

CONCEPT

Fresh perspectives on the River Continuum Concept require trophic ecology approaches focussed on food web structure and energy mobilisation routes

Javier Sánchez-Hernández 

Departamento de Biología y Geología,
Física y Química Inorgánica, Universidad
Rey Juan Carlos, Móstoles, Madrid, Spain

Correspondence

Javier Sánchez-Hernández
Email: javier.sanchezh@urjc.es

Funding information

European Commission, Grant/Award
Number: PCI2022-132991; Universidad
Rey Juan Carlos, Grant/Award Number:
M3006

Handling Editor: Julien Cucherousset

Abstract

1. Stream-dwelling communities are expected to show a gradual replacement of the dominant feeding types following the type of resources found along the river continuum. Yet, the underlying longitudinal gradients in food web structure and energy flow-paths remain poorly understood.
2. Here, I synthesise novel research on the River Continuum Concept (RCC) and identify promising areas for future research linked to longitudinal changes in food-chain length and energy mobilisation routes. For example, feeding links and connectance should reach maximum values in mid-order rivers and then decrease to river mouths following uncovered longitudinal diversity patterns. Regarding energy mobilisation routes, a gradual replacement in the food web fuelling between allochthonous (leaf litter) and autochthonous (periphyton) resources should be expected.
3. Beyond longitudinal changes in primary basal resource to consumer paths, other allochthonous (e.g. riparian arthropod inputs) and autochthonous (e.g. fish prey) inputs subsidising higher level consumers may show longitudinal changes, that is, terrestrial invertebrates decreasing but piscivory increasing downstream. However, the role of these inputs, that can alter predator niche variation and have indirect community-based effects, on both food web structure and energy flow-paths along the river continuum is not clear yet.
4. Incorporating energy mobilisation and food web structure into RCC principles is necessary for a broad understanding of ecosystem functioning and trophic diversity in riverine systems, driving the emergence of novel insights. How function and structure of riverine food webs adapt to longitudinal changes in physical and biological environments represent a challenge for next generation of stream ecologists.

KEYWORDS

animal communities, bottom-up mechanisms, energy flow-paths, freshwater ecology, meta-community, meta-ecosystem, river network, spatial changes

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Author. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Although spatial changes in animal communities of freshwater ecosystems are well documented, our comprehension of such changes is incomplete because we currently lack holistic concepts that apply to spatially diverse systems and regions. The River Continuum Concept (RCC) is a long-standing framework in stream ecology that describes lotic ecosystems from headwaters to river mouths (Vannote et al., 1980). In particular, the RCC predicts a continuous gradient in the structure of animal communities (both macroinvertebrates and fish) according to physical (stream discharge, stream width and riparian vegetation) and biophysical (energy input and organic matter for production and stream metabolism or P/R) conditions (Vannote et al., 1980). Here, I review the historical background of the RCC, addressing the knowledge gaps, new ways of thinking about the RCC and some methodological pitfalls to be considered in future research. Overall, I hope this paper will stimulate scientific debate and bring increased attention to the recognition of new patterns in energy mobilisation routes and food web structure along the river continuum and its importance for a comprehensive understanding of stream ecology.

2 | HISTORICAL CONTEXT

Ever since the RCC was introduced in the late-20th century (Vannote et al., 1980), much attention has been paid to validate

the RCC's predictions with a steep increase in the number of publications over the last decade mainly focused on macroinvertebrate communities (Figure 1). The RCC has been considered appropriate at the level of the flow-through time of a river but the view of a longitudinal succession on a geological time scale is wrong, thus validity of theories with a worldwide perspective may depend on the temporal dimensions (Minshall, 1988). Regarding spatial scales, the RCC can be broadly applied to typical temperate systems (Greathouse & Pringle, 2006; Larsen et al., 2019; Rosi-Marshall & Wallace, 2002) and many riverine ecosystems can be generally accommodated within the RCC (Minshall, Cummins, et al., 1985). For example, Tomanova et al. (2007) highlighted that RCC's principles can be accommodated to neotropical streams, showing that longitudinal changes of macroinvertebrate communities in neotropical streams are similar to temperate riverine systems. However, the RCC may not apply to all river types and biomes (Doretto et al., 2020; Ryder & Scott, 1988; Winterbourn et al., 1981). In fact, Winterbourn et al. (1981) questioned the validity of the RCC to New Zealand streams due to physical (geomorphology and hydrology) and biological differences. These include, for example, heavy rainfalls, mountainous areas, short rivers having a stream order of only 6 or 7, low proportion of shredders, paucity of deciduous trees and low riparian vegetation in upland catchments (Ryder & Scott, 1988; Winterbourn et al., 1981). Thus, it is reasonable to expect some deviations from the expected RCC pattern in rivers of high altitude, latitude and xeric regions (Statzner & Higl, 1985). In addition, the RCC was formulated for perennial rivers with

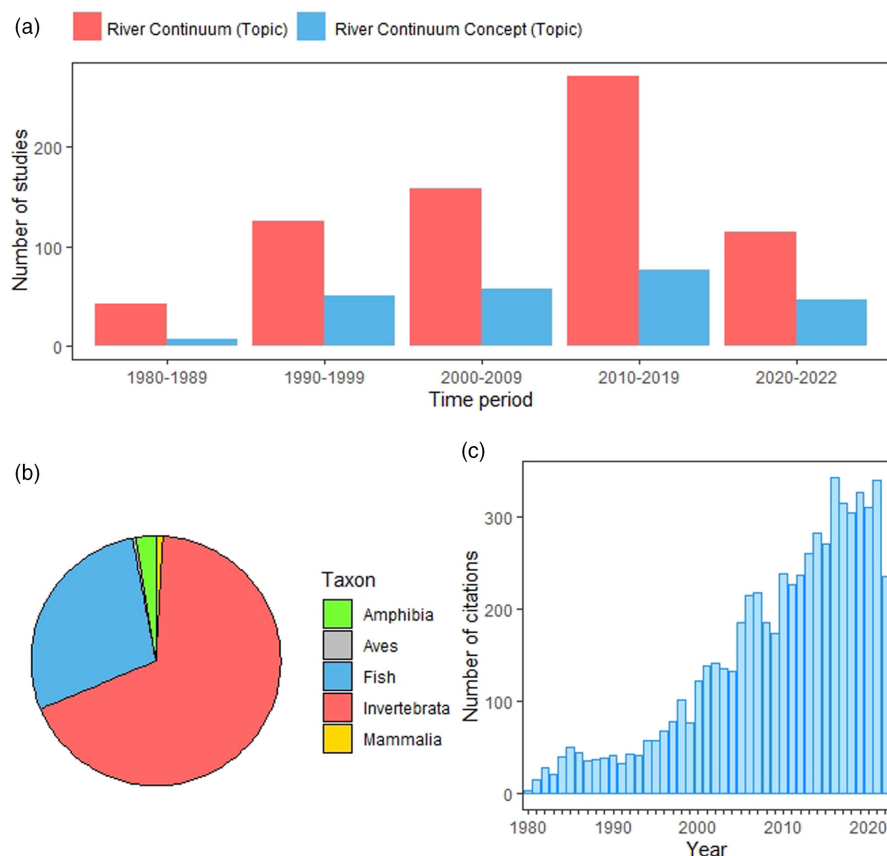


FIGURE 1 Metrics of the River Continuum Concept (RCC; Vannote et al., 1980) as indicated by a Web of Science search. (a) Number of studies examining the RCC over time (1980–2022) [the search was performed using the key words: (i) 'River Continuum' (black bars) and (ii) 'River Continuum Concept' (grey bars)]. (b) Model organisms used to test RCC's predictions. (c) Number of citations over time for the RCC. Note, although representative, this search might underestimate the real number of published studies or citations to date.

permanent flow (Vannote et al., 1980), being not compatible for intermittent rivers (Datry et al., 2014). Still, similar patterns are expected to be found among riverine systems with comparable climate and geomorphology conditions. However, we currently do not know whether patterns remained the same at global scales within those similar river systems like, for example, permanent rivers found in Mediterranean climate regions (i.e. areas surrounding the Mediterranean Sea and parts of America, Australia, Africa and Asia). Thus, research covering broad geographic territories should be prioritised to corroborate or refute general conclusions about the RCC principles.

Over the last decades, emergent developments such the meta-ecosystem and the river wave concepts have been relevant for improving our understanding of stream ecology integrating aquatic and terrestrial ecosystems across ecosystem boundaries (e.g. Gounand et al., 2018; Humphries et al., 2014; Loreau et al., 2003), perspectives that have recently highlighted for studies aiming to explore research questions relate to the RCC (Doretto et al., 2020). For example, the river wave concept by Humphries et al. (2014) proposes that rivers are commonly dominated by both local autochthonous and allochthonous inputs in normal situations, but the origin of allochthonous input shows substantial differences over the phases of the flood pulse. That is, floodplain allochthonous production during the peaks and upstream allochthonous production during ascending and descending flows (Humphries et al., 2014). This underlines longitudinal and lateral aspects of energy mobilisation in riverine systems, which has been recently explored by Guo et al. (2021) in one-predator scenario (through brown trout *Salmo trutta* L. as apex organism and macroinvertebrates as mid-level consumers), showing the importance of longitudinal shifts in energy mobilisation other than detritus-bound nutrients to consumer paths such as, for example, periphyton. However, the importance of considering multi-predator systems and different aspects of competition theory (e.g. intraguild predation and competitive interactions among species) are still needed to reach extensive generalisations in ecological research about longitudinal shifts in energy mobilisation.

The exploration of changes in energy mobilisation routes of other allochthonous (i.e. riparian arthropod inputs) and autochthonous (cannibalism and intraguild predation such as for example piscivory) resources, that can alter predator niche variation and have indirect community-based effects (Nakano et al., 1999; Sánchez-Hernández et al., 2021), remains unexplored from a RCC perspective. Terrestrial invertebrates and fish prey can subsidise higher level consumers, representing an important resource budget with important biological benefits (growth and survival) for animal communities (e.g. Kawaguchi & Nakano, 2001; Mittelbach & Persson, 1998; Sánchez-Hernández, 2020b). In addition, decreases in riparian arthropod inputs have an indirect effect on stream benthic communities by altering the intensity of fish predation in the food web, that is, predators increase the feeding on aquatic invertebrates which drives a subsequent increase in periphyton biomass via cascading trophic effects (Nakano et al., 1999). Because resource availability commonly shows spatial differences (e.g. Sánchez-Hernández,

Finstad, et al., 2019), it is pertinent to ask if those allochthonous (terrestrial invertebrates) and autochthonous (macroinvertebrates and fish prey) energy sources fuelling food webs maintain consistent support for higher trophic levels along the river continuum. Despite some incipient studies about allochthonous and autochthonous carbon flows in food webs, showing that the principal energy source is allochthonous (riparian forest) in tropical forest streams (Neres-Lima et al., 2017), we need to know whether energy flow-path patterns and food web structure vary longitudinally and can be linked to the RCC principles. This would engage novel approaches focussed on structural and functional responses of food webs, enabling insights into understanding how riverine food web fuel differs longitudinally and how animal communities adapt to such changes.

Thus far, little attention has been paid to studies directed towards verifying whether food web structure shows longitudinal changes. A remarkable exception can be found in Romanuk et al. (2006), who observed that the increasing connectance downstream is due to an increased number of links, likely because the increasing probability that consumers are themselves resources for other consumers. Thus, we should expect longitudinal changes in consumer–resource relationships driving changes in the trophic niche of predators and food web structure through bottom-up mechanisms (e.g. Curtis et al., 2018; Romanuk et al., 2006; Sánchez-Hernández, Finstad, et al., 2019).

3 | PROMISING AREAS FOR FUTURE RESEARCH: INTEGRATING TROPHIC ECOLOGY INTO THE RCC PRINCIPLES

Trophic ecology can be integrated into RCC principles through changes in predator–prey relationships, food web structure and energy mobilisation routes along the river continuum (Figure 2). The RCC supports the view that headwater macroinvertebrate communities show a large reliance on riparian vegetation via allochthonous resources (tree leaves and leaf detritus), but the importance of such resource decreases along the river continuum (Vannote et al., 1980). Guo et al. (2021) have recently demonstrated that the proportion of long-chain polyunsaturated fatty acids in periphyton increased longitudinally, such differences were also reflected in consumers (grazers) and predators (invertebrate and fish) via trophic transfer through riverine food webs. Thus, energy mobilisation among trophic levels can be expected to follow a longitudinal gradient in terms of basal food sources; that is, a progressive shift from allochthonous (leaf litter consumed by shredders mainly in the headwaters) to autochthonous-based (periphyton and detritus via grazers and collectors respectively) food webs (Vannote et al., 1980). However, terrestrial invertebrates, congeners (cannibalism) and fish prey (piscivory) are key food resource fuelling species at higher trophic levels (e.g. fish and salamanders) in riverine food webs (Kawaguchi & Nakano, 2001; Mittelbach & Persson, 1998; Sánchez-Hernández, 2020b), which have not been considered into RCC principles.

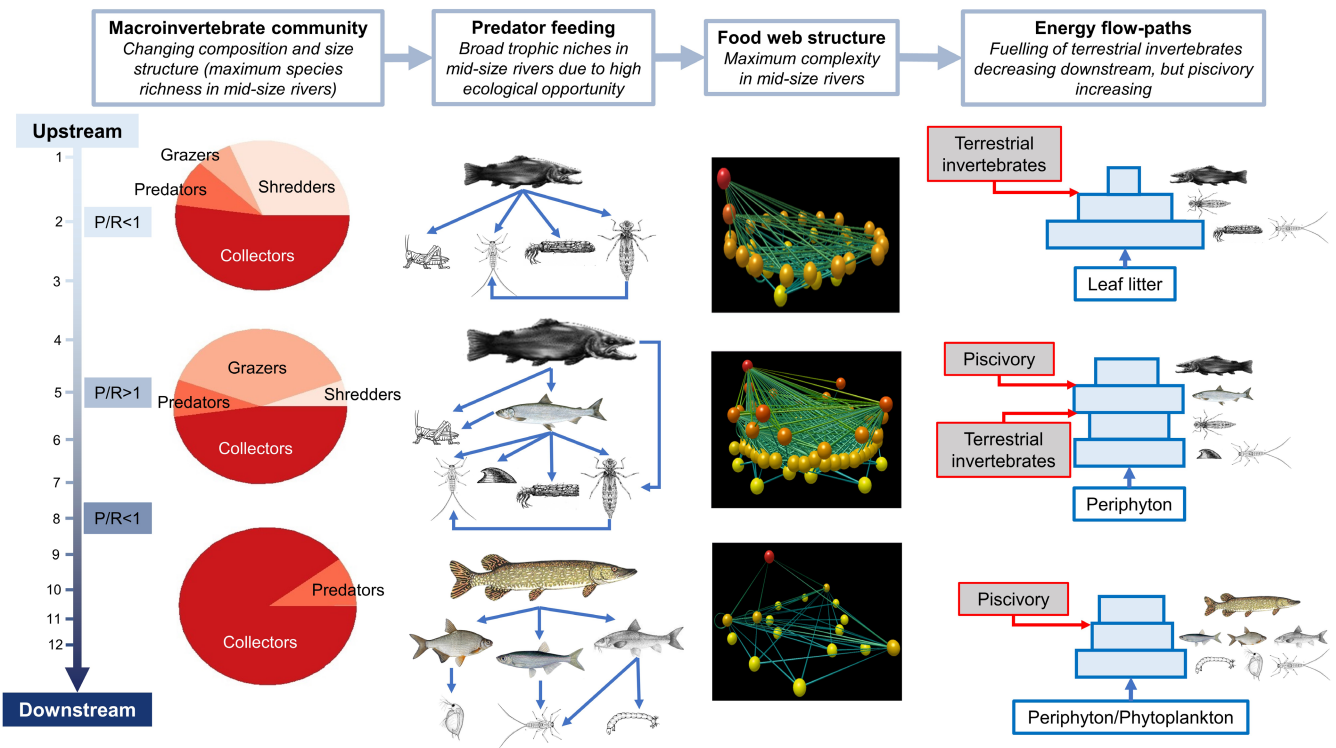


FIGURE 2 Illustrative example of changes in food web structure and energy mobilisation routes along the river continuum (modified from Vannote et al., 1980).

Terrestrial invertebrates are key to understand the maintenance of riverine food webs, for example, sustaining fish biomass, allowing predators to coexist (via food resource partitioning) and reducing fish predation pressure on benthic communities with concomitant effects on periphyton biomass (Edwards & Huryn, 1996; Nakano et al., 1999; Sánchez-Hernández et al., 2016). However, terrestrial invertebrate inputs to the riverine systems greatly depend on riparian canopy cover (Edwards & Huryn, 1996; Kawaguchi & Nakano, 2001; Ryan & Kelly-Quinn, 2015) and sparse riparian vegetation is commonly found towards river mouths compared to headwaters (Vannote et al., 1980). In this context, Syrjänen et al. (2011) observed a weak relationship between the consumption of terrestrial invertebrates by salmonids and channel width in streams flowing through deciduous forests, but they did not provide evidence for a longitudinal association in terrestrial feeding. Thus, it is possible that the consumption of terrestrial invertebrates decreases downstream, but the longitudinal perspective in the transfer of animal energy and biomass from terrestrial into aquatic ecosystems represents an important pitfall in the current state of knowledge. Future longitudinal studies, applying meta-ecosystem concepts, on the flux of terrestrial into the aquatic food webs will allow us to have important insights into how the donor system (terrestrial) contributes to the maintenance of communities in the recipient system (river) according to longitudinal physical and biological changes. In addition, the suggested future research direction may help disentangle whether terrestrial prey can mitigate deficiencies of aquatic energy flow-paths (detritus and periphyton-based via aquatic macroinvertebrate communities), considering that terrestrial prey supplies occur

primarily during summer, when aquatic invertebrate biomass is usually low in many riverine systems (Nakano & Murakami, 2001).

From another standpoint, study designs testing the RRC principles require more attention to biotic interactions among multiple trophic levels instead of focusing only on the aquatic macroinvertebrate community (e.g. Larsen et al., 2019; Tomanova et al., 2007). The integration of trophic interactions between mid-level consumers (macroinvertebrates) and the main predators (fish and salamanders) can improve our understanding of ecological processes (e.g. predator-prey relationships and cascading trophic interactions) and food web structure (e.g. food-chain length and trophic position) along the longitudinal physical and biological gradients. Food web structure is expected to change along the river continuum, as both connectance and number of links have been shown to increase downstream (Romanuk et al., 2006). The variation in these food web structural properties likely depends on patterns in species richness along the longitudinal gradient. It is possible that the higher species richness (both macroinvertebrates and fish) downstream (e.g. Minshall, Petersen, et al., 1985; Oberdorff et al., 1993; Vannote et al., 1980) may play an important role in determining longitudinal variation in food web structure, primarily due to changes in the trophic relationships between the fish species (Romanuk et al., 2006). However, longitudinal patterns in taxa richness are not continuous as both macroinvertebrate and fish species richness increase with stream size, reaching maximum values in mid-size rivers, but then decrease in large rivers (e.g. Minshall, Petersen, et al., 1985; Oberdorff et al., 1993; Vannote et al., 1980). Prey communities, especially prey diversity rather than abundance, have a pivotal role

in shaping niche variation and trophic specialisation of riverine animals expecting niche expansion and a higher number of feeding links when prey diversity increases (Sánchez-Hernández et al., 2021). Thus, structural properties of food webs likely follow shifts in species richness, reaching maximum complexity (e.g. connectance and number of links) in mid-size rivers (Figure 2). The little knowledge on this research topic comes from the study of Romanuk et al. (2006), which only covered a specific geographic area (South Saskatchewan River Basin in Alberta, Canada) and may not include large (high order) river systems despite covering longitudinal shifts from mountain to prairie regions. Thus, conclusions may not apply to broad geographic zones, especially considering that the number of feeding links based on predator(fish/salamanders)–prey(macroinvertebrates) interactions can show remarkable geographical variation (Sánchez-Hernández, 2020a; Sánchez-Hernández, Finstad, et al., 2019). That said, how food web structure changes consistent with the RCC has not been resolved yet and represents a challenge in animal ecology research.

Size structure of many fish populations in terms of mean length at age, such as salmonids, increases downstream (Parra et al., 2009), and this comes with increases in the piscivorous behaviour which, in turn, increases species' trophic position, food-chain length and complexity of food webs (Sánchez-Hernández, 2020a; Sánchez-Hernández, Nunn, et al., 2019). Thus, if larger individual fish are found in higher stream orders, food-chain length, trophic position of piscivorous species and energy mobilisation routes are expected to change along the river continuum (Figure 2) but remains unexplored and should be prioritised for further research.

4 | THINKING OUTSIDE THE MAIN STEM RIVER: META-ECOSYSTEM, META-COMMUNITY AND RIVER NETWORK CONCEPTS

We require novel approaches to examine dynamics and functioning of ecosystems along longitudinal environmental gradients integrating meta-ecosystem, meta-community and river network concepts (Doretto et al., 2020 and references therein), as flow connectivity across longitudinal and lateral (aquatic–terrestrial linkage) dimensions aligns well with meta-ecosystem and meta-community perspectives (Humphries et al., 2014). Network topology is crucial to understand response of meta-community to changing connectivity by altering dispersal patterns (Carraro & Altermatt, 2022; Lee et al., 2022), but also changing connectivity regimes impact on species richness as local species richness is mediated by spatial loss of connectivity (Lee et al., 2022). As already pointed out, food web structure and energy mobilisation routes may respond to biodiversity patterns along the river continuum (Figure 2). Thus, changes in food web structure and trophic transfer along the river continuum are expected to be dynamic integrating local and spatial processes in meta-communities and thus dependent on species-specific dispersal dynamics and aquatic–terrestrial linkages at the landscape scale.

Moreover, changes in resource availability linked to flood pulse dynamics can be reflected in consumers' feeding and energy mobilisation routes through stable isotopes (e.g. Pool et al., 2017). Thus, flood pulse concepts can be accommodated with trophic ecology considerations (energy flow-paths and food web structure) on the RCC. However, methodological approaches should be closely linked to the research questions to be addressed. For example, short-term diet-tracing techniques like stomach-content analysis could be used to evaluate changes in food web structure (feeding links and connectance) during specific time moments of pulse phases (e.g. increasing, peaking and decreasing), whereas long-term diet-tracing techniques (e.g. stable isotopes and biomarkers) are recommended to explore changes in energy mobilisation routes over broader time periods such as dry and wet seasons (Pool et al., 2017).

The RCC predicts a shift from cold-stenothermal and invertivores fish species to warm-eurythermal and piscivorous fish species (Vannote et al., 1980), which has been empirically demonstrated, showing that the proportion of piscivorous and omnivorous fish increases with river size (Oberdorff et al., 1993). Apex predators and omnivorous species are expected to increase food-chain lengths (Sommer et al., 2018), therefore feeding guilds of the fish communities emerge as key factor to understand longitudinal changes in food web structure within river dendritic networks. In addition, generalist consumers with numerous prey types increase food web structural properties (number of links, connectance and linkage density) (Sánchez-Hernández, 2016). Thus, the increasing presence of apex predators along stream-size gradients would increase food-chain length and food web complexity, especially when apex predators are specialised on generalist consumers. However, the perception of food web becoming increasingly complex along the river continuum as consequence of apex predators increase may have some exceptions as food web structure rely largely on prey richness, and thereby expecting to be maximum at mid-size rivers (Figure 2).

It should be noted that lakes and tributaries may cause deviations from the expected RRC pattern, that is, serial discontinuities, through local variation of biotic (animal communities), physical (water and sediment fluxes) and biophysical (energy input and organic matter) conditions (e.g. Doretto et al., 2020; Jones, 2010; Malmqvist & Brönmark, 1985; Rice et al., 2001). The physical and biological consequences that natural discontinuities (lake or tributary) might have on the RRC principles can be dependent on its position and size within the river system (Jones, 2010; Jones & Schmidt, 2016; Rice et al., 2001). For example, large tributaries can revert functional composition of animal communities towards those expected upstream, whereas small tributaries may accelerate longitudinal trends of animal communities (Doretto et al., 2020). Another important point is that environmental variation has a greater importance than branching on determining diversity maintenance at the watershed scale, but hierarchical dendritic branching pattern can affect stream community structure when streams are small relative to the scales of environmental change or dispersal (Holt & Chesson, 2018). Thus, large main stem rivers buffer the effect of small tributaries without causing noticeable changes,

whereas the effect is more evident in headwaters of main stem rivers (Jones & Schmidt, 2016). The role of terrestrial invertebrates in aquatic food web fuelling may likely increase after a tributary confluence, which provides terrestrial inputs available for predators in the main stem (Figure 3). Lakes are another natural discontinuity in river-lake systems, species diversity increases with distance below lakes in support of the serial discontinuity concept (Green et al., 2022). Overall, I posit that environmental and ecological changes downstream of the discontinuity (tributary confluence or lake) are expected to drive changes in food web structure and energy mobilisation routes as part of the complex and dynamic processes involved in dendritic river networks. However, despite

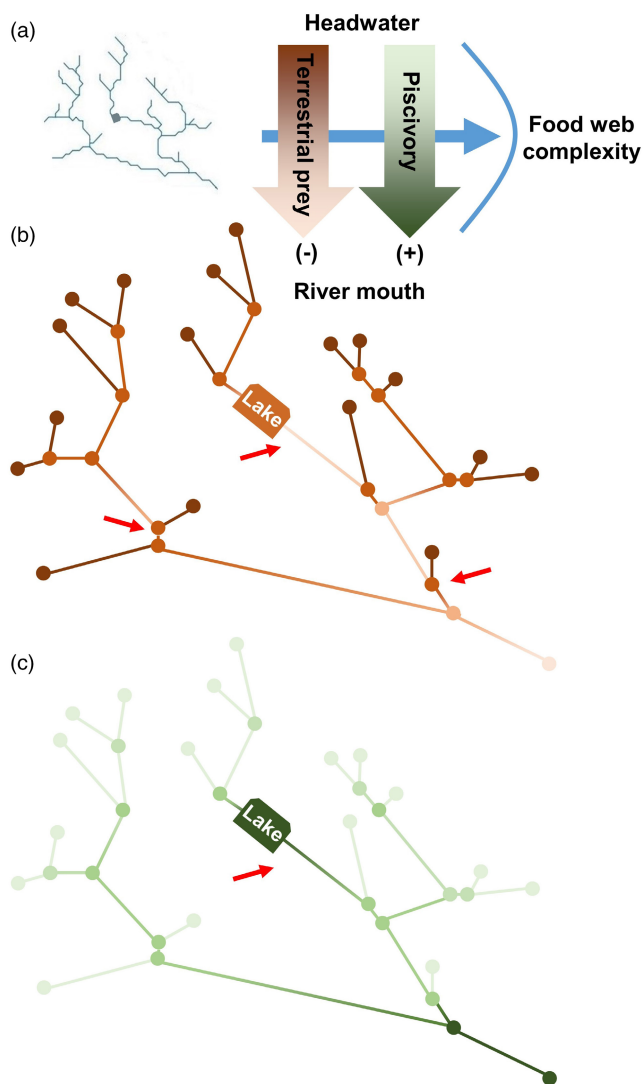


FIGURE 3 Importance of terrestrial invertebrates and fish prey in aquatic food web fuelling along the river continuum. A hypothetical river network (a) and the same network rendered as a graph showing longitudinal trends in the consumption of terrestrial invertebrates (b) and fish prey (c). Darker and lighter colours represent high and low values respectively. Red arrows show discontinuity (lake or tributary confluence) in the longitudinal patterns of energy mobilisation routes involved in dendritic river networks.

punctual deviations could be found downstream of natural discontinuities (Figure 3), overall trends in food web structure and energy mobilisation routes should prevalence at broader spatial scales following the tenets proposed in this concept (Figure 2).

5 | WHAT IS THE BEST PREDICTOR TO EXPLORE APPROACHES RELATED TO THE RCC?

Research questions related to the RCC have been commonly explored using stream order as predictor (e.g. Curtis et al., 2018; Larsen et al., 2019; Rosi-Marshall & Wallace, 2002), but less explored using altitude (Tomanova et al., 2007) and distance from the stream source (Miserendino, 2004). Quantitative geomorphic methods developed to measure stream order, such as Strahler stream order (Strahler, 1957), can reflect continuous variables measuring longitudinal scales of riverine such as, for example, distance from the stream source or altitude. This relies on the premise that high stream orders are located downstream where altitude is lower, but distance to the stream source is higher, compared to headwaters. However, locations with the same stream order can be situated differently along the longitudinal river gradient and hence with different environmental conditions (e.g. temperature and riparian canopy cover; Tomanova et al., 2007). Following the same reasoning, distance from the stream source may not completely overlap with stream order. Thus, the choice of the variable used to measure river continuum (stream order, distance from the stream source or altitude) in ecological studies can be key to avoiding misleading results. Because the concept behind the RCC is one of continuous change from source to sea, it is likely that a much more convincing statistical approach would be including the position of the sampling site as a continuous variable (distance from the stream source or altitude) rather than a categorical one (stream order). This would help to adopt spatial-scale approaches more accurate to explore trophic considerations (here food web structure and energy mobilisation routes) relate to environmental heterogeneity along the river continuum because consumer's feeding can be explained by site-specific prey community structures along environmental gradients through bottom-up mechanisms (Sánchez-Hernández, Finstad, et al., 2019).

6 | CONCLUSIONS AND OUTLOOKS

This concept details several ways that a trophic ecology perspective can help meet challenges facing ecologists today to provide a holistic understanding of the function and energy transfer in animal communities in response to changes along spatially diverse systems and regions. Because aquatic communities are structured according to cascading trophic mechanisms, a food web approach on the RCC would improve our understanding of the structure and functioning across several ecological scales (community and ecosystem levels).

- Consumer's diet can be integrated into the RCC because stream-dwelling species can follow a gradual replacement of the dominant food resources along the river continuum through bottom-up mechanisms (Figure 2). So, energy flow-paths are expected to change between headwaters (leaf litter) and downstream (biofilm and detritus) via changes in aquatic macroinvertebrate communities, but we currently do not know the role that terrestrial invertebrates and fish prey (piscivory) play in such transition. This represents a unique opportunity to test research hypotheses exploring spatial differences in terrestrial-aquatic linkages aiming to uncover the role of terrestrial invertebrates in aquatic food web fuelling and for the maintenance of aquatic communities, especially when aquatic invertebrate biomass can be limiting due to both natural (seasonal life-history traits such as hatching and emergence) and anthropogenic (e.g. water contamination and habitat alteration) causes. In this regard, stoichiometric and stable isotope approaches (e.g. Evans-White & Halvorson, 2017; Middelburg, 2014) emerge as key methods to understand how riverine food webs are fuelled along spatially diverse systems and regions, and thus in line with the RCC principles.
- Trophic ecology considerations (energy flow-paths and food web structure) on the RCC represent novel research lines and emerging frameworks that should receive further attention. The few available works (Guo et al., 2021; Romanuk et al., 2006) could be replicated geographically along biomes or climatic domains to provide generalisation of outcomes. For example, Englmaier et al. (2020) observed that biodiversity patterns (maximum at mid-size river systems) are similar in Afrotropical compared to temperate regions, which might match with tenets proposed in this concept supporting highest food web complexity at mid-size river systems regardless of geographic regions.
- The inclusion of meta-ecosystem theories underlying longitudinal patterns of riverine networks may be relevant for a broader range of systems than those mountainous temperate and forested headwater catchments described in the original RCC conception. Meta-analyses approaches (Sánchez-Hernández, Finstad, et al., 2019 and references therein) could be implemented to test longitudinal shifts in terrestrial-aquatic linkages (consumption of terrestrial prey) to uncover broadscale patterns in energy flow-paths according to RCC principles. Also, the exploration of longitudinal changes in cannibalism and intraguild predation within size-structured communities represent promising insights into the development of the RCC.
- For a standardisation of methods for studies addressing RCC principles, it may be preferably combining continuous (preferably, distance from the stream source) with categorical variables (stream order) to obtain more reliable conclusions and avoid misleading results.

AUTHOR CONTRIBUTIONS

All stages of producing this manuscript were carried out by Javier Sánchez-Hernández.

ACKNOWLEDGEMENTS

I thank three anonymous reviewers for their helpful comments. My current research on trophic ecology is supported by BiodivRestore (project PCI2022-132991) and Impulso (project M3006) funding.

CONFLICT OF INTEREST STATEMENT

The author declares that he has no conflict of interest.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

ORCID

Javier Sánchez-Hernández  <https://orcid.org/0000-0001-9684-4774>

REFERENCES

- Carraro, L., & Altermatt, F. (2022). Optimal Channel networks accurately model ecologically-relevant geomorphological features of branching river networks. *Communications Earth & Environment*, 3, 125.
- Curtis, W. J., Gebhard, A. E., & Perkin, J. S. (2018). The river continuum concept predicts prey assemblage structure for an insectivorous fish along a temperate riverscape. *Freshwater Science*, 37, 618–630.
- Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: A challenge for freshwater ecology. *Bioscience*, 64, 229–235.
- Doretto, A., Piano, E., & Larson, C. E. (2020). The river continuum concept: Lessons from the past and perspectives for the future. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 1853–1864.
- Edwards, E. D., & Hury, A. D. (1996). Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia*, 337, 151–159.
- Englmaier, G. K., Hayes, D. S., Meulenbroek, P., Terefe, Y., Lakew, A., Tesfaye, G., Waidbacher, H., Malicky, H., Wubie, A., Leitner, P., & Graf, W. (2020). Longitudinal river zonation in the tropics: Examples of fish and caddisflies from the endorheic Awash River, Ethiopia. *Hydrobiologia*, 847, 4063–4090.
- Evans-White, M. A., & Halvorson, H. M. (2017). Comparing the ecological stoichiometry in green and brown food webs—a review and meta-analysis of freshwater food webs. *Frontiers in Microbiology*, 8, 1184.
- Gounand, I., Little, C. J., Harvey, E., & Altermatt, F. (2018). Worldwide cross-ecosystem carbon subsidies and their contribution to ecosystem functioning. *Trends in Ecology & Evolution*, 33, 36–46.
- Greathouse, E. A., & Pringle, C. M. (2006). Does the river continuum concept apply on a tropical Island? Longitudinal variation in a Puerto Rican stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 134–152.
- Green, M. D., Herbst, D., Spasojevic, M. J., & Anderson, K. E. (2022). Rethinking biodiversity patterns and processes in stream ecosystems. *Ecological Monographs*, 92, e1520.
- Guo, F., Ebn, N., Bunn, S. E., Brett, M. T., Hager, H., & Kainz, M. J. (2021). Longitudinal variation in the nutritional quality of basal food sources and its effect on invertebrates and fish in subalpine rivers. *Journal of Animal Ecology*, 90, 2678–2691.
- Holt, G., & Chesson, P. (2018). The role of branching in the maintenance of diversity in watersheds. *Freshwater Science*, 37, 712–730.
- Humphries, P., Keckeis, H., & Finlayson, B. (2014). The river wave concept: Integrating river ecosystem models. *Bioscience*, 64, 870–882.
- Jones, N. E. (2010). Incorporating lakes within the river discontinuum: Longitudinal changes in ecological characteristics in stream-lake networks. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1350–1362.
- Jones, N. E., & Schmidt, B. J. (2016). Tributary effects in rivers: Interactions of spatial scale, network structure, and landscape characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 503–510.

- Kawaguchi, Y., & Nakano, S. (2001). Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology*, *46*, 303–316.
- Larsen, S., Bruno, M. C., Vaughan, I. P., & Zolezzi, G. (2019). Testing the River Continuum Concept with geostatistical stream-network models. *Ecological Complexity*, *39*, 1007732.
- Lee, F., Simon, K. S., & Perry, G. L. W. (2022). Network topology mediates freshwater fish metacommunity response to loss of connectivity. *Ecosphere*, *13*, e4286.
- Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, *6*, 673–679.
- Malmqvist, B., & Brönmark, C. (1985). Reversed trends in the benthic community structure in two confluent streams; one spring-fed, the other lake-fed. *Hydrobiologia*, *124*, 65–71.
- Middelburg, J. J. (2014). Stable isotopes dissect aquatic food webs from the top to the bottom. *Biogeosciences*, *11*, 2357–2371.
- Minshall, G. W. (1988). Stream ecosystem theory: A global perspective. *Journal of the North American Benthological Society*, *7*, 263–288.
- Minshall, G. W., Cummins, K. W., Petersen, R. C., Cushing, C. E., Bruns, D. A., Sedell, J. R., & Vannote, R. L. (1985). Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1045–1055.
- Minshall, G. W., Petersen, R. C., Curtis, J. R., & Curtis, F. N. (1985). Species richness in streams of different size from the same drainage basin. *The American Naturalist*, *125*, 16–38.
- Miserendino, M. L. (2004). Effects of landscape and desertification on the macroinvertebrate assemblages of rivers in Andean Patagonia. *Archiv für Hydrobiologie*, *159*, 185–209.
- Mittelbach, G. G., & Persson, L. (1998). The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1454–1465.
- Nakano, S., Miyasaka, H., & Kuhara, N. (1999). Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, *80*, 2435–2441.
- Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 166–170.
- Neres-Lima, V., Machado-Silva, F., Baptista, D. F., Oliveira, R., Andrade, P. M., Oliveira, A. F., Sasada-Sato, C. Y., Silva-Júnior, E. F., Feijó-Lima, R., Angelini, R., Camargo, P. B., & Moulton, T. P. (2017). Allochthonous and autochthonous carbon flows in food webs of tropical forest streams. *Freshwater Biology*, *62*, 1012–1023.
- Oberdorff, T., Guilbert, E., & Lucchetta, J. C. (1993). Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia*, *259*, 157–167.
- Parra, I., Almodóvar, A., Nicola, G. G., & Elvira, B. (2009). Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales. *Journal of Fish Biology*, *74*, 2355–2373.
- Pool, T., Holtgrieve, G., Elliott, V., McCann, K., McMeans, B., Rooney, N., Smits, A., Phanara, T., Cooperman, M., Clark, S., Phen, C., & Chhuoy, S. (2017). Seasonal increases in fish trophic niche plasticity within a flood-pulse river ecosystem (Tonle Sap Lake, Cambodia). *Ecosphere*, *8*, e01881.
- Rice, S. P., Greenwood, M. T., & Joyce, C. B. (2001). Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 824–840.
- Romanuk, T. N., Jackson, L. J., Post, J. R., McCauley, E., & Martinez, N. D. (2006). The structure of food webs along river networks. *Ecography*, *29*, 3–10.
- Rosi-Marshall, E. J., & Wallace, J. B. (2002). Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, *47*, 129–141.
- Ryan, D. K., & Kelly-Quinn, M. (2015). Effects of riparian canopy cover on salmonid diet and prey selectivity in low nutrient streams. *Journal of Fish Biology*, *86*, 16–31.
- Ryder, G. I., & Scott, D. (1988). The applicability of the River Continuum Concept to New Zealand streams. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, *23*, 1441–1445.
- Sánchez-Hernández, J. (2016). Do age-related changes in feeding habits of brown trout alter structural properties of food webs? *Aquatic Ecology*, *50*, 685–695.
- Sánchez-Hernández, J. (2020a). Drivers of piscivory in a globally distributed aquatic predator (brown trout): A meta-analysis. *Scientific Reports*, *10*, 11258.
- Sánchez-Hernández, J. (2020b). Reciprocal role of salamanders in aquatic energy flow pathways. *Diversity*, *12*, 32.
- Sánchez-Hernández, J., Finstad, A. G., Arnekleiv, J. V., Kjærstad, G., & Amundsen, P.-A. (2019). Drivers of diet patterns in a globally distributed freshwater fish species. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*, 1263–1274.
- Sánchez-Hernández, J., Finstad, A. G., Arnekleiv, J. V., Kjærstad, G., & Amundsen, P.-A. (2021). Beyond ecological opportunity: Prey diversity rather than abundance shapes predator niche variation. *Freshwater Biology*, *66*, 44–61.
- Sánchez-Hernández, J., Glaber, H.-M., & Amundsen, P.-A. (2016). Food resource partitioning between stream-dwelling Arctic charr *Salvelinus alpinus* (L.), Atlantic salmon *Salmo salar* L. and alpine bullhead *Cottus poecilopus* Heckel, 1836: An example of water column segregation. *Hydrobiologia*, *784*, 105–115.
- Sánchez-Hernández, J., Nunn, A. D., Adams, C., & Amundsen, P.-A. (2019). Causes and consequences of ontogenetic dietary shifts: A global synthesis using fish models. *Biological Reviews*, *94*, 539–554.
- Sommer, U., Charalampous, E., Scotti, M., & Moustaka-Gouni, M. (2018). Big fish eat small fish: Implications for food chain length? *Community Ecology*, *19*, 107–115.
- Statzner, B., & Higler, B. (1985). Questions and comments on the river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1038–1044.
- Strahler, A. N. (1957). Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union*, *38*, 913–920.
- Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., & Muotka, T. (2011). Stream salmonids as opportunistic foragers: The importance of terrestrial invertebrates along a stream-size gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 2146–2156.
- Tomanova, S., Tedesco, P. A., Campero, M., Van Damme, P. A., Moya, N., & Oberdorff, T. (2007). Longitudinal and altitudinal changes of macroinvertebrate functional feeding groups in neotropical streams: A test of the River Continuum Concept. *Fundamental and Applied Limnology*, *170*, 233–241.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 130–137.
- Winterbourn, M. J., Rounick, J. S., & Cowie, B. (1981). Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research*, *15*, 321–328.

How to cite this article: Sánchez-Hernández, J. (2023). Fresh perspectives on the River Continuum Concept require trophic ecology approaches focussed on food web structure and energy mobilisation routes. *Journal of Animal Ecology*, *92*, 957–964. <https://doi.org/10.1111/1365-2656.13928>