How disrupted spatial fluxes reshape food web structure along the river–sea continuum

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Abstract

Anthropic disturbances and ecosystem processes transcend the artificial boundaries between land, freshwater, and sea. While these systems are interconnected through species and material fluxes, they are often studied in isolation. In response, the concept of metaecosystem has emerged as a powerful framework to understand how fluxes among ecosystems shape their functions and dynamics. Disrupting these fluxes can have dramatic consequences that ripple across entire landscapes. In aquatic systems, dams and nutrient pollution are known to strongly affect fish communities. Yet, little is still known about how these effects propagate and potentially accumulate, through hydrographic basins and ultimately to the sea. Using bayesian spatio-temporal statistical models (R-INLA), we aim to analyse existing data on food-web structure across France, combined

with environmental variables (dams, nutrients, …), to quantify how breaking or increasing fluxes among systems disturbs food-web structure locally and how these disturbances spread throughout the metaecosystem.

Keywords: *foodweb ecology, stream network, spatial autocorrelation, bayesian statistics.*

Introduction

While patterns in community change within river network have been well studied, these studies have mostly focus on specise richness (Bonnaffé et al. 2024), or roughly defined functional composition (Vannote et al. 1980).

River-estuary-sea continuum

- Xenopoulos et al. (2017) highlights the importance of accounting for the full gradient from headwater to the sea. Freshwater and coastal ecosystems are connected by flux of carbone and nutrients (N, P), as well as, movement of migratory species. Reviews work connecting river and sea, that said, most of them focus on chemical fluxes, remain relatively local, and none of them focused on the food web structure.
- Catchment land-use impacts macro-invertebrates along the river-sea continuum with no dilution effect (Bierschenk et al. 2017).
- The Land-to-Ocean Continuum (LOAC) concept has been used to study carbon fluxes between land and ocean, and how these fluxes, and feedback loop influence the carbon storage by oceans (**Regnier-etal-2022?**).

Freshwater ecosystems

- The River Continuum Concept has shaped the freshwater ecology researsh by links physical gradients along rivers to predictable changes in community structure, energy sources, and ecosystem functioning (Vannote et al. 1980; Doretto et al. 2020).
- Serial Discontinuity Concept is a framework to predict the impact of discontinuities, such as dams, on biotic and abiotic variables along the river continuum (Ward and Stanford 1995).
- The Flood Pulse Concept (FPC) complements the RCC as it focuses on the lateral dimension of rivers and its role in explaining community productivity, while the RCC focused on the longitudinal aspect. The FPC states that its the rythm of flood and recession – that is, the pulse – which structures ecosystem productivity, not the flow (Junk et al. 1989).
  - Terrestrial organic matter (leaf litter, vegetation, soil nutrients) gets dissolved and mobilized into the water

  - Aquatic plants and algae explode in productivity in the shallow, sunlit floodwaters
  - Fish and invertebrates move onto the floodplain to feed and reproduce
  - When waters recede, nutrients and organic matter flush back into the main channel

- The River Wave concept as unifying framework of different concepts of freshwater ecology (Humphries et al. 2014).
- Community richness and hence food web structure is expected to be driven by nutrient availability (Ho et al. 2023).

Multiple stressors

- Synergistic and antagonistic effects of multiple stressors (Jackson et al. 2021; Orr et al. 2024).
- Temperature can interact with nutrients and impact food web structure in a nonlinear way Binzer et al. (2012).
- (Danet et al. 2021; Bonnaffé et al. 2024).

Connectivity

- Small dispersal stabilizes through spatial structure and asynchrony (LeCraw et al. 2014; McCann et al. 2005; Pillai et al. 2011).
- A metaecosystem model shows that dispersal of living organisms (that consume nutrients) is stabilising,while dispersal of non-living compartments such as nutrients or detritus is destabilising (Gounand et al. 2014).
- Prey switching of mobile top predators can stabilize connected food webs through 'spatial coupling' (LeCraw et al. 2014; McCann et al. 2005; Pillai et al. 2011).
- At high dispersal/connectivity the stabilizing effect wanes as strongly connected patches behave as a single patch (LeCraw et al. 2014; McCann et al. 2005).
- Studies between pairs of the following connectivity, complexity and stability are common. However, studies investigating how these are interconnected are rare (LeCraw et al. 2014).
- Connectivity has 4 dimensions: longitudinal, lateral, vertical and temporal (Grill et al. 2019).
- We identified five pressure factors to represent the main human interferences within the four dimensions of fluvial or river connectivity (Grill et al. 2019):

  (1) river fragmentation (longitudinal);
  (2) flow regulation (lateral and temporal);
  (3) sediment trapping (longitudinal, lateral and vertical);

(4) water consumption (lateral, vertical and temporal);
(5) infrastructure development in riparian areas and floodplains (lateral and longitudinal).

- In freshwater system, fish dispersal is limited. A meta-analysis found that the mean dispersal kernel is around 10km (Comte and Olden 2018).
- Neutral metacommunity model explains biodiversity pattern in the Missisipi river, showing the key role of dispersal in explaining community structure along the river continuum (Muneepeerakul et al. 2008).
- Connectivity structures and mititgates effect of drying events in macroinvertebrates communities (Chalmandrier et al. 2025).
- It is key to adopt a network perspective to understand how diversity is created and maintained within riverine ecosystems (Altermatt 2013). With this perspective one can account for the dendritic network and so the spatial processes that shape diversity.
- From points (Death and Winterbourn 1995)… to lines (RCC, SDC)… to dendritic networks (Shepherd and Ellis 1997).
- River network characteristics, local network properties and their interaction were important individual contributors to explaining local species richness of aquatic insects (Altermatt et al. 2013). Effect of connectivity on richness supported experimentally (Carrara et al. 2012).

Dams

- Decrease river connectivity / reduce migration (Dean et al. 2023; He et al. 2024; Pedersen et al. 2012).
- Reservoir, lotic from lentic conditions, can result in hypoxic conditions. Favor phytoplancktons and macrophytes (Ding et al. 2026; Dean et al. 2023). Facilitate the spread of invasive species (Johnson et al. 2008).
- Reservoir increase residence time of nutrients upstream and decrease the downstream output, which can result in a decrease in primary productivity.
- Hydropeaking - that is, the sudden release of large water to answer the higher electric demand - can harm riverine community due to sudden change in water level and water flow.
- Cumulative impact of dams can reduce the nutrient input in deltas (Dean et al. 2023).
- A review (Ellis and Jones 2013) suggests that two recovery gradients exist in regulated river:

  1) a longer, thermal gradient of around 100 km;
  2) a shorter resource subsidy gradient of around 1-4 km.

Methods

Food web inference

To infer local food web structure, we used a metaweb approach. That is, we build a web compiling the potential feeding interactions between all species of the dataset. Importantly, our metaweb takes into account intra-specific variation in species diet. We did so by defining trophic interactions at different life stages for each species.

Metaweb nodes

The nodes of our metaweb represent a species at a given lifestage. Specifically, fish species were divided into nine body class sizes evenly distributed. Each body size class within a given species is what we call a 'trophic species' assuming that conspecifics of the same body size class share similar trophic interactions because trophic interactions are largely determined by predator–prey body size ratio in freshwater ecosystems (Brose et al. 2006).

In addition of fish species, seven basal nodes (resources) were added at the base of the metaweb: detritus, biofilm, phytoplanckton, zooplanckton, macrophytes and zoobenthos. We represent the basal food web structure in the Appendix (see Figure S1). We assumed that these resources were present at all sampling sites.

Infer missing fish lengths

Most length of fishes are measured but not all. Yet, we need individual fish length to determine their diet based on their ontogeny. We infer missing fish size using information on the given fishing operation. When there are more than three observations of the fish species, we use a truncated normal distribution (package truncdist; Nadarajah and Kotz (2006)). The mean and variance are given by the modes of the observed distribution of the fishing operation. The minimum and maximum of the distribution are given by the minimal and maximal length observed on the entire data set for that species. We do so to avoid infering irrealistic lengths.

Get fish diet

We use fishbase as a primary source to extract fish diet at their different life stages, to get on which basal categories species feed on and whether they are piscivorous or not. We detail in the Supporting Information how made the correspondance between our categories and the one of fishbase. We remove species that have an occurence lower than 10 in the entire dataset which comprise 69 species. This enable to avoid retrieving diet information of species that will have a minimal impact on food web structure due to their rarity. We add a larvae stage when missing, assuming that fish larvae feed on zooplankton (Dabrowski 1984). We assume that fish individuals are larvae if they measure less than 2 cm. To classify individuals as juvenile or adult we use the length at maturity of the species as a threshold. When this information was not available we used a single stage (*combined*) by merging the diets of the two stages. We did not consider a recruit stage.

The metaweb

Predation window are assumed to be 0.03 to 0.45 of individual body size for piscivorous species. We then use the package foodwebbuilder to build the metaweb and the local food webs through subsampling. We investigated the effect of the number of size classes on the structure of the reconstructed metaweb. We observed little influence of the number of size classes on the metaweb connectance Figure S3. So, we decided to split each species 5 size classes as in Bonnaffé et al. (2024).

> **Note**
>
> The choice of a constant predation window has an important implication. It implies that what only matters in terms of ecosystem functioning is the individual size (once the species is known to be piscivorous). In this setting, two piscivorous individual of different species but same size will eat the very same things.

Subsampling the metaweb to get local food webs

Results

Discussion

Limitations

Regarding food web structure, we have simplified the base of the web and exclude macro-invertebrates. This choice naturally emphasizes the functional role of fishes in shaping food web structures. Yet, it would be valuable to include macro-invertebrates within the food web to get a more exhaustive picture of how aquatic community respond to stressors along the riversea continuum.

Supporting Information

Structure of the food web base

Model DAG

Put model DAG here using targets.

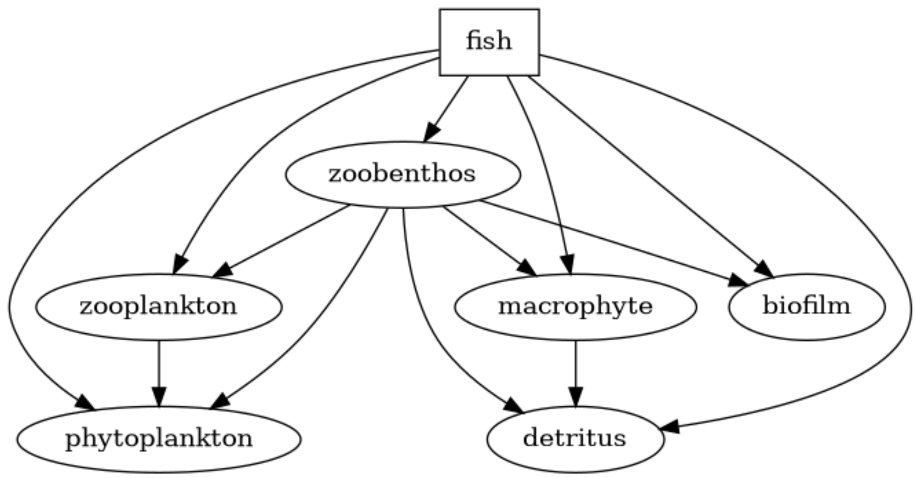

Figure S1: Assumed structure of the food web base.

Venn diagramm

Number of size classes and metaweb structure

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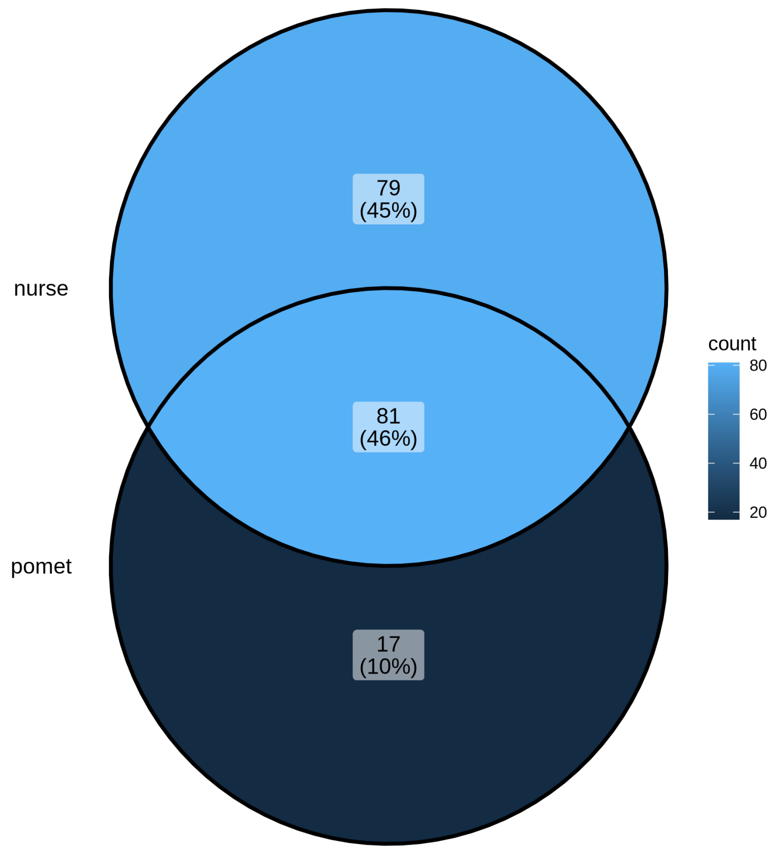

Figure S2: Venn diagram of common species between surveys.

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```
targets::tar_read(plot_metaweb_connectance)
```

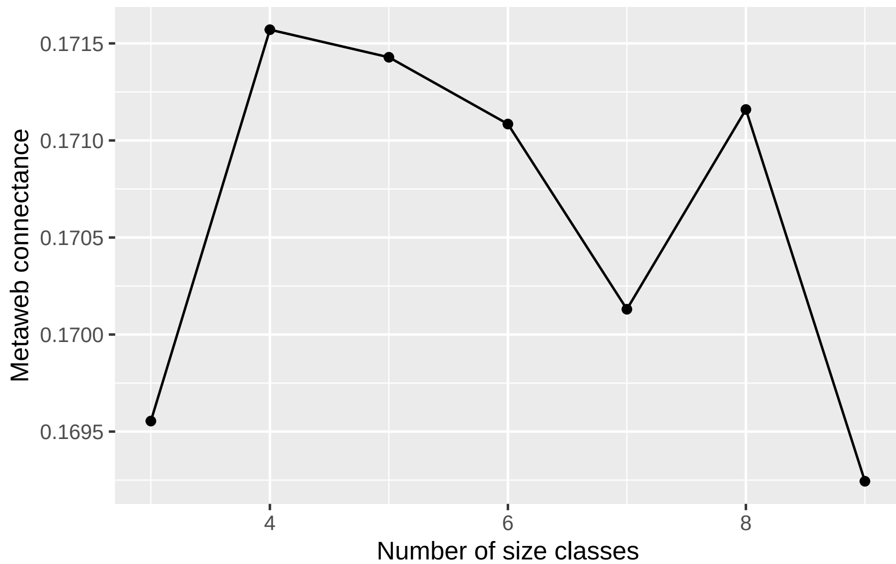

Figure S3: How metaweb connectance varies with the number of size classes.

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