



Freshwater fish in mid and northern German rivers – Long-term trends and associated species traits

Martin Friedrichs-Manthey^{a,b,c,*}, Diana E. Bowler^{a,b,c,d}, Jörg Freyhof^e

^a Institute of Biodiversity, Friedrich Schiller University Jena, Dornburger Straße 159, 07743 Jena, Germany

^b Helmholtz Centre for Environmental Research - UFZ, Department of Ecosystem Services, Permoserstr. 15, 04318 Leipzig, Germany

^c German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103 Leipzig, Germany

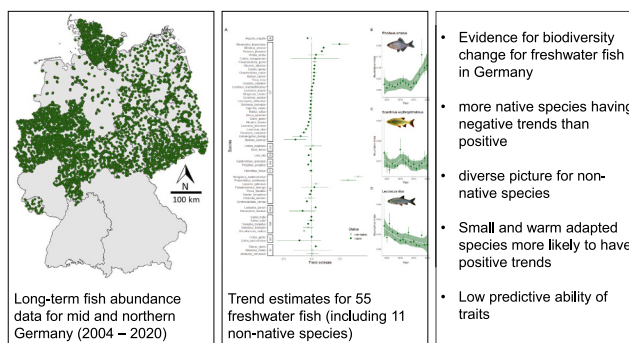
^d UK, Centre, for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

^e Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, 10115 Berlin, Germany

HIGHLIGHTS

- Species' long-term population trends are essential to understand biodiversity change.
- We analysed a new data-set for freshwater fish in mid and northern Germany.
- We detected strong evidence for a change in freshwater fish biodiversity.
- Small species, spawning at higher temperature more likely to have positive trends.
- Overall traits had only limited predictive power to predict trends.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Damià Barceló

ABSTRACT

To understand biodiversity change and support conservation decision-making, estimates of species' long-term population trends at regional and national scales are essential. However, such estimates are missing for many freshwater taxa, despite the diverse range of threats that they face. For this study, we mobilised monitoring data on riverine freshwater fish abundance collected across different regions of Germany. We applied generalized mixed effect models to estimate the population trends for 55 native species and 11 non-native species between 2004 and 2020. In addition, we used boosted regression trees to identify trait-based predictors of species trends and assessed their predictive ability. We found evidence of increasing abundance trends for 14 species and decreasing trends for 15 species; while the remaining species were mostly stable (26 species). Native species were more typically decreasing than increasing (14 vs 10 species); while non-native species were more often increasing (4 vs 1 species). Important traits associated with trends were maximum length, spawning temperature, and water quality tolerance, with small species, those spawning at high temperatures, and those preferring unpolluted waters, being most likely to have positive trends. Despite these associations, overall trait-based models showed limited power to predict trends in terms of direction as well as magnitude. Our results

* Corresponding author at: Department Biodiversity and People, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, D-04103 Leipzig, Germany.

E-mail address: martin.friedrichs-manthey@idiv.de (M. Friedrichs-Manthey).

<https://doi.org/10.1016/j.scitotenv.2024.177759>

Received 3 September 2024; Received in revised form 20 November 2024; Accepted 23 November 2024

Available online 28 November 2024

0048-9697/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

highlight the ongoing change in riverine fish communities and the importance of on-going species-level monitoring. The trait-based associations also indicate climate change and invasive species as important drivers of change in European freshwater rivers.

1. Introduction

Freshwater ecosystems are biodiversity hotspots (Su et al., 2021) with rivers and lakes covering <1 % of the earth's surface but providing habitat for numerous species, including 15,000 fish species, representing one-fourth of all known vertebrates (Lévêque et al., 2008). The current state of freshwater biodiversity, based on the most recent Living Planet Index (LPI) aggregating data worldwide, shows an average population decline of 83 % (WWF, 2022). This estimated rate of decline is much higher than those for terrestrial or marine biodiversity (WWF, 2022). Also, according to the IUCN, roughly one-third of all known freshwater fish species face the threat of extinction (IUCN, 2021). Especially rivers suffer from diverse threats such as fragmentation, pollution, invasive alien species, and climate change (Tickner et al., 2020).

While the LPI is important for conservation policy, it averages data across different species as an indicator of mean biodiversity change, so it does not provide an understanding of species level change. Species trend estimates are, however, needed to develop specific conservation action plans. The IUCN Red List Assessments, and almost all regional equivalents, require population trend assessments at the species-level, but they are still often qualitative due to a lack of data. Freshwaters are under-represented in large scale monitoring (Maasri et al., 2022; van Rees et al., 2021), especially for freshwater fish (García-Girón et al., 2023; Schmidt-Kloiber and De Wever, 2018) and data availability is only improving slowly (Hering et al., 2010). Freshwater policy in Europe, including the Water Framework Directive (WFD) 2000/60/EC (EC., 2000) and the Habitats Directive (HD) 92/43/EEC (EC., 1992), has promoted structured freshwater monitoring programs that produce standardised abundance data for a wide range of freshwater taxa. But these data are still often scattered, and access and harmonisation remain difficult and time-consuming. Quantitative species-level trend estimates at national or sub-national scales are still needed to strengthen the evidence-base for conservation action, especially for freshwater ecosystems (Ledger et al., 2023).

Recent analysis for freshwater invertebrates have suggested some recovery of freshwater ecosystems in Europe (Haase et al., 2023), which may be partly explained by improved wastewater treatment. However, it is unclear whether such recovery is also apparent in freshwater fish populations. The WFD, and partly the HD, have directed conservation efforts towards freshwaters, but since the implementation of the WFD in 2000, only 40 % of surface waterbodies have reached a good ecological status, with little to no improvement for the past 10 years (Vermeulen et al., 2019). As one likely consequence, to date, >40 % of all known European fish species are thought to face the threat of global extinction (plus 15 are already considered extinct) (Darwall and Freyhof, 2015). However, in the absence of structured data, this estimate is based on distribution ranges plus threat assessments.

In addition to gaps in knowledge on trends, there are gaps in data to describe threats, preventing explicitly linking suspected threats to population declines (Joppa et al., 2016). As a short-cut, trait-based analyses have shown to be a promising alternative to identify possible causes of change (Bowler et al., 2017). Traits represent the biological and ecological characteristics of a species, such as its life history, habitat and diet preferences (Gutiérrez-Cánovas et al., 2024). Of particular interest are 'response' traits, which are those that affect how species respond to specific environmental gradients and provide insights into key drivers of change. For instance, increases in species classed as 'warm-adapted species' indicate a likely role of climate change in reshaping biological communities. Over the last decades, a growing

number of databases have been built that organize trait data for species that facilitate trait-based analyses (Thorson et al., 2023).

One of the most appealing aspects of trait-based approaches is the potential to build predictive frameworks of species trends. If there are associations between species traits and population trends, traits can be used to predict population trends for species where data are scarce. Previous studies have shown that traits have the potential to explain variation in the estimated trends of different species across a range of taxa (Jiguet et al., 2007; Kamp et al., 2021; Morelli et al., 2020). However, there are also numerous cases where traits had only a limited capacity to predict trends (Coulthard et al., 2019; Poccock, 2011; Skálová et al., 2022).

Here, we compiled a large-scale time-series dataset across northern and mid Germany for riverine freshwater fish abundance collected from official authorities for monitoring purposes (e.g. WFD or HD) from 2004 to 2020 (Friedrichs-Manthey and Klasen, 2023). First, we used these data to estimate long term population trends for 55 freshwater fish species occurring in northern and mid German rivers. Second, we combined trend estimates with species traits to identify species characteristics associated with increasing or decreasing trends. We choose traits reflecting vulnerability to climate change, habitat change, and exploitation, as well as adaptive capacity of a species. We did both steps for the full data set (55 species) and a reduced data set only including native species with self-sustaining populations (42 species). Lastly, we used boosted regression trees and linear models in a leave-one-out approach to assess the predictive performance of traits.

2. Methods

2.1. Data compilation and cleaning

In collaboration with conservation agencies from 12 federal states of Germany (excluding Bavaria, Rhineland Palatinate, Baden Württemberg, and Hamburg), we compiled a spatially explicit data-set consisting of 174,558 abundance counts for 72 fish species between 1985 and 2020 (Friedrichs-Manthey and Klasen, 2023). We merged all sampling sites along the same waterbody within a distance of 100 m together as one sampling site. This procedure was necessary because i) between years some sampling sites were slightly moved along the water course (e.g. a certain location falls dry in one year) in the original data set and ii) some sampling sites had no unique ID but rather only coordinates. After this process the data-set consisted of 12,007 sites. We further cleaned this data set as follows. At first, because not all federal states delivered data for the same period of time, we removed all years before 2004 for which the spatial coverage was insufficient, as assessed visually (Supplementary Fig. 1). Then, since we were interested in species population trends over time, we removed all sites that had been only sampled once. We also removed all species that do not have self-sustaining populations in Germany (e.g. *Ctenopharyngodon idella*, *Hypophthalmichthys* spp.) as well as entries that were not identified to species level (e.g. *Lampetra* sp.). Finally, to make sampling effort comparable, we only include data from rivers sampled via electrofishing, which was the most typical method (>95 % of the data). The final data-set consists of a time-series ranging from 2004 to 2020 with 131.633 abundance measures for 62 freshwater fish species over 5497 sites that had been at least sampled twice within this time-frame (Fig. 1, see Supplementary Fig. 1 for spatial coverage of sampling points for different timeframes).

2.2. Trend estimation

To calculate species-specific population trends, we first completed the site-specific species list for all years that a site was sampled. This was necessary because the dataset only contained the abundance for detected species and zeros for undetected species were not reported. However, zero data were collected since the surveys could be assumed to sample the whole community present. We added zeros as follows: if a site had been sampled twice, e.g., 2004 and 2005, and three species were found in 2004, and six species were found in 2005 (3 from 2004 plus 3 new species), we added three entries to the data set for 2004 for each species that has been found at that site in 2005 but not in 2004, and set the abundances for those species to zero. We choose this approach, because 1) all samples were taken with the same method, so it can be assumed that all species that are at least have been caught once are generally catchable (although some species are more likely to be caught than others), and 2) if a monitoring site would theoretically have been in unfavourable environmental condition at the time the monitoring should have taken place, WFD as well as HD allows to either move the sampling area in a certain range up- or downwards the river or move the sampling day, so that it can be assumed that species that have been caught once were not excluded in the next event due to environmental conditions. Based on this data-set, we fitted for each species a generalized linear mixed effect model with abundance as the response and year as the main predictor, assuming a negative binomial distribution for abundance. We also included the day of the year of the sampling event as a predictor to account for variation in sampling dates. We also accounted for variation in sampling effort by including effort (length of river sampled) as an offset term (logged to match the scale of the linear predictor). Random effects were used to account for mean site-level differences in abundance and to account for random variation in trends at the site-level around the mean fixed effect of year. Models were fit using Bayesian inference with the brms package. Chain convergence

was assessed visually and using the Brooks–Gelman–Rubin criterion (Rhat). We achieved convergence with all Rhat <1.01.

2.3. Trait analysis

For all trait-based analyses, we collected traits from Freyhof and Kottelat (2007), freshwaterecology.info (Schmidt-Kloiber and Hering, 2015), and fishbase.org (Froese and Pauly, 2010) (Table S1). Since not all traits were available for all species, we i) screened available literature, or ii) used expert opinion to fill gaps. In total we collected nine traits: two representing species sensitivity to climate change (spawning temperature and temperature tolerance), two affecting species sensitivity to habitat change (rheophily and water quality tolerance), two on species sensitivity and exposure to exploitation (maximum body size and gamefish), and three reflecting species adaptive capacity towards threats (nativeness, female age at first maturity, and its current frequency in Germany). Please note that “gamefish” here refers to species that are regularly targeted by recreational anglers and that are also harvested in amounts that could potentially affect population sizes (Arlinghaus et al., 2020).

2.3.1. Trend-trait-relationship

To assess associations between the calculated species trends and their traits, we used boosted regression trees (BRT) with the trend estimate as response and the nine traits as predictors. BRTs are nonparametric models that combine regression (decision trees) and machine learning (boosting) techniques. BRTs are able to fit complex non-linear relationships between predictors and the response. In addition, they are robust to outliers and can handle metrics of varying scales. Although they are also robust against correlation, we made visually sure that there were no obvious strong correlations between our predictors. We fitted our BRTs using the `gbm.step` function in the `dismo` package with a “Gaussian” family. We used the default settings of the `gbm.step` function

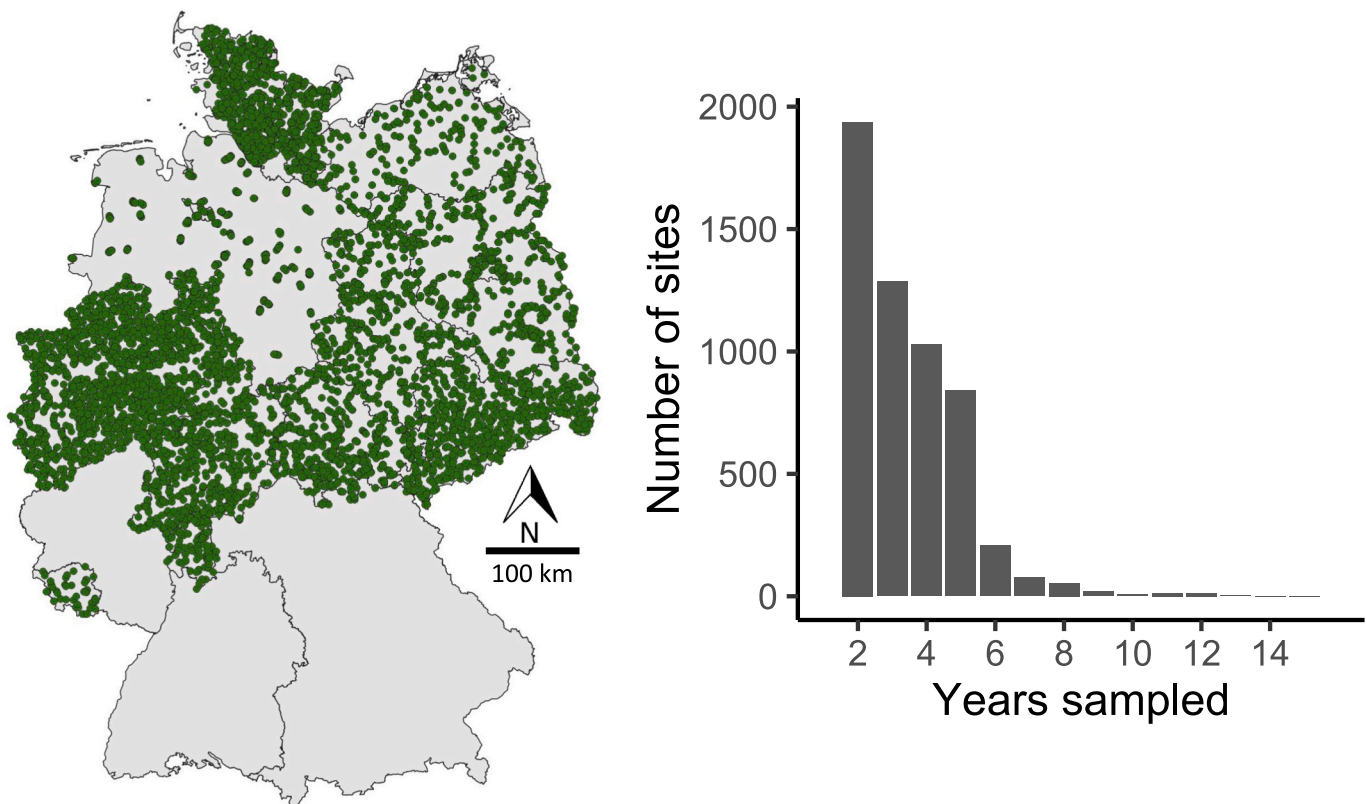


Fig. 1. Distribution of 5497 sampling sites across 12 federal states of Germany, excluding Bavaria, Baden Württemberg, Rhineland Palatinate, and Hamburg (left panel). Number of sites and how often they have been sampled (right panel).

except for the learning rate, which was set to 0.0001 to reach a sufficient number of trees. To define the relative importance of traits on trend estimates, we used a leave-one-out approach on the full data-set (all species for which we could calculate trend estimates, $n = 55$) and on a reduced data-set, where non-native species, common carp (*Cyprinus carpio*) and salmon (*Salmo salar*) were excluded ($n = 43$, from here on called native species data-set). We decided to exclude the common carp from this native species list despite it being considered native in Germany, because, i) natural reproduction is very limited, especially in rivers (Freyhof et al., 2023) and ii) its current distribution and population size is mainly maintained by stocking initiatives from recreational anglers. Therefore, a trend estimate reflects stocking intensity over the past years. Similarly, for salmon, the current population is only maintained by stocking initiatives with almost no natural reproduction (Freyhof et al., 2023). The aim of additionally running the trait analysis with this native species list was to make sure that observed trend-trait combinations are not influenced by non-native, potentially invasive species that are currently in an accelerating phase of their invasion history.

2.3.2. Predictive ability

To assess the predictive ability of traits, we used a leave-one-out approach and predicted the trend for each species using the predictions of the trend model built on all data except for that species. Based on the predictions, we assessed if the model was able to predict the direction of a trend and its magnitude. In addition, we compared the predictions of the BRT against a simple linear model with those three traits as predictors that showed the highest relative importance in the BRT analysis.

Data cleaning and analysis was done using the software R Version 4.4.1 (R Core R-Core-Team, 2024).

3. Results

3.1. Trend estimation

We were able to calculate trend estimates for 55 freshwater fish species (model convergence shown by $r_{hat} < 1.01$; Fig. 2 and Table S1). Of these 55 species, 11 species are considered as non-native to German rivers. The highest population trend (0.83), was estimated for the non-native *Neogobius melanostomus*. Since this species was almost absent in the beginning of the study period, but was very abundant at the end, the number of individuals caught at a site has increased by 54.500 %. The lowest population trend (-0.29) was estimated for the native *Ballerus ballerus*. The mean number of individuals caught at a specific site has shrunk by 98 %. We observed more significant negative trends ($n = 15$) than significant positive trends ($n = 14$), while the remainder were stable ($n = 26$). This overall negative pattern becomes more pronounced, when only native species (i.e. the native species data-set; $n = 44$) are considered (negative trends = 14; positive trends = 10; stable trends = 20).

3.2. Trait analysis

Our BRT analysis based on the full data-set showed that maximum length (63.0 %), water quality tolerance (14.1 %), and spawning temperature (9.2 %) were the three main predictors that explained an increasing or decreasing long term population trend (Fig. 3A and B). For the full data-set, we found that small-sized species, with a low water quality tolerance and a high spawning temperature are most likely to have positive population trends (Fig. 3B).

The general pattern for the native species data-set was similar to the full data-set. However, the relative importance of single traits was different. For the native species, spawning temperature was with a relative importance of 68.3 % by far the most influential trait. Followed by maximum length (25.2 %) and water quality tolerance (4.0 %).

Similar to the full data-set, a small-sized species, with a low water quality tolerance and high spawning temperature was most likely to have a positive population trend.

3.3. Predictive ability

The predictive ability of all trait models was low. We found MSE values ranging from 0.014 for the BRT based on the native species data-set to 0.033 for the BRT based on all species. The linear models ranged in between those extremes. The BRT based on the full data set predicted the correct direction of the population trend for only 36.4 % of the species ($n = 55$). The mean absolute distance to the true trend was 0.1 ± 0.15 (Fig. 4 left panel red dots). In comparison, the linear model based on the full data-set predicted for 52.0 % of species ($n = 52$) the correct direction. The absolute distance to the true trend was 0.09 ± 0.14 (Fig. 4 right panel blue dots). The BRT based on the native species data-set predicted for 65.9 % of the species ($n = 43$) the correct direction and the mean absolute distance to the true trend was 0.07 ± 0.09 (Fig. 4 left panel green dots). In comparison, the linear model based on the native species data-set predicted for 50.0 % of the species ($n = 40$) the correct direction and the mean absolute distance to the true trend was $0.1 + - 0.09$ (Fig. 4 right panel purple dots).

4. Discussion

By using a newly mobilised almost German-wide abundance data-set for freshwater fish, we estimated the long-term population trends (2004 to 2020) for 55 native and non-native species. Our analyses gave evidence for a change in freshwater fish biodiversity in Germany, with more native species having negative trends ($n = 14$) than positive ($n = 10$) and a diverse picture for non-native species. We combined trend estimates with species-specific traits representing sensitivity to climate change, habitat change, and exploitation, as well as species' adaptive capacity towards threats. In this way, we tried to identify key traits explaining positive or negative trend estimates. Our trait analysis showed that no matter if all or just native species are considered, body length and spawning temperature were among the most influential traits. Despite that, traits had only a very limited capacity to predict trends.

4.1. Native species trends

We calculated long-term population trends for 43 native freshwater fish species. Ten of the 43 species showed significant increasing trends. In contrast, 20 species showed either significant negative trends ($n = 14$) or gave a strong indication for negative trends (upper CI very close to 0; $n = 6$), indicating a general loss of population sizes of native species. A phenomenon observed by several studies across Europe (Benitez et al., 2022; Darwall and Freyhof, 2015; Santos et al., 2021).

Among the increasing species, we found that spiralin (*Alburnoides bipunctatus*) showed the highest increase in population size over the past 16 years. The strong increase stands in contrast to a study focusing on headwater streams of large rivers in Europe, which showed a decrease of spiralin (Mueller et al., 2020). However, two reasons are likely for this discrepancy. First, our data did not cover the main distribution range of spiralin, but rather included the northern edge of its distribution. Thus, it is likely that spiralin increases in abundance in our study area due to e.g. climate change and that its distribution range in general moves northward. Second, Mueller et al. (2020) included data only until 2013 and attributed the decline of spiralin to waste water sewage disposal. Our data included a more recent time period and, therefore, probably covers a longer period with improvements in wastewater management.

Among the decreasing species were "expected" species such as *Thymallus thymallus* or *Lota lota*. Both species are listed nationally as critically endangered and are known to be negatively affected by diverse threats such as pollution, predation, fragmentation, and climate change.

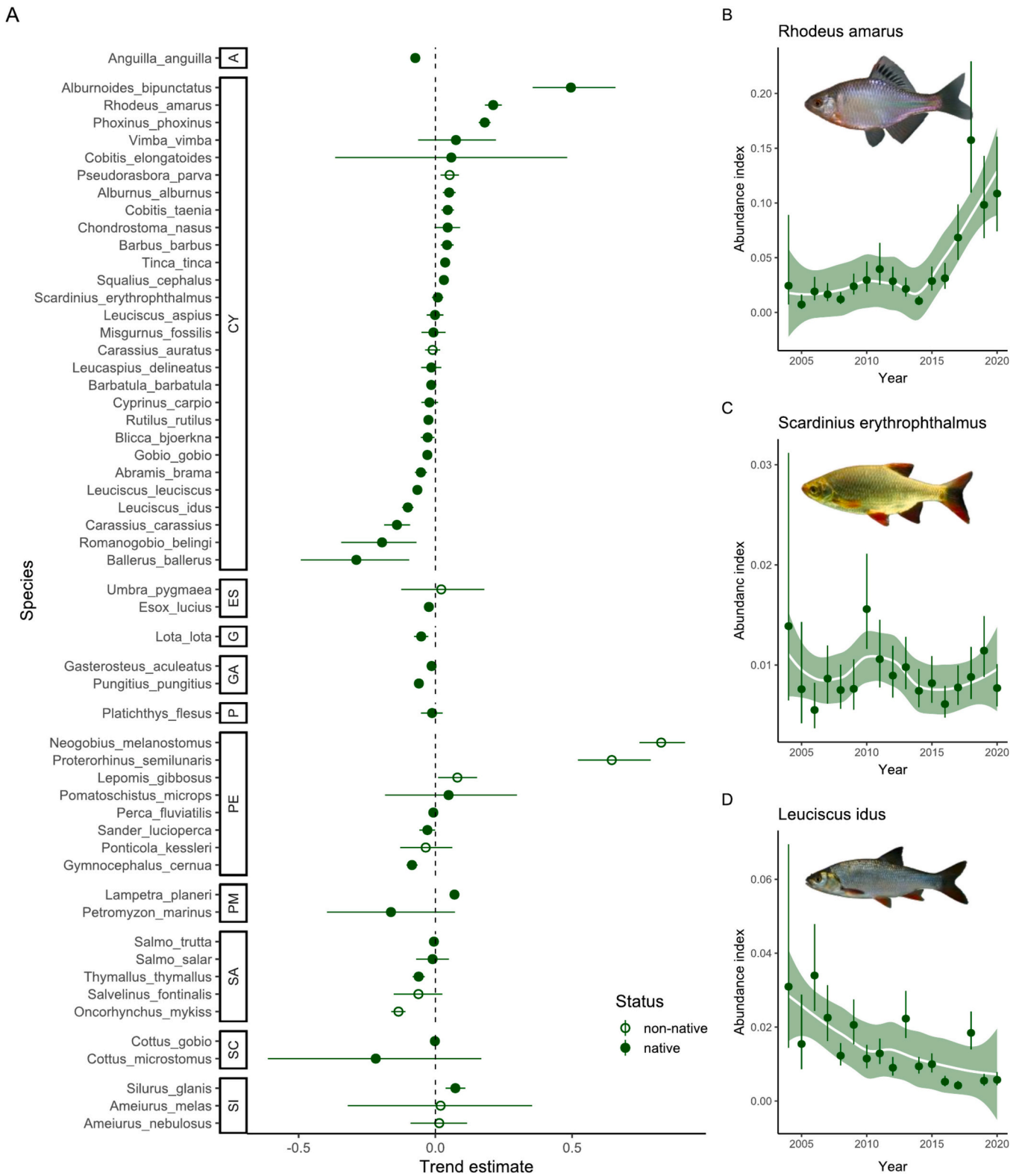


Fig. 2. Population trend estimates for all analysed species and specific examples. A) Calculated population trend estimates for 55 freshwater fish species in Germany. Y-axis indicates the species (and its order). X-axis indicates the trend estimate. Dots indicate the trend estimate and green lines its associated 95% confidence interval. The vertical dashed line indicates the line of no change in population size. Trend estimates for native species are indicated by solid dots and for non-native species by open dots. For a better visualisation, we grouped species according to orders. A= Anguilliformes, CY= Cypriniformes, ES= Esociformes, G= Gadiformes, GA= Gasterosteiformes, P= Pleuronectiformes, PE= Perciformes, PM= Petromyzontiformes, SA= Salmoniformes, SC= Scorpaeniformes, SI= Siluriformes. B to D) Example of time series (significant positive (B), stable (C), significant negative (D)) for: *Rhodeus amarus* (B), *Scardinius erythrophthalmus* (C), *Leuciscus idus* (D). The time series for all species are shown in Supplementary Figure 1.

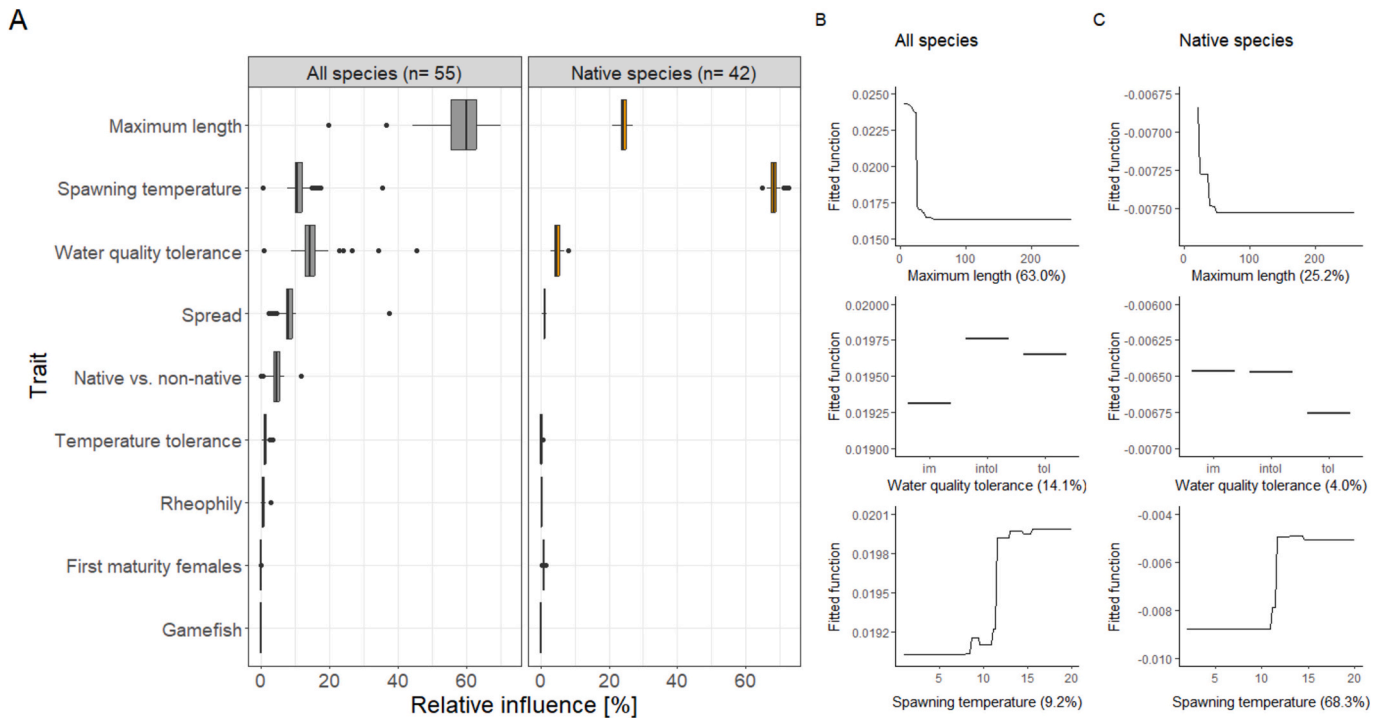


Fig. 3. A) Relative influence of traits on trend estimates, based on a leave-one-out approach, where we re-run BRT models with the trend estimate as response and traits as predictors (left: based on all analysed species; right: based on native species only). B and C): Partial plots for BRT models (B: based on all analysed species; C: based on native species only).

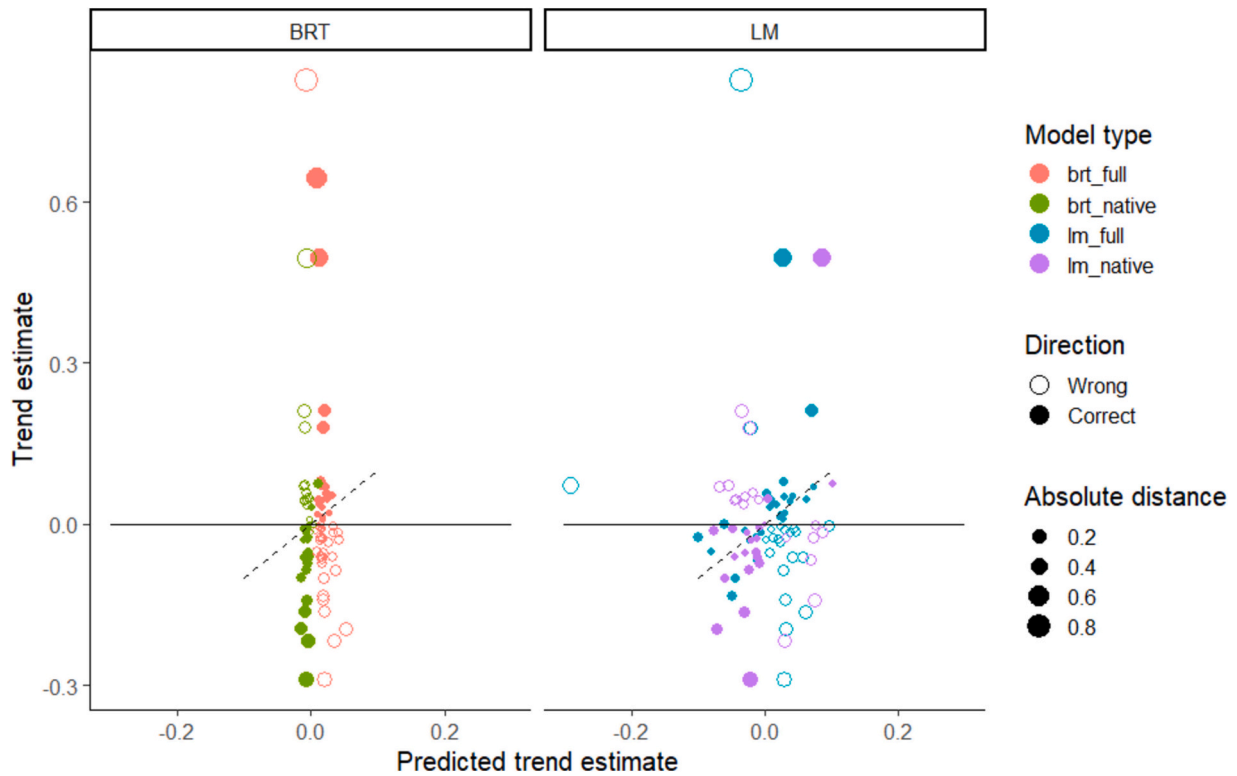


Fig. 4. Predictive ability of boosted regression tree (BRT) models (left panel) in comparison to linear regressions with only the three traits with the highest relative importance as predictors (right panel). The dashed line indicates $x=y$. Solid circles indicate the correct predicted direction of a trend. The size of the circles indicates the absolute distance of a prediction to the true trend. If trend predictions based on traits would have a high predictive power, we would expect to see many small solid circles along the dashed line.

For both species, multiple stocking and conservation initiatives exist in Germany, which, apparently, seem to be insufficient to halt the population decline. However, we also identified several non-threatened and widespread species, such as *Abramis brama* and *Esox lucius*, among the group of decreasing species. Although, those common or very common, non-threatened species are generally expected to be less affected by drivers such as fragmentation or climate change (Jaric et al., 2019), the number of studies, which identified significant decreases for common species is increasing steadily (Benitez et al., 2022; Santos et al., 2021).

4.2. Non-native species trends

Overall, non-native species were present at 44 % of all sites at least once. In the first three years (2004 to 2006), they were present at 23 % of all sites and at 25 % in the last three years (2018 to 2020). This indicates a relatively stable distribution pattern of non-native species in mid and northern Germany. In extreme cases, non-native species made up to roughly 50 % of the total fish caught at those sites. For example, at a sampling event in Hesse in 2018, spanning 500 m of river length, in total 8432 individuals from 18 species were caught. Five of those species were non-natives, summing up to 4013 individuals, from which again *N. melanostomus* made up 3924 individuals. Four, out of 12, non-native species in Germany had significant increasing population trends. Non-native *N. melanostomus* and *Proterorhinus semilunaris* represent the two species with the highest population trend increases at all. Those two species can be considered in their accelerating phase of invasion, which is characterised by rapid range expansion and a dramatic increase in population size. Similar trends for those species have been observed in different European countries (Azour et al., 2015; Jüza et al., 2018). However, here it is worth mentioning that a similar invasive species, *Ponticola kessleri*, was found to have a stable population trend. *P. kessleri* was among the first non-native goby species that arrived in German rivers (Gaye-Siessegger et al., 2022). In their accelerating phase, they expanded rapidly and increased in population size. However, after the arrival of other goby species, the population size of *P. kessleri* seems to be stable or even slightly decreasing. A trend that could be expected and had been observed in other places as well (Gaye-Siessegger et al., 2022; Janáč et al., 2018), given an increase in competition due to other goby species and an additional increase in predation rate due to the acceptance of gobies as natural prey by native predators (Všetičková et al., 2018). The other two non-native species with increasing population trends are *Lepomis gibbosus* and *Pseudospina parva*. Similar increases in population sizes for both species have also been reported for Alpine streams in central Europe (Niedrist et al., 2023). Both species probably benefit from e.g. climate change and unintentional stocking from recreational anglers (Baltazar-Soares et al., 2020; Rakauskas et al., 2021; Yavno et al., 2020). The only non-native species with a decreasing trend is *Oncorhynchus mykiss*. Despite a high stocking intensity over the past hundreds of years, *O. mykiss* has only rarely established self-sustaining populations in Germany, thus, similar to common carp, this negative trend is rather reflecting stocking intensities (Freyhof et al., 2023; Stanković et al., 2015).

4.3. Trait analysis

Species' preferred spawning temperature was positively associated with long-term population trends and for the native species, spawning temperature was by far the most influential parameter associated with population trends. This finding supports the general assumption that the impacts of climate change favour warm-dwelling or thermally tolerant species. For Europe, this pattern has been shown for example, for some French rivers (Daufresne et al., 2004), but also by several trait-based or predictive studies on a European scale (Jaric et al., 2019; Markovic et al., 2014). However, several recent studies have found either no support or more nuanced patterns for freshwater fish biodiversity. Bowler et al. (2017) did not find a shift towards warm-dwelling or thermally tolerant

species in several freshwater datasets across Europe. Similarly, a predictive study by Buisson et al. (2008) forecasted range expansion for many cold- and warm-water species in France. On a species level, Daufresne et al. (2004) found increasing long-term population trends for *Squalius cephalus* and *Barbus barbus* (both warm-adapted), while *Leuciscus leuciscus* (cold-adapted) showed a decreasing trend. In this line, our study also gives evidence for a more nuanced interpretation, at least for the decreasing species. We found no cold-adapted species with increasing population trends and many cold-adapted species, such as *L. leuciscus*, *L. lota* and *T. thymallus*, with significant negative trends. However, we also found many significant negative trends for warm-water adapted species, such as *A. brama*, *Rutilus rutilus*, or *Carassius carassius*, indicating that warming is just an element of change in German rivers.

Species length was for both data-sets (all species and only native species) among the most important traits explaining population trends. Considering all species, including non-native species, the importance was larger compared to only the native species. For both sets, smaller species were more likely to have positive trends than larger species. He et al. (2018) suggested exploitation to be among the main reasons for the dramatic decline in large fish species. However, exploitation is very likely not the cause for the observed pattern in Germany, as there is almost no commercial fishing pressure existing in inland waters in Germany and we cover exploitation by recreational anglers by the trait "game fish". This trait turned out to be of minor importance in our analysis. Although many studies found severe effects of angler exploitation on fish stocks, there was no such signal in our dataset (Blackwell et al., 2019). More likely, larger species are associated with long spawning migrations, lower adaptive capacity, and long life-spans and generation times, making them generally more vulnerable to change (He et al., 2018). It might be speculated that those are characteristics that could lead to shrinking population sizes in a highly variable, human-dominated river landscape.

Not surprisingly, size was much more important when non-native species were included, as these (*Lepomis*, *Pseudorasbora*, *Neogobius* and *Proterorhinus*) are all small-sized species. Again, this points towards a connection between size and adaptive capacity, which is known to be often higher for non-native species and especially for invasive species such as the aforementioned (Rosecchi et al., 2001).

We found that water quality tolerance was an important trait explaining species trends. For both data-sets, water quality intolerant species were slightly more likely to have positive trends than tolerant or indifferent species. Organic pollution and eutrophication are among the most prevalent pressures for freshwater fish communities in rivers in Europe (Schinegger et al., 2016). Especially, eutrophication leads to oxygen depletion and hypoxia (Teichert et al., 2016), causing catastrophic events and mass mortality in fish assemblages (Petriki et al., 2021). In Europe, since 1990, improvements in water quality have been on the agenda. Several directives, such as the Nitrate Directive 91/676/EEC (EC., 2002), the Urban Waste Water Treatment Directive 91/271/EEC (EC., 1999), and probably most importantly the WFD (EC., 2000), have been set into force and recent papers show that they are at least partly effective (Cooper and Hiscock, 2023; Vigiak et al., 2023). Consequently, it could be assumed that our finding supports the theory of recovery of water quality intolerant species due to water quality improvements, similar to what is assumed for freshwater insects (van Klink et al., 2020). However, in contrast to a recent study by Haase et al. (2023), we had no evidence for any sort of plateauing, especially, since Haase et al. (2023) found this effect mainly for richness and not for abundance, which was our focus here. In our case, the native species with the highest increase in population size, *A. bipunctatus*, is considered poor-water-quality intolerant. The same is true for some other significantly increasing species, such as *B. barbus* and *Rhodeus amarus*. However, in many more cases, we found significant and strong decreases for water quality tolerant and indifferent species, such as *A. brama* or *Ballerus ballerus*. Therefore, the importance of water quality tolerance as an

explaining trait for species trends, should, in our opinion, be interpreted as a result of decreases in population sizes of tolerant and indifferent species, rather than an increase in population sizes of intolerant species.

4.4. Predictive ability of traits

For data-deficient taxa, traits are considered an effective tool to identify conservation priorities (Jaric et al., 2019). We tried to predict species trends based on our trait models. However, this approach was only very limited in power. Only for the direction of trends, the BRT model (based on the native species data-set) was able to predict the correct direction for 66 % of native species. All other models performed worse. The magnitude of trends was not well predicted by any of the models. This finding is in line with other approaches that tried to use traits to predict trends. Coultard et al. (2019) showed for moth species (Lepidoptera) that trait-based models were able to predict the correct direction for declining species in almost 90 % of the cases; however, for species with positive population trends, this success rate was reduced to <50 %. Poccock (2011) showed for birds that models based on a trait-trend relationship in one region had almost no ability to predict vulnerable species in another region. For grassland communities, Skálová et al. (2022) found that traits were able to predict short-term dynamics. However, long-term trends were rather determined by environmental change. For non-native fish species, Rosacchi et al. (2001) found that invasiveness is a result of phenotypic plasticity rather than determined by a certain set of traits pre-adapted to invasion.

In contrast, especially for birds and butterflies, several studies have found that traits such as habitat preference or life history, explain some of the variation among species in their long-term trends (Jiguet et al., 2007; Kamp et al., 2021; Morelli et al., 2020).

In our study, the low predictive ability of traits has likely several reasons. First, the relatively low sample size reduces the amount of intraspecific variability to explain trends by traits. Traits explain the interspecific variation of trends; hence, can only be useful when there is considerable variation. Second, even with a large sample size, species with the same traits might not show the same trends. For example, the two goby species with the highest long-term population trends share exactly the same set of traits with another goby species, *P. kessleri*, that has a stable long-term trend. Third, our traits are mostly categorical, except for the maximum length and the spawning temperature. More continuous trends likely have a higher predictive power, especially when the sample size and the intraspecific variability are rather low. Fourth, there is also the chance that we have missed some key traits. For example, Jaric et al. (2019) found that the centroid of the distribution range was a good predictor to identify climate change susceptible species across Europe. However, Jaric et al. (2019) did not confirm predictions by actual data and a lot of species classified as not susceptible show negative long-term trends based on our national data set.

4.5. Concluding remarks

For the purpose of this study, we mobilised, archived and published the first data set on fish occurrence and abundance in inland rivers for a large part of Germany (Friedrichs-Manthey and Klasen, 2023). Initial data mobilisation was part of the process for a new national red-list assessment for freshwater fish in Germany (Freyhof et al., 2023). Despite its importance in identifying large-scale patterns in biodiversity change and consequently setting conservation priorities, monitoring data for fish and other taxa in Germany are generally scattered around different data holders (e.g. federal institutes, conservation agencies and NGOs, natural history societies). Data mobilisation is often only possible with strong commitments from those diverse data holders. In addition, a significant amount of time, financial resources, taxonomic knowledge, and technical expertise are prerequisites for data harmonisation of different data sources and initial curation. However, timely research and evidence-based actions are needed to reverse or stop biodiversity loss.

Consequently, data accessibility according to FAIR(+)-principles needs to be fostered, which will involve the establishment of trustworthy national (and European) data infrastructures to support the diverse landscape of data holders with data mobilisation, archiving and publication (Luther et al., 2022). Our paper reveals the wealth of existing data for freshwater fish in Germany, and shows the value of bringing data together. However, in an ideal case for conservation purposes (since rivers regularly cross administrative borders), we could have presented a German (or European) wide analysis based on a FAIR+ dataset.

CRedit authorship contribution statement

Martin Friedrichs-Manthey: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Diana E. Bowler:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis. **Jörg Freyhof:** Writing – review & editing, Writing – original draft, Supervision, 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.

Acknowledgements

MFM was supported by the German Research Foundation (DFG) within the project “Establishment of the National Research Data Infrastructure (NFDI)” in the consortium NFDI4Biodiversity (project number 442032008). MFM gratefully acknowledge the support of the German Centre for Integrative Biodiversity Research (iDiv) funded by the German Research Foundation (DFG-FZT 118, 202548816). Diana Bowler appreciates the support of the German Research Foundation (DFG) for funding the sMon working group (Trend analysis of biodiversity data in Germany) through the iDiv (DFG FZT 118, 202548816). JF wants to thank the German Red-List-Centre for constant support with a special thanks to Jürgen Wolf, Esra Sohlsström, Jürgen Brück, Jonas Bunte, Steffen Caspari, Miriam Lindenmeier und Günter Matzke-Hajek. In addition, we want to thank all colleagues who invested their time to mobilise the fish occurrence data-set: Tanja Berg, Rainer Bock, Frank Bonell, Ingo Borkmann, Matthias Brunke, Birgit Budszuhn, Margret Bunzel-Drüke, Julia von Dassel-Scharf, Thomas Dietert, Ute Dreyer, Michael Effenberger, Frank Franken, Gert Füllner, Jens Görlach, Jens Götzinger, Arne Haybach, Hannes Hoffmann, Bernd Kammerad, Stephan Karger, Martin Krappe, Kamilla Kubaczynski, Christian von Landwüst, Christoph Mayr, Bernd Mockenhaupt, Eva Christine Mosch, Milan Müller, Franziska Neumann, Achim Pätzold, Stefanie Pleines, Jens Puchmüller, Lasse Rennebeck, Reinhold Sangen-Emden, Elisabeth Schlag, Michael Schubert, Jean Signer, Nikola Theißen, Martina Völkel, Thomas Wanke, Arno Waterstraat und SteffenZahn

We also thank Marcel Jentsch for data handling and general data support at Museum für Naturkunde Berlin.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.177759>.

Data availability

All data that has been used, was previously published by us and is cited in the manuscript.

References

- Arlinghaus, R., Beardmore, B., Riepe, C., Pagel, T., 2020. Species-specific preference heterogeneity in German freshwater anglers, with implications for management. *J. Outdoor Recreat. Tour.* 32, 100216. <https://doi.org/10.1016/j.jort.2019.03.006>.
- Azour, F., van Deurs, M., Behrens, J., Carl, H., Hüsey, K., Greisen, K., Ebert, R., Möller, P. R., 2015. Invasion rate and population characteristics of the round goby *Neogobius melanostomus*: effects of density and invasion history. *Aquat. Biol.* 24 (1), 41–52. <https://www.int-res.com/abstracts/ab/v24/n1/p41-52/>.
- Baltazar-Soares, M., Blanchet, S., Cote, J., Tarkan, A.S., Záhorská, E., Gozlan, R.E., Eizaguirre, C., 2020. Genomic footprints of a biological invasion: introduction from Asia and dispersal in Europe of the topmouth gudgeon (*Pseudorasbora parva*). *Mol. Ecol.* 29 (1), 71–85. <https://doi.org/10.1111/mec.15313>.
- Benitez, J.-P., Dierckx, A., Rimbaud, G., Nzau Matondo, B., Renardy, S., Rollin, X., Gillet, A., Dumonceau, F., Poncin, P., Philippart, J.-C., Ovidio, M., 2022. Assessment of fish abundance, biodiversity and movement periodicity changes in a large river over a 20-year period. *Environments* 9 (2), 22. <https://www.mdpi.com/2076-3298/9/2/22>.
- Blackwell, B.G., Kaufman, T.M., Moos, T.S., 2019. Angler exploitation of an unexploited walleye population in the northern Great Plains. *Fish. Res.* 216, 59–64. <https://doi.org/10.1016/j.fishres.2019.03.026>.
- Bowler, D.E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R.W., Dekoninck, W., Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., Böhning-Gaese, K., 2017. Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution* 1 (3), 0067. <https://doi.org/10.1038/s41559-016-0067>.
- Buisson, L., Blanc, L., Grenouillet, G., 2008. Modelling stream fish species distribution in a river network: the relative effects of temperature versus physical factors. *Ecol. Freshw. Fish* 17 (2), 244–257. <https://doi.org/10.1111/j.1600-0633.2007.00276.x>.
- Cooper, R.J., Hiscock, K.M., 2023. Two decades of the EU water framework directive: evidence of success and failure from a lowland arable catchment (river Wensum, UK). *Sci. Total Environ.* 869, 161837. <https://doi.org/10.1016/j.scitotenv.2023.161837>.
- Coulthard, E., Norrey, J., Shortall, C., Harris, W.E., 2019. Ecological traits predict population changes in moths. *Biol. Conserv.* 233, 213–219. <https://doi.org/10.1016/j.biocon.2019.02.023>.
- Darwall, W. R., & Freyhof, J. (2015). Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. In M. K. a. J. D. O. G. P. Closs (Ed.), *Conservation of Freshwater Fishes* (pp. 1–35). Cambridge University Press.
- Daufresne, M., Roger, M.C., Capra, H., Lamouroux, N., 2004. Long-term changes within the invertebrate and fish communities of the upper Rhône River: effects of climatic factors. *Glob. Chang. Biol.* 10 (1), 124–140. <https://doi.org/10.1046/j.1529-8817.2003.00720.x>.
- EC., 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Off. J. Eur. Union* 206 (7), 50.
- EC., 1999. Implementation of Council Directive 91/271/EEC concerning urban wastewater treatment—summary of the measures implemented by the member states and assessment of the information received pursuant to articles 17 and 13 of the Directive, COM(98)775 final. *Official Journal of the European Communities*.
- EC., 2000. 60/EC of the European Parliament and of the council of 23 October 2000 establishing a framework for community action in the field of water policy. *Off. J. Eur. Communities* 22 (12), 2000.
- EC., 2002. Implementation of Council Directive 91/676/EEC Concerning the Protection of Waters against Pollution Caused by Nitrates from Agricultural Sources: Synthesis from Year 2000 Member States Reports. Office for Official Publications of the European Communities.
- Freyhof, J., Kottelat, M., 2007. *Handbook of European Freshwater Fishes*. Publications Kottelat.
- Freyhof, J., Bowler, D., Broghammer, T., Friedrichs-Manthey, M., Heinze, S., Wolter, C., 2023. Rote Liste und Gesamtartenliste der sich im Süßwasser reproduzierenden Fische und Neunaugen (Pisces et Cyclostomata) Deutschlands. *Naturschutz und Biologische Vielfalt* 170 (6), 63.
- Friedrichs-Manthey, Freyhof, J., & Klases, B. (2023). *Harmonised freshwater fish occurrence and abundance data for 12 federal states in Germany* Version 1.10.) Leibniz Institute for the Analysis of Biodiversity Change (LIB). doi: 10.15468/c75fky.
- Froese, R., Pauly, D., 2010. *FishBase*. Fisheries Centre, University of British Columbia.
- García-Girón, J., Bini, L.M., Heino, J., 2023. Shortfalls in our understanding of the causes and consequences of functional and phylogenetic variation of freshwater communities across continents. *Biol. Conserv.* 282, 110082. <https://doi.org/10.1016/j.biocon.2023.110082>.
- Gaye-Siessegger, J., Bader, S., Haberbosch, R., & Brinker, A. (2022). Spread of invasive Ponto-Caspian gobies and their effect on native fish species in the Neckar River (South Germany). *Aquatic Invasions. European Research Network on Aquatic Invasive Species (ERNAIS)*, 17(2), 207–223. <https://doi.org/10.3391/ai.2022.17.2.05>.
- Gutiérrez-Cánovas, C., Stubbington, R., von Schiller, D., Bolpagni, R., Colls, M., Datry, T., Marcé, R., & Bruno, D. (2024). Use of trait concepts and terminology in freshwater ecology: historic, current, and future perspectives. *Freshwater biology*, n/a(n/a). doi: <https://doi.org/10.1111/fwb.14230>.
- Haase, P., Bowler, D.E., Baker, N.J., Bonada, N., Domisch, S., Garcia Marquez, J.R., Heino, J., Hering, D., Jähnig, S.C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, G., Angeler, D.G., Archambaud-Suard, G., Jorrín, I.A., Aspin, T., Azpiroz, I., Weltri, E.A.R., 2023. The recovery of European freshwater biodiversity has come to a halt. *Nature* 620 (7974), 582–588. <https://doi.org/10.1038/s41586-023-06400-1>.
- He, F., Bremerich, V., Zarfl, C., Geldmann, J., Langhans, S.D., David, J.N.W., Darwall, W., Tockner, K., Jähnig, S.C., Iacona, G., 2018. Freshwater megafauna diversity: patterns, status and threats. *Divers. Distrib.* 24 (10), 1395–1404. <https://doi.org/10.1111/ddi.12780>.
- Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C.K., Heiskanen, A.-S., Johnson, R.K., Moe, J., Pont, D., Solheim, A.L., de Bund, W., v., 2010. The European water framework directive at the age of 10: a critical review of the achievements with recommendations for the future. *Sci. Total Environ.* 408 (19), 4007–4019. <https://doi.org/10.1016/j.scitotenv.2010.05.031>.
- IUCN. (2021). The IUCN Red List of Threatened Species. Retrieved 18.08.2021 from <https://www.iucnredlist.org>.
- Janáč, M., Roche, K., Slapanský, L., Poláčik, M., Jurajda, P., 2018. Long-term monitoring of native bullhead and invasive goboids in the Danubian rip-rap zone. *Hydrobiologia* 807 (1), 263–275. <https://doi.org/10.1007/s10750-017-3398-6>.
- Jaric, I., Lennox, R.J., Kalinkat, G., Cvijanovic, G., Radinger, J., 2019. Susceptibility of European freshwater fish to climate change: species profiling based on life-history and environmental characteristics. *Glob. Chang. Biol.* 25 (2), 448–458. <https://doi.org/10.1111/gcb.14518>.
- Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Chang. Biol.* 13 (8), 1672–1684. <https://doi.org/10.1111/j.1365-2486.2007.01386.x>.
- Joppa, L.N., O'Connor, B., Visconti, P., Smith, C., Geldmann, J., Hoffmann, M., Watson, J.E.M., Butchart, S.H.M., Virah-Sawmy, M., Halpern, B.S., Ahmed, S.E., Balmford, A., Sutherland, W.J., Harfoot, M., Hilton-Taylor, C., Foden, W., Minin, E. D., Pagad, S., Genovesi, P., Burgess, N.D., 2016. Filling in biodiversity threat gaps. *Science* 352 (6284), 416–418. <https://doi.org/10.1126/science.aaf3565>.
- Jůza, T., Blabolil, P., Baran, R., Bartoň, D., Čech, M., Drašík, V., Frouzová, J., Holubová, M., Ketelaars, H.A.M., Kočvara, L., Kubečka, J., Muska, M., Prchalová, M., Říha, M., Sajdllová, Z., Šmejkal, M., Tušer, M., Vašek, M., Vejřík, L., Peterka, J., 2018. Collapse of the native ruffe (*Gymnocephalus cernua*) population in the Biesbosch lakes (the Netherlands) owing to round goby (*Neogobius melanostomus*) invasion. *Biol. Invasions* 20 (6), 1523–1535. <https://doi.org/10.1007/s10530-017-1644-5>.
- Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B., Karthäuser, J., Kunz, F., Mitschke, A., Schwarz, J., Suddfeldt, C., 2021. Population trends of common breeding birds in Germany 1990–2018. *J. Ornithol.* 162 (1), 1–15. <https://doi.org/10.1007/s10336-020-01830-4>.
- Ledger, S.E.H., Loh, J., Almond, R., Böhm, M., Clements, C.F., Currie, J., Deinet, S., Galewski, T., Grooten, M., Jenkins, M., Marconi, V., Painter, B., Scott-Gatty, K., Young, L., Hoffmann, M., Freeman, R., McRae, L., 2023. Past, present, and future of the living planet index. *Npj. Biodiversity* 2 (1), 12. <https://doi.org/10.1038/s44185-023-00017-3>.
- Lévêque, C., Oberdorff, T., Paugy, D., Stiassny, M.L.J., Tedesco, P.A., 2008. Global diversity of fish (Pisces) in freshwater. In: Balian, E.V., Lévêque, C., Segers, H., Martens, G. (Eds.), *Freshwater Animal Diversity Assessment*. Springer, Netherlands, pp. 545–567. https://doi.org/10.1007/978-1-4020-8259-7_53.
- Luther, K., Güntsch, A., Koenig-Ries, B., Fichtmueller, D., 2022. NFDI4Biodiversity: a German infrastructure for biodiversity data [10.3897/biss.6.93869]. *Biodiversity Information Science and Standards* 6, e93869. <https://doi.org/10.3897/biss.6.93869>.
- Maasri, A., Jähnig, S.C., Adamescu, M.C., Adrian, R., Baigun, C., Baird, D.J., Batista-Morales, A., Bonada, N., Brown, L.E., Cai, Q., Campos-Silva, J.V., Clausnitzer, V., Contreras-MacBeath, T., Cooke, S.J., Datry, T., Delacámara, G., De Meester, L., Dijkstra, K.-D.B., Do, V.T., Worischka, S., 2022. A global agenda for advancing freshwater biodiversity research. *Ecol. Lett.* 25 (2), 255–263. <https://doi.org/10.1111/ele.13931>.
- Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdius, H., Darwall, W., Richardson, D., 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>.
- Morelli, F., Benedetti, Y., Callaghan, C.T., 2020. Ecological specialization and population trends in European breeding birds. *Global Ecology and Conservation* 22, e00996. <https://doi.org/10.1016/j.gecco.2020.e00996>.
- Mueller, M., Bierschenk, A.M., Bierschenk, B.M., Pander, J., Geist, J., 2020. Effects of multiple stressors on the distribution of fish communities in 203 headwater streams of Rhine, Elbe and Danube. *Sci Total Environ* 703, 134523. <https://doi.org/10.1016/j.scitotenv.2019.134523>.
- Niedrist, G.H., Hilpold, A., Kranebitter, P., 2023. Unveiling the rise of non-native fishes in eastern alpine mountain rivers: population trends and implications. *J. Fish Biol.* 103 (5), 1085–1094. <https://doi.org/10.1111/jfb.15508>.
- Petriki, O., Patsia, A., Vafeiadou, A., Tekidis, I., Michalopoulou, P., Samartzis, S., Mallinis, D., Bobori, D.C., 2021. Tracking the causes of a mass fish kill at a Mediterranean River within a protected area. *Water* 13 (7), 989. <https://www.mdpi.com/2073-4441/13/7/989>.
- Pocock, M.J.O., 2011. Can traits predict species' vulnerability? A test with farmland passerines in two continents. *Proc. R. Soc. B Biol. Sci.* 278 (1711), 1532–1538. <https://doi.org/10.1098/rspb.2010.1971>.
- Rakauskas, V., Virbickas, T., & Steponėnas, A. (2021). Several decades of two invasive fish species (<i>Perccottus glenii</i> and <i>Pseudorasbora parva</i>) of European concern in Lithuanian inland waters; from first appearance to current state. *Journal of Vertebrate Biology*, 70(4). doi: 10.25225/jvb.21048.
- R-Core-Team, 2024. *R*: a language and environment for statistical Computing. In R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rosecchi, E., Thomas, F., Crivelli, A.J., 2001. Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. *Freshwater Biology* 46 (6), 845–853. <https://doi.org/10.1046/j.1365-2427.2001.00715.x>.

- Santos, R., Poulet, N., Besnard, A., 2021. Life-history traits correlate with temporal trends in freshwater fish populations for common European species. *Freshw. Biol.* 66 (2), 317–331. <https://doi.org/10.1111/fwb.13640>.
- Schinegger, R., Palt, M., Segurado, P., Schmutz, S., 2016. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. *Sci. Total Environ.* 573, 1079–1088. <https://doi.org/10.1016/j.scitotenv.2016.08.143>.
- Schmidt-Kloiber, A., De Wever, A., 2018. Biodiversity and freshwater information systems. In: Schmutz, S., Sendzimir, J. (Eds.), *Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future*. Springer International Publishing, pp. 391–412. https://doi.org/10.1007/978-3-319-73250-3_20.
- Schmidt-Kloiber, A., Hering, D., 2015. www.freshwaterecology.info – an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecol. Indic.* 53, 271–282. <https://doi.org/10.1016/j.ecolind.2015.02.007>.
- Skálová, H., Hadincová, V., Krahulec, F., Pecháčková, S., Herben, T., 2022. Dynamics of a mountain grassland: environment predicts long-term trends, while species' traits predict short-term fluctuations. *J. Veg. Sci.* 33 (3), e13138. <https://doi.org/10.1111/jvs.13138>.
- Stanković, D., Crivelli, A.J., Snoj, A., 2015. Rainbow trout in Europe: introduction, naturalization, and impacts. *Reviews in Fisheries Science & Aquaculture* 23 (1), 39–71. <https://doi.org/10.1080/23308249.2015.1024825>.
- 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>.
- Teichert, N., Borja, A., Chust, G., Uriarte, A., Lepage, M., 2016. Restoring fish ecological quality in estuaries: implication of interactive and cumulative effects among anthropogenic stressors. *Sci. Total Environ.* 542, 383–393. <https://doi.org/10.1016/j.scitotenv.2015.10.068>.
- Thorson, J.T., Maureaud, A.A., Frelat, R., Mérigot, B., Bigman, J.S., Friedman, S.T., Palomares, M.L.D., Pinsky, M.L., Price, S.A., Wainwright, P., 2023. Identifying direct and indirect associations among traits by merging phylogenetic comparative methods and structural equation models. *Methods Ecol. Evol.* 14 (5), 1259–1275. <https://doi.org/10.1111/2041-210X.14076>.
- Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclere, D., Lynch, A.J., Leonard, P., McClain, M.E., Muruvu, D., Olden, J.D., Young, L., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *Bioscience* 70 (4), 330–342. <https://doi.org/10.1093/biosci/biaa002>.
- van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368 (6489), 417–420. <https://doi.org/10.1126/science.aax9931>.
- van Rees, C.B., Waylen, K.A., Schmidt-Kloiber, A., Thackeray, S.J., Kalinkat, G., Martens, K., Domisch, S., Lillebø, A.I., Hermoso, V., Grossart, H.-P., Schinegger, R., Decler, K., Adriaens, T., Denys, L., Jarić, I., Janse, J.H., Monaghan, M.T., De Wever, A., Geijzendorffer, I., Jähnig, S.C., 2021. Safeguarding freshwater life beyond 2020: recommendations for the new global biodiversity framework from the European experience. *Conserv. Lett.* 14 (1), e12771. <https://doi.org/10.1111/conl.12771>.
- Vermeulen, J., Whiteoak, K., Nicholls, G., Gerber, F., McAndrew, K., Cherrier, V., Cunningham, E., Kirhensteine, I., Wolters, H., Verweij, W., & Schipper, P. (2019). Fitness check evaluation of the Water Framework Directive and the Floods Directive: Final evaluation report. <https://edepot.wur.nl/509764>.
- Vigiak, O., Udías, A., Grizzetti, B., Zanni, M., Aloe, A., Weiss, F., Hristov, J., Bisselink, B., de Roo, A., Pistocchi, A., 2023. Recent regional changes in nutrient fluxes of European surface waters. *Sci. Total Environ.* 858, 160063. <https://doi.org/10.1016/j.scitotenv.2022.160063>.
- Všetičková, L., Mikl, L., Adámek, Z., Prásek, V., Roche, K., Jurajda, P., 2018. The diet of reservoir perch before, during and after establishment of non-native tubenose goby. *Knowl. Manag. Aquat. Ecosyst.* 419, 4. <https://doi.org/10.1051/kmae/2017052>.
- WWF, 2022. *Living Planet Report 2022 – Building a Nature-Positive Society*. WWF.
- Yavno, S., Gobin, J., Wilson, C.C., Vila-Gispert, A., Copp, G.H., Fox, M.G., 2020. New and Old World phylogeography of pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758): the north American origin of introduced populations in Europe. *Hydrobiologia* 847 (2), 345–364. <https://doi.org/10.1007/s10750-019-04095-y>.