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Habitat suitability, niche unfilling and the potential spread of *Pterois miles* in the Mediterranean Sea

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ABSTRACT

The common lionfish *Pterois miles* has rapidly spread across the eastern Mediterranean Sea. We compiled occurrence data from both native and invaded range under the framework of Species Distribution Modelling (SDM). Through a construction of an environmental suitability model and estimation of spread rates we investigated the lionfish climate niche in both its native and invaded domains, this latter represented by the Mediterranean region. Model projections allowed to identify suitable areas for lionfish establishment in the Mediterranean. Spread analysis suggested that a further geographical expansion in this basin could be completed within the next years. Our results did not provide evidence for niche expansion but highlighted a high degree of niche unfilling thus prospecting a likely spread of Mediterranean lionfish invasion beyond the predictions of current SDMs. These findings provide novel inputs to forecast the future geographical evolution of the lionfish in the Mediterranean Sea and asses the related risk of invasion.

1. Introduction

The lionfishes *Pterois volitans* (Linnaeus, 1758) and *Pterois miles* (Bennett, 1828) are native to the Pacific Ocean and Indian Ocean, respectively (Kulbicki et al., 2012). They gave rise to one of the most disruptive marine biological invasions worldwide (Albins and Hixon, 2008, Hixon et al., 2016). In the last three decades, these two species rapidly spread throughout the tropical and subtropical coasts of the western Atlantic, the Gulf of Mexico and the Caribbean Sea (Whitfield et al., 2002, Semmens et al., 2004, Johnston and Purkis, 2014). This unprecedented invasion extended across a wide range of natural habitats (Morris, 2012, Albins and Hixon, 2013, Côté et al., 2013), severely impacting coastal biodiversity and ecosystem processes and functions (Albins, 2015; Ballew et al., 2016; Andradi-Brown et al., 2017). Recently, a new lionfish invasion has begun in the Mediterranean Sea; the most invaded marine basin worldwide.

This invasion started in 2012, when two individuals of the common lionfish *Pterois miles* were recorded from the Lebanese coasts (Bariche et al., 2013). Since then, *P. miles* population increased and rapidly spread westwards, reaching Sicily and Tunisia (Kletou et al., 2016; Dailianis et al., 2016; Azzurro et al., 2017). Molecular analyses revealed that the invading *P. miles* population is of Red Sea origin initiated by individuals immigrating through the Suez Canal (Galil et al., 2017; Samaha et al., 2016; Zenetos et al., 2017) in multiple introductions (Dimitriou et al., 2019). There are serious concerns about the potential ecological impact of this incipient invasion, since the Mediterranean Sea is a biodiversity hotspot and the world's most invaded marine region (Coll et al., 2010; Edelist et al., 2013). Assessing *P. miles*' environmental requirements and predicting its potential geographic distribution in the Mediterranean Sea is today one of the most urgent research objectives, with concrete applications in conservation, early-warning and invasive-species management.

Here, we employed species distribution model (SDM) framework to assess the habitat suitability of Mediterranean waters to the lionfish invasion. SDM combine species occurrence records and oceanographic data to model species' distributions based on marine environmental

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variables and have been frequently used to predict range limits of invading species (Franklin, 2010). SDM can be trained on occurrence records from the native domain where species are considered in equilibrium with their environment. However, invasions of new geographic areas often occur in environments that fall outside the native climatic range (Lauzeral et al., 2011). Therefore, SDM trained on occurrence records from a native domain often require unreliable extrapolations of the species-climate relationship outside of the training data (Owens et al., 2013). Conversely, training SDM on occurrence records from the invaded domain avoids the problem of extrapolation but violates the assumption of equilibrium with the climatic environment (De Marco et al., 2008, Elith and Leathwick, 2009). If the species' geographic range is still expanding, SDM that use occurrence data from the invaded domain cannot distinguish between an absence due to incomplete invasion or due to unsuitable climate. In such cases, SDM may underestimate the potential range limits of the invading species.

The proper interpretation of SDM predictions of invasive species requires comparing predictions based on species occurrences in the native and invaded domains along with analysis on whether the climatic niche changed during invasion (Parravicini et al., 2015; D'Amen and Azzurro, 2019). The analysis of a species' climatic niche can identify niche space that is unoccupied in the native but occupied in the invaded domain (i.e. niche expansion), or niche space that is occupied in the native but unoccupied in the invaded domain (i.e. niche unfilling) (Petitpierre et al., 2012). Since niche expansion violates the niche constancy assumption and niche unfilling violates the equilibrium assumption, niche analysis provides information necessary to interpret the SDM predictions for an invasive species. Since locations in niche space can be mapped into geographic space, approaches that determine which areas in climatic niche space are occupied by a species (Broennimann et al., 2012) can be used to predict which geographic areas are climatically suitable for a species. Such an approach uses different assumptions than the assumptions used for SDMs and therefore provides a useful alternative.

The aim of this study was to investigate the potential spread of the invasive *P. miles* in the Mediterranean Sea. To this aim, we constructed an environmental suitability model based on the Maximum Entropy approach and evaluated the degree of niche expansion and niche unfilling, which are key information for species distribution modelling (SDMs), when applied to invasive species (Parravicini et al., 2015). Based on sea surface characteristics and historical chronology, we also estimated the lionfish invasion speed to evaluate its maximum potential of dispersal assuming no other limiting factors.

2. Methods

2.1. Occurrence data & environmental variables

A total of 623 geo-referenced records were extracted from the GBIF database (GBIF Secretariat, 2017), 530 of which were included since they were from native areas according to Schofield et al. (2017). An additional 254 Mediterranean records were extracted from the literature and included in the analysis (Turan and Öztürk, 2015; Mytilineou et al., 2016; Azzurro et al., 2017). The data from both the native (Red Sea and Indian Ocean) and non-native areas (Mediterranean Sea) were subjected to an occurrence thinner filter (10 km radius) using spThin R package (Aiello-Lammens et al., 2015) to reduce sampling bias, resulting in a final data set of 146 (SDM_{ALL}). From them for the Mediterranean remain 37 presence data points (SDM_{INV}) and for the native range remain 109 presence data points (SDM_{NAT}) (Sup File, Fig. S1). Marine abiotic data on variables related to seabed morphology, sea surface salinity (SSS) and sea surface temperature (SST) were obtained from the MARSPEC data set (Sbrocco and Barber, 2013); the spatial resolution of the variables is 1×1 km^2. The environmental data were limited to a depth of 300 m (Schofield et al., 2017). Variance Inflator Analysis (VIF) using USDM R package (Naimi et al., 2013) has been used in order to reduce multicollinearity among predictors. In addition, all variables with an estimated percentage contribution < 1% were excluded from the model.

2.2. Distribution modelling

The probability of lionfish occurrence in the Mediterranean Sea was estimated using MaxEnt ver. 3.4.1 (Phillips et al., 2017). A re-sampling jackknife test used to examine the importance of each environmental variable used in the model for the distribution of *P. miles*. The accuracy of the model was evaluated using the Receiver Operating Characteristic curve (ROC) and the Area under Curve (AUC) values (Fielding and Bell, 1997). AUC-values of 0.5 indicate a model prediction no better than random one, while a value of 1.0 indicates a model with a perfect fit to the data. Three different models have been designed: SDM_{ALL} = Native and Mediterranean presence data, SDM_{INV} = Mediterranean presence data only and SDM_{NAT} = native presence data only. The results from the SDM_{INV} and SDM_{NAT} were used to calculate niche similarity, whilst the SDM_{ALL} was used to calculate the potential distribution across the Mediterranean Sea. All models have run using beta values from one to five to determine whether the prediction of Mediterranean occurrence was influenced by overfitting or sampling bias. Following the recommendations by Barbet-Massin et al. (2012)), for each model different background (bg) point numbers have been selected for optimal model tuning (SDM_{ALL} = 14,600, SDM_{INV} = 3700 & SDM_{NAT} = 10,900). For the SDM_{MED}, a 3-fold cross-validation approach has been selected in order to have enough numbers of data for each fold while for the SDM_{NAT} and the SDM_{ALL} a 5-fold cross-validation has been selected. The final beta value for models has been selected using the model selection function of ENMTools package (Warren et al., 2010) based on the lowest AICc value.

2.3. Niche and analysis

Considering the potential expansion of *P. miles* into areas beyond its native climatic niche (Parravicini et al., 2015) we compared the native (Red Sea/Indian Ocean) and non-native (Mediterranean Sea) climate niches (i.e. abiotic factors) following the method proposed by Broennimann et al. (2012) and Petitpierre et al. (2012). We therefore performed the analysis in the two-dimensional niche space, to make the results less dependent of the specific set of variables measured. In order to define a two-dimensional niche space we applied two approaches: we first used as two axes the two principal components of a Principal Component Analysis (PCA) applied to background samples from native and non-native areas of the same environmental variables as used in the species distribution model (SDM). These two components account for 70% of the variation in the data. The niche analysis was performed using the R package *ecospat* (Di Cola et al., 2017). Since we do not know whether the first two principal components are ecologically relevant for the lionfish, we used in a second approach the mean annual temperature and salinity as the two axes, based on our a priori ecological judgement. We refer to these two different niche spaces as “PCA-based” and “raw niche space” in the main text.

2.4. Spread analysis

Invasion speed was estimated by analysing to which extent the distance between *P. miles* records and the point of entry increased over time. Since the Mediterranean Sea is a heterogeneous environment with an irregular coastline and variable oceanographic characteristics, least-cost distances were used in this analysis, instead of straight-line geographic distances. The least-cost distance describes the distance between two points along the path of the least resistance on a map of conductance values, i.e. values that indicate the ease of spread between any pair of neighbouring cells (van Etten, 2017). The conductance values between two grid cells on the map were either calculated based on occurrence probabilities of *P. miles*, provided by the distribution modelling of the native occurrence data or based on sea current data. The conductance based on occurrence probabilities was calculated as the geometric mean of the occurrence probabilities of the two cells. Since any area with a depth below 300 m was not considered a habitat, some Mediterranean records occurred in 'habitat islands' i.e. areas that could not be reached from the Suez Canal via a contiguous path through cells with non-zero occurrence probabilities. More details on the methods are included at the methods supplementary file.

3. Results

3.1. Distribution modelling

Prediction accuracy was high in both models that included Mediterranean occurrence data set (SDM_{ALL} and SDM_{INV}). The average area under the receiver-operating curve (AUC) was 0.94 ± 0.001 and 0.96 ± 0.006 std. for SDM_{ALL} and SDM_{INV}, respectively (Supplementary Fig. S2). The most important variables, as indicated by the Jackknife test and variable contribution analysis were bathymetry, mean annual sea surface salinity (SSS), SSS of the saltiest month, mean annual sea surface temperature (SST), and SST of the warmest month (Table 2, Supplementary Fig. S3). The niche overlap between the three model outputs was low (Supplementary Table S1). The model trained only with the native data set (SDM_{NAT}) displayed the highest AUC for a beta of 5 (test AUC 0.579) but this AUC was lower than when the Mediterranean occurrence data set was included in the training (SDM_{ALL} and SDM_{INV}). SDM_{INV} showed that the eastern Mediterranean has the highest environmental suitability for *P. miles* (red and yellow in Fig. 1). Probability of occurrence decreases along the southern parts of the central Mediterranean and in the southern coasts of the western Mediterranean Sea, but on a similar level to some areas where the *P. miles* has already been recorded but with few observations (light blue areas in Fig. 1). The Adriatic Sea, Ionian Sea the Gulf of Lion, the Tyrrhenian Sea and the Alboran Sea in the northern Mediterranean were found to be areas unfavorable for the lionfish invasion (Fig. 1; Supplementary Fig. S4). (See Table 1.)

3.2. Test for climatic niche conservatism

We tested for niche equivalency between the native and the invaded domain using different niche space definitions, minimum density cut-offs, and niche overlap metrics. The result of the niche equivalency test depended on the minimum density cut-off. When this measure was set at 5%, niche equivalency was rejected for both niche representations and overlap metrics ($P < .001$ in PCA-based or raw niche space for both metrics). However, with a minimum density cut-off of 0%, niche equivalency was rejected in raw niche space ($P < .001$ for both metrics) but not necessarily in PCA-based space ($P = .82$ for D metric and $P = .01$ for I metric). Hence, in seven out of eight tests (combinations of niche space, minimum density cut-offs, and overlap metric) the observed niche overlap between *P. miles* occurrences in the Indian Ocean and the Mediterranean Sea was significantly lower than the niche overlap between random splits of pooled *P. miles* occurrences (Supplementary Table S2). Tests for niche similarity between the native and invaded domain showed no significant deviation from the null distribution, regardless of niche space representation, minimum density cut-off, or overlap metric. Hence, the observed niche overlap between *P. miles* occurrences in the Indian Ocean and the Mediterranean Sea was not significantly higher than the overlap between the native niche and random niche samples from the Mediterranean Sea. The niche expansion and unfilling indices were, respectively, 0.24 and 0.89 in PCA-based niche space, and zero and 0.51 in the raw niche space when a minimum density threshold of 0% was used. No expansion or unfilling indices could be calculated for a minimum density threshold of 5% since there was either no intersection between niche space in the native and invaded range (PCA-based space) or no non-zero *P. miles* density in the invaded range (according to raw niche space).

Mapping areas from niche space into the geographic space revealed that niche areas with non-zero lionfish densities occur in many parts of the Mediterranean Sea, some of which with no *P. miles* records so far (Fig. 4). In PCA-based niche space, all cells with non-zero *P. miles* densities in the invaded and zero densities in the native range (expansion areas) mapped into the Red Sea in the native domain (Supplementary Fig. S5). Stable niche areas, i.e. areas in niche space where *P. miles* occur in the native and invaded range, mapped mostly into the northern Red Sea and the southern Mediterranean, regardless of whether PCA-based or raw niche space were used (Fig. 4). The geographic

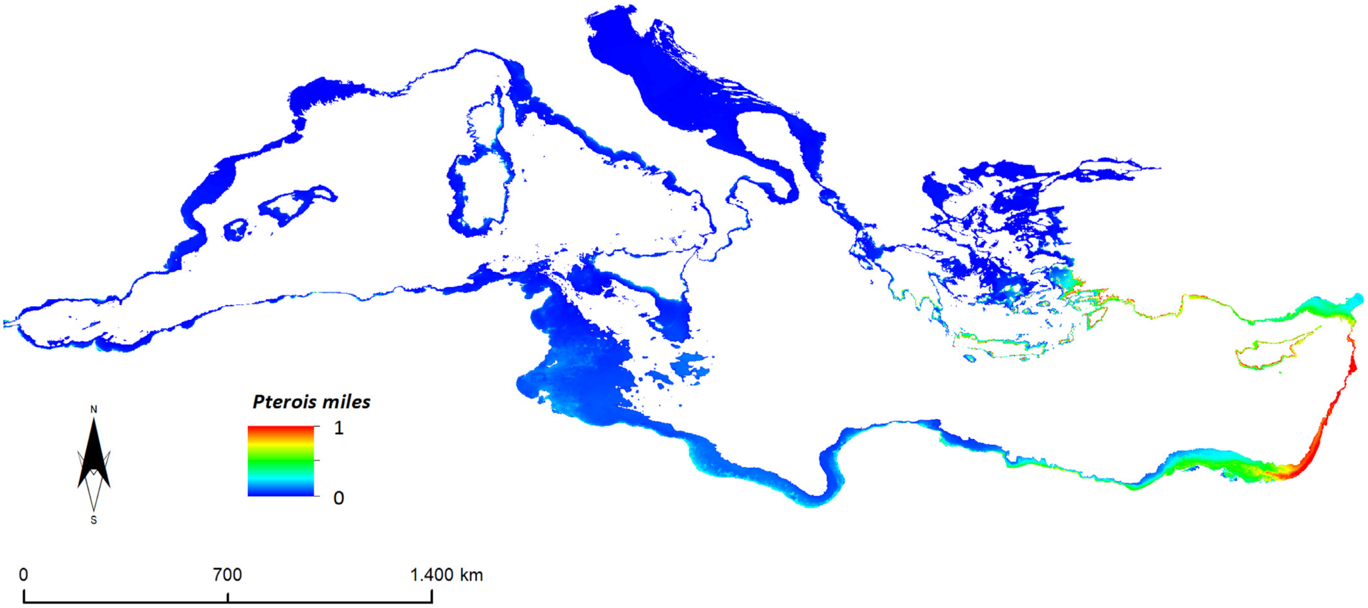

Fig. 1. Probability of *P. miles* occurrence in the Mediterranean Sea based on occurrence data in the native range and the Mediterranean Sea. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Table 1
The MARSPEC variables; ***bold*** indicating variables used in the MaxEnt model.

Parameter code	Description	Parameter code	Description
Bathymetry	***Depth of the seafloor (m)***	biogeo09	***SSS of the freshest month (psu)***
biogeo01	East/West Aspect (radians)	biogeo10	***SSS of the saltiest month (psu)***
biogeo02	North/South Aspect (radians)	biogeo11	***Annual range in SSS (psu)***
biogeo03	Plan Curvature	biogeo12	***Annual variance in SSS (psu)***
biogeo04	Profile Curvature	biogeo13	***Mean Annual SST (°C)***
biogeo05	Distance to Shore (km)	biogeo14	***SST of the coldest month (°C)***
biogeo06	Bathymetric Slope (degrees)	biogeo15	***SST of the warmest month (°C)***
biogeo07	Concavity (degrees)	biogeo16	***Annual range in SST (°C)***
biogeo08	***Mean Annual SSS (psu)***	biogeo17	***Annual variance in SST (°C)***

Table 2
Percentage contribution and permutation importance of the environmental variables used in the model.

Variable	Percent contribution (%)	Permutation importance (%)
Mean Annual SST	32.9	25.2
Mean Annual SSS	18.9	5.1
Bathymetry	13.2	8
Annual variance in SST	11.8	5.8
SST of the warmest month	7.2	2.2
SSS of the freshest month	6.2	3.3
SSS of the saltiest month	4.9	5.8
SST of the coldest month	2.3	6.5
Annual variance in SSS	1.6	19.3
Annual range in SST	0.6	17.1
Annual range in SSS	0.3	1.7

location of unfilling niche areas, i.e. areas in niche space where lionfish occur in the native and but not in the invaded range, depended on the niche definition.

Niche unfilling was found remarkably high regardless of the technique employed to depict the climatic niche (PCA-based = 0.89; raw niche space = 0.51). Unfilling niche cells in raw niche space (i.e. cells in niche space that are occupied in the native range and unoccupied in the invaded range) map into the South African coast in the native range and into four distinct regions of the Mediterranean Sea, two of which occur in the northern Mediterranean Sea (Fig. 4). Stable niche cells (i.e. cells in niche space that are occupied in the native range and in the invaded range) map into the northern Red Sea and most of the southern coast of the Mediterranean Sea (Fig. 4).

These unfilling areas in raw niche space mapped into the South African coast and different parts of the Mediterranean Sea (Fig. 4), whereas unfilling niche areas in the PCA niche space mapped into the coast of India and Thailand and different parts of the Mediterranean Sea (Supplementary Fig. S5). The only variable for which niche equivalency was rejected according to both overlap metrics (Schoener's D and Warren's I) was annual variance in SSS ($P < .001$ for both metrics). For this variable, the expansion and unfilling indices were, respectively, 0 and 0.16 (Fig. 5).

3.3. Spread analysis

Invasion speed was estimated by analysing to which extent the least-cost distance between *P. miles* records and the point of entry increased over time. The conductance values between two grid cells on the map were either calculated based on the occurrence probabilities predicted by SDMs or based on sea current data. In the first scenario, the least-cost path from the first (2012) to the westernmost record moved along the southern shores of the Mediterranean. In contrast, when calculations were based on sea currents, the least-cost path moved north of the islands of Cyprus and Crete (Fig. 2). The patterns of temporal expansions were similar for both distance measures (Fig. 3). No increase in distance was found for 2013 according to the two distance measures, followed by a slight increase in 2014 and a strong increase in 2015. The percentage of the cost distances between the Suez Canal and the Strait of Gibraltar that the lionfish has covered so far differed between the two distance methods used. According to occurrence probability-based distances, *P. miles* expanded annually by 8% of the distance between the Suez Canal and the Strait of Gibraltar, while according to sea current-based distances, it expanded by 13% annually. The total percentage of the cost distance between the Suez Canal and the Strait of Gibraltar that *P. miles* has reached so far is 32% according to the occurrence probability-based distances and 54% according to the sea current-based distances (Fig. 3). The putative time of arrival at Gibraltar was estimated to be 2025 and 2019, respectively.

4. Discussion

4.1. SDMs and niche analysis

Our model allowed us to identify areas in the Mediterranean Sea that are climatically suitable to be conquered by the invasive lionfish *P. miles*. Among the three lionfish occurrence data sets used to train the SDM's (i.e. native range, Mediterranean, or both), native occurrences only resulted of little value for predicting the lionfish Mediterranean distribution. This poor model fitting, when calibrated in the native range only, was somehow expected due to tendency of these species to shift their climatic niche when translocated to distant locations (Parravicini et al., 2015; and D'Amen and Azzurro, 2019). At the same time, the combined (native plus Mediterranean) occurrences allowed a much better model fit, with projected probability occurrence (Fig. 1) that closely agree with the most recent outputs of SDMs developed by D'Amen and Azzurro (2020) for the same species.

This conclusion is also supported by eight different niche equivalency tests, which were used to check for the lionfish climatic niche shift. Seven out of eight tests showed a significant deviation from niche equivalency (Supplementary Table S2), which may be the result of either niche expansion or niche unfilling (Parravicini et al., 2015). Evidence for niche expansion occurred only in PCA-based niche space (Table S2) and many of these cells mapped into the Mediterranean Sea and into tropical waters along the coast of Malaysia and Sumatra (Supplementary Fig. S5) which are the east boundaries of the native distribution (Schofield et al., 2017). However, since the first two principal components of environmental variables were not always suitable to describe niche space (Supplementary Fig. S5), further research is needed to determine whether the limitations of PCA-based niche space, as shown in our study, occur only in this data set of occurrences and predictors or also other oceanographic data sets.

Eastern Mediterranean climates, closely resembled to the northern Red Sea conditions, mainly Gulf of Suez (Fig. 4), from where the lionfish invasion originates (Bariche et al., 2017). Similarly, for other Lessepsian fishes, the most suitable conditions occur in the eastern Mediterranean (Azzurro et al., 2013; D'Amen and Azzurro, 2020) with stable niche cells (stable points in Fig. 4). Nevertheless, possibilities of a further expansion of the climatic niche of *P. miles* in the Mediterranean Sea

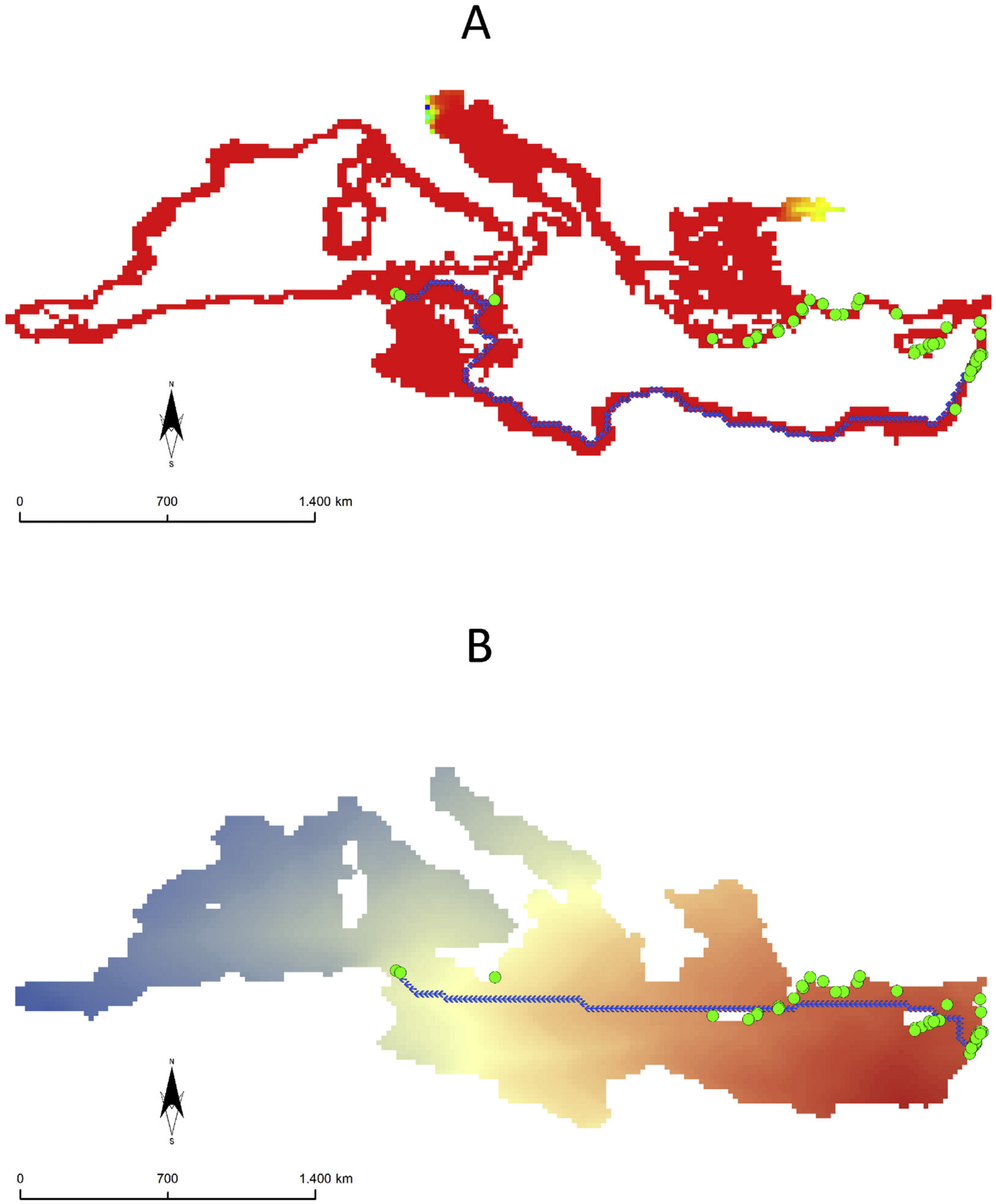

Fig. 2. Movement cost according to least-cost distances. Coloured pixels show the least cost distance from the Suez Canal to every point on the map. Least-cost distances were either calculated based on occurrence probabilities (A) or sea current velocities (B). The red lines indicate the least-cost path from the first record in 2012 to the westernmost record and red dots show records of *P. miles*. Green points show the presence records used in the analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

seems to be likely, due to the high degree of niche unfilling. Possibilities of local adaptation (Conover et al., 2006) and propagule spread are also elements to be considered to properly evaluate the risk of future invasion. Indeed, the mapping of cells from raw niche space into geographic space would result in wide suitable areas along the eastern and southern sectors of the Mediterranean (Fig. 4). By critically considering the outputs of both, the SDMs and niche analyses, these could be interpreted as the less and most conservative projections of the space the lionfish could occupy, respectively.

4.2. Spread analysis

Outcomes of SDMs and niche analysis are here enriched by spread analyses. According to our findings, sea currents could have contributed to the mismatch between *P. miles* occurrence and climatically suitable areas in the Mediterranean Sea. The least-cost path based on sea currents between the first and westernmost *P. miles* record passed along the southern coast of Turkey and Crete, areas that possess the most Mediterranean *P. miles* records (Fig. 2). Sea currents are therefore a possible contributing reason why *P. miles* still hasn't established yet along the coast of Libya and Egypt, even though temperature and salinity in these regions are similar to the northern Red Sea and therefore suitable for the establishment of this species. The regression of least-cost distance vs. time also indicates that *P. miles* is still not in equilibrium with its environment since there is no evidence that the geographic expansion has slowed down. Our extrapolation of the temporal trends indicates that, If the Mediterranean was all suitable to be colonized by *P. miles*, this species could reach the Strait of Gibraltar

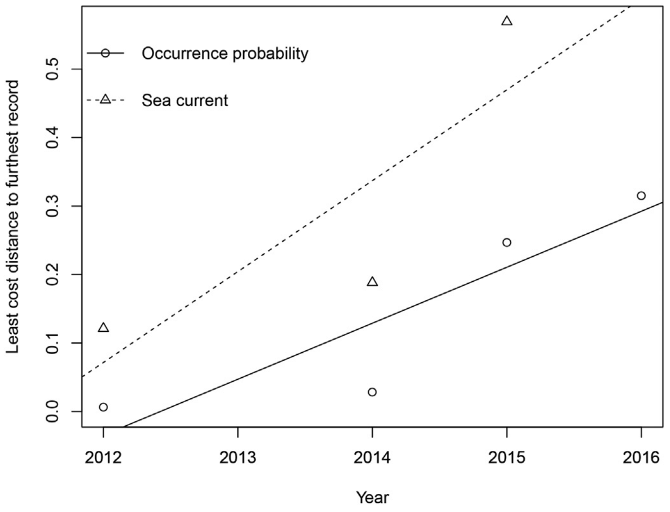

Fig. 3. Furthest least-cost distance per year. The plot shows the furthest distance to the Suez Canal among all records for each year in which the distance increased compared to all previous years. Lines show results of least-square regressions. Least-cost distances were calculated based on occurrence probabilities or sea currents. Different distances were divided by the cost distance to Gibraltar.

within a few years. Certainly, the dispersal ability of this species will not help the lionfish to colonize unsuitable habitats, but could allow the species to reach suitable areas of the Mediterranean. The continuous westward spread of *P. miles* is illustrated by both the scientific literature (see Azzurro et al., 2017) and citizen's generated observations (Giovos et al., 2019) would support the idea of a rapid spread and high connectivity of the Mediterranean lionfish, controverting the initial hypothesis of Johnston and Purkis (2011). Certainly, our estimated spread rates should be interpreted with caution since they were based on published first records, rather than systematic surveys. Furthermore, data points in the plot of least-cost distance vs. time were not independent of each other. The fitted regression lines are therefore illustrations of the trends in the data, rather than precise estimates of spread. Nevertheless, the rate of spread obtained from our analysis is in line with the spread rates observed by *P. miles* invasion in the Caribbean Sea (Johnston et al., 2011) and comparable to the most rapid fish invasions in the Mediterranean Sea (Azzurro et al., 2013; Lasram et al., 2010).

5. Conclusions

The invasive *P. miles* has rapidly expanded through the eastern Mediterranean but so far it has been never reported from some suitable areas, including Egypt and Libya. This is well illustrated by the combined evidence arising from the SDMs, niche analysis and the least-cost paths, which would explain the present picture as a combination of incomplete invasion and sea currents. Predictions of climatic suitability based on the raw niche space based on mean SST and SSS might be significantly improved by the inclusion of other relevant climatic variables and complex relationships, such as those arising from biotic interactions, that have been demonstrated to have a primary role in predicting the invasion success (Azzurro et al., 2013). It is therefore reasonable to interpret our two climatic suitability predictions, SDMs and niche analysis, as the two ends of a spectrum.

Specifically, SDM predictions (Fig. 1) would represent our less conservative projection (the lower end), whilst the niche-based approach, include unfilling areas (Fig. 4) as the most conservative one, the upper end of the potential geographic range that *P. miles* can occupy. The final equilibrium distribution that *P. miles* will reach in the Mediterranean Sea will most likely fall somewhere between these two extremes. It is important to note that even the low-end scenario (Fig. 1) shows climatically suitable areas in currently unoccupied areas of the southern Mediterranean rim (e.g. Egyptian coast to western Tunisia and southern Aegean Sea to Saronikos Gulf).

Finally, our results can contribute towards the development of an Early Warning Systems and Information tools (EWSI) for reporting newly arrived and emerging non-indigenous species in support of the D2 "Exotic Species" of the Marine Strategy Framework Directive. As such, early views of newly arrived species or species with a well up to now defined invasion which are potential harmful to the e.g. fishermen

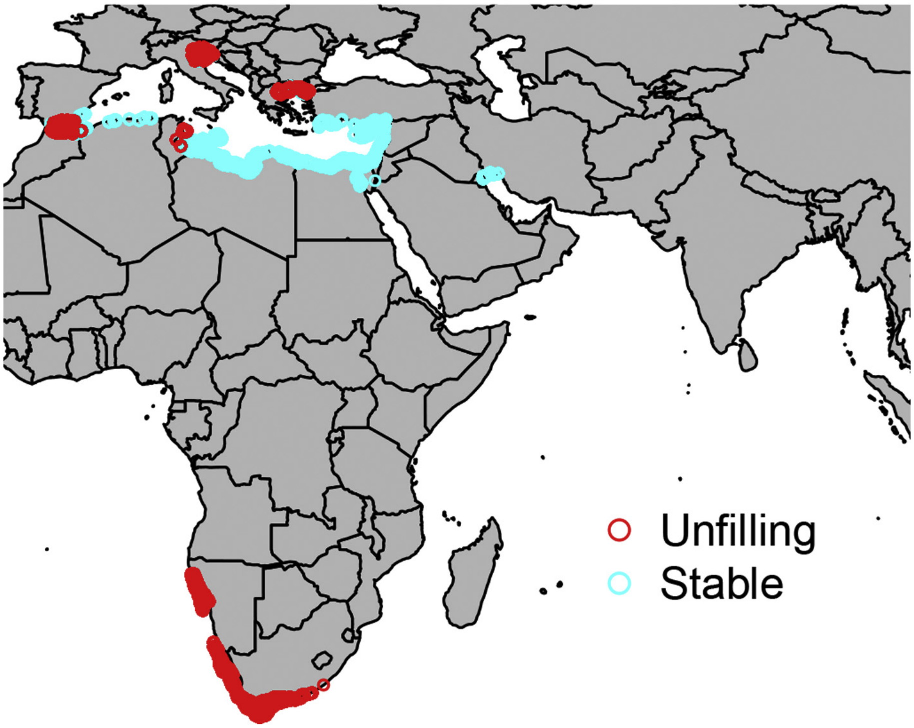

Fig. 4. Background samples that fall in niche space cells with non-zero lionfish densities. Points are distinguished between stable (niche space occupied in invaded and native range) and unfilling (niche space occupied only in native range but not in invaded range). The plot is based on niche space defined by mean annual SST and SSS.

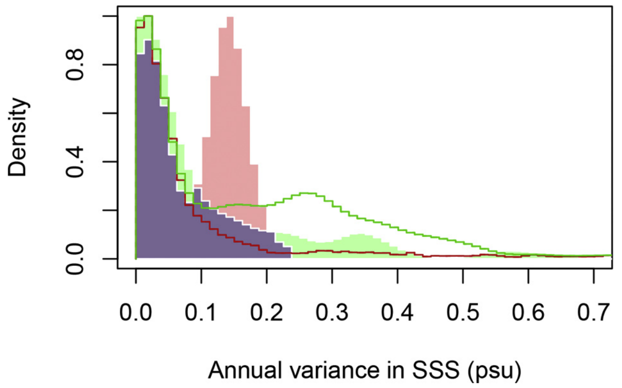

Fig. 5. Probability density functions of variable and species distributions for annual variance in SSS. Solid lines show distribution of variable values and shaded areas show species occurrence distribution. Native range is shown in green and invaded range in red. Overlapping species distribution is shown in purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and citizens of the coastal zone; that could rapidly respond to social issues that may arise (EEA, 2010) can be addressed and communication providing spatial maps for their potential distribution, acknowledging the limitations of the methods (Katsanevakis and Moustakas, 2018).

Such systems are widely used in several other fields e.g. water resources management Koutsoyiannis et al., 2003), environmental management (McIntosh et al., 2011), fire and flood management (Noonan-Wright et al., 2011) but rarely used in the field of conservation and management of invasive species (Aracena, 2013; Maguire, 2004). In 2004, the international convention on the control and management of ships ballast water and sediments (BMW Convention) was adopted with the aim to prevent the spread of alien species and entered into force in September 2017. Alien species are one of the six key objectives in the EU Biodiversity Strategy (COM/2015/0478, 2015). The threat posed by the introduction of alien species to global diversity loss is considered to rank second after habitat destruction.

Raised concerns regarding the establishment of alien species outside their native range led the European Union to adopt the marine strategy framework Directive 2008/56/EC, 2008 with a descriptor for alien (or non-indigenous) species Crise et al., 2015). Once an alien species is established in a large marine ecosystem such as the Mediterranean Sea, it cannot be eradicated (Kalogirou, 2011, Pluess et al., 2012, N'Guyen et al., 2016). Removal programs can be useful to control *P. miles* invasion at the local scale but eradication of this species through removal is unfeasible (Barbour et al., 2011; RELIONMED-LIFE, 2017). Other management implications for *P. miles* could include fishmongers and civil training on removing venomous spines, informing the fisheries sector, and promoting local culinary (Morris Jr et al., 2011). Our study could support stakeholders in decision-making and development of early warning systems.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

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Appendix A. Supplementary data

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