestimated by traditional linear sampling approaches.

richness from all headwater streams in a catchment with that for all the mid-order streams in the same catchment (a 'network' approach, Fig. 1b) may reveal the highest combined taxonomic richness in the headwaters. The most likely explanation of such a pattern would be greater dissimilarity among individual headwater streams within a catchment (i.e. high β -diversity). Work is currently underway in our research group

collecting data to explore such diversity patterns by quantifying the partitioning of α - and β -diversity of macroinvertebrates in headwater stream networks.

Analyses of biodiversity patterns in freshwater systems largely have ignored β -diversity (Ward, Tockner & Schiemer, 1999) and headwater streams are no exception (although see Heino, Muotka & Paavola, 2003; Monaghan *et al.*, 2005; Costa & Melo, 2008). While there has been little examination of β -diversity of aquatic macroinvertebrates in headwater streams, recent work indicates that a large proportion of taxa in headwater streams is unique to particular sites or regions. Monaghan *et al.* (2005) found high taxonomic turnover within and among streams and that paired sites within streams often shared $\leq 50\%$ of taxa. Moldenke & Linden (2007) studied insect emergence in 14 first-order streams in the Pacific Northwest (U.S.A.) and found that almost 40% of the species were unique to one or another of the five geographic regions sampled. Danehy *et al.* (2007) examined 18 headwater streams in Oregon (U.S.A.), finding that 42 of the macroinvertebrate taxa were found at only one site, while only seven taxa were ubiquitous. Assemblage composition in four streams in the Rocky Mountains showed a significantly lower assemblage similarity among small alpine stream sites than those at lower altitudes (Finn & Poff, 2005). Frady, Johnson & Li (2007) found that similarity among sites from three pairs of adjacent headwater basins was $\leq 72\%$.

A similar pattern appears in genetic structure of some headwater stream macroinvertebrates. Finn, Blouin & Lytle (2007) found that 16 of 24 populations of the giant water bug *Abedus herberti* (Hidalgo) in headwater streams contained at least one 'private' haplotype (i.e. haplotype found only in one population). Populations of the stonefly *Yoraperla brevis* (Banks) in small montane streams were more similar within than among streams, due to limited aerial dispersal (Hughes *et al.*, 1999). Finn *et al.* (2007) proposed a 'headwater model' to describe spatial patterns of genetic diversity for species that are headwater specialists, which predicts that genetic variance is partitioned according to higher-altitude 'islands' of suitable habitat and so populations of headwater specialists are often highly isolated. However, Hughes *et al.* (1999) noted that gene flow in populations of stream insects depends on dispersal ability and Wilcock *et al.* (2007) found that this

'headwater model' does not hold when upland headwater species have strong dispersal ability.

Mechanisms potentially generating diversity patterns in headwater streams

Whilst it is important to describe diversity patterns of aquatic macroinvertebrates, we must also attempt to determine the mechanisms that drive these patterns. Vinson & Hawkins (1998) reviewed the major conceptual advances of the past 50 years regarding the factors that influence insect biodiversity in streams and many of these probably apply equally to headwater streams. However, there may be additional factors driving diversity patterns in headwater streams that are unique to these systems, or operate in a way that is different to higher-order streams. We explore here how (i) dispersal ability and opportunity and (ii) spatial structure of dendritic networks might operate to generate unique diversity patterns of macroinvertebrates in headwater streams.

Dispersal ability and opportunity. Dispersal is a key process determining the partitioning of diversity into α and β components (Loreau & Mouquet, 1999). The architecture of drainage basins leads to low physical connectivity among headwater streams within a catchment (Gomi *et al.*, 2002). For species lacking an aerial dispersal stage, patches that are spatially 'nearby' may effectively be very remote (Fagan, 2002). High rates of genetic differentiation within species (Hughes *et al.*, 1999) and low rates of immigration of new species into local assemblages from the regional species pool are expected. Headwaters often are disconnected and isolated from other headwaters within catchments by large inhospitable rivers and the distance along the network to reach new sites, thereby limiting dispersal opportunities through higher-order streams (Richardson & Danehy, 2007). These isolated components of the river network also have the fewest possible pathways for recolonization in the event of local population extinctions (Fagan, 2002; Richardson & Danehy, 2007).

Hughes (2007) reviewed genetic data for a range of freshwater species (42) and found that, in general, contemporary dispersal across catchment boundaries is negligible and dispersal among streams within catchments is more limited than previously thought. Similar results were noted by Griffith, Barrows &

Perry (1998) who studied lateral dispersal of adult Plecoptera and Trichoptera in four headwater streams draining adjacent catchments in West Virginia. They found that mean maximal dispersal distances for most species were usually less than half the distance among adjacent headwater streams, suggesting that lateral dispersal into neighboring headwater streams in this region is uncommon for many species. Similarly, a study of lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream in the U.K. by Petersen *et al.* (1999) revealed that 90% of trapped individuals travelled less than 51 m from the stream channel. However, there is also growing evidence to suggest that inter-catchment dispersal of insects may be greater than previously thought. Studies of adult stoneflies have shown evidence of dispersal among small streams (Briers *et al.*, 2004; Macneale, Peckarsky & Likens, 2005). Masters *et al.* (2007) investigated inter-catchment dispersal of adult Ephemeroptera, Plecoptera and Trichoptera to test the hypothesis that acid-sensitive invertebrates are unable to disperse into recovering headwaters because of geographical isolation across catchments. They found that, although some species caught as adults occur exclusively around streams occupied by their larvae, other species showed evidence of inter-catchment dispersal. Similarly, Miller, Blinn & Keim (2002) found that dispersal capabilities of aquatic insects are highly variable and that the use of hierarchical indicators of genetic differentiation are not always a good proxy for investigating dispersal.

Given the wide range of dispersal capabilities noted for aquatic insects in the literature a conceptual partitioning of α - and β -diversity in two, adjacent

headwater networks that might be generated from a regional species pool of six species (A–F) with differing dispersal abilities and opportunities is shown in Fig. 2. Species A has high dispersal ability with a long-range aerial stage able to cross a mountain range separating the two headwater networks. This species has a wide distribution across the two catchments (e.g. many insect taxa). Species B has good dispersal ability with an aerial stage, but is unable to cross the mountain range. Absences of species A or B from individual streams are due either to lottery effects (Sale, 1974) or inability to survive under local environmental conditions (Poff, 1997). Species C, D and E have either very limited aerial dispersal ability or are able to colonize only immediately adjacent reaches through instream drift or limited overland travel (e.g. aquatic beetles). Species F has no aerial dispersal ability and no opportunity to colonize adjacent reaches because the distance through the stream network is too great and cannot be made without travelling through inhospitable higher-order streams. The overland distance to other suitable headwater streams in the network also is too far for species F. Restriction of the range of species F is a function of both its dispersal ability and opportunity (e.g. opportunity dictated by spatial position of that headwater stream in the stream network).

Different dispersal ability or differences in habitat requirements can also generate patterns of biotic nestedness (Atmar & Patterson, 1993; Cutler, 1994). Biotic nestedness occurs when the biota of species-poor assemblages are non-random subsets of the biota in richer assemblages (Patterson & Atmar, 1986). Biotic nestedness generally is regarded as the opposite

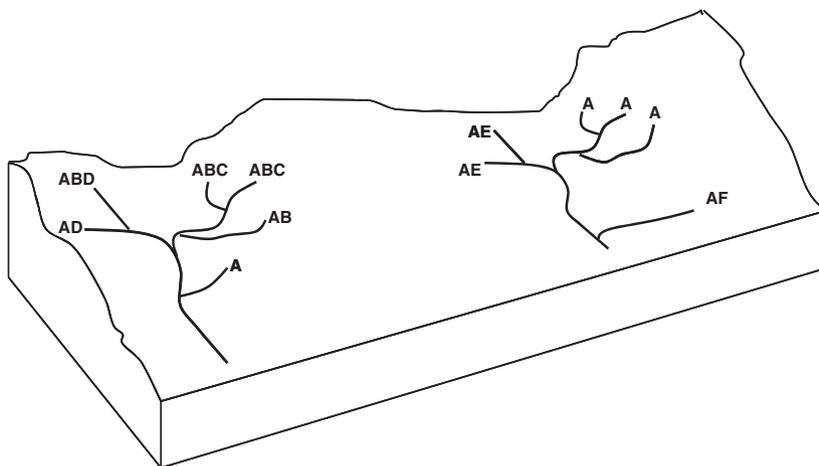


Fig. 2 Theoretical patterns of α and β -diversity generated in two headwater networks with a regional species pool (γ -diversity) of six species (A–F) with differing dispersal abilities and opportunities across two adjacent catchments separated by a mountain range.

phenomenon to high species turnover among sites (Leibold & Mikkelsen, 2002) and thus provides an alternative idea for how diversity patterns of aquatic macroinvertebrates might be structured in headwater systems. Heino (2005b) found that midge assemblages in headwater streams were nested, although they also showed some evidence of alternative structuring, such as species turnover and Gleasonian gradients (e.g. species turnover but with a random arrangement of species ranges along the gradient). In a study of 88 streams, Malmqvist & Hoffsten (2000) also found evidence of nested distribution patterns for Ephemeroptera, Plecoptera, Trichoptera and Simuliidae. Monaghan *et al.* (2005) found some evidence that assemblage structure was nested among 22 alpine headwater sites, but also reported a high number of 'rare' species, which indicates that species turnover (e.g. β -diversity) may be high. A prevalence of 'rare' species was also found by Malmqvist, Zhang & Adler (1999) when analysing patterns of biotic nestedness in blackfly larvae. There was little evidence that the distribution of blackfly larvae was nested. Future studies assessing whether the macroinvertebrate fauna of headwater streams is a nested sub-set of the fauna present at downstream sites are required to further enhance our understanding of the contribution that headwater streams make to γ -diversity. For example, Sabo *et al.* (2005) found that riparian habitats contributed to high γ -diversity by harbouring a unique complement of species, rather than high species richness.

Spatial structure of river networks. The network geometry of river basins can be classified as dendritic, or branching, whereby bifurcation results in a 'main-stem' and 'branches' with a greater number of branches encountered as one moves upwards through the network (Grant *et al.*, 2007). This branching pattern often generates a familiar drainage basin shape, where the widest part of the basin is located at the top of the network and the narrowest at the bottom. A consequence of this spatial structure is that the distance between the two farthest first-order streams is likely to be larger than the distance between the two furthest second-order streams and so on (Fig. 3). The distance between streams is important ecologically as it may lead to patterns of spatial autocorrelation, whereby the similarities in biota diminish in sites that are further apart (Legendre, 1993). However, this general pattern of spatial auto-

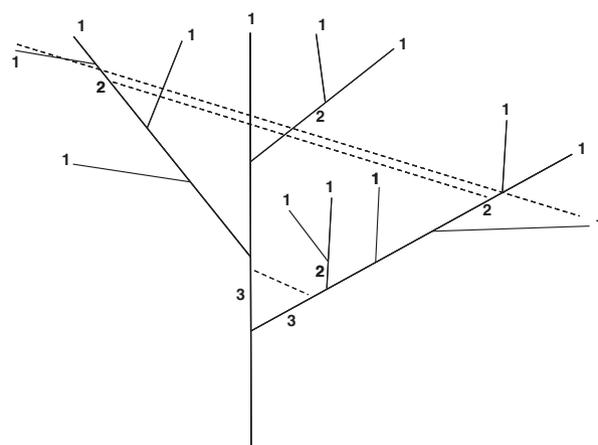


Fig. 3 Generalized spatial structure of a dendritic river network illustrating how the branching geometry of river basins may generate a pattern whereby the distance between the two furthest first-order streams is greater than the distance between the two furthest second-order streams and so on. Such a pattern may generate high spatial autocorrelation of macroinvertebrate assemblages in headwater streams compared to higher-order streams.

correlation is likely to be confounded by differing abilities and opportunities for dispersal. Spatial autocorrelation of assemblages may also be driven by spatial autocorrelation of habitats or local environmental conditions (Lloyd, Mac Nally & Lake, 2005). As outlined above, a greater distance between the two furthest first-order streams in a catchment, in comparison to higher-order streams, may also result in a greater range of environmental conditions being encompassed in the uppermost parts of the stream network. Much work is needed to determine the scales at which spatial autocorrelation affects macroinvertebrate assemblage composition (Lloyd *et al.*, 2005) and headwater stream networks may prove to be an ideal system in which to study such patterns.

The structure of drainage basins is dictated by the power law, a signature of the well-characterized fractal behaviour of river networks (Rinaldo *et al.*, 1993), where each time the area drained by a streams doubles, the number of such streams decreases by a factor of about 2.7 (Buchanan, 2002). This high proportion of small streams, and their subsequent confluences, is concentrated in the uppermost parts of the stream network. Riverine heterogeneity has been linked to confluences (Rice, Greenwood & Joyce, 2001) and is, therefore, also likely to be non-uniformly distributed within catchments (Benda *et al.*, 2004). Stream ecologists have often related changes in

taxonomic richness to physical riverine heterogeneity (Vinson & Hawkins, 1998) and thus a concentration of riverine heterogeneity (related to confluences) in the headwaters of catchments may drive high rates of species turnover in headwater streams. More studies investigating the ecological processes occurring at confluences are required as stream ecologists have mostly worked at the reach-scale and have neglected a crucial property of stream architecture, namely the junctions or nodes (Lake, 2007). Gooderham, Barmuta & Davis (2007) suggested that greater physical heterogeneity in headwater streams may be driven by a lack of competence – ability to move material on the bed and banks – in small streams. Greater physical heterogeneity also may provide opportunities for greater numbers of rare species. Rare species may make a significant contribution to β -diversity in headwater streams and thus contribute substantially to γ -diversity at the catchment scale.

While there are likely to be other mechanisms (e.g. neutral and niche processes) generating local patterns of diversity (Hubbell, 2001; Thompson & Townsend, 2006) it is clear that conceptual advances regarding the determinants of macroinvertebrate diversity in headwater streams may be made by considering how the geometry of river networks generates biological diversity (Benda *et al.*, 2004; Grant *et al.*, 2007). While such advances are being made for fish assemblages (Osborne & Wiley, 1992; Schlosser, 1995; Fagan, 2002; Grenouillet, Pont & Herisse, 2004) and for riparian vegetation (Muneepeerakul *et al.*, 2007), few studies have addressed the role that spatial structure plays in determining local species richness and assemblage composition of aquatic macroinvertebrates (although see Rice *et al.*, 2001).

Implications for conservation management

Studies are needed to examine the patterns and determinants of macroinvertebrate diversity in headwater streams to provide information for managers and policy makers about how best to halt, and where possible reverse, declines in riverine biodiversity (Dudgeon *et al.*, 2006). An understanding of patterns in taxonomic richness is critical to preventing the loss of biodiversity (Vinson & Hawkins, 1998) and such information also will provide valuable inputs for systematic conservation planning and reserve design to protect riverine biodiversity. For example, in

headwater systems structured by biotic nestedness, it may be possible to protect most species by preserving just the (often large) species-rich areas (Malmqvist *et al.*, 1999; Malmqvist & Hoffsten, 2000). Where species turnover is high, a network of smaller reserves across the whole catchment may be required to protect most of the species. Planning for the conservation of macroinvertebrates in headwater streams is a task that has become more urgent in the face of global climate change because the ecological consequences of climate change for upland streams are anticipated to be substantial (Durance & Ormerod, 2007).

Vulnerability (the possibility that future condition will change in a negative direction) and irreplaceability (the extent to which the loss of an area will compromise regional conservation targets) are two key attributes to consider when planning for aquatic conservation (Linke *et al.*, 2007). Headwater streams may be at higher risk of biodiversity loss than lowland rivers because tight aquatic–terrestrial linkages make these systems particularly vulnerable to disturbance in the surrounding catchment (Lowe & Likens, 2005). Such disturbance is amplified by the vague definition of what constitutes a headwater stream and their subsequent exclusion from many early forest practice regulations and catchment management programmes (Adams, 2007; Bryant, Gomi & Piccolo, 2007; Mac Nally *et al.*, 2008). Macroinvertebrate assemblages also may be highly distinctive at both the assemblage and genetic levels (and thus more irreplaceable) and recolonization from other source populations often may be limited. Hughes (2007) found that five out of six invertebrate species studied from upland streams showed negligible dispersal among streams within catchments and that local extinctions in these cases probably would be ‘final’. It is thus critical that restoration programmes recognize the added difficulty that headwater streams may pose for the recolonization of macroinvertebrates, especially those that do not have an aerial dispersal stage. Lake, Bond & Reich (2007) recognized this when highlighting the need for special attention to be paid to the unique geometry of drainage basins when attempting to re-establish populations.

In conclusion, headwater streams clearly play an important role in catchments, acting as areas of streamflow generation (Sidle *et al.*, 2000), sources of organic matter and invertebrates (Wipfli *et al.*, 2007),

critical sites for nutrient processing (Bilby & Likens, 1980) and are potentially important areas for aquatic biodiversity (Meyer *et al.*, 2007). We examined empirical studies of macroinvertebrate diversity in headwater streams and found that, although local species richness often may be low in individual headwater streams, the overall contribution of headwater streams to regional diversity may become more apparent at larger scales and that β -diversity may be an important component of macroinvertebrate diversity in headwaters. Embracing the emerging view of river basins as networks, rather than as linear, reach-scale segments, is likely to bring new understanding on how diversity patterns are generated at the landscape scale. With the widespread adoption of systems thinking by many biological disciplines (Chong & Ray, 2002; Kitano, 2002), it should not be a surprise that the importance of headwater streams to regional macroinvertebrate diversity might be found when examining the catchment (system) as a whole rather than by studying its individual components in isolation.

Exploring the role that β -diversity plays in generating spatial patterns of macroinvertebrate diversity in headwater streams is a nascent area of research and is likely to be a critical one (Monaghan *et al.*, 2005). Future studies of diversity patterns in headwater streams have much to gain from moving beyond linear conceptual models of stream ecosystems to consider the role that spatial structure of river networks might play in determining diversity patterns at the landscape scale (Grant *et al.*, 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Studies included in Table 1 a,b

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(Manuscript accepted 16 May 2008)

Supporting Information: Appendix S1. Studies included in Table 1.

Study	Location
Heino <i>et al.</i> 2003	Finland
Moore and Palmer 2005	Maryland, USA
Haggerty <i>et al.</i> 2002	Washington, USA
Grubaugh <i>et al.</i> 1996	Appalachian Mountains, North Carolina, USA
Boyero and Bailey 2001	Coiba Island, Republic of Panama
Cole <i>et al.</i> 2003	Coast Range Mountains, Oregon, USA
Liljaniemi <i>et al.</i> 2002	Finland and Russia
Nislow and Lowe 2006	New Hampshire, USA
Monaghan <i>et al.</i> 2005	Swiss Alps
Feminella 1996	Alabama, USA
Churchel and Batzer 2006	Piedmont Region, Georgia, USA
Megan <i>et al.</i> 2007	Mid-Atlantic Coastal Plain, USA
Dieterich and Anderson 2000	Corvallis, Oregon, USA
Herlihy <i>et al.</i> 2005	Western Oregon, USA
Townsend <i>et al.</i> 2004	Otago Province, New Zealand
Angradi 1996	Appalachian Mountains, West Virginia, USA
Sponseller <i>et al.</i> 2001	Southern Appalachian Mountains, Virginia, USA
Heino <i>et al.</i> 2004	Northern Finland
Guerold <i>et al.</i> 2000	Vosges Mountains, northeast France
Fraday <i>et al.</i> 2007	Cascade Mountains, Oregon, USA
Danehy <i>et al.</i> 2007	Coast Range, Oregon, USA
Robson <i>et al.</i> 2005	Otway Ranges, Victoria, Australia
Woodcock and Huryn 2005	Maine, USA
Hernandez <i>et al.</i> 2005	Prince of Wales Island, southeastern Alaska

Declaration for Thesis Chapter 2

This thesis chapter (Clarke *et al.* 2010) is in the same form as the final manuscript published in the peer-reviewed journal *Canadian Journal of Fisheries and Aquatic Sciences*. The full reference for the published paper is:

Clarke A, Mac Nally R, Bond N & Lake, PS (2010) Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment. *Canadian Journal of Fisheries and Aquatic Sciences*, in press.

Declaration by the candidate

In the case of Chapter 2, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution
I performed 100% of the fieldwork, 100% of the laboratory work, 60% of the statistical analyses and was the primary author of the manuscript.	70%

The following co-authors contributed to the work:

Name	Nature of contribution
Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work, conducted the hierarchical Bayesian model analyses and co-authored the manuscript.
Nick Bond	Nick Bond contributed ideas to the work, calculated the cumulative streamflow deviation and co-authored the manuscript
PS Lake	PS Lake contributed ideas to the work and co-authored the manuscript

Candidate's signature		Date
----------------------------------	--	-------------

Declaration by co-authors

The undersigned hereby certify that:

- (1) the above declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria;
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor of publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (6) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Locations(s)

School of Biological Sciences, Monash University

		Date
Signature 1		
Signature 2		
Signature 3		

Chapter 2 - Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment

Abstract

Drying can be a common disturbance affecting macroinvertebrate communities in headwater streams. Whether intermittent and ephemeral streams have a lower diversity and/or unique assemblage structure relative to physically similar and nearby perennial streams is still debated. We investigated changes in the diversity and assemblage composition of aquatic macroinvertebrates occupying debris dams in three headwater streams with a gradient of flow permanence (perennial, intermittent and ephemeral) during a dry period in the austral summer of 2007 and a wet period in the spring of 2008. In the dry period, mean taxon richness and abundance in debris dams were lower in the intermittent and ephemeral streams than the perennial stream, and the length of time without connected surface flow appeared to produce different patterns in community composition. However, during the wet period, mean taxon richness, abundance and community composition of macroinvertebrates were very similar among the three streams. Hierarchical Bayesian modeling showed evidence for a strong effect of permanence on taxon richness, abundance and evenness within debris dams. Taxa from the perennial stream were extremely efficient at colonizing seasonally dry nearby streams. Differences in assemblage structure between these temporary and permanent headwater streams may only arise seasonally and also appear related to flow permanence.

Introduction

Drying of stream ecosystems is a local and regional disturbance for stream biota (Lake 2003) and a major factor influencing macroinvertebrate assemblage structure (Williams 1996). The temporary absence of surface flow is particularly common in headwater streams (springs excluded) and they can be highly responsive to single precipitation events (Richardson and Danehy 2007). Temporary waters can be subdivided into those which are dry at times of the year that are more or less predictable (intermittent) and those which contain water on an unpredictable basis (ephemeral) (Williams 1996). High heterogeneity of the physical habitat in headwater streams (Gooderham *et al.* 2007) and highly variable local discharge (Gomi *et al.* 2002) mean that single catchments often contain headwater streams that are both permanent and temporary.

Poff and Ward (1989) argued that macroinvertebrate diversity should be low under conditions of intermittency and Vinson and Hawkins (1998) found that most studies reported lower richness in temporary streams than in permanent streams and that richness generally increased with increasing flow duration. Conversely, some studies have found taxon richness in temporary streams to exceed that of perennial streams (Dieterich and Anderson 2000). Taxa inhabiting temporary streams require one or more strategies to cope with the onset of drying and may possess functional traits that allow them to persist under such conditions. These may include: short or flexible life cycles, long-lived propagules, resistance to desiccation, good dispersal ability or behavioral adaptations such as drifting or seeking refuge (Williams 1996; Humphries and Baldwin 2003; Bêche *et al.* 2006). Therefore, temporary streams may harbour unique or distinctive macroinvertebrate communities that differ from nearby perennial streams (Feminella 1996; Williams 1996).

Taxa without these functional traits may not persist in temporary streams or may seek refuge on a seasonal basis and return during periods of increased hydrologic connectivity through aerial or overland dispersal or drift.

We investigated aquatic macroinvertebrate communities in three nearby and physically similar headwater streams that differed primarily in their level of flow permanence to determine whether, 1) flow permanence affects diversity, 2) flow permanence affects community composition, and 3) which macroinvertebrate taxa (or groups of taxa) show the strongest response to flow permanence. We focused on seasonal drying (over one year), but the study was undertaken during a time of severe and prolonged drought affecting streams in south eastern Australia over the past decade (Rose *et al.* 2008; McGowan *et al.* 2009).

Methods

Study area and design

The study was conducted in 3 unnamed 1st-order streams in the Wallaby Creek Designated Water Supply Catchment Area (37°4'S, 145°2'E). This 9965 ha closed catchment is located at the southern end of the Hume Plateau on top of the Great Dividing Range in Victoria, Australia (Ashton 2000) and is approximately 50 km NE of the state capital, Melbourne. In the wider catchment, annual mean rainfall was 1207 mm over the period 1995-2006 (Martin *et al.* 2007) and elevation ranges from 600 – 800 m A.S.L. The vegetation is dominated by ecologically mature, eucalypt forest that encompasses a mixture of Ecological Vegetation Classes including: restricted pockets of Cool Temperate Rainforest, Wet Forest, Damp Forest, Shrubby Foothill Forest and Riparian Forest (Frood *et al.* 2001).

Ecological Vegetation Classes (EVCs) are the recognized units of the Victorian Government vegetation classification system and represent groupings of vegetation communities based on floristic, structural and ecological features. The catchment area is closed to the general public and is primarily managed for protection of water quality and water supply (Parks Victoria 1998). At the time of this study the area was largely undisturbed, but there are historic disturbances (mostly occurring in the mid-late 1800s) including bushfire, aqueduct construction, logging, human settlement and bullock grazing (Ashton 2000).

All studied streams are tributaries of Silver Creek within 2 km of each other. Streams are similar with respect to width (< 0.5 m), gradient (very low, no riffles present in any of the study streams), drainage area (< 1.4 km²), Ecological Vegetation Class (Riparian Forest), geology (Chesney Vale granite) and soils (rich krasnozemic loam, which has a high organic matter content in the uppermost layers) but have a range of flow permanence from perennial to ephemeral. Permanency was calculated as the proportion of site visits in which a stream was flowing. Twelve site visits were made over a period of 26 months commencing three months before the first sampling period and concluding one week after the last sampling period. The perennial stream was flowing 10 / 12 visits ($F = \text{flow permanence} = 0.83$), the intermittent stream was flowing 7 / 12 visits ($F = 0.58$) and the ephemeral stream was flowing on only one occasion ($F = 0.08$).

It was not possible to obtain replicates of each stream type as there were no other streams in this catchment that displayed a high degree of permanency. Additionally, of the small number of headwater streams in the catchment (approx. 10), several streams were inaccessible or had been artificially modified by the construction of small aqueducts. In

light of this, we recognize that our findings cannot provide generalizations about patterns and processes in all temporary streams, but nonetheless they can provide an insight to the patterns and processes occurring in this catchment which is an important example of mature and largely undisturbed forest with high biological integrity that would have been more widespread in the past.

Regional drying and drought history (1961 - 2008)

Ecological patterns and processes in streams (e.g. diversity patterns or life history strategies) may be correlated with long-term flow patterns (Lytle and Poff 2004), but also confounded by drying and drought events occurring at smaller temporal or spatial scales (Bêche and Resh 2007). To assess how representative flow conditions were during our study, we examined several decades (1961 – 2008) of daily stream flow data from a gauging station approximately 10 km north-east of the study site on King Parrot Creek at Flowerdale (Station No. 405231) to determine whether the severity of the current drought was greater than previous periods of drying or drought in the past half century. We calculated the cumulative streamflow deviation (mm) for any run of consecutive wet or dry years. When there was a transition from an above-average or below-average streamflow year, we reset the deviation to zero.

Macroinvertebrate sampling

All study streams were located within the ‘Riparian Forest’ EVC. The structure of this EVC is generally open forest to tall woodland with a layered understory comprising a range of eucalypt species. The tall *Eucalyptus viminalis* is usually the dominant species and occurs with *Eucalyptus melliodora*, *E. obliqua*, *E. radiata* ssp. *radiata* and *E. ovata*. The dominance of eucalypt species beside these streams has considerable influence on in-stream

habitat because, unlike many streams in North America and Europe, eucalypt species are not deciduous but have continuous leaf litter inputs throughout the year (with a peak in summer) and much slower rates of leaf breakdown (Pozo *et al.* 1997). This means that features such as leaf packs and debris dams are common habitats in temperate Australia streams, and contribute significantly to the structural heterogeneity of low gradient sand-bottom reaches. This is particularly true in small headwater streams where there is a high ratio of structural component size to stream width due to lack of stream competence to move material that has fallen onto the bed and banks (Gooderham *et al.* 2007).

Initial field observations of all headwater streams in the study area revealed only two dominant habitat types, sandy benthic areas and debris dams. We followed the definition of debris dams of Smock *et al.* (1989) as “any wood > 5 cm in diameter in contact with sediment and spanning at least one-fourth of the channel. Also included were root masses from living riparian vegetation.” The debris dams in the study streams generally were characterized by one larger piece of wood causing a partial obstruction of the channel and an accumulation of smaller pieces of wood, twigs and leaves. Subsequent work for another study in the Silver Creek catchment quantified the previously observed dominance of the debris dam habitat type in the study area through records of the percentage of streambed in 30 m reaches occupied by debris dam habitats. In 2007, the percentage of reach length occupied by debris dam habitats ranged from 33 – 53% and in 2008 it ranged from 13 – 73% (A. Clarke, unpublished data). This study therefore focused on macroinvertebrate assemblages in debris dam habitats and the findings will be relevant only to this particular habitat type. It is likely that the effects of flow permanence on macroinvertebrate assemblages in sandy benthic habitats will be greater than those in debris

dams because these sections of the stream are the first to dry out when flow ceases and have little organic matter that can retain moisture. Debris dams also have long been considered to provide important habitat for macroinvertebrates and are the dominant source of energy in heavily forested streams (Bilby and Likens 1980; Smock *et al.* 1989).

Macroinvertebrates were sampled from debris dam habitats twice, once during the austral summer low-flow period (January 2007) and again during the spring high-flow period (November 2008). During the high-flow period, all sites had connected surface flow. During the dry period, the ephemeral stream had no surface water present and the stream bed was dry, although damp just below the surface. The intermittent stream had very little surface water present although the stream bed was slightly damp. The perennial stream had connected surface flow.

Ten debris dams were selected randomly from a 30 m reach in each stream and sampled by collecting one small handful of organic matter from the centre of the debris dam and preserving all material in 70% ethanol. Although these samples were not strictly quantitative, the use of this sampling technique in the catchment for other, related investigations revealed no relationship between taxa richness and AFDW (g) of organic material collected in one handful ($R^2 = 0.10$ during 2007 and $R^2 = 0.03$ during 2008), despite some inevitable variation in the amount of organic material collected in one handful (4.71 - 32.47 g AFDW in 2007 and 3.82 - 31.98 g AFDW in 2008). Samples were washed over a 300 μm sieve in the laboratory and insects were identified to the lowest possible taxonomic resolution (usually genus). Diptera were identified to family except Chironomidae, which were identified to sub-family. Oligochaeta and Nematoda were not

identified further. Terrestrial taxa found in the samples were not included in any of the analyses presented here.

Data analysis

We plotted mean taxon richness and mean abundance for the three streams during both the dry and the wet period. The distribution of abundance (evenness) among taxa was graphically explored using rank-abundance plots, where one axis of the curve represents the taxon rank in a community and the other represents taxon abundance (Tokeshi 1990) and taxon abundance was plotted on a log scale.

Given that we had three reaches of differing permanence over two flow seasons, we used a regression approach to analyse the response variables. The model was:

$$(1) \quad L(\mu_{ik(j)}) = \alpha_1 + \alpha_2 \delta_i + (\alpha_3 + \alpha_4 \delta_i) P_j + b_j; \delta_i = \begin{cases} 0 & \text{for dry} \\ 1 & \text{for wet} \end{cases}$$

$L()$ is a link function appropriate for measured values, $Y_{ik(j)}$, where the subscript i denotes season (0 = dry, 1 = wet), j is reach (1, ..., 3), and k is “replicate” debris dam within reach ($N = 10$). Note that the k subscripts are nested within the corresponding reaches j (hence $k(j)$). α_1 is the general intercept; α_2 is the effect of season, which is measured as a deviation from the dry season occurring in the wet season (hence the δ); α_3 is the regression parameter relating the response variable to the measure of permanence (F_j) in the dry season; and α_4 is an interaction that modifies the response–permanence relationship for the wet season. F_j is a continuous variable and was not selected a priori as a “factor.” The

b s are reach-specific random effects having zero mean and common variance σ_b^2 (these are used because of the “repeated measures” for each reach).

Different generalized linear models were developed to analyze patterns of richness ($L = \text{Poisson}$, deemed appropriate for non-negative counts data), total abundance ($L = \text{log-normal scale}$) and evenness ($L = \text{Beta distribution}$) in the three reaches. Evenness was calculated using the preferred (Jost 2007) Shannon’s equitability [$E(H)$] where $E(H)$ has a value between 0 and 1, with 1 indicating complete evenness (e.g. all taxa having equal abundances). Adequacy of model fit was assessed using Bayesian posterior predictive assessment (Gelman *et al.* 1996), which have been regarded as “Bayesian P -values.” “Importance” of the parameters (i.e., do these differ substantially from zero?) was assessed using posterior probability distributions and odds ratios (OR). ORs are ratios of posterior to prior odds, and measure how much the data change our initial expectations. ORs > 10 are strong evidence supporting one hypothesis over another, and $3 < \text{OR} < 10$ signal positive evidence (Kass and Raftery 1995). For negative parameters, inverse ORs hold (i.e., ORs $< 1/10$ are strong evidence). Inferences in the Results section use $\text{OR} \geq 10$ (or $\leq 1/10$) as the threshold.

WinBUGS Bayesian modeling software was used (Spiegelhalter *et al.* 2003). Model runs had “burns-in” of 10,000 and parameter samples of 10,000. Usual appraisals of model convergence were employed (Smith 2006). More complete specifications of the Bayesian modelling are presented in the Supplementary Material.

Multivariate analysis exploring changes in community composition was undertaken using non-metric multidimensional scaling (NMDS) for untransformed taxon abundance data. The ordination solution was generated from 100 random starts and is displayed in 2

dimensions due to low stress for this dimensionality (< 0.15). The use of MANOVA or ANOSIM to assess differences between groups was not undertaken because of the lack of true replicates (i.e. samples were sub-samples at the reach scale). Centroids and 90% confidence ellipses were plotted for each group of 10 sub-samples (R 2005 v 2.4.1). Effects of permanence on community composition were determined by visual inspection of the ordination plot.

Results

Regional drying and drought history (1961 - 2008)

The current period of drying in the region (2001 – 2008) was the longest period of consecutive years that streamflow has been below average since 1961 (Fig. 2). While the cumulative streamflow deviation was large (in a negative direction), the deviation from any single year in the period 2001 – 2008 was not substantially greater than other negative annual streamflow deviations that have occurred in the past half century. In particular, the annual streamflow deviation in 1982 was very large (i.e. far below average) and annual streamflow deviations in 1962, 1967 and 1980 were also large.

Aquatic macroinvertebrate diversity in temporary vs permanent streams

Seventy-four aquatic taxa (21 557 individuals) were found in the three headwater streams over the two sampling periods. Diptera was the most diverse order with 11 families (Athericidae, Empididae, Ceratopogonidae, Chironomidae, Culicidae, Dixidae, Tipulidae, Psychodidae, Stratiomyidae, Simuliidae and the rare Tanyderidae). Ephemeroptera, Plecoptera and Trichoptera (EPT) collectively made up 35% of the total number of taxa recorded. Ten of the 25 freshwater Trichoptera families known to occur in Australia were

found (13 genera), all four Plecoptera families known to occur in Australia (8 genera) but only two of the seven Ephemeroptera families (5 genera).

Taxonomic richness

Using the odds-ratio (OR) criterion, all parameters differed from 0 with high certainty (all ORs infinite) (Table 1). Mean random effects for reaches (b_j) differed little from 0 when compared with their SDs of estimates (all < 10%). Model results are consistent with the data presented in Fig. 2a. Dry-season richness increased substantially with degree of permanence [from a mean of 4.9 ($F = 0.08$) to 26.2 ($F = 0.83$)]. Wet-season richness was little related to the stream's permanence (Fig. 2a), which is consistent with the interaction effect for wet season as a function of permanence, which essentially eliminated the permanence relationship ($\alpha_3 + \alpha_4 = 2.28 + -2.29 = -0.01$).

Pooling all samples for each stream over the two sampling times revealed increasing total richness with degree of stream permanence: 42 ($F = 0.08$), 54 ($F = 0.58$) and 63 ($F = 0.83$).

Total abundance of aquatic macroinvertebrates

All parameters differed substantially from 0 (all ORs > 16, Table 1). Stream permanence had a marked positive effect on numbers of individuals in the dry season, increasing on average from about 12 individuals ($P = 0.08$) up to 454 ($P = 0.83$) (Fig. 2b). Permanence depressed numbers for the wet season data given a net difference of $\alpha_3 + \alpha_4 = (4.8 - 5.9) = -1.1$ in the model parameters. Thus, the model supports the evident interaction in which the wet-season total abundance decreased with flow permanence from an average of about 663 individuals ($P = 0.08$) to 347 ($P = 0.83$) (Fig. 2b). Mean random effects for reaches again

were small differed little from 0 when compared with their SDs of estimate, and also absolutely (< 0.09).

Rank-abundance plots showed that during the dry period evenness was not markedly different among the three streams, although the plots appear quite different because of the reduced abundance and taxon richness in the two more temporary streams (Fig. 3a). During the wet period, the slope of the three plots was very similar indicating that evenness, abundance and taxon richness were all similar among the three streams (Fig. 3b).

Evenness of abundances among taxa

All parameters differed greatly from 0 (all ORs > 32 , Table 1). The baseline dry season average evenness exclusive of permanence effects was 0.90. When the latter were included, fitted means (actual means in brackets) for the permanent, intermittent and ephemeral streams were 0.71 (0.66), 0.78 (0.79) and 0.89 (0.80) respectively. Thus, evenness decreased slightly with permanence for the dry season. The wet season effect (exclusive of the permanence effect) reduced the baseline value to 0.47. The interaction term changed the regression coefficient for the permanence effect from -1.6 to $+1.4$ for the wet season. The fitted (actual) means for perennial, intermittent and ephemeral streams were 0.74 (0.74), 0.67 (0.60) and 0.50 (0.57) respectively. Hence, evenness increased with permanence for the wet season. Mean random effects for reaches differed little from 0 when compared with their SDs of estimate. These results are supported by the rank abundance curves for each stream during the wet and dry periods which graphically display patterns of evenness (Fig. 3).

Aquatic macroinvertebrate assemblage structure in temporary vs permanent streams

In the dry period, each stream had a distinct macroinvertebrate assemblage occupying debris dams with a clear grouping of samples separated by the difference in flow permanence for each stream (Fig. 4). The taxon list for each stream showed that during the dry period, the two temporary streams had twelve taxa that did not occur in the perennial stream. The other taxa present in the two temporary streams were a nested sub-set of the taxa present in the perennial stream at the same time.

However, during the wet period, macroinvertebrate assemblages from each stream were very similar. Therefore, there is limited evidence from this study to support the idea that temporary streams in our region permanently harbour unique or distinctive macroinvertebrate communities associated with debris dams. Ordination based on presence / absence data revealed similar patterns (not shown).

Taxonomic responses to flow permanence in headwater streams

The Orthoclaadiinae (Diptera) showed the weakest response to flow permanence because this taxon was the most widely distributed across all streams and both sampling periods, absent from only three samples in the ephemeral stream during the dry period. The EPT group showed a very strong negative response to drying stress because sampling during the dry period in the intermittent stream found no taxa from the Plecoptera or Ephemeroptera and only three genera from the Trichoptera. Sampling in the ephemeral stream during this period revealed the absence of any genera from the EPT group. However, subsequent sampling of these streams during the wet period showed that eight genera of Plecoptera, three genera of Ephemeroptera and four other genera of Trichoptera had colonized the intermittent stream, although one Trichopteran genus (*Lectrides* sp.) which had been

present during the dry period was not recorded during the wet period). In the ephemeral stream, sampling during the wet period revealed that one genus of Plecoptera, two genera of Ephemeroptera and two genera of Trichoptera had colonized the previously dry stream.

Of the 12 taxa found exclusively in the two temporary streams during the dry period, five were coleopterans [(*Notohydrus sp.* (Hydrophilidae), *Hydraena sp.* (Hydraenidae), *Sclerocyphon sp.* (Psephenidae), Hydrochidae and Curculionidae)]. Two dipteran taxa that appeared to be exclusively associated with driest conditions were in the families Ceratopogonidae (Forcipomyiinae) and Stratiomyidae as these were only recorded in the temporary streams and only during the dry period.

Discussion

Regional drying and drought history (1961 – 2008)

The streamflow deviation data indicate that the current drought represents the longest period of consecutive years of below average streamflow in the study region since at least 1961, which is consistent with the widely reported descriptions of the prolonged nature of the drought that is currently affecting south eastern Australia (Pezza *et al.* 2008; Rose *et al.* 2008; McGowan *et al.* 2009). However, the occurrence of large (negative) annual streamflow deviations in earlier parts of the record (e.g. 1962, 1967, 1980 and 1982) means that macroinvertebrate communities in the region have previously been exposed to the pressure of highly variable and well-below-average streamflow. We might infer that macroinvertebrates in these systems may have evolved and maintained adaptations (e.g. life-history, morphological and behavioral) to cope with this highly variable flow regime, which is punctuated by drying and drought. Thus, differences in patterns of

macroinvertebrate diversity between permanent and more temporary streams are likely to reflect structuring of communities in response to long-term patterns in hydrologic variability rather than just short-term responses to the current supra-seasonal drought. However, if the current period of drought continues, the cumulative streamflow deviation in the region may become so severe that the hydrologic regime of some headwater streams will shift so that previously perennial streams become ephemeral and so on with consequent effects on the biota.

Effect of flow permanence on aquatic macroinvertebrate diversity

Stream ecologists have predicted that macroinvertebrate diversity should be low under conditions of intermittency because loss of hydrologic connectivity constrains exchanges of matter, energy and organisms between patches (Poff and Ward 1989; Ward *et al.* 1999). This prediction may be less applicable to regions with naturally high levels of stream intermittency because periods of seasonal drying occur with a high level of predictability, allowing for development of adaptations to cope with the seasonal reduction or absence of flow. Several studies of macroinvertebrate responses to predictable, seasonal drying in Mediterranean-climate streams in regions such as California and Spain have found that intermittent and ephemeral streams do not always harbour a lower macroinvertebrate diversity than their perennial counterparts (Bonada *et al.* 2006; Bonada *et al.* 2007). A study in Oregon found that a temporary headwater contained 125 species compared to only 100 species in a nearby permanent headwater (Dieterich and Anderson 2000).

In this study, we investigated the effects of flow permanence on macroinvertebrate assemblages in debris dam habitats and found that summer taxon richness was lower in the two temporary streams than in the permanent stream, but taxon richness in the intermittent

stream was much higher than the ephemeral stream. Taxon richness was similar in all streams during the wet period, which suggests that although many taxa might be seasonally extirpated or move from the channel into nearby refugia, they are extremely effective at recolonizing temporary streams upon resumption of flow.

The permanent stream had higher total (pooling sampling periods) taxon richness than either of the temporary streams, indicating that during the dry period, taxa are lost from the temporary streams but very few 'new' taxa more tolerant of the dry conditions arrive to take their place. The ephemeral stream, which experienced the longest period without connected surface flow, had much lower taxon richness than the intermittent stream and so annual taxon richness appears to be positively correlated with flow permanence. Similarly, Dieterich and Anderson (2000) found that although temporary streams may harbour as many or more taxa than nearby permanent streams, species richness was lowest at the most ephemeral sites. Boulton and Lake (1992) compared macroinvertebrate assemblages between sites on two intermittent rivers in southern Australia and also found that species richness generally increased with longer flow duration.

Evenness was relatively high in all three streams, even during the dry period when the temporary streams contained few taxa. This pattern was driven by many taxa in the dry period occurring only as one or two individuals and no single taxon occurred in exceptionally high abundances. This result is consistent with a study of headwater streams by Heino *et al.* (2008), who found high evenness in small streams and inferred that this phenomenon might reflect so called 'small stream effects' where abundances are more evenly divided among species because of inherent heterogeneity and variability in the conditions of small headwater streams.

Effect of flow permanence on macroinvertebrate assemblage structure

Towns (1985) suggested that fauna inhabiting temporary waters are highly specialized with unique life-history adaptations to intermittent flow. However, several studies have reported only slight differences in the faunal composition of permanent and intermittent sites (Boulton and Lake 1992; Feminella 1996; Price *et al.* 2003). We found that although there were seasonal differences in assemblage structure, patterns were mostly driven by loss of taxa and there was a high degree of faunal overlap between the three sites once flow resumed. Only 12 taxa (16%) were found exclusively in the temporary streams. These findings suggest that the temporary streams in our study region do not contain a significant suite of specialist taxon adapted to intermittent flow and that for the many taxa that are seasonally extirpated from the temporary streams recolonization from populations in the permanent stream is likely to occur in the wetter months.

Taxon responses to flow permanence in headwater streams

Orthoclaadiinae appeared to be the best adapted to a range of flow permanence, which is not surprising since they are known to occupy the widest range of habitats of all the Chironomidae (Oliver 1971). A substantial number of species from the Orthoclaadiinae are multivoltine with continuous recruitment for much of the year (Pinder 1986).

Of the EPT group, the Trichoptera appeared to have the greatest ability to withstand or recover from drying stress in our study, although their ability to survive in temporary streams during the dry period seemed limited to genera known to build a case or retreat of some type (*Caenota* sp., *Lectrides* sp. and Genus Calocidae B). Larval case building by caddisfly taxa has previously been suggested as a form of resistance to drying or drought (Zamora-Munoz and Svensson 1996). While eight genera of stoneflies colonized the

intermittent stream once flow had resumed, only one genus was found to have colonized the ephemeral stream during the wet period, *Dinotoperla* sp. [see also (Boulton and Lake 1992)].

Most aquatic Coleoptera and the Tipulidae (Diptera) pupate out of the stream channel in cells formed by damp soil and moss, a habitat that is prevalent when flow recedes or ceases (Cummins and Wilzbach 2005). This may explain the prevalence of coleopteran and dipteran taxon found in the temporary streams in our study (Boulton and Lake 1992). Price *et al.* (2003) found that intermittent and ephemeral streams tended to be richer in dipteran taxon and Bêche *et al.* (2006) found that during the dry season density of air-breathing macroinvertebrates with strong body armouring, such as the Coleoptera, increased. The success of dipteran taxa in colonizing temporary habitats is likely to be due to a suite of functional and life-history traits that prove advantageous, such as short life cycles, simple bodies, survival in a wide range of habitats and high dispersal ability of adult stages (Oliver 1971; Pinder 1986).

Implications for management of intermittent headwater stream systems

Periods of drying and drought are an integral part of the Australian climate (Rose *et al.* 2008) and indigenous macroinvertebrate communities from such Mediterranean-type climates are likely to be adapted to naturally occurring low-flow or zero-flow conditions (Boulton 2003; Lake 2003; McMahon and Finlayson 2003) or have highly efficient mechanisms for recolonization when flow resumes, as suggested by the findings of our study. However, taxa may not be as resilient or resistant to the interactive effects of predictable seasonal drying and longer-term supra-seasonal drought (Lake 2003), such as the current severe and prolonged drought occurring in south eastern Australia (Rose *et al.*

2008; McGowan *et al.* 2009). Analysis of long-term rainfall records in southeastern Australia (1910 – 2005) showed a decline in most rainfall indices, particularly since the 1950s when total autumnal rainfall began decreasing by approximately 11 mm per decade, contributing to a significant decrease in total annual rainfall of approximately 20 mm per decade (Gallant *et al.* 2007). Further intensifying the effects of natural intermittency of some headwater streams are increasing levels of water extraction from unregulated rivers, and the future effects of climate change that are predicted to be substantial for upland streams (Durance and Ormerod 2007).

Managing freshwater systems in the face of growing demand for water resources and the predicted impacts of climate change will be challenging, but it is critical that actions to protect freshwater biodiversity are taken (Dudgeon *et al.* 2005). While intermittent streams may harbour a lower diversity than their perennial counterparts during some parts of the year, it appears from our study that intermittent headwater streams may regain their full complement of taxa upon resumption of flow. These findings are however limited to macroinvertebrate assemblages in debris dam habitats, and the effect of flow permanence on macroinvertebrate assemblages in sandy, benthic areas may be more pronounced due to the rapid onset of drying in these sections of stream once flow ceases. The permanent stream in our study may have provided a critical over-summering refuge for many taxa; Boulton (1989) highlighted the importance of such streams as sources of recolonization. In this system, taxa from the perennial stream appear extremely efficient at colonizing the seasonally dry, temporary streams. When planning for reserve design or disturbance mitigation, it may be important to ensure that intermittent headwater streams are not disconnected from nearby permanent streams by blocking or fragmenting aerial and

upstream migration pathways. This study also highlighted the potential loss of diversity, at least seasonally, that may occur as the local and regional climates become drier and previously perennial and intermittent streams shift towards more ephemeral flow regimes.

Acknowledgements

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Table 1. Model parameter estimates (mean \pm SD) for the analyses of species richness, abundance and evenness.

Variable	Link/error	α_1	α_2	α_3	α_4	PPP *
Richness	Log _e /Poisson	1.4 \pm 0.3	1.8 \pm 0.2	2.4 \pm 0.6	-2.29 \pm 0.2	0.88
Abundance	Log _e /log-normal	1.9 \pm 0.5	4.7 \pm 0.3	4.8 \pm 1.0	-5.9 \pm 0.5	0.78
Evenness	Logit/Beta	2.2 \pm 0.5	-2.3 \pm 0.3	-1.6 \pm 1.0	3.0 \pm 0.4	0.69

* PPP = posterior predictive probability, values < 0.05 or > 0.95 suggest a poor model fit to the data

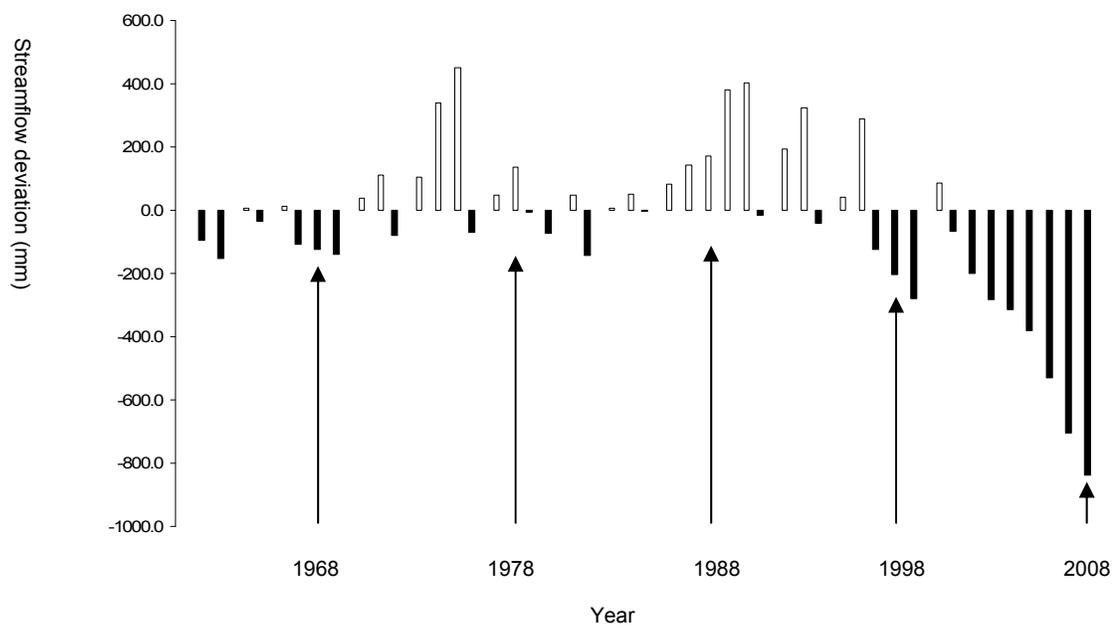


Figure 1. Regional drying and drought history in the region represented by cumulative annual streamflow deviation for the period 1961 – 2008.

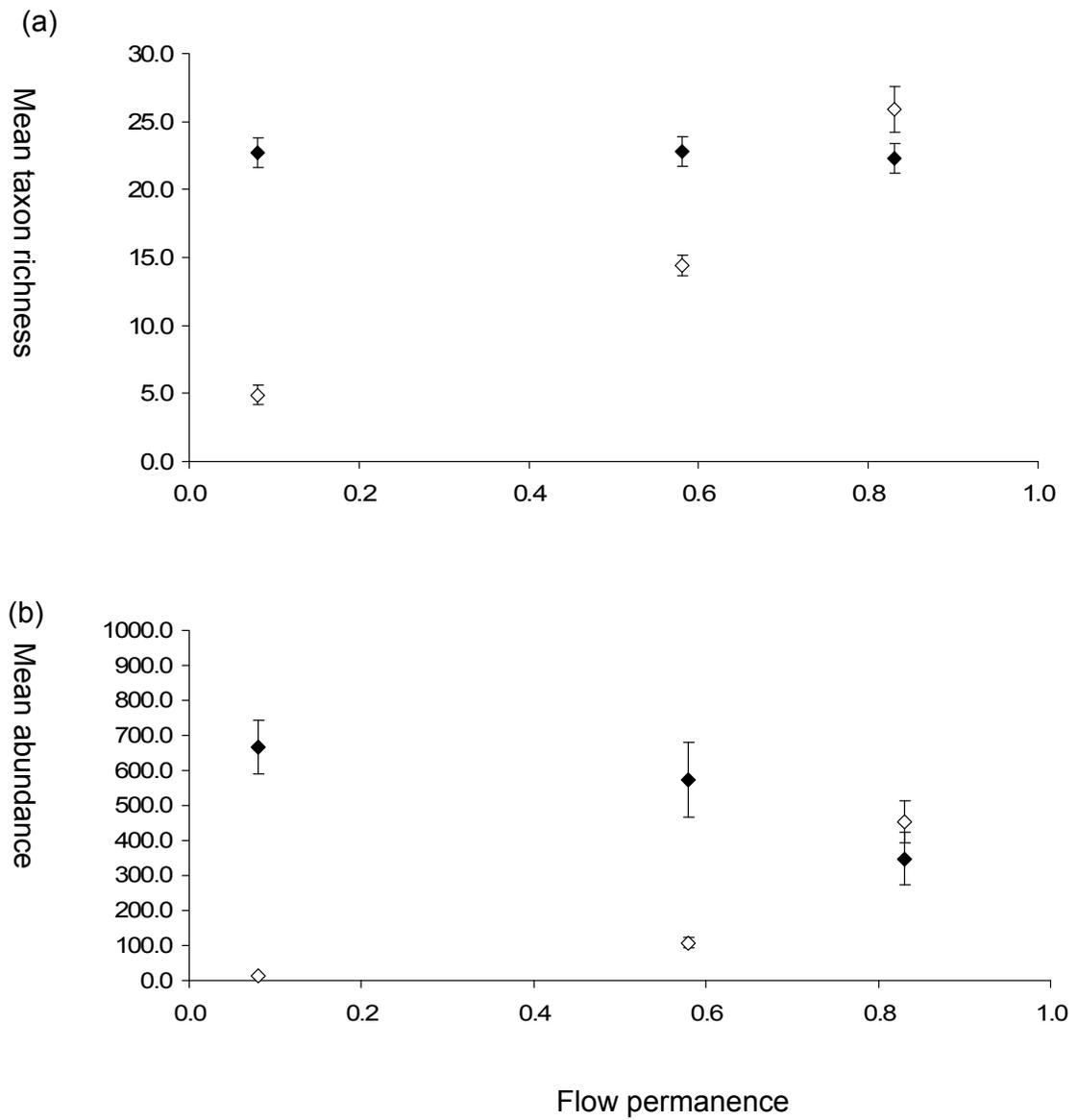


Figure 2. a) Mean taxon richness and b) mean abundance with standard error bars in the three headwater streams during the wet period (black diamonds) and the dry period (white diamonds).

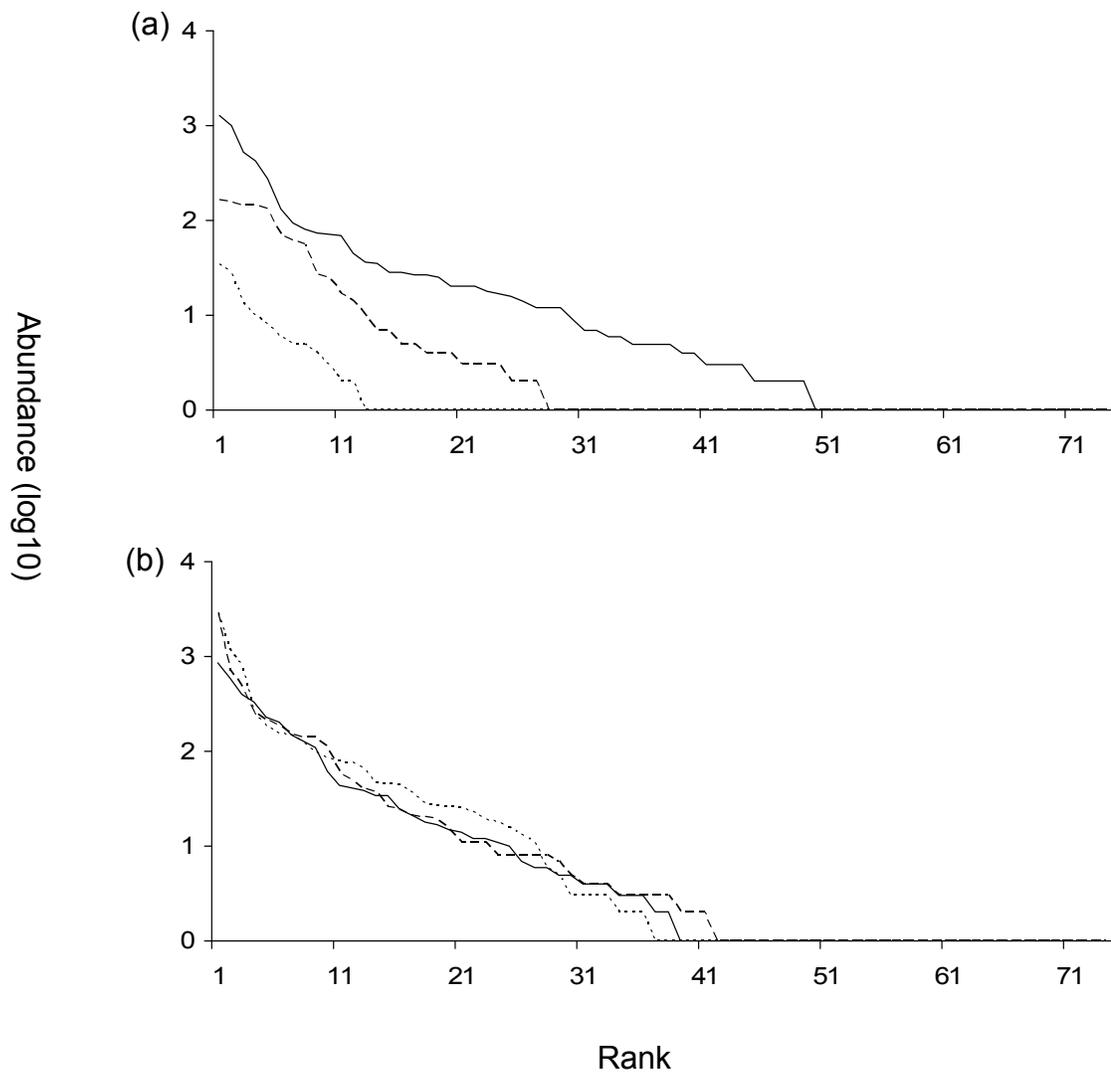


Figure 3. Rank abundance curves for a) dry period and b) wet period (perennial = solid line, intermittent = dashed line, ephemeral = dotted line).

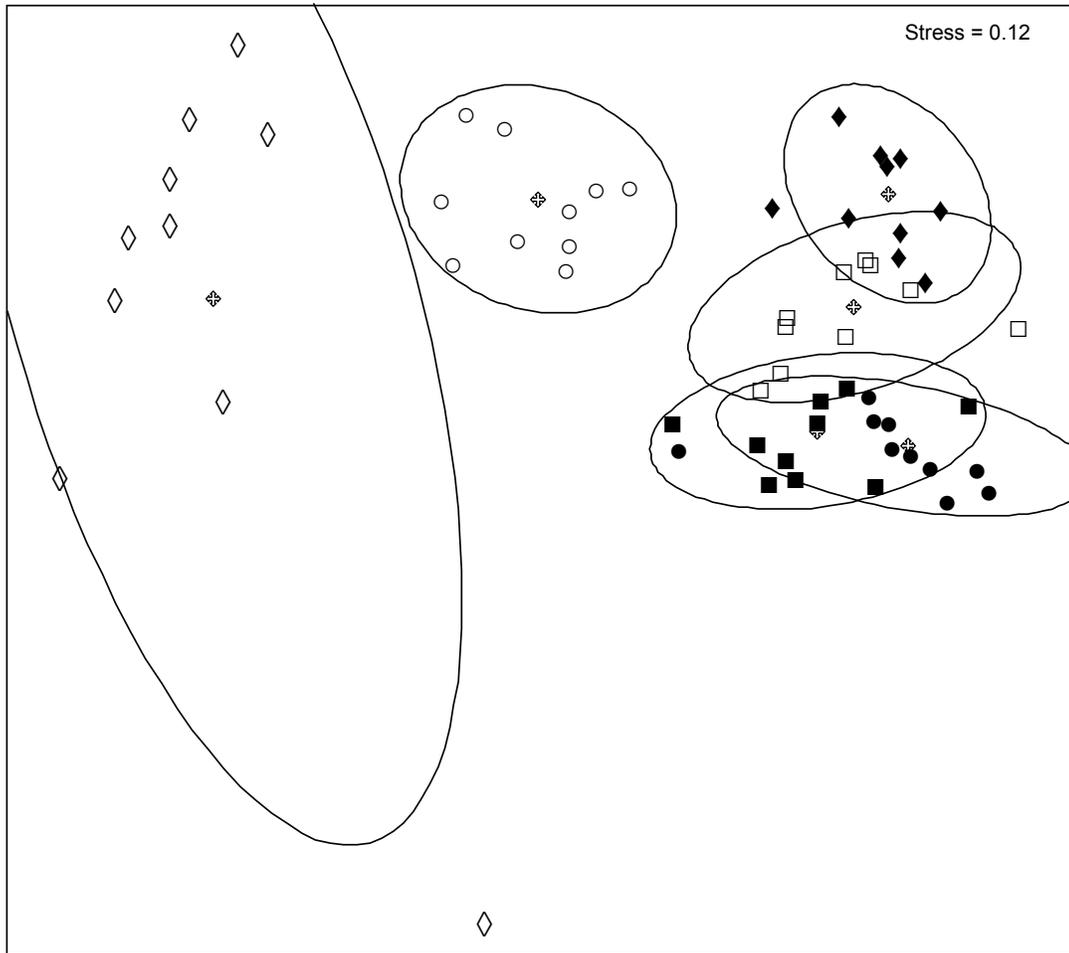


Figure 4. NMDS ordination of 60 samples from the three headwater streams (perennial = squares, intermittent = circles, ephemeral = diamonds) during the wet period (black) and the dry period (white).



Plate 2. Dry headwater streams in the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia.

Declaration for Thesis Chapter 3

This thesis chapter (Clarke *et al.* 2010) is in the same form as the final manuscript published in the peer-reviewed journal *Diversity and Distributions*. The full reference for the published paper is:

Clarke A, Mac Nally R, Bond N & Lake, PS (2010) Conserving macroinvertebrate diversity in headwater streams: The importance of knowing the relative contributions of α and β diversity. *Diversity and Distributions*, in press.

Declaration by the candidate

In the case of Chapter 3, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution
I performed 100% of the fieldwork, 100% of the laboratory work, 100% of the statistical analyses and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Nick Bond	Nick Bond contributed ideas to the work and co-authored the manuscript.
PS Lake	PS Lake contributed ideas to the work and co-authored the manuscript.

Candidate's signature		Date
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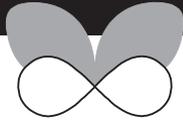
Declaration by co-authors

The undersigned hereby certify that:

- (1) the above declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria;
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor of publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (6) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Locations(s) **School of Biological Sciences, Monash University**

	Date	
Signature 1		
Signature 2		
Signature 3		



Conserving macroinvertebrate diversity in headwater streams: the importance of knowing the relative contributions of α and β diversity

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ABSTRACT

Aim We investigated partitioning of aquatic macroinvertebrate diversity in eight headwater streams to determine the relative contributions of α and β diversity to γ diversity, and the scale dependence of α and β components.

Location Great Dividing Range, Victoria, Australia.

Methods We used the method of Jost (*Ecology*, 2007, 88, 2427–2439) to partition γ diversity into its α and β components. We undertook the analyses at both reach and catchment scales to explore whether inferences depended on scale of observation.

Results We hypothesized that β diversity would make a large contribution to the γ diversity of macroinvertebrates in our dendritic riverine landscape, particularly at the larger spatial scale (among catchments) because of limited dispersal among sites and especially among catchments. However, reaches each had relatively high taxon richness and high α diversity, while β diversity made only a small contribution to γ diversity at both the reach and catchment scales.

Main conclusions Dendritic riverine landscapes have been thought to generate high β diversity as a consequence of limited dispersal and high heterogeneity among individual streams, but this may not hold for all headwater stream systems. Here, α diversity was high and β diversity low, with individual headwater stream reaches each containing a large portion of γ diversity. Thus, each stream could be considered to have low irreplaceability since losing the option to use one of these sites in a representative reserve network does not greatly diminish the options available for completing the reserve network. Where limited information on individual taxonomic distributions is available, or time and money for modelling approaches are limited, diversity partitioning may provide a useful ‘first-cut’ for obtaining information about the irreplaceability of individual streams or subcatchments when establishing representative freshwater reserves.

Keywords

Alpha diversity, beta diversity, diversity partitioning, headwater stream, irreplaceability, macroinvertebrates.

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INTRODUCTION

The focus of conservation science is moving from protecting single species and isolated protected areas (Poiani *et al.*, 2000) to conserving entire communities within regions (Chandy *et al.*, 2006). For assemblages with relatively few species, or those in which individual species distributions are known,

conservation planning frequently proceeds by predicting the distribution of individual species across the landscape and then selecting priority areas for inclusion in conservation reserves based on the extent to which a suite of reserves can encompass the full complement of species (e.g. Linke *et al.*, 2007; Spring *et al.*, 2010). However, such approaches require a good understanding of the distribution of individual species,

information that frequently is lacking (Thuiller *et al.*, 2004). An alternative approach is to consider community composition (or turnover) and the spatial scales (and hence suitable conservation planning units) over which biodiversity patterns (and hence species complements) differ. Conservation reserve networks then are developed with an understanding of the relevant spatial scales at which additional reserves probably will lead to an increase in the numbers of species being protected as a function of the regional species pool (Spring *et al.*, 2010). Spatial variation in species richness and/or community composition is increasingly being incorporated into spatial prioritization routines for systematic conservation planning (Arponen *et al.*, 2008), with recent recognition that the importance of relationships between the distribution of surrogate species (or communities) and environmental or spatial factors has generally been overlooked in systematic conservation planning (Ferrier & Drielsma, 2010).

While such approaches do not require a complete understanding of the distribution of individual species, they still require an understanding of how diversity patterns are generated and maintained across multiple spatial scales. Such knowledge is critical because regional diversity (γ) can be generated in different ways and may require tailored conservation planning and reserve design depending on the relative contributions of α (within-assemblage) and β (among-assemblage) diversity. Patterns of species diversity also are scale dependent (Chandy *et al.*, 2006; Crist & Veech, 2006), so the relative importance of α and β components may change depending on the scale of investigation.

The partitioning of diversity across multiple spatial scales, such that γ diversity on one spatial scale becomes α diversity at a larger scale (Stendera & Johnson, 2005), is useful for studying diversity patterns in streams, which long have been recognized as spatially nested, hierarchical systems (Frissell *et al.*, 1986). The scale-invariance of the physical structure of stream networks (Rodriguez-Iturbe & Rinaldo, 1997) also means that there is no particular spatial scale at which streams should be studied, and so, any investigation of ecological patterns in stream systems should be conducted at multiple spatial scales (Webb *et al.*, 2007). Despite this, analyses of species diversity patterns in streams largely have been restricted to longitudinal reach scales (Lloyd *et al.*, 2005; Lowe *et al.*, 2006). Also, the importance of the physical topology of stream systems (i.e. branching-networks or ramifications) in determining spatial patterns of species diversity has been little explored (Fisher, 1997; Poole, 2002) despite the potential for this branching structure to restrict dispersal and isolate assemblages (e.g. Fagan, 2002). Therefore, the highly branched headwaters of stream networks are valuable systems within which to explore the relative contributions of α and β diversity to γ diversity.

We previously have suggested that, while individual headwater streams may have low α diversity, their overall contribution to γ diversity may be more important when viewed at the landscape scale because of potentially high β diversity (Clarke *et al.*, 2008). However, despite the ubiquity of

headwater streams, their aquatic fauna and contribution to γ diversity have been relatively understudied (Cole *et al.*, 2003; Heino *et al.*, 2003), and little is known about the partitioning of diversity in these systems (Clarke *et al.*, 2008).

Here, we investigated partitioning of aquatic macroinvertebrate diversity in eight headwater streams to determine: (1) the relative contributions of α and β diversity to γ diversity, and (2) the scale dependence of α and β components using the partitioning approach described by Jost (2007). We discuss the implications that these findings may have for conservation planning of macroinvertebrate communities in headwater streams. We also developed conceptual models comparing theoretical dispersal paths of terrestrial taxon and riverine taxon among landscape patches arranged identically to our study sites but with two different dispersal geometries (planar and dendritic). From this, we hypothesized that β diversity would make a substantial contribution to regional (γ) diversity at both the reach and catchment scales, but would be greater at the catchment scale because of reduced dispersal among catchments (compared to reaches within catchments) and greater differences in local catchment environments.

METHODS

Study area

The study was conducted in eight first-order streams (Fig. 1) in the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia (37°4' S, 145°2' E). This 9965-ha catchment is located at the southern end of the Hume Plateau (Ashton, 2000) and is dissected into a south-facing slope and north-facing slope by the cross-cutting Great Dividing Range. The study area is *c.* 50 km north-east of the state capital, Melbourne. Mean annual rainfall in the catchment area was 1207 mm from 1995 to 2006 (Martin *et al.*, 2007) and elevation ranges from 600 to 800 m A.S.L. The vegetation is dominated by ecologically mature, eucalypt forest that encompasses a mixture of Victorian vegetation classes (Mac Nally *et al.*, 2008). The area is closed to the public for protection of water quality and water supply (Parks Victoria, 1998). At the time of this study, the area was largely undisturbed, but there are historic legacies (mostly occurring in the mid- to late 1800s) that include bushfire, aqueduct construction, logging, some human settlement and bullock grazing (Ashton, 2000).

Data collected (for a separate investigation) on these eight streams showed that local environmental conditions were quite variable among the eight sites, despite the relatively small spatial scale of the study area. The streams differed in riparian vegetation type (three different classes), aspect (two south-facing and six north-facing), number of debris dams per reach (5–21), total volume of organic material per reach (1069.6–68652.3 m³), mean pH (5.5–7.2), mean dissolved oxygen (3.1–12.9 p.p.m.), mean conductivity (48.1–106.2 μ m), mean water temperature (6.9–11.4 °C), mean wetted width (27.5–102.5 cm), mean water depth (1.8–7.4 cm) and mean discharge (1.2–58.8 cm³ s⁻¹).

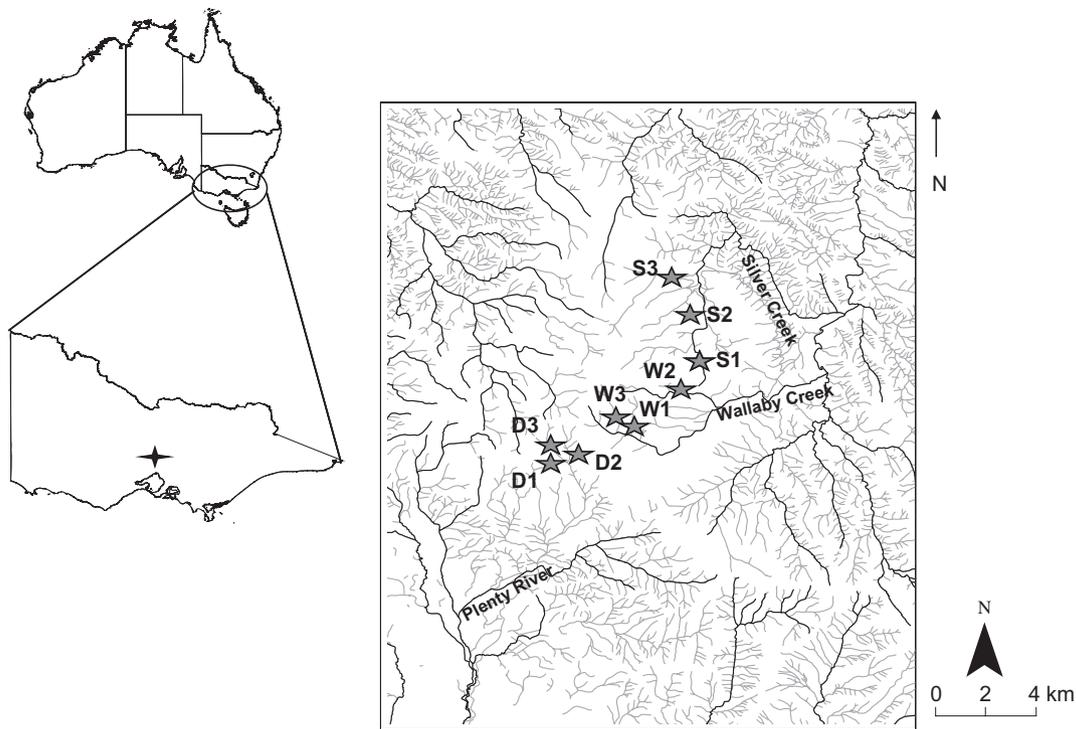


Figure 1 Location of study sites within the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia. Disappointment Creek catchment (D), Wallaby Creek catchment (W), Silver Creek catchment (S).

Pilot study

Grubaugh *et al.* (1996) and Parsons & Norris (1996) highlighted the problems with sampling only one habitat type and suggested that proportional sampling based on the dominant habitat types present provides a more accurate reflection of the macroinvertebrate assemblage at a site. Visual inspection of the study streams revealed two dominant macroinvertebrate habitat types, sandy benthic areas ('B') and debris dams ('D'). We followed the definition of debris dams of Smock *et al.* (1989) as 'any wood > 5 cm in diameter in contact with sediment and spanning at least one-fourth of the channel. Also included were root masses from living riparian vegetation'. The debris dams in the study streams generally were characterized by one larger piece of wood causing a partial obstruction of the channel and an accumulation of smaller pieces of wood, twigs and leaves. A pilot study was undertaken in one stream from the Silver Creek catchment, randomly selected from the eight study streams, to determine whether macroinvertebrate assemblages differed between the two habitat types (thus requiring stratified random sampling). The pilot study also explored the number of samples required to ensure that taxon rarefaction curves in the main study would begin to approach the asymptote, indicating that the majority of the taxa in the community had been sampled (Gotelli & Colwell, 2001).

Twenty-seven samples (15 B, 12 D) were collected over 2 days from a 20-m reach in the pilot study stream in December 2006 (early austral summer). Benthic samples were randomly collected from the sandy stream bed using a current-

independent pump sampler (Boulton, 1985). A 10 × 10 cm patch of benthic habitat was isolated within a square frame, and the benthos disturbed to a depth of 5 cm while the manual diaphragm pump was operated for 1 min. Each debris dam sample was collected from a randomly selected debris dam by collecting one handful of organic material from the centre of the dam and transferring the material to a zip lock plastic bag (Poff *et al.*, 1993). All samples were preserved in 70% ethanol and returned to the laboratory for identification. In the laboratory, samples were washed over a 300-µm sieve, and all macroinvertebrates were counted and identified to the lowest possible taxonomic resolution (usually genus). Diptera generally were identified to family, except Chironomidae, individuals of which were identified to subfamily. Oligochaeta and Nematoda were not identified further.

Data analysis for the pilot study

Differences in assemblage composition between the two habitat types were examined by visual inspection of an ordination plot using non-metric multidimensional scaling (NMDS) for untransformed, taxon-abundance data. The ordination solution was generated from 100 random starts and in two dimensions. ANOSIM was used to test for significant differences between samples from the two *a priori* defined habitat types. Individual-based rarefaction curves, randomized 100 times, were generated using ESTIMATES 8.0 (Colwell, R.K. 2006) to determine whether the number of individuals collected exceeded the shoulder on the accumulation curve.

Rarefaction curves are means of repeated resampling of all pooled samples and so represent the statistical expectation for the corresponding taxon accumulation curves (Gotelli & Colwell, 2001).

Visual inspection of the ordination plot revealed two groupings of samples according to habitat type, with a small region of overlap, indicating that several taxa are shared between the two habitat types (see Fig. S1 in Supporting Information). This grouping by habitat type was further confirmed by the results of a one-way ANOSIM (Global R : 0.51, $P < 0.001$). Rarefaction curves for the two habitat types showed that the two samples sizes (12 and 15) were more than adequate to pass the shoulder of the accumulation curve for each habitat type (see Fig. S2). Given the findings of the pilot study, stratified random sampling was adopted for the main study with a total of 15 samples to be collected in each reach based on the proportion of the two habitat types present.

Sampling design and site selection for the main study

We used a hierarchically nested sampling design with the hierarchical levels corresponding to two spatial scales: catchments and reaches within catchments. Of the four small catchments in the study area, only three were included in the study because the remaining catchment was dry during all initial site visits. Two of the catchments were on the north-facing slope (Wallaby Creek and Silver Creek) and one catchment was on the south-facing slope (Disappointment Creek). Three reaches were randomly selected in each of the three catchments, followed by a site inspection to check that the reach was accessible and contained enough water to be sampled. Of the nine study streams, one reach in the Disappointment Creek catchment did not contain enough connected surface water to be sampled in either 2007 or 2008 and was, therefore, excluded from the study. No other suitable replacement reaches in the Disappointment Creek catchment could be found.

Macroinvertebrate sampling was conducted in the austral spring 2007 (October) and austral spring 2008 (October). Prior to sampling, 30-m study reaches were measured for the proportions of benthic habitat and debris-dam habitat, determined by recording the total downstream length of each habitat type over the 30-m reach to the nearest cm, and calculating the percentage of reach length of each. We then determined the allocation of samples for benthic and debris dam habitats ($N = 15$) based on this proportion.

The location of all debris dams in a reach was recorded, and each was given a number. Debris dams for sampling were chosen randomly from the total number available by using random numbers. Macroinvertebrate samples from debris dams were collected as described for the pilot study.

The positions of benthic samples were determined by splitting the reach into 30 × 1 m sections with a measuring tape and selecting the required amount of numbers (e.g. numbers of benthic samples needed) using random numbers. For each number drawn, the benthic sample was taken from

the closest available sandy benthic habitat to the position on the measuring tape matching the number. Benthic samples were collected as described for the pilot study.

All samples were preserved and washed as described for the pilot study, and all macroinvertebrates were identified as described previously. After sorting all macroinvertebrates from the debris-dam samples, we dried the remaining organic matter from each 'grab' sample in a 60 °C oven to constant mass, weighed and ashed the organic matter in a muffle furnace for ≥ 2 h at 550 °C and reweighed them to obtain the ash-free dry mass (AFDM). Given the expected variation in the volume and mass of organic material collected in each sample, we investigated whether taxon richness from the debris dam samples was correlated with the AFDM of the sample. We found no relationship with taxon richness in 2007 ($R^2 = 0.11$) or 2008 ($R^2 = 0.03$).

Data analysis

Taxon richness generally increases with the number of individuals collected, so taxon richness among sites with different numbers of individuals cannot be validly compared unless an accumulation curve has reached its asymptote (Gotelli & Colwell, 2001). We constructed individual-based rarefaction curves, as described for the pilot study, to enable valid comparisons of taxon richness among reaches based on a comparable number of individuals. That number was the smallest number of individuals recorded for a reach in each year and was 1365 in 2007 and 725 in 2008. This > 50% reduction in the number of individuals collected in 2008 compared to 2007 is likely because of decreasing rainfall and increasing streamflow deficit between the 2 years as a result of the severe drought affecting south-eastern Australia for the past 13 years (Rose *et al.*, 2008). Thus, values of rarefied taxon richness for each reach in this study should not be compared between years. Taxon richness at the fixed count was determined by fitting a logarithmic function to the rarefaction curve and using the associated equation to determine taxon richness.

Visual inspection of patterns in assemblage composition was undertaken from ordination plots, as described for the pilot study. Ninety-percentile confidence ellipses were plotted for each group of 45 samples from the three catchments. A two-way nested ANOSIM was used to determine whether there were differences in assemblage composition between catchments and between reaches (nested within catchments).

Given that most diversity indices (excluding species richness) measure entropy rather than actual diversity (i.e. they measure the uncertainty in the outcome of a sampling process), the direct application of values derived from diversity indices can give misleading results (Jost, 2006). These entropies must first be transformed to their effective number of elements in a system, or 'numbers equivalents', before they can be literally interpreted (Jost, 2006). Jost (2007) showed that using the numbers equivalents of diversity indices is also the only way to derive β that is independent from α and that

Whittaker's multiplicative rule for diversity partitioning (1960;1972) is true for the numbers equivalents of all indices. Conversely, if β is defined as γ minus α , e.g. the recent widespread use of additive partitioning (Loreau, 2000; Wagner *et al.*, 2000; Gering *et al.*, 2003; Stendera & Johnson, 2005; Crist & Veech, 2006; Erős, 2007), then β must approach zero whenever α diversity is high, regardless of the actual turnover between samples. Therefore, β does not behave as one would intuitively expect it to as a result of the 'hidden' dependence of β on α (Jost, 2007).

For diversity partitioning, individual samples within reaches were pooled to obtain a taxon list with abundance data for the reach. We partitioned data for aquatic macroinvertebrate diversity into independent α and β components for two spatial scales by using the multiplicative relationship between α and β for the numbers equivalents of taxonomic richness and Shannon diversity (Jost, 2007). Given that taxonomic richness is a direct measure of diversity (and not entropy), it does not require transformation to obtain a numbers equivalent. The numbers equivalent of Shannon diversity (H) is e^H (Jost, 2006). We used Shannon diversity because Jost (2007) showed that Shannon diversity is the only standard diversity measure than can be partitioned into independent components when community weights (e.g. number of individuals) are unequal.

At the reach scale, γ is the total number of taxa recorded within one catchment, α is the mean number of taxa across the reaches within one catchment, and β is the effective number of taxonomically distinct reaches (Jost, 2007).

At the catchment scale, the Disappointment Creek catchment data were excluded from analysis because there were only two reaches sampled in this catchment and so these could not be compared with the other catchments that had three. γ is the total number of taxa recorded across both the Silver and Wallaby Creek catchments, α is the mean number of taxa across the two catchments, and β is the effective number of taxonomically distinct catchments (Jost, 2007). From β , we calculated indices of homogeneity:

$$H = ((N/\beta) - 1)/(N - 1),$$

where N is the number of reaches or catchments sampled. H ranges from 0 to unity and decreases with increasing β diversity (Jost, 2007).

RESULTS

Macroinvertebrate diversity and assemblage composition

Some 45,523 individuals from 92 taxa were collected in the eight headwater streams during the two sampling periods. Rarefaction curves for the eight streams were more similar to each other in 2007 than in 2008 (see Figs S3 and S4, respectively). Many of the curves in 2008 appeared to be truncated in comparison with the 2007 curves because of the smaller number of individuals collected for all streams in 2008, except S3. In 2007, rarefied taxon richness was highest in D3

(43.6) and lowest in W1 (32.2). In 2008, rarefied taxon richness was highest in W3 (37.4) and lowest in S3 (21.1).

There was considerable faunal overlap between samples from the Wallaby and Silver Creek catchments in 2007, but only a small region of overlap with samples from the Disappointment Creek catchment (Fig. 2). Samples from two of the eight reaches (D3 and W1) were less similar than samples from the remaining reaches. There was a significant difference between reaches (Global R : 0.29, P = 0.001) and between catchments (Global R : 0.62, P = 0.007). In 2008, there was a similar pattern, with considerable overlap between samples from the Wallaby and Silver Creek catchments, but the samples from the Disappointment Creek catchment were more similar to the other two catchments in 2008 than in 2007 (Fig. 3). Samples from reaches D3 and W1 in 2008 were less similar than the other reaches. In 2008, samples from S3 also were less similar to samples in the remaining reaches. There was a significant difference among reaches (Global R : 0.42, P = 0.001), but not between catchments (Global R : 0.31, P = 0.08).

Diversity partitioning at the reach and catchment scale

Following Jost (2007), the numbers equivalents of diversity components will be referred to as the 'true' diversity (e.g. true α diversity in this case is the numbers equivalent of α diversity for either taxonomic richness or Shannon diversity). True α diversity for both taxonomic richness and Shannon diversity (at the reach scale) was much higher than true β diversity in all three catchments, in both years (Table 1). True α diversity for both taxonomic richness and Shannon diversity (at the catchment scale) was also much higher than true β diversity (Table 1). True β diversity was generally lower at the catchment scale than the reach scale (Table 1).

DISCUSSION

The additive partitioning of diversity into hierarchical components is a common method of diversity analysis, but this comparison of β diversity among hierarchical levels generally is not valid because it is usually conducted by comparing β values that have a 'hidden' dependence upon α values (Ricotta, 2009). Here, by using the methods of Jost (2007), where α and β components of a diversity index are independent when their numbers equivalents are multiplied, we partitioned macroinvertebrate diversity into α and β components for two spatial scales and determined the relative importance, and scale dependence, of these components.

The relative contributions of α and β diversity to γ diversity

Ecological studies of landscapes mostly have dealt with 'planar' geometries, where patches extend in two dimensions and can theoretically 'fill' the entire landscape (Mac Nally *et al.*, 2004;

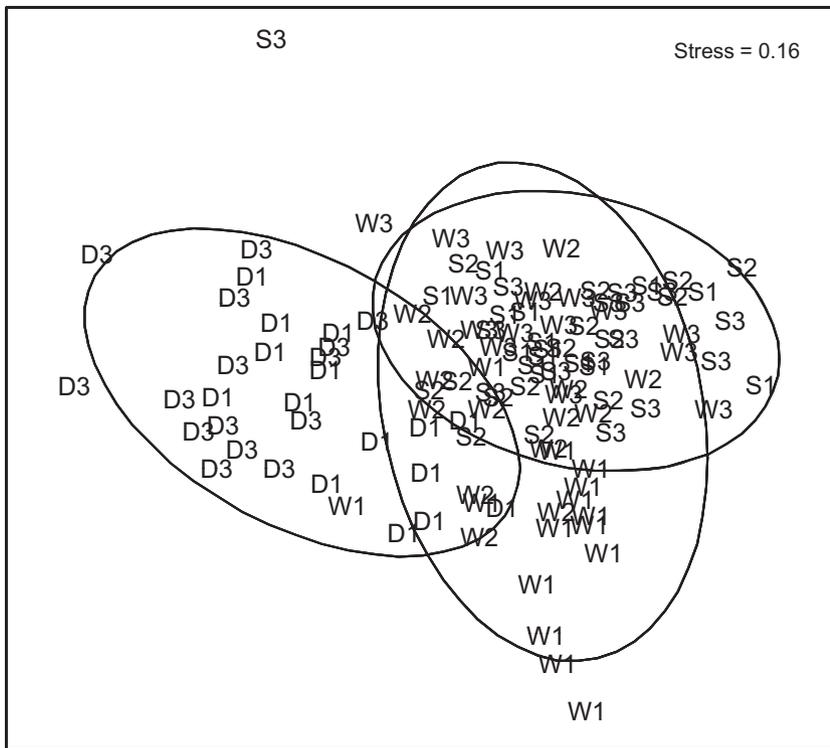


Figure 2 Ordination plot using non-metric multidimensional scaling for all 2007 samples with 90% confidence ellipses for the three catchments.

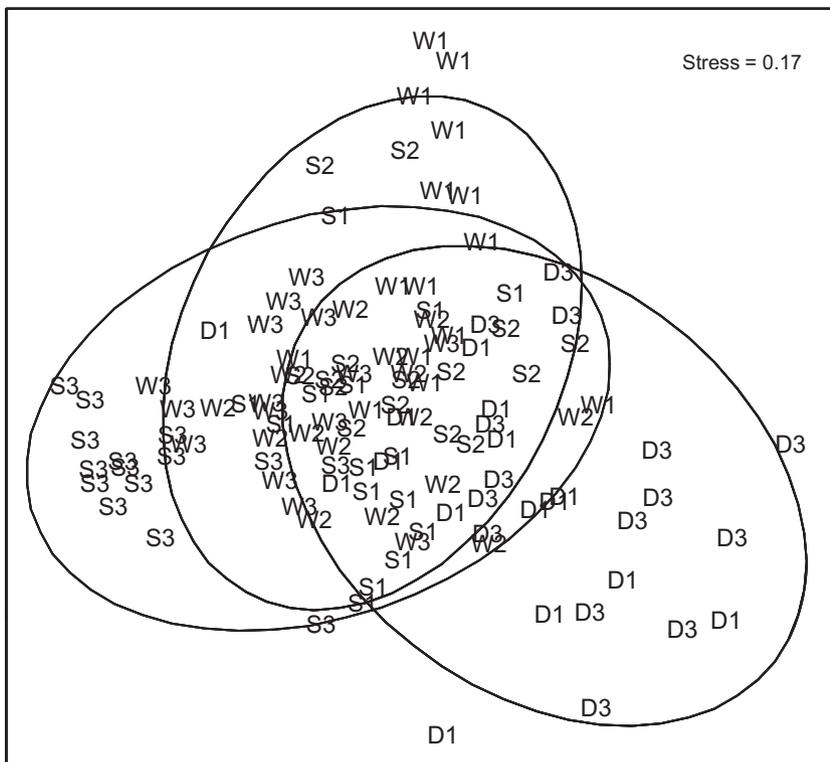


Figure 3 Ordination plot using non-metric multidimensional scaling for all samples in 2008 with 90% confidence ellipses for the three catchments.

Fagan *et al.*, 2009). There has been little consideration of other natural geometries and their effects on the spatial structure of biodiversity (Fisher, 1997; Grant *et al.*, 2007; Mac Nally *et al.*, 2010). The hierarchical, dendritic structure of river networks may impose landscape-scale dispersal constraints that are

particularly important for fish and aquatic macroinvertebrate species that cannot disperse well by flight (Fagan, 2002). Consequently, river network structure has been posited to have particularly strong effects on β diversity because of the containment effect of the largely inhospitable terrestrial

Table 1 Partitioning of diversity components for two spatial scales (reach and catchment) showing true* diversities for taxon richness and Shannon diversity for (a) 2007 and (b) 2008

	Reach scale		
	Wallaby Creek	Silver Creek	Disappointment Creek
Taxon richness			
(a)			
True* α (reach)	48.33	49.67	40.50
True β (reach)	1.32	1.37	1.28
True γ	64	68	52
Homogeneity	0.63	0.60	0.56
	Catchment scale (Wallaby and Silver only)		
True α (catchment)	66		
True β (catchment)	1.20		
True γ	79		
Homogeneity	0.67		
	Reach scale		
	Wallaby Creek	Silver Creek	Disappointment Creek
Shannon diversity			
True α (reach)	7.37	7.10	7.99
True β (reach)	1.25	1.13	1.13
True gamma	9.23	7.98	9.04
Homogeneity	0.70	0.83	0.77
	Catchment scale (Wallaby and Silver only)		
True α (catchment)	8.58		
True β (catchment)	1.12		
True γ	9.62		
Homogeneity	0.78		
	Reach scale		
	Wallaby Creek	Silver Creek	Disappointment Creek
Taxon richness			
(b)			
True α (reach)	48.67	45.34	35
True β (reach)	1.38	1.46	1.26
True γ	67	66	44
Homogeneity	0.59	0.53	0.59
	Catchment scale (Wallaby and Silver only)		
True α (catchment)	66.5		
True β (catchment)	1.17		
True γ	78		
Homogeneity	0.71		
	Reach scale		
	Wallaby Creek	Silver Creek	Disappointment Creek
Shannon diversity			
True α (reach)	7.92	8.10	11.46
True β (reach)	1.45	1.04	1.11
True γ	11.51	8.45	12.72
Homogeneity	0.53	0.94	0.80
	Catchment scale (Wallaby and Silver only)		
True α (catchment)	9.87		
True β (catchment)	1.136		
True γ	11.21		
Homogeneity	0.76		

*True α diversity in this case is the numbers equivalent of α diversity for either taxonomic richness or Shannon diversity.

landscape separating river reaches (Clarke *et al.*, 2008; Munepeerakul *et al.*, 2008).

We used conceptual models to compare theoretical dispersal paths of terrestrial taxon and riverine taxon among landscape patches arranged identically to our study sites but with two different dispersal geometries, planar for terrestrial taxon and dendritic for aquatic taxon (Fig. 4). From this, we hypothesized that β diversity would make a large contribution to the γ diversity of macroinvertebrates in our dendritic riverine landscape, particularly at the larger spatial scale (among catchments) because of limited dispersal among sites and especially among catchments (Hughes, 2007). Several studies of diversity partitioning for both fish and macroinvertebrates in riverine landscapes have found similar patterns of small α components and a large β component (Monaghan *et al.*, 2005; Stendera & Johnson, 2005; Erős, 2007). The conceptual model illustrates the potential for topographic boundaries (in this case the cross-cutting Great Dividing Range) to limit further the already restricted dispersal paths in the dendritic landscapes, particularly for taxa without an aerial dispersal stage (Fig. 4b). Previous authors have highlighted the ability of intervening steep topography to drastically limit among-drainage dispersal (Hughes *et al.*, 1999; Monaghan *et al.*, 2002; Downes & Reich, 2008) and the ability of heterogeneity created by topographic boundaries to lead to greater β diversity (Kerr *et al.*, 2001).

We found that for the numbers equivalents of both taxon richness and Shannon diversity, true α diversity made a very large contribution to regional diversity at both spatial scales and in both years, with β diversity contributing much less. Given that all sites were contained within a < 10,000 ha reserve, β diversity may have been lower than hypothesized because of relatively small distances between sites and the presence of many macroinvertebrate taxa with an aerial dispersal stage that could facilitate high levels of dispersal among reaches and catchments in this area. However, studies over larger distances and more dissimilar sites have also reported high contributions of α diversity to γ diversity (Fleishman *et al.*, 2003; Novotny *et al.*, 2007; Hulcr *et al.*, 2008). High α diversity and low β diversity may also indicate a non-interactive and unsaturated local community, where excess niche space is available and interactions such as competition are weak (Cornell & Lawton, 1992).

A recent meta-analysis of terrestrial arthropod diversity patterns suggested that at scales relevant to insects, rainforests often represent relatively large tracts of homogeneous habitat in which the local species pool (i.e. α diversity) typically represents a large portion of the diversity in the region (Lewinsohn & Roslin, 2008). This may also be the case in our system, where the closed water supply catchment represented a continuous tract of relatively undisturbed vegetation through which stream insects with an aerial dispersal stage can freely move among reaches and catchments. Although β diversity was generally low among all reaches and catchments, ordination plots revealed that community assemblages from the south-facing Disappointment Creek catchment were more different

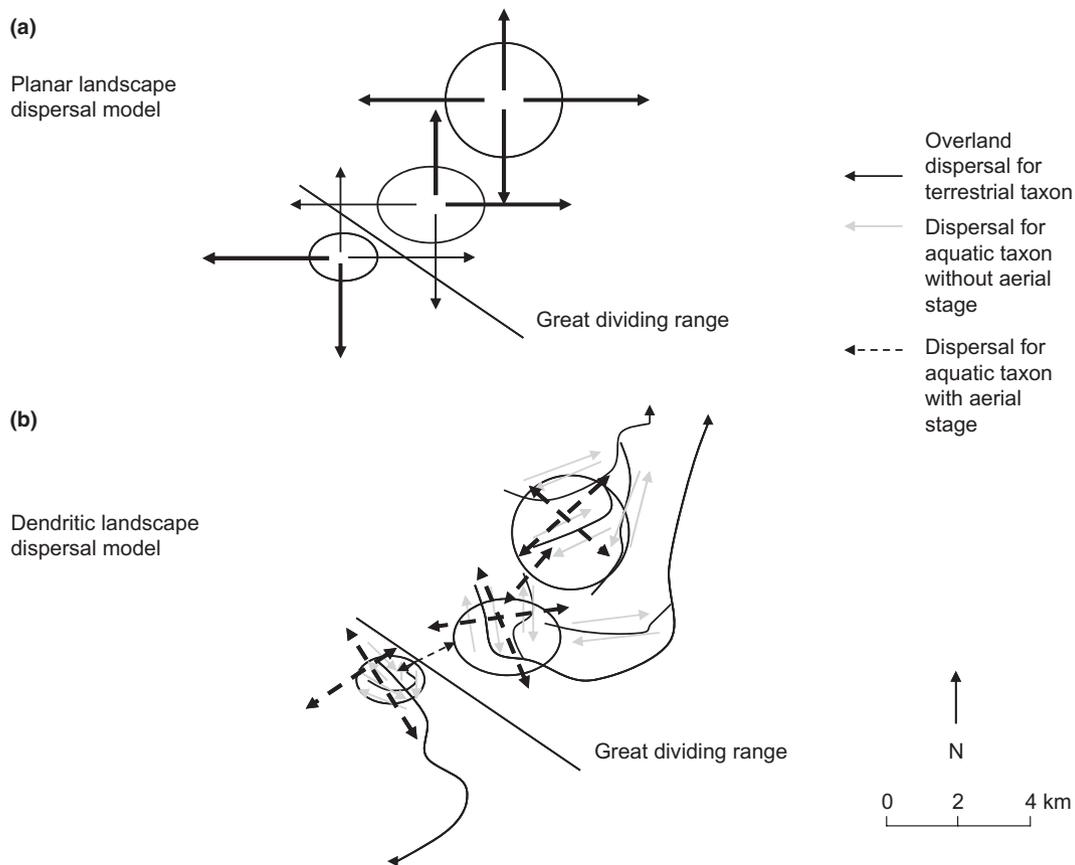


Figure 4 Hypothetical dispersal paths across landscape patches approximating our study sites for (a) terrestrial taxon (planar geometry) and (b) aquatic taxon (dendritic geometry). Increased length and thickness of arrows indicate increased distance and ease of dispersal, respectively.

from the two north-facing catchments (Silver and Wallaby Creek catchments) than they were to each other. This was not a straight-line distance effect (Fig. 1). It seems that there may be more dispersal than expected across the peak of the Great Dividing Range in the study area, and this could be because of the relatively low relief on either side of peak, because of the presence of the Hume Plateau. It is also possibly because of the influence of the Wallaby Creek channel that connects the Wallaby and Silver Creek catchments to the south-facing side of the Great Dividing Range, acting as a conduit for movement of biota. However, this is considered unlikely because the channel was dry for the majority of this study because of low streamflow caused by the severe drought, spanning more than a decade, currently affecting south-eastern Australia (Rose *et al.*, 2008).

In this study, we defined regional richness as the pooled richness of the three reaches (at the reach scale) or pooled richness of the three reaches for both catchments (at the catchment scale). It is almost certain that other reaches in the catchment had at least some different taxa, so our estimate of γ diversity is likely lower than the actual diversity of the region, thus making the contribution of α diversity seem higher than its probable actual contribution and the contribution of β diversity seem lower than its probable actual contribution.

Without exhaustive surveys of a region or previous studies upon which to draw for a complete taxonomic list of a region, this type of problem will often be encountered in diversity partitioning studies.

The scale dependence of α and β components

Ecological patterns and processes occur across a wide range of scales, yet many diversity studies are undertaken at only a single scale, usually that of the original sample plots (Chandy *et al.*, 2006). Aquatic macroinvertebrate communities in streams are likely to be structured by a combination of dispersal limitation and environmental factors (Thompson & Townsend, 2006), so it is important to consider that macroinvertebrate communities respond to multiple environmental gradients, many of which are scale related (Stendera & Johnson, 2005). Thus, diversity patterns also may be scale dependent because various landscape components differ in their contribution to species diversity and various mechanisms may drive diversity at different scales (Fleishman *et al.*, 2003). An understanding of the scale dependence of diversity partitioning is critical to the application of management and conservation strategies, which typically extend beyond the small-scale studies often conducted by ecologists to entire

regions or catchments (Lowe *et al.*, 2006; Thomson *et al.*, 2009).

Our expectation was that dispersal limitation and environmental factors would lead to greater differences in macroinvertebrate communities among catchments than among reaches, so that β diversity would be higher at the catchment scale. However, we found that β diversity generally was higher at the smaller spatial scale (i.e. among reaches within catchments). So, in this system, it seems that relatively small-sized reserves would most efficiently maintain aquatic macroinvertebrate diversity in the region. β diversity at the reach scale may be generated by high-habitat heterogeneity among even very close sites. Small headwater streams are often structurally complex because their morphology is largely determined by the stochastic distribution of obstructions, such as rocks, tree roots and woody debris, which cannot easily be moved because of low stream power (Gooderham *et al.*, 2007). Stendera & Johnson (2005) also found that β diversity was inversely related to spatial scale in their study of macroinvertebrate diversity partitioning over three spatial scales. However, Monaghan *et al.* (2002) found little evidence of scale dependence in diversity partitioning of macroinvertebrate assemblages in alpine streams, with β diversity making a large contribution to γ diversity at all three spatial scales studied. Scale dependence of diversity partitioning is also likely to vary depending on the organisms studied. For example, Fleishman *et al.* (2003) found that α diversity within canyon segments was the dominant component of overall species richness of butterflies but not of birds and emphasized that the most appropriate scales for studying and conserving different taxonomic groups are often not the same. This sentiment is echoed by Heaney (2007) who suggested that the search for general paradigms of island biogeography may be somewhat futile since even closely related sets of organisms in a single region can comprise species with very different patterns of dispersal and gene flow, making broad generalizations about spatial patterns of biodiversity difficult.

Implications for riverine conservation planning

Linke *et al.* (2007) suggested that riverine conservation planning must consider three key attributes of catchments: irreplaceability, condition and vulnerability. Irreplaceability of a site (or river reach) can be defined as the extent to which the options for a representative reserve system are lost if that site is lost (Pressey *et al.*, 1994). In our study, individual headwater streams each had high α diversity and low β diversity, and each contained a large portion of the estimated macroinvertebrate diversity in the study region. If a planner could afford to protect only one of these headwater streams as part of a broader representative reserve system, the results of diversity partitioning for these eight streams tell us that it may matter little which of these eight streams is chosen. Even if half the sites were identified as being unavailable to the planner (e.g. because of high cost), there are still several options

remaining for the contribution to the reserve system and thus these eight sites could be interpreted as having low irreplaceability, as defined by Pressey *et al.* (1994). Such low irreplaceability of these streams means that after protecting one of these sites, the most efficient additional conservation gains are likely to be made by protecting more headwater streams from dissimilar landscapes in adjacent catchments or reaches further downstream that may harbour different taxa, in preference to further protecting more headwater streams within the area.

Directly calculating irreplaceability is often computationally difficult, or almost impossible (for large areas), because of the combinatorial nature of the problem (Linke *et al.*, 2008). Where limited information on individual species distributions is available, diversity partitioning may provide an alternative method for assessing the irreplaceability of individual streams or subcatchments to reserve designs aiming at protecting the entire regional species pool. It can also be undertaken without the detailed information on species distributions required by more intensive modelling approaches. Diversity partitioning may provide information that is useful as a quick 'first-cut' for conservation planning when followed up with targeted studies on the distribution of individual species, or be useful in its own right where time or resources for conservation planning are severely limited.

Diversity partitioning is a useful tool for examining diversity patterns and their scale dependence but careful consideration must be given to the use of additive or multiplicative partitioning. In our system, 30-m reaches had high α and low β diversity and contained a high proportion of the estimated total macroinvertebrate diversity of headwater streams in the study area, making their individual irreplaceability low. Future investigation into how diversity patterns are generated and maintained across multiple spatial scales will provide ecologists with a deeper understanding of the mechanisms that drive these patterns and is crucial for the effective management and conservation of aquatic biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Ordination plot of benthic (B) and debris dam (D) samples from the pilot study.

Figure S2 Rarefaction curves for benthic samples (bottom) and debris dam samples (top) in the pilot study.

Figure S3 Individual-based rarefaction curves for the eight study streams in 2007.

Figure S4 Individual-based rarefaction curves for the eight study streams in 2008.

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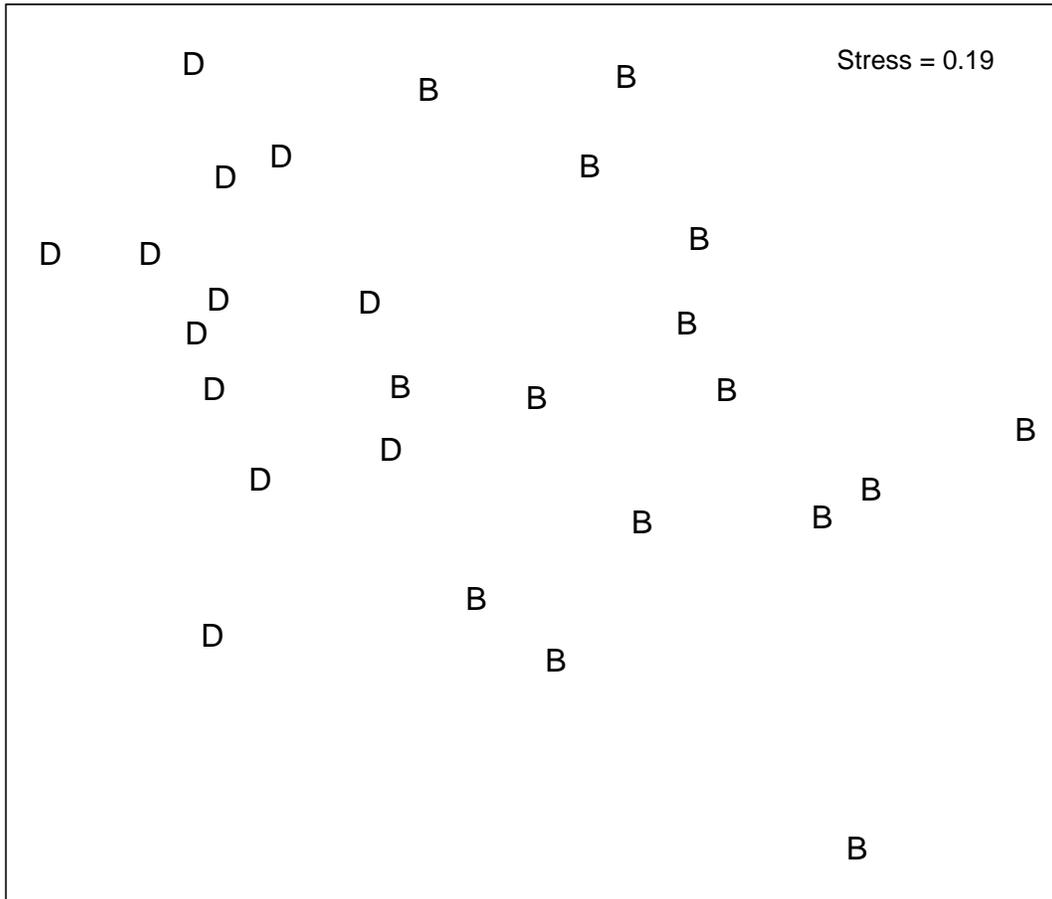
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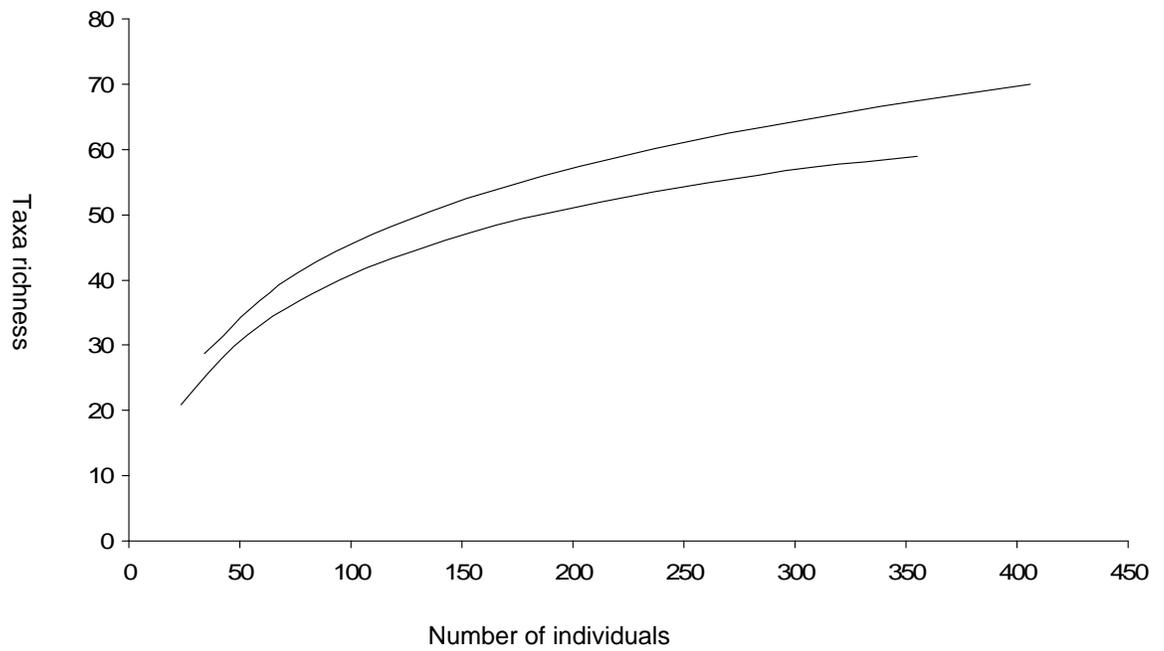
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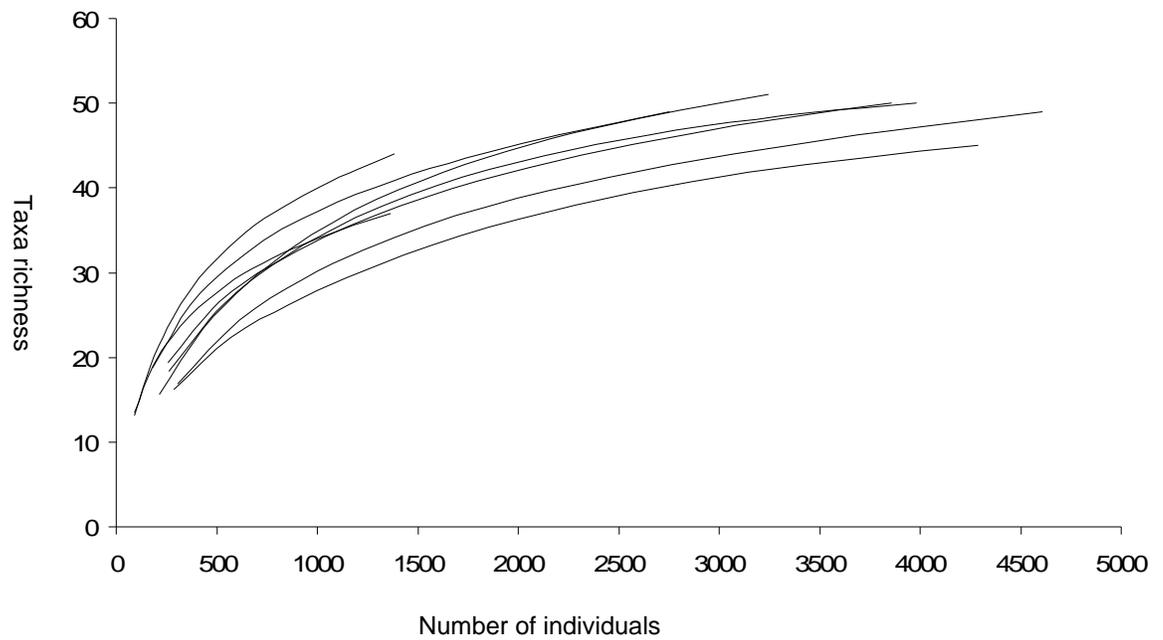
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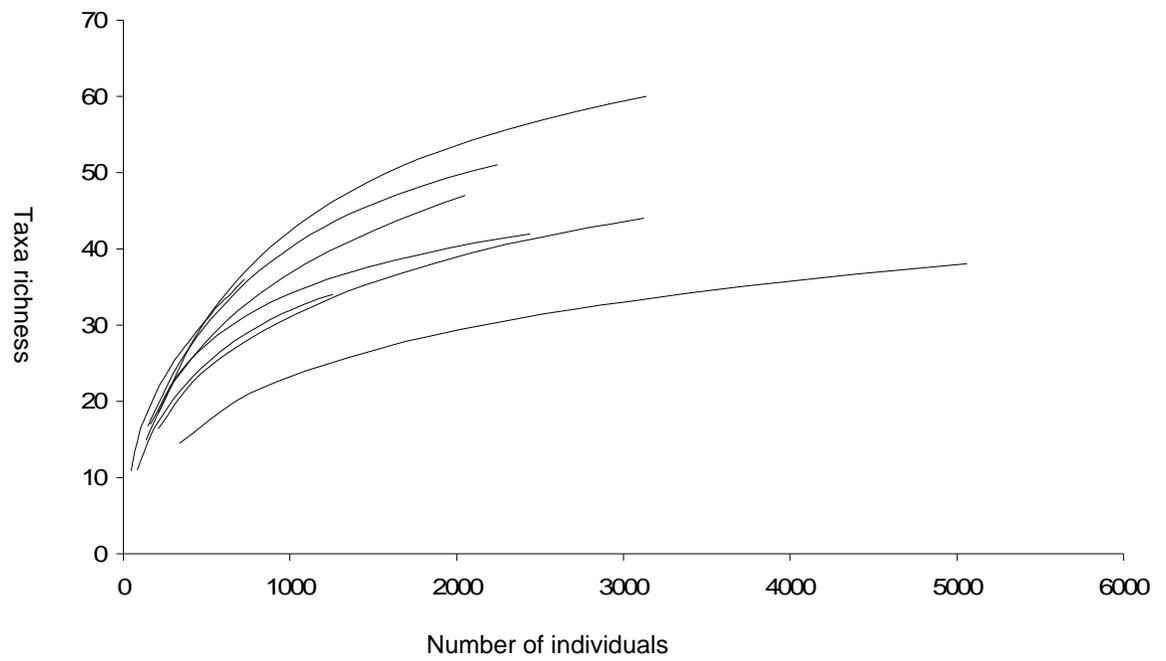
Supporting Information: Figure S1. Ordination plot of benthic (B) and debris dam (D) samples from the pilot study.



Supporting Information: Figure S2. Rarefaction curves for benthic samples (bottom) and debris dam samples (top) in the pilot study.



Supporting Information: Figure S3. Individual-based rarefaction curves for the eight study streams in 2007.



Supporting Information: Figure S4. Individual-based rarefaction curves for the eight study streams in 2008.

Declaration for Thesis Chapter 4

This thesis chapter (Clarke *et al.* in review) is in the same form as the draft manuscript that has been submitted to a peer-reviewed journal.

Declaration by the candidate

In the case of Chapter 4, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution
I performed 100% of the fieldwork, 100% of the laboratory work, 100% of the statistical analyses (with advice from Jim Thomson) and was the primary author of the manuscript.	80%

The following co-authors contributed to the work:

Name	Nature of contribution
Ralph Mac Nally	Ralph Mac Nally contributed ideas to the work and co-authored the manuscript.
Nick Bond	Nick Bond contributed ideas to the work and co-authored the manuscript.
PS Lake	PS Lake contributed ideas to the work and co-authored the manuscript.

**Candidate's
signature**

	Date
--	-------------

Declaration by co-authors

The undersigned hereby certify that:

- (1) the above declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria;
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor of publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (6) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Locations(s)

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Chapter 4 - Metacommunity structure of macroinvertebrate assemblages in headwater streams

Abstract

Empirical work seeking to discriminate among metacommunity models has focused mostly on testing the neutral model described by Hubbell's unified neutral theory of biodiversity (Hubbell 2001) and this work has generally been conducted in terrestrial ecosystems with a focus on tropical rainforest plants. Relatively few studies of metacommunity structure have been undertaken in stream systems despite the obvious potential for spatial structuring of local communities as a result of the characteristic branching shape of stream networks. Here, we investigated in successive years (2007 and 2008) how much variation in assemblage structure was related to environmental (local) factors vs. spatial (regional) factors, whether macroinvertebrate assemblages in headwater streams showed metacommunity structure matching any of the four metacommunity models, and if any of the individual environmental variables were significant in structuring assemblages. We found a limited role for environmental factors structuring macroinvertebrate assemblages in this system. In both years, a spatially structured environmental component was a major factor affecting macroinvertebrate assemblages and is likely due to the presence of a mountain range that dissects the study region. Evidence of metacommunity structure was found only in 2008, when the presence of a significant spatial variation component (independent of environmental factors) aligned with predictions for the neutral/patch dynamic metacommunity model. Given previous findings of low β diversity in these same streams, it appears that high neighbourhood dispersal is potentially the main structuring

agent affecting macroinvertebrate assemblages in this system. Future genetic or tracking studies would be valuable to directly measure levels of macroinvertebrate dispersal and provide more support for this conclusion.

Introduction

Ideas from metapopulation dynamics, coupled with the rise of landscape ecology, have greatly influenced the way that ecologists think about the mechanisms that structure local assemblages (Holyoak *et al.* 2005). Much community theory was developed on the assumption that local assemblages were closed and isolated (Leibold *et al.* 2004), with the most important structuring mechanisms those arising from *in situ* species interactions, such as competition and predation (Connell 1961), or how species respond to local environmental conditions (Hutchinson 1959; Levin 1970). Community ecologists then recognized the need to explicitly incorporate regional factors (e.g. processes having a spatial component such as dispersal) into models of community assembly (Legendre and Fortin 1989; Menge and Olson 1990; Wiens 1989). It is now clear that local communities often are linked by dispersal of potentially interacting species. These interconnected local communities are defined as ‘metacommunities’ (Gilpin and Hanski 1991; Wilson 1992). Communities are defined as the individuals of all species that potentially interact within a local area of habitat (locality) (Leibold *et al.* 2004). The relative importance of local (environmental) and regional (dispersal) processes in structuring metacommunities is a topic of much debate (Cottenie 2005), particularly tests of the validity of the neutral model of biodiversity (Hubbell 2001) and other metacommunity models (Ricklefs 2006).

Currently there are four main metacommunity models: the ‘patch-dynamic’, ‘species-sorting’, ‘mass-effects’ and ‘neutral’ models (Leibold *et al.* 2004). In the patch-dynamic and neutral models, habitats and species (respectively) are ecologically equivalent such that dispersal is the only factor maintaining community structure. In the species-sorting model, which draws on long-established theory about niche separation and coexistence, species distributions are closely linked to local ecological conditions (Leibold *et al.* 2004). Environmental conditions and dispersal jointly affect community structure because dispersal is the mechanism by which species arrive at localities with suitable environmental conditions, but, importantly, this type of metacommunity structure will not result in spatial patterns *independent* of environmental variables because its effect is confounded within the environmental processes (Cottenie 2005). In mass-effects models, local environmental conditions also are important in structuring communities, although these factors are diluted by high rates of dispersal. This results in spatial patterns occurring independently of environmental patterns (and to environmental patterns occurring independently of spatial patterns) and is therefore more correctly regarded as a species-sorting + mass-effects model (Cottenie 2005).

Empirical work seeking to discriminate among these metacommunity models has focused mostly on testing the neutral model (Hubbell 2001), and has been conducted largely in terrestrial ecosystems with a focus on tropical rainforest plants (Condit *et al.* 2002; Tuomisto *et al.* 2003; Chave 2004; Soininen *et al.* 2007). Relatively few studies of metacommunity structure have been undertaken in stream systems, despite the obvious potential for spatial structuring of communities due to the characteristic branching shape of stream networks, where patches of habitat (particularly in the headwaters of a catchment or

watershed) are separated by often inhospitable (terrestrial) terrain. One recent exception is a study explicitly investigating the influence of riverine network structure on metacommunity dynamics that found little role for spatial factors (i.e. dispersal) in structuring macroinvertebrate assemblages in headwater streams (Brown and Swan 2010). Evidence has also been found for a joint effect of environmental and spatial factors on macroinvertebrate assemblages in stream systems (Thompson and Townsend 2006).

In the system we consider here (Wallaby Creek Designated Water Supply Catchment Area, see Methods), we previously found that isolated reaches each had relatively high taxon richness and high α diversity (within-reach diversity), while β diversity (among-reach diversity) contributed little to γ diversity (regional diversity) at both the reach and catchment scales (Clarke *et al.* 2010). This was counter to the expectation that headwater streams have high β diversity (Clarke *et al.* 2008) due to limited dispersal within and among catchments (Finn *et al.* 2007; Hughes 2007) and high habitat heterogeneity among streams. Low β diversity may have arisen from high levels of dispersal reducing differences in assemblages among sites (Soininen *et al.* 2004) or may reflect similar local ecological conditions among sites.

Here, we investigated metacommunity structure of macroinvertebrate assemblages in the Wallaby Creek Designated Water Supply Catchment Area by: (1) identifying whether there was a relationship between macroinvertebrate assemblage composition and measured environmental variables; (2) determining the relative importance of regional (spatial) factors and local (environmental) factors in structuring macroinvertebrate assemblages; and (3) considering whether species-sorting (SS), mass-effects/species-sorting (ME/SS) or

neutral/patch dynamics (N/PD) metacommunity models best represented our system, based on the predictions for each model (Table 1a, adapted from Cottenie 2005).

Methods

Study area

The study was conducted in eight 1st-order streams (Fig. 1) in the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia (37°4'S, 145°2'E). This 9965 ha catchment is located at the southern end of the Hume Plateau atop the Great Dividing Range (Ashton 2000). Mean annual rainfall in the catchment area was 1207 mm from 1995-2006 (Martin *et al.* 2007) and elevation ranges from 600–800 m A.S.L. The vegetation was dominated by ecologically mature, eucalypt forest (Ashton 2000). The area is closed to the public to provide protection of water quality and water yield (Parks Victoria 1998). At the time of this study, the area was largely undisturbed, but there were historic legacies (mostly occurring in the mid- to late-1800s) including fire, aqueduct construction, logging, some human settlement and bullock grazing (Ashton 2000). About 98% of the catchment was severely burnt in the catastrophic February 2009 bushfires (Cai *et al.* 2009).

Study design

Of the four small catchments in the study area, only three were included in the study because the streams in the other were dry during all initial site visits. Three reaches were randomly selected in each of the three catchments, followed by a site inspection to check that the reach was accessible and contained enough water to be sampled. Of the nine study streams, one reach in the Disappointment Creek catchment did not contain enough connected surface water to be sampled in either 2007 or 2008, and so was excluded. Suitable replacement reaches in the Disappointment Creek catchment could not be found.

Vegetation in the study area is dominated by various species of the genus *Eucalyptus* and this has considerable influence on instream habitat. Unlike many deciduous northern hemisphere species, eucalypts are evergreen but still produce relatively continuous leaf fall throughout the year and have much slower rates of leaf breakdown (Poza *et al.* 1997). Therefore, features such as leaf packs and debris dams are common habitats in temperate Australian streams (Boulton 1991; Gooderham *et al.*, 2007). This is especially true in small headwater streams where low discharge means streams are often unable to move material that has fallen onto the bed and banks (Gooderham *et al.* 2007). Initial field observations revealed two dominant habitat types: sandy benthic areas and debris dams. We used the definition of debris dams proposed by Smock *et al.* (1989) as “any wood > 5 cm in diameter in contact with sediment and spanning at least one-fourth of the channel. Also included were root masses from living riparian vegetation.” We required a total of 15 samples in each reach based on the proportion of the two habitat types present (for description of pilot study see Clarke *et al.* 2010).

Macroinvertebrate sampling

Macroinvertebrate sampling was conducted in the austral springs (October) of 2007 and 2008. Prior to sampling, 30 m study reaches were measured for proportions of benthic habitat and debris dam habitat by recording the total length of each habitat type over the 30 m reach to the nearest cm. These were converted into proportions. We then determined the allocation of samples for benthic and debris dam habitats (total $N = 15$) based on these proportions.

Debris dams for sampling were chosen using random numbers. Macroinvertebrate samples were collected by obtaining one, similarly sized handful of organic material from

the centre of each dam and transferring the material to a ziplock plastic bag (Poff *et al.* 1993). In 2008, we also recorded the total volume of the selected debris dams to investigate whether taxon richness in samples was related to the total size of the debris dam from which samples were taken, but there was no relationship ($R^2 < 0.01$).

The positions of benthic samples were determined by splitting the reach into 30 1-m sections with a measuring tape and then selecting the appropriate number of sections using random numbers. For each number drawn, the benthic sample was taken from the closest available sandy benthic habitat to the position on the measuring tape matching the number. Macroinvertebrate samples were collected from the sandy stream bed using a current-independent pump sampler (Boulton 1985). A 10 x 10 cm patch of benthic habitat was isolated within a square frame and the benthos disturbed to a depth of 5 cm while a manual diaphragm pump was operated for 1 min.

All samples were preserved in 70% ethanol and returned to the laboratory for identification. Samples were washed over a 300 μm sieve and all macroinvertebrates were counted and identified to the lowest possible taxonomic resolution (usually genus). Diptera generally were identified to family, except Chironomidae, individuals of which were identified to sub-family. Oligochaeta and Nematoda were not identified further.

Local environmental variables

A range of reach-scale environmental variables was measured at each site prior to macroinvertebrate sampling. Environmental variables were chosen by conducting a literature search on determinants of macroinvertebrate diversity in small streams and compiling a list of those with some evidence of an association with macroinvertebrate diversity or assemblage composition (papers included; Angradi 1996; Heino *et al.* 2002;

Heino *et al.* 2003b; Arscott *et al.* 2005; Heino 2005; Herlihy *et al.* 2005; Megan *et al.* 2007). From this list, we chose 12 variables that we considered relevant to temperate, southern-hemisphere headwater streams. We measured mean water temperature, dissolved oxygen, pH and conductivity with a Horiba (U-10, Fukuoka, Japan) by taking measurements at three randomly selected locations in each reach. For each reach, we recorded the number of debris dams and their total and mean volume by measuring the length, width and height of each to the nearest cm. Three cross-sectional transects were randomly located in each reach to determine mean discharge, mean wetted width and mean depth. Riparian vegetation type was determined by identifying the Ecological Vegetation Class from an online interactive GIS program maintained by the State Government. Ecological Vegetation Classes (EVCs) are an ecosystem-based classification scheme used is one component of biodiversity management in Victoria (Mac Nally *et al.* 2002). An EVC consists of one or several floristic communities that appear to be associated with a recognizable environmental niche. Aspect was determined from a contour map. Data for all environmental variables are outlined in Table S1, Supporting Information.

Data analysis

Heino (2004) suggested that, in assemblage-level analysis, sample-to-sample variability probably represents stochastic sampling effects rather than true or ecologically meaningful variation in assemblage composition. Therefore, after macroinvertebrate identification and full enumeration of each sample, a single taxonomic list with pooled abundance data was compiled for each of the eight study streams for 2007 and 2008. All analyses here were performed on the pooled reach data.

Relative importance of the 12 environmental variables

Differences in assemblage composition were examined by inspection of ordination plots using non-metric multidimensional scaling (NMDS). Ordination plots were generated from Bray-Curtis dissimilarities for abundance data using the 'MASS' package (Venables & Ripley 2002) for R (R Development Core Team 2008). The ordination solution was generated from 100 random starts and in two dimensions. We used stress to measure the goodness-of-fit (where higher stress equals lower goodness-of-fit). Relationships between NMDS axes and individual environmental variables were examined by fitting vectors to these ordination plots using the 'envfit' function of the vegan package (Oksanen *et al.* 2007) for R (R Development Core Team 2008). Fitted vectors are shown as arrows that point to the direction of the most rapid change in the environmental variable (i.e. steepest gradient) and their lengths are proportional to the correlation between the ordination and the variable. Correlation coefficients and *P*-values are also given (from permutations).

Relative importance of regional (spatial) processes and local (environmental) processes

We were interested in the relationships between three sets of variables: community composition, environmental factors and spatial factors. Determining the independent effects of environmental and spatial factors on community assemblages is difficult because environmental variables often are spatially autocorrelated. That is, two ecological variables may appear to be correlated just because they are both linked to a third, common variable such as spatial location (Reynolds and Houle 2002).

While Mantel and partial Mantel tests are useful for identifying correlations between data sets (e.g. community, environmental, spatial), they cannot tell us the fraction of the variation in a community matrix explained by either the environmental variables or

We used the function ‘rda’ in the vegan package (Oksanen *et al.* 2007) for R (R Development Core Team 2008) for partial redundancy analyses. Input data are community composition, environmental variables relevant for structuring that particular community, and spatial configuration (xy coordinates) of the sampled sites. Cottentie (2005) noted the importance of limiting spatial and environmental variables to the most parsimonious subset of significant variables to reduce overfitting and multicollinearity. We used the output of the environmental vector fitting from the first analysis to identify the three variables with the highest correlation to community composition in each year and used these as the environmental data input. Spatial data consisted of only two variables (geographic coordinates of the sites) and describe simple linear spatial patterns in the data. We did not fit a higher-order terms model, but these can be a useful way of detecting more complicated

spatial features, such as patches and gaps (Mykrä *et al.* 2007). We considered distance between sites as a surrogate for detecting the influence of dispersal as a regional factor structuring assemblages because only genetic or mark-recapture/tracking studies can detect actual dispersal. Thus, distance is thought to indicate the relative difficulty of dispersal among sites.

Relative contributions of the variance components were calculated and displayed graphically following the method of Borcard *et al.* (1992). Corresponding *P*-values were determined for each component with an ‘ANOVA-like’ permutation test using the function ‘anova.rda’ in the vegan package (Oksanen *et al.*, 2007) for R (R Development Core Team 2008). The significance structure of the variance components was compared to the predictions of significance structure for each of the four metacommunity types (Cottenie 2005) in each year to determine if there was evidence of metacommunity structure matching any of the four metacommunity models. Given that this approach is correlative, using variance components and their *P*-values as estimates for the observational evidence that particular factors (environmental vs spatial) are important in structuring assemblages, we did not adjust the *P* -values for multiple testing (Cottenie 2005; Quinn and Keough 2002).

Results

Some 45,523 individuals from 92 taxa were collected in the eight headwater streams during the two sampling periods. Of the 92 taxa sampled, 70.6% were identified to genus. The fauna was dominated by taxa belonging to the order Diptera (32%) and to the sensitive

Ephemeroptera, Plecoptera and Trichoptera (EPT) orders (28%). The most abundant taxon was Oligochaeta, with 14,001 individuals collected over the two years.

Assemblage composition in 2007 showed sites were significantly grouped according to the catchment to which they belonged (ANOSIM, $R = 0.687$, $P = 0.007$, Fig. 2a). However, there was no significant grouping of sites by catchment in 2008 ($R = 0.252$, $P = 0.108$, Fig. 2b) because four sites from the Silver and Wallaby Creek catchments had an almost identical assemblage composition and, therefore, were positioned together in the centre of the ordination plot. An ordination based on presence/absence data for the same year did not exhibit this same clumping of sites (not shown here). Therefore, the high degree of assemblage similarity between the four sites in 2008 is due primarily to changes in abundance rather than diversity (i.e. taxa present).

Relative importance of 12 environmental variables

Environmental vectors (shown as arrows) were fitted to the ordination plots for 2007 (Fig. 2a) and 2008 (Fig. 2b). Only two variables were significantly correlated with macroinvertebrate assemblage structure in 2007: aspect ($R^2 = 0.925$, permutation $P = 0.001$) and mean water temperature ($R^2 = 0.730$, $P = 0.039$). In 2008, aspect was the environmental variable most significantly correlated with assemblage structure ($R^2 = 0.910$, $P = 0.001$) as was mean dissolved oxygen ($R^2 = 0.773$, $P = 0.024$) and number of debris dams ($R^2 = 0.750$, $P = 0.029$). As indicated above, the three environmental variables most highly correlated to assemblage composition in each year were used in the environmental data matrices for the partial redundancy analysis. In 2007, the three variables were aspect, mean water temperature and number of debris dams. In 2008, the variables were aspect, mean dissolved oxygen and number of debris dams.

Relative importance of regional (spatial) processes and local (environmental) processes

In 2007, 95% of the total variation in community data was explained by the combination of environmental and spatial factors, with 23% explained by pure environmental factors, 18% by pure spatial factors and 54% by spatially structured environmental factors (Fig. 3a). In 2008, spatial autocorrelation was reduced and pure spatial factors played a more important role in structuring macroinvertebrate assemblages. In 2008, 96% of the total variation in community structure was explained by environmental and spatial factors together, 20% by pure environmental factors, 43% by pure spatial factors and 33% by spatially structured environmental factors (Fig. 3b).

Comparison of the significance structure of variance components (Table 1b) with the predictions for the four metacommunity models (Table 1a) revealed no evidence to support any of the four metacommunity types in 2007, with the significance structure most closely aligned with the predictions for ‘undetermined’ metacommunity type. In 2008, there was some evidence to support the neutral model/patch dynamics metacommunity model because the variance component attributed to spatial factors independent of environmental factors was significant (Table 1b, $P < 0.05$).

Discussion

We sought to discern the relative importance of environmental (local) and spatial (regional) factors in structuring macroinvertebrate assemblages, and search for evidence of metacommunity structure matching any of the four metacommunity models currently debated in the ecological literature. We found that environmental variables alone (i.e. independent of spatial factors) played a limited role in structuring macroinvertebrate

assemblages in this system. Evidence of metacommunity structure was found only in 2008, where the presence of a significant spatial variation component (independent of environmental factors) aligned with predictions for the neutral/patch dynamic metacommunity model.

Relative importance of the 12 measured environmental variables

Relationships between local environmental conditions and macroinvertebrate assemblages have long been studied (Faith and Norris 1989; Minshall 1984; Richards *et al.* 1993; Malmqvist and Maki 1994), with investigations specifically exploring headwater streams being relatively more recent. A wide range of local environmental factors appear to be important for explaining variation in macroinvertebrate assemblage structure in headwater streams (Heino *et al.* 2002; Cole *et al.* 2003; Arscott *et al.* 2005; Stendera and Johnson 2005; Johnson *et al.* 2007; Brown and Swan 2010). In our study, aspect was significantly correlated with macroinvertebrate assemblages in both 2007 and 2008, separating the two south-facing sites from the six north-facing sites. The influence of aspect on macroinvertebrate assemblages is probably related to the dissimilar micro-climates of the north-facing and south-facing slopes. The south-facing slopes are sheltered and intercept frontal cloud systems, which condense and result in considerable fog drip, supporting wet gullies and growth of the Cool Temperate Rainforest EVC in the riparian areas of the Disappointment Creek catchment (Ashton 2000). However, the north-facing slopes generally are drier because they are subjected to the hot, sometimes ferocious, northerly winds that occur in Victoria each summer.

Mean water temperature also was correlated with macroinvertebrate assemblage structure in 2007. However, none of the other environmental variables showed any

relationship with macroinvertebrate assemblages. In 2008, nine of the 12 environmental variables showed no relationship with macroinvertebrate assemblages. This was an unexpected result given the many studies that have noted significant relationships between environmental variables and macroinvertebrate assemblages in headwater streams. It is possible that there are environmental variables strongly related to macroinvertebrate assemblages in our system that we did not measure, particularly since our list of variables was generated from studies that were conducted in countries other than Australia and generally in the northern hemisphere. Most environmental variables are context-specific and scale-dependent and few factors are likely to be universally important correlates of macroinvertebrate assemblage composition (Marchant *et al.* 1999; Mykrä *et al.* 2007). Our ability to detect significant relationships between macroinvertebrate assemblages and local environmental variables may have been diminished by the level of taxonomic identification used for the diverse Chironomidae family, for which individuals were identified only to sub-family. The chironomids are a highly heterogeneous group of species with differing responses to environmental gradients (Heino *et al.* 2003a) and, by lumping several, potentially different, species together at the sub-family level, this could dampen the influence of environmental variables on assemblage structure.

These potential issues aside, our finding that few reach-scale environmental variables were significantly related to assemblage composition appears to confirm the results of the partial redundancy analysis that indicted a limited role for local environmental factors in structuring macroinvertebrate assemblages. Little relationship between headwater stream assemblages and environmental variables at larger spatial scales (i.e landscape-catchment scale variables) have been reported (Hawkins *et al.* 2000; Sandin & Johnson

2000; Heino *et al.* 2008), indicating the possibility that other mechanisms, such as dispersal, might play a significant role in structuring assemblages.

Relative importance of regional (spatial) processes and local (environmental) processes

The relative importance of regional and local factors in determining assemblage structure has attracted much interest across a wide range of ecological systems (Menge & Olson 1990; Ricklefs and Schluter 1993; Heino *et al.* 2003b), particularly in the context of conducting empirical tests of the neutral model (Condit *et al.* 2002; Tuomisto *et al.* 2003; Thompson and Townsend 2006). In our system, we found a very limited role for structuring of macroinvertebrate assemblages by pure environmental effects (i.e. independent of spatial effects). This is contrary to findings of similar studies in headwater streams that found pure environmental effects were more important in structuring macroinvertebrate assemblages than spatial factors, generally lending support to the species-sorting metacommunity model (Mykrä *et al.* 2007; Brown and Swan 2010). The relative importance of environmental factors can differ with spatial scale (Wiens 1989), and the independent influence of environmental factors is more important at greater spatial scales for Amazonian forest species when more diverse habitats are considered (Tuomisto *et al.* 2003). Given the comparatively small spatial scale of our study region, it is possible that environmental conditions did not vary widely enough to play a significant role in structuring assemblages. However, Mykrä (2007) studied the proportion of variation explained by pure effects of environmental variables at three different spatial scales in headwater streams in Finland and found that the portion of variation explained by pure environmental effects increased with decreasing geographical extent.

While aspect is an environmental variable, it is confounded by inherent spatial structuring. In our study area, the effect of sheltered, moist slopes vs more exposed, drier slopes is dependent on the spatial location of the sites in relation to the Great Dividing Range. This may explain the high percentage of variation in community composition, in both years, that was explained by the spatially structured environmental component. The effect of aspect (as an environmental variable) on macroinvertebrate assemblages also is confounded with dispersal because aspect in this system is determined by the presence of the cross-cutting Great Dividing Range. Intervening steep topography may limit among-drainage dispersal (Hughes *et al.* 1999; Monaghan *et al.* 2002). Other studies have found spatial structuring of environmental variables, such as water chemistry (conductivity, pH, iron content) at small scales, even within drainage systems (Mykrä *et al.* 2007).

Evidence of metacommunity structure was found only in 2008, where the presence of a significant spatial variation component (independent of environmental factors) aligned with predictions for the neutral/patch dynamic metacommunity model. This indicates that some type of spatial dynamics was a significant factor structuring macroinvertebrate assemblages in 2008. Mykrä *et al.* (2007) also found relatively strong spatial structure of macroinvertebrate assemblages in headwater streams, unrelated to local environmental conditions, even at the smallest spatial scale studied (within drainage systems). High levels of spatial autocorrelation in 2007 meant that a significant component of variation could not be attributed to either environmental or spatial factors independently of the other, so there was no evidence supporting any of the four proposed metacommunity models in that year.

Debates around the neutral model focus on dispersal limitation as the major spatial dynamic structuring assemblages, but dispersal can also be a structuring force whereby a

constant flux of individuals move between closely connected sites and generate more similar assemblages among these localities than at sites that are further apart (Cottenie *et al.* 2003). Therefore, both dispersal limitation and neighbourhood dispersal processes may cause spatial structure in assemblages (Mykrä *et al.* 2007). Increased dispersal reduces β diversity among habitat patches (Shurin *et al.* 2009), which we have reported for the Wallaby Creek Designated Water Supply Catchment Area (Clarke *et al.* 2010). This pattern is consistent with the structuring mechanism of high levels of neighbourhood dispersal outlined above. Many studies have suggested or shown that the exchange of individuals among localities in headwater streams generally is low (Griffith *et al.* 1998; Finn *et al.* 2007; Hughes 2007; Brown and Swan 2010). However, where assemblages are dominated by stream insects with aerial dispersal by adults, many individuals may have a high dispersal potential and should be able to reach any location in a drainage system with appropriate environmental conditions (Mykrä *et al.* 2007). In our study, macroinvertebrates (mostly insects with an aerial dispersal stage) were sampled over a relatively small (< 10, 000 ha) and contiguous patch of largely undisturbed forest. Collectively, these factors are all likely to promote high dispersal among sites. A similar conclusion was drawn by Cottenie *et al.* (2003) who studied zooplankton assemblages in highly connected ponds and suggested that dispersal limitation probably was unimportant due to the small geographic area of the study and the continuous dispersal of individuals through connecting elements. Future studies directly measuring dispersal in the field or genetic studies of differentiation among our study sites would be a valuable tool for evaluating the conclusion that high levels of neighbourhood dispersal are the dominant force structuring macroinvertebrate assemblages in this system. Increasing the spatial scope of the study area

and re-assessing the relative importance of environmental and spatial factors would provide additional information about the scale-dependence of the relationships that have been observed in this study. However, this is not possible now (at least for decades) due to the devastating fires of February 2009 (Cai *et al.* 2009). Increases in the spatial scale of a study region generally lead to a more diverse selection of habitats being covered and higher potential for dispersal limitation to occur (Cottenie 2005).

Future testing of the validity of the four metacommunity models should move towards developing a synthetic perspective on metacommunities, because it is unlikely that all interacting species in real metacommunities, or in all metacommunities across different taxonomic groups, will uniformly fit into just one of the four models (Leibold *et al.* 2004). Recent meta-analyses searching for evidence of a dominant type of metacommunity structure found an overriding pattern of dual control of assemblage structure by both niche-based processes and by neutrality (Soininen *et al.* 2007), but also for dominant control of assemblage structure by species-sorting dynamics (Cottenie 2005). Ecologists and landscape geneticists need to combine their skills on questions of metacommunity structure in ecological systems. Direct quantification of the influence of dispersal may be the key to developing a comprehensive understanding of the dynamics that control local assemblages.

Acknowledgements

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Table 1a. Predicted relationships between significance structure (S = significant, NS= not significant; $\alpha = 0.05$) of the important variation components for each of the metacommunity paradigms (adapted from Cottenie (2005)). None of the four models specifically predicts a significant relationship between assemblage structure and either pure environmental or spatial data so they are not shown here.

Metacommunity type	Environment effect independent of spatial (E/S)	Spatial effect independent of environment (S/E)
Neutral/patch dynamic	NS	S
Species sorting	S	NS
Species sorting + mass effects	S	S
Undetermined	NS	NS

Table 1b. Significance structure of the important variation components for the study streams in 2007 and 2008, $\alpha= 0.05$

	Environment effect independent of spatial (E/S)	Spatial effect independent of environment (S/E)
2007 (undetermined)	0.12	0.17
2008 (neutral/patch dynamic)	0.18	< 0.05* (0.0496*)

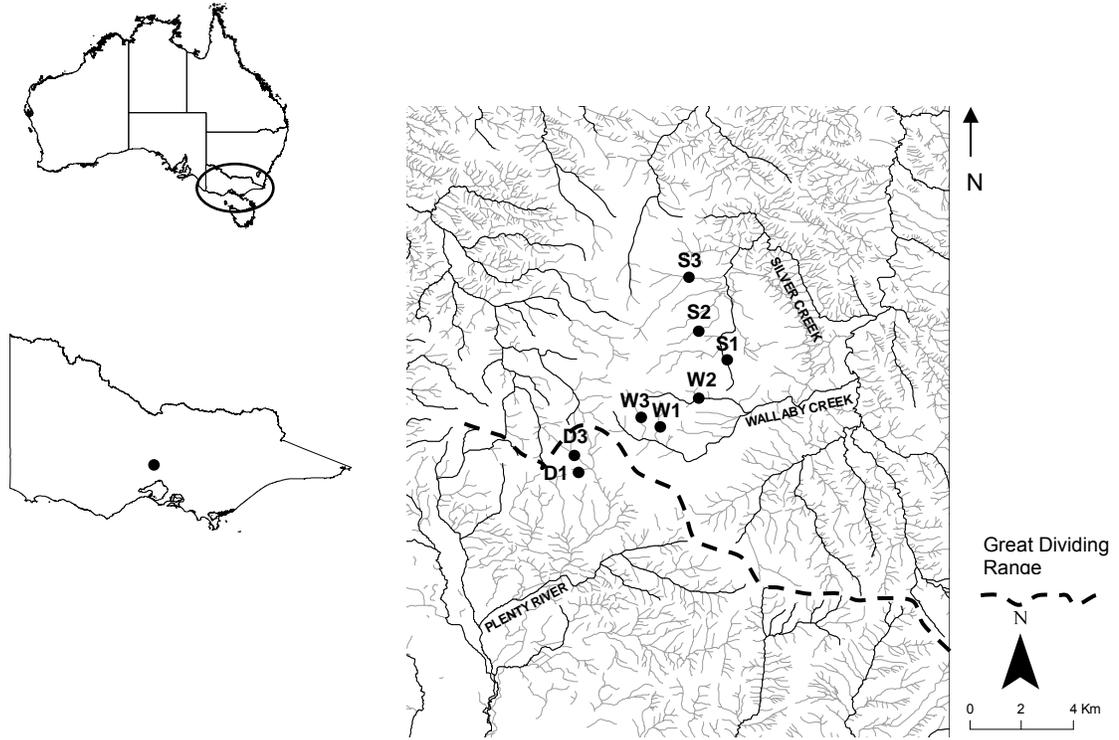


Figure 1 – Location of study sites within the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia. Disappointment Creek catchment (D), Wallaby Creek catchment (W), Silver Creek catchment (S).

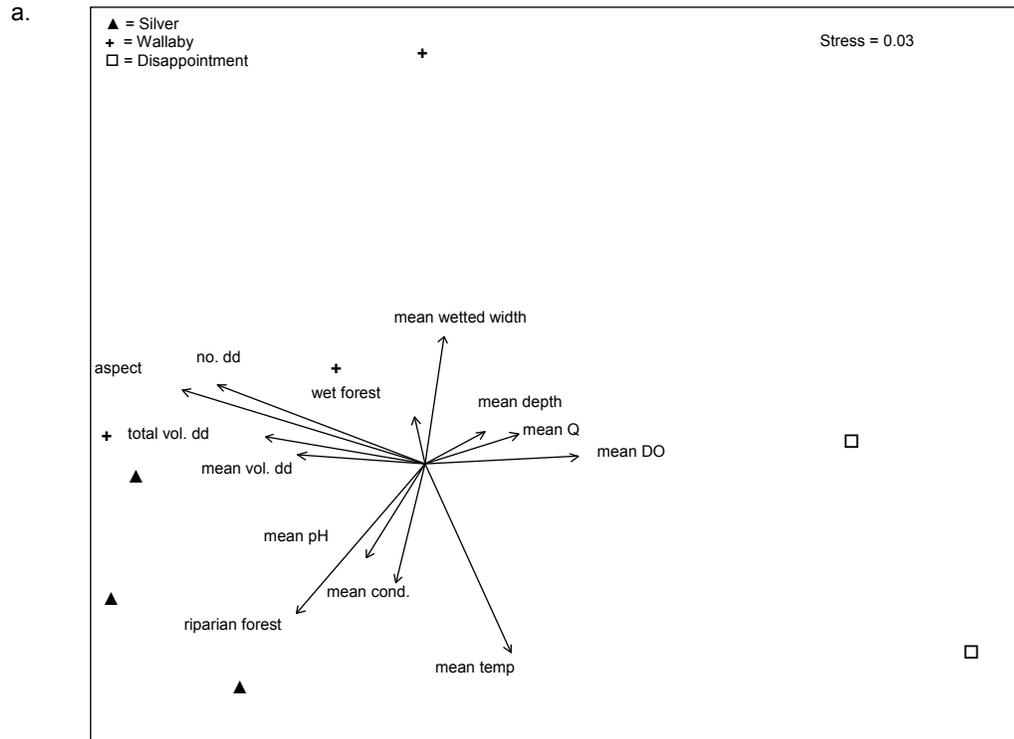


Figure 2a – NMDS of the eight study sites with environmental vectors overlaid for 2007.

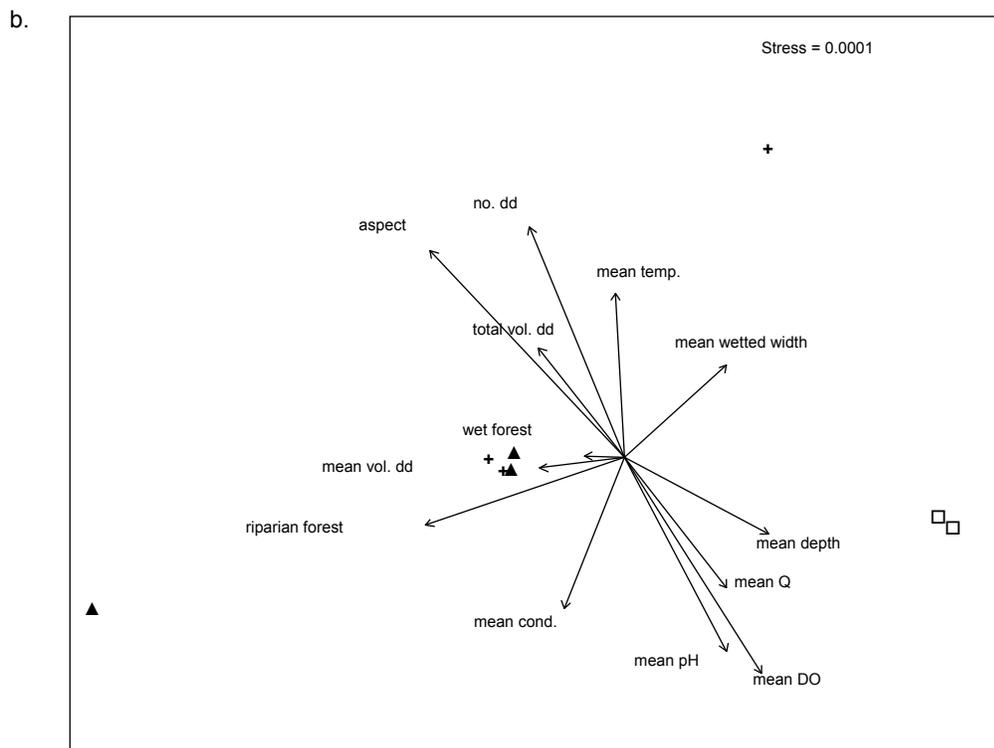


Figure 2b – NMDS of the eight study sites with environmental vectors overlaid for 2008.

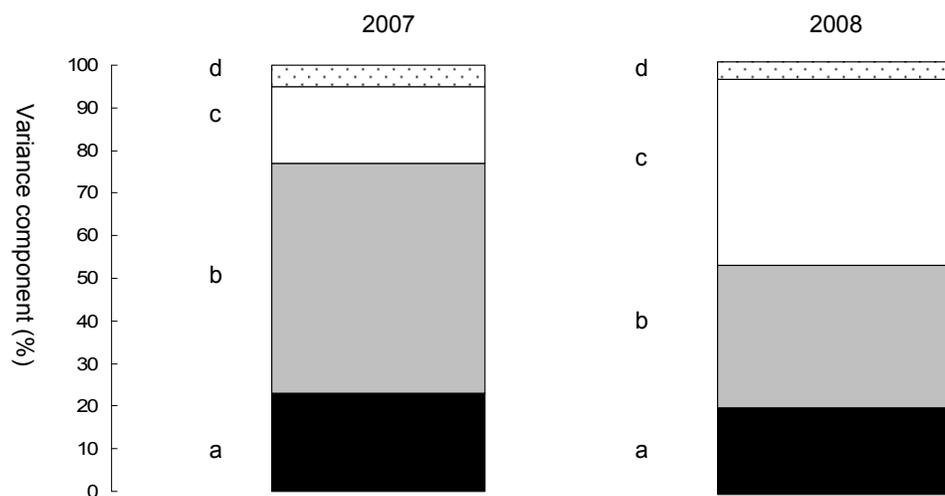


Figure 3 - Components of variation of the macroinvertebrate community data matrix in 2007 and 2008 where a = pure environmental component, b = spatially structured environmental component, c = pure spatial component and d = unexplained variation.

Supporting Information: Table S1 - List of environmental variables measured for the eight sites in a) 2007 and b) 2008.

a.

Variables	Sites							
	W1	W2	W3	S1	S2	S3	D1	D3
No. debris dams per reach	20	18	17	21	14	17	4	5
Total volume of debris dams per reach (m ³)	16 660	5 670	40 100	3 901	7 515	37 387	2 975	1 454
Mean volume of debris dams per reach (m ³)	833	315	2 358	185	536	2 199	743	290
Mean pH	6.1	6.3	6.0	6.5	7.2	6.5	6.3	6.3
Mean DO (ppm)	8.4	10.3	9.8	10.1	8.5	3.1	10.6	11.5
Mean conductivity (µm)	59.1	48.1	54.9	70.1	77.0	106.2	72.7	70.3
Mean temperature (°C)	9.5	10.0	10.1	10.6	10.8	10.9	11.4	11.2
Mean water depth (cm)	3.7	5.1	6.3	2.8	1.8	2.3	2.7	5.8
Mean wetted width (cm)	102.5	65.0	92.5	67.5	97.5	27.5	70.0	77.5
Mean discharge (cm ³ /s)	13.6	21.4	27.0	9.4	6.4	1.2	9.6	28.1
Ecological vegetation class	Cool temperate rainforest	Wet forest	Cool temperate rainforest	Riparian forest	Riparian forest	Riparian forest	Cool temperate rainforest	Cool temperate rainforest
Aspect	North-facing	North-facing	North-facing	North-facing	North-facing	North-facing	South-facing	South-facing

b.

Variables	Sites							
	W1	W2	W3	S1	S2	S3	D1	D3
No. debris dams per reach	16	12	15	9	13	10	8	5
Total volume of debris dams per reach (m ³)	42 522	1 069	68 652	5 931	19 171	44 816	6 792	17 405
Mean volume of debris dams per reach (m ³)	2 657	89	4 576	659	1 474	4 481	849	3 481
Mean pH	5.6	5.7	5.5	6.0	6.4	6.1	6.5	6.6
Mean DO (ppm)	7.8	11.6	10.8	11.5	10.8	8.4	12.8	12.9
Mean conductivity (µm)	57.8	51.6	51.3	59.3	72.4	92.6	69.3	65.9
Mean temperature (°C)	8.3	6.9	8.1	7.6	7.2	7.5	7.3	7.6
Mean water depth (cm)	5.0	6.4	7.4	4.9	6.2	3.6	6.5	6.3
Mean wetted width (cm)	80.0	48.3	100.0	91.7	95.0	40.0	73.3	85.0
Mean discharge (cm ³ /s)	11.2	30.5	58.8	40.3	35.8	5.3	31.8	58.2
Ecological vegetation class	Cool temperate rainforest	Wet forest	Cool temperate rainforest	Riparian forest	Riparian forest	Riparian forest	Cool temperate rainforest	Cool temperate rainforest
Aspect	North-facing	North-facing	North-facing	North-facing	North-facing	North-facing	South-facing	South-facing

Declaration for Thesis Chapter 5

This thesis chapter (Clarke *in review*) is in the same form as the draft manuscript that has been submitted to the peer-reviewed *Journal of the North American Benthological Society*.

Declaration by the candidate

In the case of Chapter 5, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution
I was the sole author of the manuscript.	100%

Candidate's
signature

	Date
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Chapter 5 - River basins as complex networks: extending the ‘rivers as networks’ paradigm in stream ecology

Abstract

In decades past, little research in stream ecology considered the influence that the underlying structure of river networks might have on the functioning of whole river basins. More recently, stream ecologists have embraced the emergent paradigm of ‘rivers as networks’ and research that explicitly considers the influence of the structural architecture of whole river basins is proliferating. However, much of this work is undertaken without consideration of the vast literature on networks that already exists in the fields of physics, mathematics and network theory. Here, I discuss three examples of how recent advances in network theory might be applied to research areas in stream ecology and illustrate that irrespective of the local properties of river basins, their large-scale behaviour may be best understood by considering some universal principles that govern complex networks and how these might apply to river basins.

Introduction

Many of the major advances in stream ecology over the last few decades were driven by 'local and linear' studies of stream ecosystems that identified the important components of streams and how they function. While such studies proved invaluable for elucidating the mechanics of processes such as nutrient spiraling (Newbold *et al.* 1982) and organic matter processing (Fisher and Likens 1973; Bilby and Likens 1980), this reductionist approach to stream ecology was not well-suited to a deeper understanding of the collective functioning of whole river basins. Additionally, there is much inertia surrounding the development of general theories in stream ecology which may be a legacy effect of past research overlooking collective system behavior in favor of more detailed understanding of processes and interactions at local scales.

Fisher (1997) encouraged stream ecologists to make a more deliberate effort to generate new, creative ideas about streams with the hope of enhancing contributions to general ecological theory. Since then, the emergent paradigm of conceptualizing rivers as networks (rather than as isolated, linear reaches) is arguably one of the most significant advances in generating new approaches to research in stream ecology. The idea of viewing rivers as networks has become increasingly popular over the last decade (Fagan 2002; Benda *et al.* 2004; Lowe and Likens 2005; Grant *et al.* 2007; Hitt and Angermeier 2008; Chaput-Bardy *et al.* 2009; Brown and Swan 2010). However, the application of the network concept in stream ecology has focused largely on incorporating the spatial configuration of study sites into analyses of pattern and process. Although the explicit recognition of stream ecosystems as spatially structured networks has undoubtedly increased our understanding of ecological patterns and processes (Grant *et al.* 2009), recent advances in the study of networks, particularly in the fields of physics and network theory,

offer a multitude of findings on the universal properties of different network topologies that could considerably extend the current application of the network concept in stream ecology.

This paper explores how some universal properties of complex networks (unearthed in the fields of physics and network theory) could be used to further extend the current ‘rivers as networks’ paradigm in stream ecology. First, I outline some general definitions of networks and explain how river basins can be considered as a special class of complex networks called scale-free networks. I then draw on a selection of existing knowledge and recent advances in the study of networks from seemingly unrelated areas such as epidemic spreading, error tolerance and attack vulnerability and percolation theory to illustrate that irrespective of the local properties of river basins, their large-scale behaviour may be best understood by considering the universal principles that govern complex networks and how these might influence the system dynamics of processes occurring in river basins. The explosive rate of advance in the study of complex networks crosses many disciplines and offers exciting possibilities for stream ecology to further extend the current ‘rivers as networks’ paradigm.

Tangled webs: defining and classifying networks

The link between observed patterns in the formation of river systems and the organizing principles governing their structure has recently begun to be explained in a holistic way combining insights from mathematics, physics and network theory. The characteristic branching structure of river basins exhibits a pattern which is **fractal** and can be described mathematically using a **power law** (see Glossary, Table 1). This simple mathematical expression of underlying pattern in the structure of river systems is echoed in the structure of many real-life networks including the World Wide Web, the Internet, cellular networks

and the citation patterns of scientific publications (Albert and Barabasi 2002). Many real-world networks (including river basins) belong to a special class of networks termed scale-free networks, but to understand why requires some definitions and an understanding of how networks are differentiated into classes based on their structural properties, or topologies.

Networks

Networks play a central role in our understanding of a diverse range of systems from seemingly disparate disciplines such as biology, information technology, economics and physics (Caldarelli *et al.* 2004a). Not surprisingly, there is no single definition of what constitutes a network but rather iterations based around the two central components that make up networks: nodes (vertices) and edges (links). Amaral and Ottino (2004) defined a network as '*a system of nodes with connecting links*' and Fisher *et al.* (2004) described a network as an '*arrangement of interwoven or connected linear structures*'. The most simple types of networks are lattice networks – every node connected with a well-defined set of closest neighbors, and random networks – every node with the same probability of being connected to other nodes (Amaral and Ottino 2004). Ecological systems can also be defined as networks where '*the vertices are the elements of the systems and the edges represent the interactions between them*' (Latora and Marchiori 2001) but these real-life networks are not well-described by the simple network models outlined above (Amaral and Ottino 2004).

Complex networks

Caldarelli *et al.* (2004a) described complex networks as '*made by many components whose microscopic interactions give rise to global structures and dynamical evolutions often characterized by emergent collective behaviors and complex topological properties*'. Thus,

complex networks may have one or more distinctive properties not found in simple networks such as a high clustering coefficient, degree distributions which decay as power laws, scale invariance or a hierarchical structure (Strogatz 2001; Albert and Barabasi 2002; Newman 2003; Ravasz and Barabasi 2003). Most importantly, these features cannot be explained by simply extrapolating the local properties of individual nodes (Caldarelli *et al.* 2004b).

Scale-free networks

In many real complex networks, nodes differ in the number of edges (or links) they possess (i.e. their **degree**) (see Glossary, Table 1). This effect can be characterized by a distribution function $P(k)$, which gives the probability that a randomly selected node has k links (Ravasz and Barabasi 2003). A crucial development in the understanding of complex networks was the discovery that for a large number of real complex networks the degree distribution decays as a power law (Albert and Barabasi 2002), free of characteristic scale (Albert *et al.* 2000). Networks with this type of degree distribution are referred to as ‘scale-free’ or **scale invariant** (see Glossary, Table 1) due to the lack of an intrinsic scale in some of the properties of these networks (Petermann and De Los Rios 2004a). River basins have been shown to fit into this classification (Rodriguez-Iturbe and Rinaldo 1997).

Given the definitions above, it is clear that river systems can be broadly defined as networks since they are made up of nodes (confluences) and edges (stream segments).

River systems can also be considered complex networks as they comprise many components whose interactions give rise to global structures and emergent properties that are not necessarily evident at local scales (e.g. the hierarchical structure of river systems and their fractal properties). Finally, rivers fit the definition of scale-free networks as their degree distribution has been shown to decay as a power law (Maritan *et al.* 1996,

Rodriguez-Iturbe and Rinaldo 1997). The structure of river basins is also characterised by many other power-law relationships (e.g. power law structure of elevations, aggregated areas and power expenditure in river networks), reflecting the scaling invariance of the processes involved (Rodriguez-Iturbe and Rinaldo 1997).

River basins as complex networks

The structure and dynamics of complex networks have been widely studied in recent years (Grabowski and Kosinski 2004). It is now appreciated that these systems follow universal laws independent of the local details of the system (Amaral and Ottino 2004) and that the topology and evolution of real networks are governed by strict organizing principles (Ravasz and Barabasi 2003). A consequence of these findings is that advances made in one discipline or one type of system are transferable to many other disciplines or systems (Amaral and Ottino 2004) and greatly enhance our understanding of the behavior of structurally similar objects (e.g. different types of complex networks).

The many advances that have been made in the fields of complexity science and network theory share an important common theme; movement away from the traditional reductionist approach towards an understanding of the interconnectedness of elements in a system and the importance of their collective behaviors over their local interactions. Many problems in science and biology are now being redressed from a complexity perspective (Proctor and Larson 2005) and there is an increasingly voiced need to understand the behavior of systems as whole entities, rather than as individual components (Albert and Barabasi 2002). One area of stream ecology that is already well progressed in using advances from network theory to further their own field of knowledge is the study of

ecological food webs (Solé and Montoya 2001; Dunne *et al.* 2002; Power and Dieterich 2002).

The following section provides three examples of how some general findings about the behavior and organising principles of complex networks might be applied to current research issues in stream ecology including; managing the spread of invasive species, predicting the robustness of river networks to disturbance and using concepts from network theory to guide large-scale conservation planning. These examples aim to provide general stimulus for stream ecologists to take advantage of established knowledge from other fields to further extend the current application of the network concept in their research.

Predicting and managing epidemic spreading in river networks

The spreading of infectious agents (e.g. ideas, fads, technologies, animals and diseases) is a phenomenon currently driving much cross-disciplinary research, as spreading processes share several properties which make them amenable to generalized analysis (Amaral and Ottino 2004). A computer virus spreading on the Internet or HIV spreading through the web of human sexual contacts are two processes that illustrate how epidemic spreading occurs in complex networks (Petermann and De Los Rios 2004b). These two examples are of particular importance since they also represent cases where an infectious agent is spread through a specific type of complex network; a scale-free network. Researchers have recently discovered two general features that characterize epidemic spreading in scale-free networks including the absence of any epidemic threshold below which an infectious agent cannot initiate a major outbreak and the hierarchical spread of epidemic outbreaks in the form of a cascade from **hubs** (see Glossary, Table 1) to intermediate and then small degree vertices (Barthelemy *et al.* 2005; Yan *et al.* 2005). Importantly, these features are not exhibited by other types of networks and so scale-free networks are generally more prone

than other types of networks to the spreading and persistence of infectious agents, independent of the spreading rate of the epidemic agent (Pastor-Satorras and Vespignani 2001). This general theoretical framework of epidemic spreading in complex networks is of great interest given the ubiquity of these systems (Barthelemy *et al.* 2005) and it is also worth noting that these recent discoveries regarding disease spreading in complex networks were entirely unexpected results that radically changed many widely held beliefs about epidemic spreading (Pastor-Satorras and Vespignani 2001). These discoveries may provide stream ecologists with new insight when considering the spreading of invasive species, animal or plant disease, or polluting agents through river networks. For example, the finding that epidemic spreading in complex networks has a hierarchical structure means that natural resource managers may predict the spread of a potential invasive species, from initial introduction in the highly connected hub(s) and then towards vertices with a smaller value of k and finally those with the lowest degree that are typically last to be infected (Barthelemy *et al.* 2005). This generic prediction may prove invaluable for optimizing limited resources to prevent the introduction or limit the spread of invasive species and hence protect the majority of the river network. Consideration of network architecture is also important to predict the speed at which an invasive species might spread through a river network once introduced. Barthélemy *et al.* (2005) found that initial conditions play a key role in epidemic spreading and if an introduction initially occurs in a hub the outbreak will be fast, however if an introduction occurs in a part of the network with a low degree spread of the invasive species will be far slower.

Other recent findings have suggested that scale-free networks share the unusual feature of not obtaining global immunity via random immunization of individual nodes (even in the presence of unrealistically high densities of randomly immunized individuals)

and that any immunization scheme for epidemic spreading in scale-free networks should be delivered in a priority order based on the degree of the individual nodes, beginning with the hubs and working down to the nodes with the lowest degree (Dezso and Barabási 2002; Amaral and Ottino 2004). Again, this general finding may help natural resource managers optimize the use of preventative measures by directing the majority of effort and funding for prevention of invasive species introduction towards the most crucial parts (hubs) of the network. There is currently much interest in the epidemiological field about designing optimal containment strategies (Yan *et al.* 2005) and these may well prove useful to stream ecologists and natural resource managers studying the spread of invasive species, disease or pollutants in river networks.

Some recent studies have begun to apply this type of thinking directly to problems of stream ecology by examining the fundamental role that the network structure plays in driving spreading processes in river basins. Bertuzzo *et al.* (2007) analysed the effects of network structure on wave propagation of migration fronts (e.g. the effect of river network structure on spreading processes, such as invasive species) using quantitative models of dispersion along fractal and real river networks and found that wave speed is affected mostly by the gross structure encountered by the front while propagating along the network (i.e the nodes or bifucations in the river network). They highlighted the ability of these network models to be used to predict the first colonization time distributions of all sites in the network (Bertuzzo *et al.* 2007). Such predictive models have powerful potential to help fight the spread of agents, such as invasive species, through river networks. The exact role that river network structure plays in the evolution of living communities in explicitly spatial landscapes is a relatively new area of research (Rodriguez-Iturbe *et al.* 2009), but one that is rapidly growing, particularly in relation to the spatio-temporal dynamics of the spread of

water-borne disease. Bertuzzo *et al.* (2008) used quantitative models of spreading in river networks to accurately predict outbreaks and spreading behaviour of a cholera epidemic as they occurred in a well-documented outbreak in South Africa during the summers of 2000/01 and 2001/02 and highlighted the significant role that waterways and the river networks play as an ecological corridor for the pathogen. These advances in understanding the dynamics of spreading of infectious agents through rivers systems all stem from the application of network theory to ecological problems occurring in real-life networks.

Predicting the robustness of river networks to disturbance

Many real-world complex networks are of considerable economic importance (e.g. the power grid, the World Wide Web, the Internet, email communities etc.) so it is not surprising that research into the robustness of complex networks is a rapidly growing field (Amaral and Ottino 2004; Paul *et al.* 2004). The robustness of networks may be compromised by unexpected failure of one or more nodes (error) or by intentional disruption of one or more nodes (attack). For example, faulty wiring of a telegraph pole (error) may compromise the power distribution network by cutting off electricity to the adjoining houses, or all houses on the street. Alternatively, deliberate destruction of a sub-station (attack) may leave the network unable to deliver power to all houses in the surrounding suburb. Network theory is now being used to address questions of the robustness of complex networks to both failure and directed attack (Amaral and Ottino 2004) and this approach could potentially be used to help model the effects of various disturbances in river networks. Such information could aid decisions about where best to site damaging activities in the catchment (e.g. forestry, agriculture) so that minimal effects are observed throughout the rest of the river basin, or to identify areas for restoration and

management activities that would be likely to strengthen the robustness of the entire river network.

Researchers studying error tolerance and attack vulnerability in different types of networks have found that networks with a given degree distribution may be very resilient to one type of attack but not to another (Paul *et al.* 2004). For example, the overall functioning of scale-free networks is highly resistant to the failure of random vertices as the majority of the vertices in the network have a small degree (i.e. they are not highly connected to other vertices in the network). As such, there appears to be a functional advantage to scale-free architecture (Strogatz 2001) in that a large portion of nodes in a scale-free network are essentially redundant because any random node attacked is most likely to have a small degree and is thus expendable with minimal or no loss to the overall functioning of the network. So, random failure is most likely to affect the functioning of only a very small part of the network and the majority of vertices remain connected together in what is known as a **giant component** (see Glossary, Table 1). One important finding of network theory is the existence of a critical probability at which this occurs, such that below this threshold a network is composed of isolated clusters, but above the threshold a large cluster (i.e. a giant component) spans the entire network (Albert and Barabasi 2002). This concept is the focus of a field of mathematics known as percolation theory but it also has practical implications for a large array of phenomena related to real-world networks. Whilst being more robust to random failure than single-scale networks, scale-free networks are very susceptible to targeted attack of the highest degree nodes, that is, the highly connected ‘hubs’ of the network (Albert *et al.* 2000; Petermann and De Los Rios 2004b), as these parts of the network play a crucial role in holding together the whole network (i.e. maintaining the giant component).

These general properties regarding the robustness and fragility of complex networks, and the concept of the giant component, provide a strong theoretical basis for trying to predict the effects of disturbances in river networks. There are currently several theoretical efforts trying to characterize the percolation transition, that is, the critical fraction of nodes that would need to be removed before the giant component breaks up (Albert and Barabasi 2002). For example, work has already been undertaken in ecological networks investigating the effects of species deletions from food webs on the overall functioning of the food web network. A study of three species-rich ecosystem food webs showed that despite differences in the characteristics of the networks, all three food webs were very robust against random removals of species but very fragile when a selective approach targeting specific species was used, with the food web fragmenting into disconnected sub-webs (Solé and Montoya 2001). Similarly, modelling river basins as scale-free networks will allow researchers to explore the impacts of damaging or fragmenting different parts of the river network and to explore the cumulative effect of these actions by identifying thresholds beyond which species are no longer able to move through the majority of the river network or beyond which the movement of important constituents such as nutrients and organic matter can no longer be effectively transported through the river network. By identifying those river reaches that are the well-connected hubs of the river network, disturbances to these important parts of the network can be prohibited or minimised and so large-scale impacts on the robustness of the whole river network will be less likely to occur and the integrity of the system maintained.

Quantifying the connectivity of individual nodes in a network is necessary to identify the hubs of the network, although connectivity of individual nodes is not necessarily related to the importance of a particular node to the entire network. Consider an

example (Fig. 1) where a major disturbance, such as the construction of a new dam wall for generation of hydro-electricity, is considered in a hypothetical river basin consisting of two main branches ('East' and 'West'). If we accept that a dam wall largely restricts the movement of critical constituents above and below it, we can see that constructing the dam wall at Location 1, slightly upstream of Node C (which has three neighbouring nodes), would restrict movement of constituents from Nodes A to B but movement throughout the remainder of the river network below Node C will be unaffected. Now consider the dam wall at Location 2, slightly upstream of Node Z which also has three neighbouring nodes (i.e. the same local connectivity as Node C) but has far greater importance in keeping large parts of the network connected because it acts as a 'bridge' for movement between the East and West branches of the river (Fig. 1). Blocking movement through Node Z essentially breaks the river network into two disconnected components and thus Node Z is a 'cut-vertex' in the language of network theory. Nodes like these are critical to the overall functioning of a network, despite often not having a high local connectivity themselves. This concept of how 'important' a node is to the overall connectivity of the network is known as the 'betweenness centrality' of a node and is quantified as the fraction of shortest paths going through a given node (Barthelemy 2004). Moving the dam to Location 3 just slightly downstream of Node Z allows the two major branches of the river network to stay connected though Node Z (Fig. 1). So, borrowing relatively simple quantitative measures of connectivity and centrality from network theory has the potential to provide a powerful tool for predicting and better quantifying the effects of local disturbance on the functioning of whole river networks.

These concepts from network theory are beginning to emerge in stream ecology. A study by Cote *et al.* (2009) developed a Dendritic Connectivity Index for quantifying the

longitudinal connectivity within river networks, highlighting the enormous potential for these general concepts of connectivity and centrality from network theory to be used in stream ecology.

Using concepts from network theory as a theoretical basis for large-scale conservation planning

Large-scale conservation planning for terrestrial species generally considers species as living and dispersing in two-dimensional 'planar' landscapes, where dispersers may move between pairs of patches via many possible dispersal routes (Fagan 2002). For riverine systems, this is only possible for taxon with an aerial flight stage in their life history (e.g. stream insects) or the ability to make short terrestrial excursions between adjacent reaches (e.g. salamanders). Most dispersers are constrained to move within the hierarchical 'dendritic' landscapes imposed by the physical structure of river networks. So, it is critical that riverine reserve design considers the constraints that this network structure may have on dispersal and connectivity of populations living within it.

In the previous section, the related concepts of network hubs and the giant component were introduced with respect to predicting the effects of random error or targeted attack on scale-free networks. Network hubs and the giant component also have direct relevance to ecological questions regarding connectivity and fragmentation of systems, two related concepts that are of central concern to large-scale conservation planning. Hubs, the highly connected nodes of scale-free networks, are known to play an important role in keeping complex networks together (Ravasz and Barabasi 2003) with one or more hubs contributing to a giant component in scale-free networks. The concept of the giant component may provide a quantifiable goal for the overall connectivity of a riverine reserve network as it represents the threshold at which the majority of the nodes are

connected together in one large network, thus allowing wide-spread dispersal throughout the river basin. Network theory also offers a quantitative method of assessing the importance of different nodes in a river network to connectivity of the whole network using the concept of betweenness centrality. This ‘importance’ of nodes in a river network may be an important parameter to consider in reserve design algorithms for freshwater reserves, in addition to established concepts such as comprehensive, adequate and representative suites of reserves (Dunn 2003) and more recently suggested attributes such as irreplaceability, condition and vulnerability (Linke *et al.* 2007).

These quantitative measures from the field of network theory have recently begun to be applied to research in landscape ecology and conservation biology (Urban *et al.* 2009). A study of a heavily fragmented agricultural landscape in Madagascar used centrality measures to assess the importance of individual habitat patches in relation to their effect on different aspects of landscape connectivity and also the criticality of an individual patch to the provision of large-scale connectivity (Estrada and Bodin 2008). This research is clearly analogous to the central research questions in the field of percolation theory and has much to gain from knowledge that has already been generated in this area. While there are some very early adopters of these ideas in stream ecology that have been utilizing concepts from network theory to inform studies of landscape-scale connectivity and fragmentation for several years (Fagan 2002; Grant *et al.* 2007; Grant *et al.* 2009), there is enormous scope for these concepts to be more widely applied across the field of stream ecology.

Conclusions

Fisher *et al.* (2004) highlighted that further advancing our knowledge of whole drainage basins will require more than a mere summation of our knowledge about individual stream

segments. Embracing the concept of ‘rivers as networks’ has assisted both researchers and managers in progressing beyond downstream ‘fixes’ to a more systemic understanding of whole catchments (Everard and Powell 2002) and provided a deeper understanding of ecological patterns and process across spatial scales (Grant *et al.* 2009). However, I contend that the ‘rivers as networks’ paradigm still has a vast potential to grow and that further exploration of how the universal properties of different network topologies could be applied to river basins provides an opportunity to greatly extend the application of the network concept in stream ecology.

The increasing breakdown of boundaries between disciplines has allowed ecologists to borrow concepts from areas of research that were traditionally limited to physicists and mathematicians. Understanding some of the organising principles and general properties of complex and scale-free networks is a vital approach to better understanding of the collective functioning of whole river basins and further promoting the use of the network concept in stream ecology.

Here, I discussed several examples of how concepts from network theory might be applied to current research issues in stream ecology, with the aim of stimulating stream ecologists to re-consider some common research questions from a different angle and build upon the advances already made by other disciplines. While such approaches are already underway by a handful of early-adopters, the aim here was to bring these important concepts from the fields of network theory and physics to the attention of researchers in stream ecology that do not have the time or resources to thoroughly investigate the literature in the fields of network theory and physics for general concepts that might be applicable to their research. Considering rivers as networks has already emerged as one of the most important new paradigms in stream ecology and it would seem imprudent not to

draw on the strong theoretical advances made in the fields of physics, mathematics and network theory to further advance our understanding of riverine systems as networks and the universal principles that govern them.

Acknowledgements

I would like to thank (then) Associate Professor Frank Fisher for his 2004 class in 'Systems Thinking' which introduced me to the concept of general systems theory that inspired me to read the material on network theory that is presented in this paper. I also thank Ross Thompson and Nick Bond for many informal discussions about networks and stream ecology.

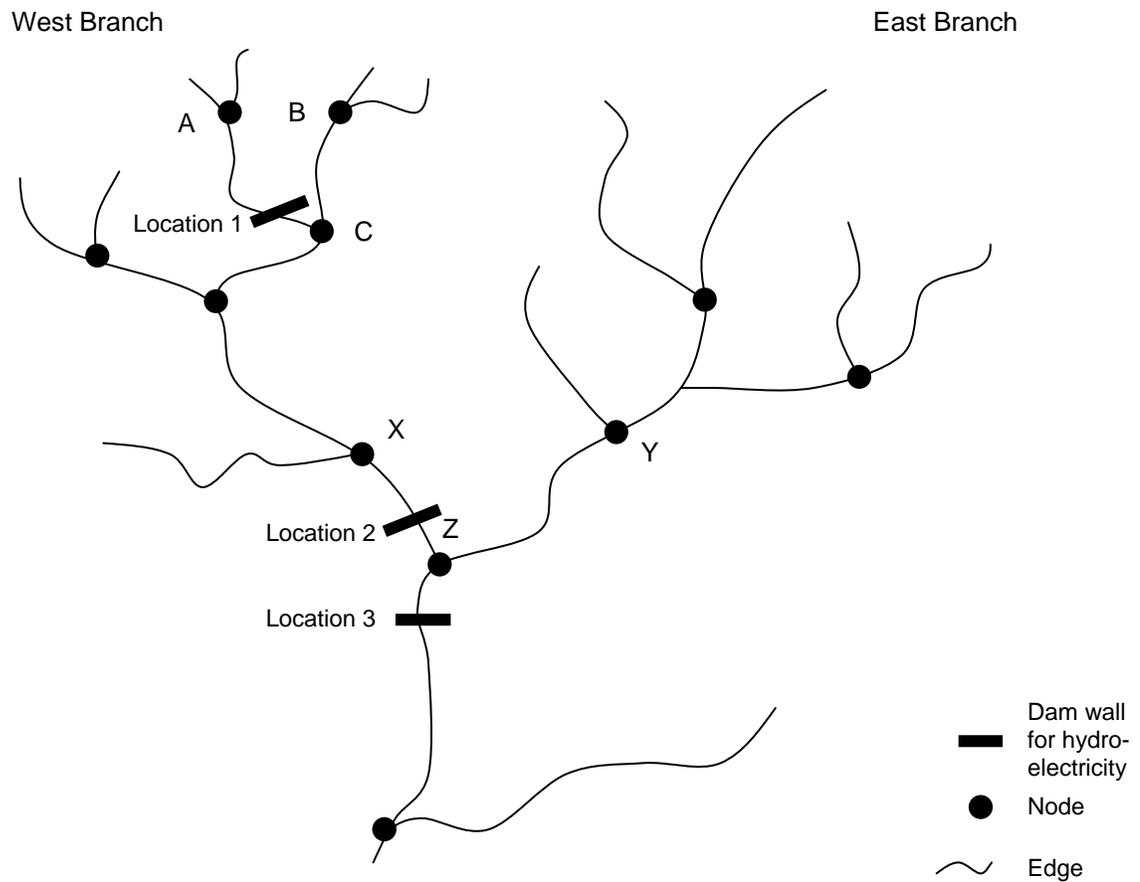


Figure 1. Borrowing the concept of ‘betweenness centrality’ from network theory offers the potential to predict the effects of local disturbances on the overall connectivity of river networks by quantifying the ‘importance’ of each node in a network to the overall connectivity of the network.

Table 1 – Glossary of key terms

Fractal

Fractals are rough geometric shapes that produce (at least approximately) reduced-size copies of the whole when subdivided across a large range of scales (Sornette 2006). Many natural objects are approximate fractals (e.g. clouds, snowflakes, ferns, lightning), including river networks, and are thus self-similar over a wide range of spatial and temporal scales.

Power-law

Power law relationships are common in physical and natural systems, arising as probability or frequency distributions of the form $f(x) = \beta x^\alpha$ (Marquet et al. 2005) that exhibit the property of scale invariance (see below) which is an exact form of self-similarity.

Scale invariance

Scale invariant phenomena possess the same statistical properties at all scales and thus are not associated with any particular or characteristic scale (Marquet et al. 2005).

Degree distribution

$P(i)$ - The probability that a randomly chosen node will have degree i , that is be linked to i other nodes.

Scale-free

Networks with no characteristic number of links per node, a feature of networks with power-law degree distributions.

Hubs

The nodes of a network possess a larger probability of developing connections pointing to other nodes (Pastor-Satorras and Vespignani 2001).

Giant component

A connected sub-network that contains a majority of the networks nodes.

General Discussion

The increasing breakdown of boundaries between scientific disciplines has allowed ecologists to borrow concepts from areas of research, such as network theory, that were traditionally limited to physicists and mathematicians. The concept of viewing rivers as networks has become increasingly popular over the last decade (Fagan 2002; Benda *et al.* 2004; Lowe and Likens 2005; Grant *et al.* 2007; Hitt and Angermeier 2008; Chaput-Bardy *et al.* 2009; Brown and Swan 2010). The explicit recognition of stream ecosystems as spatially structured networks has increased our understanding of ecological patterns and processes (Grant *et al.* 2009) and provided the impetus for this research.

Headwater streams are held to be ‘important’ areas for biodiversity in river networks (Gomi *et al.* 2002; Lowe and Likens 2005; Meyer *et al.* 2007; Richardson and Danehy 2007). There is limited evidence to assess this view because of the paucity of studies on spatial and temporal patterns of diversity in headwater streams, and streams in general. Considering the role that the spatial structure of river networks might play in determining diversity patterns in landscapes is important because dendritic networks have characteristic effects on the distribution of species (Grant *et al.* 2007). When river basins are conceived as dendritic networks in landscapes, spatial patterns of diversity in headwater streams can be examined by assessing the relative contributions of α (within-assemblage) and β (among-assemblage) diversity to γ (regional) diversity.

River network structure has been posited to have particularly strong effects on β diversity due to the isolation effect of the largely inhospitable terrestrial landscape separating river reaches (Clarke *et al.* 2008; Muneeppeerakul *et al.* 2008). I expected that β diversity would make a large contribution to the γ diversity of macroinvertebrates in the

study area, particularly at the larger spatial scale (among catchments) due to limited dispersal among sites and especially among catchments. Diversity partitioning showed that reaches each had high α diversity, while β diversity made only a small contribution to γ diversity at both the reach and catchment scales (Fig. 3a). β diversity may have been lower than hypothesized due to relatively small distances between sites and the presence of many macroinvertebrate taxa with an aerial dispersal stage that could facilitate high levels of dispersal among reaches and catchments. This result resembles that of rainforests, which often are large tracts of relatively homogeneous habitat in which the local species pool (i.e. α diversity) typically represents a large portion of the diversity in the region (Lewinsohn and Roslin 2008). A similar effect may have been operating in my study area whereby the relatively continuous tract of undisturbed vegetation facilitates high dispersal within and among headwater stream catchments.

Evidence to quantify dispersal can be obtained through genetic methods that provide an estimate of the average movement between populations over time (Hughes 2007). Determining the role that dispersal plays in structuring assemblages can also be investigated by assessing the relative importance of local (environmental) and regional (e.g. dispersal) processes. The relative importance of these processes also reveals much about how macroinvertebrate assemblages are structured across the landscape (i.e. metacommunity structure). The relative importance of factors structuring metacommunities is a topic of much debate (Cottenie 2005), particularly for testing of the validity of the neutral model of biodiversity (Hubbell 2001) and other metacommunity models (Ricklefs 2006).

In this study system, there was a limited role for environmental factors structuring macroinvertebrate assemblages (Fig. 3b). This was contrary to the findings of several studies that have found environmental factors to be important for explaining variation in macroinvertebrate assemblage structure in headwater streams (Heino *et al.* 2002; Cole *et al.* 2003; Stendera and Johnson 2005; Johnson *et al.* 2007; Brown and Swan 2010). I also found that a spatially structured environmental component was a major factor affecting macroinvertebrate assemblages (Fig. 3c) and is likely to be due to the presence of a mountain range dissecting the study region that has different micro-climates on either side. In one year (2008), spatial factors (independent of environmental factors) were the dominant factor structuring macroinvertebrate assemblages (Fig. 3d). This indicated that metacommunity structure in the study region aligns most closely with the predictions for the neutral/patch dynamic metacommunity model (Fig 3e).

Debates on the neutral model focus on dispersal limitation as the major spatial dynamic structuring assemblages, but dispersal can also be a structuring force when a constant flux of individuals moves among closely connected sites and generates more similar assemblages among these sites than those that are further apart (Cottenie *et al.* 2003). Therefore, both dispersal limitation and neighbourhood dispersal processes may cause spatial structuring in assemblages (Mykrä *et al.* 2007). Increased dispersal reduces β diversity among habitat patches (Shurin *et al.* 2009) and I found evidence of low β diversity in headwater streams in the study area. My finding of spatial structuring coupled with low β diversity suggests that high neighbourhood dispersal is potentially the main structuring agent affecting macroinvertebrate assemblages in this system (Fig. 3f). Many studies have suggested or shown that the exchange of individuals among localities in headwater streams

generally is low (Griffith *et al.* 1998; Finn *et al.* 2007; Hughes 2007; Brown and Swan 2010). However, where assemblages are dominated by stream insects with aerial dispersal by adults, many individuals may have a high dispersal potential and should be able to reach any location in a drainage system with appropriate environmental conditions (Mykrä *et al.* 2007). Future studies directly measuring dispersal in the field or studies of genetic differentiation of species among these study sites (Hughes 2007) would be useful for evaluating my conclusion that high levels of neighbourhood dispersal are the dominant force structuring macroinvertebrate assemblages in this system (Fig. 3g).

Although most of the measured environmental variables did not play a significant role in structuring macroinvertebrate assemblages in this system, the flow-related variables may have been important in structuring assemblages if they were measured during periods of low flow in the study region. In a study of flow permanence in one catchment (Silver Creek), I found that differences in macroinvertebrate assemblages in a permanent, an intermittent and an ephemeral stream could only be detected in the dry, summer period. Flow permanence in this study area has only a seasonal effect on macroinvertebrate diversity (Fig. 3h) and reveals that there is a temporal component to the spatial diversity patterns in this system. The intermittent and ephemeral streams in the Silver Creek catchment do not appear to harbour a specialized aquatic invertebrate fauna that is distinct from that in a nearby perennial stream. Therefore, taxa from the perennial stream appear to be efficient at colonizing seasonally dry, nearby streams and the perennial streams in this catchment may provide a critical over-summer refuge for many taxa.

Implications for management of biodiversity in freshwater systems

The conservation of biodiversity in freshwater ecosystems is a pressing issue, particularly because freshwater biodiversity is now considered to be declining faster than biodiversity in terrestrial ecosystems (Abell 2002; Dudgeon *et al.* 2006). Freshwater ecosystems are poorly protected around the world, despite harbouring unique flora and fauna and providing substantial ecosystem services that should be a strong imperative for their protection (Moilanen *et al.* 2008). Headwater streams, in particular, provide habitat for a vast array of algae, bacteria, fungi, plants, invertebrates, vertebrates and birds (Meyer *et al.* 2007), but are globally threatened by human activities such as mining, forestry, agriculture, water extraction and increasing urbanisation (Meyer and Wallace 2001). Headwater streams are especially vulnerable to disturbance due to their small size and close coupling to hillslope processes in surrounding catchments (Gomi *et al.* 2002) and are likely to be more greatly affected than larger rivers by the future predicted effects of climate change (Durance and Ormerod 2007; Heino *et al.* 2009).

Understanding how α , β and γ diversity are related along geographical and environmental gradients has important implications for biodiversity conservation in freshwater ecosystems (Heino 2009). Studies developing protected area reserves for marine and terrestrial ecosystems have delivered many advances in the field of systematic conservation planning over the past two decades, although the application of these ideas has only recently begun to be widely applied to freshwater systems (Linke *et al.* 2008; Moilanen *et al.* 2008; Nel *et al.* 2009; Linke *et al.* 2010). Systematic conservation planning aims to stem the loss of biodiversity by prioritising areas for conservation action in a spatially efficient configuration (Nel *et al.* 2009). Four key principles are generally

addressed in modern conservation planning: comprehensiveness, adequacy, representativeness and efficiency (Linke *et al.* 2010). *Adequacy* addresses how a conservation area network should be designed to ensure persistence of all biodiversity attributes and the inherent connectivity of river basins makes this aspect of conservation planning more difficult than for terrestrial or marine ecosystems (Linke *et al.* 2010). The branching geometry of river basins also has characteristic effects on the distribution and abundance of species in river systems (Fagan 2002; Grant *et al.* 2007) that mean traditional reserve designs are unlikely to be effective for freshwater ecosystems.

Determining the relative contributions of α and β diversity to γ diversity, and the scale dependence of α and β components, provides vital information for conservation planning because optimal reserve designs will differ depending on how diversity is partitioned across the landscape. My finding of high α and low β diversity indicated that each stream in the study area can be considered to have low irreplaceability and the capacity to contribute a large portion of species to regional conservation targets. I showed that where limited information on individual taxonomic distributions is known, or resources for intensive modelling are not available, diversity partitioning may provide a useful surrogate measure of the irreplaceability of individual streams or sub-catchments to freshwater reserves trying to protect the entire regional species pool.

Conclusions

This study has revealed important information about the spatial patterns of biodiversity in headwater streams and the processes that are important in driving these patterns (Fig. 3). Although headwater streams have been posited to have high β diversity due to habitat

heterogeneity or limited dispersal within and among catchments, this clearly does not hold for all systems. I found that reaches had high α and low β diversity at two spatial scales. Also, while many studies have shown that environmental (local) factors are important factors structuring macroinvertebrate assemblages in headwater streams, this generally was not the case in my study area. Spatial (regional) factors were the dominant factor structuring assemblages and indicated that the metacommunity structure more closely resembles the predictions for the neutral/patch dynamic model than other models of metacommunity structure. These findings, together, indicate that the dominant processes driving spatial patterns of diversity in the study region may be high levels of neighbourhood dispersal. Proving this hypothesis would require genetic studies to quantitatively assess the rates of dispersal among headwater streams and this provides a promising avenue for future research in the study area to build upon my findings.

Information on diversity patterns is urgently required for systematic conservation planning for freshwater reserves if we are to halt the rapid decline in global freshwater biodiversity. While it is important to protect downstream sites, it is hard to see how any freshwater reserve aiming to protect long-term ecological integrity and biodiversity could succeed without a foundation of intact and functional headwater streams (Lowe and Likens 2005).

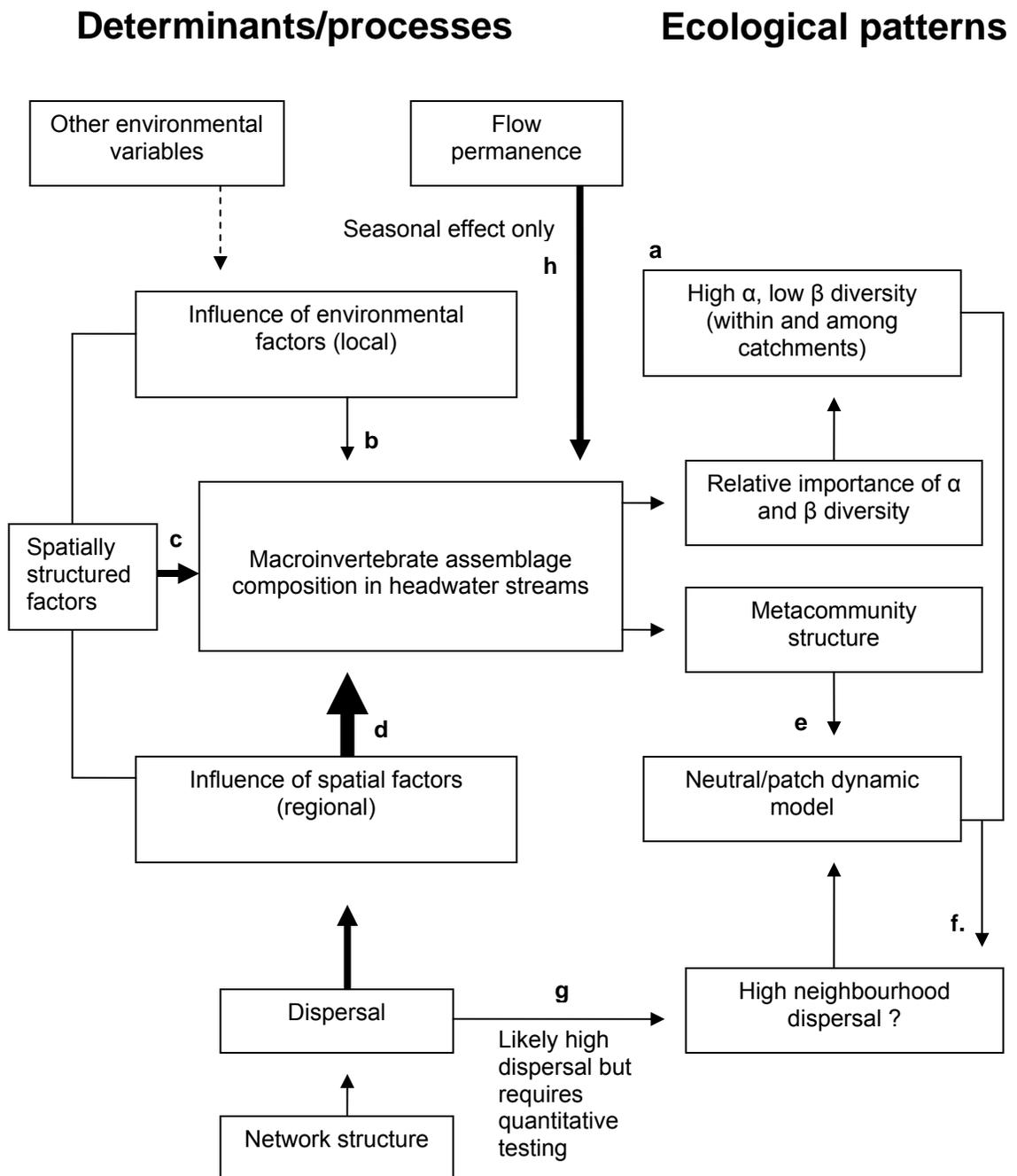


Figure 3. Conceptual model of the processes driving spatial patterns of macroinvertebrate diversity in headwater streams in the Wallaby Creek Designated Water Supply Catchment Area, Victoria, Australia. Increased thickness of arrows indicates greater evidence for the pattern/process as shown by this research.

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Appendix 1 – List of macroinvertebrate taxa collected

The following taxa were found in the eight study streams of the Wallaby Creek Designated Water Supply Catchment Area:

Nematoda	<i>Molophilus sp.</i>
Nematomorpha	<i>Dactylobasis sp.</i>
Oligochaeta	<i>Limonia sp.</i>
<i>Corbicula sp.</i>	<i>Hexatoma sp.</i>
Hydrobiidae	<i>Epiphragma sp.</i>
<i>Glacidorbis sp.</i>	<i>Dolichopeza sp.</i>
Acarina	<i>Dasyomma sp.</i>
Ostracoda	Empididae (SRV6)
Copepoda	Empididae (SRV7)
<i>Crenoicus sp.</i>	Psychodidae
Cladocera	Stratiomyidae
<i>Neoniphargus sp.</i>	Chironominae
<i>Pseudomoera sp.</i>	Orthoclaadiinae
<i>Austrochiltonia sp.</i>	Tanypodinae
Hypogasturidae	Podonominae
Isotomidae	Ceratopogoninae EPA 42
Sminthuridae	<i>Aphrotenia sp.</i>
<i>Nannochorista sp.</i>	<i>Aphroteniella sp.</i>
Osmylidae	<i>Eutanyderus sp.</i>
<i>Austroneurorthus sp.</i>	<i>Austrosimulium sp.</i>
Tipulidae (unidentified sp.)	<i>Paradixa sp.</i>
<i>Cryptolabis sp.</i>	<i>Nothodixa sp.</i>
<i>Limnophila sp.</i>	Tabanidae

Dolichopodidae

Eusthenia sp.

Austropentura sp.

Austrocercella sp.

Illiesoperla sp.

Leptoperla sp.

Acruroperla sp.

Dinotoperla sp.

Reikoperla sp.

Atalophlebia sp.

Ulmerophlebia sp.

Koormonga sp.

Nousia sp.

Coloburiscoides sp.

Tasmanophlebia sp.

Edmundsiops sp.

Caenota sp.

Oecetis sp.

Taschorema sp.

Condocerus sp.

Hydrobiosella sp.

Daternomina sp.

Aphilorheithrus sp.

Genus Cal. B

Lectrides sp.

Triplectides sp.

Apsilchorema sp.

Austroaeschna sp.

Eusynthemis sp.

Telephlebia sp.

Notriolus sp.

Curculionidae

Notohydrus sp.

Hydrochidae

Hydraena sp.

Scirtidae

Byrronectes sp.

Sclerocyphon sp.

Austrolimnius sp.

Macrogyrus sp.

Australphilus sp.

Chostonectes sp.

Hydrophilidae

Microvelia sp.