

SPECIAL REVIEW

Review of theoretical developments in stream ecology and their influence on stream classification and conservation planning

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SUMMARY

1. We review some of the classic literature on geomorphology and ecology of streams in an effort to examine how theoretical developments in these aquatic sciences have influenced the way fresh flowing waters are classified. Our aim was to provide a historical examination of conceptual developments related to fluvial classification, and to discuss implications for conservation planning and resource management.
2. Periods of conceptual influences can be separated into three overlapping phases each distinguished by theoretical, analytical or technological advances: (i) early Darwinian perspectives; (ii) the quantitative revolution; and, (iii) age of the computer, hierarchy and scale.
3. During the first phase, stream geomorphologists were largely influenced by Darwinian metaphors. The study of stream origin and change through time became more important than the study of stream systems themselves. The idea that streams progress deterministically through successive stages of development seemed to create a veil, most prevalently in North America, that barred analysis of the full scope of variability in these systems for over 50 years.
4. The quantitative revolution brought about many new ideas and developments, including the laws of stream numbers. This period focused on predictive and mechanistic explanations of stream processes, setting the stage for physically based stream classifications that assume that streams can be restored by engineering their physical characteristics.
5. In the most recent 'age of the computer', concepts from the fields of geographic information science and landscape ecology have been incorporated into stream ecology and aquatic classification. This has led to investigations in stream and aquatic ecosystems at hierarchical spatial scales and along different dimensions (upstream/downstream, riparian/floodplain, channel/ground water and through time). Yet, in contrast to terrestrial landscapes, flowing waters are not as easily classified into spatially nested hierarchical regions wherein upper levels can be subdivided into smaller and smaller regions at finer spatial scales. Riverscapes are perhaps best described as directionally nested hierarchies: aquatic elements further downstream cannot be rendered equivalently to elements upstream. Moreover, fully integrated aquatic ecosystem classifications that incorporate lake and river networks, wetlands, groundwater reservoirs and upland areas are exceedingly rare.
6. We reason that the way forward for classification of flowing waters is to account for the directionally nested nature of these networks and to encode flexibility into modern digital freshwater inventories and fluvial classification models.

Keywords: conservation/biodiversity, ecosystem, fresh waters, large-scale ecology, running water/rivers

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We have long since discarded the idea of treating the whole stream or river as a single ecological entity... it is only stream segments, stream sections, or (preferably) stream habitats which may be properly compared and contrasted from place to place.

Pennak, 1971

The whole-ecosystem approach and appropriate measurement and monitoring strategies needed to predict an impending state change are only now beginning to emerge.

Stanley, Powers & Lottig, 2010

Introduction

A history of fluvial ecosystem classification begins around the turn of the 20th century (1890–1914), but efforts to classify unique ecosystems, in general, really began to intensify around the 1970s and early 1980s (e.g., Pennak, 1971; Lotspeich & Platts, 1982; Bailey, 1983). This period was the dawn of the computer age, during which time many fields saw a profound increase in classificatory work (Sokal, 1974). Efforts to understand how streams differed from one another prior to the 1970s were already well underway, and numerous classifications of stream communities into longitudinal zones can be found (Thienemann, 1912; Steinmann, 1915; Carpenter, 1927, 1928; Huet, 1954, 1959; Illies, 1961). But, with computers and remote sensing technologies came the ability to automate data collection at spatial scales that were hitherto unachievable. The use of computers led to the development of algorithms for finding multivariate similarities (e.g., clustering algorithms), which enabled more quantitative and efficient approaches to classification (Sokal, 1974).

Concurrent with this rise in computing power came the rise in the environmental movement. Social and biological scientists were turning their attention to studying relationships between unconstrained population growth, pollution and human encroachment on undeveloped landscapes. The social context was one of political discord over environmental issues. For example, Earth Day movements in the early 1970s took place with the participation of nearly 20 million Americans (US EPA, 2010). The time was ripe for identifying sensitive, rare and unique ecosystem types.

Over time, more attention became focused on the conservation of terrestrial ecosystems, despite evidence to suggest that freshwater biodiversity is at an even greater risk of extinction (Ricciardi & Rasmussen, 1999; Abell *et al.*, 2002; Turak & Linke, 2011). Lakes, rivers, wetlands and streams within protected areas seemed to be

viewed as an afterthought, used to support terrestrial species or to define reserve boundaries, rather than garnering protection for their own sake (Hermoso *et al.*, 2011). How did this happen? There are a number of potential explanations: aquatic ecosystems are implicitly 'out of sight' and 'out of mind' because one cannot easily peer beneath the surface of a water body. Moreover, these systems generally lack charismatic mega-fauna typical of terrestrial ecosystems, and aquatic systems are not well protected because the scientific and policy frameworks for their protection are poorly developed (Hermoso *et al.*, 2011; Nel *et al.*, 2011).

Freshwater aquatic ecosystems are dynamic, changing through time and space, and connected by flowing water. The idea that you can set aside a section of stream as a bounded and protected area and thereby preserve a representative sample of aquatic biodiversity does not fit well with freshwater aquatic ecosystems (Nel *et al.*, 2011). Only recently have we begun to determine exactly what aquatic representation actually means, and a recent special issue in the journal of *Freshwater Biology* presents nine articles that explore the topics of representation (Nel *et al.*, 2011), persistence (Turak *et al.*, 2011) and assigning conservation priorities in fluvial systems (e.g., Heiner *et al.*, 2011). Many of these prioritisation schemes rely on some kind of classification (or map) of riverine ecosystem diversity (Leathwick *et al.*, 2011).

Much of the primary literature on river-stream classification is based on research done in forested, mountainous areas where lakes and wetlands do not dominate the landscape (e.g., Frissell *et al.*, 1986; Seelbach *et al.*, 2006). However, flowing waters are intimately connected with slow moving waters like lakes and wetlands in many, if not most, regions of the world, and this is particularly true in areas with low topographical relief (Jones, 2010). Despite the need for an integrated approach to understanding freshwater systems, our main focus in this review is on the influence of theoretical developments in stream ecology and stream geomorphology on the classification of flowing waters. A complete review of theoretical developments in lake or wetland ecology is beyond our scope. Thus, we ignore obvious lake classification schemes based on trophic status or productivity (e.g., oligotrophic, mesotrophic, and eutrophic) and we do not discuss influential wetland and deepwater habitat classifications such as Cowardin *et al.*'s (1979) classification of wetlands in the United States. But, we believe that there is a real need for an integrated approach to aquatic ecosystem classification, and we hope that this review provides some insights towards the development of such classifications. A great

deal of freshwater aquatic research around the world focuses either on lakes or rivers and streams, but generally not both (Jones, 2010).

Background on classification

Classification systems are an effective reflection of the current state of knowledge in an area (e.g., on river function, Frissell *et al.*, 1986). Essentially, all classificatory efforts aim to satisfy the following four general principles. First, classifications organise information and describe what is known. The hope is that the description captures the true nature of the objects or relationships described. When classes reflect the actual processes that have led to the groupings themselves, then by studying the classification, we can learn about the laws governing the behaviour of the objects classified (Sokal, 1974; Portt, King & Hynes, 1989). This allows us to make inductive generalisations about objects in each class. Second, classifications achieve what Sokal (1974) called, an 'economy of memory'. Just as language allows us to attach convenient labels to things to aid communication, classifications provide a consistent spatial context for monitoring, inventory, reporting and reference. Indeed, most languages use common words to classify running waters according to their size (e.g., rill, rivulet, brook, creek, stream, river). Third, classifications are easy to understand and manipulate such that new objects can be easily classified. Fourth, classifications represent hypotheses about how we think ecosystems behave. Ideally they are probabilistic representations of ecosystem classes, based on sound theory, and treated as hypotheses rather than definitive representations of reality (Goodwin, 1999). They stimulate interest and raise questions about how the perceived order was generated (Sokal, 1974).

Yet, a major challenge facing freshwater ecosystem classification is the lack of an explicit link between the objectives of conservation management and the design of a fluvial classification system or its associated end points (e.g., maps and categories, Soranno *et al.*, 2010). Fluvial classifications can help satisfy many specific management purposes including: mapping areas expected to contain unique species; assessing ecosystem sensitivity (e.g., to pollutants, dams, water extraction); providing a common ecosystem framework for monitoring and reporting; and characterising reference physical conditions. But no single classification can serve all purposes. Care must be taken to ensure that managers and decision makers are involved in the design of classification systems intended for their use.

An accepted way to test the strength of a classification is to determine whether or not ecosystem classes correspond well with sampled data on biotic communities (e.g., fish) within each class (Van Sickle, 1997; Hawkins *et al.*, 2000; Snelder *et al.*, 2004). Such tests are presumably most suited to an examination of classifications designed to capture diversity in particular taxonomic groups at specific scales. Most ecosystem classifications are not designed to be the best framework for any one particular suite of species or resource but rather are designed as research, assessment and management aids (Omernik & Bailey, 1997). Other valid criteria to assess the utility of a classification can be considered as well (e.g., cost, ease of use, theoretical grounding).

Some have argued that classification is one of the earliest endeavours in a new field of study (Goodwin, 1999). According to this line of reasoning, classification eventually gives way to the development of empirical relationships, which in turn lay the foundations for overarching theories (or laws), under which the fundamental processes of interest are understood (Goodwin, 1999). Although theory frequently follows methodological innovations in classification, many classification systems are based on *a priori* logical or philosophical grounds, and both approaches have their advantages and disadvantages (Sokal, 1974). Certainly, many authors in various parts of the world describe their country's fluvial classification system by first establishing a conceptual basis for the classification itself (e.g., Wiley, Kohler & Seelbach, 1997). Bailey, Zoltai & Wiken (1985) argued that it is imperative to clarify and elaborate on the conceptual underpinnings of a classification to improve communication and understanding. Indeed, one of Goodwin's (1999) recommendations was that fluvial classifications should have a sound foundation based on empirical laws and stream theory.

Scientific researchers tend to be well aware that theories, understanding and technologies change through time and are profoundly influenced by paradigm shifts (Kuhn, 1962). Despite a general recognition that the ways in which rivers are conceptualised influences the development of aquatic ecosystem classifications (Hudson, Griffiths & Wheaton, 1992; Gordon *et al.*, 2004; Thorp, Thoms & Delong, 2008), there has been little or no discussion of the implications these influences had on conservation planning and resource management. This article fills that gap by providing a historical examination of theoretical developments in stream ecology as they relate to fluvial classification. We make brief detours to outline salient technological advances that have in turn played a role in shaping our efforts to classify fluvial ecosystems.

Organisation of this review

We organise our discussion of conceptual influences on fluvial classification into three phases, each distinguished by theoretical, analytical or technological advances. The first phase (late 1800s to early 1900s) is distinguished by stream geomorphic perspectives that were influenced by Darwinian metaphors. The metaphorical explanation by Davis (1899) of '*The Geographical Cycle*', as an evolution of streams and landforms through *young*, *mature* and *old* stages, provides a suitable example of how theoretical developments in other fields can be seen to influence stream classification. This period was also marked by a tension between seemingly dogmatic ideas about climax community types and debate about the importance of chance events in the field of ecology. The second phase is marked by a quantitative revolution in stream geomorphology as well as by ideas that nature is ordered, mechanistic and predictive (though the latter view of the balance of nature has origins that date back much further in time – Botkin, 1990; Cuddington, 2001). During this period, the law of stream numbers was derived and extended (Horton, 1945; Strahler, 1957; Shreve, 1966). The third phase is delineated by the 'age of the computer' as well as by technological and analytical advances that allowed data to be collected at increasingly large spatial extents and higher resolutions (e.g., remote sensing technologies). Concepts from the field of landscape ecology have been incorporated into stream ecology and classifications for the last several decades (see Johnson & Host, 2010 for an in-depth discussion on landscape approaches to the study of aquatic ecosystems). Many recent aquatic classifications have an *a priori* logical grounding in hierarchy theory, aiming to integrate ecological and physical aspects of rivers across hierarchical scales. We examine how the logic of hierarchy theory is applied in these classifications. Finally, we come to the present day. The social context is one in which communications are increasingly made using digital data sent via computer networks. Digital mapping and visual analysis are usurping the pre-eminence of text (Schuurman, 2000). Fair access to adequate remotely sensed data as well as spatially explicit information on species distributions, abundance and models in digital formats are widely needed around the world to help identify priority areas for conservation (Scholes *et al.*, 2008). Modern ecosystem classifications stand to benefit from these digital mapping technologies. Certainly they need to remain flexible enough to sustain changing conceptual models and policy frameworks. We suggest a way forward for conservation and resource

management practices that rely on classifications of ecosystem types.

Before we proceed, however, we wish to caution the reader that our portrayal of these three periods of conceptual influences as linear and distinct is rather subjective. We fully admit that theoretical and conceptual ideas have overlapping periods of influence and that intellectual developments tend to be much more patchy and halting than we depict them. However, we believe that our portrayal has heuristic value by providing the reader with some insight into the literature. Moreover, these periods or phases have been well recognised by both historians and scientists. For example, the quantitative revolution was described by Burton in 1963, and the age of the computer is recognised by many scientists as the 'information age' or the 'digital age' (Sokal, 1974; Wilson, 2003), and these phases are linked to key methodological and technological advances.

Early Darwinian perspectives

The earliest phase in the development of theoretical ideas in stream ecology (between 1890 and the 1940s) was marked by the influence of evolutionary theory and the newly established field of ecology itself. Terms like *biome* (Clements, 1916), *ecosystem* (attributed to Tansley, 1935), *niche* (Grinnell, 1917), *ecological succession* (Clements, 1916) and *climax communities* (Clements, 1916) were introduced (Fig. 1). During this phase, William M. Davis, a professor of physical geography at Harvard University, used Darwinian metaphors to describe his cyclic theory of land formation and stream origin (Stoddard, 1966). Davis suggested that streams have evolved through a cycle of distinct stages from young to mature and old (Davis, 1899; Fig. 1), incorporating the organismal metaphor of ageing as well.

A young land-form has young streams of torrential activity, while an old form would have old streams of deliberate or even of feeble current."..."A whole series of forms must be in this way evolved in the life history of a single region, and all the forms of such a series, however unlike they may seem at first sight, should be associated under the element of time, as merely expressing the different stages of development of a single structure."

W.M. Davis (1899)

Davis believed that evolutionary principles could bring diverse facts together into meaningful relationships, and he promoted the application of evolutionary concepts in all lines of study (Stoddard, 1966). Indeed, his ideas were enormously popular most likely because they provided a

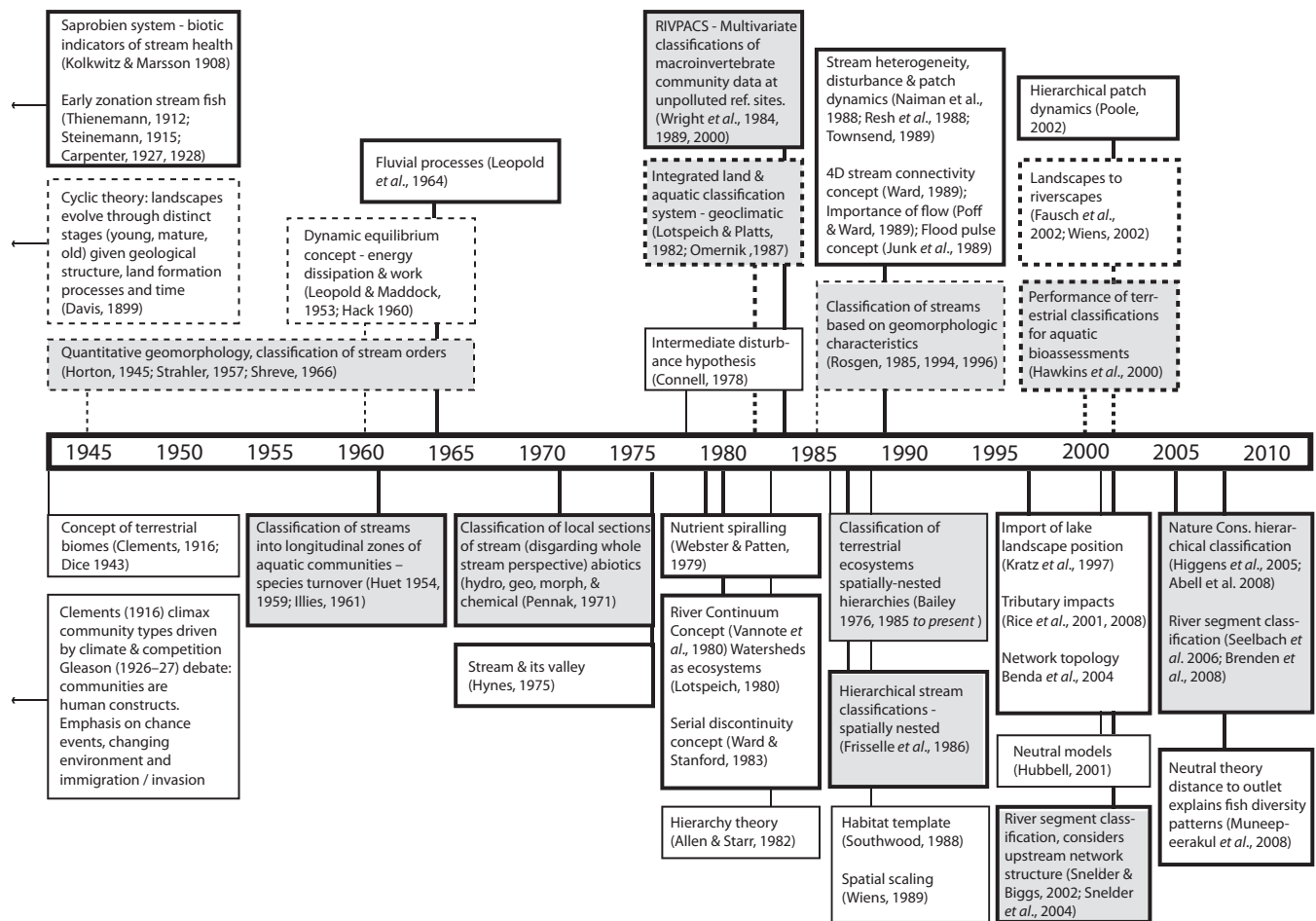


Fig. 1 Timeline of significant theoretical contributions to stream ecology with an emphasis on those that have influenced aquatic classifications. Note that concepts are not necessarily fixed in time; they develop, overlap and intermingle with other ideas over the entire timeline with different levels of emphasis. Line types relate to developments in different fields: stream geomorphology (*thin dashed*), ecology (*thin black*), stream ecology (*thick black*), integrated terrestrial-aquatic systems (*thick, dashed black*); shaded boxes denote particular aquatic classifications.

resonant unifying principle at the time; he brought a varied taxonomy of nominal stream classes together into an orderly progression of development. But what for Darwin was a process of speciation became for Davis a history of individual stream origin and ageing (Stoddard, 1966). Davis classified streams according to their underlying geological structure, the processes that shape land formation, and stages through time. Cyclic theory assumed that all streams and landforms erode towards a base grade after an initial uplift in the earth's crust: this process of erosion advanced streams through stages of youth (and irregular stream gradients), maturity and old age (to streams with smooth low gradients). Unique features of streams themselves were largely ignored, and the importance of chance events and random variation was exchanged for Newtonian orderliness and temporal determinism (Stoddard, 1966). Random variation, stochasticity and chance were also largely ignored, possibly

because well established *a priori* theological arguments about design were dominant at the time (Stoddard, 1966).

Frederic Clements, an American contemporary of Davis, wrote about succession and climax community types in the field of plant ecology, adopting a similar perspective to that of Davis concerning temporal determinism (Stoddard, 1966). Using metaphorical terms that linked development of a climax community to development of an organism through stages of growth, maturity and death, Clements (1916; Fig. 1) suggested that climax communities were analogous to organic entities that go through 'a series of invasions, a sequence of plant communities marked by change from lower to higher life-forms.' Around the same time, Shelford (1911) classified fish communities in different reaches of streams draining into Lake Michigan, suggesting that the graded distribution of fish species from source to mouth could be explained by temporal ecological succession. He suggested that fish communities

in the 'youngest' headwater streams were most similar to each other and that these communities were displaced successively further downstream by fish communities associated with progressive stages of stream maturity (i.e., in the 'older', longer streams with more gradual gradients). The ideas of Davis and Clements on ecosystem development and succession had an impact well into the mid-twentieth century as reflected in Shelford's writings (1911) and in later writings by Margalef (1960) and Odum (1969), both of whom wrote explicitly about ecosystem maturity and immaturity.

By contrast, Western European river classifications in the early part of the twentieth century were developing along somewhat independent lines of thought (reviewed in detail by Hawkes, 1975). Early German biologists, such as Thienemann (1912) and Steinmann (1915), worked on the fauna of mountainous streams and described river zones in utilitarian terms according to the dominant game fish species that were present (i.e., trout, grayling, barbel, bream and flounder). Classification of rivers by longitudinal zonation was generally accepted and taught in many standard German textbooks early in the twentieth century (e.g., Steinmann, 1915, Thienemann, 1925), and the zonation concept spread to other parts of Europe and the world (Carpenter, 1927; Huet, 1959; Illies, 1961). Later research focused on refining longitudinal zones in different regions of the world: to determine their general applicability; to describe associated biota such as invertebrate fauna (e.g., Thienemann, 1925; and many others); to characterise the ecological types of zones and their animal associations (e.g., calm eddies or backwaters with characteristic surface skimming Hemiptera, Carpenter, 1927, 1928), and to quantify the physiographic, morphometric (Huet, 1954, 1959) and related physicochemical conditions of zones ordered sequentially along a stream (e.g., Carpenter, 1927, 1928; Illies, 1961; Fig. 1).

In the German literature on longitudinal zonation, as well as in pursuant work written in English, terms like biotope (from the German word, *biotop*) and biocoenosis were used. Biotope was used to describe a region (or longitudinal stream zone) with a particular set of environmental conditions plus the biotic community, or *biocoenosis*, of plants and animals associated with that region. According to Hawkes (1975), a biotope can describe the basic ecological unit of a river, but because fish range over large areas, fish zones embrace several different biotopes (Hawkes, 1975). These terms differ somewhat from the term biome (*sensu* Clements), which relates more to early notions of climax plant and animal communities as well as succession. The meaning of the word biome, however, has changed since its inception and

the term is now frequently recognised to be a region on earth where climate and geology interacts with biota and substratum to produce large, easily recognisable community units (Odum, 1971; Odum & Barrett, 2004). Many current land-based (Dice, 1943; Hills, 1961; Aldrich, 1966; Bailey, 1983) and a few global freshwater classifications at broad spatial scales are based on the biome concept (Illies, 1978; Abell *et al.*, 2008; Fig. 1).

By the 1940s, both the cyclic theory of stream formation and classical ideas about community succession had fallen out of favour in response to a variety of concerns. There was growing awareness that the Earth's crust is mobile, and that climate and geomorphic processes are in continual states of flux that are not inevitably cyclic (Ortne, 2007). The cyclic theory of landforms proved to be too limited in its description of stream types and was later replaced by principles of dynamic equilibrium (Leopold & Maddock, 1953; Leopold, Wolman & Miller, 1964; Fig. 1), which emphasised a balance between energy dissipation and energy use efficiency (work) along a stream continuum (Hack, 1960; Fig. 1). In terms of community succession, the importance of chance events, a changing environment, ecological gradients, immigration and invasion were increasingly recognised as strong drivers of community composition (Gleason, 1926, 1927; Whittaker, 1953).

How did these early ideas influence conservation planning and resource management, and what are the implications of these influences? The idea that streams progress deterministically through successive stages of development in time (*sensu* Davis) seemed to create a veil, most prevalently in North America, that barred analysis of the full scope of variability in these systems for up to 50 years. A great deal of work during the early Darwinian period focused on understanding general patterns of longitudinal zonation, and this research did prove useful in river and fish management (e.g., in determining fish stocking policies and for flow regulation, Hawkes, 1975), although it is now recognised that the concept of faunal zones has limitations due to historic, geographic and climatic influences (Hawkes, 1975). In addition, zones are sometimes separated by such long transitions that the transitions between zones are longer than the zones themselves. Generally, no evident demarcation between recognisable biotic communities can be observed, but rather there are gradual transitions in species associations, interrupted by marked changes below significant tributaries (Hawkes, 1975; Bruns *et al.*, 1984). It has proven difficult to divide rivers up into distinct biotic community types when the majority of aquatic species are able to disperse large distances up and downstream, utilising

lakes and tributaries during different life stages. Moreover, when climate and physiography are considered, geographically distinct freshwater basins and catchment boundaries do not generally match up neatly with known climatic and physiographic zones (Omernik, 1987). Any attempt to force continuous variables and diverse systems into stereotyped categories may be doomed (Usinger, 1956), but broadly based ecological classifications can prove useful for conservation, management and a generalised understanding. In the 1940s, researchers recognised the need for a quantitative and predictive understanding of stream ecology and geomorphology. The quantitative revolution was about to begin.

Quantitative revolution

The fields of geography and stream geomorphology underwent a radical shift in the 1940s as researchers emphasised the pre-eminence of using mathematical equations, deterministic models and inferential statistics in the advancement of their work (Burton, 1963). Strahler (1957) reasoned that classical *descriptive* analysis of land-form evolution and stream origin was of little practical value in engineering and military applications. Not surprisingly, military applications were on many people's minds during World War II and the decades that followed (e.g., Strahler, 1952a). Mathematical models and quantitative methods gained acceptance as higher forms of scientific achievement than those of qualitative study because they could be used to make reliable predictions (Strahler, 1952a; Burton, 1963). This belief in the superiority of numbers, measurement and quantitative analysis has led to enduring debates about the merit of scientific positivism in the field of geography (see Schuurman, 2000; for a review). Most believe that quantitative analyses are here to stay (Burton, 1963).

Robert Horton (1945; Fig. 1) was a pioneer in quantitative stream geomorphology. He developed a system of stream ordering which effectively inverted earlier European attempts to classify streams on the basis of branching or bifurcation (i.e., Gravelius, 1914). Rather than designate the extensively branched main stem as order one, Horton designated all small, unbranched, headwater tributaries as order one, reserving the highest orders for the main stem. In this system, later refined by Strahler (1952b), streams receiving tributaries have their order increased to $n + 1$ only in cases where an incoming tributary has order n , and where n is the order of the main stem branch. Horton (1945) derived two famous laws using this system of stream classification: the law of stream numbers and the law of stream lengths. These laws

take the form of inverse geometrical series that relate number (or length) of streams in different orders to dimensionless properties of the drainage basin, such as stream bifurcation ratios and stream-length ratios.

Ronald Shreve (1966; Fig. 1) went on to show that the law of stream numbers arises as a result of a large number of randomly merging stream channels, dictated by the laws of chance as much as governed by the general tendency of erosional processes to produce dendritic networks. He showed that in the absence of (local) geological controls, the branching of stream segments in a drainage basin will be topologically random. Work by Horton, Strahler and Shreve on stream network geomorphology is still highly relevant today, and these works will very likely generate a resurgence of interest given the current push to understand influences of stream network topology on lotic ecosystem function (Benda *et al.*, 2004; Grant, Lowe & Fagan, 2007; Poole, 2010). Stream order encapsulates compound hydrological and geomorphic information, providing an indication of stream size, power and position in the drainage network (Poole, 2010).

Numerous modern freshwater classifications use Strahler's stream order directly as one piece of information in multi-scale, multi-metric classifications that aim to provide an overall indication of river character (e.g., Frissell *et al.*, 1986; Snelder & Biggs, 2002; Higgins *et al.*, 2005). However, stream order can be considered a subjective measure for a variety of reasons: assignment of stream order varies depending on selection of a particular mapping scale, it is difficult to map the origin of perennial streams and stream segments of the same order can have vastly different discharge (Poole, 2010). For these reasons, catchment or drainage area is often used in place of stream order in aquatic classifications (e.g., Snelder, Dey & Leathwick, 2007; Brenden, Wang & Seelbach, 2008; Soranno *et al.*, 2010).

Also during the quantitative revolution, Leopold & Maddock (1953) described longitudinal profiles of streams using a series of eight predictive equations for flow, discharge, particle size changes, changes in sediment concentration, slope, bed and bank erodability, as well as energy dissipation and work. Amongst others, most notably Hack (1960; Fig. 1), these authors developed the theory of dynamic equilibrium to explain how regular changes downstream in key physical characteristics (i.e., width, depth, sediment and discharge) are related to regular enlargements of drainage area and a balance between the processes of erosion and the resistance of rocks undergoing uplift. Assuming that erosion and uplift occur at constant rates, dynamic equilibrium suggests that high topographical relief creates great potential energy,

which provides enough erosional energy to balance the uplift. This then leads to a steady state in topography as long as similar rocks are exposed at the surface (Hack, 1960). The theory of dynamic equilibrium replaced Davis' cyclic theory of stream origin, and emphasis in stream geomorphology shifted from a focus on equilibrium processes in evolutionary time (i.e., producing gradual reductions in stream topography) to equilibrium processes in space (i.e., producing longitudinal adjustments in stream topography, Hack, 1960).

The River Continuum Concept (RCC) is really the biological analogue to this theory of dynamic energy equilibrium in geomorphology (Vannote *et al.*, 1980; Fig. 1). Biota are seen to respond to longitudinal patterns in the physical and hydrological characteristics of a stream: organic matter from surrounding riparian areas is differentially loaded, transported, used and stored along the length of a river; and consistent downstream patterns of community structure and function are the result (Vannote *et al.*, 1980). The RCC has had considerable influence on research in stream ecology over the last quarter century (Poole, 2010). The concept represents an elegant, idealised and simplified view of community changes along a river continuum under conditions of dynamic equilibrium in physical conditions. However, when heterogeneities, discontinuities, stream network confluences, lakes chains and tributaries are ignored, the RCC can become an over-simplified, perhaps even dogmatic conceptual scaffolding (Poole, 2010).

Research on longitudinal zonation in Europe during the early 1900s was another obvious precursor to Vannote's RCC, and this observation highlights the nonlinear and patchy nature of periods of conceptual influence. For instance, Kathleen Carpenter (1927, 1928) examined and classified biotic associations between macroinvertebrates and fish in longitudinal zones of Cardiganshire (Wales) streams that varied in their physical and chemical attributes. One of the very first zonation schemes she would have been exposed to in her work on mineral pollution from lead mining (Carpenter, 1924, 1925) took water quality and anthropogenic influences into account (Kolkwitz & Marsson, 1908, 1909). Carpenter's German contemporaries, Kolkwitz & Marsson (1908, 1909), distinguished four different river zones: polysaprobic or extremely polluted; α -mesosaprobic & β -mesosaprobic or severely to moderately polluted; and oligosaprobic or slightly polluted. Their zonation scheme focused on organic matter pollution and differences in the presence of organisms that process decaying organic matter (i.e., the *saprobies*) in addition to the level of oxygen in the system. Whereas Carpenter's research may have been a

precursor to both the RCC and multivariate classifications of macroinvertebrate communities in relation to physico-chemical variables (Wright *et al.*, 1984; Marchant *et al.*, 1985, 1997), the 'Saprobien System' for biological assessment of pollution is a good example of where the metaphor of stream health and 'self-purification' was galvanised.

The notion that ecosystems can be healthy stems from a combination of metaphors: one that the earth is a well-organised and '*beautiful machine*' (Hutton, 1788; writing incidentally at a time of increased mechanisation during the industrial revolution; Scrimgeour & Wicklum, 1996), and two that the earth is an organised body, which may be naturally repaired again and again (Hutton, 1788; cited in Scrimgeour & Wicklum, 1996). There is some discussion in the literature about whether or not the 'health' metaphor is appropriate in a scientific context, on the one hand suggesting that the concept is obviously value-laden, and on the other suggesting that 'health' is not an observable ecological property (Scrimgeour & Wicklum, 1996; Gordon *et al.*, 2004). However, the idea of ecosystem health has wide public appeal and stream managers can draw on a universal understanding of personal health to effectively communicate results of scientific pollution assessments in streams to the general public and policy officials (Gordon *et al.*, 2004). Classifications of stream health have been widely employed using a variety of assessment approaches that measure physicochemical, habitat-based, hydrological and/or biotic aspects of streams (Gordon *et al.*, 2004 and references therein).

Longitudinal zonation and related biologically based assessments of stream health are still often used to classify river types, and they are a central component of the European Union (EU) Water Framework Directive (Council of the European Communities, 2000; Gordon *et al.*, 2004). Numerous studies report zonation patterns in fish (contemporary studies include Petry & Schulz, 2006, Brazil; Ibanez *et al.*, 2007; Africa; Noble, Cowx & Starkie, 2007; England and Wales) and macroinvertebrate communities (e.g., Reese & Batzer, 2007), suggesting that zonation has broad relevance for assessments of expected stream diversity in relation to environmental conditions. In the UK, multivariate classifications of macroinvertebrate community data at unpolluted reference sites were used by Wright *et al.* (1984); Wright, Armitage & Furse (1989); Wright, Sutcliffe & Furse (2000) to develop a system for the biological assessment of water quality (the river invertebrate prediction and classification scheme or RIVPACS, Fig. 1). The Australian river assessment system (AUSRIVAS) is also based on RIVPACS principles and

methodologies such that observed richness of macroinvertebrate communities can be compared with an expected richness derived from measurements at unpolluted reference sites (Simpson & Norris, 2000; Turak *et al.*, 2011).

Most research in this area benefited from increased computing power and analytical developments made during the 'age of the computer', but they are discussed in this section because longitudinal zonation and studies of river continua have occurred throughout the 21st century. Technological advances in multivariate statistics and clustering allowed predictive modelling of community types from continuous environmental data. Numerous analytical methods were more easily executed with the aid of computers. For example, RIVPACS was promoted as a '*computer-based system*' in 1989, designed to perform multivariate biological assessment of freshwater quality (Wright *et al.*, 1989). Two contemporary multivariate analysis techniques were employed: detrended correspondence analysis (DCA, Hill & Gauch, 1980) and TWINSpan (two-way indicator species analysis; Hill, 1979). DCA is an ordination technique that places similar sites together along compound gradients by reciprocal averaging of species data (presence/absence). TWINSpan is a divisive, hierarchical clustering method that finds groups of similar species and sites. Species groupings along DCA axes were then related to physical and chemical variables at each site using multiple discriminant analysis (MDA). These environmental variables were used to predict TWINSpan species groupings with MDA. Many other researchers employ similar approaches (cluster analysis and ordination) to find overlapping groups of species along compound environmental gradients (e.g., Marchant *et al.*, 1985, 1997; Biggs *et al.*, 1990; Turak & Koop, 2008). Recent versions of RIVPACS (Wright *et al.*, 2000) incorporate prediction error estimation and were found to be more accurate than methods based on Illies (1978) freshwater ecoregions (Davy-Bowker *et al.*, 2006).

Reminiscent of earlier deterministic approaches to stream geomorphology created during the quantitative revolution is Rosgen's stream classification system (1985, 1994, 1996; Fig. 1). Rosgen's system was designed from an engineering perspective and is based on the premise that channel morphology is governed by the laws of physics through fluvial processes and readily observable features of stream channels. In Rosgen's system, river valley segments are hierarchically classified into distinct morphological groups based on specific breaks in valley slope, cross-sectional profile, degree of constraint by valley walls, predictably patterned channels and hydraulic

habitats such as pools, glides and riffles. An implicit assumption in Rosgen's system is that if you restore the physical structure of the stream itself, then you restore the important (biotic) aspects of the system. Though his classification methods are widely used in the United States for the design of river restoration projects (Gordon *et al.*, 2004), Rosgen's system has been criticised by several authors for neglecting to adequately consider the surrounding catchment (Gordon *et al.*, 2004), neglecting how species arrive (time dependence) and neglecting to account for multiple stable states and unpredictability (Juracek & Fitzpatrick, 2003).

Clearly, several existing stream classifications are based on ideas developed in stream geomorphology during the quantitative revolution. The prevalence of ideas that physical and corresponding biotic processes in streams are in a kind of dynamic mathematical equilibrium or balanced continuum state is apparent during this period. Usage of mathematical equilibria in ecology can be linked to the 'balance of nature' metaphor, which invokes ideas that nature operates to strike a balance between disparate forces resulting in community persistence and regular fluctuations in populations and species number (Cuddington, 2001). This 'balance of nature' metaphor plays a fundamental role in many fields, and seems to imbue value-neutral terms like 'dynamic equilibrium' with positive and negative connotations (Botkin, 1990; Cuddington, 2001). For example, if all streams can be characterised as gradual and stable river continua with a continuously apt suite of riverine communities, this is a desirable state for conservation and management. However, the idea that river systems are in a state of dynamic equilibrium has provoked some controversy (Schoener, 1987; Townsend, 1989). Botkin (1990) argued that such equilibrium views are outdated and no better than believing that nature is like a mechanistic machine: constant, ordered and deterministic.

Age of the computer, hierarchy and scale

If the period following World War II can be described as a quantitative revolution for its emphasis on quantitative modelling, prediction and control, the period since 1970 can be described as a truly expansive age: the age of the computer, hierarchy and scale. As numerous authors note, we have witnessed huge expansions in our technological sensory perception over the last 40 years: remote sensing satellite platforms allow us to view the world from multiple spatial and temporal scales whereas a profound increase in computing power has allowed us to automate data collection and changed the way we process large

amounts of information. A by-product of the use of computers is the development of algorithms for classification, which has led to more objective and efficient approaches to classification (Sokal, 1974), as discussed above. In response to the availability of environmental information at increasingly large spatial scales, the fields of landscape ecology and geographic information science (GIS) were established, providing us with ways to understand and study ecology at multiple spatial and temporal scales. In the paragraphs that follow, we describe how concepts from the fields of landscape ecology and GIS were incorporated into stream ecology and fluvial classification.

In the early days of this period, Hynes (1975) published an article on the importance of the valley surrounding a stream to the maintenance of key processes, characteristics and functioning in the stream environment. He urged his colleagues to truly appreciate that '*the valley rules the stream*', and he did so by reviewing the cycling of ionic, organic and energetic (allochthonous) inputs from the surrounding land. He emphasised that streams are largely heterotrophic, deriving most of their energy (and inputs) from uphill. His article was in part a pithy reaction against field-scale stream classifications (e.g., Pennak, 1971; Fig. 1) based solely on abiotic fish habitat characteristics measured at fine spatial scales. Hynes (1975) shifted the emphasis in stream ecology towards incorporating factors and processes that operate beyond the site level.

The highly influential RCC (Vannote *et al.*, 1980), mentioned previously, soon provided the framework to link multiple processes along a longitudinal river continuum, from headwater streams in upland areas to mid- and larger order river ecosystems (Johnson & Host, 2010). Around the same time, it was recognised that longitudinal and lateral movement of water along streams creates a nutrient spiral (Nutrient Spiralling Concept, NSC, Webster & Patten, 1979), which transports nutrients downstream from areas that have reached their in-stream capacity to recycle nutrients (Gordon *et al.*, 2004). An enormous body of work conducted over the last quarter of a century stemmed out of the structural and functional predictions, refinements and limitations of the RCC and NSC (Johnson & Host, 2010; Mulholland & Webster, 2010; Poole, 2010). Advances following these conceptual developments reasonably mark the birth of a new era in the field of stream ecology, but these advances were not easily implemented into aquatic classificatory frameworks. It is difficult to develop science-based policy to protect flowing water ecosystems that vary continuously over multiple terrestrial ecoregions. In addition, established aquatic classification methods such as early stream zonations

(Illies, 1961) and stream engineering approaches (Rosgen, 1985) had institutional momentum, exerting historical constraints on classification frameworks (Ward, Robinson & Tockner, 2002).

Shortly after the RCC was introduced, Ward & Stanford (1983) proposed the 'Serial Discontinuity Concept', recognising that the RCC did not adequately account for disruptions in the continuum (such as reservoirs) that interrupted the natural longitudinal pattern. Bruns *et al.* (1984) examined how tributary streams modify the RCC where the magnitude of modification depends on tributary size relative to the mainstem and the physical, chemical and biological characteristics of the tributary (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004). Junk, Bayley & Sparks (1989) suggested that the main driver of aquatic biomass and diversity in rivers is the large pulse of discharge and lateral exchange between the floodplain and the river channel that occurs during periodic and seasonal flood events – the 'Flood Pulse Concept'. Their views stood in contrast to the RCC, which emphasised the longitudinal transfer of nutrients and organic matter downstream. Ward (1989) described a four dimensional framework for flowing waters that included the longitudinal (e.g., RCC and NSC), lateral, vertical and temporal dimensions.

In the same year, Poff & Ward (1989) wrote a groundbreaking paper that integrated many of the then current ideas in stream ecology. These authors described a conceptual model relating the importance of flow disturbance and variability to processes that structure lotic communities, and their model effectively classified streams into nine types, from harsh intermittent to perennial flashy, snowmelt driven, and mesic groundwater-sourced. Their working hypothesis was that high variability and/or unpredictable flow regimes result in a physical environment in which abiotic processes are the main drivers of lotic community patterns, whereas low variability and predictable stream flow result in an environment in which biotic interactions (i.e., competition and predation) are stronger drivers of community structure. Poff *et al.* (1997) suggested that a wide range of hydrological variability is critical to sustain the ecological integrity of stream ecosystems. To best conserve and restore stream ecosystems, managers should restore the natural flow regime as closely as possible to its natural pattern of variability (Poff *et al.*, 1997).

Recognition of the role of disturbance in stream ecology and the intermediate disturbance hypothesis developed by Joseph Connell in the field of ecology (IDH, Connell, 1978; Fig. 1) challenged both the dominant paradigm of dynamic equilibrium (i.e., of the RCC and Leopold &

Maddock, 1953) and the view that ecological communities were deterministically structured (Death, 2010; Stanley *et al.*, 2010). With these developments, emphasis shifted from studies that emphasised community turnover and biotic interactions towards studies that emphasised the importance of disturbance. For example, Townsend & Hildrew (1994) focused on classifying stream environments into habitat templates along two dimensions: temporal heterogeneity as a function of disturbance frequency and spatial heterogeneity as a function of changes in the physicochemical environment. Their habitat classification was designed to be used as a testable predictive model that described differences in species traits and community characteristics. Species richness was expected to peak at intermediate levels of temporal variation.

Stochastic disturbances from droughts, floods, confluences and tributaries, in addition to gradual downstream physical changes, competition and other biotic factors, are now thought to be the major driving forces behind community structure in streams (Resh *et al.*, 1988; Poff, 1992; Lake, 2000; Rice *et al.*, 2001, 2008; Fig. 1). Lake (2000) described how these disturbances create patchiness in the stream environment. During floods, large volumes of water move and redistribute bottom materials (sand and rocks), plants, detritus, snags and debris, resulting in the removal and displacement of biota. Recovery can be rapid depending on whether or not the biota has access to environmental refugia. Droughts generally cause a dramatic reduction in stream habitat as the loss of water traps biota without access to refugia. Water quality deteriorates, temperatures climb and pools begin to form. These patchy environments do not necessarily form uniformly throughout a catchment. For example, deeper downstream pools may persist longer than shallower upstream ones (Lake, 2000). Rice *et al.* (2001) hypothesised that tributaries and confluences are responsible for moderate and large-scale variations in stream characteristics along river channels as they add water, sediment and organic matter to the main channel. These physical changes have an important impact on in-stream biotic communities (Rice *et al.*, 2008), and on how we view classification of stream tributary networks.

Themes of patchiness (Naiman *et al.*, 1988; Townsend, 1989; Lake, 2000; Fig. 1), habitat heterogeneity (Southwood, 1977), stochastic and temporal disturbance (Resh *et al.*, 1988; Southwood, 1977; Fig. 1), habitat templates (Townsend & Hildrew, 1994) and hierarchical scaling (Frissell *et al.*, 1986; Fig. 1) thus arose in the field of stream ecology over the last quarter century; and these themes have obvious links with the field of (landscape) ecology

and GIS (Benda *et al.*, 2004; Johnson & Host, 2010). Naiman *et al.* (1988) suggested that it might be more informative to view lotic systems as a collection of resource patches, a river mosaic, rather than a river continuum, taking their cue from landscape ecologists like Forman & Godron (1986). The idea that a river contains a mosaic of resource patches focused attention on the inherent habitat heterogeneity of the system and implied that the spatial distribution and structure of these patches can be investigated relative to both longitudinal (upstream-downstream) and lateral (channel-riparian) linkages in energy and material exchange (Naiman *et al.*, 1988). These authors proposed that lotic patches can be classified by quantifying the scale and intensity of processes that create and maintain patch boundaries at hierarchical spatial and temporal scales (as per Frissell *et al.*, 1986).

More recent papers by Fausch *et al.* (2002), Poole (2002) and Wiens (2002) continue to stress the importance of applying key concepts and techniques developed in the field of landscape ecology to rivers, and the value of doing research at hierarchical spatial and temporal scales. For example, Fausch *et al.* (2002) highlight three key landscape ecological concepts that can be transferred to rivers: one, the importance of spatial scaling, where both grain (spatio-temporal resolution) and extent (study area and duration) dictate the scale of processes that can be understood (Wiens, 1989); two, the scale dependence of patch heterogeneity; and three, ecological processes that operate at landscape scales. Poole (2002) proposed a hierarchical patch dynamics (HPD) perspective to describe the discontinuous nature of a river punctuated by confluences: the HPD views lotic ecosystems as a discontinuum of hierarchically nested and interactive elements in which the functional linkages across scales need to be studied.

In his review of the role of disturbance, Death (2010) points out that patch dynamic models rely on trade-offs between the colonisation ability and competitive ability of organisms for which there is little evidence in stream communities. He reasons that many aquatic organisms are highly mobile and tend to have disjunct life history stages, suggesting that dispersal ability rather than niche diversification is the dominant factor shaping community structure in rivers. Fittingly, Hubbell's (2001; Fig. 1) neutral model of community structure has stimulated much interest due to its emphasis on the role of dispersal in structuring aquatic communities (e.g., Muneerpeerakul *et al.*, 2008; Fig. 1).

Despite all these advances in stream ecology, progress in terrestrial classification systems far surpassed aquatic ecosystem classifications during the age of the computer,

hierarchy and scale. Terrestrial landscapes are often perceived as nested spatial hierarchies in which different levels correspond to structural and functional units at distinct spatial and temporal scales (Bailey, 1976, Bailey, 1985). The idea that well developed complex ecosystems are essentially hierarchically structured is a predominant view in ecology today (Wu & David, 2002). Hierarchies simplify complex ecosystems by identifying the characteristic scales and extents of key ecological processes and disaggregating the landscape into homogeneous structural and functional units that are increasingly detailed at lower and lower levels (Valentine & May, 1996; Wu & David, 2002). There are many examples of spatially nested hierarchical land-based classifications of ecosystems in the literature (e.g., Bailey, 1985; ECOMAP, 2007; Crins *et al.*, 2009; Fig. 1), and these types of classifications are used around the world for conservation planning and assessment. Such regionalised classifications subdivide land according to observed patterns of variation in vegetation communities (often from the top-down) and they generally have their theoretical underpinnings in Allen & Starr's (1982) hierarchy theory from the fields of complex systems analysis and landscape ecology. Several authors attempted to integrate terrestrial classifications with aquatic ecosystem processes (Lotspeich & Platts, 1982; Omernik, 1987) but considerable research indicates that terrestrial landscape classifications have limited application in aquatic bioassessments (reviewed by Hawkins *et al.*, 2000; Fig. 1).

Logic of hierarchy theory and modern aquatic classifications

Frissell *et al.* (1986) were the first to apply Allen & Starr's (1982) conceptual framework of the hierarchical nature of ecological systems to stream habitat classification. In their framework, whole streams (10^3 m) are less susceptible to disturbance than segments (10^2 m), reaches (10^1 m), pools/riffles (10^0 m) and microhabitats (10^{-1} m). Each level in the system is controlled by processes operating over shorter and shorter temporal periods from evolutionary processes (glaciation to annual sedimentation) to developmental processes (e.g., from denudation to the break-down of organics). They recommend a number of general, invariant variables for classification at each level (segment, reach, pool/riffle, microhabitat), which relate to processes of interest in aquatic habitat classifications. Today, streams are generally described as natural hierarchical systems in which climate, geology and topography at large scales set the context for geomorphic processes that maintain heterogeneity at smaller scales (Fausch *et al.*, 2002). More than a few authors suggest that

hierarchical classification systems should be of fundamental value in assessing conservation potential in aquatic systems (e.g., Naiman *et al.*, 1992; Hawkins *et al.*, 2000; Snelder & Biggs, 2002). Hierarchical aquatic classifications in use currently have uppermost levels at scales much larger than Frissell *et al.*'s original classification (e.g., at ecoregional scales up to 10^5 – 10^6 km²; Higgins *et al.*, 2005; Soranno *et al.*, 2010).

Hierarchical aquatic ecosystem classifications such as that of Higgins *et al.* (2005) are generally created from the top down by subdividing a unit of land according to observed patterns of variation in zoogeographical species distributions and catchment boundaries. In practice, upper levels are often essentially sketched on the basis of expert opinion and knowledge of post-glacial expansion limits, climate constraints and physiography (Omernik, 1987; Higgins *et al.*, 2005; Kleynhans, Thirion & Moolman, 2005; Abell *et al.*, 2008). Lower level groupings are typically created from the bottom up by clustering fluvial attributes of interest (Seelbach *et al.*, 1997, 2006; ECOMAP 2007). Bottom-up approaches differ in principle from the identification of spatially homogeneous freshwater ecoregions and subregions because they group sites together based on similarities in environmental or biological attributes, independent of their geographical location. Bottom-up, place-independent approaches may be more ecologically relevant (Leathwick *et al.*, 2011).

Given that numerous recent classification systems have their conceptual underpinnings grounded in hierarchy theory, we briefly examine herein how the logic of hierarchy theory is applied in these classifications. First, a bit more background is necessary. Hierarchical classifications assume that larger-scale and longer-term systems or processes set constraints on shorter-term systems operating at smaller and smaller scales (Frissell *et al.*, 1986), and this assumption is generally reflected in the spatially nested hierarchical framework of land-based classifications. Furthermore, hierarchy theory assumes that the relationship between upper and lower levels is generally asymmetrical: upper levels (long-term, large-scale dynamics) exert constraints on lower levels (short-term, small scale dynamics), and lower levels provide initial conditions for upper levels, but small scale dynamics may not have the same impact on the system as a whole (Frissell *et al.*, 1986; Wu & David, 2002). Any event that causes shifts in a large-scale system will change the capacity of all lower-level systems it encompasses, but events that affect smaller-scale habitat characteristics may not affect larger-scale system characteristics (Frissell *et al.*, 1986; Naiman *et al.*, 1992).

Hierarchies can be either nested or non-nested. The classic example of a nested hierarchy is an army, which is made up entirely of its soldiers. Other examples of nested hierarchies come from different fields, such as: molecular biology, where molecules are nested within cells, which are then nested within the tissues of an organ; biological classification, where species are nested within genera, families, orders and so on; land-based classification, where ecodistricts are nested within ecoregions and ecozones; and ecology, where organisms are nested within populations and communities. Military command is an example of a non-nested hierarchy because a general cannot be disaggregated into his/her soldiers (Allen, 1999). Much of the theory described by Allen & Starr (1982) is only pertinent to nested hierarchies where upper levels completely contain the next lower levels (Valentine & May, 1996; Wu & David, 2002).

Whereas it may seem counterintuitive, a river is a non-nested hierarchy in the same way that a phylogenetic tree, or a real tree for that matter, is a non-nested hierarchy (Valentine & May, 1996). The trunk of a tree cannot be divided up into its leaves, just as the main stem of a river cannot be divided up into different headwater streams. Valentine & May (1996) refer to this type of hierarchy as a "hierarchical" positional structure that lacks hierarchical properties. This realisation runs counter-intuitively to much of the literature describing hierarchical stream systems. With few exceptions, most notably work on Michigan's river valley segment classification (Seelbach *et al.*, 2006; Brenden *et al.*, 2008), the literature on hierarchical stream classifications describes stream networks as completely nested hierarchies, wherein all river reaches, pools and segments are equivalently nested within a broader catchment area (as per Frissell *et al.*, 1986; Fig. 2a). Seelbach *et al.* (2006) make a distinction between Frissell *et al.*'s (1986) concept of hierarchically nested

stream segments and a system that differentiates neighbouring segments based on differences in the areas that they drain. This view of nestedness and overlapping catchments is standard in hydrological analyses (Fig. 2). Along these lines, if a river system is nested at all, it may be referred to as a '*directionally nested network*' because the main-stem catchment consists of all headwater catchments above it, but a headwater catchment does not likewise consist of all catchments below it (Fig. 2b). A new conceptual framework is needed to address directionally nested network hierarchies.

We dare speculate that the majority of hierarchical stream classifications may have misinterpreted the principles of hierarchy theory when applied to aquatic systems. Indeed, misunderstandings are common in applications of hierarchy theory (Valentine & May, 1996; Wu & David, 2002; Thorp *et al.*, 2008). Perhaps some of the confusion arises because water in headwater stream catchments ultimately flows through the mainstem and river outlet at some point in time. Water at the outlet is made up of water from most other parts of a river network. But the reverse is not true: water in the outlet does not flow through headwater streams. Moreover, contrary to the assumption in hierarchy theory that smaller-scale characteristics may not affect larger-scale system characteristics, small scale events in headwater streams directionally impact everything in the network below them. Rivers are directed networks (Newman, 2003), and must be considered as such: segments further down in the network cannot be rendered equivalent to segments further up.

We recognise that it is often critically important to consider upstream processes as well. Biota such as fish and adult insects with aquatic larval stages are not restricted to movement in a single direction, though upstream movements may be slower and more energetically expensive (Osborne & Wiley, 1992). Pringle (1997) highlighted the need for more research on downstream-upstream linkages, exemplifying the many human alterations in lower reaches of a river that can produce biophysical legacies in upstream reaches. Urbanisation, aggregate extraction, dams, impoundments and channel modifications are generally situated in the lower reaches of a river and they can cause genetic isolation, population level changes (e.g., immigration of exotic species; loss of native species through source-sink dynamics), and changes in nutrient cycles and decomposition (e.g., when the release of nutrients from decomposing migratory fish is blocked, Pringle, 1997). Models of aquatic networks that adequately account for the directed nature of these systems, the processes of interest, and the importance of

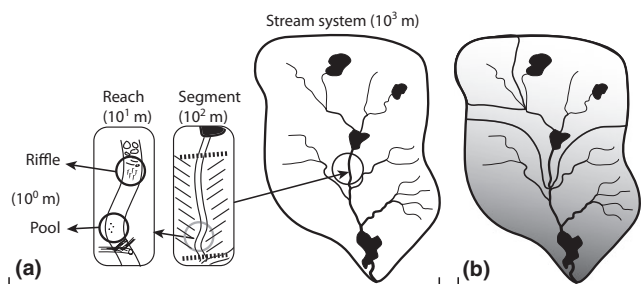


Fig. 2 (a) Frissell *et al.*'s (1986) hierarchy showing all stream segments, reaches, riffles/pools and microhabitats nested within the entire sub-catchment. (b) Example of directionally nested and overlapping catchments typically used in hydrological analysis (figures adapted from Frissell *et al.*, 1986 and Seelbach *et al.*, 2006).

network position could aid in the study of downstream-upstream linkages.

The importance of landscape and network position has not gone unnoticed in the field of aquatic ecology (Poole, 2002), but incorporating these ideas into aquatic classification has just begun. Benda *et al.* (2004; Fig. 1) proposed the Network Dynamics Hypothesis to describe how stream habitat heterogeneity in space and time is a function of the spatial arrangement and relative size of tributaries, resultant confluences and stochastic catchment processes. To classify streams, there is a real need for catchment-based measures of aquatic networks and network positional metrics that relate to aspects of ecosystem function at larger spatial scales.

The way forward

Ideally the aim of classification is to capture the 'true' nature of systems classified. When classes reflect aquatic ecological processes, then by studying the classification, we can determine if those systems behave as expected (Sokal, 1974). Classifications represent how much we know about the systems under study but, once established, an accepted classification system has an institutional momentum. Thus, care must be taken to avoid essentialist systems 'whose philosophical origins date back to Aristotle' (Sokal, 1974). What this means is that sometimes classifications lead to essentialist ideas that assume all things have an underlying or true essence, which conforms to existing concepts and understanding. For example, in reference to the use of land-based classifications in aquatic bioassessments, Hawkins & Norris (2000) suggested that predictions about biotic variation in different ecotypes were rarely based on a mechanistic understanding of how environmental variation at larger scales influenced the biota. Rather, predictions were frequently based on axiomatic statements such as '*if stream segment X flows through ecoregion B, its expected condition is therefore BX*' (Hawkins & Norris, 2000). Such prescriptive statements can lead to assumptions that because one thing follows another, the latter must have been caused by the former. Ehrenfeld (2003) calls this an ancient logical fallacy. Segment X may be influenced as much by upstream processes in other (eco)regions as by local conditions, depending on the ecological process of interest and its direction of flux (Pringle, 1997).

In this article we have reviewed theoretical advances in stream ecology and showed that they are commonly based on metaphors derived from other fields. The process of scientific development routinely relies on the use of metaphor to elucidate novel ideas and metaphor-

ical language can in turn have a profound influence on our thought process (Botkin, 1990; Cuddington, 2001). Metaphors allow us to temporarily escape from established cognitive and cultural norms, and so long as these ideas remain suggestive and transformative, they provide an aid to scientific understanding (Ehrenfeld, 2003). But when the way in which rivers are conceptualised prescriptively influences our interpretation of how things came to be, this can lead to false conclusions and mistakes. Classifications are hypotheses that need to be tested.

So, how should we proceed, besides being cautious, so as to avoid erroneous assumptions that if things are alike in some senses, they are alike in others? To begin with, it is important to ensure that the terminology used to describe aquatic classifications is consistent with theoretical assumptions and knowledge of aquatic hydrology: for example, 'spatially nested' means different things on land and water. In addition, current ideas in the literature on aquatic ecosystem classification and stream ecology support the need for an integrated approach that considers network ecology and the 'fluvial landscapes' of Poole (2002). This is the logical next stage or 'natural progression' of ideas, and as such we can only dimly glimpse where the road ahead will lead - perhaps towards incorporating network theory and directionally nested hierarchies. But can we begin to foresee and avoid some potential issues?

Graph theory and existing network thinking may not be ideally suited to aquatic networks given that rivers have such a restricted, directional structure, but these research areas are likely to be fruitful starting points (Newman, 2003; Grant *et al.*, 2007; Olden *et al.*, 2010). Confluences, lakes or wetlands all form different kinds of breaks in a directed network, and these breaks can be represented by different kinds of 'nodes' and analysed accordingly (Newman, 2003). Even significant geological features such as narrows, rock transformations and waterfalls can form breaks in directed aquatic networks. Certainly it has long been known that geological controls, such as underlying bedrock, structural fractures, tectonics and land formations, can influence stream drainage (Zernitz, 1932), and classifications of drainage network patterns (dendritic, trellis, rectangular, parallel, pinnate, etc.) can provide an indication of the conditions under which networks form (Zernitz, 1932; Mejia & Niemann, 2008). Perhaps measures of network pattern based on expectations from graph theory may provide additional insight. For instance, the shapes of basins tend to be self-similar and dendritic in the absence of structural controls (Mejia & Niemann, 2008), and the average length of channels between confluences (i.e., mean link length) is different for different network

types (Mejia & Niemann, 2008). Parallel networks that follow parallel topographical features such as drumlins (i.e., ridges of elongated hills made up of glacial till) have longer links, whereas trellis or lattice-like networks along folded or tilted strata have shorter links (Ichoku & Chorowicz, 1994).

The physical structure of aquatic networks dictates that headwater systems behave differently from mid- and lower-order systems (Fullerton *et al.*, 2010). Headwater systems tend to be occupied by a suite of different biota, such as colonising specialists with excellent dispersal abilities and species with the ability to withstand more unstable environmental conditions, than downstream systems (Mcgarvey, 2010). Mean annual discharge, channel size, alluvial habitat and contributing area all generally increase in a downstream direction, which results in predictive species-discharge relationships that are similar to land-based, species-area curves (Poff *et al.*, 2001; Mcgarvey, 2010; Olden *et al.*, 2010), albeit streams in arid regions may be an exception because they can sometimes lose flow as catchment area increases. Increases in discharge and contributing area, however, may not linearly correspond with increases in key stream environment characteristics that serve as habitat for a variety of species (Olden *et al.*, 2010). Perhaps we need classifications that treat streams differently according to their network position, stream order or mean contributing area.

Modern classifications need to remain flexible enough to accommodate emerging conceptual models and policy frameworks. Indeed, the need for 'a flexible scheme as fluid as the medium' has long been recognised (Carpenter, 1928). Remote sensing and GIS technologies enhance our ability to monitor spatio-temporal environmental change and these technologies are forging a new era in earth observation (Scholes *et al.*, 2008) that may help us remain flexible. Fittingly, GEOBON (2010) was established through the voluntary partnership of 73 national governments to provide a global biodiversity observation network tasked with collecting, managing, analysing and reporting on the status of the world's biodiversity. A global classification of freshwater ecosystems is considered an essential step towards this goal (GEOBON, 2010), and the recent map of freshwater ecoregions around the world (Abell *et al.*, 2008) will be used as a broad-scale starting point for recognising (and modelling) distinctions among freshwater ecosystems at finer scales within these ecoregions (GEOBON, 2010). We can expect different views of the aquatic environment to be modelled as multiple working hypotheses, and encoded in a variety of classification maps.

We suggest programming flexibility into an aquatic inventory or classification mapping approach that allows

users to retrieve different classification models to suit a variety of resource management purposes and spatial scales (site, segment, catchment, etc.). Such an approach would allow collaborative (multiple research laboratory) creation of classification models or views of river systems based on different suites of ecological drivers. For example, in many cases historical information on glaciation and related geological predictors are expected to be strongly related to fish (Mandrak, 1995; Abell *et al.*, 2008) and mussel (Strayer, 1983) species distributions, but such information may not be a significant driver of aquatic invertebrates with aerial dispersal mechanisms (Neff & Jackson, 2011). Furthermore, a flexible and up-to-date inventory would allow physically based, abiotic classifications to be combined with predictive models of climate change to forecast potential shifts in the distribution of various freshwater biotas. Given the likelihood of climate change and the dynamic nature of aquatic systems, large shifts in freshwater classification maps are expected. Therefore, the dynamic nature of these systems must be considered.

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