

SPECIAL REVIEW

Macroinvertebrate diversity in headwater streams: a review

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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 |

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[†]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

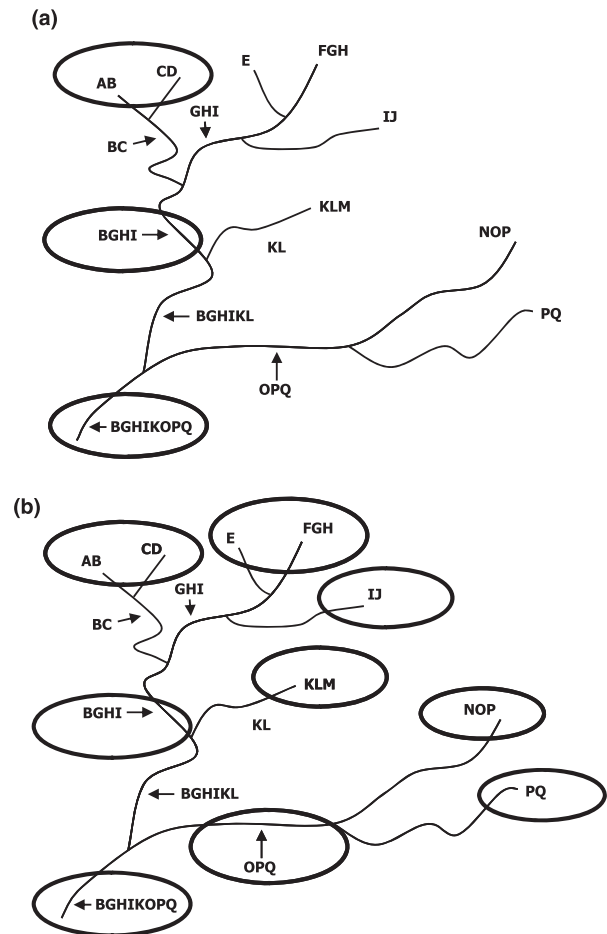


Fig. 1 Contrasting sampling designs for investigating longitudinal changes in taxonomic richness of macroinvertebrates: (a) a traditional 'linear' sampling approach to studying longitudinal patterns in taxonomic richness. Circles represent sampling sites. This sampling approach assumes that by sampling 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

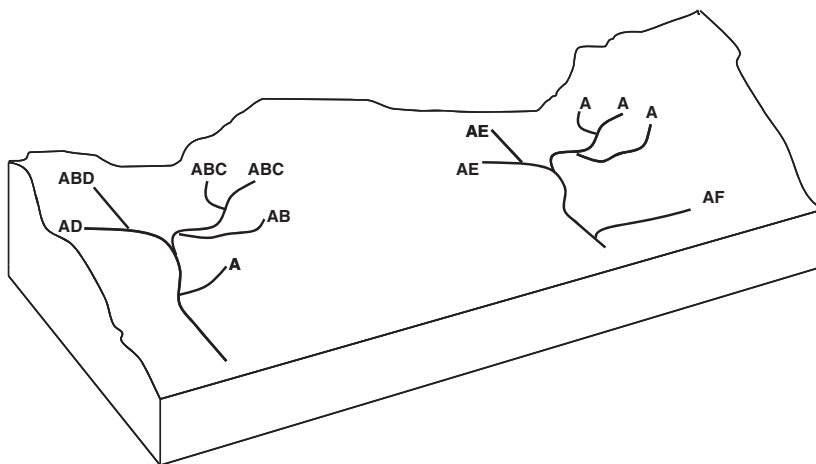


Fig. 2 Theoretical patterns of α and β -diversity generated in two headwater networks with a regional species pool (γ -diversity) of six species (A–F) with differing dispersal abilities and opportunities across two adjacent catchments separated by a mountain range.

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-

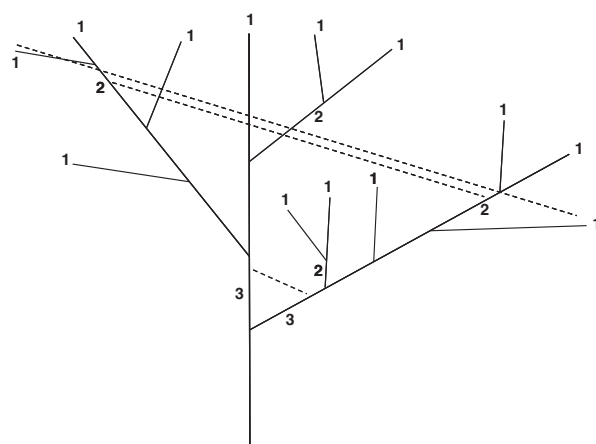


Fig. 3 Generalized spatial structure of a dendritic river network illustrating how the branching geometry of river basins may generate a pattern whereby the distance between the two furthest first-order streams is greater than the distance between the two furthest second-order streams and so on. Such 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).

Acknowledgments

This is contribution no. 145 from the Australian Centre for Biodiversity. We thank two anonymous reviewers and Alan Hildrew for their thoughtful and constructive comments. This work is funded by a Victorian *Our Water Our Future* Postgraduate Scholarship, a eWater Cooperative Research Centre Postgraduate Scholarship and a Wentworth Group Science Program Scholarship.

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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)