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Ecological topics related to food webs: a review with emphasis on global freshwater fish communities

Tópicos ecológicos relacionados con las redes alimentarias: una revisión con énfasis sobre comunidades mundiales de peces de agua dulce

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Abstract

Understanding the structure and dynamics of freshwater food webs remains a challenge for ecologists, mainly due to factors, mechanisms, and processes that maintain communities must be considered. This study aims to analyze the state-of-the-art on food web on freshwater fish communities through a systematic literature review and applying the co-words bibliometric technique. Particularly, developed countries have increased the study of food webs in the last years. The evaluation of the different ecosystem components like phytoplankton, zooplankton, and aquatic macroinvertebrates are important to considered in food webs, and stable isotope analysis accompanied by stomach content as methodologies. Food web is usually represented by models (e.g., Ecopath with Ecosim) or diagrams (food networks connecting species). Further research is needed on describe food webs in freshwater system from developing countries.

Keywords: Communities, trophic structure, stable isotopes analysis, gut content, ecological network analysis.

Resumen

Comprender la estructura y la dinámica de las redes alimentarias en sistemas de agua dulce sigue siendo un desafío para los ecólogos, principalmente debido a los factores, mecanismos y procesos que deben tenerse en cuenta para que se mantengas las comunidades. Este estudio tiene como objetivo analizar el estado del arte en el tema de la red alimentaria en las comunidades de peces de agua dulce a través de una revisión sistemática de la literatura y aplicando la técnica bibliométrica de co-palabras. Particularmente, las redes alimentarias se han estudiado más en los países desarrollados en los últimos años. La evaluación de los diferentes componentes del ecosistema como el fitoplancton, el zooplancton y los macroinvertebrados acuáticos son importantes para considerar en las redes alimentarias y el análisis de isótopos estables, acompañado del contenido estomacal como metodologías. La red alimentaria generalmente se representa mediante modelos (por ejemplo, Ecopath con Ecosim) o diagramas (redes alimentarias que conectan especies). Se necesita más investigación para describir las redes alimentarias en el sistema de agua dulce de los países en desarrollo.

Palabras clave: Comunidades, estructura trófica, análisis de isótopos estables, contenido estomacal, análisis de redes ecológicas.

1. Introduction

Food webs are one of the principals thematic in ecological science, the first depictions of community-wide feeding relationships were published in the early 20th century (Egerton, 2007). Yet, many people associate the dawn of food web ecology with Charles Elton (Elton, 1927). Through time, several authors have been added more specific ideas and important terms to Elton´s contributions: the flow of energy through ecosystems, trophic dynamic (Lindeman, 1942), food web complexity and stability (May, 1972), generalized food web models (Cohen, 1978), functional food webs (Paine, 1980), ecological network analysis (Polovina, 1984), stable isotopes perspectives of food web structure (Van der Zander and Rasmussen, 1999), trophic cascades (Carpenter, 1985), intraspecific trophic variation (Bolnick, 2003), keystone species (Libralato *et al.,* 2006), between others.

Food web in communities describes either species and networks that represent interactions among a group of organisms, populations, or trophic units, the energy and biomass flow among compartments, species are represented by nodes, and trophic relationships are represented by links (Jordán and Scheuring, 2002). These depictions of feeding relationships can provide insight into almost every area of ecological research, ranging from population dynamics to the cycling of nutrients through ecosystems.

It is challenging to find a specific sub-discipline of ecology that is not related to, or relevant for, understanding of food webs, mainly due to having implications at the population (Winemiller, 1990), community (Paine, 1980), ecosystem (Carpenter *et al.,* 2001) and evolutionary (Post and Palkovacs, 2009) levels. In this context, one of the taxonomic groups that must be considered is fish species because they are economically and ecologically important worldwide, mainly due to important food resources for humans; they also perform many functions within ecosystems (*bottom-up and top-down* theory, details coming later). Unfortunately, anthropogenic activities such as climate change, habitat degradation, pollution, the introduction of nonnative species, and overfishing are causing a decrease in fish populations (O'Reilly *et al.,* 2015), leading many species to face extinction, thereby inducing cascade effects in ecosystems, for example, competition for resource between species (Devlin *et al.,* 2017). Fish are mobile sources of critical nutrients like nitrogen and phosphorus (Samways and Cunjak, 2015); spatiotemporal variations in the production and biomass of fish create patterns in the freshwater and riparian food webs generally (García *et al.,* 2015). Therefore, fish are represented on practically every trophic level, from herbivores to tertiary predators and decomposers (Delong *et al.,* 2019). Some species are highly specialized to feed on items such as scales and fins, while others are generalists with broad diets, especially when exploiting abundant resources (Nelson, 2015).

In addition, fish act as energy regulators between adjacent ecosystems by transforming and exporting energy from primary producers, and are the components of 90% of the nekton, as well maintaining energy reserves within food webs and are bioindicators (Dudgeon *et al.,* 2006).

Freshwater ecosystems including rivers, streams, lakes, wetlands, are critical for biodiversity, providing habitat for one third of all the vertebrate species, including approximately 40% of fish species, also they are some of the most important resources in the replenishment and purification of water sources used by humans (Lynch *et al.,* 2016).

Despite covering only 0.01% of the Earth's total surface, they supply essential ecosystem services such as food, water, and energy provision to billions of people (Mota *et al.,* 2014). Unfortunately, they are also one of the most highly degraded ecosystems, suffering from chemical contamination by waste and plastics, overexploitation of aquifers, eradication of wetlands, and others (Carpenter *et al.,* 2011).

The objective of this research was to carry out a bibliometric review of the literature to understand better freshwater ecosystem food webs related to the fish community. The analysis of important topics in recent years provides an informative reference on the basic concepts and advantages in quantifying the food webs in communities and their applications to freshwater fish. Besides, we attempted to identify and comment on general gaps in the study of food webs in freshwater fish communities and give directions for further studies concerning this subject.

2. Methods

The research was focused on articles in the Scopus database and Web of Science-Thompson Reuters, these databases were selected because they are considered the largest abstract and citation database of peer-reviewed literature, with more than 60 million records, covering over 21,500 peer-reviewed journals from over 5000 international publishers in different scientific areas (Joshi, 2016).

In the first phase, articles were selected that used the terms *Freshwater* Fish* Community** and *Food web** in the title, abstract, or keywords. As a result, an initial sample of 359 documents in Scopus and 972 documents in Web of Science was found. The topic of food webs has been aborded since the last century (Elton, 1927), however, this study aims to examine the most recent and innovative literature, a six-year timeframe was selected covering the period between 2015 and 2021, resulting in 164 documents in Scopus and 447 documents in Web of Science. The review was limited to "Article," "Review," and "Books" documents because they are the source of most up-to-date knowledge and probably have a greater impact on the field. The literature that only presented anthropology, archaeology, phytochemical, immunological data were excluded. Only articles with the language "English" were considered, since the dissemination of scientific knowledge is fundamentally done in this language and is a criterium used in various reviews (e.g., Thompson *et al.,* 2012).

3. Results

3.1 Descriptive information

A total of 117 documents in Scopus and 388 documents in Web of science were obtained. After reading the abstracts and eliminating those that do not refer to freshwater fish and food webs, the final number of articles was 358 in both databases. The study of the freshwater fish communities and food web has been maintained a constant number of publications in Web of Science, with a decline in 2021, whereas Scopus databases showed in 2015 the lowest number of publications and increased in 2021 (Figure 1). The year with the highest number of articles was 2020, with 60 articles on Web of Science.

The publications are led by the Freshwater Biology journal, followed by Freshwater Science and Ecology, most of the journals are quartile one, only Ecology of Freshwater Fish and Journal of Great Lakes research are quartile 2. The highest impact factor is in Ecological monographs (10.31), following of Ecology (5.49)

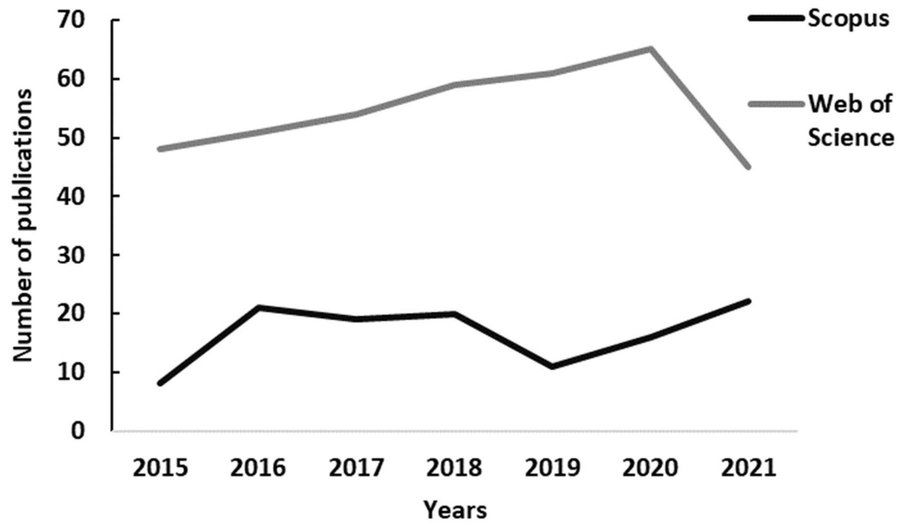

Figure 1. Total of articles published during 2015 to 2021 in Scopus databases and Web of Science.

(Figure 2). The study fields of environmental science, ecology, freshwater ecology, and fisheries have extensive studies in freshwater fish communities and food web in Scopus database and Web of Science.

In this research, the results showed that the United States is the country that published the most articles about the food web in freshwater fish communities, followed by Canada and Germany (Table 1).

The principal institutions are United States Geological Survey and United States Department of the Interior from USA (Table 2).

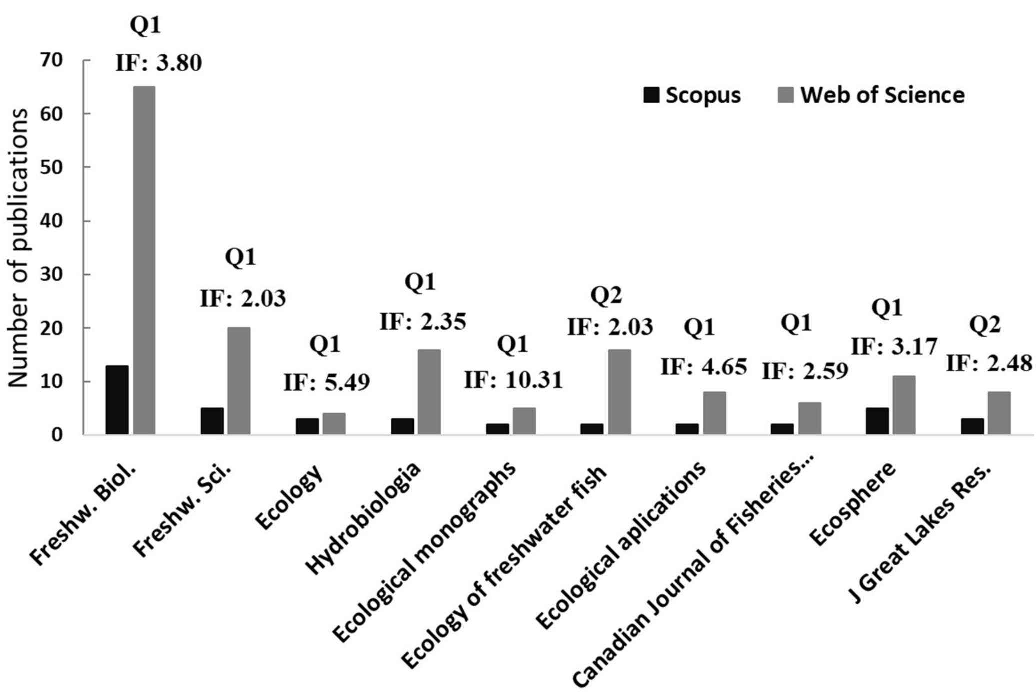

Figure 2. Main journals with their impact factor and quartils, per number of articles published in Scopus database and Web of Science. FI = impact factor, Q= Quartils.

Table 1
Main countries with a number of articles published by Scopus database and Web of Science.

Country	Number of articles in Scopus	Number of articles in Web of Science
United States	45	78
Canada	20	56
Germany	11	28
China	5	28
England	10	23
Australia	7	22
Spain	5	20
México	2	6

Table 2
Principal institutions and their origin country, and the number of publications per database (Scopus and Web of Science)

Scopus Institution and country	Number of publications	Web of Science Institution and country	Number of publications
United States Geological Survey (USA)	15	United States Department of the Interior (USA)	27
Aarhus University (Denmark)	9	United States Geological Survey (USA)	25
CNRS Centre National de la Recherche Scientifique (France)	9	CNRS Centre National de la Recherche Scientifique (France)	23
University of Washington, Seattle (USA)	8	University of California System (USA)	21
University of Wisconsin-Madison (USA)	8	CNRS Institute of Ecology Environment INEE (France)	14
The University of British Columbia (Canada)	7	Aarhus University (Denmark)	12

3.2 Theories

Not all articles handle theories to test, some of them only mention fundamental concepts within the document. Twelve percent of the articles mention the theory of b*ottom-up* and *top-down,* this is the main approach theory used to explain the study of the determinants of biomass pyramids (i.e., the patterns of the biomass of organisms at different trophic levels of an ecosystem) within and across ecosystems. This theory was first mentioned in 1986, established resource use *versus* consumer limitation (McQueen *et al.,* 1986).

The "*trophic cascade"* is a concept considered by some authors in the documents reviewed (8% of the documents), this is for understanding trophic interactions, resulting in alternating abundance, biomass, or production across more than one trophic levels in an ecosystem (e.g., Leroux and Loreau, 2015; Rodríguez-Lozano *et al.,* 2016). Trophic cascades have often been applied to explain indirect top-down effects in ecosystems. Broadly defined, trophic cascades refer to the indirect effects of an ecosystem perturbation (i.e., change in soil nutrients or predation rate) throughout an ecosystem (Carpenter *et al*., 1985).

The assembly rules are also included in some documents reviewed (5%), they have helped provide a means to generate realistic food web structures (Fath *et al.,* 2007; Fath *et al.,* 2019). They are used to describe general principles arising from mechanisms operating within the community and to which the assemble of a community conforms, for example relationship between community temporal dynamics and ecological stochasticity of an ecosystem, probably caused by anthropogenic activities (e.g., Li *et al.,* 2021).

4. Approaches in consideration in the food web

Within the revised articles, some important topics are maintained that must be considered within the evaluations of food webs, for example, the diet of the species, trophic position, habitat use, the ecosystem functions as a biological, geochemical and physical process, like the decomposition, production, nutrients cycling and nutrient energy flows between species in the community, to determines how an ecosystem responds to perturbations and thus is key to understanding the ability to respond to perturbation without loss of essential functions (Ives *et al.,* 2018).

The review of the studies indicates that fish play an important role in the trophic dynamics in freshwater ecosystems; through predation on zooplankton, planktivorous fish may promote cascading trophic effects (top-down) leading to increased phytoplankton biomass and reduced water clarity (Laske *et al.,* 2017). Hence the literature has been centered on better understanding how the structure of the fish community may change depending on biotic and abiotic factors. Spatial and temporal variation in the relative abundance of dominant and other species likely is influenced by species differences in habitat selection, reproduction, and recruitment (e.g., Grubh and Winemiller, 2018). Fish community patterns were primarily attributable to seasonal changes instead of spatial gradient and habitat types (Sather *et al.,* 2016). Various studies have suggested the importance of biotic interactions across habitats (littoral, benthic and pelagic zone).

Nowadays, one of the main focuses within the reviewed articles is the interactions of native and nonnative species, and several authors mention that invasive species are causing damage in native fauna (e.g., Pereira and Vitule, 2019). Introductions of nonnative species and their subsequent dispersal can change the structure and composition of entire communities (Gallardo *et al.,* 2016). Moreover, present nonnative species simultaneously occupy different trophic levels and interact across trophic levels, leading to increased and often unforeseeable effects due to the prevalence among predators (Martins *et al.,* 2021). The ecological consequences of nonnative freshwater fish introductions have been well documented (Cucherouset and Olden, 2011). However, most studies of the effects of nonnative fishes address solely direct effects rather than indirect interactions, such as cascading effects on other ecosystem compartments, that can alter ecosystem functioning in unpredictable ways.

The effects of nonnative fishes can cascade beyond conventionally defined habitat boundaries and have significant consequences for food web dynamics (Gallardo *et al.,* 2016). However, such effects often are overlooked because researchers typically limit the scope of their studies to one system or even a single system component. For example, in some aquatic systems, lakes and rivers are physically connected, thereby generating the potential for several modes of interaction via resource use (Gou *et al.,* 2018).

5. The design of the study, methodology

Different methodologies were used in the articles analyzed during the review process. The main methodology used was the Stable Isotope Analysis (SIA) of carbon ($\delta^{13}C$; information on food resources) and nitrogen ($\delta^{15}N$; information on trophic position). This methodology provides a powerful tool for measuring the trophic structure by describing the relative trophic positions of consumers within a community and the contributions of distinct basal resources (Svanbäck *et al.,* 2015). This technique permits various fish tissues to be analyzed, but soft tissue, generally muscle, has typically been preferred. It is easy to collect and prepare material, and it provides the means to analyze several isotopic tracers (carbon $\delta^{13}C$, nitrogen $\delta^{15}N$, oxygen $\delta^{18}O$, sulfur $\delta^{34}S$).

Furthermore, this technique has been developed to investigate the consequences of nonnative fish species introductions on trophic structures (Sagouis *et al.,* 2015). They provide a powerful approach to predict the invasion impacts of nonnative species and the degree of dietary competition pressure felt by native species (Hill *et al.,* 2015).

The gut content analysis usually complements the stable isotope methodology (e.g., Laske *et al.,* 2018). The gut content analysis consists of dissecting the fish stomach, and prey items are identified to the lowest taxonomic level possible. A prey accumulation curve must be elaborated for the fish species to determine whether the number of analyzed stomachs that accurately described the diet (Márquez-Velásquez *et al.,* 2019).

Two indices were mainly mentioned in the reviewed articles to evaluate the contribution of each prey item to the diet of the fish species, the index of relative importance (IRI) (Yáñez-Arancibia *et al.,* 1976) and prey-specific index of relative importance (PSIRI) (Brown *et al*., 2012). In addition, other two important index are the diet overlaps between taxa, which is possible to assess by the Horn´s index and trophic niche width calculated using the standardized Levin´s index (Krebs, 1989).

The use of multiple approaches allows more robust assertions about the trophic patterns and trophic interactions among species (Weidner *et al.,* 2017). Stable isotopes and gut content analyses complement each other to gain more insight into the feeding relationships of fish species and the degree of dietary resource sharing (Mwijage *et al.,* 2018). Gut content may underestimate niche widths if there is limited diet information for each individual in the population, for example, if stomach size is small or resource competition constrains the number of preys consumed per individual (Svanbäck *et al.,* 2015). The use of stable isotopes is important, especially when characterizing the diet and feeding interaction of predatory fish species that sometimes have high prey regurgitation and stomach vacuity (Hill *et al.,* 2015).

6. Aquatic components from the system

Phytoplankton and zooplankton biomass and composition were evaluated as complementary components in several documents reviewed (e.g., Kovalenko *et al.,* 2019), considered important drivers of the aquatic ecosystem function. The phytoplankton assemblage composition is essential to predict food web responses to stressors, including increased nutrient loading, changes in surface temperature, and thermocline depth (Vesterinen *et al.,* 2016). The zooplankton moderate effects of fish on phytoplankton biomass (Beaver *et al.,* 2019). Another important group in food webs are the macro-invertebrates, they are considered a good biological indicator in aquatic systems and play an important role in trophic transfer within and across ecosystems, linking energy flow from basal food sources to upper trophic levels such as fish and eventually respond to a wide range of anthropogenic impacts (Dedieu *et al.,* 2015). Phytoplankton, zooplankton, and macroinvertebrates can affect the food web by periphyton assimilation, species identity, functional feeding groups, and seasonal and spatial environmental variations, mainly due because their functional role in linking the energy flow from basal food sources to higher trophic levels (Guo *et al.,* 2018).

7. Mathematical modeling

In the selected works reviewed, the trophic structure is usually represented by models (Ecopath with Ecosim) or diagrams (food networks connecting species), but it can also be assessed by a more simplified approach based on the use of trophic guilds (Konan *et al.,* 2015).

The Ecopath and Ecosim (EwE) modeling approach was primarily developed to answer 'what if…' questions that could not be addressed with single-species assessment models (Christensen and Walters, 2004). The Ecopath model can be seen as a toolbox offering a large collection of methods to analyze various ecological phenomena, for example, it has been widely used to analyze the trophic structure and energy flow between all species occurring in the aquatic ecosystems and predict trends in their development (Deehr *et al.,* 2014). It is recognized as a core new-generation tool for studying aquatic ecosystems worldwide (Ortiz *et al.,* 2015). The EwE modeling complex consists of a suite of three main sub-models: (1) Ecopath, static and descriptive, (2) Ecosim, dynamic and predictive, and (3) Ecospace, spatially explicit, dynamic, and predictive (Christensen and Walters, 2004).

On other hand, diagrams analysis considers interaction strength may identify species whose impacts on their communities are disproportionately large relative to their abundances (Reis *et al.,* 2020). The diagrams analysis provides an effective method to understand and describe the topological structures, dynamic characteristics, and the complexity of functions between species within the food web (Jiang and Zhang, 2015). In addition, an ecological network analysis is an important tool to understand whole-system interactions in the food web, which include the energy-matter flow of who eats whom, and non-feeding pathways to detritus (Fath *et al.,* 2007; Fath *et al.,* 2019). Other modeling options have been also used in food webs are for example STELLA (Spieles and Mitsch, 2003), EcoNet (Kazanci, 2007), and statistics packages for the program R (e.g., enaR, Borrett and Lau, 2014).

8. Current limitations

Determining the disturbances' effects on the biotic communities represents a major challenge in most of the reviewed articles. To understand the effects of climate change at an ecosystem level, ecologists need to better understand their impact across the trophic structure; the disturbances occur over long-temporal scales, and it is difficult to isolate the effects of these interlinked stressors. Given changing environmental conditions and anthropogenic impacts on freshwater communities, understanding the adaptive capacity of food webs supporting important resources, such as commercial fisheries are vital to ecological and economic stability.

Although the effects of environmental variability on the trophic structure of fish assemblages have been investigated, most works are based on short-term sampling focusing mainly on local factors (e.g., temperature, turbidity, and salinity) (Nelson *et al.,* 2015). However, many ecological processes and environmental phenomena occur on a long-term time scale or are cyclical processes, requiring several years or even decades of continuous monitoring and investigation to understand their influences on the biota.

9. Future directions

The study of food webs in freshwater fish communities has grown in recent years in developed countries, based in the increase of the number of publications (Figure 1). However, we consider that certain questions can help us expand our knowledge about the relationship between food webs, freshwater communities' structure, and ecosystems' functioning. Further research is needed on what traits best describe food webs in a freshwater system. In this sense, there are important advances in the homogenization of criteria in the main use methodologies as stable isotopes analysis inconjunct with stomach content and mathematical models. However, it could be interesting to incorporate the molecular-based approaches, which have made DNA techniques more available to ecologists for reconstructing consumers' diets, identifying species interactions, showing how food webs are structured. By amplifying genes and comparing sequences to existing DNA libraries of known species. Few studies have examined food web involving interacting species across several trophic levels, establish their interactions are critical to restoring function to degraded freshwater ecosystems. It is important to consider the evaluation of food webs in tropical and subtropical lakes and hots spots with endemic species. The articles reviewed in this study focused mainly on big lakes and rivers in template areas, less instream, ponds and in tropical and subtropical areas.

10. Conclusions

This research is focus on food webs on freshwater fish communities, this issue being more examined in developed countries in the last years. There is a concern about the methodologies that could be used to evaluate a project, targeted not only in international researchers but also to grad students in higher education institutes.

Considering its deeper multidisciplinary nature, the articles included in this systematic literature review were published in a great diversity of journals, analyzing various themes such as ecology, environmental sciences, fisheries, and water resources.

The studies on significant aspects such as the changes in abundance, species richness, size distribution, life history of the species, feeding habits (diet), space use, and trophic dynamics will improve the understanding of the changes in food webs in freshwater fish community structure and dynamics, and the potential cascading effects (bottom-up and top-down). Evaluating periphyton, phytoplankton, and zooplankton is vital to understand the roles and the limitations of the species, finding their position in the trophic cascade (filter-feeding herbivorous fish, predator control, omnivorous fish). Stable isotope analyses of carbon and nitrogen together with gut content analysis provide a powerful approach to predicting the invasion impacts of nonnative species and the degree of dietary competition pressure felt by native species. Thereby enhancing the chances of preserving the freshwater ecosystems with high diversity.

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