Consequences of connectivity on aquatic food webs in Metropolitan France

Conséquences de la connectivité sur les réseaux trophiques aquatiques en France métropolitaine

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RÉSUMÉ

La fragmentation des habitats naturels menace la biodiversité, notamment dans les écosystèmes aquatiques d'eau douce, où barrages et seuils bloquent les migrations de poissons nécessaires au frai et à l'alimentation. Théoriquement, la connectivité des habitats influence les communautés piscicoles et leurs interactions, mais les validations empiriques restent rares. Ce travail analyse des données de pêches standardisées sur plus de 630 stations en France métropolitaine pour explorer les liens entre connectivité et réseaux trophiques. En utilisant des graphes mathématiques intégrant la structure hydrographique et les barrages, plusieurs résultats émergent : la connectivité aval-amont, conforme au River Continuum Concept, explique la richesse et la longueur des chaînes trophiques, qui augmentent de l'amont vers l'aval, tandis que la connectance diminue. La centralité des tronçons, en tant que carrefours du réseau fluvial, renforce la structuration des réseaux trophiques. Les barrages infranchissables accentuent cette influence en réduisant la connectivité. Enfin, l'impact de la connectivité varie entre écosystèmes lotiques et lentiques. Ces résultats approfondissent les liens entre paysage et réseaux biotiques, essentiels pour une gestion durable des milieux aquatiques.

ABSTRACT

The fragmentation of natural habitats poses a major threat to biodiversity, particularly in freshwater ecosystems, where dams and weirs block the migration routes of fish essential for spawning and feeding. Theoretically, habitat connectivity influences fish communities and their interactions, but empirical validations remain scarce. This study analyzes standardized fishing data from over 630 sites across metropolitan France to explore the relationships between connectivity and trophic networks. Using mathematical graphs that integrate hydrographic structures and dams, several key findings emerge: downstream-upstream connectivity, consistent with the River Continuum Concept, explains the richness and length of trophic chains, which increase from upstream to downstream, while connectance decreases. The centrality of river segments, as key junctions in the fluvial network, further shapes trophic networks. Impassable dams amplify this influence by reducing connectivity. Finally, the impact of connectivity differs between lotic and lentic ecosystems. These findings advance our understanding of the links between landscape structure and biotic networks, crucial for the sustainable management of aquatic environments.

KEYWORDS

Barriers, connectivity, empirical study, fish communities, trophic networks

Connectivité, communautés piscicoles, étude empirique, obstacles, réseaux trophiques

1 INTRODUCTION

Human infrastructures pose a major threat to natural habitats and biodiversity by directly destroying ecosystems and causing fragmentation (Haddad et al., 2015). Fragmentation, defined as the division of ecosystems without significant habitat loss, often arises from linear structures like roads and dams. This fragmentation reduces connectivity between habitat patches, hampers recolonization, limits interspecific and intraspecific interactions, and disrupts genetic mixing (Fahrig, 2003). Despite theoretical predictions (LeCraw et al. 2014), few empirical studies have explored its functional consequences, particularly on trophic networks, which provide insights into ecosystem structure and dynamics through predator-prey interactions.

Theoretical models suggest that landscape connectivity influences trophic networks by affecting species colonization and interactions (Leibold 2004). Predictions include a positive relationship between connectivity and trophic richness and chain length but a negative relationship with connectance, reflecting a shift toward more specialized interactions (LeCraw et al., 2014). However, these hypotheses lack empirical validation.

Freshwater ecosystems are ideal for studying connectivity's impact on trophic networks due to their dendritic structure, directional flow, and biodiversity richness (Kopf et al., 2015). In France, over 15,000 dams fragment rivers, limiting fish migration critical for spawning and feeding. Downstream sections typically exhibit higher trophic richness and complexity, influenced by upstream ecological processes (Ho et al., 2023). This study aims to empirically test theoretical predictions on habitat connectivity and trophic network structures using standardized fish sampling data from over 629 French stations. Key hypotheses include greater trophic richness and chain length but lower connectance in highly connected habitats, with connectivity metrics incorporating dam influence offering stronger explanatory power.

2 MATERIALS AND METHODS

This study examines the connectivity and trophic networks of freshwater ecosystems in metropolitan France. Fish sampling was conducted across 629 stations, including 373 river and 256 lake sites, using standardized methods (electrofishing for rivers and gillnetting for lakes). Fish individuals were identified to species level and measured, with trophic networks reconstructed based on taxonomy and body size classes to account for dietary shifts. Seven basal resources were included, and key indices—trophic richness, food chain length, and connectance—were calculated to evaluate ecosystem complexity and resilience.

Eighteen hydrographic units, representing major river basins such as the Rhône, were mapped using the Carthage database. Dams were identified as impassable from the French registry of flow obstacles were incorporated into connectivity analyses. The hydrographic data were modeled as mathematical graphs in R software, where hydrological segments formed nodes, and water flow determined directed links. Connectivity was quantified using the Ecologically Scaled Landscape Index (ESLI, Vos et al., 2001) under three scenarios: downstream connectivity, absolute centrality, and fragmented centrality, reflecting the influence of physical barriers.

Structural Equation Models (SEMs) were used separately for rivers and lakes, exploring the direct and indirect effects of spatial connectivity on trophic indices. Comparisons between scenarios with and without barriers highlighted dam impacts on network properties, including trophic richness, food chain length, and connectance.

3 RESULTS

3.1 Trophic Network Properties in Lakes and Rivers

The analysis included 576 trophic networks (220 from lakes and 356 from rivers). Trophic richness ranged from 10 to 91 nodes, with an average of 35.3 ± 13.5. The mean food chain length (MFCL) ranged between 3.35 and 5.66 nodes, averaging 4.59 ± 0.37, highlighting vertically structured networks capable of sustaining apex predators. Connectance values ranged from 0.05 to 0.23 (mean = 0.14 ± 0.03), suggesting low realized interaction rates relative to potential ones. Significant differences were observed between lakes and rivers in trophic richness, MFCL, and connectance. Lake networks showed higher trophic richness and MFCL but lower connectance compared to river networks.

3.2 Structural Equation Model (SEM) Selection

The SEMs compared different scenarios of spatial connectivity: absolute centrality (free movement) versus fragmented centrality (accounting for barriers). Fragmented centrality, which incorporates dam impacts, provided better explanatory power across both lakes and rivers. Models with fragmented centrality consistently had lower AIC values and good overall fit (p-values > 0.05 in Fisher tests). In the following analyses, we thus focused on fragmented centrality SEMs to explore relationships between connectivity and trophic network properties.

3.3 Direct and Indirect Relationships Between Connectivity and Trophic Network Structure in Lakes

The SEM for lake ecosystems showed a good fit (C = 8.95, p = 0.18), retaining 5 of the 9 hypothesized direct pathways. It explained 30% of the variance in trophic richness, 24% in mean food chain length, and 35% in connectance. Including hydrological units as random effects captured substantial variation, particularly in trophic richness. Sampling stations with high downstream connectivity (RCC, for the River Continuum Concept) and fragmented centrality exhibited more trophic nodes (rδ = 0.19 and 0.21, respectively; Fig. 1a). However, these connectivity metrics did not directly influence connectance or food chain length but affected them indirectly through trophic richness.

Trophic richness positively influenced mean food chain length (rδ = 0.49), while connectance was shaped by opposing processes: increasing trophic nodes reduced connectance (rδ = -0.46), but longer food chains indirectly enhanced it (rδ = 0.59). In summary, both types of connectivity similarly increased the number of trophic nodes in lake ecosystems, demonstrating their shared role in shaping trophic network structure.

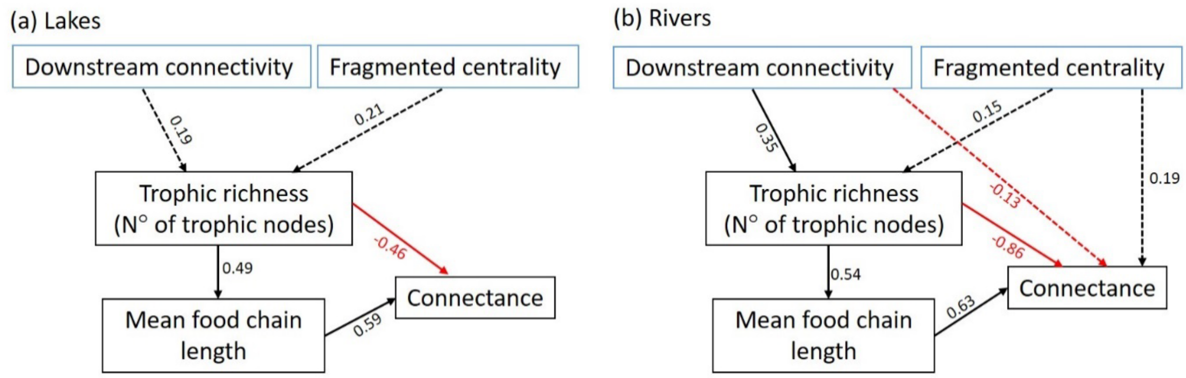

Figure 1. Effects of connectivity indices (downstream legacy and fragmented centrality) on food web structure in (a) lakes and (b) rivers. Full and dotted arrows represent highly significant (*p* < 0.001) and significant (*p* < 0.05) direct effects, respectively. Black and red arrows represent in positive and red negative direct effects, respectively.

3.3 Direct and Indirect Relationships Between Connectivity and Trophic Network Structure in Rivers

The Structural Equation Model (SEM) effectively described the relationships between spatial connectivity and river trophic network structures, explaining 35% of the variance in trophic richness and mean food chain length and 55% in connectance. Including hydrographic units as random effects captured significant variability, especially in trophic richness. Sampling stations with high downstream connectivity (RCC) and fragmented centrality exhibited more trophic nodes (Fig. 1b). RCC connectivity had contrasting effects: it negatively influenced connectance directly but increased it indirectly via longer food chains, while also reducing it through increased trophic richness. In contrast, fragmented centrality positively influenced connectance and food chain length but less strongly than RCC connectivity. Overall, downstream connectivity had a more significant impact than fragmented centrality, highlighting the critical role of flow continuity versus barriers in shaping riverine trophic networks.

4 DISCUSSION

This study explored the relationships between the connectivity of freshwater aquatic habitats and the associated trophic networks. The results highlight two critical and complementary spatial parameters in dendritic networks: the centrality of a habitat patch within the watershed and the downstream connectivity inheritance, as described by the River Continuum Concept (RCC, Vannote et al., 1980). Both connectivity indices are statistically linked to key trophic network metrics such as trophic richness, food chain length, and connectance. Higher downstream connectivity is associated with increased trophic richness, elongation of food chains, and decreased connectance

(Ho et al., 2023). This positional and functional indicator reflects the hierarchical structure of aquatic habitats, with headwater streams hosting simpler trophic structures and downstream zones supporting more complex networks. In upstream habitats, primary production is limited, and organic material mainly comes from adjacent terrestrial ecosystems. This favors shredders like insect larvae and small predators such as trout. In contrast, downstream regions benefit from higher connectivity, greater nutrient inputs, and more diverse habitats, supporting generalist species, intermediate consumers, and apex predators. These findings align with the RCC and more recent studies (e.g. Zatkos et al., 2021) and reveal how increased connectivity fosters complex trophic networks but can reduce connectance due to specialized interactions.

Centrality positively influences trophic richness and food chain length. However, barriers such as dams disrupt fish migrations, reducing connectivity and altering trophic structures in upstream habitats. Migratory species like salmon and trout may be particularly impacted, as their movements are blocked which may explain the trophic homogenization we found in isolated habitats. Adjusting connectivity metrics to account for barriers improves their explanatory power, underscoring the ecological importance of mitigating such disruptions with management measures like fish passes. Connectivity has a stronger impact on trophic structures in rivers compared to lakes. This is attributed to ecological differences: lakes, being lentic systems, are less dependent on upstream inputs and feature greater habitat heterogeneity, supporting higher trophic diversity. Rivers, in contrast, rely heavily on downstream connectivity for nutrient flow and trophic complexity.

This work demonstrates that key areas of high connectivity, such as central watershed patches and downstream zones, host richer and more complex trophic networks. These findings support ecological management frameworks, such as green and blue corridors, aimed at preserving biodiversity by maintaining habitat connectivity. By advancing our understanding of the spatial and functional dynamics of freshwater ecosystems, this study contributes valuable insights to the sustainable management of aquatic biodiversity.

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