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

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Abstract

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 temporally and/or spatially: 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 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, or the distribution of functional uniqueness and redundancy. The reduction of functional diversity is concerning since human activities are removing specific functions from natural environments and results in the dominance of traits related to generalist ecological strategies. Despite the general patterns of reduction, local features are determinants on how the community will answer to human activity and therefore we highlight the importance of understanding the environment and fauna at the local scale, and the mechanisms by which each activity might affect FD.

Keywords: anthropogenic pressure, assembly rules, land use

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 (Cantera et al., 2022; Lo et al., 2020). 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; Baumgartner et al., 2017; Lima et al., 2016; Ortega et al., 2021; Virgilio et al., 2018), a growing body of research has focused on the ecological traits present in affected communities (Bonilla-Valencia et al., 2022; Campbell & Mandrak, 2020; Lourenço et al., 2023; Sagouis et al., 2017) since species traits are related to the environment (Maciel et al., 2024; Santos et al., 2019). 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 (Niche Filtering hypothesis; Mouillot et al., 2007; Zobel, 1997).

Changes in functional traits are frequently quantified using three main functional diversity components (richness, divergence, regularity) (Mason et al., 2005, 2013). These three complementary components describe the functional niche space based on the ordination of trait values of, in our case, species, and 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. Regularity indices quantify the abundance distribution within the functional space and are related to an equitable occupation of the functional space. Divergence indices quantify relative differences between species in the functional space.

Although the theoretical framework of functional diversity clearly establishes the mechanisms and effects that anthropogenic impacts can have on freshwater communities (Helmus et al., 2010) (*i.e.*, pristine environment have higher diversity), published evidence commonly disagrees with expected patterns (Silva et al., 2022; Teresa & Casatti, 2012; Wang et al., 2021). 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 functional diversity (*e.g.*, Wilkinson et al. 2018), others show that deforestation produces a more heterogeneous environment and promotes higher fish functional diversity (Teresa & 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 functional richness if they display divergent traits from the native community (Campbell & Mandrak, 2020; Rojas et al., 2021). Thus, the literature on community-level functional responses shows contrasting outcomes on how human impacts affect the functional diversity of freshwater communities (but see Lo et al., 2020).

One of the reasons for these contrasting outcomes might be the choice and the number of functional traits and indices (*e.g.,* de Bello et al. 2021; Villéger et al. 2017). Another source of uncertainty in predicting functional diversity responses to human activities depends on the differences in environmental patterns and dynamics, as well as the geological history that shaped current regional species pools and their ecological traits (Su et al., 2022; Toussaint, et al., 2016). 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 high functional redundancy (*i.e.,* more species playing the same ecological role), which could indicate more resistance to impacts; on the other hand, the low number of species in temperate regions can lead to higher biological vulnerability than in the tropics (Toussaint, et al., 2016). 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 functional diversity and drive conservation actions.

Given the growing body of evidence on the response of functional diversity 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 functional diversity of fish communities in face of human activity. Fish communities are good models for understanding how human impacts affect water bodies, since they encompass high species and trait diversity (Nelson et al., 2016), are shown to be sensitive to environmental changes (Silva et al., 2022; Teresa et al., 2015), and directly contribute to human populations (Holmlund & Hammer, 1999). This study assesses how different human activities related to freshwater affects the functional diversity of fish communities through a meta-analytical approach. To do so, we posed three main questions: (i) Is there a general effect of human activities on each component of functional diversity? (ii) How does each human activity type affect each component of functional diversity? (iii) 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 replaced by generalists. Due to the high magnitude of changes caused by reservoirs and that it usually accompanies other human activities (Agostinho et al., 2016; Dias et al., 2021), we expect reservoirs to have the strongest negative effect on functional diversity. We expect that fish invasions have the smallest negative effect on functional richness because successful invasions are likely to be of functionally unique species that could increase FD (MacDougall et al., 2009), but a strong effect on regularity given the dominance of invaders (Bernery et al., 2022; Campbell & Mandrak, 2020). 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 disproportionally to the functional space (Leitão et al., 2016) and the local redundancy vulnerability (Benone et al., 2022).

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 (i) evaluated changes in the functional diversity indices of (ii) freshwater (iii) fish communities in (iv) 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 appeared 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. A PRISMA diagram (O’Dea et al., 2021) depicting the search and screening processes and the list of articles and treatment type are available in the supporting material.

Data extraction

The relationships between human impact and functional diversity were classified as: (i) categorical, including those that compared means of functional diversity indices between natural (or less disturbed by human activity) and sites disturbed by human activity; or (ii) 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 replicate number of 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 the R environment (R Core Team, 2023) to extract data from graphs.

For each observation, we classified the functional diversity index used into the three components of functional diversity (richness, regularity, and divergence), we also noted the human activity studied and the mean coordinates to determine the climate region (tropical or temperate).

Table 1. List of moderators used in this meta-analysis, functional diversity component, type of impact and climate. Each one has a brief description, the number of papers that contains 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	Component of functional diversity that quantifies the range of traits in the functional multidimensional space. In this paper, it was composed by the indices, functional richness and functional structure	34	57
	Functional Divergence	Component of functional diversity 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 by functional dispersion, divergence, originality, similarity, specialization, redundancy, uniqueness and Rao's quadratic entropy	29	81
	Functional Regularity	Component of functional diversity that quantifies the regularity of the distribution of the organisms in the functional space. Composed by the indices, functional entropy and functional evenness	22	40
Impact	Deforestation	Impact related to removing trees near the waterbody. Are included in this category studies that evaluate different land use type.	11	74
	Fragmentation	Impact related to loss of connectivity of some lakes to a river. Both studies were conducted in the same basin.	2	6
	Homogenization	Impact related to loss of habitat heterogeneity inside water	3	9
	Invasion	Impact related to the addition of non-native species in the waterbody	11	30
	Multiple	When the study did not specify a major impact that is being evaluated or when they used an integrity index to evaluate the environment.	10	35
	Pollution	Impact related to the chemicals input into the waterbody	2	16
	Reservoir	Impact related to the construction of a river barrier and the change from a lotic to a lentic environment.	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

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, 2009; Schürings et al., 2022). We calculated Hedges' g as:

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

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

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

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:

$$g = \left(\frac{2 * \mathrm{r}_i}{\sqrt{1 - \mathrm{r}_i{}^2}}\right) * J$$

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

$$Vg\ (means) = \frac{Nt_i + Nc_i}{Nt_i * Nc_i} + \frac{{g_i}^2}{2(Nt_i + Nc_{i)}}$$

And

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

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 the R environment (R Core Team, 2023).

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 different range of variance. Models were performed with the rma.mv function of the metafor package (Viechtbauer, 2010).

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 to a human activity through 178 observations of difference between means (124 observations) or simple regression (54 obs.). From these studies, 23 (81 observations) were sampled in the temperate region and 18 (97 obs.) in the tropics. Several functional indices were applied, with Functional Richness (FRic - 34 articles and 57 obs.) and Functional Divergence (FDiv – 29 articles and 81 obs.) being more common than Functional Regularity (FReg – 22 articles and 40 observations). Only 17 studies evaluated all three components of functional diversity.

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 obs.) evaluated multiple human activity influencing functional diversity. Reservoirs and habitat homogenization appeared in three papers (8 and 9 obs., respectively). Fragmentation (6 obs.) was analyzed in two studies based in the same basin, but in different years, and pollution was evaluated in two studies (16 obs.). Specific information about the articles and the moderators can be found in the supplementary material.

The observed idiosyncrasy eliminates the possibility of finding a global effect of human activity on functional diversity (Figure 1). Despite this, functional richness (Effect Size (ES) = -0.62, Confidence Interval (CI) = -1.13, -0.12) and regularity (ES = -1.79, CI = -2.32, -1.27) showed consistent decline in the tropics, and although the results for functional divergence was not statistically significant it seems to follow the same trend (ES = -0.51, CI = -1.02, 0.00) (Figure 2).

Type of human impact. Following the general pattern, most of the human activities did not affect any component of functional diversity. Of the seven assessed human activities, none of them had a significant global pattern of impact on functional divergence. Reservoirs (ES = -1.92, CI = -3.51, -0.33) and fragmentation (ES = -2.27, CI = -4.46, -0.08) reduced functional richness (Figure 3), while deforestation reduced functional evenness (ES = -1.77, CI = -2.47, -1.07) (Figure 3).

Human activity in each climate region. The decrease of functional richness 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) (Figure 4). Also in the tropics, deforestation decreased functional regularity (ES = -1.76, CI = -2.43, -1.09) (Figure 4). On the other hand, no human activity besides fragmentation (ES = -2.31, CI = -3.88, -0.74) reduced any component of functional diversity in the temperate region (Figure 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 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.

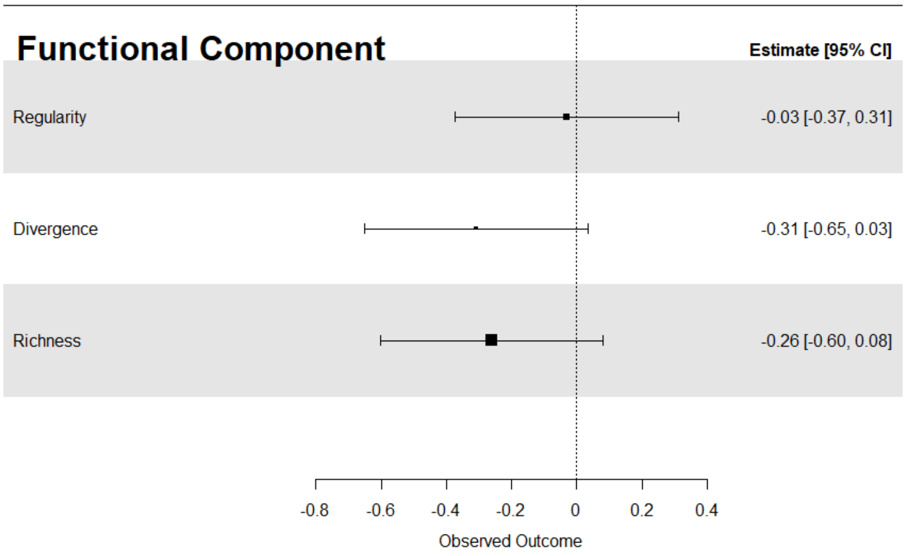

Figure 1. Effect size for each functional component, functional regularity, functional divergence and functional richness, based on all observations. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line 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 the human activity

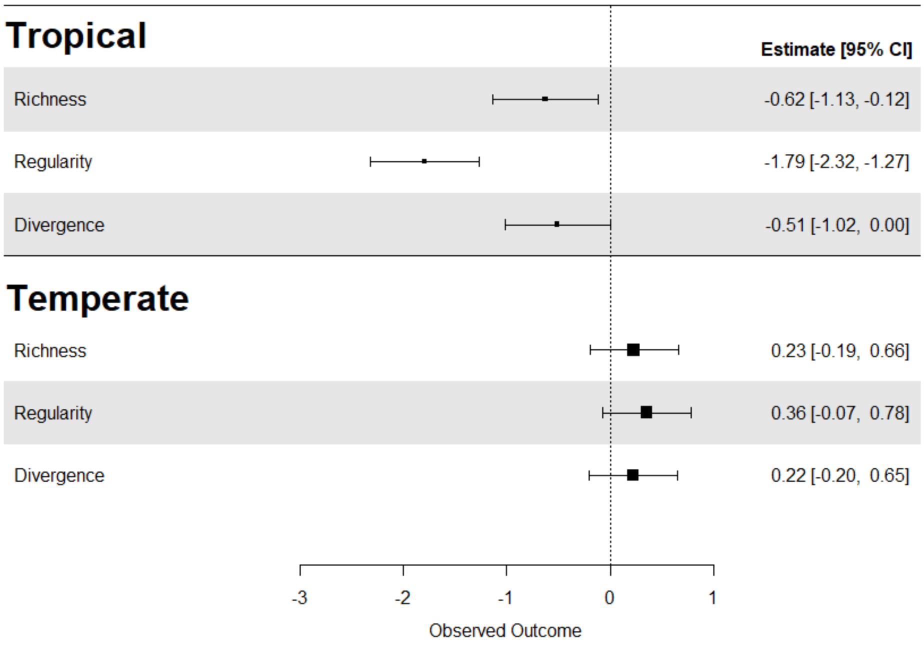

Figure 2. Effect size for each functional component in each climate region. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches the vertical dotted line there is no significant effect of human activities on

that functional component. Values on the left side of the dotted line represents negative effects of the human activity

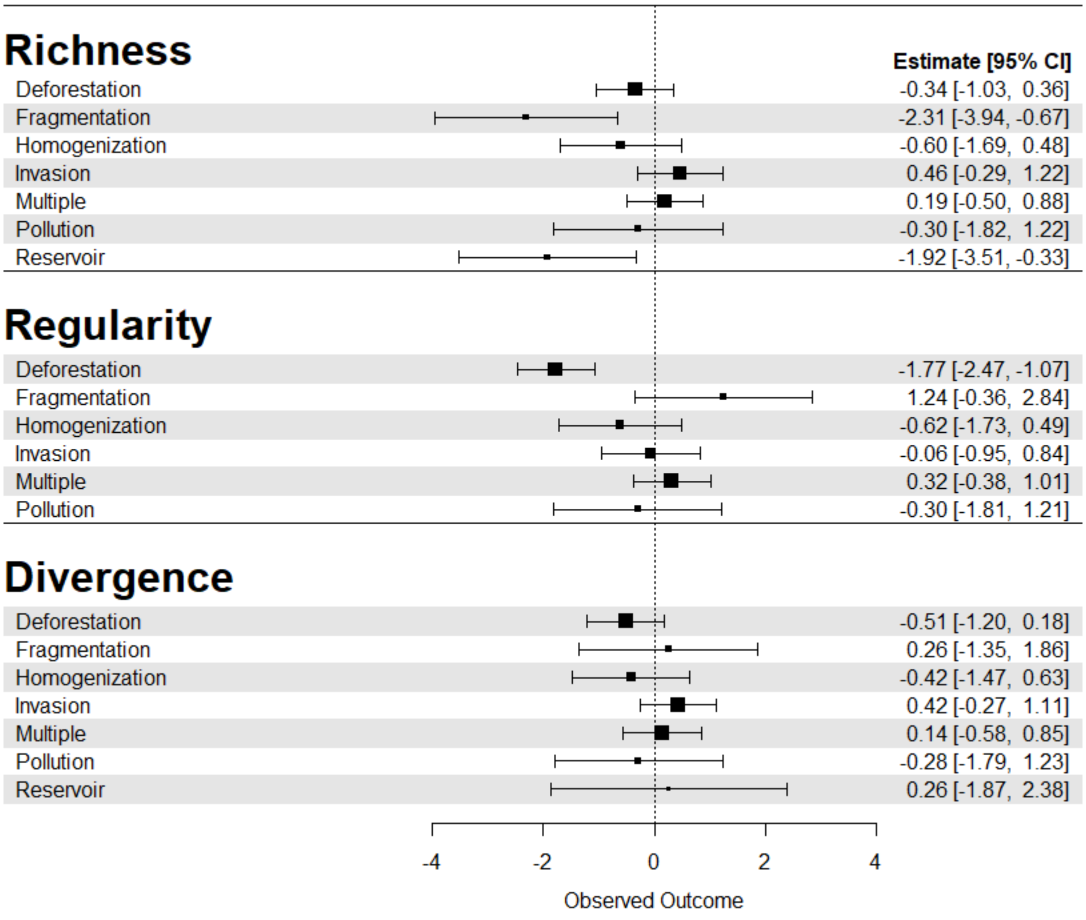

Figure 3. Effect size of each functional component divided by the human activity. Each line represents the effect of the human activity in the respective functional component. The black square is the effect size, and the horizontal line is its confidence interval. When the confidence interval touches 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 the human activity

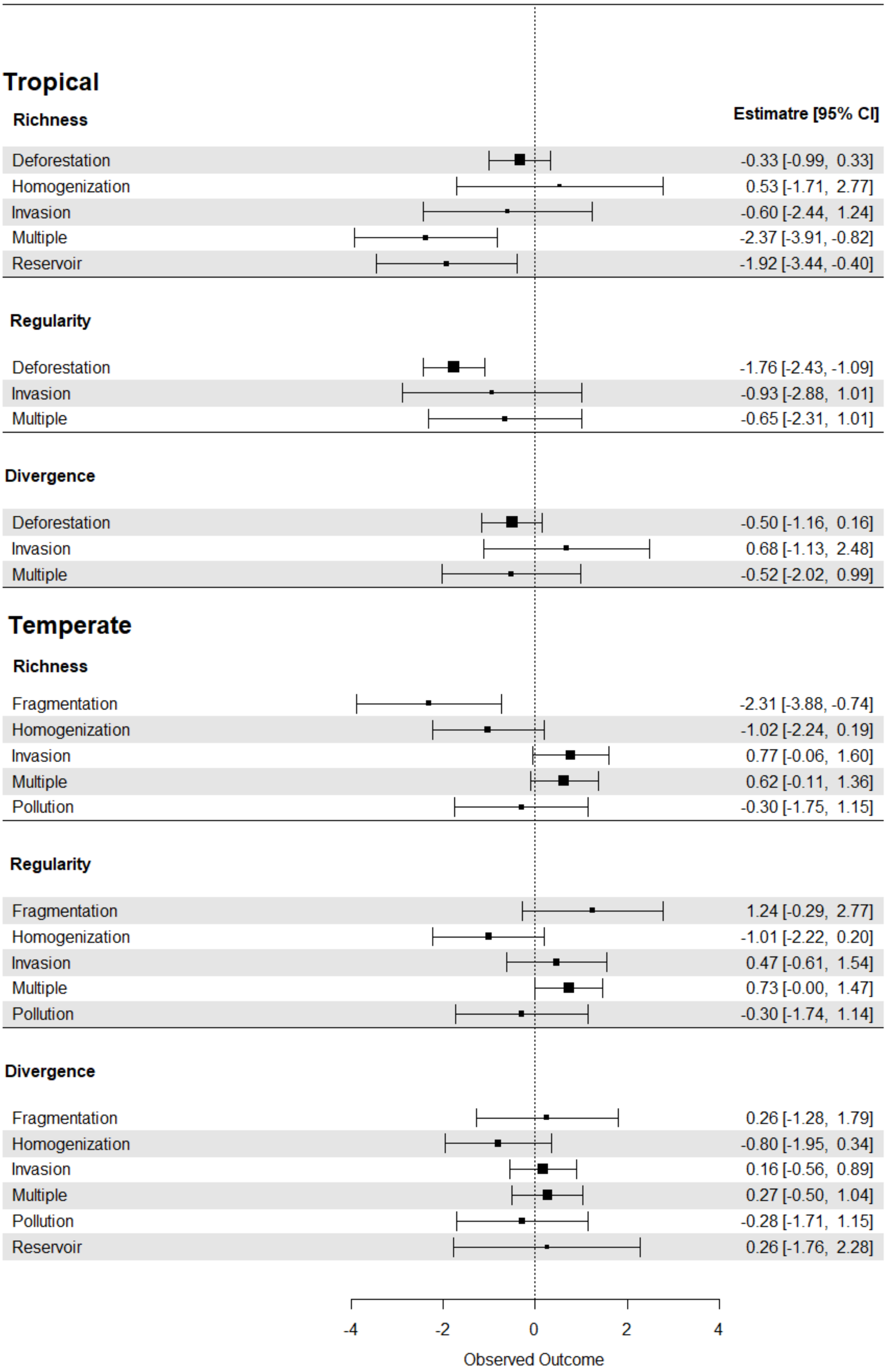

Figure 4. Effect size of each functional component divided by the human activity and the climate region. Each line represents the effect of the human activity in the respective

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 the human activity

Discussion

We predicted that human activities reduce functional diversity, that reservoirs should display the largest effects, biological invasions display the smallest effects, and that tropical regions display higher intensity of reduction. Our results partially support our main hypothesis 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 decreasing. 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 functional richness and regularity in the tropics. Also, there is a tendency to reducing functional divergence, 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.

The contrasting results found across articles, even when studying the same human activity type, scale up as a lack of generalized effect over the functional diversity 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 & Casatti, 2012).

Likewise, non-native fish species can promote higher functional diversity, especially if they have distinct traits (Rojas et al., 2021; Toussaint et al., 2018), but also, non-native species can decrease functional diversity 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 (de Bello et al., 2021; Villéger et al., 2017).

Fish functional ecology studies often rely on easily measurable traits or traits available in the 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 on 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. 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 and environments are of great importance to better understand the idiosyncrasy of each local and to create 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). 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 12 functional indices, two grouped in the functional richness component, two in the functional regularity component, and eight in the functional divergence component.

This is expected to increase the heterogeneity between observations and make it more difficult to compare the results between studies. One way to circumvent this problem 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) since they are easily calculated in the R environment.

Despite all the source of heterogeneity, we found negative effect of some human activities on functional diversity and, in the tropics, functional richness and regularity are being reduced while functional divergence seems to present the same pattern. As we expected, the negative changes on functional diversity on tropics is more intense. The reduction of functional richness 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 specific portion of the functional space which shows us that the high redundancy (Toussaint, et al., 2016) is not sufficient to refrain functional richness from decreasing. At the same time, the reduction of functional regularity shows that human activities are enhancing unbalanced distribution of organisms in the functional space (e.g. 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 (Antoniazzi et al., 2023; De Paula et al., 2022; Stefani et al., 2020). Because of this replacement, we also could expect that this unbalance is towards the center of the functional space and, consequently, directly linked to the tendency of reduction of functional divergence.

In the temperate region, we have smaller functional richness when compared with tropical sites and high trait complementarity (i.e. low redundancy) (Toussaint, et al., 2016). We could expect that the functional diversity would be sensitive even to the loss or addition of few species. Instead, our results do not show any consistent effect of changing functional diversity, which might be related to how human activities are geographically distributed.

Regarding the types of human activity, our findings show that reservoirs and multiple activities decrease functional richness, and deforestation decreases functional regularity in tropical areas while fragmentation decreases functional richness on temperate area. The enormous changes that reservoirs cause in the environment are well documented in the literature (Agostinho et al., 2008; Baxter, 1977; Carpenter et al., 2011; Rosenberg et al., 1995; Soukhaphon et al., 2021; Wu et al., 2019). Reservoirs change 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 & Mello, 1990). Reservoirs also lead to environmental homogenization (Poff et al., 2007), facilitate the introduction of non-native species (Bernery et al., 2022; Han et al., 2008; Turgeon et al., 2019), and constrain the migration of migratory species (Pelicice et al., 2015). All these changes favor generalist species with sedentary behavior (Cunico & Agostinho, 2006; Perônico et al., 2020), mostly nekton-benthic species (Dos Santos et al., 2017), thus reducing functional diversity.

Analyzing the distribution of human activities between tropical and temperate areas, we observed that studies focusing on the effect of reservoirs are mostly found for tropical ecosystems. This happens because articles assessing the effects of reservoirs in temperate ecosystems consider other sources of impact, usually using environmental integrity indices, then being classified as “multiple” (e.g., Wang et al. 2021; Lin et al. 2021). This type of human activity decreases the functional richness in the tropical region but not on temperate and this pattern is related both to the idiosyncrasy of the functional richness 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 reservoirs (Lin et al., 2021; Wang et al., 2021) and urbanization (Antoniazzi 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 on the temperate region, two studies evaluated the loss of connectivity of lakes with the main channel of a basin and we entitled this activity as fragmentation. This activity 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 (Jiang et al., 2021; Liu & Wang, 2018). Although it lowers functional richness, our results are based on two studies and should be interpreted with caution.

The functional regularity 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 (De Paula et al., 2022; Giam et al., 2015) or when it gains heterogeneity due to increased plant production (Teresa & Casatti, 2012), the changes results 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.

We found that changes in functional diversity are context-dependent, but human activities consistently exclude unique traits while increase trait dominance of tropical fish communities. As most tropical sites are in developing countries, this problem must be addressed with urgency to reduce future losses on functional diversity due to the development of these areas. At the temperate region, invasive species seems to increase functional diversity, 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 on how the environment is related to the functional traits and how human activities alter the environment to properly understand how human activities affect functional diversity. This will also enhance the robustness and predictions of the functional diversity 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 do not limit a site to a specific human activity when they probably suffer from multiple stressors. Finally, the study of functional diversity should follow standard approaches, such the Handbook of trait-based Ecology (de Bello et al., 2021) 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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Supplementary Materials

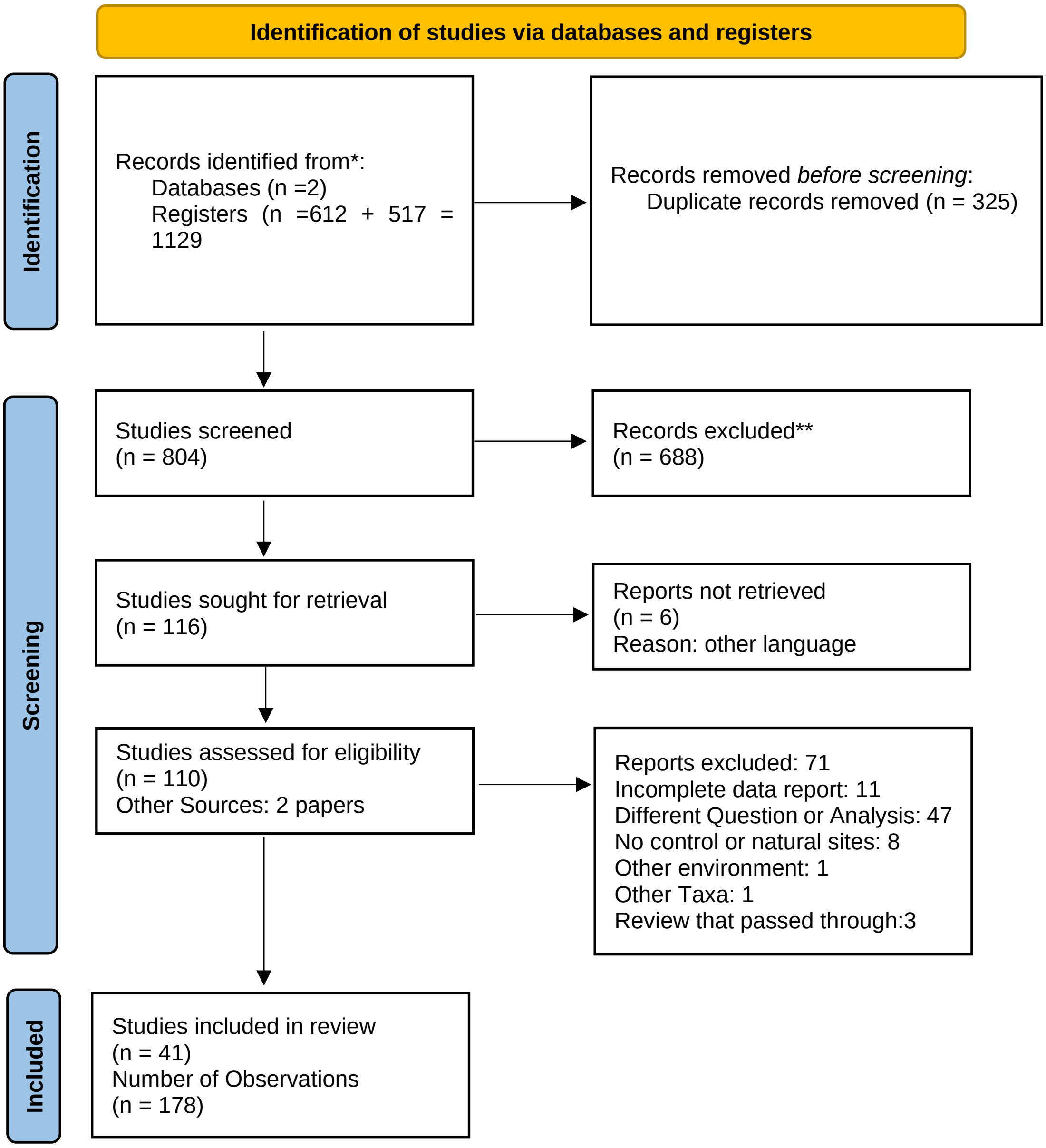

Figure 5. PRISMA diagram depicting the steps of paper selection for this meta-analysis.

Table 2. List of papers, their DOI and the set of moderators that appears on each. The last two lines are the total of observations (each sample unit of the meta-analysis) and the total of occurrence (number of papers in which some moderator appeared). Div: Functional Divergence, Reg: Functional Regularity, Ric: Functional Richness, Def: Deforestation, Frag: Fragmentation, Homo: Homogenization, Inv: Invasion, Mul: Multiple, Pol: Pollution, Res: Reservoir, Tem: Temperate, Tro: Tropical.

Article ID				Functional Component			Human Activity							Climate	
ID	**Authors**	**Year**	**DOI**	**Div.**	**Reg.**	**Ric.**	**Def.**	**Frag.**	**Homo.**	**Inv.**	**Mul.**	**Pol.**	**Res.**	**Tem.**	**Tro.**
1	Antoniazzi et al.	2023	10.3389/fenvs.2022.965291	1	1	1					3			3	
2	Brejão et al.	2020	10.1590/1982-0224-2020-0031			2							2		2
3	Cantera et al.	2022	10.1038/s41467-022-30842-2			1	1								1
4	Cantera et al.	2023	10.1186/s13717-023-00463-8	2	2	2	6								6
5	Colin et al.	2022	10.3390/w14030355	2	2							4		4	
6	Côte et al.	2022	10.1002/eap.2845		4	4					8			8	
7	Dias et al.	2022	10.1111/faf.12524	1		1					2				2
8	Freitas et al.	2021	10.1590/1982-0224-2021-0098			1	1								1
9	Giam et al.	2015	10.1111/cobi.12483	2	1	1	4								4
10	Jia	2020	10.1007/s10750-020-04244-8	1	1	1					3			3	
11	Jiang et al.	2021	10.1016/j.scitotenv.2020.144177	1	1	1		3						3	
12	Lamothe et al.	2019	10.1111/fwb.13395	2		1					3			3	
13	Larentis et al.	2022	10.1007/s10750-021-04756-x	6		1	7								7
14	Li et al.	2022	10.1002/ece3.9156	1									1	1	
15	Lin et al.	2021	10.7717/peerj.11824	1	1	1					3			3	
16	Liu & Wang	2018	10.1111/cobi.13142	1	1	1		3						3	
17	Matsuzaki et al.	2013	10.1111/geb.12067			1				1				1	
18	Matsuzaki et al.	2016	10.1111/fwb.12774			1				1				1	
19	Milardi et al.	2020	10.1016/j.scitotenv.2019.134364	1						1				1	
20	Miiller et al.	2021	10.1590/1982-0224-2020-0134	6	3	3	12								12
21	Nascimento et al.	2022	10.1007/s00027-022-00865-4	2	2	2			6					6	
22	Parra et al.	2023	10.1007/s10499-023-01096-6	3	1	1				5					5
23	Paula et al.	2022	10.1007/s10750-020-04507-4	6	2	2	10								10

Article ID				Functional Component			Human Activity							Climate	
ID	**Authors**	**Year**	**DOI**	**Div.**	**Reg.**	**Ric.**	**Def.**	**Frag.**	**Homo.**	**Inv.**	**Mul.**	**Pol.**	**Res.**	**Tem.**	**Tro.**
24	Pease et al.	2015	10.1007/s10750-015-2235-z			2					2			2	
25	Pereira et al.	2021	10.1111/btp.12896	2	2	2					6				6
26	Perônico et al.	2020	10.1007/s10750-019-04117-9			5							5		5
27	Quirino	2021	10.1007/s00027-020-00768-2			2			2						2
28	Rojas et al.	2020	10.1016/j.gecco.2020.e01355			1					1			1	
29	Rojas et al.	2021	10.1016/j.ecolind.2021.108364	3		1				4				4	
30	Sagouis et al.	2017	10.1111/eff.12306	2	2					4				4	
31	Sánches-Pérez et al.	2020	10.1016/j.scitotenv.2020.138989	3					1	2				3	
32	Shuai et al.	2018	10.1007/s10530-018-1751-y	2	1	1				4				4	
33	Silva et al.	2022	10.1007/s10452-022-09946-w	6	1	1	8								8
34	Souza et al.	2021	10.1590/1982-0224-2021-0033			1				1					1
35	Stefani et al.	2020	10.1016/j.scitotenv.2020.139902	2		1				3				3	
36	Teresa & Casatti	2012	10.1111/j.1600-0633.2012.00562.x	3	3	3	9								9
37	Torres-Bejarano et al.	2022	10.1007/s10452-021-09904-y	8	4		12								12
38	Wang et al.	2021	10.1016/j.jenvman.2021.112863	3	1						4			4	
39	Wilkinson et al.	2018	10.1016/j.biocon.2018.04.004			4	4								4
40	Zhao et al.	2019	10.1007/s00442-018-4311-3	2	1	1				4				4	
41	Zhao et al.	2021	10.1016/j.chemosphere.2020.127994	6	3	3						12		12	
Total Observations		178	-	81	40	57	74	6	9	30	35	16	8	81	97
Total of Studies		41	-	29	22	34	11	2	3	11	10	2	3	23	18

Table 3. List of papers, their DOI, the number of O**bservations** (sample unit) in each paper, the **Type** of data mean and error (Mean) or coefficient of regression value (Regression) and the **Country** where the study was conducted. *FG = French Guiana, USA = United States of America

Article ID				Other Informations		
ID	**Authors**	**Year**	**DOI**	**Observations**	**Type**	**Country**
1	Antoniazzi et al.	2023	10.3389/fenvs.2022.965291	3	Mean	USA*
2	Brejão et al.	2020	10.1590/1982-0224-2020-0031	2	Mean	Brazil
3	Cantera et al.	2022	10.1038/s41467-022-30842-2	1	Regression	Brazil, FG*, Suriname
4	Cantera et al.	2023	10.1186/s13717-023-00463-8	6	Regression	French Guiana (FG)
5	Colin et al.	2022	10.3390/w14030355	4	Mean	Chile
6	Côte et al.	2022	10.1002/eap.2845	8	Mean	France
7	Dias et al.	2022	10.1111/faf.12524	2	Regression	Brazil
8	Freitas et al.	2021	10.1590/1982-0224-2021-0098	1	Regression	Brazil
9	Giam et al.	2015	10.1111/cobi.12483	4	Mean	Borneo
10	Jia	2020	10.1007/s10750-020-04244-8	3	Mean	China
11	Jiang et al.	2021	10.1016/j.scitotenv.2020.144177	3	Mean	China
12	Lamothe et al.	2019	10.1111/fwb.13395	3	Mean	Canada
13	Larentis et al.	2022	10.1007/s10750-021-04756-x	7	Regression	Brazil
14	Li et al.	2022	10.1002/ece3.9156	1	Mean	China
15	Lin et al.	2021	10.7717/peerj.11824	3	Mean	China
16	Liu & Wang	2018	10.1111/cobi.13142	3	Mean	China
17	Matsuzaki et al.	2013	10.1111/geb.12067	1	Mean	Japan
18	Matsuzaki et al.	2016	10.1111/fwb.12774	1	Regression	Japan
19	Milardi et al.	2020	10.1016/j.scitotenv.2019.134364	1	Regression	Italy
20	Miiller et al.	2021	10.1590/1982-0224-2020-0134	12	Regression	Brazil
21	Nascimento et al.	2022	10.1007/s00027-022-00865-4	6	Mean	Brazil
22	Parra et al.	2023	10.1007/s10499-023-01096-6	5	Mean	Brazil

Article ID				Other Informations		
ID	**Authors**	**Year**	**DOI**	**Observations**	**Type**	**Country**
23	Paula et al.	2022	10.1007/s10750-020-04507-4	10	Mean	Brazil
24	Pease et al.	2015	10.1007/s10750-015-2235-z	2	Regression	USA
25	Pereira et al.	2021	10.1111/btp.12896	6	Mean	Brazil
26	Perônico et al.	2020	10.1007/s10750-019-04117-9	5	Mean	Brazil
27	Quirino	2021	10.1007/s00027-020-00768-2	2	Regression	Brazil
28	Rojas et al.	2020	10.1016/j.gecco.2020.e01355	1	Mean	Chile
29	Rojas et al.	2021	10.1016/j.ecolind.2021.108364	4	Mean	Chile
30	Sagouis et al.	2017	10.1111/eff.12306	4	Regression	France
31	Sánches-Pérez et al.	2020	10.1016/j.scitotenv.2020.138989	3	Regression	Portugal, Spain
32	Shuai et al.	2018	10.1007/s10530-018-1751-y	4	Regression	China
33	Silva et al.	2022	10.1007/s10452-022-09946-w	8	Mean	Brazil
34	Souza et al.	2021	10.1590/1982-0224-2021-0033	1	Regression	Brazil
35	Stefani et al.	2020	10.1016/j.scitotenv.2020.139902	3	Regression	Italy
36	Teresa & Casatti	2012	10.1111/j.1600-0633.2012.00562.x	9	Mean	Brazil
37	Torres-Bejarano et al.	2022	10.1007/s10452-021-09904-y	12	Mean	Colombia
38	Wang et al.	2021	10.1016/j.jenvman.2021.112863	4	Mean	China
39	Wilkinson et al.	2018	10.1016/j.biocon.2018.04.004	4	Mean	Malasyan Borneo
40	Zhao et al.	2019	10.1007/s00442-018-4311-3	4	Regression	France
41	Zhao et al.	2021	10.1016/j.chemosphere.2020.127994	12	Mean	China
Total of Studies: 41			Total of Observations: 178			

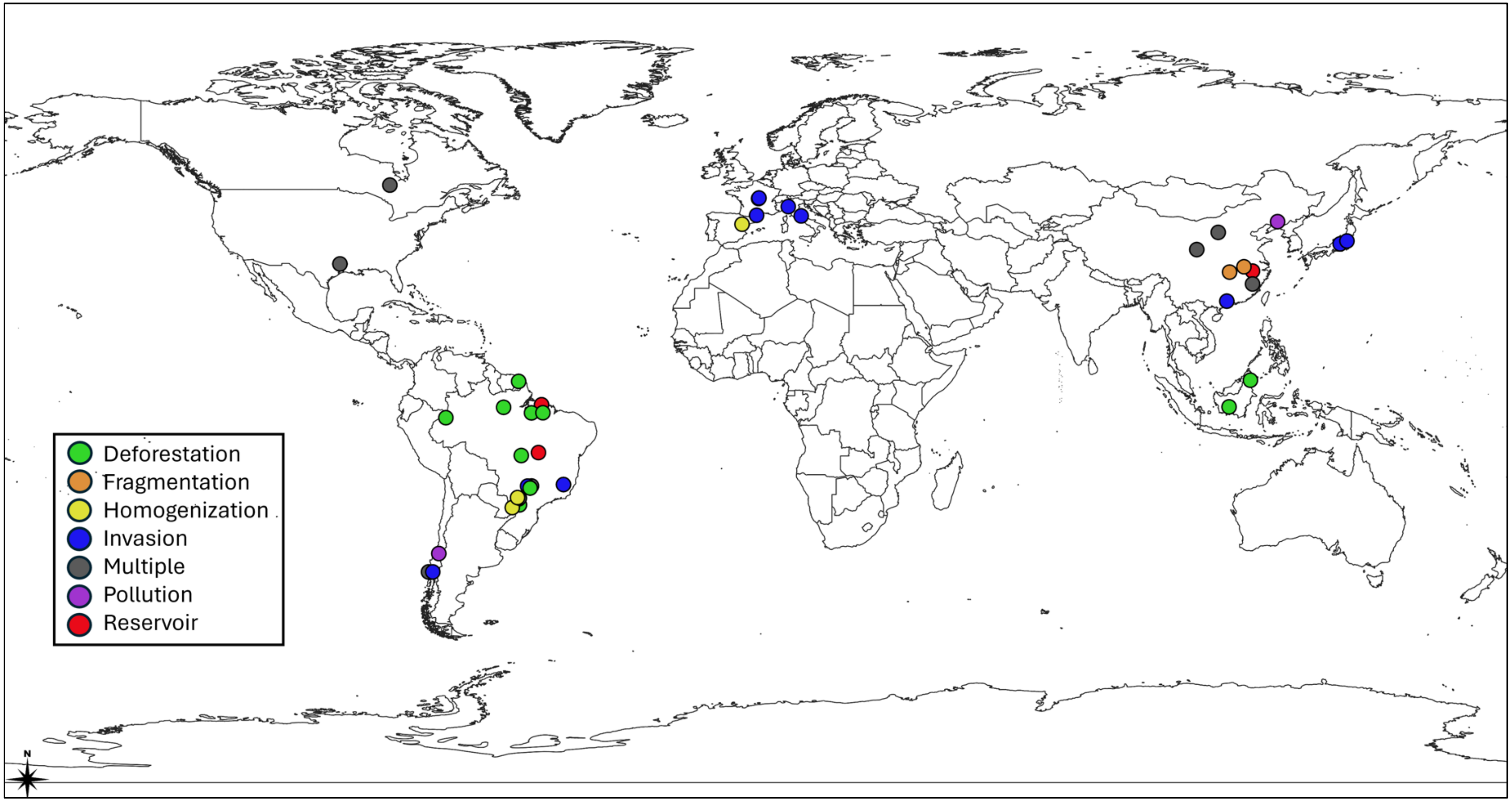

Figure 6. Global distribution of assessed studies. Each dot is the mean coordinates of the study.