



## Lessepsian fish invasion in Mediterranean marine protected areas: a risk assessment under climate change scenarios

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Mediterranean marine protected areas (MPAs), designed to achieve long-term nature conservation, are progressively conquered by invasive species of tropical origin, posing novel challenges for managers and policymakers of the 21st century. In this study, we assessed the vulnerability of 142 coastal Mediterranean MPAs to nine of the most invasive fishes under current and future climatic conditions. We predicted invasive species' habitat suitability using an ensemble modelling approach, calibrating models on the entire distribution of the species. We categorized three risk levels for Mediterranean MPAs, based on the assumption that more suitable habitat conditions make protected areas more prone to invasion. Future projections forecasted an increase of suitable areas for all considered species in the Mediterranean basin. In the Levantine Sea, almost all MPAs are at high risk of invasion by the considered species both in the current and future scenarios. MPAs located in the other Mediterranean sectors have currently a low suitability for most invasive species, but their risk level will increase overall by 2050, especially in the South Adriatic Sea and off South Western Italy. By identifying spatial priorities in a global change context, we fill critical information gaps on the vulnerability of MPAs to the future expansion of warm-water invaders.

**Keywords:** global change, invasion risk, invasive species, marine conservation, Mediterranean Sea, protected area network

### Introduction

Marine protected areas (MPAs) are nature-based tools for repairing environmental damages and sustaining the wide array of services provided by marine ecosystems (MedPAN & UNEP-MAP-SPA/RAC, 2016). Well-managed MPAs, indeed, effectively protect natural habitats and species from multiple local stressors such as destructive fishing and pollution (Sala *et al.*, 2018). Current protection measures, however, may not be effective in preserving these areas from global threats, particularly those posed by climate change and invasive species (Keller *et al.*, 2009; Monzón *et al.*, 2011), which represent an increasing and underestimated challenge for conservation (Katsanevakis *et al.*, 2014). Comprehensive recommendations have been made for improving ocean policy in light of these threats (e.g. RAC/SPA—UNEP/MAP, 2014; Mazaris and Katsanevakis, 2018). At the same time, there is a pressing need to provide resource managers with

approaches and information that can help to conceive appropriate strategies for mitigating related impacts (Fulton *et al.*, 2015).

Climate change is redistributing species across the globe, including marine invaders (e.g. Occhipinti-Ambrogi, 2007; Cheung *et al.*, 2009; Marras *et al.*, 2015). Indeed, these species often benefit from novel climatic conditions (Hiddink *et al.*, 2012; Bruno *et al.*, 2018) and spread into previously uncolonized areas, with significant ecological and socioeconomic consequences (Katsanevakis *et al.*, 2014). By modifying species interactions and food web dynamics, marine invaders can cause population declines, local extinctions, and alter the structure and functioning of ecosystems (Occhipinti-Ambrogi, 2007) and their related services (Pimental, 2002). Yet, the major problem for conservationists is that invasive species cannot be directly kept out from protected areas (Simberloff, 2000, but see Roberts *et al.*, 2017). Management efforts should, therefore, aim to anticipate the

vulnerability to invasion and provide at-risk areas with the adaptive capacity to cope with anticipated pressures (Bradley *et al.*, 2010; Fulton *et al.*, 2015). A key issue for guiding invasion control would be to assess the vulnerability of natural ecosystems ahead of invasion, but in the marine environment, relatively few efforts have been dedicated to improve predictions of the spatial distributions of these species under different climate scenarios (Marras *et al.*, 2015; Coro *et al.*, 2018). Today, this knowledge is urgently needed for the Mediterranean Sea, one of the world's most invaded marine regions (Edelist *et al.*, 2013; Katsanevakis *et al.*, 2014), which is warming faster than the global average (i.e. with annual mean basin sea surface temperature expected to increase from 1.5°C to 3°C by the end of the 21st century; Giorgi, 2006).

With 186 MPAs now representing 1.60% of the Mediterranean Sea, the surface covered by nationally designated sites has nearly doubled since 2012 to achieve the Convention on Biological Diversity (CBD, 2010) Aichi target 11 of 10% marine protection by 2020 (MedPAN & UNEP-MAP-SPA/RAC, 2016). In this study, our aim was to assess the vulnerability of Mediterranean MPAs to the progressive penetration of invasive fishes of tropical origin, being several species (hereafter referred as Lessepsians) already established in this region due to the opening of the Suez Canal in 1869. The extreme urgency of anticipating current and future potential impacts of these invasive species on protected ecosystems has been stressed by several Mediterranean scientists (Giakoumi *et al.*, 2017; Galil *et al.*, 2019). Recent evidence also indicates that Levantine MPAs are already overwhelmed by non-indigenous species, having partly failed to achieve their conservation objectives.

To this end, we fitted species distribution models (SDMs) to estimate the species-specific suitability of environmental conditions in Mediterranean MPAs in the present and under four climate change scenarios by 2050. SDMs have recently emerged as a powerful tool for inferring the spatial distribution of suitable habitats and to estimate how suitability would vary under changing environmental conditions (Bradley and Mustard, 2006; Vicente *et al.*, 2010). Because Lessepsian species have a tropical origin, climate warming is believed to facilitate them expanding into new areas, especially towards the Western and Northern colder Mediterranean sectors (Hiddink *et al.*, 2012). In this scenario, our expectation is an increasing risk of MPAs to be conquered by alien organisms. Although SDMs are increasingly applied to predict the geography of species' invasions under a changing climate, they have been mostly applied to terrestrial systems (e.g. Barbet-Massin *et al.*, 2013; Bellard *et al.*, 2018), with a very limited number of studies focused on the marine taxa (e.g. De Rivera *et al.*, 2011; Jones *et al.*, 2013; Bellard *et al.*, 2018), and very few on individual Lessepsian species (Coro *et al.*, 2018).

Spatio-temporal assessments of invasion risk are urgently requested for Mediterranean MPAs (Tulloch *et al.*, 2015) because several taxa of both native and exotic origin are displaying rapid spatial rearrangements under warming water conditions (Ben Rais Lasram *et al.*, 2010). Predictive modelling studies indicate a substantial increase of climatically suitable habitats for warm-adapted fishes (Marras *et al.*, 2015; Coro *et al.*, 2018), whilst opposite trends are apparent for native boreal and endemic species (Ben Rais Lasram *et al.*, 2010; Albouy *et al.*, 2012; Marras *et al.*, 2015), highlighting a priority for conservation. Here, based on SDM projections and assuming a positive relationship between environmentally suitability and invasion risk, we provide a first estimate of the vulnerability of each Mediterranean MPA to nine

of the most invasive fishes in the Mediterranean basin. We conduct this assessment under current conditions and future climate change scenarios, accounting for species-specific dispersal rates.

## Methods

### Species selection, occurrence records, and environmental data

We considered nine of the Lessepsian fishes known to be most invasive in the Mediterranean Sea (Streftaris and Zenetos, 2006; Katsanevakis *et al.*, 2014; Supplementary Appendix A). Occurrence records in the Mediterranean were derived by updating the geo-referenced database ORMEF (Occurrence Records of Mediterranean Exotic Fishes), which has been already used for invasive species modelling (e.g. Parravicini *et al.*, 2015). Literature updates were performed by searching the available information on spatially explicit records of the nine selected species, considering only studies based on Mediterranean countries (Supplementary Appendix B). Geo-referenced records were mostly extracted from published papers. Literature search was performed with the help of databases such as Scopus and Web of science. Only those species with more than 30 records in the invaded range were selected, excluding taxa with challenging taxonomy such as *Sargocentron rubrum* (Bariche *et al.*, 2015). The final list of species retained for the analyses included: *Fistularia commersonii*, *Lagocephalus scleratus*, *Pterois miles*, *Siganus luridus*, *Siganus rivulatus*, *Stephanolepis diaspros*, *Upeneus moluccensis*, *Hemiramphus far* and *Sphyrna chrysotaenia* (Supplementary Appendix A). Noteworthy, six of these species (*F. commersonii*, *L. scleratus*, *S. luridus*, *S. rivulatus*, *S. diaspros*, and *U. moluccensis*) are included in the Blacklist of Marine Invasive species (Otero *et al.*, 2013), with five of them (*L. scleratus*, *S. rivulatus*, *S. luridus*, *F. commersonii*, and *P. miles*) considered as priority species for the purposes of the UNEP-MAP and GFCM joint study in the eastern Mediterranean [UNEP(DEPI)/MED WG.445/4]. The Mediterranean distributional data for these species were based overall on 206 references (Supplementary Appendix B). We only used occurrence records from populations presumed to be stable, and excluding geographically extreme records from vagrant individuals, which were located far away from, and clearly outplaced with respect to, the known distribution of our target species. This decision was mainly supported by the CIESM Atlas (<http://www.ciesm.org/atlas/appendix1.html>, which provides maps on the Mediterranean distribution of exotic fishes in the Mediterranean and distinguished such isolated records) and subjected to expert evaluation (co-author E.A.).

We derived native range information from the open-source datasets OBIS (OBIS, 2018) and GBIF (GBIF.org, 2018). Records were filtered to consider only those coming from reliable sources and with precise co-ordinate information. The distributions were compared with the AquaMaps dataset (Kaschner *et al.*, 2016) for overall geographic reliability, further excluding doubtful records. For each species, we finally pooled the data from the invaded and native ranges. These datasets were thinned to the resolution of 5 arcmin to match environmental layer grids. The final datasets used for model calibration contained a total of 2795 geo-referenced observations, ranging between 51 and 641 records/species (Supplementary Appendix C).

We downloaded environmental marine layers from the open-access BIO-ORACLE database at the resolution of 5 arcmin (Assis *et al.*, 2018). We selected six predictors based on the result of a

previous assessment of variable importance for NIS species (D'Amen and Azzurro, unpublished data): pH, salinity (mean and range), sea surface temperature (mean and range), and mean primary productivity (see [Supplementary Appendix D](#) for a description).

The environmental layers included both current (calculated as a mean over the period 2000–2014) and future conditions in 2050. Four scenarios were available for this time slice, developed for the IPCC AR5 under the new representative concentration pathways (RCP) ([Van Vuuren et al., 2011](#)): (i) the RCP26, representing a peak-and-decline scenario, with very low greenhouse gas concentration levels by the end of this century. This would be reached with substantial reductions of greenhouse gas emissions (and, indirectly, emissions of air pollutants) over time; (ii) the RCP45, which is a stabilization scenario whereby the total radiative forcing is stabilized before 2100 thanks to technological advancements and reduction of greenhouse gas emissions; (iii) the RCP60, which is also a stabilization scenario, where greenhouse gas concentration levels stabilize; (iv) the RCP85, which is a pessimistic scenario under which increasing emissions over time will lead to high greenhouse concentration levels. Differences among scenarios can be attributed in part to differences between the applied models and scientific, economic, and technological assumptions. Only the square cells located in coastal waters, with a depth limit of 750 m, were used for pseudo-absence sampling, model calibrations and projections, as the fish presence records occurred mainly in this bathymetric range.

### Species distribution models and dispersal

Recently, concerns have been raised that applying SDMs to invasive species could be challenged by the possible violation of the niche conservatism assumption (e.g. [Li et al., 2014](#)). In fact, invasive species can occur in areas with different environmental conditions than experienced in their native ranges ([Beaumont et al., 2009](#)). To cope with this potential niche shift, we calibrated our models with data from the entire (native and invaded) known distribution: this allows a better characterization of species' fundamental niches and supports improved forecasts of potential expansion under climate change ([Beaumont et al., 2009](#)).

We applied an ensemble modelling approach that consists of producing multiple realizations of predictions and averaging them to obtain a final consensus that accounts for model uncertainty. This approach has been shown to improve modelling outcomes ([Araújo and New, 2007](#)). As only presence information was available, we performed 10 runs of pseudo-absences generation, by randomly selecting points within the species' extent of occurrence (pooling native and invaded ranges), maintaining a prevalence of 50%. We used three top-performing statistical modelling techniques, commonly used in predictive studies: (i) Generalized Boosting Models, also known as Boosted Regression Trees (GBM, [Elith et al., 2008](#)), (ii) Random Forests (RF, [Breiman, 2001](#)), and (iii) MaxEnt ([Phillips et al., 2006](#)). We ran the models using the `biomod2` package ([Thuiller, et al., 2016](#)), in the R platform, version 3.5.1 ([R Core Team, 2018](#)), with model parameters left at their default settings to facilitate repeatability ([Supplementary Appendix E](#)). For each species, we obtained an index of habitat suitability, HS ([Phillips et al., 2006](#)) ranging between 0 and 1000 (lowest and highest suitability, respectively) for the Mediterranean basin under current and future environmental conditions (2050, four RCP scenarios). Model performance was

determined with a 10-fold cross-validation using (i) the area under the curve (AUC) of a receiver operating characteristic (ROC) plot, where an area of 1 represents a perfect test and an area of 0.5 represents a worthless test ([Fielding and Bell, 1997](#)), and (ii) the true skill statistic (TSS), which ranges from  $-1$  to  $+1$ , where  $+1$  indicates perfect agreement and values of zero or less indicate a performance no better than random ([Allouche, et al., 2006](#)). At each iteration, the dataset was split into 90% data used for training, and 10% data used for evaluation. For each species, the projections generated by the combination of modelling technique and initial dataset were finally combined into single HS consensus forecasts, for current conditions and for each RCP scenarios for 2050. To generate consensus projections, we used a weighting average approach by TSS scores; models with a TSS score lower than 0.70 were excluded from the final consensus.

Based on the ORMEF dataset, we reconstructed the chronological series of the progress of dispersion for each invasive species. An estimate of specific dispersal rate was calculated as the least-cost distance between consecutive point pairs. We created a conductance layer that measures the local "friction" of the landscape, assigning maximum permeability to the continental shelf area and decreasing permeability values for areas of increasing depth. See [Supplementary Appendix F](#) for further details on the calculation of the spread rate.

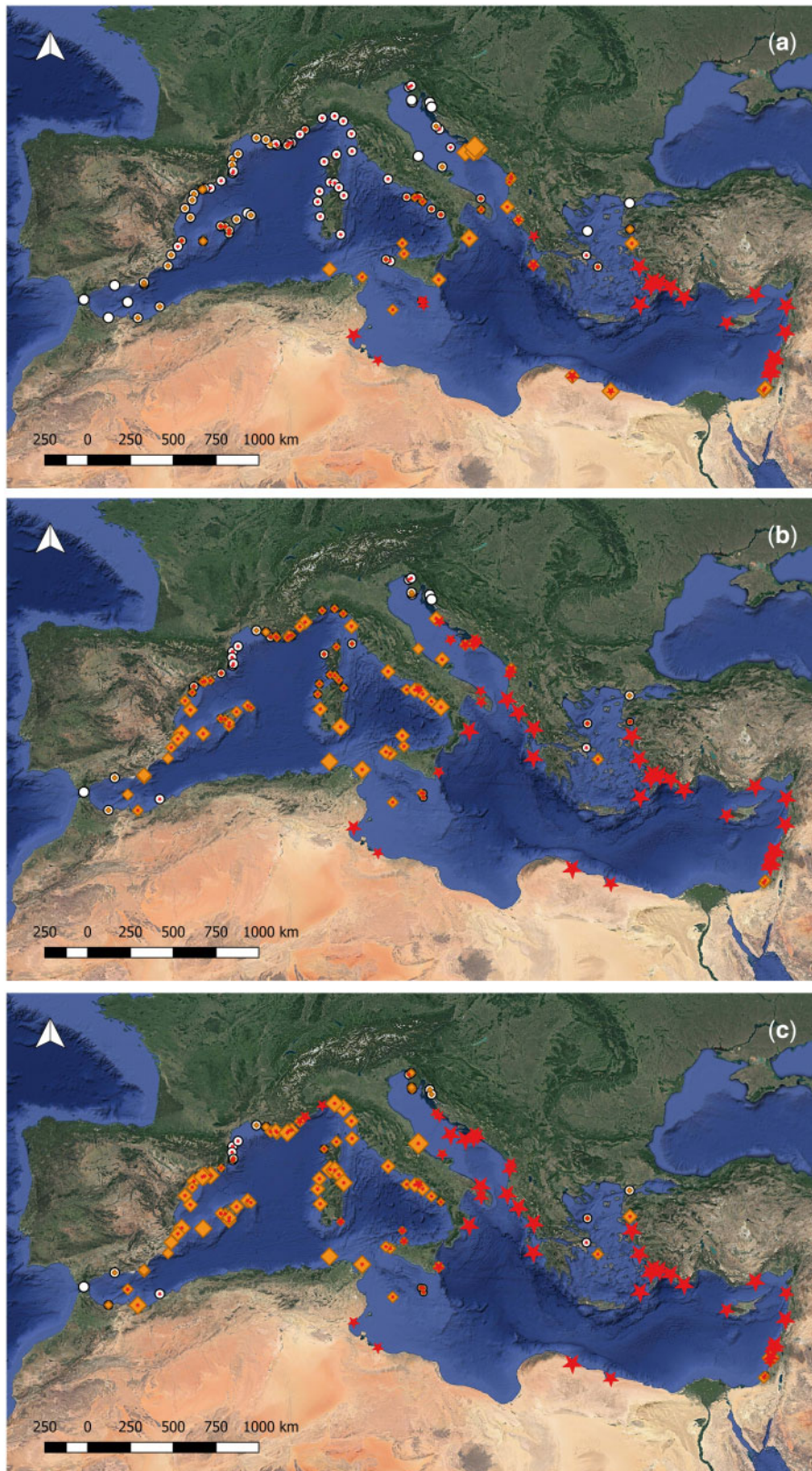
Data preparation and analyses were carried using functions from the following R packages: `gdistance` ([Van Etten, 2017](#)), `ggplot2` ([Wickham, 2016](#)), `raster` ([Hijmans, 2017](#)), `rgbif` ([Chamberlain, et al., 2016](#)), and `sdmpredictors` ([Bosch, 2018](#)).

### Marine protected areas dataset and risk assessment

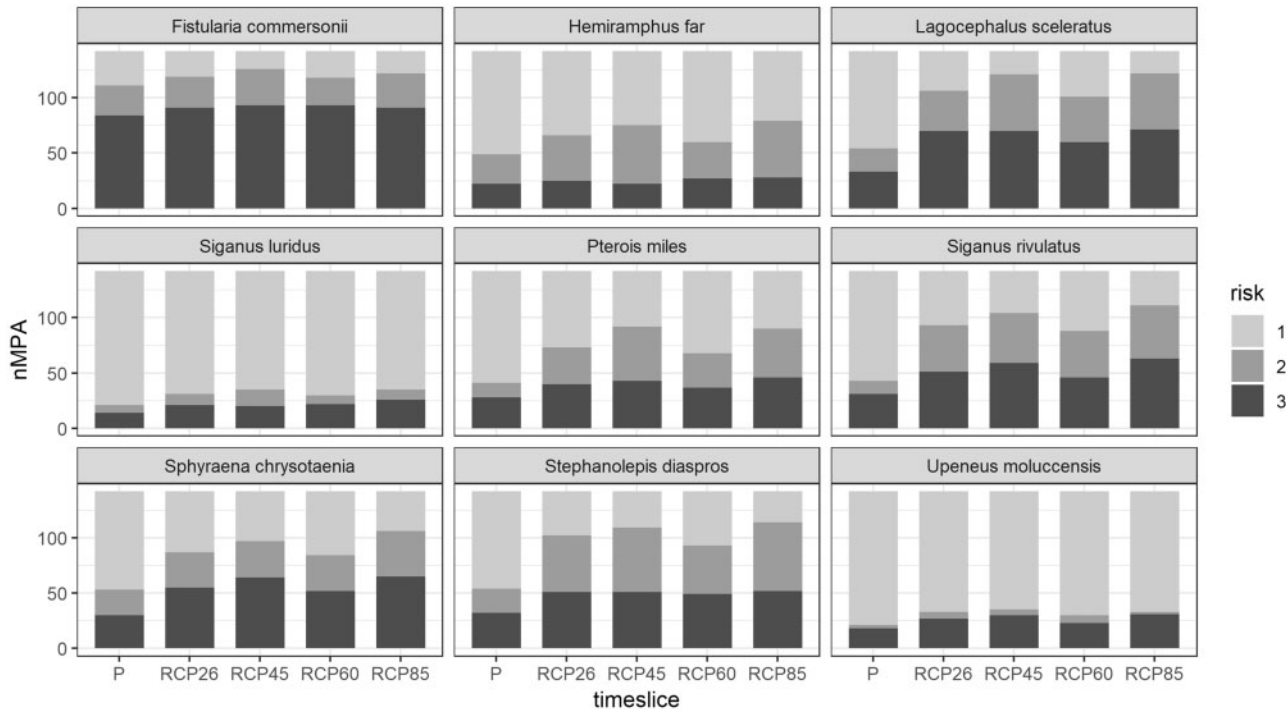
Data on the location of existing marine protected areas in coastal Mediterranean Sea were derived from the MPAs in the Mediterranean GIS database (MAPAMED), which gathers information on MPAs and on sites of interest to the conservation of the marine environment of the Mediterranean ([www.medpan.org](#); [Supplementary Appendix G](#)). To identify current and future potential spatial conflicts between MPAs and invasive non-indigenous fishes, we used the final consensus projections. For each species, we extracted the mean, minimum, and maximum HS values predicted under current and future conditions in each MPA overlapping the marine coastal area considered in this study (for a total of 142 MPAs, [Figure 1](#) and [Supplementary Appendix D](#)). To examine how the potential risk from the nine invasive species would change given global warming, we tested whether HS values in the MPA network would significantly increase between the current conditions and each RCP scenarios for 2050, using a paired  $t$ -test statistic. In addition, we reclassified the HS maps in three arbitrary classes, following [Georgian et al. \(2019\)](#) ( $<400$  = low suitability,  $400-800$  = moderate suitability, and  $>800$  = high suitability), with the aim of representing three risk categories for MPAs useful for conservation planning and management.

### Results

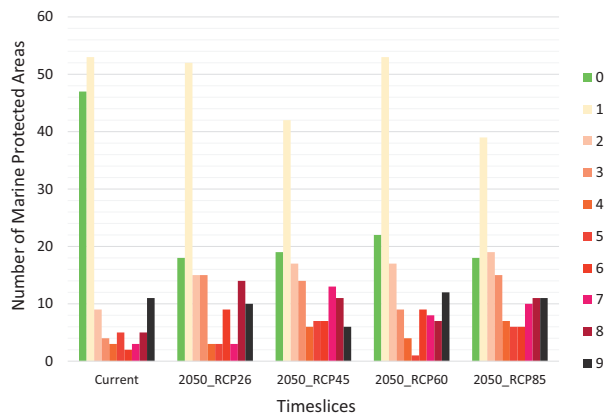
The cross-validation evaluation scores of the single SDMs were fair to good and similar across all species, with the best performance achieved by RF (TSS  $\geq 0.72$ , AUC  $\geq 0.91$ ), followed by GBM (TSS  $\geq 0.63$ , AUC  $\geq 0.90$ ) and last MAXENT (TSS  $\geq 0.5$ , AUC  $\geq 0.76$ ), (see [Supplementary Appendix H](#) for the summary statistic for each species and modelling technique and



**Figure 1.** Location of the considered MPAs and risk assessment of their potential invasion by nine non-indigenous fishes in current (a) and 2050 conditions under the most optimistic (b) and the most pessimistic (c) scenarios. Dots: low risk (i.e. species with habitat suitability  $< 400$ ). Diamonds: medium risk (i.e. species with  $400 < \text{habitat suitability} < 800$ ). Stars: high risk (i.e. species with habitat suitability  $> 800$ ). The size of symbols is proportional to the number of species in the corresponding category. For each MPA, symbols are visible in the following order: high–medium–low risk categories.



**Figure 2.** Number of marine protected areas (nMPA, y-axis) in the three risk classes (1= low risk i.e. habitat suitability <400; 2 = medium risk, i.e. 400< habitat suitability <800; and 3 = high risk i.e. habitat suitability >800) for each of the considered species under present climatic conditions (P), and by 2050 under the four socioeconomic scenarios (RCP26, RCP45, RCP60, RCP85; timeslice, x-axis).



**Figure 3.** Cumulative high risk of MPA invasion by none or 1–9 species under current climatic conditions and by 2050 under the four socioeconomic scenarios.

Supplementary Appendix I for output maps in the Mediterranean).

Future projections forecasted an increase of suitable areas for all species in the Mediterranean basin (Supplementary Appendix I). Consensus models showed congruent patterns and highly correlated HS values among the alternative RCP scenarios for 2050 for all species. Overall, the projections point to a general increase of potential suitable conditions along the Tyrrhenian and Balearic Sea coasts and the North Adriatic Sea. *Fistularia commersonii* projections were largely uniform across RCP scenarios, forecasting an increased suitability in currently unsuitable areas such as the

North Adriatic Sea, part of the Gulf of Lion, and in the Balearic Sea. For *H. far*, the increase of suitable areas was more pronounced under RCP45 and RCP85 scenarios, forecasting new suitable areas in the South Adriatic Sea, the Balearic and Tyrrhenian Seas, along the coast of central Italy, and in small areas along western and eastern Sardinia. Potential suitable areas for *L. scleratus* were predicted to increase in the coastal waters of both the Adriatic and Tyrrhenian Seas. According to 2050 projections, almost all the Adriatic Sea could be suitable for *L. scleratus* expansion, as well as the coastal waters of the Balearic Sea. The environmental suitability for this species is also expected to increase along the coasts of Algeria and Tunisia and across the entire Aegean Sea. *Siganus luridus* projections by 2050 show a great increase of potential suitable areas towards the eastern Mediterranean sectors, which are currently unoccupied and predicted to be unsuitable (Balearic and Tyrrhenian Sea coasts, Adriatic Sea and Strait of Sicily). A similar potential expansion pattern was predicted for the congeneric species *S. rivulatus*. In both cases, the potential expansion is especially pronounced under RCP45 and RCP85 scenarios. The 2050 projections for *S. chrysoaenia* agree in the potential increase of HS values along the Tyrrhenian and Adriatic Sea coasts, but no further eastern expansion was predicted. *S. diaspros* projections indicated a potential increase of HS along the coast of Africa up till the Gulf of Gabès, and new potentially suitable areas along the Tyrrhenian and Adriatic Sea coasts. A moderate increase of HS was also predicted along the Balearic Sea coasts and in Algerian and Tunisian coastal waters. The predicted expansion of suitable conditions of *U. moluccensis* and *P. miles* under 2050 scenarios was limited to the southern Adriatic Sea and Italian Ionian sea coasts (Supplementary Appendix I). The rates estimated based on the

past speed of invasion for the considered species indicate that all species would be potentially able to reach all the newly suitable areas in the Mediterranean within the next 30 years (Supplementary Appendix F).

Most MPAs currently have a low risk of invasion, being poorly suitable for all the considered species ( $HS < 400$ ), according to SDM predictions in the Mediterranean Sea (Figure 2, Supplementary Appendix L). *Fistularia commersonii* represents an exception because it already poses a high risk of invasion (i.e. would find a highly suitable habitat) in more than 80 MPAs (Figure 2). This situation is expected to change drastically according to SDMs projections by 2050 (Supplementary Appendix L). Suitability values (mean, minimum, and maximum) for each species will increase significantly in the MPA network, under all the four RCP scenarios (paired  $t$ -tests  $p < 0.05$  after Bonferroni correction; Supplementary Appendix L). *Fistularia commersonii* is predicted to have the smallest increase in HS within the MPAs network, finding already high suitability in the MPAs under current conditions. *Lagocephalus sceleratus*, which currently would find highly suitable habitats in only 33 MPAs, will potentially be able to invade up to 71 MPAs according to SDM projections for 2050. Similarly, *S. luridus*, *S. rivulatus*, and *S. chrysothaenia* have the potential to invade nearly twice as many MPAs in the future (28 up to 46 MPAs, 31 up to 63 MPAs, and 30 up to 65 MPAs; Figure 2 and Supplementary Appendix M).

Under current conditions, around one-third of MPAs are at low or medium risk for all the considered non-indigenous fishes. By contrast, only 12–16% MPAs would maintain these levels of risk by 2050, according to our analyses (Figure 3). The number of MPAs at high risk of being invaded by one non-indigenous fish species is predicted to remain stable in comparison to the current conditions (between 30% and 37% of MPAs). Conversely, under future conditions, the number of MPAs potentially at high risk of being invaded by more than five species increases by a factor of four under the most pessimistic RCP scenario (Figure 3). The predicted increase of MPA invasion risk by Lessepsian fishes has a westward direction (Figure 1). In current conditions, most of the MPAs located along the Tyrrhenian and Ligurian coasts, and most of the Spanish MPAs are subject to a low invasion risk for most or all the considered species (Figure 1a). The same situation is currently observed for the North Adriatic coasts. According to model projections for future conditions, in the western Mediterranean sectors, an increasing number of MPAs will be at medium risk of invasion, i.e. at high risk for one or two non-indigenous species. Invasion risk will increase in the South Adriatic sector and along the southern coasts of Italy especially under the RCP85 scenario (Figure 1b and c).

## Discussion

We predicted the current and future areas of climate suitability in the Mediterranean Sea for nine invasive fishes using an ensemble of three top-performing SDM techniques and four different climate change scenarios by 2050. In doing so, we provide a spatially explicit evaluation of how climate change may increase the number of MPAs at risk of invasion. Our results are species-specific and projected into spatio-temporal suitability maps, which clearly illustrate specific gradients of invasion risk across the Mediterranean MPAs. This represents a novel and valuable source of information for multiple applications in conservation biology (Tulloch *et al.*, 2015) and for the management of MPA networks (Katsanevakis *et al.*, 2014).

Under current conditions, our model predictions highlight the eastern Mediterranean as the most problematic sector. Indeed, many Levantine MPAs are already dominated (in terms of both number of species and biomass) by invasive organisms of Lessepsian origin (Giakoumi *et al.*, 2019b; Galil, 2019). Many of these species have already started to expand towards the western and northern sectors of the basin (Azzurro *et al.*, 2013; Azzurro *et al.*, 2017a; Coro *et al.*, 2018), yet the MPAs located in the Western Mediterranean, as well as in the northern Adriatic Sea and North Aegean Sea currently exhibit low risks of invasion due to unfavourable climates. By 2050, invasive species will potentially gain new suitable areas along the South Western coast of Italy and in the South Adriatic Sea, with West Mediterranean MPAs becoming less resistant to invasion.

Among the nine considered fishes, *F. commersonii* has already spread over most Mediterranean coasts (Azzurro *et al.*, 2013) and, in term of climatic requirements, is the only invasive fish that currently poses a risk more than half of Mediterranean MPAs. Nevertheless, by 2050, suitable habitats for *L. sceleratus* are also projected to increase over almost half of the current MPA network. This is consistent with the predictions made by Coro *et al.* (2018), who suggested that *L. sceleratus* will continue its rapid spread, if no countermeasures are taken. Interestingly, the common lionfish *P. miles* is predicted to find suitable habitats only in the Eastern Mediterranean sector, without significantly expanding its range of suitable environments due to climate change. However, a recent analysis of the niche dynamics for this species evidenced a high degree of niche unfilling (Poursanidis *et al.*, in preparation) and possibilities of a further expansion of the climatic niche of *P. miles* in the Mediterranean Sea cannot be excluded (Parravicini *et al.*, 2015). These traits, along with ecological evidence for the broad thermal tolerance of *P. miles* (Kimball *et al.*, 2004) would explain the progressive expansion of this species up to the central sectors of the basin (Azzurro *et al.*, 2017b; Dimitriadis *et al.*, in preparation).

Finally, our regional analysis illustrates that, by 2050, the Levantine sectors will keep providing the most suitable climates for invasive fishes, potentially exacerbating the competition with native species, such as *S. rivulatus* vs. *Sarpa salpa* (Marras *et al.*, 2015). Considering that the efficacy of several Mediterranean MPAs could be progressively affected by the arrival of warm-adapted invaders in the next few decades, and that a strong turnover of the native community is expected (Ben Rais Lasram *et al.*, 2010), our species-specific results should be taken into account to reduce uncertainty in spatial planning decision processes (Rilov *et al.*, 2019) and to design long-term mitigation strategies. These latter must take the form of adaptation plans, include regular monitoring and implement a series of species-specific actions, including the promotion of selective removals, protection of natural predators, public awareness and participation (see Giakoumi *et al.*, 2019a).

The assessment of invasion risk is here based on the evaluation of species-specific environmental suitability within the MPAs, an approach commonly used in conservation biology (e.g. Zalba *et al.*, 2000; Thuiller *et al.*, 2005; NTA, 2009). In fact, it is well known that unsuitable environmental conditions may halt invasions (Levine, 2008), and their regulatory role is typically appreciated at large biogeographic scales, as shown here. Indeed, once tropical species are introduced to a temperate sea such as the Mediterranean, their persistence and geographical spread is expected to be strongly limited by abiotic conditions, including unfavourable seasonal temperatures and salinity (Azzurro *et al.*,

2014; Coro *et al.*, 2018). We did not consider biotic interactions in this study, which are also important in determining species distributions. However, biotic resistance, i.e. the ability of resident species to reduce the success of exotic invasions (Elton, 1958), is estimated to be low for most of the invaders that we modelled. Indeed, most of these fishes are characterized by unique traits that would allow them to use wide niche space, avoiding direct competition with resident species (Azzurro *et al.*, 2014). This is also the reason of their great success in invading the Mediterranean Sea. For example, species such as the common lionfish *P. miles* or the blue-spotted cornetfish, *F. commersonii*, can be considered as novel predators, which use novel predatory tactics and take advantage by the reduced antipredatory defenses of native prey (Sih *et al.*, 2010); the rabbitfishes (*S. rivulatus* and *S. luridus*) are favoured by the paucity of competing herbivorous species in the hosting community (Fanelli *et al.*, 2015).

Our results are based on the application of SDMs. To optimize the analyses for invasive species, we calibrated the models on data pooled across invaded and native ranges, so as to capture a larger spectrum of suitable conditions under which the species may spread (Broennimann and Guisan, 2008). This choice was supported by results of a previous test on *S. luridus*, which showed a better predictive accuracy of the ongoing invasive range if the models were calibrated within the pooled native and invaded ranges (D'Amen and Azzurro, unpublished data). Accounting for the native range is also recommended when the final goal of the study is to project the models in different conditions (Broennimann and Guisan, 2008). On the other hand, such practice may lead to merging data from many different sources, which may weaken the models' performance (Phillips *et al.*, 2009). To partially reduce issues surrounding spatial bias, we thinned the presence dataset to the resolution of 5 arcmin. Other approaches could also have been applied, e.g. creating a set of background data that reflect the same bias as the occurrence data (Phillips *et al.*, 2009; Georgian *et al.*, 2019). In this study, we selected random points for the models' background from the area that "includes but not exceeds all areas that are accessible to the taxon", as prescribed by the gold standard for best practices in SDM recently identified by Araújo *et al.* (2019).

MPAs are cornerstone for marine conservation (Simberloff, 2000; Francour *et al.*, 2010; Galil *et al.*, 2019), but this role may be compromised under growing xenobiotic pressure. Alien fishes are mostly ignored in conservation planning, even if their negative impacts are now largely recognized (Mačić *et al.*, 2018). In many MPAs, protection regimes may even favour invasive populations (Schlaepfer *et al.*, 2011; Yokes *et al.*, 2012). This is reasonably the case of many Lessepsian fishes that are commercially exploited in the eastern Mediterranean and may take direct advantage from no-take regulations. A major challenge is thus to provide stakeholders with precise guidelines on how to manage these environmental issues, translating these principles into a realistic, integrated ecosystem-based approach.

Different perspectives can be evaluated for conservation planning: can we actually do something or just leave nature do its job? Shall we allow fishing alien species in the protected areas? Shall we engage recreational divers in the removal of invasive species? Are these measures ecologically and economically sustainable? MPA managers would certainly benefit of much practical guidelines for addressing this kind of questions; however, management strategies need to be site-specific and tailored to the particular conditions of each MPA (Otero *et al.*, 2013). Frameworks designed to support

decisions must consider many factors (Katsanevakis *et al.*, 2018), including their impacts on native biodiversity, ecosystem services, and human health and prioritization processes are highly advisable due to the intrinsic subjectivity of management options (Epstein *et al.*, 2018). Moreover, participatory actions and education among the general public and specific groups may help to manage invasive species and to limit their impacts. Finally, it is important to recognize that some alien species can also have positive impacts, for example by maintaining biodiversity representativeness, providing food, and securing ecosystem processes (Schlaepfer *et al.*, 2011; Katsanevakis *et al.*, 2014; Mačić *et al.*, 2018). These functions need to be carefully evaluated, especially at the easternmost edge of the Mediterranean, where climate change has already caused multi-species collapses (e.g. Rilov, 2016; Yeruham *et al.*, 2015), and where tropical organisms might actually replace lost ecological roles.

## Conclusion

MPA managers of the 21st century will be forced to carefully consider the major biodiversity and functional alterations that climate change is driving by displacing species in coastal Mediterranean ecosystems. Some MPAs are already facing these impacts, whereas others will likely face them in the next few decades. There is, therefore, an urgency to develop biodiversity conservation plans and to prioritize monitoring efforts in areas of increasing vulnerability to climate-empowered invaders. By providing information on the geographical sectors where invasive species pressures are most likely to occur, our spatially explicit findings provide a key tool for optimizing the usually limited resources and planning monitoring schemes (IPCC, 2014; Garrabou *et al.*, 2018). Certainly, although projections provided by this analysis are useful for understanding regional risk resulting from invasive species, adaptive measures need to be implemented at the local level. In this context, management strategies should be planned with the scope to help marine biodiversity (and human populations) to adapt to these pressures (Bradley *et al.*, 2010). As for climate change hotspots, where many irreversible changes have already occurred, strategies for shifting from a species-based to an ecological functions or socioeconomic-based approach in conservation planning is ought to be evaluated (Mačić *et al.*, 2018), but further research is needed to address the inherent uncertainty in socio-ecological responses (Katsanevakis *et al.*, 2014). In conclusion, our species-specific projections provide additional inputs to long-term management plans that can help identify spatial priorities for invasive species mitigation in the upcoming decades. This information is expected to be useful for regional conservation strategies and to coastal management bodies, which are called to monitor, detect, anticipate, and promptly react to the challenges posed by a rapidly changing marine region.

## Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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