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Cover Caption: The striped eel catfish *Plotosus lineatus*, an Indo-Pacific species established in the Mediterranean Sea
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LETTER

Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders

Valeriano Parravicini,^{1,2,3*} Ernesto Azzurro,⁴ Michel Kulbicki² and Jonathan Belmaker^{5*}

Abstract

Climatic niche conservatism, the tendency of species-climate associations to remain unchanged across space and time, is pivotal for forecasting the spread of invasive species and biodiversity changes. Indeed, it represents one of the key assumptions underlying species distribution models (SDMs), the main tool currently available for predicting range shifts of species. However, to date, no comprehensive assessment of niche conservatism is available for the marine realm. We use the invasion by Indo-Pacific tropical fishes into the Mediterranean Sea, the world's most invaded marine basin, to examine the conservatism of the climatic niche. We show that tropical invaders may spread far beyond their native niches and that SDMs do not predict their new distributions better than null models. Our results suggest that SDMs may underestimate the potential spread of invasive species and call for prudence in employing these models in order to forecast species invasion and their response to environmental change.

Keywords

Biological invasion, niche conservatism, niche expansion, niche shift, species distribution models.

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INTRODUCTION

Climate change has already triggered profound responses of natural systems (Walther *et al.* 2002; Hoegh-Guldberg & Bruno 2010). Among them, the spread of invasive species and the poleward shift of warm-adapted organisms represent two major causes of current biodiversity changes (Parmesan *et al.* 1999; Parmesan & Yohe 2003; Araújo *et al.* 2005; Cheung *et al.* 2009; Pereira *et al.* 2010). Understanding the degree of species climatic niche conservatism, the tendency of species climatic niche to remain unchanged across space and time, is pivotal to forecasting the spread of invasive species and climate-related distributional shifts (Pearman *et al.* 2010; Wiens *et al.* 2010). Indeed, if species maintain their climatic niche, species distribution models (SDMs) could predict their future ranges on the basis of the current environment in which the species are observed. However, if species are able to expand into novel climates, attempts to predict range shifts following environmental change may be largely futile.

Despite its relevance, the generality of climatic niche conservatism is still under intense scientific debate (Guisan *et al.* 2012; Petitpierre *et al.* 2012; Webber *et al.* 2012). Some conceptual issues arise from the fact that SDMs use observed-locality data and hence may estimate the realized and not the fundamental niche of the species (Godsoe 2010; Warren 2012; McInerny & Etienne 2013). For instance, SDMs do not incorporate biotic interactions which may shape species distribution beyond climate itself (Wiszniewski *et al.* 2013). Despite these

limitations, SDMs have been shown to perform well in predicting species distribution in the terrestrial realm (Pearson & Dawson 2003; Araújo *et al.* 2005; Soberón & Nakamura 2009). One of the main obstacles to a broader assessment of SDMs is the availability of independent data across many species which are seldom available, especially in the marine realm.

In this context, biological invasion represents a valuable source of information (Petitpierre *et al.* 2012; Guisan *et al.* 2014) as it typically generates two separate and independent geographical distributions (Broennimann & Guisan 2008; Pearman *et al.* 2008): the native and invaded ranges of species. Comparing these distributions may allow us to assess patterns of: (1) climatic niche expansion (the environmental shift of species beyond their climatic limits in their native ranges), niche unfilling (the presence of favorable climate in the invaded domain not yet occupied by the species) and climatic niche conservatism (also termed stability, i.e. the match in environmental conditions between native and invaded ranges). Recent comprehensive assessments of reptiles, amphibians, plants and birds have found convincing evidence for climatic niche conservatism (Broennimann *et al.* 2012; Petitpierre *et al.* 2012; Strubbe *et al.* 2013), while only a few assessments, mostly focusing on a single or few species, have documented niche expansion (Broennimann *et al.* 2007; Medley 2010; Lauzeral *et al.* 2011). Moreover, niche expansion detected in later studies may be partly due to methodological artefacts (Broennimann *et al.* 2012). However, no comprehensive assessment of

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climatic niche expansion by invasive species is currently available for the marine environment.

We compiled two extensive data sets consisting of all the available information on the distribution of Indo-Pacific tropical marine fish species currently spreading into the Mediterranean Sea, the world's most invaded marine basin. Since the opening of the Suez Canal in 1869, the Mediterranean has been experiencing a large influx of Red Sea organisms, also known as 'Lessepsian species' (Galil 2008; Zenetos *et al.* 2010), with profound ecological and economical consequences (Sala *et al.* 2011; Edelist *et al.* 2013). In the open debate concerning whether the degree of climatic niche conservatism is sufficient to allow accurate predictions of invasion risk, the invasion of the Mediterranean by tropical taxa offers a unique, unplanned biogeographical experiment. The complete distributional data for these invasive species in their native and exotic ranges, as well as the distribution of the entire pool of non-invasive Red Sea species, allowed us to employ a suite of novel niche conservatism tests at an unprecedented scale for the marine realm.

METHODS

Species distribution data and environmental variables

We compiled a database on the distribution of tropical coastal fish occurrences in the Indo-Pacific, i.e. the native range of species (Belmaker *et al.* 2013; Kulbicki *et al.* 2013; Parravicini *et al.* 2013). Information was obtained from 548 references (Supplementary References 1), including 289 checklists, 27 new records of species for specific locations, 38 global, 137 regional and 57 local reviews for specific families or genera. For each checklist, we cross-verified the information against the other sources of information (i.e. new records and reviews) and used maps in the original publication to define in GIS database (Geographical Information System) the area to which each species list pertains. Using this spatial layer, we extracted the geographical distribution of Lessepsians (30 species) and the entire pool of Red Sea non-invasive coastal fish (805 species) using a 100×100 km grid (Belmaker *et al.* 2013). The final data employed for the analysis consisted of 2355 grid cells covering the entire Indo-Pacific region (see Fig. S1). Checklists are actually sampled locations and have lower false-absence as well as lower false-presence rates than data derived from range maps, thereby representing one of the best available information for calibrating SDMs.

Mediterranean distributions were extracted from the OR-MEF database (Azzurro *et al.* 2013), for the 30 coastal Lessepsian species for which we had extensive information on both the Mediterranean Sea and their native ranges. The Mediterranean distributional data for these species is based on 250 references (Supplementary References 2) corresponding to 1805 geo-referenced observations. This occurrence data were coarsened to a 100×100 km grid of Mediterranean shallow water habitat (< 100 m depth), so that a species was deemed present in a grid cell if it was observed within it at least once.

Since taxonomic uncertainty is common in macroecological research, we identified species that have been subject to recent taxonomic revisions or species which can be confounded with

others (see Table S1). For these species, we built a 'minimal distribution' containing the smallest range of the potentially confounded species and a 'maximal distribution' reporting the joint distribution across all the potentially confounding species (Table S1). Results were highly consistent between the minimal and maximal distributions and in the main text we report only the most conservative results derived from the maximal data set (the results for the minimal distribution may be found in the Supplementary Information).

Climatic variables for both the Mediterranean and Indo-Pacific were extracted using a 100×100 km grid. Climatic layers were based on Tyberghein *et al.* (2012) with a resolution of 5 arcmin. In accordance with previous work on Lessepsian fishes (Belmaker *et al.* 2013), we described the climatic niche of species according to eight variables: mean annual salinity (PSS); minimum, maximum and range sea surface temperature ($^{\circ}\text{C}$); minimum, maximum, mean and range chlorophyll a concentration (mg m^{-3}) as a proxy of productivity. We calculated the mean values within each grid cell in both native and invaded ranges.

Testing for climatic niche conservatism

To determine climatic niche overlap between native and non-native ranges, we compared the climatic niche of species in the Indo-Pacific with the niche occupied by the same species in the Mediterranean (Fig. 1). We first calculated a PCA on

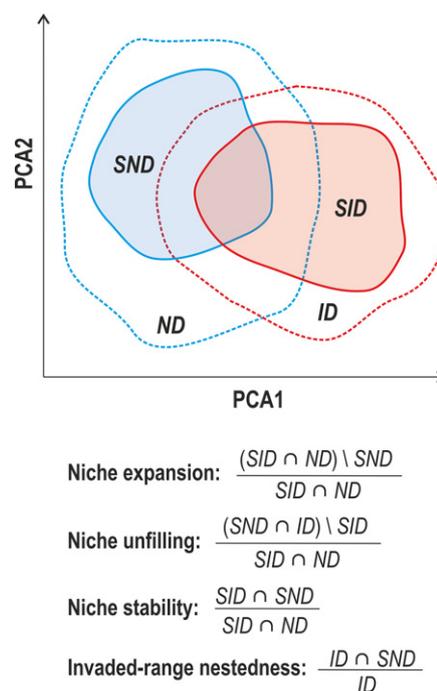


Figure 1 Graphical illustration of the indices employed to assess niche expansion, niche unfilling, niche stability, and invaded-range nestedness (i.e. the degree of nestedness of the Mediterranean Sea climate within the climatic niche of the species in the native range) according to the PCA-kernel method. Dotted lines refer to Native Domain (ND, blue) and Invaded Domain (ID, red). Filled polygons represent the niche of species inferred from the Species Native range Density (SND, blue) or Species Invaded range Density (SID, red).

all environmental data from both the Indo-Pacific and the Mediterranean. The first two axes explained 80% of the variance and were retained for further analyses. The environmental space depicted by the first two PCA axes was then divided into a grid of 100×100 cells and a Gaussian kernel density estimator was applied to estimate, for each grid cell, the smoothed density of occurrences. For each species, overlap between the climatic niche in the invaded and native ranges was assessed, after correcting for environmental availability, using the Schoener's D metric (Warren *et al.* 2008; Broennimann *et al.* 2012). This index measures the degree of overlap between the two climatic niches, i.e. how much the niche in the native domain is similar to the niche in the invaded domain, and ranges between 0 (no overlap) and 1 (complete overlap). Although this method can be used with as few as five occurrences (Broennimann *et al.* 2012), we decided to use a more conservative cut-off of seven records as the minimum sampling effort for depicting a climatic niche. This cut-off resulted in the selection of the 30 invasive species to be included in analyses, ranging from 7 to 273 occurrences in the Mediterranean and from 14 to 1717 occurrences in the Indo-Pacific (see Table S3).

In order to test for climatic niche conservatism, we first used two well-established procedures, i.e. the 'niche equivalency' test and the 'niche similarity' test (Warren *et al.* 2008). The former tests whether the native and invaded climatic niches are identical, while the latter tests whether the similarity between the native and invaded niches is higher than expected by chance alone. According to the method proposed by Broennimann *et al.* (2012), we tested for niche equivalency by randomly reallocating the occurrences in the entire climatic space (Mediterranean and Indo-Pacific) before calculating overlap and for niche similarity by comparing the overlap between Indo-Pacific and Mediterranean distributions to a random draw of grid cells in climatic space (the same size as the observed number of occurrences) from the Mediterranean. In both cases, 999 random draws were employed.

Since in the specific case of Lessepsian invasion, species are forced to enter the Mediterranean by the Suez Canal, we further tested whether the overlap between native and invaded distributions was different than expected, given the climatic constraints in the South-Eastern Mediterranean. For this, we randomly selected grid cells in the Mediterranean Sea, with probabilities decreasing with distance to the entry point in the Suez Canal. We assigned a cell-specific probability of occurrence using the negative exponential probability distribution:

$$P = \lambda e^{-\lambda x} \quad (1)$$

where P is the probability of a grid cell in the Mediterranean Sea of being selected, λ is the range parameter and x is the distance of the cell from the Suez Canal (km). The tests were conducted using five different values of λ , i.e. 100, 500, 1000, 5000 and 10 000 km (Fig. S2). Using these probabilities, we randomly selected the number of grid cells to match the observed number of Mediterranean occurrences and repeated the procedure over 999 randomisations. Analyses were conducted with R using 'ade4' package and additional functions provided by Broennimann *et al.* (2012).

Deconstructing the invaded distribution: niche expansion, unfilling and stability

While the overlap between the two climatic niches provides evidence for conservatism, a lack of niche overlap may be due to distinct phenomena, niche expansion or niche unfilling (Fig. 1). Climatic niche expansion occurs when the non-overlapping portion of the niche corresponds to a shift towards new climates (i.e. climates not occupied by the species in the native domain). On the other hand, niche unfilling occurs when the non-overlapping portion of the niche corresponds to climates not yet filled by the species in the invaded domain (i.e. climates occupied by the species in the native domain but not occupied in the invaded domain). Since invasive species are unlikely to have reached climatic equilibrium in the invaded domain, climatic niche unfilling may be very common and attest the future potential spread of the species. Finally, climatic niche stability is the inverse of niche expansion and is calculated as the proportion of the climatic niche in the invaded domain which overlaps with the native climatic niche.

The Schoener's D metric is not able to distinguish between climatic niche expansion and niche unfilling. However, within the context of biological invasion, niche expansion represents a lack of climatic niche conservatism, while niche unfilling cannot inform about processes as the assumption of equilibrium is not met. We thus calculated indices for climatic niche stability, expansion and niche unfilling using the following formulas (see Fig. 1):

$$Stability = \frac{SID \cap SND}{SID \cap ND} \quad (2)$$

$$Expansion = \frac{(SID \cap ND)/SND}{SID \cap ND} \quad (3)$$

$$Unfilling = \frac{(SND \cap ID)/SID}{SID \cap ND} \quad (4)$$

where SID (Species Invaded range Density) represents species occurrence densities in the invaded range, SND (Species Native range Density) represents the densities in the native range, ID (Invaded range Density) is the densities of the entire invaded range and ND (Native range Density) is the densities of the entire native range. Hence, $Expansion$ represents the percent of densities in the invaded distribution which are not present in the native distribution; $Unfilling$ represents the percent of densities in the native distributions which are not present in the invaded ones.

We used the 75th density percentile to reduce the effect of marginal climates (Petitpierre *et al.* 2012). However, using different percentiles (i.e. 75, 80, 85, 90, 95 and 100) had no effect on the metrics (Kruskal–Wallis rank sum test never found significant differences; Fig. S3). To present results comparable to those of recent assessments, we defined as expanding species only those showing a niche expansion higher than 10% (Petitpierre *et al.* 2012).

The calculations of climatic niche expansion can be applied in two versions, either after removing cells with non-analog climates (i.e. only at the intersection between ID and ND) or retaining these cells. These two methods have slightly different assumptions and both have been advocated as ecologically superior (Petitpierre *et al.* 2012; Webber *et al.* 2012). However,

in our analyses including or excluding non-analog climate had little effect on our results and we therefore present the most conservative results after excluding non-analog climate.

While it is rarely tested, detecting climatic niche expansions may be constrained by the novelty of climates in the invaded range. At the extreme, if the entire invaded domain is climatically similar to the species native range, niche expansion will always be absent just because it cannot be detected. To test whether climatic niche expansion and stability were related to constraints related to the available climate within the invaded domain, we calculated a metric of 'Invaded-Range climatic nestedness' (IR_{ness}) as the degree of nestedness of the entire climate of the Mediterranean Sea within the niche of the species in the native range:

$$IR_{ness} = \frac{ID \cap SND}{ID} \quad (5)$$

Although the assessment of the climatic niche using PCA and kernel density estimation in environmental space is presently considered the most reliable technique, detecting niche expansion may be method-dependent (Broennimann *et al.* 2012). To assess the robustness of our estimates to methodological choices, all the analyses were also performed with an alternative method based on the geographical space: the Multivariate Environmental Similarity Surfaces (MESS) method (Elith *et al.* 2010). The MESS technique is similar to bioclimatic envelope methods (Busby 1991), but extended in order to differentiate the level of dissimilarity when outside the environmental envelope of the species in its native range (i.e. the reference envelope). Positive values (high climatic similarities) are obtained when a cell in the invaded range is found within the climatic envelope of the native range while negative values (low climatic similarities) are obtained when a cell in the invaded range is found outside the climatic envelope of the

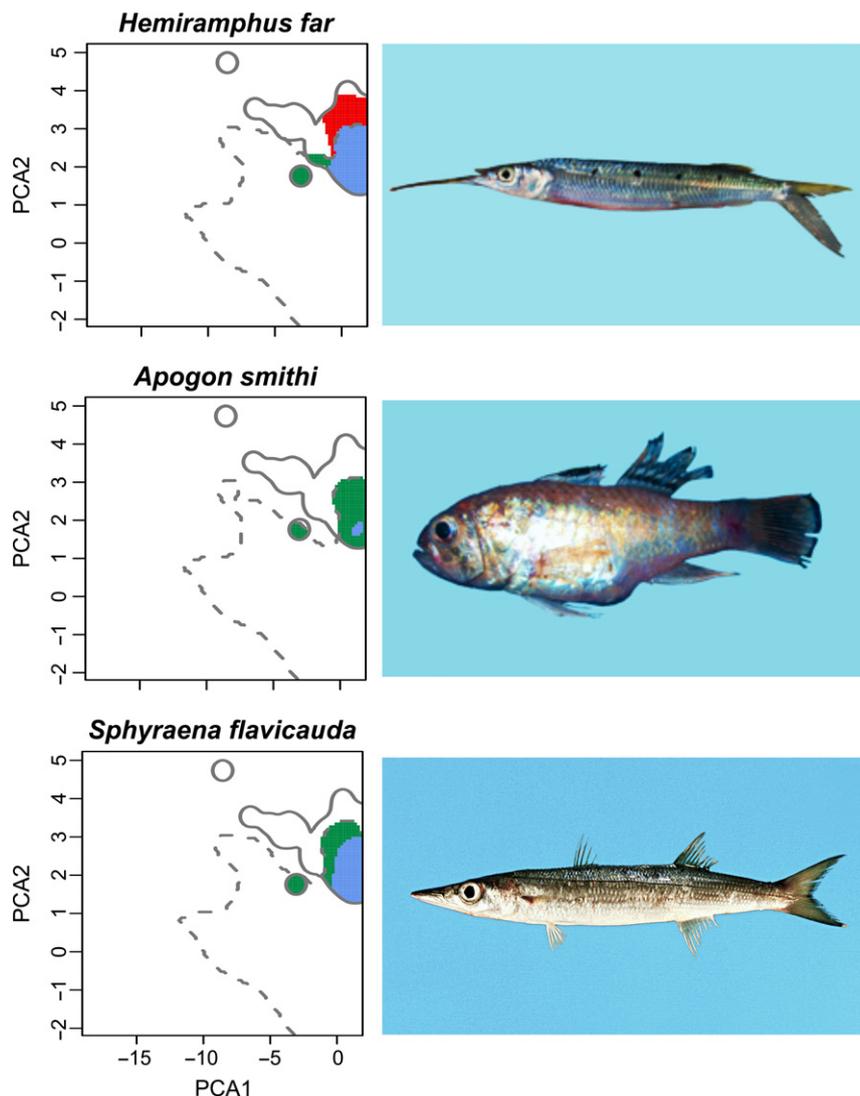


Figure 2 Examples of Lessepsian species climatic niche behaviors. *Hemiramphus far* (photo E. Azzurro) is an example of a species with large climatic niche expansion (see Methods), *Apogon smithi* (photo E. Azzurro) is an example of species with large niche unfilling while *Sphyraena flavicauda* (photo D. Golani) is an example of a species displaying climatic niche stability. Left panels represent climatic space defined by the first two PCA axes. Red areas represent niche expansion, green areas represent niche unfilling and blue areas represent niche stability. Continuous lines represent the entire Mediterranean Sea climate, while dotted lines represent the native climatic niche of species in the Indo-Pacific.

native range. For each species, we obtained a map of the Mediterranean Sea highlighting the cells climatically similar and dissimilar to the climate in the native range. We applied the same calculation of climatic niche expansion and unfilling as described above using the PCA-kernel method in environmental space (see Fig. S4).

Evaluating the potential of species distribution models to forecast invasion risk

We further assessed the potential of the climatic niche to detect the invasion potential by constructing species distribution models (SDMs) to predict the presence of invasive species in the Mediterranean. We calibrated maximum entropy SDMs (MaxEnt; Phillips *et al.* 2006) using the native distribution of species in the Indo-Pacific. The number of grid cell occurrences in the Indo-Pacific was high (sample sizes ranged between 14 and 1717 occurrences) which allowed us to perform model validation procedures. Thus, during model building, data for the native range were randomly split into 80% training and 20% testing, and subject to 10 evaluation runs. We largely used default settings, but due to concerns about over-fitting we chose not to use products between predictors as well as hinges and thresholds. The quality of the model was evaluated using the AUC (Area Under the ROC Curve) and the continuous Boyce index (Hirzel *et al.* 2006). These indices were calculated by comparing the probabilities predicted for the Mediterranean by MaxEnt models calibrated using the native distribution of species with the true occurrences in the Mediterranean Sea. All the analyses were conducted in R using the 'biomod2' package.

Comparison with Red Sea species distributions

Distributional data typically show high spatial autocorrelation, raising the concern that climate-based analyses may show spuriously high predictive power (Beale *et al.* 2008). To further discern the true predictive power of SDMs in the context of invasion from constraints associated with range-cohesion and environmental spatial autocorrelation, we compared the observed ability of native range data to predict Mediterranean occurrences with those based on the Indo-Pacific distributions of non-invasive Red Sea coastal species (805 species). We used Red Sea species as they constitute the entire source pool of invasion. We first tested whether the climatic niche overlap between native and invaded distributions was different than the overlaps between the true invaded distributions and each species within the entire pool of non-invasive Red Sea species. In addition, we tested whether the AUC and Boyce index values obtained from the original SDMs models were higher than those obtained by models calibrated on each of the non-invasive Red Sea species.

RESULTS

We found little evidence of climatic niche similarity between fishes in their invasive Mediterranean range and native range within the Indo-Pacific. First, we found no evidence of niche equivalency in any of the studied species (Table S2). Second, while we found evidence of significant climatic niche similarity

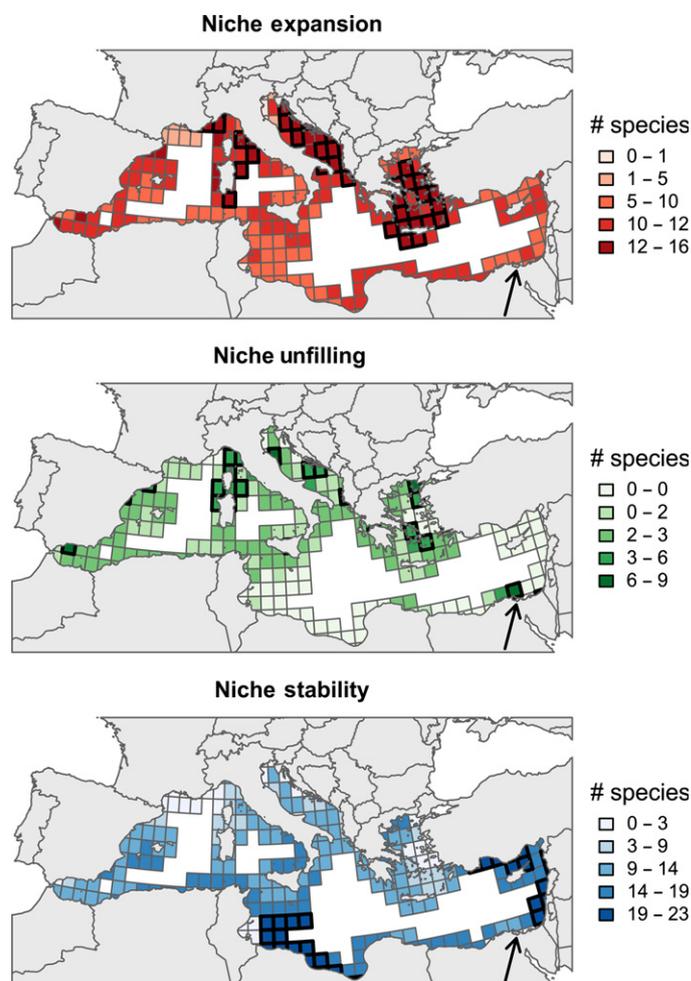


Figure 3 Number of Lessepsian species showing climatic niche expansion, stability and unfilling (see Methods) estimated using the PCA-kernel method measured in environmental space and projected into geographical space. The arrow on the maps highlights the entry point of Lessepsian species in the Mediterranean (i.e. the Suez Canal). Grid cells in the maps with thick borders represent hotspots of expansion, stability and unfilling defined as the cells with the highest 10% of species. The northern sectors of the Mediterranean Sea were identified as hotspots of niche expansion while niche stability (i.e. overlap between native and invaded niches) is common in the southern Mediterranean, especially in the Levant Sea.

between the native and invaded ranges for 11 species out of 30, this number further decreased to nine species when accounting for the constrained entry point of invaders through the Suez Canal (Table S2). Finally, a comparison of the observed overlaps between native and invaded climatic niches with the overlaps between the climatic niches of invasive species in the Mediterranean and random Red Sea non-Lessepsians revealed that only seven species show a niche overlap significantly higher than expected according to the distributions of Red Sea species. In other words, taking a species distribution at random from the Red Sea pool of species often produces larger climatic niche overlaps than found when using the actual distribution of the invaders in their native ranges (Table S2).

We then analyzed two distinct phenomena that may explain non-overlapping climatic niches, each with markedly different

implications: niche expansion and niche unfilling (Fig. 2). Considering as expanding species only those showing a niche expansion larger than 10%, the PCA-kernel method identified expansion for 33% of the species, while the MESS techniques for 53% of them (Table S3). These values become even larger when using the data set based on the minimal distribution (40% using the PCA-Kernel method and 66% using MESS). This tendency of species to expand towards new climates in the Mediterranean was not related to fish habitat affinity (i.e. reef-associated, soft bottom, or pelagic) or to fish resident time in the invaded basin (Figs S5 and S6).

Across species, the north-eastern sectors of the Mediterranean basin, especially the Aegean and the Adriatic Sea, represent hotspots of climatic niche expansion (Fig. 3). Climatic niche stability (i.e. overlap between native and invaded range climates) is common in the southern Mediterranean, and especially in the Levant Sea. Niche unfilling, instead, is common in the north-western parts of the Mediterranean suggesting that these regions may be climatically favorable for several species but not yet filled.

We found a significant negative relationship between invaded-range nestedness, the proportion of the Mediterranean climate nested within the native niche of species, and the degree of niche expansion ($R^2 = 0.47$, $P < 0.001$; Fig. 4). This indicates that climatic niche expansion is found predominantly in species for which the Mediterranean climate has little overlap with the native Indo-Pacific range, allowing these species to have a comparatively larger potential to expand.

Evaluating the performance of SDMs in predicting risk of invasion into the Mediterranean, we found that for a majority of the species, (83% and 50% using the Boyce and AUC indices, respectively) SDMs calibrated using the native range of species do not perform better than those obtained when using randomly selected non-invasive species from the Red Sea species pool (Table S4).

DISCUSSION

We used the invasion of the Mediterranean basin by Indo-Pacific species through the Suez Canal as a case study for testing the generality of climatic niche conservatism. The

removal of a physical barrier by humans revealed a surprising capacity of tropical species to enter new environments. The extensive distributional data for Lessepsian fishes in both their native and invaded ranges, in addition to the clearly delineated source pool of non-invasive Red Sea species that can serve as a control, allowed us to employ a suite of novel tests of niche conservatism. These include the assessment of the invaded-range nestedness (i.e. the *a priori* possibility of detecting niche expansion), which has not been considered in previous studies. Overall, our results highlight a substantial climatically labile response by Lessepsian fish with 33% of the invaders clearly showing climatic niche expansion in the Mediterranean. Even considering the most conservative estimate, this percentage is much higher than that recently documented for plants, where niche expansion was detected in only 17% of the species (Petitpierre *et al.* 2012), which suggests that processes alternative to climate alone may play a substantial role in shaping marine species distributions.

Climatic niche expansion cannot always be detected due to constraints imposed by the climate in the invaded domain. In fact, when the region experiencing invasion is climatically nested within the native niches of species, expansion of the climatic niche is not possible although there may be no underlying climatic constraints. Ignoring this may potentially lead to substantial overestimation of climatic niche conservatism, because species not able to display climatic niche expansion will be considered as evidence for niche conservatism. Nevertheless, explicit tests for the detectability of niche expansion are generally missing in studies assessing conservatism, probably because clear boundaries for the native and invaded domains may be hard to delineate. In our study, the clear distinction between the Mediterranean (invaded) and Indo-Pacific (native) basins made estimating the potential for detecting niche expansion possible. The strong negative association found between the degree of niche expansion and invaded-range nestedness (i.e. the degree of nestedness of the entire invaded-range climate within the native niche of the species; Fig. 4) suggests that the apparent climatic stability detected for some species is simply an outcome of the absence of novel climates for these species in the Mediterranean. This implies that previous studies may overestimate climatic niche conser-

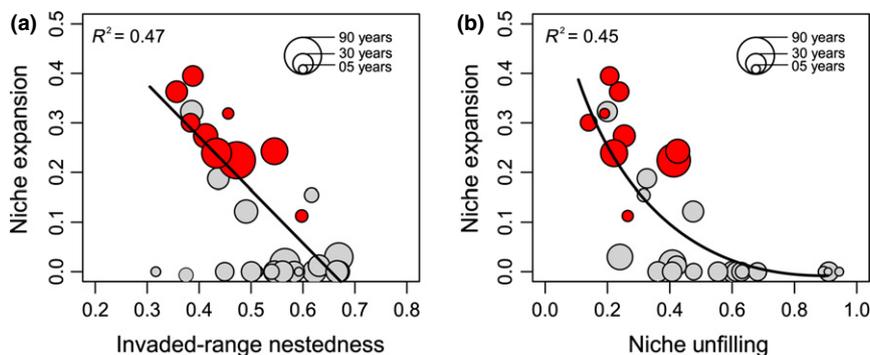


Figure 4 (a) Linear regression between invaded-range nestedness (i.e. the proportion of the Mediterranean climate within the native climate of the species) and niche expansion. (b) Power regression between niche unfilling and niche expansion. Red circles indicate species for which the PCA-kernel and MESS methods qualitatively agree in detecting niche expansion (i.e. expansion higher than 10%). The size of the circles is proportional to species resident time in the Mediterranean Sea. Climatic niche expansion and unfilling estimates are based on the PCA-kernel method, those obtained according to the MESS method can be found in Fig. S5.

vatism when the ability to detect niche expansion given the climate available in the invaded range is not assessed.

The labile climatic response of invaders poses serious concerns regarding the potential utility of SDMs in predicting areas of likely future invasion or species response to changing climate. We demonstrated that for only a minority of the species, SDMs calibrated using the actual native distributions performed better than null models which take climatic niches at random from the Red Sea species pool. This finding is striking and suggests that the potential to predict range shifts using SDMs may be far less accurate than anticipated when using classical model evaluation criteria. Indeed, although model performance is good (e.g. the AUC of the calibrated models is high, often exceeding 0.8) this performance is seldom better than what can be obtained from using null models (Table S4). This result indicates that caution is warranted when using model evaluation criteria, such as AUC and the Boyce index, to assess the accuracy of species distribution models.

In SDMs locality data is used to construct estimates of ecological tolerances of species using the Grinnellian niche concept (Soberón & Nakamura 2009), thus focusing on climatic variables which are non-interactive and non-consumable to define niche space. Thus, altered biotic processes such as reduced competition (Azzurro *et al.*, 2014), predation or parasitism in the Mediterranean Sea or changes in the available resources may all explain the general tendency of species to expand towards apparently unfavorable climates (Pearman *et al.* 2008; Lavergne *et al.* 2010). For instance, *Siganus luridus*, which is an Indo-Pacific herbivore, may find a surprisingly favorable habitat in the Mediterranean Sea, in which shallow reefs are algae-dominated and occupied by only two potential fish competitors (i.e. *Sarpa salpa* and *Sparisoma cretense*; Bariche *et al.* 2004; Azzurro *et al.* 2007). At the same time, our results of substantial niche expansion can be explained by biotic processes or dispersal limitation acting predominantly in the native domain of species and thus preventing them from realizing their full climatic potential in the Indo-Pacific.

While incorporating processes such as biotic interactions and dispersal limitation into SDMs is an active line of research (Kissling *et al.* 2012; Zarnetske *et al.* 2012; Wisz *et al.* 2013), accurately predicting the future potential of invasive species will likely require detailed species-specific ecological knowledge that is seldom available across many species. We note that the incorporation of these processes might be especially important for invading species (Sorte *et al.* 2010). Thus, the generality of our findings to native species experiencing climate-induced range shifts still needs to be established.

Here, we provide the first large quantitative assessment of climatic niche conservatism for the marine realm and show that the potential to predict invasion risk using existing species distribution models may be by far less accurate than hoped for. Interestingly, while for terrestrial species climatic niche conservatism has been often confirmed, a tendency towards niche expansion is found in other aquatic studies (e.g., Lauzeral *et al.* 2011). Although too few studies are available to detect generalities, it is possible that aquatic organisms are comparatively less constrained by dispersal, and hence may have an intrinsically higher tendency

towards climatic niche expansion. Our results demonstrate that, at least for Lessepsian fishes, using climatic constraints alone will underestimate range expansion and thus return biased conclusions. Consequently, wide scale range-expansion of biological invaders could be the rule rather than the exception.

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AUTHORSHIP

VP, JB, MK, EA conceived the study. MK, EA, VP participated in the data collection. VP and JB conducted the analyses. All the authors contributed substantially to the writing of the manuscript.

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