Northeast Fisheries Science Center Technical Memorandum 447

How Most Influential Ecological and Geomorphologic River Concepts Shaped Modern Aquatic Ecology and Restoration

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ABSTRACT

Freshwater ecosystems have been significantly transformed by human impacts on watersheds, resulting in major decreases in the abundance and diversity of fish populations. To address these transformations, increased fish abundance is a common motivator of river restoration projects. Despite the central importance of fish as a provider of numerous ecosystem services (including food, cultural services, and critical ecological roles in river systems, biological processes), influential ecological models of rivers often ignore their role. As a result, restoration too often considers fish as simply a product of other elements of river structure and function. This leads to restoration actions frequently assuming that restoring physical complexity will also result in biological complexity—not necessarily targeting actions directly toward biological processes. Moreover, due to time and budget constraints, restoration is often planned at a spatiotemporal scale that does not yield measurable benefits for the targeted species (e.g., reach scale and over a few seasons). Here, we review the major conceptual models informing our view of freshwater ecosystems and how they shaped our view of habitat restoration, examining if this could be the reason restoration focus the physical habitat aspects, with a rare integration of the biological ones.

INTRODUCTION

River systems are essential components of the human environment that provide a wide array of ecosystem services, including fostering biological and habitat diversity, maintaining ecological balance through nutrient cycling and energy flux, and supporting human drinking water, food, transport, and energy needs (Albert et al., 2019; Ouellet et al., 2022). River processes create and maintain the landscape that most humans live on. Worldwide, the central societal importance of rivers has also made them one of the most dramatically altered ecosystems due to drainage, channelization, urbanization, dams, water withdrawals, and road crossings (Chin, 2006; Reid et al., 2019; Woodward et al., 2010). Transformations occur through multiple nested impacts that operate at different spatio-temporal scales and impact various processes.

Given the challenges that freshwater ecosystems face, there is a growing concern that the delivery of ecosystem services will be even more substantially impacted as freshwater habitats continue to deteriorate (Albert et al., 2021). In this light, river restoration has become key in trying to reverse changes due to human pressures (Piégay et al., 2023). Fish are often the target of habitat restoration, but restoration efforts rarely incorporate biological targets such as their food to go beyond the physical habitat components. Even when the restoration target is a particular fish species, restoration should integrate river ecological health, sustainability, climate resilience, and both physical and biological processes. To better understand why biological processes are not fully integrated into the restoration process, we revisit some of the most influential ecological and geomorphologic river concepts to: 1) examine their major contributions to shaping modern aquatic ecology and restoration and 2) understand key concepts necessary to a better integration of the biological processes that can lead us toward a more holistic watershed restoration.

HOW 45 YEARS OF RIVER CONCEPTUAL MODELS SHAPED MODERN STREAM ECOLOGY AND RESTORATION

The River Continuum Concept (RCC) was one of the most influential conceptual models in the field of stream ecology (Vannote & Sweeney, 1980). The model shifted science approaches from descriptive to predictive while emphasizing the need for interdisciplinary research (Doretto et al., 2020; Minshall et al., 1985). Since then, other approaches have emerged, and we review the conceptual models that shaped ecological understanding of rivers and views of watershed and habitat restoration (Figure 1, Table 1). We then describe how these concepts influenced a more common understanding of complex ecological processes and the connections and gaps between this understanding and stream restoration. Understanding these connections can help improve our working knowledge of stream ecology and make restoration more targeted and effective.

Timeline

Past → Present

Physical processes	Biological processes
River Continuum Concept - 1980	
Continuum of energy distribution along the stream network	Energy flow along the river network continuum acts as a template that explain macroinvertebrates organization
Flood Pulse Concept – 1989/2004	
Notion of system resets cause by floods and droughts that affect energy distribution and add lateral connectivity	Resets as the main biota drivers
Serial Discontinuity Concept -1983/1995/2001/2002	
System are rarely continuous and conditions resets as the downstream distance from disturbance (dams) increases	The resets toward more natural conditions include environmental heterogeneity and biota
Process Domain Concept – 1999	
Introduce multiscale drivers of ecosystems structure and watershed scale disturbances processes	Geomorphological patches control habitat and biological communities in it
Network Dynamics Hypothesis – 2004	
Importance of network structure in influencing spatiotemporal heterogeneity	Biota heterogeneity follow the habitat heterogeneity, and tributaries influence local drivers of heterogeneity
Riverine Ecosystem Synthesis – 2006	
Rivers are downstream arrays of hydrogeomorphic and climatic patches.	Biota distribution is driven by the hydrogeomorphic patches
River Wave Concept – 2014	
Unify of previous model using wave concept and attributes to explain network organization and energy flow.	
Channel Evolution model – 1984/1986 & Stream Evolution Model – 2014/2019	
Geomorphologic processes are key to river form and spatial organization and vary according evolutionary stage	Evolution stages are linked to specific physical and vegetative attributes that influences the species richness and trophic diversity
River Wetland Corridor -2021	
Connectivity between surface and subsurface hydrology to create and maintain an interacting system of channels, wetlands, and floodplain ponds and lakes	Consider the feedbacks between the geomorphologic/hydrology drivers and the wetlands complex
Waterscape Continuum Concept - 2022	
River ecosystems are nested within a much broader continuum, one that expands and contracts across and through landscapes and riverscapes	Typography, geologic composition, climate influence ecohydrological processes (and therefore biota)

Figure 1: Tabular synthesis of the major ecological concepts since the River Continuum Concept and their main contribution to the understanding of physical and biological processes. Collectively they form an information matrix of stream structure and function. More details on each concept are listed in Table 1.

The longitudinal stream organization of the RCC emerged from the concept of entropy in landscape evolution proposed by Leopold and Langbein (1962). This concept stated that several geomorphologic forms are explained by the most probable energy distribution and influenced by diverse constraints guiding the longitudinal evolution of river drainage channels. This foundational concept informed the macroinvertebrate communities component in the RCC (Vannote & Sweeney, 1980), which was complemented by the Flood Pulse Concept (Junk et al., 1989; Junk & Wantzen 2004) that integrated system ‘resets’ due to floods and drought as primary drivers of biota and expanded on the lateral connectivity of the river and its floodplain. Subsequently, Ward (1989) expanded this general connectivity framework to four dimensions: longitudinal, lateral, vertical, and temporal.

Because rivers are dynamic, and often interrupted longitudinally, the concept of discontinuity was developed (Stanford, 1983a; Ward & Stanford, 1995) with the Serial Discontinuity Concept (SDC) where dams act as spatial resets. Ward & Stanford (1995) integrated the concept of environmental heterogeneity describing how ecological conditions reset toward natural/unregulated conditions as the downstream distance from a discontinuity increased. Stanford & Ward (2001) expanded the concept of vertical connectivity, further expanding to a framing of a river corridor. The ecological relevance of discontinuities was further integrated by Poole (2002) with the proposed framework for fluvial landscape ecology. He described rivers as a patchy discontinuum from headwater to mouth that was integrated across the three dimensions of connectivity (lateral, longitudinal and vertical), along with the fourth dimension of time that is also related to the FPC and seasonal fish migrations (Ward 1989; Ouellet et al., 2022).

The Network Dynamics Hypothesis (NDH; Benda et al., 2004) further described habitat heterogeneity by documenting how the spatial arrangement and size of tributaries interacts with stochastic watershed processes to influence overall spatiotemporal heterogeneity. Effects depend on the network's structure, such as the basin size, shape, pattern, and size differences between confluent channels, drainage density, confluence density, local network geometry, stream power, and erodibility potential. The Riverine Ecosystem Synthesis (RES) viewed rivers and their organization as downstream arrays of large hydrogeomorphic patches resulting from catchment geomorphology, and climate characteristics (Thorp et al., 2006a). Humphries et al. (2014) further integrated these arrays into the River Wave Concept (RWC) to unify previous concepts (RCC, FPC) and the Riverine Productivity Model- RPM), where the spatial and temporal flow variations are described using the wave concept and associated attributes (shape, magnitude, wavelength, and frequency) linked to geomorphologic and climate characteristics. The Channel Evolution Model (CEM; Schumm, 1993; Simon & Hupp, 2006), considered geomorphological processes as key to river forms and spatial organization. An updated and expanded version of the Stream Evolution Model (SEM; Cluer & Thorne, 2014) further detailed the biogeomorphic and hydrologic links with evolutionary stages of streams and their valleys, and how this ultimately could be linked to manage and sustainably restore dynamic river systems. The SEM has been instrumental in promoting the view that there are alternate stable (in human time frame) river conditions that influence ecosystem functions in a non-linear process that cycles between stages and can be triggered by natural and/or anthropogenic disturbances, including human interventions. As such, restoration can influence a stable-state approach, with varying timelines, while recognizing the need to revisit and understand where sediment-transport shaping processes (like in alluvial floodplains) exist versus where channels are being shaped by structural controls (e.g., bedrock eskers). The River-Wetlands Corridor (RWC) further linked surface and sub-surface hydrology interactions and how this creates complex systems of channels, wetlands, and floodplain ponds and lakes (Wohl et al., 2021). Finally, the Waterscape Continuum Concept and its template (WCC) reinforced the idea that river ecosystems are nested under a discontinuous continuum of topographic, geologic, and climatic drivers that ultimately influence the ecohydrological processes (O'Sullivan et al., 2022a).

The organization of biological processes and biota in the RCC stems from the habitat template theory (Southwood, 1977) with habitat units driving population reproductive success, associated ecological species strategies, and the resulting community composition and spatio-temporal evolution- "As populations march through their habitats in space and time, their position and magnitude will wax and wane". The RCC was influential in explaining how the macroinvertebrate community varies. Shredder and collector species dominate upstream communities, primarily driven by the allochthonous energy inputs from leaves and other coarse particulate organic matter) and downstream the dominance of grazers and collectors increases as energy inputs shift to autochthonous sources ranging from periphyton to fine particulate organic matter from upstream. Predator guilds also vary along the continuum while representing a somewhat similar proportion of the overall community composition throughout a waterway. The continuum idea helped promote and shape the understanding of ecological spatial dynamics. This organizational idea was built into the Network Position Hypothesis (Brown & Swan, 2010a; Henriques-Silva et al., 2019) that clarified that local environmental drivers controlled headwater communities, while downstream communities were controlled by both environmental and dispersal factors. Species distribution patterns were further expanded by the FPC and SDC, which explained how flood pulse and discontinuities control/reset the distribution of in-stream vegetation, macroinvertebrates, and fish. The RES detailed how different hydrogeomorphological patches influence biota distribution and composition. In contrast, the SEM highlighted how the different watershed process domains and the stream evolution stages nested within the domains are linked to specific physical and vegetative attributes that influence species richness, trophic diversity, and species productivity. Although the RWC mainly focuses on aquatic vegetation, it does integrate the notions of feedback between the plant communities and the geomorphologic drivers of wetlands (Wohl et al., 2021), an idea missing from the previous concepts. In contrast, the WCC explains how drivers at different scales are controlling the ecohydrological processes that ultimately influence biota's distribution (O'Sullivan et al., 2022). The stream Evolution Triangle (SET, Castro & Thorne, 2019) is the only concept that fully integrates geology, hydrology, and biology by recognizing biology as a driver of stream form and processes, as proposed by Schumm (1985), thereby integrating all the components of previous conceptual models. However, it is essential to note that the ultimate connection of the three process categories in the SET to the evolution stage is specifically applicable to alluvial systems. Therefore, selecting a river evolution stage based on the SET should not inform restoration without a strong consideration to the river's stream power and erodibility index as originally framed by Schumm (1985).

Modern concepts integrate different categories of processes, consider the river corridor and the hydrology that's ultimately driven by topographic, geologic, and climatic factors. Modern concepts were foundational in focusing restoration towards processes that reestablish and maintain functional habitats vis-à-vis (Beechie et al., 2008; Grabowski et al., 2016 and Stefankiv et al., 2019). Although the ultimate goal is to achieve a holistic restoration that accounts for the physical and biological processes, ecological health, sustainability, and climate resilience, the literature presents a variety of approaches regarding the timeline presented in Figure 1. In some regions, process-based restoration has been more fully integrated, while in other regions, in-stream habitat structures are still dominating the restoration actions. However, even in areas where there is better consideration of physical processes and riverscape, as highlighted by Whitney et al. (2020), the restoration community generally overlooks biological considerations.

CONCLUSION

From the RCC to the WCC (Figure 1), the relevant spatial scale evolved from segments arranged along a longitudinal continuum river network to a corridor that includes lateral connectivity with the floodplain and the riparian area and vertical connectivity between the hyporheic zone and water column. The idea that river ecosystems are more than a single unidirectional channel but an integrated floodplain system is well embedded in modern aquatic ecology of a river corridors and the WCC (Biron et al., 2018; Kline & Cahoon, 2010; O'Sullivan et al., 2022; Wohl et al., 2005). Collectively, these models fostered a greater understanding of all the dimensions and connections of flowing rivers, and how processes interact to produce a habitat mosaic that varies over time and space frames. Our collective understanding of community distribution and composition evolved from a simpler longitudinal organization, to a more complex heterogeneous one where disturbances, water movements, local and river reach environmental and climatic drivers all play a dynamic role in framing species abundance and diversity. However, like many new scientific concepts, the application of this spatial organization in the stream restoration community has lagged. Perhaps because until recently, there was a lack of a practical framework about how to factor that level of organization into practical restoration. (O'Sullivan et al., 2022b)(T. Beechie et al., 2008; T. J. Beechie et al., 2021, 2023; Booth et al., 2016)(Ashley Steel et al., 2016; Dunham et al., 2018; Erős et al., 2018; Humphries et al., 2020; Torgersen et al., 2021).

Similarly, although the food web science has advanced (Cross et al., 2013; Scholl et al., 2023), it has not fully been incorporated into these ecological concepts, which might explain the lag in incorporating food webs into restoration (Benjamin et al., 2020; Whitney et al., 2020) . The initiative to integrate that type of information into our understanding of riverine habitats and their evolution has been stronger over the last few years, and the practice is mainly lagging behind this integration. This is most likely because we still lack simplified ways to make specific predictions about the composition, interactions, and responses of food webs to restoration actions; a tool practitioners can use to guide their restoration. (Ouellet et al., 2025; Rossi et al., 2024). Nonetheless, as result, biological consideration such as fish abundance, diversity, food, etc. are rarely included and often the target species is treated as the end product of the other biota and habitat organization without full consideration of all the linkages, including feedback mechanisms, i.e. how fish influence other biological and physical processes. Naman et al., (2022) described the link between all the biological components, stating that food webs offer insight into understanding species interactions, trophic relationships and energy flow, which underpin fish populations' characteristics such as survival, growth and reproduction. Recent papers on foodscape are proposing specific actions to help move in that direction, but there are a couple of needs to first improve our understanding of foodscape to then be able to develop predictive models that could support restoration decision-making (Ouellet et al., 2025; Rossi et al., 2024). Until the science behind the biological processes matures in ways similar to our knowledge of spatiotemporal organization, we can initiate small steps to better incorporate biological processes such as thinking of drivers of abundance and diversity, energy flux through food web and predatory interactions, etc.

Many restoration projects remain focused mainly on physical processes in stream organization, and restoration and have not aligned with current scientific thinking about the scale of organization and the complexity of the biological processes. Our review confirmed that the major organizational concepts have strongly influenced our restoration views. However, there is a lag between the most recent concepts and the field applications. Most likely, this lag results from the time it takes to update the most recent scientific findings and integrate them into practice, which can sometimes be hindered by the lack of an applied framework and the daunting complexity of biological and large-scale processes. he WCC (O'Sullivan et al., 2022b) and the increased baseline of process-based restoration literature (Beechie et al., 2008; Beechie et al., 2021, 2023; Booth et al., 2016) can certainly help provide actionable examples of work at a riverscape scale (Ashley Steel et al., 2016; Dunham et al., 2018; Erős et al., 2018; Humphries et al., 2020; Torgersen et al., 2021).

Table 1: Theoretical evolution of biological river system concept since the river continuum concept

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
River Continuum Concept (RCC)	Proposes that understanding of the biological strategies and dynamics of river requires consideration of the gradient of physical factors formed by the drainage network	Static	Continuum along a regular stream order	No disruption of longitudinal connectivity	Macroinvert-ebrates	River network	(Vannote et al., 1980)
Flood Pulse Concept (FPC)	Explain how the periodic inundation and drought (flood pulse) are important dynamics of river system, controlling lateral exchanges of water, nutrients, and organisms between the main river channel (or lake) and the connected floodplain (flood pulse is the major driver of biota)	Dynamic (flood event)	Propose that river network is not the main determinant, but concept applied to natural system, so some level of discontinuity only	Consider lateral connectivity with the floodplain more than the longitudinal connectivity	Plants, macroinvert-ebrates and fish are the result of the flood pulse, do not consider their interactions or interactions with the processes	Unmodified large river floodplain system (complemen-tary to RCC)	(Junk et al., 1989; Junk & Wantzen, 2004)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
The Serial discontinuity concept (SDC)	Address the river network discontinuities, arguing that rivers reset ecological conditions toward natural or unregulated conditions as downstream distance from discontinuity increases (e.g., dams). Was expanded to include lateral and vertical connectivity	Attempt to include some environmental heterogeneity (as a proxy for spatial and temporal effect)	Discontinuum (dam only, discontinuity distances)	Original concept only included longitudinal, revised to include lateral and vertical	Plants, macroinvert-ebrates and fish are the result of changes in environment al parameters and energy fluxes below dam, do not consider their interactions or interactions with the processes	Revised version: river corridor	(Stanford, 1983b; Stanford & Ward, 1993, 2001)
Process Domain Concept (PDC)	First concept to bring the multi-scale aspect: 1) at smaller scale the spatial variability in geomorphic processes governs temporal patterns of disturbances that influence ecosystem structure and	Dynamic	Discontinuum	Mostly longitudinal	Geomorpho-logic patches influence habitats and therefore, biological communities in each unit	Sets channel reach into a context of watershed disturbance processes	(Montgomer y, 1999)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	dynamics; 2) at coarse scale, regional climate, geology, vegetation, and topography control the suite of geomorphic processes that are distributed over a landscape						
The Riverine Productivity Model (RPM)	Proposed for shallow and constrained systems, with a firm substrate and aphotic zone, where energetic pathways function differently than in the main channel. For instance, the authors argue that the downward leakage of FPOM as the main source of organic carbon in large rivers (as postulated by the RCC) is	Static	Continuum	Consider connection with riparian zone, but not lateral stream connectivity (constraint channel)	Macroinvert-ebrates	Mainstem	(Thorp & Delong, 1994)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	overemphasized compared with the in-stream primary production.						
River Wave Concept (RWC)	Combined the RCC, FPC, and RPM into a unifying model that includes the spatial and temporal variation in river flow described as a wave (shape, magnitude, wavelength, and frequency) and use climate and geomorphologic attributes to define the wave characteristics.	Dynamic	Longitudinal discontinuities considered from a wave point of view (i.e., how they modify the wave characteristics)	Longitudinal and lateral	Describe how wave characteristic s influence habitat without getting into specific biota details	River corridor	(Humphries et al., 2014)
Riverine ecosystem synthesis (RES)	Conceptualizes rivers as “downstream arrays of large hydrogeomorphic patches (e.g., constricted, braided,	Dynamic	Discontinuum	Longitudinal and lateral	Can apply to different biota as distribution and composition is explain by	River corridor	(Thorp et al., 2006b)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	and floodplain channel areas) formed by catchment geomorphology and climate”). Conceptual marriage of eco-geomorphology (ecological aspects of fluvial geomorphology) with a terrestrial landscape model describing hierarchical patch dynamics				the patterns and the processes		
Network Position Hypothesis (NPH)	Proposed that the local environment should exclusively control headwater communities, given their isolation and their more heterogeneous nature; while downstream	Mainly static	Continuum	Longitudinal	Benthic diatoms, macrophytes, macroinvert-ebrates and fish	Stream network	(Brown & Swan, 2010b; Henriques-Silva et al., 2019)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	communities should be regulated by both environmental and dispersal processes linked to the riverscape connectivity.						
(Benda et al., 2004)	Geomorphic framework describing how tributary confluence effects vary in terms of the specific attributes of a network's structure, including basin size, basin shape, network pattern, size difference between confluent channels, drainage density, confluence density, local network geometry, and the power law of stream sizes and how stochastic watershed disturbances such as	Dynamic	Discontinuum	Longitudinal and lateral	Do not use biological data but states that increasing habitat heterogeneity including channel width and depth, bed substrate, wood storage, and water velocity, should increase total macroinvert-ebrates and fish species	Stream network	Brenda et al., 2004

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	floods, fire, and storms impose temporal heterogeneity on confluence effects, reflecting the controls exerted by the underlying network structure.				richness		
Channel Evolution Model (CEM)	Assumption that the stream has a bed and banks that are sufficiently erodible so that they can be shaped by the stream over the course of years or decades	Dynamic but in one river archetype (single-thread channel)	Account for disturbance through erosion processes	Longitudinal, lateral and vertical	Geomorphologic only	River corridor	(Schumm, 1993)
Stream Evolution Model (SEM) / Stream Evolution Triangle (SET)	Links the evolutionary stages of stream adjustment to indicators of habitat and lotic ecosystem benefits, which might be used to better understand, strategically manage and sustainably	Dynamic	Discontinuum	Longitudinal, lateral and vertical	Biodiversity, biology and ecosystem services, but mainly geomorphologic and hydrologic	River corridor	(Castro & Thorne, 2019; Cluer & Thorne, 2014)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
	restore freshwater aquatic systems The SET recognize the biology as process driver						
River Wetland Corridor (RWC)	River-wetland corridor as a relatively wide valley floor within which there is space for persistent alluvial deposits and Sufficient connectivity between surface and subsurface hydrology to create and maintain an interacting system of channels, wetlands, and floodplain ponds and lakes	Dynamic	Highlights that river-wetland corridors can be longitudinally continuous but also interspersed with singlethread reaches in narrower portions of the valley	Multidimensional	Wetlands vegetation, but consider interactions and feedbacks between the drivers and the wetlands complex	River corridor/river valley	(Wohl et al., 2021; Wymore et al., 2023)
Waterspace Continuum Concept and	Defined as the spatially and temporally dynamic	Dynamics	Proposes to reconcile concepts of	Multidimensional	Focus on the ecohydrolog-ical	Watershed	(O'Sullivan et al., 2022a)

Concept	Main point	Consider river dynamism?	Continuum/ Discontinuum	Connectivity and dimension	Functional guild	Ecotype (e.g. watershed, mainstem, …)	Reference
Template (WCC)	water upon and within the critical zones to link terrestrial and aquatic ecohydrological processes across a continuum Considers as "river ecosystems" being nested upon and within a much broader continuum, one that expands and contracts across and through landscapes and riverscapes		continuity from RCC and discontinuity from SDC		processes rather than the biological communities		

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