Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean

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Abstract

Alien species are considered one of the prime threats to biodiversity, driving major changes in ecosystem structure and function. Identifying the traits associated with alien introduction has been largely restricted to comparing indigenous and alien species or comparing alien species that differ in abundance or impact. However, a more complete understanding may emerge when the entire pool of potential alien species is used as a control, information that is rarely available. In the eastern Mediterranean, the marine environment is undergoing an unparalleled species composition transformation, as a flood of aliens have entered from the Red Sea following the opening of the Suez Canal in 1869. In this study, we compile data on species traits, geographical distribution, and environmental affinity of the entire pool of reef-associated fish species in the Red Sea and more generally across the Indo-Pacific. We use this extensive data to identify the prime characteristics separating Red Sea species that have become alien in the Mediterranean from those that have not. We find that alien species occupy a larger range of environments in their native ranges, explaining their ability to colonize the seasonal Mediterranean. Red Sea species that naturally experience high maximum temperatures in their native range have a high probability of becoming alien. Thus, contrary to predictions of an accelerating number of aliens following increased water temperatures, hotter summers in this region may prevent the establishment of many alien species. We further find that ecological trait diversity of alien species is substantially more evenly spaced and more divergent than random samples from the pool of Red Sea species, pointing at additional processes, such as competition, promoting ecological diversity among alien species. We use these results to provide a first quantitative ranking of the potential of Red Sea species to become established in the eastern Mediterranean.

Keywords: bioinvasion, introduction, lessepsian migration, marine, reef fish, tropicalization

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Introduction

Global environmental change in marine ecosystems is associated with warming temperatures, mass mortalities, shift in species distribution, and accelerated biological introductions (Harley *et al.*, 2006; Albouy *et al.*, 2012). The introduction of alien (i.e., nonindigenous) species and their spread are considered among the most pervasive and immediate threats to biodiversity worldwide (Mack *et al.*, 2000; Molnar *et al.*, 2008; Walther *et al.*, 2009). Alien species have been shown to induce profound phase shifts in indigenous communities (Sala *et al.*, 2011; Edelist *et al.*, 2013).

The identification of alien species before they arrive and establish themselves may greatly improve the chances of alleviating their impact as prevention is much easier than mitigation (Mack *et al.*, 2000). Thus, many attempts have been made to identify the species and environmental characteristics correlated with introduction success (i.e., species profiling; Safriel & Ritte, 1980; Kolar & Lodge, 2002; Garcia-Berthou, 2007; Lasram *et al.*, 2008a,b; Blackburn *et al.*, 2009; Sol *et al.*, 2012). However, when characterizing alien species, it is challenging to correctly identify the appropriate control group (Hayes & Barry, 2008). Comparing indigenous and alien species or comparing alien species that differ in abundance or impact, the most common comparisons (Hayes & Barry, 2008), does not easily translate into the identification of species characteristics favoring initial introduction. Thus, when the aim is to predict the identity of new alien species, it is important to use the pool of potential alien species, which is rarely known. In this study, we make use of a unique 'natural experiment' in which the entire pool of potential alien species is known to test several key hypotheses about the processes facilitating alien species introduction.

Species traits are receiving increasing attention as an important way to understand underlying community assembly processes. Two types of processes may

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differentiate traits of successful vs. unsuccessful aliens. On one hand, only species from similar native environments (climatic matching) or with traits predisposing them to disperse may establish alien populations (Safriel & Ritte, 1980; Hayes & Barry, 2008; Lasram *et al.*, 2008a; Luiz *et al.*, 2012). These 'environmental' and 'dispersal' filters may cause shifts in trait values (deviation from the mean) or trait clustering (reduction in trait variance) compared with the range of traits represented in the source species pool. On the other hand, competition among already established alien species might reduce introduction success of species with similar trait combinations, leading to patterns of trait overdispersion (Kraft *et al.*, 2008; Belmaker & Jetz, in press). Thus, the trait make up of alien species in relation to the pool of potential migrants may elucidate mechanisms underlying successful introduction.

The Mediterranean Sea, an inland sea that comprises only 0.32% of the global oceanic volume, contains ca. 18% of all known marine species (Bianchi & Morri, 2000) and has been compared with a scale model of world's oceans for understanding global change (Lejeusne *et al.*, 2010). A large introduction of Red Sea species into the Mediterranean has followed the opening of the Suez Canal (Galil, 2009; Lasram & Mouillot, 2009; Rilov & Galil, 2009; Golani, 2010). These alien species, known as Lessepsian migrants (Por, 1971), constitute a large proportion of total fish biomass in this area, sometimes exceeding 90% (Goren & Galil, 2005; Edelist *et al.*, 2011), and may pose a threat to indigenous fish (Coll *et al.*, 2010; Lasram *et al.*, 2010; Abdul Malak *et al.*, 2011). The rate of alien species introduction and the consequent changes in species composition in the eastern Mediterranean far exceeds the values attained in any other open marine system (Edelist *et al.*, 2013). As the ichthyofauna of both the Red Sea and the Mediterranean are well known (Goren, 1993; Golani, 1996, 1999, 2005; Belmaker *et al.*, 2007; Zenetos *et al.*, 2010; Cinar *et al.*, 2011; Mouillot *et al.*, 2011) the ensuing influx of Lessepsian species offers a unique opportunity to study fish traits associated with successful introduction.

Several attempts have been made to characterize Lessepsian species. A high proportion of Lessepsian species are shallow water, benthic carnivores (Rilov & Galil, 2009) and many species are schooling (Golani, 2010). In addition, the relative success of Lessepsian species within the Mediterranean, measured by rate of spread, is associated with coarse-scale climatic match with the native range (Lasram *et al.*, 2008a). It has thus been suggested that increased ocean temperatures and salinity will facilitate further introductions from the largely tropical Red Sea (Bianchi, 2007; Lasram & Mouillot, 2009; Raitsos *et al.*, 2010). Studies to date usually examine the relative success of Lessepsian species already established in the Mediterranean. However, a predictive framework for future introduction risk should allow the identification of Red Sea species that can potentially, but have yet to, establish populations in the Mediterranean. The only study to directly compare Lessepsian and non-Lessepsian Red Sea species found Lessepsian species to be particularly common in Red Sea sandy habitats (Golani, 1993).

In this study, we take a fresh look at the characteristics that distinguish Lessepsian species from non-Lessepsian species in the Red Sea. We compile two large data sets that describe the ecological traits and the geographical distribution of Red Sea and, more generally, Indo-Pacific fish species. Species geographical distributions are used to estimate their environmental affinity. We thus characterize species according to their ecological traits, geographical distribution, and environmental affinity and test the following hypotheses: (1) Traits associated with elevated dispersal ability such as large home range size or wide geographical distribution (Hayes & Barry, 2008; Luiz *et al.*, 2012) will be higher for Lessepsian than for non-Lessepsian species. (2) Climatic affinity of species in their native range will influence introduction probabilities. (3) The multivariate trait distribution of Lessepsian species may display either clustering or overdispersion, depending on whether environmental filters or competitive processes dominate. Together, testing these hypotheses in this unique system provides a comprehensive view of the factors that are associated with successful introduction.

Materials and methods

Geographical distribution

We compiled an extensive database on shallow-water reef-associated fish species. We defined species as reef-associated if they are either: observed over reefs (including noncoralline reefs) or observed in association with reefs. We obtained species distributional data from 199 locations, of which 149 are found within the Indo-Pacific. For each location, presence–absence was collected from published works, regional checklists, monographs on specific families or genera, and gray literature (appendix S1). Species were categorized as found within the Red Sea based on Golani & Bogorodsky (2010). In sum, the data include 6933 species of which 6352 species are found in the Indo-Pacific, including Red Sea. The list of Lessepsian species was based on Belmaker *et al.* (2009) and Golani (2010) but updated to 2010 using Zenetos *et al.* (2010) and D. Golani (personal communication). The final list includes 85 Lessepsian fish species. However, only 54 of these were considered shallow reef-associated species which were retained for analyses (appendix S2).

For each location we defined, according to maps and descriptions in the original publications, the area of the

continental shelf (sea-bottom between 0 and 200 m depth) to which the location pertains. The continental shelf was defined using SRTM30_PLUS bathymetry (Shuttle Radar Topography Mission) available at http://topex.ucsd.edu/WWW_html/srtm30_plus.html. Using a global equal area Behrmann projection, the world was divided into 10 000 km^2 cells (100 × 100 km) and the geographical distribution of each species determined by an intersection between this grid with the above locations. We then calculated the following variables: (1) *LatRange* (km). Maximum latitudinal distance between cells in which a species was observed. (2) *LongRange* (km). Maximum longitudinal distance between cells in which a species was observed. (3) *RangeSize* (km^2). Range size area was estimated using an alpha hull algorithm (Pateiro-Lopez & Rodriguez-Casal, 2010), which is a generalization of the convex hull and retrieves more accurate estimates of nonconvex polygons. We present the results using a value of α = 1000 km, but results were similar when other α values were used (500–2000 km). (4) *ShelfArea* (km^2). The area of continental shelf (0–200 m depth) summed over all locations in which a species was observed. (5) *DepthMax* (m). Maximum depth in which a species was observed. *DepthMax* was extracted from 'Fish Base' (http://www.fishbase.org). All the above variables were log$_{10}$ transformed to reduce heteroscedasticity.

Environmental affinity

The overlay of species occurrences from all 199 locations with environmental layers was used to extract species-specific environmental affinities. Global marine environmental layer, at a resolution of 5 arcmin, was based on Tyberghein *et al.* (2012), and include: *SalMax* – maximum salinity (PSS); *SSTrange* – mean temperature range (warmest–coldest month, °C); *SSTmin* – minimum of the minimum monthly average temperature (°C); *SSTmax* – maximum of the maximum monthly average temperature (°C); *SSTmean* – average annual mean temperature (°C); *ProdRange* – mean range of net Primary productivity (December/June, g C m^{-3} d^{-1}). Productivity was based on satellite data collected from 2003 to 2007 (http://www.science.oregonstate.edu/ocean.productivity/index.php) and calculated using the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997).

Ecological traits

Ecological traits were compiled from published literature augmented with expert opinion information (Kulbicki *et al.*, 2011). These traits describe species-level attributes and do not accommodate intraspecific variation in trait values. Ecological traits include: (1) *Diet*. One of five categorical groups: H – herbivore (macro algae, sea grass, turf, and filamentous algae or other undefined vegetal material), C – Invertebrate feeder (large and small benthic invertebrates, sessile invertebrates), D – detritus (detritus and other undefined organic material), P – nekton (large organisms living in the water column, usually fish and cephalopods as well as benthic fish), Z – plankton and small organisms which migrate in the water column. (2) *Home range*. One of three ordinal categories: S – small.

Sedentary or territorial species, species staying in a restricted area (less than a few 100 m²) for extended periods (at least a month). M – medium. Mobile species, which will move from reef to reef or travel large distances over a reef. W – wide. Species which frequently change reefs or which daily travel large distances over a reef. (3) *Activity*. Dial activity pattern. One of three ordinal categories: D – diurnal species. Fish active during day time hours. B – both. species active at all times, both night and day. N – night. Nocturnal species. (4) *Schooling* level. One of five ordinal categories: S – solitary species. Fish usually living alone (but they may group for reproduction or some other specific need). P – pairing species. Fish usually seen in pairs. F – species living in small groups (3–20 individuals). Groups do not need to be schools. M – species in groups of 20–50 individuals. L – species living in large groups or schools (>50 individuals). (5) *Height*. Height in the water column. One of three ordinal categories: B – species staying on the bottom at all times. L – species living slightly above the bottom but which may at time rest on the bottom. H – species spending most of their active time high above the bottom (several meters). (6) *Body size*. Due the difficulty of obtaining a standard and reliable measure of body size, we separate all species into one of six size classes 1: <5 cm; 2: 6–10 cm; 3: 11–20 cm; 4: 21–40 cm; 5: 41–80 cm; 6: >80 cm.

Analyses

Introduction correlates. We were first interested in examining whether single characteristics can explain which Red Sea species become Lessepsian. This was determined using a mixed-effect logistic regression (generalized linear mixed model, GLMM) where the presence or absence of Red Sea species in the Mediterranean was the response variable and fish family was added as a random effect. Similar results were obtained when no random effect was used (i.e., a standard logistic regression; Table S1).

First, we examined the performance of single predictors and compared them to intercept-only models using the second-order Akaike Information Criterion (AICc). As each predictor was examined separately, we were not concerned at this stage about possible collinearity between predictors. Next, predictors from each group (ecological traits, geographic distribution, and environmental affinity) that received the best support (and better than the intercept-only model) were used to construct several candidate multipredictor models that were again compared using AICc. At this stage, care was taken to exclude variables that displayed high collinearity (i.e., *ProdRange* and *SSTrange*; Figures S1, S2).

We used pseudo-R^2 as a measure of goodness of fit, calculated as one minus the deviance explained relative to the null deviance. Null deviance was determined either using a model with only a fixed intercept or a model with a random effect (fish family). The former provides an overall assessment of goodness of fit whereas the latter quantifies the contribution of the fixed effects alone. As a measure of model discriminative capacity we used the area under the receiver operating characteristic curve (AUC, Fielding & Bell, 1997). Values of 0.5 represent random performance while values of 1 mean perfect correspondence between observed and predicted values.

Multivariate trait composition. To assess changes in the dispersion of Lessepsian multivariate ecological trait structure, we first constructed a trait distance matrix between all Red Sea species using the Gower dissimilarity that allows the use of categorical, ordinal, and continuous variables (Pavoine *et al.*, 2009; Laliberte & Legendre, 2010). All the variables were given equal weights but results were robust to variation in weighting scheme. We examined difference in trait values between Lessepsian and non-Lessepsian species using analysis of similarity (ANOSIM). We then quantified Lessepsian trait structure using three indices representing relatively independent trait axes: trait richness, trait evenness, and trait divergence (Villeger *et al.*, 2008; Mouchet *et al.*, 2010). Trait richness (TR) measures how much of the potential trait space is filled. High trait richness values mean that Lessepsian species possess a large proportion of the Red Sea species trait combinations. Trait evenness (TE) measures the regularity in the distribution of Lessepsian species traits. Finally, trait divergence (TD) measures the relative position of Lessepsian species traits, where high values indicate traits further away from the trait-space center and hence niche differentiation.

Low Lessepsian trait richness, compared to expectations based on random draws from the Red Sea species pool, may indicate the operation of environmental filters, dispersal filters, or competition with indigenous species, which may all restrict assemblage multivariate trait composition. In contrast, higher trait richness evenness and divergence may all be a sign of competition among Lessepsian species (e.g., 'limiting similarity', Mouchet *et al.*, 2010). However, similar patterns may also form due to facilitation or the presence of multiple vacant niches in the Mediterranean.

Quantification of trait richness was based on the convex hull approach (Cornwell *et al.*, 2006). Trait evenness was calculated using a minimum spanning tree, and trait divergence using the summed deviance from the trait center of gravity (Villeger *et al.*, 2008). For trait richness and divergence, we used 10 PCoA axes to represent the original dissimilarity, which resulted in reduced-space representation quality (Laliberte & Legendre, 2010) of 0.99. To control for species richness influences, trait diversity indices were compared with values predicted from null models based on random draws of Red Sea species (500 iterations). Analyses were based on the Package FD (Laliberte & Legendre, 2010) within the R programming language (R Development Core Team, 2008).

Results

Introduction correlates

We find several characteristics that distinguish Red Sea species found in the Mediterranean from those which are not. Among the environmental attributes we find that Lessepsian species are found in regions that have higher temperature range, higher productivity range, and higher maximum SST compared with non-Lessepsian Red Sea species (Fig. 1, Table 1; see Figures S3 and S4 for results for each fish family). Geographical attributes such as latitudinal range or range size were

not strongly supported (Table 1). Thus, environmental correlates do not simply reflect a correlation between geographical attributes and the range of environments to which species are exposed. Among the ecological traits we find that Lessepsian species tend to occupy large home ranges, to be schooling species and to be higher in the water column relative to non-Lessepsian Red Sea species (Fig. 2, Table 1). Similar results, with minor modifications, were found when using GLMs instead of GLMMs (Table S1).

When considering combinations of predictors, we find that the strongest support is found for models that include home range size and schooling behavior as well as large temperature range and a high maximum temperature (Table 2). The combined influence of both temperature range and maximum temperature is particularly strongly supported among the environmental affinity group (AIC weights = 1) and conforms to expectations based on environmental matching between native and alien ranges. We did not detect any relationship between model residuals and the year a species was first recorded in the Mediterranean (Fig. 3). We used the best multipredictor model to assign each non-Lessepsian Red Sea species its predicted probability of introduction (appendix S3).

Multivariate trait composition

We find little trait differences between Lessepsian and non-Lessepsian species (ANOSIM's $R = 0.11$; $P = 0.13$). However, as mean trait values might conceal differences in the multivariate trait structure we further tested for differences in trait richness, trait evenness, and trait divergence. While observed trait richness was well within the range of null values (observed value fall at the 66th quantile of the random distribution; $P = 0.67$), we find that trait evenness and divergence are high relative to null expectations (both at the 100th quantile; $P < 0.05$). Hence, Lessepsian species contain trait combinations which tend to be more regularly distributed and further away from the trait center of gravity than values predicted from random assembly of Red Sea species (Fig. 4).

Discussion

We use information on ecological, geographical, and environmental characteristics of the pool of reef-associated Indo-Pacific species to understand the processes associated with alien fish introduction. We find that introduction probability can be explained by species climatic affinities and ecological traits such as home range size, schooling, and height above the substrate. Surprisingly, we find that high water temperature in the native
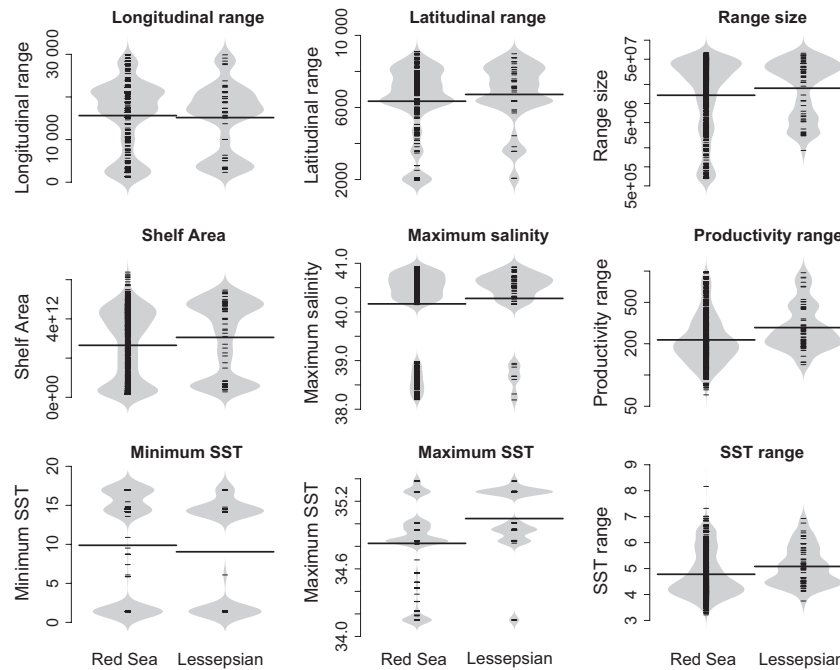
Fig. 1 Beanplots comparing variables related to geographical distribution and environmental affinity between Red Sea non-Lessepsian (Red Sea) and Lessepsian species. Thick bars represent mean values per group. SST, Sea Surface Temperature.

range is associated with increased introduction success, suggesting that the warm water adaptation may be a prerequisite for introduction into the higher latitude Mediterranean. We further find that the multivariate trait make up of Lessepsian species is nonrandom, consistent with the operation of additional biological constraints on introduction. These results provide a unique understanding of the processes associated with biological introduction, which is used to score the introduction probability of Red Sea species yet to be recorded from the Mediterranean (appendix S3).

We find strong evidence for climatic filters, as high temperature range (*SSTrange*), high productivity range (*ProdRange*), and high SST (*SSTmax*) in the native range are all associated with Lessepsian introduction. The strong statistically effect of *SSTrange* and *ProdRange* suggests that coping with environmental fluctuation may be a major factor limiting introduction. As the Mediterranean is a temperate seasonal ocean only species that are adapted to both low winter and high summer extremes may be capable of establishing viable populations.

It has been argued that the tropical origin of Lessepsian species implies that increased water temperatures in the Mediterranean will accelerate their establishment (Lasram & Mouillot, 2009; Raitsos et al., 2010). Such an influence of higher temperatures on increased survival of tropical species in temperate regions has been demonstrated in Australian fish (Figueira & Booth, 2010).

However, we find that Lessepsian species actually experience higher maximum water temperatures (*SSTmax*) in their native range compared with Red Sea species that have not yet been observed in the Mediterranean (Table 1). While the eastern Mediterranean is temperate, warm conditions during summer may exceed the values for tropical regions and have been suggested to contribute to low fishery yields in that region (Golani, 1996; Sonin et al., 2007). Thus, only species that are already adapted to high temperatures may become established in the eastern Mediterranean. This implies that elevated water temperatures in the Mediterranean (Nykjaer, 2009) will decrease the proportion of Red Sea species with the necessary thermal adaptations. Consequently, and contrary to some recent suggestions, increased warming may actually *decrease* the future introduction probability of some species due to increased inability of Red Sea fish to cope with Mediterranean summer heat.

Interestingly, salinity, considered to limit the passage of fish through the Suez Canal (Golani, 2010), does not explain the difference between Lessepsian and non-Lessepsian Red Sea fish (Table 1). Hence, at present salinity tolerance does not seem like a barrier to successful introduction. While the salinity of the bitter lakes may have limited introductions in earlier years, salinity level have dropped to below 43‰ during much of the year by 1955 (Morcos & Messieh, 1973). The salinity is now probably reduced even further due to

Table 1 Model comparison for single predictor mixed-effect models with fish family as random effect. Models with AICc (second-order Akaike Information Criterion) values lower than the model which contains the intercept only (in bold) are better supported by the data. SalMax, maximum salinity; SSTrange, temperature range; SSTmin, minimum temperature; SSTmax, maximum temperature; SSTmean, mean temperature; ProdRange, productivity range; LatRange, latitudinal range (km). LongRange, longitudinal range; DepthMax, maximum depth; Home Range, home range size; Schooling, size of typical groups; Height, height in the water column; Activity, dial activity pattern; ShelfArea, summed area of species occurrences over continental shelf

Predictor	Estimate	Standard error	Z value	P value	AICc
SSTmax	2.2	0.6	3.4	0.0***	364.1
SSTrange	0.7	0.2	3.8	0.0***	365.0
Home range					366.2
Linear	1.19	0.32	3.74	0.00***	
Quadratic	−0.24	0.31	−0.77	0.44	
ProdRange	0.0	0.0	3.8	0.00***	366.3
Schooling					367.1
Linear	5.76	302.44	0.02	0.99	
Quadratic	3.67	255.60	0.01	0.99	
Cubic	−9.56	604.87	−0.02	0.99	
^4	7.30	457.24	0.02	0.99	
Height					374.7
Linear	0.82	0.35	2.32	0.02*	
Quadratic	−0.07	0.34	−0.20	0.84	
Body size	0.2	0.1	1.6	0.1	376.3
Intercept	**−2.6**	**0.2**	**−12.1**	**0.0***	**376.9**
SSTmean	−0.3	0.2	−1.3	0.2	377.3
LongRange	−0.5	0.4	−1.2	0.2	377.6
DepthMax	0.2	0.2	1.0	0.3	377.9
SalMax	0.2	0.2	0.8	0.4	378.2
Activity					378.6
Linear	−0.01	0.35	−0.03	0.97	
Quadratic	−0.51	0.33	−1.55	0.12	
SSTmin	0.0	0.0	0.3	0.8	378.9
Range size	−0.1	0.3	−0.2	0.8	378.9
LatRange	0.2	1.0	0.2	0.9	378.9
ShelfArea	0.0	0.4	0.0	1.0	379.0
Diet					383.6
D	−12.89	1056.55	−0.01	0.99	
H	0.09	0.67	0.14	0.89	
P	0.19	0.44	0.43	0.67	
Z	0.29	0.46	0.62	0.54	

*P value < 0.05, ***P value < 0.001.

the continual enlargement of the Suez Canal (Golani, 2010), eliminating the need for high salinity adaptations as a prerequisite for successful introduction.

From the ecological traits examined, we find strong support for home range size as a predictor of introduction. Thus, species with large home ranges are more likely to become Lessepsian than species with small home ranges. As home range size is likely correlated with adult dispersal ability, this partially supports the notion that passage through the Suez Canal is mostly accomplished by adult active swimming (as opposed to passive drift by larvae). Nevertheless, we note that many small home range species are also obligate coral dwellers that may have a lower probability of surviving in the Mediterranean as it is devoid of hermatypic corals (but see Goren *et al.*, 2011). Thus, the virtual lack of corals in the Mediterranean may provide an alternative reason for the observed correlation between home range size and introduction success.

Schooling level was found to be an independent predictor of Lessepsian invasion, with species that form schools having higher introduction probabilities, in accordance with previous findings (Golani, 2010). We feel that this is a likely signal of an alee effect, in which small (founder) populations experience lower per capita growth rates than larger populations. Some support for small founder populations are found in genetic studies identifying population bottlenecks in select Lessepsian species (Golani *et al.*, 2007)(we note that evidence for bottlenecks is absent in many species; Bernardi *et al.*, 2010). Hence, species introduced into the Mediterranean individually or in small groups may be less likely to find mates or have lower genetic diversity than schooling species that disperse in large numbers (see Lewis & Kareiva, 1993 for theoretical considerations).

Combining multiple ecological traits to characterize the Lessepsian fish assemblage, we find that Lessepsian trait evenness and divergence are high relative to random draws from the Red Sea pool. Hence, Lessepsian species have trait combinations that tend to be regularly dispersed and further from the trait center of gravity relative to null expectations. The operation of environmental or dispersal filters should be detected as trait clustering causing low trait richness, evenness, and divergence (Mouchet *et al.*, 2010). Thus, the observed patterns hint at additional nonrandom biological structuring forces. For example, competition among Red Sea species with similar traits may hinder their establishment success in the Mediterranean and cause successful Lessepsian species to display trait complementarity and high trait evenness and divergence. Alternatively, facilitation among invading Red Sea species may also promote Lessepsians trait complementarity (Emerson & Gillespie, 2008). Finally, multiple vacant niches within the Mediterranean, each necessitating a different set of trait combinations, may also cause the observed patterns. A fuller understanding of Lessepsian trait distribution may be achieved by concurrently comparing Lessepsian and non-Lessepsian

Table 2 Model comparison for multiple-predictor mixed-effect models with fish family as random effect. First, we considered all single predictors that are better supported by more than two Akaike Information Criterion (AICc) units from the intercept-only model (Table 1). We excluded predictors that displayed high colinearity (i.e., ProdRange was excluded and SSTrange was retained). Next, within each group (ecological traits and environmental affinities only; geographical distribution was not used as no predictors within this group were supported) we examine all possible predictor combinations. Finally, we constructed a combined model that is composed from the predictors from the best model within each group. We note, that when using a binary response R^2 will be lower than when comparing two continuous variables and influenced by the ratio of presences to absences (Ash & Shwartz, 1999)

| Model | Pseudo-R^2 | | AUC | Log-likelihood | AICc | AIC weight |
	Relative to fixed intercept	Relative to random effect				
Ecological traits						
HomeRange + Schooling	0.090	0.067	0.70	−173.88	363.97	0.55
HomeRange	0.063	0.040	0.66	−179.07	366.2	0.18
Schooling	0.071	0.048	0.66	−177.47	367.06	0.12
HomeRange + Schooling + Height	0.091	0.068	0.72	−173.74	367.79	0.08
HomeRange + Height	0.067	0.044	0.69	−178.24	368.59	0.05
Level + Schooling	0.073	0.050	0.67	−177.14	370.49	0.02
Height	0.040	0.017	0.61	−183.33	374.72	0
Environmental affinity						
SSTrange + SSTmax	0.132	0.110	0.78	−165.95	339.97	1
SSTrange	0.061	0.037	0.68	−179.02	364.07	0
SSTmax	0.063	0.040	0.68	−179.49	365.01	0
Combined models						
SSTrange + SSTmax + HomeRange + Schooling	0.184	0.164	0.81	−155.96	332.24	
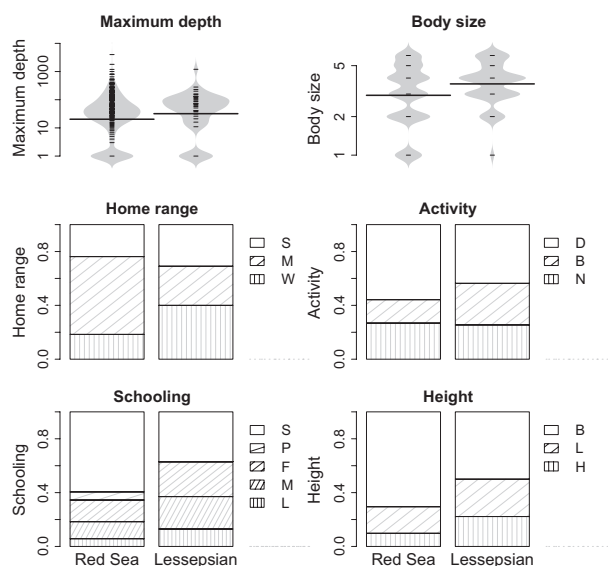
Fig. 2 Ecological attributes of Red Sea non-Lessepsian (Red Sea) and Lessepsian species. Maximum depth (m), although being a geographical traits, was added here and not in Fig. 1 for visual appeal. Beanplots are depicted for continuous predictors, where thick bars represent mean values. Barplots are shown for categorical and ordinal predictors, with values proportional to the total number of species (54 Lessepsian, 748 Red Sea species).
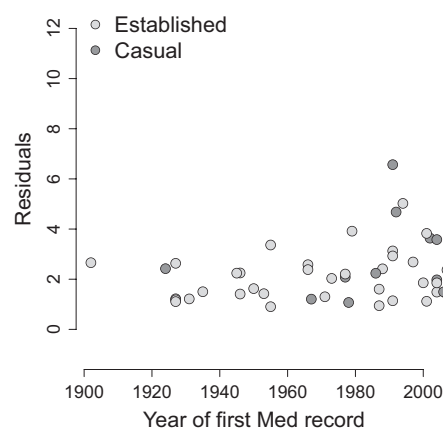

Fig. 3 Residuals from the best-supported model predicting Lessepsian introduction (Table 2) vs. the year of first sighting in the Mediterranean. Lessepsian species were further separated to those with established populations and those only casually observed (less than three records).

Red Sea species with indigenous Mediterranean species, a comparison that can be used to directly assess the niche associations between fish groups.

The evidence presented here for trait filters superficially contradicts a previous study that found Lessepsian
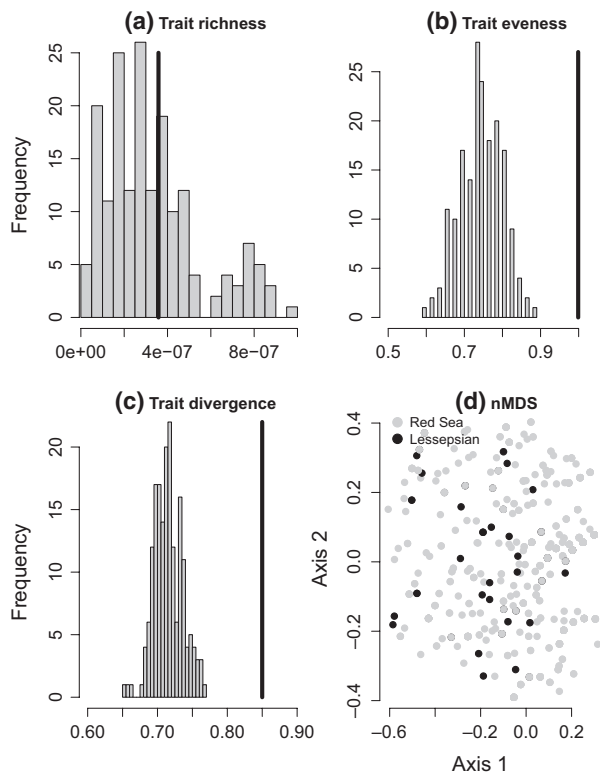
Fig. 4 Three indices of multivariate assemblage trait composition (a–c) and a nMDS visualizing the multivariate distribution of Red Sea species ecological traits (d). In a–c, the solid vertical black lines represent the values attained by the Lessepsian species assemblage while the histograms depict null values obtained from 500 random draws from the pool of Red Sea species. Lessepsian trait evenness and divergence are both higher than expectations based on a random draw null models.

introduction to be a largely stochastic process (Belmaker *et al.*, 2009). However, Belmaker *et al.* (2009) made inference only on the subset of Red Sea species suitable to the Mediterranean environment. In contrast, this study includes all reef-associated Red Sea species and identifies characteristics that discern the species that may establish populations in the Mediterranean from those that may not. Reconciling the two studies, the subset of Red Sea species capable of living in the Mediterranean may be determined by species characteristics, while the identity of specific introduced species out of this subset seems to be a largely stochastic event. The stochastic nature of introduction within the subset of species capable of living in the Mediterranean is supported by the lack of correlation between model residuals and time of introduction (Fig. 3). A deterministic introduction process should show species that have arrived earlier to have larger residuals (and hence higher introduction probabilities). Interestingly, the colonization of the Red Sea by Indian Ocean fish species over much longer time

frames also seems to be largely stochastic (Kiflawi *et al.*, 2006). The stochastic introduction processes imply that while we might be able to estimate the probability of Red Sea species to become Lessepsian (appendix S3), it will be difficult to accurately predict the timing of these species introductions.

We find that factors related to geographical range size (Luiz *et al.*, 2012) did not explain introduction success. Thus, either geographical range size is unrelated to dispersal ability or dispersal ability is not a strong predictor of introduction. The proposition that geographical range size is related to dispersal ability has received mixed support. For example, while long pelagic larval durations (PLD) may be associated with increased dispersal abilities, fish dispersal abilities' influence on range size appears to be complex and contingent on evolutionary age (Lester *et al.*, 2007; Mora *et al.*, 2012). Thus, it may be that geographical range is simply a poor proxy of dispersal abilities. Alternatively, dispersal abilities may not be the prime factor restricting introduction. The climatic constraints found in this study suggest that at least part of the limitation on introduction success is associated with environmental suitability, and the nonrandom multivariate trait structure points at additional biological filters. Both of these may be stronger than filters associated with dispersal through the Suez Canal.

In this study, we only examine whether Red Sea species have established populations in the Mediterranean. However, different stages of introduction are probably associated with different fish characteristics. For example, while arrival into the Mediterranean may be associated with dispersal capacities, relative success in the Mediterranean may be controlled by climate or ecological processes. Moreover, we implicitly assume a single mode of introduction – active dispersal of early life stages or adults through the Suez Canal. Multiple modes of introduction, such as human transport through ship ballast water (Wonham *et al.*, 2000), may contribute to Lessepsian introduction, although a clear example of such a species has yet to be found. Thus, by only using presence–absence data we are conflating the different stages of a biological invasion (e.g., introduction, establishment, spread; Blackburn *et al.*, 2011) and possibly also different modes of introduction (e.g., active dispersal, ballast water, accidental releases of fish from the aquarium trade). Currently, data limitation prevents quantitative analyses of species relative success – only several species in select localities have accurate abundance estimates. However, we expect that with the continual input of high quality data, especially through international collaborative projects, it will be possible to extend similar analyses to predict not only whether a Red Sea species becomes introduced but also

whether it becomes invasive or detrimental to indigenous species diversity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The sources used for estimating species lists for each locality. Species lists were compiled using two major types of information: (1) species checklists; (2) descriptions or revisions of species, genus, or families.

Appendix S2. The list of Lessepsian species used in this study. Only reef-associated shallow-water species were examined.

Appendix S3. Predicted probabilities of Red Sea species to establish populations in the Mediterranean, extracted from the best-supported multipredictor model (see Table 2).

Appendix S4. Supplementary tables and figures.