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Citation

Scherer, L., Boom, H. A., Barbarossa, V., & Bodegom, P. M. van. (2023). Climate change threats to the global functional diversity of freshwater fish. *Global Change Biology*, 29(13), 3781-3793. doi:10.1111/gcb.16723

Version: Publisher's Version

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Note: To cite this publication please use the final published version (if applicable).

Climate change threats to the global functional diversity of freshwater fish

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Abstract

Climate change impacts on freshwater ecosystems and freshwater biodiversity show strong spatial variability, highlighting the importance of a global perspective. While previous studies on biodiversity mostly focused on species richness, functional diversity, which is a better predictor of ecosystem functioning, has received much less attention. This study aims to comprehensively assess climate change threats to the functional diversity of freshwater fish across the world, considering three complementary metrics—functional richness, evenness and divergence. We built on existing spatially explicit projections of geographical ranges for 11,425 riverine fish species as affected by changes in streamflow and water temperature extremes at four warming levels (1.5°C, 2.0°C, 3.2°C and 4.5°C). To estimate functional diversity, we considered the following four continuous, morphological and physiological traits: relative head length, relative body depth, trophic level and relative growth rate. Together, these traits cover five ecological functions. We treated missing trait values in two different ways: we either removed species with missing trait values or imputed them. Depending on the warming level, 6%–25% of the locations globally face a complete loss of functional diversity when assuming no dispersal (6%–17% when assuming maximal dispersal), with hotspots in the Amazon and Paraná River basins. The three facets of functional diversity do not always follow the same pattern. Sometimes, functional richness is not yet affected despite species loss, while functional evenness and divergence are already reducing. Other times, functional richness reduces, while functional evenness and/or divergence increase instead. The contrasting patterns of the three facets of functional diversity show their complementarity among each other and their added value compared to species richness. With increasing climate change, impacts on freshwater communities accelerate, making early mitigation critically important.

KEYWORDS

climate extremes, freshwater ecosystems, functional divergence, functional evenness, functional richness, functional traits, global warming, streamflow change

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1 | INTRODUCTION

Within an era of massive biodiversity loss, freshwater ecosystems are especially threatened (Collen et al., 2014; WWF, 2016). Freshwater ecosystems occupy less than 2% of the surface (>3% are lakes, ponds and impoundments according to Downing et al., 2006, but almost half of the lakes are saline according to Shiklomanov, 1993) and about 0.01% of the water volume on the Earth (Shiklomanov, 1993), but comprise about 9.5% of all known animal species (Balian et al., 2008) and a similar number of, for example, ray-finned fish species (Actinopterygii) as in marine environments (Vega & Wiens, 2012). However, vertebrate populations declined much faster in freshwater than in terrestrial or marine environments (WWF, 2016), and freshwater vertebrates face a higher extinction risk than their terrestrial equivalents (Collen et al., 2014).

These declines are, among others, related to climate change, which has profound impacts on freshwater ecosystems. It warms the water and alters the flow pattern (Barbarossa et al., 2021). Besides such direct effects, it can also amplify other stressors, such as species invasions (Rahel & Olden, 2008) or harmful cyanobacterial blooms in water affected by eutrophication (Visser et al., 2016). Even at the level of climate change up to now, there is evidence that 23 of 31 freshwater ecological processes (74%) at different levels of biological organisation, from genes to the ecosystem, have been affected by climate change (Scheffers et al., 2016). For example, organisms are shrinking in body size, species shift their ranges, populations change in abundance and communities change in composition, resulting in new species interactions. This can also affect human societies, for example, through reduced fishery yields and novel disease vectors (Scheffers et al., 2016). Fish play important functional roles within their communities as predators, mediators of nutrient fluxes and some also as ecosystem engineers (Villéger et al., 2017).

Responses of freshwater fish species to climate change vary over geographical areas, which highlights the importance of providing a global perspective. This was shown most markedly by Barbarossa et al. (2021), who investigated the effects of climate extremes on the species richness of freshwater fish globally at a grid level. Species richness is a commonly measured feature of biodiversity, but functional diversity is a better predictor of ecosystem functioning because the diversity of traits links more strongly to ecosystem functioning than does the number of species (Ahmed et al., 2019; Gagic et al., 2015).

The only study known to the authors that has already examined the effects of climate change on functional diversity at a global scale was conducted by Manjarrés-Hernández et al. (2021). However, for functional diversity, they only presented boxplots with the variability across river basins, that is, without showing any spatial patterns, and only analysed functional richness. Functional richness alone cannot capture the different facets of functional diversity (Scherer et al., 2020; Villéger et al., 2008). Moreover, they have only used categorical traits to estimate functional richness, and these do not capture the variation between species as well as continuous traits (Scherer et al., 2020). Their range of climate scenarios is also limited

compared to that used by Barbarossa et al. (2021). Therefore, there is a demand to further explore the impacts of climate change on freshwater fish functional diversity.

This study aims to comprehensively assess the climate change threats to the functional diversity of freshwater fish across the world. We built on spatially explicit projections of geographical ranges under two dispersal assumptions for 11,425 riverine fish species as affected by changes in streamflow and water temperature extremes following four warming levels between 1.5°C and 4.5°C from Barbarossa et al. (2021). The two dispersal assumptions—either no dispersal beyond the historical geographical range or maximal dispersal within the same drainage basins and freshwater ecoregions—are expected to provide upper and lower estimates of functional diversity loss. Overall changes, including losses and gains, are more difficult to anticipate and could also be stronger under maximal dispersal because both species losses and gains can cause changes. We use continuous traits to estimate three complementary functional diversity metrics—functional richness, evenness and divergence.

2 | MATERIALS AND METHODS

2.1 | Functional diversity metrics

Different computation methods exist to describe each of the facets of functional diversity. Ahmed et al. (2019) evaluated various functional diversity metrics and recommended the three metrics developed by Villéger et al. (2008), covering the three facets investigated here: functional richness, evenness and divergence. Functional richness describes the volume of functional space filled by the (fish) species in a community, while functional evenness and divergence describe how evenly and distant from the centre of gravity the species are distributed within that space (Villéger et al., 2008). Functional evenness and divergence are constrained between 0 and 1, whereas functional richness represents an absolute volume and, thus, has no upper limit (Villéger et al., 2008).

Functional diversity metrics were computed using the function *dbFD_parallel* (Kim, 2018), which implemented the three metrics by Villéger et al. (2008). Kim (2018) adjusted the original *dbFD* function from the 'FD' package (Laliberté & Legendre, 2010) to reduce the computation time for large datasets. For this study, we adjusted the *dbFD_parallel* function further to reduce the computation time of the functional evenness component. The computation of functional evenness requires a minimal spanning tree. This process was optimised by replacing the *mst* function from the 'ape' package (Paradis & Schliep, 2019) with the *spanntree* function from the 'vegan' package (Oksanen et al., 2020).

Input data to compute the functional diversity metrics were twofold: (1) trait data for the freshwater fish species (section 2.2) and (2) presence–absence data per species per geographical location on a world grid for different climate scenarios (section 2.4). Ideally, abundance data would be used instead of presence–absence data. However, species abundance was unknown, and

the functional diversity metrics are also suitable for presence-absence data (Villéger et al., 2008). Before the functional diversity metrics computation, the trait data (all continuous values) were standardised to a mean of 0 and unit variance. Additionally, for the presence-absence data of each climate scenario, a hypothetical geographical location was added where each species was present. This ensured that, during the functional diversity computations for each scenario, the same list of species was considered and, thereby, the functional diversity metrics were comparable across the scenarios.

2.2 | Trait data

The selection of fish traits was based on their (1) relevance to and broad joint coverage of ecological functions and ideally also trait categories, (2) availability in the FishBase database (Froese & Pauly, 2021) and (3) complementarity through a weak correlation among them, similar to the selection of plant traits by Scherer et al. (2020).

The relevance of commonly used traits to ecological functioning was analysed through a literature review. The fish traits were related to five ecological functions: food acquisition, locomotion, nutrient processing, reproduction and predator-prey interactions (also known as survival) (Villéger et al., 2017). Additionally, they were classified into four trait categories: morphology, life history, physiology and behaviour (Martini et al., 2021). A trait within a specific trait category can relate to multiple ecological functions.

Forty-two traits were selected and extracted from FishBase (Table S1.1) by using the R package 'fishbase' (Boettiger et al., 2012). Where multiple observations were available per fish species, the values were aggregated through the arithmetic mean for continuous traits and the mode for categorical traits. The trait set was reduced by excluding traits with 70% or more missing values (except for food type with 72% missing values to evaluate the correlation with the trophic level later on). This resulted in 16 traits (Table S1.2). We also analysed the co-occurrence of missing trait values across species by multivariate statistics to lower the number of affected species (Figures S1.1 and S1.2).

Functional diversity estimates depend, among others, on the trait selection. We intentionally selected only continuous traits. The inclusion of categorical traits could potentially have lowered the number of missing trait values (e.g., the categorical body shape contains fewer missing values than the continuous relative body depth we selected) or allowed for the consideration of additional trait categories (the categorical reproduction mode is a life history trait, while we only considered morphological and physiological traits). Categorical traits also avoid issues with inconsistent measurement methods, as categorical traits are unitless, which might make them more reliable and comparable (Ladds et al., 2018). However, several functional diversity metrics, including the ones used here, were designed for continuous traits. Although there are some workarounds to make them applicable to categorical traits, such procedures can lead to

information loss or the meaning of the metrics changes. Therefore, Schleuter et al. (2010) advise against using categorical traits.

Based on optimal coverage across ecological functions and trait categories, our final selection of traits consisted of the following four: relative head length, relative body depth, trophic level and relative growth rate, making it a balanced coverage of two morphological and two physiological traits. These traits covered all five ecological functions (Table S1.2). The relative head length and trophic level covered food acquisition (Da Silva et al., 2019; Pease et al., 2012, 2015; Wiedmann et al., 2014). The body depth represented locomotion (Buisson et al., 2013; Frimpong & Angermeier, 2009; Pease et al., 2012, 2015). The relative body depth and trophic level covered nutrient processing (Villéger et al., 2017). The relative growth rate and trophic level represented reproduction (Frimpong & Angermeier, 2009). Finally, the trophic level (Wiedmann et al., 2014) and relative head length (Da Silva et al., 2019; Ford & Roberts, 2020) covered predator-prey interactions. The four selected traits contained about 37% of missing values, and in most cases, such missing values occurred with the same species (Figure S1.2). Spearman's rank correlation coefficients ranged from -0.19 to 0.35 (Figures S1.3 and S1.4).

To detect potentially erroneous trait values, the four selected traits were checked for their natural bounds and outliers. This was done for the original data extracted from FishBase before aggregating traits in the case of multiple observations per species. One negative value indicated an erroneous value and was removed (Table S2.3). Possible outliers were identified by applying the interquartile method (Salgado et al., 2016) (Figure S2.6). Outliers that were found either seemed accurate according to the original references linked in FishBase or could not be verified due to a lack of references. Thus, outliers were neither excluded nor replaced.

The computation of functional diversity metrics was based on two different fish trait datasets (Scherer et al., 2023): (1) removing species with one or more missing trait values and (2) imputing missing trait values across fish species. Removing species with missing trait values resulted in a trait dataset for 3792 fish species.

Three imputation methods were examined: phylogenetic imputation, Multiple Imputation by Chained Equations (MICE) and imputations with random forest algorithms (missForest). These methods were used before to handle missing trait values (Johnson et al., 2021; Penone et al., 2014; Taugourdeau et al., 2014). The phylogenetic imputation is a trait evolution analysis that requires a phylogenetic tree. It was conducted by using the R package 'Rphylopars' (Goolsby et al., 2017) and data from the Fish Tree of Life (Rabosky et al., 2018) through the R package 'fishtree' (Chang et al., 2019). Matching fish species from the phylogenetic tree with those used in this study would disregard about 55% of the species. Although a stochastically resolved phylogenetic tree would lead to much fewer unmatched species, Rabosky (2015) generally advises against their use in analyses involving traits. Therefore, phylogenetic imputation was excluded. For MICE, the predictive mean matching method was applied. With this method, data were imputed by matching observed values between traits (Johnson et al., 2021). MissForest is a

nonparametric imputation method that uses trained random forest predictions (Penone et al., 2014) (see Appendix S2 for further details on the imputation methods). The most accurate imputation method was selected by fivefold cross-validation with three performance indicators: the normalised root mean square error (NRMSE), per cent bias (PBIAS) and coefficient of determination (R^2). Given that two out of three indicators (NRMSE and R^2) suggested that the missForest imputation performed better (Table S2.4), this method was chosen to impute missing trait values across species.

2.3 | Species' geographical ranges

The geographical ranges of 11,425 riverine fish species were obtained from Barbarossa et al. (2021), who compiled them from multiple data sources. Most of them are from the IUCN Red List of Threatened Species database (IUCN, 2018). Others are from the Amazonfish dataset (Jézéquel et al., 2020) or Barbarossa et al. (2020), who delineated them based on point occurrence records, following a similar approach as used for the IUCN database. The dataset covers partially or entirely lotic fish species (living in flowing water) but excludes entirely lentic species (living in standing water). Moreover, it includes both native and exotic species.

2.4 | Climate scenarios

The climate scenarios were based on spatial data at a resolution of 5 arcminutes (~10 kilometres at the equator) from Barbarossa et al. (2021), who considered the five global climate models (GCMs) included in the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP) (Warszawski et al., 2014): HadGEM2-ES from the Met-Office Hadley Centre, IPSL-CM5A-LR from the Institute Pierre Simon Laplace Climate Modelling Centre, MIROC-ESM-CHEM from a Japanese consortium (University of Tokyo, NIES and JAMSTEC), GFDL-ESM2M from the Geophysical Fluid Dynamics Laboratory and NorESM1-M from a consortium of Norwegian universities and institutes. The historical scenario represented the period 1976 to 2005. For future scenarios, the five GCMs were combined with four Representative Concentration Pathways (RCPs) (RCP 2.6, 4.5, 6.0 and 8.5) that represent trajectories of greenhouse gas emissions towards a certain radiative forcing in 2100. The future scenarios represented four warming levels—1.5°C, 2.0°C, 3.2°C and 4.5°C—relative to the pre-industrial reference period 1850–1900. The warming levels were reached at different points in time for each GCM-RCP combination and sometimes only outside of the modelling period until 2100. This resulted in 42 future scenarios.

Based on these scenarios, Barbarossa et al. (2021) defined five climate extremes: the maximum and minimum weekly water temperature, maximum and minimum weekly streamflow and the number of zero-flow weeks. For each climate extreme, species-specific thresholds were defined and estimated from each species' geographical range for a historical scenario (Barbarossa et al., 2021). For

each future scenario and each grid cell, it was evaluated whether a climate extreme exceeded the threshold of a fish species within its (potentially extended) geographical range. Exceeding one or more climate extreme thresholds implied that the respective fish species was assumed to become absent at that location. As in Barbarossa et al. (2021), we made two dispersal assumptions. First, 'no dispersal' of fish species occurs, where species cannot move beyond the geographical range they occupy in the historical scenario. Second, 'maximal dispersal' occurs, where fish species can move beyond their historical geographical range within a surrounding region delineated by the intersection of the physical boundary represented by the drainage basins and ecological conditions represented by freshwater ecoregions. Under this assumption, the geographical ranges in the historical situation were also adjusted to account for dispersal (Barbarossa et al., 2021). To get from 42 scenarios to aggregated scenarios for the historical situation and the four warming levels, presence-absence estimates of fish species were aggregated using its median value within a grid cell. After aggregation for each species individually, all fish species were combined in one presence-absence matrix per aggregated scenario, containing the locations on a world grid and the fish species.

2.5 | Functional diversity loss calculation

Functional diversity loss (subscript loss) was assessed for each functional diversity metric (FD) by comparing the functional diversity under environmental pressure to the reference situation (Scherer et al., 2020), here the different warming levels (subscript warming) and the historical scenario (subscript historical):

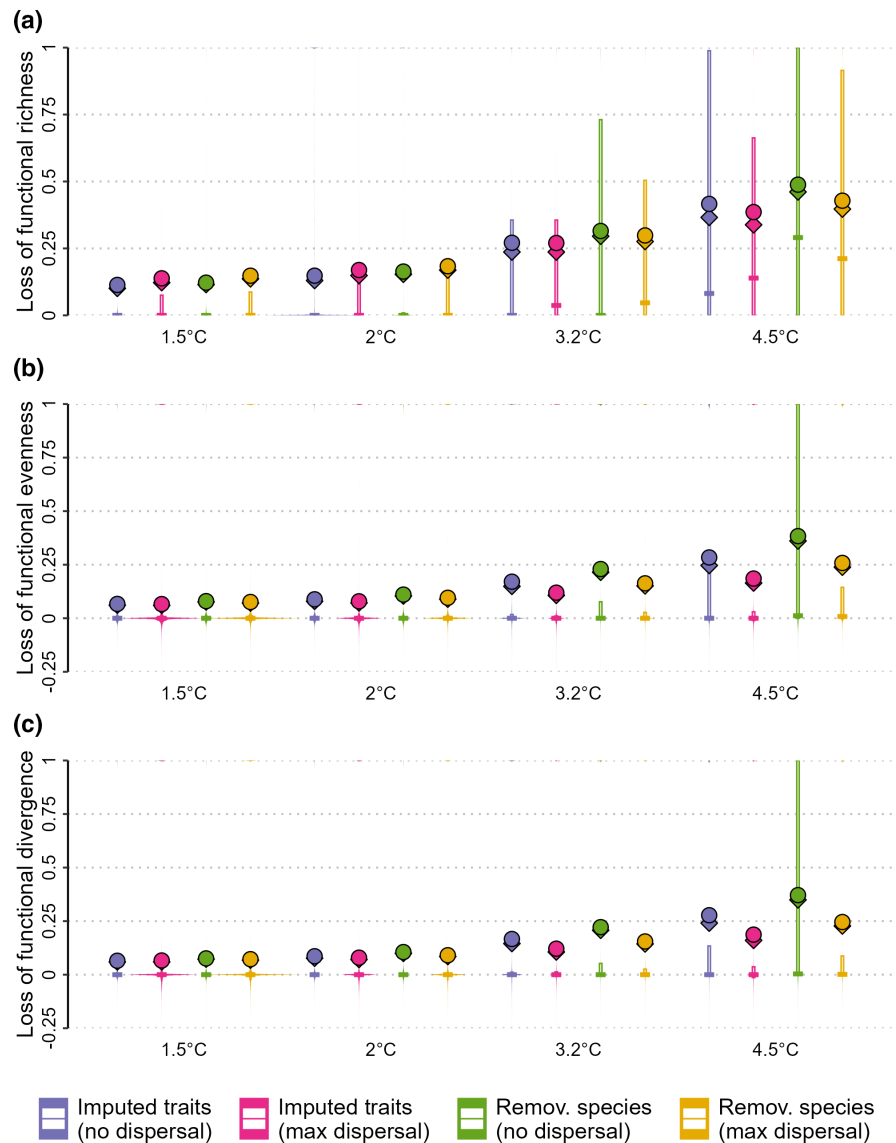
$$FD_{\text{loss}} = 1 - \frac{FD_{\text{warming}}}{FD_{\text{historical}}}$$

A loss of 1 indicates a complete loss of functional diversity for a specific metric, whereas 0 indicates no loss. The range between 0 and 1 indicates a partial loss. For functional evenness and divergence and, in general, under maximal dispersal, it is also possible to achieve gains instead of losses, implying negative loss values. For functional richness, the assumption of no dispersal prevents any gains. The spatial data on functional diversity and its loss are available from Scherer et al. (2023).

3 | RESULTS

Climate change threatens all three aspects of fish functional diversity at all warming levels (Figure 1). At some locations, there were small gains in functional evenness and divergence (represented by negative losses), especially under maximal dispersal. Functional richness could only stay constant or reduce when assuming no dispersal, but there were also never gains in functional richness when assuming maximal dispersal. Overall, losses of functional richness are

FIGURE 1 Loss of functional richness (a), evenness (b) and divergence (c) at different warming levels and with different trait datasets and dispersal assumptions. The violins show the distribution across grid cells. Within each violin, the white boxes represent the interquartile range; the horizontal line, the median; the diamonds, the unweighted average; and the circles, the area-weighted average. Note that values below -0.25 are cut off for visualisation purposes.



higher than for evenness and divergence (Figures S3.25–30). Losses are higher when weighing them by the grid-cell areas, as losses are generally higher at lower latitudes where the grid-cell areas are larger (Figure S4.40).

Using the dataset with imputed trait values as opposed to the dataset where species with missing trait values had been removed results in slightly lower losses (Figure 1). The dataset with fewer species (i.e., without imputation) lacks grid cells especially in high latitudes where the functional diversity losses are smaller (Figure S3.7). Removing these locations in the imputed dataset, however, results in losses that more closely resemble those based on the imputed dataset with all locations than those based on the dataset with fewer species, especially for functional evenness and divergence (Figures S4.38 and S4.39). Hence, the consideration of fewer species has a larger influence than fewer locations. This suggests that any lost species has a larger proportional effect in a dataset with fewer species or that the species that had to be removed were generally less sensitive to climate threats. Functional richness is clearly influenced by both factors. Overall, it shows that the imputation of

missing trait values was important to cover both more species and locations and, thus, produce a more representative projection of functional diversity impacts.

Assuming maximal dispersal rather than no dispersal, losses can sometimes be higher at lower warming levels, given that the historical diversity is also assumed to be higher and more species can get lost. However, latest at a warming level of 3.2°C , climate change adaptation through dispersal reduces functional diversity loss across all metrics (Figure 1).

Functional diversity loss generally accelerates with increasing warming levels (steeper lines in Figure 2). In fact, it slows down a bit between 1.5°C and 2.0°C , especially when assuming maximal dispersal, but accelerates afterwards, especially when assuming no dispersal. The losses are faster for functional richness, but the acceleration is stronger for functional evenness and divergence.

Different functional diversity components can respond differently to climate change. At some locations, functional richness still remains intact, while functional evenness and divergence decrease. At other locations, functional richness reduces, while functional

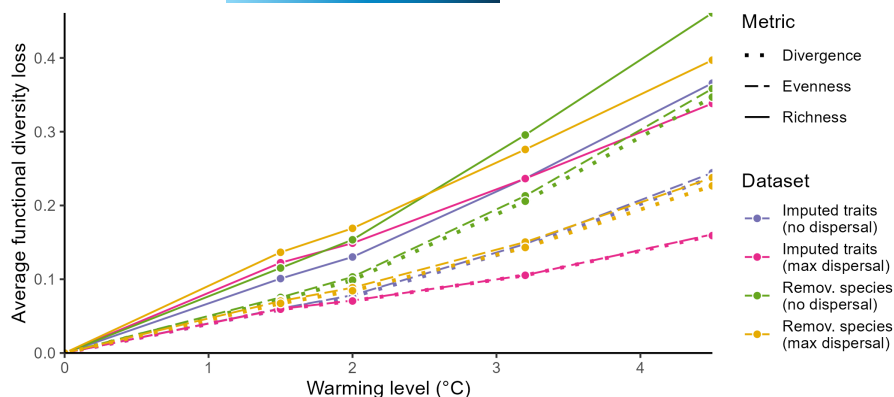


FIGURE 2 Average functional diversity loss by warming level.

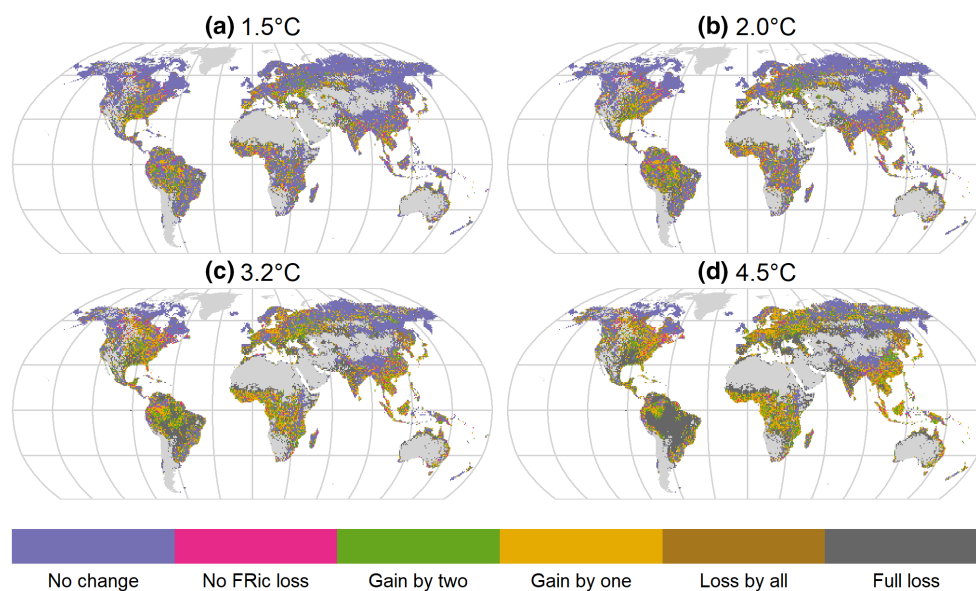


FIGURE 3 Functional diversity change categories at warming levels of 1.5°C (a), 2.0°C (b), 3.2°C (c) and 4.5°C (d), assuming no dispersal. In the underlying fish trait data, missing trait values were imputed. No change: no species get lost, and thus functional diversity does not change; no FRic loss: functional richness remains constant but functional evenness and divergence decrease; gain by two: functional evenness and divergence increase and functional richness decreases; gain by one: functional evenness or divergence increases and the other two decrease; loss by all: all functional diversity components decrease; full loss: all species and thus the entire functional diversity get lost. The original data at a 5-arcmin resolution (~10km at the equator) are displayed here with a World Robinson projection. Light grey denotes no data areas (insufficient species occurring to estimate functional diversity or no data available). See Figures S3.25, S3.27 and S3.29 for maps of the change in the individual functional diversity components, Figure S3.34 for functional change categories aggregated to the river basin level, and Figure S3.32 for maximal dispersal.

evenness, divergence, or both increase (Figure 3). The latter is especially common under maximal dispersal (Figure S4.42). Such divergent responses can occur almost anywhere around the world. However, it is more likely that no functional diversity change occurs in high northern latitudes (Figure S4.40) like polar freshwaters and temperate coastal rivers (Figure S4.45). It should be noted that any gains in some of the functional diversity components might only be temporary and transition to losses later on, such as at some locations in the Amazon River basin (Figure 3, Figures S3.32, S4.40 and S4.41).

The largest continuous area affected by a complete loss of functional diversity at higher warming levels is in the adjacent Amazon and Parana River basins in South America. Other large

river basins where complete loss at a warming level of 4.5°C is the most frequent change category across grid cells when assuming no dispersal are the Mississippi and Nelson Rivers in North America, the Danube River in Europe, the Ob, Indus and the Tigris–Euphrates Rivers in Asia, the Niger and Orange Rivers in Africa, and the Murray Darling River in Australia (Figure S3.34). Xeric freshwaters and endorheic (closed) basins like the Sahara and the Arabian Peninsula are especially affected but often data-poor (Figure 3, Figure S4.45).

While 6% of grid cells face a complete loss of functional diversity at a warming level of 1.5°C, this share increases to almost 25% at 4.5°C, assuming no dispersal (Figure 4; 17%, assuming maximal dispersal, Figure S4.42). At 4.5°C, another 7% (10%) face partial losses

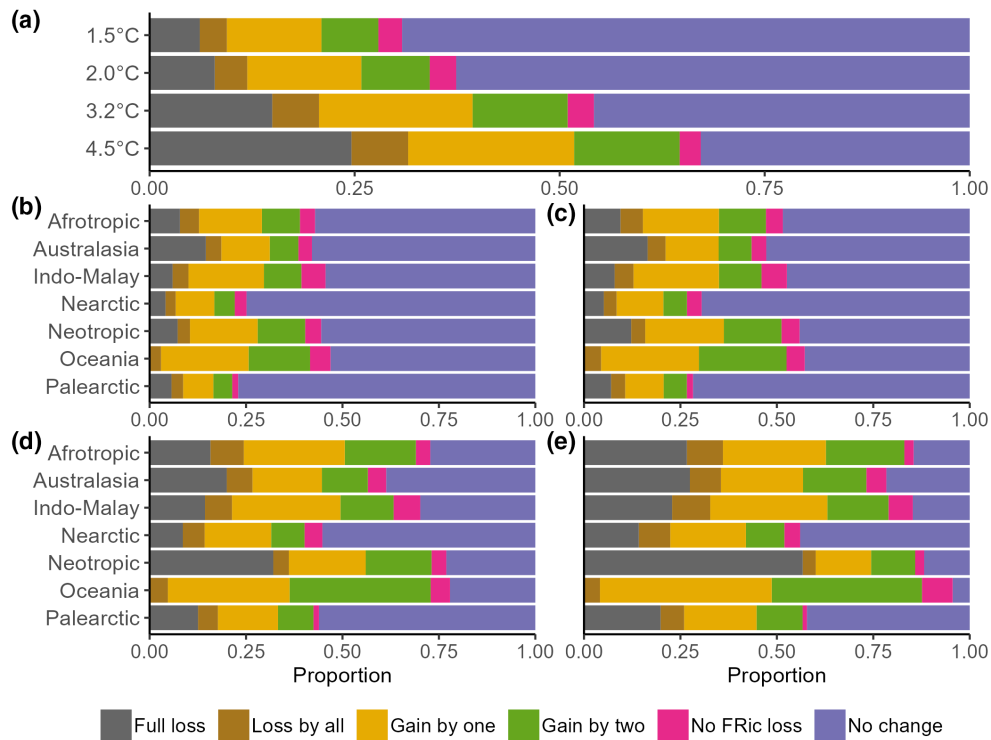


FIGURE 4 Functional diversity change categories across different warming levels (a) and biogeographic realms at warming levels of 1.5°C (b), 2.0°C (c), 3.2°C (d) and 4.5°C (e), assuming no dispersal. In the underlying fish trait data, missing trait values were imputed. No change: no species get lost, and thus functional diversity does not change; no FRIC loss: functional richness remains constant but functional evenness and divergence decrease; gain by two: functional evenness and divergence increase and functional richness decreases; gain by one: functional evenness or divergence increases and the other two decrease; loss by all: all functional diversity components decrease; full loss: all species and thus the entire functional diversity get lost. See [Figure S4.43](#) for the functional diversity change categories across different warming levels and fish trait datasets, and [Figures S4.42](#) and [S4.44](#) for maximal dispersal.

in all three functional diversity components, almost 36% (57%) show diverging patterns with gains in one or two functional diversity components or losses in functional evenness and divergence but no change in functional richness, and the remaining about 33% (17%) remain unaffected by climate change. Across biogeographic realms, Oceania is the least affected at all warming levels ([Figure 4](#)). Only a negligible amount of grid cells face complete loss at the highest warming level, and it contains the highest share of grid cells with gains in one or two functional diversity components. This is similar to the picture for oceanic islands as a major habitat type, which characterises Oceania ([Figure S4.45](#)). Australasia contains the highest share of grid cells with complete loss at lower warming levels. At higher warming levels, however, the Neotropics, where the Amazon and Paraná Rivers are located, show the highest complete losses when assuming no dispersal, while Australasia stays highest when assuming maximal dispersal.

Functional change is moderately to very strongly positively correlated with species loss ([Figure 5](#); it can be very weak for individual data points of functional evenness and divergence when assuming maximal dispersal, [Figure S4.47](#)), that is, the more species get lost, the more likely it is that functional diversity decreases as well. This applies to all three aspects of functional diversity, but the relationship is stronger for a change in functional richness than for

evenness and divergence, although the correlation of the latter two increases with warming. Functional richness is also very strongly correlated with species richness, whereas functional evenness and divergence show a very weak or weak and negative correlation with species richness ([Figure S4.48](#)), demonstrating their complementarity. A very weak or weak and negative correlation between species richness and functional change further indicates that a higher species richness makes it less likely for functional diversity loss to occur.

Although all functional change categories can occur across a wide range of historical species richness, we observe no functional richness loss or a gain in one or two functional diversity components rather at locations with higher historical species richness ([Figure 6](#)), even when species richness declines. Moreover, at the lowest warming levels, a complete loss tends to occur at locations with low species richness. In contrast, at the highest warming level, locations with complete loss exhibit the highest average historical species richness when assuming no dispersal (the average historical species richness of locations with complete loss also increases with warming when assuming maximal dispersal, but locations with gains keep the highest species richness, [Figure S4.49](#)). It demonstrates that high species richness only provides a temporary buffer against climate change threats.

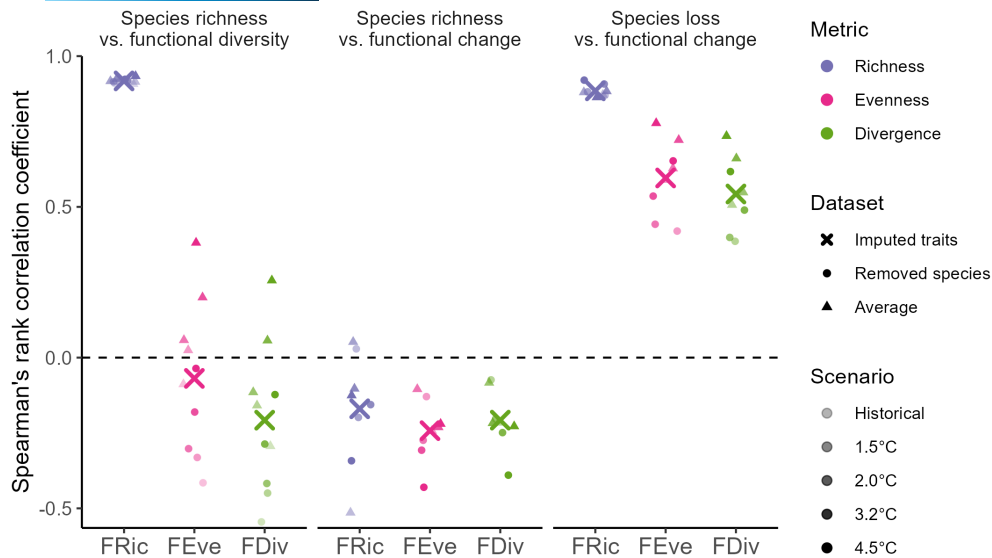


FIGURE 5 Spearman's rank correlation between species richness and functional diversity or changes thereof, assuming no dispersal. Points of one colour represent the different warming levels and the two datasets (imputed traits vs. removed species). Crosses represent the averages. The points include random horizontal noise (jitter) to avoid overlaps. See [Figure S4.47](#) for maximal dispersal.

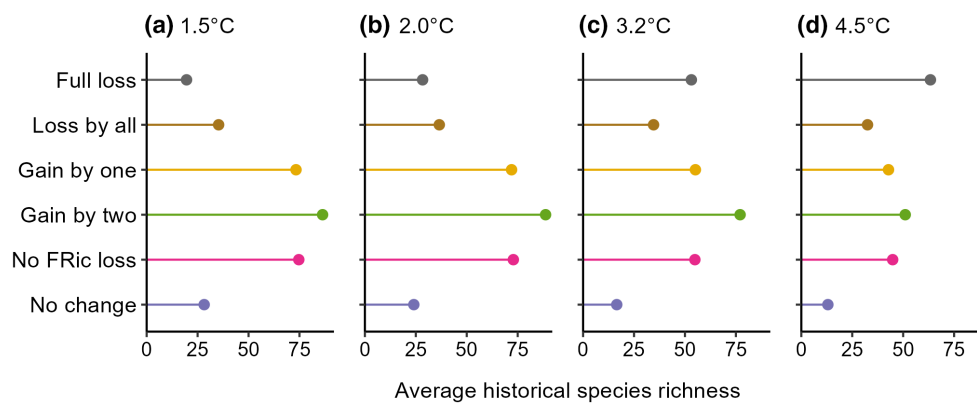


FIGURE 6 Average historical species richness across functional diversity change categories at warming levels of 1.5°C (a), 2.0°C (b), 3.2°C (c) and 4.5°C (d), assuming no dispersal. In the underlying fish trait data, missing trait values were imputed. No change: no species get lost, and thus functional diversity does not change; no FRic loss: functional richness remains constant but functional evenness and divergence decrease; gain by two: functional evenness and divergence increase and functional richness decreases; gain by one: functional evenness or divergence increases and the other two decrease; loss by all: all functional diversity components decrease; full loss: all species and thus the entire functional diversity get lost. See [Figure S4.49](#) for maximal dispersal.

4 | DISCUSSION

Assessments of functional diversity changes provide complementary information to species losses. Although functional richness is strongly correlated with species richness, which was already assessed in global climate change scenarios by Barbarossa et al. (2021), these two facets of biodiversity do not change consistently everywhere. In 6%–12% of grid cells apart from those with either no or complete biodiversity loss, no functional richness loss occurs despite species loss. Furthermore, functional evenness and divergence are only weakly and negatively correlated with species richness, and even their relative changes are only moderately correlated with relative species losses when assuming no dispersal and weakly

correlated when assuming maximal dispersal. Thus, assessing functional diversity changes provides new insights.

Consideration of functional diversity is more complex and data-intensive than species richness. In addition to spatially explicit information on species, it requires species-specific information on functional traits. Such traits are not available for all species, implying that either species need to be removed or missing trait values imputed. We have done both and found significant differences in the assessments with both datasets. An assessment with fewer species and, thus, fewer locations considered leads to an overestimation of functional diversity loss. Although imputation entails uncertainties, we believe that the gains in the number of species and the spatial coverage are more important.

The spatial patterns differ among the three facets of functional diversity and their responses to climate change. For example, at some locations, functional richness is not yet affected despite species loss, while functional evenness and divergence start decreasing. At other locations, it might even happen that some facets are losing, while others are gaining (evenness and/or divergence). Alahuhta et al. (2018) confirmed through their literature review that climate change could have multiple and contrasting effects on functional diversity across different facets (and species groups). These contrasts demonstrate the complementarity and the importance of considering more than one facet of functional diversity. It also seems remarkable that, at the lower warming levels (1.5°C and 2.0°C), the majority of locations (>60%) do not yet face functional diversity change when assuming no dispersal, although this share reduces to about a third when assuming maximal dispersal.

The contrasting patterns in biodiversity change depend on the type of species that get lost. For example, only the species with the most extreme trait values determine functional richness, and it is independent of the abundance of species with such extreme trait values (Villéger et al., 2008). So, if the species that get lost and reduce species richness are species with less extreme trait values or species that are functionally redundant to others with the same extreme trait values, it does not affect functional richness. Functional evenness and divergence seem to be especially good predictors of ecosystem functions provided by animals. High functional evenness and divergence suggest functional complementarity, making the relationship with ecosystem functioning mostly positive, although it can sometimes also be negative (Gagic et al., 2015). Functional evenness can increase when some of the species that are functionally most similar to other species get lost, leading to less functional overlap and a more even distribution across the functional space of the remaining species. Functional divergence can increase when the species that get lost are more generalist species close to the centre of gravity of the functional space, making the remaining specialist species with more extreme trait values relatively more abundant (Hitt & Chambers, 2014; Villéger et al., 2010). Gains in functional evenness and divergence may also be a side effect of a lower functional richness because this reduction restricts the functional space available to functional evenness and divergence (Hitt & Chambers, 2014).

Even under maximal dispersal, functional richness never increased under climate change in our scenarios. This finding is consistent with the finding by Barbarossa et al. (2021), on whose study we built, that species richness does not increase compared to the historical baseline. Although the geographical ranges of some species, especially warm-water species, are expected to expand (Comte et al., 2013), this may not be sufficient to lead to a net increase in species richness, as the ranges of other species, especially cold-water species, are expected to contract. However, others projected increases in freshwater fish species richness under climate change in some parts of the world (Markovic et al., 2014). Even if species richness increased, functional richness would not necessarily increase as well, but it could also increase proportionally more than species

richness (Toussaint et al., 2018). The change in functional richness depends on the functional similarity of the newcomers versus the loss in functional richness due to the species losses.

The Amazon River basin is one of the most strongly impacted by climate change and stands out for its large area of complete fish functional diversity loss at the higher warming levels. The Amazon rainforest might similarly face massive dieback by the end of this century as induced by deforestation and climate change. Empirical evidence already shows a pronounced loss of forest resilience, suggesting a transition towards critical thresholds (Boulton et al., 2022). In the case of freshwater ecosystems, the Amazon River basin sees relatively strong reductions in minimum and maximum weekly flow and increases in the number of zero-flow weeks and minimum and maximum weekly water temperature (Figure S5 in Barbarossa et al., 2021). According to our results, the high species richness of the Amazon River basin can only provide a buffer against such changes in climate extremes up to a certain level and then cannot withstand them any longer.

Toussaint et al. (2016) also examined the functional diversity of freshwater fish at the global scale, though they only considered functional richness as the only facet of functional diversity and only at the broad level of biogeographic realms. Instead of assessing specific threats to functional diversity like climate change, they assessed the functional vulnerability to species loss, which they defined as the share of functional diversity that is supported by threatened species. They found the largest functional richness in the neotropical realm, similar to our findings with a hotspot especially in the Amazon River basin (Figure S3.34). They also found that functional richness is negatively but not significantly correlated with functional vulnerability. This is consistent with our findings that species richness (strongly correlated with functional richness) is only very weakly and negatively correlated with functional richness loss. In contrast, they also did not find an association between the number of threatened species and functional vulnerability, whereas we found a moderate positive correlation between species loss and functional richness loss.

Su et al. (2021) investigated changes in functional richness globally at the river basin scale between roughly pre-industrial and current times. They related the changes to four environmental and four anthropogenic variables, none of which is anthropogenic climate change as assessed here. They found that functional richness in most basins increased, including the Amazon River basin. Basins with losses in functional richness are especially found in Siberia, like the Lena River, but not in western Siberia, like the Ob River. Their observations contrast the spatial patterns modelled in our assessment, where high northern latitudes like Siberia are generally little affected by climate change threats, but the Ob River is among the major rivers projected to lose more than 50% of functional richness at a warming level of 4.5°C when assuming no dispersal (Figure S3.36; functional richness loss in the Ob River is lower when assuming maximal dispersal but still higher than in most other parts of Siberia, Figure S3.37).

The magnitude of functional diversity loss depends on the dispersal assumption. We assumed either no dispersal of fish species, that is, each fish species is confined to its current geographical

range, or maximal dispersal within a fish species' current watershed and freshwater ecoregion. Like Barbarossa et al. (2021), we generally found lower threat levels for freshwater fish species when assuming maximal instead of no dispersal (with some exceptions at lower warming levels). Both dispersal assumptions are likely to be unrealistic, and the truth lies somewhere between the two. Freshwater fish species have been shown to shift their ranges in response to climate change, yet their pace is likely to be too slow to keep up with climate change, and they are constrained by the upstream–downstream structure of the river basins as well as potential physical barriers like dams (Comte & Grenouillet, 2013). River fragmentation due to dams is likely to increase considerably in the future (Barbarossa et al., 2020) due to a global boom in hydropower (Zarfl et al., 2015), especially in megadiverse tropical rivers (Winemiller et al., 2016), which further limits dispersal. In contrast, dispersal might also occur across river basins and go beyond what we considered maximal dispersal in the case of human-assisted intentional and unintentional translocation of species (Bernery et al., 2022; Su et al., 2021). While generally presenting results for both dispersal assumptions, it is not always convenient, and we then focus on the no-dispersal assumption to follow a precautionary principle (Brysse et al., 2013). For future research, we recommend considering partial-dispersal scenarios, which, however, increase the data and computational requirements (Bateman et al., 2013).

The accelerating climate change impacts make early mitigation even more important. Any climate change impacts we can already observe nowadays will be less than the magnitude of the impacts in the future. Moreover, it is more difficult to predict what we can expect from the future. The acceleration also implies that limiting climate change makes an even bigger difference because future functional diversity losses will be larger than expected under a simple linear extrapolation.

The projections of functional diversity loss under climate change can help make conservation planning more effective. Only by considering ongoing and future threats in conservation planning, biodiversity persistence can be safeguarded (Reside et al., 2018). Designing conservation actions with a view into the future may be suboptimal in the short run but will pay off in the long run (Scherer et al., 2017). However, it requires further research on how to define conservation priorities under trade-offs between different facets of functional diversity.

It would be beneficial to conduct similar studies for other taxa and ecosystem types. For example, Odonata (dragonflies and damselflies) have been suggested as an indicator taxon for the impacts of climate change that could serve as a proxy for wider biodiversity, among others, because they respond to climate change strongly in multiple ways (Hassall, 2015). However, invertebrates like Odonata receive less attention in research than vertebrates like fish, and data availability is poorer. Besides freshwater ecosystems, such assessments could also be extended to terrestrial and marine ecosystems. Trisos et al. (2020) performed a similar analysis for terrestrial and marine ecosystems as Barbarossa et al. (2021) did for freshwater

ecosystems, simulating the exceedance of climate niche limits. As we built on the results from Barbarossa et al. (2021), one could similarly build on the results from Trisos et al. (2020) to estimate the impacts of climate change on the functional diversity of terrestrial and marine ecosystems.

5 | CONCLUSIONS

Climate change poses severe threats to freshwater fish communities and their functional diversity. This study assessed the functional diversity change of freshwater fish caused by climate change due to changes in streamflow and water temperature extremes at four global warming levels (1.5°C, 2.0°C, 3.2°C and 4.5°C). Losses accelerate towards higher warming levels. Globally, 6%–25% of the locations face a complete loss of functional diversity when assuming no dispersal (and 6%–17% when assuming maximal dispersal). An additional 3%–7% (6%–10%) face a partial loss in functional diversity in all three investigated facets: functional richness, evenness and divergence. The adjacent Amazon and Paraná River basins stand out as hotspots of functional diversity loss. The three facets of functional diversity do not always follow the same pattern. Sometimes, functional richness is not yet affected despite species loss, while functional evenness and divergence start decreasing. At other locations, functional richness decreases, while functional evenness and/or divergence increase. This contrasting pattern shows the complementarity of functional diversity and its three facets compared to species richness, which is most commonly assessed. Considering future threats through the projections of functional diversity loss under climate change, as done here, can help make conservation planning more effective and protect biodiversity persistence.

AUTHOR CONTRIBUTIONS

Laura Scherer conceived the idea. Hidde A. Boom and Laura Scherer performed the analysis. Laura Scherer drafted the manuscript and designed the figures. All authors provided critical feedback and helped shape the research, analysis and manuscript.

ACKNOWLEDGEMENTS

This work was performed using the computational resources from the Academic Leiden Interdisciplinary Cluster Environment (ALICE) provided by Leiden University.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Zenodo at <https://doi.org/10.5281/zenodo.7831404>. These data were derived from the following resources: The species' geographical ranges and the effects of different climate scenarios and dispersal assumptions on them are taken from Barbarossa et al. (2021), and

the related R code is available at <https://github.com/vbarbarossa/fishsuit>. The fish trait data are taken from FishBase and available at www.fishbase.org (Froese & Pauly, 2021).

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REFERENCES

- Ahmed, D. A., van Bodegom, P. M., & Tukker, A. (2019). Evaluation and selection of functional diversity metrics with recommendations for their use in life cycle assessments. *The International Journal of Life Cycle Assessment*, 24(3), 485–500. <https://doi.org/10.1007/s11367-018-1470-8>
- Alahuhta, J., Erős, T., Kärnä, O.-M., Soininen, J., Wang, J., & Heino, J. (2018). Understanding environmental change through the lens of trait-based, functional, and phylogenetic biodiversity in freshwater ecosystems. *Environmental Reviews*, 27(2), 263–273. <https://doi.org/10.1139/er-2018-0071>
- Balian, E. V., Segers, H., Martens, K., & Lévêque, C. (2008). The freshwater animal diversity assessment: An overview of the results. In E. V. Balian, C. Lévêque, H. Segers, & K. Martens (Eds.), *Freshwater animal diversity assessment* (pp. 627–637). Springer Netherlands. https://doi.org/10.1007/978-1-4020-8259-7_61
- Barbarossa, V., Bosmans, J., Wanders, N., King, H., Bierkens, M. F. P., Huijbregts, M. A. J., & Schipper, A. M. (2021). Threats of global warming to the world's freshwater fishes. *Nature Communications*, 12(1), 1701. <https://doi.org/10.1038/s41467-021-21655-w>
- Barbarossa, V., Schmitt, R. J. P., Huijbregts, M. A. J., Zarfl, C., King, H., & Schipper, A. M. (2020). Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences*, 117(7), 3648–3655. <https://doi.org/10.1073/pnas.1912776117>
- Bateman, B. L., Murphy, H. T., Reside, A. E., Mokany, K., & VanDerWal, J. (2013). Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling. *Diversity and Distributions*, 19(10), 1224–1234. <https://doi.org/10.1111/ddi.12107>
- Bernery, C., Bellard, C., Courchamp, F., Brosse, S., Gozlan, R. E., Jarić, I., Teletchea, F., & Leroy, B. (2022). Freshwater fish invasions: A comprehensive review. *Annual Review of Ecology, Evolution, and Systematics*, 53(1), 427–456. <https://doi.org/10.1146/annurev-ecolsys-032522-015551>
- Boettiger, C., Lang, D. T., & Wainwright, P. C. (2012). Rfishbase: Exploring, manipulating and visualizing FishBase data from R. *Journal of Fish Biology*, 81(6), 2030–2039. <https://doi.org/10.1111/j.1095-8649.2012.03464.x>
- Boulton, C. A., Lenton, T. M., & Boers, N. (2022). Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nature Climate Change*, 12(3), 271–278. <https://doi.org/10.1038/s41558-022-01287-8>
- Bryse, K., Oreskes, N., O'Reilly, J., & Oppenheimer, M. (2013). Climate change prediction: Erring on the side of least drama? *Global Environmental Change*, 23(1), 327–337. <https://doi.org/10.1016/j.gloenvcha.2012.10.008>
- Buisson, L., Grenouillet, G., Villéger, S., Canal, J., & Laffaille, P. (2013). Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biology*, 19(2), 387–400. <https://doi.org/10.1111/gcb.12056>
- Chang, J., Rabosky, D. L., Smith, S. A., & Alfaro, M. E. (2019). An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. *Methods in Ecology and Evolution*, 10(7), 1118–1124. <https://doi.org/10.1111/2041-210X.13182>
- Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., Pollock, C., Richman, N. I., Soulsby, A.-M., & Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, 23(1), 40–51. <https://doi.org/10.1111/geb.12096>
- Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639. <https://doi.org/10.1111/fwb.12081>
- Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, 36(11), 1236–1246. <https://doi.org/10.1111/j.1600-0587.2013.00282.x>
- Da Silva, V. E. L., Silva-Firmiano, L. P. S., Teresa, F. B., Batista, V. S., Ladle, R. J., & Fabr e, N. N. (2019). Functional traits of fish species: Adjusting resolution to accurately express resource partitioning. *Frontiers in Marine Science*, 6, 303. <https://doi.org/10.3389/fmars.2019.00303>
- Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., McDowell, W. H., Kortelainen, P., Caraco, N. F., Melack, J. M., & Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, 51(5), 2388–2397. <https://doi.org/10.4319/lo.2006.51.5.2388>
- Ford, B. M., & Roberts, J. D. (2020). Functional traits reveal the presence and nature of multiple processes in the assembly of marine fish communities. *Oecologia*, 192(1), 143–154. <https://doi.org/10.1007/s00442-019-04555-1>
- Frimpong, E. A., & Angermeier, P. L. (2009). Fish traits: A database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries*, 34(10), 487–495. <https://doi.org/10.1577/1548-8446-34.10.487>
- Froese, R., & Pauly, D. (2021). *FishBase*. www.fishbase.org
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tschamtkke, T., Weisser, W., & Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, 282(1801), 20142620. <https://doi.org/10.1098/rspb.2014.2620>
- Goolsby, E. W., Bruggeman, J., & An e, C. (2017). Rphylopar: Fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution*, 8(1), 22–27. <https://doi.org/10.1111/2041-210X.12612>
- Hassall, C. (2015). Odonata as candidate macroecological barometers for global climate change. *Freshwater Science*, 34(3), 1040–1049. <https://doi.org/10.1086/682210>
- Hitt, N. P., & Chambers, D. B. (2014). Temporal changes in taxonomic and functional diversity of fish assemblages downstream from mountaintop mining. *Freshwater Science*, 33(3), 915–926. <https://doi.org/10.1086/676997>
- IUCN. (2018). *The IUCN red list of threatened species: Version 2018-2*. <https://www.iucnredlist.org/>
- J ez quel, C., Tedesco, P. A., Bigorne, R., Maldonado-Ocampo, J. A., Ortega, H., Hidalgo, M., Martens, K., Torrente-Vilara, G., Zuanon, J., Acosta, A., Agudelo, E., Maure, S. B., Bastos, D. A., Gregory, J. B., Cabeceira, F. G., Canto, A. L. C., Carvajal-Vallejos, F., Carvalho, L. N., Cella-Ribeiro, A., ... Oberdorff, T. (2020). A database of freshwater fish species of the Amazon Basin. *Scientific Data*, 7(1), 96. <https://doi.org/10.1038/s41597-020-0436-4>
- Johnson, T. F., Isaac, N. J. B., Paviolo, A., & Gonz alez-Su arez, M. (2021). Handling missing values in trait data. *Global Ecology and Biogeography*, 30(1), 51–62. <https://doi.org/10.1111/geb.13185>
- Kim, S. (2018). *dbFD_parallel.R* [Source code]. <https://doi.org/10.6084/m9.figshare.6167903.v1>
- Ladds, M. A., Sibanda, N., Arnold, R., Dunn, M. R., & Giordani, P. (2018). Creating functional groups of marine fish from categorical traits. *PeerJ*, 6, e5795. <https://doi.org/10.7717/peerj.5795>

- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. <https://doi.org/10.1890/08-2244.1>
- Manjarrés-Hernández, A., Guisande, C., García-Roselló, E., Heine, J., Pelayo-Villamil, P., Pérez-Costas, E., Pérez-Costas, E., González-Vilas, L., González-Dacosta, J., Duque, S. R., Granado-Lorencio, C., & Lobo, J. M. (2021). Predicting the effects of climate change on future freshwater fish diversity at global scale. *Nature Conservation*, 43, 1–24. <https://doi.org/10.3897/natureconservation.43.58997>
- Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdius, H., & Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, 20(9), 1097–1107. <https://doi.org/10.1111/ddi.12232>
- Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B. E., Bittner, L., Castilla, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaud, E., Usseglio-Polatera, P., Vogt, M., ... Ayata, S.-D. (2021). Functional trait-based approaches as a common framework for aquatic ecologists. *Limnology and Oceanography*, 66(3), 965–994. <https://doi.org/10.1002/lno.11655>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2020). *Vegan: Community ecology package. R package version 2.5-7*. <https://CRAN.R-project.org/package=vegan>
- Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pease, A. A., González-Díaz, A. A., Rodiles-Hernández, R., & Winemiller, K. O. (2012). Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. *Freshwater Biology*, 57(5), 1060–1075. <https://doi.org/10.1111/j.1365-2427.2012.02768.x>
- Pease, A. A., Taylor, J. M., Winemiller, K. O., & King, R. S. (2015). Ecoregional, catchment, and reach-scale environmental factors shape functional-trait structure of stream fish assemblages. *Hydrobiologia*, 753(1), 265–283. <https://doi.org/10.1007/s10750-015-2235-z>
- Penone, C., Davidson, A. D., Shoemaker, K. T., Di Marco, M., Rondinini, C., Brooks, T. M., Young, B. E., Graham, C. H., & Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*, 5(9), 961–970. <https://doi.org/10.1111/2041-210X.12232>
- Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth-death polytomy resolvers for downstream comparative analyses. *Evolution*, 69(12), 3207–3216. <https://doi.org/10.1111/evo.12817>
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559(7714), 392–395. <https://doi.org/10.1038/s41586-018-0273-1>
- Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, 22(3), 521–533. <https://doi.org/10.1111/j.1523-1739.2008.00950.x>
- Reside, A. E., Butt, N., & Adams, V. M. (2018). Adapting systematic conservation planning for climate change. *Biodiversity and Conservation*, 27(1), 1–29. <https://doi.org/10.1007/s10531-017-1442-5>
- Salgado, C. M., Azevedo, C., Proença, H., & Vieira, S. M. (2016). Noise Versus Outliers. In M. I. T. Critical Data (Ed.), *Secondary analysis of electronic health records* (pp. 163–183). Springer. https://doi.org/10.1007/978-3-319-43742-2_14
- Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., & Bickford, D. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Scherer, L., Boom, H. A., Barbarossa, V., & van Bodegom, P. M. (2023). Climate change threats to the global functional diversity of freshwater fish [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.7831404>
- Scherer, L., Curran, M., & Alvarez, M. (2017). Expanding Kenya's protected areas under the Convention on Biological Diversity to maximize coverage of plant diversity. *Conservation Biology*, 31(2), 302–310. <https://doi.org/10.1111/cobi.12792>
- Scherer, L., van Baren, S. A., & van Bodegom, P. M. (2020). Characterizing land use impacts on functional plant diversity for life cycle assessments. *Environmental Science & Technology*, 54(11), 6486–6495. <https://doi.org/10.1021/acs.est.9b07228>
- Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469–484. <https://doi.org/10.1890/08-2225.1>
- Shiklomanov, I. (1993). World fresh water resources. In P. H. Gleick (Ed.), *Water in crisis: A guide to the world's fresh water resources*. Oxford University Press.
- Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science*, 371(6531), 835–838. <https://doi.org/10.1126/science.abd3369>
- Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O., & Amiaud, B. (2014). Filling the gap in functional trait databases: Use of ecological hypotheses to replace missing data. *Ecology and Evolution*, 4(7), 944–958. <https://doi.org/10.1002/ece3.989>
- Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P. A., Tedesco, P. A., Brosse, S., & Villéger, S. (2018). Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecology Letters*, 21(11), 1649–1659. <https://doi.org/10.1111/ele.13141>
- Toussaint, A., Charpin, N., Brosse, S., & Villéger, S. (2016). Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific Reports*, 6(1), 22125. <https://doi.org/10.1038/srep22125>
- Trisos, C. H., Merow, C., & Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, 580(7804), 496–501. <https://doi.org/10.1038/s41586-020-2189-9>
- Vega, G. C., & Wiens, J. J. (2012). Why are there so few fish in the sea? *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), 2323–2329. <https://doi.org/10.1098/rspb.2012.0075>
- Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., & Vanni, M. J. (2017). Functional ecology of fish: Current approaches and future challenges. *Aquatic Sciences*, 79(4), 783–801. <https://doi.org/10.1007/s00027-017-0546-z>
- Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20(6), 1512–1522. <https://doi.org/10.1890/09-1310.1>
- Visser, P. M., Verspagen, J. M., Sandrini, G., Stal, L. J., Matthijs, H. C., Davis, T. W., Paerl, H. W., & Huisman, J. (2016). How rising CO₂ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae*, 54, 145–159. <https://doi.org/10.1016/j.hal.2015.12.006>
- Warszawski, L., Frieler, K., Huber, V., Piontek, F., Serdeczny, O., & Schewe, J. (2014). The inter-sectoral impact model intercomparison project (ISI-MIP): Project framework. *Proceedings of the National Academy of Sciences*, 111(9), 3228–3232. <https://doi.org/10.1073/pnas.1312330110>
- Wiedmann, M. A., Aschan, M., Certain, G., Dolgov, A., Greenacre, M., Johannesen, E., Planque, B., & Primicerio, R. (2014). Functional

- diversity of the Barents Sea fish community. *Marine Ecology Progress Series*, 495, 205–218. <https://doi.org/10.3354/meps10558>
- Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I. G., Darwall, W., Lujan, N. K., Harrison, I., Stiassny, M. L. J., Silvano, R. A. M., Fitzgerald, D. B., Pelicice, F. M., Agostinho, A. A., Gomes, L. C., Albert, J. S., Baran, E., Petrere, M., Jr., ... Sáenz, L. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, 351(6269), 128–129. <https://doi.org/10.1126/science.aac7082>
- WWF. (2016). *Living planet report 2016: Risk and resilience in a new era*. Gland.
- Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, 77(1), 161–170. <https://doi.org/10.1007/s00027-014-0377-0>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Scherer, L., Boom, H. A., Barbarossa, V., & van Bodegom, P. M. (2023). Climate change threats to the global functional diversity of freshwater fish. *Global Change Biology*, 29, 3781–3793. <https://doi.org/10.1111/gcb.16723>