RESEARCH ARTICLE

Who will be where: Climate driven redistribution of fish habitat in southern Germany

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Abstract

To improve the robustness of projections of freshwater fish distributions under climate change, species distribution models (SDMs) were calculated for six fish species in southwestern Germany with different ecological requirements along an upstream-downstream gradient in a multi-general circulation model (GCM) approach. Using the maximum entropy (Maxent) algorithm and a high number of occurrence records (N = 4684), species distributions were projected to future climate conditions derived from 13 GCMs across the most likely representative carbon pathways (RCP4.5 and 8.5) and two time spans (near future 2050, and far future 2070), resulting in 104 distribution maps per species that were then used for the statistical analysis of future trends. Climate change is likely to affect the distribution of four of the six fish species. The potential ranges of salmonids are predicted to decline by up to 92% (brown trout) and 75% (grayling). In contrast, habitat suitability for perch and roach is predicted to increase by up to 108% and 53%, respectively. Even when accounting for broad variation in GCMs and realistic RCPs, these results suggest climate change will drive a significant redistribution of fish habitat. Salmonid-dominated communities in headwaters seem more sensitive to climate change than the fish communities of downstream sections. Because headwaters are a prevailing element of the hydrographic network in southwestern Germany, such changes may result in large-scale regressions of valuable fish communities that currently occupy broad geographic niches.

Introduction

Anthropogenic climate change is a major threat challenging the stability of the world's economic and natural systems [1] and has already been identified as a major driver of biodiversity loss [2], with species across diverse taxonomic groups responding to recent climate alterations by shifting their ranges or becoming locally extinct [3,4]. Accelerated climate change may even threaten species that show a high potential for adaption or dispersal, for instance when these capabilities cannot compensate for the high rate of habitat loss in their current distribution area [5,6]. This threat is particularly pronounced in freshwater ecosystems [7], that already

experience massive ongoing biodiversity losses [8–10] through multiple stressors [11,12], including changing catchment land-use [13], habitat fragmentation by hydropower [14], and the introduction of invasive non-native species [15,16]. Climate changes are expected to drive further alterations in water temperature and streamflow that will severely affect the character and biota of freshwater habitats [17,18].

Freshwater fish provide essential ecosystem services [19] and, with an estimated number of 18,260 species and high levels of endemism, significantly contribute to vertebrate species diversity [20,21]. In many locations, such as southwestern Germany, they are also of primary socio-economic importance via recreational or commercial fishing of wild stocks [22] or via aquaculture [23]. As ectothermic organisms, the life cycles of fish are closely linked to local climatic conditions [24] and their zoogeographies are strongly influenced by the range of temperatures to with they are adapted [25].

Species distribution models (SDMs), also known as ecological niche models or climate envelope models, represent a primary tool to assess impacts of climate change on fish species [26,27]. SDMs relate species occurrence data to environmental data and use these relationships to predict the habitat suitability of any location [28–31]. They have been applied extensively to project future species distributions under climate change and to guide conservation and management measures [27,32,33].

A major source of uncertainty in SDM projections arises from the choice of global climate models (GCMs) and representative carbon pathways (RCPs) [34,35]. A wide variety of GCMs has been published that make projections for future climates and the choice of GCMs can introduce a high variance in projections of climate suitability. Between-GCM variability of SDM projections may even exceed the variability arising from the choice of RCP [35]. Studies of climate change effects on fishes and other freshwater biota typically include climate projections from only a few GCMs (cf. [18,26,36,37]). Pre-selection of particular GCMs is valid when there is evidence that these make the most appropriate representation of variation at a local geographical scale. However, given the broad range of available GCMs [38], this approach fails to capture the variability or similitude resulting from including the full range of future climate projections [39]. Furthermore, and unfortunately, it has become evident that projections calculated from the frequently used low-emission scenario (RCP2.6) that keeps global temperature rise below 2 ˚C [40,41] are unrealistic and potentially misleading, as humanity remains set on a path towards mid- to high-emission scenarios (RCP4.5 and 8.5) that leads towards a global warming of approx. 3 ˚C by the end of the century [42].

The aim of this study was to take the wide variety of GCMs into account to make robust predictions for the impact of climate change on habitat suitability for a typical assembly of temperate zone freshwater fishes in southwestern Germany. The underlying hypothesis is that there will be different reactions to the expected change among the native fish species. SDMs were calculated for six species with different ecological requirements and distributions along the upstream–downstream gradient (Table 1) and projected to future climate conditions derived from 13 GCMs across two RCP scenarios (4.5 and 8.5) and two time spans (near future 2050, and far future 2070). The RCPs used reflect moderate (RCP4.5) and high emission (RCP8.5) scenarios within the likely trajectory of the Earth system given current global climate policies [5,43,44]. The results may prove indicative for other geographic regions with comparable habitat conditions.

Methods

Study area, species selection and occurence data

The study was carried out in the federal state of Baden-Württemberg, south-western Germany, a Central European region with an exceptional diversity of freshwater habitats and fish

Table 1. Primary habitat, thermal guild, distribution and angling interest of the study species in southwestern Germany.

Species	Common name	Primary habitat	Thermal guild#	Distribution##	Angling interest
S. trutta	brown trout	headwater streams (rhithral zone)	cold	0,86	high
T. thymallus	grayling	streams and small rivers (lower rhithral zone)	cold	0,37	high
B. barbatula	stone loach	streams and rivers (rhithral to potamal zone)	cool	0,74	none
P. fluviatilis	perch	potamal rivers and lakes	cool	0,58	medium
R. rutilus	roach	lakes and rivers	cool	0,67	medium
S. glanis	wels catfish	large potamal rivers and lakes	warm	0,32	medium

based on FiCli [45].

proportion of 10x10 km UTM grid cells where the species is known to occur.

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diversity (58 native species, [46]). The state is rich in mid-elevation mountainous areas with rhithral rivers characterized by swift currents, cool water and high levels of dissolved oxygen [47], which drain into the catchment areas of the rivers Rhine and Danube (Fig 1). The river network is largely composed of headwater streams and small rivers but also comprises low-gradient potamal sections of the Rhine and Danube Rivers.

For the purpose of this study, a set of six fish species with different niche requirements along the upstream–downstream gradient and a wide spectrum of angling interest was selected (Table 1). All of selected species can be considered to exhibit equilibrium distribution within the study area, i.e., they are commonly present in environmentally suitable areas and absent from unsuitable ones, which is a major assumption for SDMs [30,46], and are present in all

Mountanious regions
1 Odenwald
2 Black Forrest
3 Swabian Jura
4 Allgäu

Drainage areas
- Danube
- Upper Rhine
- High Rhine
- Lake Constance (Rhine)
- Neckar (Rhine)
- Main (Rhine)

Surface water bodies
- Potamal streams
- Rivers
- Rhithral rivers
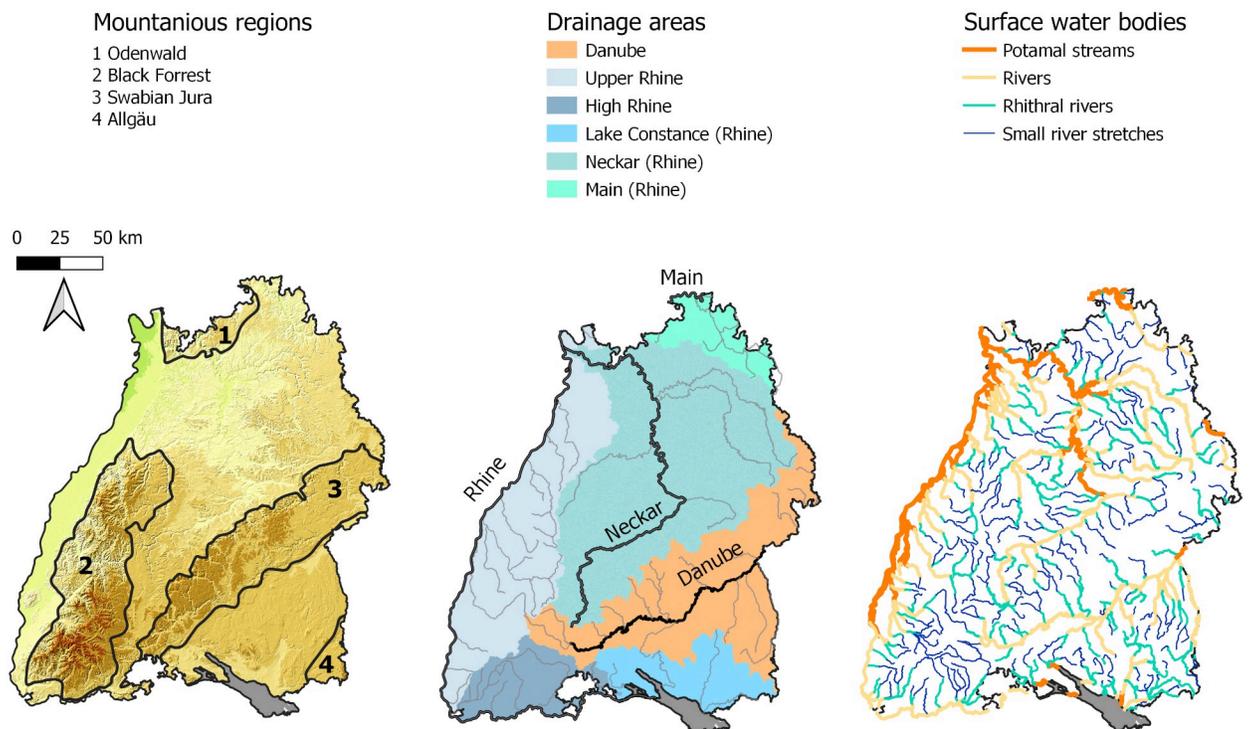- Small river stretches

Fig 1. Study area (federal state of Baden-Württemberg; southwestern Germany), including elevation gradients, main drainage areas, and classification of lotic water bodies (Base layer of the map, drainage areas and water bodies are from https://udo.lubw.baden-wuerttemberg.de/public/).

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major catchments, i.e., forecasted range shifts are unlikely to be restricted by major watersheds. Brown trout (*Salmo trutta* Linnaeus 1758) and grayling (*Thymallus thymallus* Linnaeus 1758) represent stenothermic cold-adapted specialists, while perch (*Perca fluviatilis* Linnaeus 1758), roach (*Rutilus rutilus* Linnaeus 1758) and wels catfish (*Silurus glanis* Linnaeus 1758) can be considered as eurythermic habitat generalists [48]. To highlight potential climate-change consequences for recreational fisheries, the assessed species cover a full spectrum of angling interest, from zero interest in the case of stone loach (*Barbatula barbatula* Linnaeus 1758), to popular game fish, such as grayling, trout, and perch [49].

Species occurrence data were extracted from the database of the Federal State of Baden-Württemberg (FiAKa), which contains more than 25,000 georeferenced records of fish occurrence. For the purpose of the present study, occurrence points for brown trout (n = 1,645), grayling (n = 167), stone loach (n = 1,331), perch (n = 345), roach (n = 788) and wels catfish (n = 408) were extracted for the years 1996 to 2018 (supplementary S1 Data). Most records arise from electro fishing surveys that were carried out in summer and autumn. To minimize possible bias from misidentified specimens or erroneous records, only records with secure species identification were considered. To prevent pseudo-replication, records that fell within the same 30 arcsec grid cells (approximately 0.625 km^2 in the research area) were entered as one case in the SDM model.

Niche models

For each of the six study species, potential distribution, i.e., habitat suitability, was assessed using niche-based SDMs constructed in Maxent (version 3.4.1., [50]). Maxent makes use of a machine-learning maximum entropy framework to relate environmental conditions at species occurrence sites to the background environment of the study area, which is obtained by sampling 10,000 random locations. The established relationships are then used to predict habitat suitability across the landscape. In contrast to most other SDM algorithms, Maxent does not require *a priori* assumptions about species absence, thereby allowing for seamless application to the presence-only dataset used in this study [30,50–52]. Bioclimatic predictors were obtained from WorldClim (http://www.worldclim.org, [53]), at a resolution of 30 arcsec. Environmental data included slope and Strahler order as a measure of stream size. Slope was calculated from elevation maps using the gdal slope plugin in QGIS (v. 3.4) and Strahler order numbers were extracted from the European Catchments and Rivers Network System provided by the European Environment Agency (Ecrins, version 1, Jun. 2012, Denmark). Values range from 1 (small rhithral headwaters) to 8 (large rivers). Similar sets of candidate predictors have been previously used in ecological niche models for freshwater fish and macroinvertebrates in Baden-Württemberg [15,54,55].

The following variables were selected to represent variation in temperature (see supplementary Table A in S1 Text for justification): mean diurnal range (MDR, bio2), isothermality (ISO, bio3), temperature seasonality (TS, bio4), mean summer temperature (SuT, bio10), and mean winter temperature (WiT, bio11). Values for mean summer precipitation (SuP, bio18) and mean winter precipitation (WiP, bio19) were retained as predictors of precipitation.

The Maxent training and prediction area was limited to grid cells covering lotic surface waters. To correct for uneven sampling effort across the investigation area, a sampling bias grid was specified in Maxent, which indicated relative sampling effort based on the number of sampling sites per cell [30]. For each species, 20 replicate models were fitted with cross-validation [30,50,55]. For this, occurrence data were randomly split into 20 equal-sized folds, and models were run leaving out one fold at a time. In each model iteration, the left-out fold of occurrence data was then used for model evaluation. Using this approach, each occurrence

point was used at least once for training and evaluation of the models. Final projections were obtained by averaging the 20 replicate models. Models were run using the default settings, except for the regularization multiplier, which was set to 1.5 (*cf.* [54,56]). For perch and wels catfish, the regularization multiplier was adjusted to 3 to eliminate overfitting and implausible response curves encountered in preliminary model runs with the multiplier set at 1.5.

For further analysis, the logistic model outputs were converted to binary presence-absence maps using the '10th percentile training presence' threshold (10P) to assess the 'core distribution' areas with suitable environment for the assessed fish species [30]. In addition, the 'equate entropy of thresholded and original distributions' threshold (EET) was used, which generates less conservative predictions than the 10P (data for EET are presented as supplementary Table F in S1 Text).

Distribution projection

To forecast future occurrence probabilities for the six fish species, final models were projected to future climate conditions derived from 13 GCMs on basis of the CMIP5 data set (supplementary Table B in S1 Text; worldclim.org) across two representative carbon pathways (RCP4.5 and 8.5) and two time spans (near future, '2050', average for 2041–2060, and far future, '2070', average for 2061–2080). RCP4.5 and RCP8.5 correspond to 'moderate' and 'high' emission climate change scenarios, respectively, and were used to cover the most likely outcomes of future global change [40,57]. The moderate scenario envisages a 'emissions-reduction' future (RCP4.5) that might be more appropriate if climate mitigation policies are put into place and tipping points are not reached. The high emission scenario represents climate change under a 'fossil fuel intensive' future with highest changes in temperature and precipitation (RCP8.5).

This multi-GCM approach resulted in a total of 104 binary distribution maps per species. Forecasted changes in habitat suitability were subsequently presented either as change in suitable area (given as percentage of the total area). Ternary plots were drawn to illustrate the dynamic changes i.e. loss *vs.* gain of suitable habitat and potential migrations of fish species over time. When comparing forecasted habitat suitability between present and future conditions, three potential outcomes can be assumed for each grid cell: 1) 'stay´ –the cell is predicted as suitable under present and future conditions, 2) 'loss´ –the cell is predicted as suitable under current but not future conditions, and 3) 'gain´ –the cell is predicted as unsuitable under current conditions but will probably become suitable in the future. These potential outcomes were taken as endpoints for triangular plots to visualize the relative contribution of each process (stay, loss, and gain) to the predicted change in habitat suitability. This was done for all future predictions, whereby hulls were drawn for each combination of time span and RCP, connecting the extreme coordinates of the 13 different climate models.

Management and statistical analysis of georeferenced data

Data preparation, analyses and visualizations were performed in QGIS (version 3.10.3) and R (version 3.6.3 running in Rstudio Version 1.4.1103), while ecological niche modelling was done using Maxent (version 3.4.0). To assess the accuracy of the Maxent models, the area under the receiver operating characteristic curve (AUC) is given. AUC values range between 0.5 for random prediction to 1.0 for perfect prediction [30], values below 0.5 are worse than random guess, and values lower than 0.7 indicate low accuracy of the model, while values higher than 0.7 represent adequate discrimination capacity [58,59]. In addition, response curves of the predictor variables were checked for ecologically plausible behavior and signs of potential overfitting, e.g., random curve behavior. Distribution graphs were drawn with R

(packages: ggplot2, ggtern). Statistics were calculated with R (packages: emmeans, gtools, PMCMRplus, stats) and Past (version 4.01, [60]). Effects of the two main factors, i.e. time span (year) and RCP, on species habitat suitability (percentage of total area predicted as suitable) and on the median elevation at which the species is expected to be distributed were examined using least square linear models (ANOVA with Tukey´s HSD post hoc test)

Results

The average SDM outputs for current distributions of the six fish species are shown in Fig 2 and the respective model statistics are summarized in Tables 2 and 3 presenting the average AUC scores, 10th percentile training presence thresholds, and variable contributions. Presence probabilities were mostly determined by stream size, followed by temperature and precipitation variables. Individual variable contributions and response curves are summarized by species in supplementary (Table C in S1 Text).

Suitable existing habitat for brown trout is predicted almost throughout Baden-Württemberg (Figs 2A and 3A), although the predicted core distribution range (based on the 10P threshold) excludes most of the Upper Rhine plain and low-gradient streams north of the Black Forest. Under future climatic changes the area of suitable habitat for brown trout is predicted to decline considerably under both RCP scenarios (F = 109.2, p < 0.001) and time spans (F = 10.14, p = 0.008). Predicted future projections suggest that less than 15% of currently suitable area in Baden-Württemberg will remain suitable for trout populations (Table 2), and only 1–2% of new habitat will be gained. It appears that future brown trout habitat will be concentrated in the elevated mountainous regions of the Black Forrest, Swabian Jura and prealpine regions of the Allgäu, indicated by an upwards shift of the average elevation range of more than 100 m (current: 489 m to future median 645–668 m, see Table D and E in S1 Text, Figs B and C in S1 Text for details). Ternary plots indicate severe range reductions: all but one model showed habitat loss under future conditions (Fig 4A).

Under current conditions, suitable habitat for grayling in Baden-Württemberg is mostly predicted in lowland river stretches (Fig 2B). With ongoing climate changes this area of suitable habitat will decline significantly by 2070 (6.5–7.6% reduction, F = 16.31, p <0.001), with minimal predicted area gain (0.1%, Table 2). Most climatic models indicate a decrease in distribution area or describe a stable situation with little changes (Fig 4B).

The habitat suitability model for the stone loach estimates 43.6% suitable habitat of Baden-Württembergs grid cells covering lotic surface waters under current climatic conditions (Fig 2C). Notwithstanding a trend towards range reduction, the models predict no significant changes resulting from future conditions (year: $F_{2,24}$ = 2.7, p = 0.08; RCP: $F_{1,12}$ = 0.3, p = 0.58). This is due to the wide variation in predictions based on the RCP8.5 scenario (red shaded area, Fig 3C) in which loach are predicted to experience both habitat loss (9.4–19.8%) and habitat gain (2050: 5.1–5.3%, Table 2). These dynamics are also visualized in the ternary plot, where values range from the remain/increase section (mostly RCP4.5 models, Fig 4C) to the extreme habitat decrease section on the opposite side (mostly RCP8.5 models).

The model for perch predicts 42.7% suitable habitat in Baden-Württemberg and reflects the species wide distribution in particular along the Rhine valley and in northern and southern low mountain ranges (Odenwald, Allgäu). Irrespective of the underlying RCP, perch habitat is likely to increase vastly (28.4–38.6% near future 2050, 40.7–46.3% in the far future, Table 2) under predicted future conditions, a prediction reinforced by colored areas in the 'increase' section of the ternary plot (Fig 4D).

Roach habitat in Baden-Württemberg is currently limited to northern and western lowland river stretches (median elevation of 330 m) and is very similar to the distribution of perch,
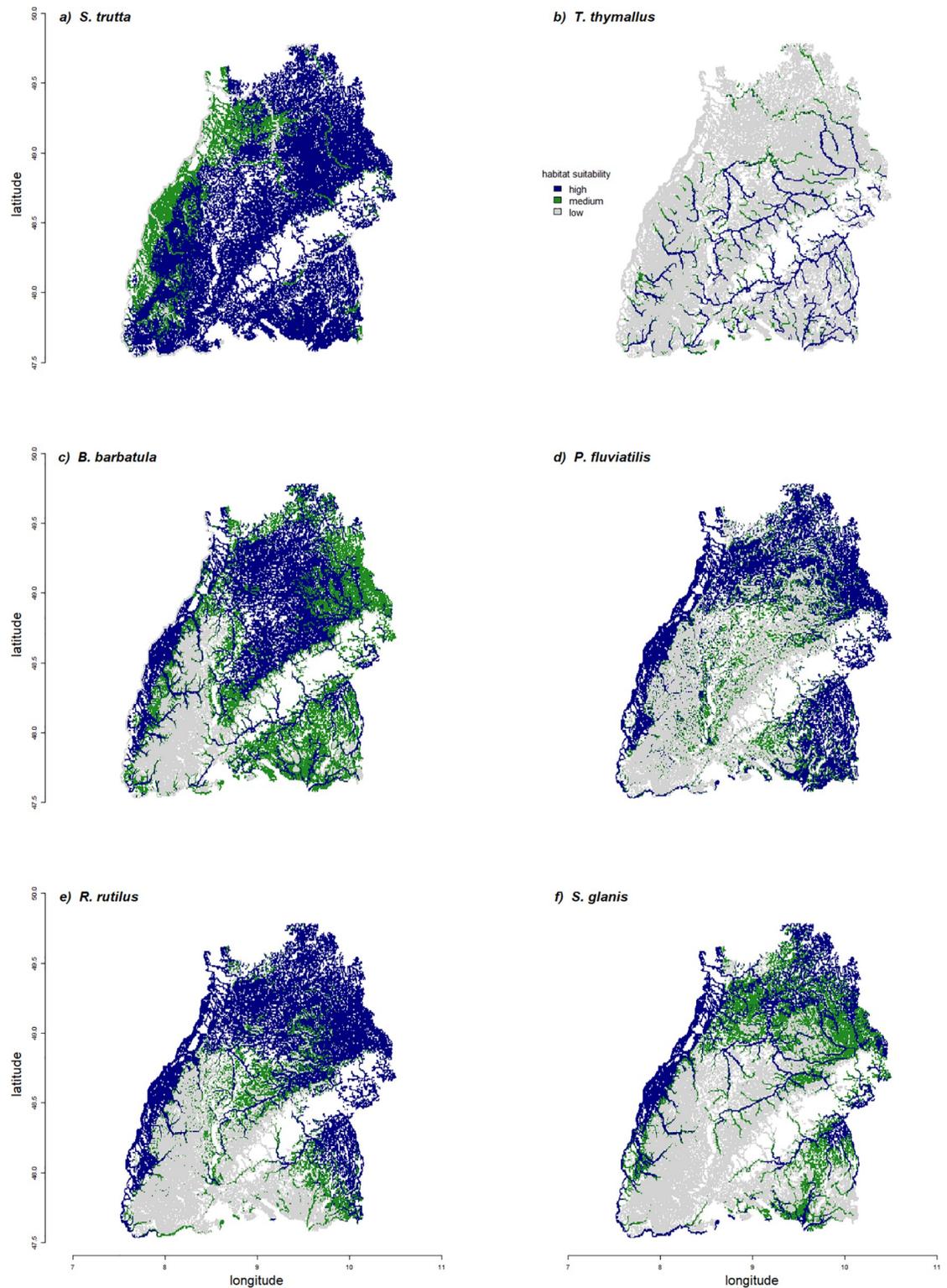
Fig 2. Predicted habitat suitability for six fish species in southwestern Germany under current climatic conditions (a: Brown trout, b: Grayling, c: Stone loach, d: European perch, e: Common roach, and f: Wels catfish). Areas with high suitability are colored blue (10th percentile cut off), habitats with moderate conditions are green (EET), unsuitable areas are gray. (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/).

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Table 2. Species distribution model parameters for six fish species in southwestern Germany and predicted habitat suitability (median and interquartile range, 25%-75%, 10th percentile cut off) under current and future climatic conditions derived from 13 different climate models (see Table B in S1 Text for details) across two RCP pathways.

Species	Mean AUC	Current	Suitable range [%]											
			2050						2070					
			RCP4.5			RCP8.5			RCP4.5			RCP8.5		
			Stable	Loss	Gain	Stable	Loss	Gain	Stable	Loss	Gain	Stable	Loss	Gain
S. trutta	0.62 (±0.03)	79.7 (79.5–80.0)	15.0 (10.1–26.8)	64.7 (52.9–69.6)	2.2 (1.7–3.3)	11.3 (2.7–18.6)	68.5 (61.1–77.0)	2.4 (0.3–2.8)	8.9 (2.5–13.3)	70.9 (66.5–77.3)	1.9 (0.9–2.5)	5.3 (1.0–11.5)	74.4 (68.3–78.7)	1.4 (0.1–1.9)
T. thymallus	0.88 (±0.04)	10.0 (9.4–10.2)	6.1 (4.9–7.5)	3.8 (2.4–4.9)	0.5 (0.2–0.8)	5.3 (3.9–7.0)	4.6 (2.8–5.9)	0.5 (0.1–0.6)	3.3 (1.5–6.3)	6.5 (3.6–8.4)	0.1 (0.0–1.0)	2.2 (0.3–4.6)	7.6 (5.2–9.5)	0.1 (0.0–0.4)
B. barbatula	0.71 (±0.03)	43.6 (43.2–44.0)	34.3 (24.6–39.6)	9.4 (4.1–19.1)	5.3 (1.0–14.9)	30.7 (19.2–41.0)	13.0 (2.7–24.5)	5.1 (0.7–17.8)	34.3 (23.1–38.4)	9.4 (5.3–20.6)	3.9 (0.5–13.0)	23.9 (17.9–39.4)	19.8 (4.2–25.8)	0.4 (0.2–12.7)
P. fluviatilis	0.83 (±0.04)	42.7 (42.0–43.4)	42.5 (38.8–42.6)	0.2 (0.1–3.9)	28.4 (12.2–41.3)	42.1 (38.0–42.6)	0.6 (0.0–4.6)	38.6 (14.3–48.6)	42.5 (34.0–42.6)	0.1 (0.0–8.7)	40.7 (10.3–47.8)	42.6 (39.5–42.7)	0.1 (0.0–3.2)	46.3 (22.9–53.2)
R. rutilus	0.79 (±0.04)	49.4 (49.2–49.5)	45.8 (41.2–46.3)	3.6 (3.1–8.2)	15.1 (6.5–19.1)	46.0 (35.6–48.4)	3.4 (0.9–13.8)	19.9 (0.3–32.8)	47.0 (40.7–49.3)	2.4 (0.1–8.7)	25.1 (3.2–41.1)	47.7 (38.9–49.3)	1.7 (0.0–10.5)	28.0 (1.1–48.3)
S. glanis	0.83 (±0.04)	26.0 (25.0–27.2)	25.7 (21.5–25.7)	0.1 (0.1–4.3)	32.1 (2.7–37.6)	25.7 (12.7–25.8)	0.1 (0.0–13.1)	34.2 (0.2–39.8)	25.7 (14.4–25.8)	0.1 (0.0–11.4)	24.4 (0.2–43.2)	25.7 (12.2–25.8)	0.1 (0.0–13.6)	42.4 (0.2–50.5)

Values for habitat suitability correspond to the percentage of total area predicted as suitable. Maxent AUC for test data is given as mean ± SD.

with higher elevations being not suitable (Fig 2E). Under expected climatic changes, roach habitat will increase significantly (year: $F_{2,24} = 6.17$, $p = 0.007$; RCP: $F_{1,12} = 6.26$, $p = 0.028$), with a wide range of variation in the model predictions (Table 2, e.g., habitat gain ranges from 0.3–32.8% interquartile range for 2050 RCP8.5; Fig 3E, shaded area). Hence while most future distribution models for roach show stable distributions ('stay'), others predict extreme increases or declines (Fig 4E).

Current wels catfish habitat is limited to lowland regions of Baden-Württemberg in areas similar to those occupied by roach and perch but more restricted to big streams and their major tributaries (Fig 2F and Table C in S1 Text: 61% importance by stream size, Table D in S1 Text: median elevation of 277 m). This distribution is unlikely to undergo significant changes under climate change (year: $F_{2,24} = 3.11$, $p = 0.06$; RCP: $F_{1,12} = 0.91$, $p = 0.36$). In detail wels catfish are set to lose very little of their current areas (0.1–0.1% range of means, 0–13.6%

Table 3. Effects of time (year) and RCP on habitat suitability (percentage of area predicted as suitable) for six different fish species in southwestern Germany (estimated marginal means/least square means).

	ANOVA									Least square means		
	year			RCP			Year:RCP			2000–2050	2000–2070	2050–2070
	Sum Sq	F value	P value	Sum Sq	F value	P value	Sum Sq	F value	P value	P value	P value	P value
S. trutta	251.59	109.2	**<0.001**	5.14	10.14	**0.008**	2.57	5.32	**0.012**	**<0.001**	**<0.001**	**0.013**
T. thymallus	31.88	16.31	**<0.001**	2.02	10.89	**0.006**	2.11	9.08	**0.001**	0.056	**<0.001**	**0.009**
B. barbatula	5.13	2.74	0.085	0.06	0.32	0.582	0.06	0.32	0.728	0.326	0.073	0.674
P. fluviatilis	45.99	13.93	**<0.001**	1.35	4.15	0.064	0.71	2.02	0.154	**0.003**	**<0.001**	0.371
R. rutilus	25.05	6.17	**0.007**	2.41	6.26	**0.028**	1.47	4.82	**0.017**	0.330	**0.005**	0.112
S. glanis	31.10	3.11	0.063	0.29	0.91	0.36	0.20	0.84	0.444	0.157	0.069	0.903

Significant effects are highlighted in bold.
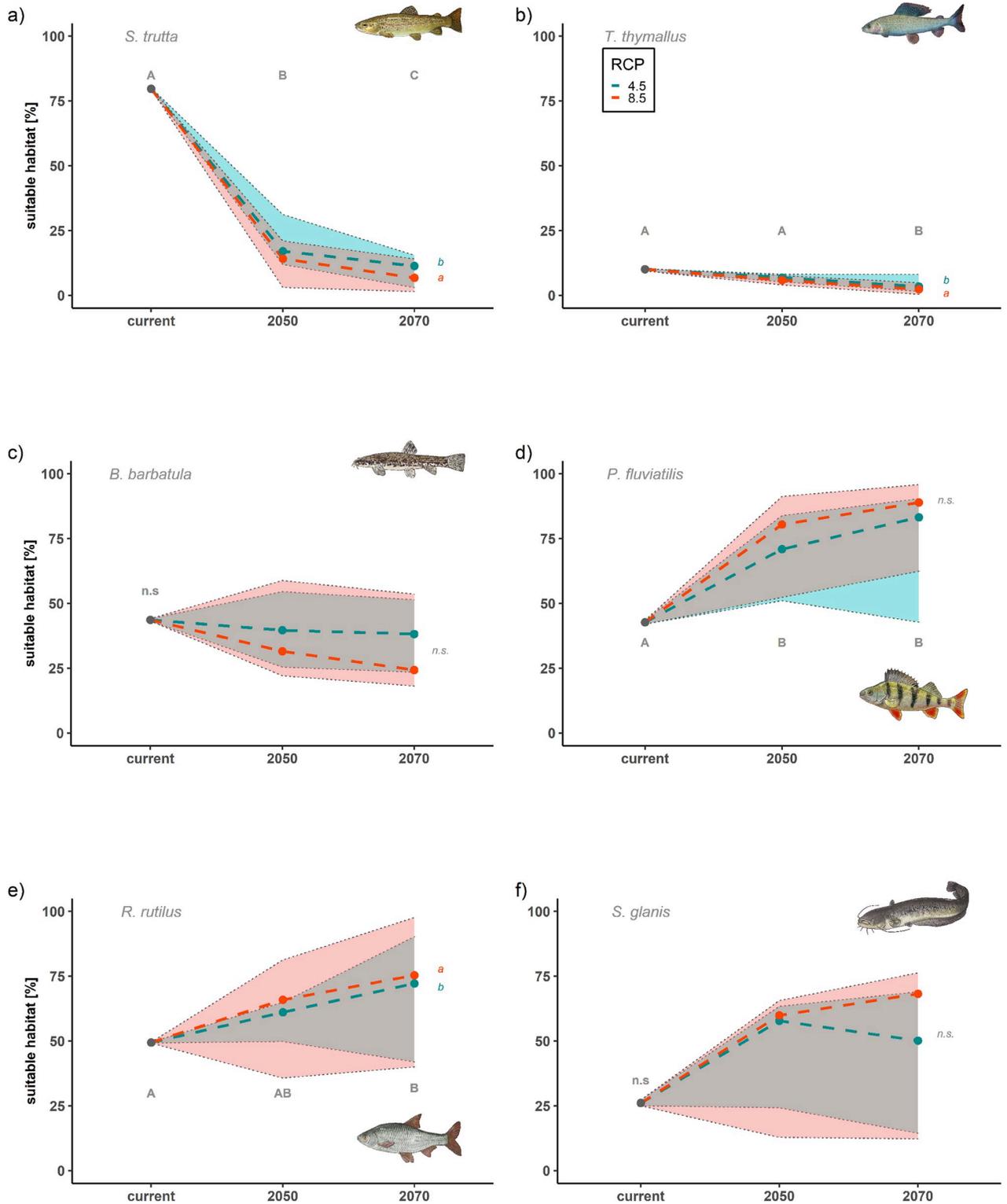
Fig 3. Predicted changes in suitable habitat area for six fish species in southwestern Germany under anticipated climate change (a: Brown trout, b: Grayling, c: Stone loach, d: European perch, e: Common roach, and f: Wels catfish). Data is presented for 13 different climate change models (10th percentile cut off; see Table B in S1 Text for details) as median (points, dashed line) and most likely variation (interquartile range: 25–75 interquartile range % percentiles, shaded area) for different RCP pathways (green: RCP4.5 and red: RCP8.5). Significant changes (One-Way ANOVA with Tukey HSD) between time spans (capital letters, bold) and RCP pathways (lowercase letters, italic) are highlighted.

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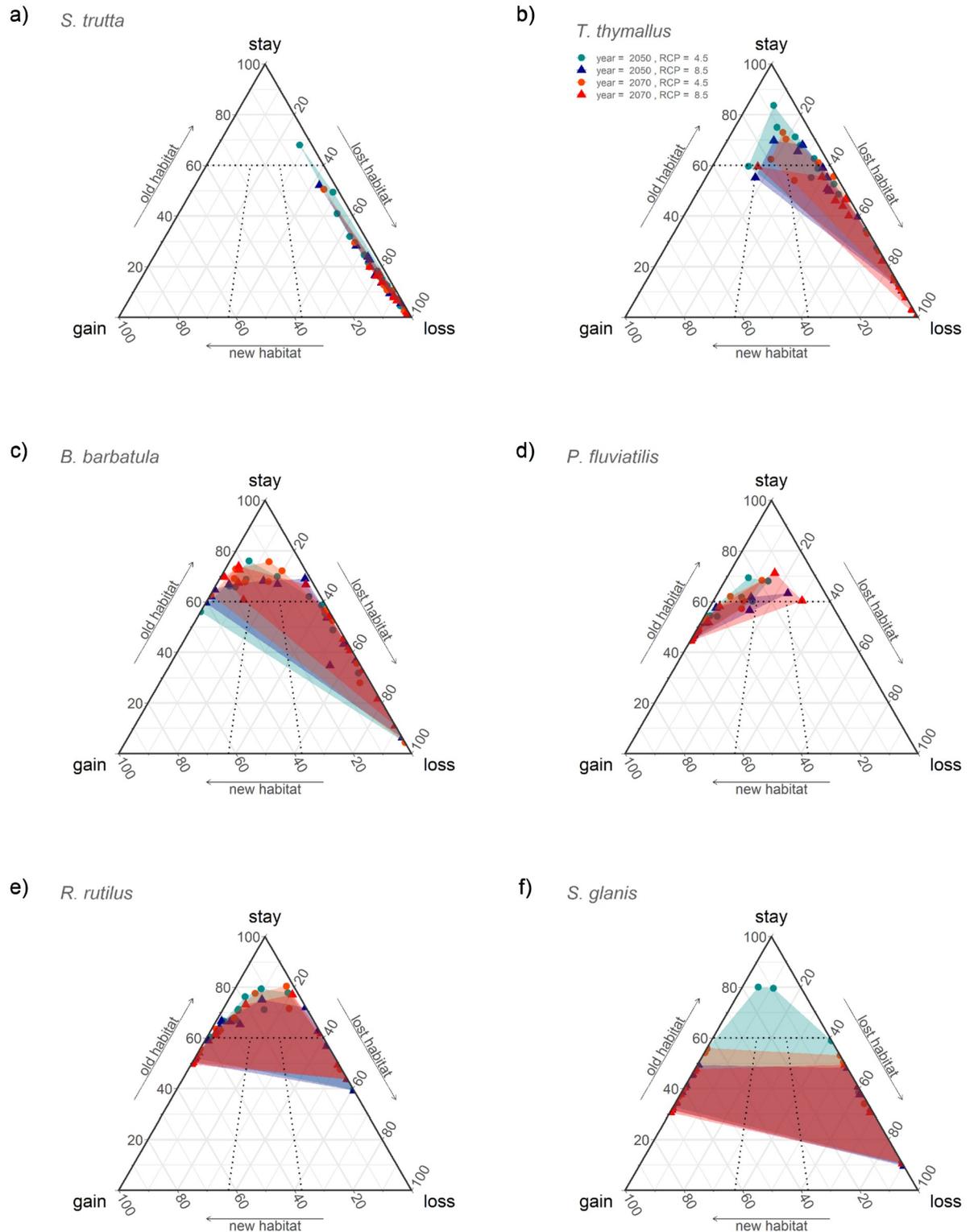
Fig 4. Triangle plots of predicted distribution changes between current conditions and predicted future conditions (a: Brown trout, b: Grayling, c: Stone loach, d: European perch, e: Common roach, and f: Wels catfish). Suitable habitat range shifts are displayed for "stay" (suitable under current and future conditions), "loss" (current: Suitable, future: Not suitable) and "gain" (current: Not suitable, future: Suitable) (see Fig A in S1 Text for explanation). Symbols represent distribution changes between current conditions and individual future predictions (13 different climatic models across two RCP scenarios and years; see Table B in S1 Text for details); hulls were drawn for each year-RCP combination connecting the extreme coordinates of the predicted changes.

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IQR loss, Table 3), but appear to gain some areas that are currently not suitable for their distribution (24.4–42.4% range of mean, 0.2–50.5% IQR win). Under severe RCP8.5 scenarios wels catfish appear to gain more habitat than under the moderate RCP4.5 (Table 2), indicated by the line plot showing this indifferent pattern of habitat shift under far future conditions (2070, Fig 4F). A few models predict a decrease in distribution area (right side, Fig 4F), whereas most model runs showed future distribution increase with marginal losses (left side, Fig 4F).

Discussion

Niche-based SDMs are a powerful tool in understanding species' environmental niches and potential ranges [61,62] and are widely used in freshwater ecology to relate fish community structure to environment [31,63,64] and to predict future distributions under changing conditions [18,37,53]. In southwestern Germany, SDMs were recently used to underpin risk assessment and conservation planning for endangered freshwater crayfish [15,54] and to assess the risk of fish disease spread under projected climate change in a single-GCM approach [55]. This study went beyond previous SDM applications by integrating projections from 13 different GCMs across two realistic RCP scenarios in an effort to account for the inherent variability of climate models and to arrive at robust predictions [35,36]. This multi-GCM approach is likely to better capture trajectories of future species distributions than SDM projections based on single or only few GCMs [35].

The developed SDMs were able to capture the known ranges of all of the six fish species and the response curves exhibited ecologically plausible behavior (Figs C-H in S1 Text) in accordance with existing knowledge of the modelled species and landscapes [46,48]. The AUC values of the SDMs also indicate good model performance (AUC 0.7–0.9 for all species except brown trout; (cf. [65]). The lower AUC score of the SDM for brown trout (0.6) is probably related to its exceptionally wide distribution in the study area, since great niche breadth is known to decrease AUC [54,62]. The set of predictor variables might also miss environmental variables important to the occurrence of brown trout, although this is deemed unlikely based on the well-known environmental requirements of this species [46,47]. Notwithstanding the low AUC score, the brown trout model shows plausible behavior and realistic predictions, consistent with understanding of the species' biology [48,66,67]. The presented models are therefore considered indicative of future fish distributions under anticipated climate change.

Climate change effects on fish distributions

Anticipated climate change, as assessed by the 13 GCMs, is likely to affect the distribution area of four out of the six modelled fish species. Specifically, the potential ranges of grayling and brown trout are predicted to decline over time (up to 75 and 92% under RCP8.5, far future conditions), whereas habitat suitability for roach and perch is predicted to increase (up to 53 and 108% respectively). The potential distribution area of wels catfish and stone loach meanwhile are not predicted to undergo significant change, although the extent of suitable habitat for the former is predicted to increase in most climate models (increases of up to 163%). These findings are generally consistent with previous research predicting climate 'losers´ or 'winners´ and those less sensitive to climate change [18,26,68].

The cold-adapted stenothermic such as brown trout and grayling are consistently predicted to be losers to climate change, while perch and roach, both eurythermic habitat generalists, are predicted to be winner. This distinct pattern provisionally supports the use of species-level traits for quick assessment of the climate-change susceptibility of fishes (cf. [69]) and hints at differential susceptibility of fish communities along the upstream–downstream gradient under climate-change. Salmonid-dominated communities in the upper stream reaches seem

particularly sensitive when compared to the cyprinid-dominated fish communities in downstream sections (*cf.* [26,70]). The hydrographic network of Baden-Württemberg is dominated by headwaters and small rivers, which are highly sensitive to climate change. This may result in large-scale regression of fish species that are currently occupying broad geographic niches, exemplified by the brown trout in this study.

The predicted changes in habitat suitability in face of expected global warming result from a composite of loss areas and gain areas, and areas that maintain suitability over time (stay areas). Considering the relative contributions of these processes can help to identify range shifts that may go unnoticed if only the combined picture is considered. For instance, about 10% of the potential future range of stone loach is associated with gains that are outweighed by losses. This indicates that the predicted range of loach is geographically shifting over time, despite no significant overall quantitative change in suitable habitat is predicted for the study area. Notably, brown trout is also predicted to gain habitat in high-elevation areas as part of an uphill shift; but this gain cannot even remotely compensate for the losses of suitable habitat predicted in lower-elevation areas. With regard to potential gain areas, it is also important to note that the predicted changes in habitat suitability will probably occur faster than fish populations can adapt and disperse [18]. Furthermore, potential gain areas may not be accessible to fish because of artificial migration barriers, such as river dams, or natural barriers to dispersal, such as catchment boundaries or unfavorable hydromorphological conditions. Predicted gain areas should therefore be interpreted with care, as opposed to loss areas, which are likely to manifest directly.

The magnitude of forecasted climate change, *i.e.* the underlying RCP scenario, had a distinct effect on the potential ranges of the two salmonid species and of roach, with stronger predicted range loss (salmonids) or gain (roach) occurring under the high emission scenario. This finding re-emphasizes the notably high sensitivity of salmonids to climate-change effects (*cf.* [26,55,70–72]) and the fact that detrimental effects of global warming scale with the magnitude of climate change [1,73]. In this regard, it is important to highlight that this study contrasts two realistic emission scenarios rather than best- and worst-case scenarios, which typically span a wider spectrum of potential future climates. The scenarios used in this study fall within the likely trajectory already set by humanity [73–75] and findings shown here indicate that the moderate emission scenario (RCP4.5) holds considerably less drastic implications for fish.

Regardless of the scenarios used, cold water adapted species such as trout and grayling will decline in their distribution in the future, with expected consequences for freshwater habitats, their conversation purposes and value for fisheries. Warm-water adapted or generalist species like wels or perch on the other hand can benefit from anticipated changes, provided that potential new habitat is also accessible to the fish. In addition to range expansion, these species may further increase in abundance within their range, as currently reported for wels [46,68].

Implications for species management

Anticipated climate change will inevitably impact fish communities (this study, [6]) and exacerbate existing stressors [11,14,16,55,76], with cascading effects on ecosystem functioning and services like shifts in body size and biomass fluxes, decoupling of food web interactions or even partial collapses of food webs when predators decline [77–80]. Besides functioning, ecosystem services will as well face climate induced changes. For instance, a decline in salmonid fisheries under future climate change, as forecasted in this study, is likely to carry negative economic implications (*cf.* [81,82]), even if future angling interests shift

towards climate-change winners, such as perch or wels catfish (this study, [26,68]). Furthermore, current conservation policies have virtually no experience with wide range shifts of fish communities and their ecosystems. Finally, species may venture into new habitats where they might have to establish new inter-species relationships that may become competitive or mutualistic, parasitic or pathogenic. This may require a paradigm shift in how to deal with migrations of species to localities where these were rarely seen and the way we think about protective areas [83–85].

Efforts to preserve functioning and ecosystem services of freshwater ecosystems must therefore account for climate change, and mitigation actions to restore and increase the resilience of fish habitats to higher ambient temperatures and extreme weather effects are urgently needed [86–88]. Salmonid fish, for example, would greatly benefit from shading of headwaters by fostering native riparian woods [89,90], restauration of habitat connectivity [88,91–93] and preservation of cold-water refugia [94,95], in addition to measures that secure natural surface water runoffs, in particular during drought conditions [86,88]. Finally, and above all, limiting global warming, as pledged under the Paris Agreement [96], is imperative in maintaining native fish communities and their ecosystem services, especially since ecosystem disruption may occur abruptly [97].

Supporting information

S1 Data. Fish occurrence points used for SDM analysis.
(CSV)

S1 Text. Tables (A-F) and Figs (A-H) with additional information for the study. Table A: Predictor variables of fish species presence probability used in the species distribution models, including justification for inclusion and data source. The range and average values of under current climate conditions are given for study area. Table B: Thirteen different climate change data sets were used to generate future predictions for fish species. All data were obtained from the Worldclim.org database website. Table C: Estimates of relative contributions of the environmental variables to the Maxent model for different fish species under current conditions in Baden-Württemberg. Table D: Elevation range of Maxent model for fish species under current and future conditions in Baden-Württemberg (average median and interquartile range, 25%-75%, 10th percentile cut off). Table E: Analysis of Variance Model with Post Hoc Test (estimated marginal means/least square means) for elevation distribution of six different fish species in southwestern Germany under current and future climatic conditions. Significant differences to current distribution are highlighted in bold. Table F: Species distribution model parameters for fish species in Baden-Württemberg. Suitable range (median and interquartile range, 25%-75%, 'equate entropy of thresholded and original distributions threshold' cut off) is given for current and future climatic conditions for 13 different models (see Table B in S1 Text for details), two timespans and two different RCP pathways. The values correspond to percentage of total assessed area. Maxent AUC for training and test are given as mean ± SD. [Compare with Table 2 for 10th percentile cut off values for more conservative/restrict future estimations]. Fig A: Triangle plot of theoretical species distribution changes between current conditions and predicted future conditions. X axis ("new habitat") illustrates a gain of new suitable habitat, y axis ("old habitat") represents percentage of area remaining suitable for the species whereas z-axis ("lost habitat") highlights a reduction in suitable habitat. The population "remains" in its original space, when more than 60% of habitat stays suitable. If the portion of lost habitat is greater than the portion gained the overall population will "decrease" (loss>gain, right sector), if vice versa the population will "increase" (gain>loss, left sector). If the proportions of loss and gain are almost equal, a species migration will occur ("migrate", lower middle

sector). Fig B: Elevation range of Maxent models for fish species (A: Trout, B: Grayling, C: Stone loach, D: Perch, E: Roach, F: Catfish) under current (solid black line) and future conditions in Baden-Württemberg (light blue 2050, RCP 4.5; blue: 2050, RCP 8.5; orange: 2070 4.5, red: 2070 RCP8.5). Gray bars represent the elevation range of the study area in southern Germany. Fig C: Species occurrence and distribution map of brown trout (*Salmo trutta*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat speciconditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/). Fig D: Species occurrence and distribution map of grayling (*Thymallus thymallus*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat conditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/). Fig E: Species occurrence and distribution map of stone loach (*Barbatula barbatula*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat conditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/). Fig F: Species occurrence and distribution map of perch (*Perca fluviatilis*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat conditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/). Fig G: Species occurrence and distribution map of roach (*Rutilus rutilus*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat conditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/). Fig H: Species occurrence and distribution map of catfish (*Silurus glanis*) under current and future climatic conditions in the study area of Baden-Württemberg. Species occurrence (blue points) results in a Maxent binary map under current conditions (10P cut off, blue area), future graphs display gradient maps for 13 different climatic models (10P cut off) for near (2050) and far future (2070) under two different RCP scenarios. White area contains no surface water bodies; grey indicates unsuitable habitat conditions. The more models predict suitability, the darker the colors (Base layer of the map is from https://udo.lubw.baden-wuerttemberg.de/public/).
(DOCX)

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