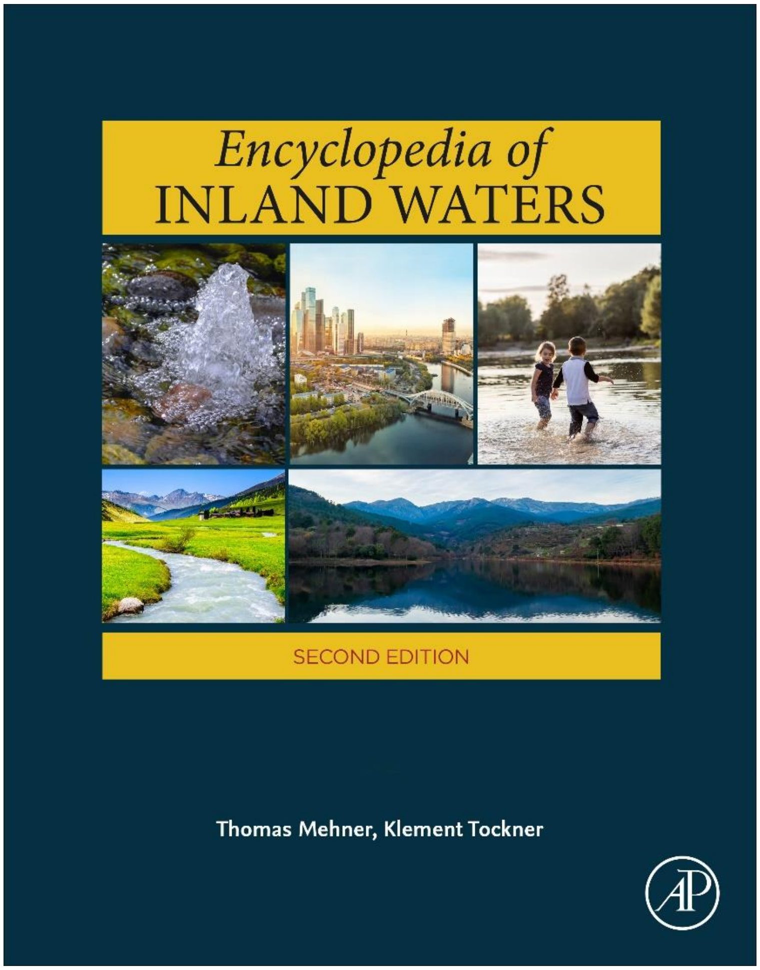




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# The River Continuum Concept

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## Glossary

**Allochthonous** Carbon produced outside the stream in the terrestrial habitat, which falls or washes into the stream.
**Autochthonous** Carbon produced by primary producers in the stream or river.
**Collector-gatherers** Animals that collect small organic particles (living or dead) for food.
**Ecosystem respiration (ER)** The sum of respiration (i.e., the process involving the intake of oxygen and the release of carbon dioxide from the oxidation of organic substances) by all heterotrophs and autotrophs in an ecosystem. Units are in mass per area per time or mass per volume per time.
**Filter feeders** Animals that collect particles in suspension in the water column.
**Functional feeding groups** Classification of organisms based on their ecological role, particularly their trophic position in a food web. Often used to classify animals.
**Gross primary production (GPP)** The total carbon fixation in an ecosystem. It can also be represented by dissolved oxygen flux. Units are in mass per area per time or mass per volume per time.
**Invertivores** Animals that feed on invertebrates.
**Macrophytes** Aquatic plants that have adapted to living in aquatic environments.
**Net Ecosystem Production** The gross primary production (GPP) minus the ecosystem respiration (ER) that indicates net carbon gain in a system. It is sometimes represented as GPP/ER where net carbon gain is represented by values greater than one.
**Periphyton** The complex film of algae and other organisms attached to solid surfaces in freshwater environments.
**Piscivores** Animals that feed on fishes.
**Planktivorous** Animals that feed on plankton, including zooplankton and phytoplankton.
**Riparian zone** The zone near the edge of a river or stream.
**Scraper-grazers** Animals that scrape biofilms from solid surfaces, usually periphyton (i.e., attached algae). Also refers to animals that eat macrophytes (aquatic plants). Grazer implies consumption of photosynthetic organisms.
**Shredders** Animals that break down leaves or wood for nutrition.

## Introduction

The River Continuum Concept (RCC, Vannote et al., 1980) is almost a half-century old, and as of September 2021 Google Scholar counts over 12,000 citations and the more restrictive Web of Science lists over 6300 citations. At the core of this concept is the idea that at each specific location in a watershed, inputs from upstream interact with the local terrestrial riparian habitat to control ecosystem characteristics. These interactions then shape river ecosystem metabolism, energetics, and biological communities. Whether considered a milestone in stream ecology that shaped stream ecology research or a concept that needs revision, it has the merit of spurring considerable research, conceptual advance, and debate in stream ecology. Here, we explain the RCC, and how it has evolved over the years since first proposed by Vannote et al. (1980), including support and critiques. We end with ideas of how researchers might use the concept into the future.

The original concept centered on the continuous connection from a temperate forested high elevation stream flowing through ever-bigger channels into a large lowland river (Fig. 1). The organic material entering from nearby riparian vegetation, the organic material transported from upstream, and the light entering the flowing water driving photosynthesis are the factors that control the sources of carbon and their identity. In small streams with dense canopy cover, the light is low for much of the year, so primary production (autochthonous carbon) is limited and most carbon enters the system in the form of terrestrial leaves, dissolved organic carbon, and other detritus (allochthonous carbon). This leads to a system dominated by heterotrophic respiration (mostly microbial) that relies upon the organic material. In this case, gross primary production (GPP) is low, ecosystem respiration (ER) is high, net ecosystem production is negative, and GPP/ER is less than one. In the middle-sized streams further down the continuum, the stream widens, and light can stimulate productivity. While the light promotes primary production, allochthonous carbon also enters the stream from nearby riparian vegetation and washes in from the small streams above. In this case, GPP rates balance ER, and net ecosystem production approaches or is greater than zero. Note the original paper suggested GPP/ER greatly exceeded one in middle- sized streams, but subsequent research suggests it rarely does by much. Once the flow reaches large rivers, the system is almost completely dependent upon carbon transported from above or gross primary production by any primary producers in the water if turbidity is low enough so that ample light can be transmitted into the river.

This basic pattern in carbon and light supply then controls function and composition of the communities of invertebrates and fishes. The relative dominance of invertebrates is categorized by their functional feeding groups. These include (1) shredders that consume large organic detritus, (2) collector-gatherers that filter or collect smaller particles, (3) scrapers-grazers that consume periphyton or macrophytes, and (4) predators. Changes along the continuum are driven mainly by relative availability of allochthonous and autochthonous carbon sources. In small streams, invertebrate communities rely heavily on allochthonous particulate organic matter, such as leaf litter, decomposed detritus, pollens, and other organic debris, or the microbes on this organic matter. Communities of small streams are, therefore, predicted to be dominated by shredders and collector-gatherers. Shredders process primarily coarse particulate organic matter (>1 mm diameter), while collector-gatherers process the finer fraction of this particulate matter. Both shredders and collector-gatherers depend upon microbial biomass and the byproducts of microbial metabolism for their nutrition. In middle-sized streams, communities shift to dominance by collector-gatherers and scraper-grazers. The development of periphyton as more light reaches the stream in a relatively open canopy characterizing middle-sized streams drives increased relative abundance of grazers. Farther down the continuum, an increase in water turbidity and a sharp reduction of relative importance of locally produced allochthonous detrital coarse particulate carbon are expected. The concept predicts that associated invertebrate communities in these larger systems will be dominated by collector-gatherers including filter feeders.

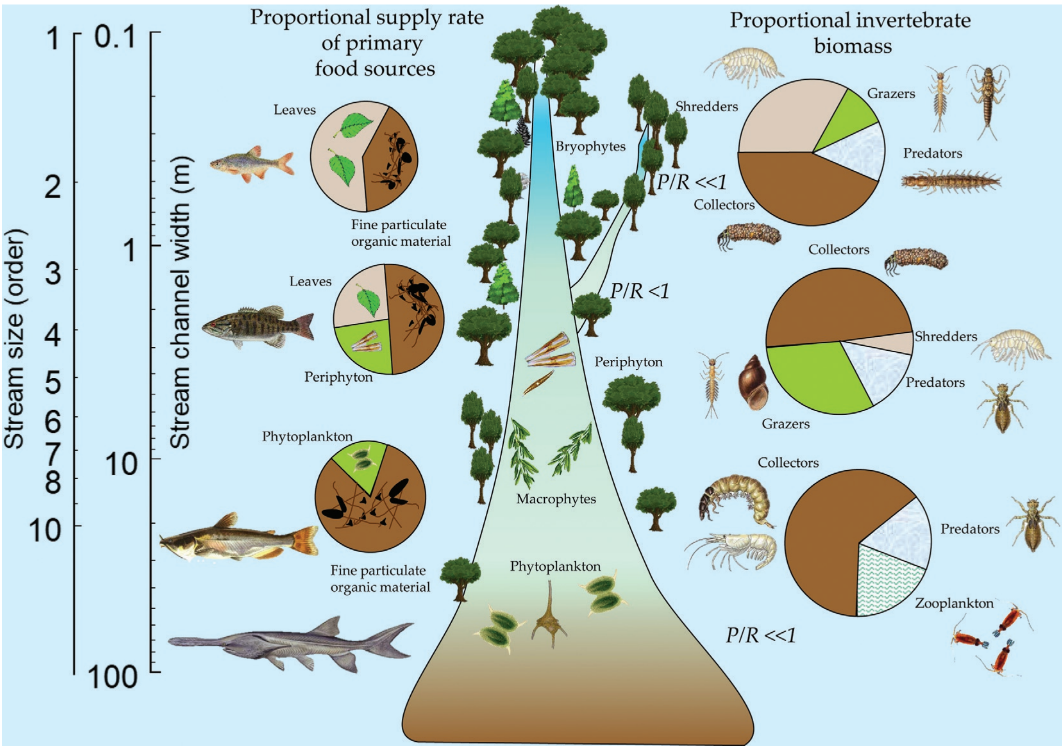


**Fig. 1** A diagram of the River Continuum Concept. Modified from Vannote RL, Minshall CW, Cummins KW, Sedell JR and Cushing CE (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.

The original paper, therefore, argues that the longitudinal pattern in invertebrate communities reflects an adaptation to optimize energy use. Thus, energy in the form of organic carbon that is not used in the upstream parts of the stream moves downstream and the downstream community benefits from it. Stated differently, the invertebrate communities have evolved to efficiently use the balance of organic carbon generated locally (either allochthonous or autochthonous) and that being transported from upstream.

The concept predicts fish communities will be dominated by invertivore species in small streams and headwaters, by invertivores and piscivores in middle-size streams and further downstream along the river continuum. In the largest sections of the river, often associated with low slope, planktivorous species will become more prevalent reflecting the semi-lentic (i.e., lake-like) nature of such waters. Many of the species in large rivers are adapted to high turbidity/low light conditions. The original concept also states that this shift in fish communities reflects changes in affinity to water temperature. Headwater and small stream communities exhibit low diversity and affinity to cool water, while further along the continuum, fish communities are more diverse with increasing affinity to warmer water.

## The original concept

The RCC used five components to describe how it should apply to stream ecosystems. Here, we discuss components that "went forward" or received substantial attention in the scientific community, as well as those that were "set aside" or were less commonly examined.

### Components that went forward and why

In general, these components went forward because they provided easily testable hypotheses. They are also simpler to understand, so they form the basis of teaching efforts and appeal to a wide range of types of scientists. The common image associated with the RCC found in many textbooks is based on these components (e.g., Fig. 1).

#### *Stream size and ecosystem structure and function*

This component is, by far, the most widely examined and has shaped much of the stream ecology research subsequent to the RCC. It stipulates that based on stream size (expressed as stream order) a longitudinal shift in loadings of carbon shape communities of invertebrates and fishes. The ratio of stream GPP/ER characterizes the longitudinal change in carbon inputs. When photosynthesis is the dominant pathway of incoming carbon the GPP/ER is expected to be greater than 1. This component has been tested in multiple ecoregions and on different types of rivers spanning temperate and tropical ecosystems (see, table of supporting case studies below, Table 1). Researchers have also thoroughly examined changes in community composition of fishes and invertebrates and shifts in their trophic guilds to validate the predictions of the RCC. The bioenergetic influences along the river continuum are also widely considered by stream researchers.

#### *Ecosystem processing along the continuum*

This component stipulates that unused or partially processed materials in a river ecosystem will be transported downstream where communities are structured to capitalize on the so-called "inefficiencies" of upstream processing. The fate of unprocessed material and the examination of retention, leakages, and downstream adjustments are topics often researched in the context of watershed functioning as a whole.

**Table 1** A few important case studies.

| *Site* | *Country* | *Latitude* | *Longitude* | *Main topic covered* | *Reference* |
|---|---|---|---|---|---|
| North Carolina | United States | 35.05977° | −83.43022° | Regulation of stream detritus dynamic by macroinvertebrates | Wallace et al. (1982) |
| Pennsylvania | United States | 39.752086° | −75.775300° | Organic matter inputs and turnover | Minshall et al. (1983) |
| Michigan | United States | 42.405863° | −85.344884° | Organic matter inputs and turnover | Minshall et al. (1983) |
| Oregon | United States | 44.232134° | −122.190617° | Organic matter inputs and turnover | Minshall et al. (1983) |
| Idaho | United States | 44.123941° | −114.870759° | Organic matter inputs and turnover | Minshall et al. (1983) |
| Pennsylvania | United States | 39.752086° | −75.775300° | Shift in metabolism from net heterotrophy to primary production downstream | Bott et al. (1985) |
| Michigan | United States | 42.405863° | −85.344884° | Shift in metabolism from net heterotrophy to primary production downstream | Bott et al. (1985) |
| Oregon | United States | 44.232134° | −122.190617° | Shift in metabolism from net heterotrophy to primary production downstream | Bott et al. (1985) |
| Idaho | United States | 44.123941° | −114.870759° | Shift in metabolism from net heterotrophy to primary production downstream | Bott et al. (1985) |
| Quebec | Canada | 50.384993° | −65.315187° | Carbon flux and standing stocks | Naiman et al. (1987) |
| North Carolina | United States | 35.0598622° | −83.430618° | Invertebrate secondary production | Grubaugh et al. (1997) |
| Idaho | United States | 44.123941° | −114.870759° | Invertebrate diets | Rosi-marshall et al. (2016) |
| Tennessee | United States | 36.350833° | −85.565000° | Food webs | Curtis et al. (2018) |

### Components that were set aside

In general, these concepts are more difficult to understand than those that went forward. They are not as easily tested, as they require long periods of time (e.g., geomorphological change or biological evolution) or space for time substitutions for confirmation. They are not simple to explain graphically and thus have seen less interest in the research and teaching communities.

#### *River ecosystem stability*

This component stipulates that ecosystem stability may be viewed as the tendency to reduce fluctuation in energy flow and other variables of the physical system while the structure and function of the biota are maintained. We note that river ecologists and geomorphologists have developed a differing view of "stability" than in some other branches of ecology (e.g., Connell and Sousa, 1983). In general, the idea of a dynamic equilibrium in geomorphology suggests an overarching stability in the face of continuous change that can include catastrophic events such as intense floods (Schumm and Lichty, 1965). This view of a dynamic equilibrium suggests a sort of stability at longer periods used by river geomorphologists that strongly influenced the framers of the RCC. Ecosystem stability is therefore achieved by a dynamic interplay between physical and biological components that change along the river ecosystem from low to high stream orders. In highly fluctuating environments (e.g., fluctuation in temperature, dissolved oxygen concentrations, or water discharge), the biota may assume a critical role in stabilizing the energy flux through an entire system, whereas in highly stable environments the role of the biota in ecosystem stability will be reduced. Only more recently have stream ecologists approached system stability through the concepts of thresholds and alternative stable states (e.g., Dodds et al., 2010). Furthermore, most stream research on stability and disturbance does not directly reference the RCC. Finally, until recently ecologists have not considered stability or dynamic equilibria in the face of global climate change and the prevalence of invasive species that may come to dominate energy flows and change the predictions of the RCC.

#### *Temporal adjustments in maintaining an equilibrium of energy flow*

This component stipulates that stream ecosystems will tend towards uniformity of energy flow on an annual basis. Synchronized change in biological communities to temporal patterns of energy sources over an annual cycle controls uniformity of energy flow. Thus, biological systems move towards equilibrium by a trade-off between a tendency to optimize the use of energy inputs and a tendency towards a uniform rate of energy processing throughout the seasons. While this principle has been validated in streams of temperate forested regions (Minshall et al., 1983; Bott et al., 1985), little attention has been given to examining this principle in streams of other biomes. In general, most stream researchers do not produce annual budgets of carbon flux, so few data are available to test this idea. However, longer-term carbon flux estimates are becoming available (e.g., Roberts et al., 2007; Uehlinger, 2006), but only a few are available for larger rivers on an annual basis (e.g., Dodds et al., 2013), and these are not paired with estimates of production by different functional groups of animals. Factors that disrupt systems such that the species evolved in a particular area are no longer as well suited for the habitat (e.g., anthropogenic disturbances, directional climate change, species invasions) will interfere with this "equilibrium."

#### *The invariance and the absence of succession in stream communities*

This temporal equilibrium component stipulates that biological systems of each stream order are in equilibrium with the physical system at that point of the continuum. Temporal succession is not explicitly considered under the framework of the RCC, instead, biological systems present only a spatial shift along the continuum. Losses and gains of species occur primarily in low probability cataclysmic events and in response to evolutionary channel development. The lack of observation of successive biological stages is attributed to communities being a continuous heritage of species rather than an isolated temporal composition of species within a sequence of discrete successive stages. Thus, slow evolutionary processes shaping stream channel development are the main drivers of this invariance (or absence of succession) of stream communities at a non-evolutionary period. Little research has examined this principle to date, the main obstacles being the availability of extensive temporal data, and the numerous major alterations that have affected river ecosystems globally in the last century making it challenging to dissociate the contributions of natural and anthropogenic changes to the succession in stream communities.

## Critique and support

The conceptual framework of the RCC received both critiques and support since its publication. Several papers supporting the overarching predictions of the RCC appeared soon after the original paper (see table of supporting case studies, Table 1). Minshall et al. (1983) documented the greatest inputs of allochthonous materials in headwaters in four stream networks across the United States. Bott et al. (1985) documented decreases in the relative importance of heterotrophic metabolism relative to primary production in four watersheds across the continental US as predicted, but noted that seasonal variation and that the shift happened at different stream orders. Rosi-Marshall et al. (2016) visited the same Idaho sites used in the previous two studies and re-sampled invertebrates. They found, as the RCC predicts, the greatest amount of reliance on leaf litter in headwaters. However, the authors also noted that there were substantially more autochthonous materials in the guts of stream invertebrates than predicted in the lower order streams. Lately, Curtis et al. (2018), tested the RCC predictions by explicitly linking consumer groups and found that the RCC predictions are integrated into the food webs, transcending, therefore, assemblage boundaries.

The main critiques can be grouped into four major divisions: (1) The limited applicability of the concept arguing that it was developed only for temperate river systems with forested headwaters and rivers flowing in relatively undisturbed landscapes, ignoring, therefore, the complexity of river systems globally. Many argued that the concept applies only to one type of river system excluding, just to cite a few, intermittent rivers, grassland rivers with reduced woody riparian, endorheic rivers, and tropical rivers. (2) The concept failed to integrate lateral habitats and floodplains and their contributions to both river functioning and biodiversity. Critics argued that the relative contribution of lateral connectivity becomes more and more important with increasing stream order and the contribution of lateral habitats in meandering and braided river sections, for example, cannot be ignored when conceptualizing river ecosystems. (3) geomorphological patterns and others that form the template for habitat often do not reliably follow the upstream-downstream continuum of the RCC and local processes may depend more heavily on local conditions than transport from upstream. (4) The concept did not account for the general framework of meta-community theory and identified only local environmental heterogeneity as the main driver for changes in the composition of stream communities.

The first critique, that the RCC only covers temperate forested headwater streams and does not apply to other biomes, is somewhat unfair. The Vannote et al. (1980) paper explicitly said that "At higher elevations and latitudes, and in xeric regions where riparian vegetation is restricted, the transition to autotrophy may be in order 1". This statement acknowledges that the authors understood that the patterns they were describing were potentially biome-specific. However, several critiques and modifications have addressed this issue. Soon after the original publication, Winterbourn et al. (1981) criticized the RCC by showing the limited applicability of the concept to New Zealand river systems with unpredictable rainfall patterns and low forest biomass. Barmuta and Lake (1982) responded to this critique that the lack of invertebrates following the expected patterns in New Zealand rivers could have been related to unusually high disturbance rates in the rivers studied by Winterbourn et al. (1981). Dodds et al. (2004) modified the RCC for application to grassland streams, and this approach was taken further subsequently, to predict the way that biomes modified the predictions of RCC (Dodds et al., 2015). Greathouse and Pringle (2006) studied freshwater invertebrates in tropical streams of Puerto Rico. They found that predators, scrapers, and shredders followed the prediction of the RCC patterns, but that filterers and omnivorous freshwater shrimps did not. They suggested that spatially restricted predation on the shrimps by fishes could explain part of the deviation from the patterns expected by the RCC. Tomanova et al. (2007) found patterns of invertebrate structure and function mostly followed the RCC in Bolivian streams once the corrected for altitude.

The second avenue of criticism, that the RCC failed to integrate lateral habitats and floodplains and their contributions to both river functioning and biodiversity has been discussed by several researchers. Sedell et al. (1989) noted the RCC did not predict the importance of side habitats (e.g., backwaters and weakly connected oxbow lakes) connected to large rivers that are vital habitats for fishes and important locations of high ecosystem productivity. Junk et al. (1989) formalized the idea that large rivers experience high flows that connect lateral habitats to the main channel, further developing ideas of ways that large rivers are not completely explained by the RCC. However, materials carried into lateral habitats can originate from upstream.

The third avenue of criticism, that geomorphological patterns that form the template for habitat often do not reliably follow the upstream-downstream continuum of the RCC, and that local processes may depend more heavily on local conditions than transport from upstream has also received consideration. This avenue relates to the second avenue discussed in the last paragraph. Minshall et al. (1985), further refined by Montgomery (1999), suggested a "process domain" framework could allow the application of geomorphological considerations at various scales to make the RCC more broadly predictive. Thorp et al. (2006) took this idea further in their Riverine Ecosystem Synthesis (RES). They viewed streams as nested hierarchies of patch mosaics, with ecosystem dynamics resulting from a composite of intra and inter patch processes. Functional process zones, as identified in the RES, controlled therefore local processes. They stressed the non-equilibrium processes that result in "quasi-equilibrial metastable states". This synthesis led to 14 predictions on ecological characteristics in streams. This synthesis allows for upstream linkages upon which the RCC depends, but it focuses much more heavily on local conditions and views ecological processes in rivers and streams as substantially more insular than the RCC does. The degree to which local processes dominate relative to control by position in the watershed and location on a continuum from headwaters to large rivers is still an active area of research in stream ecology. More recently, Maasri et al. (2021) and Collins et al. (2018) have shown that despite considering rivers through a discreet model like the RES, the longitudinal and progressive downstream gradient of responses to abiotic and biotic features will be observed in communities and processes, thus forming a partial biotic continuum as predicted by the RCC.

The idea of breaks in the RCC as spawned a number of publications on the river "discontinuum" For example, when a tributary enters a stream, the discharge downstream is abruptly greater (Poole, 2002), and such tributaries create unique habitats above and below the main channel (Benda et al., 2004) disrupting the concept of a smooth continuum. Natural features such as beaver dams (Burchsted et al., 2010), lakes (Jones, 2010), and subsurface stream flow (Di Lorenzo et al., 2013) have all been described as discontinua. These researchers present a view that is closer to the RES than the RCC.

The fourth, and most recent, avenue of criticism states that the RCC failed to integrate the contribution of the theoretical framework of meta-community ecology in explaining changes in communities along the continuum (see review by Doretto et al., 2020). This avenue needs to be considered with respect to the relatively recent rapid development of research in meta-community theory. Meta-community theory postdates the RCC (see, Hanski, 1994, Leibold, 1995, or Leibold et al., 2004), with only a few exceptions referring to the role of dispersal limitation or stochasticity as drivers of ecological communities that can be dated to the early 20th century (Chase and Myers, 2011).

Some further modifications to the RCC have been proposed in addition to the four areas of criticisms to broaden the applicability and scope of inference of the RCC. Statzner and Higler (1985) proposed to simplify the concept and reduce its theoretical ballast by excluding components that are either unexpected, unsupported by evidence, or restricted to particular geographic areas. Those components dealt mainly with the absence of succession in stream ecosystems, the temporal sequence of species replacement, or longitudinal patterns of biodiversity, shifting, therefore, the RCC towards an energetics based concept, with emphasis on photosynthesis, respiration, and on the status of organic matter and corresponding organization of communities. This suggested simplification was prescient, and Statzner and Higler (1985) suggested dropping the components that we listed above as "not going forward"; it appears that the stream research community has taken this recommended approach for the most part.

The RCC developed in a time when ecologists often focused on "natural" conditions and abiotic and biotic drivers of stream networks as relatively constant over time (e.g., no climate change or invasive species). However, human impact has increased substantially as we move into the Anthropocene. Dams are ubiquitous in watersheds of most areas with human inhabitation, and Stanford and Ward (2001) modified the RCC by considering how human-constructed impoundments disrupt the continuum. While reservoirs strongly influence the continuum, other features can as well. Anthropogenic influences can disrupt or enhance connectivity by activities such as water abstraction drying stream channels, channelization of flows, and construction of impoundments.

Additionally, deforestation, row crop agriculture, and urbanization can lead to large disruptions in the expected continuum by altering flow, riparian conditions, and natural sediment regimes. The RCC does at least provide a framework under which to understand some implications of these changes to river ecosystems.

## Conclusion

The RCC has received great attention, in part, because it took a landscape view of how position in the watershed influenced stream ecosystems. River ecologists were primed to receive this view because of the obvious influence of the watershed on aspects such as water quality, discharge, flood intensity, and biotic components (Hynes, 1975). These types of ideas still have relevance. For example, the meta-ecosystem framework (Loreau et al., 2003) was proposed as a new avenue for landscape ecology, but the RCC already fits into that framework in that it includes multiple linked systems that are spatially distributed and have specific interactions based on how they are linked. The second reason that the RCC has been successful is that the components that went forward are conceptually simple and based on obvious abiotic properties such as the fact that stream channels generally get wider further down in the watershed and flow moves materials downstream. The RCC provides testable hypotheses, and they are easy to modify as new approaches have arisen. Even if some of the specifics do not hold (e.g., streams are not all in the temperate biomes originally considered), it is easily modified based on basic geomorphological and ecological principles (e.g., riparian canopies can intercept light, the balance of metabolism in ecosystems, functional adaptations of stream invertebrates) to provide a new framework applicable to local conditions.

## Knowledge gaps

- How does the continuum vary with the biomes that rivers and streams are embedded in?
- What is the relationship of the continuum with local processes such as floodplain dynamics and functional processing zones?
- What is the influence of humans on the expectations/predictions of the RCC, including land cover/land use change, climate change, and eutrophication?
- Does biogeography influence the RCC (e.g., do areas with functional groups of organisms with different evolutionary history display different patterns)?
- Do any of the less studied predictions of the RCC hold (e.g., can paleoecology get at the idea of animals in ecosystem optimizing energy flow)?
- How does the RCC relate to meta-community concepts?

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