RESEARCH PAPER

WILEY Journal of Biogeography

Multiple stressors facilitate the spread of a non-indigenous bivalve in the Mediterranean Sea

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Abstract

Aim: The introduction of non-indigenous species (NIS) via man-made corridors connecting previously disparate oceanic regions is increasing globally. However, the environmental and anthropogenic factors facilitating invasion dynamics and their interactions are still largely unknown. This study compiles and inputs available data for the NIS bivalve *Brachidontes pharaonis* across the invaded biogeographic range in the Mediterranean basin into a species distribution model to predict future spread under a range of marine scenarios.

Location: Mediterranean Sea.

Methods: A systematic review produced the largest presence database ever assembled to inform the selection of biological, chemical and physical factors linked to the spread of *B. pharaonis* through the Suez Canal. We carried out a sensitivity analysis to simulate current and future trophic and salinity scenarios. A species distribution model was run to determine key drivers of invasion, quantify interactive impacts arising from a range of trophic states, salinity conditions and climatic scenarios and forecast future trajectories for the spread of NIS into new regions under multiple-parameter scenarios (based on the main factors identified from the systematic review).

Results: Impacts on invasion trajectory arising from climate change and interactions with increasing salinity from the new opening of the canal were the primary drivers of expansion across the basin, the effects of which were further enhanced by eutrophication. Predictions of the current distribution were most accurate when multiple stressors were used to drive the model. A habitat suitability index developed at a subcontinental scale from model outputs identified novel favourable conditions for future colonization at specific locations under 2030 and 2050 climatic scenarios.

Main conclusions: Future expansion of *B. pharaonis* will be enhanced by climate-facilitated increased sea temperature, interacting with increasing pressures from salinity and eutrophication. The spatially explicit risk output maps of invasions represent a powerful visual product for use in communication of the spread of NIS and decision-support tools for scientists and policymakers. The suggested approach, the observed distribution pattern and driving processes can be applied to other NIS

species and regions by providing novel forecasts of species occurrences under future multiple stressor scenarios and the location of suitable recipient habitats with respect to anthropogenic and environmental parameters.

1 | INTRODUCTION

Climate change is driving poleward range shifts across a wide range of marine benthic taxa (Helmuth, Mieszkowska, Moore, & Hawkins, 2006; Mieszkowska, Sugden, Firth, & Hawkins, 2014; Mieszkowska et al., 2006; Pecl et al., 2017) and is thought to be exacerbating the invasion success of non-indigenous species (NIS) (Pederson et al., 2011). Climate change exerts a significant and growing impact on global biodiversity and potential "globalization" of marine biota resulting in biodiversity loss, alteration of ecosystem function and degradation of ecosystem services (Gallien, Münkemüller, Albert, Boulangeat, & Thuiller, 2010). The majority of marine NIS that have successfully colonized new regions beyond those accessible via natural modes of dispersal are thought to proliferate in their introduced ranges due to their greater tolerances for one or more environmental parameters when compared to native species within the invaded community (Lenz, da Gama, & Gerner, 2011). Advances in our ability to track biogeographic range shifts and invasions have increased awareness of the complexity of environmental and anthropogenic processes involved in biological invasions in a changing world. Beyond a simplistic, unilateral response to warming of the global oceans, scientists seek new, integrated approaches to predict future biogeographic shifts of NIS (Burrows, Schoeman, & Richardson, 2014). The development of predictive models that can be run for a range of multiple anthropogenic factor (hereafter termed stressors) scenarios will increase the accuracy of quantitative forecasts for ecological and economic costs of invasion, and provide useful guidance for planning management or control strategies that form part of the mitigation and adaptation management processes (Chapman, Makra, & Albertini, 2016).

A specific mode of invasion is that observed for Lessepsian invasive species, those utilizing the Suez Canal (a man-made corridor between previously unconnected seas) as a pathway to colonize new environments far removed from their origin. This canal connects the Indo-Pacific and the Red Sea with the Mediterranean Sea, the "Eastern door" through which NIS invade the Mediterranean basin by planktonic larvae in a "stepping stone" fashion and via shipping vectors of hull fouling and ballast water transport (Galil, Boero, & Campbell, 2015). This situation is not unique, with man-made corridors providing connective pathways for marine invasions around the world (e.g. Panama, White Sea–Baltic Sea, Kiel and Danube–Black Sea Canals). Shipping and shipping-related constructions are thus contributing to the movement of marine species around the world,

shaping the origin, frequency and magnitude of movements by providing new introduction routes for Lessepsian invasions (Katsanevakis, Zenetos, Belchior, & Cardoso, 2014).

The key to a successful invasion is the presence of suitable habitats (sensu resistance hypothesis; Ruiz et al., 2000) with respect to physical, chemical and trophic conditions in those areas where new NIS propagules arrive (Hulme, Bacher, & Kenis, 2008). Climatic and anthropogenic forcing of the marine environment, coupled with an increase in shipping traffic from the Levantine basin are thought to have amplified both the habitat suitability (HS) and the propagule pressure for NIS within the Mediterranean in recent years (Katsanevakis et al., 2014); however, this has not been quantitatively investigated for most recorded NIS.

Here we investigate how anthropogenically driven changes to the marine environment may exacerbate the existing impacts of NIS on native species, communities and ecosystems and alter their trajectory of future spread. We use the recent expansion of the Suez Canal via a second parallel seaway as a case study system to test the impacts of multiple anthropogenic stressors on the invasion trajectory of a Lessepsian NIS within the Mediterranean Sea, and address how such infrastructure can result in wider implications for both Lessepsian and global species invasions. The second waterway will have a large impact on the biological (e.g. increase of the propagule pressure for a wide variety of species), physical and chemical characteristics of basin. Biotic changes have already occurred as a result of several previous enlargements of the existing canal, resulting in environmental changes initiated in the Eastern basin propagating across the entire area (Katsanevakis et al., 2014). Invasion dynamics are predicted to accelerate with exposure to these human- (e.g. eutrophication; Nixon, 2009) and climate-related factors (e.g. modification of temperature and wind-driven hydrodynamics; Adloff et al., 2015) which are already driving range shifts in the distributions of native species, altering community structure, diversity and resilience, thus favouring biological invasions (Pecl et al., 2017). We predict that these drivers will interact with those deriving from the new Suez Canal opening, exposing Mediterranean biodiversity to large modifications of chemical and physical properties.

The focal species of this study is the Lessepsian mussel, *Brachidontes pharaonis* (Fischer 1870), a bivalve classified as a "pest model NIS" (Galil, 2009), widely reported to be invading the Mediterranean littoral rocky habitat. However, knowledge of the ecology and physiology of this species is lacking in comparison with other marine NIS. *Brachidontes pharaonis* has a planktonic larval phase and a protracted,

year-round reproductive cycle. This species has a wide thermotolerance range (9–31°C) and can tolerate salinities from 35 to 53 psu, traits typical of most Lessepsian NIS (Sarà, Romano, Widdows, & Staff, 2008; references listed in Appendix S1). *Brachidontes pharaonis* exerts strong local-scale effects on hard substrata biodiversity by creating biogenic habitat that promotes local species richness, out-competing native species for resources and space (Safriel & Sasson-Frostig, 1988; Appendix S1). The biology and invasion ecology of this species is typical of NIS with respect to wide ecophysiological tolerance ranges for environmental parameters including temperature, salinity and pH, making *B. pharaonis* a suitable model species with which to study how human- and climate-related factors will drive biological invasions from the present day to 2050.

While recent approaches based on mechanistic trait-based models (Sarà, Palmeri, Rinaldi, Montalto, & Helmuth, 2013) are able to reliably predict the current spatial distribution of NIS, they require huge amounts of data in order to provide reliable predictions of NIS spread in the future when assessing the effects of environmental change, including climate. Unfortunately, the investigation of impacts arising from multiple anthropogenic factors is still far from the application's range of mechanistic trait-based modelling. To provide a valuable, effective and immediate tool for decision-making in NIS management, we employed an integrated classical correlative approach to NIS modelling, bringing the novelty of the interaction between multiple stressors (salinity and temperature as proxies of tropicalization and eutrophication as a proxy of local urbanization) tested through a set of sensitivity analyses. Thus, we derived reliable and exploitable information to: (1) generate risk maps of future biological invasions (sensu Hulme, 2009) to feed strategic and tactical pest management decisions; (2) forecast relevant outcomes to inform scientists and managers on ecological and socio-economic potential impacts generated by ongoing invasions; (3) fulfil emergent regulations, policy drivers and directives in the framework of European Parliament and Council; and (4) provide strategies for managing NIS as part of a realistic, integrated, ecosystem-based approach, which is a major challenge for the scientific community, stakeholders and decision makers.

2 | MATERIALS AND METHODS

2.1 | Literature search

An extensive literature analysis was completed *viz.* a systematic review, designed to investigate the past and present distribution of *B. pharaonis* across the Mediterranean basin and identify factors potentially affecting its ability to colonize new habitats. The search was carried out using prominent or substantial keywords forming a simple search string ("*Brachidontes pharaonis*" AND "Mediterranean"). The search ranged from the year 1900 to the present day. The search string was entered into scientific computerized databases including: ISI Web of Sciences, Scopus, BioOne, CAB Abstracts, Aquatic Sciences and Fisheries Abstracts (since 1971), Directory of Open Access Journal and J-STOR. Additional general search engines

were used (Google and Google Scholar) limiting the search for appropriate data to the Word, PDF and/or Excel documents and to the first 50 hits (Mangano & Sarà, 2017a, 2017b). A hand search was performed on bibliographies of relevant review articles to identify any additional references. Data on presence records were searched in specific database and information systems showing current and past distribution maps (e.g. shapefiles, polygons, points); Ocean Biogeographic Information System—http://www.iobis.org/; Global Biodiversity Information Facility—http://www.gbif.org/; AquaNIS—http://www.corpi.ku.lt/databases/index.php/aquanis; DAISIE—http://www.europe-aliens.org, EASIN—http://easin.jrc.ec.europa.eu; World Register of Introduced Marine Species—http://www.marinespecies.org/introduced/aphia. Authors of relevant articles not readily available online were contacted to provide missing data and unpublished material or further recommendations (search ended at 21 August 2015). Hits generated from the search were collated in a database, examined for relevance and critically appraised (Table A1 in Appendix S1). Data and evidence extraction from peer-review and grey literature were organized and synthesized according to specific criteria, e.g. geographic area, habitat preferences, associated species, with a complete list of the collated studies for each Mediterranean sector (Table A1 in Appendix S1). All quantitative information from each paper were extracted to draw up the most correct and precise picture of the ecological status of *B. pharaonis* in the Mediterranean basin and on the environmental parameters influencing its distribution.

2.2 | MAXENT modelling

Presence data that represented the current known distributions for *B. pharaonis* extracted through the systematic review process were used to build the occurrence dataset within the study area. Data and evidence from the review process were used to populate a presence-only maximum entropy (MAXENT) species distribution model (SDM) to forecast habitat suitability (Phillips, Anderson, & Schapire, 2006) for *B. pharaonis*. MAXENT represents the most effective correlative modelling approach in context of SDM (Guisan & Zimmermann, 2000), providing an important ecological tool for the prediction of NIS geographic distribution within the context of climate change (Elith & Leathwick, 2009; Walther et al., 2009). These scenarios were used to forecast how the potential habitat suitability for *B. pharaonis* will vary across three trophic statuses (oligotrophication, no change and eutrophication) in combination with 11 salinity conditions across a gradient from decreasing, no change to increasing salinity with respect to two climate scenarios (2030 and 2050; Med-Cordex Regional Climate Model, Representative Concentration Pathways 4.5). Trophic and salinity conditions were simulated through sensitivity analyses, an alternative tool to explore the robustness of models' outputs within an uncertain context (Payne, Barange, & Cheung, 2015).

Data cleaning was required to remove data duplicates and incorrect records. Sampling bias is a well-known factor influencing SDMs (Phillips et al., 2006), leading to spatial autocorrelation of records

and artificial spatial clusters of observations, violating the assumption of independence (Dormann, McPherson, Araújo, Bivand, & Bolliger, 2007). This bias can be avoided by sampling one point *per* cluster in the environmental space, which was carried out using the software OccurrenceThinner (Verbruggen, 2012). OccurrenceThinner identifies areas of high record density based on the species occurrence records and a two-dimensional kernel surface grid file representing the region of study to filter occurrence records (Verbruggen et al., 2013). Ten pseudo-replicate datasets produced through OccurrenceThinner, each with reduced sampling bias, were run in order to reduce densely sampled regions. After this procedure, the occurrence dataset contained 98 unique presence records. These were used, with eight physical, chemical and biological variables selected after the collinearity tests (Variance Inflation Factor—VIF, Table A2 in Appendix S1), to model the current distribution of *B. pharaonis* in the invasive range (Figure 1).

Environmental climatic NetCDF data (Network Common Data Form) were downloaded from the Med-CORDEX website (https://www.medcordex.eu/). NetCDF files were extracted and manipulated employing the Climate Data Operator (CDO) software (1.6.4 version; Max-Planck Institut für Meterologie). Layers of chlorophyll concentration data were obtained from Copernicus project (http://marine.copernicus.eu/). For the future scenarios, we assumed a magnitude of change in chlorophyll-a concentrations of +10%, coded as eutrophication scenario, and −10%, coded as oligotrophication scenarios. Similarly, we generated 11 salinity scenarios: no change, five salinity decrease scenarios (from −0.1 to −0.5) and five salinity increase scenarios (from +0.1 to +0.5).

Prior to analysis, all environmental data were rescaled at 1 km applying the nearest neighbour interpolation. Eight environmental variables were selected (Table A1 in Appendix S1) based on their biological relevance, as potential predictors of habitat distribution for *B. pharaonis*. Species distribution models were applied using MAXENT 3.3.3k (Phillips et al., 2006). The default settings including logistic output, regularization multiplier 1 and 10,000 background points were used. The model evaluation was carried out through the random test percentage, splitting the whole dataset in training (70%) and test data (30%), subsamples (equal to the number of observation) and 5,000 iterations, using the easily interpretable logistic output format with habitat suitability values. MAXENT generates an estimate of species probability presence ranging from 0 (unsuitable habitat) to 1 (optimal habitat) representing the distribution in geographic space of suitable habitat (i.e. Habitat Suitability Index—HSI; Elith et al., 2006; Phillips & Dudík, 2008). Subsample replicates from MAXENT were used as proxies for different single-models to reach a consensus scenario, reduce model inter-variability and avoid
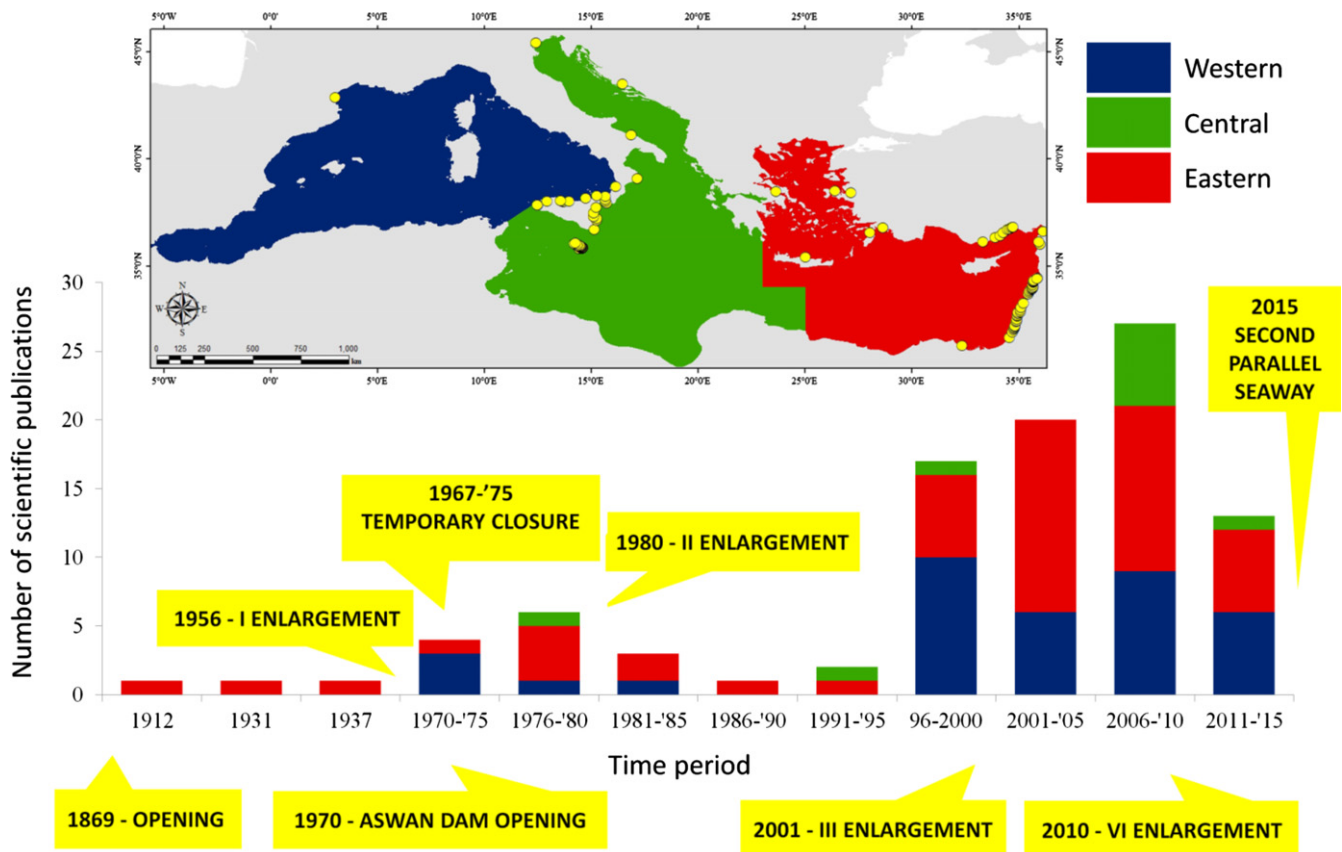

FIGURE 1 Temporal trend of the number of scientific publications across the three considered Mediterranean basin (total number of plotted hits 98 except global and regional reviews; search performed at 20 July 2015). Presence records of *Brachidontes pharaonis* extracted from literature and employed to run MAXENT models (yellow points on the map). The main evolutions of the Suez Canal are reported (yellow labels on the graph, data derived from "http://www.suezcanal.gov.e.g/"\t"_blank") [Colour figure can be viewed at wileyonlinelibrary.com]

potentially compromising policy decisions. To construct current distributions, we converted the continuous suitability predictions to binary predictions using the "threshold equal training sensitivity and specificity" command in MAXENT. The sensitivity is the probability that the model correctly predicts an observation (true positive rate), while specificity is the probability that a known absence is correctly predicted (true negative rate). This is the most reliable threshold allowing to minimize the absolute difference between sensitivity and specificity (Nenzén & Araújo, 2011) and to balance the accuracy of areas correctly modelled as present and absent in the training and test data. Specifically, at this threshold the chance of missing suitable distribution and assigning unsuitable distribution is the same.

The performance model was assessed by calculating the area under the curve (AUC) of the receiver operator characteristic (ROC), a measure of discrimination capacity of generated models (Delong, Delong, & Clarke-Pearson, 1988). Models with an AUC of 0.5 corresponded to the expected performance of a random classifier, 0.7–0.8 are considered an acceptable prediction, 0.8–0.9 are excellent and >0.9 are outstanding (Hosmer & Lemeshow, 1989).

Prior to running the models, all environmental data were remapped using the nearest neighbour interpolation, employing CDO in order to achieve the highest possible spatial resolution (1 km), with the same extent and spatial projection used for all variables. Subsequently, the entire environmental dataset was clipped with the Mediterranean coastline. Collinearity between predictors was tested applying the vifstep function from the 'usdm' package in R (Naimi, 2013) and the predictor variables were selected.

In order to assess the rate of expansion of *B. pharaonis* in response to recent and short-term future climate change, models were run for the time-steps 2010, 2030 and 2050. For the future distribution models, 66 scenarios of salinity (11 scenarios) and chlorophyll-a concentration parameters (3 scenarios) were calculated and the obtained results were divided for the three Mediterranean basins: Eastern, Central and Western (Figure 1). From these scenarios, HSI was derived for each time step across the basins (Figures 3 and 4) and presented as geographic forecast maps. The percentage of variation of mean HSI was estimated in comparison to 2010 (Figure 2) for each of the 66 simulated scenarios respectively for 2030 and 2050 under different trophic and salinity scenarios (Table A1 in Appendix S1). The invasion risk of this species was tested by calculating the frequency of scenarios in which the HSI was greater than 0.7 to highlight the suitable areas for colonization under the possible future environmental states. Potential interactions between HSI and the environmental variables considered in 2010 were analysed as absolute Pearson correlations and kernel density overlays (Feld, Segurado, & Gutiérrez-Cánovas, 2016).

3 | RESULTS

Studies published on *B. pharaonis* during the 2000s (Figure 1) show the introduced range spreading westwards throughout the Mediterranean Sea, following the anticlockwise direction taken by most

Lessepsian NIS (Katsanevakis et al., 2014). The outputs of the systematic review identified the ability of this NIS to compensate for large changes in temperature and salinity regimes, with wider thermotolerance ranges and increased tolerance of higher salinities in comparison to native Mediterranean bivalves (Table A1 in Appendix S1). No evidence exists within the current literature on the effect of trophic status on the presence of *B. pharaonis*, although as most filter feeder diets comprise of fresh particulate organic matter and detritus, will likely be affected by trophic condition shifts as expressed by changes in suspended chlorophyll-a.

Under future scenarios, 2030–2050, eight predictors were identified, with chlorophyll-a, salinity and surface temperature exerting the greatest influence on the invasion pathway for *B. pharaonis* (Figures A2 & A3; Tables A1–A3 in Appendix S2). Chlorophyll-a (adopted as proxy of local urbanization; Nixon, 2009), salinity and surface temperature (proxy of tropicalization; Azzurro, Soto, Garofalo, & Maynou, 2013) were the predictors accounting for the highest percentage of the modelled current distribution (Figure A1 and Table A1 in Appendix S2), which was in accordance with values from the literature (AUC = 0.816 ± 0.052; Figure 2 current scenario, 2010). For the 2010 model, the marginal response of *B. pharaonis* to the selected environmental variables is reported in Figure A4 in Appendix S2. Of all stressor predictor variables tested, salinity change will be the most important driver modifying Lessepsian NIS distribution pathways (Galil, Marchini, Occhipinti-Ambrogi, & Ojaveer, 2017; Rilov & Galil, 2009). As already known from the literature, this species shows a marked hypersaline affinity (Sarà et al., 2008) and the forecasted increase in salinity will likely promote the spatial spread of the propagules towards the Western basin.

3.1 | Habitat suitability

In 2030, the contribution of climate-related factors will increase the forecasted habitat suitability HSI by 47%, 25% and 14% for the Eastern, Central and Western basins respectively (Table 1) in comparison to 2010 (Figures 2 and 3). Estimating the HSI likelihood under increasing salinity scenarios arising from the new Suez Canal opening (from +0.1 to +0.5 psu; Table 1) and under no change trophic conditions (i.e. no change; Table 1), in 2030 HSI will increase by 161%, 53% and 27% per basins. In 2050 under no change trophic conditions, HSI will increase by 182%, 75% and 40% respectively. If the trophic conditions of the three Mediterranean basins become more eutrophic, the HSI will also dramatically increase (Table 1 right panels; Figures 3 and 4). Conversely, an overall reduction in HSI values will occur for the whole Mediterranean Sea under conditions of decreased salinity and oligotrophication (Table 1 left panels; Figures 3 and 4). The effect of changes in chlorophyll-a concentrations depends on the basin considered. For the scenario with no change in salinity in 2030, eutrophication leads to increase in HSI by 16.30%, while decrease by −2.08% is expected for more oligotrophic conditions in the Eastern basin. The exact opposite pattern, however, occurs in the Western basin with a decrease by −2.03% in case of eutrophication and increase of 26.02% for oligotrophication.
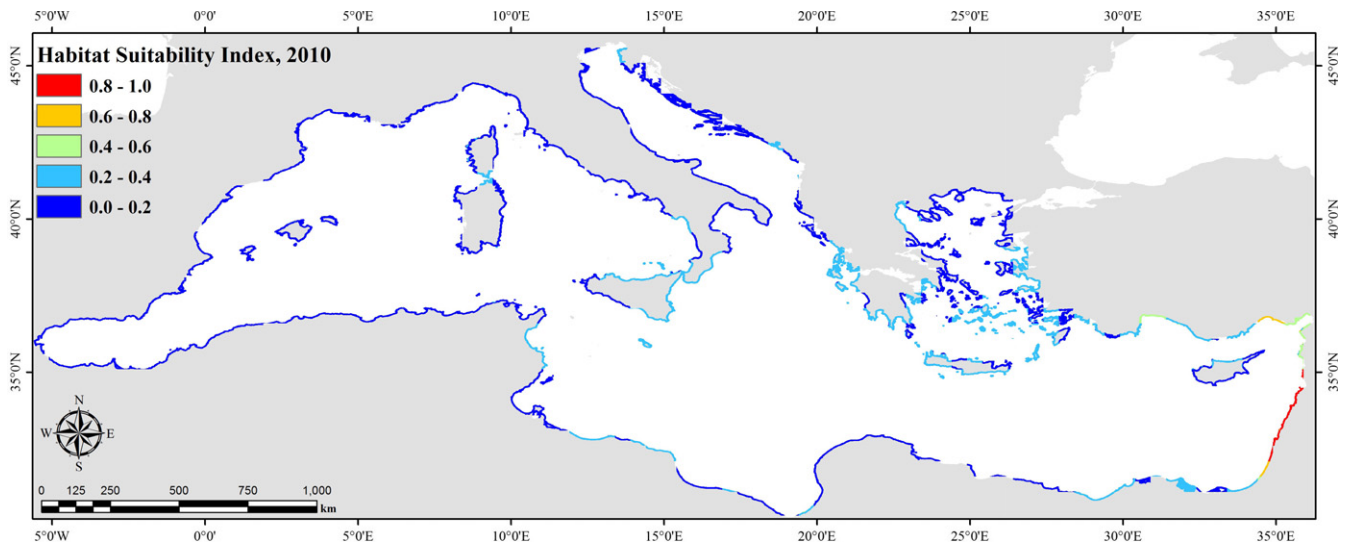
FIGURE 2 Spatial distributions of predicting suitable habitat of *Brachidontes pharaonis* under 2010 current scenario (AUC = 0.809 ± 0.043) for the Mediterranean Sea [Colour figure can be viewed at wileyonlinelibrary.com]

Similarly, when the salinity is increasing by +0.5 psu, HSI in the Western basin increases more strongly for oligotrophication (+48.84%) than for eutrophication scenario (+27.28%), but the opposite response occurs in the East (+129.15% vs. +153.69%).

The interactions between HSI and the environmental variables considered in 2010 were reported in Figure A5 (Appendix S2—predictor environmental variables). The results highlighted that the salinity (0.45) and the SST (0.38) were the most correlated environmental variables with the HSI.

Figures 5 and 6 represent the number of scenarios in which the HSI resulted greater than 0.7 for the 2030 and 2050 respectively. The frequency of agreement between models outputs in both time periods, were higher in the Eastern portion of the Mediterranean, while the area of the Aegean Sea and the South-Eastern Italy in the Western portion of the Mediterranean presented lowest values. HSI never exceeded 0.7 within the Western Mediterranean basin in the scenarios analysed.

3.2 | Multiple stressors

In 2030 and 2050, the combined effects of multiple stressors will generate a synergistic effect under increased salinity scenario. In contrast, effects of multiple stressors will generate an antagonistic response under decreasing salinity scenarios. The climate change stressors (SST and wind stress) will increase HSI by 11%, 18% and 8% in 2030 and 32%, 41% and 32% in 2050 (Eastern, Central and Western basins respectively; Table 1). A synergistic effect is evident with changes in trophic status conditions (HSI will range from −2% to 26% in 2030 and 19% to 48% in 2050; Table 1). Under future decreasing salinity scenarios there will be a decrease in the mean HSI, whereas HSI will increase under increasing salinity scenarios, with the effect being more marked in 2050 (Table 1). Potential interactions, representing the response of HSI to pairwise

stressor combinations are reported in Appendix S2 (Figures A4 and A5).

4 | DISCUSSION

The forecast scenarios show unexpected consequences when climate change interacts with increasing salinity derived from the new Suez Canal opening, further altered by changing trophic conditions produced by local human pressures (sensu Nixon, 2009). The main predicted effect of the doubling of the Suez Canal will be the increase of the propagule pressure for a variety of species that are likely to colonize the Levantine waters. The future westwards spread of *B. pharaonis* is forecast for both periods 2030 and 2050 under a 10% increase in eutrophication scenario, when climate change and salinity increase are modelled together, with interaction effects evident. The pathway from the current, localized distribution within the introduced range in the western basin is predicted to predominantly follow a north-westerly trajectory, with colonization of new sites forecast along the northern coastline. Some colonization of the southern coastline is also predicted, but to a far lesser extent. Secondary introductions (e.g. through ballast waters) in a westerly direction from Levantine waters are a more complex phenomenon, potentially related to the warming of the sea and to additional hydrographic changes that are a consequence of the global climate change (e.g. salinity and trophic factors). The interregional differences showed by our modelling are predominantly related to the spatial variation in the productivity across the Mediterranean Sea, with more oligotrophic conditions prevailing in the Eastern sector. Considering the preference of *B. pharaonis* for average levels of productivity, the 10% increase in productivity should facilitate the spread throughout the Eastern basin, but at the same time hinder the invasion in western eutrophic waters.

TABLE 1 Percentage of variation of mean habitat suitability index (HSI), in comparison to 2010, within the three considered Mediterranean basins (Eastern, Central (Sicilian Channel, Ionian and Adriatic seas) and Western (Tyrrhenian, Balearic and Alboran seas) for each of the 66 simulated scenarios respectively for 2030 and 2050 under different trophic and salinity scenario (OLIGOTROPHIC = OLIGOTROPHICATION; EUTROPHIC = EUTROPHICATION) [Colour table can be viewed at wileyonlinelibrary.com]

		DECREASE ←					2030 SALINITY	INCREASE →				
		0.5	0.4	0.3	0.2	0.1	0	0.1	0.2	0.3	0.4	0.5
OLIGOTROPHIC	Eastern	−26.44	−17.48	−18.12	−13.26	−10.05	−2.08	44.43	68.73	135.26	129.59	129.15
	Central	−6.62	5.16	2.65	10.57	14.05	14.73	17.11	20.53	30.87	42.80	106.07
	Western	1.92	13.24	12.00	18.35	23.77	26.02	27.99	27.02	35.33	48.31	48.84
NO CHANGE	Eastern	−12.66	−13.19	−8.03	−1.26	0.66	10.91	61.73	116.12	116.84	122.62	139.13
	Central	0.36	0.47	1.21	12.45	11.77	18.23	19.92	29.67	30.00	45.71	111.71
	Western	−1.87	−5.21	−2.28	6.47	5.58	7.74	13.56	20.51	19.74	26.71	36.08
EUTROPHIC	Eastern	−8.96	1.49	0.65	−0.87	3.94	16.30	67.72	107.24	145.66	147.54	153.69
	Central	−2.73	6.46	5.80	6.82	6.51	15.91	21.49	32.32	27.63	48.51	115.16
	Western	−16.47	−9.35	−7.65	−6.33	−8.67	−2.03	6.55	19.68	7.60	19.99	27.28
		DECREASE ←					2050 SALINITY	INCREASE →				
		0.5	0.4	0.3	0.2	0.1	0	0.1	0.2	0.3	0.4	0.5
OLIGOTROPHIC	Eastern	−1.58	3.09	5.57	8.54	11.46	18.88	74.91	113.07	154.10	160.10	181.08
	Central	20.74	22.98	25.91	30.05	37.90	41.39	43.21	48.61	62.12	70.00	134.15
	Western	25.14	25.96	35.27	30.34	41.31	48.01	49.60	51.49	61.96	64.04	67.59
NO CHANGE	Eastern	7.99	15.40	18.36	24.32	27.76	31.83	90.10	137.55	136.39	167.72	185.92
	Central	18.98	25.07	32.71	37.33	34.94	40.69	55.54	58.17	61.25	68.12	136.67
	Western	7.53	11.77	21.91	24.60	21.39	31.63	41.01	37.26	39.76	34.83	53.24
EUTROPHIC	Eastern	19.12	23.41	35.41	31.29	32.80	44.61	94.62	133.33	150.93	177.08	192.60
	Central	24.29	27.82	40.95	35.45	38.31	46.81	48.83	52.88	66.50	74.81	136.41
	Western	0.38	7.34	17.64	15.86	17.04	22.11	22.22	27.05	33.71	34.21	35.32

Synergistic interactions cause the equilibrium of native communities to shift, favouring NIS invasions. A climate-facilitated expansion will likely result from future increases in temperature, as the spread of *B. pharaonis* will be promoted under conditions of interacting stressors of trophic and salinity changes.

To date, however, there is a lack of biogeochemical models and the availability of projected datasets for salinity and eutrophication is still scant. Thus, the reliability of projected scenarios is widely debated and considered less confident than that of other variables considered in this study (e.g. sea surface temperature, wind stress, etc.). Following the precautionary principle, a set of sensitivity analysis was performed to cover all possible expected changes.

A number of criticisms have been advanced against the use of SDMs, e.g. these tools do not consider biotic interactions, evolutionary change and species dispersal (Pearson & Dawson, 2003). However, the SDM approach can provide useful first results, giving an approximation of the impact of environmental change including climate on species distributions (Guisan, 2013). Despite limitations, SDMs may be useful in conservation planning by contributing to strategic decisions about environmental change impacts, and can play a key role by highlighting likely shifts of suitable habitat of NIS invasion (Araujo, Alagador, Cabeza, Nogues-Bravo, & Thuiller, 2011). One of the main problems of SDMs could be due to the potential underestimation of the potential spread of these species and consequentially the suitable habitat predicted can represent only a conservative estimate (Parravicini, Azzurro, Kulbicki, & Belmaker, 2015).

The use of SDM tools remains challenging, but the potential to assess future invasion risk by identification of areas vulnerable to

FIGURE 3 Spatial distributions of predicting suitable habitat of *Brachidontes pharaonis* under 2030 future scenario, considering the scenarios with a decrease (−0.5 psu, panels a and c) and increase (+0.5 psu panels b and d) of salinity, and both oligotrophication (−10%; on the left, panels a and c) and eutrophication (+10%; on the right, panels b and d) conditions [Colour figure can be viewed at wileyonlinelibrary.com]
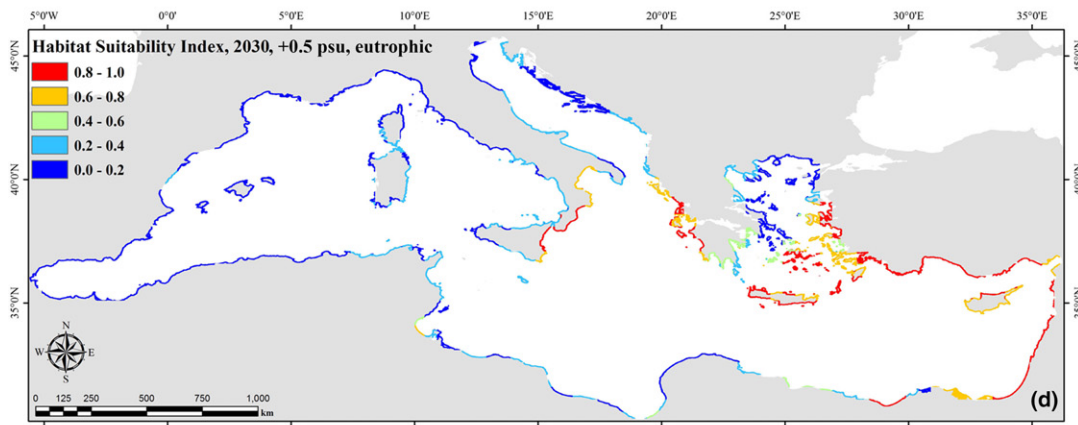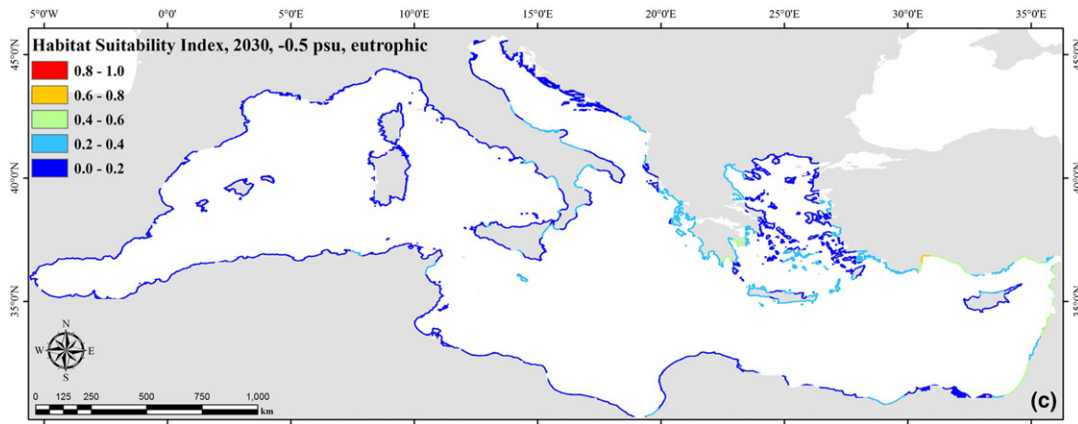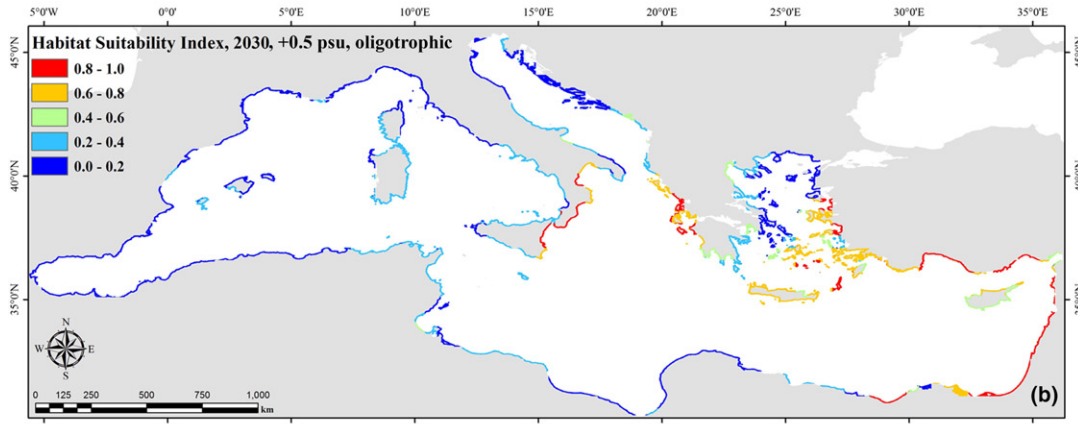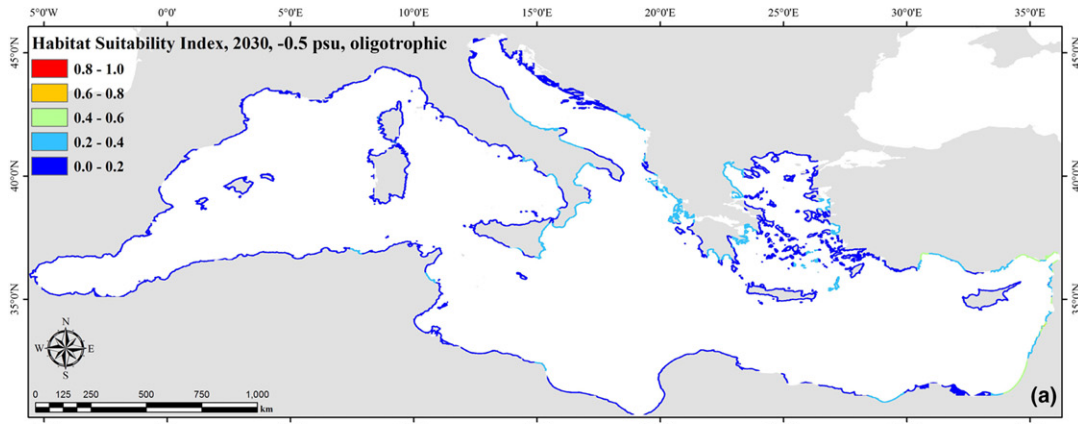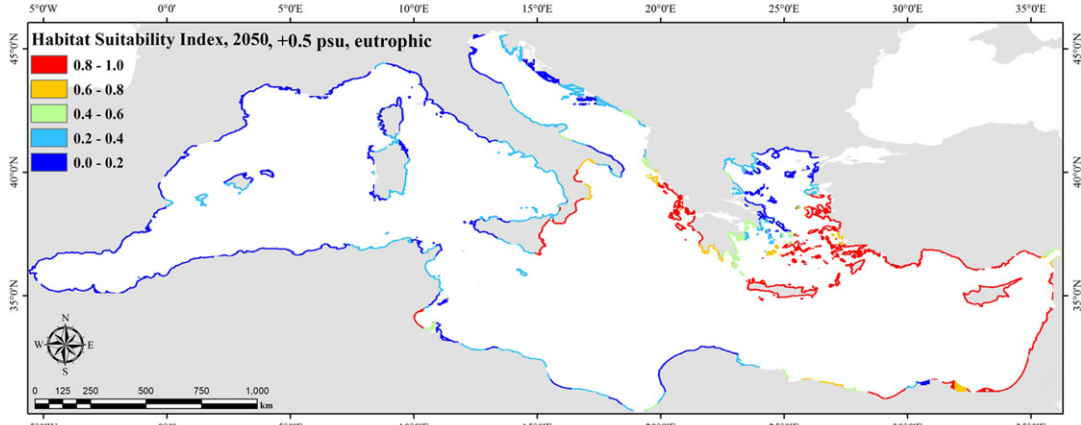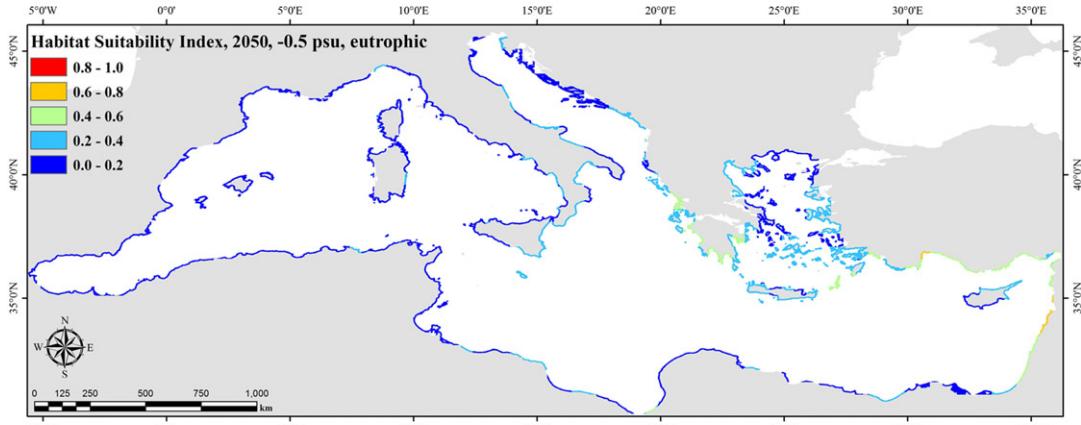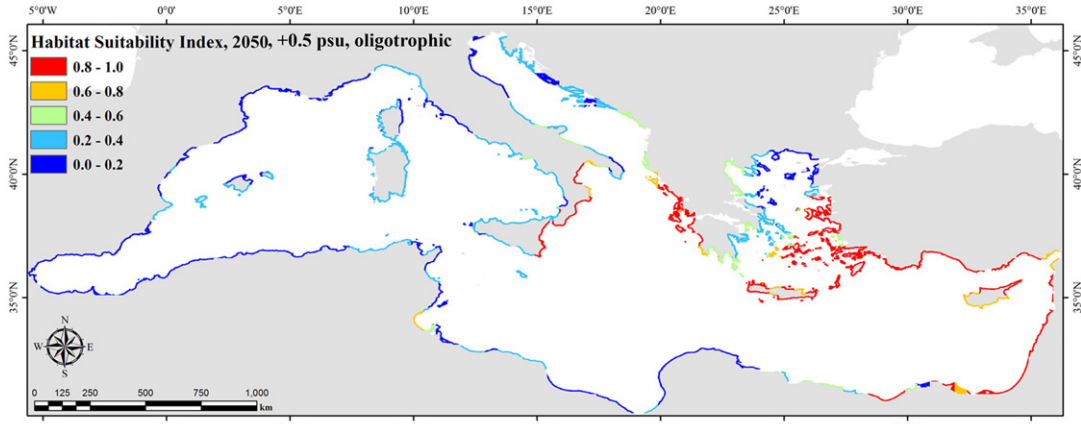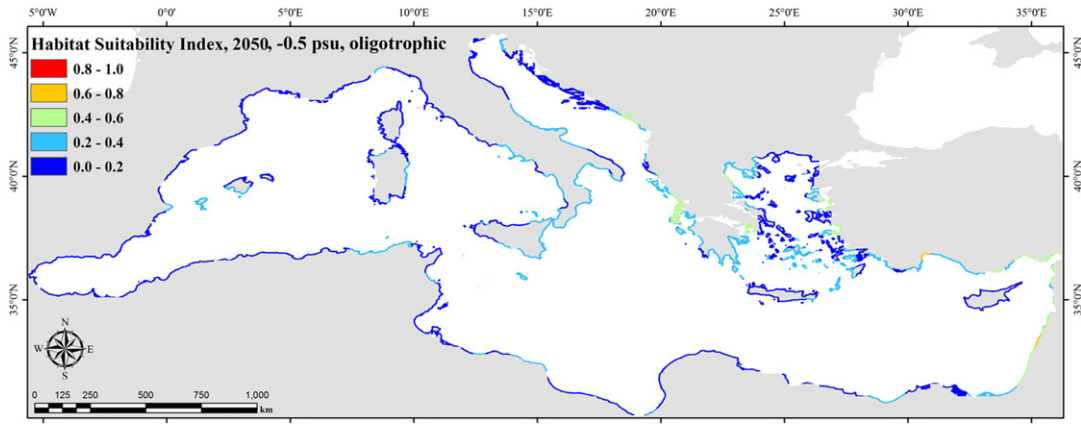
invasion demonstrates their value for predicting potential NIS distributions.

4.1 | Future range expansion

Although a degree of uncertainty inherent in all modelling approaches may complicate projections of future biodiversity (Thuiller et al., 2005; Walther, 2007), SDMs represent the best approach to date with which to forecast biological invasions. Our predictions represent an excellent test to evaluate invasive distribution shifts within marine systems using models developed and validated for terrestrial ecosystems (Fernández & Hamilton, 2015). When coupled with functional trait-based approaches based on the fundamental niche (Sarà et al., 2013), such results may improve the ability to predict changes from current to future spatial distributions of NIS. The model outputs support hypothesis that *B. pharaonis* will proliferate from its current invasive distribution to 2050 under future salinity and eutrophication scenarios, being able to colonize hard substrata across the Mediterranean (Figure 4). This NIS will expand its invasive range by more than 1,000 km in a westerly trajectory with respect to hydrographic conditions, reaching the Spanish coasts and the Gibraltar Strait by 2050. This is consistent with predictions made by Sarà et al. (2013) based on mechanistic functional trait-based models, which tested the reliability of that approach to predict current physiologically suitable habitats for this species. Although there were no historical records of occurrence further west in the North Atlantic in the literature, the likelihood of *B. pharaonis* being present was also predicted along the African, Southern Italian Peninsula and northern Sardinia coasts both during 2030 and 2050 (Figures 3 and 4; Table 1).

4.2 | Policy implications of invasion

Our results demonstrate that current European management actions and marine spatial planning frameworks, solely based on measures to manage ballast waters and hull fouling as the primary vector of invasion (Ojaveer, Galis, & Minchin, 2014), may be rendered ineffective by the construction of man-made corridors such as the new Suez Canal opening. The SDM approach provides a new tool with which to realistically predict habitat suitability for NIS, *via* a worked example for one NIS model species, *B. pharaonis*.

Our invasion maps (Figures A6 and A7 in Appendix S2) will assist managers to identify areas of vulnerability for native ecosystems. These geospatial model outputs will facilitate the development and implementation of new, effective mitigation actions to prevent novel, favourable conditions for the introduction of NIS and subsequently address the related risks and cost to policymaking and administration

at the national and European levels (Hulme et al., 2008). In addition, these models can be more widely applied to coastal marine systems globally to forecast invasion dynamics for benthic marine species under a range of multiple stressor scenarios.

At the European scale, these quantitative, georeferenced, spatially explicit risk maps of biological invasions under changing environmental conditions provide powerful visual communication and decision-support tools with which to describe where and when species might invade, and provide geospatial trajectories of future spread. The need to predict the NIS distribution pathways within the context of multiple stressors, including environmental and anthropogenic drivers is a primary, essential step to identify and evaluate management options and decisions to regulate and prevent new introductions. SDMs are useful statistical toolkits with which to geospatially map past, current and future biogeographic ranges for NIS, accommodating multiple stressor scenarios to enable more realistic forecasts of environmental and anthropogenic stressors and the resultant impacts on the range and spread of NIS into new areas.

Risk/pest maps are a valuable tool for the accurate assessment of Good Environmental Status (GES) for member state compliance with the EU Marine Strategy Framework Directive. GES targets are set against a background of "prevailing physiographic, geographic and climatic conditions" for MSFD Descriptor 1 "Biodiversity" and 2 "Non-indigenous species" (European Union, 2008). At the present time, there are no standard methods to calculate the future distribution and status of native and invasive species in European waters with respect to uncontrollable environmental drivers such as climate change, salinity, eutrophication, etc. termed "prevailing... conditions" (EU, 2008).

Pest maps will provide additional information on the ecological and economic impacts of invasion, predicting future risks areas, discussing and addressing related costs relevant to policy and management practices. By combining and overlapping our maps with outputs from a mechanistic trait-based approach (Sarà et al., 2013) and human use layers (aquaculture farms, Brigolin, Porporato, Prioli, & Pastres, 2017; major ports, international maritime transport hubs, D'Alessandro et al., 2016) or layers of spatial management measures (e.g. Marine Protected Areas, Galil et al., 2017; Special Protection Areas, Sarà et al., 2013), locations predicted to be highly suitable for colonization by *B. pharaonis* may overlap with protected or highly anthropic areas that are highly likely to receive new propagules. The same exercise can be done using the major shipping routes within the Mediterranean Sea or using the circulation patterns or other local maritime use layers.

This approach can be more widely applied to any marine species for which current distributional, ecological and environmental tolerance data are available and thus has wide potential applications for

FIGURE 4 Spatial distributions of predicting suitable habitat of *Brachidontes pharaonis* under 2050 future scenario, considering the scenarios with a decrease (−0.5 psu, panels a and c) and increase (+0.5 psu panels b and d) of salinity, and both oligotrophication (−10%; on the left, panels a and c) and eutrophication (+10%; on the right, panels b and d) conditions [Colour figure can be viewed at wileyonlinelibrary.com]

quantitatively determining the changes in GES with respect to the relative contributions of a range of drivers, including uncontrollable environmental change and local/regional anthropogenic stressors. This species shares similar distribution patterns with other invasive species whose biogeographic ranges are driven by temperature (e.g. the European green crab, *Carcinus maenas*; Compton, Leathwick, & Inglis, 2010; and other benthic invertebrates; de Rivera, Steves, Fofonoff, Hines, & Ruiz, 2011) and specifically with other Lessepsian invaders clearly showing climatic niche expansion in the Mediterranean (Parravicini et al., 2015). Given the vastly different ecology of these species (fish, benthic foraminifera and mussels), the consistency of the obtained results might represent a major step in making broader generalizations about the future spread of Lessepsian species under changing climate conditions. A combination of chlorophyll-a and salinity was the most influential environmental variables explaining the expansion or abiotic resistance to this invasion of the bluespotted cornetfish *Fistularia commersonii* (Azzurro et al., 2013). Both for fish and large foraminifera, the main future areas of environmental suitability were identified along the northern coasts of the Levantine Sea with suitability continuously increasing towards the
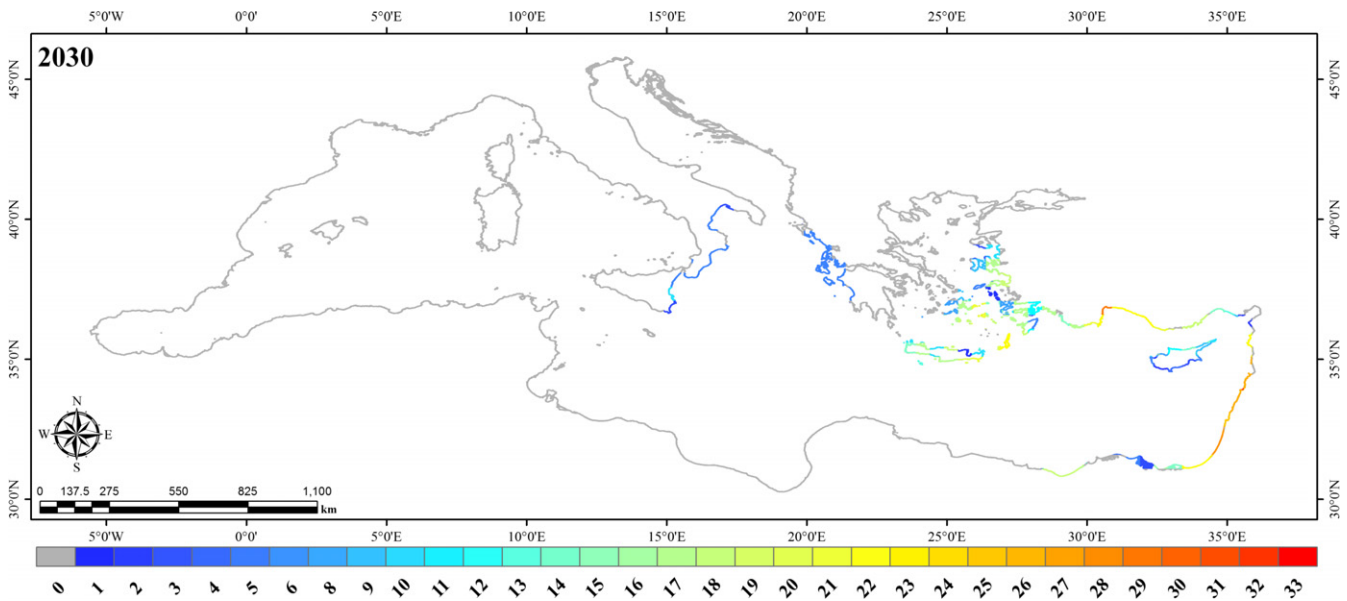

FIGURE 5 Spatial distributions of frequency of predicted habitat suitability of *Brachidontes pharaonis* under 2030 for all the 33 scenarios [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 6 Spatial distributions of frequency of predicted habitat suitability of *Brachidontes pharaonis* under 2050 for all the 33 scenarios [Colour figure can be viewed at wileyonlinelibrary.com]
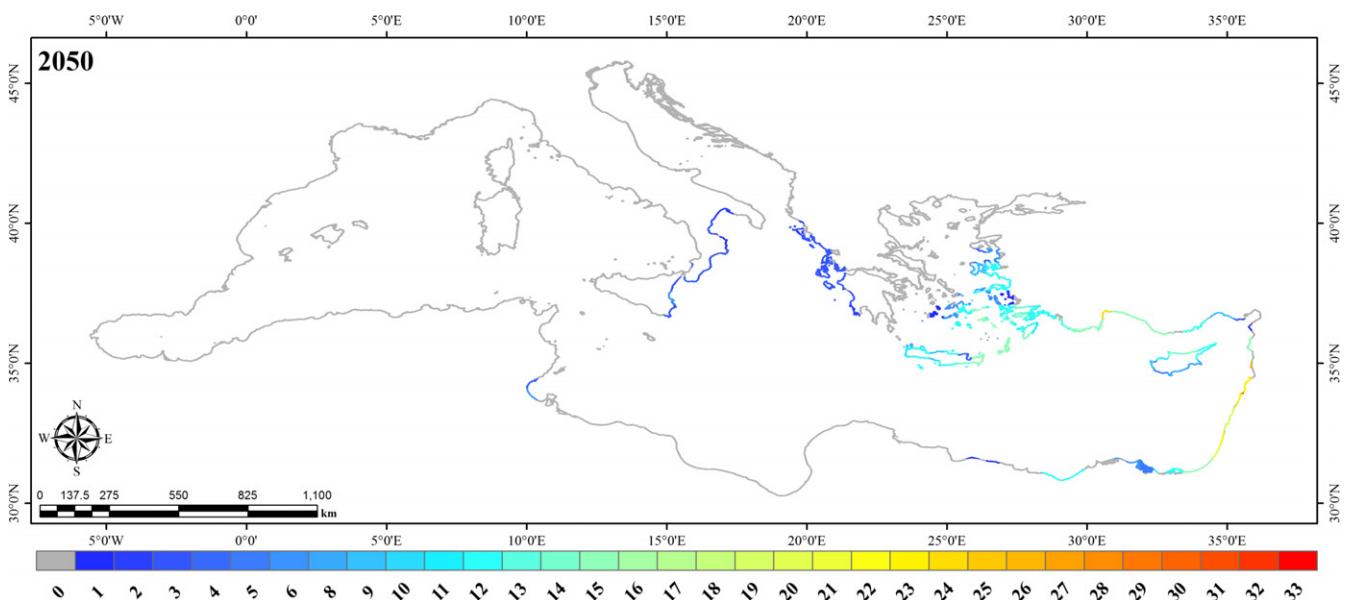
Central and Western Mediterranean Sea (Weinmann, Rödder, Lötters, & Langer, 2013).

An additional finding of the literature assessment suggests that in situ monitoring is the most effective option to support biological invasion management, via the provision of early detection warnings, and a rapid response derived from field data. Active and ongoing NIS monitoring programmes should be continued to track new introductions and spread of NIS, evaluate changes in species composition and assess the status of both vulnerable and resilient ecosystems (Butchart, Walpole, & Collen, 2010). Prevention seems to be the only feasible management alternative when facing the need to take post-invasion adaptive management actions to control biological invasions in marine ecosystems. Information on future invasion spread combined with data of propagule pressure and the roles that climatic and anthropogenic drivers play in altering invasion dynamics will be crucial in informing prevention and monitoring strategies, suggesting where to focus monitoring plans and target management options at appropriate scales and frequencies (local to regional) to successfully mitigate invasions and minimize their impact on native biodiversity, ecosystem services and human activities (McDonald-Madden, Runge, Possingham, & Martin, 2011).

Using data collected from observational and experimental research on multiple stressors and target species as input variables ensures scientific rigour of the SDM outputs encourages a "call for collection of …" species occurrence and environmental data, at both finer scales and in additional spatial regions. Such research-based, integrated approaches are a priority over the coming decades as climate-facilitated biological invasions will create new and unexpected challenges for biodiversity conservation.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA ACCESSIBILITY

Rasters derived from the habitat suitability models will be available as raster grids from the Pangaea database.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

BIOSKETCH

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Author contributions: G.S. conceived the idea and addressed the objective of analyses, and with N.M. equally led the writing, provided funds, hardware and software facilities; E.M.D.P. carried out the predictive modelling and led the modelling writing; M.C.M. performed the systematic review, led the review and the management issues writing and with other authors equally contributed to draft this manuscript.