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Review

Freshwater fish functional diversity shows diverse responses to human activities, but consistently declines in the tropics

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Freshwater environments are intertwined with human activities and the consequence has been environmental degradation and biodiversity loss. Fish provide key ecological and economic benefits, and fish abundance and diversity can be affected by human activities resulting in functional diversity (FD) changes that might scale up to ecosystem impacts. Changes in FD can be expressed by quantifying its three main FD components: richness, regularity and divergence. There is no consensus about how human activities affect the main components of FD. In addition, human activities might affect the functional diversity of communities differently in temperate and tropical regions because of differences in the regional species pools and the distribution of functional traits. Here, using a meta-analytical approach, we assess how different human activities (e.g. deforestation, invasion, reservoirs) in freshwater systems affect FD components in fish communities. We compiled information from 2012 to 2023, and we found highly idiosyncratic patterns globally, but consistent loss of functional richness and regularity in face of human activities in the tropics. This idiosyncrasy could be related to high environmental heterogeneity or the multiple ways in which communities can be affected by human activities, including species loss or introduction of non-native species, or the distribution of functional uniqueness and redundancy. The reduction of functional diversity in tropical regions reveals that high redundancy alone does not prevent declines in functional diversity, and that human activities are removing specific ecological functions from natural environments. Despite the general patterns of reduction observed, local features play a crucial role in shaping how communities respond to human activities. Therefore, it is essential to understand these patterns at a local scale and to investigate the mechanisms by which specific activities impact FD.

Keywords: anthropogenic pressure, assembly rules, ichthyofauna, land use, niche filtering



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Introduction

Freshwater environments are crucial for the maintenance of life on Earth and support numerous human activities, such as transport, food and energy provisioning. These and other activities cause environmental changes that affect freshwater ecosystems, reducing both biodiversity and ecosystem functioning. For example, deforestation of lands near aquatic ecosystems, which are frequently converted to agriculture or pasture lands, can decrease habitat heterogeneity and resources through reduction of allochthonous inputs into aquatic ecosystems (Lo et al. 2020, Cantera et al. 2022). Agriculture and cattle farming often result in the release of nitrogen, herbicides, and phosphates, leading to drastic changes in water quality (Bănăduc et al. 2022, Schürings et al. 2022). Other activities can alter water flow and river connectivity, such as impoundments (Lees et al. 2016), or affect biotic interactions, such as the introduction of non-native species (Bernery et al. 2022). In general, human activities disrupt biotic and abiotic interactions within ecosystems, which pose challenges for local aquatic communities.

Although several studies highlight anthropogenic impacts on species taxonomic diversity (Agostinho et al. 2008, Lima et al. 2016, Baumgartner et al. 2017, Virgilio et al. 2018, Ortega et al. 2021), a growing body of research has focused on the ecological traits present in affected communities (Sagouis et al. 2017, Campbell and Mandrak 2020, Bonilla-Valencia et al. 2022, Lourenço et al. 2023) since species traits are related to the environment (Santos et al. 2019, Maciel et al. 2024). Environmental conditions might act as filter for species selecting species from the regional pool through their functional traits (sensu Violle et al. 2007), thus generating local pools of species with a limited set of traits (Zobel 1997, niche filtering hypothesis; Mouillot et al. 2007).

Changes in functional traits are frequently quantified using three main functional diversity (FD) components (richness, divergence, regularity) (Mason et al. 2005, 2013) that are quantified by several indices (Villéger et al. 2008, Mason et al. 2013, Carmona et al. 2016, de Bello et al. 2021). These three complementary components describe the functional niche space based on the ordination of trait values of, in our case, species, which is believed to be related to the ecological niches of species (Villéger et al. 2008). Richness indices quantify the range of trait values, commonly as the volume that a community occupies in the functional space. Functional richness (FRic) can be reduced if one or more species with unique traits (i.e. positioned at the edges of the functional space) are lost, and conversely increased if distinct species are introduced. Regularity indices quantify the abundance distribution within the functional space and are related to an equitable occupation of the functional space. The functional regularity (FReg) will be lower when specific traits dominate the community. Divergence indices quantify relative differences between species in the functional space or between species and the centroid of the functional space. Functional divergence (FDiv) is low when species are closer to each other or to the centroid of the functional space.

Although the theoretical framework of diversity studies clearly establishes the mechanisms and effects that anthropogenic impacts can have on freshwater communities (Helmus et al. 2010, Mouillot et al. 2013) (i.e. pristine environment has higher diversity), published functional diversity studies commonly disagree with expected patterns (Teresa and Casatti 2012, Wang et al. 2021, Silva et al. 2022). Some studies in freshwater ecosystems show that some activities can generate adequate conditions to maintain a functionally diverse community. For example, while studies show that deforestation lowers FD (Wilkinson et al. 2018), others show that deforestation produces a more heterogeneous environment and promotes higher fish FD (Teresa and Casatti 2012). Inconsistencies are also shown in invasion studies. Although often reported as a major cause of homogenization of species pools (Sala et al. 2000), non-native species might increase FRic if they display divergent traits from the native community (Campbell and Mandrak 2020, Rojas et al. 2021). Thus, the literature on community-level functional responses shows contrasting outcomes on how human impacts affect the FD of freshwater communities (Lo et al. 2020).

These contrasting outcomes in predicting functional diversity responses to human activities might be due to methodological particularities of each study (Villéger et al. 2017, de Bello et al. 2021) or due to the differences in environmental patterns and dynamics, as well as the geological history that shaped current regional species pools and their ecological traits (Toussaint et al. 2016, Su et al. 2022). Thus, if the regional pool of species in each region is different, we might expect that the same human activity alters the functional pools in different ways. For example, the high number of species in tropical areas could indicate strong specialization (Janzen 1967, Tewksbury et al. 2008) or high functional redundancy (Toussaint et al. 2016). While both could indicate more resistance to human pressure (Cadotte et al. 2012, Toussaint et al. 2016, Biggs et al. 2020), a pressure that excludes specific functionally specialized species might disproportionately reduce the functional diversity (Leitão et al. 2016, Benone et al. 2022). Thus, it is important to understand how biogeographic patterns might interact with shared environmental changes to better understand the mechanisms that determine global patterns of FD and drive conservation actions.

Given the growing body of evidence on the response of FD to human activities in freshwater habitats and the reporting of contrasting results, this study aims to systematically assess the current knowledge on the topic and elucidate general trends in the response of the FD of fish communities in face of human activity. Fish communities are good models for understanding how human pressure affects water bodies, since they encompass high species and trait diversity (Nelson et al. 2016), are shown to be sensitive to environmental changes (Teresa et al. 2015, Silva et al. 2022), have limited dispersal capacity (Martins et al. 2024), and directly contribute to human populations (Holmlund and Hammer 1999). This study assesses how different human activities related to freshwater affect the functional diversity of fish

communities through a meta-analytical approach. To do so, we posed three main questions: 1) is there a general effect of human activities on each component of functional diversity? 2) How does each human activity type affect each component of functional diversity? 3) Is there a difference between functional diversity responses to impacts in temperate and tropical environments?

As human activities often disrupt community structure, we expect that all three components of fish functional diversity will be reduced in face of human pressure because of the loss of functionally unique species or the replacement of these species by generalist species. Due to the high magnitude of changes caused by dam construction and that it usually accompanies other human activities (Agostinho et al. 2016, Dias et al. 2021), we expect dams to have the strongest negative effect on functional diversity. On the other hand, we expect that fish invasions will have the smallest negative effect on FRic, considering FRic for both native and non-native species. This is because successful invasive species may exhibit traits similar to native species, enabling them to thrive in a new environment, but they must also have functionally unique traits that reduce competition, thereby facilitating species establishment, as postulated by the Darwin's naturalization conundrum (Darwin 1859, Diez et al. 2008), particularly on smaller scales (Campbell and Mandrak 2017). This could increase FD (MacDougall et al. 2009) but also have a negative effect on regularity given the dominance of invaders (Campbell and Mandrak 2020, Bernery et al. 2022). Furthermore, we expect reduction in all the three components in both temperate and tropical regions, but a steeper reduction in tropical communities given the high number of rare species that contribute disproportionately to the functional space (Leitão et al. 2016).

Material and methods

Search

A search was conducted in Web of Science and Scopus for papers published until the end of 2023 with the following search terms: fish* AND river* OR stream* OR lake* OR reservoir* OR floodplain* OR freshwater* OR "inland water*" OR pond AND impact* OR disturb* OR "human activit*" OR "anthropogenic activit*" OR deforest* OR pollut* OR impound* OR "climate change" OR inva* OR connectivity OR nonnative OR non-native OR fragment* OR dam* OR tourism OR homogen* OR heterogeny* OR "temporal chang*" OR "spatial chang*" OR "land us*" OR "land cover" OR warm* OR exotic AND "functional diversity" OR "functional richness" OR "functional evenness" OR "functional dispersion" OR "functional divergence" OR "functional redundancy" OR "functional originality" OR "functional group" OR "functional rarity" OR "functional complementarity" OR "functional trait" OR "response trait" OR "trait diversity" OR "functional similarity" OR "functional differentiation" OR "functionally redundant" OR

"functionally original" OR "functionally different" OR "functional novelty" OR "functional uniqueness" OR "functional distinctiveness".

The search resulted in 1129 articles from the two platforms, from which 325 were duplicates that were removed. We screened 804 articles' titles and abstracts and selected for data extraction articles that 1) evaluated spatial or temporal changes in the functional diversity indices of 2) freshwater 3) fish communities in 4) response to a human activity, totaling 116 articles after initial screening from which six were written in Chinese language and therefore, not retrieved. From the 110 remaining, 71 papers were excluded due to incomplete data reported (11 articles), different questions or analyses indicated (47 articles), no control or natural sites compared (8 articles), other type of environment than freshwater (1 article), other taxa (1 article), and 3 reviews that passed through the previous filters. Two additional articles that did not appear in this search were selected from previous searches. As a result of these filters, we ended up with 41 articles totaling 178 functional diversity vs. impact relationships. The date of publication of the selected articles ranged from 2012 to 2023. A PRISMA diagram (O'Dea et al. 2021) depicting the search and screening processes and the list of articles and treatment types are available in the Supporting information.

Data extraction

The relationships between human activity and functional diversity (FD) were classified as: 1) categorical, including those that compared means of FD indices between natural (or less disturbed by human activity) and sites disturbed by human activity, this comparison could be spatial (different location at the same time) or temporal (same location in different periods); or 2) regression, those that related the value of functional indices to a gradient of human activity. For the categorical relationships, we extracted the mean, standard deviation (when standard error was reported, we transformed it to standard deviation), and the number of replicates for each treatment. For the regression relationships, we extracted the coefficient of correlation (r) and the number of replicates. Each relationship was used as a sample unit (for now on, an observation) in the meta-analysis. When the values were not available in tables or text, we used the 'metaDigitise' package (Pick et al. 2018) in R (www.r-project.org) to extract data from graphs.

For each observation, we classified the FD index used into the three components of FD (richness, regularity and divergence). This classification was based on previous literature (Mouchet et al. 2010, Tucker et al. 2017, de Bello et al. 2021) and the description and initial purpose of the indices (Villéger et al. 2008, Laliberté and Legendre 2010). Functional richness includes indices that quantify the range of traits calculating the sum of traits, the length of dendrogram branches or the volume of a convex hull; functional regularity includes only functional evenness which evaluates the regularity in the distribution of abundances inside the functional space; and functional divergence primarily includes indices that calculates

the distance between species and the centroid of the functional space. Due to lower observation number of indices such as functional redundancy or functional originality, which are attempts to measure functional redundancy (Mouillot et al. 2013, Ricotta et al. 2016), and due to the similar description of the indices (they measure species distance to a referential point inside functional space) we grouped those together with functional divergence indices. Rao's quadratic entropy, another index with a low number of observations, was also classified into FDiv component. This index, together with functional dispersion might be strongly related to richness if not properly controlled (Mason et al. 2013) but also showcase other facets of functional diversity (Laliberté and Legendre 2010). We decided to group both RaoQ and FDis into the FDiv component first because their purpose is to measure FDiv and second to not put indices that measure anything else than FRic inside the FRic component. We found that each functional component presented different effect sizes from each other and indices inside the same functional component show no difference (Supporting information).

We also noted the human activity studied and the mean coordinates to determine the climate region (tropical or temperate). Some methodological information was also noted (e.g. number of observations per freshwater type, if the study was a spatial or a temporal comparison, number of traits used), and further information is available in the Supporting information.

Analysis

We used Hedges' g as the effect size metric because it can incorporate mean and deviance information, as well as corrections of biases related to small or different sample sizes. Also, because it is possible to convert the correlation values into Hedges' g (Borenstein et al. 2009, Schürings et al. 2022). We calculated Hedges' g as:

$$g = \left(\frac{Mt_i - Mc_i}{SDp} \right) \times J$$

Where, Mt and Mc are the diversity index mean of impacted (treatment) and less impacted (control) environments, respectively. SDp is the pooled standard deviation:

$$SDp = \sqrt{\frac{(Nt_i - 1) \times sdt_i^2 + (Nc_i - 1) \times sdc_i^2}{Nt_i + Nc_i - 2}}$$

And J is the correction factor calculated by:

$$J = 1 - \frac{3}{4(Nt_i + Nc_i - 2) - 1}$$

Where, for the two previous formulas, Nt and Nc are the sample sizes, and sdt and sdc are the standard deviations for

both the impacted (treatment) and less impacted (control) environments, respectively.

When the article used linear regressions, Hedges' g was calculated as:

$$g = \left(\frac{2 \times r_i}{\sqrt{1 - r_i^2}} \right) \times J$$

Where r is the coefficient of correlation of some impact variable and the FD index. The variance of means and correlations of coefficient values were calculated as:

$$Vg(\text{means}) = \frac{Nt_i + Nc_i}{Nt_i \times Nc_i} + \frac{g_i^2}{2(Nt_i + Nc_i)}$$

and

$$Vg(\text{correlation}) = J^2 \times \frac{4v_d}{(1 - r^2)^3}$$

To calculate Hedges' g , we used the *escalc* function of the 'metafor' package (Viechtbauer 2010) and we transformed the coefficient of correlation into Hedges' g using the *res* function of the 'compute.es' package (Re 2013) in R (www.r-project.org).

A random-effects model (REM) was built to assess how different human activities drive changes in the functional diversity of fish assemblages. We considered Hedges' g as the dependent variable in these models and produced the model including all studies because we expected that all three components would reduce in face of human activity. Given the high amount of heterogeneity in the produced model, and given that we expected that although diminishing, each functional component could respond differently, we performed mixed-effects models (MEM) to test each functional component, impact, and climate as moderators to answer how each impact affects each component of functional diversity and how these components are affected in different climates. In each model, the article was categorized as a random variable because they usually present more than one observation that are not independent between them, and each paper might have a different range of variance. Models were performed with the *rma.mv* function of the 'metafor' package (Viechtbauer 2010). Since we had multiple moderators that we could use and some moderator we could use in multiple ways (e.g. decimal latitude *vs.* climate categories) we choose models based on our major questions and used Akaike's information criterion (AIC) to support the choice of models (Burnham et al. 2002). The AIC values and further moderator analyses are available in the Supporting information.

To search for publication bias, the funnel plot was observed along with the adjustment of a trim and fill model.

This method estimates the number of missing observations based on the distribution symmetry of known observations, considering that an unbiased review would have a symmetric distribution towards the effect value. We tested the heterogeneity of each model and the unexplained heterogeneity to evaluate the robustness of each effect.

Results

Our search resulted in 41 published studies that evaluated the response of functional diversity (FD) to human activity through 178 observations of difference between means (124 observations) or simple regression (54 observations). From these studies, 23 (81 observations) were sampled in the temperate region and 18 (97 observations) in the tropics. Several functional indices were applied, with Functional richness (FRic – 34 articles and 57 observations) and functional divergence (FDiv – 29 articles and 83 observations) being more common than functional regularity (FReg – 21 articles and 38 observations). Only 17 studies evaluated all three components of FD.

We found a total of seven human activities studied (Table 1). The most studied were deforestation (11 papers and 74 observations) and invasion (11 papers and 30 observations). Ten studies (35 observations) evaluated multiple human activity influencing FD. Dam construction and habitat homogenization appeared in three papers (8 and 9

observations, respectively). Lateral disconnectivity (6 observations) was analyzed in two studies based in the same basin, but in different years, and pollution was evaluated in two studies (16 observations). Specific information about the articles and the moderators can be found in the Supporting information. We also provide additional information on freshwater habitat types in the Supporting information, but we are unable to test how distinct human activities affect different habitat types given a low number of observations.

The observed idiosyncrasy eliminates the possibility of finding a global effect of human activity on functional diversity (Fig. 1). Despite this, FRic (effect size (ES) = -0.62 , confidence interval (CI) = $-1.13, -0.12$) and FReg (ES = -1.79 , CI = $-2.31, -1.27$) showed consistent decline in the tropics, and although the results for FDiv were not statistically significant it seems to follow the same trend (ES = -0.51 , CI = $-1.02, 0.001$) (Fig. 2).

Type of human impact

Following the general pattern, most of the human activities did not affect any component of FD. Of the seven assessed human activities, none of them had a significant global pattern of impact on FDiv. Reservoirs (ES = -1.92 , CI = $-3.51, -0.33$) and fragmentation (ES = -2.27 , CI = $-4.46, -0.08$) reduced FRic (Fig. 3), while deforestation reduced FReg (ES = -1.77 , CI = $-2.47, -1.07$) (Fig. 3).

Table 1. List of moderators used in this meta-analysis, functional diversity (FD) component, type of impact and climate. Each one has a brief description, the number of papers that contain it and the number of observations (the sample unit of the meta-analysis) included in all papers.

Moderator	Categories	Description	Papers	Obs.
Functional diversity component	Functional index			
	Functional richness (FRic)	Component of FD that quantifies the range of traits in the functional multidimensional space. In this paper, it was composed of the indices, functional richness and functional structure	34	57
	Functional divergence (FDiv)	Component of FD that quantifies the dispersion between organisms in the functional space. This dispersion could be related to the center of the functional space or to each pair of species. Composed of functional dispersion, divergence, originality, similarity, specialization, redundancy, uniqueness and Rao's quadratic entropy	29	83
	Functional regularity (FReg)	Component of FD that quantifies the regularity of the distribution of the organisms in the functional space. Composed of the functional evenness index	21	38
Impact	Deforestation	Removal of trees near the waterbody. Are included in this category studies that evaluate different land use type.	11	74
	Lateral disconnectivity	Loss of lateral connectivity of lakes to the main channel.	2	6
	Habitat homogenization	Loss of habitat heterogeneity inside water	3	9
	Invasion	Addition of non-native species in the waterbody	11	30
	Multiple	When the study did not specify a major human activity that is being evaluated or when they used an integrity index to evaluate the environment pristine status.	10	35
	Pollution	Related to chemicals input into the waterbody	2	16
	Dam construction	Construction of a barrier that changes the environment from lotic to lentic.	3	8
Climate	Temperate	When sample sites were above or equal the latitude 23 or below or equal to latitude -23	23	81
	Tropical	When sample sites were between the latitude -23 and 23	18	97

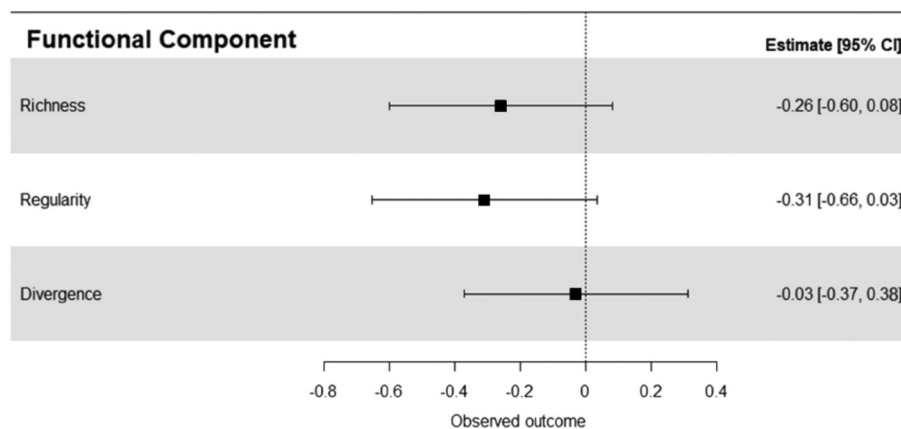


Figure 1. Effect size for each functional component, functional regularity, functional divergence and functional richness, based on all observations. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line there is no significant effect of human activities on that functional component. Values on the left side of the dotted line represents negative effects of human activity.

Human activity in each climate region

The decrease of FRic in face of human activities in the tropics was mostly because of reservoirs ($ES = -1.92$, $CI = -3.44$, -0.40), and multiple activities in the same environment ($ES = -2.37$, $CI = -3.91$, -0.82) (Fig. 4). Also in the tropics, deforestation decreased FReg ($ES = -1.76$, $CI = -2.43$, -1.09) (Fig. 4). On the other hand, no human activity besides lateral disconnectivity ($ES = -2.31$, $CI = -3.88$, -0.74) reduced any component of FD in the temperate region (Fig. 4).

Publication bias

The trim and fill model shows that there are no missing studies. The test of heterogeneity shows that the model without

moderators showed high heterogeneity, which supports the necessity of testing different moderators. All models with moderators showed significant heterogeneity between groups of observations, validating the models. And as expected when dealing with large and heterogeneous dataset, all models showed significant unexplained heterogeneity. From all models, the one with the lower AIC value was the model that considered all moderators (climate region, functional component and type of human activity) together.

Discussion

We expected that human activities would reduce functional diversity (FD), that reservoirs should display the largest effects, biological invasions display the smallest effects, and

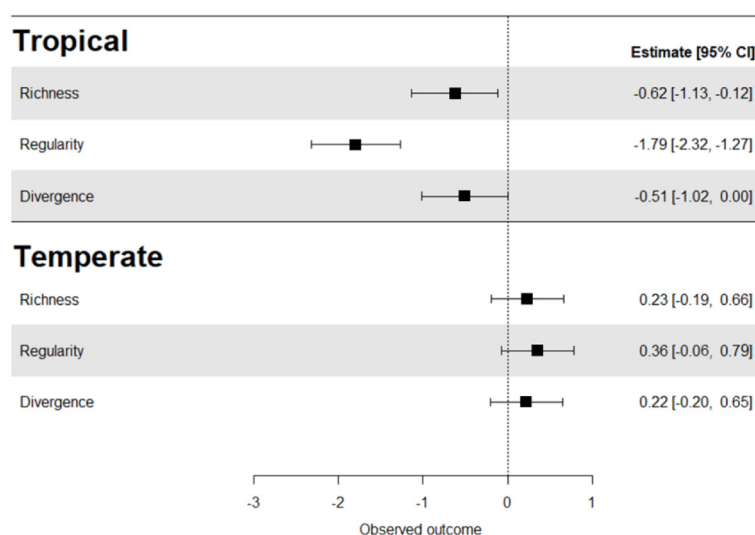


Figure 2. Effect size for each functional component in each climate region. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line there is no significant effect of human activities on that functional component. Values on the left side of the dotted line represent negative effects of human activity.

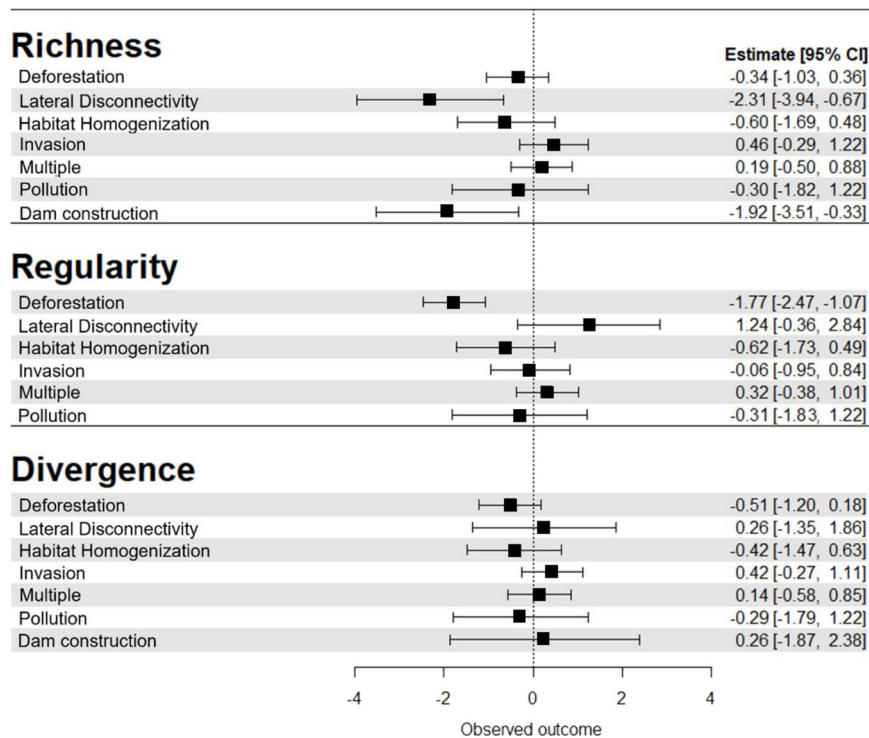


Figure 3. Effect size of each functional component divided by human activity. Each line represents the effect of human activity in the respective functional component. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line there is no significant effect of human activities on that functional component. Values on the left side of the dotted line represents negative effects of human activity.

that tropical regions display higher intensity of reduction. Our results partially support our main expectations since human activities did not lead to an overall decrease in functional diversity, but functional richness and regularity showed a reduction in tropical areas, with reservoirs and multiple activities (FRic) and deforestation (FReg) as the major causes of FD decreases. The high heterogeneity between studies and the lack of effect in temperate regions might have led to the lack of a global FD reduction, but despite all the heterogeneity, our results show that human activities are reducing the FRic and FReg in the tropics. Also, there is a tendency to a reduction in FDiv, which can be related to an unbalanced distribution of traits towards the center of the functional space or/and because of the increasing of the functional redundancy (i.e. higher cooccurrence of species with similar traits).

The contrasting results found across articles, even when studying the same human activity type, scale up as a lack of generalized effect over the FD of fish communities. The high environmental heterogeneity found in nature, and the multiple ways in which communities can be affected by human pressure might partially explain the lack of an effect. For example, deforestation can negatively influence fish diversity by lowering habitat heterogeneity and food input (Lo et al. 2020); on the other hand, light input results in the growth of grasses in deforested streams, which can also increase habitat heterogeneity and create habitat for novel species (Teresa and Casatti 2012). Likewise, non-native fish species

can promote higher FD, especially if they have distinct traits (Toussaint et al. 2018, Rojas et al. 2021), but also, non-native species can decrease FD through competition, predation, or indirect effects (Matsuzaki et al. 2016). Thus, understanding the local environment is important to predict how human activities affect aquatic biota, and must be the first step to properly construct the study design (Villéger et al. 2017, de Bello et al. 2021).

Fish functional ecology studies often rely on easily measurable traits or traits available in literature (Gomes et al. 2023), such as morphological or life-history traits, without proper justification for their use. This happens because of a lack of resources and the difficulty in measuring physiological or behavioral traits that might be more related to the fish functional role in the ecosystem. Nevertheless, this practice might weaken the results when traits are chosen considering what is available rather than the importance of the trait to ecological phenomena. Although this was not the focus of this meta-analysis, for a subset of our data, we found that the higher the number of traits used, the higher was the magnitude of the effect size (Supporting information). Therefore, it is important to carefully select traits during the study design with clear hypothesis on how they relate to the objective of the study for each trait used. For that, the publishing of studies that test relationships between fish traits and environmental variables, such as the seminal works of Gatz (1979) and Watson and Balon (1984), for different regions

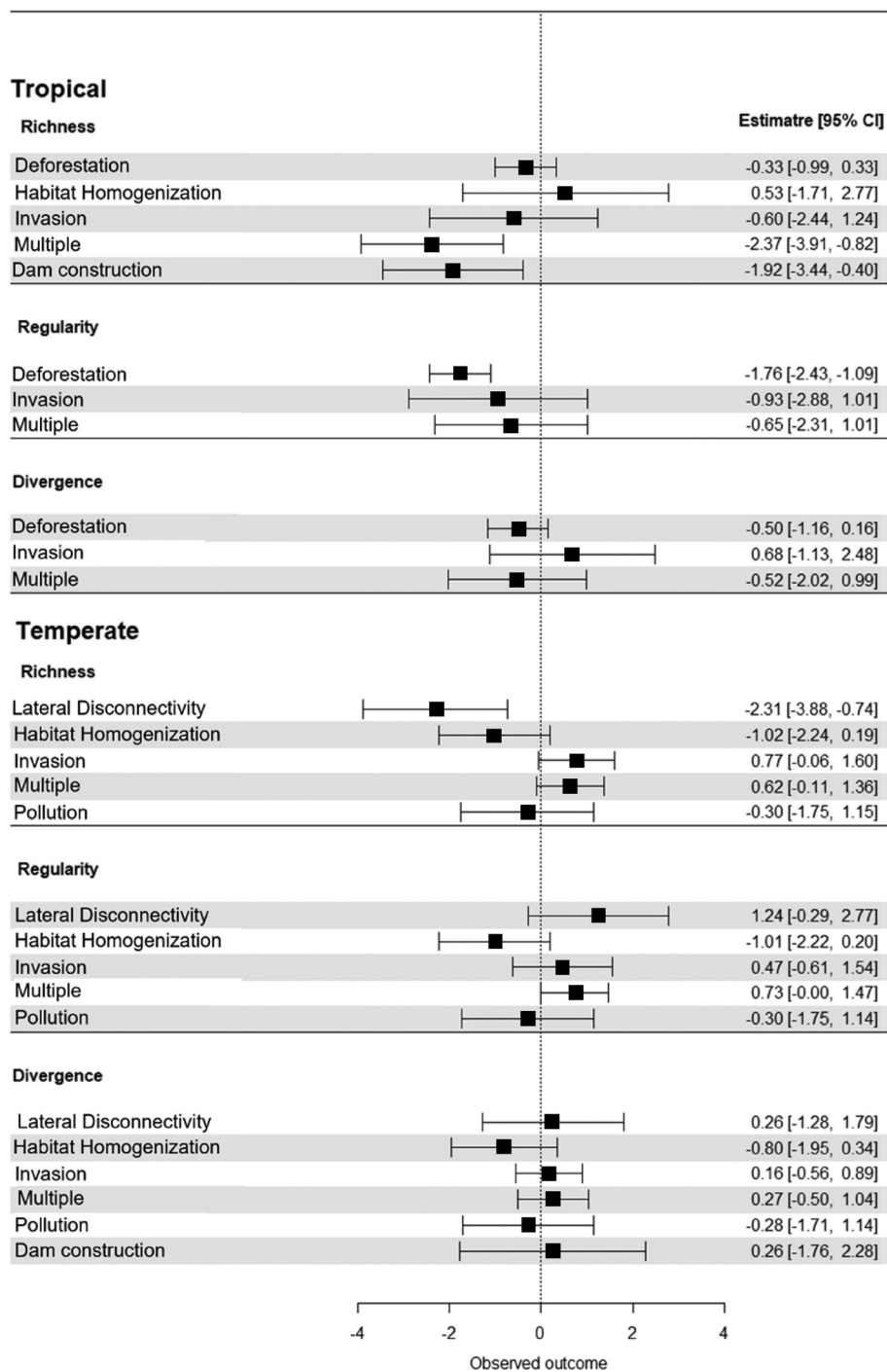


Figure 4. Effect size of each functional component divided by human activity and climate region. Each line represents the effect of human activity in the respective functional component. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line there is no significant effect of human activities on that functional component. Values on the left side of the dotted line represents negative effects of human activity.

and environments are of great importance to better understand the idiosyncrasy of each local and to create a pertinent hypothesis for the phenomena studied. Also, contributing to global-scale data consortiums are a pathway to better understand ecological phenomena at larger scales, such as Biotime (Dornelas et al. 2018) and RivFishTIME (Comte et al.

2021). We also suggest studies considering how the choice of traits, in terms of trait meaning and quantity, might influence FD outcome.

Another source of variance between studies is the plethora of functional indices available (Carmona et al. 2016, de Bello et al. 2021, Gomes et al. 2023). Our search found 18

different ways of measuring functional diversity nested into 13 functional indices (their description and classification can be found in the Supporting information), three grouped in the FRic component, two in the FReg component, and eight in the FDiv component. This is expected to increase the heterogeneity between observations and make it more difficult to compare the results between studies. Also, as any classification attempt, this also has its problems, and indices inside the same component might quantify that functional space component differently than others due to mathematical particularities (Villéger et al. 2008 for differences between FDiv and FDis, see Laliberté and Legendre 2010) or they might present relationship with more than one component. For example, RaoQ and functional dispersion, which were classified into functional divergence, can be related to the richness component (Mason et al. 2013), if the calculation does not control the number of species. One way to circumvent these problems and control this source of heterogeneity is to make data available for future reviews or meta-analysis studies, including indices not included in the main text (as did Silva et al. 2022), considering their own calculation particularities (de Bello et al. 2021), since they are easily calculated in the R environment. Also, as species richness can largely affect FD indices, accounting for it through null models is recommended. This standardization could reduce heterogeneity between studies due to differences in species richness.

Despite all the sources of heterogeneity, we found negative effects of some human activities on FD. In the tropics, FRic and FReg are being reduced while FDiv seems to present the same pattern. As we expected, the negative changes in FD in the tropics are more intense. The reduction of FRic in tropical regions could be explained by two non-exclusive mechanisms. The loss of rare species with unique traits, that have disproportional contribution to the functional space (Leitão et al. 2016) or/and the human activity is targeting a specific portion of the functional space which shows us that the high redundancy (Toussaint et al. 2016) is not sufficient to refrain FRic from decreasing. At the same time, the reduction of FReg shows that human activities are enhancing unbalanced distribution of organisms in the functional space (Giam et al. 2015), i.e. disturbed sites have higher trait dominance. In fact, this is what many studies find in disturbed sites: the replacement of rare species by generalist species that have less unique traits (Stefani et al. 2020, De Paula et al. 2022, Antoniazzi et al. 2023). Because of this replacement, we also could expect that this imbalance is towards the center of the functional space and, consequently, directly linked to the tendency of reduction of FDiv. In the temperate region, we have smaller FRic when compared with tropical sites and high trait complementarity (i.e. low redundancy) (Toussaint et al. 2016). We could expect that the FD would be sensitive even to the loss or addition of few species. Instead, our results do not show any consistent effect of changing FD, which might be related to how human activities are geographically distributed.

Regarding the types of human activity, our findings show that dam construction and multiple activities decrease FRic,

and deforestation decreases FReg in tropical areas while lateral disconnectivity decreases FRic on temperate area. The enormous changes that dam construction causes in the environment are well documented in the literature (Baxter 1977, Rosenberg et al. 1995, Agostinho et al. 2008, Carpenter et al. 2011, Wu et al. 2019, Soukhaphon et al. 2021). River damming changes the water flow dynamics, turning a lotic environment into lentic; thus, the reduced and human-controlled flow due to the dam operation jeopardizes the aquatic–terrestrial interactions and the nutrient cycling (Baxter 1977, Junk and Mello 1990). The dam also leads to environmental homogenization (Poff et al. 2007), facilitates the introduction of non-native species (Han et al. 2008, Turgeon et al. 2019, Bernery et al. 2022), and constrains the migration of migratory species (Pelicice et al. 2015). All these changes favor generalist species with sedentary behavior (Cunico and Agostinho 2006, Perônico et al. 2020), mostly nekton-benthic species (Dos Santos et al. 2017), thus reducing FD.

Analyzing the distribution of human activities between tropical and temperate areas, we observed that studies focusing on the effect of dam construction are mostly found for tropical ecosystems. This happens because articles assessing the effects of dams in temperate ecosystems consider other sources of impact, usually using environmental integrity indices, then being classified as ‘multiple’ (Lin et al. 2021, Wang et al. 2021). Multiple human activities decrease the FRic in the tropical region but not on temperate and this pattern is related both to the idiosyncrasy of the FRic of each region and the role of non-native species. On the tropics, articles categorized in the ‘multiple’ category (Dias et al. 2021, Pereira et al. 2021) use environmental protocols that consider multiple environmental features to categorize their sites as disturbed or not, such as the physical structure or the influence of urbanization and agriculture. While some studies do this at temperate region, other studies perform past vs. current approach and do not constrain the environment to only one type of activity. Also, most studies inside this category present invasion as one of the multiple activities and those studies somewhat converge to the explanation that the negative effects of dams (Lin et al. 2021, Wang et al. 2021) and urbanization (Antoniuzzi et al. 2023) is diminished by the new traits that invasive species add to the functional space. This increase might occur in the temperate region because the higher probability of an introduced species to show unique traits in relation to the regional pool of traits (Toussaint et al. 2016).

Still in temperate regions, two studies evaluated the loss of connectivity of lakes with the main channel of a basin. This lateral disconnectivity also reduces functional richness by hampering dispersal between water bodies and preventing fish to assess laterally connected ecosystems, leading to the loss of species (and their traits) that needs to locomote between places (Liu and Wang 2018, Jiang et al. 2021). Although it lowers FRic, our results are based on two studies and should be interpreted with caution.

The FReg component is also negatively affected by human activity on the tropics. Although there are multiple ways

in which deforestation can change habitat heterogeneity, when the environment loses heterogeneity due to the lack of allochthonous input (Giam et al. 2015, De Paula et al. 2022) or when it gains heterogeneity due to increased plant production (Teresa and Casatti 2012), the changes result in the increasing of the dominance of some specific traits. For example, changes in the water body due deforestation can facilitate the dominance by schooling species and the loss of specific groups related to microhabitats lost in deforested streams (Giam et al. 2015), thus resulting in the higher dominance of traits.

When assessing how human activities affect biodiversity, it is also important to consider the intensity of the pressure, as well as the temporal and spatial scales of influence of human activity. FD outcomes might change depending on the spatial scale evaluated. For example, Cantera et al. (2022) found that deforestation 30 km upstream the sampled site was more correlated with diversity declines even at low intensity levels and Matsuzaki et al. (2013) discussed that regional assessment might not identify local negative effects of fish invasion, since species extirpation is more likely to happen at a local scale. Also, the duration of the pressure or the response time of the fauna can influence the outcome found, invasive species are likely to take time to spread further and cause negative effects regionally, in fact Matsuzaki and collaborators (2013) predicted future FD homogenization for fish fauna (Rojas et al. 2021). In another example, Baumgartner and collaborators (2018) found that FD correlations with river regulation reached its peak more than 1.5 years after the regulation and when a dam is constructed, the first year results in high accumulation of resources near the barrier which increases diversity, these resources decrease in the following years stabilizing the diversity at low levels (Lima et al. 2016, Perônico et al. 2020). Despite their importance, our observations were not sufficient to test these factors, therefore we promote the publication of more studies evaluating FD changes in fish communities to enhance the number of observations which would support to explore better how these particularities affect FD.

We found that changes in FD are context-dependent, but human activities consistently exclude unique traits while increasing trait dominance of tropical fish communities. As most tropical sites are in Global South countries, this problem must be addressed with urgency to reduce future losses on FD due to the development of these areas. At the temperate region, invasive species seems to increase FD, which might lead to cascading effects on those ecosystems. Due to the observed idiosyncrasy, fish functional ecologists should make more effort toward a better understanding of how the environment is related to the functional traits and how human activities alter the environment to properly understand how human activities affect FD. This will also enhance the robustness and predictions of the FD response in face of human impacts. Thus, studies that evaluate traits vs. environmental variables and contributing to large-scale assessments are important towards this goal. Also, the use of environmental

protocols to measure integrity and how they relate to functional traits and diversity might be a way to reduce variation between different types of human activities and might be an emerging pathway to homogenize methodologies since it is based on environmental variables and does not limit a site to a specific human activity when they probably suffer from multiple stressors. Finally, the study of FD should follow standard approaches, such the Handbook of trait-based ecology (de Bello et al. 2021, Gonçalves-Souza et al 2023) and the review of functional ecology for fishes (Villéger et al. 2017), to increase the robustness of future meta-analytical approaches and to better assess changes due by different stressors in different regions.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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