







Three hundred years of past and future changes for native fish species in the upper Danube River Basin—Historical flow alterations versus future climate change

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Abstract

Aim: Rivers belong to the most threatened ecosystems on Earth. Historical anthropogenic alterations have, and future climate change will further affect rivers and the species therein. While many studies have projected climate change effects on species, little is known about the severity of these changes compared to historical alterations. Here, we used a unique 300-year time series of hydrological and climate data to explore the vulnerability of 48 native fish species in the upper Danube River Basin to past and potential future environmental changes.

Location: Upper Danube River Basins (Germany and Austria).

Methods: We applied a climate niche factor analysis and calculated species-specific vulnerability estimates based on modelled and observed hydrological and climate data from 1800 to 2100. We compared the estimated species vulnerabilities between two historical time intervals (1800–1830 and 1900–1930) and a future time interval (2070–2100, including the two representative concentration pathways 4.5 and 8.5) to an observed reference time interval (1970–2000). In addition, we identified the

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main environmental drivers of species vulnerability and their change over the past 200 years and for the predicted 100 years in the future.

Results: Our results showed that (i) in the past, species vulnerability was mainly driven by changes in discharge, while (ii) future potential vulnerabilities would be due to temperature. Moreover, we found that (iii) future environmental conditions for riverine fish species driven by temperature would change at a similar magnitude as past hydrological changes, driven by anthropogenic river alterations. Future changes, projected for the RCP 4.5, would result in moderate species vulnerability, whereas for the RCP 8.5, the vulnerability for all species would substantially increase compared to the historical conditions.

Main Conclusion: Accounting for an extended timeline uncovers the extent of historical pressures and provides unprecedented opportunities to proactively plan conservation strategies that are necessary to address future challenges.

KEYWORDS

CENFA, climate change, COSERO, Danube, fish, flow alteration, freshwater, river

1 | INTRODUCTION

Fresh waters belong to the most threatened ecosystems on Earth (Dudgeon, 2019; Reid et al., 2018), with almost one-third of all freshwater species facing the threat of extinction (Collen et al., 2014). Among all known freshwater fish species, one quarter faces extinction (Su et al., 2021). Fish species in river ecosystems are sensitive to alterations in discharge (Beatty et al., 2014; Rolls & Arthington, 2014; Ward et al., 2015; Xenopoulos & Lodge, 2006) and temperature (Buisson et al., 2008; Buisson & Grenouillet, 2009; Comte et al., 2013; Kriauciūnienė et al., 2019; Lyons et al., 2010). Globally, discharge has been anthropogenically altered in the past, such that fish have been detrimentally impacted in abundance, demography and diversity (Poff & Zimmerman, 2010). While the effects of historical temperature changes on fish species distribution and occurrence remain largely unknown (but see Clavero et al., 2017), recent pronounced temperature increases (IPCC, 2022) have already been shown to lead to a constant northward migration of fish species and to increase the occurrence rate of fish die-offs (Ebersole et al., 2020; Osland et al., 2021). In contrast, for the future, studies suggest that the significant rise in temperature and changes in precipitation patterns (with regionally diverse but consequential changes in discharge) will be the main driver of vulnerability, that is, susceptibility to being negatively affected (Pacifiçi et al., 2015), for riverine species (Jaric et al., 2019; Kriauciūnienė et al., 2019; Reid et al., 2018).

The majority of large rivers globally have been modified by humans over centuries to meet social and economic demands such as transportation and navigation, energy production, flood and disease control or drinking and agricultural water supply (Grill et al., 2019; Grizzetti et al., 2017; Jungwirth et al., 2014), resulting in a severe loss of natural characteristics of rivers (Cazzolla Gatti, 2016; Wohl, 2019). Climate change scenarios predict a further

significant increase in pressures for river ecosystems within the near future (Dudgeon, 2019; Grill et al., 2019; Jaric et al., 2019; Rodell et al., 2018). For example, climate change will result in increased water temperatures (IPCC, 2017), which often results in a reduction of suitable habitats for native species (Markovic et al., 2014) (but see Isaak et al., 2016) and/or an increase in thermal stress as species will be subject to their upper thermal boundaries (Crear et al., 2020; Till et al., 2019) as well as in potential interactions of stressors (van Vliet et al., 2013). In addition, an expected increase in water use and changes in the amount and spatial distribution of precipitation (Rodell et al., 2018) will add additional hydrologic pressures on biotic communities in rivers (Kakouei et al., 2018; Rolls & Bond, 2017; Yoshikawa et al., 2014).

One of the many river basins with a long history of human alteration and expected severe, future climate-change effects is the Danube River Basin (Figure 1a,b). The Danube is one of the largest and most diverse rivers regarding fish species in Europe (Jungwirth et al., 2014). A glimpse on the history of the Danube River Basin reveals that in the 19th century, engineering measures were dedicated to flood prevention and channelisation, especially in the upper part (Jungwirth et al., 2014) and its tributaries (Heckmann et al., 2017; Hohensinner et al., 2020). Severe impacts on the fish fauna started to occur towards the end of the 19th century, when channelisation reached its maximum (Hohensinner et al., 2020) and soon after hydroelectric power stations were established in the catchment (Jungwirth et al., 2014; Zauner & Schiemer, 1994). The first hydroelectric power station was completed in 1924 in the Inn River, followed by one in the main channel which was completed in 1927. To date, more than 70 hydroelectric power stations exist only in the main stem of the upper Danube River (Jungwirth et al., 2014). Considering future alterations, mean annual temperature is predicted to steadily increase with an accelerating rate (IPCC, 2017) in the upper Danube River Basin (Jacob et al., 2014). However, the

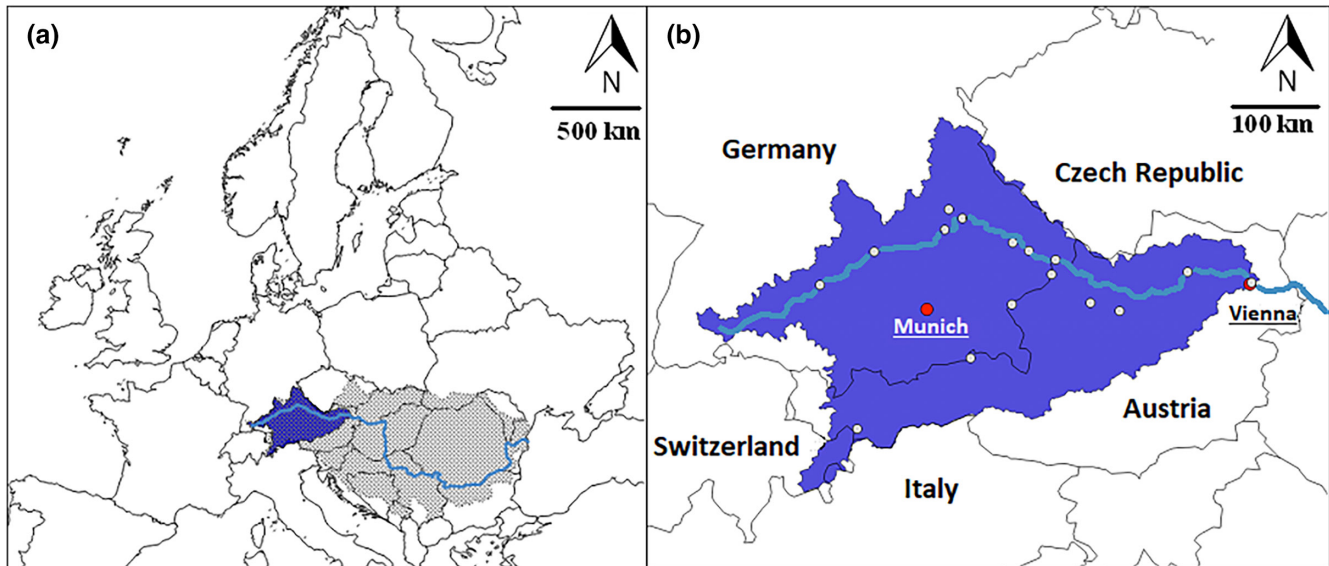


FIGURE 1 Overview of the study area. (a) The location of the upper Danube River Basin in Europe. The dark blue-shaded area represents the study area, that is, the upper part of the Danube River Basin whereas the remaining basin is shown by the light grey-shaded area. The light blue line shows the Danube main stem. (b) Grey circles show the distribution of the gauging stations used to extrapolate discharge values across the study area (see 'Hydrological data' for details). Red circles indicate the location of Munich and Vienna areas for orientation.

predicted precipitation changes are variable and effects on the fish fauna are difficult to anticipate (Giorgi et al., 2016). For instance, a general reduction in precipitation in the summer months is expected; however, several regional climate models also predict an increase in precipitation with a change from rain to snow in higher alpine areas (Giorgi et al., 2016).

When assessing conservation needs for freshwater biodiversity under future climate change scenarios, it is important to address the often dramatic historical environmental alterations and their impact on species or populations (Wohl, 2019). Without quantifying past alterations and their impact on species, future predictions can only deliver the estimates of vulnerability relative to the current point in time. In addition, predictions often come with high uncertainties (Yates et al., 2018) and while these estimates emphasise the importance of temperature, it is important to bear in mind that the spatial units of analysis impact such results (Friedrichs-Manthey et al., 2020). In addition, (ii) the expected rapid increase in temperature is likely to be more pronounced than a gradual change in discharge driven by precipitation changes. Consequently, such uncertainties hinder practical implications of modelling results (McShea, 2014; Porfirio et al., 2014; Schuwirth et al., 2019). In this regard, it is beneficial to set predicted future changes into a historical context, that is, consider the type and magnitude of change that species have been exposed to in the past, and if applied at a relevant spatial resolution, such approaches would provide crucial and much-needed knowledge for species conservation (Bonebrake et al., 2010; Novaglio et al., 2020; Pont et al., 2015).

To this end, we employ a unique 300-year time series of observed (from 1800) and modelled (until 2100) climate and hydrological data for the upper Danube River Basin area (Figure 1). The long period allows comparing the effects of major historical alterations

in discharge and temperature on the vulnerability of fish species (Jungwirth et al., 2014; Zauner & Schiemer, 1994) with predicted effects for the future driven by modelled alterations in climate conditions (Kling et al., 2012; Stanzel & Kling, 2018). In addition, the time series allows quantifying the causes of vulnerability between the historical and potential future environmental drivers.

We first used habitat suitability models (HSMs) to map the present-day suitable habitats for 48 native fish species in the upper Danube River Basin. We then used the present-day predicted fish habitat distributions for a climate niche factor analysis to assess species historical, and potential future vulnerabilities to climate change. We hypothesised that (i) historical vulnerability estimates will be mainly driven by discharge, and when moving towards the future, temperature will be the main factor. In addition, we hypothesised (ii) that historical discharge alterations caused by damming and channelisation have impacted riverine fish species more than the combined, predicted changes in temperature and flow would in the future. We expected that this difference will be expressed by overall higher historical vulnerability estimates compared to those under future scenarios.

2 | METHODS

2.1 | Study region

Our study region is the upper Danube River Basin from its source in Germany's Southwest up to the gauging station close to Vienna, Austria, covering 102,113 km² and roughly 1000 km of the Danube River main stem (Figure 1). The upper Danube River Basin mainly covers parts of Germany and Austria (>90%) and smaller areas of

Switzerland, Italy and the Czech Republic (Figure 1b). For subsequent analyses, we divided the study area into 18,708 sub-basins as the spatial units of analysis (Figure 2a) using the GRASS-GIS (Neteler et al., 2012) function 'r.watershed' (Ehlschlaeger, 1989; for further details on how the sub-basins are created, see Friedrichs-Manthey et al., 2020) and considered each sub-basin with at least one fish occurrence as a sub-basin with said species presence, resulting in a presence-absence sub-basin map per species (Figure 2b).

2.2 | Fish distribution data

We compiled fish species presence-only data from four different sources. For the German part of the upper Danube River Basin, we used occurrence data which were collected by the Federal Ministries of Bavaria and Baden-Württemberg to comply with the EU Water Framework Directive. For the Austrian part of the upper Danube River Basin, we used occurrence data collected for the project 'Improvement and Spatial extension of the European Fish Index' (EFI+, Pont et al., 2009). From these sources, we created our species

list of 48 native fish species for our study area (Table S1). We further complemented the fish records in our list with data from Brunken et al. (2008), from whom we only used data collected by acknowledged sources, such as universities and federal ministries. We filtered all fish occurrence data for sampling dates between 1970 and 2016, where 40% of the data were sampled from 1970 to 2000 and 60% from 2000 to 2016.

2.3 | Environmental data time series

2.3.1 | Hydrological data

We obtained data on discharge and climate from the German Federal Institute of Hydrology (BfG; Stanzel & Kling, 2018). We collected monthly discharge data from 16 gauging stations located in the study area (Figure 1b). These data were obtained using the COSERO precipitation run-off model, covering a time span of 300 years from 1800 to 2100 (Stanzel & Kling, 2018). Historical discharge simulations from COSERO are based on gridded monthly temperature data and precipitation data which are available in the HISTALP database

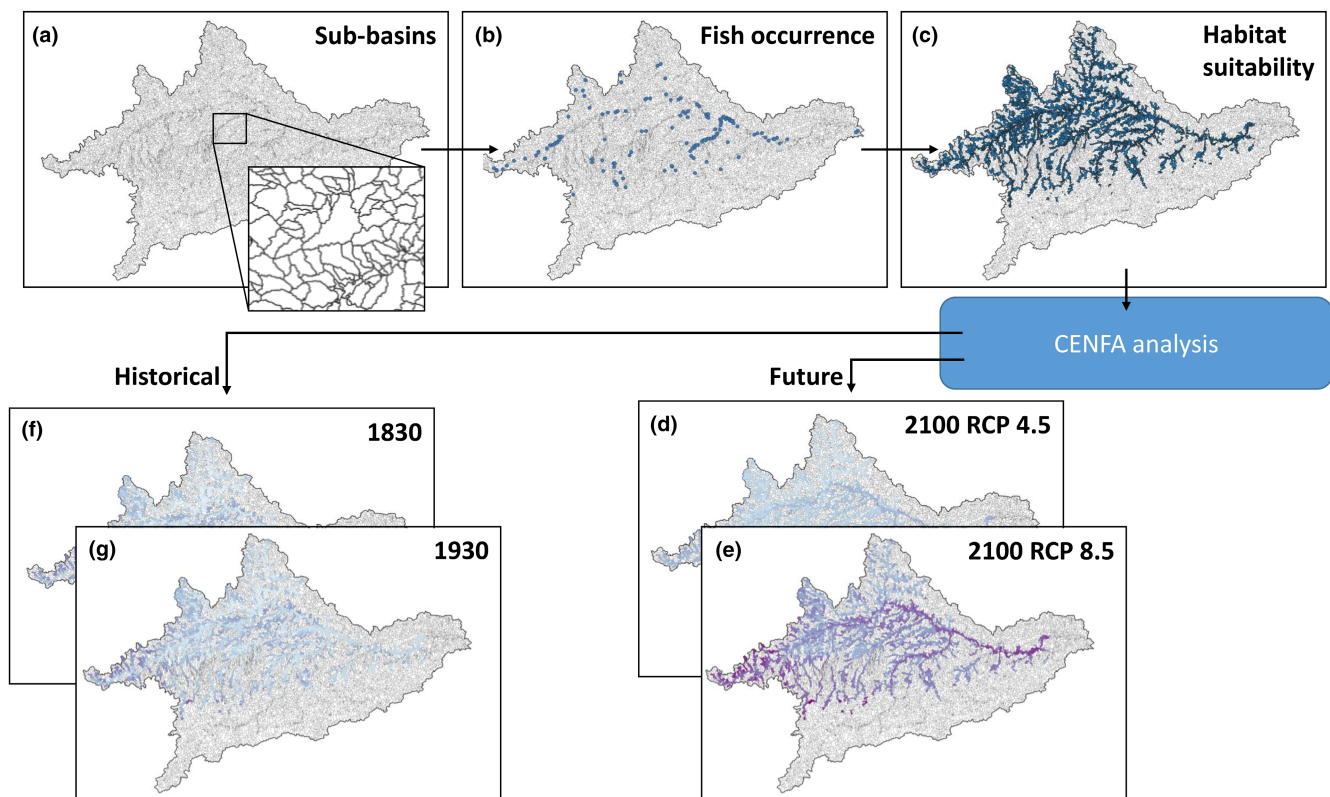


FIGURE 2 Description of the workflow. (a) The study area divided into 18,708 sub-basins with a mean area of $8 \pm 8 \text{ km}^2$. The inset illustrates exemplary sub-basins in detail. (b) Fish point records were used to create fish presence-absence sub-basin maps, here shown for the common bream, *Abramis brama*. (c) For each of the 48 fish species, each occurring in at least 10 sub-basins, we estimated the present-day habitat suitability using six environmental predictors (i.e. mean annual temperature, temperature annual range, mean monthly discharge, coefficient of variance of monthly discharge, mean northness and roughness range; Friedrichs-Manthey et al., 2020). Based on the resulting distribution maps, we applied a species-specific CENFA analysis (Rinnan & Lawler, 2019). (d–g) For each species, we estimated sub-basin-specific vulnerabilities for the three time intervals and climate change scenarios (for details, see section CENFA: Departure and vulnerability analysis).

(Auer et al., 2007; Chimani et al., 2013). Future discharge simulations are based on temperature and precipitation projections of regional climate models (RCMs) from the EUR-11 ensemble of the EURO-CORDEX initiative (Jacob et al., 2014). We used future discharge simulations based on 10 different global-regional climate model (GCM/RCM) combinations (i.e. CERFACS-CNRM-CM5/CCLM4-8-17, EC-EARTH/CCLM4-8-17, HadGEM2-ES/CCLM4-8-17, M-MPI-ESM-LR/CCLM4-8-17, EC-EARTH/RACMO22E, HadGEM2-ES/RACMO22E, EC-EARTH/HIRHAM5, IPSL-CM5A-MR/WRF331F, CERFACS-CNRM-CM5/ALADIN53, M-MPI-ESM-LR r2i1p1/REMO2009) and for the two representative concentration pathways 4.5 and 8.5 (Stanzel & Kling, 2018). For further details on COSERO and its performance, see Kling et al. (2012). To create discharge estimates for each sub-basin, we extrapolated the modelled discharge values from the 16 gauging stations using a linear model of flow accumulation (number of grid cells contributing to a given stream grid cell) and monthly discharge (see also Kuemmerlen et al., 2014). From the entire time series of simulated monthly discharge data, we extracted two historic time intervals (1800–1830 and 1900–1930; from here on addressed as 1800s and 1900s, respectively), a present-day time interval (1970–2000) and a future time interval (2070–2100) with two scenarios (RCP 4.5 and RCP 8.5, from here on 2070s RCP 4.5 and 2070s RCP 8.5, respectively). These time intervals cover historically the phases of river channelisation and straightening (~1800–1900) and damming (~1900–2000) for the entire catchment. For the future, we expected the effects of climate change to be most pronounced towards the end of the century. For each time interval and scenario, we calculated the coefficient of variance of monthly discharge and the mean annual discharge for each sub-basin (see Table 1 for an overview of the raw values). We used both variables as predictors in the HSMs (only the present-day time interval) and the climate niche factor analysis (CENFA: historical and future time intervals, Table 1).

2.3.2 | Temperature data

In the absence of range-wide water temperature data, we used air temperature as a surrogate to assess the effects of climate change on freshwater species (Kirk & Rahel, 2022). Especially for small lowland rivers, which form a large part of the rivers within the study area, the relationship between air and water temperature can be considered robust (Paul et al., 2019; Stefan & Preud'homme, 1993). In addition, as we used 30-year averages of mean annual temperature and the range of those values, the relationship between air and water temperature can be expected to be robust even for snow- and glacier-fed rivers at higher altitudes (southern part of the study area), as has been shown previously for rivers in the Austrian Alps (Webb & Nobilis, 1997). To be consistent with the discharge model COSERO, we used the same monthly temperature data (i.e. the same historic data and the same RCMs) in our analyses. COSERO is driven by temperature data, which was downscaled to 61 hydrological response units within the study area with elevation as a covariate

(Kling et al., 2012). We used the downscaled monthly climate data to aggregate mean annual temperatures as well as annual ranges of temperature across sub-basins and the four time intervals and scenarios (1800s, 1900s, present-day, and 2070s with RCP 4.5 and RCP 8.5; see Table 1). Mean annual temperature and annual range of temperature were used as predictors for the habitat suitability modelling (only the 2000; see *Habitat suitability models*) and the CENFA analysis (Table 1, see CENFA: *Departure and vulnerability analysis*).

2.3.3 | Topographical data

We used topographical data for the present-day HSM, since topography-related predictors were found to strongly contribute to modelled fish habitat suitability in the upper Danube River Basin (Friedrichs-Manthey et al., 2020). Since topography did not change over the 300-year time period, we used topographical predictors only in the HSM to obtain the best possible present-day predictions of habitat suitability (and excluded them from the CENFA analyses). We obtained northness and roughness layers from the EarthEnv topography data set (Amatulli et al., 2018) on a 1-km² resolution, and aggregated these to mean northness and the range of roughness across sub-basins (Table 1).

2.4 | Habitat suitability models (HSMs)

We used HSMs to estimate the occurrence probability for each species across our study area (Elith & Leathwick, 2009). HSMs use a statistical relationship between species occurrence data and environmental predictors to create predictions of habitat suitability for the species. We used the *biomod2* package in R (R-Core-Team, 2013; Thuiller et al., 2009) and a weighted ensemble model approach (Marmion et al., 2009) comprising five machine learning and regression algorithms (Artificial Neural Networks, ANN; Maximum Entropy, MaxEnt; Multivariate Adaptive Regression Splines, MARS; Generalised Linear Model, GLM; Generalised Additive Model, GAM) that are widely applied in HSM studies (Araújo & New, 2007; Merow et al., 2014). We modelled potential habitat suitability only for species that had records in at least 10 unique sub-basins (van Proosdij et al., 2016) and for each species, we used a fixed number of one-third of randomly drawn sub-basins as pseudo absences. As predictors, we used six environmental variables from three different categories, which had a correlation coefficient of less than |0.7| (Dormann et al., 2013) and have shown to be appropriate to model habitat suitability of fish species in the upper Danube River Basin (Friedrichs-Manthey et al., 2020): hydrology—average annual discharge and coefficient of variance of monthly discharge, climate—mean annual temperature and temperature annual range and topography—the average northness and the range of roughness in the sub-basins. We assigned proportional weights to all single models (i.e. derived from single algorithms) before combining them to a final ensemble model for each species.

TABLE 1 Summary statistics of predictors used for the HSM and CENFA analyses.

Time interval	Predictor	Mean (\pm SD)	Median (1st and 3rd quartile)	Maximum	Minimum
1800s	CoV of monthly discharge	2.2 (0.9)	2.7 (1.6; 3.0)	3.1	0.3
	Mean annual discharge (m ³ /s)	322.3 (747.0)	67.7 (61.6; 120.9)	3251.5	8.3
	Temperature annual range (°C)	26.0 (2.6)	26.6 (26.1; 27.3)	28.4	3.3
	Mean annual temperature (°C)	6.7 (2.0)	7.1 (6.7; 7.8)	8.5	-3.0
1900s	CoV of monthly discharge	2.3 (1.0)	2.8 (1.6; 3.1)	3.1	0.3
	Mean annual discharge (m ³ /s)	313.9 (744.4)	61.5 (55.6; 113.4)	3268.1	7.5
	Temperature annual range (°C)	24.2 (2.6)	24.8 (24.4; 25.7)	26.5	3.1
	Mean annual temperature (°C)	6.4 (2.0)	6.8 (6.3; 7.5)	8.1	-3.3
Present-day	CoV of monthly discharge	1.5 (0.6)	1.7 (1.1; 1.9)	1.9	0.2
	Mean annual discharge (m ³ /s)	337.4 (741.2)	85.4 (79.5; 137.7)	3276.1	10.5
	Temperature annual range (°C)	24.7 (2.6)	25.3 (24.9; 26.1)	27.1	3.2
	Mean annual temperature (°C)	7.1 (2.0)	7.7 (7.0; 8.3)	8.8	-2.6
2070s RCP 4.5	CoV of monthly discharge	1.3 (0.5)	1.6 (1.0; 1.7)	1.7	0.2
	Mean annual discharge (m ³ /s)	332.3 (741.6)	80.4 (74.5; 132.4)	3266.2	9.9
	Temperature annual range (°C)	25.2 (2.6)	25.8 (25.3; 26.6)	27.5	3.2
	Mean annual temperature (°C)	9.0 (2.0)	9.5 (9.0; 10.2)	10.8	-0.4
2070s RCP 8.5	CoV of monthly discharge	1.5 (0.7)	1.8 (1.0; 2.0)	2.1	0.2
	Mean annual discharge (m ³ /s)	314.9 (741.4)	64.3 (58.7; 113.3)	3273.4	7.9
	Temperature annual range (°C)	25.2 (2.5)	25.9 (25.2; 26.6)	27.6	3.2
	Mean annual temperature (°C)	10.6 (1.9)	11.0 (10.6; 11.7)	12.4	1.0
All	Mean northness	-0.01 (0.1)	-0.01 (-0.07; 0.05)	0.74	-0.79
	Range of roughness	85.8 (96.1)	47.8 (19.5; 117.6)	701.3	0.0

Note: For each time interval and scenario, we show the mean \pm standard deviation (SD), the median with the first and third quartile and the minimum and maximum.

Abbreviation: CoV, coefficient of variance.

The assignment of weights allows capitalising on the best algorithm without discarding information provided by other algorithms (Araújo & New, 2007). Weights were assigned according to the True Skill Statistic (TSS, Allouche et al., 2006). In general, TSS values range between -1 and +1, with values around zero indicating that a model is not better than random and values of +1 indicating a perfect fit. The final ensemble models were evaluated using TSS by means of data splitting: We used 10 separate model runs, where 70% of the data were used for calibration and 30% for model validation. Predicted habitat suitability was transformed to a binary presence/absence information (Figure 2c; which we refer to as species suitable habitats) using a species-specific cut-off value that minimises the absolute difference between the true-positive rate (i.e. how well a model depicts the true known presences of a certain species) and the true-negative rate (i.e. how well a model depicts the randomly created pseudo absences) (França & Cabral, 2019).

2.5 | Departure and vulnerability analysis

We followed the CENFA framework (Rinnan & Lawler, 2019) to calculate species-specific vulnerability estimates for the two historical

time intervals and the future time interval. The CENFA approach expands the environmental niche factor analyses (ENFA; Hirzel et al., 2002), by the possibility of projections and to calculate three metrics to assess projected environmental changes on species: departure, sensitivity and vulnerability.

The basis for any projections is the so-called environmental departure (i.e. environmental distances between time steps). We define the environmental departure as the change between baseline habitat conditions (present-day environmental conditions) and the historic or the future environmental conditions (Rinnan & Lawler, 2019). The departure estimate is always positive and has no upper limit. For each sub-basin, we calculated the departure from the present-day time interval backwards to the two historical time intervals and forward to the future time interval with the two different RCP scenarios. In total, we calculated 22 departure estimates for each sub-basin (2 historic, and 1 future \times 2 RCP scenarios \times 10 RCMs). As the 10 RCMs differ among each other and, hence, vary in departure estimates, we calculated the median departure to create one future departure layer for each sub-basin and RCP.

We then calculated the species-specific environmental sensitivity. For each species, the environmental sensitivity for one given predictor is calculated as the hypervolume of the range of

environmental conditions a species tolerates compared to a reference area (i.e. the entire study area). The sensitivity can thus be considered a species niche estimate, with high sensitivities indicating a small estimated niche and vice versa. The sensitivity is always positive and allows comparisons across species with identical reference areas. The sensitivity can only be extracted for the current point in time and the current (predicted) distribution.

To estimate vulnerability, the departure and sensitivity are combined following the equation (Rinnan & Lawler, 2019):

$$v_j = \sqrt{(1 + e_j)s_j}$$

where s and e indicate sensitivity and departure, respectively, for the j -th environmental variable and the species-specific sensitivity estimate weights the overall departure estimate for a given environmental variable (Rinnan & Lawler, 2019). Consequently, high sensitivity and departure estimates result in a high vulnerability. Vulnerability estimates can only be interpreted for one species across different time intervals or across species for the same time interval. Vulnerability is sub-basin and species-specific. We first calculated the species-specific vulnerabilities for each sub-basin in which the species was predicted to have suitable habitats (Figure 2c). Second, we averaged the sub-basin-specific vulnerabilities to an overall vulnerability estimate of the given species across its suitable habitat. We used the 10 future climate models separately and combined the results to one median vulnerability layer for each species and future scenario. We compared the spatial similarity of the four resulting median vulnerability layers using the 'modOverlap' function in the R package fuzzySim (Barbosa, 2015) and calculated Schoeners'D (Warren et al., 2008) that ranges from 0 (no overlap) to 1 (total overlap) between each time interval and the two RCPs.

3 | RESULTS

3.1 | Departure

The environmental departure in the coefficient of variance of monthly discharge was similar between the two historical time intervals (1800s: 0.58, 0.49 and 0.69; 1900s: 0.60, 0.51 and 0.72; median, 1st and 3rd quartile, respectively). However, this change was over

two times greater than the median departure observed in the 2070s under the RCP 4.5 scenario (0.23, 0.19 and 0.27). Compared to the 2070s RCP 4.5 scenario, the departure increased for the 2070s RCP 8.5 scenario (0.39, 0.32 and 0.47), but remained lower than the departure for the historic time intervals (Figure 3, light blue box-plots).

The median departure for the annual mean discharge constantly increased from the historic time interval 1800s to the historic time interval 1900s and to the future scenarios, with the highest departure for the 2070s RCP 8.5 scenario (0.13, 0.13 and 0.14; Figure 3, dark blue box plots). We found the same pattern for the median departure for the annual mean temperature, with the highest median departure for the future 2070s RCP 8.5 of 0.94 (0.94 and 0.94, Figure 3, orange box plots). We found the opposite pattern for the median departure for the annual temperature range. The median departure was highest in the historic time interval 1800s (0.1, 0.1 and 0.1) and lowest for the future 2070s RCP 4.5 scenario (0.04, 0.04 and 0.04) and only slightly higher for the future 2070s RCP 8.5 scenario (0.06, 0.06 and 0.06, Figure 3, red box plots).

3.2 | Vulnerability

Mean vulnerability for all 48 native fish species was lowest for the 2070s RCP 4.5 scenario (0.55, 0.51 and 0.66; median, 1st and 3rd quartile, respectively) and almost double for the 2070s RCP 8.5 scenario (1.02, 0.91 and 1.16; Figure 4). The vulnerability estimates for the two historic time intervals ranged between the future scenarios (1800s: 0.60, 0.47 and 0.74; 1900s: 0.65, 0.52 and 0.79; Figure 4).

The spatial structure of the mean vulnerability was more similar among historical time intervals than among the future scenarios (Table 2). The similarity was lowest when comparing any historical time interval with any future scenario (0.88 for both historical scenarios against 2070s RCP 4.5; Table 2).

4 | DISCUSSION

In our study, we showed that the drivers of species-specific vulnerability shifted in their importance from discharge in the past to

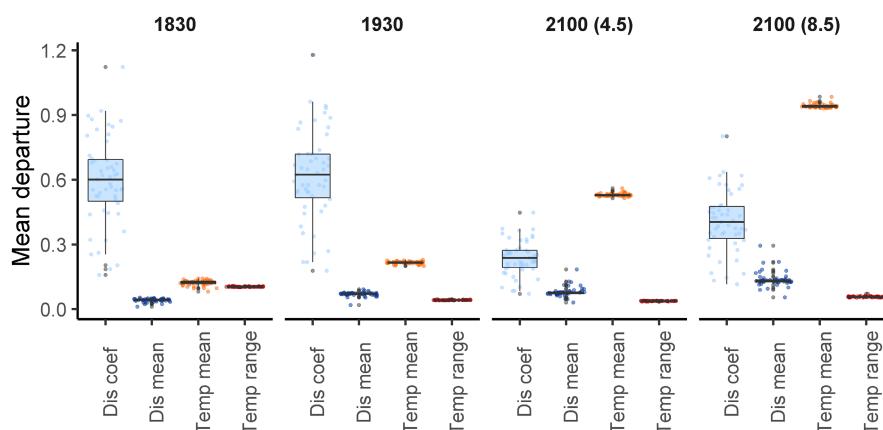


FIGURE 3 Mean departure estimates for the four environmental predictors used in the CENFA for 48 native fish species in the upper Danube River Basin. Departure is always measured as the distance between the present-day and the respective time interval or RCP scenario. Dis coef = Coefficient of variance of monthly discharge, Dis mean = Mean annual discharge, Temp mean = Mean annual temperature, Temp range = Range of mean monthly temperatures.

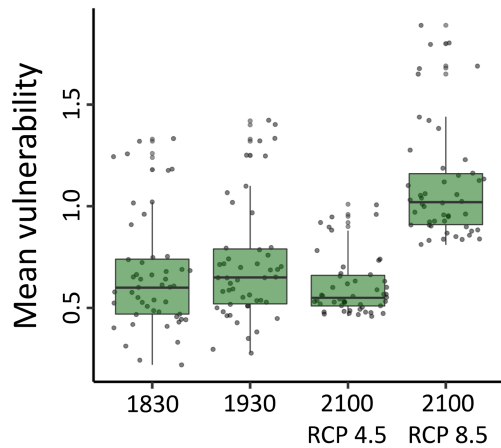


FIGURE 4 Mean vulnerability estimates for 48 native fish species in the upper Danube River Basin for the historical and future time intervals, including two future RCP scenarios.

TABLE 2 Similarity (Schoeners'D; Warren et al., 2008) between vulnerability estimates for the two historic time intervals and the future time interval with two scenarios.

Time interval	1800s	1900s	2070s RCP 4.5	2070s RCP 8.5
1800s	–	0.99	0.88	0.90
1900s	0.99	–	0.88	0.91
2070s RCP 4.5	0.88	0.88	–	0.96
2070s RCP 8.5	0.90	0.91	0.96	–

Note: Schoeners'D values range between 0 and 1. The higher the number, the more similar the spatial structure of the pairwise vulnerability estimates.

climate in the future. Resulting vulnerability estimates were, in terms of magnitude, similar between the two historical time intervals and the moderate future RCP 4.5 scenario. However, for the more severe RCP 8.5 scenario, we identified an almost twofold increase in vulnerability estimates compared to the RCP 4.5 scenario. Our study underlines the significance to widen the time span of analysis when assessing the potential impact of future pressures on freshwater species.

4.1 | Fish species vulnerability in a historical context

The human-induced regulation of the Danube River in the upper basin started as early as at the end of the 16th century (Hohensinner, 2019; Jungwirth et al., 2014) with flood control measures and improvement of inland navigation, especially for the Austrian Danube River Basin, being the main driving force. By the end of the 19th century, flood control and channelisation resulted in a pronounced loss of river length of the German and Austrian Danube main stem (approx. 15% loss of total length; Jungwirth et al., 2014) and its tributaries (approx. 5% loss; Hohensinner et al., 2020). Danube main stem alteration

peaked at the beginning of the 20th century, and to date more than 90% of the shoreline of the upper Danube mainstream is embanked (Jungwirth et al., 2014) and the same percentage of floodplains has been disconnected along the German part of the Danube (Brunotte et al., 2009). These anthropogenic changes have influenced the seasonal patterns of the discharge regime in the upper Danube River Basin with an increase of mean monthly flows during winter and a decrease in summer, whereas the overall mean annual flow remained constant over the last 100 years (Klein et al., 2011).

To interpret our results in line with the aforementioned historical development of the study area, it is important to consider that the present-day environmental conditions, and thus the modelled habitat suitability of fish species, were set as a baseline. This means our baseline study area consists of an already heavily modified catchment that is channelised and straightened and beside large dams, is fragmented by countless, mainly small (<1 MW) hydropower plants (Habersack et al., 2016). This has led to the loss of almost all free-flowing river stretches (Brinker et al., 2018; Duarte et al., 2020; Schiemer & Spindler, 1989).

We found that compared to the baseline, the vulnerability for native fish species increased for both historical time intervals (Figure 4) and that this increase was mainly driven by the variability in monthly discharge (Figure 3). Interestingly, we found no change in vulnerability from 1800s to 1900s (Figure 4). This indicates that interventions for flood control and channelisation between 1800s and 1900s have not caused any major changes for the variability of monthly discharge, probably being influenced by the location of the gauging stations in our analysis which are mainly found along the Danube main stem and large tributaries (Figure 1).

As outlined before, especially the main stem and the large tributaries have a much longer history of human interventions than the many smaller tributaries and most likely our 1800s historical time interval falls into a time period where the main stem and large tributaries were already largely impacted. While anthropogenic alterations further increased between 1830 and 1930 (Jungwirth et al., 2014), they concentrated more on smaller tributaries and had, therefore, probably fewer consequences for discharge variability for the already impacted main stem and its large tributaries.

Considering the vulnerability estimates for the future time intervals under the RCP 4.5 scenario, we found again an increase in fish vulnerability (Figure 4). This increase is mainly caused by an increase in mean annual temperature by 2°C (Figure 3, Table 1). Interestingly, the level of vulnerability projected for the future scenario RCP 4.5 falls within a similar range as in the historical time periods (Figure 4). It can be argued that returning to a state resembling the Danube River Basin's conditions around the 1930s (i.e. reducing vulnerability caused by hydrological changes) would counteract the anticipated impacts of climate change under the RCP 4.5 scenario (i.e. vulnerability caused by climate change and climate-induced hydrological changes).

Regarding the more extreme RCP 8.5 scenario, which tracks current CO₂ emissions best (Schwalm et al., 2020), we observed larger overall vulnerabilities than for all other time intervals and the RCP

4.5 scenario (Figure 4). This increase was mainly driven by an overall +4°C rise in mean annual temperature (Table 1). Interestingly in the RCP 8.5 scenario, the coefficient of variance of monthly discharge returned as an essential driver of fish vulnerability. This indicates that future climate change would cause temperature-driven flow alterations (i.e. more discharge during winter month and less during summer month; Laghari et al., 2018) that are comparable to historical anthropogenic alterations. Considering that COSERO does not account for new dams planned to be built, the cause for these discharge alterations is only a result of changes in climate and precipitation. Under these assumptions, consequences for native fish species in the upper Danube River Basin under RCP 8.5 would be a significant temperature increase and additional hydrological pressures, similar in magnitude to what they have already experienced historically.

On a species-specific level, we found that species inhabiting smaller streams with fast-flowing, well-oxygenated and cold water, such as *Phoxinus phoxinus* and *Cottus gobio*, or very range restricted species, such as *Alburnus mento* and *Cobitis elangatooides*, were predicted to experience high vulnerabilities in the future. In contrast, species such as *Abramis brama* and *Barbus barbus*, both rather warm-adapted, were predicted to experience low future vulnerabilities. However, for the cold-adapted *Lota lota*, the CENFA analysis predicted relatively low vulnerabilities as well. This is probably caused by the fact that *Lota lota* mainly occurs in the mainstem and the large tributaries of the Danube, regions considered less impacted by predicted hydrological changes.

An additional angle to our vulnerability analysis is brought by assessing the spatial similarity between historical and future vulnerability maps. We found that the spatial similarity was lowest between historical and future time intervals (Table 2). This finding indicates that not only the expected pressures caused by climate change will be in a similar (RCP 4.5) and higher (RCP 8.5) magnitude compared to the historical alterations, but they are also expected to impact different areas than those that have been especially impacted by historical alterations. A phenomenon that has been rarely assessed for fresh waters (Döll & Zhang, 2010), but is of highest importance for, for example, conservation actions (Bonebrake et al., 2018).

4.2 | Practical implications

For some organism groups, such as benthic invertebrates or marine fish (Roberts et al., 2017), a reduction in environmental pressures can promote resilience towards anticipated climatic pressures. For instance, Durance and Ormerod (2009) showed that for benthic invertebrate communities in small streams, expected changes in species communities due to warming waters over an 18-year period were buffered by a steadily increasing water quality over the same time period. Our results show a similar pattern for the upper Danube River Basin and its fish communities. The overall environmental departure caused by the historic reduction of discharge variability is similar to the overall environmental departure that is expected

under future climate change scenarios, as indicated by increased mean annual temperatures.

When comparing the fish community in the upper Danube River Basin around the year 1800 with the present-day fish community, only a few species, for example, anadromous sturgeons, went regionally extinct (Friedrich, 2018; Hensel & Holcík, 1997). For sturgeons, regional extinction was mainly caused by large dams, which acted as migration barriers, and poaching in the lower Danube regions (Jungwirth et al., 2014). Other fish populations suffered considerably in relative abundance but did not go extinct after damming (Galik et al., 2015; Schiemer & Spindler, 1989; Schmutz et al., 2013). This observation indicates that the historical fish community itself is still largely present in the upper Danube River Basin, which is an important precondition for effective fish species conservation in river ecosystems (Stoll et al., 2014). To relieve the environmental pressure induced by hydrological alterations, as predicted to play a role again in our RCP 8.5 scenario, floodplain restoration has shown to be an effective conservation action for fish communities (Ramler & Keckeis, 2019; Roni et al., 2008). In the upper Danube River Basin, approximately 25% of the historically available and nowadays unconnected floodplain area has a good potential for rehabilitation measures (Hein et al., 2016). Considering the increasing temperature pressure predicted in both RCP scenarios, the upper Danube River Basin with its many headwater regions might offer cold-water temperature refugia for sensitive fish species (Isaak et al., 2016).

Our study provides a generally promising outlook. This positive outlook is supported when considering that our CENFA analysis assumes a stable species–environment relationship. Future vulnerabilities can be expected to be lower since adaptation and evolutionary processes will likely come into play. However, on the other side, our promising results have to be interpreted carefully. First, our results might be affected by a 'survivorship bias' (Budd & Mann, 2018). Using monitoring data from 1970 to 2016, we excluded species from our analyses that went regionally extinct already before 1970. Second, using only species with more than 10 occurrence records, we excluded range-restricted species that are either hard to detect or less abundant such as *Cottus gobio* (Cruickshank et al., 2016). Third, with our habitat suitability models, we predict the potential realised niche, given the predictors and occurrence records used (Araújo & Guisan, 2006). However, the truly realised niche of fish species in the upper Danube is smaller due to, for example, migration barriers or the occurrence of non-native species. Consequently, by potentially having excluded species and the fact that we assessed the potential realised niche, we likely underestimated the effect of past environmental alterations in the upper Danube River Basin. Two examples, for which the above-described restrictions apply are the Grayling (*Thymallus thymallus*) and the Danube Salmon (*Hucho hucho*). For both species, we estimated relatively low sensitivities (0.78 and 0.87, respectively) and vulnerabilities for historic time intervals (see Table S1), despite they are assessed as endangered in the study area (Freyhof, 2009; Wolfram & Miksch, 2007). The low sensitivity and vulnerability estimates were caused by the fact that both species likely only occur in some last refugia, which have been

less affected by past hydrological alterations. The relatively low vulnerabilities estimated for future scenarios (see Table S1) indicate that these last refugia will not be significantly affected by predicted climate change effects, which is an important finding to guide the implementation of protected areas.

4.3 | A conservative approach to reduce uncertainty

In this study, we modelled how native fish species in the upper Danube River Basin were affected by historic environmental alterations and how they may be affected by future climate change. We used HSMs to fill monitoring gaps of the present-day distribution of species, but we did not use them to assess potential changes in their spatial distribution neither historically nor in the future, as it is usually done (Ehrlen & Morris, 2015; McMahan et al., 2020; Radinger et al., 2017). In contrast, we analysed the environmental conditions that defined habitat suitability for fish species in the past and would impact habitat suitability in the future. We opted for this conservative approach, since any prediction based on HSMs comes at the cost of uncertainty, especially when a model is transferred to new environments or time frames (Werkowska et al., 2017; Yates et al., 2018); however, the reduction of uncertainty is a key prerequisite to make models useful for practical conservation efforts (Schuwirth et al., 2019). We believe that the approach tested in this study as well as the results can provide guidance towards future conservation actions and conservation management by capitalising on past, observed environmental changes.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used for this study are available in the Pangaea repository at <https://doi.pangaea.de/10.1594/PANGAEA.935756>.

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BIOSKETCH

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SUPPORTING INFORMATION

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