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THE RIVERINE ECOSYSTEM SYNTHESIS: BIOCOMPLEXITY IN RIVER NETWORKS ACROSS SPACE AND TIME

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ABSTRACT

We propose an integrated, heuristic model of lotic biocomplexity across spatiotemporal scales from headwaters to large rivers. This riverine ecosystem synthesis (RES) provides a framework for understanding both broad, often discontinuous patterns along longitudinal and lateral dimensions of river networks and local ecological patterns across various temporal and smaller spatial scales. Rather than posing a completely new model, we arrange a conceptual marriage of eco-geomorphology (ecological aspects of fluvial geomorphology) with a terrestrial landscape model describing hierarchical patch dynamics. We modify five components of this terrestrial model for lotic ecosystems: (1) nested, discontinuous hierarchies of patch mosaics; (2) ecosystem dynamics as a composite of intra- and inter-patch dynamics; (3) linked patterns and processes; (4) dominance of non-equilibrial and stochastic processes; and (5) formation of a quasi-equilibrial, metastable state. Our conceptual model blends our perspectives on biocomplexity with aspects of aquatic models proposed from 1980–2004.

Contrasting with a common view of rivers as continuous, longitudinal gradients in physical conditions, the RES portrays rivers as downstream arrays of large hydrogeomorphic patches (e.g. constricted, braided and floodplain channel areas) formed by catchment geomorphology and climate. The longitudinal distribution of these patches, which are identifiable using standard geomorphic techniques, varies amongst rivers and is difficult to forecast above ecoregional scales. Some types of hydrogeomorphic patches may reoccur along this downstream passage. Unique ecological 'functional process zones' are formed by individual types of hydrogeomorphic patches because of physiochemical habitat differences which affect ecosystem structure and function.

The RES currently includes 14 tenets predicting how patterns of individual species distributions, community regulation, lotic ecosystem processes, and floodplain interactions will vary over spatiotemporal scales, especially as they relate to the functional process zones formed by hydrogeomorphic differences in the river network. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: eco-geomorphology; floodplains; flood pulse concept; headwaters; hierarchical patch dynamics; hydrogeomorphic patches; inshore retention concept; large rivers; river continuum concept; riverine productivity model

HISTORICAL PERSPECTIVES AND PHILOSOPHICAL FOUNDATION

Understanding the ecological structure and function of natural and/or altered lotic ecosystems is a common goal of many stream and river ecologists. This has spurred development of numerous conceptual models, shaped empirical research and funding, and occasionally altered government policies on river conservation, management and rehabilitation. Formation of conceptual theories can expand our knowledge of factors regulating river networks as long as popular theories are viewed as the 'latest best approximations' rather than iron-clad truths and if ecologists seek to test theories and comprehend why concordance or incongruity emerge.

A lucid and widely accepted understanding of how most ecosystems are naturally regulated has eluded terrestrial and aquatic ecologists. This challenge is especially rigorous in river networks because they are open systems whose physical structure changes dramatically over many spatial and temporal scales. Early attempts to cope with this complexity by dividing lotic ecosystems into specific, longitudinally ordered zones (e.g. Hawkes, 1975)

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proved untenable (Townsend, 1996). This was followed by a portrayal of lotic systems as intergrading, linear networks by the river continuum concept (RCC; Vannote *et al.*, 1980), one of the most influential lotic papers of the twentieth century. This basic depiction of a river network as an ecological continuum is still largely accepted for headwaters through medium rivers (but see Statzner and Higler, 1985). However, the RCC's predictions for the importance to downstream food webs of organic matter derived from upstream trophic leakage has been criticized from a lateral floodplain perspective by the flood pulse concept (Junk *et al.*, 1989; Junk and Wantzen, 2004) and from an autochthonous production standpoint by the riverine productivity model (Thorp and Delong, 1994, 2002).

Many original lotic theories and models adapted from other ecosystems have been proposed to explain patterns of structural and functional biocomplexity across spatiotemporal scales in river networks. Some have addressed aspects of longitudinal processes (i.e. upstream-downstream changes), such as concepts involving energy sources and allocation (Vannote *et al.*, 1980), nutrient spiralling (Newbold *et al.*, 1982), river network and landscape interactions (e.g. Montgomery, 1999; Gomi *et al*., 2002; Benda *et al.*, 2004), and serial discontinuity and dams (Ward and Stanford, 1983). Others have examined processes operating at mid to fine scales and involving hierarchical habitat templates (Frissell *et al*., 1986; Poff, 1997), flow regime (Poff *et al*., 1997; Thoms and Parsons, 2003; Lytle and Poff, 2004), general perturbations (e.g. Townsend *et al*., 1997; Lake, 2000), inshore retention (Schiemer *et al*., 2001a; Hein *et al*., 2005; Thoms *et al*., 2005), patch dynamics (Pringle *et al*., 1988, Townsend, 1989), river discontinua (Poole, 2002), and sediments and/or stream hydraulics (Statzner and Higler, 1986; 'link discontinuity concept' of Rice *et al*., 2001). Numerous useful reviews and analyses of other aspects of stream regulation have been published, including those by Minshall *et al*. (1985), Statzner and Higler (1985), Junk *et al.* (1989), Ward (1989), Petts (1994), Johnson *et al*. (1995), Townsend (1996), Lorenz *et al*. (1997), Poff (1997), Ward and Tockner (2001), Woodward and Hildrew (2002), and Winemiller (2004), to name a few. However, no model explaining broad aspects of community structure and ecosystem functioning from small streams to great rivers has gained preeminent support since publication of the RCC, and few have attempted the complex task of integrating these longitudinal processes with patch-scale dynamics into a single model.

Our purpose is not to propose a completely new model but to blend an existing landscape model, pertinent aspects of lotic models proposed from 1980–2004, and our perspectives on characteristics of river networks from headwater streams to great rivers into the *riverine ecosystem synthesis* (RES). In particular, we focus on a conceptual marriage of the terrestrially-derived hierarchical patch dynamics model (Wu and Loucks, 1995) with ecogeomorphology (Thoms and Parsons, 2002), a research area that, for rivers, emphasizes ecological aspects of fluvial geomorphology. We propose an integrative framework to facilitate understanding of both: (a) broad, often discontinuous patterns along longitudinal and lateral dimensions from headwaters to great rivers; and (b) local or regional ecological patterns across various temporal and smaller spatial scales. Although we examine upstream-downstream patterns, this focus does not imply agreement with either a continuous gradient (*sensu* Vannote *et al.*, 1980) or a predictable but non-continuous gradient (e.g. Hawkes, 1975) of biocomplexity. We define biocomplexity as structural and functional phenomena arising from dynamic interactions amongst biotic elements of the ecosystem and between these components and the physiochemical environment.

ESSENTIAL ELEMENTS OF THE RIVERSCAPE AND RIVERINE LANDSCAPE

Two seemingly simple, but important tenets upon which we have based the RES are that lotic ecosystems possess a four-dimensional nature (Ward, 1989) and that rivers are more than a single thread passing through a terrestrial landscape (cf., Ward and Tockner, 2001). The longitudinal and lateral (riparian inputs) nature of rivers was emphasized in the RCC, but Ward (1989) also focused attention on vertical (e.g. hyporheic) and temporal dimensions. The lateral dimension and temporal variability of rivers formed the core of the flood pulse concept (Junk *et al*., 1989), and the temporal dimension was emphasized by the natural flow regime paradigm (Poff *et al*., 1997).

Rivers are often erroneously discussed as being either a single channel of flowing water or as the main channel plus river floodplains. This has been reinforced by a common research emphasis on headwater streams, the linear nature of influential theories such as the RCC and the nutrient spiralling theory (Newbold *et al*., 1982), a paucity of research on structurally complex floodplain rivers, and artificial channelization of many floodplain rivers (Thoms and Sheldon, 2000). As Fisher (1997) pointed out, the major paradigms and research foci in stream ecology over the past quarter century '. . . have been based upon a linear ideogram—an image which is at best incomplete and at worst, incorrect'. Furthermore, the continually flowing portions of rivers are called lotic, whereas the usually non-advective regions of the river are often given the easily misleading and divisive label of semi-lentic (Ward *et al.*, 2002), when in reality both areas are interdependent and perhaps equally integral to functioning of streams and rivers. During the last decade, a research emphasis on floodplain rivers has caused some scientists and governments to view rivers as permanently submerged main channels and temporarily wetted floodplains. In fact, structurally complex rivers consist of the main channel, various slackwater habitats, sub-bankfull inundation areas, and supra-bankfull floodplains. Slackwater habitats are nearly continuously wetted habitats where directional water currents are minimal or nonexistent except during high water (Thorp and Casper, 2002). They include many shorelines, shallow to deeply incised bays, secondary and side channels, alluvial wetlands, and backwaters (where rising waters back up into semi-enclosed areas lacking upstream connections except during some flood periods). These hydrological retention areas correspond closely to the terms 'dead zone' and 'storage zone' often used by European scientists.

The main channel and slackwaters constitute the riverscape (*sensu* Wiens, 2002), which is linked functionally and structurally to the riverine landscape. The latter consists of: (1) the riverscape; (2) sub-bankfull inundation areas (= the lower portion of the aquatic/terrestrial transition zones, or ATTZ, of Junk *et al.*, 1989); and (3) supra-bankfull inundation areas (including the remainder of the ATTZ) and permanently wetted, but usually disconnected floodplain lakes. Other appropriate approaches to characterizing river landscapes were described by Ward *et al.* (2002). We suggest that structural features and functional processes of the riverscape differ substantially from those found in other aquatic portions of the riverine landscape, as discussed in part below. Moreover, we agree with Tockner *et al.* (2000) that the hydrological flow pulse may be as important ecologically in these sub-bankfull areas as the flood pulse has proved to be in supra-bankfull, floodplain areas.

DO PATTERNS EXIST ALONG A LONGITUDINAL DIMENSION IN RIVER NETWORKS?

Historical perspectives on continua within the river network

Central to the RCC (Vannote *et al.*, 1980) are the linked concepts that: (a) physical variables within a river network present a 'continuous gradient' of physical conditions from headwaters to a river's mouth; and (b) this longitudinal gradient '. . . should elicit a series of responses within the constituent populations resulting in a continuum of biotic adjustments and consistent patterns of loading, transport, utilization and storage of organic matter along the length of a river'. This emphasis on lotic ecosystems as longitudinally interlocked entities contrasted sharply with previous perspectives that rivers were composed of specific and somewhat isolated zones distributed in a predictable fashion along a longitudinal dimension of the river network (reviewed in Hawkes, 1975).

The concept of river networks as ecological continua is widely accepted and continues to be taught in many universities, but this generic portrayal and the predictability of biotic responses along a longitudinal dimension are increasingly considered suspect. Rather than networks consisting of a steady gradient of stream hydraulics, Statzner and Higler (1986) identified discontinuities where transitions in water flow and resulting substrate size were the critical determinants of changes in species assemblages. In a similar vein, Benda *et al.* (2004) identified tributary junctions with the main channel as biological hot spots in their 'network dynamics hypothesis'. Perry and Schaeffer (1987) found only a weak downstream gradient in benthic species in a tributary of the Gunnison River in Colorado and no gradient in functional guild composition; they characterized species distributions as punctuated gradients. Townsend (1989) concluded that the idealized downstream pattern of the RCC in primary trophic resources '. . . is remarkable primarily because it is not usually realized and cannot provide a world-wide generalization'. Montgomery (1999) concluded that a continuum perspective was valid only for low-relief watersheds with relatively constant climate and simple geology; whereas his 'process domains concept', based on the importance of local geomorphic conditions and landscape disturbances, was applicable in regions with high relief, variable climates, and complex geology (e.g. the U.S. Pacific Northwest). Poole (2002) proposed that: (a) rivers are composed of patchy discontinua where the community responds to local features of the fluvial landscape; and (b) a community within a stream segment is not necessarily more similar structurally and functionally to communities in adjacent segments than it is to groups located farther upstream or downstream. A core problem in describing river networks as hydrological, physical, and ecological

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continua seems to be that this portrayal does not work physically because it ignores differential geology within a catchment, tributary effects and historical geomorphic influences.

Hydrogeomorphic patches and associated functional process zones (FPZs)

How predictable are river conditions and ecological elements along a longitudinal dimension of a river network? The answer is complex because scale-dependent phenomena are involved, but we can draw some general conclusions. Our perspectives are based on numerous general studies of fluvial geomorphology (e.g. Rosgen, 1994; Church, 2002; Benda *et al.*, 2004) and a specific project by Thoms and Parsons (2003) which employed 230 hydrological and geomorphic variables to describe river areas. The latter study supports the concept that spatial zonation of hydrological characteristics, each with different temporal patterns, is a fundamental property of rivers.

Contrasting with a common view of rivers as continuous, longitudinal gradients in physical conditions, we view rivers as downstream arrays of large hydrogeomorphic patches formed by catchment geomorphology and flow characteristics. Climatic conditions influence these patches by influencing runoff (water, sediment, organic matter and nutrients), riparian/floodplain vegetation, and aquatic vegetation (e.g. macrophyte beds, mangroves etc.). Hydrogeomorphic patches result from shifts in hydrological and geomorphic conditions, which distinguishes them from more common but relatively arbitrary, spatially defined units such as reaches, sections and segments. Physical boundaries between hydrogeomorphic patches may be sharp or indistinct, as can be their ecological differences, but they can be delineated using techniques and terminology standard to geomorphology. They have different flow regimes, flow histories, flood pulses and stream hydraulics (moving from long to short temporal scales). Some examples of these patches in large rivers are areas with constricted, braided or anabranch channels, extensive slackwater areas, and broad floodplains. The physical template characterizing each type of hydrogeomorphic patch is unique and differs in terms of size, vertical and lateral shape, internal structural/hydrological complexity and other habitat characteristics (e.g. mean substrate size)—all critical factors shaping biotic communities and delimiting ecosystem processes. This portrayal of rivers is broader than, but consistent with, the division of rivers into geological 'lithotopo' units, as proposed by Montgomery (1999), and it is compatible with perspectives of Poole (2002).

The various types of hydrogeomorphic patches differ in physical and chemical conditions and, therefore, biocomplexity should vary significantly amongst these patches in numerous ways, including in their characteristic productivity, system metabolism, organic matter dynamics, nutrient spiralling, and community composition. This conclusion is consistent with the widely acknowledged, critical role of hydrological characteristics in ecosystem structure and function (e.g. Poff *et al.*, 1997). Hence, physical hydrogeomorphic patches, which are of direct interest to fluvial geomorphologists, serve as a template for ecological 'functional process zones' (FPZs; Figure 1), which are a research province of aquatic ecologists. Evidence that ecosystem function varies with types of FPZs is abundant (e.g. comparisons between constricted and floodplain channel rivers, as in Sedell *et al.*, 1989). Yet, a systematic, ecological comparison amongst many types of FPZs has not been attempted to our knowledge. Another critical step in understanding differences amongst FPZs will be evaluating the proportional importance and distribution of individual habitats within the FPZs and transitions between them (Klement Tockner, pers. com.). Key ecological nodes within FPZs could include, for example, tributary confluences, divergence and convergence areas in braided/anastomosing rivers, vegetated islands, parafluvial ponds (Karaus and Tockner, unpublished), and various slackwater areas in general.

Although these ecosystem functional patches are depicted as 'zones', they do not correspond to the historical characterization and arrangement of fixed lotic zones (e.g. Hawkes, 1975) as being present in specific regions of a river network and non-repetitive along a longitudinal dimension. Moreover, they differ from the process domains of Montgomery (1999), which were geomorphic regions affected by terrestrial landscape disturbances acting on fundamental geological conditions of those local areas.

Describing the distribution of hydrogeomorphic patches and associated FPZs along a longitudinal dimension of the river network requires appreciation of scale dependence. Because the temporal signature of flow disturbance varies as you move downstream, the occurrence of some hydrogeomorphic patches in a given area is more likely than others. For example, the nature of the short-term flood pulse (which has some relationship to flashiness) is most important in headwater, while attributes of long-term flow history (e.g. recent history of floods and droughts)

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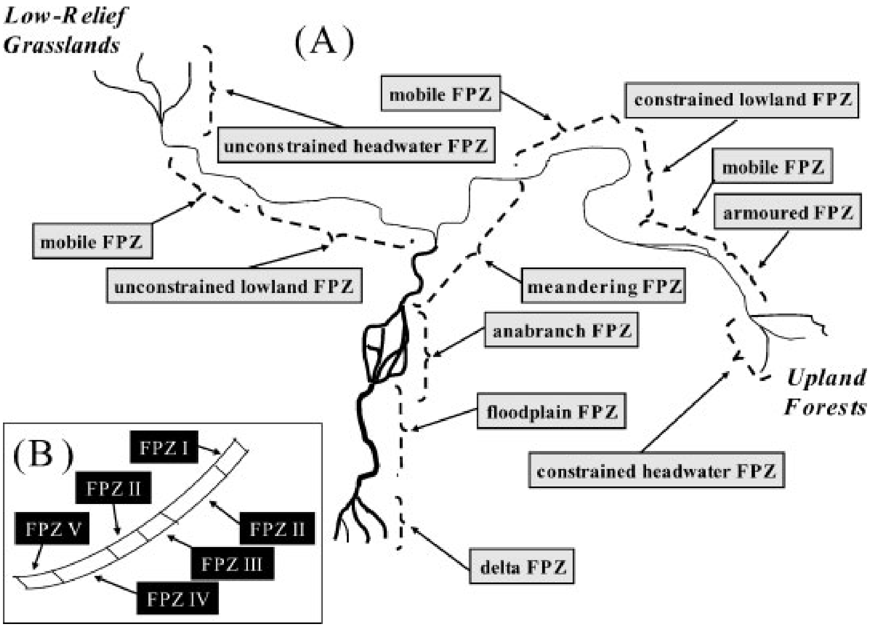

Figure 1. (A) Schematic view of a complex river catchment showing various ecological functional process zones (FPZs) present from headwaters (in forested and grassland ecoregions) to the river delta that are formed by large hydrogeomorphic patches; (B) the same type of FPZ (e.g. FPZ II) may be present in more than one part of a single tributary and be arranged in an order that is not always predictable; the downstream length of an FPZ will vary with and among types of FPZs

tend to be most important to lowland rivers. Headwaters tend to have shorter retention times for organic matter than do downstream river-floodplain areas, but intermediate locations may vary greatly in retention times depending on what kind of hydrogeomorphic patch is present. As one moves through the river network, variations in other geomorphic, hydrological, and climatic conditions alter watershed and river conditions, affecting both the nature of the local FPZ and the investigators ability to identify potential longitudinal trends (Figure 2). Another complicating factor is that the same general type of hydrogeomorphic patch may appear repeatedly along a longitudinal dimension of a river network in a pattern that is not consistent amongst rivers.

The distribution of hydrogeomorphic patches and associated FPZs within rivers varies amongst rivers along a gradient from somewhat predictable to nearly unpredictable, depending on the scale of analysis. Within ecoregions one tends to find, as a matter of course, similar geomorphic, hydrological, climatic, and botanical conditions (Figure 2). For example, headwater reaches are often portrayed (e.g. Church, 2002) as being constrained channels, whereas downstream areas are depicted as meandering or braided reaches. However, this is true primarily for some headwater streams found at high elevation and in areas with prominent bed slopes. Headwater streams in areas of low relief, especially those in non-forested areas, are mostly unconstrained. Indeed, from a global perspective, a high percentage of headwater streams are unconstrained, especially when you include those in Africa (pers. com., Bernhard Statzner). The nature of the river and longitudinal distribution of its hydrogeomorphic patches will reflect these similar conditions to some degree, but the relationship will be complex. Above the ecoregional scale, it becomes increasingly difficult to predict distribution of these patches along a longitudinal dimension of the river network.

One might assume from the preceding arguments that predicting longitudinal progression of physical and linked biological features in a river network is impossible, but this task is not entirely hopeless. Statzner and Higler (1986) contended that physical characteristics of flow (stream hydraulics) were, '. . . the most important environmental factor governing the zonation of stream benthos on a world-wide scale'. Rather than a steady gradient of stream hydraulics postulated by continuum models, they identified discontinuities where transition zones in flow and resulting substrate size were the critical determinants of changes in species assemblages. These essentially large-scale hydrogeomorphic patches consisted of: (a) upstream regions of relatively low hydraulic stress; (b) a

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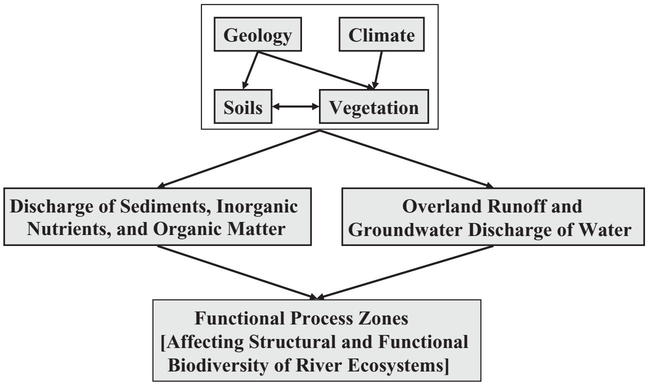

Figure 2. Schematic drawing showing the effects of terrestrial conditions on discharge of water, sediments, inorganic nutrients, and organic matter into rivers and the ultimate effects on biocomplexity within functional process zones

transition zone; (c) a reach of high slope and hydraulic stress; (d) another transition zone where the slope levels off; (e) a reach of low hydraulic stress; and ending with (f) a broad downstream segment that is interrupted by large-scale discontinuities in hydraulic stress. Transitions between these patches would qualify as hydrogeomorphic ecotones within a riverscape (*sensu* Wiens, 2002). Hence, knowledge of the progression of hydrogeomorphic patches along a river network would permit approximate forecasting of changes in biocomplexity within the FPZ. Longitudinal patterns in biocomplexity could be present within an FPZ, as a result of smaller-scale hydrogeomorphic patches (e.g. flow-substrate interactions). These changes, however, are probably less than those evident between different types of FPZs because of more pronounced differences in hydrogeomorphic patches at larger scales.

Despite the above arguments, a relatively progressive, downstream gradient of responses to abiotic and biotic features is observable for some community and ecosystem attributes, thus forming a partial biotic continuum as predicted by the RCC. Examples of physical conditions that are affected by local conditions but that also change longitudinally (as well as laterally) are substrate size and temperature regime. For instance, water temperatures along a North American river network flowing through eastern deciduous forests in a southerly direction will tend to increase in a roughly continuous gradient from headwaters to the river's mouth, and this will simultaneously contribute to a gradient in dissolved oxygen conditions. On the other hand, different downstream patterns in temperature and oxygen, either consistent or variable longitudinally, could be exhibited in other systems, for example in rivers flowing toward the poles, originating in non-forested headwaters, present in tropical regions, and/or passing through variable and repeated constricted and floodplain zones.

For most ecosystem attributes, however, biocomplexity should be more similar in the same general type FPZ located throughout the network than in adjacent patches up or downstream (cf., Montgomery, 1999; Poole, 2002) with different FPZs. Even where a longitudinal progression of FPZs is reasonably predictable, changes along a longitudinal dimension rarely reflect a continuous gradient. The spatial arrangement of FPZs along a longitudinal dimension might significantly influences biocomplexity, but this hypothesis remains untested. Further research into longitudinal patterns (continuous or discontinuous) is needed.

HIERARCHICAL PATCH DYNAMICS MODEL—BRIEF DESCRIPTION

A description of how biocomplexity changes from headwaters to great rivers is an initial step in development of a comprehensive model of ecosystem function, but it does not fully explain what regulates biocomplexity at various temporal and smaller spatial scales of the river network, such as within a single FPZ. For answers to that component of our model, we applied the hierarchical patch dynamics (HPD) model (Wu and Loucks, 1995; Wu, 1999) to lotic systems. This model integrates a general theory of spatial heterogeneity (patch dynamics) with hierarchy theory by expressing relationships amongst pattern, process and scale in a landscape context. It should not be confused with the more restricted concept of nested hierarchical classifications, which was linked to a stream's physical template by Frissell *et al*. (1986). Relevant aspects of this concept are summarized below, and the model is described in detail by Wu and Loucks (1995). Following this brief review, we examine the application of the HPD model to lotic ecosystems.

In our analysis, we are defining 'patch' as a spatial unit differing from its reference background in nature and appearance. The size of the patch is scale-, organismal-, and process-dependent and can vary greatly in temporal dimension and size (e.g. individual rock to a river segment or a floodplain area). Furthermore, species of different sizes, life histories and evolutionary traits will experience physical hierarchies and patches from often contrasting perspectives (cf., Hildrew and Giller, 1994), and the discreteness of the habitat boundary hinges upon the organism's mobility (Tokeshi, 1994).

The HPD model is composed of five principal elements (modified from Wu and Loucks, 1995). First, ecological systems are viewed as 'nested, discontinuous hierarchies of patch mosaics'. This allows one to analyse the role of small patches (e.g. substrate types) within large patches (e.g. FPZs). It also enables investigators to factor in seasonal and aperiodic changes in the nature and role of patches. The presence of patches within a hierarchy of regulatory factors reflects the action of different disturbances and other independent variables operating over fluctuating spatiotemporal scales. Second, the dynamics of ecological systems are derived from a composite of intra- and inter-patch dynamics. This interaction amongst patches produces an emergent property of lotic ecosystems which is not evident when studying patches in isolation. Third, pattern and process are interlinked and scale-dependent. Various processes (e.g. nutrient spiralling) may create, modify or eliminate patterns on spatial and temporal scales, while at the same time certain spatial and temporal patterns (e.g. differences in flow characteristics) can substantially alter ecological processes. Scale-dependent interrelationships can change from a riffle-sized patch to a channel-floodplain patch and, therefore, may require different approaches to elucidate. For example, if one asked what controls community diversity within a riffle during the summer, conducting resource-limitation and predator-prey experiments might prove fruitful. In contrast, understanding ecosystem functional responses to variability in flow patterns might be a more profitable approach at the FPZ scale within a floodplain river. Fourth, non-equilibrium conditions and stochastic processes play a dominant role in so-called 'ecosystem stability'. Deterministic processes can still contribute significantly to community regulation within a given patch; but on a hierarchical scale, stochastic processes amongst patches are more important. Fifth, a quasi-equilibrial, metastable state can develop at one hierarchical level through incorporation of multiple, non-equilibrial patches from the adjacent, lower level—in essence, 'out of chaos comes order!'

APPLYING THE HIERARCHICAL PATCH DYNAMICS MODEL TO LOTIC ECOSYSTEMS

Selective spatiotemporal scales

A simultaneous benefit and disadvantage of the HPD model is its lack of temporal or spatial scales where analyses must start. Frissell *et al*. (1986), in their hierarchical framework for stream habitat classification, listed events and processes controlling stream habitats on different spatiotemporal scales. At stream and segment scales, these included geomorphic and hydrological processes operating through periods ranging from hundreds to over 100,000 years. Substantial alterations of stream channels and watersheds, resulting from major climatic shifts, tectonic processes, glaciation etc., can occur over such lengthy periods. During the same or longer period, evolutionary and long-term ecological processes can interact with abiotic and biotic environmental characteristics to produce the species pool from which lotic communities are drawn. Linking the appropriate spatiotemporal scales with their relevant ecological processes (ecosystem to individuals) may be critical to understanding natural functioning of rivers (Thoms and Parsons, 2002), managing them properly, and rehabilitating them where appropriate.

We confine our present analysis to ecological time frames (i.e. shorter than evolutionary and long-term geological processes) because this scale is most relevant to community regulation and the ecosystem processes observable by researchers. The spatial scales discussed below extend from the entire longitudinal and lateral extent of a river network down to microhabitat patches. In this spatial approach, we have a greater chance of understanding differences in the importance of various regulatory factors from small streams to great rivers and in applying this information to management and rehabilitation of rivers.

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Element I: nested, discontinuous hierarchies of patch mosaics

Stream ecologists have often implicitly included spatial patches as a research variable, but few thought in terms of temporal patches until recently. The patches most commonly studied have rarely exceeded dimensions of riffles or pools, and most were no larger than individual cobbles or resource patches (cf. Woodward and Hildrew, 2002). Initial research on small patches focused on biotic interactions, principally competition and predation/herbivory (e.g. Peckarsky, 1979; Georgian and Thorp, 1992) along with succession (reviewed in Fisher, 1983). This was followed in the late 1980s and 1990s by a greater appreciation of the role of flow disturbance in regulating species within patches (e.g. Statzner and Higler, 1986) in concert with the broader ecological trend recognizing the importance of stochastic factors in non-equilibrial environments. There now exists widespread agreement in aquatic ecology that organisms are greatly influenced by interactions between physical habitat and flow patterns, the latter being considered the master control variable by many scientists (Power *et al*., 1995; Poff, 1997; Resh *et al*., 1998). These observations promoted application of the habitat template model to streams (Frissell *et al*., 1986; Townsend and Hildrew, 1994). Because temporal scales of biotic interactions are usually different from those related to disturbances from flow variability, a temporal hierarchy of regulatory factors develops, even within small spatial patches (cf., Fisher *et al*., 1998). The result is a mosaic of dynamic patches in small streams which vary in composition, size, and recovery stage (quasi-successional?). One of many possible schematic models of a hierarchically nested, mosaic of patches in lotic ecosystems is shown in Figure 3.

The RCC, which was written for a generalized stream, implicitly recognized segment-scale patches that were central to its interpretation of species composition and trophic food webs along its proposed river continuum. These included: (a) stream patches with a canopy cover from riparian trees (e.g. headwater streams in forested

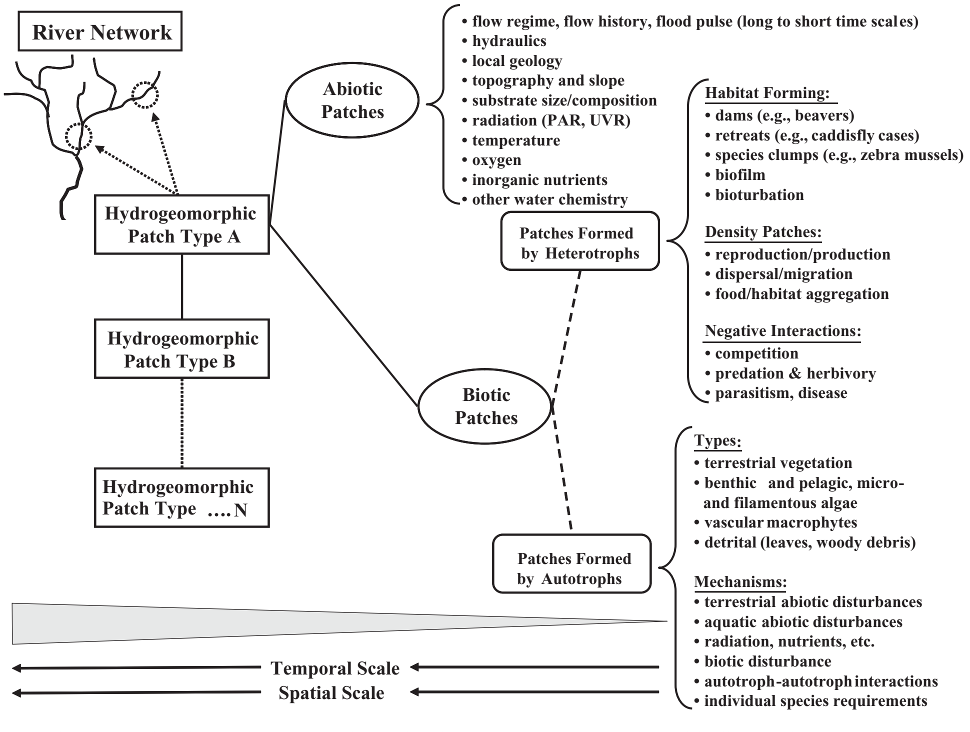

Figure 3. A schematic model of a hierarchically nested mosaic of some patches present in an idealized lotic ecosystem. Within a hierarchical classification, a river network and the basin it which it lies occupy the greatest spatial and temporal scales shown here. They may lie entirely within an ecoregion or be spread over multiple ecoregions. The next level below is represented by various types of hydrogeomorphic patches and the functional process zones they form. These are composed, in turn, of various abiotic (physical, chemical, and radiation) and biotic patches which vary in extent and nature over time. Riverine landscape patches can be present on land or in water, with the latter being in the channel, slackwater areas, or floodplains, and in pelagic, benthic, or hyporheic zones. Bulleted items within brackets represent types of patches and/or mechanisms causing them. Both abiotic and biotic patches are influenced by climate at different spatiotemporal scales. Abiotic patches are often, but not exclusively, present over greater spatiotemporal scales than are biotic patches

ecoregions) or without a riparian canopy (e.g. grasslands); and (b) patches where light penetrated to the bottom in open streams (small to medium rivers) or failed to reach it because of depth and/or turbidity (medium to large rivers). Based on the energy equilibrium theory of fluvial geomorphologists, Vannote *et al*. (1980) hypothesized that the biotic structure and function of a stream community conforms over time to the mean state of the physical system. For simplicity sake, the model assumed an uninterrupted gradient of physical conditions in natural rivers where physical conditions gradually alter as one moves downstream. Other authors modified the RCC for the patch-forming effects of tributaries and dams (e.g. Ward and Stanford, 1983). From knowledge of how physical conditions alter the input or generation of allochthonous and autochthonous organic matter, the RCC postulated a predictable, unidirectional change in functional feeding groups from small streams to large rivers. Although the RCC was not explicitly a hierarchical model, Poff (1997) considerably elaborated on this approach in his 'categorical niche model' where he defined scaled habitat features as 'filters' that influence probabilities of occurrence by species with appropriate traits (see also Malmqvist, 2002). [In the parlance of hierarchical theory, these filters are equivalent to 'holons', or boundaries between horizontal levels (Allen and Starr, 1982; Wu, 1999).] Parsons *et al*. (2003) described the distribution of benthic macroinvertebrates within a hierarchical classification based principally on geomorphologically derived scales. Statzner and Higler (1986) also implicitly identified large-scale patches created by the physical characteristics of flow (stream hydraulics); however, they disagreed with the RCC's portrayal of streams as a steady gradient of stream hydraulics. Instead, they emphasized the ecological importance of discontinuities of flow at transitions between hydrogeomorphic patches.

Changes in the nature and variability of patches often modify community composition (e.g. see references in Vannote *et al*., 1980; Pringle *et al*., 1988). For example, Brown *et al*. (1998) suggested that pulmonate snails are more common in temporary headwater streams and shallow littoral margins of lotic systems because of a greater physiological adaptation in variable habitats, while prosobranchs dominate the gastropod fauna of larger rivers (and in spring-fed rivers) because of greater competitive ability, lower risk of predation, and/or less-variable physical and chemical regimes.

With increased study of large rivers, the potential importance of large lateral patches (e.g. floodplains and large slackwaters) became evident. The flood pulse concept (Junk *et al*., 1989) emphasized a significant lateral component in extensive floodplains. Trophic dynamics within these functional process zones were shown to be distinctly different and divorced from upstream areas. This contrasted with the prevailing idea that they were linked by FPOM derived as a consequence of upstream processing inefficiencies. In recognition of this lateral component, Sedell *et al*. (1989) indicated that the RCC was still applicable to upstream reaches and large constricted-channel rivers but was an inappropriate model for floodplain rivers. At a different spatial scale compared to those in large rivers, small streams can also have large (e.g. beaver dam pools; e.g. Naiman, 1997) and moderate-sized patches (e.g. riffles and pools).

Publication of the flood pulse concept helped greatly expand a formerly small trend of research in large rivers (e.g. Winemiller, 2004). Scientists began recognizing the importance of channel complexity around the world (e.g. Walker *et al*., 1995; Thoms and Sheldon, 1997; Amoros and Bornette, 2002; Robinson *et al*., 2002) and initiated studies comparing ecological structure and functioning amongst and within large patches (FPZs) formed by channel braiding, anabranches, various forms of slackwaters, floodplains etc. Often these large patches were created, eliminated or altered extensively on seasonal or aperiodic temporal scales by sub-bankfull flow pulses (Tockner *et al*., 2000; Burgherr *et al.*, 2002) or supra-bankfull flood pulses (Junk *et al*., 1989). Recognition of the ecological importance of differences in flow velocity, turbulence, and retention time in large rivers led to development of the inshore retention concept (Schiemer *et al*., 2001a). A growing number of scientists are now finding that large lateral, flow-related patches in large rivers are responsible for major differences in structural and functional attributes of river ecosystems for plankton, benthic macroinvertebrates, nutrient cycling, productivity and trophic food webs (e.g. Vranovsky, 1995; Reynolds and Descy, 1996; Hein *et al*., 2003; Thorp and Casper, 2003). It has also well established that fish perceive patches at small (substrate) to large (e.g. floodplain areas) size ranges and use them differently depending on season and their life history characteristics (Schiemer *et al*., 2001b; Galat and Zweimüller, 2001). The impacts of reduced patch complexity and decreased connectivity amongst lateral patches is a rapidly growing area of research in rehabilitation of large lowland rivers (e.g. Hein *et al*., 2005).

Even though large patches are present in large rivers, important small patches exist within a hierarchy of larger spatiotemporal patches. These include substrate patches, which presumably function in the same way as in small

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streams. Some substrate patches develop in response to geomorphic and/or hydrological processes, while others are formed biotically (e.g. macrophyte beds and wood snags). Macrophyte patches, which predominately occur from small open-canopy rivers to slackwaters in large rivers, can be characterized by different substrate size, oxygen conditions, benthic organic content, and nutrient relationships compared to the more homogeneous surrounding habitats of bare substrate. Their presence in large rivers is tightly bound spatially to stream hydraulics, and their patch size also fluctuates seasonally. Consequently, the benthic and littoral plankton assemblages associated with macrophyte beds are influenced by a spatiotemporal hierarchy of biotically and abiotically controlled patches. In some ways, some small patches become even more important in large rivers because hard substrates are often relatively more abundant in small streams than in large rivers where silt and sand often predominate. For example, the distribution of isolated rock outcroppings are vital to interactions between sympatric species of prosobranch snails in the Ohio River (Greenwood and Thorp, 2001). Water-column patches of nutrients and plankton are also present in rivers, but these have not been thoroughly investigated.

Ecologists have identified a large range of patch sizes in river networks, but research is needed to link spatiotemporal patches into a modelled hierarchy suitable for testing. In some cases, we also need better evidence that the patches we identify for motile invertebrates are really applicable for the target processes we have selected (e.g. Malmqvist, 2002). For instance, Peckarsky *et al*. (2000) demonstrated that patches seemingly appropriate for studying the dynamics of mayfly species in Rocky Mountain streams were in fact too small because processes operating at a large regional patch determined dispersal rates. This also could be an example of metapopulation dynamics at work. Moreover, Ward and Tockner (2001) suggested that hydrological connectivity controls biodiversity at the floodplain scale; whereas at the even larger catchment scale, biogeographical factors are more important. Likewise, Grimm (1994) noted that algal biomass was strongly influenced by disturbance-related flow regime on an annual basis but by nitrogen availability during shorter temporal scales. Statistically demonstrating the hierarchical importance of different spatiotemporal patches in lotic ecosystems is not an easy task, but the problem can be approached with both experimental and modelling techniques. Whilst in the past it was sufficient to show that biotic interactions influenced species densities and distribution on a small spatial scale (e.g. interactions amongst larval insects on a rock), researchers should now be encouraged to take the next step and explicitly determine how important that process is for larger spatiotemporal patches where other independent variables operate. Ecologists should also examine how a given process varies longitudinally and laterally along the river network. Finally, aquatic ecologists may need to match the scale of environmental processes with the appropriate scale of biological organization from individuals to ecosystems (Thoms and Parsons, 2002).

Element II: Ecosystem dynamics as a composite of intra- and inter-patch dynamics

It has been known for at least two decades that the structure and functioning of an ecosystem at any given time are the sum of dynamic, deterministic and stochastic processes occurring within and amongst patches of different spatiotemporal scales (e.g. Pickett and White, 1985). This aspect of system dynamics is considered an emergent property of the ecosystem (Wu and Loucks, 1995) which could not be ascertained by only studying, for example, competitive interactions amongst periphyton scrapers on a rock. Moreover, the consequences and significance of any focal level process will not be revealed in a hierarchically organized system without investigation at the next higher (horizontal) level, nor can the mechanisms be demonstrated without studying one or more levels down from the focal process (O'Neill, 1988). This can be illustrated by the community dynamics of zooplankton in rivers. The local importance of deterministic processes can be studied with *in situ* experiments testing effects of mussel and fish predation on density and relative abundance of rotifers, cladocera and copepods (e.g. Jack and Thorp, 2000, 2002; Thorp and Casper, 2002, 2003). Community responses that seem to involve a trophic cascade (Thorp and Casper, 2003) are evident only by studying mechanisms of predation and competition at a finer level and by understanding relative differences amongst major taxa of zooplankton in reproductive rates and reactions to river currents and turbulence. The reach-scale significance of these deterministic processes occurring within plankton patches should then be evaluated at higher hierarchical levels, such as between main channel and slackwater patches where disparate hydrodynamic forces may predominate. They could also be studied amongst seasons where differences in both abiotic (temperature and hydrological regime) and biotic conditions (e.g. variable phytoplankton productivity) may alter the importance of trophic cascades. Finally, it could be crucial to understand

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interactions amongst patches which occur via corridors (an aspect that the HPD model does not emphasize explicitly), especially those that change seasonally in response to floods.

Deciphering codes of community regulation in river networks will probably always be a formidable challenge because ecosystems are so complex. Nonetheless, researchers can lighten the task by focusing on adjacent hierarchical levels, where the strength and frequency of interactions are greater than between more distant portions of the hierarchy (Wu, 1999). The resulting loss of information is often insignificant but will vary with processes, patterns and scales examined.

Element III: Linked patterns and processes

Pattern and process are interlinked and scale-dependent. By ‘pattern’ we mean an observable configuration of living or inanimate objects or processes in space and/or time. A few of the many examples of patterns in river networks are the alternating distribution of riffles and pools in streams, life history characteristics of species adapted for intermittent streams versus large permanent rivers, changes in functional feeding groups from headwaters to large rivers, and species replacements of microalgae colonizing rocks over time. Processes are series of actions leading to change over time and to new or recurring patterns. Some examples of processes are species evolution, riparian leaf decomposition, algal primary production, nutrient spiralling, trophic cascades, sediment transport and flooding.

Pattern does not imply process, but sometimes one can cautiously infer processes from interlinked patterns and *vice versa*. This can be seen, for example, in both natural rivers (Junk *et al.*, 1989) and ones with modified channels (Hein *et al.*, 2003) where productivity and diversity vary with hydrological connectivity (fluvial distance between slackwaters and the main channel or periodicity of flooding in intermittently isolated floodplain lakes). Patterns of biocomplexity across a gradient of hydrological connectivity sometimes appear to fit an intermediate disturbance model (Ward and Tockner, 2001, based on the model of Connell, 1978). The causation of this pattern, however, may relate to numerous factors acting individually or in concert (e.g. current velocity, temperature, suspended sediments, predator and resource types and levels) and could vary over time. Consequently, successful inferences about causation of patterns must factor in spatial and temporal scales in hierarchically arranged ecosystems (Fisher, 1993). Extreme caution must be used, however, in extrapolating conclusions about causal mechanisms amongst disparate spatiotemporal scales because regulatory factors operating at one spatiotemporal scale may be completely dissimilar from those present at another scale and because non-linear ecological relationships and inter-component feedbacks are common amongst scales (Wu, 1999).

Processes and patterns may create, modify, or eliminate one another, depending on the spatiotemporal scale examined. For example, patterns of distribution and abundance of both debris dams and beaver dams in streams influence the process of nutrient spiralling on different spatial scales by changing rates of downstream transport, but nutrient spiralling may in turn control patterns of distribution and productivity of periphyton. Likewise, the rate of primary productivity may limit density of suspension feeding bivalve molluscs, but the distribution and abundance of exotic mussels influence the number of type of phytoplankton (Cohen *et al.*, 1984; Caraco *et al.*, 1997).

Element IV: Dominance of non-equilibrium and stochastic processes

Depending on the temporal and spatial scales of observation, ecological units within the river network can be interpreted as exhibiting non-equilibrial, transient or unstable dynamics, but rarely could these open, environmentally fluctuating ecosystems be portrayed as existing in a true equilibrial state. However, one’s view of the equilibrial status in a river network may depend on whether the focus is on patterns (e.g. community composition) or processes (e.g. primary and secondary production, nutrient spiralling, etc.), and the level of discrimination of each. As an example, a flood event in the ephemeral Sycamore Creek of the arid southeastern USA can remove greater than 90% of the benthic insect biomass and much of the attached algae (Grimm and Fisher, 1989). Fisher (1993) suggested that the rapid recovery of functional processes indicates a system that is stable because of strong resilience (though weak resistance), whereas the eventual return to a similar community composition points to system that is stable because of the opposite attribute, resistance of structural biodiversity! He noted that both viewpoints were correct, depending on which observation set was selected. Other investigators focusing on the same responses but shorter time scales or the same time scale but on relative species abundances might perceive the system as

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clearly unstable and dominated by stochastic processes. Indeed, a reasonable hypothesis for retention of species is that the stochastic nature of hydrological events in Sycamore Creek prevents equilibria from developing and thereby reduces chances of extirpation of local species by interspecific competition. It is relevant to note, however, that stochastic processes do not necessarily work against stability but may, instead, constitute a mechanism underlying the apparent stability of ecological systems at different scales (Wu, 1999). 'Thus, equilibrium and non-equilibrium are not absolute and context-free, but relative and scale-dependent (Wu, 1999)'.

Over the last quarter-century, there has been a shift in general ecological perceptions to the viewpoint that lotic ecosystems are driven chiefly by stochastic forces related primarily to floods (e.g. Ward *et al.*, 2002) or droughts (Lake, 2003; Dodds *et al.*, 2004). Stochastic processes operate across broad spatial and temporal scales in lotic systems, but small-scale processes generally tend to be more stochastic and less predictable (cf., Wu, 1999). In contrast, the importance of deterministic factors appears more restricted to the smaller spatial scales where predator-prey, host-parasite and interspecific competitive interactions operate.

Current evidence suggests that deterministic factors are relatively more prominent in slackwater areas, whereas stochastic factors achieve their greatest importance in flowing channels where hydraulic stress is greater (Johnson *et al.*, 1995; Thorp and Casper, 2003). However, stochastic processes could also be crucial along the moving littoral border of the aquatic-terrestrial transition zone, as described in Junk *et al.* (1989). Consequently, the structure of hydrogeomorphic patches should influence the relative importance of deterministic and stochastic factors in FPZs.

A productive area for future research could entail analysis of relative importance of stochastic and deterministic processes in river networks as one moves from cobble- to reach-sized patches for different types of functional process zones. Is the importance of stochastic factors related mostly or essentially only to hydrological patterns or do other environmental factors play a role in streams? Are hydrological events always or mostly stochastic, or can they act as deterministic factors at some spatiotemporal scales (cf., Sparks *et al.*, 1990; Delong *et al.*, 2001)? Does the tendency of a hydrological event to be stochastic versus deterministic vary with stream size and/or bed motility? Do relative roles of non-equilibrial factors vary laterally and/or longitudinally by the size of the stream or hydrogeomorphic patch? How do these relationships differ with organismal life history patterns and ecoregion?

Element V: Formation of a quasi-equilibrial, metastable state

Depending on which variables one uses to evaluate equilibrium and over what spatiotemporal scales, many if not all natural rivers exist in a non-equilibrial or perhaps quasi-equilibrial state (= statistical equilibrium). Ecologists could reasonably question whether river networks can ever achieve true equilibrium because they are open systems subject to major hydrological variations over several temporal scales which introduce substantial stochasticity within and amongst patches. Nonetheless, it is theoretically possible for a quasi-equilibrial, metastable state to develop at one level of an ecosystem through incorporation of non-equilibrial processes operating within multiple patches at a lower hierarchical level (Paine and Levin, 1981; O'Neil *et al.*, 1989). In one sense, this property allows naturalists to note inter-year similarities in stream species richness even though relative abundances and absolute densities vary.

The presence of metastability at one hierarchical level does not necessarily imply its presence at another level. Hence, metastability of diverse fish communities does not mean that individual species occur in metapopulations. Indeed, ecologists and conservation biologists have just begun to explore the potential importance of species metapopulations in river networks. Metapopulation dynamics and stability can be examined at several spatial dimensions along a four-dimensional river network. Research on repopulation of stream sections denuded by hydraulic spates has often emphasized recolonization from longitudinal (e.g. upstream dispersal by flying aquatic insects, swimming by amphipods and fish and crawling by snails), lateral (e.g. inter-stream, cross-land migration of crayfish and adult insects), and vertical dimensions (recolonization from hyporheic refuges) (see examples in Giller and Malmqvist, 1998; Thorp and Covich, 2001). For some species habitat recolonization in small streams constitutes intra-population recruitment from refugia. In other cases, however, this may represent the action of a metapopulation. The latter explanation is especially appropriate where recruitment is derived from a separate stream in the same or different river network or if clearly demarcated patches exist within the same stream and intra-patch recruitment chances exceed inter-patch dispersal. Metapopulation models (e.g. Levins, 1969) have been applied to fish (e.g. Dunham and Riemanm, 1999) and exotic mussel populations in rivers (e.g. Stoeckel *et al*., 1997), but the theoretical suitability of specific models (e.g. the island-mainland model of Harrison *et al*., 1988) is occasionally challenged (Gotelli and Taylor, 1999).

A more puzzling problem that potentially involves metapopulation dynamics is how plankton populations are maintained in advective environments, given the great difficulty phytoplankton, protozoa, rotifers and microcrustaceans have swimming against currents. Aside from likely recruitment for some taxa via resistant eggs blown from dried floodplain habitats, metapopulation studies of river plankton are beginning to focus on the role played by both small (e.g. eddies and shoreline habitats) and large patches (e.g. lateral slackwater and floodplain habitats). Hydraulic storage resulting from channel morphology may account for river phytoplankton recruitment and production, according to Reynolds and Descy (1996), and this may explain metastability in the broader lotic community. Retentivity of slackwater areas has also been shown to be vital for recruitment of 0+ aged fish, production of zooplankton (Schiemer *et al*., 2001a), and diversity, relative abundance and fecundity of riverine zooplankton (Thorp and Casper, unpublished data). Similar observations led to development of the inshore retention concept (Schiemer *et al*., 2001a). The first step in proving that slackwater and floodplain patches generate metastability within the larger river network is to document a significant export of recruits into the main channel habitat. Such movement as been noted in the River Danube by Schiemer *et al*. (2001a) who found high correlations between rotifer populations in the main channel and sinuosity index values in the river (which are related to the degree of hydraulic retention). Junk *et al*. (1989) concluded that Amazonian floodplains energetically support main channel populations of fish, but the export of living and detrital organic matter from large floodplains seem insignificant in the tropical Orinoco River (e.g. Hamilton *et al*., 1992; Lewis *et al*., 2000) and has been questioned for the Amazon (Hedges *et al*., 1986).

Research on metapopulations from lateral slackwaters and floodplains could be a fertile research area. Determining export rates from hydraulically complex slackwater and floodplain sites will be the first significant challenge. Another major task will be evaluating whether large patches constitute different populations and whether those in the main channel are dependent for recruitment on populations in lateral patches. This research avenue could be crucial, however, because river channelization on several continents has reduced lateral patch complexity and severely impinged on ecological integrity in a high percentage of lowland river ecosystems (e.g. Hein *et al*., 2005). Finally, stream ecologists need to determine which models of population sustainability are most appropriate (e.g. see Gotelli and Taylor, 1999).

A CONTRIBUTION TO CONCEPTUAL COHESIVENESS IN LOTIC MODELS

While the drive within lotic ecology to develop conceptual cohesiveness is not comparable in fervour to physicists seeking a unified field theory, attainment of this ecological goal would still be monumental. As in evolutionary biology (Mayr, 1970), a viable theory is unlikely to be a single factor model and would probably include a balance of conflicting forces. An effective synthesis could draw upon special case theories (e.g. the flood pulse concept in lowland floodplain rivers; Junk *et al*., 1989), but should be more than a compilation of such models. Indeed, we would be better served in seeking this goal by actively discarding non-viable theories, but the easier (more collegial?) way is usually to let time accomplish that chore. Our contribution to this quest for a general lotic theory is the heuristic *riverine ecosystem synthesis* (RES). As described above, the RES is an integrated model derived from aspects of other aquatic and terrestrial models proposed from 1980–2004, combined with our perspectives on functional process zones and other aspects of riverine biocomplexity.

Many testable hypotheses can be generated from the RES, but manuscript space and time limit what we can initially propose. Consequently, we define below 14 model tenets which describe the functioning of epigean portions of lotic ecosystems on ecological time scales. We made an effort to frame most of the tenets as testable hypotheses, at least in part. We make no claim to originality for all these tenets. Some of these ideas are well supported in the scientific literature, whereas others may be controversial or border on being educated guesses. They are focused more on the riverscape than the entire riverine landscape (*sensu* Wiens, 2002), an emphasis partially reflecting the more recent developments in river-floodplain research. The RES describes the functioning of pristine river networks, but it could be used to test effects of human activities (as described in a chapter of the book we are currently preparing about the RES). The first set of tenets concerns factors influencing species distributions or, in effect, composition of the species pool. The next section on community regulation relates to factors controlling species diversity and abundance within the assemblage of species potentially present in the environment. Both density independent and dependent factors are included. The final set of tenets covers processes at the ecosystem and riverine landscape levels. The list of tenets is not meant to be exhaustive, and we hope our colleagues will add and test additional tenets derivable from the RES.

Distribution of species

> *Model Tenet 1: Species distributions in a river network are associated primarily with the distribution of small to large spatial patches formed principally by hydrogeomorphic forces and modified by climate and vegetation.*

Because the temporal signature of flow disturbance varies as you move downstream, the probability of occurrence of particular functional process zones (FPZ) in a given region of the river network may be enhanced, but the same type of FPZ may appear repeatedly along a longitudinal dimension in a complex pattern which becomes less predictable above the ecoregional level. The unique habitat template characteristic of each hydrogeomorphic patch limits the potential species pool and alters biocomplexity within the associated FPZ. Absolute and relative abundance of species within FPZs are related primarily to the physiochemical nature of the FPZ and constituent species.

> *Model Tenet 2: Distributions of species and ecotypes and community diversity from headwaters to a river's mouth primarily reflect the nature of the functional process zone rather than the position along the longitudinal dimension of the river network.*

Biotic communities in comparable types of FPZs should be more similar to each other than either is to adjacent assemblages in different types of FPZs. This contrasts with a continuum perspective of species distributions where a relatively smooth transition of species is predicted to occur along a longitudinal dimension and community dissimilarity should increase with separation distance. Various authors have concluded that species diversity in river networks bears little relationship to stream order (e.g. Statzner, 1981; Minshall *et al.*, 1982; Statzner and Higler, 1985; Townsend, 1989). While we see some evidence of gross patterns of diversity and abundance for broad taxonomic groups along a longitudinal dimension (e.g. for fish, molluscs, crustaceans and insects), these patterns are highly variable and more responsive to variations amongst FPZs. However, it is possible that the spatial arrangement of FPZs along a longitudinal dimension significantly influences biocomplexity.

> *Model Tenet 3: Species diversity is maximum at ecological nodes representing transitions between hydrogeomorphic patches or areas of marked habitat convergence and divergence within functional process zones.*

These ecological nodes are formed primarily in response to transitions in hydrogeomorphic processes but can also be influenced by other habitat-forming processes. The importance to benthic species of transition areas along a longitudinal dimension was emphasized soon after publication of the RCC by Statzner and Higler (1985). More recently, scientists have emphasized transitions within channels (e.g. tributary confluences, divergence and convergence areas in braided/anastomosing rivers, and vegetated islands; e.g. Thorp, 1992), between flowing water channels and slackwaters (e.g. Schiemer *et al.*, 2001a; Thorp and Casper, 2002), and between slackwaters and subbankfull areas, such as parafluvial ponds (e.g. Burgherr *et al.*, 2002; Karaus and Tockner, in review). Hyporheic transition areas may also serve as a form of permanent or temporary ecological node (cf., Ward and Voelz, 1994).

> *Model Tenet 4: Species diversity and density vary significantly with current velocity throughout the river network and are positively correlated with hydrological retention within the riverscape of larger rivers, except where other abiotic environmental conditions (e.g. oxygen, temperature, substrate type) restrict many taxa.*

Rivers are distinguished from lentic environments by their persistence of directional flow, but all lotic ecosystems—from those with simple constricted channels to ones with complex, intertwined secondary channels and broad floodplains—include areas where directional currents are low or nearly permanently absent and turbulence

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is greatly reduced. These slackwater areas function as refuges from the physical stress of flowing water. They also serve as nursery and/or high productivity reservoirs for many fish, other vertebrates, plankton, benthic invertebrates, vascular macrophytes and some periphyton. Moreover, they retain food longer and cycle nutrients differently than faster-flowing channel areas. While access to these areas is not necessarily essential for most fish species in some rivers, such as temperate rivers with aseasonal flood cycles, it usually greatly enhances overall fish recruitment (Humphries *et al*., 1999, 2002; Winemiller, 2004). Hydrological retention areas are an essential element of lotic ecosystems ensuring the natural functioning of healthy lotic ecosystems, as demonstrated repeatedly (e.g. see references in Sedell *et al.*, 1989; Thorp, 1992; Thorp and Delong, 2002) and modelled by the inshore retention concept (Schiemer *et al*., 2001a). The degree and importance of hydrological retention vary with the type of FPZ.

Community regulation

Factors regulating community structure are likely to vary significantly over spatiotemporal scales and are influenced by the type of FPZ, its position within a river network, and the nature of the surrounding ecoregion. The relative importance of density dependent and independent factors could change seasonally (e.g. Ward and Uehlinger, 2003) and will certainly vary with taxonomic group. Nonetheless, we list below some general conclusions applicable across broad spatial scales.

> *Model Tenet 5: The most important feature of the environment regulating community composition is a hierarchical habitat template, as determined primarily by interactions between geomorphic habitat features and both short- and long-term flow characteristics.*

Gaining some semblance of unanimity on the relative importance of factors regulating lotic communities is a major challenge, but the factor that would probably be ranked highest by most stream ecologists is a hierarchically-scaled, habitat template (cf., Frissell *et al*., 1986; Hildrew and Giller, 1994; Townsend and Hildrew, 1994). This factor, or really nested series of factors, integrates effects on species of interactions between geomorphic features of the aquatic and terrestrial habitat and flow characteristics (magnitude, frequency, duration, timing and rate of change of hydrological conditions; see Poff *et al*., 1997).

Research on the significance of flow characteristics has been especially prominent in the scientific literature within the last decade, but the relative importance of mean and variability of flow patterns has not been firmly established. Vannote *et al*. (1980) hypothesized in the RCC, '. . . that the structural and functional characteristics of stream communities are adapted to conform to most probable position or mean state of the physical system'. In contrast, Palmer *et al*. (1997) and others have argued that environmental variability itself may be a controlling factor. It is possible, therefore, that observed biocomplexity is as much in response to characteristic variability within a FPZ or whole stream as it is to the probable mean state of the environment. Given that variability of flow is inversely related to stream size, the importance of short-term hydrological variability in community regulation is probably greatest in headwater streams. In addition to in-channel flow control of community structure and ecosystem function (e.g. nutrient spiralling), sub-bankfull flow pulses (Tockner *et al*., 2000) and supra-bankfull flood pulses (Junk *et al*., 1989; Winemiller, 2004) are critical to sustaining biodiversity, probably more so in downstream portions of the river network.

The relative and absolute effects of geomorphical features and hydrological conditions on biocomplexity will vary with the nature of the FPZ. This reflects in part the observation that both short- and long-term variability and predictability of environmental conditions differ amongst types of hydrogeomorphic patches both within and amongst rivers.

> *Model Tenet 6: Both deterministic and stochastic factors contribute significantly to community regulation, but their relative importance is scale- and habitat-dependent; however, stochastic factors are more important overall and throughout the river network.*

Stochastic, non-equilibrium processes in lotic ecosystems are primarily associated with stream hydraulics (e.g. direct effects of water velocity and turbulence and indirect effects from substrate movement), floods and droughts.

Climatic impacts related to high temperatures, oxygen content and ice scouring are occasionally important (especially in smaller streams), and stochastic factors influencing the watershed can also be consequential. These latter could include vegetation loss from fires which would then temporarily increase runoff of water, sediment, inorganic nutrients and organic matter into streams as well as changing detrital constituents of the floodplain, thus modifying effects of the flood pulse cycle (pers. com., Wolfgang Junk). Stochastic factors operate over broad spatiotemporal scales but are especially important at small scales. Their role is probably greater in channel habitats compared to slackwaters and possibly at ecotones between both adjacent FPZs and river-landscape habitats.

Deterministic processes contributing to community regulation in river networks are mostly related to interspecific competition, predator-prey interactions and host-parasite interactions. The current evidence for interference (space) competition (e.g. Hart, 1983; Georgian and Thorp, 1992) is stronger than for exploitative (primarily food) competition. Nonetheless, some studies have demonstrated resource competition can influence population size in zooplankton (e.g. Pace *et al.*, 1998), snails (e.g. Brown, 2001) and other organisms. Deterministic processes tend to be more influential on shorter rather than longer time scales and where physical stress is diminished. Therefore, one would more likely find significant biotic interactions in lateral slackwater habitats or in the main channel in areas or times of minimal hydraulic stress. Although not as often reported as in lentic environments, trophic cascades have been suggested for some lotic systems (e.g. Pace *et al.*, 1999; Woodward and Hildrew, 2002; Thorp and Casper, 2003).

The intermediate disturbance hypothesis (Connell, 1978) has been applied to small streams through large rivers (reviewed in Ward and Stanford, 1983; Townsend *et al*., 1997; Ward and Tockner, 2001) in terms of predator and flow regime effects on community attributes, but a definitive demonstration of this phenomenon has rarely been attempted (cf., field experiment of Thorp and Cothran, 1984). Moreover, Wootton (1998) questioned the application of this theory to some complex, multi-trophic lotic systems, such as lotic communities. For a thorough discussion of patterns of environmental perturbations (disturbances and responses), see Lake (2000).

Model Tenet 7: A quasi-equilibrium is maintained by a dynamic patch mosaic.

A true equilibrial state is problematic in river networks because they are open, advective systems subject to major hydrological variations which introduce large measures of stochasticity within patches at various scales. Despite the predominance of stochastic, non-equilibrial processes at most spatiotemporal scales and habitats, we believe that lotic communities are generally maintained in a quasi-equilibrial state. This results from incorporation of multiple, non-equilibrial or short-term equilibrial processes operating at lower hierarchical levels in a dynamic mosaic of patches characterized by multiple spatial and temporal dimensions (cf., Paine and Levin, 1981; O'Neil *et al*., 1989).

The study of metapopulations in open, advective systems is in its infancy, and it is too early to ascertain their importance for lotic populations. Defining a metapopulation for lotic communities, however, is somewhat risky. Does recolonization of intermittent streams reflect the action of a metapopulation? Likewise, does recruitment of fish and invertebrates into channel habitats from large lateral patches constitute metapopulational dispersal? One of the more likely examples of the effects of a metapopulation concerns recruitment of resistant potamoplankton propagules from one catchment to another via prevailing winds or waterfowl movement; however, the relative importance of this process has not been sufficiently evaluated.

Model Tenet 8: (a) Classical (facilitative) succession is primarily limited to terrestrial elements of the riverscape (on ephemeral islands) and riverine landscape (riparian and floodplain habitats), and it occurs in response to hydrogeomorphic processes; (b) the relative importance of simple seasonal species replacement versus true, non-facilitative succession (e.g., a blend of inhibition and tolerance succession) within wetted portions of the riverscape varies directly with stream size and inversely with hydrological variability.

Evaluating the importance of succession in lotic ecosystems is challenging because of the many disparate definitions of the process. Classical succession, or facilitation (described in Connell and Slatyer, 1977), should be limited mostly to terrestrial elements of the riverscape and riverine landscape and results from hydrogeomorphic processes operating on medium time scales of one to hundreds of years. Some examples of riverine

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landscape succession are given in Robertson and Augspurger (1999) and Friedman and Lee (2002). Primary, facilitative succession principally entails predictable vegetative seres both on initially bare alluvial islands within the active river corridor of the riverscape and on bare alluvium deposited in the floodplain following episodic floods (cf., Ward *et al.*, 2002). Terrestrial succession in these areas significantly impacts biocomplexity in the linked aquatic ecosystem. Newly formed floodplain lakes within the riverine landscape will also undergo succession which can ultimately lead to terrestrialization unless reset by a new flood; Ward *et al.* (2002) refers to this as hydrarch succession. Long-term hydrogeomorphic processes lasting thousands of years or more will also gradually shift characteristics of the channel and lateral habitats causing development of new FPZs and successional communities.

While facilitative succession rarely, if ever, occurs in wetted portions of the riverscape, many authors have concluded that other forms of succession are present. In some cases, this putative succession is merely annually repeated, seasonal cycles of species replacements or perhaps the simple cumulative effects of dispersal into a previously disturbed environment to fill empty niches (as predicted by island biogeography theories even without facilitative succession). In other instances, however, an interaction of species over time and/or a response to changing environmental conditions following a hydraulic disturbance will cause a predictable shift in ecosystem processes (e.g. Fisher *et al.*, 1982) and sometimes species composition (e.g. Flory and Milner, 2000; Biggs and Smith, 2002). These latter forms of true, non-facilitative succession may represent various blends of the tolerance and inhibition successional categories described by Connell and Slatyer (1977). Whilst most successional studies in the riverine landscape have focused at the macroscale, the importance and form of succession could be different in the microscale landscapes of the meiobenthos (e.g. Robertson and Milner, 1999) and lotic biofilms (e.g. Sekar *et al.*, 2002).

The relative importance in wetted portions of the riverscape of simple 'seasonal species replacements' versus 'true, non-facilitative succession' occurring in response to hydraulic disturbance (e.g. as a result of increased overland runoff or blockage from in-channel, large woody debris) should vary directly with hydrological predictability and inversely with hydrological variation. These hydrological and hydraulic conditions will, in turn, differ amongst ecoregions and longitudinal position within the river network. If this hypothesis is valid, then the importance of true, non-facilitative succession should be greatest in lotic systems of arid ecoregions and should diminish with increasing stream size.

Ecosystem and riverine landscape processes

> *Model Tenet 9: (a) On an annual basis, autochthonous autotrophy provides, through an algal-grazer food web pathway, the trophic basis for most metazoan productivity for the river network (riverscape) as a whole, but allochthonous organic matter may be more important for some species and seasons and in shallow, heavily canopied headwaters; (b) however, a collateral and weakly linked, decomposer food pathway (the microbial-viral loop) is primarily responsible (with algal respiration in some cases) for a river's heterotrophic state (P/R < 1).*

Averaged over the year and river network, autochthonous autotrophy provides >50% of the energy supporting metazoan production in channel and slackwater sites. Exceptions will occur where autotrophs have not adequately adapted photosynthetically to low light or nutrients caused by factors such as a dense, enclosing canopy in headwaters, certain geological features and possibly high inorganic turbidity. The trophic-basis of production should shift from a relative emphasis on benthic to pelagic autotrophs from headwaters to mouth but is also influenced by the nature of the local FPZ. Although the metazoan community as a whole depends primarily on instream primary production, individual species may rely on allochthonous organic matter for most of their energy annually and/or seasonally.

Other than the RCC (Vannote *et al.*, 1980) and its modifications (e.g. Ward and Stanford, 1983; Minshall *et al.*, 1985; Sedell *et al.*, 1989), no lotic model has addressed changes in food resources or functional feeding groups along the entire river network. The RCC stipulated for a generalized river that the primary food sources along the longitudinal dimension of the river network are: (a) allochthonous organic matter (principally riparian leaves) in headwater streams with a heavy canopy cover; (b) benthic autotrophs in shallow mid-order rivers; and (c) fine

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particulate organic matter (FPOM) in large rivers that was derived from terrestrial organic matter via leakage from upstream food webs.

The primary energy supporting metazoan food webs in headwaters seems to be a combination of autochthonous production and riparian inputs of particulate and dissolved organic matter, with the relative balance dependent on the extent of canopy cover (Vannote *et al.*, 1980). Finlay (2001) showed that consumer δ^{13}C values in temperate headwaters through medium-sized rivers are more strongly related to algal than terrestrial δ^{13}C. However, he found a clear transition from terrestrial to algal carbon sources as watershed area increased, which was linked to decreasing canopies.

In mid-order streams, autochthonous autotrophy usually predominates as an energy source for Metazoa because such streams are typically shallow with minimal canopy and adequate light for benthic microalgae (Vannote *et al.*, 1980). However, macrophytes, though often abundant in mid-order streams, are unlikely to contribute in a substantial and direct way to metazoan production (cf., Winemiller, 2004) and are probably not even a major indirect contributor because of their recalcitrant detritus.

The source of energy fuelling large river food webs has been more controversial. A popular view (e.g. Sedell *et al.*, 1989; and the flood pulse concept of Junk *et al.*, 1989) has been that terrestrial detritus and aquatic macrophytes on submerged floodplains are the predominant nutrient sources in floodplain rivers rather than FPOM from upstream. Others have concluded from stable isotope data that the primary, annual energy source supporting overall metazoan production of most constricted and floodplain rivers ($\geq$ 4th order) is autochthonous primary production entering food webs via algal-grazer and decomposer pathways (see review and a discussion of the riverine productivity model in Thorp and Delong, 2002). However, a decomposer (microbial-viral loop) food pathway may process most of the transported, allochthonous and autochthonous carbon and contribute substantially to the heterotrophic state ($P/R < 1$) of many large rivers (Thorp and Delong, 2002). A weak coupling between microbial and metazoan production has also been noted by Lewis *et al.* (2001) and Delong and Thorp (2005). [See further discussion of floodplain food webs in Model Tenet 10.]

Interestingly enough, a common assumption in most lotic models is that FPOM in large rivers primarily originates as terrestrial CPOM (coarse particulate organic matter) transformed by, and then leaking from (as FPOM), headwater food webs. In contrast, recent analyses of seston composition using stable isotope and C:N ratios demonstrated that living and detrital autochthonous matter, principally phytoplankton, is an important or even majority constituent of transported POM in temperate and some tropical rivers (Thorp *et al.*, 1998; Delong *et al.*, 2001; Delong and Thorp, 2005). The predominance of autochthonous organic matter in seston has been shown for the Mississippi, Colorado, Rio Grande, and Columbia Rivers (Kendall *et al.*, 2001), for a floodplain reach of the River Danube (Hein *et al.*, 2003), and for the Upper Mississippi's main channel during the summer (Delong and Thorp, 2005). Although seston composition varies among seasons and rivers, the predominance of autochthonous organic matter in seston extends for much of the year but is especially prevalent during periods of maximum consumer productivity.

Model Tenet 10: Algal production is the primary source of organic energy fueling aquatic metazoan food webs in the floodplains of most riverine landscapes during supra-bankfull floods, especially in rivers with seasonal, warm-weather floods.

Based on earlier studies by Bayley (1989), Junk *et al.* (1989), and others, most aquatic ecologists probably still accept the proposition that metazoan food webs in flooded riverine landscapes are primarily fuelled by direct or detrital consumption of vascular macrophytes and terrestrial plant matter. However, the importance of allochthonous carbon to Metazoa as a whole has been challenged recently for tropical and temperate floodplain rivers (e.g. Hamilton *et al.*, 1992; Forsberg *et al.*, 1993; Lewis *et al.*, 2001; Winemiller, 2004). These studies support the preeminent role of grazer and detrital consumption of benthic, attached, and/or suspended algae in floodplain food webs. This may seem anomalous because of the inherently larger biomass of terrestrial and aquatic macrophyte detritus in floodplains, but apparently much of the FPOM assimilated by detritivorous fishes is derived from algae, even in floodplains where macrophytes dominate primary production (Araujo-Lima, 1986; Winemiller, 2004; Winemiller and Akin, unpublished data). Moreover, overall fish production in most rivers is dominated by relatively few species and short food chains, even in species-rich tropical floodplain rivers (Winemiller, 2004). This

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efficient transfer of energy may explain why large fish stocks in tropical floodplains can be supported by a seemingly minor component of the ecosystem's autotrophic production (Lewis *et al.*, 2001; Winemiller, 2004). Clearly, however, some floodplain ecosystems contain taxa specializing on consumption of terrestrial plant matter and aquatic macrophytes, especially in the tropics (Winemiller, 2004).

> *Model Tenet 11: Average current velocity and nutrient spiral length are positively correlated with river discharge, but both decrease in functional process zones with extensive lateral components.*

Nutrient spiralling is a foundation concept of modern lotic ecosystem ecology which combines nutrient cycling and downstream transport of solutes and gases (Webster and Patten, 1979; Newbold *et al.*, 1982; Newbold, 1992). Research has focused on biotic processing and physical retention by instream material, such as large woody debris (Valett *et al.*, 2002) and the hyporheic zone. Despite the inherent longitudinal component of this concept, researchers have concentrated almost exclusively on spiralling in the main channel of headwater systems, undoubtedly because spiralling is easier to measure and manipulate in very small permanent and intermittent streams (e.g. Mulholland *et al.*, 2002). While this research is clearly important, the potentially vital roles of lateral nutrient cycling and physical retention of nitrogen and other elements in medium to great rivers has rarely been examined.

Lateral habitats of the riverine landscape compress nutrient spirals in three basic ways. First, they retard downstream transport of solutes and gases because of minimal currents and floodplain storage of detritus and sediments. Second, biotic sequestration and biotic emigration are enhanced by: (a) greater primary and secondary production compared to main channel habitats; (b) the presence of some longer-lived species compared to upstream (e.g. larger and older fish); and (c) emigration to other ecosystems with waterfowl which have fed within slackwaters and alluvial wetlands. Third, anoxic microhabitats should be relatively more common in slackwaters than in the main channel and headwaters, thus affording more opportunities for microbially linked processes, such as nitrification and denitrification. Because the extent of lateral habitats varies among types of hydrogeomorphic patches, nutrient spiralling will differ significantly among categories of FPZs.

> *Model Tenet 12: Naturally dynamic hydrological patterns are necessary to maintain the evolved biocomplexity in river networks.*

The importance of hydrology and hydraulics to system functioning has long been acknowledged by ecologists working mostly in wadeable streams (e.g. Statzner and Higler, 1986), but it was not until publication of the flood pulse concept (Junk *et al.*, 1989) that the role of floods as necessary ecological events in large rivers became widely acknowledged. The influential 'natural flow regime' publication by Poff *et al.* (1997) demonstrated not only the crucial part played by floods in maintaining ecological integrity of naturally flowing rivers but also underscored their significance for river conservation, management and rehabilitation. The five flow regime components often considered most important are discharge magnitude, frequency of a given level, duration of specific flow events, seasonality-predictability of flow events, and rate of change (flashiness) between levels. Seasonal changes in hydrology are especially important in the tropics where photo-radiation and temperature show little seasonal variation. At the opposite extreme from floods, the ecological importance of droughts has recently begun receiving increased scientific scrutiny (e.g. Lake, 2003; Dodds *et al.*, 2004) and may, in fact, operate more as a mechanism of disturbance than floods in lotic ecosystems (Sparks *et al.*, 1990; Delong *et al.*, 2001).

> *Model Tenet 13: The frequency of flood-linked life history characteristics increases directly with the seasonal predictability of floods and their concurrence with periods of maximum system primary productivity.*

The importance of the flood pulse to life history characteristics of aquatic organisms and general biocomplexity was elegantly described for tropical rivers in the flood pulse concept (Junk *et al.*, 1989; Junk and Wantzen, 2004), but its role in temperate rivers has remained problematical. Recently, however, Winemiller (2004) explicitly linked the expression of flood-linked life history characteristics to the degree to which flooding occurs in phase with warm temperatures and enhanced system productivity. He identified three types of floodplain rivers: temperate stochastic, temperate seasonal and tropical seasonal. Reproduction/development, secondary production and food web complexity are linked in tropical rivers with highly predictable, long periods of flooding occurring against a backdrop of minimal seasonal fluctuations in temperature. Linkage of life history characteristics with flooding is weakest in temperate stochastic rivers with their aseasonal (unpredictable) flood regimes. Even in temperate seasonal floodplain rivers, maximum secondary production and selection for flood-linked life history characteristics depend on the flood pulse occurring in the late spring or summer.

> *Model Tenet 14: Biocomplexity generally peaks at intermediate levels of connectivity between the main channel and lateral aquatic habitats of the riverine landscape, but the relationship varies substantially among types of connectivity, evolutionary adaptation of taxa to flowing water, and functional processes examined.*

Spatiotemporal complexity of the riverine landscape—which varies amongst types of hydrogeomorphic patches—begets dynamic stability and influences ecological biocomplexity. The two principal forms of surface water connectivity affect stability and biocomplexity in ways differing amongst taxa and functional processes. In floodplains, connectivity refers to the frequency of surface water connection at supra-bankfull floods between the river proper and the floodplain lakes and temporally isolated river channels. By contrast, in slackwaters of the riverscape—which are connected continually or frequently by sub-bankfull river stages—connectivity pertains to the distance that water must flow between the main channel and the slackwater habitats, which affects, for example, oxygen, nutrients, dispersing life stages etc. Connectivity of slackwaters, however, is also linked to discharge magnitude. Increases in discharge, even within sub-bankfull river stages, can enhance exchanges between the channel and slackwaters (Delong and Bruesewitz, unpublished manuscript).

Biota, inorganic nutrients and particulate and dissolved organic matter move at different rates amongst elements in the riverine landscape (cf., Wiens, 2002) according to spatiotemporal dimensions, adjacent patch context, abundance of edges, extent of corridors and steepness of the boundary ecotones (which obviously differ for an organism vs. a nutrient molecule). The basis of understanding of this connectivity in riverine landscapes is mostly theoretical at this stage, and investigations have been limited primarily to hydrological connectivity of the wetted riverscape with terrestrial and lentic components of the floodplain (e.g. Bornette *et al.*, 1998; Tockner *et al.*, 1999; Ward *et al.*, 2002; Hein *et al.*, 2003). Flood waters impact terrestrial vegetation and initiate or reset successional processes. Likewise, many floodplain lentic systems may follow a successional pathway from a fluvial origin to terrestrialization if not reset by subsequent floods. Ward and Tockner (2001) concluded that overall biodiversity peaks at intermediate levels of connectivity, and Tockner *et al.* (1998) showed that the connectivity-biodiversity relationship varied considerably with the taxa being analysed. Such fundamental research has been applied directly to rehabilitation strategies (e.g. Hein *et al.*, 2005).

The effects of connectivity between channel and slackwater areas of the wetted riverscape on biocomplexity should be different than for river-floodplain (terrestrial and lentic) connectivity. Within the riverscape, increased hydrological connectivity should influence landscape diversity (i.e. structural complexity), current velocities and processes affected by flow (e.g. productivity and nutrient spiralling). Although the relationship between landscape diversity and inundation level seems to vary amongst types of rivers (Ward and Tockner, 2001), research on ecologically significant changes in structural complexity with inundation levels for habitats above and below the air-water interface in the riverscape have rarely been attempted. Increased connectivity within the riverscape at high water should depress population densities, productivity and community diversity for most aquatic macrophytes and for many metazoa, algae and prokaryotes that poorly tolerate currents, turbidity and/or sedimentation. For some taxa, however, this negative relationship may be counterbalanced by advantages linked to currents, such as higher oxygen tension in somewhat stagnant areas and greater additions of organic and inorganic nutrients to replace levels depressed, for example, by competition or sedimentation.

Although this last tenet predicts maximum biocomplexity at intermediate levels of connectivity, the current evidence supporting this seemingly simple relationship is sparse and the theoretical basis is not refined, especially when relying solely on application of the intermediate disturbance hypothesis (IDH) of Connell (1978). Plots of community structure or functional processes versus connectivity that result in intermediate relationships could produce not only a normal-shaped curve (as often illustrated for the IDH) but also ones characterized by extreme positive through negative skewness. This could reflect differences in adaptation of taxa to aquatic environments in

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general (e.g. fish, amphibians and birds) and to flowing waters in particular and differences in functional processes examined. Clearly additional research is needed in this area.

CONCLUSION AND CAVEAT ON THE RIVERINE ECOSYSTEM SYNTHESIS

Ecological systems are inherently complex and almost always frustrate the desire of scientists, conservationists, river managers and government regulators for simple models. Bearing that in mind, our contribution toward conceptual cohesiveness (the RES) consists of: (a) a *perspective* on the longitudinal organization of river networks (i.e. functional process zones formed by hydrogeomorphic patches); (b) selective application of a landscape model (hierarchical patch dynamics) as an *analytical framework or tool* for understanding lotic ecosystems; and (c) a series of mostly testable, *model tenets* to guide future research. We remind readers, however, that this is intended to be an heuristic model. Thus, it is meant as a pathway for exploration not as the destination. Consequently, we expect it to be modified by ecologists as research in different ecoregions around the world demonstrates where well-documented concordances or incongruities emerge.

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