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# Fish functional diversity responses to total phosphorus in the rivers of the Baltic Sea catchment area☆

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ABSTRACT

Eutrophication results from nutrient overload in aquatic ecosystems and affects primary productivity patterns, which impacts the living conditions of aquatic organisms. The rivers in the catchment area of the Baltic Sea are greatly affected by eutrophication, but impacts on fish functional diversity are poorly understood. This study, therefore, evaluates the effects of freshwater eutrophication on fish functional diversity in the rivers of the Baltic Sea catchment area. Total phosphorus is used as the eutrophication indicator. Functional richness, evenness, and divergence values were calculated using comprehensive fish trait and occurrence databases. Functional evenness was found to be negatively related to eutrophication. In contrast, functional divergence demonstrated a positive relation. Functional richness showed no or a negative response, depending on whether environmental covariates were considered. As a comparison, species richness revealed a negative relationship and was the most responsive to increasing eutrophication of all measures evaluated. Hence, this study demonstrates the varying nature of responses of multiple diversity indices and comprehensively describes the response of fish communities to increasing eutrophication in the area. The results show that functional redundancy helps to reduce adverse effects of species losses on functional diversity, which provides an important starting point for impact assessment. The findings illustrate that actions to limit nutrient discharge to freshwater are needed to maintain sustainable riverine ecosystems.

## 1. Introduction

Rivers contribute to human well-being in numerous ways – by providing drinking water, cooling the air, serving as buffers for flood protection, and more (Böck et al., 2018). To fulfil the societies' nutritional and economic needs, the maintenance of sustainable aquatic ecosystems is a must. One of the anthropogenic pressures affecting aquatic ecosystems and one of the most widespread water quality impairments (Le Moal et al., 2019) is eutrophication, which impacts both marine and freshwater ecosystems. Key drivers of eutrophication are the increasing use of artificial fertilisers in agriculture, the rising demand for energy production, and the expansion of agricultural land (World Resources Institute, n.d.). In the Baltic Sea, where 97 % of the total area is estimated to be affected by eutrophication, it is also commonly seen as one of the potential causes of fish biodiversity loss due to worsening conditions for feeding (HELCOM, 2018). As a consequence of the eutrophic state, the world's largest dead zone (oxygen-depleted area) is located in the Baltic Sea (European Environment Agency, 2019). The eutrophication levels of the Baltic Sea coastal areas are closely linked to the eutrophic state of rivers and river basins feeding them (Voss et al., 2011), with river-borne nutrient loads as the main driver of its eutrophication (Meier et al., 2019).

So far, most studies on the impacts of eutrophication on biodiversity focussed on species richness (e.g., Azevedo et al., 2013). Daam et al. (2019), in their overview of the links between aquatic biodiversity and ecosystem functioning, note that trait-based analyses could be a promising future research direction. Functional diversity describes the diversity of species traits in ecosystems (Ahmed et al., 2019) and provides a usual metric for the implementation of trait-based approaches. In the context of aquatic environments and fish, functional diversity can be measured by examining traits that relate to life history (for example, life span), morphology (for example, body length), physiology (for example, trophic level), and behaviour (for example, swimming speed) (Martini et al., 2020). Such variety of traits for each species as examined within functional diversity measures provide a more comprehensive assessment of the ecosystem at hand than, for example, species richness.

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The goal of this research was to quantify the effects of eutrophication on fish functional diversity in rivers of the Baltic Sea catchment area. We focus on freshwater ecosystems, as they are more threatened globally; their vertebrate populations declined much more than in marine environments (McRae et al., 2017). Moreover, tackling eutrophication in rivers also benefits the seas into which they flow. While we conducted a case study in a region that is especially affected by eutrophication, wider applicability can be drawn by following this research approach and analysing data on the functional diversity and eutrophication or other water quality indicators in other regions.

## 2. Methods

### 2.1. Study region

The study region is the catchment area of the Baltic Sea. The Baltic Sea is a sea in Northern Europe connected to the Atlantic Ocean. It is bordered by Denmark, Sweden, Finland, Russia, the Baltic countries, Poland, and Germany. Some of the largest rivers in the region are the Neva, Vistula, Daugava, Nemunas, Kemijoki, Oder, and Göta Älv. The combined discharge of these rivers accounts for almost half of the total long-term mean flow via rivers into the Baltic Sea (HELCOM, 2015).

### 2.2. Eutrophication indicators

To determine the effect freshwater eutrophication has on fish functional diversity, an appropriate eutrophication indicator was selected first while keeping in mind that no single indicator can capture the entirety of eutrophication. Potential water quality indicators were extracted from water monitoring stations from Waterbase of the European Environment Agency (EEA) (2021). Data compiled in Waterbase are reported by EEA member countries and cooperating countries based on the WISE SoE - Water Quality ICM and other reporting obligations (EEA, 2021). Waterbase contains data aggregated by year for each observed property (indicator) and monitoring station (EEA, 2015). The initial dataset included 47,314 water monitoring stations located in the rivers of the catchment area of the Baltic Sea. Potentially erroneous values were removed from the water indicator data set (Section A1 in the Supplementary Material).

As the temporal coverage of the data was quite wide – including data points from the years 1965–2019 – the values per indicator in a monitoring station over the last three years available were selected. If there was more than one value representing the same year, indicator, and station combination, the value based on most observations was taken. To obtain a single value per indicator per water monitoring station, the arithmetic mean of the values over the three most recent years was calculated. After these steps, data was available for 377 different water indicators. The 63 indicators with at least 500 stations available are listed in Table A1.

Of the 63 water quality indicators, 15 were related to eutrophication impacts and can be grouped into nutrient-related, oxygen-related, or algae-related indicators (Table A2). The selection of the most suitable eutrophication indicator was based on i) the indicator most relevant for analysing river ecosystems, ii) the previous impact assessment studies done with this indicator, and iii) the coverage of stations with indicator values available.

Considering the characteristics of the potential eutrophication indicators, research findings on freshwater eutrophication, and data availability, total phosphorus was chosen as the eutrophication indicator to be applied in further analysis. This selection assumes that phosphorus is the limiting nutrient for freshwater environments, which is a rule of thumb that is often reasonable (Norris, 2002). McDowell et al. (2020) also identified most areas in the Baltic Sea catchment area as phosphorus-limited, which applies especially to those areas with undesirable periphyton growth. As pointed out by Morelli et al. (2018), most (life cycle) impact assessment methods apply phosphorus as the sole indicator for freshwater eutrophication. Moreover, total phosphorus is the nutrient with the most data points available in the water quality indicator dataset. Stations that had a value for total phosphorus were selected for the next steps, resulting in 1914 water monitoring stations in the catchment area.

### 2.3. Fish occurrences

#### 2.3.1. Data and pre-processing

Occurrences of fish species in the area of interest, i.e., rivers of the catchment area of the Baltic Sea as delineated by HELCOM (2008), were retrieved from GBIF (2022). The taxonomic groups of Actinopterygii, Sarcopterygii, Elasmobranchii, Holocephali, Myxini, and Cephalaspidomorphi were considered. In total, 4,228,103 occurrences were available within the bounding box of the catchment area.

Multiple filters were applied. Firstly, occurrence records with relatively high coordinate uncertainty reported were excluded. The literature rarely documents the appropriate thresholds for filtering occurrence records by coordinate uncertainty. Zizka et al. (2020) used 100 km as the threshold. However, considering the scope of this study and the importance of location precision when evaluating the diversity in water areas with varying eutrophication levels, 76,382 occurrence points with reported coordinate uncertainty values above 1 km were removed from the dataset. Moreover, the 4305 occurrence records that stated "fossilized specimen" as the basis of record were removed. Occurrences that were outside the catchment of the Baltic Sea were also filtered. After this step, 3,589,548 fish occurrence records remained. These occurrence values were used as the basis for extracting the list of fish species present in the area of interest.

The species names present in the occurrence dataset were extracted and compared to the species names used in FishBase (used for the fish trait data; see Section 2.4). The number of fish occurrences representing 259 species within the area of interest was 3,424,164 or 95.39 % of the occurrences identified before matching species names and removing species living in lakes (see Section A2).

Of these 259 species, 172 species had all values available for the set of traits chosen (see Section 2.4.1). The occurrence points of species which did not have all trait values available were removed, resulting in 3,274,767 occurrences (94.61 %) in the data set for the next steps of the analysis.

#### 2.3.2. Presence-absence matrix

To calculate functional diversity values, a species presence-absence matrix is required. The presence-absence matrix depicts which species are present in which locations. To create this matrix and later compare fish functional diversity with total phosphorus levels in the area, buffer zones around water monitoring stations were created. The fish observed in the buffer zones were assumed to live in conditions similar to those at the station's location.

The buffer zones were created based on the following rules (see also Section A7).

1. There are at least three species observed in each buffer zone. This is the minimum condition for the functional diversity calculations.
2. Each buffer zone covers a similar length of rivers, allowing for a deviation of 1 % over or under the desired length within the buffer zone. A similar river length ensured that the buffer zones had a similar potential for occurrences.
3. There is no overlap between the buffer zones.
4. The river length targeted under condition 2 to be covered in the buffer zones is not too large.
5. A reasonable sample size of station buffers is achieved.

As a result, there were 313 non-overlapping stations left with buffers ranging from 10 km to 21.55 km, river coverage in buffers ranging from 89.22 km to 91.32 km containing 3 to 39 different fish species (Fig. A5).

In this data set, there were occurrences of 114 species.

### 2.4. Functional diversity

#### 2.4.1. Fish trait selection

FishBase (Froese & Pauly, 2022) was chosen as the source for data on fish traits, as it contains extensive information about 34,800 fish species. Fish traits were selected based on ecological relevance, species coverage, and the correlation coefficients among traits, following Scherer et al. (2020). While the use of multiple traits is encouraged for functional diversity estimates, a larger number of traits is not always beneficial. Too many traits might discriminate species to the extent that it negates a functional approach, it increases the chances of relationships among some of the traits, which can lead to misleading results (Lefcheck et al., 2015), and in our case without the imputation of any trait values, it would also have implied losing more species for the analysis. Therefore, we opted for a limited but well-chosen set of complementary traits. The research of Martini et al. (2020) was taken as the basis for categorising the traits, as it provides the broadest framework for classifying aquatic traits, although it is not fish-specific. The authors categorise commonly used traits into two types of groups - by trait type and function. Table A4 shows the 43 fish traits examined and categorized based on Martini et al. (2020) and own interpretation.

Traits with categorical values (for example, body shape and food type) were removed, as, for this research, functional diversity indices developed by Villéger et al. (2008) were used (see Section 2.4.2), which demands continuous traits, although there would be possibilities for categorical trait transformations if needed (Villéger et al., 2008).

To ensure a reasonable species coverage, traits which had values available for less than 60 % of species from the species list (259 species) were removed. As a result, 13 traits with continuous values remained in the next steps.

Trait values were scrutinized for potential outliers or erroneous values. As a result, 20 trait values were examined, 3 were modified, and 7 were removed from the dataset. Histograms of normal and log-transformed trait values and the values examined and modified are available in Tables A5–A17.

As the data from FishBase at times offers multiple trait values for a single fish species, the data was summarized with the arithmetic mean to obtain a single trait value per species.

The subset of 13 traits was assessed by running a correlation analysis with the Spearman correlation coefficients (Fig. A1). By removing highly correlated coefficients, a final selection of numerical traits was obtained that together cover three of four trait categories – morphological, physiological, and behavioural, but not life history – and all four ecological functions – resource acquisition, growth, reproduction, and survival.

1. **Growth rate** (physiological trait): Growth is distinguished as a separate ecological function in Martini et al. (2020).
2. **Relative head length** (morphological trait): Pease et al. (2012) argue that head length reflects the use of resources, and Stefani et al. (2020) examine head length in relation to dietary preferences, both pointing to resource acquisition.
3. **Relative body depth** (morphological trait): According to Pease et al. (2012) and Stefani et al. (2020), this trait relates to swimming behaviour and habitat use. This trait was useful to include for the coverage of swimming and locomotion dimensions.
4. **Trophic level** (physiological/behavioural trait): It describes the feeding characteristics relevant to resource acquisition. It is also related to predation vulnerability and, thus, survival. The trophic level is one of the most used traits in fish functional diversity studies.
5. **Minimum depth** of occurrence in the water column (physiological/behavioural trait): This trait is categorized under habitat use in Lamothe et al. (2019), and is considered to represent environmental tolerances in Ford and Roberts (2020), which is relevant to all ecological functions. This trait shows the least correlation with any other trait selected.

#### 2.4.2. Functional diversity calculation

The indices developed by Villéger et al. (2008) were applied for calculating functional diversity: functional richness, functional evenness, and functional divergence. Functional richness relates to the functional space filled by the species set and is the only index not dependent on species abundances, while it is strongly correlated with species richness. The regularity at which the species, weighted by their abundance, fill the functional trait space describes functional evenness. Functional divergence describes the distribution of abundance in terms of distances from the centre of gravity in the functional trait space. The indices are complementary and can be used together to link biodiversity more closely to ecosystem functioning (Villéger et al., 2008). These indices were also recommended to be used by Ahmed et al. (2019), based on their relation with ecosystem functioning and desirable structural properties. Due to the lack of data on species abundance in the areas of interest, presence-absence was considered instead (see Section 2.3.2). The programming language R with the package *FD* (Laliberté et al., 2014) was used to calculate the functional richness, functional evenness, and functional divergence values. In the calculation of functional diversity measures, the option to standardize the functional richness values was applied, ensuring that all functional diversity values will fall between 0 and 1 for ease of comparison.

#### 2.4.3. Species richness

While species richness was not a central indicator in this study, the relationship between species richness and eutrophication was explored. This was done to compare the outcomes and explore the difference between functional diversity and species richness and their response to increased eutrophication levels. The comparison also served as a sensitivity check of the results obtained with functional diversity measures.

### 2.5. Relationship between eutrophication and functional diversity

#### 2.5.1. Regression analysis

Based on the data distributions of functional diversity measures and total phosphorus levels in the 313 locations (Fig. 1), a linear mixed-effects model was fitted between (natural) log-transformed values of total phosphorus and the original values of functional diversity. The model considered the time difference between the mean occurrence year for each station and the mean of the last three years of water indicator values of the station as an additional fixed effect. The grouping of stations in three freshwater ecoregions (FEOW, 2008) was considered as a random effect for random intercepts. Such ecoregions are derived from biogeography considerations almost exclusively focussing on fish, considering aspects such as catchments, broad climatic patterns, and historical geographical events (Abell et al., 2008). To avoid negative values, the values of total phosphorus were multiplied by 1000 before transforming to a natural logarithm, converting the unit from mg/L to g/L.

The regression coefficients depict the impact of eutrophication on functional fish diversity and species richness and indicate how much one more unit of phosphorus entering the riverine environment in the Baltic Sea catchment area could impact fish diversity. Additionally, the proportion of diversity gained or lost as total phosphorus increases was estimated. It was calculated as the range of the fitted values by the linear mixed-effects model over the largest fitted value for functional richness, evenness, and species richness, and over the smallest fitted value for functional divergence (based on the positive or negative relations found).

#### 2.5.2. Covariate analysis

Since environmental factors other than eutrophication may influence functional diversity simultaneously and bias the results, a covariate

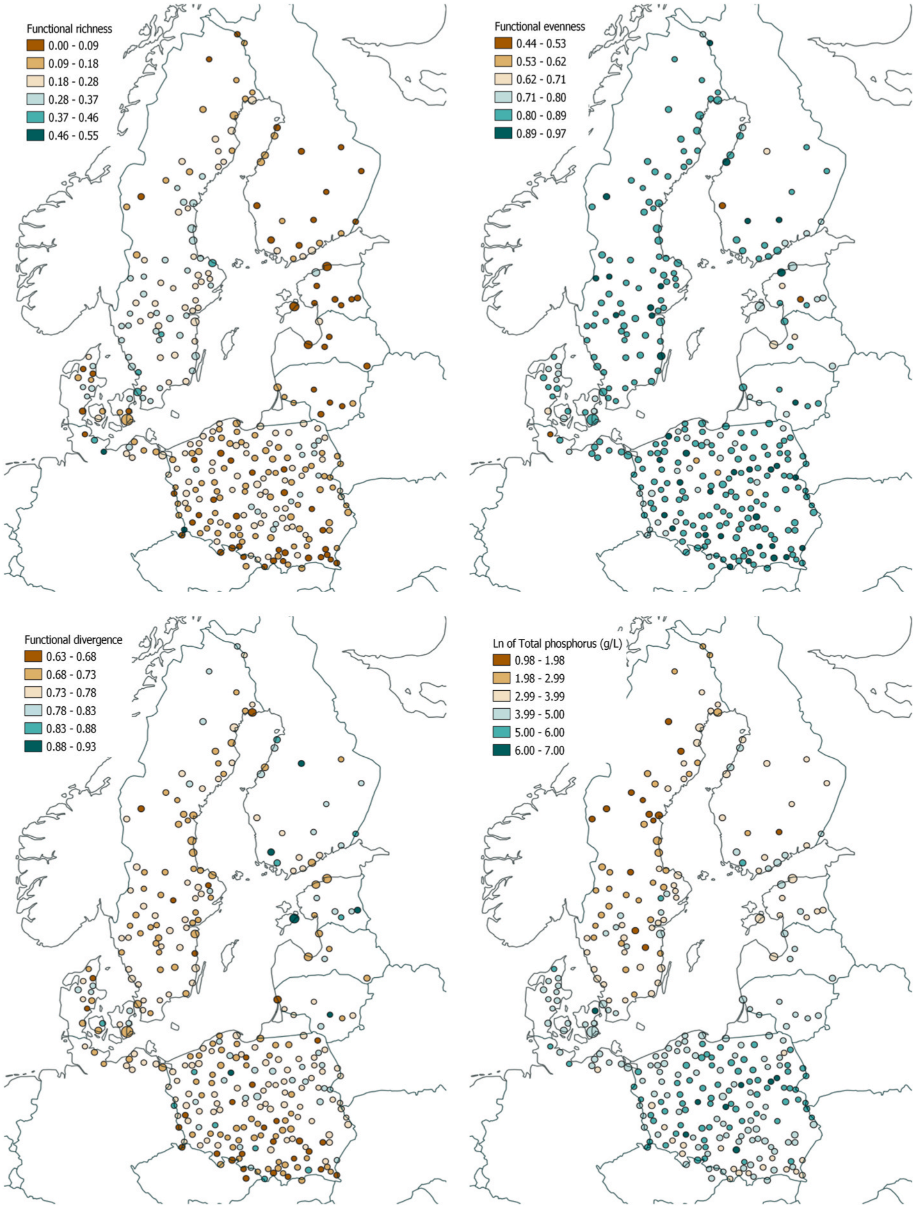


**Fig. 1.** Functional diversity and log-transformed values of total phosphorus in the final sample set of water monitoring stations across the catchment area of the Baltic Sea.

analysis was pursued. This analysis was done to test if, by applying weighting factors to control for other environmental factors (covariates), the relations of eutrophication to functional diversity measures change and in which way.

Potential covariates were extracted from Waterbase (EEA, 2015) and grouped based on the type of impact the indicators could signal according to scientific literature and classification found in regulatory documents. The three key groups of potential covariates identified were acidification, salinity, and toxicity. In addition to these three categories, there were parameters which could not be grouped but are still important for characterising the water conditions, such as total organic carbon, temperature, and hardness (Table A18).

To select a set of covariates to be used for generating weights to control for other environmental factors, several rules were applied.

1) A reasonably extensive coverage of stations should be achieved with the covariate values combined.
2) The covariates should not have Spearman correlation coefficients over an absolute value of 0.5 within the covariate set.
3) The covariates should cover various categories described above – acidity, salinity, toxicity, and ungrouped indicators.
4) The covariate set should have a relatively high sum of absolute correlation coefficients with the mean of functional diversity measures (FDMean).
5) The covariate set should be relatively well-balanced in the weighted sample.

The Spearman correlation matrix (Fig. A1) was assessed together with the missing value counts. With the choice of covariates made, the next step of the analysis was to create weights for the sampling points of interest. The R package WeightIt (Greifer, 2022) was used to generate the weights using generalised linear models. The choice of covariates was considered balanced if the threshold of 0.1 was not exceeded for both the Spearman correlation coefficients (Zhu et al., 2015) and the mean differences (Stuart et al., 2013) between the weighted and unweighted samples. Based on these criteria, three covariate sets were distinguished (Section A6).

#### 2.5.3. Outlier analysis

Since outliers could bias the results, the Minimum Covariance Determinant (MCD) approach was used to detect and exclude potential multivariate outliers. The MCD method analyses all possible sets of observations of a given sub-sample size that would not be considered outliers and computes their mean and covariance matrix, in the end choosing the most central sub-sample as identified by the smallest determinant of the covariance matrix (Leys et al., 2018). The outliers were detected and excluded using the R package *Routliers* (Delacre & Klein, 2019).

The breakdown point within the MCD approach relates to the proportion of observations of the estimator which, when replaced by arbitrary values, would cause the estimator to no longer give useful estimations (Hubert et al., 2018). A breakdown point of 0.25 was applied in determining outliers. This value was recommended by Leys et al. (2018) to be applied if there is no serious doubt that more than 25 % of the data analysed might be classified as outliers. The values that were classified as outliers using the MCD method (Figs. A7–A14) were further examined to evaluate whether there is any objective reason why the data points may be erroneous and should be removed, and the underlying species counts and characteristics, as well as the total phosphorus values, were checked. The linear mixed-effects model was fitted to data with the potential outliers excluded and compared with the initial results to see if major discrepancies from the overall trends in the data could be found.

#### 2.5.4. Model selection

The Akaike Information Criterion (AIC) was calculated to compare the relative quality of the models before and after covariate analysis and before and after the exclusion of potential outliers. AIC assesses the quality based on the trade-off between the models' fit and parsimony. To make the AIC estimates comparable, the same underlying subset of the data was used. Ranking of the models was done based on the difference in AIC values compared to the model with the lowest AIC (Tables A19-20). This information was used to select one of the three considered covariate sets.

Additionally, we assessed the model performance through the standard error of the slope and the marginal and conditional $R^2$'s. Since the AIC values of the models with and without outliers are not directly comparable due to different underlying data, the other performance metrics were used to decide whether to focus on the model with or without outliers in the main results.

## 3. Results

### 3.1. Relationship between eutrophication and functional diversity

The fish functional diversity indices exhibited diverse geographic patterns (Fig. 1).

When not considering any confounding variables, a close to zero and highly insignificant positive trend was observed for fish functional richness. Locations with higher total phosphorus levels tended to have lower fish functional evenness, as illustrated in a negative trend of the regression line (Fig. 2). Functional divergence, however, tended to increase with growing total phosphorus levels. The slope was statistically significant at a significance level of 0.1 or lower for functional divergence only (Table 1).

Functional divergence gains proportionally the most as total phosphorus increases, with about 6 % more modelled functional divergence across the range of total phosphorus observed. The effect is smaller for functional evenness, losing almost 5 % as total phosphorus increases. For functional richness, the proportion gained with increasing phosphorus is only about 1 %.

### 3.2. Covariate analysis

To demonstrate the effect of applying weights, the regression considering the covariate set with the most stations available is depicted in Fig. 3. This covariate set includes water temperature, pH, zinc and its (zinc) compounds. Out of three covariate sets analysed, this set also provides the best AIC values following the unweighted model, except for functional evenness, where it even performs best overall. The weighing factors generated to control for this covariate set show a directional shift in the regression line for functional richness, turning it negative. In this weighted model, the regression line for functional evenness shows a minor downwards shift. For functional divergence, the impact of weights representing this covariate set is more severe, depicting an even

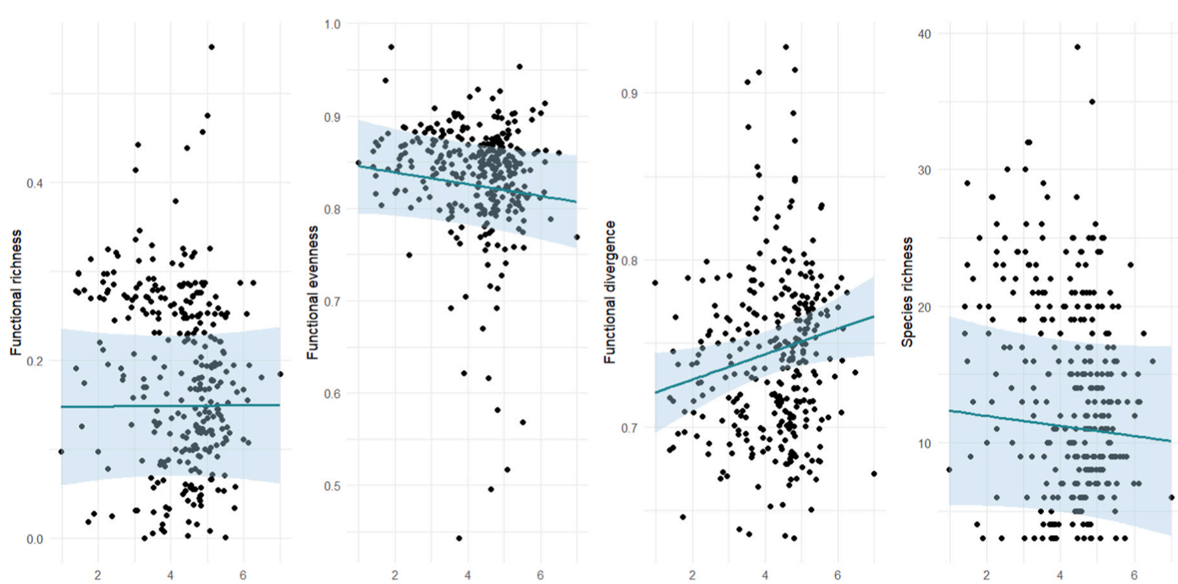


**Fig. 2.** Relationship between biodiversity and log-transformed total phosphorus concentrations. Biodiversity is represented by functional diversity and species richness. The green line is the marginal fit of the linear mixed-effects regression line, and the blue-shaded area is the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 1**
Statistics of the linear mixed-effects models of biodiversity and log-transformed total phosphorus. ● = p-value ≤0.1, * = p-value ≤0.05, ** = p-value ≤0.01.

| Biodiversity measure | Intercept | Slope of regression line (biodiversity measure/ln total phosphorus) | P-value of slope | Standard error of slope | Marginal $R^2$ of regression | Conditional $R^2$ of regression | % modelled biodiversity gained/lost as TP increases |
|---|---|---|---|---|---|---|---|
| Functional richness | 0.14 | 3.24E-04 | 0.962 | 0.0067 | 0.01 | 0.38 | 1.32 |
| Functional evenness | 0.85 | −0.01 | 0.122 | 0.0041 | 0.01 | 0.33 | −4.54 |
| Functional divergence | 0.71 | 0.01 | 0.025* | 0.0033 | 0.03 | 0.07 | 6.40 |
| Species richness | 12.07 | −0.37 | 0.462 | 0.4968 | 0.01 | 0.42 | −17.87 |

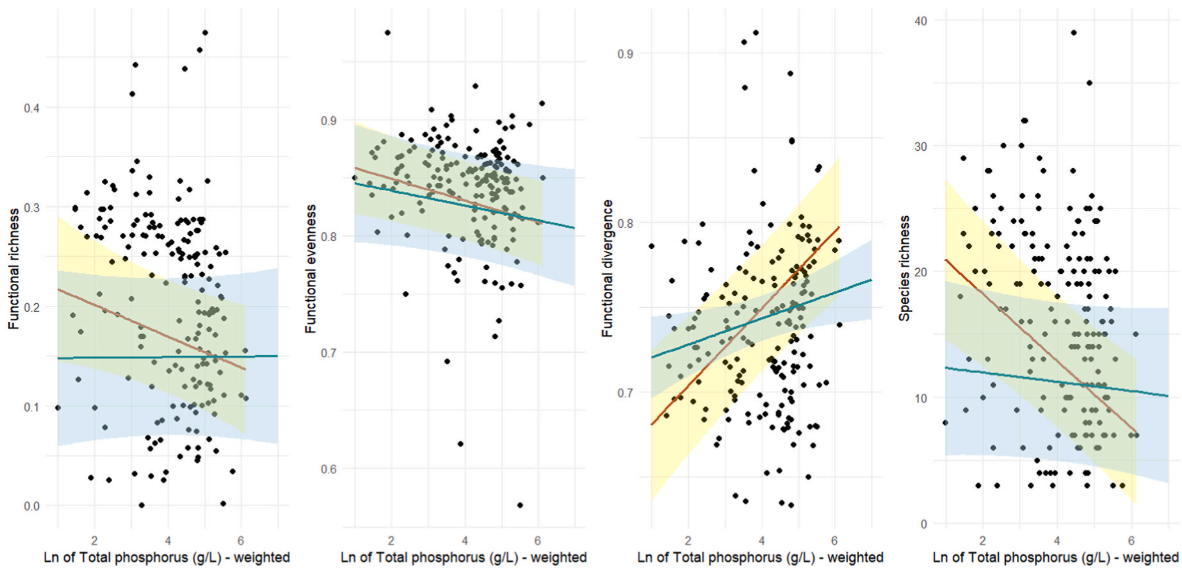


**Fig. 3.** Relationship between biodiversity and log-transformed total phosphorus concentrations before and after applying weights from the covariate set with water temperature, pH, zinc and its (zinc) compounds. Biodiversity is represented by functional diversity and species richness. The dark green line is the marginal fit of the linear mixed-effects regression line before applying weights, the brown line is the marginal fit of the linear mixed-effects regression line after applying weights, the blue-shaded area is the 95 % confidence interval before applying weights, and the yellow-shaded area is the 95 % confidence interval after applying weights. N = 184. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

stronger positive relation to increasing phosphorus. All regression slopes are statistically significant at a significance level of 0.1 or lower (Table 2).

Functional richness displays the largest loss as phosphorus increases, losing about 37 % of modelled biodiversity as phosphorus increases. The second largest proportional response to increasing phosphorus is for functional divergence, increasing by about 17 %. Functional evenness displays a similar result as in the unweighted model, equalling to a loss of slightly above 5 % of modelled biodiversity as phosphorus increases.

### 3.3. *Outlier analysis*

Overall, no substantial reason was found to remove the potential outlier stations in the data examined. Even if these outliers were removed, the general relation between functional diversity measures and eutrophication was influenced only for functional richness. Like when considering covariates in Section 3.2, the removal of potential outliers led to a distinct downward slope of the regression line of functional richness compared to the near-zero slope generated with the original, unweighted data set. Excluding potential outliers did not lead to improved statistical significance of the regression line slopes. Outlier analysis on the model that considers the covariate set of water

**Table 2**
Statistics of the mixed-effects models of biodiversity and log-transformed total phosphorus after applying weights from the covariate set with water temperature, pH, zinc and its (zinc) compounds. ● = p-value ≤0.1, * = p-value ≤0.05, ** = p-value ≤0.01.

| Biodiversity measure | Intercept | Slope of regression line (biodiversity measure/ln total phosphorus) | P-value of slope | Standard error of slope | Marginal $R^2$ of regression | Conditional $R^2$ of regression | % modelled biodiversity gained/lost as TP increases |
|---|---|---|---|---|---|---|---|
| Functional richness | 0.22 | −0.02 | 3.68E-02* | 0.0075 | 0.04 | 0.21 | −37.39 |
| Functional evenness | 0.87 | −0.01 | 7.80E-03** | 0.0035 | 0.04 | 0.31 | −5.61 |
| Functional divergence | 0.65 | 0.02 | 9.15E-08** | 0.0041 | 0.14 | 0.36 | 17.24 |
| Species richness | 22.9 | −2.66 | 1.45E-05** | 0.5974 | 0.11 | 0.32 | −65.47 |

temperature, pH, zinc and its (zinc) compounds did not introduce any major shifts in regression lines.

### 3.4. Comparison with effects on species richness

Species richness decreases as eutrophication levels increase, as signalled by the downward-facing regression line (Figs. 2 and 3). Species richness was more responsive to total phosphorus concentrations than functional diversity; it faces the largest proportional loss across the range of total phosphorus observed at about 18 % for the unweighted model and 65 % for the model considering covariates (Table 1, Table 2). The slope of the species richness and phosphorus regression line was statistically significant at a significance level of 0.01 or lower for the weighted model only.

## 4. Discussion

This study showed divergent, but mostly negative, effects of eutrophication on different functional diversity metrics and species richness. The model with water temperature, pH, zinc and its (zinc) compounds as covariates showed more pronounced effects and higher statistical significance of all regression slopes. The unweighted model with the original data set produced the lowest AIC values for all but one biodiversity measure, which suggests a better model performance, considering the lower model complexity. However, the less pronounced effects and the lack of statistical significance (except for functional divergence) suggest that the effects of phosphorus were masked by the effects of confounding environmental conditions. Therefore, the consideration of covariates seems valuable to shed light on the effects of eutrophication on functional diversity despite the increased model complexity.

Functional richness decreased as total phosphorus levels increased in the model weighted with covariates, as well as the unweighted and weighted models after outlier removal. The proportion of functional richness lost as total phosphorus increases is noteworthy and in line with the expected results and ecologic theory. The increasingly eutrophic conditions in rivers brought by nutrient concentrations reduce the quality of the aquatic habitat. As explained by Hitt and Chambers (2014) in a study of fish functional diversity in relation to mountaintop mining, reduced functional richness could signal niche filtering processes, which lead to less niche space available. Less niche space also limits the potential trait space available. As species communities with a variety of traits ensure better functioning of the ecosystem, the impact observed in this study raises concern about the damage done to riverine environments by freshwater eutrophication. However, the results from the unweighted model including outliers displayed a near-zero and highly insignificant positive slope for the response of functional richness to increasing phosphorus.

Functional evenness showed a decrease as total phosphorus levels increased in all models considered. The direction of the effect is the same as observed with functional richness in most models, while it is smaller in extent, based on the slopes and proportional losses of diversity when eutrophication increases. This effect illustrates that once eutrophication pressures cause species to disappear, the trait space of the species in the area becomes less evenly distributed. The species remaining could be more clustered in groups of trait value ranges. In the fish functional diversity study by Hitt and Chambers (2014), both functional evenness and functional divergence increased under the pressure of mountaintop mining, while functional richness decreased. In a study of fish functional diversity responses to habitat complexity, a similar pattern was found – with greater habitat complexity, functional richness increased, but functional evenness and divergence decreased (do Nascimento et al., 2022). These findings partially contrast the results of this study, in which functional evenness and divergence respond differently to eutrophication.

Functional divergence is the only measure that responded positively to increasing levels of total phosphorus in all models considered. In addition to the studies cited above, opposite directions of response to pressures for functional richness and functional divergence were also found in a study of biological invasions and fish functional diversity (Shuai et al., 2018). The proportion of functional divergence gained with increasing total phosphorus indicates that the effect is not negligible. This is an interesting finding about the dynamics of functional diversity measures when it comes to responses to eutrophication. It could be assumed that, in more eutrophic waters, the trait space of the species is increasingly divergent – meaning that the extreme ends of the trait values are more prevalent. As Mouchet et al. (2010) explained, increasing functional divergence could signal that niche differentiation is increasing, indicating that the set of species remaining in the more eutrophic environments faces less competition.

Species richness exhibits a negative relation to total phosphorus levels, like functional richness and functional evenness. This outcome confirms previous observations that functional richness is linked to species richness (Villéger et al., 2008; Scherer et al., 2023). Species richness has the highest fraction of biodiversity lost along the regression line among the measures evaluated. It demonstrates that species richness is the most responsive to eutrophication. This finding indicates that, with increasing eutrophication, the effects on species richness do not fully coincide with those on functional richness. Thus, disappearing species are not a random draw from the total species pool but are -to some extent-functionally similar species, allowing functional richness to decrease less. This comparison also proves the usefulness of the functional diversity measures, as they depicted a variety of potential dynamics in fish diversity under increased eutrophication.

To reduce the negative effects on functional diversity explored in this study, various management measures should be advanced to limit the amount of nutrient discharge into freshwater. In the latest Baltic Sea Action Plan developed by HELCOM (2021), the key actions for reducing the eutrophication levels in the sea relate to promoting sustainable agricultural practices such as buffer zones, precision fertilization and organic farming, as well as managing nutrient discharge from wastewater, for example by eliminating phosphorus in detergents and ensuring that the proportion of untreated wastewater entering waters is kept to a minimum. Considering that riverine inputs are the leading sources of nutrients entering the Baltic Sea (HELCOM, 2021), these practices could help improving the eutrophication status of this study area.

The results depend on data quality, and while large and reputable databases were used, there were limitations in terms of the spatial and temporal distribution of the occurrence and water quality data. Data obtained from GBIF originated from various sources with likely different underlying sampling methods, including capture and non-capture methods (Radinger et al., 2019). While this approach may introduce biases, GBIF is still considered the largest compilation of biodiversity data and remains valuable for ecological research like this (Gaiji et al., 2013). Moreover, the temporal scales of data were considered in this study only as fixed effects. A potential bias might have been caused by creating buffer zones around river monitoring stations to gather a set of fish occurrences. While a uniform set of criteria was applied to select stations to be included in the analysis, the resulting sample stations were clustered in regions with the highest data availability, leading to an inevitable bias. Data on fish trait values, especially for traits belonging to the life history category, would be a good addition to the trait set. However, efforts were put into reducing the potential flaws of the data, and the approach of this study is a useful tool for further exploration of the topic.

To improve impact assessment, further research could be dedicated to expanding this study's approach to obtain a broader spatial coverage of the effects. The methods developed could be transferred to other regions. For example, evaluating the relationship between fish functional diversity and eutrophication on the European level could be done by using the same databases as in this study. Back-transforming the data could make the slope illustrate what fraction of functional diversity is lost at a given point as one unit of total phosphorus enters the aquatic environment, but this slope would differ depending on the reference point, which must be carefully chosen. Moreover, it would be interesting to relate the proportional functional diversity loss to the "ideal" or unaffected state, in which the fish functional diversity is not yet affected by eutrophication.

This study was not only useful for demonstrating a method for impact assessment but also for describing the dynamics of fish functional diversity and eutrophication in the catchment area connected to one of the most eutrophic seas in the world. The outcomes made evident that eutrophication is an important pressure to be monitored and reduced to maintain the quality of riverine ecosystems in the area. Emissions of total phosphorus both harm fish diversity in rivers and contribute to the ongoing eutrophication of the Baltic Sea. Considering that only the effects of total phosphorus increase in freshwater were analysed, future research could employ other potential eutrophication indicators such as nitrogen as a co-limiting nutrient or dissolved oxygen as an intermediate indicator between nutrient emissions and biodiversity loss. Moreover, the method can be adapted to lakes and marine environments. Studying how eutrophication impacts other taxonomic groups would give a more comprehensive view of functional diversity dynamics in the aquatic ecosystem and possibly reveal whether the loss of functional diversity in other taxa is interrelated with the functional diversity of fish.

## 5. Conclusions

This study determined the relationship between fish functional diversity and eutrophication in the rivers of the catchment area of the Baltic Sea. The results of this study provide insights into the responses of biodiversity in aquatic ecosystems when total phosphorus emissions increase. The decrease in functional richness illustrates that the variation in trait values decreases as eutrophication occurs. The decreasing functional evenness signals that the species remaining at more eutrophic conditions are more clustered in specific trait value ranges, and the distribution of the species' trait values becomes increasingly more irregular as eutrophication increases. The increase in functional divergence with increasing eutrophication illustrates that, in more phosphorus-rich areas, the fish communities represent more of the extreme trait values than they would in less eutrophic areas.

Eutrophication affects both the functional and taxonomic diversity of fish in riverine environments. When controlled for water temperature, pH, zinc and its (zinc) compounds as covariates, the linear mixed-effects model for species richness and total phosphorus modelled that 37 % of the functional richness and 65 % of the species richness is lost across the range of observed total phosphorus levels. These results illustrate the damage to riverine ecosystems caused by eutrophication, which is largely an anthropogenic pressure in the region. Considering the exceptionally eutrophic state of the Baltic Sea and the results of this study, actions towards decreasing nutrient inputs to freshwater are urgent and should be extensive. This research also provides an approach that can be applied in studies of similar pressures to the aquatic environment in different regions and across various taxa.

## CRediT authorship contribution statement

**Māra Deksne:** Writing – original draft, Visualization, Methodology, Formal analysis. **Peter M. van Bodegom:** Writing – review & editing, Supervision, Methodology. **Laura Scherer:** Writing – review & editing, Supervision, Methodology, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2025.126062.

## Data availability statement

The data required to reproduce the above findings are publicly available. The outline of the Baltic Sea catchment area can be retrieved from HELCOM (2008). Data on river coverage can be obtained from the hydroRIVERS database (Lehner & Grill, 2013). The water quality data can be obtained from Waterbase of the European Environment Agency (2021). The species occurrence data can be downloaded from GBIF (2022). The trait data can be downloaded from FishBase (Froese & Pauly, 2022). The Freshwater Ecoregions of the World can be downloaded from FEOW (FEOW, 2008).

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