Science of the Total Environment 883 (2023) 163689

Contents lists available at ScienceDirect

Science of the Total Environment

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

Streams in the Mediterranean Region are not for mussels: Predicting extinctions and range contractions under future climate change

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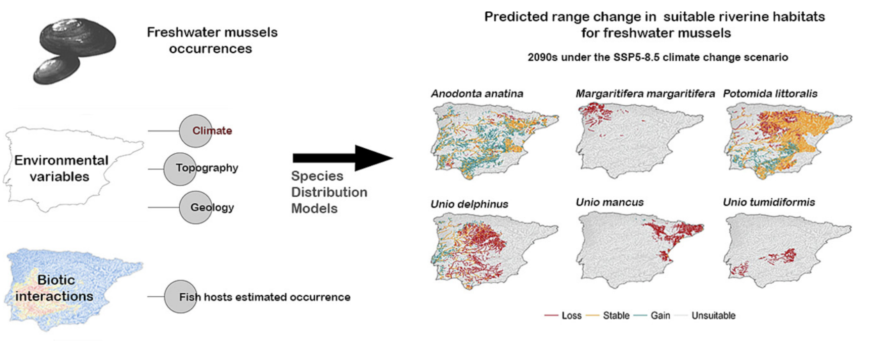
HIGHLIGHTS

- Species distribution models were built with environmental variables and fish hosts.
- Climate change is expected to severely impact the distribution of Iberian FMs.
- Disregarding biotic interactions underestimated future climate change impacts.
- Species with narrow ranges may face regional/global extinction due to habitat loss.
- Restoring suitable habitats and river connectivity is critical for conservation.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Damia Barcelo

Keywords:
Biodiversity conservation
Biotic interactions
Fish hosts
Habitat loss
Range shift
Species distribution models

ABSTRACT

Climate change is becoming the leading driver of biodiversity loss. The Mediterranean region, particularly southwestern Europe, is already confronting the consequences of ongoing global warming. Unprecedented biodiversity declines have been recorded, particularly within freshwater ecosystems. Freshwater mussels contribute to essential ecosystem services but are among the most threatened faunal groups on Earth. Their poor conservation status is related to the dependence on fish hosts to complete the life cycle, which also makes them particularly vulnerable to climate change. Species Distribution Models (SDMs) are commonly used to predict species distributions, but often disregard the potential effect of biotic interactions. This study investigated the potential impact of future climate on the distribution of freshwater mussel species while considering their obligatory interaction with fish hosts. Specifically, ensemble models were used to forecast the current and future distribution of six mussel species in the Iberian Peninsula, including environmental conditions and the distribution of fish hosts as predictors. We found that climate change is expected to severely impact the future distribution of Iberian mussels. Species with narrow ranges, namely *Margaritifera margaritifera* and *Unio tumidiformis*, were predicted to have their suitable habitats nearly lost and could potentially be facing regional and global extinctions, respectively. *Anodonta anatina, Potomida littoralis,* and particularly *Unio delphinus* and *Unio mancus,* are expected to suffer distributional losses but may gain new suitable habitats. A shift in their distribution

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http://dx.doi.org/10.1016/j.scitotenv.2023.163689
Received 5 March 2023; Received in revised form 18 April 2023; Accepted 19 April 2023
Available online 24 April 2023

to new suitable areas is only possible if fish hosts are able to disperse while carrying larvae. We also found that including the distribution of fish hosts in the mussels' models avoided the underprediction of habitat loss under climate change. This study warns of the imminent loss of mussel species and populations and the urgent need of management actions to reverse current trends and mitigate irreversible damage to species and ecosystems in Mediterranean regions.

1. Introduction

Climate change will likely become the leading environmental challenge of the 21st century for human societies. Despite the observed environmental impacts around the globe (World Wide Fund for Nature, WWF, 2022) and the consequent humanitarian crisis (Institute for Economics & and Peace, 2022), global government commitments to reduce greenhouse gas emissions continue to fail (IPCC, 2022). In the meantime, climate change is becoming a major driver of biodiversity loss, as one million plant and animal species are currently threatened with extinction (Bellard et al., 2012; WWF, 2022).

The Mediterranean Region is strongly affected by ongoing climate change because of its naturally low water availability and high levels of human demand for water resources (García-Herrera and Barriopedro, 2018). Effects are emerging differently around the world, and southwestern Europe is already facing some of the severest consequences (Bolotov et al., 2018; Cresswell-Clay et al., 2022; Filipe et al., 2013a; Hastie et al., 2003). An abnormal expansion of the Azores High - a semi-permanent centre of high atmospheric pressure over the North Atlantic – following the industrial revolution has been recently linked to unprecedented dry conditions in the Iberian Peninsula (Cresswell-Clay et al., 2022). Accordingly, progressively higher temperatures are being recorded each year, in addition to worrisome increases in aridity and frequency of extreme weather events (Díaz-Poso et al., 2023; Pereira et al., 2021). In addition, the Mediterranean Region is located within one of the 25 Global Biodiversity Hotspots (Myers et al., 2000) and harbours unique biodiversity which includes a great number of endemic species, thus being an urgent case for examining the potential climate change impacts on Mediterranean-type ecosystems (Benson et al., 2021; Hermoso and Clavero, 2011; Tierno de Figueroa et al., 2013).

Iberian freshwater biodiversity includes a remarkable diversity of species, many endemic, which are responsible for valuable ecosystem functions and services, and consequently contribute to important livelihoods (Darwall et al., 2008; Dudgeon, 2019; Reid et al., 2019). Freshwater ecosystems are particularly vulnerable to climate change, given the dependence of thermal and hydrological regimes on climate conditions (Filipe et al., 2013a; Markovic et al., 2014). Consequently, drastic alterations in the stationarity of freshwater ecosystems (sensu Milly et al., 2008) are causing unparalleled species losses and changes in species' abundances and distributions that typically far surpass declines in terrestrial and marine systems (Darwall et al., 2018; Harrison et al., 2018; Markovic et al., 2014; Reid et al., 2019; WWF, 2022). Such extreme trends of freshwater biodiversity loss can also be the result of a multitude of other threats (e.g. pollution, river regulation, water abstraction, overexploitation, and the introduction of non-native species), but impacts will most likely be further intensified by ongoing climate change (Darwall et al., 2018; Dudgeon, 2019; Markovic et al., 2014; Reid et al., 2019).

Within freshwater ecosystems, freshwater mussels of the order Unionida Gray 1854 (hereafter, mussels) are declining rapidly and are among the most threatened faunal groups on Earth (Böhm et al., 2021; Ferreira-Rodríguez et al., 2019; Lopes-Lima et al., 2018). This severe decline is partly related to their unusual life cycle: during reproduction, a parasitic larva (glochidia) must attach to a suitable fish host to metamorphose into a juvenile (Modesto et al., 2018). Furthermore, declines are also attributed to climate change by the impacts of i) warming water temperature (Akiyama and Iwakuma, 2007; Ferreira-Rodríguez and Pardo, 2017; Ganser et al., 2015; Hastie et al., 2003; Pandolfo et al., 2010; Taeubert et al., 2014), ii) increased frequency and severity of extreme floods (Hastie et al., 2001; Sousa et al., 2012) and droughts (Bódis et al., 2014; Gagnon et al., 2004; Mouthon and Daufresne, 2006; Nogueira et al., 2021; Sousa et al., 2018), and iii) alterations of the mussel-host dynamics, both by changing the phenology, distribution and population structure of fish hosts or by potentially disrupting the ecological functionality of their obligatory interaction, which could undoubtedly lead to extinction cascades (Bellard et al., 2012; Clavero et al., 2017; Filipe et al., 2013b, 2009; Miller-Struttmann et al., 2015; Modesto et al., 2018; Spooner et al., 2011; Xenopoulos et al., 2005).

Maintaining healthy and recruiting mussel populations requires that mussels and fish hosts' distributions overlap (Modesto et al., 2018; Schwalb et al., 2013). Species distributions models (SDMs) are the most common tool to predict species' distributions facing climate change, though they often fail to consider essential biotic interactions such as this mussel-fish relationship (Araújo and Luoto, 2007; Bush and Hoskins, 2017; Giannini et al., 2013; Lois et al., 2014; Markovic et al., 2014). Accordingly, species distributions are primarily driven by environmental conditions, dispersal constraints, and biotic interactions (Elton, 1927; Grinnell, 1917; Hutchinson, 1957). Because of this, disregarding this key contribution, particularly concerning obligatory interactions such as the mussel-fish host, can lead to weaker model performance and an overestimation of species' distributions (Araújo and Luoto, 2007; da Silva et al., 2022; Flores-Tolentino et al., 2020; Giannini et al., 2013; Hof et al., 2012; Khosravi et al., 2021). This is a major shortfall because safeguarding mussels' diversity implies the most accurate prediction of current and future distributions that can inform improved conservation strategies (Ferreira-Rodríguez et al., 2019; Lopes-Lima et al., 2021; Pearson and Dawson, 2003; Sousa et al., 2023).

Mussel assemblages in the Iberian Peninsula are usually characterized by low species richness, but most of those species have high conservation value and some present narrow distributions (Araujo et al., 2009; Lopes-Lima et al., 2017). There are currently 10 recognized species of mussels in the Iberian Peninsula. Within these, we predicted the current and future distribution of six species, namely *Margaritifera margaritifera* (Linnaeus, 1758), *Anodonta anatina* (Linnaeus, 1758), *Potomida littoralis* (Cuvier, 1798), *Unio mancus* Lamarck, 1819, and the endemic species *Unio delphinus* Spengler, 1793 and *Unio tumidiformis* Castro 1885, while accounting for the distribution of their fish hosts. We excluded *Pseudunio auricularius* (Spengler, 1793), *Unio gibbus* Spengler, 1793, *Unio ravoisieri* Deshayes, 1847, and *Anodonta cygnea* (Linnaeus, 1758) from the study due to their very restricted distribution or lack of knowledge regarding suitable fish hosts (Araujo et al., 2009; Lopes-Lima et al., 2017). Given the downward trajectory of this faunal group, their complex life histories, and their high sensitivity to human disturbances, appropriate research to understand how climate change will influence these species, and which are most at risk, is urgent. In addition, given the already evident environmental effects of climate change in the Iberian Peninsula, this region has the potential to illustrate impacts on freshwater biodiversity that may soon affect other territories around the world. As such, we aimed at: i) modelling and projecting the current distribution of mussels in the Iberian Peninsula, ii) forecasting potential range shifts of six Iberian mussels as a result of three climate change scenarios for the 2050s and 2090s time periods; and iii) quantifying the proportion of the current distributional ranges that will likely be lost for each mussel and climate scenario. We hypothesise that climate change will lead to range shifts of Iberian mussels, although the proportion of current distributional loss will vary by mussel species and climate scenario, with habitat specialist species with restricted distributions being more vulnerable to climate change.

2. Material and methods

2.1. Study area

The Iberian Peninsula is the south-westernmost region of the European continent. Covering an area of approximately 583,200 km^2, Iberia is bordered by the Atlantic Ocean (north, west, and southwest) and the Mediterranean Sea (south, east and southeast). In the north, it is separated from Europe by the Pyrenees, which represents a known biogeographic barrier. Due to its location and temperate Mediterranean dominant climate, this region covers substantial ranges of temperature and precipitation, and is highly vulnerable to climate change in the future as shown by the predicted expansion of the Arid climate area (Beck et al., 2018). Specifically, southern and eastern areas are characterized by hot and dry summers, and mild and rainy winters, while some areas in the northwest have a more Atlantic climate with cooler temperatures and higher rainfall (Beck et al., 2018; Cresswell-Clay et al., 2022). Accordingly, highest annual precipitation values exceeding 2200 mm are recorded in mountainous areas in the north. In contrast, the lowest values are found in the south, with average annual rainfall below 300 mm. Regarding temperature conditions, average annual maximum air temperature varies between 17/20 °C and 32/35 °C during summer months. In the winter, average minimum air temperature varies between values below 0 °C in areas of high altitude, and around 15 °C in the southern coastal regions (Cunha et al., 2011).

Most river basins in Iberia flow to the Atlantic Ocean in a north-eastern to south-western orientation, due to the similar orientation of the main orographic structures. The main exceptions are the Ebro, Segura, and neighbouring basins in the east, flowing to the Mediterranean in a northwest to south-east direction parallel to the Pyrenees. Due to the seasonal variation in precipitation and temperature patterns, all Iberian rivers register a seasonality in flow, with high winter and low summer discharges. The amplitude of flow levels is generally high, increasing from north to south.

2.2. Species data

Mussels' occurrences were compiled from numerous sampling campaigns between 2000 and 2022 and complemented with data from scientific and grey literature including technical reports and museum collections (Araujo et al., 2005; Ayres, 2008; Barros, 2014; Bragado et al., 2010; Comas and Carrera, 2004; Confederación Hidrográfica del Guadiana, 2009; Genoher et al., 2002; Gómez and Araujo, 2008; Lois, 2010; Lois et al., 2014; Madeira et al., 2007; Martín et al., 2007; Morales et al., 2004; Pérez Quintero et al., 2002; Rovira et al., 2009; Soler et al., 2006; Toledo, 2006; Velasco and Romero, 2005; Velasco Marcos et al., 2002). Fish host records were obtained from the Spanish Fish Chart (Iberian Society of Ichthyology, 2017, last accessed in June 2022) and the Global Biodiversity Information Facility database (GBIF, last accessed in June 2022 – Table S1). All data were manually checked with removal of incorrect entries and filtered to the period 2000–2022. Occurrence records were thinned using the R package 'spatialEco' (Evans, 2021). Species included in the analyses and corresponding number of presence records are shown in Table S1. Knowledge regarding the whole range of fish hosts compatibility for *A. anatina*, *U. delphinus* and *P. littoralis* is currently unavailable. Because of this, we selected the fish species that are known to be suitable hosts for the development of glochidia into juvenile mussels from Araujo et al. (2009), Douda et al. (2013), Lopes-Lima et al. (2020) and Ramos (2011) and further included congeneric fish species occurring in the Iberian Peninsula, assuming that they would present similar suitability to tested species. For example, *Luciobarbus bocagei* was previously tested for host compatibility, but it only occurs in Atlantic basins from the Minho basin in the north to the Tagus and Sado basins in the south (Collares-Pereira et al., 2021). However, other *Luciobarbus* spp. occur in the Iberian Peninsula, overlapping with mussels' distributional ranges, namely *L. microcephalus* (Guadiana basin)*, L. comizo* (Tagus and Guadiana basins), and L. *graellsii* (from Ebro to Ter and Ason basins), among others, which were also included as suitable hosts. From all the assumed suitable fish hosts for the studied mussels in the Iberian Peninsula (Table S2), we excluded *Achondrostoma* spp., *A. occidentale, Barbus meridionalis, Luciobarbus steindachneri, Squalius aradensis, S. torgalensis* and *S. castellanus* from the analyses due to the low number of presence records ($N < 10$).

2.3. Environmental data

An initial set of environmental variables was downloaded from public databases and clipped to the study area (Table S3). Subsequently, each variable was depicted to the 12th level of the river network delineation defined in HydroRivers by Lehner and Grill (2013), which ensured concordance of variables' resolution. Because large-scale information on in-stream conditions is not currently available, this set of variables included correlates that have been widely used in modelling freshwater species (e.g., Filipe et al., 2002; Low et al., 2020; Yiwen et al., 2016), and intended to describe conditions that are known to influence the distribution of mussels and fish hosts, namely climate (Filipe et al., 2013a; Hastie et al., 2003), topography and hydrology (Filipe et al., 2002; Friedrichs-Manthey et al., 2020), geology and soil (Mcrae et al., 2004), and landcover and anthropogenic impacts (Amoatey and Baawain, 2019; Gillis et al., 2017; Maceda-Veiga et al., 2017).

Future climate conditions were obtained from downscaled CMIP6 projections as provided by WorldClim (Coupled Model Intercomparison Project Phase 6; Eyring et al., 2016). The future projections according to Weng et al. (2020) include three different Shared Socioeconomic Pathways of IPCC (SSPs) for 2050s (average 2041–2060) and 2090s (average 2081–2110): sustainability (SSP1–2.6), middle of the road (SSP2–4.5), and fossil-fuelled development (SSP5–8.5), upgraded from representative concentration pathways (RCPs) of a significant reduction in carbon emissions (RCP 2.6), a peak in carbon emissions in 2040 (RCP 4.5), and emissions continue to rise or business-as-usual (RCP 8.5), respectively. The average of eight global circulation models (GCMs) that have different assumptions for climate change was considered (BCC-CSM2-MR, CNRM-CM6-1, CNRM- ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0) to explicitly account for model uncertainties when predicting future species distributions (Thuiller et al., 2019), but a comparison between climate model projections can be consulted in Tebaldi et al. (2021). Climate variable values of each SSP and GCM were calculated as the weighted average of the total watershed area upstream of each stream reach, as defined in HydroRIVERS (Lehner and Grill, 2013), using the Network Toolkit RivTool v. 2.1. We assumed the remaining non-climatic variables will not change significantly during the future decades considered.

2.4. Model fitting

Choosing to include important biotic interactors as model predictors over an extensive collection of readily available environmental variables in correlative SDMs is not straightforward (Anderson, 2017; Dormann et al., 2018). However, the lack of important biotic variables may lead to underestimating climate change consequences for biodiversity (Araújo and Luoto, 2007; Bellard et al., 2012). Accordingly, disregarding fish hosts for predicting the impacts of climate change on mussels distribution was previously shown to lead to an overestimation of distributional ranges (da Silva et al., 2022). Because of that, we fitted two candidate models for each mussel species as follows: A) model ENV, only including environmental variables as predictors, and B) model ENV + FH, including both environmental variables and fish host estimated occurrences as predictors.

Prior to model building, we ensured that a maximum of $n/5$ environmental variables (where n is the number of presence records) were selected, to avoid overfitting that could result from the ratio between many predictors and small sample size (Fielding and Bell, 1997). As such, eight predictor variables were selected to each species per model. To do so, we ran Random forests (RF) (Valavi et al., 2021) using an initial set of variables (Table S3) and evaluated variable importance based on mean decreased accuracy. RF were chosen because they are widely used in ecology

(Valavi et al., 2021) and are usually able to identify variables that are good predictors of the response even when highly correlated with other variables (Cutler et al., 2007). From that, we removed the least contributing variables of highly correlated pairs and retained the variables that seemed ecological relevant for the species through visual inspection of variable response curves resulting from univariate models. For the final models, only the weakest correlated variables were kept (Spearman's correlation<0.7).

Fish hosts variables represented fishes' continuous probability of occurrences resulting from SDMs fitted to each fish species occurrence data. For each mussel species, we calculated the maximum probability of occurrence of a suitable fish host regardless of the identity of the fish species, and only that variable was used as a predictor in the mussels' models. This choice was made because some of the studied mussels are host generalists that can complete their life cycle in a wide range of fish species (Table S2). Consequently, including the probability of occurrence of all suitable hosts as additional variables would lead to model overfitting (Fielding and Bell, 1997).

Presence-absence data was available for mussels, while presence-only data was available for fish hosts. Species distribution models (SDMs) were built using an ensemble of tuned individual models: generalised linear models (GLM), generalised additive models (GAM), gradient boosting machines (GBM) and random forests down-sampled (RF) according to the findings of Valavi et al. (2022) and Zurell et al. (2020). Models were tuned using the R package ‘flexsdm’ v1.3.2 (Velazco et al., 2022), and details on algorithm tuning parameters and model implementation can be found on Table S4.

Due to the importance of limiting background extent to only include locations that are accessible to the species (Elith et al., 2011; Jarnevich et al., 2017; Merow et al., 2013), and because most fish are not able to disperse across river basins, pseudo-absences were drawn only from the main basins where each fish species was recorded (i.e., basins with confirmed presences). Up to ~25,000 pseudo-absences were selected, depending on the total number of streams within the main basin(s) with confirmed presences of fish hosts. A similar procedure was used for mussels, whereby absence records that fell outside species ranges were excluded from the analyses.

Data was split into calibration (70 %) and validation (30 %) and each model was calibrated 10 times using the R package ‘biomod2’ v4.2-1 (Thuiller et al., 2022). For each species, variable importance was evaluated using a permutation procedure whereby each variable was permuted 10 times. Models' performance and predictive ability was evaluated using the area under the receiver operating characteristic curve (AUC), kappa statistic and true skill statistic (TSS) (Fielding and Bell, 1997). Differences in the resulting model evaluation metrics of the ENV and ENV + FH models were compared using Wilcoxon signed-rank tests for related samples (Araújo and Luoto, 2007; Giannini et al., 2013). The predictions that resulted from each algorithm were combined in an ensemble model, including only individual models with ROC values above 0.7.

2.5. Ensemble forecasting

Ensemble models were used to predict consensus current and future distributions of mussels (Araújo et al., 2005). Future distributions were forecasted using eight GCMs and averaged to obtain a more accurate future species probability of occurrence. Forecasts of models fitted with the predictor datasets including information about fish host distributions were built using the maximum probability of fish hosts' presence projected for future climate conditions. Models' binary predictions were obtained through a reclassification of continuous occurrence probability model outputs using the threshold method that maximises the sum of sensitivity and specificity (Liu et al., 2016). Binary predictions were used to calculate changes in mussels' ranges as the proportion of streams defined by the 12th level of the river network delineation defined in HydroRivers by Lehner and Grill (2013) that were lost or gained as a result of future climate scenarios (Pearson and Dawson, 2003).

3. Results

3.1. Distribution modelling

Overall, candidate ensemble models performed very well in terms of predictive accuracy, discriminatory ability and agreement between models, and minor differences were found between the evaluation metrics of models ENV (i.e., only environmental variables as predictors) and ENV + FH (i.e., including both environmental variables and fish hosts predicted occurrences) (<0.08; Table 1). Wilcoxon signed-rank tests showed small but statistically significant differences ($p < 0.05$) between ten cross-validated evaluation metrics for some mussel species, although results were not consistent across species and evaluation metrics (Table 2). Specifically, the predictive accuracy of *A. anatina*'s model ENV + FH was significantly greater than the model ENV (Table 2). For *M. margaritifera*, model ENV + FH significantly improved AUC values over the model ENV, although differences in the remaining metrics were not significant (Table 2). Models ENV + FH significantly increased Kappa and AUC values for *U. tumidiformis*, but no significant differences were found in TSS (Table 2). Differences between models ENV and ENV + FH were not significant for *P. littoralis, U. delphinus* and *U. mancus* (Table 2).

Future ensemble model predictions showed that models ENV + FH predicted far greater losses in suitable habitats than models ENV for *A. anatina, M. margaritifera, P. littoralis* and *U. delphinus*, under all emission scenarios and time frames considered (Table 3). For *U. mancus* and *U. tumidiformis,* the differences between ensemble model predictions were almost negligible (Table 2). As such, and because small differences in performance between the two candidate models for each mussel were found (Tables 1 and 2), models ENV + FH were selected over models ENV for predicting current and future distributions to avoid the possibility of overpredicting future distributional ranges for most of the studied mussel species.

3.2. Current distribution

The projected distribution of *A. anatina* included almost the whole latitudinal and longitudinal ranges of the Iberian Peninsula, although the proportion of rivers and streams with high probability of occurrence was moderate and mostly corresponded to Iberian larger rivers (Fig. 1). Within the rivers of higher order, highly suitable habitats are expected to present mean temperatures above ~10 °C in the wettest quarter (Fig. S1). River order was largely the most important variable in explaining the distribution of *A. anatina*, followed by mean temperature of wettest quarter (Bio8), additionally to a small contribution of calcium carbonate content and the occurrence of fish hosts (Fig. 2).

Margaritifera margaritifera presented a narrow distribution, restricted to the north-western area of the Iberian Peninsula (Fig. 1). Maximum temperature of warmest month (Bio5) had the largest contribution for predicting the distribution of *M. margaritifera*, although forest cover extent and distance to river source were also important (Fig. 2). Highly suitable habitats are expected to mainly represent upstream areas near the river source,

Table 1
Freshwater mussels' ensemble models mean evaluation metrics. Models ENV were built including only environmental variables as predictors, and models ENV + FH including both environmental variables and fish host estimated occurrences as predictors. Kappa: Cohen's Kappa; AUC: area under curve of the receiver operating characteristic; TSS: true skill statistic.

	Model ENV + FH			Model ENV		
	Kappa	AUC	TSS	Kappa	AUC	TSS
Anodonta anatina	0.61	0.89	0.64	0.69	0.94	0.71
Margaritifera margaritifera	0.80	0.97	0.81	0.79	0.97	0.84
Potomida littoralis	0.66	0.94	0.71	0.65	0.93	0.70
Unio delphinus	0.77	0.96	0.77	0.79	0.96	0.79
Unio mancus	0.79	0.96	0.80	0.74	0.95	0.76
Unio tumidiformis	0.66	0.94	0.71	0.65	0.91	0.71

Table 2

Effects of including fish hosts predicted occurrences in freshwater mussels' distribution models. Values refer to the mean difference in ten cross-validated evaluation metrics for the 4 algorithms used in the ensembles between the ENV + FH and the ENV models. Positive values (+) indicate average increase, and negative (−) indicate average decrease. Values in bold report statistically significant differences ($p < 0.05$) in Wilcoxon signed-rank tests for related samples.

	Variation		
	Kappa	AUC	TSS
Anodonta anatina	**+0.05**	**+0.03**	**+0.06**
Margaritifera margaritifera	−0.02	**+0.02**	−0.02
Potomida littoralis	−0.02	−0.02	−0.03
Unio delphinus	−0.02	−0.01	−0.02
Unio mancus	+0.02	+0.04	+0.03
Unio tumidiformis	**+0.06**	**+0.05**	+0.04

with high forest cover and, more importantly, where maximum temperature conditions in the warmest month do not rise above ~27 °C (Fig. S2).

Potomida littoralis was projected to occur widely in the Iberian Peninsula, although a skewed distribution of highly suitable habitats in the east was noteworthy. In the west, this species was mostly confined to larger rivers (Fig. 1). River order and precipitation of the wettest quarter (Bio16) were the most important variables, although calcium carbonate content in the soil was also relevant (Fig. 2). Models predicted high habitat suitability in larger rivers (higher order), with decreasing precipitation levels in the wettest quarter, and particularly in areas with higher percentage of calcium carbonate content in the soil (Fig. S3).

Table 3

Expected loss and gain (%) of freshwater mussels' suitable niche distribution and respective range size differences between the current and future projections predicted by models ENV + FH and models ENV. Predictions were made for the 2050s and 2090s time frames under three climate change scenarios (sustainability [SSP1-2.6], middle of the road SSP2-4.5], and fossil-fuelled development [SSP5-5.8]).

		ENV + FH			ENV		
Time frame	Emission Scenario	Loss (%)	Gain (%)	Range change (%)	Loss (%)	Gain (%)	Range change (%)
		Anodonta anatina					
SSP1-2.6	2050s	24.6	24.2	−0.4	16.2	48.3	32.1
	2090s	22.4	28.2	5.8	14.9	53.5	38.7
SSP2-4.5	2050s	22.3	32.1	9.7	15.6	57.1	41.5
	2090s	19.7	47.0	27.3	16.5	82.6	66.2
SSP5-8.5	2050s	20.3	46.9	26.6	16.0	70.4	54.3
	2090s	10.4	107.3	96.8	8.7	149.8	141.1
		Margaritifera margaritifera					
SSP1-2.6	2050s	76.2	0.6	−75.5	54.3	10.5	−43.9
	2090s	76.0	0.6	−75.4	55.0	9.7	−45.3
SSP2-4.5	2050s	81.7	0.2	−81.6	60.4	10.0	−50.5
	2090s	96.1	0.0	−96.1	84.3	5.2	−79.0
SSP5-8.5	2050s	91.7	0.0	−91.7	72.8	7.0	−65.9
	2090s	100.0	0.0	−100.0	100.0	0.0	−100.0
		Potomida littoralis					
SSP1-2.6	2050s	15.9	2.0	−13.9	6.6	1.8	−4.9
	2090s	14.2	2.7	−11.4	6.1	2.2	−3.9
SSP2-4.5	2050s	14.2	3.5	−10.8	5.9	3.5	−2.5
	2090s	16.7	6.4	−10.4	7.2	6.2	−1.0
SSP5-8.5	2050s	16.7	4.9	−11.7	7.1	4.2	−2.9
	2090s	18.0	14.4	−3.7	7.0	20.8	13.9
		Unio delphinus					
SSP1-2.6	2050s	38.9	19.6	−19.3	17.2	12.9	−4.3
	2090s	40.1	19.4	−20.7	17.7	13.2	−4.5
SSP2-4.5	2050s	45.5	18.9	−26.7	17.2	13.9	−3.3
	2090s	55.1	13.9	−41.2	21.1	14.5	−6.6
SSP5-8.5	2050s	49.4	15.9	−33.5	19.8	14.0	−5.8
	2090s	72.9	15.1	−57.8	22.4	20.2	−2.2
		Unio mancus					
SSP1-2.6	2050s	59.8	6.7	−53.0	60.4	4.8	−55.7
	2090s	54.5	6.8	−47.7	53.0	5.7	−47.3
SSP2-4.5	2050s	60.6	7.8	−52.8	60.5	5.5	−55.0
	2090s	75.9	5.7	−70.2	77.1	3.4	−73.6
SSP5-8.5	2050s	72.8	5.7	−67.1	74.0	3.2	−70.8
	2090s	98.4	1.1	−97.2	99.5	0.2	−99.3
		Unio tumidiformis					
SSP1-2.6	2050s	97.2	0.0	−97.2	96.7	0.0	−96.7
	2090s	97.2	0.0	−97.2	96.6	0.0	−96.6
SSP2-4.5	2050s	97.9	0.0	−97.9	97.6	0.1	−97.5
	2090s	100.0	0.0	−100.0	100.0	0.0	−100.0
SSP5-8.5	2050s	99.9	0.0	−99.9	99.8	0.0	−99.8
	2090s	100.0	0.0	−100.0	100.0	0.0	−100.0

Unio delphinus was predicted to be widespread in the Iberian Peninsula, with highly suitable habitats mainly representing main Iberian Rivers (Fig. 1). Distribution range was mostly predicted by river order and, to a lesser extent, mean temperature of driest quarter (Bio9). Higher habitat suitability was predicted in larger rivers (higher river order), where temperatures in the driest quarter were not below ~20 °C (Fig. S4).

Unio mancus was projected to occur in the northeast of the study area and its distribution was mainly explained by temperature (Figs. 1 and 2). Highly suitable habitats mostly corresponded to areas of higher mean temperatures in the wettest quarter (Bio8) and lower temperature seasonality (Bio4) (Fig. S5).

Unio tumidiformis distribution was limited to a few sub-basins in the south of the Iberian Peninsula, and highly suitable areas were mostly predicted in the eastern part of its narrow distribution (Fig. 1). Mean temperature of driest quarter and (Bio9) was the most contributing variable for the predicted distribution of this species, followed by human footprint, slope, annual precipitation (Bio12), and river order (Fig. 2). Highly suitable habitats for this species were predicted to encompass areas with mean temperature conditions of up to ~25 °C in the driest quarter, low human footprint, gentle slope, and annual precipitation of less than ~550 mm (Fig. S6).

3.3. Future distribution

The future timeframes and emission scenarios considered in this study are expected to have substantial effects on the distribution of mussel species (Fig. 3). The most severe reductions were forecasted for *M. margaritifera, U. mancus* and *U. tumidiformis* (Fig. 3). Smaller contractions in the distributions of *P. littoralis* and *U. delphinus* were also predicted, whereas *A. anatina* could potentially expand its range (Fig. 3).

Specifically, the distribution of the suitable habitats of *A. anatina* in the 2050s was forecasted to be similar to current projections (Fig. 3). In the 2090s, an increase in suitable areas is expected, particularly for the scenario of fossil-fuelled development (Fig. 3). Mild losses of suitable areas are expected for all time frames and emission scenarios (Table 3). The range size of this species was forecasted to mostly expand due to the increased percentage gain (5.8–96.8 %) of suitable habitats that surpassed the loss (10.4–24.6 %) (Table 3). The distributional range seemed to increase under the middle of the road and fossil-fuelled development scenarios over the sustainability scenario, although new areas generally showed moderate suitability (probability of occurrence<0.8) (Table 3 and Fig. 3). New suitable habitats in the future were forecasted broadly across the whole study area (Fig. 4).

Margaritifera margaritifera future distribution is likely to contract to a few streams in the north of the Iberian Peninsula (Fig. 3). Losses between 76 % and 100 % of its current suitable habitats are expected (Table 3). Under the suitability scenario, losses of up to 76.2 % were predicted in the 2090s, while for the middle of the road scenario these increased to 81.8 % in the 2050s, and 96.1 % in the 2090s. Considering the scenario of fossil-fuelled development, this species was predicted to lose 100 % of suitable habitats in the 2090s (Table 3). Furthermore, models predicted negligible to no gains in suitable habitats (Table 3 and Fig. 4). The few habitats that are likely to remain suitable in future forecasts were restricted to the highest latitudes of its current distribution, although probability of occurrence decreased from current predictions (Fig. 3).

The distribution of *P. littoralis* was predicted to contract, and habitat suitability notably decreased throughout its distribution (Fig. 3). Between 14.2 % and 18.0 % of current suitable habitats are expected to be lost in the future, and 2.0 to 14.4 % of new suitable areas are expected to be gained (Table 3). Overall, range size was predicted to decrease between 3.7 % and

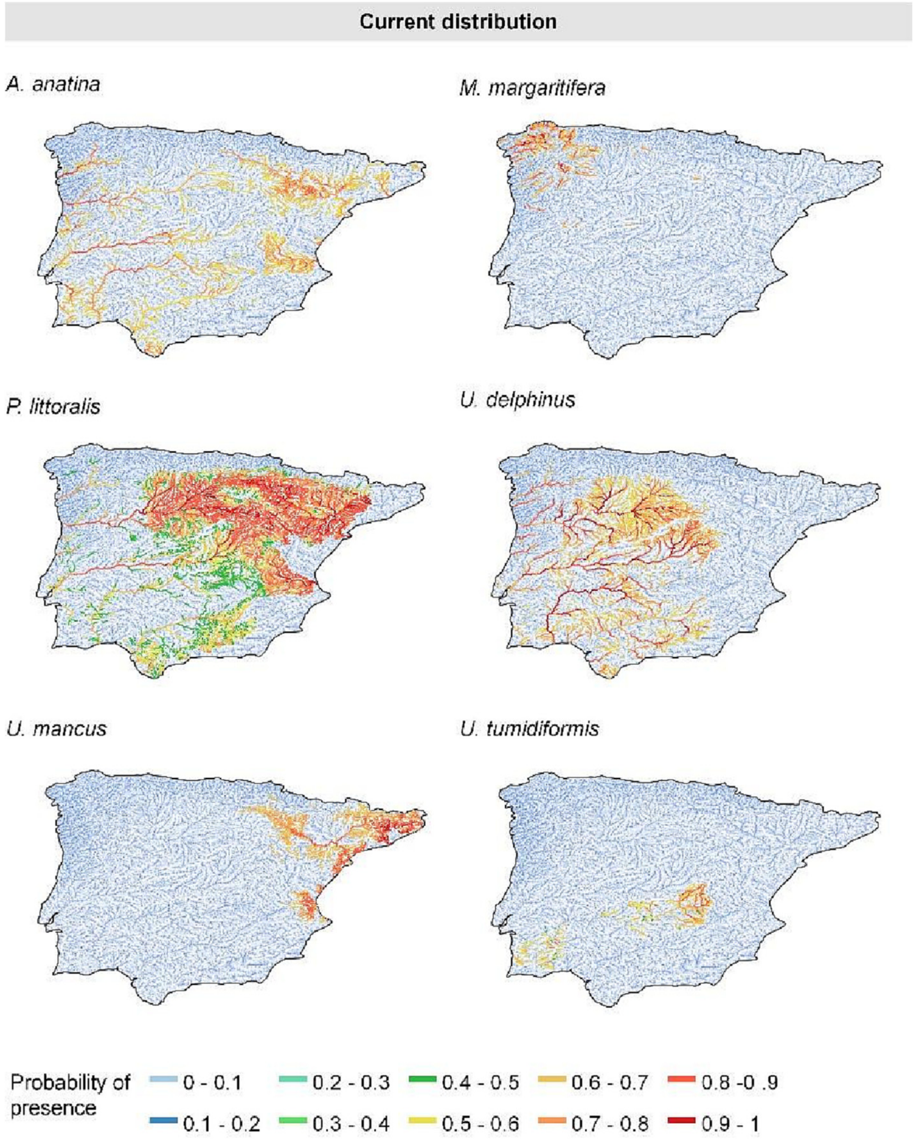


Fig. 1. Ensemble models projections of current distributions of six freshwater mussels (*Anodonta anatina*, *Margaritifera margaritifera*, *Potomida littoralis*, *Unio delphinus*, *Unio mancus* and *Unio tumidiformis*) in the Iberian Peninsula.

13.9 % in the future (Table 3). Higher losses were mostly predicted under the middle of the road and fossil-fuelled development scenarios (Table 3). Low to moderate probabilities of occurrence were predicted generally across its future range (Fig. 3). Most of its current distribution in the east of the study area is expected to remain suitable in future conditions (Fig. 4).

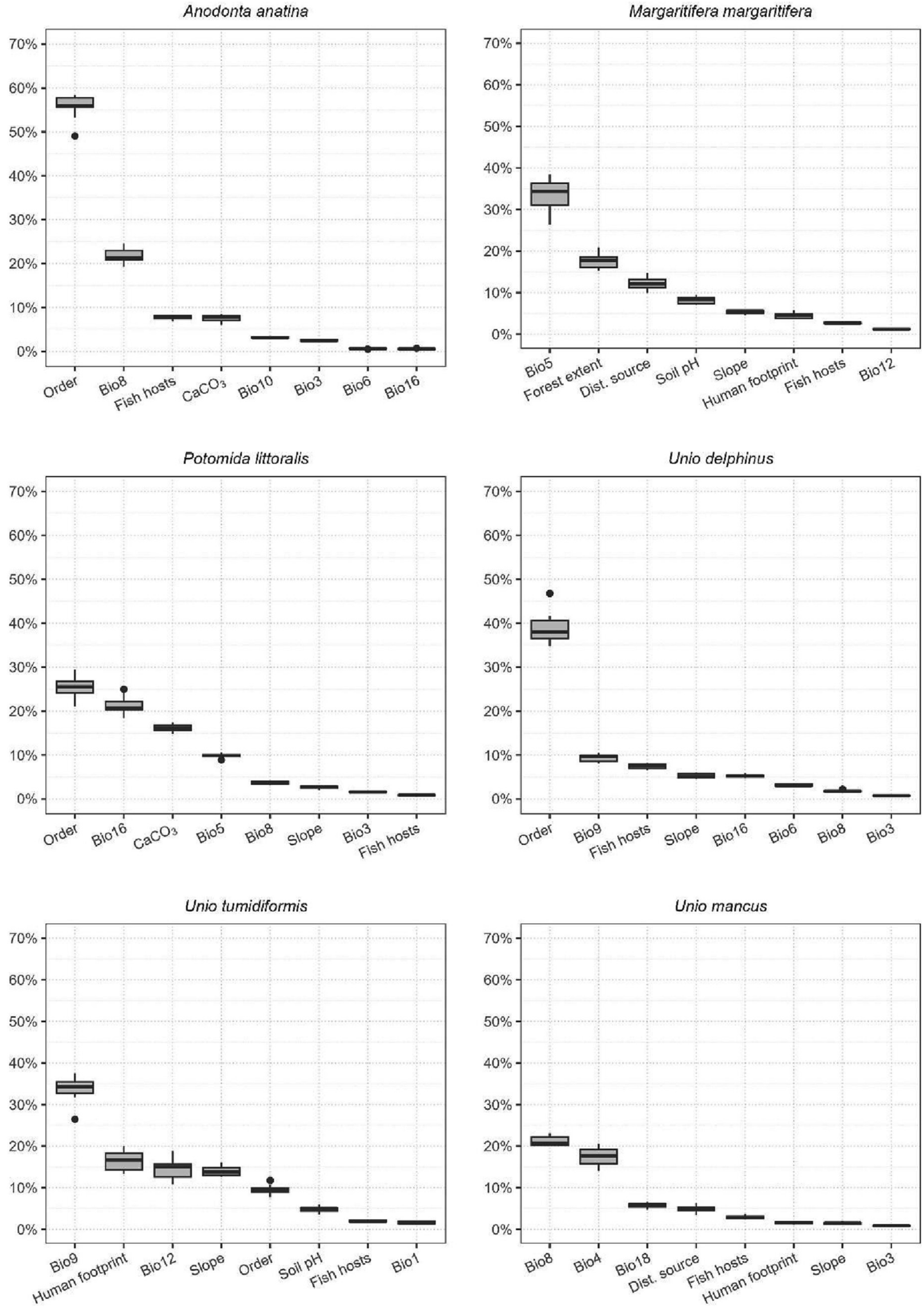
The distribution range of *U. delphinus* was forecasted to decrease in all time frames and emission scenarios, particularly in the 2090s under the fossil-fuelled development scenario (Fig. 3). From 38.9 % to 72.9 % of suitable habitats were predicted to be lost for this mussel (Table 3). Expected gains in suitable areas varied between 15.1 % and 19.6 %, which resulted in range losses between 19.3 % and 57.8 % (Table 3). Stable suitable habitats in the future were scattered within the current distribution of *U. delphinus*, and new suitable areas were mainly located north of its current distribution or near the coast (Fig. 4).

The future distribution of *U. mancus* is expected to decrease under all emission scenarios and time frames considered, but particularly in the 2090s under the fossil-fuelled development scenario, where this species is expected to nearly disappear from the Iberian Peninsula (Fig. 3). Accordingly, losses of suitable habitats are expected to vary between 53.0 % and 97.3 % (Table 3). Gains of 1.1 % to 7.8 % were predicted for this species, resulting in range losses between 47.7 % under the sustainability scenario and 97.3 % under the fossil-fuelled development scenario in the 2090s (Table 3). Habitats that were forecasted to remain suitable in the future were mostly located in the east of its current range (Fig. 4). Predicted gains in suitable habitats were mainly located in the northwest of current distribution (Fig. 4).

The largest contraction in distribution was predicted for *U. tumidiformis*, with losses of suitable habitats between 97.2 % and 100 % (Table 3). Suitable habitats were forecasted to be virtually lost for all emission scenarios and timeframes considered (Fig. 3). This mussel was forecasted to completely disappear in the 2090s under the middle of the road and fossil-fuelled development scenarios (Figs. 3 and 4). Models predicted no gains in suitable areas (Table 3 and Fig. 4). Only one to 25 streams are expected to remain suitable in the future, under the fossil-fuelled development scenario in the 2050s and sustainability scenario in the 2090s, respectively) (Fig. 4). These streams were confined to the southwest of its current distribution, although the probabilities of occurrence in these sites only varied between 0.5 and 0.7 (Fig. 3).

4. Discussion

Freshwater mussels are a diverse and remarkable group of aquatic molluscs responsible for important ecosystem functions and services (Lopes-



Anodonta anatina

Margaritifera margaritifera

Potomida littoralis

Unio delphinus

Unio tumidiformis

Unio mancus

Fig. 2. Variables selected for building ENV + FH ensemble models and respective percent contribution for explaining the distribution of Iberian freshwater mussels. Bio1: Annual Mean Temperature; Bio3: Isothermality; Bio4: Temperature Seasonality; Bio5: Maximum Temperature of Warmest Month; Bio6: Minimum Temperature of Coldest Month; Bio8: Mean Temperature of Wettest Quarter; Bio9: Mean Temperature of Driest Quarter; Bio10: Mean Temperature of Warmest Quarter; Bio12: Annual Precipitation; Bio16: Precipitation of Wettest Quarter; Bio18: Precipitation of Warmest Quarter; CaCO3: Calcium Carbonate content; Dist. Source: Distance to the most upstream location along the river network; Fish hosts: Maximum probability of occurrence of a suitable fish host; Forest extent: Forest Cover Extent; Order: River order (Strahler ordering system); Slope: Average terrain slope; Soil pH: pH in the soil.

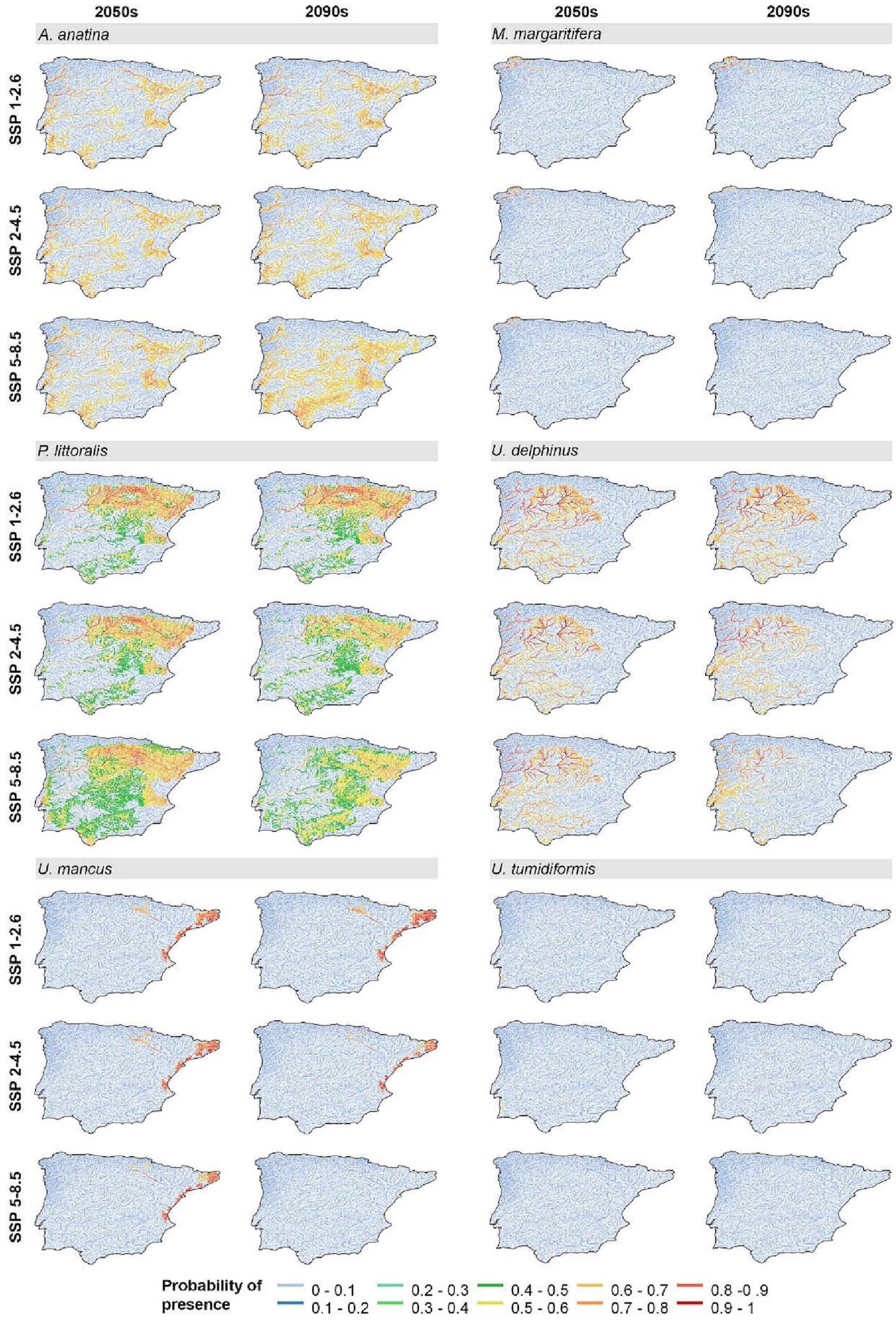


Fig. 3. Ensemble model results showing the future (2050s, 2090s) predicted distribution ranges of six freshwater mussels occurring in the Iberian Peninsula (*Anodonta anatina, Margaritifera margaritifera, Potomida littoralis, Unio delphinus, Unio mancus* and *Unio tumidiformis*) under three climate change scenarios (sustainability [SSP1–2.6], middle of the road [SSP2–4.5], and fossil- fuelled development [SSP5–8.5]).

Lima et al., 2017, 2018; Zieritz et al., 2022). In this study, we demonstrate the potential impact of future climate scenarios on freshwater mussel species in the Iberian Peninsula. The six mussel species investigated here show distinct potential distributions and the ability to cope with climate change. Overall, climate and topography were mainly responsible for shaping their distributions in the Iberian Peninsula. Interestingly, mussels' responses to environmental conditions and distributions are highly variable. *Anodonta anatina*, *P. littoralis*, and *U. delphinus* are generally

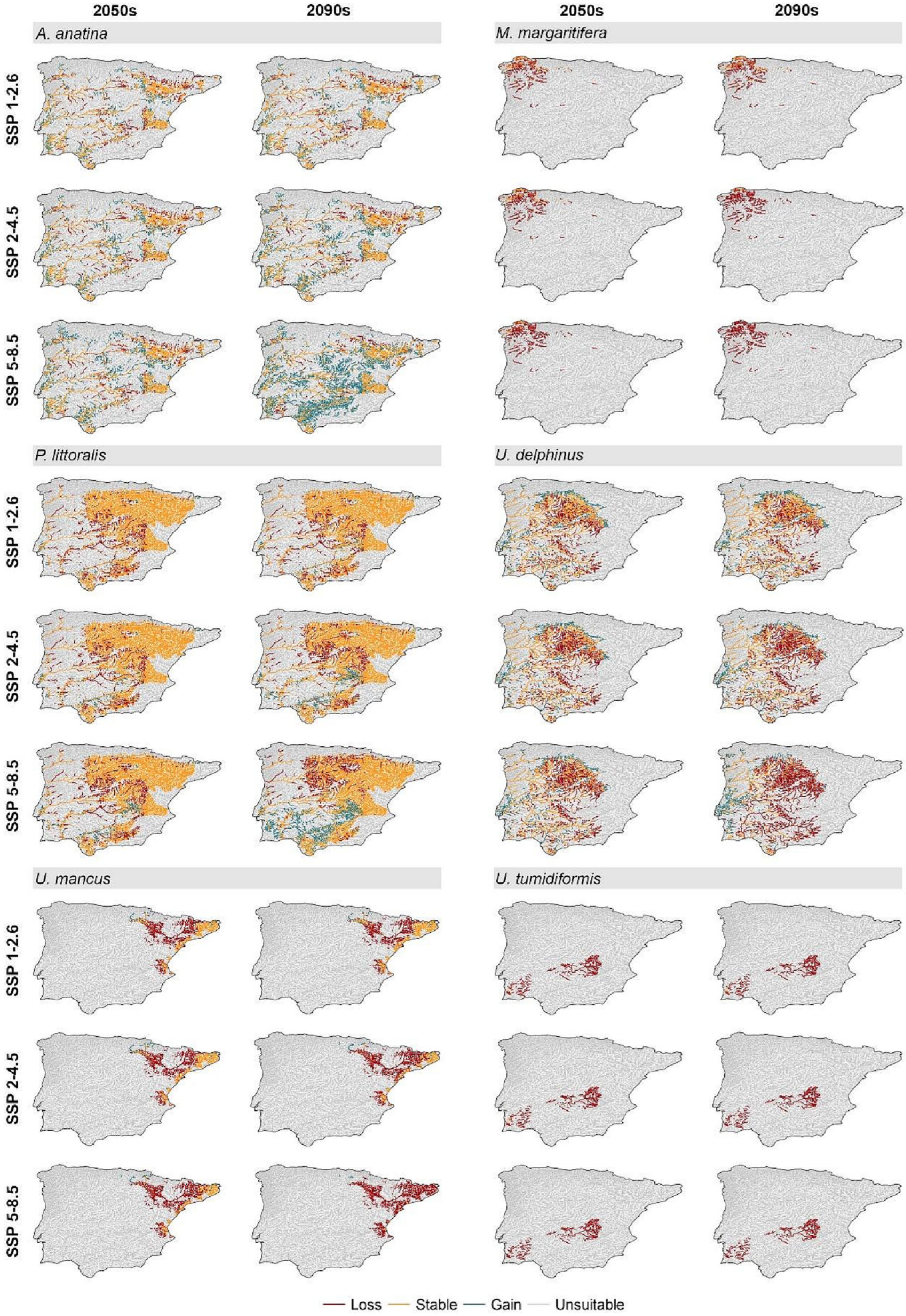


Fig. 4. Predicted changes in the suitable streams of freshwater mussels in the Iberian Peninsula (*Anodonta anatina*, *Margaritifera margaritifera*, *Potomida littoralis*, *Unio delphinus*, *Unio mancus*, and *Unio tumidiformis*) in future climate conditions. Predictions were made by model ENV + FH for the 2050s and 2090s time frames under three climate change scenarios (sustainability [SSP1-2.6], middle of the road SSP2-4.5], and fossil-fuelled development [SSP5-5.8]).

widespread, *U. mancus* is confined to the Mediterranean basins in the north, and *M. margaritifera* and *U. tumidiformis* present very small ranges in the north and south, respectively. Furthermore, climate change should have a massive impact on the future distribution of Iberian mussels, being responsible for the disappearance of many suitable habitats. Our findings showed that *M. margaritifera* in the north and *U. tumidiformis* in the south are likely to become the most affected species, closely followed by *U. mancus*. Additionally, milder but still substantial effects of climate change are expected for *A. anatina, P. littoralis*, and *U. delphinus*.

Margaritifera margaritifera and *U. tumidiformis* are recognized as habitat specialists with narrow distributions in the study area (Araujo et al., 2009; Reis and Araujo, 2009; Sousa et al., 2015). Endemic or rare species with restricted ranges may be more vulnerable to climate change, facing a greater risk of extinction (Bellard et al., 2012; Markovic et al., 2014; Urban, 2015). Accordingly, *U. tumidiformis* is expected to completely disappear during the next decades, regardless of the carbon emission scenario considered, while *M. margaritifera* may be confined to a few small northern streams as soon as 2050s. This was not surprising, given the poor conservation status and decreasing population trends already described for both species (Araujo, 2011a; Lois et al., 2014a, 2014b; Moorkens et al., 2017; Reis, 2010; Sousa et al., 2015; Varandas et al., 2013).

Even though *M. margaritifera* is widely distributed across Europe and North America, the Iberian Peninsula represents the southernmost range boundary of its distribution (Geist, 2010; Sousa et al., 2015). Within range boundaries, environmental conditions are often less than optimal, so any changes to habitat may promptly shift distributional edges to higher latitudes or altitudes (Thomas, 2010). Furthermore, this species is a habitat specialist that exclusively occurs in well-oxygenated, oligotrophic streams across its entire range (Geist, 2010; Lopes-Lima et al., 2017; Varandas et al., 2013). Accordingly, our findings support and highlight its vulnerability to high temperatures, with suitable habitats reduced to headwater streams shadowed by a dense riparian canopy (Bolotov et al., 2018; da Silva et al., 2022). Nonetheless, due to their small size, headwater streams may heat up quickly because of extreme climatic events such as droughts and heatwaves (Hastie et al., 2003; Sousa et al., 2018; Nogueira et al., 2021). Consequent water shortages in these systems will potentially hamper individuals' survival. These events are already common in the Iberian Peninsula but are expected to become more frequent in the next decades (Cresswell-Clay et al., 2022; Pereira et al., 2021), putting the last suitable habitats of *M. margaritifera* in Iberia at imminent risk of complete disappearance. Its endangered conservation status (Moorkens et al., 2017) calls upon urgent management to reverse decreasing Iberian population trends and preserve its genetic diversity (Perea et al., 2022b). For that, propagation, artificial rearing, and culturing of juveniles to increase the number of individuals in suitable areas should be accomplished. Furthermore, restoring riparian vegetation in areas with confirmed presences could help mitigate future temperature increases (Santos et al., 2015; Sousa et al., 2018).

Here we found that increasing temperatures, particularly in the summer, may be widely responsible for forecasted extirpations of *U. tumidiformis*, and likely be exacerbated by other human impacts (water abstraction, invasive species, changes in land use). This species is endemic to the southwestern Iberian Peninsula, with low density populations occurring in threatened temporary Mediterranean-type streams, where flow is reduced to isolated pools in the summer (Reis and Araujo, 2009). In addition, suitable climatic conditions are expected to vanish completely from its current range, increasing its vulnerability to other threats. *Unio tumidiformis* was listed as Vulnerable in the last assessment of the IUCN Red List of Threatened Species (Araujo, 2011a), but our results suggest that the current conservation status may be even poorer and in urgent need of an update. In this case, because restoring suitable habitats may be impossible (due to the expected lack of water in the summer), artificial rearing and assisted migration, i.e., translocating individuals to basins located at higher latitudes, may be the only alternative to prevent the imminent extinction of this species (Perea et al., 2022a). Nevertheless, the trade-offs of such a strategy should be carefully considered before implementation (due to, for example, the risk of moving parasites and diseases; Brian et al., 2021).

Unio mancus is restricted to France, Italy, and Spain and population declines have been described throughout most of its current range, mostly associated with pollution, habitat loss and invasive species (Araujo et al., 2009; Lopes-Lima and Seddon, 2014). We found that, in the Iberian Peninsula, these reported declines may soon be severely exacerbated by future changes in climate conditions, as this species is forecasted to suffer losses of at least 50 % in the next decades. Furthermore, if greenhouse gases emissions are not reduced very soon, *U. mancus* may be completely extirpated from this region. Accordingly, populations of Mediterranean river basins are particularly at risk, given their recognized restricted distributions and apparent weak potential to recover from past declines (Lopes-Lima and Seddon, 2014). Our results suggest the urgent need to further study the biological traits of *U. mancus* and update Iberian population status and trends (see for example recent extirpations in anthropogenic canals documented by Nakamura et al., 2023). Additionally, it is essential to analyse the geographic genetic structure of this species across its entire range to help developing specific conservation actions that could prevent the loss of genetic variability.

Unio delphinus is here predicted to suffer great distributional losses, particularly if human development falls within the business-as-usual scenario, although gains of new suitable areas could help mitigate climate change impacts. Currently listed as Near Threatened, significant range declines have been observed in the past decades (Araujo, 2011b; Araujo et al., 2009; Lopes-Lima et al., 2020). Our findings show that climate change will likely contribute to accentuate losses, potentially leading to the extirpation of many populations. Transforming current human development practices towards sustainability is essential to safeguard this species, additionally to the improvement of river conditions through the implementation of effective water management plans and efforts to minimize pollution (Araujo, 2011b).

The effects of upcoming climate conditions on *A. anatina* and *P. littoralis* seem to be less severe. We predict similar losses in suitable habitats for both mussels, although the future range change highly differs between the two species. *Potomida littoralis* expected gains in habitat suitability are generally moderate, which leads to the overall contraction of its potential distribution. *Potomida littoralis* is currently listed as Endangered and accelerated declines have been observed in Portugal and Spain (Lopes-Lima et al., 2014). Nevertheless, no conservation actions are known for this mussel, which lacks and needs legal habitat protection and restoration actions. Conversely, *A. anatina* is forecasted to gain a considerable percentage of suitable habitats under climate change, giving the impression that this species may expand its range in the future. If dispersion to new suitable habitats is attainable, mussel assemblages in the Iberian Peninsula may progressively become dominated by *A. anatina* over other native mussel species. Caution should be taken when interpreting this result, given the evidence for regional population declines and high geographic genetic differentiation of its populations across Iberia (Froufe et al., 2014; Lopes-Lima, 2014). For example, the extirpation of local populations (e.g. Ebro basin; Nakamura et al., 2023) could mean the loss of unique genotypes and genetic lineages within the Iberian Peninsula (Lopes-Lima et al., 2016). Habitat protection and further research, for example regarding genetically distinct populations and their autecology, is still required to define adequate conservation strategies.

The differences found between Iberian mussels are not surprising. *Anodonta anatina*, *P. littoralis* and *U. delphinus* are usually considered habitat generalists, whereby *A. anatina* and *U. delphinus* can occur in most river systems, and *P. littoralis* mainly occurs in middle to lower river sections (Araujo et al., 2009; Lopes-Lima et al., 2017, 2014). A broader physiological tolerance allows some species to survive, grow and reproduce in more productive environments with, for example, lower oxygen levels, when compared to other mussels, such as *M. margaritifera* (Lopes-Lima et al., 2017). But all species have physiological limits, outside which they cannot survive (Pecl et al., 2017). As climate conditions change and fall outside tolerance thresholds, species either adapt or shift their distribution to avoid extinction (Bellard et al., 2012; Hastie et al., 2003; Pecl et al., 2017). In this vein, mussels face great challenges to cope with climate change. First, their long lifespan makes it difficult to quickly adapt to a changing environment. (Hastie et al., 2003; Lopes-Lima et al., 2017; Markovic et al., 2014). Second, mussels' limited dispersal ability makes them highly dependent on fish hosts' movement to disperse (Modesto et al., 2018). Nevertheless, freshwater fish face many natural (i.e., due to the topographic and dendritic nature of river basins) and anthropogenic (e.g., dams, weirs, habitat degradation) barriers to dispersal, which may hinder their ability to reach new suitable habitats, when these are available at all (Filipe et al., 2013a; Modesto et al., 2018; Olden et al., 2010). The overall gains in suitable habitats predicted here can only be accounted for if fish hosts are able to reach those areas while transporting glochidia. Because of this, range changes found in this study may overestimate the potential distribution of Iberian mussels in the future. For example, *U. delphinus* distribution may contract up to 70 % if dispersal to suitable conditions is not attainable. Considering such strong constraints calls attention to the importance of investing funds in protecting and restoring current suitable habitats that are predicted to remain stable in the future. Additionally, the removal of barriers to increase river connectivity, and ensuring effective passage for fish can help conserve both mussels and their fish hosts (Hermoso et al., 2021; Hermoso and Filipe, 2021; Markovic et al., 2014).

Underestimating the potential impacts of climate change may be problematic for the future of biodiversity (Bellard et al., 2012). Here, we believe that we have partly considered this issue in a novel and innovative way by including the distribution of fish hosts to predict the distribution of mussels. Accordingly, suitable habitat losses were far greater when models included the biotic predictor for most mussel species. Improved geographic projections of *M. margaritifera* in Europe upon adding the distribution of fish hosts were already found by da Silva et al. (2022). These findings support the hypotheses that biotic predictors should be considered when evaluating the potential impacts of climate change on species' distributions, particularly when highly specific or specialised interspecific interactions occur, for example when one species needs another to survive. However, the importance of considering biotic interactions should be further addressed, since recent studies highlight that losing biotic interactions as a result of global change may weaken community resilience, severely damaging the integrity of ecological networks (Strona and Bradshaw, 2022).

Despite our efforts to achieve accurate predictions of distributional ranges, our findings may still be overestimating the future distribution of mussels in the Iberian Peninsula because our models did not consider the impacts of other threats to freshwater mussels and their fish hosts. These species are facing a multitude of threats, namely habitat loss and fragmentation, pollution, and biological invasions, which sometimes may have synergistic effects, potentially exacerbated by climate change (Bellard et al., 2012; Dudgeon, 2019; Gallardo and Aldridge, 2013; Reid et al., 2019; Sousa et al., 2020; Sousa et al., 2023). Furthermore, considering climate change effects on early life stages (i.e., glochidia and juveniles) that are more sensitive to warming temperatures remains challenging (Pandolfo et al., 2010; Weiskopf et al., 2020), but should be a future avenue of research. On the other hand, fish species used in this study included potentially important hosts, but not all were previously tested for host compatibility with *A. anatina*, *P. littoralis*, *U. delphinus,* and *U. mancus*. We assumed that congeneric fish species would all similarly produce viable juvenile mussels (Table S2). From this assumption, the biotic predictor included in the mussels' models was calculated as the maximum probability of presence of a suitable fish host, regardless of the identity of the fish species. However, we acknowledge that we may have included fish that are not suitable hosts for these mussels and, consequently, mussels' distribution may still be overestimated.

Due to the restricted distributions of the Iberian mussels that were not investigated here, our results suggest similar, or even harsher, effects of climate change are likely for *P. auricularius*, *U. gibbus*, *U. ravoisieri*, and *A. cygnea*. Further concerns arise when considering fish hosts population trends. In the Iberian Peninsula, many freshwater fish species are declining due to the same threats as described above for freshwater mussels (e.g. habitat loss and fragmentation, pollution, water demands, climate change and the spread of non-native species; Clavero et al., 2017; Costa et al., 2021; Garcia-Raventós et al., 2020; Maceda-Veiga, 2013; Maceda-Veiga et al., 2017; Anastácio et al., 2019). For mussels, the impact of these threats is amplified, by directly affecting their populations, but also indirectly by impacting their fish hosts (Modesto et al., 2018). In summary, the above-mentioned impacts, the inability of non-native fish species to be effective hosts (Douda et al., 2013; Lopes-Lima et al., 2020), in addition to the impact that they have on fish host populations, stand as important challenges for the conservation of mussels.

This study warns of the massive impact that climate change will have on freshwater mussels. Current legal conservation actions and networks of protected areas do not seem sufficient to reverse the decreasing trends of many mussels, even for the already Endangered *M. margaritifera*, which has been receiving most of the research and conservation funding among European invertebrates (da Silva et al., 2022; Mammola et al., 2020). Additionally, similar impacts are expected very soon for several other species across the Mediterranean region. We highlight that, beyond the loss of irreplaceable species and related intrinsic value of biodiversity, the disappearance of mussel species may jeopardise the maintenance of important ecosystem functions and services, namely water purification, nutrient cycling, and provision of habitat for other species (Ilarri et al., 2018). Disrupting these processes can have major cascading effects on other organisms and ultimately on human well-being (Vaughn, 2018; Zieritz et al., 2022). Furthermore, not only distributional losses, as predicted here, are expected, but also severe decreases in the abundance of these species within climate refugia that will further imperil the above-mentioned ecosystem functions and services across large areas.

Anticipating the effects of climate change on species distributions is critical to alert society and inform policy decisions and proactive conservation actions to ensure the persistence of populations, species, and healthy ecosystems. The conservation of freshwater ecosystems demands immediate and combined local, regional, and international efforts, including the protection of critical areas, the implementation of adequate management measures, and the promotion of sustainable practices to ensure the well-being of generations to come.

5. Conclusion

In this study we found that future climate change is expected to lead to the disappearance of many suitable habitats for Iberian mussels. Accordingly, species with already restricted distributions and poor conservation status within our study area seem to be on the brink of extinction. Simultaneously, widespread species may still experience significant declines that could reduce genetic variability and/or push them to the forefront of becoming threatened. We also showed that including the distribution of fish hosts in our models to predict the distribution of mussels lead to greater predicted losses of suitable habitats. As such, we suggest that taking into account species interactions in the modelling of species distribution that involve obligatory interactions is essential to avoid underestimating the effects of climate change. Conservation of freshwater mussels (and their fish hosts) in the Mediterranean Region poses many challenges and several management measures must be taken into consideration. These include protecting and restoring habitats, especially those that are currently suitable and projected to remain so in the future, but also the implementation of species-specific management and legal protection. Additionally, artificial propagation and assisted migration may be considered for species that are more prone to extinction.

CRediT authorship contribution statement

Janine P. da Silva: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization. **Ronaldo Sousa:** Conceptualization, Validation, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Duarte Vasconcelos Gonçalves:** Conceptualization, Validation, Writing – review & editing, Investigation. **Rafael Miranda:** Validation, Data curation, Writing – review & editing, Investigation. **Joaquim Reis:** Validation, Data curation, Writing – review & editing, Investigation. **Amílcar Teixeira:** Validation, Writing – review & editing, Investigation, Funding acquisition. **Simone Varandas:** Validation, Data curation, Writing – review & editing, Investigation, Funding acquisition. **Manuel Lopes-Lima:** Conceptualization, Validation, Investigation, Data curation, Writing – review & editing, Funding acquisition. **Ana Filipa Filipe:** Conceptualization, Validation, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

Data will be made available on request.

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.

Acknowledgments

This work was supported by the Portuguese Foundation for Science and Technology (FCT) and the European Social Fund through the North Portugal Regional Operational Programme through a doctoral Grant to J.S. (SFRH/ BD/146492/2019) and under Stimulus of Scientific Employment contract to MLL (2020.03608.CEECIND), DVG (2020.03848.CEECIND), and to AFF (2020.03872.CEECIND). FCT through national funds also supported this research under the project EdgeOmics - Freshwater Bivalves at the edge: Adaptation genomics under climate-change scenarios (PTDC/CTA-AMB/3065/2020). Additional strategic funding was provided by FCT UIDB/04423/2020 and UIDP/04423/2020. Fish data were collected under the project Updating of the national inventory and evaluation of the conservation status of Iberian fish (PRCV00858) funded by the Fundación Biodiversidad of the Ministry for Ecological Transition and the Demographic Challenge of Spain. Mussel data was partially obtained under the project POA 1.100021 (Documentos Estruturantes) of the Instituto da Conservação da Natureza (Portugal).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163689.

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