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# IsoFresh: A global stable isotope database of freshwater food webs

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**Abstract** – Ecologists seek to understand the ways that human activities are altering the structures and processes that support biodiversity and nature's contributions to people. Food web research at the interface of community and ecosystem ecology is promising in this regard. An industry of studies has utilized stable isotopes in recent decades to rapidly characterize energy and material transfer among organisms in freshwater food webs. Nevertheless, these efforts have been somewhat siloed and mainly locally-based, and lack of a centralized database has limited efforts to tackle questions about food web change using isotopes at a global scale. Here we present IsoFresh, a freshwater food web database that contains species-level carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) stable isotope values for 15343 organisms, representing 1001 food webs and including > 1600 fish species and associated potential prey, from 65 countries around the globe. Our hope is that IsoFresh is used to explore fundamental and applied food web questions, contributing new knowledge about global environmental change so that human societies can better conserve and manage freshwater ecosystems along desirable future trajectories.

**Key-words:** Stable isotope analyses / food web architecture / trophic interaction / trophic niche / fish / macroinvertebrates / human perturbations / freshwater ecosystems

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## **1** Introduction

Globalisation has led to conspicuous changes in biological diversity with profound impacts on ecosystem structure and function (Cardinale et al., 2012; Naeem et al., 2012). Yet, elucidating links between the structure of biodiversity and ecosystem functioning remains a fundamental challenge that is driven, in part, by the large disconnection between community and ecosystem ecology (Loreau, 2010). On the one hand, community ecologists often use macroecological approaches to describe global patterns of biodiversity, and grapple with the difficulty of translating how community changes may affect ecosystem processes. On the other, ecosystem ecologists investigate the interplay between ecosystem functions and a host of determinants (e.g. temperature, nutrient availability), yet persistently struggle to understanding how species contribute to ecosystem function and respond to changes. What progress has been made on establishing a connection between the structure of biodiversity and ecosystem functioning is largely limited to experimental settings or small-scale studies, predominantly in terrestrial ecosystems. New global initiatives are needed to better understand how ecosystem processes respond to changing biodiversity across broad scales, and how species and environments modulate these responses (Loreau, 2010; Burley et al., 2016; Gonzalez et al., 2020). Because they describe energy flow among species, food web approaches offer an opportunity to reconcile community and ecosystem ecology (Thompson et al., 2012). This is only possible due to a paradigm shift in the way in which food webs are studied. Traditional food web data, obtained using dietary observations (e.g. stomach contents) to document trophic interactions are problematic to assemble and interpret at global scales for a number of reasons including methodological variability. In addition, attaining time-integrated food webs at the whole- community level requires significant resources, limiting the ability to rapidly assemble many comparable food webs (Polis, 1991; Nielsen et al., 2018). Stable isotope analyses, because they reflect the consequences of energy flow, provide an integrative approach to reflect the net transfer of energy of resources to consumers and to characterize the trophic niche of diverse taxa (e.g. zooplankton, benthic invertebrates and fish) and food web structure (isotopic food webs). Stable isotopes of carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) are principally used by ecologists to quantify the nature and origin of resources consumed and the trophic position of consumers, respectively (Fry, 2006). There is a well established history of trophic investigations using stable isotope analyses in freshwater ecosystems. For instance, stable isotope analyses can reveal the role of predatory fish in coupling pelagic and littoral food chains in a simplified food web lake (Vander Zanden et al., 1999) or quantify the ecological consequences of global change such as biological invasions, habitat fragmentation, and pollution (e.g. Alp and Cucherousset, 2022). Stable isotope approaches provide accurate tools for comparing a first compilation food webs and population diets between ecosystems, notably by incorporating methods such as baseline corrections of the stable isotope values of consumers (Post, 2002; Quezada-Romegialli et al., 2018).

The development of rigorous stable isotope analyses in freshwater ecology provides a powerful, yet still underused, data archive to address questions at the intersection of community and ecosystem ecology, with a focus on global change, biodiversity loss, and food web architecture. However, despite the increased use of stable isotope analyses and the existence of a global stable isotope repository (IsoBank, Pauli et al., 2017), large-scale investigations of global ecological responses of food webs based on stable isotope analyses are still rare. In one of the first global investigations in aquatic ecosystems, food chain length patterns were investigated in freshwater and marine ecosystems across the globe (Vander Zanden and Fetzer, 2007). More recently, a compilation of stable isotope values of freshwater fish has been used to investigate several global-scale questions related to: (i) the influence of biological invasions on the stable isotope structure of freshwater fish communities in lentic and lotic ecosystems (Sagouis et al., 2015); (ii) resource partitioning and niche conservatism of non-native freshwater fish (Comte et al., 2016, 2017); (iii) the link between different facets of biological diversity in fish communities (Pool et al., 2016); and (iv) habitat coupling-trait relationships in lakes (Stiling et al., 2023). Altogether, these studies have revealed the importance, added-value and potential of large-scale stable isotope databases for evaluating of freshwater ecosystems to global change.

We present the IsoFresh database, a global stable isotope database of freshwater fish that also includes other organisms (non-fish) present in the food webs, compiles the species-level  $\delta^{15}$ N and  $\delta^{13}$ C values of 1001 freshwater food webs from the published materials in 65 countries from 1992 and 2023. Our motivation for compiling this database is to identify and understand the fundamental structure and processes of the earth's freshwater food webs and to assess the ways that these structures and processes are being altered by human-driven global change.

## 2 Methods

#### 2.1 Data extraction

The IsoFresh database was initiated in 2011 and was updated regularly until end-2023, with the more recent updates to improve the geographical coverage of the database. IsoFresh is a global stable isotope database of freshwater fish in which we included all other organisms analysed for stable isotopes and used to interpret food webs. We first used online search engines to collect stable isotope values ( $\delta^{15}N$  and  $\delta^{13}C$ ) in journal articles, academic theses and reports. Specifically, we first searched Clarivate Analytics' Web of Science online database using the following search terms: "TS=(isotope\* AND fish\* AND carbon AND nitrogen), (community\* OR communities\* OR assemblage\*) and (freshwater\* OR lake\* OR reservoir\* OR river\* OR stream\*)". We also searched Google Scholar with similar terms. Then, we followed a more supplementary approach by searching for references cited in the selected publications and for literature published by the same group of scientists.

We applied a set of criteria to select a subset of studies for inclusion in the database from among all the publications identified by the initial search. Our first criterion of inclusion focused on identifying that the studies were conducted in freshwater ecosystems *sensus stricto* while excluding studies performed in estuarine, brackish and marine environments. Secondly, we included only the studies in which  $\delta^{15}$ N and  $\delta^{13}$ C values were simultaneously investigated. Thirdly, only studies





Fig. 1. Distribution of the publication year of the food webs (n=1001) included in the IsoFresh database.

including both stable isotope values for each species were included. Here each species must, at least, include an average  $\delta^{15}$ N and  $\delta^{13}$ C value irrespective of the number of individuals analysed per species. Fourth, we only included studies with comprehensively studied fish communities. To conclude comprehensiveness, we required that a statement was provided in the methods indicating that species known to be present in the local fish community were represented in the sample, or a comprehensive freshwater fish sampling protocol was presented indicating an effort to assay the whole fish community. It is therefore very likely that rare species were underrepresented in these studies. Studies assessing the trophic niche of only a subset of species within a given community were excluded. Finally, the presence of organisms other than fish was not used as a criterion for inclusion in the IsoFresh database but, when available, the stable isotope values of these organisms (i.e. baselines, potential prey) were included.

For each food web, information about site name, the type of freshwater ecosystem, the country, continent and the geographic coordinates (latitude and longitude) were extracted. The database could include distinct food webs for multiple sites sampled within the same drainage or for the same site sampled at different seasons or years. In cases when the geographical information was missing in a literature source, we digitalised the coordinates based on maps provided in the source and/or used online maps to localize the study site. For each food web, we extracted the mean  $\delta^{15}$ N and mean  $\delta^{13}$ C values of each fish species from tables, supplemental appendices or figures using WebPlotDigitizer (https://autome ris.io). In addition, we collected the variability associated with mean  $\delta^{15}$ N and mean  $\delta^{13}$ C values (e.g. standard error, standard deviations), the number of individuals and the type of tissue (e.g. muscle, fin) analysed for stable isotope analyses. When  $\delta^{15}\!N$  and  $\delta^{13}C$  values were reported at the individual level or

were provided for different age classes or subspecies, they were averaged to obtain a single value per species. Further fish taxonomy (species, orders and families) was obtained using rfishbase (Boettiger *et al.*, 2012) or manually retrieved and confirmed if not available in FishBase. When available (77.1% of all food webs), we also extracted the stable isotope values (mean, associated variability and number of samples analysed for  $\delta^{15}$ N and  $\delta^{13}$ C values) of other taxa, including non-aquatic organisms that were collected to represent baselines and potential prey. These include primary producers such as macrophytes, phytoplankton, and detritus and consumers such as zooplankton and macroinvertebrates. We followed the same approach regarding the extraction of stable isotope data for these other organisms.

#### 2.2 Database formatting

The database is organized in a folder containing multiple files. The first file is a README file (IsoFresh read.me.txt) that describes the content of each column in each subsequent file. Each food web has a unique identifier (Food Web\_ID) which is the first column of each spreadsheet and links the different information contained in each spreadsheet. The second file "IsoFresh FoodWeb.csv" contains information about the food webs and includes a DOI link or URL access to the original source, the author's name, the publication title and year and the source type. The third file "IsoFresh Ecosystem. csv" contains information about the location where the food web was sampled and includes the site name reported in the original source, the type of freshwater ecosystem (lentic or lotic), the country (and associated ISO code), the world region, and the longitudinal and latitudinal coordinates. The fourth file "IsoFresh Isotope Fish.csv" contains information about the

Region	Food webs n	δ <sup>13</sup> C (‰)				δ <sup>15</sup> N (‰)			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Africa	74	-21.7	1.8	-24.7	-18.5	10.1	1.3	8.1	12.0
Asia	108	-25.3	1.8	-27.8	-22.9	11.2	1.4	9.3	13.1
Europe	219	-26.5	1.6	-28.5	-24.6	11.0	1.2	9.5	12.4
North America	291	-25.1	1.5	-27.2	-23.1	10.4	1.3	8.7	12.1
Oceania	178	-25.6	1.8	-28.0	-23.3	9.4	1.0	8.1	10.7
South America	131	-26.6	2.1	-30.1	-23.4	9.9	1.4	7.7	12.1

**Table 1.** Descriptive statistics of the food webs (total number) and the  $\delta^{13}$ C and  $\delta^{15}$ N values (mean, standard deviation, minimum and maximum) of freshwater fish contained in IsoFresh database for each geographical region.

fish species included in the database, including the common and scientific name of the species, its taxonomy (order, family and genus), the  $\delta^{15}$ N and  $\delta^{13}$ C values of each fish (mean, associated variability and number of individuals analysed) and the tissue used for stable isotope analyses (e.g fin, liver, muscle). The fifth file "IsoFresh\_Isotope\_Other.csv" contains information about the other organisms (common and scientific names of non-fish organisms, exactly as reported in the original source) for which  $\delta^{15}$ N and  $\delta^{13}$ C values (mean, associated variability and number of samples analysed) were available. These files, which constitute the IsoFresh database (Boulêtreau *et al.*, 2025) are available on a Zenodo repository (https://doi.org/10.5281/zenodo.14982323).

## 3 Content of the database

In total, the stable isotope data were collected from 296 studies (82.6% peer-reviewed, 8.7% academic theses, 8.7% other sources such as reports/books) Justification: Reformatted for clarity and consistency such as reports and books) published between 1992 and 2023 (Fig. 1). The IsoFresh database contains  $\delta^{15}$ N and  $\delta^{13}$ C stable isotope values in 1001 food webs located in 65 countries worldwide with a total of 15343 stable isotope values of freshwater organisms (Fig. 1). The database contains food webs in all continents except Antarctica, with a high proportion of sites located in North America (29.1%, n=291) and Europe (21.9%, n=219, Tab. 1), which is a common geographical bias previously observed with stable isotope studies in freshwater ecosystems (Cucherousset et al., 2012). The database contains 178 food webs in Oceania, 131 in South-America, 108 in Asia and 74 in Africa (Tab. 1). Food webs were located in different types of freshwater ecosystems and relatively well balanced between lotic (n = 522, mainly rivers and streams) and lentic (n = 476, mainly lakes and reservoirs) ecosystems. In addition, 3 food webs were classified as Other because sampling was performed in both lentic and lotic habitats. Thus, the IsoFresh database provides a comprehensive global database of specieslevel stable isotope data of freshwater ecosystems across the globe.

Stable isotope values were collated for a total of 1607 fish species. The most common fish species in the database were the European perch *Perca fluviatilis* (150 food webs), the brown trout *Salmo trutta* (140 food webs), the common carp *Cyprinus carpio* (123 food webs), the northern pike *Esox* 

lucius (122 food webs) and the roach Rutilus rutilus (116 food webs). The number of fish species occurring in each food web varied between geographical regions, with the lowest richness in communities in Europe (mean  $\pm$  SD; 5.4  $\pm$  2.9, maximum = 20 species) and Oceania ( $6.7 \pm 4.9$ , maximum = 24 species) and the highest richness in the communities in Africa  $(11.9 \pm 13.2, \text{ maximum} = a \text{ maximum of } 72 \text{ species})$  and South-America  $(12.5 \pm 8.7, \text{maximum} = 64 \text{ species})$  (Fig. 2 and Tab. 1). These geographic differences likely reflect natural biogeographical patterns observed in freshwater fish biodiversity (Tedesco et al., 2017). The fish species belonged to 182 families and there was a total of 609 fish species in South America (79 families, dominated by Cichlidae and Characidae), 360 in Africa (46 families dominated by Cichlidae and Cyprinidae), 318 in Asia (82 families dominated by Xenocyprididae and Cyprinidae), 248 in North America (43 families dominated by Salmonidae, Leuciscidae and Centrarchidae), 140 in Oceania (50 families dominated by Eleotridae and Terapontidae) and 77 in Europe (25 families dominated by Leuciscidae and Salmonidae). A vast majority of stable isotope analyses were performed on fish muscle (86.0 %) and 12.9% on fins and stable isotope values within each site were variable both within and between geographical regions (Tab. 1). In addition, the IsoFresh database contains 7307  $\delta^{13}$ C and  $\delta^{15}$ N values of non-fish organisms that usually consist of potential prey and baseline organisms of the studied food webs (e.g. primary producers and primary and secondary consumers). On average, each food web has the stable isotope values for 9.5 ( $\pm$ 7.5) non-fish organisms.

### 4 Conclusion and perspectives

The IsoFresh database constitutes the first comprehensive database of species-level carbon and nitrogen stable isotope values of freshwater fish and the associated baselines and putative prey present in food webs across the globe. The IsoFresh database provides a valuable opportunity to bridge the gap between community and ecosystem ecology. The global nature of the data can support broad-scale predictions related to the consequences of environmental change and predicting future trajectories of community dynamics in freshwater ecosystems. Global change is rewiring food webs across the globe (Bartley *et al.*, 2019), and by providing the means to characterize freshwater food webs, the IsoFresh database will enables a broader understanding of how natural

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Fig. 2. Locations of food webs included in the IsoFresh database (n = 1001), with the colour gradient of points representing the number of fish species in each food web.

and human-induced environmental drivers are involved in that rewiring. This is an critical knowledge gap because, in addition to limiting fundamental insights into ecological theory, it hampers our understanding of how changes in biodiversity induced by environmental changes modulate ecosystem functioning.

In addition, a longstanding challenge in ecology is to identify integrative and robust metrics that summarize complex biological interactions while concurrently providing inferences regarding ecosystem health. To date, most bioindicators are based on taxonomic composition of communities and provide only limited information about the processes shaping community structure and ecosystem functioning. In stable isotope ecology, several metrics have been developed to describe the spread of species in the stable isotope space, including the size of the community trophic niche (convex hull area or standard ellipse area), the range of nitrogen and carbon values and trophic evenness, and shifts in isotope signatures over time (Layman et al., 2007; Schmidt et al., 2007; Jackson et al., 2011; Cucherousset and Villéger, 2015). Raw stable isotope values of all organisms in the food webs can also be used in Bayesian mixing models to estimate the relative contribution of prey to the diet of consumers (Semmens et al., 2009; Stock et al., 2018). We are confident that stable isotope based-metrics have the potential to serve as more sensitive indicators of ecosystem change than indicators based on taxonomic data (Jackson et al., 2016) and the IsoFresh database can support such investigations.

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#### Data availability statement

The IsoFresh database is available at Zenodo (https://doi.org/ 10.5281/zenodo.14982323). We kindly request that users to cite this article when using data from the IsoFresh database. While the database is based on materials published until 2023, we encourage potential contributors to contact Stéphanie Boulêtreau and Julien Cucherousset to support future updates and extensions.

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