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ORIGINAL RESEARCH

Climate change reshapes freshwater fish distributions in a semi-arid basin of the middle East

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Abstract
Climate change alters habitat conditions, reshapes species distributions, and intensifies extinction risks across terrestrial, marine, and freshwater ecosystems. Freshwater systems in arid and semi-arid regions are particularly vulnerable to climate change due to their sensitivity to hydrological variability and the limited dispersal abilities of aquatic species. However, assessing these impacts is often challenged by data scarcity, particularly regarding species occurrences. We investigated how climate change will affect habitat suitability for endemic, native, and alien fishes in the Karun River basin, a critically important river system in the Middle East. We applied ensemble Species Distribution Models (SDMs) that combine Random Forest and MaxEnt algorithms with high-resolution environmental predictors. We then projected current and future habitat suitability under three general circulation models (IPSL-CM6A-LR, GFDL-ESM4, MPI-ESM1-2-HR) and two climate scenarios (SSP1-2.6 and SSP5-8.5). Ensemble models performed well across all fish groups, with mean AUC values of 0.96, 0.94, and 0.93 and mean TSS values of 0.88, 0.85, and 0.84 for endemic, native, and alien species, respectively. Sensitivity averaged 97%, 99%, and 93%, specificity 94%, 96%, and 88%, and overall accuracy 95%, 96%, and 88% across the three groups. Compound Topographic Index, temperature, and precipitation were the most important predictors of current habitat suitability. Climate change is projected to result in net habitat changes ranging from +21% to +13% for endemic species, +57% to +46% for native species, and +5% to +99% for alien species. These results suggest that alien fish may benefit from climate change, highlighting the need for local conservation and management strategies to protect vulnerable endemic species and control the potentially expanding ranges of alien species.

Keywords Species distribution models · Habitat suitability · Random Forest · Maxent · Biodiversity · Alien species

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Introduction

Environmental stressors such as global temperature rise, change in precipitation patterns, invasive species, land-use modifications, pollution, and overexploitation are leading to biodiversity decline and habitat loss for many species across the tree of life (Plesinski et al. 2018; Reid et al. 2019; Panja et al. 2021). While climate-induced warming and extreme events force many species to track their niches by shifting toward higher latitudes or elevations (Pecl et al. 2017; Comte and Olden 2017b), the capacity to respond varies among organism groups. For instance, species with narrow ecological niches, limited dispersal abilities, or restricted habitat availability are especially vulnerable to range contractions and local extinctions caused by these changes (Heino 2009; Urban 2015). In this context, endemic and native species often exhibit narrow ecological niches and require specific habitat conditions, making them particularly sensitive to climate-induced alterations (Staude et al. 2020; Yousefi et al. 2020a; Manes et al. 2021). In contrast, alien species often have broader ecological niches, allowing for more flexible physiological responses and higher dispersal capacity, thus enabling them to establish in areas that become suitable under changing environmental conditions and outcompete native populations (Hulme 2017; McKnight et al. 2021). Consequently, climate change tends to benefit alien species while putting native and endemic taxa at greater risk of extinction, especially in areas already stressed by other anthropogenic pressures (Rahel and Olden 2008; Carosi et al. 2023; Jan et al. 2025).

Cumulatively, freshwater ecosystems host a substantial part of Earth's biodiversity, with around 10% of all known animal species strongly associated with these habitats (Balian et al. 2008; Korkmaz et al. 2023; Schürz et al. 2023; Brunner et al. 2024). Their vulnerability to climate change is amplified by spatial constraints, such as habitat fragmentation and limited hydrological connectivity, which reduce the ability of aquatic organisms to respond to changing environmental conditions (Plesinski et al. 2018; Dudgeon 2019; Reid et al. 2019; Panja et al. 2021). Specific climate-related threats include rising temperatures, changing flow regimes, declining dissolved oxygen levels, and changes in precipitation patterns (Knouft and Ficklin 2017; Poff 2018; Barbarossa et al. 2021). These impacts are especially pronounced in riverine systems, where species are restricted to dendritic linear networks and often face barriers including dams, dewatered sections, and fragmented tributaries, further limiting movement and gene flow (Hermoso et al. 2011; Comte and Grenouillet 2013; Kowal et al. 2025). Consequently, many species in fragmented rivers are unable to migrate to more suitable habitats as conditions shift, leaving them isolated in degraded environments and increasing their vulnerability to local extinction (Rodeles et al. 2019; Wilkes et al. 2019; Sun et al. 2023). This is particularly relevant in semi-arid regions where highly variable precipitation, high evaporation rates, low soil water retention, and limited water availability intensify the vulnerability of freshwater ecosystems to climate change (Korkmaz et al. 2023; Masoumi et al. 2024). Therefore, predicting taxa-specific responses to climate change is essential for developing effective conservation and management strategies in such vulnerable regions.

Predicting how species distributions will shift under climate change has emerged as a key interest in ecology and conservation biology (Brooker et al. 2007; IPCC 2023; Rubenstein et al. 2023). These projections play a critical role in guiding adaptation and mitigation efforts to protect biodiversity in a rapidly changing world (Environment 2004; Thomas et al. 2004; Kwon et al. 2015). Species Distribution Models (SDMs) are widely used for predicting species' geographic distributions given their environmental preferences (Elith and Leathwick 2009; Domisch et al. 2013; Araújo et al. 2019). These models relate species occurrences to environmental predictors to estimate habitat suitability across space and time (Domisch et al. 2015; Kwon et al. 2015; Panja et al. 2021; Hong et al. 2022; Gholamhosseini et al. 2024). Model outputs can then be used to study biogeographic patterns, to understand the potential responses of species to climate change, or to support spatial conservation planning (Guisan et al. 2013; Domisch et al. 2015; Irving et al. 2022). Within this framework of ecological modeling, machine learning algorithms, particularly Random Forest (RF) and Maximum Entropy (MaxEnt), are widely favored. These models offer strong predictive performance, capture complex nonlinear relationships, and are robust, even with heterogeneous or data-limited ecological datasets (Breiman 2001; Phillips et al. 2006; Cutler et al. 2007; Elith et al. 2011; Dormann et al. 2013; Kwon et al. 2015; Luan et al. 2020; Canning et al. 2025).

Building on the efficacy of SDMs, this study aims to predict the impacts of climate change on habitat suitability of endemic, native and alien fish groups in the semi-arid Karun River basin, one of the most ecologically and economically important river systems in Iran (Zare Shahraki et al. 2021, 2024). Freshwater fish are poikilothermic, with physiological processes tied to environmental temperature, and their mobility makes their distribution strongly dependent on habitat conditions. Together, these traits increase the vulnerability of fishes to climate change impacts on reproduction and survival (Markovic et al. 2017; Masoumi et al. 2024). Reflecting this vulnerability, nearly half of all freshwater fish species globally are estimated to be at risk of extinction in the coming decades, especially in tropical and semi-arid regions (Collen et al. 2014; Barbarossa et al. 2021; Manjarrés-Hernández et al. 2021; Sayer et al. 2025). We applied SDM approach using the RF and Maxent algorithm to evaluate changes in habitat suitability for endemic, native, and alien fish species under current conditions and future climate projections. These projections were based on outputs from three General Circulation Models (GCMs) and two Shared Socioeconomic Pathways (SSPs): SSP1-2.6 (low emissions) and SSP5-8.5 (very high emissions). Specifically, we investigated the following research questions:

1. Which environmental predictors shape current habitat suitability for endemic, native, and alien fish groups in the Karun River basin?
2. How is habitat suitability expected to change under future climate projections, and do these responses differ among endemic, native, and alien fish groups?

We expect that climate change would promote habitat expansion for alien fish, due to their broader ecological niches, while leading to habitat losses for endemic fishes, which are often more specialized and vulnerable to environmental changes (Pyšek et al. 2017; McKnight et al. 2021). By assessing the most contributing environmental predictors and projecting habitat suitability changes under different scenarios, this study aims to provide essential information to guide mitigation and management strategies for freshwater biodiversity in the Karun River basin and elsewhere.

Materials and methods

Study area

The Karun River basin, the largest freshwater resource in Iran, covers approximately 67,000 km² across seven provinces in southwestern Iran (Fig. 1). As the longest Iranian river (950 km), it originates at an elevation of about 4,400 m in the Zagros Mountains and flows through diverse landscapes before discharging into the Persian Gulf. The basin encompasses diverse landscapes, from mountains and foothills to desert plains, which create strong climatic gradients with temperatures ranging from below 0 °C in winter to over 50 °C in summer. Annual mean precipitation ranges between 400 and 1200 mm in the central Zagros area to less than 200 mm in the lower Khuzestan plains. The Karun River system, with about 50 tributaries, supports important ecosystem services regarding water provisioning for agriculture, industry, drinking water, and recreation. However, in recent decades, extensive human activities, including dam construction, agriculture, and urban development, have significantly modified river ecosystems and their biotic communities (Fathi et al. 2022; Esmaeili Ofogh et al. 2024; Zare Shahraki et al. 2025).

Fish species records

We recorded fish species occurrences in 108 sites of the Karun River basin during two field surveys in 2019 and 2023 (Fig. 1). We collected these records following standardized fish sampling protocols, ensuring accurate species identification and spatial referencing (Zare Shahraki et al. 2022, 2025). Existing biodiversity records were often outdated, imprecise, or inconsistent, so we based this study on our standardized field surveys as the most reliable source of occurrence data. For alien species, we incorporated a small number of additional, verified regional occurrence records from the Global Biodiversity Information Facility (*GBIF;* https://www.gbif.org/*)* to supplement the dataset. These records were restricted to neighboring regions in Iraq, where the alien species included in this study are also alien and occur under comparable environmental conditions. Broader inclusion of additional records was not feasible due to the scarcity of reliable and geographically relevant data. These combined records formed the foundation for subsequent species distribution modeling in the Karun River Basin.

From these surveys, we compiled an initial dataset comprising 108 sampling sites and 46 fish species, classified into 14 families and 32 genera, including 17 endemic, 18 native, and 11 alien fish species (Zare Shahraki et al. 2025). The dataset comprises both fish observations and non-detections (i.e., fish absences), which we confirmed through standardized sampling protocols and by cross-checking with regional ichthyofauna publications (Jouladeh Roudbar et al. 2020; Freyhof et al. 2025). This comprehensive dataset served as the basis for selecting species suitable for robust distribution modeling.

For modeling purpose, we retained species with at least nine occurrence records, following common practice in species distribution modeling to balance limited data availability with model reliability (Pearson et al. 2007). From an initial pool of 46 recorded fish species, we selected 19 that met the threshold and collectively represented a broad range of ecological strategies, biogeographic origins (endemic, native, and alien), and dominance levels. This subset included eight endemic species (*Capoeta coadi*, *Capoeta aculeata*, *Turcinoema-*

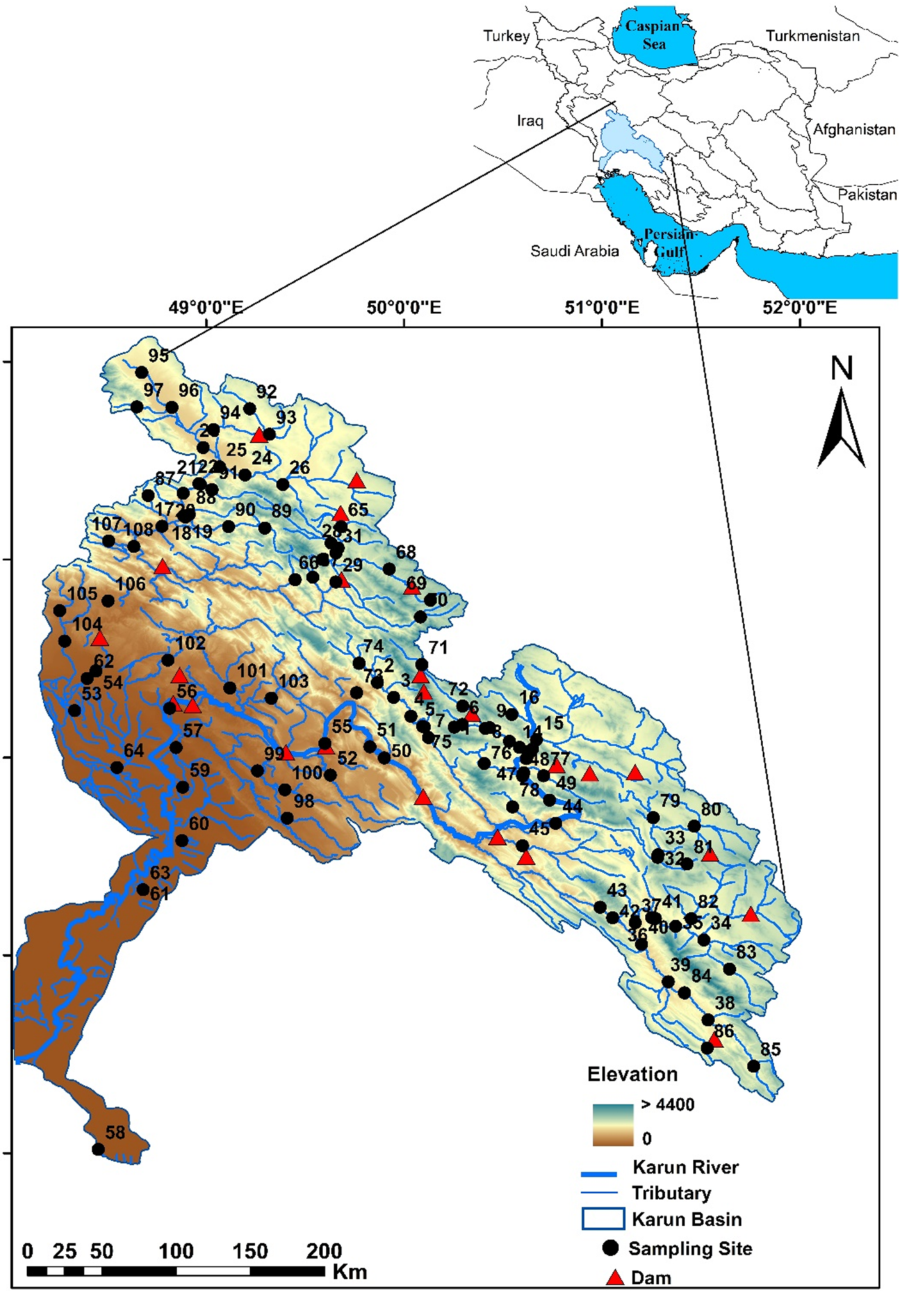

Fig. 1 Map of watersheds in Iran (small map above), and spatial distribution of dams and sampling locations across the Karun River Basin, Iran. Color shading represents the elevation gradient, triangles represent dams, and black points indicate sampling sites

cheilus ansari, *Barbus karunensis*, *Capoeta pyragyi*, *Glyptothorax alidaeii*, *Sasanidus kermanshahensis*, and *Turcinoemacheilus saadii*), eight native species (*Alburnus sellal*, *Garra rufa*, *Squalius berak*, *Arabibarbus grypus*, *Cyprinion macrostomum*, *Chondrostoma regium*, *Capoeta trutta*, and *Luciobarbus barbulus*), and three alien species (*Carassius gibelio*, *Coptodon zillii*, and *Oreochromis aureus*), ensuring ecological and spatial representativeness across the fish community. These selected species vary in habitat preferences, thermal tolerance and ecological function (Jouladeh Roudbar et al. 2020; Zare Shahraki et al. 2025), providing a robust foundation for assessing how climate change may alter habitat suitability for fish across different ecological and biogeographical groups in the Karun River Basin.

Environmental data

We built the spatial modelling framework upon the Hydrography90m stream network dataset (Amatulli et al. 2022); these data are available at www.hydrography.org and through the hydrographr R-package (Schürz et al. 2023); accessed 1.10.2024). Hydrography90m is a globally consistent, high-resolution stream network dataset derived from 90 m resolution digital elevation models, offering pre-delineated stream segments, sub-catchments, and hydrological attributes such as flow accumulation (the drainage of water into a given downstream cell), stream order, and distance to outlet (Amatulli et al. 2022). For climate data, we have relied on bioclimatic variables from the CHELSA dataset (Karger et al. 2018). The CHELSA bioclimatic variables are based on high-resolution atmospheric downscaling of daily climate data, using temperature lapse rates and orographic correction; they represent long-term climate averages and include detrended temperature and precipitation estimates (Karger et al. 2017). The present bioclimatic data represents the period from 1981 to 2010.

We extracted environmental predictors at the 316,951 sub-catchments along the river network, so that each spatial unit represents a hydrologically and ecologically meaningful stream segment. This network-constrained sub-catchment framework directly captures local habitat conditions relevant to freshwater fishes. We started with an initial candidate set of 13 predictor variables from Hydrography90m and CHELSA bioclimatic layers as predictors (Karger et al. 2017; Brun et al. 2022; Amatulli et al. 2022), which are commonly used in freshwater species distribution models (Table 1; Bond et al. 2011; Buisson et al. 2008a; Martin et al. 2013). We cropped all environmental layers (Table 1) to the extent of our study area. To account for differences in the spatial resolution of predictor layers such as 1 km for climate data and 90 m for hydrological data, we aggregated all raster values within each sub-catchment and calculated both the mean and range. This approach standardized the data to the sub-catchment scale, ensuring consistency across datasets and reducing the risk of introducing bias from resolution mismatches. We conducted pair-wise correlation tests across all sub-catchments to reduce high correlation among the predictors using a Spearman correlation coefficient threshold of $|r| \geq 0.7$ (Dormann et al. 2013). We found that annual mean air temperature and precipitation were highly correlated with most other temperature and precipitation-based variables. To avoid redundancy, only annual mean air temperature and precipitation were retained, as they capture the general climatic gradient while minimizing overlap among predictors. As a result, we used six environmental predictors in the SDMs (Table 1 - predictors in bold) to model the habitat suitability of fish species in the Karun River basin under both current and future projections.

Table 1 List of selected (in bold) and initial candidate topographical and bioclimatic predictors considered for habitat suitability modeling of 19 freshwater fish species in the Karun River basin, Iran. Topographical and bioclimatic predictors were obtained from Karger et al. (2018) and Amatulli et al. (2022), respectively. The description of each predictor is presented in appendix 1

Category	Predictor
Topographical	**Flow accumulation**
	Compound topographic index
	All stream segments and nodes attributes
	Strahler's stream order
	Distance between focal grid cell and the downstream stream node grid cell (Distance to downstream node)
	Maximum curvature between highest upstream cell, focal cell and downstream cell
	Stream power index
	Stream transportation index
	Euclidean distance between focal grid cell and the stream network (Euclidean distance to stream network)
	Elevation difference between focal cell and downstream cell
	Focal cell gradient
Bioclimatic	**Annual mean air temperature**
	Annual mean precipitation

We kept topographical predictors static, while future projections of the bioclimatic predictors for 2050 correspond to the timeframe from 2041 to 2070. Although hydrological conditions may change under future climates, incorporating such dynamics was beyond the scope of this study. We used three general circulation models (GCMs; IPSL-CM6A-LR (Boucher et al. 2020), GFDL-ESM4 (Held et al. 2019), and MPI-ESM1-2-HR (Mauritsen et al. 2019) to capture a range of potential climate change effects for the mid-21st century (2050). These GCMs represent a wide range of climate sensitivities, spatial resolution, and Earth system processes, and help to account for uncertainty in future climate projections. For each, we used two scenarios that follow the concept of the Shared Socioeconomic Pathways (SSPs), representing a framework for understanding the combined effects of greenhouse gas concentration trajectories and socioeconomic developments (O'Neill et al. 2017). We applied the GCM projections under SSP1-2.6 (a low greenhouse gas emission with limited climatic variation) and SSP5-8.5 (a very high-emissions with severe climatic variation).

Species distribution modelling

We used Random Forest and MaxEnt algorithms to model fish habitat suitability under current and future climate scenarios, and integrated their outputs into an ensemble model to produce the final habitat suitability predictions. We initially tested the models using fish observations and non-detections as true absence points. Additionally, we explored how pseudo-absences would affect model performance by randomly selecting 125, 250, 375, 500, and 750 sub-catchments as pseudo-absence locations, ensuring that these locations did not overlap with known presence points to minimize bias (Gholamhosseini et al. 2024).

We randomly split the fish occurrence dataset (including both presences and absences) into 70% for model training and 30% for testing to evaluate model performance. To account for model variability, we ran the models ten times and averaged the resulting probabilities of occurrences (Valavi et al. 2022). We evaluated model performance using area under curve

(AUC), true skill statistic (TSS), accuracy, sensitivity (true positive rate), and specificity (true negative rate) metrics (Erickson and Kitamura 2021). We calculated accuracy, sensitivity, specificity, and TSS from confusion matrices based on threshold predictions compared with observed presences and absences in both training and testing datasets, while we derived AUC from receiver operating characteristic (ROC) curves. We then modeled habitat suitability separately for each GCM and averaged the probabilistic SDM projections across the three GCMs to reduce uncertainty and improve robustness in projected future distributions (Della Rocca et al. 2019; Garza et al. 2020; Song et al. 2024). To assess the impact of climate change, we calculated differences between present and future probabilities of occurrence for each sub-catchment. We then analyzed spatial variations to identify areas of increased or decreased habitat suitability for each species.

To assess habitat changes under climate change projections, we calculated the total area (in km^2) of habitat gain, loss, and no change for each species by combining sub-catchment-level habitat suitability predictions with the area of each given sub-catchment. We performed these calculations also separately for the three GCMs, and averaged the results to account for variability among models. The total area in each habitat change category was expressed as a percentage of the overall predicted range for each species. We summed habitat suitability values across all species within each fish group (endemic, native, and alien) to quantify total group-level suitability and assess spatial trends in response to climate change.

Our modeling approach assumes full dispersal capacity, projecting that species can colonize all newly suitable habitats under future scenarios. In reality, dispersal barriers such as dams, fragmented or dewatered reaches, and limited river connectivity may restrict movements. As these constraints were not explicitly incorporated, our projections likely represent optimistic estimates of future range shifts rather than realized outcomes.

The map of the study area was created using ArcMap version 10.2 (ESRI 2011). We also used several R packages to facilitate data processing, spatial analysis, machine learning, and visualization. First, the *hydrographr* package (Schürz et al. 2023) was used for hydrographical network data handling, while *data.table* (Barrett et al. 2025) and *dplyr* (Wickham et al. 2019) enabled efficient data manipulation. Spatial data processing and raster handling were performed using *terra* (Hijmans 2025), with *tools* (R Core team 2020) and *stringr* (Wickham 2023) assisting in file management and text operations. The *biomod2* package (Guéguen et al. 2025) was used to implement RF and MaxEnt models and to generate ensemble habitat suitability projections. To enhance visualization, we used *leaflet* (Cheng et al. 2024) and *leafem* (Appelhans 2025) for interactive mapping, while *viridisLite* (Garnier et al. 2023) provided perceptually uniform color schemes. *tidyr* (Wickham et al. 2024) facilitated data restructuring, and *caret* (Kuhn 2008) was applied for model evaluation. Finally, *pROC* (Robin et al. 2011) was used to compute the AUC to assess model performance.

Results

Model performance

We compared models using true absences and various numbers of pseudo-absence points, finding that the model with 250 pseudoabsence points resulted in the best performance according to the evaluation metrics (Table 2). Overall predictive performance was very good (Table 2).

Relative importance of environmental predictors

Compound topographic index showed the highest variable importance for both endemic and native species. For alien species, annual mean air temperature and precipitation were the dominant predictors (Fig. 2). These patterns indicate that endemic and native species are strongly associated with local hydro-geomorphological conditions captured by the compound topographic index, whereas alien species respond primarily to broader climatic gradients such as temperature and precipitation.

Climate change impacts on temperature and precipitation in the Karun River basin, Iran

Temperature in the Karun River basin is projected to increase under both future climate scenarios, while precipitation shows divergent responses (Fig. 3A, B). Based on the average of three GCMs, annual mean air temperature is expected to increase by 10.4% (± 7.6% SD) under SSP1-2.6 and by 19.3% (± 14.18% SD) under SSP5-8.5. In terms of precipitation, average values are projected to increase slightly by 6.6% (± 1.37% SD) under SSP1-2.6, but decline by 6.4% (± 2.64% SD) under SSP5-8.5. These averages and standard deviations were calculated for all sub-catchments. Although with great variation among sub-catch-

Table 2 Performance metrics (AUC, TSS, sensitivity, specificity, and accuracy) of the ensemble models predicting habitat suitability for the 19 modelled fish species in the Karun River basin. Higher values indicate stronger model performance in discriminating between correctly modelled presences and absences, respectively

Category	Species	AUC	TSS	Sensitivity	Specificity	Accuracy
Endemic	*Capoeta coadi*	0.96	0.85	99.06	96.29	96.72
	Capoeta aculeata	0.99	0.94	100.00	98.80	98.93
	Barbus karunensis	0.96	0.88	99.22	97.06	97.34
	Capoeta pyragyi	0.94	0.82	96.89	93.32	93.67
	Glyptothorax alidaeii	0.94	0.87	98.88	95.83	96.09
	Sasanidus kermanshahensis	0.94	0.85	94.13	81.81	82.58
	Turcinemacheilus saadii	0.97	0.94	99.15	99.59	99.55
	Turcinemacheilus ansari	0.94	0.86	92.60	92.05	92.08
Native	*Garra rufa*	0.94	0.79	99.26	96.73	97.22
	Alburnus sellal	0.95	0.85	98.27	96.09	96.49
	Squalius berak	0.97	0.90	99.35	96.30	96.59
	Arabibarbus grypus	0.92	0.88	100.00	88.49	88.93
	Cyprinion macrostomum	0.96	0.87	99.15	96.08	96.41
	Chondrostoma regium	0.94	0.85	99.75	97.22	97.59
	Capoeta trutta	0.92	0.79	96.47	97.30	97.21
	Luciobarbus barbulus	0.95	0.90	98.21	96.67	96.78
Alien	*Carrasius gibelio*	0.89	0.75	79.87	78.91	78.97
	Coptodon zillii	0.95	0.88	100.00	94.98	95.17
	Oreochromis aureus	0.94	0.89	100.00	91.05	91.39

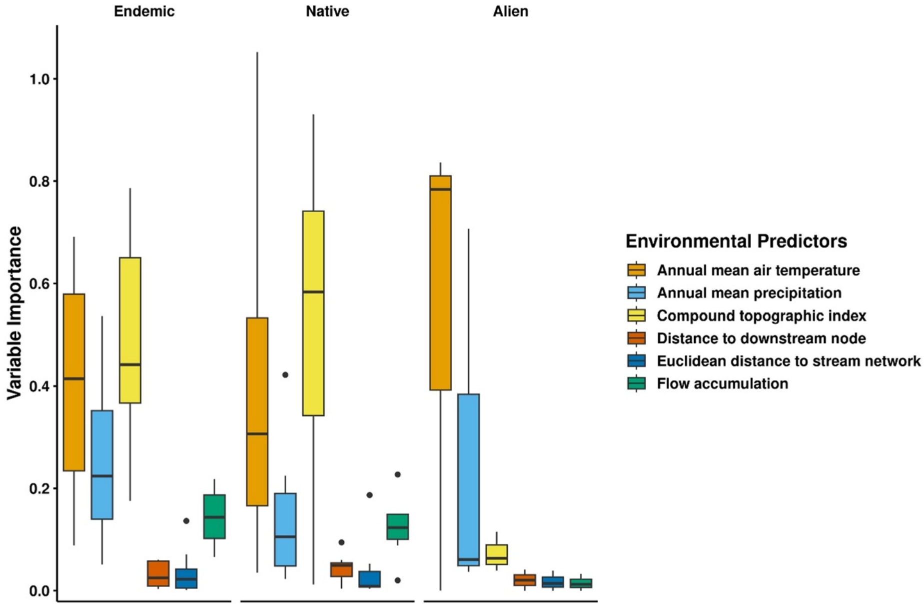

Fig. 2 Relative importance of environmental predictors in predicting habitat suitability for endemic, native, and alien fish species in the Karun River basin. Predictor importance was calculated using permutation-based changes in RF–Maxent ensemble model predictions. The boxplots summarises the distribution of permutation-based variable importance scores across species within each group: the horizontal line inside each box represents the median importance score, the box spans the interquartile range (IQR; 25th–75th percentile), and the whiskers extend to values within 1.5 × IQR. Points outside this range represent outliers

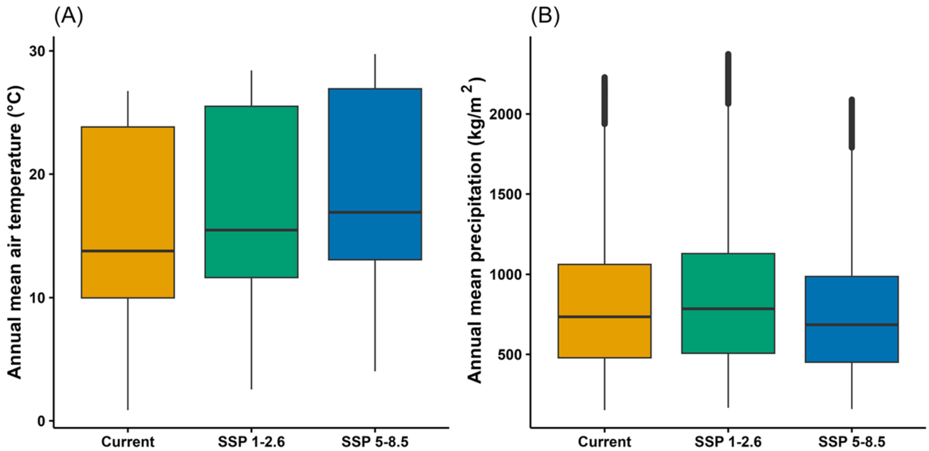

Fig. 3 Variation in annual mean air temperature (**A**) and annual mean precipitation (**B**) for current and future climate scenarios (SSP1-2.6 and SSP5-8.5) in the Karun River basin, Iran. Each projection illustrates values derived from three climate models (IPSL-CM6A-LR, GFDL-ESM4, and MPI-ESM1-2-HR), based on downscaled climate data extracted at 316,951 sub-catchment locations across the basin

ments, on average these patterns suggest a consistent warming trend across projections, accompanied by divergent precipitation responses throughout the Karun River basin.

Habitat suitability changes between current and future projections

Net habitat changes showed consistent increases across all fish groups. Endemic species exhibited a net gain of approximately 21% of the basin area under SSP1-2.6 and about 13% under SSP5-8.5. However, responses varied strongly among species. Under SSP1-2.6, species-specific net habitat change ranged from a substantial net loss of −57% to a large net gain of +96%, while under SSP5-8.5 species-specific net habitat change ranged from −23% to +87%. Several endemic species experienced net habitat losses under one or both scenarios, including *S. kermanshahensis*, *C. pyragyi*, *C. coadi*, *B. karunensis*, and *C. aculeata*. Native species showed a net gain of roughly 57% under SSP1-2.6 and 45% under SSP5-8.5. Species-specific net habitat changes for native species ranged from +8% to +95% under SSP1-2.6 and from −35% to +77% under SSP5-8.5. Notably, *A. sellal* showed a pronounced net habitat loss under SSP5-8.5. Alien species experienced the greatest expansion, with net increases of around 5% under SSP1-2.6 and 99.5% under SSP5-8.5. The only alien species showing a marked net habitat loss was *C. gibelio* under SSP1-2.6 (−91% net change). These values summarize group-level habitat changes based on aggregated ensemble predictions across all species (Fig. 4).

Regarding the spatial changes in habitat suitability (Fig. 5), the endemic fish group shows a mix of habitat gains and losses under SSP1-2.6, with gains occurring across large parts of the basin and losses concentrated mainly in the central regions. Under SSP5-8.5, losses become more widespread and pronounced in the northern and central basin. The native fish group exhibits broad habitat gains under both scenarios, but also experiences areas of habitat loss, particularly in the downstream part of the basin under SSP1-2.6 and extending into some upstream regions under SSP5-8.5. The alien fish group shows substantial habitat gains across most of the basin, with localized areas of loss under SSP1-2.6 and a marked

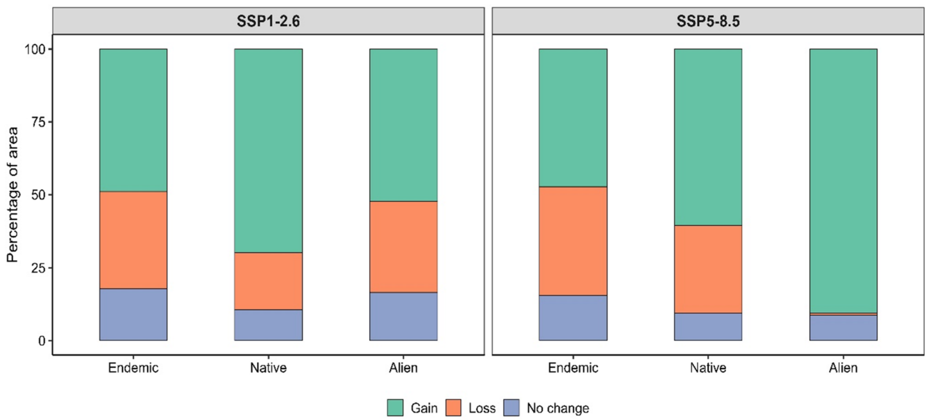

Fig. 4 Percentage of habitat area gained, lost, or unchanged under SSP1-2.6 and SSP5-8.5 for endemic, native, and alien fish groups. Values are based on group-level suitability change maps generated by averaging ensemble predictions across three GCMs and aggregating species-level layers within each group

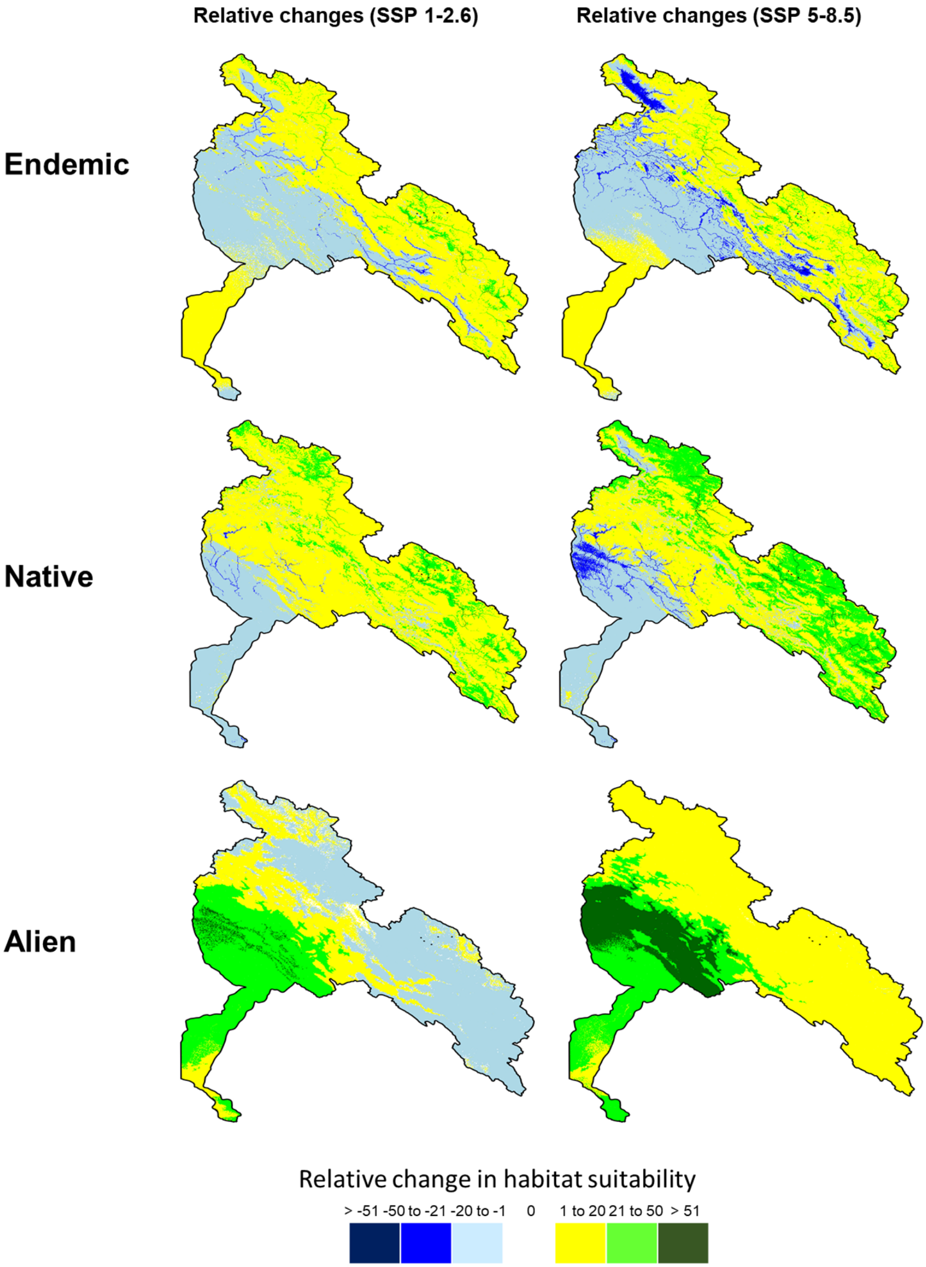

Fig. 5 Projected changes in habitat suitability between the current and future climate scenarios (SSP1-2.6 and SSP5-8.5) for three fish groups in the Karun River basin. The maps represent the summed difference in suitability across all modeled species within each group. Warm colors (yellow to green) indicate areas of habitat gain, while cold colors (light blue to dark blue) represent areas of habitat loss due to climate change

expansion of suitable habitats under SSP5-8.5. Maps are available as an interactive online resource at: https://geo.igb-berlin.de/maps/1019/view#/.

Discussion

We used species SDMs and three GCMs to evaluate how climate change may alter habitat suitability for endemic, native, and alien fish groups in the Karun River basin in Iran. The models showed high predictive performance and identified Compound Topographic Index (CTI) as the most influential predictor for endemic and native species, whereas temperature and precipitation were the most important for alien species. Endemic species exhibited regionally structured habitat gains and losses, with habitat loss becoming more extensive under SSP5-8.5. The native fish group showed a mixed pattern of habitat gains and losses under both scenarios, with losses becoming especially pronounced in downstream and some upstream sections under SSP5-8.5. The alien fish group displayed some localized habitat loss under SSP1-2.6, but a marked expansion of suitable habitat under SSP5-8.5. These patterns suggest that climate change may impact freshwater fish biodiversity in the Karun River basin not only through direct effects on habitat suitability of endemic and native species, but also indirectly through the expanded distribution of alien species.

Environmental predictors of fish habitat suitability under climate change

Compound Topographic Index (CTI) emerged as the most important predictor of the current habitat suitability of endemic and native fish groups, on average. CTI is a topographic wetness index (Beven and Kirkby 1979) that integrates upstream contributing area and slope, serving as a proxy for spatial variation in moisture accumulation, hydrological storage, and long-term soil and surface–water saturation (Raduła et al. 2018). Its strong contribution to the models suggests that geomorphological controls on water retention and baseflow stability act as key environmental filters for these fish groups, supporting the persistence of species that are closely associated with more hydrologically buffered and moisture-retaining landscape positions.

For alien species, temperature and precipitation emerged as the dominant predictors, suggesting that their distributions are more strongly associated with coarse-scale climatic gradients than with local geomorphological conditions. However, these climate-based predictions should be interpreted cautiously, because changes in air temperature do not necessarily translate linearly into stream thermal regimes due to mechanisms such as groundwater discharge, riparian canopy shading, hyporheic exchange, and the thermal inertia of lotic systems (Kaandorp et al. 2019; Rey et al. 2024). Elevated water temperatures can further reduce dissolved oxygen concentrations, increase toxin solubility, and promote harmful algal blooms, thereby increasing stress and mortality and making ecosystems more vulnerable to other stressors (Dastorani and Poormohammadi 2016; Rahimi et al. 2019; Makki et al. 2021; Korkmaz et al. 2023; Johnson et al. 2024).

At the same time, extreme hydrological events such as droughts and floods, which are not fully captured by mean climatic or hydrological indicators such as average precipitation or flow accumulation, may impose additional stress on freshwater fish communities by disrupting habitat connectivity, altering flow regimes, and reducing survival (Parasiewicz et al. 2019). These considerations highlight the importance of interpreting our projections with caution, recognizing that species' responses will be influenced by both gradual climatic trends and hydrological extremes.

Climate-induced responses among fish groups

Although habitat suitability models were developed for all 18 fish species, we focused our interpretation on group-level patterns to ensure a clearer overview of broader trends. The summed habitat suitability maps (Fig. 5) reveal that the alien fish group is projected to gain more suitable habitats than the endemic and native fish groups, particularly under the high-emission scenario. While the endemic and native fish groups also show habitat gains, their spatial patterns closely resemble those of alien species, suggesting almost similar climate-driven responses for these groups. These group-level shifts likely reflect differences in ecological traits and climate tolerances among endemic, native, and alien fish groups, resulting in varying magnitudes of habitat gain or loss under future scenarios (Palmer et al. 2015; Xiang et al. 2023).

For instance, the endemic and native fish groups, which are often more specialized, may experience physiological stress, reduced growth, and lower reproductive success even under moderate warming (Kwon et al. 2015; Knouft and Ficklin 2017; Barbarossa et al. 2021). In contrast, many alien species are ecological generalists and show broad environmental tolerances, including high thermal tolerance and adaptability to warming conditions and changes in precipitation (Ficke et al. 2007; Durance and Ormerod 2009; Xiang et al. 2023). In addition, they often have rapid reproductive rates and flexible feeding strategies (Özgür 2011; Yalçın Özdilek et al. 2019; Geletu et al. 2024; Radtke and Bernas 2025; Tang et al. 2025). These unequal responses can result in biotic homogenization, a process where biological communities become more similar as generalist species expand and endemic or native specialists decline (Hellmann et al. 2008; Olden et al. 2004). This pattern aligns with prior studies highlighting the importance of both topographical (e.g., CTI, stream order, flow accumulation) and climatic (e.g., temperature, precipitation) predictors in shaping fish distributions in both regional and global contexts (Panja et al. 2021; Sharma et al. 2021; Makki et al. 2023a; Souza et al. 2025).

Moreover, Jan et al. (2025) reported that climate change can simultaneously reduce suitable habitat for native species and increase environmental overlap with alien species, thereby intensifying interspecific competition. This dual threat is particularly pronounced in altered habitats where alien species might establish. As a result, even endemic and native species that initially appear to benefit from warming conditions may face indirect biotic pressures that threaten their long-term persistence, especially since many alien species are strong competitors (McCluney et al. 2014; Alexander et al. 2016; Winkowski et al. 2024). Trophic flexibility might contribute to both the success of alien species and to range shifts of native species to cope with climate change (Comte et al. 2017a).

Building on the trait-based differences discussed above, alien species are widely recognized as climate "winners" and are therefore more likely to expand their distributions under future warming (Perdikaris et al. 2012; Carosi et al. 2023; Xiang et al. 2023; Geletu et al. 2024; Zare Shahraki et al. 2025). Our results are consistent with findings from other regions (Table 3) where alien species are projected to extend their distribution under warming conditions (Rahel and Olden 2008; Sharma et al. 2009; Britton et al. 2010; Le Hen et al. 2023).

Table 3 Summary of selected studies assessing the impacts of climate change on freshwater fish species across different climatic regions

Study	Region	Climate zone	Species or group	Climate scenario	Projected habitat change
Hong et al. (2022)	South Korea	Temperate	Two alien species	RCP4.5 and RCP8.5	Significant habitat expansion; increased distribution under warming conditions
Markovic et al. (2014)	Europe	Temperate	European freshwater fishes	Not specified	100% habitat loss (8 species); 50% with no suitable habitat
Buisson et al. (2008b)	France	Temperate	Stream fish	IPCC SRES A2, B1	Habitat loss for cold-water species; expansion for cool- and warm-water species
Panja et al. (2021)	Ganges	Subtropical	*Neolissochilus hexagonolepis*	RCP6 and RCP8.5	Significant habitat loss
Xiang et al. (2023)	China	Subtropical	Five alien species	SSP 2.6 and SSP 8.5	Significant expansion in suitable habitat for all five species
Makki et al. (2023b)	Iran	Arid and Semi-arid	131 freshwater fish species	RCP 4.5 and RCP 8.5	Habitat loss (48 species), gain (17), mixed (61), no change (6)
Yousefi et al. (2020b)	Iran	Arid and Semi-arid	15 endemic species	RCP 8.5	Habitat loss (5 species), gain (10)

For instance, Xiang et al. (2023) reported dramatic range expansions for five alien species, ranging from 39% to 292% in China. Similarly, Hong et al. (2022) documented significant habitat changes for two invasive alien fish species in South Korea under climate change projections. These examples support the view that climate-driven habitat expansion may be a common outcome for alien fish species, particularly in warming systems (Le Hen et al. 2023) (Table 3).

Range shifts, dispersal, and habitat connectivity

Our results showed that the alien fish group would experience greater habitat gains under climate change compared to endemic and native fish groups. These projected range shifts are based on the full dispersal model, which provides a theoretical estimate of potential habitat change but likely overestimates actual colonization capabilities, especially for species with limited mobility or occurring in fragmented habitats (Conti et al. 2015; Haase et al. 2023). In reality, colonization success depends not only on environmental suitability but also on life-history traits, connectivity, reproductive capacity, and species interactions (Kraft et al. 2011; Burrows et al. 2014; Dahlke et al. 2020; Panja et al. 2021; Makki et al. 2023a). While species occupying large, connected river systems may benefit from broader dispersal opportunities, those confined to smaller or isolated tributaries are more likely to face local extinctions due to their limited capacity to track shifting climate niches (Beecher et al. 1988; Yousefi et al. 2020b; Panja et al. 2021).

Study limitations

While our models provide valuable insights into potential future patterns, certain limitations should be considered when interpreting the projections. First, consistent with the full-dispersal assumption discussed above, our models may overestimate the ability of species to colonize newly suitable habitats, particularly in fragmented river systems. Second, we relied on static hydrological predictors (e.g., flow accumulation) due to the lack of high-resolution future hydrology projections, although actual hydrological conditions may change under future climates. Incorporating dynamic hydrological variables was beyond the scope of this study but remains an important direction for future work. Third, our models do not account for biotic interactions, adaptive capacity, or microhabitat variability, which may also influence species persistence and responses. These simplifications are common in large-scale SDMs and underscore the need to interpret projections as potential outcomes rather than definitive responses under climate change. In addition, including more occurrence data, especially for alien taxa from their non-native range, will enhance model reliability and inform more effective management strategies.

Implications and constraints of SDM-based management under climate change

SDMs provide a useful basis for anticipating how climate change may alter habitat suitability and species distributions, thereby informing proactive conservation planning. Model projections can help identify climatically stable headwaters and potential cold-water refugia that may serve as priority areas for protection (Isaak and Young 2023). At the same time, SDMs often indicate that future suitable habitats may occur outside current species ranges, emphasizing the need to maintain or restore longitudinal connectivity to support dispersal and range tracking (Davis et al. 2024). By distinguishing areas of projected habitat loss, gain, or persistence, SDMs can also guide restoration and management investments toward locations that are more likely to remain suitable under future climates. Because projections are influenced by uncertainty in climate scenarios, dispersal assumptions, and model structure, SDM outputs are most effective when used within an adaptive management framework in which monitoring and model updates are iteratively integrated into decision making.

When climate-induced habitat loss cannot be reversed, assisted migration or translocation may be considered, particularly where SDMs indicate future suitable habitats beyond current dispersal limits. However, relocation remains challenging due to ecological, disease, and community-level risks, and long-term viability is often undermined by ongoing anthropogenic pressures such as habitat fragmentation, land-use change, water extraction, and pollution (Mawdsley et al. 2009; Munday et al. 2017; Yousefi et al. 2020a; Makki et al. 2023a, b).

Conclusion

Our study indicates that global change, particularly rising future temperatures, is likely to facilitate the spread of the alien fish species in the Karun River Basin, as evidenced by their pronounced range expansions and projected shifts in habitat suitability. These findings underscore the growing ecological pressure associated with alien species and highlight the need for conservation and management strategies aimed at safeguarding endemic and native fish communities in the long term. In situations where climate-induced habitat loss cannot be reversed, management actions such as assisted migration or translocation of vulnerable species may be considered, provided that ecological risks are carefully evaluated.

We further emphasize the importance of regular and coordinated monitoring of freshwater ecosystems in the Karun River Basin. Such monitoring can help detect changes in species distributions, richness, and community composition, identify newly established or declining species, and provide essential information to support adaptive conservation planning under ongoing anthropogenic and climatic pressures.

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Declarations

Competing interests The authors declare no competing interests.

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