Ecological Indicators 160 (2024) 111857

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Climate change drives contrasting shifts in fish species distribution in the Mekong Basin

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ARTICLE INFO

Keywords:
Mekong basin
Climate change
Human population density
Species distribution model
Freshwater fish
Range shift

ABSTRACT

Global changes are causing significant alterations to terrestrial, marine, and freshwater ecosystems worldwide, with substantial implications for plant and animal populations, potentially leading to species extinctions. While freshwater ecosystems are recognized as particularly vulnerable to these impacts, there has been limited research conducted in tropical regions on how these changes will affect them. Here, we assessed the relative impacts of change in climate and human population density on fish species distribution between current (1970–2000) and future (2050s) time periods in the Mekong River. We analyzed occurrence data for 195 fish species from 10 functional guilds and employed species distribution models (SDMs) to evaluate potential changes in fish species distribution under the independent and combined impacts of changes in climate and population density. Our results show that climate change, with significant change in temperature and precipitation rather than minor population shifts, will be the primary driver of future change in fish species distribution in the Mekong River with all fish guilds likely to expand their suitable habitats. However, contrasted distributional changes were observed among fish species, with certain guilds projected to gain more suitable habitat than others. Out of the 195 species examined, the majority of fish species studied (i.e., 84 %) are expected to undergo a northward distributional shift, while 49 species may experience a reduction in their suitable habitats. Additionally, significant declines in species richness are projected to occur in currently diverse areas (i.e., Tonle Sap Lake and River), while the highest increases in fish species richness are projected to occur in the 3S (Sesan, Sekong, and Srepok) River Basins. These findings highlight potential hotspots for mitigating the impacts of environmental changes, providing an opportunity for conservation practitioners and planners at the national and regional levels to develop and implement adaptation and mitigation measures.

1. Introduction

Evidence indicates that climate change has already altered terrestrial, marine, and freshwater ecosystems worldwide. Biological responses, encompassing both functional and structural facets (i.e., physiological adaptations and distributional range shifts), have proven insufficient to cope with recent climate change, potentially leading to declines in numerous plant and animal populations and, ultimately, species extinctions (IPCC, 2022). Studies have shown strong associations between climate variability and changes in population abundances across various species groups, including birds, mammals, amphibians, fish, invertebrates, and plants (Pearce-Higgins et al., 2015). In Asia, both terrestrial and freshwater ecosystems, along with their associated species, populations and communities, are experiencing changes that can be directly attributed to climate change (IPCC, 2022). In response to climate change, many species are expected to shift their historical ranges, which will significantly impact local and regional biodiversity (Elliott et al., 2022; Hu et al., 2022; Pound et al., 2021).

Compared to terrestrial and marine ecosystems, freshwater ecosystems have been more significantly impacted by climate change (IPCC,

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https://doi.org/10.1016/j.ecolind.2024.111857
Received 20 November 2023; Received in revised form 15 February 2024; Accepted 5 March 2024

2022; Jenkins, 2003), with freshwater species likely to experience five times greater losses than terrestrial ones (Revenga et al., 2005). Under projected changes in hydrological regimes and a warming climate, freshwater fish appear to be at a high risk of extinction (Collen et al., 2014). However, the effects of climate change on fish species are not uniform, with cold-water fish losing suitable habitats, while other warm-water fish can expand their habitat ranges due to climate change (Comte et al., 2013; Sharma et al., 2007; Tekip, 2021). Fish distributions and biodiversity are influenced by temperature and precipitation, with temperature being more significant, since fish cannot regulate their body temperature and are highly sensitive to their surrounding temperature (Feng et al., 2017; Griffiths et al., 2014; Hochachka and Somero, 2002; Mostafavi et al., 2014).

The Mekong River is one of the largest and most productive rivers in the world, ranking third globally in terms of fish diversity, following the Amazon and Congo River Basins (Harrison et al., 2018; Jézéquel et al., 2020; Mekong River Commission, 2018a; Nuon et al., 2020; Winemiller et al., 2016). The distribution of Mekong fish varies significantly from its headwater to the Mekong Delta, with few fish found in the headwater and a plethora of fish in the lower part of the river. This disparity can be attributed to the higher slope in the headwaters, resulting in fast and variable water flow. In contrast, the lower part features larger surrounding floodplains and diverse habitats, providing suitable conditions for a wide range of fish species (Kang and Huang, 2022). Moreover, certain species, such as *Pangasianodon gigas* and *Catlocarpio siamensis,* hold significant importance for conservation efforts due to their critical endangered status. Fisheries resources of the Mekong are crucial to nearly 70 million people whose livelihoods partially or entirely depend on it (Mekong River Commission, 2018b). Additionally, the annual fisheries production in the Lower Mekong Basin (LMB) amounts to approximately 2.3 million tonnes of wild fisheries, valued at US$ 11 billion, making the LMB one of the most productive fisheries basins in the world (Mekong River Commission, 2018a). However, despite these statistics highlighting the significant ecological and socioeconomic benefits provided by the Mekong, its ecosystem is under severe stress due to human activities, such as hydropower, irrigation, navigation, sand mining, agriculture development, and overfishing (Arias et al., 2019; Bravard et al., 2013; Mekong River Commission, 2019; Nuon et al., 2020). Several studies have revealed that these stressors have led to changes in fish community composition, functional diversity, and a decline in catch rates (Chea et al., 2020; Mekong River Commission, 2021a; Montaña et al., 2020; Ngor et al., 2018a).

In addition to human-induced stressors, climate change is expected to significantly impact Mekong fish abundance and diversity. Several researchers have observed and predicted changes in temperature and precipitation regimes, as well as sea-level rise in the Viet Nam Mekong Delta, due to ongoing and future climate change (Eastham et al., 2008; Mekong River Commission, 2018b; Trisurat et al., 2018). Projected temperature changes by 2030 suggest a rise of 0.7–0.8 °C across most Upper Mekong Basin catchments, with more pronounced increases expected in the northern region. Specifically, the coldest Upper Mekong catchment is projected to experience the greatest rise (exceeding 1 °C), while catchments in Northern Thailand and Laos will undergo increases ranging from 0.8 to 0.9 °C (Eastham et al., 2008). Future precipitation projections for 2030 carry higher uncertainty. According to the same study by Eastham et al. (2008), the most probable scenario suggests an average increase of approximately 200 mm across the basin. However, this precipitation increase exhibits significant variability across different catchments, with increments ranging from less than 50 mm to over 300 mm. Regarding the river discharge, peak discharge is expected to notably increase in the future conditions (2076–2100). Chiang Saen and Kratie anticipate an average surge exceeding 50 % and 43 %, respectively, compared to present conditions (1980–2014). These heightened peak discharge levels are expected to expand the flooded area in the Lower Mekong Basin (Ly et al., 2023). As a result, it is crucial for practitioners and planners to gain a better understanding of these impacts to design effective management programs with appropriate measures to minimize adverse effects. Although the Mekong Basin is highly vulnerable to climate change (Mekong River Commission, 2018b), there has been a lack of research investigating the impacts of these changes on fish species distribution, especially on a large spatial scale covering the entire basin and accounting for various fish functional guilds.

Recently, there has been a significant increase in the use of species distribution models (SDMs) to investigate shifts in species distribution (Hu et al., 2022; Melo-Merino et al., 2020; Zhang et al., 2020). SDMs, also known as bioclimatic envelope models, ecological niche models, or habitat suitability models, have found applications in various fields, including wildlife management, biodiversity assessments, and spatial conservation prioritization (Araújo and Peterson, 2012; Booth, 2018; Khoury et al., 2020). In this study, we employed SDMs to establish relationships between fish species occurrence and environmental variables, allowing us to assess the current and predict the future distribution of 195 fish species. Therefore, the objectives of this study were twofold: (i) to assess the potential changes in fish species distribution due to alterations in environmental conditions; and (ii) to identify potential hotspots that are susceptible to climate and human-induced habitat alterations to inform and improve conservation and management strategies for Mekong fishes.

2. Materials and methods

2.1. Study area

The Mekong River originates in the Tibet plateau at an elevation of approximatively 5,000 m, and flows through six countries: China, Myanmar, Lao People's Democratic Republic (Lao PDR), Thailand, Cambodia, and Viet Nam. As a transboundary river, it ranks as the 12th longest river in the world, with a total length of 4763 km, and boasts an extensive catchment area of 810,000 km^2 with an annual average discharge of 446 km^3 (Mekong River Commission, 2018a). Geographically, the river can be divided into two primary sections (Fig. 1), the Upper Mekong Basin, which includes China and Myanmar, and the Lower Mekong Basin, comprising the remaining countries (Mekong River Commission, 2005).

2.2. Species occurrence data

In this study, we analyzed occurrence data for 571 fish species mainly based on a previous study by Nuon et al. (2020). To ensure model accuracy, species with less than 50 occurrences were excluded from the analyses, as they may have limited data to reliably predict their distribution (Guisan et al., 2017). Thus, we focused on 195 species from 46 families (Table S1), which were further categorized into 10 functional guilds (Table S2) (Mekong River Commission, 2021a): rhithron residents (27 species), long-distance white fishes (13 species), short-distance white fishes (61 species), floodplain spawners or grey fishes (27 species), generalist fishes (21 species), black fishes (16 species), estuarine residents (21 species), anadromous fishes (2 species), catadromous fishes (1 species), and marine visitors (6 species). It is worth noting that the Mekong River Commission (2021b) classified Mekong fish into these functional guilds using the guild classification of Welcomme et al. (2006), which groups fish species based on their reproductive strategies and habitat associations. Additionally, the occurrence data for Mekong fish species were sourced from three main databases: (i) Fish Abundance and Diversity Monitoring Programme of the Mekong River Commission (https://www.mrcmekong.org/). Through this programme, fish catch data were collected daily at 38 monitoring sites across the LMB. Furthermore, the fish data used in this study spanned from 2007 to 2018. For the details of the fish sampling procedure, interested readers can refer to (Mekong River Commission, 2021a); (ii) the International Union for Conservation of Nature range maps (IUCN;

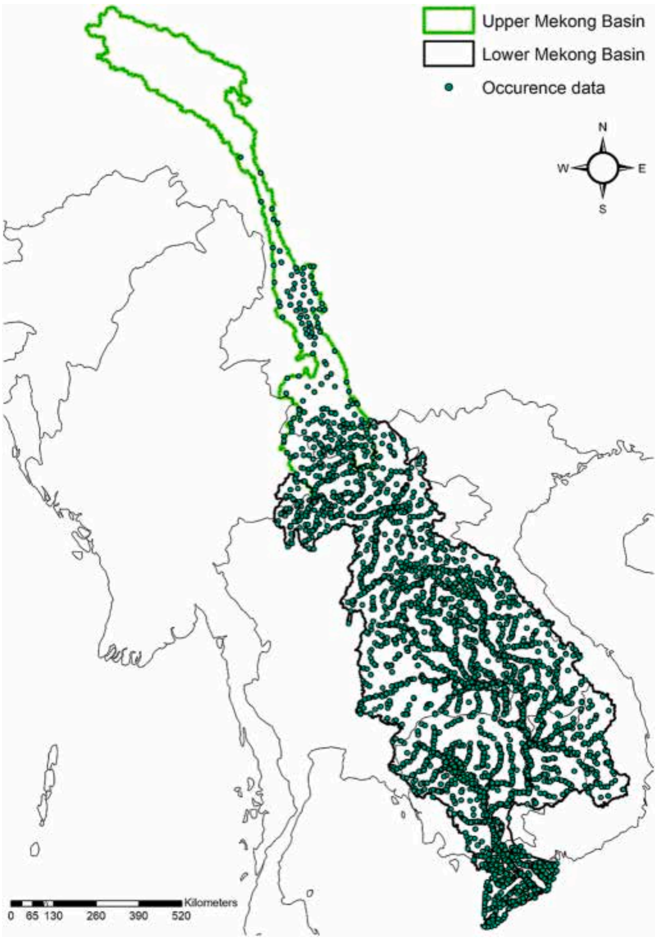

Fig. 1. Mekong Basin map and occurrence data of 195 fish species.

https://www.iucnredlist.org/); and (iii) the Global Biodiversity Information Facility (GBIF; https://www.gbif.org).

Before consolidating data from the three sources, the expert-based range maps of the IUCN for each fish species were converted into point data. This transformation involved sampling 300 points within the range of each species, ensuring comprehensive coverage of their distribution (Fourcade, 2016). Subsequently, we merged occurrence records from all data sources and conducted a quality check. Any occurrences located outside the Mekong Basin were removed from the dataset. To address issues related to spatial autocorrelation, we excluded occurrences within a 10 km radius of each other (Boria et al., 2014). Additionally, we implemented spatial rarefying to minimize the impact of uneven sampling effort. This involved retaining only one occurrence per environmental grid cell measuring 1 km^2 (Hu et al., 2022), using the fishnet tool in ArcGIS 10.5.2.

2.3. Predictor variable selection

Nineteen bioclimatic variables were obtained from the WorldClim database (https://www.worldclim.org). These variables consisted of eleven temperature-related variables and eight precipitation-related variables (Table S3) for both current conditions (1970–2000) and future climatic conditions (2041–2060; hereafter 2050s), with a spatial resolution of approximately 1 km^2 (i.e. 30 arc-seconds resolution). For future climatic projections, we used the representative concentration pathways (RCP) 8.5 (i.e., "business as usual" scenario), based on a multi-model average from three global circulation models (GFDL-CM3, GISS-E2-R and IPSL-CM5A-LR) selected for their suitability in the Mekong region (CCAI, 2015). In addition to the climatic variables, two non-climatic variables (i.e., human population density and elevation) were incorporated, as they are ecologically meaningful for the spatial distribution of fish species (Larentis et al., 2022; Luck, 2007; Suvarnaraksha et al., 2012). Human population density was derived from a global population dataset downscaled to a $\sim$ 1-km^2 resolution with a base year of 2000 and projections at ten-year intervals from 2010 to 2100 (Gao, 2020). However, only the projection in 2050 under SSP5 (Shared Socioeconomic Pathways) was selected for this study to align with the climatic dataset. Elevation data with the same spatial resolution as the other variables was obtained from the WorldClim database. Both the climatic and non-climatic datasets were clipped to the boundaries of the Mekong Basin using ArcGIS 10.5.2. To ensure robust performance of the SDMs, multicollinearity issues were addressed by removing strongly correlated variables and computing the variance inflation factor (VIF). Consequently, eight variables were retained for the analysis: mean diurnal range (Bio2), maximum temperature of the warmest month (Bio5), precipitation of the wettest month (Bio13), precipitation of the driest month (Bio14), precipitation seasonality (Bio15), precipitation of the warmest quarter (Bio18), precipitation of the coldest quarter (Bio19) and human population density (HPD) (Table S3).

2.4. Species distribution models

To enhance reliability and reduce uncertainty in model predictions, ensemble models with an unweighted average approach were employed in this study. Ensemble models have been shown to consistently outperform individual models, providing more robust and accurate predictions (Araújo and New, 2007; Grenouillet et al., 2011; Ngor et al., 2023). Four single models were selected: generalized linear model (GLM), generalized boosting model (GBM), random forests (RF) and multiple adaptive regression splines (MARS). These models have been widely used in ecological niche modeling and were chosen for their effectiveness (Elith et al., 2006; Liu et al., 2019; Zhang et al., 2020). The algorithms of these models were fitted using the default settings of the "sdm" package (Naimi and Araújo, 2016) in R (R Development Core Team 2022).

For pseudo-absences selection, a randomization method was applied with 10,000 pseudo-absences for GLM, 100 for MARS and equal amounts of presences for RF and GBM (Barbet-Massin et al., 2012). The presence and absence records for each species were split into training (70 %) and testing (30 %) datasets for algorithm calibration and evaluation, respectively. To ensure unbiased data splitting, this process was repeated 10 times, resulting in 40 different habitat suitability predictions for each species. The model performances were assessed using two metrics: the area under the ROC curve (AUC; Fielding & Bell, 1997) and the true skill statistics (TSS; Allouche et al., 2006). To develop the ensemble models using an unweighted average approach, models with AUC values below 0.8 and TSS values below 0.6 were excluded (Araujo et al., 2005; Rew et al., 2020).

Finally, a Principal Component Analysis (PCA) was performed to visualize the variable importance for each species and the relationships between variable importance and fish ecological guilds. The PCA model and graphical illustration were performed through "stats" and "factoextra" packages, respectively, in R.

2.5. Potential impacts on habitat suitability, distributional ranges, and species richness

To analyze the current and future probabilities of species occurrence or habitat suitability generated by the SDMs, binary maps were produced by transforming the continuous probability values into presence (1) and absence (0) areas. This transformation was conducted using a threshold determined by the sensitivity–specificity sum maximization approach recommended by Liu et al. (2005) and computed using the "sdm" package in R. Then, the changes in habitat suitability were assessed by overlaying the raster data of both current and future conditions, allowing to identify areas of stability, unsuitability, extirpation, and colonization as follows: (i) areas which were identified as suitable habitat for both current and future conditions were considered as “stable”; (ii) areas deemed unsuitable habitat for both current and future conditions were considered as “unsuitable habitat”; (iii) areas currently suitable but unsuitable in the future were considered as “extirpation”; and (iv) areas not currently suitable, but suitable in the future were categorized as “colonization”.

Distributional range shifts were quantified for all fish species using the centre of gravity of their distribution (i.e., range centroid), corresponding to the mean latitude and longitude of all the locations where a species is present. By comparing the current and projected species distributions, we computed the distance (in km) and the direction (in degrees) of the range centroid shift.

Finally, the current and future species richness were produced by overlaying the current and future species occurrences, respectively, and we computed the projected changes in species richness for each grid cell.

3. Results

3.1. Model performances and variable importance

Across the different fish species, AUC and TSS values from selected models ranged from 0.8 to 0.98, and from 0.6 to 0.97, respectively (Table S1). Regarding fish guilds, the model performances significantly varied among all the guilds for both AUC and TSS (Fig. S1). Notably, marine-related guilds (Guilds 7, 8, 9 and 10) demonstrated relatively high performance.

The importance of environmental variables in shaping fish species distributions varied between fish guilds (Fig. 2). Among the eight variables considered, Bio2 (Mean diurnal range) and Bio5 (Max Temperature of warmest month) emerged as the most influential variables, followed by Bio15 (Precipitation seasonality). The distributions of fish species from guilds 7 (Estuarine residents), 8 (Anadromous fishes), 9 (Catadromous fishes) and 10 (Marine visitors) were primarily driven by Bio2, while those from guilds 2 (Long-distance white fishes), 4 (Floodplain spawners or grey fishes), 5 (Generalist fishes) and 6 (Black fishes) were more influenced by Bio5. In contrast, the precipitation-related variables (i.e., Bio15) played an important role in shaping the distribution of fish species from guild 1 (Rhithron residents). Fish species from guild 3 (Short-distance white fishes) exhibited distributions influenced by both temperature and precipitation-related variables (Bio5 and Bio15, respectively).

3.2. Impacts of climate and human population changes on potential future fish species distribution

Remarkable changes were observed in the distribution of suitable habitats among fish guilds under the different scenarios (i.e., HPD, climate change (CC), and combined impacts of HPD and CC). Overall, the results showed that changes in human population density hardly affected the distribution of suitable habitats for all fish guilds (Fig. 3), while climate change emerged as the primary driver of projected changes in fish species distribution. Under climate change and combined impact scenarios, all fish guilds were predicted to expand their suitable habitats with guilds 2 (Long-distance white fishes) and 6 (Black fishes) experiencing the most substantial gains (about 24 % increase) (Table S4). Guilds 1 (Rhithron residents), 3 (Short-distance white fishes), and 5 (Generalist fishes) anticipate gains of approximately 22 %, while guilds 7 (Estuarine residents), 9 (Catadromous fish) and 10 (Marine visitors) exhibit minor increases, each expanding by less than 10 %.

Despite these similarities among the responses of the ten fish guilds, very contrasted distributional changes were observed among fish species. These changes ranged from 0 to 97 % of reduction in suitable habitat (mean ± sd = 25 % ± 27). On the other hand, some species experienced a significant increase in suitable habitat, ranging from a negligible increase (0.02 %) to a 235 % increase (mean ± sd = 70 % ± 42) (Table S5 and Fig. S5). Out of the 195 species analyzed, 49 (i.e., *Amblyrhynchichthys micracanthus*, *Vanmanenia striata* and *Pangasius bocourti*) were projected to experience reduced suitable habitats under both climate change and combined impact scenarios (Table S1). In contrast, several species (i.e., *Cyclocheilos enoplos*, *Hypsibarbus lagleri* and *Poropuntius deauratus*) emerged as potential winners in response to climate change. Overall, the results highlighted that the magnitude of

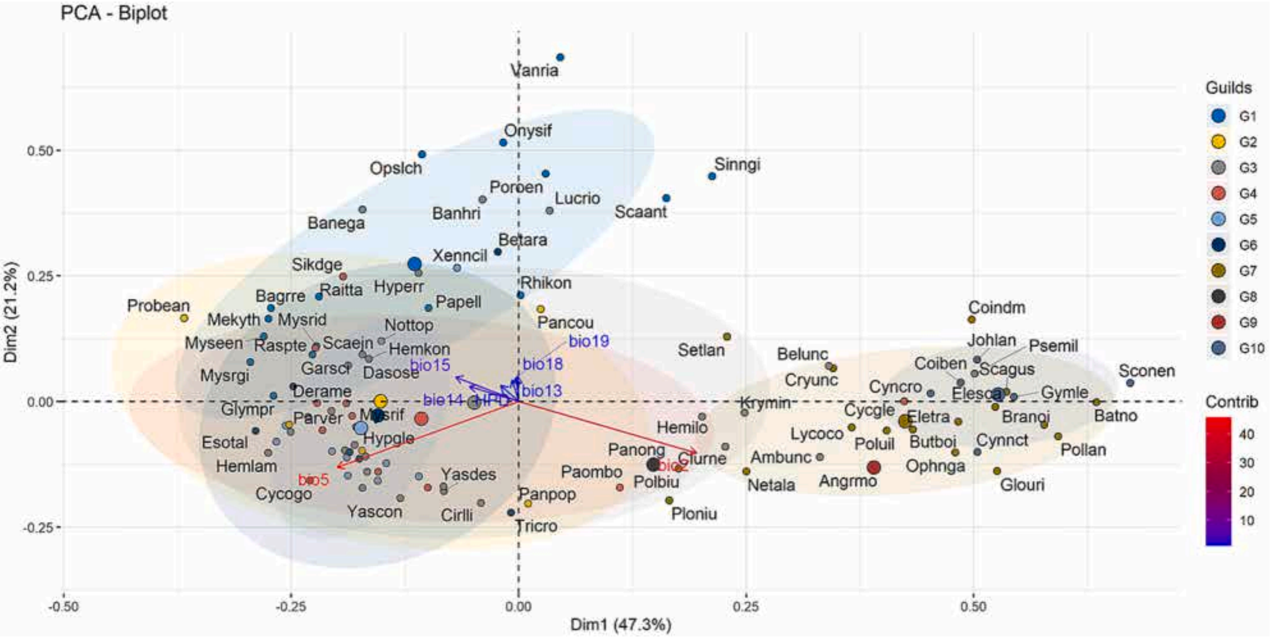

Fig. 2. PCA biplot of ten fish functional guilds, showing the contribution of eight variables to principal components. The centroids of each guild are represented by large dots. The colors of the arrows denote the contribution of the variables to principal components, with blue representing low contribution and red representing high contribution. Full species names are shown in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

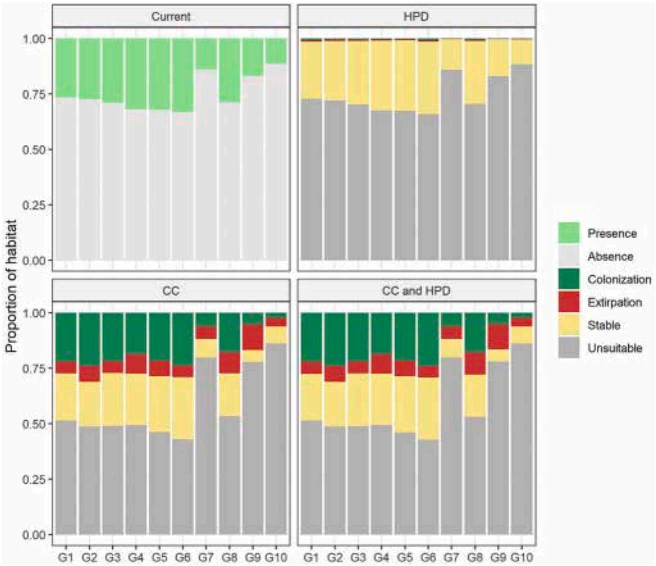

Fig. 3. Gain and loss in suitable habitat of fish functional guilds under different scenarios. CC stands for climate change and HPD stands for human population density.

habitat reduction was comparatively smaller than that of habitat expansion.

Finally, by the 2050s, most of the fish species studied (i.e., 84 %) would undergo a distributional shift northward (Fig. 4), with shifts in their range centroid ranging from 8 to more than 300 km (mean ± sd = 118 km ± 75).

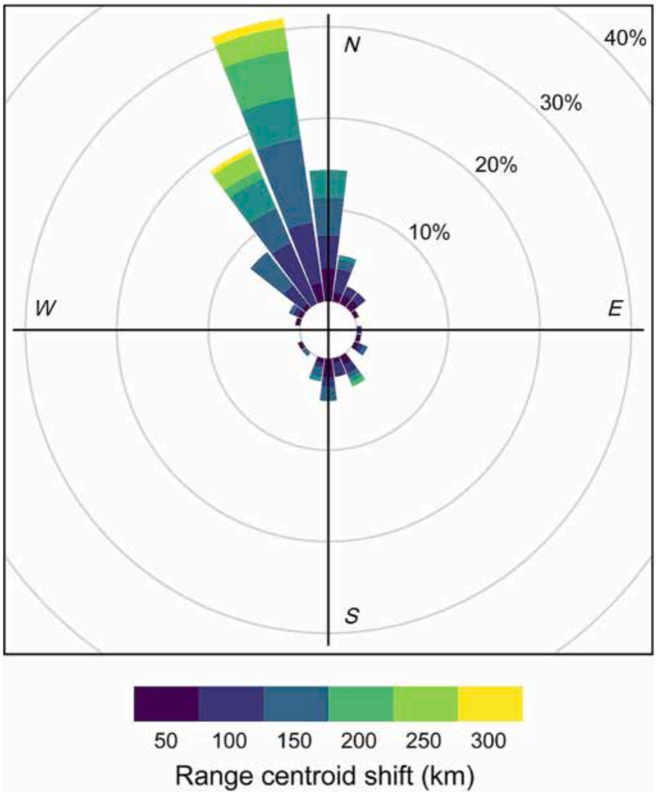

Fig. 4. Frequencies of projected direction and magnitude of changes in the range centroid (i.e., center of gravity of the species distribution) for the 195 fish species studied.

3.3. Changes in species richness

Among the three scenarios considered, climate change and the combined impact scenarios were likely to have the most significant impact on the current spatial pattern in fish species richness in the Mekong Basin, particularly in the LMB (Fig. 5). Currently, the highest number of fish species was observed in the Mekong Delta, the TSLR, and the mainstream extending from Stung Treng province in Cambodia to Vientiane in Lao PDR. However, under the aforementioned scenarios, significant declines in species richness were projected to occur in these areas, particularly in the TSLR. Conversely, the highest increases in fish species richness were projected to occur in the 3S (Sesan, Sekong, and Srepok) River Basin, extending up to Borikhamxay province of Lao PDR. Furthermore, the upper part of the LMB in Lao PDR (i.e., Xayabury, Luangprabang, Oudomxay and Bokeo provinces) and the northeastern regions of Thailand (i.e., Maha Sanakham, Khon Kaen and Nakhon Ratchasima provinces) were projected to experience increases in fish species richness. Similarly, small increments in species richness were predicted to occur in the lower part of UMB encompassing Myanmar and Yunnan.

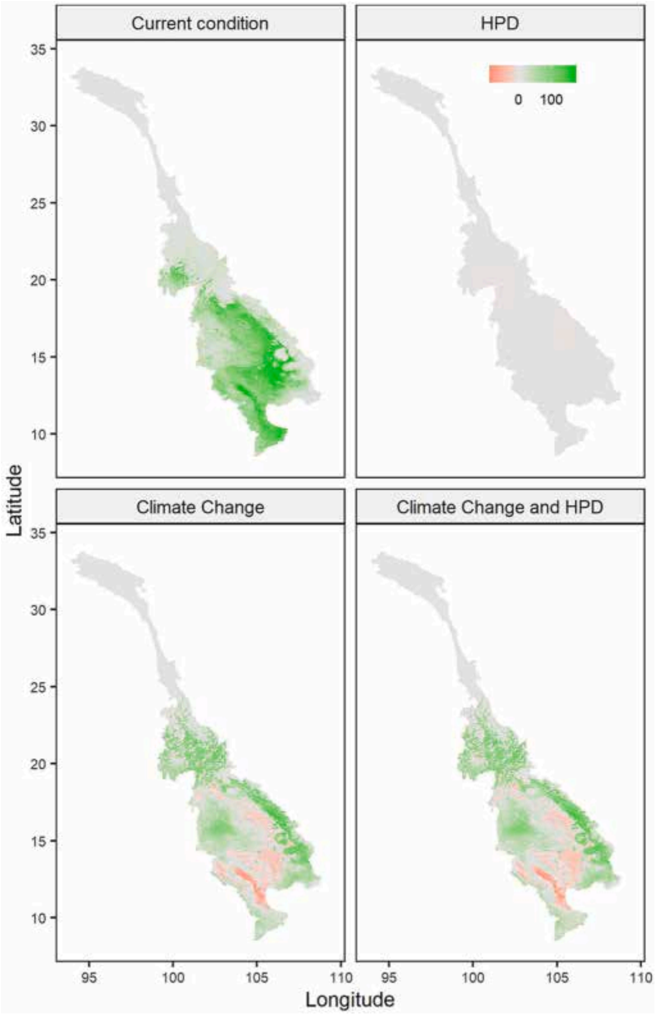

Fig. 5. Spatial patterns of projected changes in fish species richness in the Mekong Basin under independent and combined impacts of climate change and HPD. The colors represent the different levels of species richness, with red representing loss of species richness, grey representing no loss of species richness, and green representing high species richness. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Factors influencing species range shifts

Tropical fish species are more diverse than those in other regions (Oberdorff et al., 2015) and are among the most vulnerable to climate change (Barbarossa et al., 2021). Despite this vulnerability, studies using SDMs to assess the impacts of climate change on fish range shifts in the tropics have been limited (Comte et al., 2013). While some recent studies have employed SDMs for this purpose (Herrera-R et al. (2020); Hu et al., 2022; Liu et al., 2019), none have focused on the Mekong Basin. Our study is the first to use SDMs to investigate the impacts of climate change, including human pressures, on fish species distribution across the entire Mekong Basin, accounting for ten fish functional guilds.

Our study revealed that the future changes in HPD had the least significant impact on fish suitable habitats in the Mekong Basin due to a minimal difference between the current and future HPDs (Appendix S1 and Fig. S4). Such small changes are expected to have limited effects on fish habitat diversity, as demonstrated by Larentis et al. (2022), who linked increased human pressure, such as urbanization, to reduced habitat diversity in stream environments. It is important to acknowledge that our study solely focuses on the effects of HPD on fish suitable habitats, without accounting for the energy demands of the basin's residents. Consequently, the observed effects of HPD may appear relatively modest. However, the inclusion of energy demands in our analysis could reveal a more profound impact of HPD. This is particularly relevant in the Mekong Basin, where hydropower serves as a crucial energy resource (Mekong River Commission, n.d.). Notably, the number of hydropower projects increased from 59 to 89 between 2015 and 2019, with corresponding total installed capacities of 10,017 MW and 12,285 MW, respectively (Mekong River Commission, 2018a, n.d.). Previous studies consistently underscore the strong negative impact of hydropower dams on fish biodiversity, communities, and distribution, especially for migratory species (Benejam et al., 2016; Jellyman and Harding, 2012; Ngor et al., 2018a; Nuon et al., 2020; Sor et al., 2023). In contrast, climate change emerged as the primary driver of changes in fish suitable habitats in the Mekong Basin, leading to both habitat contraction and expansion. Notably, nearly all fish guilds exhibited greater sensitivity to temperature-related variables than to precipitation-related variables. Previous studies have similarly emphasized temperature as a crucial factor in determining habitat suitability for fishes (Feng et al., 2017; Griffiths et al., 2014; Hochachka and Somero, 2002; Mostafavi et al., 2014).

As ectotherms and poikilotherms, most fishes are highly sensitive to alterations in water temperature due to their lack of mechanism to generate and maintain body heat (Helfman et al., 2009; Roessig et al., 2005). Consequently, temperature can impact their metabolic rates, as well as their feeding, growth, and reproductive activities (Helfman et al., 2009; Wootton, 1992). When water temperature increases, fishes face additional environmental challenges such as low pH, diurnal oxygen depletion, parasites and bacteria, which can lead to mortality or migration to other suitable areas to complete their life cycle (Almeida-Val et al., 2005; Kang and Huang, 2022; Wootton, 1992). For instance, a significant fish mortality event occurred in Boeng Tonle Chhmar Ramsar site, located at the northeast fringe of the Tonle Sap Lake, where approximately 65 tonnes of fish died due to high temperature reaching about 42 °C (Chheng & David, 2016). Moreover, elevated temperature are projected to cause a dramatic decline in species richness in the Tonle Sap Lake and River by the 2050s. Marine and estuarine-related fish guilds are particularly vulnerable to increased temperature, with many species from these guilds projected to lose between 3 and 50 % of their suitable habitat by the 2050s. Similar findings have been reported in previous studies investigating the impacts of climate change on estuarine fish (Gillanders et al., 2011). Furthermore, our study revealed that the habitat suitability of these two fish guilds were relatively small and located at low latitudes, making them more vulnerable to shifting temperature conditions. Evidence suggests that fish species inhabiting high and low latitudes exhibit narrower thermal tolerances compared to those inhabiting intermediate latitudes (Rijnsdorp et al., 2009). For example, *Vanmanenia striata*, which inhabits the high latitudes (mid-UMB) and has a small distribution range, is likely to become extinct as its current range is expected to be almost completely lost by the 2050s.

In addition to its adverse effects, climate change provides opportunities for fishes to access additional favorable thermal habitat. For instance, with an increased temperature, 75 % of the studied fish from almost all fish guilds were anticipated to gain suitable habitats in the future. Moreover, most of these fishes are projected to expand their range northward, suggesting that the benefits of temperature change outweigh the negative impacts for most species. This trend is primarily due to the fact that the majority of studied fishes are warm-water fishes, well-adapted to living in warm environments with maximum summer daily mean temperatures typically ranging from 24 to 29 °C (Roghair and Adams, 2019; Wootton, 1992). Importantly, most studied fishes (except marine and estuarine-related guilds) have a broad habitat range and occupy intermediate latitudes, and generally exhibit high tolerance to elevated water temperature and can withstand a wide range of thermal conditions (Laikre et al., 2005; Rijnsdorp et al., 2009). As a result, the suitable habitats of warm-water fishes expand, allowing them to access new favorable thermal habitats (Comte et al., 2013; Sharma et al., 2007; Tekip, 2021).

Our study found that climate change is driving a significant shift in fish species richness, with new potential habitats emerging in some provinces of Thailand (Maha Sarakham, Khon Kaen, Nakhon Ratchasima), as well as between 3S River Basin and upper LMB in Lao PDR (Fig. 5). These findings are consistent with the previous studies (Buisson et al., 2008; Buisson and Grenouillet, 2009) that have predicted a shift in species richness to new areas under climate change. The new potential habitats identified in our study are essential for future conservation efforts and should be considered as important habitats for fish species adaptation.

4.2. Implications for conservation

The species range shifts predicted by this study have significant implications for conservation planning and management. Firstly, it is important to acknowledge that while fishes may have the capacity to track new favorable habitats under climate change, their ability to disperse and reach these destinations is a major concern. The migration paths of fish species may be obstructed by physical barriers, particularly in the Mekong Basin where numerous hydropower dams have been constructed along the mainstream and tributaries. Some of these dams overlap with potential habitats, such as those in the 3S basin, in the provinces of upper Vientiane, Lao PDR, and the lower part of the Upper Mekong Basin in China (Ngor et al., 2018b; Nuon et al., 2020; Sor et al., 2023). These physical barriers can have detrimental impacts on fish migration, reproduction, and habitat availability (Fuller et al., 2015), ultimately leading to changes in fish communities as documented in the upper LMB and Sesan River (Ngor et al., 2018a; Nuon et al., 2020). Therefore, it is crucial to prioritize conservation and management efforts in potential habitats that exhibit high species richness. Additionally, maintaining and restoring longitudinal and lateral connectivity of river networks is essential for facilitating fish migration and completing their life histories. This can be seen as an adaptive strategy for aquatic ecosystems (Mekong River Commission, 2021b; Tingley et al., 2019).

Lastly, it is crucial to prioritize the management and conservation of habitats that are projected to be adversely impacted by climate change. This includes the habitats of marine and estuarine-related guilds in the Mekong Delta and habitats of most fish species in TSLR. These habitats are already facing numerous threats, such as deforestation of flooded and mangrove forests, pollution, overfishing, sand mining, irrigation and hydropower dams (Daly et al., 2020; Hackney et al., 2020; Nuon et al., 2020; Shivakoti and Bao, 2020; Sovannara, 2020; Tonle Sap

Authority, 2019; Young, 2009). The combined effect of these threats and climate change will exacerbate the challenges faced by fish populations, necessitating urgent conservation efforts at both national and regional levels. At the national level, conservation practitioners can consider initiatives such as reforestation of flooded forests and mangroves in Tonle Sap Lake, Cambodia and the Mekong Delta, Vietnam, respectively. These actions not only provide habitat for a diverse range of fish and other fauna and flora but also contribute to carbon storage. Collaboration with relevant stakeholders is crucial for developing preventive measures and controlling pollution arising from improper pesticide use and untreated wastewater disposal. Maintaining high water quality is essential to protect aquatic biota from the increased toxicity of pollutants associated with rising water temperatures (Ficke et al., 2007; Roghair and Adams, 2019). Furthermore, restoring connectivity within floodplains is important for fish species that require migration between floodplains and local tributaries for spawning, feeding, and refuge. This is particularly relevant for fishes belonging to guilds G4 (Floodplain spawners or grey fishes), G5 (Generalist fishes), and G6 (Black fishes) (Mekong River Commission, 2017). Additionally, the establishment of community fish refuges should be considered as they provide shelter for fish during the dry season, benefiting fish populations, household incomes, and food security (Joffre et al., 2012). Addressing the challenges posed by climate change, conservation requires a joint effort among the Mekong countries. It is crucial to urgently implement the “Mekong strategy for basin-wide environmental management for environmental assets of regional importance” developed by the Mekong River Commission in 2021. The strategy includes key actions such as developing or updating management plans for environmental assets, enhancing habitat connectivity, implementing spatial planning and zoning mechanisms to manage shifting habitats, and prioritizing activities such as reforestation, co-management and overfishing control (Mekong River Commission, 2021b). Successful implementation of this strategy will not only benefit aquatic and terrestrial biodiversity but also support human adaptation to a changing environment.

4.3. Limitation and future work

Our primary findings are derived from SDMs based on correlations between fish species occurrence and temperature- and precipitation-related variables, as well as human population density. However, this approach does not take into account the potential influence of hydropower dams and climate change-induced alterations in water flow patterns on fish species distribution. This limitation should be acknowledged in our study, and further research should explore these factors in the future. Additionally, in this study, we assume that all fish can freely and equally migrate, regardless of fish body sizes and biogeographical barriers, such as dams. Therefore, the capacity for fish dispersal needs attention in the future work.

While this study proposes several promising conservation measures, their feasibility is limited by several factors. Securing the significant funding required for large-scale reforestation, connectivity restoration, and co-management programmes across multiple Mekong countries can be difficult, especially given competing priorities and limited budgets. Additionally, ensuring effective implementation requires overcoming challenges related to cross-border collaboration, governance structures, and potential conflicts between diverse stakeholder interests. Future work should explore these challenges in more detail and investigate potential solutions such as innovative financing mechanisms and improved stakeholder engagement strategies.

5. Conclusion

Our findings strongly indicate that climate change is a major driver of potential changes in the distribution of fish functional guilds, with temperature-related variables playing a significant role in determining habitat distribution. We predicted that a smaller number of species would experience future range contractions, and among the guilds studied, marine and estuarine-related guilds could be particularly affected by increased temperatures. Our results suggest a decrease in species richness in Tonle Sap Lake and River, and most mainstream areas, while an increase in species richness is expected in the 3S basin up to Borikhamxay province, northeastern regions of Thailand, the upper part of the LMB in Lao PDR (i.e., Xayabory, Luangprabang, Oudomxay and Bokeo provinces) and the lower part of UMB (Myanmar and Yunnan). These findings highlight the habitats that are potential candidates for conservation and the areas that would be the most impacted, providing valuable information for conservation practitioners and planners at both national and regional levels. This knowledge can also aid in the planning, formulation, and revision of measures to adapt to global changes.

CRediT authorship contribution statement

Vanna Nuon: Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Ratha Chea:** Writing – review & editing, Supervision, Conceptualization. **Sovan Lek:** Writing – original draft, Methodology, Conceptualization. **Nam So:** Writing – review & editing, Conceptualization. **Bernard Hugueny:** Writing – review & editing, Conceptualization. **Gaël Grenouillet:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

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

Data availability

Data used in this study were sourced from IUCN, GBIF, WorldClim and MRC. While the data from IUCN, GBIF and WorldClim are publicly accessible, those from the MRC cannot be shared without explicit permission from the MRC.

Acknowledgment

This study was financially supported by Institut de Recherche pour le Développement (No.253535) through Laboratory of Freshwater Ecology (ECOFRESH). The authors express sincere thanks to the Mekong River Commission Secretariat for providing the fish data. Centre de Recherche sur la Biodiversité et l’Environnement was supported by “Investissement d’Avenir” grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111857.

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