

LETTER

External morphology explains the success of biological invasions

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Abstract

Biological invasions have become major players in the current biodiversity crisis, but realistic tools to predict which species will establish successful populations are still unavailable. Here we present a novel approach that requires only a morphometric characterisation of the species. Using fish invasions of the Mediterranean, we show that the abundance of non-indigenous fishes correlates with the location and relative size of occupied morphological space within the receiving pool of species. Those invaders that established abundant populations tended to be added outside or at the margins of the receiving morphospace, whereas non-indigenous species morphologically similar to resident ones failed to develop large populations or even to establish themselves, probably because the available ecological niches were already occupied. Accepting that morphology is a proxy for a species' ecological position in a community, our findings are consistent with ideas advanced since Darwin's naturalisation hypothesis and provide a new warning signal to identify invaders and to recognise vulnerable communities.

Keywords

Abundance, biological invasions, geometric morphology, Lessepsian fish, limiting similarity, Mediterranean Sea, morphological niche, species coexistence.

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INTRODUCTION

In a borderless world, the intentional or inadvertent human-assisted translocation of species beyond their natural ranges is a global phenomenon irreversibly altering the biological landscape (Vitousek *et al.* 1996). Some of these immigrants become numerically and ecologically dominant in their new environment, causing profound ecological impacts and huge economic costs, but others fail to thrive (Simberloff & Rejmánek 2011). Predicting which species will fall in one or the other category is a pressing but challenging task for ecologists to the extent that some consider it the ultimate goal for invasion biology (e.g. Kolar & Lodge 2001). Accurate prediction methods have long been sought in the characteristics of both the invaders and the invaded ecosystems (Catford *et al.* 2009), but so far few studies have found traits related to invasiveness, and all require gathering difficult data, such as data on life-history (Olden *et al.* 2006), phylogeny (Schaefer *et al.* 2011; Violle *et al.* 2011; Park & Potter 2013) and network structure (Romanuk *et al.* 2009).

Most theories share the idea that successful invaders somehow differ from native species (Van Kleunen *et al.* 2010), recalling concepts that have early origins in ecology. In *The Origin of Species*, Darwin (1859) intuited that differences, intended as phylogenetic distances, are a benefit for invasive flora because the struggle for existence is greater

between closely related species than between distantly related species (Violle *et al.* 2011). This intuition, known as 'Darwin's naturalization hypothesis', is one of the earliest and most influential theories in the field. The concept of a limit to the ecological similarity of coexisting species is also at the basis of classical principles in community ecology (Elton 1958; Hardin 1960). Indeed, according to the limiting-similarity hypothesis (MacArthur & Levins 1967), species that are similar to others are predicted to have less opportunity to become abundant, owing to greater interspecific competition. More recent theories about invasions share the idea that these differences, understood as taxonomic, ecological or functional in nature, allow invaders to use unexploited niche opportunities to avoid direct competition with resident species (Shea & Chesson 2002). Other hypotheses, such as the 'empty niche hypothesis' and the 'biotic resistance hypothesis', also incorporate the central relationship between niche similarity and competition (see Catford *et al.* 2009 for a review). Thus, at the heart of all these theories we find the same commonly accepted assumption that niche space within the recipient community influences the success probability of these newcomers. These 'niche opportunities' (Shea & Chesson 2002) would emerge for an invasive species when it possesses traits that fit with the receiving environmental conditions but are not shared by native species (Olden *et al.* 2006).

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Despite the long history of these ideas, and some experimental validation (e.g. Schaefer *et al.* 2011; Violle *et al.* 2011), empirical approaches have been quite ineffective so far (Blackburn *et al.* 2011). Moreover, on some occasions (e.g. Ricciardi & Mottiar 2006), also considered by Darwin (1859), degrees of pre-adaptation to the local environment may render species that are similar to native ones more likely to succeed once introduced, outweighing the potential disadvantage of stronger competition from close relatives (e.g. Duncan & Williams 2002).

Our case study is the Mediterranean Sea, a hotspot of biological invasions. This basin, owing to its recent history, has been considered a system where much ecological space is still 'available' (Oliverio & Taviani 2003), and the idea of 'unsaturated', 'empty' or 'vacant' niches' has often been advanced to explain the success of non-native species in this marine region. The opening of the Suez Canal in 1869 allowed the passage of hundreds of organisms from the Red Sea (Galil 2009), including more than 90 fishes recorded so far (Golani *et al.* 2013; Golani personal communication), by far the most fish invasions for any one region (Edelist *et al.* 2013). This phenomenon, commonly known as 'Lessepsian migration' (after Ferdinand de Lesseps, who engineered the Canal), is one of the greatest biogeographic events of the contemporary world (Por 2010), with an apparent accelerating rate of introductions in recent decades (Galil 2009; Golani 2010).

Other great biotic connections, such as those established by the Panama Canal, resulted in only subtle changes in species interactions among local assemblages but suggest that unsaturated communities will accommodate morphologically distant invaders without necessarily leading to local extinction of native fauna, at least at a decadal scale (Smith *et al.* 2004). By contrast, the Lessepsian migration dramatically affected the Mediterranean biota, with a number of native fish species locally displaced by competition with these invaders (Galil 2009; Golani 2010). Nevertheless, because no extinction has been documented at the basin level, the introduction of new species is also increasing the diversity of species at the regional level.

Apart from its growing impact on the ecology and economy of the Mediterranean Sea (Galil 2009), Lessepsian migration is increasingly seen as a unique opportunity to explore ecological and evolutionary processes in the marine environment and a unique unplanned ecological experiment for studying biological invasions. In fact, the timing of invasion, the invasion route, and the invaders' geographic source are known, but most importantly, the success or failure of these organisms is known, especially for fishes, which are a conspicuous and well-studied group of organisms. In order to identify traits related to outcomes of Lessepsian invasions, Belmaker *et al.* (2013) compiled ecological, morphological and geographical data for the entire pool of reef-associated Red Sea fishes, comparing those that invaded the Mediterranean to those that had not. They found that home range size can predict introduction well, but they also observed a substantial increase in the disparity of ecological traits of Lessepsian fishes with respect to those of a random sample of potential invaders (Red Sea species). These results were used to acknowledge the potential for undisclosed ecological

processes, primarily interspecific competition, to explain the success of Lessepsian species.

Here we take a conceptually simple approach to predict the outcome of an introduction, which follows Darwin's view of naturalised invaders as species being of 'highly diversified nature' compared to indigenous ones (Pearson *et al.* 2012). Darwin observed a link between the evolutionary relatedness of organisms and the ecological processes that determine their abundance (Park & Potter 2013). In ecology, we can assume that morphological relatedness is correlated with ecological similarity (Ricklefs & Miles 1994); thus a species' morphology can be a proxy for its ecological role in a community. A species that differs greatly from those in the native pool is predicted to become abundant because it can have access to new resources and/or because it would use new strategies to exploit them. Therefore, we explore to what extent the abundance of an introduced fish can be explained by its morphological traits, testing the hypothesis that morphological relationships are related to population abundance.

MATERIALS AND METHODS

Conceptual approach

We define the morphospace of the indigenous community and examine how introduced fishes of Lessepsian origin distribute in this space. If ecological differences exist between successful and unsuccessful invaders in terms of available niche space (Elton 1958), they should be detectable as a preferential placement of successful invaders in less occupied parts of morphological space (Ricklefs & Miles 1994). To test this hypothesis, we examine the relative positions of introduced fishes with respect to the morphological space defined by the resident assemblage, then correlate our observations with their abundances, which are determined from bibliographic sources (see below).

The morphological space of the receiving fish community was delimited by a multidimensional convex hull. The convex hull, a measure derived from computational geometry, constitutes the minimum convex geometry that includes all the observations (Cornwell *et al.* 2006). This construct, which is the multivariate equivalent of range, is increasingly used to represent the space of traits occupied by a community (e.g. Villéger *et al.* 2008), and we adopted it here to address the question of limiting similarity.

Using a landmark-based procedure, we calculated the convex hull of existing morphologies (recipient community), and we examined the relative position of a newly introduced species in relation to its abundance in its invaded range.

The resulting morphospace is defined as the area inside the convex hull C associated with a guild of resident species (Cornwell *et al.* 2006). Each C was then decomposed into Voronoi polygons V , determined by distances among species in a two-dimensional plot (Mellen & Mishra 2010). Voronoi polygons set the space limits of individual species in relation to their close neighbours and can be used to estimate the available ecological space around each species in a community (e.g. Du *et al.* 2012). Each such polygon is defined by the set of points closer to a particular species than to any other. In

this way, we create a unique partition of C associated with the resident community, which can then be distorted by addition of a new species.

The addition of a newly introduced species S_x to a guild of resident species E_k , may occur according to three scenarios (Fig. 1). The new species might appear: (I) within the morphological range of the resident assemblage C_k , occupying less morphological space than the closest neighbour species S_{pk} ($V_{xk} < V_{pk}$) (Fig. 1c); (II) within C_k with more morphological space than the closest neighbour species ($V_{xk} > V_{pk}$) (Fig. 1d) and (III) outside C_k (Fig. 1e), hence occupying a morphological domain not occupied by the resident assemblage. These three cases would define three different levels of niche opportunities (*sensu* Shea & Chesson 2002), from low to high, and they should correlate with the abundances of the invaders according to our hypothesis.

Species lists and rank of abundance

The Lessepsian species list was compiled from Golani *et al.* (2013) by selecting those teleost fishes for which the mode of introduction through the Suez Canal (and no others such as ballast waters) was indicated. The native species list was obtained from available bibliographic sources updated with the most recent literature (see Supporting References). Because Lessepsian fishes typically occupy shallow depths (Golani *et al.* 2013), those species distributed at minimum depths deeper than of 50 m were filtered out. Depth ranges were obtained from the FAO guides (see Supporting Information) plus specific bibliographic searches. Overall, a total of 79 introduced and 323 Mediterranean fishes (Table S2) were included in the analyses.

The invasion process can be divided into two essential stages: transport of organisms to a new location, and establishment and population increase in the invaded locality (Shea & Chesson 2002). Here we focus on this second stage, because the probability of developing an abundant population can be strictly related to species interactions and hence to the opportunities provided by the invaded community. In the absence of density data on all Lessepsian fish species, abundance levels (in the form of an ordered qualitative variable) were determined from the available atlas (Golani *et al.* 2013) and guides (see also Supporting Information), which provide descriptive information on the status (established-not established) and abundance of these species. Therefore, we assigned each of the 79 introduced fishes to one of the following categories: (1) not established or rare; (2) occasional to common but never very abundant; (3) very abundant or dominant (Table 1).

Definition of guilds

Morphological analyses were performed on 13 fish groups (Table S1 and S2), which were primarily defined on the basis of taxonomy. These sets of species embraced different families and/or orders, according to commonly accepted ecological and morphological criteria (e.g. Wainwright & Reilly 1994; Hobson 2006). All species belonging to the same family and order (except Perciformes) were included in the same guild. Perciformes, which contains the greatest number of species of any order of fish (and vertebrates), was further split according to phylogenetic relatedness (Hobson 2006).

Fish groups consist of fishes with similar morphology and lifestyles and might be seen as ecological 'guilds' (Simberloff & Dayan 1991; Hobson 2006). Thus, in the absence of

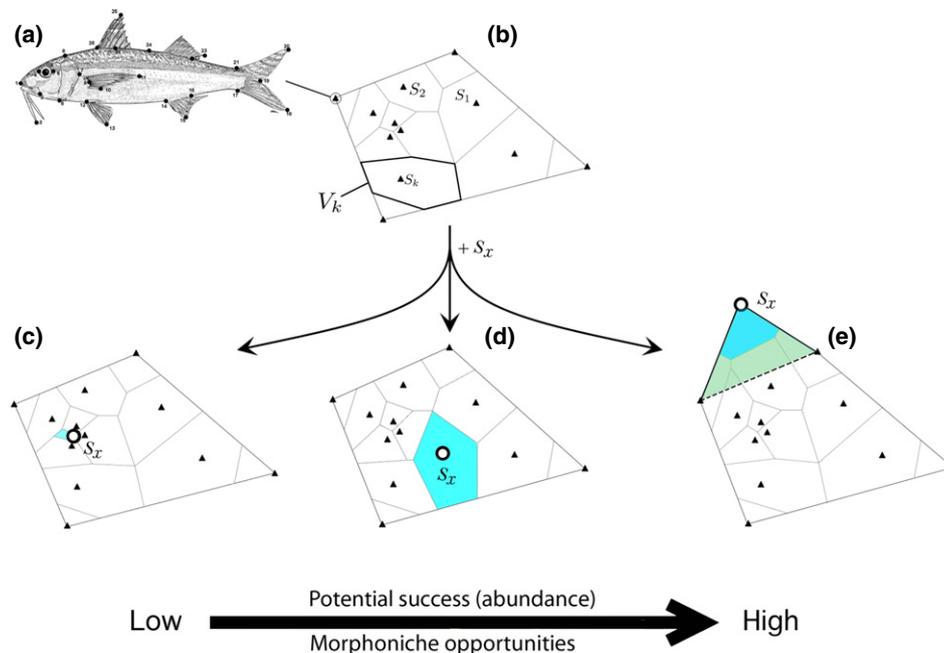


Figure 1 Schematic representation of conceptual framework. (a) Morphological landmarks ($N = 27$) define the position of each species. Given a hypothetical original assemblage, species positions are projected on a two-dimensional space (b). The area of the morphological space occupied by a new immigrant S_x and its position with respect to members of the original assemblage (c–e), are the basis of prediction for invasive success. With morphology as a proxy for ecological position, a positive significant relationship between morphological niche opportunities (which are assumed to increase from c to e) and the probability that a new invader becomes abundant can be established.

Table 1 Introduced fishes used in the analysis with indication of the year of first detection in the Mediterranean Sea; Morphological position (I, II, III), corresponding to the cases illustrated in Fig. 1c, d, e respectively, and three *a priori*-known levels of abundance: (1) not established or rare; (2) occasional to common but never very abundant; (3) very abundant or dominant

Family	Species	Year of first detection	Morphological position	Abundance rank
Chaetodontidae	<i>Chaetodon austriacus</i>	2011	I	1
Serranidae	<i>Epinephelus coioides</i>	1966	I	1
Serranidae	<i>Epinephelus malabaricus</i>	1966	I	1
Muraenidae	<i>Gymnothorax reticularis</i>	2013	I	1
Lutjanidae	<i>Lutjanus argentimaculatus</i>	1977	I	1
Platycephalidae	<i>Papilloculiceps longiceps</i>	1986	I	1
Pomacanthidae	<i>Pomacanthus maculosus</i>	2009	I	1
Platycephalidae	<i>Sorsogona prionota</i>	1947	I	1
Terapontidae	<i>Terapon jarbua</i>	2009	I	1
Terapontidae	<i>Terapon puta</i>	1973	I	1
Apogonidae	<i>Cheilodipterus novemstriatus</i>	2010	I	2
Syngnathidae	<i>Hippocampus fuscus</i>	1994	I	2
Mugilidae	<i>Liza carinata</i>	1924	I	2
Terapontidae	<i>Pelates quadrilineatus</i>	1969	I	2
Sphyraenidae	<i>Sphyraena flavicauda</i>	1991	I	2
Clupeidae	<i>Sprattelloides delicatulus</i>	1973	I	2
Callionymidae	<i>Callionymus filamentosus</i>	1953 or before	I	3
Carangidae	<i>Decapterus russelli</i>	2005	I	3
Clupeidae	<i>Herklotsichthys punctatus</i>	1943	I	3
Gobiidae	<i>Oxyurichthys petersi</i>	1982	I	3
Sparidae	<i>Acanthopagrus bifasciatus</i>	2010	II	1
Chaetodontidae	<i>Chaetodon larvatus</i>	2011	II	1
Gobiidae	<i>Coryogalops ochetica</i>	1924	II	1
Sparidae	<i>Crenidens crenidens</i>	1970	II	1
Serranidae	<i>Epinephelus fasciatus</i>	2011	II	1
Gobiidae	<i>Favonigobius melanobranchus</i>	1978	II	1
Hemiramphidae	<i>Hyporhamphus affinis</i>	1964	II	1
Muraenesocidae	<i>Muraenesox cinereus</i>	1979	II	1
Mullidae	<i>Parupeneus forsskali</i>	2000	II	1
Blenniidae	<i>Petroscirtes ancydon</i>	1988	II	1
Pomacanthidae	<i>Pomacanthus imperator</i>	2009	II	1
Scorpaenidae	<i>Pterois miles</i>	1991	II	1
Scorpaenidae	<i>Rastrelliger kanagurta</i>	1967	II	1
Sparidae	<i>Rhabdosargus haffara</i>	1991	II	1
Congridae	<i>Rhynchoconger trewavasae</i>	1987	II	1
Scaridae	<i>Scarus ghobban</i>	2001	II	1
Gobiidae	<i>Silhouetta aegyptia</i>	1972	II	1
Synanceiidae	<i>Synanceja verrucosa</i>	2010	II	1
Ostraciidae	<i>Tetrosomus gibbosus</i>	1987	II	1
Apogonidae	<i>Jaydia queketti</i>	2004	II	2
Platycephalidae	<i>Platycephalus indicus</i>	1953 or before	II	2
Haemulidae	<i>Pomadasystris stridens</i>	1950	II	2
Engraulidae	<i>Stolephorus insularis</i>	2009	II	2
Tetraodontidae	<i>Torquigener flavimaculosus</i>	1987	II	2
Carangidae	<i>Alepes djedaba</i>	1927 or before	II	3
Hemiramphidae	<i>Hemiramphus far</i>	1927	II	3
Tetraodontidae	<i>Lagocephalus sceleratus</i>	2003	II	3
Nemipteridae	<i>Nemipterus randalli</i>	2005	II	3
Apogonidae	<i>Ostorhinchus fasciatus</i>	2008	II	3
Diodontidae	<i>Cylichthys spilostylus</i>	1992	III	1
Leiognathidae	<i>Equulites elongatus</i>	2011	III	1
Chaetodontidae	<i>Heniochus intermedium</i>	2002	III	1
Ostraciidae	<i>Ostracion cubicus</i>	2011	III	1
Priacanthidae	<i>Priacanthus sagittarius</i>	2009	III	1
Gobiidae	<i>Trypauchen vagina</i>	2009	III	1
Exocoetidae	<i>Parexocoetus mento</i>	1935 or before	III	2
Labridae	<i>Pteragogus pelycus</i>	1991	III	2
Apogonidae	<i>Apogonichthyoides pharaonis</i>	1946	III	3

(continued)

Table 1. (continued)

Family	Species	Year of first detection	Morphological position	Abundance rank
Atherinidae	<i>Atherinomorus forskalii</i>	1902 or before	III	3
Cynoglossidae	<i>Cynoglossus sinusarabici</i>	1953 or before	III	3
Clupeidae	<i>Dussumieria elopsoides</i>	1948	III	3
Leignathidae	<i>Equulites klunzingeri</i>	1924	III	3
Clupeidae	<i>Etrumeus golanii</i>	1961	III	3
Fistulariidae	<i>Fistularia commersonii</i> *	2000*	III	3
Apogonidae	<i>Jaydia smithi</i>	2007	III	3
Tetraodontidae	<i>Lagocephalus spadiceus</i>	1950	III	3
Tetraodontidae	<i>Lagocephalus suezensis</i>	1977	III	3
Pempheridae	<i>Pempheris rhomboidea</i>	1978	III	3
Plotosidae	<i>Plotosus lineatus</i>	2001	III	3
Holocentridae	<i>Sargocentron rubrum</i>	1945	III	3
Synodontidae	<i>Saurida undosquamis</i>	1952	III	3
Scomberidae	<i>Scomberomorus commerson</i>	1935 or before	III	3
Siganidae	<i>Siganus luridus</i>	1955	III	3
Siganidae	<i>Siganus rivulatus</i>	1927 or before	III	3
Sillaginidae	<i>Sillago suezensis</i>	1977 or before	III	3
Sphyracnidae	<i>Sphyracna chrysotaenia</i>	1931 or before	III	3
Monacanthidae	<i>Stephanolepis diaspros</i>	1927 or before	III	3
Mullidae	<i>Upeneus moluccensis</i>	1946 or before	III	3
Mullidae	<i>Upeneus pori</i>	1942	III	3

*Evidence of an isolated observation in 1975 also exists

detailed information on all species' ecology and distribution, these guilds were used to assess the position in the morphospace of introduced species classified in the same groups by the same criteria. This procedure is aimed at surmounting the difficulties of studying a large set of species all at once (Simberloff & Dayan 1991), such as the fact that mixing too many disparate species, regardless of guild membership or ecology, will obscure patterns of species co-existence [the 'dilution effect', Diamond & Gilpin (1982)].

Morphological landmarks

Fish images were obtained both from the collection of the Laboratory of Renewable Marine Resources of the Institute of Marine Sciences of Barcelona and from Fishbase. For each species, we used 27 landmarks with anatomical, ecological and taxonomic significance (Recasens *et al.* 2006; Farré *et al.* 2013) based on standardised images of the left side of an adult individual (Lombarte *et al.* 2012) – using tpsDig, 2.16 (Rohlf 2001) (Fig. 1). We digitised landmarks using tpsDig software (Rohlf 2001) for geometric morphometric analysis.

Direct analysis of landmark coordinates contains other components unrelated to shape such as position, orientation or size, this latter accounting for most of the variability among samples. To remove these distortions, a generalised least-squares superimposition (GLS) procedure (generalised Procrustes) was applied, translating all specimens to a common centroid position in the coordinate system, scaling them to unit centroid size and rotating them to minimise the distances between corresponding landmarks (Kassam *et al.* 2002). A relative warp analysis of superimposed images was conducted using tpsRelw v. 1.49 (Rohlf 2001).

Morphospace analysis

The morphometric analysis was performed on a single sample image per species, assuming it to be a representative of the entire species (e.g. Antonucci *et al.* 2009). Changes in shape were computed sequentially, based on the date of first record of each Lessepsian species, and visualised using Relative Warp Analysis (RWA) (Rohlf & Marcus 1993). Each relative warp axis represents a set of specific morphological characteristics that summarise variation among species, allowing particular morphological attributes to be analysed directly. This kind of approach is currently used for studies of morphological integration (e.g. Kassam *et al.* 2002). The first three relative warps that explained the most overall morphological variation (32.2, 22.6 and 8.6%, accounting for a total of 63.5%) were retained for analysis of groups. The first two warps that explained the most variation in each group (Table S1) were used to project the morphological position of each species/group in a two-dimensional plot (Fig. 2, Fig. S3). Convex hull and Voronoi polygons were obtained using Delone software (v 1.0.1.19). Areas of Voronoi polygons were measured with an image analysis programme (Image-Pro Plus, v. 5.0., Media Cybernetics).

To test our hypothesis, we regressed the level of abundance (1, 2, 3) of introduced species on the predictors: relative position in morphospace (I, II, III), year of first detection and number of species within the receiving community, using ordered linear regression. The model selection process was based on comparing models of increasing complexity with one, two or three predictors against the null model with none of the predictors. We selected the model with the lowest value of Akaike's Information Criterion (Akaike 1973). The routine

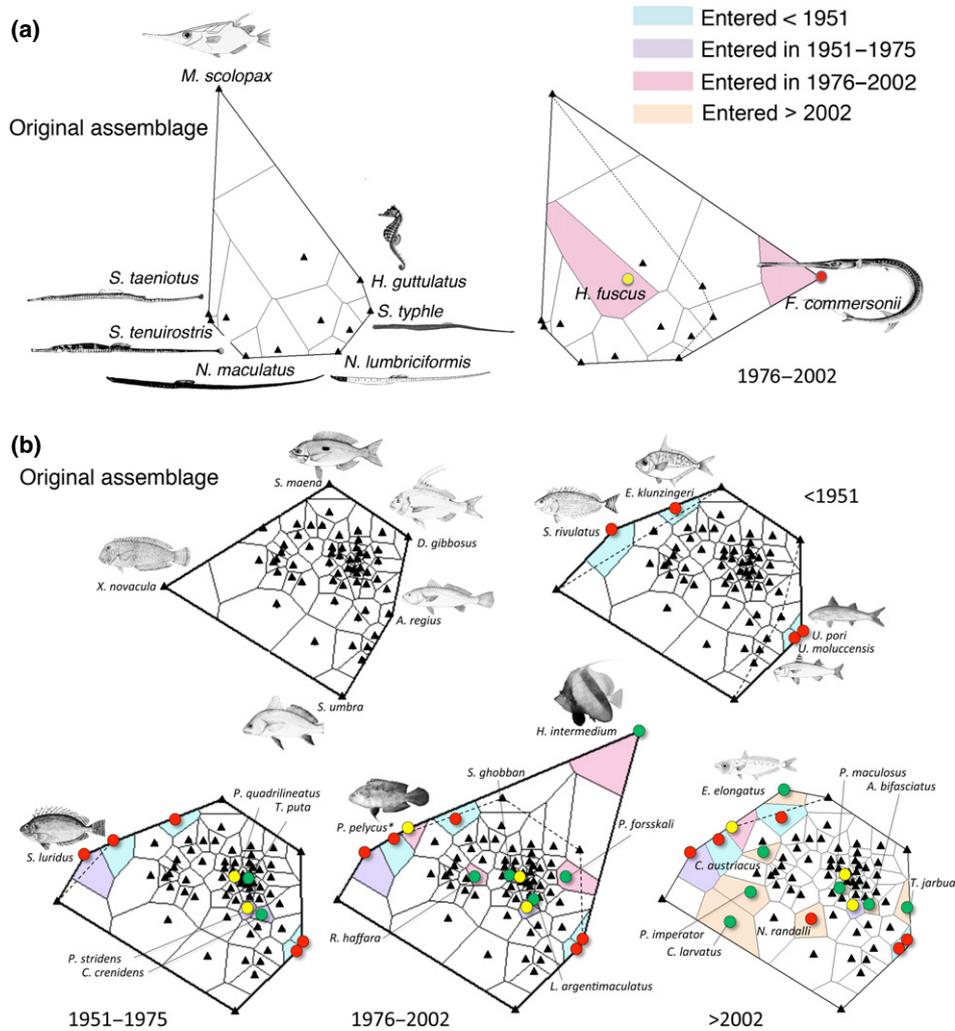


Figure 2 Morphological position of native and introduced species according to three *a priori* known levels of abundance. Black triangles = native species; circles = non-indigenous species: (1) green = not established or rare; (2) yellow = occasional to common but never very abundant; (3) red = very abundant. Successful invaders are generally added outside of or at the margins of the original convex hull, whereas unsuccessful species are mostly found within the original morphospace. Here two different examples of how this occurs are depicted: (a) Guild 3 and (b) Guild 5. On the left the native assemblages, on the right the new assemblages after the arrival of non-indigenous species and according to four temporal windows.

for ordered linear regression is available in Agresti (2010) in the MASS library of the R computing package (function `polr` in R 3.0.2).

RESULTS

In Figure 2, we show examples of successful and unsuccessful invasion events. A systematic analysis revealed that new species occupying locations outside the receiving assemblage typically became numerically abundant (Table 2, Fig. S1). The clearest result relates to group III, where 22 out of 30 species located outside of the original morphological space developed abundant populations, whereas most of the species assigned to categories I and II were rare or not established (Table 1). Results of the ordered linear regression are shown in Table 2. The model with morphological position and year of introduction significantly explained introduced species abundance (chi-square test $P < 0.001$), regardless of the size of the receiving guild. Morphological position III was twice (coefficient 2.025,

$P < 0.05$) as likely to result in abundant population levels as position I, while morphological position II did not differ significantly from position I ($P > 0.05$). Additionally, species

Table 2 Results of the ordered linear regression showing the model selection process and the coefficients of the selected model

NULL Model	AIC = 169.27		
Model 1: Morphological position	AIC = 150.75		
Model 2: Morphological position + Year + Size of receiving group	AIC = 147.29		
Model 3 (Selected) : Morphological position + Year	AIC = 141.83		
Predictor of Model 3	Coefficients (SE)	t-value	P
Morphological position II	0.085 (0.592)	0.144	0.391
Morphological position III	2.025(0.641)	3.157	0.0048
Year	-0.029 (0.0002)	-125.4	0.0001

Coefficients of the selected model show effects relative to morphological position I and year of first record in the Mediterranean Sea (Year)

introduced earlier were more likely to be abundant now (coefficient -0.029 , $P < 0.05$).

Examples of successful invaders that match our predictions (located outside the convex hull) can be seen by comparing the relative position of these species with their ranks (Table 1, Fig. S1): *Plotosus lineatus*, (Guild 1); the bluespotted cornetfish *Fistularia commersonii* (Guild 2); *Stephanolepis diaspros*, *Lagocephalus suezensis* and *L. spadiceus* (Guild 3); *Saurida undosquamis* (Guild 5); *Siganus* spp., *Upeneus* spp. and *Equulites klutzingeri* (Guild 8); *Atherinomorus forksalii*, *Dussumeria elopoides* and *Etrumeus golanii* (Guild 10); *Sphyræna chryso-taenia* (Guild 11); *Scomberomorus commerson* (Guild 12) and the majority of Apogonids and other nocturnal species such as *Pempheris rhomboidea* and *Sargocentron rubrum* (Guild 13) are all abundant invaders in eastern Mediterranean communities. By contrast, unsuccessful species are generally found within the original morphological ranges provided by the receiving assemblages. Introduced fishes belonging to families such as Serranidae (Guild 7) and Sparidae (Guild 8), which are well represented in the native assemblages of the Mediterranean Sea and are closely packed in their morphological spaces, generally did not establish or remained at low population values (Fig. S1).

DISCUSSION

Our findings demonstrate that external morphology, and by inference niche space, can be used to predict which introduced species will develop abundant populations and which will not. Overall, 73% of species located outside of the convex hull became abundant or dominant (Class 3) in their invaded range, and a regression model including position in the convex hull and year of first detection was statistically significant ($P < 0.001$). A weaker efficacy of our method in distinguishing between the non-abundant species groups (Class 1, 2) may be due to the fact that these earlier phases of 'introduction' and 'establishment' are less related to competitive interactions, depending largely on abiotic (especially climatic and environmental conditions) and stochastic factors (Schaefer *et al.* 2011). On the contrary, the stage of population increase would largely depend on species composition of local ecosystems (Schaefer *et al.* 2011), and if strong competition among species were to occur, it likely would be at this stage.

The approach presented here is based on integrating ecological, morphological and taxonomic traits in a single morphospace and assumes that morphological relatedness captures niche similarity (Ricklefs & Miles 1994; Ricklefs 2012). Although it ignores abiotic factors and phylogenetic and geographical components, the purely morphological allocation of these species provides a simple, reliable basis to evaluate expectations for newly introduced species.

Species such as the bluespotted cornetfish *Fistularia commersonii* or the eel catfish *Plotosus lineatus* constitute absolute 'novelties' for the Mediterranean community, and their morphological distinctness is reflected by their tremendous success in their new environment (Golani *et al.* 2013). Other species, like the invasive mullids (*Upeneus pori*, *U. moluccensis*) or siganids (*Siganus luridus* and *S. rivulatus*), are morphologically similar to only a few native species (*Mullus barbatus*, *Mullus*

surmuletus and *Sarpa salpa* respectively) and have high niche opportunities, as their morphologies place them outside of the receiving trait space.

By contrast, entire families of introduced fishes, such as Blenniidae, Gobiidae, Serranidae and Sparidae, are closely packed within the receiving morphological space and generally failed to develop invasive populations. For these families that will likely continue to be introduced to the Mediterranean Sea, we predict low probability of prominence as invaders.

Despite the reliable explanatory basis provided by our morphological framework, limitations may arise because of other factors, not only species interactions, can strongly influence both survival and population dynamics of introduced species. For instance, species like the butterflyfishes (Chaetodontidae: e.g. *Heniochus intermedius*) present really novel morphologies with respect to Mediterranean fishes and fall outside of the range of existing morphologies (Class III). Nevertheless, these fishes are strictly associated with coral reefs (Golani *et al.* 2013), and we expect them not to become established, owing to the lack of appropriate habitat in their introduced environment. Our approach based on external morphology may fail to account for aspects of invasion success associated with protracted lag times or specific life-history traits. For example, species such as *Pteragogus pelycus* may still be at low abundances simply because they have not had enough time to grow to large numbers since their first detection in 1991. Generally, the more time elapsed since colonisation, the better the opportunity to succeed, and our regression model (Table 2) significantly confirms this hypothesis advanced by Golani (2010).

From a methodological perspective, how guilds are defined constitutes a core step of this procedure, necessary to simplify large sets of species. The ability to predict accurately will critically depend on the morphologies used to construct the morphospace, as is also highlighted in analogous studies (Sidlauskas 2008). The lionfish (*Pterois miles*) was introduced to the Mediterranean but has not thrived yet, and our model predicts low probabilities of success for this species in the Mediterranean Sea. Nevertheless, the morphological peculiarities (e.g. the elongated fin rays with respect to confamilial species) of this species complex (*Pterois miles* – *P. volitans*) are considered so novel along the western Atlantic coasts that these are often adduced to explain the great success of this predatory invader (Albins & Hixon 2013). In summary, a careful interpretation of our results is advised when dealing with species such as the lionfish that were strikingly successful when introduced elsewhere.

Despite the aforementioned limitations, this work shows how the hypothesis of limiting similarity can easily be extended to morphology with a significant level of confidence. Our approach can help elucidate mechanisms underlying invasions (e.g. biotic vs. environmental filtering), and it could be extended to other systems for which meaningful morphological data are available and appropriate eco-morphological groups can be defined.

Because of its simplicity and efficacy, the analysis of external morphology could be a key addition to tools presently available for ecological assessment of invasive potential, at least for aspects related to population increase. It can help overcome the difficulty of rigorously assessing realised ecological niches (Belmaker *et al.* 2013), with both theoretical and

methodological implications. Invasive species are difficult to control, particularly in the marine environment (Barbour *et al.* 2011), making the ability to understand what species can develop abundant populations vitally important for assessing the risk of unwanted introductions. According to our predictive framework, we can evaluate the potential of newly introduced species as soon as they are recorded in their new environment. We can also screen the entire pool of potential invaders to infer the success probabilities of each species. On the contrary, we cannot predict which species from the Red Sea will be introduced, because this phase (i.e. crossing the Suez Canal) is less related to species interactions and strongly influenced by stochastic events (Belmaker *et al.* 2009, 2013).

Species lists and morphological data are relatively easy and inexpensive to obtain, and they can be systematically applied using computational geometry techniques. This will allow our findings to be tested in many other systems and in every situation in which both the morphological traits of the invader and of the invaded communities can be taken into account. Because of the urgency of detecting early warning signals (Scheffer *et al.* 2009) and in particular of estimating the probability that a given species will become invasive, our method could be useful for those introduced species that, though not yet naturalised, might constitute a threat in the future.

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AUTHORSHIP

ARP gathered morphological data from all fish images employing the landmarks technique; VT and AL developed and performed the morphological analyses; FM conducted statistical analyses and supported the formulation of the hypothesis along with all authors; DS supervised the rationale behind the morphological niche concepts; EA conceived the initial idea and wrote the main paper in collaboration with DS, RS and the other authors. All authors discussed results and implications, providing significant inputs to the manuscript at all stages.

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