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# Climate-driven range expansion of the invasive silver-cheeked toadfish (*Lagocephalus sceleratus,* Gmelin 1789) in the Mediterranean: modelling habitat suitability

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## Abstract

Rates of alien species introductions in European waters continue to increase rapidly. As a fundamental concern for the European Commission, the identification of novel and potential Invasive Alien Species (IAS) in the region is essential to realise implementation of current EU regulations. The silver-cheeked toadfish, *Lagocephalus sceleratus*, has recently been identified as a significant threat to local biodiversity, fisheries, and human health in the region. In order to assess the potential for further range expansion, and to support potential mitigation strategies for this species, we employed species distribution models (SDMs) to assess the past, current and future habitat suitability of the silver-cheeked toadfish in Europe. Species distribution models (SDMs) indicate that habitat suitability for *Lagocephalus sceleratus* will increase in the Eastern Mediterranean, the Adriatic and Ligurian Seas, and the Strait of Sicily, extending toward the North African coast under a realistic climate scenario. Additionally, rising temperatures between 2000 and 2020 possibly enhanced the species' migration through the Suez Canal into the Mediterranean Sea, which had remained uncolonized since its opening in 1863 until the first record of this species presence in 2003. Given the establishment and rapid expansion of the silver-cheeked toadfish in the Mediterranean, complete eradication is no longer feasible, necessitating a shift toward adaptive management and mitigation strategies. Key priorities include public education to reduce poisoning incidents, support for the fisheries sector through technological and financial measures, and the promotion of collaborative governance among scientists, fishers, and policymakers.

**Keywords:** Range expansion; Geographical distributions; Invasive species; silver-cheeked toadfish; Species distribution modelling; machine learning.

## Introduction

Invasive alien species (IAS) are widely recognised as one of the most significant threats to biodiversity, with harmful and often far reaching consequences for native communities, and the potential to cause irreversible ecological and economic damage (Galil, 2007; Grosholz, 2002; Katsanevakis *et al.*, 2014a; Otero *et al.*, 2013; Simberloff, 2013; Tsiamis *et al.*, 2020).

Ecological impacts range from individual species interactions, resulting in reduced fitness for native species to changes in community composition, habitat structure, population decline, local extinctions, and changes in ecosystem functioning (Blackburn *et al.*, 2014; Giangrande *et al.*, 2020; Katsanevakis *et al.*, 2014a).

Although the economic impacts of IAS are not always easy to assess (Courchamp *et al.*, 2017; Vilà *et al.*, 2010), it is understood that many species impede the provision of ecosystem services, including food provision, recreation and tourism (Katsanevakis *et al.*, 2014b). Aquatic IAS are estimated to have cost over US$345 billion to the global economy (Cuthbert *et al.*, 2021).

The rate of IAS introductions continues to increase as a result of globalization and increasing anthropogenic activities, including fisheries, aquaculture, shipping, and trade (Ojaveer *et al.*, 2018). European marine environments are thought to be among the worst affected, hosting approximately 1400 species (Tsiamis *et al.*, 2020), with more expected to invade and become problematic in the region in the near future (Tsiamis *et al.*, 2018). Climate change is thought to further exacerbate these invasions through species range shifts, facilitation of new introductions, and altered effectiveness of control measures, especially combined with increasing trade and expanding global transport networks (Hellmann *et al.*, 2008). More specifically, climate change is known to facilitate range increases in some species; for example, the Pacific Oyster, *Crassostrea gigas*, the Asian club tunicate, *Styla clava* (Cook *et al.*, 2013) and the comb jelly, *Mnemiopsis leidyi* (Oliveira, 2007). However, within Europe the effects of climate change on ongoing and potential invasions is complex and thus improving knowledge on potentially harmful species and their current and future distributions, based on climate predictions can help to inform decision making (Townhill *et al.*, 2017).

The effective management of marine invasive species has only been achieved with early detection and rapid management responses (Giakoumi *et al.*, 2019). Furthermore, given the known and potential future impacts of invasive species in Europe, their mitigation has become an important variable to address in management and policy decisions (Giangrande *et al.*, 2020). As a result, policy instruments including the Convention on Biodiversity (CBD) and the European Commission's Marine Strategy Framework Directive (MSDF) aim to enhance the protection of marine ecosystems (Outinen *et al.*, 2024) by providing recommendations on integrating invasive species into their marine management strategies (Tsiamis *et al.*, 2021). The inclusion of specific invasive species descriptors and indicators have created national-level obligations (Tsiamis *et al.*, 2019) and have led to increased scientific attention aiming to identify presence and explore impact and potential mitigation in the region (Zenetos & Galanidi, 2020).

Of the large numbers of non-indigenous species, some that have not yet become fully established in the region are already impacting European waters (Tsiamis *et al.*, 2020). The silver-cheeked toadfish, *Lagocephalus sceleratus*, for example, is a predatory species currently presenting substantial challenges for fishermen, consumers, and ecosystems (Sabatino *et al.*, 2024; Ulman *et al.*, 2022; Ünal *et al.*, 2015). Native to the Indo-Pacific the species has been observed in shallow waters in areas outside its natural range, including Mozambique and the Red Sea (Akyol *et al.*, 2005) and was first reported in the Mediterranean Sea in 2003 (Akyol *et al.*, 2005). The species is regarded as a top predator in the eastern Mediterranean (Ulman *et al.*, 2022), thereby posing a threat to European marine biodiversity, including local crustaceans, fish, and cephalopods (Ulman *et al.*, 2022). Predation has been reported only scarcely for its introduced range, with juvenile specimens found in the stomach contents of garfish (*Belone belone*), common dolphinfish (*Coryphaena hippurus*), and of adult silver-cheeked toadfish in the Mediterranean (Ulman *et al.*, 2021). However, in Europe, adult specimens have only been documented being preyed upon by loggerhead turtles (*Caretta caretta*) (Ulman *et al.*, 2021). The scarcity of natural enemies for *L. sceleratus* is attributed to its robust defence mechanisms (Ulman *et al.*, 2021). The species is capable of inflating as a defence mechanism, which involves pumping water into its stomach to increase its size and asphyxiate its predators (Ulman *et al.*, 2021). In addition, the species is highly poisonous as it has high levels of tetrodotoxin (TTX) in its tissues including its muscles, skin and specific organs.

High levels of TTX also pose a threat to humans. So far consumption of the species in Europe has resulted in five reported fatalities (Ulman *et al.*, 2021). Furthermore, TTX levels in silver-cheeked toadfish have been linked to elevated levels in multiple marine organisms, such as the blue mussel (*Mytilus edulis*), which is consumed by humans (Sabatino *et al.*, 2024). Prior to the 21st century, the presence of TTX in marine organisms was not considered a threat in temperate regions; however, the introduction of the silver-cheeked toadfish in these areas has led to a significant increase in TXX levels in blue mussel (Sabatino *et al.*, 2024). Moreover, the economic losses experienced by fishermen are attributable to the damage the species inflicts on fishing gear, as they bite and cut-off parts of the nets (Ünal *et al.*, 2015). Consequently, the presence of the silver-cheeked toadfish has the potential to exert a detrimental influence on ecological, socio-economic, and health-related aspects of the environment and human well-being.

In order to effectively manage the impact of this invasive species, it is imperative to understand its current and potential distribution in European marine ecosystems. Species distribution models (SDM) can be utilized to map the species' habitat suitability by modelling occurrence records and gridded environmental parameters such as pH, temperature, and nutrient levels (Marx & Quillfeldt, 2018; Miller, 2010). Such models can be based on various statistical and machine learning algorithms (Marx & Quillfeldt, 2018). SDMs have been used to predict the habitat suitability of different marine fish and crustaceans (Bond *et al.*, 2011; Weterings *et al.*, 2025; Zhang *et al.*, 2019, 2020a). Panzeri *et al.* (2024) used species distribution models to project the future habitat suitability of fish and other demersal species in the Adriatic and Ionian seas, combining various modelling algorithms and concluding that several significant commercial species are projected to migrate northward under changing climatic conditions (Panzeri *et al.*, 2024). For silver-cheeked toadfish, such models have not yet been developed. Here, we aimed to model habitat suitability of this species in Europe. Known occurrences within its invasive range, its current habitat suitability, and its habitat suitability under a realistic climatic scenario were mapped using species distribution models based on 4 different algorithms: maxent, support vector machine, gradient boosting machines and random forest.

## Methods

### *Occurrence records*

All occurrence data (n=3,902) were retrieved from the Global Biodiversity Information Facility (GBIF, 2025). These data included global records of the species' observations with concerning coordinates and additional information (GBIF, 2025). Records from both the native and invasive range of the species were included to fully capture the entire environmental tolerance range for the species. The data were filtered to include only field observations and exclude collection records. Inaccurate coordinates were identified and removed to ensure that each record fell within the correct raster cell. Coordinates were considered inaccurate if they had less than three decimals in the WGS84 coordinate system. Additionally, records falling outside the extent of the environmental layers were removed.

Spatial bias is common in occurrence data and, if not properly addressed, can lead to overfitting (Boria *et al.*, 2014; Fourcade *et al.*, 2014; Gaul *et al.*, 2020). Spatial bias arises when certain areas are densely sampled while others are under sampled, as was seen in our occurrence data, with a heavily sampled native range compared to a sparsely sampled invasive range. However, factors such as sample size and model choice have been shown to exert a greater influence on predictive performance than spatial bias alone (Gaul *et al.*, 2020). The most effective way to remove sampling bias is through systematic sampling across the species' entire range (Fourcade *et al.*, 2014). Nonetheless, this approach is often unrealistic and costly, particularly given the vast amount of occurrence data already available in repositories such as GBIF and Observation.org. To reduce overfitting, we applied a robust spatial filter with a grid size of 0.2 × 0.2 degrees, which removed a substantial number of occurrence points from the densely sampled native range and only few points from the sparsely sampled invasive range. Spatial filtering can improve model performance as long as the remaining sample size is sufficient (Lamboley & Fourcade, 2024). Caution is advised when applying stringent filters to small datasets. In our case, the sample size remained relatively large after filtering. The final set of occurrence records for analysis comprised 780 records of which 41 records were from its invasive range and 739 from its native range (Fig. 1). Due to the unavailability of true absence data, we used pseudo-absence points (n=1,000). Unlike true absence points, which represent environments where the species does not occur, pseudo-absence points represent the available environment within the study area. When combined with the environmental range covered by the occurrence records, they can be used to model suitable versus unsuitable habitat. A thousand randomly distributed pseudo-absence points were generated in ArcGIS Pro.

### *Environmental data*

All environmental data were retrieved from Bio-Oracle version 3.0 (Bio-Oracle, n.d.). Bio-Oracle provides a substantial number of climatic variables representing the period from 2010 to 2020. These data are modelled using both in situ and remote sensed data and were downloaded as raster layers with a cell size of 0.05 degrees. Five specific environmental variables were selected based on the biological traits of the silver-cheeked toadfish and previous research on species distributions in marine environments. These environmental variables represent the conditions at the surface of the ocean. Bathymetry (m) was included as one variable because the species is usually found in shallow waters (Akyol *et al.*, 2005). Mean ocean temperature (°C) was included because temperature is known to strongly affect the species' spawning behaviour (Ulman *et al.*, 2021). In addition, winter temperatures are often limiting a species range (Qian *et al.*, 2022) therefore the long term minimum ocean temperature (°C) was also added. Given that the majority of toadfish species inhabit the marine environment, while some species inhabit both fresh and brackish waters, salinity (PSS) was included as a variable to account for the potential variation in salinity preferences across species (Ulman *et al.*, 2021). Final-

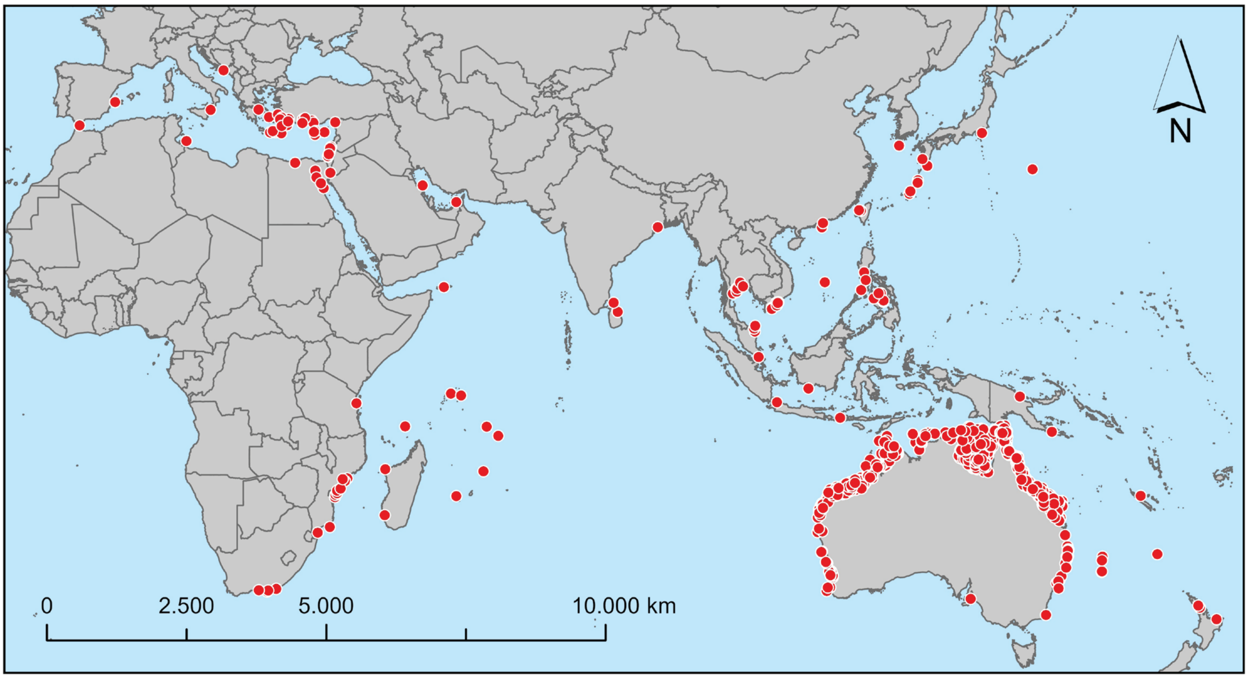

***Fig. 1:*** Red dots represent occurrence records of silver-cheeked toadfish that were retained after rigorous filtering. In the bottom right, along the coast of Australia (native range), occurrence records were still very dense compared to other regions.

ly, mean primary productivity was included as a proxy for food availability. The efficacy of these five layers in studying fish distributions in European waters has been previously demonstrated (Schickele *et al.*, 2021). To assess collinearity among environmental variables, we calculated Variance Inflation Factors (VIFs) using the car package in R. Variables with VIF values greater than 3 were removed from the analysis (Weterings *et al.*, 2025), which resulted in the removal of mean temperature. In addition to climatic variables representing current environmental conditions, we employed forecasted environmental data for the period 2030–2040 and historical data for the period 2000–2010. These datasets were also obtained from Bio-Oracle v3.0. These forecasted data are modelled using complex models that incorporate changes in Earth systems, greenhouse gases, and socioeconomic factors and are known as the Shared Socioeconomic Pathways (SSP). These data are provided for a variety of climate scenarios. For the purposes of this study, the SSP 4.5 was selected as the most likely scenario (Huard *et al.*, 2022).

### *Species distribution modelling*

Species distribution models were built using the SDM, Wallace R and caretSDM packages (Naimi & Araújo, 2016) in RStudio (version 2024.04.2) built on R version 4.4.1 (R Core Team, 2024). We built SDMs using four modelling algorithms namely MaxEnt, Support Vector Machine (SVM), Random Forest (RF) and Gradient Boosting Machines (GBM). Hyperparameters for these machine learning algorithms were tuned using caretSDM and Wallace R (for MaxEnt) and model selection was based on the accuracy, which is a measure for the proportion of correctly classified presence/absence predictions. The MaxEnt model was tuned to a beta multiplier of 0.5 and used hinge, product, linear, and quadratic feature classes. The random forest model was tuned to 1,000 trees with one variable tried at each split (mtry = 1). The gradient boosting machine model was tuned to 50 trees, a shrinkage rate of 0.1, an interaction depth of 7, and a minimum of 10 observations per terminal node. The support vector machine model was tuned to a sigma of 2 and a cost of 1. We ran five repetitions for each model -s using a fivefold split of the occurrence data into training data (80%) and testing data (20%) for cross-validation (Zhang *et al.*, 2020b). Results from these repetitions were averaged resulting in a single output.

In species distribution modelling, the Area Under the Curve (AUC) is a commonly used indicator of a model's predictive performance and often used for model weighing in ensemble models. The AUC discriminates between presence and background points but does not indicate the magnitude of differences in suitability scores. It can sometimes be inflated depending on the spatial distribution of points, the size of the study area, or the dominance of a single variable within the model, as these factors can make separation of the modelled environment relatively easy (Elith & Graham, 2009; Lobo *et al.*, 2008; Merow *et al.*, 2013). Instead of the AUC, we used the Continuous Boyce Index (CBI) for model assessment and weighing. The CBI measures predictive performance by assessing differences in suitability scores (Sorbe *et al.*, 2023). CBI values range between –1 and 1, where positive values indicate a strong correlation between predicted suitability and presences, values near zero indicate random predictions, and negative values indicate performance worse than random.

In addition, we calculated the standard deviation of the predicted values across all repetitions and cross-validation folds in order to provide a spatial overview of model uncertainty, which allows to detect unstable or overfit regions and where caution is needed with interpretation. The response of silver-cheeked toadfish to environmental predictors was visualized using response curves. These response curves were plotted based on the response of silver-cheeked toadfish to the range of sample values for the four predictor variables. We plotted mean curves with confidence intervals based on all 25 model runs for each modelling algorithm. Variable importance was calculated using a permutation-based approach, where each predictor variable's values are randomly shuffled to assess the resulting decrease in model performance. The magnitude of performance loss after permutation reflects the relative contribution of each variable to the predictive accuracy of the model.

## Results

All models demonstrated good predictive power, with all CBI scores higher than 0.6 (Table 1). The MaxEnt model exhibited the highest predictive power followed

**Table 1.** Evaluation metrices for all four models: CBI, TSS and deviance (dev.). The last four columns give the variable importance for long term minimum temperature (Temp.), mean salinity (Sal.), total primary production (Prim.) and bathymetry (Bathy.)

| Model | CBI | TSS | Dev. | Temp. | Bathy. | Sal. | Prim. |
|---|---|---|---|---|---|---|---|
| Maximum Entropy | 0.907 (0.07) | 0.96 | 0.45 | 84.5% | 4.1% | 0.0% | 0.0% |
| Gradient Boosting Machine | 0.874 (0.09) | 0.96 | 0.15 | 94.2% | 2.0% | 1.1% | 0.1% |
| Random Forest | 0.874 (0.06) | 0.97 | 0.14 | 56.0% | 9.2% | 1.2% | 1.5% |
| Support Vector Machine | 0.693 (0.17) | 0.96 | 0.18 | 61.0% | 21.1% | 2.9% | 3.8% |

by the random forest model. Nonetheless, all models showed similar responses to the predictor variables. Variable importance across models differed in percentages (Table 1), but for all models the long term minimum temperature was the most important variable followed by bathymetry. Whereas mean salinity and primary production were unimportant in all models reflecting consistency among models. For long term minimum temperature and bathymetry the response curves were also comparable (Fig. 2). The data indicated that the species was primarily observed in shallow waters, with a median depth of 37 meters (IQR = 35), and in areas with a median long term minimum temperature of 23°C (IQR = 3.0°C).

The MaxEnt model showed the least variation across the different runs, with no areas exhibiting high uncertainty, as indicated by low standard deviations (<10%) mapped throughout the study area (Fig. 3 A). The RF model also displayed minimal variation in predictions across regions (Fig. 3C). In contrast, the GBM (Fig. 3B) and especially the SVM (Fig. 3D) models revealed greater inconsistencies in specific regions –particularly the eastern Mediterranean. These regions generally showed lower habitat suitability (Fig. 4), suggesting that the observed inconsistencies are unlikely to result in overestimations of habitat suitability. These differences are also reflected in the response curves of the SVM and GBM models, which showed more irregular patterns for the variables salinity and primary productivity (Fig. 2). The ensemble model produced predictions closely aligned with those of the MaxEnt and RF models (Fig. 5b).

When comparing the three time periods, habitat suitability has remained mostly stable in the larger Mediterranean over the past two decades. However, a strong increase was observed in the region surrounding the Suez canal and the coastal areas of the Red Sea (Fig. 5). Projections for the next 20 years indicate a further increase in habitat suitability throughout the Mediterranean Sea and in particular the Eastern Mediterranean basin, parts of the Adriatic sea, the Ligurian Sea, and south of Sicily (Fig. 5 D-E).

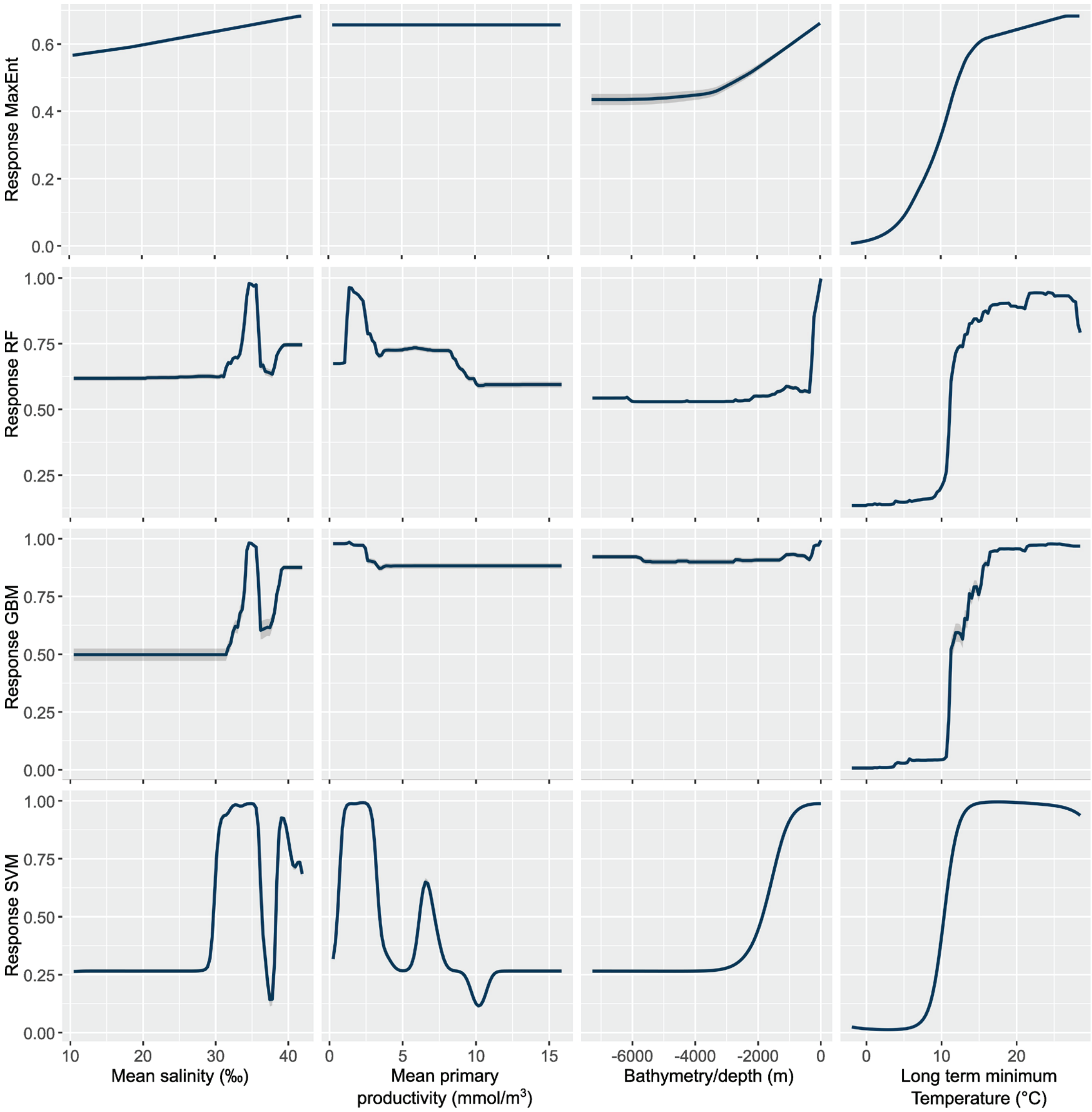

***Fig. 2:*** Response curves for all four modelling algorithms. Each row of graphs gives the plots for one algorithm whereas the column all depict a certain variable. The plots show strong agreement for variables that the models considered important (long term minimum temperature and bathymetry).

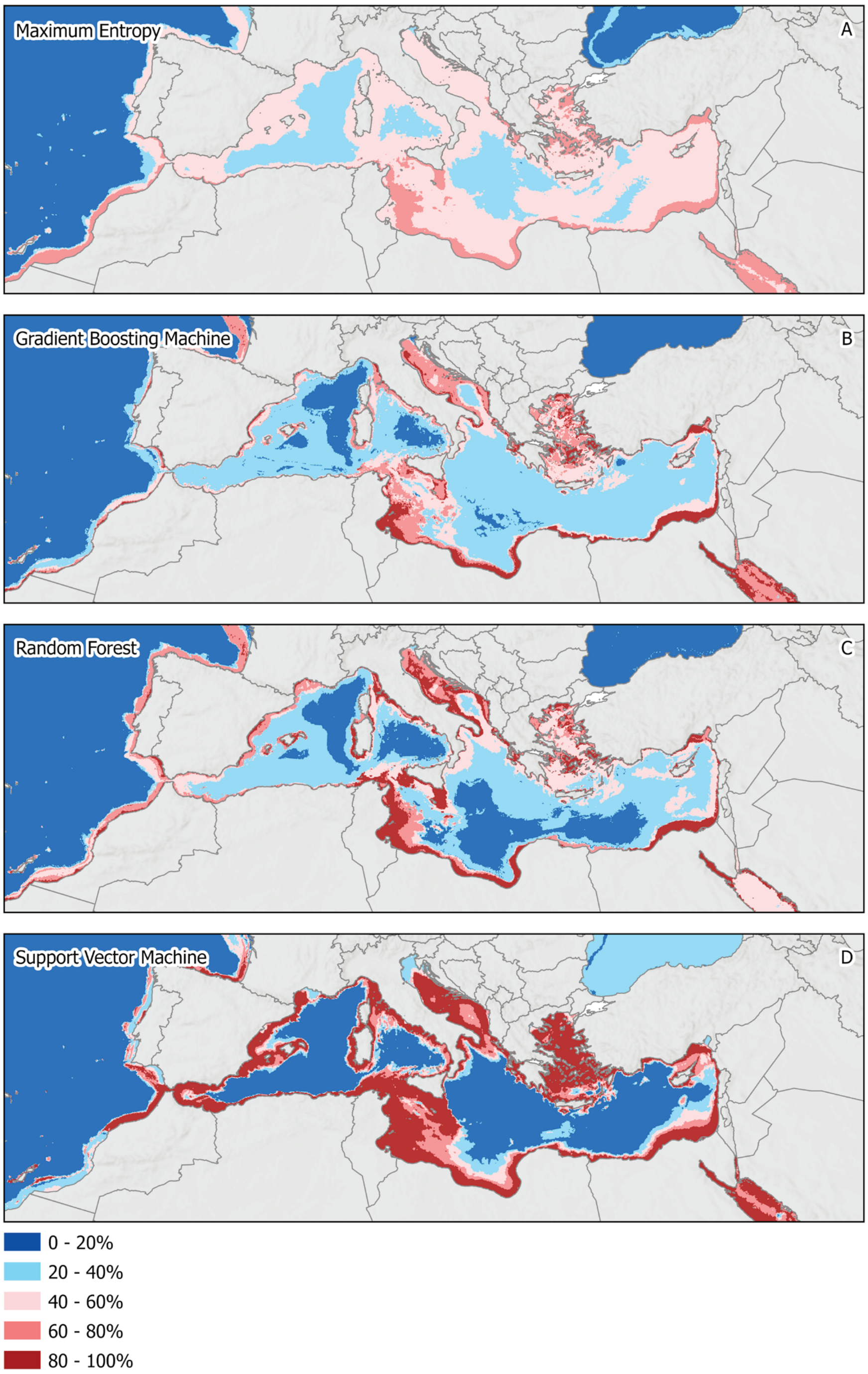

***Fig. 3:*** Habitat suitability maps based on the mean of all cross-folds for the maxent model. Percentages indicate how suitable an area is based on the maxent (A), gradient boosting machine (B), random forest (C) and support vector machine (D) algorithms.

## Discussion

Our SDMs consistently showed that the Adriatic, Aegean, and Ligurian Seas are experiencing – and will continue to experience– increased habitat suitability for *L. sceleratus* over the coming decades, under a realistic climate scenario. The models indicate that between 2000 and 2020, the coastal areas of the Red Sea and the region surround the Suez canal had already become more suitable for this species. During this period, increasing temperatures possibly facilitated migration through the Suez Canal, since the canal opened in 1863 but no record of this species presence can be found until 2003. A further increase in temperature is likely to drive continued range expansion and increased abundance of the silver-cheeked toadfish in the Mediterranean, as predicted by our models. The eastern part of the Mediterranean Sea is generally warmer than in the west and is also expected to experience the most significant warming in response to climate change, compared to other subregions (Adloff *et al.*, 2015). This is thought to be, at least in part, due to the semi-enclosed nature, increased heat flux, and reduced colder freshwater inflow from the Black Sea (Montanari *et al.*, 2023; Stanev *et al.*, 2019). Furthermore, reports of increasing numbers of invasive species in the Aegean Sea since 2020 –most of which originated from the western Indo-Pacific– indicate further climate-driven range expansion of Lessepsian migrants (Ragkousis *et al.*, 2023).

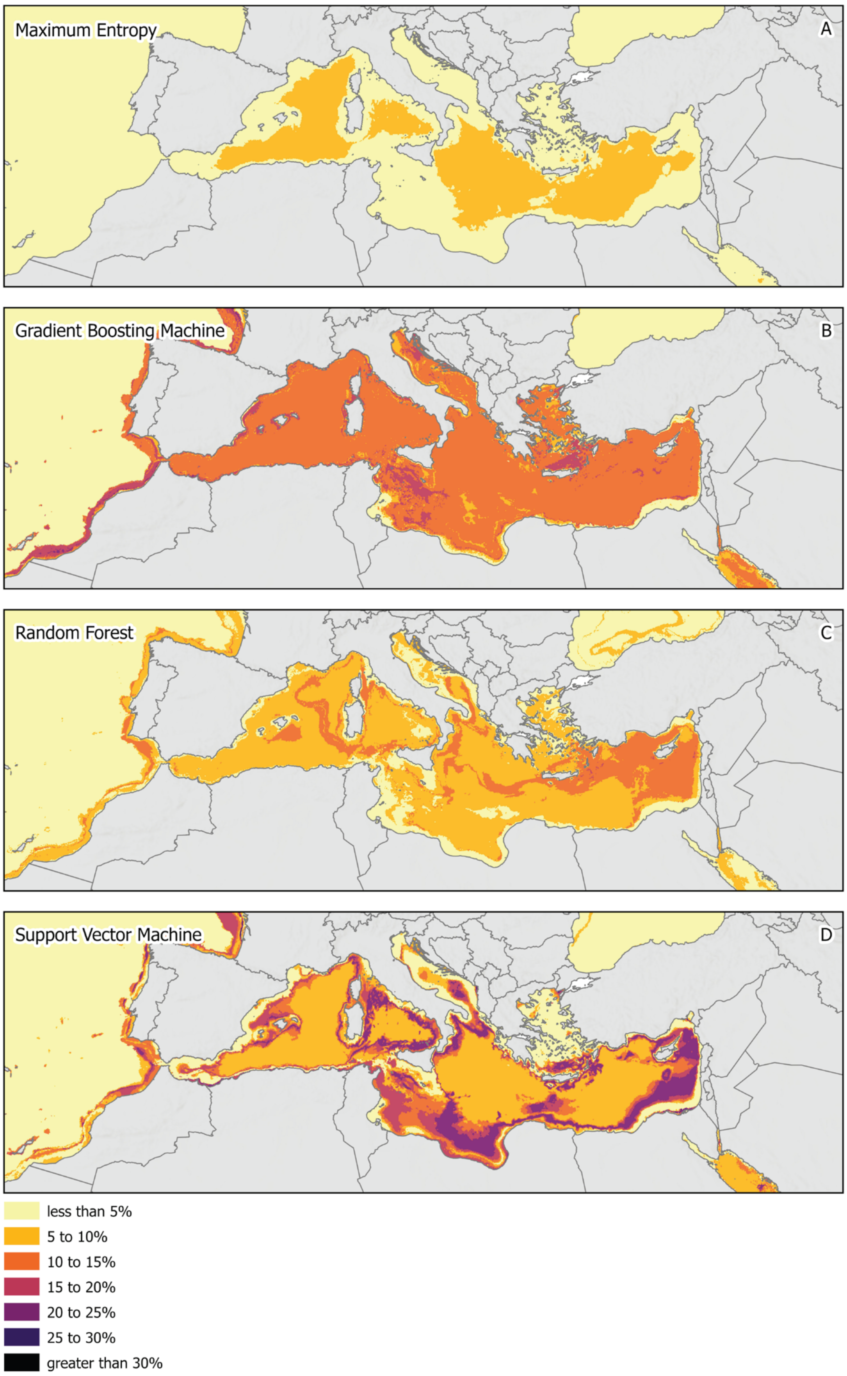

***Fig. 4:*** Maps showing the standard deviation of habitat suitability maps based on all cross-folds for the maxent (A), gradient boosting machine (B), random forest (C) and support vector machine (D) algorithms.

In the Eastern Mediterranean, the silver-cheeked toadfish is already becoming more abundant and are reaching larger sizes than in their native range (Ulman *et al.*, 2022). This may be the result of ecological release, where the invader experiences reduced competition or a lack of predators as is also seen in other fish species (Ord *et al.*, 2017; Syslo *et al.*, 2020). This may have implications for the interpretation of our models. In the current approach, we combined occurrence data from both the native and invasive ranges. Consequently, the environmental predictors primarily reflected conditions in the native range. However, the environmental niche in the native range does not necessarily represent the species' full tolerance limits, particularly when constrained by factors such as competition (Bates & Bertelsmeier, 2021). Previous research has shown that model performance declines when extrapolating to regions with sparse occurrence data (Nguyen & Leung, 2022) or when niche shifts are present (Liu *et al.*, 2022). As such, it is likely that our models underestimate the potential range of suitable habitat and should be interpreted as conservative in terms of the predicted distribution of the silver-cheeked toadfish. An alternative and widely recommended approach is to model native and invasive occurrence records separately (Gallien *et al.*, 2012; Stiels *et al.*, 2015). We tested this by constructing a separate model using 41 invasive-range occurrence records. This model produced distribution patterns, response curves, and performance metrics simi-

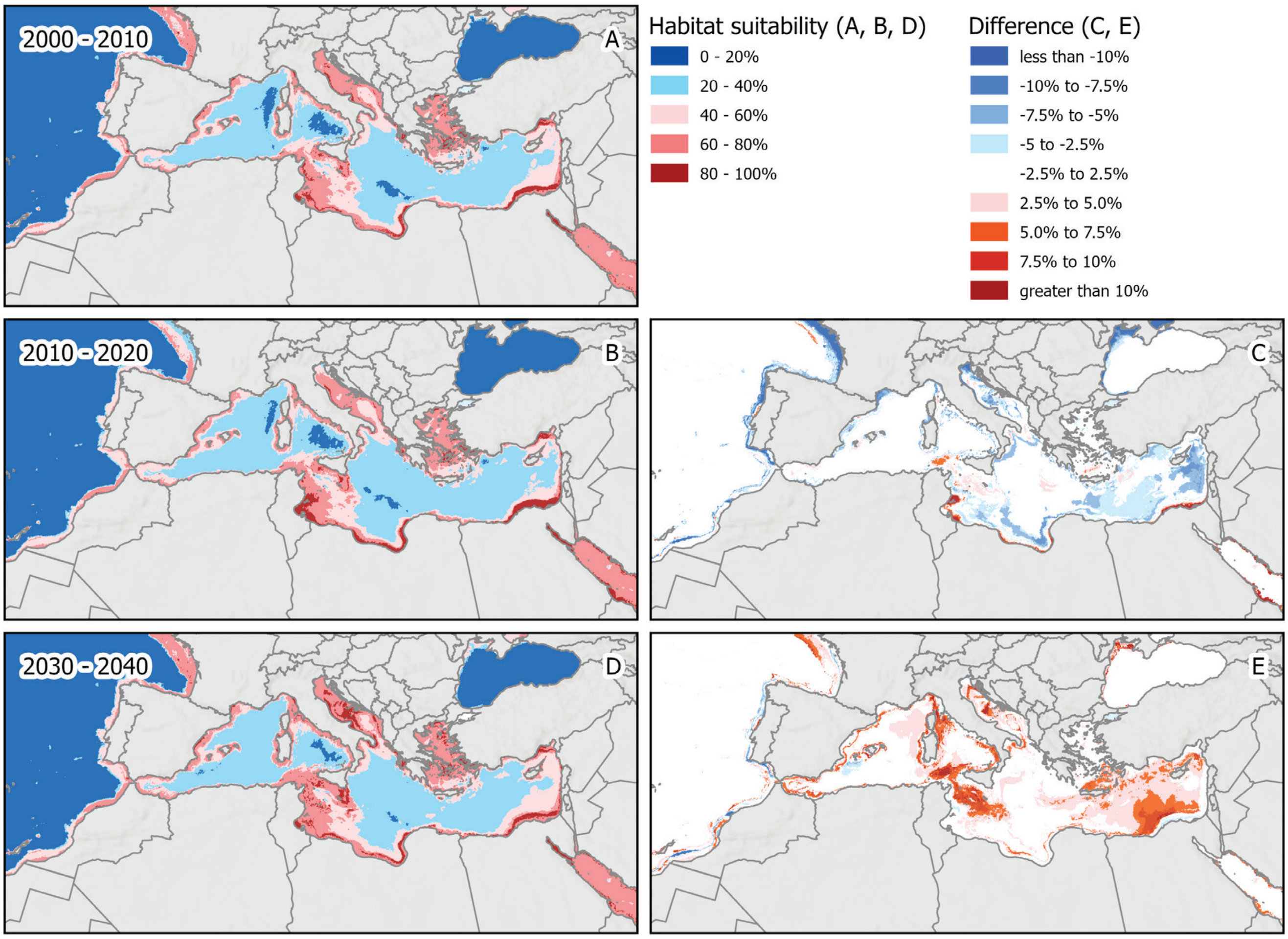

***Fig. 5:*** Predicted habitat suitability maps based on a weighted ensemble model (2010-2020). This ensemble model was used to hindcast (2000-2010) and forecast (2030-2040) habitat suitability. Changes in habitat suitability between the period 2000-2010 and 2010-2020 (C) and for the period 2010-2020 and 2030-2040 (E) are given in the figures on the right.

lar to those of the combined model. However, due to the limited sample size and minimal additional explanatory power, we did not include this model in the final analysis.

All four modelling algorithms treated the environmental variables in a similar manner, resulting in comparable regions that are more suitable than others, but with some differences in the height of suitability scores indicating model robustness. CBI scores differed across the models, with MaxEnt predicting habitat suitability very well and SVM producing less accurate predictions. However, this metric assesses only predictive power (Hirzel *et al.*, 2006) and do not adequately capture model accuracy (Fourcade *et al.*, 2014). Notably, 94% of SDM studies do not report model uncertainty (Robinson *et al.*, 2017). To address this limitation, we mapped the standard deviation of predictions across cross-validation folds, which offers insight into regions where model performance may be less reliable. For example, the SVM model exhibited lower residual deviance, typically suggesting better performance (Guisan & Zimmermann, 2000). However, analysis of the standard deviation across 25 cross-fold predictions revealed that several areas showed higher variability in predicted values compared to the other models. This indicates a potential for overfitting and suggests that the SVM model may not perform as well as the other models. On the other hand, MaxEnt showed very low variability in all regions, while this model had the highest deviance. This may indicate, not just reduced model fit, but actual absence of overfitting to unimportant variables such as salinity and phytoplankton (Franklin, 2012). All cross folds resulted in very similar models. Maxent exhibited the lowest spatial variation in Standard deviations of all models. This is likely the consequence of how this algorithm operates in comparison to the other machine learning algorithms (Li, 2013). MaxEnt's regularization framework penalizes overfitting and tends to produce more conservative predictions when extrapolating to novel environmental conditions (Phillips *et al.*, 2006). Importantly, the standard deviation maps also showed consistently low variation within areas predicted to have high habitat suitability across all four models. This supports the conclusion that regions identified as highly suitable are indeed very suitable.

Based on the SDM models the silver-cheeked toadfish is expected to continue expanding across the Mediterranean in the coming decades, leading to increasing socio-economic challenges (Christidis *et al.*, 2024; Sabatino *et al.*, 2024; Ünal & Bodur, 2017). One major issue is its impact on fisheries. The species' powerful beak-like teeth are capable of biting through fishing nets and lines, with a recent report of various fishing gears (nets, hooks and lines) found in their stomach contents (Gomes *et al.*, 2025). In some regions, fishers report daily damage to gear, resulting in rising costs and reduced profitability (Christidis *et al.*, 2024). These interactions lead to reduced catches and extra gear repair costs, causing significant economic losses to both small-scale and commercial fisheries (Christidis *et al.*, 2024; Gomes *et al.*, 2025; Ünal & Bodur, 2017), with some fishers pointing to this species as a contributor to the reduction of local cephalopod stocks, through predation (Nader *et al.*, 2012). Indeed, Gomes *et al.* (2025) confirmed that cephalopods occur in stomach contents of this species and indicate that predation by *L. sceleratus* may, in combination with climate change and increasing temperatures in the Mediterranean, be contributing to the decline in cephalopod stocks in the region. Recent studies also classify the silver-cheeked toadfish as a top predator in its invasive range (Ersönmez *et al.*, 2023; Gomes *et al.*, 2025) and as the populations continue to grow, such damages are expected to become more frequent and widespread.

Another significant concern is the toxicity of *L. sceleratus*. The species contains tetrodotoxin, which can be fatal to humans even in small doses (Bentur *et al.*, 2008). Despite repeated warnings, incidents of poisoning from both accidental and intentional consumption continue to be reported, particularly in regions where public awareness is limited. From an ecological perspective, however, the species appears to exert a deterring effect on other exotic species. For example, significant differences between the reactions of potential native versus exotic prey has been reported, with native species largely indifferent to the presence of silver-cheeked toadfish, while exotic species exhibited strong avoidance behavior (Chaikin *et al.*, 2023). Furthermore, gut content analysis from the same study revealed that the silver-cheeked toadfish primarily preyed on exotic species. Typically, the indifference of native species to an invasive predator is interpreted as a result of evolutionary naivety, which would suggest that native species should appear more frequently in the predator's diet (Salo *et al.*, 2007). However, this was not the case. Ulman *et al.* (2022) made similar observations, noting that silver-cheeked toadfish predominantly preyed on invasive species such as lionfish, long-spined sea urchins, and even their juveniles of the same species. However, they suggested that this pattern may be density-dependent, with higher densities of invasive prey resulting in a greater proportion of such species in the diet. In a system like the Mediterranean Sea, characterized by a high number and abundance of invasive species (Ulman *et al.*, 2022), it is possible that the silver-cheeked toadfish will exert a stronger ecological impact on other invasive species than on native ones.

Completely halting the spread of the silver-cheeked toadfish in the Mediterranean is no longer a realistic goal, given its established populations and rapid range expansion. Instead, adaptive management and mitigation strategies are essential. Foremost among these is public education, as most poisoning cases result from a lack of awareness regarding the species' toxicity. Community outreach, including efforts targeting small and isolated communities, and focused awareness campaigns can help prevent consumption and reduce associated health risks. Additionally, there is increasing interest in developing alternative uses for the species. Although human consumption is unsafe, some researchers have proposed investigating its potential applications in pharmaceuticals, due to its content of certain bioactive peptides, or processing it into fishmeal or fertilizer (Çavaş *et al.*, 2020; Doğdu *et al.*, 2019). Finally, supporting the fisheries sector is crucial. Innovations in gear design, the implementation of compensation schemes, and the development of gear insurance could help offset economic losses. Promoting collaborative approaches involving scientists, fishers, and policymakers will be essential for effectively managing the impacts of silver-cheeked toadfish in the years to come.

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**Author contribution:** RW conducted the analysis, produced figures, and wrote the manuscript. AR prepared the data, conducted preliminary analysis, and contributed to writing the manuscript. RdV contributed to the study design and reviewed the manuscript. TS conducted parts of the analysis. TC supervised and wrote the manuscript.

## References

Adloff, F., Somot, S., Sevault, F., Jordà, G., Aznar, R. *et al.*, 2015. Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. *Climate Dynamics*, 45 (9), 2775-2802.

Akyol, O., Ünal, V., Ceyhan, T., Bilecenoglu, M., 2005. First confirmed record of *Lagocephalus sceleratus*(Gmelin, 1789) in the Mediterranean Sea. *Journal of Fish Biology*, 66 (4), 1183-1186.

Bates, O.K., Bertelsmeier, C., 2021. Climatic niche shifts in introduced species. *Current Biology*, 31 (19), R1252-R1266.

Bentur, Y., Ashkar, J., Lurie, Y., Levy, Y., Azzam, Z. *et al.*, 2008. Lessepsian migration and tetrodotoxin poisoning due to *Lagocephalus sceleratus* in the Eastern Mediterranean. *Toxicon : official journal of the International Society on Toxinology*, 52 (8), 964-8.

Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M. *et al.*, 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biology*, 12 (5), e1001850.

Bond, N., Thomson, J., Reich, P., Stein, J., 2011. Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. *Marine and Freshwater Research*, 62 (9), 1043-1061.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological*

*Modelling*, 275, 73-77.

Çavaş, L., Bilgin, Y., Yılmaz-abeşka, Y., 2020. Can bioactive peptides of Lagocephalus sceleratus be evaluated in the functional food industry? *Biotech Studies*, 29 (2), 77-84.

Chaikin, S., De-Beer, G., Yitzhak, N., Stern, N., Belmaker, J., 2023. The invasive silver-cheeked toadfish (*Lagocephalus sceleratus*) predominantly impacts the behavior of other non-indigenous species in the Eastern Mediterranean. *Biological Invasions*, 25, 983-990.

Christidis, G., Batziakas, S., Peristeraki, P., Tzanatos, E., Somarakis, S. *et al.*, 2024. Another One Bites the Net: Assessing the Economic Impacts of Lagocephalus sceleratus on Small-Scale Fisheries in Greece. *Fishes*, 9 (3), 104.

Cook, E.J., Jenkins, S., Maggs, C.A., Minchin, D., Mineur, F. *et al.*, 2013. Impacts of climate change on non-native species. *Marine Climate Change Impact Partnership: Science Review*, 155-166.

Courchamp, F., Fournier, A., Bellard, C., Bertelsmeier, C., Bonnaud, E. *et al.*, 2017. Invasion Biology: Specific Problems and Possible Solutions. *Trends in Ecology & Evolution*, 32 (1), 13-22.

Cuthbert, R.N., Pattison, Z., Taylor, N.G., Verbrugge, L., Diagne, C. *et al.*, 2021. Global economic costs of aquatic invasive alien species. *Science of The Total Environment*, 775, 145238.

Doğdu, S., Turan, C., Ayas, D., 2019. *Isolation and Characterization of Collagen and Gelatin From Skin of Silver Cheeked Pufferfish Lagocephalus sceleratus for Pharmaceutical and Biomedical Applications*. *Natural and Engineering Sciences*, 4 (3), 308-314.

Elith, J., Graham, C.H., 2009. Do They? How Do They? Why Do They Differ? On Finding Reasons for Differing Performances of Species Distribution Models. *Ecography*, 32 (1), 66-77.

Ersönmez, H., Özyurt, C.E., Mavruk, S., Yıldız, T., Ulman, A., 2023. An in-depth study of the biology, trophic ecology and catchability of the invasive pufferfish *Lagocephalus sceleratus* from southern Turkey, eastern Mediterranean Sea. *Scientia Marina*, 87 (4), 1-69.

Fourcade, Y., Engler, J.O., Rödder, D., Secondi, J., 2014. Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLOS ONE*, 9 (5), e97122.

Franklin, J., 2012. *Mapping Species Distributions: spatial inference and prediction,* 1861(1900).

Galil, B.S., 2007. Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine Pollution Bulletin*, 55 (7-9), 314-322.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E., Thuiller, W., 2012. Invasive species distribution models – how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, 21 (11), 1126-1136.

Gaul, W., Sadykova, D., White, H.J., Leon-Sanchez, L., Caplat, P. *et al.*, 2020. Data quantity is more important than its spatial bias for predictive species distribution modelling. *PeerJ*, 8, e10411.

GBIF, 2025. GBIF.

Giakoumi, S., Katsanevakis, S., Albano, P.G., Azzurro, E., Cardoso, A.C. *et al.*, 2019. Management priorities for marine invasive species. *Science of The Total Environment*, 688, 976-982.

Giangrande, A., Pierri, C., Del Pasqua, M., Gravili, C., Gambi, M.C. *et al.*, 2020. The Mediterranean in check: Biological invasions in a changing sea. *Marine Ecology*, 41 (2), e12583.

Gomes, R.V.C., Christidis, G., Peristeraki, P., Somarakis, S., Tserpes, G., 2025. The diet and feeding habits of Lagocephalus sceleratus in the eastern Mediterranean: A case study carried out off the island of Crete (southern Greece). *Mediterranean Marine Science*, 26 (1), 97-114.

Grosholz, E., 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution*, 17 (1), 22-27.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*, 135 (2), 147-186.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five Potential Consequences of Climate Change for Invasive Species. *Conservation Biology*, 22 (3), 534-543.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, 199 (2), 142-152.

Huard, D., Fyke, J., Capellán-Pérez, I., Matthews, H.D., Partanen, A.-I., 2022. Estimating the Likelihood of GHG Concentration Scenarios From Probabilistic Integrated Assessment Model Simulations. *Earth's Future*, 10 (10), e2022EF002715.

Katsanevakis, S., Coll, M., Piroddi, C., Steenbeek, J., Ben Rais Lasram, F. *et al.*, 2014a. Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science*, 1.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E. *et al.*, 2014b. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, 9 (4), 391-423.

Lamboley, Q., Fourcade, Y., 2024. No optimal spatial filtering distance for mitigating sampling bias in ecological niche models. *Journal of Biogeography*, 51, 1783-1794.

Li, X., 2013. Applying various algorithms for species distribution modeling. *Integrative Zoology*, 8 (2), 124-135.

Liu, C., Wolter, C., Courchamp, F., Roura-Pascual, N., Jeschke, J.M., 2022. Biological invasions reveal how niche change affects the transferability of species distribution models. *Ecology*, 103 (8), e3719.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17 (2), 145-151.

Marx, M., Quillfeldt, P., 2018. Species distribution models of European Turtle Doves in Germany are more reliable with presence only rather than presence absence data. *Scientific Reports*, 8 (1), 16898.

Merow, C., Smith, M.J., Silander Jr, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36 (10), 1058-1069.

Miller, J., 2010. Species Distribution Modeling. *Geography Compass*, 4 (6), 490-509.

Montanari, A., Nguyen, H., Rubinetti, S., Ceola, S., Galelli, S. *et al.*, 2023. Why the 2022 Po River drought is the worst in the past two centuries. *Science Advances*, 9 (32), eadg8304.

Nader, M.R., Indary, S., Boustany, L.E., 2012. *The puffer fish Lagocephalus sceleratus (Gmelin, 1789) in the Eastern Mediterranean*.

Naimi, B., Araújo, M., 2016. sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, 39, 001-008.

Nguyen, D., Leung, B., 2022. How well do species distribution models predict occurrences in exotic ranges? *Global Ecology and Biogeography*, 31 (6), 1051-1065.

Ojaveer, H., Galil, B.S., Carlton, J.T., Alleway, H., Goulletquer, P. *et al.*, 2018. Historical baselines in marine bioinvasions: Implications for policy and management. *PloS One*, 13 (8), e0202383.

Oliveira, O.M.P., 2007. The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. *Aquatic Invasions*, 2 (3), 185-189.

Ord, T.J., Summers, T.C., Noble, M.M., Fulton, C.J., 2017. Ecological Release from Aquatic Predation Is Associated with the Emergence of Marine Blenny Fishes onto Land. *The American Naturalist*, 189 (5), 570-579.

Otero, M., Cebrian, E., Francour, P., Galil, B., Savini, D., 2013. *Monitoring Marine Invasive Species in Mediterranean Marine Protected Areas (MPAs): A strategy and practical guide for managers*, 1-136.

Outinen, O., Katajisto, T., Nygård, H., Puntila-Dodd, R., Lehtiniemi, M., 2024. National assessment on the status, trends and impacts of marine non-indigenous species for the European Union marine strategy framework directive. *Ecological Indicators*, 158, 111593.

Panzeri, D., Russo, T., Arneri, E., Carlucci, R., Cossarini, G. *et al.*, 2024. Identifying priority areas for spatial management of mixed fisheries using ensemble of multi-species distribution models. *Fish and Fisheries*, 25 (2), 187-204.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190 (3), 231-259.

Qian, H., Zhang, Y., Ricklefs, R.E., Wang, X., 2022. Relationship of minimum winter temperature and temperature seasonality to the northern range limit and species richness of trees in North America. *Journal of Geographical Sciences*, 32 (2), 280-290.

R Core Team, 2024. R A language and environment for statistical computing. R Foundation for Statistical*, Computing*.

Ragkousis, M., Sini, M., Koukourouvli, N., Zenetos, A., Katsanevakis, S., 2023. Invading the Greek Seas: Spatiotemporal Patterns of Marine Impactful Alien and Cryptogenic Species. *Diversity*, 15 (3), 353.

Robinson, N.M., Nelson, W.A., Costello, M.J., Sutherland, J.E., Lundquist, C.J., 2017. A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice. *Frontiers in Marine Science*, 4, 421.

Sabatino, L., Esposito, G., Meloni, D., 2024. Occurrence of silver-cheeked toadfish *Lagocephalus sceleratus* (Tetraodontiformes: Tetraodontidae) and tetrodotoxins in the Mediterranean Sea: Implications for the Italian fishing sector? *Regional Studies in Marine Science*, 75, 103562.

Salo, P., Erkki, K., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences*, 274 (1615), 1237-1243.

Schickele, A., Guidetti, P., Giakoumi, S., Zenetos, A., Francour, P. *et al.*, 2021. Improving predictions of invasive fish ranges combining functional and ecological traits with environmental suitability under climate change scenarios. *Global Change Biology*, 27 (23), 6086-6102.

Simberloff, D., 2013. *Invasive species: what everyone needs to Know.* OUP Us.

Sorbe, F., Gränzig, T., Förster, M., 2023. Evaluating sampling bias correction methods for invasive species distribution modeling in Maxent. *Ecological Informatics*, 76, 102124.

Stanev, E.V., Peneva, E., Chtirkova, B., 2019. Climate Change and Regional Ocean Water Mass Disappearance: Case of the Black Sea. *Journal of Geophysical Research: Oceans*, 124 (7), 4803-4819.

Stiels, D., Gaißer, B., Schidelko, K., Engler, J.O., Rödder, D., 2015. Niche shift in four non-native estrildid finches and implications for species distribution models. *Ibis*, 157 (1), 75-90.

Syslo, J.M., Brenden, T.O., Guy, C.S., Koel, T.M., Bigelow, P.E. *et al.*, 2020. Could ecological release buffer suppression efforts for non-native lake trout (Salvelinus namaycush) in Yellowstone Lake, Yellowstone National Park? *Canadian Journal of Fisheries and Aquatic Sciences*, 77 (6), 1010-1025.

Townhill, B., Pinnegar, J., Tinker, J., Jones, M., Simpson, S. *et al.*, 2017. Non-native marine species in north-west Europe: Developing an approach to assess future spread using regional downscaled climate projections. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27 (5), 1035-1050.

Tsiamis, K., Zenetos, A., Deriu, I., Gervasini, E., Cardoso, A.C., 2018. The native distribution range of the European marine non-indigenous species. *Aquatic Invasions*, 13 (2), 187-198.

Tsiamis, K., Palialexis, A., Stefanova, K., Gladan, Ž.N., Skejić, S. *et al.*, 2019. Non-indigenous species refined national baseline inventories: A synthesis in the context of the European Union's Marine Strategy Framework Directive. *Marine Pollution Bulletin*, 145, 429-435.

Tsiamis, K., Azzurro, E., Bariche, M., Çinar, M.E., Crocetta, F. *et al.*, 2020. Prioritizing marine invasive alien species in the European Union through horizon scanning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30 (4), 794-845.

Tsiamis, K., Palialexis, A., Connor, D., Antoniadis, S., Bartilotti, C. *et al.*, 2021. *Marine Strategy Framework Directive - Descriptor 2, Non-Indigenous Species, Delivering solid recommendations for setting threshold values for non-indigenous species pressure on European seas*.

Ulman, A., Kalogirou, S., Pauly, D., 2022. The Dynamics of Maximum Lengths for the Invasive Silver-Cheeked Toadfish (Lagocephalus sceleratus) in the Eastern Mediterranean Sea. *Journal of Marine Science and Engineering*, 10 (3), 387.

Ulman, A., Yildiz, T., Demirel, N., Canak, O., Yemişken,

E. *et al.*, 2021. The biology and ecology of the invasive silver-cheeked toadfish (Lagocephalus sceleratus), with emphasis on the Eastern Mediterranean. *NeoBiota*, 68, 145-175.

Ünal, V., Bodur, H.G., 2017. The socio-economic impacts of the silver-cheeked toadfish on small-scale fishers: A comparative study from the Turkish coast. *Ege Journal of Fisheries and Aquatic Sciences*, 34 (2), 119.

Ünal, V., Goncuoglu, H., Durgun, D., Tosunoglu, Z., Deval, M.C. *et al.*, 2015. Silver-cheeked toadfish, *Lagocephalus sceleratus* (Actinopterygii: Tetradontiformes: Tetradontidae), causes substantial economic losses in the Turkish Mediterranean coast: A call for decision makers. *Acta Ichthyologica et Piscatoria*, 15, 231-237.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P. *et al.*, 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8 (3), 135-144.

Weterings, R., Zhang, Z., Cornwell, T.O., 2025. The effects of climate change on European distributions of four alien marine crab species. *Web Ecology*, 25 (2), 137-156.

Zenetos, A., Galanidi, M., 2020. Mediterranean non indigenous species at the start of the 2020s: recent changes. *Marine Biodiversity Records*, 13 (1), 10.

Zhang, Z., Xu, S., Capinha, C., Weterings, R., Gao, T., 2019. Using species distribution model to predict the impact of climate change on the potential distribution of Japanese whiting *Sillago japonica*. *Ecological Indicators*, 104, 333-340.

Zhang, Z., Mammola, S., McLay, C.L., Capinha, C., Yokota, M., 2020a. To invade or not to invade? Exploring the niche-based processes underlying the failure of a biological invasion using the invasive Chinese mitten crab. *Science of The Total Environment*, 728, 138815.

Zhang, Z., Mammola, S., Zhang, H., 2020b. Does weighting presence records improve the performance of species distribution models? A test using fish larval stages in the Yangtze Estuary. *Science of The Total Environment*, 741, 140393.