Functional diversity: a review on freshwater fish research

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Functional diversity is an emergent approach in ecology that has been applied globally to better understand the relationships between organisms and the environment. However, assessing the functional diversity of freshwater fish is a challenge for scientists. Aiming to summarize the evolution of scientific knowledge on fish functional diversity, we performed a systematic review of the literature published from 1945 to 2021 using the Web of Science. Based on the 101 articles reviewed, we found that publications about functional diversity of fishes have increased over time, mainly in Neotropical, Indomalayan and Palearctic regions. Most studies were conducted in lotic ecosystems, especially to assess environmental impacts such as biological invasions and land use. Functional diversity has been assessed mainly by morphological traits that reflect feeding and locomotion dimensions. Functional richness was the most common index used in the studies. Our findings suggest that political neglect and lack of investments may hamper the research development in several places. The missing information about the functional traits of many species may limit the use of the functional approach. We also highlight the need for the incorporation of functional diversity in conservation programs once functional diversity is a key facet of biodiversity to maintain freshwater ecosystem functioning.

Keywords: Aquatic ecosystems, Biogeographic realms, Functional ecology, Functional traits, Systematic review.

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A diversidade funcional é uma abordagem emergente na ecologia que tem sido aplicada globalmente para melhor compreender as relações entre os organismos e o ambiente. No entanto, avaliar a diversidade funcional de peixes de água doce é um desafio para os cientistas. Com o objetivo de sumarizar a evolução do conhecimento científico sobre a diversidade functional de peixes de água doce, foi realizada uma revisão sistemática da literature publicada entre 1945 e 2021, utilizando a base de dados Web of Science. Baseado em 101 artigos revisados, houve um aumento no número de publicações sobre diversidade funcional de peixes ao longo do tempo, principalmente nas regiões Neotropical, Indomalaia e Paleártica. A maioria dos estudos foram conduzidos em ambientes lóticos, especialmente para avaliar impactos como a invasão biológica e uso da terra. A diversidade funcional tem sido avaliada principalmente através de traços funcionais morfológicos que refletem as dimensões da alimentação e locomoção. A Riqueza Funcional foi a métrica mais comumente usada nos estudos. Esses resultados sugerem que a negligência política e a falta de investimentos podem dificultar o desenvolvimento de pesquisas em diversas regiões. A falta de informações sobre os traços funcionais de muitas espécies limita o uso da abordagem funcional. Destaca-se também a necessidade de incorporar a diversidade funcional em programas de conservação, uma vez que a diversidade funcional é uma faceta chave da biodiversidade para manter o funcionamento dos ecossistemas de água doce.

Palavras-chave: Ecossistemas aquáticos, Ecologia funcional, Regiões biogeográficas, Revisão sistemática, Traços funcionais.

INTRODUCTION

Functional diversity is a key facet of biodiversity that can be defined as the diversity of functions performed by organisms within ecosystems (Petchey, Gaston, 2006). There is an increasing recognition that functional diversity, rather than species diversity, is a better approach to enhancing our understanding of ecological patterns and processes operating in nature (Gross *et al*., 2017). While species diversity studies consider only the taxonomic component (*i.e*., the number of individuals from different species), functional diversity studies are based on the variability of species' functional traits (Mason *et al*., 2005; Cadotte *et al*., 2011). Functional traits are components of an organism's phenotype that influence ecosystem-level processes. Traits can be morphological, physiological, reproductive, or behavioral aspects of an organism directly related to an ecological function (Violle *et al*., 2007). Thereby, functional traits reveal ecological differentiation between species (*i.e*., ecological roles of species) instead of their taxonomic identity only. The functional diversity approach helps to explore temporal changes in the functional structure of communities (Cheng *et al*., 2014; Fitzgerald *et al*., 2017; Oliveira *et al*., 2018), elucidate responses to environmental impacts (Dala-Corte *et al*., 2016; Macnaughton *et al*., 2016; Teresa, Casatti, 2017; Dias *et al*., 2020), predict local extirpations and extinctions (Angermeier, 1995; Parent, Schriml, 1995; Olden *et al*., 2008), and estimate ecosystem functioning (Mouillot *et al*., 2011, Moore *et al*., 2017;

Moi *et al*., 2021). Hence, it is a valuable tool for improving theoretical knowledge and supporting management plans for conservation.

Since the functional approach has become an important tool in functional ecology research, many indices have been developed to estimate functional diversity. There is extensive published literature that reviews the properties and applicability of each one (Petchey, Gaston, 2006; Cianciaruso *et al*., 2009; Maire *et al*., 2015; Calaça, Grelle, 2016; Teresa *et al*., 2021). These indices can be based on functional groups, distance matrices, functional dendrograms, and multidimensional functional spaces. However, although the concept of functional diversity is relatively simple to grasp, a plethora of different indices (Mouchet *et al*., 2010; Gómez-Ortiz, Moreno, 2017; Palacio *et al*., 2021) and potencial functional traits for measuring (Winemiller *et al*., 2015; Villéger *et al*., 2017; Junker *et al*., 2022) makes it difficult for researchers to decide the best approach. Then, this would generate a lot of between-study variation in terms of what is being calculated as functional diversity and how, which would make things less comparable to each other.

Facing the increasing degradation of freshwaters worldwide (Reid *et al*., 2019), it is necessary to identify and protect species and their functions in the ecosystems. Freshwater ecosystems are home to an extraordinay biodiversity and also they provide essential services for human population. Because the massive alterations of the aquatic ecosystems the biodiversity has dramatically declined and a lot of fish species are facing with extinction (Tickner, 2020). In addition, there is a lack of knowledge about species' traits and their ecological function (Hortal *et al*., 2015), which can hinder the selection of conservation priority areas. Thus, it is urgent to understand what we already know and what we can improve in order to assess the functional diversity of freshwater fish.

This concern prompted us to ask a central question: How, where, and why has functional diversity in freshwater fish assemblages been assessed over time? We answered this question by performing a systematic review to identify global trends in studies on the functional diversity of freshwater fish. Specifically, our study focuses on a) exploring how functional diversity has been applied to different biogeographic realms and environments, b) identifying the general background (*i.e*., the central objective of the study) and the main interest by researchers over time, c) verifying which functional traits and indices have been used to assess functional diversity. To contribute to a theoretical framework on the functional diversity of freshwater fish, we discuss the main gaps found in this study and describe the key perspectives to guide future research. We anticipate that this synthesis will contribute to improving the assessment of functional diversity in freshwater fish assemblages given the relevance of this topic for understanding ecosystem functioning and the current expansion of human effects on aquatic ecosystems.

MATERIAL AND METHODS

In August 2022, we conducted a literature search using the indexed database – the Web of Science (Clarivate Analytics), selecting articles from 1945 up to 2021. This database was used because of the quality of scientific journals encompassing a wide range of publications. For the survey, we used the following Boolean combination of relevant keywords in the "Topic" field: TS = ((fish*) AND (freshwater* OR river* OR stream*

OR reservoir* OR aquatic* OR lake* OR lagoon* OR floodplain*) AND ("function* diversit*" OR "function* trait*" OR "environmental trait*" OR "function* richness*" OR "ecological trait*")). As a result, an initial pool of 1123 articles was retrieved. We screened the titles and abstracts following PRISMA guildelines (Moher *et al.*, 2009) to identify whether articles met the criteria for inclusion in this systematic review. To be included in our review, an article must have: i) been a peer reviewed, original research article (no conference abstracts or reviews), and ii) addressed functional diversity of freshwater fish. We excluded Non-English languages studies and articles non related with fish.

We extracted the following information from each article: a) Year of publication; b) Biogeographic realm in which the research was carried out; c) Freshwater environment type; d) General background, *i.e.*, the main objectives of the study; e) Functional traits; f) Functional category; and g) Functional diversity index (Tab. 1). The temporal trend of the number of published articles was investigated using an exponential regression. Since most studies present several objectives, the classification of "general background" reflects the central objective covered by the study and not a specific objective. For example, the studies that addressed the effects of land use on taxonomic and functional structure were classified into "land use" category. Functional traits and functional category were expressed by the total number of traits found in all documents. The total number of articles were used to express the biogeographic realm, freshwater environment type and functional diversity index. Traits occurrence represents the number of times a trait was used in all the articles. Traits with similar nomenclature and meaning were considered only once.

TABLE 1 | Extracted data from the articles, description of the classification and application for each topic analyzed.

Extracted data	Classification	Application
a) Year of publication	1945–2021	Used to determine the temporal trend of publications.
b) Biogeographic realm	Palearctic, Nearctic, Neotropical, Indomalayan, Australian, Afrotropical, and Global (when the study assessed more than one region).	Used to identify the distribution of research effort among biogeographic realms.
c) Freshwater environment	River, Stream, Lake, Reservoir, Floodplain, and several (when the study assessed more than one environment).	Used to verify the type of freshwater ecosystem most assessed.
d) General background	1) Biological invasion; 2) Climate change; 3) Conservation; 4) Environmental factors; 5) Environmental filtering; 6) Flood pulse; 7) Functional structure; 8) Habitat heterogeneity; 9) Impoundments; 10) Land use; 11) Lateral connectivity; 12) Methodological; 13) Multiple stressors; 14) Taxonomic and functional patterns	Classification based on the main objectives of the studies.
e) Functional trait	Ecological traits; morphological traits	Classification based on the type of trait measure. Used to identify the traits most applied to assess functional diversity.
f) Functional category	Feeding; Habitat use; Life History; Locomotion; and Physiology (Classified according to Villéger *et al.*, 2017).	Identify which functional category with the greatest number of traits evaluated.
g) Functional diversity index	All indices found in the reviewed studies.	Used to identify the main index applied to quantify the functional diversity of fish.

RESULTS

We reviewed the full text of 101 articles (Tab. **S1**). There was an increase in the number of published articles over the years ($R^2 = 0.91$; $p < 0.001$), mainly after 2013 (Fig. 1). The Neotropical region concentrated the highest number of studies (46 articles), while the Afrotropical region the lowest (1 article) (Fig. 2A). The freshwater ecosystems most assessed in the studies include streams (n = 40 studies) and rivers (n = 28 studies). Reservoirs were the least evaluated environment (n = 4 studies) (Fig. 2B).

We recorded 14 general backgrounds linked to the functional diversity of fish. Among these, *biological invasion*, *land use*, and *environmental filtering* covered 50% of the studies reviewed (Fig. **S2**). There was an increase in published articles addressing *land use* and *biological invasion* after 2015 (Fig. 3A). *Biological invasion* was the most recorded approach in the Indomalayan region, while *land use* was addressed mainly in the Neotropical region (Fig. 3B). The other topics showed relatively homogeneous distributions with few studies in each biogeographic realm (Fig. 3B).

Morphological traits were the most applied type of traits (n = 167), while ecological traits were the least used (73 traits) (Fig. 4A; Tab. **S3**). Feeding and locomotion were the most common categories of traits (Fig. 4B; Tab. **S3**).

We identified the use of 16 functional diversity indices in the studies reviewed. The most applied indices were Functional Richness (63% of studies), Functional Evenness (45% of studies), Functional Divergence (33% of studies), and Functional Dispersion (33% of studies) (Tab. 2).

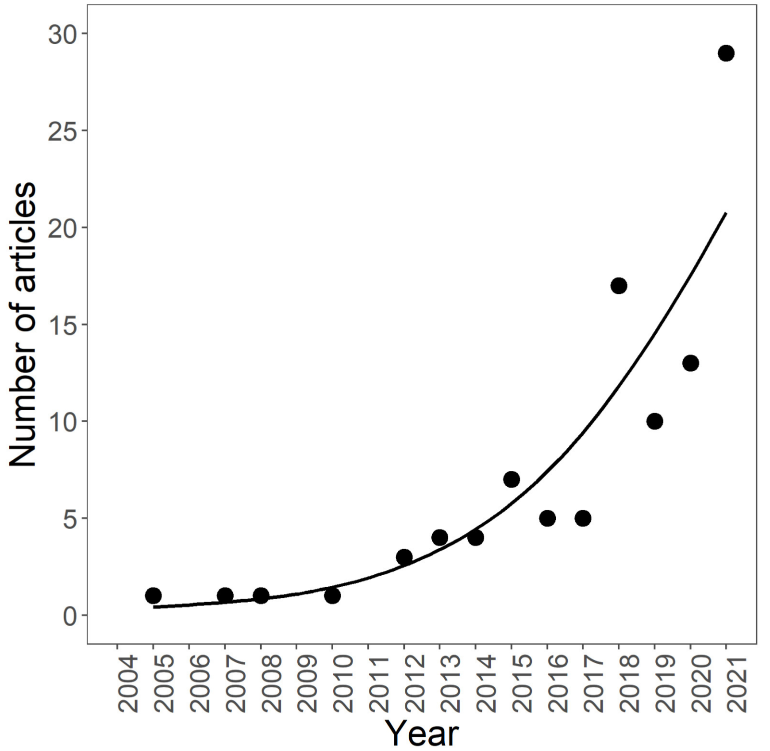

FIGURE 1 | Temporal trend of the number of published articles on the functional diversity of fish in freshwater ecosystems.

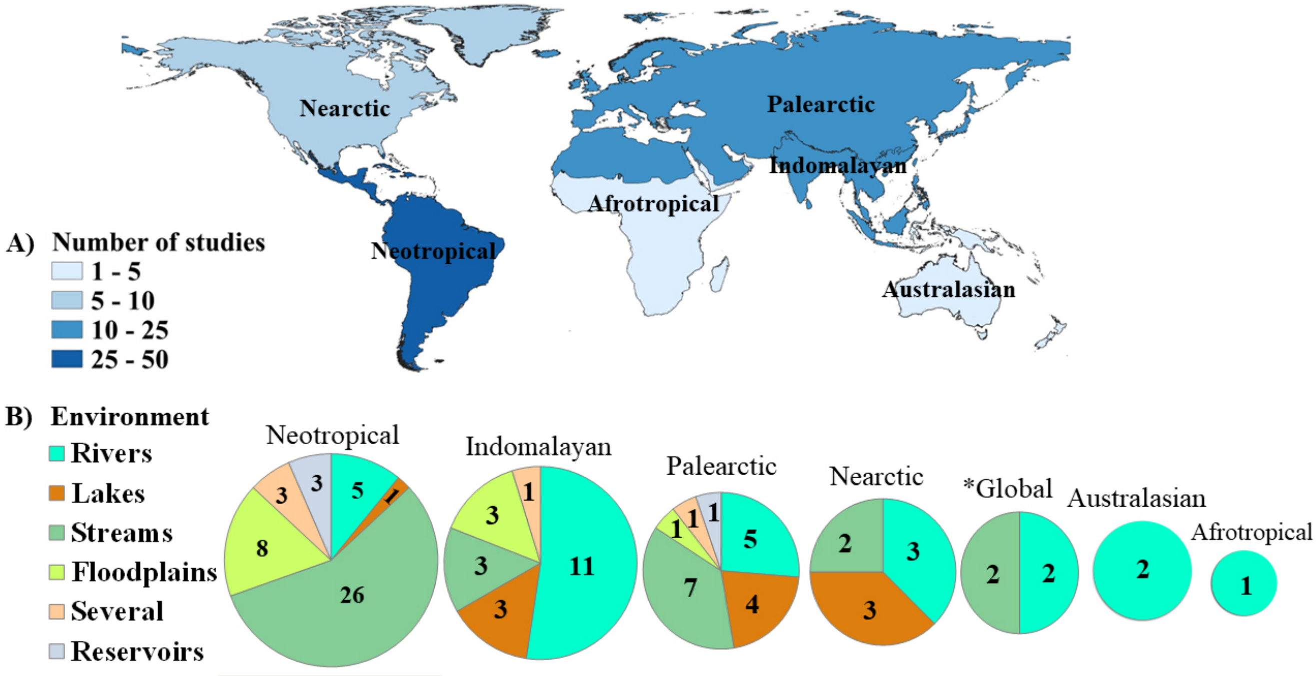

FIGURE 2 | **A.** World map showing the distribution of research effort among biogeographic realms; **B.** Pie charts represent the number of studies in each type of aquatic environment per realm. *Global: studies that evaluated more than one biogeographic realm.

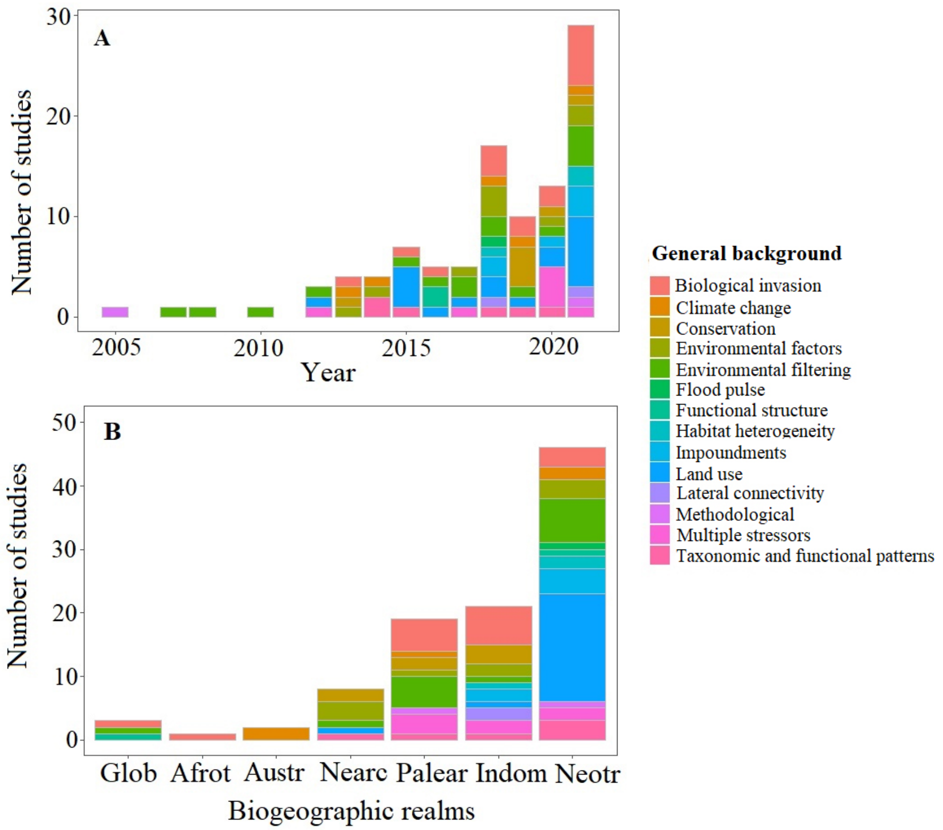

FIGURE 3 | **A.** Distribution of the general backgrounds in studies on the functional diversity of freshwater fish over time; **B.** Distribution of the central objectives in studies in each biogeographic realm.

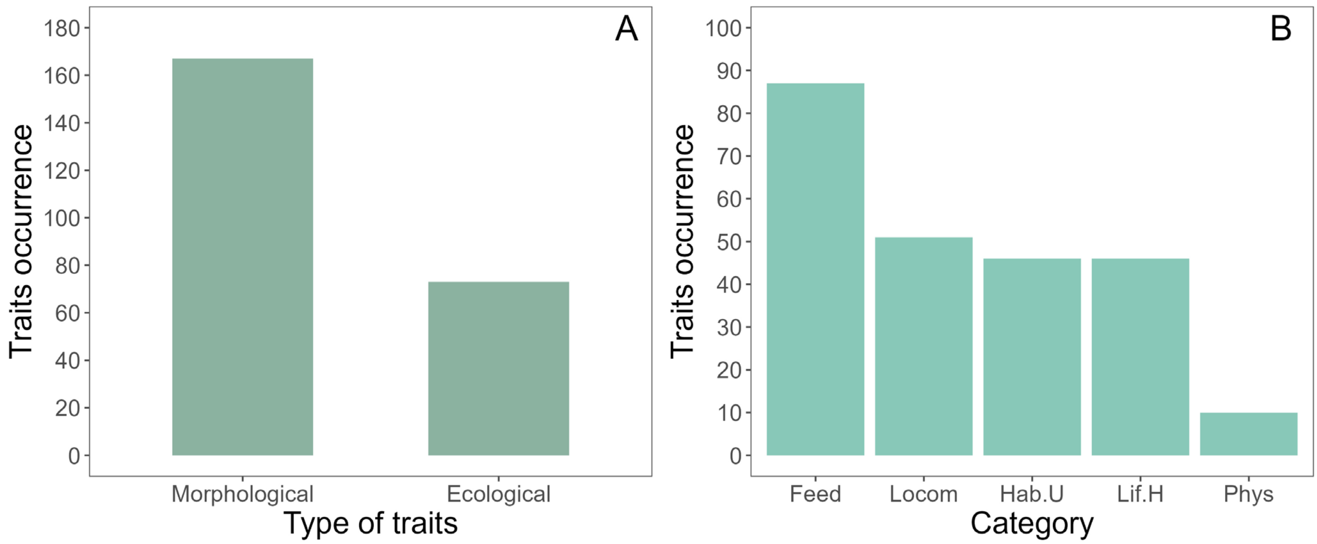

FIGURE 4 | **A.** Total number functional traits types found in our review; **B.** Total number of functional traits in each category. (Feed = Feeding, Locom = Locomotion, Hab.U = Habitat use, Lif.H = Life history, Phys = Phsysiology) (see Tab. **S3**).

TABLE 2 | List of functional diversity indices in the reviewed studies, number of studies that used the index and a brief description of each index. *The number of studies does not correspond to the total number of studies reviewed, but the number of studies that used functional indices to measure the functional diversity.

Functional diversity index	Number of studies*	Description	References
Functional Richness (FRic)	64	Volume of the functional space occupied by the community	Mason *et al.* (2005), Villéger *et al.* (2008)
Functional Evenness (FEve)	46	Sum of the minimum spanning tree branch length weighted by relative abundance of the two species	Mason *et al.* (2005), Villéger *et al.* (2008)
Functional Divergence (FDiv)	34	Species deviance from the mean distance to the center of gravity weighted by relative abundance	Mason *et al.* (2005), Villéger *et al.* (2008)
Functional Dispersion (FDis)	34	Mean distance in functional space of individual species to the centroid of all species	Laliberté, Legendre (2010)
Rao (Q)	19	Sum of species distance weighed by abundance	Botta-Dukát (2005), Ricotta, Moretti (2011)
Functional Originality (FOri)	10	Mean distance between each species and its nearest neighbour in the functional space	Mouillot *et al.* (2013)
Functional Specialization (FSpe)	8	Mean Euclidean distance between each species and the average position of all species in the functional space	Mouillot *et al.* (2013)
Functional Redundancy (FRed)	8	Difference between species diversity (Gini-Simpson diversity index) and Rao; average number of species or as mean abundance or biomass per functional group	de Bello *et al.* (2007), Laliberté *et al.* (2010)
Functional Diversity (FD)	3	Sum of the largest branch of the functional dendrogram	Petchey, Gaston (2002)
Functional Uniqueness (FUni)	3	Ratio between Rao index and the Simpson diversity index, relating functional diversity to the maximum dissimilarity value of the community	Ricotta *et al.* 2016
Functional Identity	2	Expressed as the biomass-weighted mean trait value for a community	Mouillot *et al.* (2011)
Functional Vulnerability	2	Sum of the total number of functional entities and the number of species in functional entity	Mouillot *et al.* (2014)
Mean Pairwise Distance (MPD)	2	The average of the distances between pairs of species in the focal community	Webb (2000)
Mean Nearest Taxon Distance (MNTD)	1	The average of distances between the species of focal community with the respective functionally most similar species (“neighbor closer”)	Webb (2000)
Functional Regularity Index (FRO)	1	Species evenness in functional space weighted by species abundances	Mouillot *et al.* (2005)
Functional Distinctiveness	1	Functional dissimilarity of one species in relation to the other species of the community, representing functional redundancy	Grenié *et al.* (2017)

DISCUSSION

Functional diversity is an emergent tool in functional ecology that researchers have been applied over the last decades to address a wide range of issues encompassing at least 14 general backgrounds in studies of freshwater fish worldwide. Our literature search recorded the oldest publication in 2005 (Mouillot *et al*., 2005), a seminal methodological article in which the authors proposed a new functional diversity index. After 2015, we observed an increased number of publications covering community structure, environmental impacts, and conservation. Functional approach has helped to better understand communities' responses to environmental disturbances in order to propose more efficient conservation actions in aquatic ecosystems.

Despite the increasing number of publications on the functional diversity of freshwater fish assemblages, the distribution of studies is not homogeneous around the globe. Most of the studies were concentrated in the Neotropical region. This pattern could be due to a large number of water bodies, encompassing a high biodiversity of freshwater fish in this region (~ 4.000 species) (Toussaint *et al*., 2016; Tonella *et al*., 2022) and because of the political, economic and social issues at local or regional scales (Pelicice, 2019). In the Neotropical region, Brazil presents a strong role in the studies advance of freshwater fish. The government investments in the early 2000s in Brazil lead the country to play an important role in Latin-American and global science. In addition, the regional scientific collaboration, as well as the development of the Sociedade Brasileira de Ictiologia and the creation of the journal Neotropical Ichthyology has contributed to the progress of scientific knowledge and innovations. In contrast, we recorded only one study in the Afrotropical realm, which also harbor a large number of fishes (~2,000 species). Several countries in the tropical regions need a better governance capacity and more research investments. A combination of limited infrastructure, weak institutions, and poor funding poses challenges to biodiversity research (Barlow *et al*., 2018; Pelicice, 2019).

Another problem in several regions is the lack of investment in collecting and cataloging species. Describing new species, for instance, must be a collaborative global effort, with researchers accessing resources and specimens in many museums and collections, however this is not a simple task once the knowledge of the actual number of species on Earth is unknown. Therefore, without basic research on species and their characteristics, we cannot understand local ecosystems' biological composition or ecological function, which limits our understanding of other biodiversity topics like species' life history and functional ecology (Hortal *et al*., 2015) and our ability to conserve biodiversity (Barber *et al*., 2014).

Among the great heterogeneity of freshwater ecosystems, lotic environments were the most assessed. Historically, research on fishes in lotic systems has focused mainly on streams probably because it is easier to sample fishes in small than in large aquatic systems (Johnson *et al*., 1995; Flotemersch *et al*., 2006) and because the number of streams is greater than that of other water bodies (Teresa *et al*., 2021). Furthermore, several stream fishes are extremely sensitive to environmental changes and respond markedly to human pressures on aquatic ecosystems, which makes it possible to understand the alterations in fish communities in a short period (Cruz, Pompeu, 2020; Silva *et al*., 2020; Tirupathi, Shashidhar, 2020). Conversely, large rivers are more challenging to sample compared to streams. Both environments are under intense human activity, especially by industrial pollution, urbanization, and fragmentation (Dias *et al*., 2020; Kundu *et al*., 2020). The extensive and ever-increasing urbanization creates new landscapes, alters habitats, and causes the loss of natural vegetation cover, which triggers a series of changes in several processes in the aquatic environment (Cerqueira *et al*., 2020). River impoundments affect a variety of abiotic conditions (Zuluaga-Gómez *et al*., 2016), alter natural flow regimes (Barbarossa *et al*., 2020), cause shifts in species composition (Arantes *et al*., 2019), and facilitate the introduction of non-native species (Vitule *et al*., 2012). These examples of specific impacts on the lotic ecosystems and their consequences to communities may explain the higher number of studies in these environments.

In general, freshwater ecosystems are among the most threatened environments, and it has concerned researchers due to the rapid biodiversity loss worldwide. Unsurprisingly, biological invasion and land use have been imminent concerns of ecologists for decades. However, we noticed that only over the last five years has functional diversity been applied as an approach to evaluate the effects of such disturbances in local communities. Studies have reported alterations in fish functional diversity due to the introduction of non-native species (Shuai *et al*., 2018; Millardi *et al*., 2019; Rojas *et al*., 2020) and because of the effects of land use alterations (Leitão *et al*., 2018; Alvarenga *et al*., 2021; Larentis *et al*., 2021). Consequently, changes in functional diversity imply changes in the dynamic and stability of communities. For example, introducing non-native species can promote biotic homogenization, decreasing the functional diversity of fish communities in the long term. We also highlight the greater number of studies addressing the impacts of land use in the Neotropical region. These studies are important because the Neotropical region faces intense agricultural and livestock production, accelerating habitat loss and fragmentation. Furthermore, political neglect in many South American countries has increased deforestation rates over the last years, justifying the concerns of the academic community about the effects of land use on the ichthyofauna (Casatti *et al*., 2015; Zeni *et al*., 2017; Leitão *et al*., 2018; Larentis *et al*., 2021).

To assess the functional diversity of fish, researchers have used more morphological traits than ecological traits, probably owing to the facility to obtain these morphological measures (Villéger *et al*., 2017), especially from databases such as FishMorph (Brosse *et al*., 2021) and Fishbase (Froese, Pauly, 2023), which provides several ecomorphological traits for many fish species. Conversely, ecological traits are less representative because it is more difficult or expensive to measure (Vitule *et al*., 2017). The fishes present a wide range of traits (Nelson, 2006) that can be linked to several niche dimensions (Villéger *et al*., 2017). However, many of the traits related to the autecology of species (*i.e*., reproduction, growth, development, tolerance) remain unknown (Matthews, 2012; Teresa *et al*., 2021). Studies on the basic ecology of fish have typically concentrated on larger species or species of commercial importance (Honji *et al*., 2008; Normando *et al*., 2009; Bailly *et al*., 2011; Cook-Hildreth *et al*., 2016). As mentioned, the technical difficulties in selecting and measuring some functional traits bound researchers to use a small set of traits (Gómez-Ortiz, Moreno, 2017). For instance, when a functional trait is unavailable for one species, researchers have extrapolated some information to genus or family level (*e.g*., trophic guild) (Carvalho, Tejerina-Garro, 2015a,b; Vitorino Júnior *et al*., 2016). As a result, only a subset of the functional diversity would be assessed (Vitule *et al*., 2017; Silva *et al*., 2019).

We suggest that a starting point to contribute to this issue could be the creation of functional traits databases, on a regional scale to address more local biodiversity knowledge shortfalls and minimize geographic variation in species traits. It would allow us to compare more efficiently different datasets taking account the local role of species, which is essential to identify priority areas for conservation (Mouillot *et al*., 2014). As an example, Frimpong, Angermeier (2009) compiled over 100 traits for 809 fish species from freshwaters in the United States. However, creating a database may be challenging for ecologists as it depends on experimental and observational studies, so the effort should be a joint work of the scientific community interested in this field. The Societies such as Sociedade Brasileira de Ictiologia, has the mission of becoming an international forum for the dissemination and discussion of original research on the diversity of Neotropical marine, estuarine and freshwater fish, which has helped to expand knowledge about the diverse Neotropical ichthyofauna. Thus, we suggest that the challenges, limitations and solutions for creating the datasets would be a good point to discuss by scientists in further events.

In addition, we also highlight the importance of the authors making data available for compilation. We noticed that most studies did not provide the species lists and their functional traits. Therefore, we could be creating a more collaborative culture of providing our data and, when using someone else's dataset just asking them to collaborate in any product. Even if the functional approach is independent of taxonomic identity, providing species lists would describe local patterns and guide new research. For example, using datasets to predict changes or losses of functional diversity facing climate change, river fragmentation, biological invasions. In short, we need to know to conserve, we need to share our knowledge and our data to protect biodiversity.

Regarding the category of functional traits, our results indicate that traits related to feeding and locomotion were the most applied. Indeed, this result is associated with our findings regarding the type of traits since most morphological traits were linked with these two fundamental niche dimensions of species (Tab. **S3**). Furthermore, it has been suggested that feeding and locomotion traits are good descriptors of species' function (Villéger *et al*., 2017), which supports the application of these categories in niche width. The number of traits to describe food acquisition is high, including morpho-anatomical traits representing each step of the food acquisition process and a qualitative classification that may be based on categories describing trophic level (Villéger *et al*., 2017). However, the low number of traits representing the other categories may be associated with the type of functional trait that represents each category. For instance, life history is another fundamental niche dimension less explored because it includes poorly known traits such as fecundity, egg diameter, and spawning substrate. Finally, the low usage of some trait categories might be related to them not being directly tied to the studies' central question.

With the advance in functional ecology, numerous functional indices have been developed to assess functional diversity and obtain conclusions about community responses to environmental changes and ecosystem functioning. Functional Richness (FRic) appears to be the most widely used functional diversity index, mainly coupled with Functional Evenness (FEve) and Functional Divergence (FDiv). These indices are one of the first indices developed to assess functional diversity (Mason *et al*., 2005; Villéger *et al*., 2008) and allow the understanding of complementary facets of functional diversity (Mouillot *et al*., 2013). For example, Tucker *et al*. (2017) suggest that the intuitive, unifying framework of the phylogenetic dimensions – richness, divergence, and regularity of traits – is very useful, since it applies to biological questions at multiple ecological scales, for single or multiple groups of species, and across fields.

Our findings reveal that fish functional diversity has been globally assessed for several purposes. The main concerns addressed by scientists were the effects of biological invasions and land use on fish assemblages. The main shortfall that hampers the applicability of the functional approach is the shortage of information on the autecology of fishes. Describing basic information about species ecology is a challenge for researchers since the rapid alterations of freshwater ecosystems accelerate species loss even before knowing them. Therefore, we emphasize the need for more research related to the basic ecology of freshwater fish to improve the use of the functional approach. We also reinforce the need to incorporate the functional facet in conservation plans once the studies have reported losses on fish functional diversity in freshwater ecosystems.

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