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ORIGINAL RESEARCH

Climate change and competition by the invasive Atlantic blue crab represent a critical threat for the Mediterranean green crab

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Abstract
Biological invasions are a main threat to the integrity of marine ecosystems and a major driver of biodiversity loss. The Mediterranean Sea is an enclosed basin, and its habitats are particularly vulnerable to climate change, which, in turn, is expected to exacerbate the negative effects of biological invasions. In this study, we applied Species Distribution Models to project current and future species' distribution and habitat suitability for the Mediterranean green crab *Carcinus aestuarii* and the invasive Atlantic blue crab *Callinectes sapidus* within the Mediterranean basin. Subsequently, the models were also run factoring the effect of indirect competition by the Atlantic blue crab on the green crab's habitat and range distribution. Our hypothesis was that *C. sapidus* would expand its geographic distribution under a climate change scenario, while *C. aestuarii* would be negatively affected by the double effect of climate change and exploitative competition with the invasive blue crab. The results obtained combining the pressure exerted by climate change and the invasive competitor predicted a rapid decline in the distribution of suitable habitat for the Mediterranean green crab, eventually leading to the extirpation of this species from its native range. In contrast, environmental conditions are expected to remain favourable for the Atlantic blue crab along most of the Mediterranean coastlines. Our models raise concern about the fate of the Mediterranean green crab and call for an effective management of invasive marine species and powerful climate change mitigation actions to limit a critical loss of biodiversity in the Mediterranean Sea.

Keywords Global warming · Portunoidea · Biological invasions · Species distribution models

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Introduction

Biological invasions occur when species are introduced, involuntarily or purposefully, and become established in ecosystems they are not native to (Mainka and Howard 2010). Global trends related to shipping, aquarium trade and aquaculture activities have increased the rates of species' introductions in marine environments (Katsanevakis et al. 2014; Nunes et al. 2014). In new environments, many non-native species lack their natural enemies and other ecological limiting factors, and such conditions can favour their establishment and rapid spread (Manchester and Bullok 2000).

Non-indigenous species (NIS) have the potential to become invasive (Invasive Alien Species, IAS: Pyšek et al. 2020) and alter the structure and functioning of newly colonised ecosystems, both directly (through predation, competition, introduction of novel diseases) and indirectly (economic damage) (Nunes et al. 2014; Tarkan et al. 2021). For these reasons, biological invasions are considered a main threat to the integrity of marine ecosystems and a major driver of biodiversity loss (Seebens et al. 2020; Tarkan et al. 2021).

More than 1,000 NIS have been reported in European seas (Tsiamis et al. 2018; Öztürk 2021). In this context, the Mediterranean Sea stands out as a major hotspot for marine NIS, hosting 578 recorded species (Zenetos et al. 2022). These include approximately 56 brachyuran crab species recorded as non-native or expanding beyond their natural distribution ranges (Swart and Robinson 2019). Only a fraction (~ 10–15%) of the NIS recorded in the Mediterranean Sea, however, are considered invasive or potentially invasive based on documented impacts (Bonanno and Orlando-Bonaca 2019). Such a high number of NIS reflects the long history of human occupation of the Mediterranean and its strategic position along maritime trade routes (Galil 2000; Lejeusne et al. 2010). A major driver of these introductions has been the opening of the Suez Canal which has allowed the arrival of tropical species from the Red Sea (Tiralongo et al. 2022). Ballast waters of commercial or tourist ships as well as biofouling have also contributed to the entry of various species, including those of Atlantic origin (Galil 2000).

The Mediterranean Sea is an enclosed basin, and its habitats are particularly vulnerable to climate change (Philippart et al. 2011), which is also expected to enhance the negative effects of biological invasions (the "double trouble" *sensu* Mainka and Howard 2010). Global warming can facilitate species' introduction, colonization and successful reproduction, allowing the persistence and spread of newly arrived species, especially of species originating from warm temperate and tropical areas. IAS are generally characterised by great adaptability to disturbance and to a broad range of ecological conditions and they have high reproductive rates and good dispersion ability (Burgiel and Muir 2010). These life history traits help non-native species to successfully compete with native ones, especially those with a narrow tolerance range to environmental stressors, as well as those with specialised habitat requirements and/or unable to move to new more suitable sites (Walther et al. 2009; Mainka and Howard 2010).

Information about the distribution, spatial patterns and characteristics of the environmental variables determining a species' habitat suitability is essential to implement targeted management and conservation strategies (Cianfrani et al. 2010; Jones et al. 2016). Species Distribution Models (SDMs) use contemporary environmental layers and presence/absence data to predict the potential geographical distribution of species (Thuiller et al. 2009). They can be used to model how climate change may influence the potential distribution shifts of

natural populations, changes in their range size or, ultimately, their vulnerability to local extinctions (Miller 2012; Schwartz 2012; Jones et al. 2016). By identifying the potential loss of habitats and predicting the occurrence of new suitable ranges, SDMs can be a useful tool to guide long-term conservation efforts (Jones et al. 2016). To make predictive SDMs as accurate as possible, it is essential to consider biotic interactions, especially interspecific competition (Jones et al. 2016). Since the resilience of a species to climate change can also be influenced by its biotic interactions (Gillson et al. 2013), the effect of competition from an invasive species may be a crucial factor for the future suitability of a native species' range.

The Atlantic blue crab *Callinectes sapidus*, Rathbun 1896 (Decapoda: Portunidae), native to the Western Atlantic Ocean, is invasive in the Mediterranean Sea (Marchessaux et al. 2022; Scalici et al. 2022). Currently, it is included in the list of the 100 worst invasive species in the world due to the observed negative impacts on benthic communities and fisheries (Zenetos et al. 2005; Nehring 2011; Katsanevakis et al. 2014). By contrast, the Mediterranean green crab *Carcinus aestuarii*, Nardo 1847 (Decapoda, Carcinidae) turns out to be one of the most impacted species by *C. sapidus*, through both predation and direct and indirect competition (Kampouris et al. 2019).

In this study, we applied SDMs to project current and future species' distribution and habitat suitability for both the Mediterranean green crab and the invasive Atlantic blue crab in the Mediterranean basin, based on current environmental conditions and future projections due to climate changes. We used different models to predict the distributions of both crab species, based on an extensive collection of georeferenced occurrence records. Subsequently, SDMs were also run factoring the effect of competition by the blue crab on the green crab's habitat and range distribution. The objective of this study was twofold: (1) to identify the environmental factors predicting the potential distribution of the native and non-native crabs under the current and future climate conditions and, specifically for the native species, (2) to detect the double effect of climate change and competition caused by the arrival of the new competitor. Our hypothesis is that climate change would facilitate the geographic expansion of *C. sapidus*, while it would negatively affect the distribution of *C. aestuarii* and its habitat suitability. We also hypothesise that the native species would suffer a worse scenario due to the presence of the new competitor. Our study will help understand the climatic factors responsible for the shift in distribution over time of both the native and the invasive species within the Mediterranean basin, accounting for the double trouble of climate change and biological invasions on the distribution of the native species.

Materials and methods

Study species

The target species for this study are two crabs belonging to the superfamily Portunoidea, the Mediterranean green crab *Carcinus aestuarii* and the Atlantic blue crab *Callinectes sapidus*.

C. aestuarii is a medium size shore crab native to the Mediterranean and Black seas, where adult populations predominantly inhabit intertidal and shallow subtidal coastal habitats, including estuaries and lagoons, favouring substrates composed of sand, mud, or rocks (Piccardi et al. 2025). *C. aestuarii* shows a broad thermal tolerance and tolerates high salin-

ity fluctuations, prolonged air exposure and starvation (Taylor and Butler 1978; Leignel et al. 2014; Tepolt and Somero 2014). It also shows a broad feeding niche, ranging from predation to scavenging, and feeds on a variety of benthic invertebrates and organic matter. In the Venice Lagoon, it is fished and farmed during the moulting period for the production of "*moeche*", a seasonal fishery product (Matozzo et al. 2011).

C. sapidus is native to the Western Atlantic Ocean, ranging from Nova Scotia to Argentina (Gandy et al. 2011). Extremely euryhaline (Scalici et al. 2022), during its life cycle can be encountered in both true saltwater and shallow brackish waters (Onofri et al. 2008; Nehring 2011). It is also a true eurythermal species, capable to thrive at temperatures ranging from 0 °C to 40 °C, with optimal physiological performance observed at 24 °C (Marchessaux et al. 2022). This crab is considered a keystone species in the coastal benthic food webs, being both a predator and detritivore, and represents an important fishery resource in its native range (Virnstein 1979; Nelson 1981; Hines et al. 1990; Reichmuth et al. 2009; Nehring 2011). *C. sapidus* was introduced in Europe at the beginning of the 20th century, most likely due to ballast water discharge (Nehring 2011) and has been recorded in the Mediterranean Sea since 1949 (Mancinelli et al. 2017). Its high fecundity, strong swimming capabilities and aggressive behaviour have contributed to its recent expansion and establishment as an ecologically impactful invader in the Mediterranean Sea, particularly over the last two decades (Galil and Zenetos 2002).

Occurrence and environmental data

To calculate the current and future distribution of the two studied species, we downloaded their occurrence data from the online databases iNaturalist and GBIF (https://www.inaturalist.org/, https://www.gbif.org/; accessed in November 2024). We focused our analyses on adult stages of these species due to the lack of occurrence data for the larval stages, likely related to their pelagic development, which limits detectability and field sampling.

We chose to download only occurrence data collected by experts and provided with images for species cross-identification. Each occurrence data was manually checked to avoid sampling errors. We plotted the georeferenced occurrence data in QGIS desktop (v 3.22.2) and we used the clip function to delete points that fell outside of species' distribution maps to correct potential errors in the occurrence records in the database. Next, we used the *spThin* package in R (v 4.2.1) (Aiello-Lammens et al. 2015) to minimise sampling bias by filtering occurrences within a single grid cell. We set a threshold of 5 km to avoid spatial correlation (resolution of the environmental raster).

All covariate layers were downloaded from the public database Bio-Oracle v3.0 (Assis et al. 2024) which provides environmental variables for the decade 2010–2020 (data used here as a proxy for current conditions) and projections for the 2040s (2040–2049) and 2090s (2090–2099), considering the concentration of greenhouse gas emissions in the Representative Concentration Pathway (RCP) trajectories of climate change adopted by the IPCC (Intergovernmental Panel on Climate Change) (Tyberghein et al. 2012; Assis et al. 2018). We selected the SSP 1-2.6 and SSP 5-8.5 scenarios. The SSP 1-2.6 scenario is based on the reduction of carbon dioxide emissions in the atmosphere and an increase in mean temperature under 2 °C by 2100. Conversely, the SSP 5-8.5 is more pessimistic, based on increasing gas emissions and a rise in mean temperature of 5 °C by 2100.

Environmental predictors were downloaded from a dataset of 15 variables from the Bio-ORACLE website, based on data availability and their physiological and ecological importance to marine species. All rasters were at a spatial resolution of 2.5 min. We included minimum, mean and maximum water temperature (°C), salinity, current velocity (m/s), nitrate (mmol/m^3), dissolved molecular oxygen (mmol/m^3), primary productivity (mmol/m^3), pH, chlorophyll (mmol/m^3), air temperature (°C), bathymetry (m) and Terrain Ruggedness Index. The Ruggedness index was calculated as the mean of the absolute differences between a cell's value and its eight surrounding cells. Low Ruggedness values indicate unconsolidated substrate (i.e., mud and sand), whereas high Ruggedness values are associated with rocky substrates (Riley et al. 1999; Fonseca et al. 2017).

Before running the models, we calculated the Pearson correlation coefficients between all variables, thus excluding highly correlated variables ($r > 0.75$) from the dataset and avoid overfitting. Additionally, the selected variables were further tested using the Variance Inflation Factor (VIF) to confirm the absence of multicollinearity, ensuring the robustness of the selected predictors for the SDMs.

Species distribution models (SDMs)

Species distribution models (SDMs) were performed to predict the current and future habitat suitability of the studied species. Outputs of the SDMs for *C. sapidus* were included in the *C. aestuarii* model as a proxy to investigate the effect of exploitative competition on model performance.

In this study, we used an ensemble species distribution modelling framework contained in the package BIOMOD2 (Thuiller et al. 2016), a multi-model platform implemented in R. The BIOMOD2 procedure uses an ensemble of modelling techniques (Araújo and New 2007; Guisan et al. 2017; Thuiller et al. 2019) and we chose to test data with the following models: Generalized Linear Models (GLM), General Additive Models (GAM), Classification Tree Analysis (CTA), Surface Range Envelope (SRE), Flexible Discriminant Analysis (FDA), Random Forests (RF) and Maximum Entropy to produce consensus models, which are weighted averages among all models (Marmion et al. 2009). For our input data, we generated three random datasets of pseudo-absence records using the '*Random*' method (Hao et al. 2019). We then used a 70% random sample of initial data (presence/pseudo-absence) as training data and evaluated them against the remaining 30% of samples. We repeated the split sampling ten times to account for the uncertainty associated with data partitioning. To evaluate the performance of our models, we used the area under the Receiver Operating Characteristic curve (ROC) and True Skill Statistics (TSS). We retained a model only when both ROC and TSS were bigger than 0.7 (McPherson et al. 2004), and then created an ensemble mean model that weighted single models by their model performance (ROC) for each species (Thuiller et al. 2009; Gallardo et al. 2017). The thresholds of TSS and ROC > 0.7 are commonly used in species distribution modelling to distinguish models with acceptable predictive performance from those that are poor or only marginally better than random null models (Thuiller et al. 2009). Finally, the projections obtained with the ensemble models were reclassified to convert the continuous output into a map of presence-absence (0–1), setting the suitability threshold at 0.5.

Distribution range change and spatial overlap

To visualise and measure the range change of the target crab species under future climatic conditions, we used the "*biomod.range.size*" function implemented in the BIOMOD2 package (Guisan et al. 2017). This function provides a summary statistic on species range change, such as the gain or loss of suitable conditions for the studied species, according to Guisan et al. (2017). We applied these statistics on binary maps, multiplying the number of cells by the mean area of each raster pixel to obtain the effective area (km^2) gain or loss by the species.

Habitat suitability and binary maps were employed to apply the spatial overlap test to examine habitat divergence between species. Schoener's D and Warren's I (Warren et al. 2008, 2010) are two indices for niche or habitat identity and were calculated based on the habitat suitability comparison. Schoener's D calculates the suitable range for a given species based on the probability distributions for inhabiting specific regions (cells), calculating habitat overlap based on the abundance of species in those locations. Warren's I is based purely on probability distributions without the assumptions of Schoener's D (Warren et al. 2010).

Results

Model assessment

After the Pearson correlation test, eight uncorrelated variables were retained: bathymetry, current velocity, chlorophyll, nitrate, pH, mean sea water temperature, salinity and Terrain Ruggedness Index. All predictors exhibited VIF values ranging from 1 to 2, well below the threshold of 5, confirming the absence of problematic multicollinearity among the explanatory variables. Overall, ROC and TSS values derived from all the models achieved excellent performance, showing a high degree of discrimination between the sites where the crabs were present and those where they were absent. The obtained TSS values indicate the high ability of the applied models to correctly predict true negative (specificity) and true positive rates (sensitivity). With the exception of the SRE models (*C. sapidus*: TSS = 0.72, ROC = 0.86; *C. aestuarii*: TSS = 0.67, ROC = 0.84), all other models had TSS values greater than 0.8 and ROC greater than 0.9 for both species. As all models had a ROC value greater than 0.8, all projections obtained for every scenario and time frame were used to create the ensemble models. The evaluation metrics of the ensemble models were over 0.9 for both species, confirming the reliability of the models.

Species distribution models

Bathymetry explained 69% of the *C. aestuarii*'s models, mean sea water temperature 11%, and salinity 7%. All other variables explained less than 5% of the models (Table 1). As regards *C. sapidus*, bathymetry explained 87% of the models and mean seawater temperature 23%, while the other variables did not affect the models (Table 1). In the *C. aestuarii*'s distribution model that included the putative effect of spatial overlapping with the blue crab as a factor, the relative importance of all climate variables decreased, and co-occurrence -used as a proxy for potential exploitative competition- became the most important explanatory factor describing 39% of the model (Table 1).

Table 1 List of the environmental variables included in the species' distribution models for the Atlantic blue crab *Callinectes sapidus* and the green crab *Carcinus aestuarii* (without or with the effect of competition) and their relative contribution to the model (%)

Variables	Carcinus aestuarii	Callinectes sapidus	Carcinus aestuarii + competitor
Bathymetry	69	87	23
Sea water velocity	0.2	0.4	0.5
Chlorophyll	0.4	0.1	0.4
Nitrate	0.3	0.5	0.2
pH	0.2	0.1	0.7
Salinity	0.7	0.1	0.8
Sea water temperature	11	23	0.8
TRindex	0.3	0.2	0.5
Competitor distribution	-	-	39

For *C. aestuarii*, the ensemble model for current environmental conditions (2010–2020) identified the northern coasts of the Mediterranean as the areas with the highest presence probabilities, from the Greek Islands to the southern coast of Spain, while the African coast showed a low habitat suitability. From binary maps obtained with a 0.5 threshold of habitat suitability, we identified a potential good-quality habitat area of 84,323 km^2(Fig. 1).

Under the analysed climate change scenarios, in the first half of the present century the Mediterranean green crab is projected to experience a reduction of its optimal habitat throughout the entire Mediterranean basin, estimated at 40% in the SSP 1-2.6 scenario and 55% in the SSP 5-8.5 one (Fig. 1; Table 2). An almost total loss of optimal habitat in the southern part of the Mediterranean basin is expected under both future scenarios to 2050, especially in the one predicting the greatest temperature increase (SSP 5-8.5). Both climatic scenarios also predict the possibility of the disappearance of optimal habitat throughout the entire Black Sea basin. Under the SSP1-2.6 scenario, the model forecasted a general reduction of habitat suitability in the northernmost part of the Mediterranean basin with reduced areas maintained as an optimal habitat (Fig. 1). In contrast, in the SSP 5-8.5 scenario, many areas of the northern Mediterranean are predicted to become unsuitable as habitat for the Mediterranean green crab.

Long-term (2090–2100) predictions show more pronounced differences between the two climatic scenarios. The Mediterranean green crab will lose 43% of its optimal habitat in the SSP 1-2.6 scenario (Table 2). Under the most pessimistic scenario, a 97% optimal habitat loss is expected (Table 2), with *C. aestuarii* disappearing from the entire Mediterranean area except from the Northwest Adriatic coasts (Fig. 1).

The invasive Atlantic blue crab *C. sapidus* is currently spread in the Mediterranean basin and the ensemble model for current environmental conditions (2010–2020) identified all the Mediterranean coasts as areas with high presence probabilities, as reported in Fig. 2. From the analysis of the binary maps, we obtained a total good-quality suitable habitat of 214,025 km^2.

In 2050, the area suitable for the presence of the blue crab is forecasted to be almost unchanged with a few fluctuations, both in the SSP 1-2.6 scenario (the habitat suitability will increase by 2%) and in the SSP 5-8.5 (the suitable area will decrease by 2%) (Fig. 2; Table 2). In 2100, *C. sapidus* could increase its suitable range by 1.86% in the SSP 1-2.6 scenario (Table 2). In the SSP 5-8.5, with a temperature increase of 5 °C, the species is predicted to experience a habitat reduction of 25.75% while remaining present in almost the entire Mediterranean basin (Fig. 2; Table 2).

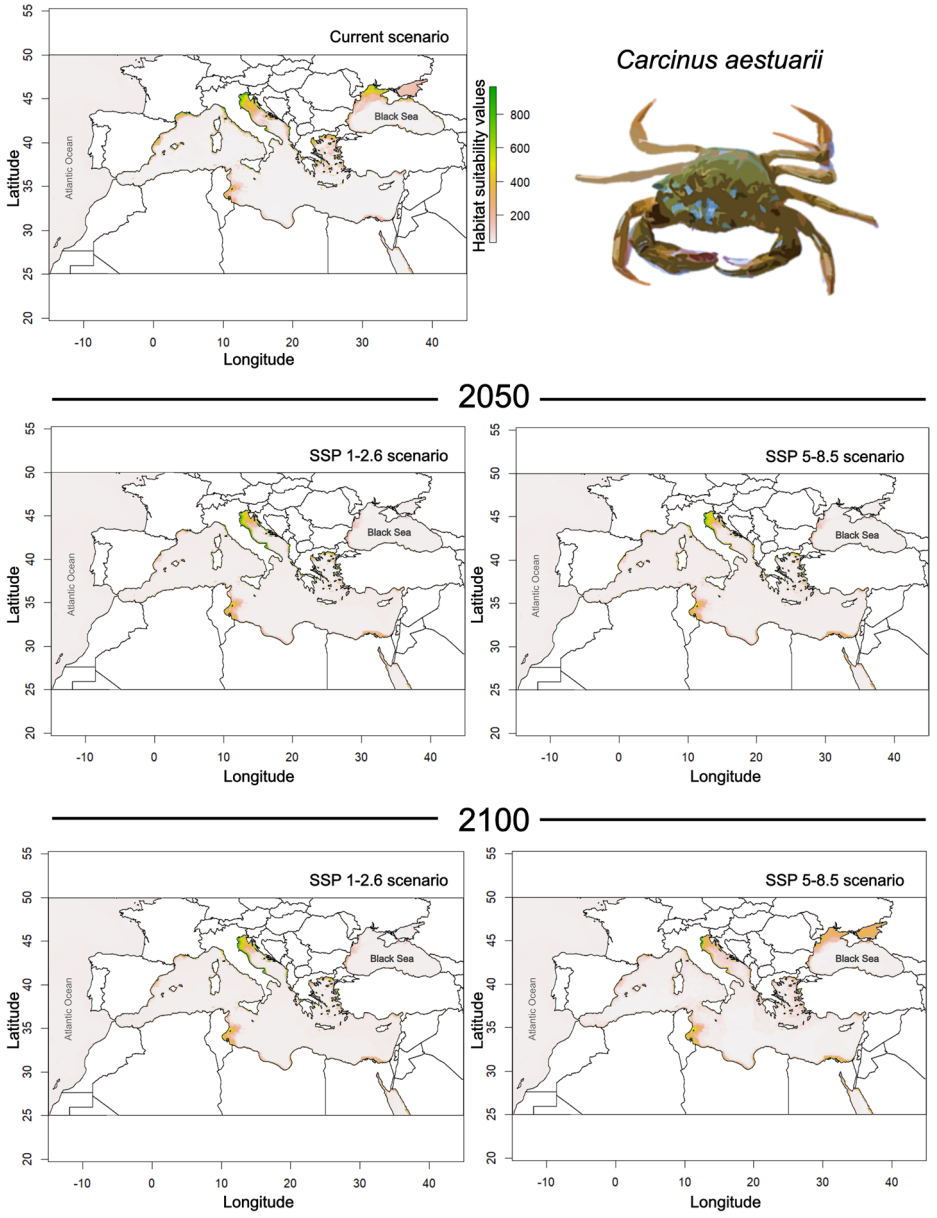

Fig. 1 Maps of predicted habitat suitability for the Mediterranean green crab *Carcinus aestuarii* under different scenarios: current environmental conditions, to 2050 with climate change scenario SSP 1-2.6 and SSP 5-8.5 and to 2100 with climate change scenario SSP 1-2.6 and SSP 5-8.5

When the SDMs for the Mediterranean green crab are run considering the distribution of the competitor *C. sapidus* as a factor, in the current climatic situation we obtain a habitat suitability scenario similar to the one calculated by SDMs run without considering the non-native species, with a binary map of 81,710 km^2 (Fig. 3).

Table 2 Range of distribution changes in future habitat suitability for *Carcinus aestuarii* and *Callinectes sapidus* under different climatic scenarios to 2050 and 2100. For *Carcinus aestuarii* the models were also run including the effect of spatial overlapping as a variable

	Range of distribution change (%)			
	SSP 1-2.6 2050	SSP 5-8.5 2050	SSP 1-2.6 2100	SSP 5-8.5 2100
Carcinus aestuarii	-40.17	-55.18	-42.95	-97.51
Callinectes sapidus	1.8	-1.86	1.86	-25.75
Carcinus aestuarii + competitor	-42.7	-59.32	-43.99	-100

In 2050, the reduction of *C. aestuarii* suitable habitat will vary between 42% and 59% throughout the entire Mediterranean basin, under the SSP 1-2.6 and the SSP 5-8.5 scenarios respectively, with the Black Sea resulting the last suitable area (Fig. 3; Table 2). For 2100, the model under the SSP 1-2.6 scenario predicts a 44% reduction in optimal habitat, while the model under the SSP 5-8.5 scenario forecasts that the Mediterranean green crab will lose 100% of its native habitat and face extreme risk of regional extirpation in the Mediterranean area (Table 2).

The two indexes representing the overlap of suitable habitat between *C. aestuarii* and *C. sapidus* (Table 3) show the same values for the binary map, indicating a current overlap of 58%, that decreases over time and with increasing temperature. The future overlap with the blue crab will remain between 45% and 42% in all scenarios except for the SSP 5-8.5 in 2100, when the green crab is predicted to occur only in the North Adriatic Sea with an overlap percentage of 80% (Table 3).

Discussion

In this study, we applied Species Distribution Models (SDMs) to assess the distribution of suitable habitats within the Mediterranean basin for the native green crab *Carcinus aestuarii* and the invasive blue crab *Callinectes sapidus*, under the current climatic conditions and under two different future climate scenarios. For the native species, we also run the models considering the effect of sympatry with the invasive species, to forecast its habitat suitability and future potential distribution range under the double effect of climate change and competition with the Atlantic blue crab. In all scenarios considered, the habitat suitability for *C. aestuarii* is projected to decrease within its own native range, i.e., the whole Mediterranean basin including the Black Sea. On the other hand, the non-native blue crab is expected to invade most of the Mediterranean coasts, representing a new competitor for the green crab *C. aestuarii*. Our results are consistent with previous studies reporting the spread of the Atlantic blue crab in the Mediterranean basin (Siddiolo et al. 2025). Our models indicate that the predicted occurrence of the blue crab is the most influential predictor shaping future habitat suitability of the Mediterranean green crab. While the inclusion of *C. sapidus* in the SDMs reflects patterns of potential co-occurrence rather than direct measures of interaction strength, the high effect of this factor is consistent with increasing ecological evidence of competitive interactions between the two species. Although alternative explanations such as shared habitat preferences or correlated responses to environmental gradients cannot be entirely excluded, the available ecological and trophic data support the interpretation that interspecific competition is likely to play a major role in shaping future distribution patterns. If the invasive blue crab will continue to spread, the native green crab could loss all his opti-

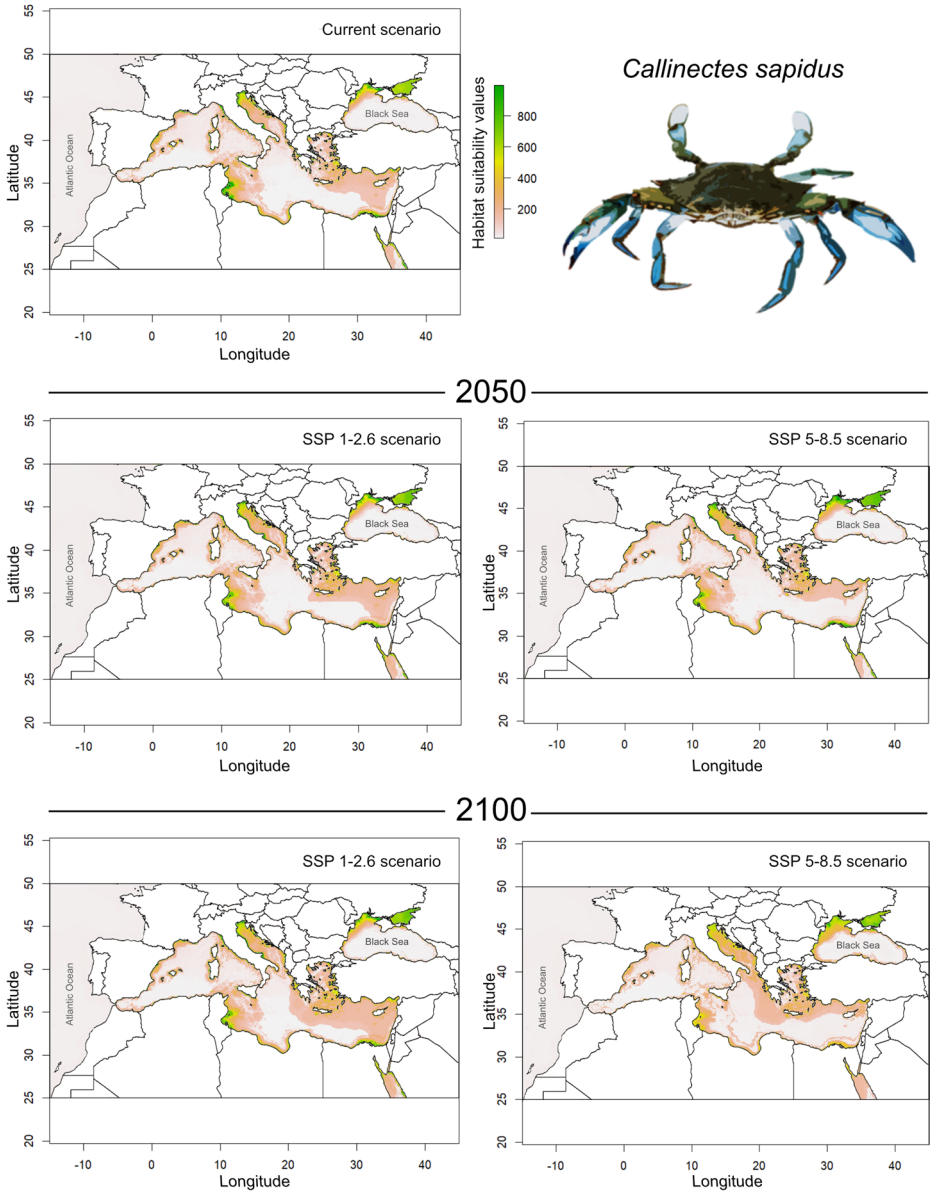

Fig. 2 Maps of predicted habitat suitability for the Atlantic blue crab *Callinectes sapidus* under different scenarios: current environmental conditions, to 2050 with climate change scenario SSP 1-2.6 and SSP 5-8.5 and to 2100 with climate change scenario SSP 1-2.6 and SSP 5-8.5

mal habitat, potentially leading to severe reduction and regional extirpation of this species in the Mediterranean basin by the end of the century.

Under current climatic conditions, the suitable habitat for *C. sapidus* encompasses the entire Mediterranean basin, significantly overlapping with the more restricted suitable areas computed for the native *C. aestuarii*. Although the current distribution range of the green

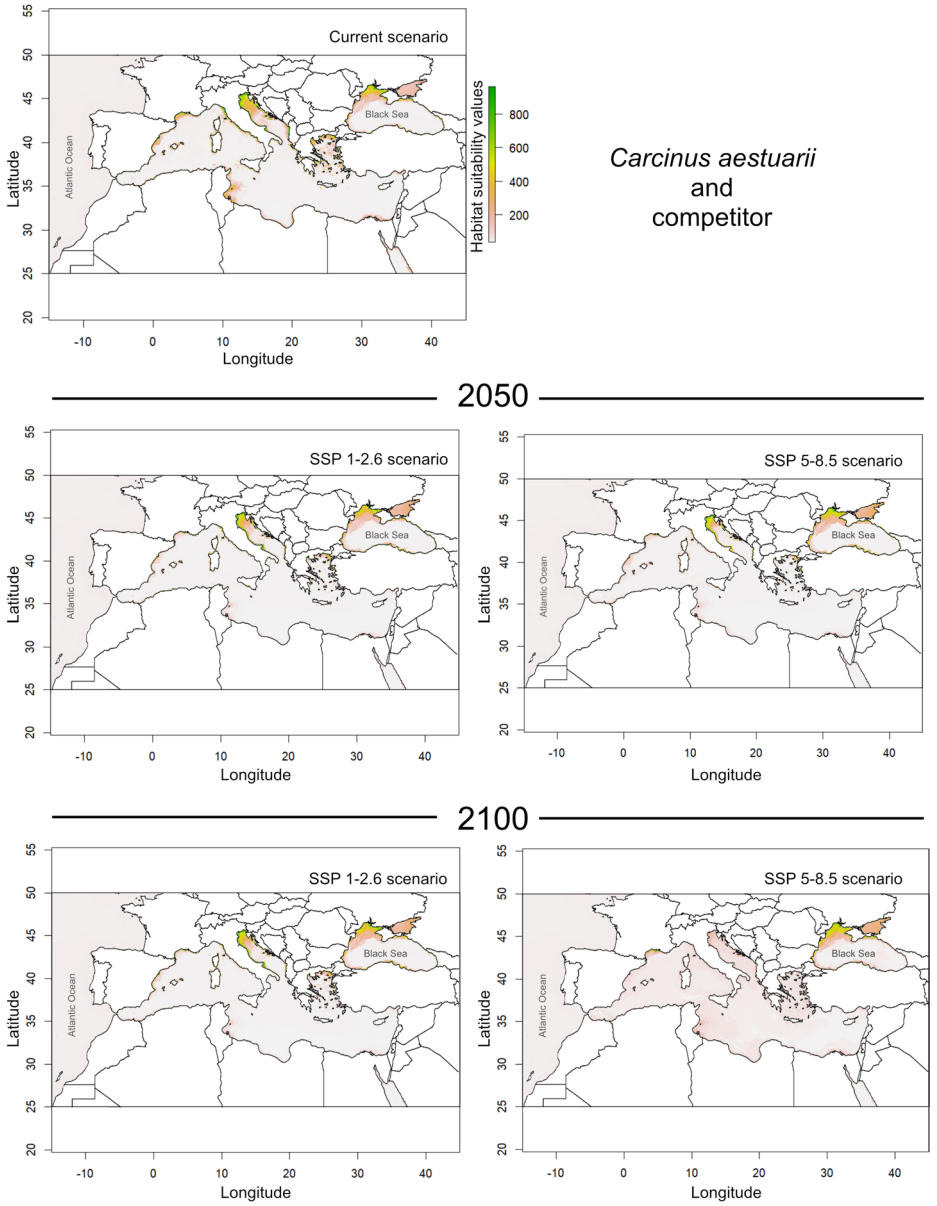

Fig. 3 Maps of predicted habitat suitability for the Mediterranean green crab *Carcinus aestuarii* considering the competition with the Atlantic blue crab *Callinectes sapidus* under different scenarios: current environmental conditions, to 2050 with climate change scenario SSP 1-2.6 and SSP 5-8.5 and to 2100 with climate change scenario SSP 1-2.6. SSP 5-8.5 scenario is not shown due to the complete loss of habitat availability

Table 3 Values of niche overlap of *Carcinus aestuarii* and *Callinectes sapidus* habitat suitability under different climatic scenarios to 2050 and 2100

	Current	SSP 1-2.62050	SSP 5-8.52050	SSP 1-2.62100	SSP 5-8.52100
Warren's I	0.92	0.89	0.89	0.89	0.92
Schoener's D	0.67	0.62	0.63	0.62	0.68
Binary map	0.58	0.45	0.42	0.44	0.08

crab still covers most Mediterranean coasts, our models indicate that the eastern and southern parts of the basin are already becoming sub-optimal. This suggests a current reduction of its ideal habitat, forcing the species to persist in marginal areas.

It is well known that both terrestrial and intertidal ectotherms can thrive in habitats where their body temperature can exceed their physiological thermal limits (Sunday et al. 2014; Jimenez et al. 2022). As many other ectotherms, green crabs are known to be able to survive in sub-optimal habitats by means of their behavioural and physiological plasticity, which allow them to avoid extreme temperatures especially during critical phases of their life (Bartolini et al. 2013). Such strategies include seeking refuge in burrows, moving to deeper or shaded waters, reducing activity during the hottest periods of the day, and adjusting the timing of key life-history events. These adaptive responses can help the species persist in marginal areas and find microclimatic refuges despite environmental stressors.

Our analyses, based on the present distribution of *C. aestuarii*, forecast a habitat reduction of about 40% under the SSP 1-2.6 scenario for the period 2050–2100 and of 55% to 97% under the SSP 5-8.5 scenario for the same period, showing a strong influence of the present global warming on its habitat suitability. The invasive blue crab, on the other hand, is forecasted to be affected by climate change only at the end of the century, and only under the worst scenario, SSP 5-8.5, when this IAS will suffer a habitat reduction of 25.75%. This pattern is consistent with the temperate geographic area of origin of *C. sapidus*, which naturally inhabits estuarine systems along the eastern coast of North America. Moderate increases in temperature may enhance its establishment and expansion in Mediterranean waters, whereas excessive warming under extreme climate scenarios may approach or exceed its physiological thresholds, thereby acting as a limiting factor. The strong influence of the forecasted expansion of *C. sapidus* across the Mediterranean on the future distribution of the green crab is supported by its wide thermal tolerance and its adaptability to very different environmental conditions. The critical thermal maximum (CTMax) experimentally established for *C. sapidus* was 40 °C (Marchessaux et al. 2022), and this thermal limit supports the hypothesis that warmer waters could favour its expansion, enhancing its growth and reproductive rates (Mancinelli et al. 2017, 2021; Marchessaux et al. 2022).

For *C. aestuarii*, the situation worsens when considering the synergistic effects of climate change and putative competition with the invasive Atlantic blue crab *C. sapidus*. While bathymetry and seawater temperature are key drivers of both species' distributions, the presence of the invasive crab emerges as the most influential factor shaping the native species' habitat suitability.

These findings suggest that the presence of the blue crab may represent a major determinant shaping the future distribution of the native green crab. The competitive advantage of *C. sapidus* can be attributed to a suite of traits, including its aggressive behaviour and larger body size, as well as highly opportunistic and omnivorous feeding habits (Darnell 1958;

Tagatz 1969; Fitz and Wiegert 1991). These characteristics have been associated with severe impacts on native biodiversity (Gennaio et al. 2006; Beqiraj and Kashta 2010; Mancinelli et al. 2017) and contribute to both direct and indirect competition with *C. aestuarii*.

In Mediterranean habitats that have been invaded by *C. sapidus*, a negative correlation has been reported between the increasing abundance of the invasive species and the decline of native taxa, including *C. aestuarii* (Gavioli et al. 2025). Although data on the trophic ecology of *C. sapidus* in the Mediterranean are still limited, emerging evidence indicates that direct predation may play a key role in this interaction. Recent dietary analyses by Vivas et al. (2025) revealed that *C. aestuarii* constituted approximately 14.7% of the gut contents of *C. sapidus* specimens, providing the first quantifiable evidence of predation pressure on the native crab species in the invaded range.

Beyond trophic interactions, *C. sapidus* also competes with *C. aestuarii* for critical habitat resources, particularly in estuarine and lagoon environments that serve as nursery and feeding grounds for both species. *C. sapidus* is known for its strong habitat plasticity, tolerating a wide range of salinities and temperatures, which allows it to colonize and dominate areas formerly occupied by native species (Nehring 2011; Mancinelli et al. 2021). In contrast, *C. aestuarii* shows a narrower ecological niche and lower mobility, which may reduce its resilience to such ecological pressures (Kampouris et al. 2019).

Although our SDMs forecast challenging scenarios within its native range, *C. aestuarii* is reported as an invasive species that established viable and expanding populations in Japan, South Africa and Argentina (Grosholz and Ruiz 1995; Carlton and Cohen 2003; Cohen et al. 1995; Le Roux et al. 1990; Hidalgo et al. 2005). The blue crab is experiencing a similar situation as a very successful invader in the Mediterranean basin, although its populations are declining within part of its native range (Childress 2014). Declines of populations within their native range and expansion into new areas are not new for a large number of invasive taxa (see Tedeschi et al. 2024 for a recent review on mammals), but it is the first time that such a mismatch is highlighted for two coastal crabs in competition with each other. More detailed analyses are necessary to understand the behavioural and physiological adaptations that could help the Mediterranean populations of *C. aestuarii* to withstand the rising water temperatures and cope with the exploitative and indirect competition with *C. sapidus*.

Conclusions

Species distribution models can be useful tools to inform conservation and management plans for both terrestrial and marine populations. The applied SDMs raise concerns about the fate of the Mediterranean green crab, projecting a scenario of total loss of suitable habitats in its native range under the synergistic effects of a worst-case climate change and competition with the invasive Atlantic blue crab. Although further studies are needed to understand the ability of native *C. aestuarii* populations to cope with this double trouble, our findings highlight the urgent need for targeted management actions, including early detection and rapid response protocols, public awareness campaigns, and, where feasible, control strategies for the Atlantic blue crab. Our analyses also showed that incorporating interspecific interactions into predictive modelling frameworks may enhance the reliability of projections under future climate scenarios, allowing for more robust conservation planning. Future research should aim to integrate spatially explicit management scenarios

into predictive frameworks, for instance by simulating localized containment or removal of Atlantic blue crab, in order to assess whether targeted interventions could alleviate competitive pressure on native Mediterranean green crab populations under climate change.

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Data availability Data will be made available on request.

Declarations

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