

## The ecohydrology of stream networks

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**Abstract** Stream ordering approaches to the study of entire stream networks are relatively simple and provide only crude estimations of the physical makeup of river ecosystems. These fail to acknowledge the importance of the hierarchical organisation of rivers and consequently use very crude variables when characterising stream networks. We provide an alternative typology for characterising the physical structure of rivers, which focuses on a specific level within the geomorphic river hierarchy, and employs a set of regional, catchment and valley criteria for developing a quantitative river characterisation scheme. Fifteen geomorphic variables were extracted from digital data using automated geographic information system modules and evaluated using a series of multivariate analyses. This allowed distinct river types within a stream network to emerge. Our approach was demonstrated in the Ovens River, Australia. The physical structure of the Ovens River stream network was further analysed using a series of community metrics: richness, composition and diversity of river types.

**Key words** riverine networks; geographic information system (GIS); physical diversity; complex systems; river characterisation

### INTRODUCTION

Ecohydrology is an interdisciplinary science that joins two or more areas of expertise into a single conceptual structure. Ecology, hydrology and fluvial geomorphology are often merged in ecohydrology studies to unravel patterns and processes in riverine ecosystems at different scales (Hughes *et al.*, 2008). Knowledge of the distribution and composition of the physical habitat within riverine ecosystems is an emerging theme of ecohydrology (Hughes *et al.*, 2008). Physical character, or habitat, provides the template upon which evolution acts to forge characteristic strategies of life history (Southwood, 1977). Therefore, the physical properties of any given habitat will influence the type, abundance and arrangement of biological assemblages found within river ecosystems. Decisions on where to invest limited resources in river conservation can be guided by the knowledge of which sites are in the greatest need of conservation or rehabilitation, and how different sites may respond to varying levels of investment (Schofield *et al.*, 2000). An understanding of the physical character of the entire river system is integral to making decisions about conservation.

River characterisation is a way to identify physical habitat within stream networks. It requires the ordering of sets of observations into meaningful groups based on similarities or differences, and attaching labels to these groups (Thorp *et al.*, 2008). There are many physical river characterisation schemes, reflecting the different contexts to which they are applied. Identification of physical habitat within river ecosystems has generally been focused at the reach or site level. Although these methods produce a wealth of data, they cannot provide information on the character and composition of physical habitat at a catchment scale. Rivers are natural hierarchical ecosystems that can be broken down into different levels of organisation. A feature of these systems is that higher levels occur at larger scales and have slower rates of behaviours, while lower levels occur at smaller scales and react more quickly. Successive levels within a hierarchical structure act like filters or constraints and, thus, data must be collected at a level or scale compatible with the scale of focus. Therefore, the characterisation of the physical habitat of entire river networks must involve data from either the regional, catchment or valley scale only (see Dollar *et al.*, 2006, for an example of a common physical river hierarchy) and not data collected at a reach or site.

The concept of stream ordering, as proposed by Horton (1945) and later modified by Strahler (1957), has become a conceptual and organisational tool in many areas of river science. It is often used to determine the physical character or habitat of entire stream networks. However, comparisons between channel networks, determined by stream ordering, can prove misleading for a number of reasons. Channel segment order depends on the criteria used to determine where first-

order channels begin within a network – no accepted standard exists for this task. The representation of a stream network in a catchment will vary, depending on the scale of the maps used to derive it. Gardiner (1995) recommended using 1:25 000 maps; other studies have used 1:100 000 scale maps (Patil *et al.*, 2002). Moreover, channel networks defined from the blue lines on a map along with information on the curvature of the contours, a critical gradient or drainage area, can differ substantially from networks identified in the field (Montgomery & Buffington, 1998). In addition to scale problems, the other main criticism of stream ordering is the absence of an inherent association between a stream order number and channel morphology or the operating fluvial processes. Stream ordering only provides an indication of relative channel size and position within the channel network. Despite these shortcomings, stream ordering has become a popular and simplistic way to describe the physical properties of a stream network (Smart, 1972).

Advances in geographic information system (GIS) technology and the availability of data covering large spatial scales are associated with the development of quantitative river characterisation approaches (e.g. Thorp *et al.*, 2008). Using data gathered from multiple sources, such as high-quality catchment digital elevation models (DEMs) and their accompanying streamlines, allows top-down multivariate approaches to characterise larger-scale river systems. The method outlined by Harris *et al.* (2008) and Thorp *et al.* (2008) is among a new set of techniques for the calculation of physical habitat at a catchment scale. Generating a data matrix from multiple sites throughout the stream network relies on a series of multivariate statistical procedures to identify similar “river types” within the stream network. These data can then be used to investigate different river-type assemblages for different stream networks.

We present results that characterise the physical habitat of a stream network at the catchment scale. We use the top-down approach supported by Thorp *et al.* (2008) to objectively determine the composition of river types within the entire network of the Ovens River catchment in northern Victoria, Australia. In addition, a series of assemblage metrics, commonly used in community ecology, are used to explore the overall physical integrity of the river network.

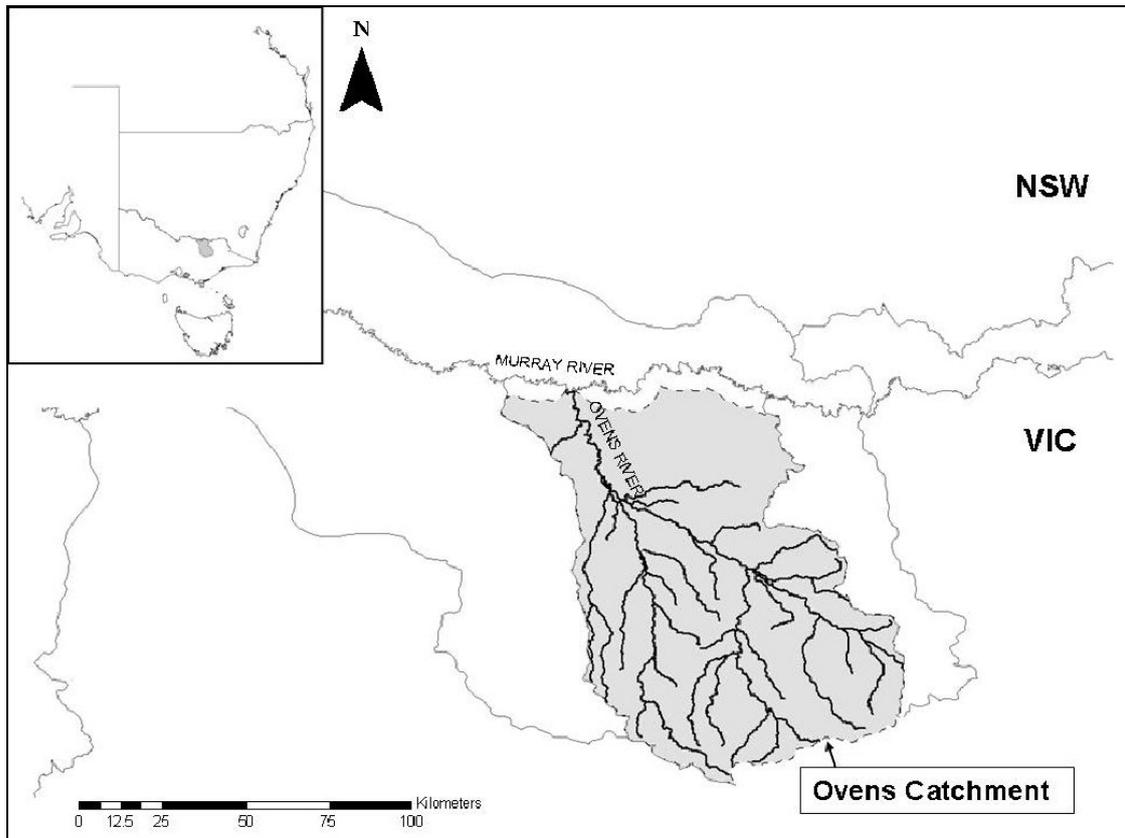
## MATERIALS AND METHODS

### Study area

The Ovens River drains 7800 km<sup>2</sup> of the alpine region in northeast Victoria, Australia (Fig. 1). There, four main subcatchments: the Kings and Ovens rivers, and Black Dog and Indigo creeks, all of which have a strong seasonal flow regime associated with spring snow melt. The Ovens River flows northwest from its headwaters at Mt Hotham (36°58'S, 147°07'E) to its confluence with the River Murray near Yarrawonga, Victoria (36°01'S, 146°00'E). The Ovens River is effectively unregulated by dams, weirs or water extractions, unlike most of the river systems in the region. It is also a significant source of water and sediment to the River Murray (Thoms & Walker, 1992). It contributes approximately 14% of the long-term average annual flow of the River Murray at Yarrawonga (1600 GL), and more than 140 000 t year<sup>-1</sup> of suspended sediment.

There are two distinct physiographical regions in the Ovens River catchment. The southern region of the catchment is relatively mountainous; the geology is dominated by the Australian Alps. This area is heavily dissected by a series of faults that are part of a large anticlinal structure that runs northwest. A distinct physiographical boundary, located approximately in the mid regions of the catchment (corresponding to the northern edge of the north–south regional anticlinal structure), separates the southern and northern regions of the catchment. North of this geological structure, the low gradient alluvial plains of the Ovens River/River Murray dominate the region. These alluvial plains slope uniformly towards the north and are associated with the contemporary meandering flood plain river system of the lower Ovens River.

The Ovens River has been identified as a high-quality ecosystem because of its regional ecological importance (DNRE, 2002). The lower sections of the Ovens River contain one of the last forested and unregulated lowland flood plains in southeast Australia (Quinn *et al.*, 2000). This area contains extensive forest stands of River Red Gum (*Eucalyptus camaldulensis*), with an array



**Fig. 1** The Ovens River catchment. Inset shows location of this catchment within southeast Australia.

of billabongs of various shapes, sizes and water permanence. Reaches of the Ovens River also contain significant populations of several native fish. Murray cod (*Maccullochella peelii peelii*), a large (up to 113 kg), iconic freshwater fish, which was once widespread and abundant throughout the Murray–Darling Basin, is present in healthy numbers in sections of the Ovens River. Populations of trout cod (*Maccullochella macquariensis*), a species that is listed as critically endangered, are also present in the Ovens River (Koehn & Harrington, 2006).

## METHODS

Initially, the network of the Ovens River was classified using Strahler's (1957) stream ordering technique. This was done digitally using a set of 100 000-scale digital streamlines for the catchment. The composition and channel lengths for each stream order were obtained from this digital data set. The stream network of the Ovens River was also described using the approach outlined in Harris *et al.* (2007) and Thorp *et al.* (2008). This desktop technique, developed for the typing of river networks, also employed the 100 000-scale digital streamlines used for the stream ordering, as well as a three-second DEM of the catchment. This method is summarised here; a full description of the data sources and technique used can be found in Harris *et al.* (2007) and Thorp *et al.* (2008).

A series of points along the Ovens stream network were created at 10-km intervals. These points became the focus for the extraction of 15 geomorphic variables, which were used to describe the morphology of the riverine landscape. Along the Ovens River stream network, 129 sites were allocated. Variables from three scales of organisation (catchment, valley and channel scales) were extracted at each site using a series of ArcGIS functions and tools. The catchment-scale variables included elevation, geology and rainfall. Elevation was determined from the 3"

DEM and mean long-term annual rainfall (1930–2007) was derived from vector contour data sourced from the Australian Bureau of Metrology. Geology was measured from a 250 000-scale vector lithology layer of the region and this was aggregated into three basic geological categories: alluvial, non-alluvial sediments and bedrock. The valley scale variables were: valley width, valley trough width, the ratio of valley width to the valley trough width, the left and right valley slopes, and down-valley slope. The six channel-scale variables were: channel belt width, channel belt sinuosity, channel wavelength, as well as channel sinuosity, wavelength, planform and the number of river channels.

This large data set (129 sites and 15 variables) was analysed using a variety of multivariate statistical techniques that identified groups of sites with a similar morphology. Initially, the data were classified using the flexible unweighted pair-group method with arithmetic averages (UPGMA) fusion strategy, as recommended by Belbin & McDonald (1993). The Gower association measure was used because this measure is range-standardised and is recommended for nonbiological data (Belbin, 1993). Groups of sites with similar morphological character were selected by viewing a dendrogram representation of the classification. Dendrogram groups were arrayed onto the streamlines of the Ovens River, to delineate the position of sites with similar morphological character (using standard GIS mapping techniques). Groups of sites with similar morphological character equate to river types. To further elucidate groups of river types, a semi-strong-hybrid multidimensional scaling ordination was performed on the data. Sites were arrayed in ordination space and then an analysis of similarity (ANOSIM) was used to assess differences between groups of sites, or river types. Finally, a SIMPER analysis was used to determine which geomorphic variables contributed to the within-group similarity. These were used to construct a river-type nomenclature for the Ovens stream network.

The typology data for the Ovens River stream network was analysed with a series of commonly-used parameters for determining the diversity of ecological communities (Magurran, 2004). This required the recognition of river networks as a community of river types, with a “river type” being analogous to a “species” in ecology. Thus, not only could the overall diversity of a community of river types within a stream network be determined, but also the individual components of abundance, evenness and richness that make up diversity (Thorp *et al.*, 2008). Diversity was measured at the whole-network scale, where richness was calculated as the number of river types present, and abundance as the total length of the channel of each river type. Evenness was measured using Simpsons evenness index, which provides a value between 0 and 1 representing the overall distribution of channel lengths between different river types. When an evenness value approaches 1, channel lengths are more evenly distributed between river types. A lumped diversity measurement for the Ovens River network was measured using the Shannon–Weiner diversity index ( $H'$ ); calculated as:

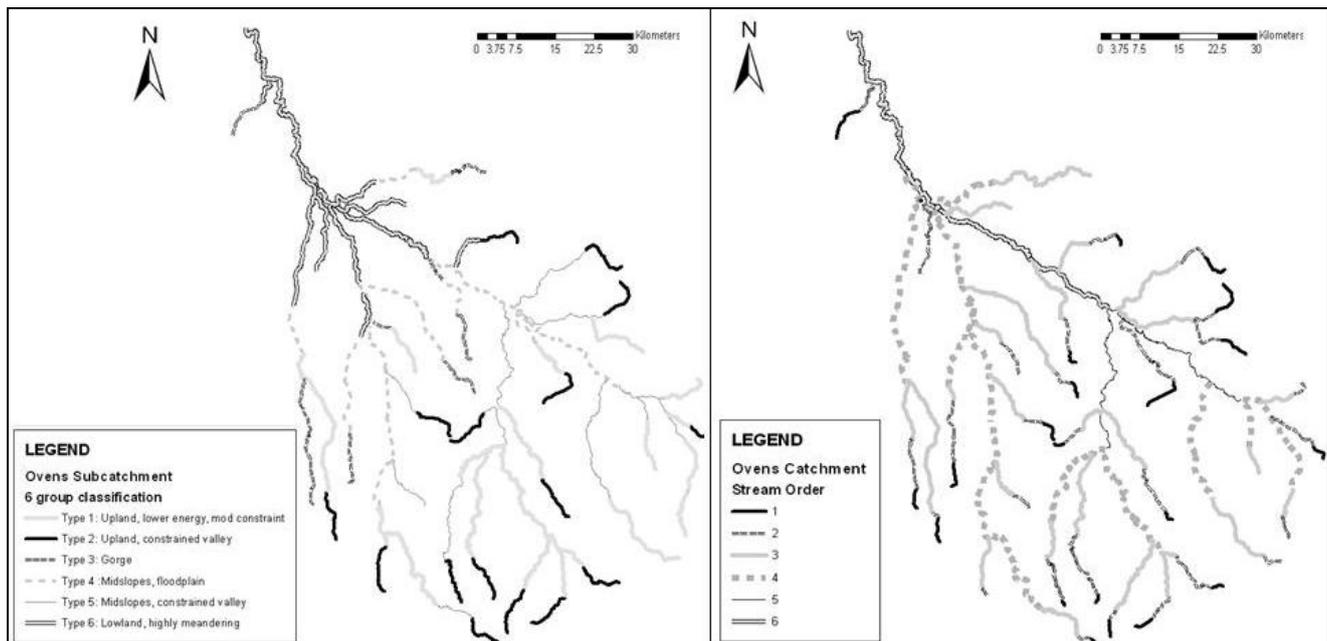
$$H' = -\sum p_i \ln p_i$$

where  $p_i$  is the proportion of channel lengths found in the  $i$ th river type (adapted from Magurran, 2004).

These measures were also calculated *within* the Ovens river network. Richness was measured as the number of disjunct river stretches within each river type and abundance as the total length of channel within each river type. Evenness (still measured using Simpsons evenness index) now calculated the distribution of channel lengths between river segments within river types. Shannon’s diversity index was measured in the same way as for the entire catchment.

## RESULTS

The Ovens River is a sixth-order catchment (Fig. 2(b)). Of the 1152 km of river channel analysed, over 50% were stream order 3 (345 km) and 4 (304 km). Stream orders 1 (85 km) and 5 (77 km) were the least abundant orders in the Ovens River. By comparison, classification of sites located along the streamlines of the Ovens River revealed six dendrogram groups at 72% similarity,



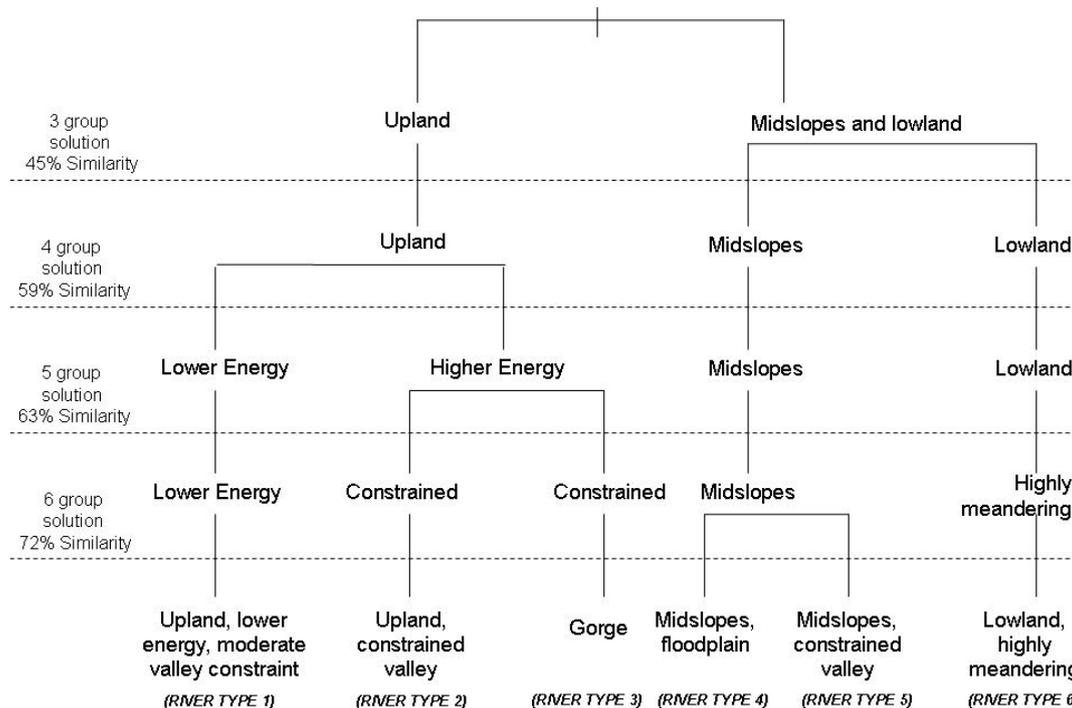
**Fig. 2** The morphological character of the Ovens River stream network. (a) The distribution of different river types and (b) the distribution of stream orders.

corresponding to six groups of sites or river types. An ANOSIM demonstrated that these six river types were statistically different to one another.

The spatial distribution of the six river types are displayed in Fig. 2(a). This spatial distribution, along with the output from the SIMPER analysis, was used to provide a description of river types for the Ovens catchment. River Types 1 and 2, located in the upland regions of the stream network (Fig. 2(a)), are characterised by highly constrained valley settings with relatively steep down-valley and valley-side slopes. River Type 1 varies from River Type 2 in that it has a lower down-valley slope; thus River Type 2 is associated with the upland, constrained valleys of the stream network. River Types 3 and 4 are characterised by relatively open valleys and have well-developed flood plain surfaces. River Type 4 has lower down-valley slopes, and hence lower stream energies than River Type 3, and is located in the mid to lower regions of the stream network catchment. River Type 3 is located in midregions only (Fig. 2(a)). River Type 5 is located in the mid to upper regions of the catchment (Fig. 2(a)) and is characterised by relatively constrained valley widths, steep valley side slopes, and moderate down-valley slopes and energy. By comparison, River Type 6 is dominated by extensive flood plain surfaces and very wide valley widths. This river type is found in the most downstream areas of the stream network (Fig. 2(a)), and therefore, contains rivers of the lowest energy in the stream network.

A SIMPER analysis for the group solutions 3–6 revealed clear separation of the variables that contributed highly to the within-group similarity (Fig. 3). The first split in the dendrogram separated River Types 1, 2 and 3 from River Types 4, 5 and 6. The former types were located in the upland and relatively higher energy regions of the catchment, while the latter types were located in the mid and lower regions of the catchment. Ultimately, the 6-group solution (72% similarity) revealed that River Type 1 was associated with those parts of the stream network located in the upland regions of the network that had lower stream energies, as distinguished by lower down-valley slopes and a moderate valley width. By comparison, River Type 6 was associated with the lowland regions of the stream network, which had highly meandering channels (cf. Fig. 3).

Overall, composition of the different river types varied in terms of their abundance, richness and evenness (Table 1). The most abundant river type was River Type 1, with a total channel length of 298 km. The next abundant river type was River Type 6, then River Type 4, River Type 5, River Type 2 and River Type 3. In terms of the number of individual segments comprising



**Fig. 3** Derivation of river types in the Owens River network using dendrogram groups formed at different levels of similarity. At each level, the variables associated with each group are given. The final river type nomenclature is presented in the bottom row.

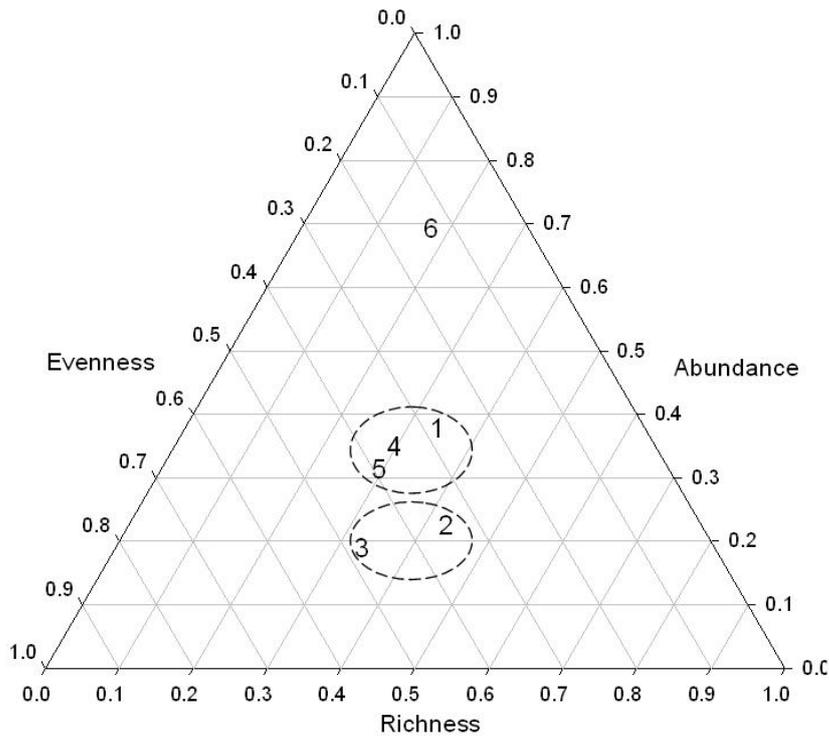
**Table 1** Composition of the six river types in the Owens stream network.

River type	Description	Abundance (%)	Total channel length (km)	Richness (no. individual segments)	Evenness (Simpson's evenness index)	Diversity (Shannon-Weiner value)
1	Upland, lower energy, moderate valley constraint	25.8	298	14	0.83	2.24
2	Upland, constrained valley	13.9	160	16	0.94	2.77
3	Gorge	7.5	86.7	8	0.83	1.92
4	Midslopes, flood plain	17.5	202	9	0.78	1.73
5	Midslopes, constrained	15.9	183	9	0.87	2.11
6	Lowland, highly meandering	19.3	222	3	0.16	0.35

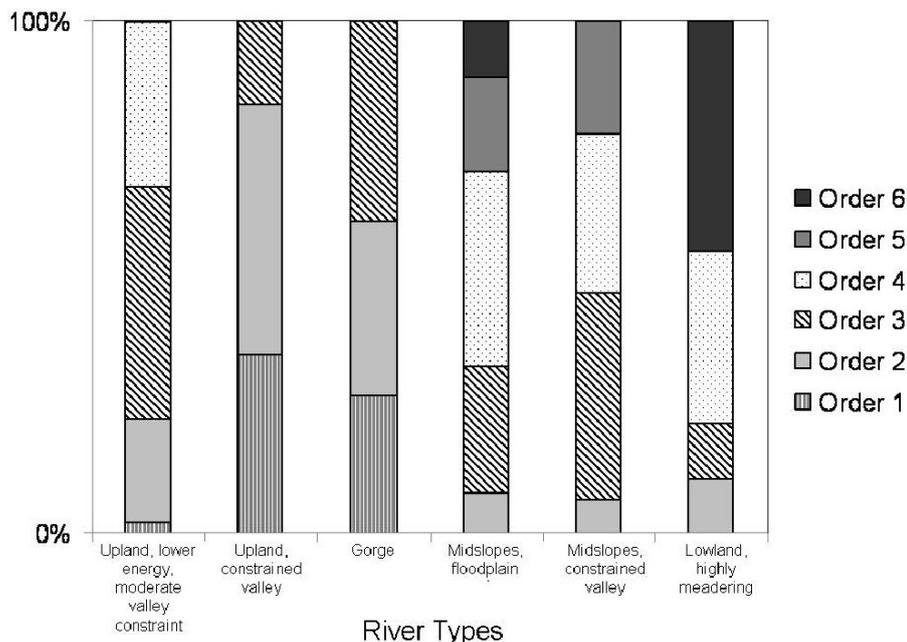
each river type (richness), River Types 2 had 16 individual segments with an average segment length of 21 km. This was followed by the River Type 1, while River Type 4 and River Type 5 had the same richness. River Type 3 had the second lowest richness with eight segments and River Type 6 recorded the lowest richness with only three individual river segments, and had an average length of 74 km.

Evenness values between river types in the Owens River stream network ranged between 0.16 and 0.94 and five of the six types had an evenness value above 0.78 (Table 1), hence segments that are similar in length. River Type 6 had the lowest evenness value, corresponding to the small number of very long segments associated with this type. River Type 2 was the most even, suggesting a high number of individual segments with similar channel lengths. River Types 1 and 3 had similar evenness values, as did River Types 4 and 5.

The abundance, evenness and richness values of the different river types suggest several clusters of river types in the Ovens River (Fig. 4). One cluster includes River Type 1, River Type 4 and River Type 5, which are characterised by high abundance and evenness. The cluster that included River Type 2) and River Type 3 had lower abundance values. River Type 6 is an outlier because of its lower richness and evenness values.



**Fig. 4** The character of identified river types in the Ovens River. Numbers 1–6 represent the different river types derived from the river characterisation outlined in the text. Circles enclose clusters of similar river types as defined by their abundance, evenness and richness.



**Fig. 5** A comparison of two river characterisation approaches: stream ordering and river typing.

In terms of the overall diversity of river types in the Ovens River stream network, Shannon–Weiner values varied – River Types 1, 2, and 5 all had diversity values greater than 2.0, and River Types 3 and 4 had diversity values of 1.92 and 1.73. River Type 6 had the lowest diversity value.

A comparison between the stream ordering and river typing approaches shows negligible correlation between the two for data collected on the Ovens River stream network (Fig. 5). Each of the six river types identified in the stream network of the Ovens River is represented by several different stream orders and there appears to be little consistency in terms of possible relationships between the two approaches. The closest correlation between stream order and river type is a 49% overlap between River Type 2 and stream order 2. Each river type is represented by at least three different stream orders; River Types 1 and 4 are associated with five different stream orders.

## DISCUSSION

No single characterisation scheme can satisfy all possible purposes, nor can it encompass the multitude of river landforms. Regardless of the approach and methods used, characterisation schemes must be based on a sound conceptual framework, underpinned by defensible scientific principles. A framework is neither a model nor a theory. Models describe how things work and theories explain phenomena. In contrast, conceptual frameworks help to order phenomena and material, thereby revealing patterns (Rapport, 1985). Frameworks serve as scientific maps for new areas of endeavour; in this case, even tentative maps are useful (Pickett *et al.*, 1999), if only because their subsequent improvement provides some measure of progress in integrative thinking. In the context of river characterisation, scientific principles act as a framework to guide the process of identifying common river types and their distinguishing features, as well as allocating river types to an existing characterisation.

Two important principles for the characterisation of river systems are as follows. First, characterising river systems must be undertaken at scales appropriate for the context in which they are to be used, or, for the questions being asked. Riverine landscapes are the result of processes operating at multiple scales (Parsons & Thoms, 2007). Teasing apart regional and local effects requires appropriate stratification of sites, along with the selection of variables at the correct scale for the study. Second, characterisation should ideally be based on a holistic range of variables (in the sense of Biggs *et al.*, 1990), which are relevant to the physical character of the river system. Consequently, knowledge of the concepts of hierarchy theory is important here. Groups of interest must be identified based on the self-emergence of groups of similar character, rather than groups being imposed or inherited from other studies or locations. Each scheme has its own inherent focus or context with which to study rivers and their character. These will not be the same for all studies. Characterisation approaches must, therefore, evolve to become more objective.

Traditional quantitative studies of river networks have been largely based on a stream ordering approach (Horton, 1945; Strahler, 1957). This is a relatively simple procedure that describes stream networks based on the hierarchy of channel tributaries. At best, it provides a crude description of the physical properties of a stream network (Smart, 1972; Thorp *et al.*, 2008). Limitations of stream ordering have been outlined in many studies (Smart, 1972; Hughes & Omnerick, 1983). Fundamental criticisms revolve around the fact that although stream order may be useful to describe relative channel size within a physiographically and climatically homogenous basin, the technique is often used beyond its capacity to address characteristics such as area, relief or discharge (Hughes & Omnerick, 1983).

By analysing stream ordering according to the two principles for river characterisation outlined here, the limitations associated with stream ordering have been highlighted. With this method, hierarchical principles of scale are not considered and the recommended scale for application of stream ordering is disputed, as the order of streams in a network will change depending on the scale of map used (Smart, 1972). Although stream orders do self-emerge, this objective approach can be interpreted to provide inaccurate information on river character. The technique does not take into account any character-defining variables, apart from position in the

network. The character of the river is assumed to change with a change in stream order, which only happens when two streams of equal order join. In the real world, changes in the physical properties of the riverine habitat are not limited to junctions in stream networks (Smart, 1972). Despite this, stream ordering is still widely used by ecologists, geomorphologists and hydrologists.

The method of river typing outlined in this manuscript provides an alternative to stream ordering. It is essentially a top-down, desktop approach that is objective and quantitative. It employs a set of 15 variables – more information than is used to determine stream order. The two techniques can be directly compared, as they are both used to provide similar physical information on riverine landscapes. Although the techniques both generated six groupings based primarily on their geomorphic position within the Ovens catchment, a comparative analysis showed little correlation between group distributions. The closest association between river type and stream order was a 49% overlap, although the river type was also associated with another two stream orders. These results highlight the problems associated with the use of the popular stream ordering technique for classifying river networks in the Ovens catchment. Both techniques were applied at the same scale and on the same streamlines, yet the outputs were quite different.

Although other physical classification schemes are available to characterise riverine habitats, most approaches to the classification of river channels tend to focus at the reach scale (Thorp *et al.*, 2008). This scale of focus weakens any attempts to classify or characterise entire river networks in a way that is meaningful and relates to forming processes. The river typing method is relatively rapid and objective, and its development parallels advances in the availability of high-quality digital elevation data, computer processing abilities and GIS tools. River typing uses readily available data sets (DEMs and streamline network models), along with information on catchment geology and climate, to derive a physical classification for rivers and flood plains at the valley scale – appropriate for classifying entire river networks. It is underpinned by hierarchy theory and, therefore, focuses only on those variables relevant to identifying valley-scale river zones within a network.

Although most large-scale river classifications provide a spatial understanding of the distribution of riverine habitats, the measurements of network diversity described here offer a more comprehensive analysis. It is already known that physical diversity and heterogeneity in streams correlate well with biological diversity (Bartley & Rutherford, 2005). Physical diversity of rivers is an indicator of stream health (Norris & Thoms, 1999) and may be used to describe the diversity of biota (Newson & Newson, 2000). Although the relationship between physical diversity in a stream and habitat diversity is recognised, there are few studies on measuring this diversity (Bartley & Rutherford, 2000). Measures that do exist are limited and commonly focus on a particular stream feature or scale.

There is a need to develop quantitative techniques to measure spatial heterogeneity (Bartley & Rutherford, 2000). The analysis technique described in this study adapts community diversity methods used in ecology to provide measures of physical diversity in stream networks. River networks form a community of river types; therefore, a “river type” is analogous to a biotic “species”. Richness is the number of disjunct river stretches within a river type, abundance is the total length of stream channel within a river type, and evenness is the distribution of channel lengths between river segments. Measurement of these enables the calculation of a lumped diversity value for each river type and for the whole catchment. The manipulation of ecological diversity metrics for application in the physical realm has not been used previously to define physical diversity in rivers. These techniques can be transferred to any other river network, and the outputs can be compared both within and between stream communities.

The physical diversity of a stream network can be associated with stream habitats, which can enable us to make inferences about biological diversity. As identified in previous studies (Bartley & Rutherford, 2000), an integrated approach by geomorphologists and ecologists is required to assess physical diversity in streams. Although the relationship between physical heterogeneity in a stream network and biological diversity is recognised, further research is needed to determine how the measures of river network diversity described here relate directly to biological communities.

## REFERENCES

- Bartley, R. & Rutherford, I. (2005) Measuring the reach-scale geomorphic diversity of streams: application to a stream disturbed by a sediment slug. *River Res. & Appl.* **21**, 39–59.
- Begon, M., Townsend, C. R. & Harper, J. L. (1986) *Ecology: from Individuals to Ecosystems*, 4th edn. Blackwell Publishing, Melbourne, Australia.
- Belbin, L. (1993) Environmental representativeness: regional partitioning and reserve selection. *Biological Conservation* **66**, 223–230.
- Belbin, L. & McDonald, C. (1993) Comparing three classification strategies for use in ecology. *J. Vegetation Sci.* **4**, 341–348.
- Biggs, B. J. F. & Smith, R. A. (2002) Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. *Limnology & Oceanography* **47**, 1175–1186.
- Dollar, E. S. J., James, C. S., Rogers, K. H. & Thoms M. C. (2007) A framework for interdisciplinary understanding of rivers and ecosystems. *Geomorphology* **89**, 147–162.
- Gardiner, V. (1995) Channel networks; progress in the study of spatial and temporal variations of drainage density. In: *Changing River Channels* (ed. by A. D. Gurnell & G. E. Petts), 65–86. Wiley, Chichester, UK.
- Hansen, W. F. (2001) Identifying stream types and management applications. *Forest Ecol. & Manage.* **143**, 39–46.
- Harris, C. D., Thoms, M. C., Rayburg, S. C. & Parsons, M. (2008) An approach for assessing the physical condition of rivers at the catchment scale. In: *Proceedings of IAHS Water Down Under 2008* (ed. by M. Lambert, T. Daniell & M. Leonard), 1879–1889. Engineers Australia, Adelaide, Australia.
- Horton, R. E. (1945) Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. *Geol. Soc. Am. Bull.* **56**, 275–370.
- Hughes, R. M. & Omernik J. M. (1983) An alternative for characterising stream size. In: *Dynamics of Lotic Ecosystems* (ed. by T. D. Fontaine & S. M. Bartell), 87–102. Ann Arbor Science Publishers, Michigan, USA.
- Hughes, V., Thoms, M. C., Nicol, S. & Koehn, J. (2008) Physical–ecological interactions in a lowland river system: large wood, hydraulic complexity and native fish associations in the River Murray, Australia. In: *Hydroecology and Ecohydrology: Past, Present and Future* (ed. by P. J. Wood, D. M. Hannah & J. P. Sadler), 387–404. Wiley, Chichester, UK.
- Koehn, J. D. & Harrington, D. J. (2006) Conditions and timing of the spawning of Murray Cod (*Maccullochella peelii peelii*) and the endangered trout cod (*M. macquariensis*) in regulated and unregulated rivers. *River Res. & Appl.* **22**, 327–343.
- Leopold, L. B., Wolman, M. G. & Miller, J. A. (1964) *Fluvial Processes in Geomorphology*. Freeman, San Francisco, USA.
- Magurran, A. E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Melbourne, Australia.
- Newson, M. D. & Newson, C. L. (2000) Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progr. Phys. Geogr.* **24**, 195–217.
- Norris, R. H. & Thoms, M. T. (1999) What is river health? *Freshwater Biology* **41**, 197–209.
- O'Neill, R. V., Johnson, A. R. & King, A. W. (1989) A hierarchical framework for the analysis of scale. *Landscape Ecol.* **3**, 193–206.
- Parsons, M. E. & Thoms, M. C. (2007) Hierarchical patterns of physical–biological associations in river ecosystems. *Geomorphology* **89**, 127–146.
- Patil, G. P. (2002) *Multiscale advanced raster map analysis system: network-based analysis of biological integrity in AU17 freshwater streams*. Center for Statistical Ecology and Environmental Statistics, Pennsylvania State University, Pennsylvania, USA.
- Pickett, S. T. A., Burch, W. R. & Grove, J. M. (1999) Interdisciplinary research: maintaining the constructive impulse in a culture of criticism. *Ecosystems* **2**, 302–307.
- Pileou, E. C. (1975) *Ecological Diversity*. Wiley Interscience, New York, USA.
- Quinn, G. P., Hillman, T. J. & Cook, R. (2000) The response of macroinvertebrates to inundation in flood plain wetlands: a possible effect of river regulation? *Regulated Rivers: Res. & Manage.* **16**, 469–477.
- Rapport, A. (1985) Thinking about home environments: a conceptual framework. In: *Home Environments* (ed. by I. Altman & C. M. Werner), 255–286. Plenum Press, New York, USA.
- Schofield, N. J., Collier, K. J., Quinn, J., Sheldon, F. & Thoms, M. C. (2000) Australia and New Zealand. In: *Global Perspectives on River Conservation: Science, Policy and Practice* (ed. by P. J. Boon, B. R. Davies & G. E. Petts), 311–334. Wiley, Chichester, UK.
- Smart, J. S. (1972) Channel networks. In: *Advances in Hydrosociences* **8**, 305–346. Academic Press, New York, USA.
- Southwood, T. R. E. (1977) Habitat, the template for ecological strategies? *J. Animal Ecol.* **46**, 337–365.
- Strahler, A. N. (1957) Quantitative analysis of watershed geomorphology. *Trans Am. Geophys. U.* **38**(6), 913–920.
- Thoms, M. C. & Walker, K. F. (1992) Channel changes related to low-level weirs on the river Murray, South Australia. In: *Lowland Flood plain Rivers: Geomorphological Perspectives* (ed. by P. A. Carling & G. E. Petts), 235–249. Wiley, Chichester, UK.
- Thorp, J., Thoms, M. & DeLong, M. (2008). *The Riverine Ecosystems Synthesis: Towards Conceptual Cohesiveness in River Science*. Academic Press, New York, USA.