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Author: Poole, Geoffrey C.

Source: Journal of the North American Benthological Society, 29(1) : 12-25

Published By: Society for Freshwater Science

URL: https://doi.org/10.1899/08-070.1

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J. N. Am. Benthol. Soc., 2010, 29(1):12–25
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DOI: 10.1899/08-070.1
Published online: 5 February 2010

Stream hydrogeomorphology as a physical science basis for advances in stream ecology

Geoffrey C. Poole[1]

Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717-3120 USA

Abstract. The disciplines of geomorphology, hydrology, and hydrogeology have had a marked influence on the evolution of systems thinking in stream ecology. The River Continuum Concept was an explicit attempt to ''translate the energy equilibrium theory from the physical system of geomorphologists into a biological analog'' (Vannote et al. 1980, p. 131). A subsequent view of rivers as corridors evolved from an improved understanding of hydrologic linkages between rivers and their catchments and among channels, alluvial aquifers, and riparian zones/floodplains. More recently, the importance of channel network topology and dynamic, 3-dimensional hydrologic connectivity across fluvial landscapes has been emphasized by stream ecologists. This progression of ecological thinking provides a useful framework for understanding the role of fluvial geomorphology, channel hydrology, and hyporheic hydrology in shaping fundamental concepts of stream ecosystem science. This progression also defines a trajectory for understanding the potential role of the nascent discipline of stream hydrogeomorphology in contributing to an improved understanding of ecological responses to a stream's dynamic physical template. Although grounded in the discipline of stream ecology, *J-NABS* has contributed substantively to our understanding of interdisciplinary linkages among ecology, geomorphology, hydrology, and hydrogeology and, therefore, is well positioned as an outlet for ecologically based contributions to advances in stream hydrogeomorphology.

Key words: geomorphology, hydrology, stream ecology, connectivity, river continuum, riparian corridor, drainage network, fluvial landscape, riverscape.

A stream can be defined as ''the bio-physical ecosystem that arises from, incorporates, and is dependent upon channelized water flow and associated sediment transport dynamics'' (GCP). As such, streams have their genesis in the physical processes of channel formation caused by the convergence of surface-water flow paths and the emergence of ground water to the Earth's surface. Thus, geomorphology, hydrology, and hydrogeology are the primary physical science disciplines that underpin stream formation, and therefore, stream ecology. Some subdisciplines—i.e., fluvial geomorphology, channel hydrology, and hyporheic hydrogeology—are especially relevant to lotic ecosystem science. When attempting to understand water movement and alluvial dynamics in streams, these subdisciplines become inexorably intertwined and interdependent. For instance, fluvial geomorphology and channel hydrology have a long-established and interrelated history (Leopold et al. 1964; Fig. 1), and the associated dynamics that structure the geomorphology of alluvial aquifers have been well described (Creuzé des Chatelliers et al. 1994). More recently, hydrogeologists have begun to rescale their thinking to understand hyporheic water fluxes (Woessner 2000), based in part, on long-established and fundamental hydrogeologic tenets, such as the fact that variation in surface topography can drive the creation of hierarchically nested groundwater flow cells that interact with surface water at multiple spatial and temporal scales (Toth 1963).

Over time, integration of fluvial geomorphology, channel hydrology, and hyporheic hydrogeology has produced a compelling 3-dimensional and dynamic view of streams as ''fluvial hydrosystems'' (Petts and Amoros 1996) along with an ongoing convergence of scientific interests and questions among those disciplines (Brown and Bradley 1995). The formalization of this convergence has been recognized by some scientists as *hydrogeomorphology*, defined by Sidle and Onda (2004, p. 598) as ''an interdisciplinary science that focuses on the interaction and linkage of hydrologic processes with landforms or earth mate-

[1] E-mail address: gpoole@montana.edu

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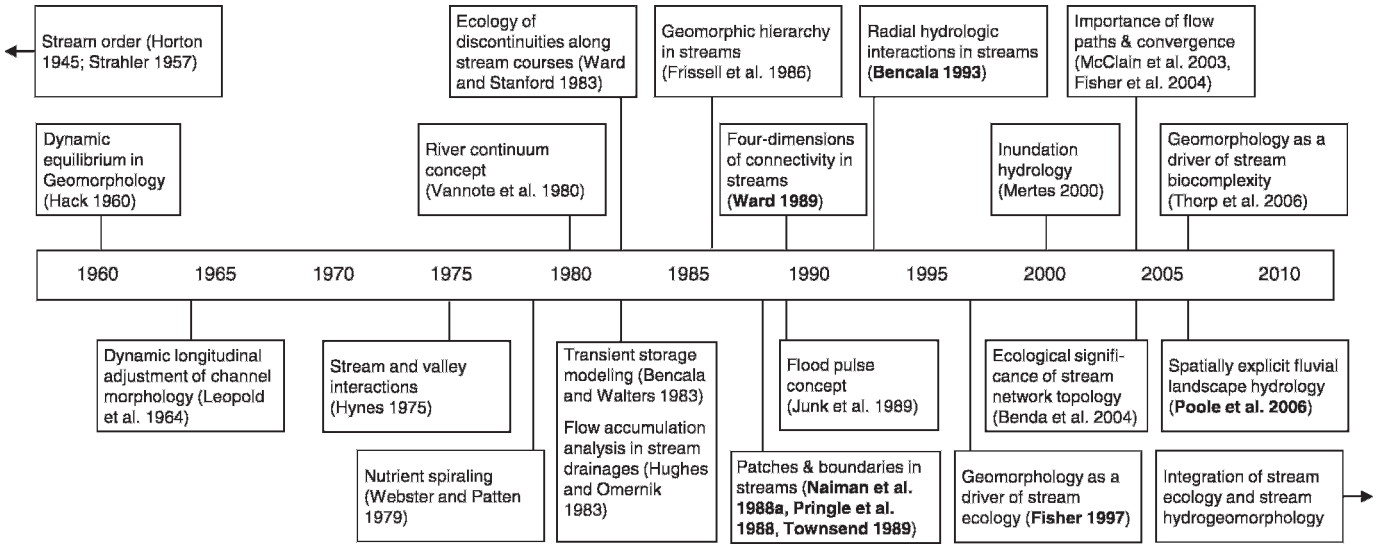


FIG. 1. Some key publications along a progression toward stream hydrogeomorphology as a physical-science basis for stream ecology. Boldface indicates papers published in *J-NABS*.

rials and the interaction of geomorphic processes with surface and subsurface water in temporal and spatial dimensions''. Within streams, then, hydrogeomorphic investigations would include describing the bidirectional interdependence between channel, floodplain, and alluvial aquifer forms and the associated spatial patterns of water movement within stream networks and fluvial corridors. In simple terms: How are streams (channels, riparian zone/floodplains, and alluvial aquifers) shaped by surface and subsurface water dynamics and how does the resulting shape influence spatial and temporal patterns of surface and subsurface water movement?

Alongside physical scientists, stream ecologists also have invoked 3-dimensional, dynamic constructs to describe lotic ecosystems (e.g., **Ward 1989**[1]; Fig. 1), and the term hydrogeomorphology is starting to be applied in the context of stream ecology (e.g., Doyle et al. 2003). Such coevolution of thought is not accidental; fluvial hydrosystems represent the fundamental physical templates upon which lotic ecosystems organize themselves. Over time, stream ecologists have described the complex interrelationships between hydrosystems and ecosystems with several conceptual constructs, each of which has contributed to the hydrologic and geomorphic underpinnings of stream ecology. In this paper, I describe a progression of scientific thought in stream ecology (Fig. 1) toward a paradigm that embraces fluvial hydrosystems as a physical template for lotic ecosystems and stream hydrogeomorphology as means of understanding that template. I trace this evolution of thought through 4 stages in the stream ecology literature: streams as 1) continua, 2) corridors, 3) networks, and 4) landscapes (Fig. 2A–D). This organizational approach provides an implicit means of describing the development of linkages between the physical underpinnings of streams (geomorphology, hydrology, and hydrogeology) and stream ecology. It also provides a natural avenue for understanding the associated role of *J-NABS*, which is a primary focus of this anniversary issue of the Journal.

The Geomorphic Basis of ''Streams as Continua''

William Morris Davis (1909) espoused the view that any landform arises from the interaction of underlying geologic structures, the processes that shape landforms, and the time over which those processes have acted. These ideas supported a general belief that geomorphologists should be able to describe precisely, and even mathematically, the developmental history and equilibrium state of landscapes from the properties of rocks and knowledge of erosive forces. Based on these concepts, Davis developed a description of landscape evolution via erosional processes through distinct states of youth, maturity, and old age.

However, Leopold et al. (1964) cited factors confounding Davis' view, including variation in uplift, weathering, erosion, and climate, and the fact that inorganic processes become functionally inseparable from organic influences of plants and animals. Leopold and colleagues instead built upon Hack's (1960; Fig. 1) ''dynamic equilibrium'' as a framework for understanding stream channel morphology (Leo-

[1] Boldface indicates paper was published in *J-NABS*

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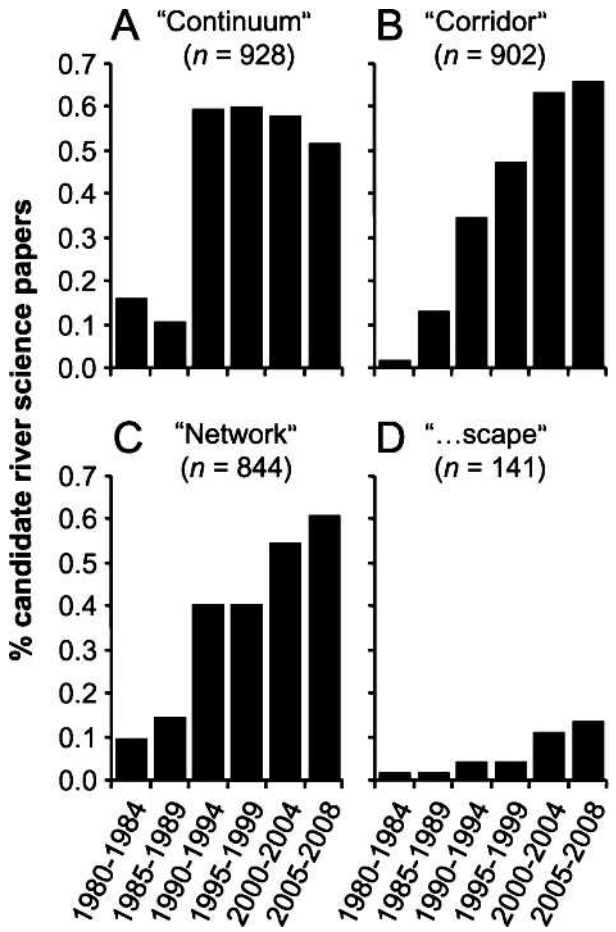


FIG. 2. Succession of published terminology used to describe river systems. Data derived from the Expanded Science Citation Index in the Institute for Scientific Information (ISI) Web of Science, which was queried in 2 stages. The initial query returned all papers referencing the terms ''river,'' ''stream,'' ''floodplain,'' or ''fluvial'' within their title, abstract, or key words during each time period, while excluding papers from inappropriate journal categories (e.g., ''data stream'' is a common term in computer science journals). This group of candidate papers was then queried for additional terms in the title, abstract, and key words: ''continuum'' (A), ''corridor'' (B), ''stream network'' or ''river network'' (C), and ''fluvial landscape,'' ''riverine landscape,'' or ''riverscape'' (D). Results are reported as the % of candidate papers in each time period that contained the phrases used in each secondary query. Plurals of each noun were included in all queries.

pold and Maddock 1953, Leopold and Langbein 1962, Leopold et al. 1964, Langbein and Leopold 1966). Using tenets of thermodynamics, they interpreted longitudinal mutual adjustments in 7 stream channel characteristics (width, depth, velocity, sediment load, sediment size, hydraulic roughness, and discharge) as a balance between the ultimately irreconcilable tendencies for uniform distribution of energy dissipation along a river and minimum total work within stream channels (Leopold et al. 1964, pp. 268–270). Thus, the concept of longitudinal adjustments in physical characteristics of streams was well established before the first publication of *J-NABS*.

Shortly before the first publication of *Freshwater Invertebrate Biology* (the precursor to *J-NABS*), Vannote et al. (1980; Fig. 1) published the River Continuum Concept (RCC) to describe longitudinal adjustments in and linkages among aquatic communities in streams. They described the RCC as an attempt to ''... translate the energy equilibrium theory from the physical system of geomorphologists into a biological analog'' (p. 131). Most stream ecologists understand that Leopold's expected hydraulic and geomorphic adjustments along a river were the basis for Vannote's idealized physical continuum in streams. However, in a more subtle nod to Leopold's approach, Vannote and colleagues framed their predictions by focusing, albeit less mathematically, on a similar assumption of uniformity of energy flow (organic matter processing) in streams ecosystems. Thus, in a very real sense, advances in fluvial geomorphology during the 1950s and 1960s provided not just a physical template but also the overall conceptual framework for developing basic concepts that shaped research in stream ecology for the past ¼ century (Fig. 2A).

After the RCC was published, studies appearing in *J-NABS* contributed markedly to the larger understanding of the applications and limitations of the RCC. *J-NABS* authors described the ecological importance of longitudinal adjustments in geomorphology (e.g., **Gooderham et al. 2007**) and associated changes in biota (e.g., **McArthur et al. 1992**, **Tachet et al. 1992**, **Bournaud et al. 1996**), downstream transport (e.g., **Miller and Georgian 1992**, **Minshall et al. 1992**, **Jones 1997**), and ecosystem processes (e.g., **McTammany et al. 2003**) in streams. In general, earlier papers in *J-NABS* tended to focus on the predictions associated with the RCC, whereas more recent papers tend to cite the RCC when speaking generally of the importance of longitudinal linkages along streams.

Given the fact that the RCC permeates the thinking of *J-NABS* authors and other stream ecologists, it is perhaps ironic that Leopold et al. (1964, pp. 273–280) went to great lengths to emphasize that there *is no physical continuum* in a given stream network. They stated: ''When there are large numbers of interrelated [hydraulic and geomorphic] factors which must adjust among themselves in response to occurrences in the environment, such as storms or flows, it should be expected that there will generally be an *indeterminacy* [emphasis added] in the manner of this mutual adjustment.'' Leopold and colleagues concluded that

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forecasting the central tendency of longitudinal changes along populations of rivers is possible, but that the specific progressions of geomorphic conditions along any particular river will be unique to the river and dynamic over time.

Thus, the original RCC was based on an idealized view of stream geomorphology (a physical continuum), which in turn, yielded an overly simplistic view of the downstream succession of patterns, such as changes in aquatic communities (in contrast, e.g., with findings and discussions by Rice et al. 2001, Poole 2002, Thorp et al. 2006 [Fig. 1]). Given the lack of a geomorphic continuum in streams, it might not be surprising that empirical observations, including those published in *J-NABS*, have failed to support the RCC (e.g., Downes et al. 1993, Statzner and Resh 1993, **Melo and Froehlich 2001**, Hoeinghaus et al. 2007) or provided only partial support (e.g., Grubaugh et al. 1996, who cited ''localized changes in stream geomorphology'' as a confounding variable). Subsequent amendments to the RCC (Ward and Stanford 1983 [Fig. 1], Minshall et al. 1985, Ward and Stanford 1995) have attempted to address its shortcomings, such as the discontinuous nature of geomorphic changes along a river course. Yet, as a concept that has been largely falsified, the enduring nature of the RCC seems puzzling, if not dogmatic. Perhaps the long-term conceptual utility of the RCC arises less from its specific predictions but more from its intuitive appeal and elegant description of the importance of longitudinal interactions in stream ecosystems (sensu Townsend 1996, Poole 2002).

The Hydrologic Basis of ''Streams as Corridors''

During the first 10 y of *J-NABS* publication (the late 1980s and early 1990s), researchers began describing stream ecosystems as corridors. Since then, the concept of the river corridor has continued to grow in popularity in the scientific literature (Fig. 2B). The idea of streams as corridors seems to have its roots in the early tenets of landscape ecology, which viewed landscapes as collections of patches and corridors set within a larger landscape matrix (**Johnson and Host 2010**). For instance, in his book *Land Mosaics: the Ecology of Landscapes and Regions,* R. T. T. Forman (1995) included a chapter entitled ''Stream and river corridors.'' Therein, he cited a substantial breadth of stream ecology literature to support his description of streams as landscape corridors, even though the cited stream ecology literature itself did not typically invoke the term corridor.

The view of rivers as corridors built upon research in the 1970s and 1980s describing the importance of linkages between stream channels and associated riparian zones, hyporheic zones, and even the broader stream catchment, which are mediated largely by channel, floodplain, and catchment hydrology. For instance, Hynes (1975; Fig. 1) provided a classic synthesis of the importance of catchment-to-stream hydrologic linkages and argued persuasively that the character of a stream's valley is a dominant control on the ecology of the stream, and that the nature of lateral hydrologic linkages between the stream and its valley mediate such interactions.

Ultimately, consideration of such lateral hydrologic linkages yielded a radial view of stream hydrology, where the channel represents a longitudinal axis and hydrologic linkages are arranged radially, extending from the catchment and bidirectionally to and from the floodplain, riparian zone, and alluvial aquifer (**Bencala 1993** [Fig. 1], Fisher et al. 1998b). For instance, the importance of such radial linkages within stream corridors was described from a systems perspective as ''nutrient spiraling'' (Webster and Patten 1979 [Fig. 1], Newbold et al. 1981); i.e., nutrient cycling driven by streambed biota (the lateral interaction) and associated with downstream (longitudinal) transport occurring when nutrients were in the dissolved or suspended portion of the cycle (**Mulholland and Webster 2010**). Nearly 3 decades after its formalization, nutrient spiraling still provides the fundamental basis of high-profile research on nutrient dynamics in stream ecosystems (Mulholland et al. 2008). In the interim, *J-NABS* has helped to advance the concept. *J-NABS* was the outlet for a perennially cited synthesis of solute transport and uptake in streams (**Stream Solute Workshop 1990**). *J-NABS* publications also have focused on factors that influence spiraling length, including stream biophysical characteristics (**D'Angelo et al. 1991**), nutrient availability (**Paul et al. 1991**), and stream order (**Minshall et al. 1992**). More recent *J-NABS* syntheses describe patterns of nutrient spiraling in natural (**Webster 2007**) and urbanized (**Meyer et al. 2005**) stream systems.

About a decade after publication of the first nutrient spiraling studies, Junk et al. (1989; Fig. 1) published their Flood Pulse Concept summarizing research that looked radially beyond the streambed and described the ecological role of river–floodplain hydrologic interactions. Their synthesis attempted to expand thinking in stream ecology, which they argue had been largely ''restricted to habitats that are permanent and lotic.'' Junk et al. (1989) described how seasonal hydrologic linkages between river channel and floodplain in large rivers are a dominant influence on nutrient transport, storage, and cycling within river systems, arguing that ''[l]ateral exchange

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between floodplain and river channel, and nutrient recycling within the floodplain have more direct impact on biota than the nutrient spiraling discussed in the RCC'' (p. 112). Based on this idea, Junk et al. (1989) concluded that the longitudinal position of a large-river floodplain within a river network had little influence on associated biota.

Simultaneously, during the late 1970s and 1980s, stream ecologists were developing a greater appreciation for the role of the riparian zone (Salo and Cundy 1987). The influences of the riparian zone on stream channel ecology (and vice versa) were summarized in a review by Gregory et al. (1991), which described riparian–channel interactions as mediated by the ''geomorphic organization of fluvial landforms'' and the resulting hydrologic processes that influence the riparian zone. Subsequently, Fisher et al. (1998b) provided a synthesis of stream ecosystem processes based on a radial view of streams by describing ''material spiraling'' among 4 radially arranged, parallel components of streams: the channel, parafluvial zone, hyporheic zone, and riparian zone. Thus, whether speaking in terms of catchments, floodplains, or riparian zones, the fundamental ecological principles describing terrestrial–aquatic interactions in stream corridors have been built upon advances in the understanding of radial hydrologic linkages between stream channels and their surrounding landscape context.

The utility and prominence of a radial view of streams is apparent when considering the functionally elegant hydrologic concept of *transient storage* (Bencala and Walters 1983 [Fig. 1], Bencala 1984), which can be used to describe the effects of radial hydrologic linkages between channels, floodplains, riparian zones, and alluvial aquifers within stream corridors. Conceptually, transient storage describes ''the temporary retention of solutes in [radial] zones of nearly stationary water and the eventual movement of that water back to the stream channel'' (**Stream Solute Workshop 1990**, p. 99). Transient storage models describe the physical movement of solutes along streams and have become the de facto hydrologic basis for quantifying nutrient spiraling metrics (e.g., spiraling length, streambed (areal) uptake rate, uptake velocity; **Stream Solute Workshop 1990**). Thus, models of transient storage have provided the quantitative basis of a large and productive arm of stream ecology that seeks to understand nutrient dynamics in stream corridors based on a radial view of steam corridor connectivity (e.g., 52 nutrient spiraling studies reviewed by Ensign and Doyle 2006). The contribution of *J-NABS* to the development of transient storage has been substantial, including Bencala's (**1993**) perspective on the implications of transient storage for solute transport in streams. *J-NABS* also has provided an outlet for several seminal papers that have had direct bearing on or have extended the hydrologic basis of transient storage (e.g., **D'Angelo et al. 1993**, **Runkel et al. 1998**, **Paul and Hall 2002**, **Runkel 2002**).

Most recently, a number of papers have identified critical limitations of associated stream tracer-based field measurements and subsequent modeling of transient storage metrics (Harvey et al. 1996, Gooseff et al. 2003, Zaramella et al. 2003, Wondzell 2006, Worman and Wachniew 2007). These studies consistently suggest that empirical measures of transient storage are accurate for short-duration, near-channel storage zones, but do not accurately capture hydrologic and ecological dynamics associated with longer-duration hydrologic storage in more distal storage zones. Thus, incorporating a more realistic and dynamic representation of stream corridor hydrology into empirical measurements and models of stream biogeochemistry remains an elusive yet worthwhile research goal (Poole et al. 2008).

The Geomorphic and Hydrologic Basis of ''Streams as Networks''

Fisher (**1997**; Fig. 1) stated that ''[t]he typical textbook of fluvial geomorphology devotes equal space to channel-scale structure, process, and dynamics, and basin-scale structure, process, and dynamics. Stream ecology has focused almost exclusively on the former'' (p. 313). He then went on to argue convincingly that the topology (patterns of connection) of a river network must indeed influence the ecology of the system. Although use of the term ''network'' in stream literature has blossomed (Fig. 2C), stream ecologists seldom investigate the nature of such influences (**Lamberti et al. 2010**). Fisher's view is supported by research on longitudinal patterns (especially of macroinvertebrates) in mainstem streams and rivers, which reveal the prevalence of discontinuities instead of continuous longitudinal trends (e.g., Perry and Schaeffer 1987). Perhaps because of the paradigm of streams as linear systems, stream ecologists identified dams (Ward and Stanford 1983), lakes (Hillbricht-Ilkowska 1999, **Myers et al. 2007**), and even floodplains (Ward and Stanford 1995) as sources of discontinuities. Yet with a few exceptions (e.g., Bruns et al. 1984, Osborne and Wiley 1992), tributary junctions were largely ignored by stream ecologists despite the fact that they are the most common natural source of discontinuities in stream networks.

Consistent with stream ecologists' conventional focus on streams as linear systems, publications in *J-NABS* typically have not examined the influence of

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stream network structure on lotic ecosystem dynamics. There are, however, 2 notable exceptions. Fisher's (**1997**) treatment of the importance of and techniques for stimulating creativity and idea generation in the scientific process yielded needed insights on the potential effects of flow network structure on ecological function. Another *J-NABS* paper (**Snelder et al. 2004**) demonstrated that a classification scheme that considers the fundamental drivers of spatial variability within a stream network (including the network structure and context) can predict community composition in streams more accurately than conventional regional classifications that ignore stream network structure.

In contrast to stream ecologists, geomorphologists have focused research on network topology for decades. Geomorphic analysis of stream network topology has yielded some of the most basic tenets of watershed hydrology. For instance, the concept of *stream order* (Horton 1945 [Fig. 1], Strahler 1957 [Fig. 1], Strahler 1964) relates stream size, power, and other hydrologic and geomorphic characteristics to stream position within the network. Stream order is a geomorphic concept that has been readily adapted by stream ecologists, perhaps because it is an exceedingly simple and relatively powerful way to characterize the network context of individual stream reaches (the scale at or below which most ecological research is conducted in streams). Although simple in concept, a stream's order is somewhat subjective because of the difficulty of defining and mapping where perennial streams begin on a landscape (*sensu* Montgomery and Dietrich 1988). In addition, vagaries in branching patterns across a stream network can yield stream segments of the same order, but with vastly different discharge. As an alternative, catchment area provides a useful index of a reach's context within a stream network, while circumventing some of the difficulties associated with stream order (Hughes and Omernik 1983; Fig. 1). Use of catchment area in place of stream order has mushroomed with the advent and widespread availability of geographic information systems (GIS) and associated tools for hydrologic analysis of digital elevation models. Such hydrologic analysis is based on the concept of *flow convergence*, or in the parlance of GIS, ''flow accumulation'' (Jenson and Domingue 1988, Jenson 1991), where hillslope water converges in channels and channels converge to form river networks.

Decades ago, geomorphologists also were describing the unique physical dynamics that occur at river junctions (e.g., Bull 1977, Rhoads 1987), the location and frequency of which are determined by network topology. Recent collaborations between geomorphologists and ecologists have propelled interdisciplinary work describing influences of tributary junctions on stream ecology (e.g., Rice et al. 2001). This trend was accelerated markedly by Benda et al. (2004; Fig. 1), who compiled a holistic synthesis of river network topology as a driver of stream ecology. Their synthesis focused in large part on the role of stream tributary junctions as key points of flow convergence, and therefore, important loci of physical and ecological dynamics within networks. Their view of stream networks as populations of ''channels and their confluences'' mirrors the approach taken by theoretical ecologists (who view ecological networks as populations of ''links and nodes'') in describing the role of complex network topology as a driver of general system behavior (Albert and Barabási 2002). This coevolution of ideas between aquatic scientists and network theorists suggests potential applications of network theory for understanding the influences of stream topology on lotic ecosystem function, especially if the definitions and functions of nodes and links from network theory are expanded to reflect distinct characteristics of dendritic ecological networks (see discussion by Grant et al. 2007).

The Hydrologic, Geomorphic, and Hydrogeologic Basis of ''Streams as Landscapes''

Streams and stream networks have been recognized as corridors within the larger landscape for decades (Forman 1995). Yet as outlined by Wiens (2002), important tenets of landscape ecology are directly applicable to lotic ecosystems when stream networks or segments are viewed as landscapes unto themselves. Specifically, Wiens (2002) argues that, for both terrestrial and fluvial landscapes: 1) patches differ in quality, 2) patch boundaries affect flows, 3) patch context matters, 4) connectivity is critical, 5) organisms are important, and 6) scale is important.

Landscape ecology concepts have been widely applied to stream ecosystems, although at rates below that of continua, corridors, or networks (Fig. 2D). *J-NABS* has been an important outlet for papers that describe the utility of viewing streams as collections of patches (**Naiman et al. 1988a**, **Pringle et al. 1988**, **Townsend 1989**, **Poole et al. 2006**; Fig. 1). Such patches exist within an explicit spatial hierarchy (Frissell et al. 1986 [Fig. 1], Townsend 1996, Poole 2002, Thorp et al. 2006). Lotic ecosystem patterns and processes (e.g., Hoeinghaus et al. 2007, Lasne et al. 2007) are influenced by the patterns of hydrologic (Pringle 2003) and ecological connectivity (Ward 1997) among patches, and by interactions among physical system components and biota, including microbes (**Hendricks 1993**), macroscopic fauna (Naiman et al.

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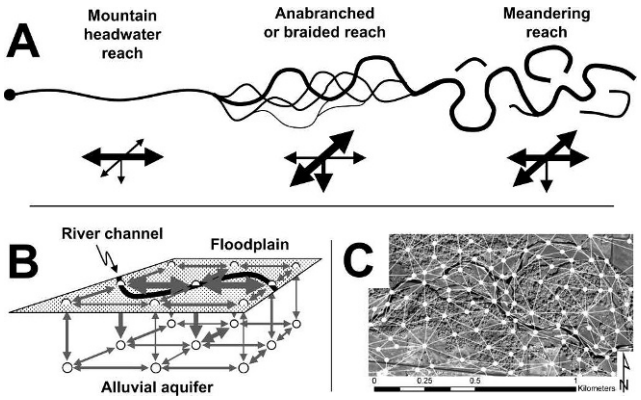


FIG. 3. Connectivity vectors in fluvial landscapes. A.—Example of arrow diagram used to illustrate changes in the relative importance of longitudinal, lateral, and vertical connectivity along a river course, largely as a function of changes in geomorphology (redrafted from Ward and Stanford 1995). B.—Arrow diagrams, such as those in panel A, depict only connection with the channel; a lattice network can represent the full range of connectivity vectors, the magnitude of which vary spatially and over time (e.g., **Poole et al. 2006**). C.—Spatial analysis of topographic controls on floodplain surface water routing reveals complex patterns of surface water connectivity across floodplains (excerpted from Jones et al. 2008a).

1988b, Onda and Itakura 1997), and vegetation (Hickin 1984, Tabacchi et al. 1998, Gurnell et al. 2002).

Terrestrial landscape ecology emerged from a general focus on lateral interactions among patches set within landscape mosaics across 2-dimensional space (Turner 1989, Forman 1995). In contrast, the 3-dimensional structure of fluvial landscape patches is critical to water movement and associated hydrologic connectivity, e.g., the topography of surface patches dictates surface water connections (Jones et al. 2008a), and the 3-dimensional juxtaposition of subsurface patches dictates patterns of vertical and horizontal interconnection in the hyporheic zone (e.g., Poole et al. 2004). Geomorphic controls on surface-water movement (Bates et al. 1998, Bates 2004) also dictate patterns of vertical hydrologic connectivity between hyporheic and surface water (**Poole et al. 2006**, **Boulton et al. 2010**), a key component of seminal thought in fluvial landscape ecology (e.g., **Dent et al. 2001**). Integrating change over time with 3-dimensional connectivity yields a 4-dimensional view of fluvial landscapes espoused in a seminal *J-NABS* publication (**Ward 1989**), which has provided a logical conceptual framework for understanding dynamic hydrologic connectivity between and within subsurface and surface components of fluvial landscapes (Stanford et al. 2005). This view underscores how the hydrology, geomorphology, and hydrogeology of streams form the physical template upon which lotic ecosystems are built (Mertes 2000 [Fig. 1], Petts 2000, Hancock et al. 2005, Malard et al. 2006) and allows conceptual integration of various prior views of rivers, e.g.: 1) a continuum or discontinuum can describe patterns of longitudinal connectivity, 2) flood pulses influence the lateral connectivity across fluvial landscapes, and 3) patterns and rates of exchange between subsurface and surface water dictate vertical connectivity (Townsend 1996, Poole 2002, Thorp et al. 2006).

Longitudinal geomorphic patterns occurring along a stream course alter the relative magnitudes and ecological influences of longitudinal vs lateral vs vertical connectivity. These along-stream changes in connectivity vectors have been postulated as rather predictable along the stream course and have been represented with various arrow diagrams (e.g., Fig. 3A) where the magnitude of hypothesized connectivity is indicated by the weight of the arrow (Ward and Stanford 1995, Townsend 1996). Although perhaps intended to represent hydrologic linkages within fluvial landscapes, such diagrams are rather channel-centric (and, in fact, more closely aligned with a radial view of stream hydrology). In these diagrams, connectivity has been represented along the channel, between the channel and floodplain surface, or between the channel and hyporheic zone. Missing are arrows representing longitudinal and lateral connectivity within the hyporheic zone; vertical connectivity among the floodplain surface, unsaturated sediments, and saturated hyporheic zone; and catchment to stream corridor connectivity. This limitation has been remedied by papers, including several published in *J-NABS*, that envision fluvial landscapes as hydrologic flux networks with a lattice structure (e.g., **Stanford and Ward 1993**, Poole et al. 2004). Such a view emphasizes the fact that subsurface and surface water fluxes are 2 facets of a single, integrated hydrosystem within fluvial landscapes (Fig. 3B), and that the hydrodynamics of neither surface water nor alluvial subsurface water can be understood if studied in isolation or at a single point in time. Instead, hydrologic connections in fluvial landscapes are driven by interactions among stream geomorphology, surface-water discharge regime, and aquifer properties, to yield complex patterns of connectivity (sensu Fig. 3C) that are dynamic over time (Wondzell and Swanson 1999, Woessner 2000, van der Nat et al. 2002, Arntzen et al. 2006, **Poole et al. 2006**).

Future Directions: Hydrogeomorphology as a Basis for Advancing Stream Ecology

For stream ecologists, the utility and importance of a shift from hydrology, geomorphology, and hydrogeol-

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ogy as related but separate disciplines toward stream hydrogeomorphology as an integrated, interdisciplinary focus of study might seem semantic at first glance. However, the fusion of these disciplines has important implications for understanding complex physical functions in stream and river ecosystems.

A spatially explicit hydrologic template

Fundamentally, hydrogeomorphology provides a means of describing the physical template of river networks as integrated surface and subsurface *hydrogeosystems*, the dynamics of which are driven by hydrogeomorphic processes and often fractal geomorphic structures that are best understood within a framework that encompasses multiple spatial scales (Dollar et al. 2007). Integrating hydrogeomorphology with stream ecology might yield advances, such as providing: 1) an improved understanding of the ecological significance of spatially explicit hydrologic processes that drive channel and floodplain inundation during flood spates (inundation hydrology), and 2) a physical context for studying the ecological consequences of patterns and locations of hydrologic flowpath divergence and convergence within lotic ecosystems.

Inundation hydrology.—Mertes (2000) defined inundation hydrology as ''the study of the water sources that contribute to inundation of a floodplain at the local scale of a river reach.'' Mertes pointed out that ''interior flooding''—inundation of the floodplain surface before the river overtops its banks—is a critical observation revealing the need for a revised look at dynamic patterns of hydrologic connectivity across floodplains in response to variation in stream discharge regime. In essence, water delivery from upstream (combined with associated changes in surface hydrologic connectivity between the floodplain and main channel) is only one potential inundation mechanism. Other water sources include floodplain tributaries, increases in water table elevation in the alluvial aquifer, and direct precipitation as mediated by local drainage patterns on the floodplain (Mertes 2000). Inundation hydrology, then, falls within the realm of stream hydrogeomorphology by attempting to understand variations in the sources and characteristics of surface water observed across floodplains and over time (sensu Malard et al. 1999, Jones et al. 2008b). Understanding and predicting patterns of inundation on floodplains require careful integration of information describing surface morphology (to incorporate geomorphic controls on surface water routing; Bates 2004, Jones et al. 2008a), aquifer properties (to assess alluvial aquifer response to changes in river stage; **Poole et al. 2006**), and the context of the floodplain within the larger river network and catchment (to determine where and how tributaries and hillslopes deliver water to the floodplain; Burt and Haycock 1996).

Thus, geomorphology (including river network topology, floodplain topography, and channel pattern) has a profound influence on lotic ecosystem dynamics, largely by influencing patterns, rates, and magnitudes of connectivity within and between surface waters and subsurface waters. These patterns of connectivity control water mixing from various sources, each of which has its own distinct characteristics, including turbidity (Mertes 1997), temperature (Arrigoni et al. 2008), and composition of dissolved constituents (**Dent et al. 2001**). Any of such characteristics can influence the ecological processes occurring within a parcel of water on a floodplain.

Flowpath divergence and convergence.—Improved descriptions of changes in ecological processes along hydrologic flow paths (e.g., Sobczak and Findlay 2002, Lewis et al. 2007) have yielded a view of stream ecosystems as collections of individual flow paths (Fisher et al. 1998a, Fisher et al. 2004 [Fig. 1], Lewis et al. 2007). If flowpath divergence, length, context, and reconvergence play critical roles in determining stream ecosystem function (McClain et al. 2003 [Fig. 1], Poole et al. 2008), then the ability to map the temporally dynamic routes of hydrologic flowpaths and identify points of hydrologic divergence and convergence over time becomes a fundamental need for understanding ecological dynamics in fluvial landscapes. Such patterns of flow divergence and reconvergence occur across a wide range of spatial scales within fluvial landscapes (Petts 2000, **Dent et al. 2001**). Whether at the streambed–channel interface, within stream reaches, or across entire floodplains, flowpaths diverge and reconverge according to the interactions of stream geomorphology and discharge regime (Cardenas et al. 2004, **Poole et al. 2006**). Such interactions are most obvious where complex channel morphology (associated with, e.g., streambed topography, debris dams, braided channel patterns, and wetland complexes) creates hydrologic gradients that drive patterns of surface water routing, subsurface water movement, and water exchange between the channel and hyporheic zone. These processes occur in both small streams (Wondzell and Swanson 1999, Gooseff et al. 2006, Zarnetske et al. 2007) and larger rivers (van der Nat et al. 2002, Jones et al. 2008b).

The ecological role of flowpath convergence has been a recent focus of study in stream ecology (e.g., McClain et al. 2003, Benda et al. 2004). Where flow paths converge, waters with different physical,

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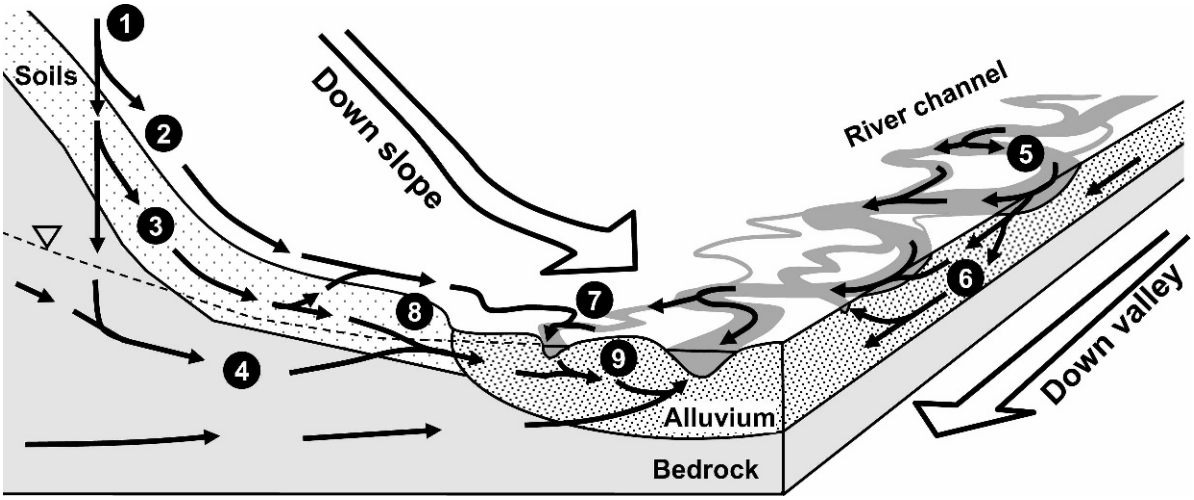


FIG. 4. When considering pathways of water movement both down slope and down valley, important locations of flowpath divergence and convergence (black arrows) are apparent. Precipitation (1) can diverge to form overland flow and infiltrating water (2), which can further separate into shallow subsurface storm flow (3) and groundwater recharge (4). River water (5) diverges among channels and between the channel and hyporheic zone (6). All of these various water types converge and mix in complex patterns on the floodplain surface (7) or near (8) or within (9) the alluvial aquifer.

chemical, and biological characteristics mix, often facilitating biological productivity, biogeochemical cycling, and biodiversity. Hydrologists and stream ecologists working at the watershed and stream network scales tend to focus on flow convergence as the hydrologic basis of stream catchments and networks; i.e., hillslope flow paths converge to form streams and streams converge to form networks. This focus on convergence is reinforced by: 1) a 2-dimensional view of stream networks and catchments (e.g., conventional GIS-based hydrologic analysis of digital elevation models or bifurcated networks), which ignores the vertical dimension of water flux both on hillslopes and in stream network corridors, and 2) the assumptions that meandering streams with a single (nonbraided) channel are the most common natural channel archetype (in contrast, e.g., with the findings of Walter and Merritts 2008). Ultimately, however, a 2-dimensional, bifurcated, single-channel flow network might prove inadequate for describing and predicting network and catchment scale ecosystem dynamics, in part because the ecological significance of flow divergence is precluded. Even simple, idealized diagrams of catchment hydrology illustrate points of hydrologic divergence that are apt to be ecologically significant (Fig. 4).

Flow divergence plays at least 2 ecologically important roles. First, where 2 flow paths diverge, one flow path often crosses an ecotone, enters a new ecological context, and brings with it dissolved and suspended constituents common in one habitat into another habitat. For instance, channel water can enter a riparian or floodplain environment or pass into the hyporheic zone. Conceptually, this transition often demarcates the beginning of a flow path, where biogeochemical transformation can occur rapidly (Fisher et al. 1998a). Second, every point of flow divergence creates a new opportunity for reconvergence of flow paths within the fluvial landscape (Fig. 4). For instance, side channels typically rejoin the main channel after diverging. Hyporheic flow diverges from the main channel, but reconverges with the channel downstream. Thus, if for no other reason, flow divergence is important because it increases the frequency of the ecologically important process of flowpath (re)convergence.

Both inundation hydrology and flowpath divergence–convergence consider spatial patterns of surface and subsurface water movement explicitly, and therefore, could be melded with recent ecological explorations, such as descriptions of biogeochemical processes and transformations along flow paths (McClain et al. 2003, Fisher et al. 2004). Such integration could allow exploration of spatially explicit representations of biogeochemical dynamics across fluvial landscapes. The obvious hydrologic and ecological implications represent fundamental research opportunities, such as: 1) understanding how the varying sources and mixing of channel, floodplain, and hyporheic water might change in response to channel engineering (e.g., dredging, diking, or straightening of channels) or stream channel restoration, and 2) describing the likely associated consequences for essential ecosystems, including biogeo-

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chemical cycling, productivity, ecosystem respiration, habitat distribution, and species distribution/community composition.

Geomorphic dynamics and biotic feedback

Thus far, I have not addressed at least 2 important issues in describing the role of hydrogeomorphology in advancing stream ecosystem science. First, fluvial landscapes are among the most consistently dynamic of any Earth surface system, yet my discussion of stream geomorphology has treated landforms as static. Second, my discussion focuses on the ecological implications of a physical (hydrogeomorphic) template without acknowledging that biological and ecological processes feed back and influence stream hydrogeomorphology. These shortcomings stem in part from my own lack of imagination, but they also largely reflect the current state of the stream ecology literature. This is not to say that stream ecologists have entirely ignored geomorphic dynamics. Recent syntheses (e.g., Stanford et al. 2005) and studies (e.g., Small et al. 2008) have progressed toward describing the influence of geomorphic dynamics in stream ecosystems. Yet in doing so, the focus is still on ecological and biological responses to structures that result from geomorphic dynamics (e.g., channel braids, aquifer deposits, channel units, wood deposits).

In essence, stream ecologists typically study complex and dynamic fluvial landscapes by presuming a period of geomorphic stasis between disturbance events that are presumed to be discrete. Alternatively, stream ecologists could choose to study complex fluvial landscapes by presuming continual, though rate-variable, geomorphic adjustment (see discussion by Molnar et al. 2002). Using such an approach, researchers could explore, e.g., the hypothesis that brief periods of high hydrologic and geomorphic activity are critical drivers to the overall function of fluvial ecosystems. For instance, coarse organic C inputs to streams during rare (e.g., 1 in 100 y) peak hydrologic events might be stored within floodplain sediments laid down during the event and could drive enhanced hyporheic microbial respiration for ensuing years or decades.

Embracing the ecological implications of geomorphic dynamics (rather than just the significance of resulting geomorphic features) will require ecologists to seek help from geomorphologists to study geomorphic processes, such as sediment transport, as a fundamental driver of lotic ecosystems (Rice et al. 2001, 2006, Benda et al. 2003, Paola et al. 2006). However, pursuing this line of inquiry heightens the need for geomorphologists to seek assistance from ecologists to incorporate the importance of biological feedbacks in fluvial geomorphology (as discussed by Poole 2002, Fisher et al. 2007, Murray et al. 2008). Such feedbacks have been identified as both floral (e.g., Murray and Paola 2003, Larsen et al. 2007) and faunal (e.g., Naiman et al. 1988b, Boulton et al. 2002, Statzner et al. 2003) influences on sediment transport and hydrologic dynamics within fluvial landscapes.

A Continuing Trajectory

Over the past 25 y of *J-NABS* publication, major concepts in stream ecology have been fundamentally influenced by advances in fluvial geomorphology, channel hydrology, and hyporheic hydrogeology. As understanding of the physical basis of stream ecosystems has improved, conceptualization of stream ecosystems has evolved from primarily linear structures (continua and corridors) to incorporate the topology of networks and the structure of landscapes. During the course of its publication, *J-NABS* has contributed substantially to this evolution of thought, especially by publishing papers that document ecological responses to geomorphic structures and hydrologic processes in streams.

The nascent discipline of stream hydrogeomorphology appears to be a promising avenue for continuing along the path of integrating more realistic representations of physical structures and dynamics into the concepts and discipline of stream ecology. Whether attempting to understand and describe inundation hydrology, flowpath divergence–convergence, or other aspects of a lotic ecosystem's physical template, stream hydrogeomorphology will provide an improved physical-science basis for viewing streams not just as channels, but instead as integrated, 3-dimensional, ecohydrological flux networks composed of geomorphically dynamic channels, alluvial aquifers, floodplains, and riparian zones. Clearly, stream ecologists will have the opportunity to benefit from and contribute to this emerging field in the coming decades. Given *J-NABS*' record of publishing papers that integrate the physical and ecological sciences, the journal will be well positioned to serve as an outlet for associated scientific advances.

Acknowledgements

I am grateful to many colleagues with whom I have interacted while developing the conceptual framework for this paper, especially Alison Appling, Emily Bernhardt, Jim Gannon, Ashley Helton, Scott O'Daniel, Leal Mertes, Jack Stanford, Steve Thomas, Bill Woessner, and Meredith Wright. The writings of Andrew Boulton, Stuart Fisher, Michael Gooseff,

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Steven Rice, and James Ward were especially thought provoking during the compilation of this paper. Ashley Helton, Krista Jones, Steven Rice, Al Steinman, Maury Valett, and an anonymous referee provided comments that substantially improved this paper.

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Received: 21 April 2008
Accepted: 14 October 2009

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