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Climate change and body size shift in Mediterranean bivalve assemblages: unexpected role of biological invasions

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Body size is a synthetic functional trait determining many key ecosystem properties. Reduction in average body size has been suggested as one of the universal responses to global warming in aquatic ecosystems. Climate change, however, coincides with human-enhanced dispersal of alien species and can facilitate their establishment. We address effects of species introductions on the size structure of recipient communities using data on Red Sea bivalves entering the Mediterranean Sea through the Suez Canal. We show that the invasion leads to increase in median body size of the Mediterranean assemblage. Alien species are significantly larger than native Mediterranean bivalves, even though they represent a random subset of the Red Sea species with respect to body size. The observed patterns result primarily from the differences in the taxonomic composition and body-size distributions of the source and recipient species pools. In contrast to the expectations based on the general temperature–size relationships in marine ectotherms, continued warming of the Mediterranean Sea indirectly leads to an increase in the proportion of large-bodied species in bivalve assemblages by accelerating the entry and spread of tropical aliens. These results underscore complex interactions between changing climate and species invasions in driving functional shifts in marine ecosystems.

1. Introduction

Body size is a key biological feature, closely related to a multitude of physiological, life-history and ecological traits of organisms, many of which determine community structure and functioning of ecosystems [1–3]. Reduction in average body size has been suggested to be a universal response of ectothermic organisms to climate warming, especially in aquatic systems [4–6]. This phenomenon can be observed across levels of biological hierarchy—from individuals to communities—reflecting cumulative and interactive effects of changes in growth and development rates of individuals, and shifts in population size structure and community composition [4,6].

Climate-induced shifts in species geographical ranges can be one of the key factors changing the distribution of body sizes at multiple spatial scales. According to Bergmann's rule (*sensu* [7]), within a broadly distributed taxonomic clade, species of smaller size tend to inhabit lower latitudes. Because climate warming triggers poleward range shifts, the proportion of smaller-bodied species is thus expected to increase, leading to a decrease in average body size in marine assemblages [4,8]. Human activities, however, including shipping, aquaculture and construction of canals, have greatly altered pathways and rates of species dispersal on a global scale [9,10], causing massive introduction of alien species originating from distant biogeographic regions. Moreover,

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climate change can facilitate this process. Warming removes physiological constraints on survival, growth and successful reproduction of subtropical and tropical alien species, and increases their competitive abilities relative to native biota [11–13]. Because species invasions can be non-random with respect to body size [14–16], a growing share of alien species may thus amplify or reverse climate-induced shifts in the size structure of receiving communities, depending on the direction and magnitude of the relative difference in body size between native and introduced species.

Large-bodied species may possess life-history traits facilitating dispersal and population establishment [5,14,17], and can be overrepresented among alien species because they were intentionally selected and introduced by humans [16,18]. Correlation between body size and invasion success, however, is not the only way in which differences in body size between alien and native species can arise. The addition of alien species can shift the interspecific size distribution of the recipient region in three general, not mutually exclusive ways (figure 1): (i) introduction of species from a region characterized by a different size-frequency distribution (species pool effect; cf. [19]); (ii) preferential introduction, establishment and/or spread of aliens belonging to particular size classes and thus representing a non-random sample of their source species pool (size-biased invasion; e.g. [14,16]); and (iii) change in average body size of alien species following their establishment in the new area relative to their native range (post-invasion size shift; e.g. [20]). Evaluating the relative importance of these scenarios requires information on both the source and recipient species pool of aliens, as well as comparative data on body size of alien species from their native and invaded range.

The Mediterranean Sea is a unique location where the ongoing warming trend coincides with an influx of alien species on an unprecedented scale [12,21,22]. The majority of the newcomers are subtropical and tropical Indo-Pacific species entering through the Suez Canal [22], the process commonly known as Lessepsian or Erythrean invasion [23]. Increasing sea surface temperatures facilitate establishment and further range expansion of warm-water alien species [23–25], leading to the so-called 'tropicalization' of Mediterranean biota [26]. Red Sea species are already becoming dominant in coastal ecosystems of the southeast Mediterranean Sea [27,28], and are increasingly spreading throughout the rest of the basin [22,29]. Importantly, because the source and recipient species pool, introduction pathway and relative success of aliens are known, the Lessepsian invasion represents a perfect system to study processes operating during marine invasions [30].

Here we evaluate the effects of the Lessepsian invasion on regional body size patterns in the Mediterranean Sea to test if the introduction of tropical alien species affects the reduction of body size in native communities expected under climate warming. We use data on marine bivalves, which are one of the most important groups taking part in the Lessepsian invasion [31]. First, we combine information on the interspecific size distribution of the entire Red Sea and Mediterranean species pools, and assess non-random size patterns among alien species to disentangle the importance of size-selective invasion and source-pool effect. Because body size is a phylogenetically conservative trait [32], we test for the taxonomic bias in the invasion and evaluate the consistency of the observed patterns within individual families and functional groups. We focus on the first stage of the Lessepsian invasion—the arrival of alien species to the Mediterranean Sea, corresponding to transport and introduction stages of Blackburn et al. [33]—because the selectivity during this phase constrains the characteristics of species potentially able to establish and become invasive in the new region [15]. Second, we use size estimates from multiple populations of two widespread invasive species to test if Lessepsian bivalves are becoming larger in the Mediterranean Sea compared with their native range.

2. Material and methods

(a) Dataset compilation

We collected species-level data on body size and ecological characteristic of bivalve fauna living at shelf depths (less than 200 m) in the Red Sea and in the Mediterranean Sea ([31]; electronic supplementary material, dataset S1). We combined information from primary literature, major monographs (e.g. [34–38]), our own field studies and museum collections (see electronic supplementary material, dataset S1 for the full list of sources). Our dataset encompassed 709 bivalve species from 66 families: 405 Red Sea species and 306 Mediterranean species, including two indigenous species shared by both basins. Specialized wood-boring teredinid and xylophagid bivalves were excluded (18 species in total); the former include many cryptogenic species and both groups are poorly studied in the Red Sea.

We use the term 'Lessepsian' to denote all Red Sea species, which have penetrated through the Suez Canal irrespective of their mode of introduction; some species are entering and spreading in the Mediterranean Sea both through the natural and human-mediated dispersal [23]. The list of Lessepsian bivalves was based on Zenetos et al. [39,40] and updated with more recent records (electronic supplementary material, dataset S1). Given a common uncertainty associated with the assessment of the establishment status of marine invertebrates, all Red Sea species with confirmed records in the Mediterranean Sea were included in the analyses.

As a proxy for body size of each species, we used the size of the largest specimen reported from its native range calculated as the $\log_2$-transformed geometric mean of the shell length and height (the metric commonly used in macroecological studies on marine bivalves; e.g. [41,42]). In all analyses addressing the interspecific size patterns, the maximum size observed in the Red Sea was used for all Red Sea species, including aliens, while the measurements recorded from the Mediterranean Sea were used for native Mediterranean species. Species were assigned to functional groups based on combination of the relationship with a substrate and feeding mode [31]. Because most of the functional groups contain no or only a few alien species [31], we addressed the patterns in body size only among epifaunal suspension feeders and infaunal suspension feeders. These two most diverse groups encompass together 80% of alien species (44 out of 55) and the majority of Red Sea and Mediterranean species (57.8% and 63.1%, respectively).

(b) Statistical analyses

Because body-size distributions tend to be skewed even after log-transformation, we used median values and employed permutation tests to compare the size of the Lessepsian species with that of native Mediterranean bivalves. After pooling size data for alien and native species, and randomly reassigning each species to one of these categories, we calculated the difference in median size between them. By repeating this procedure 10 000 times, we generated a resampling distribution of such differences, which was used to evaluate the significance of the observed size difference. Similar procedures were used to
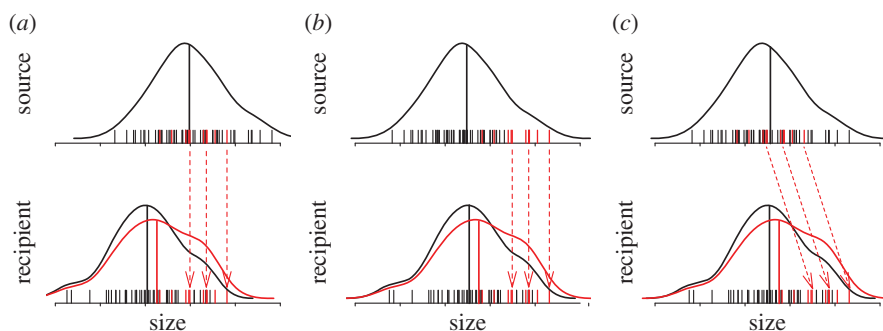
Figure 1. Three possible ways in which the addition of alien species (marked in red) can affect interspecific size distribution in a recipient region. (*a*) Species pool effect: alien species are a random subset of their source pool with respect to body size, but they originate from a region characterized by a larger average size. (*b*) Size-biased invasion: large-bodied species are more successful invaders; this correlation can occur at any stage of the invasion process. (*c*) Post-invasion size shift: successful alien species are a random subset of their source pool with respect to body size, but tend to reach larger size in the introduced range. Body size is in arbitrary units. Arrows link individual alien species between the source and recipient region; only a few of them are shown for clarity. The average size (thick vertical lines) and shape of the size distribution in a recipient region after the invasion is shown in red.

compare body size in the Mediterranean and Red Sea species pools. We report the median values on arithmetic scale (i.e. as geometric mean of shell dimensions) to facilitate interpretation.

To evaluate the non-random patterns in alien species introductions we followed the approach of Blackburn & Cassey [15]. To determine whether the 55 species that crossed the Suez Canal represent a non-random subset of the Red Sea fauna with respect to body size, we generated 10 000 random samples of 55 species taken without replacement from the total pool of 405 Red Sea species. We calculated median body size for each of these random draws to obtain a null distribution and corresponding 95% confidence intervals (CI), against which the observed median size of alien species was compared. Larger than expected body size of alien species can result from an over-representation of large-bodied clades among successful invaders. We repeated, therefore, the resampling algorithm as describe above, while controlling for family membership of alien species [15]. At each iteration, the body size of each alien was replaced by that of a Red Sea species selected at random from the same family, thus constraining the family-level composition of a simulated alien species list.

To test for the taxonomic clustering of the invasion success, we used Moran's I statistic to check for correlation between family membership and alien status coded as a binary trait (see [43,44]). This weighted correlation coefficient was introduced as a measure of spatial autocorrelation [45], but has been subsequently extended to tests of phylogenetic and taxonomic autocorrelation [46], including taxonomic patterns in extinction risk [43] and introduction success [44]. We calculated Moran's I using the R package *ape* [47] with weights denoting taxonomic proximity between two species set to 1 for co-familiar species and 0 otherwise. For individual families, we compared the observed number of alien species in each family with the null expectation assuming no taxonomic bias [15]. From the source pool of 405 Red Sea species, we sampled at random and without replacement 55 species. The number of alien species expected to belong to a given family, was calculated as the mean number of species drawn from that family in 10 000 such simulations together with corresponding 95% CI. We focused on families, because this taxonomic level explained most of the variation in body size in our dataset (electronic supplementary material, table S1), as indicated by hierarchically nested ANOVA [48].

(c) Testing for the post-invasion size shift

Because of the paucity of population-level size data for the majority of Lessepsian bivalves we focused on two extensively

studied species—*Brachidontes pharaonis* (Fisher, 1870) and *Pinctada imbricata radiata* (Leach, 1814)—for which we could obtain size measurements from multiple sites across their native (Red Sea and northwest Indian Ocean) and invaded range (Mediterranean Sea and Suez Canal; electronic supplementary material, figure S1). These two invasive aliens were among the first to cross the Suez Canal and are widely distributed in the Mediterranean Sea [23]. We combined available published records, museum collections and our unpublished data (electronic supplementary material, dataset S2), limiting the dataset to samples representing at least 20 measured individuals. If a single site was sampled during multiple seasons, individual collections were combined. We recorded the maximum size—measured as the largest shell dimension—in each sampled population and compared the mean maximum size across populations in the native and invaded range [20]. The mean shell size for individual samples was not always reported in the original studies, but when available, it was closely correlated with the size of the largest individual (Pearson's $r = 0.79$, $p < 0.001$ for 25 populations of *P. imbricata radiata*). All statistical analyses were performed in R [49].

3. Results

Fifty-five species of bivalves from 25 families—13.6% of the Red Sea species pool—crossed the Suez Canal, increasing the regional species richness of the Mediterranean Sea by 18% (from 306 to 361 species). These immigrants are significantly larger than native species (permutation test, $p < 0.001$; figure 2), with median body size of aliens (37.2 mm) being almost two times greater than that of native bivalves (19.8 mm). Thus, the addition of the Lessepsian species increases the median body size in the Mediterranean Sea by 8.6% (from 19.8 to 21.5 mm; electronic supplementary material, figure S2*a*). The observed median size of aliens is not significantly different, however, from that expected for a random selection of 55 Red Sea species (28.8 mm; 95% CI: 20.6–39.2; figure 2), especially when accounting for family membership (34.8 mm; 95% CI: 28.6–41.8). This lack of strong size-selectivity of the invasion process suggests that the larger size of alien bivalves results primarily from the differences between the source and recipient species pool. Indeed, the Red Sea bivalve fauna is characterized by a distinct size-frequency distribution (Kolmogorov–Smirnov test, $p < 0.001$) and larger median size (28.7 mm)
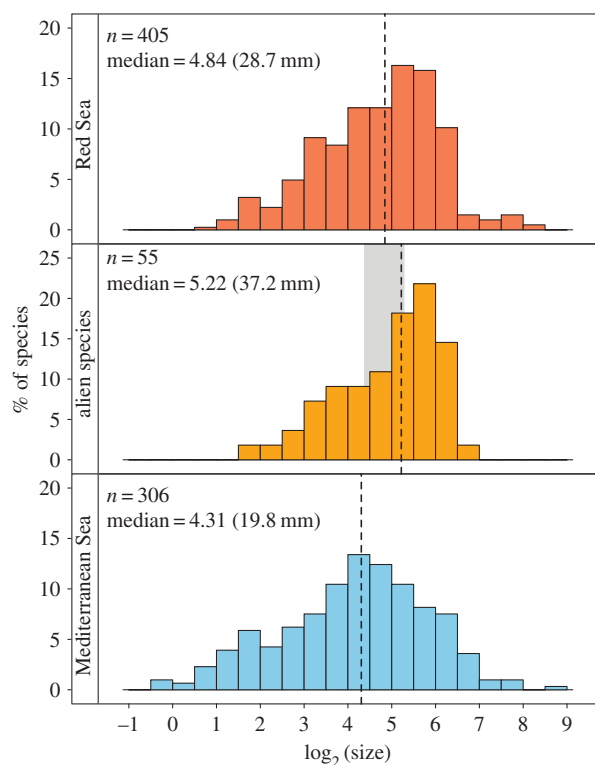
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Figure 2. Size-frequency distribution of Lessepsian bivalves compared with their source and recipient species pools—Red Sea and native Mediterranean fauna, respectively. Species' size is calculated as the geometric mean of shell length and height. Vertical dashed lines indicate median values and the grey shading represents the 95% CI based on random sampling of 55 species without replacement from the Red Sea species pool (10 000 iterations). Median sizes on an arithmetic scale are given next to the $\log_2$-transformed values for easier interpretation. (Online version in colour.)

compared with that of the Mediterranean (permutation test, $p < 0.001$; figure 2).

When the two most species-rich functional groups are considered separately (electronic supplementary material, figure S3), aliens are significantly larger than native Mediterranean species among epifaunal suspension feeders (median size of 45.6 mm and 19.7 mm, respectively; permutation test, $p = 0.006$), but not among infaunal suspension feeders (37.2 mm and 30.1 mm, respectively, $p = 0.29$). Therefore, the invasion-driven size shift in the novel Mediterranean assemblage is much stronger for the former group (increase in median size by 18.2%, from 19.7 to 23.3 mm; electronic supplementary material, figure S2). In neither of the two functional groups is the median size of aliens significantly different from that expected by a random sampling from the pool of Red Sea species representing a given ecology (electronic supplementary material, figure S3). Thus, just like in the total bivalve fauna, the magnitude of size differences between alien and native species is largely controlled by the regional size patterns: epifaunal species in the Red Sea are significantly larger than in the Mediterranean (41.9 mm versus 19.7 mm; permutation test, $p < 0.001$), but infaunal species have similar median size in both regions (30.4 mm versus 30.1 mm, $p = 0.93$).

Because particular clades tend to differ in the average size of constituent species, pooling them together in the analyses of the total assemblage may mask non-random invasion patterns occurring within individual lineages. However, comparison of alien species with Red Sea species that

belong to the same family, but did not cross the Suez Canal, failed to show any consistent size-selectivity within families (figure 3a; permutation test for difference in median size, $p > 0.05$ for all families). When alien species are compared with co-familiar Mediterranean species, similar lack of unidirectional differences in median size between alien and natives can be observed (figure 3b; permutation test, $p > 0.05$ for all families).

Variation in the species richness of families is the primary reason for distinct shapes of the Mediterranean and Red Sea body-size distributions. Due to high heritability of body size, particular bivalve clades tend to occupy different portions of a size distribution [32]. There is a lack of consistent differences in median species size between the two regions within individual families (figure 3c). Indeed, only three families (Arcidae, Carditidae and Chamidae) are significantly larger in the Red Sea and two (Donacidae and Glycymerididae) are significantly larger in the Mediterranean Sea (permutation test, $p < 0.05$). However, families grouping species with larger than average body size tend to be much more diverse in the Red Sea (figure 3d). Moreover, these species-rich and large-bodied families contain the majority of Lessepsian species (figure 3d), which explains the striking difference in body size between alien and native species evident when families are pooled together (figure 2).

Taxonomic selectivity of the invasion is weak; across all families, there is no correlation between species' taxonomic affinity and their alien status (Moran's $I = 0.03$, $p = 0.29$). Only Ostreidae (true oysters) are represented by significantly more alien species than would be expected to cross the Canal if no taxonomic bias occurred (5 species observed versus 1 species expected; 95% CI: 0–3 species).

The average maximum shell size within alien populations of *B. pharaonis* (mean ± s.e.: 30.5 ± 3.0 mm, $n = 24$) is significantly larger than those from its native range (21.4 ± 0.9 mm, $n = 9$; Welch's t-test, $t = -2.88$, d.f. = 9.52, $p = 0.02$; electronic supplementary material, figure S4a). No significant difference in size, however, occurs between the invaded (75.3 ± 3.3 mm, $n = 33$) and native range of *P. imbricata radiata* (73.7 ± 5.8 mm, $n = 14$; $t = -0.24$, d.f. = 21, $p = 0.81$; electronic supplementary material, figure S4b). Although the number of measured individuals varies greatly between samples (20–5000 shells), it is not correlated with the recorded maximum size for either species ($n = 33$, Pearson's $r = 0.28$, $p = 0.12$ for *B. pharaonis*; $n = 47$, $r = 0.18$, $p = 0.22$ for *P. imbricata radiata*).

4. Discussion

(a) Consequences of the invasion

Changes in species composition due to poleward range shifts in response to climate warming are expected to decrease average body size of marine assemblages [4,8]. The Lessepsian invasion essentially represents an expansion of subtropical and tropical species into mid-latitudes, but its outcome is directly opposite to this simple prediction: Red Sea species crossing the Suez Canal are significantly larger than native Mediterranean bivalves, thus shifting the body size distribution of the recipient biota toward larger size classes. Moreover, the ongoing rise of seawater temperatures facilitates the establishment and further spread of Lessepsian species [23–25], and thus indirectly leads to the increase in
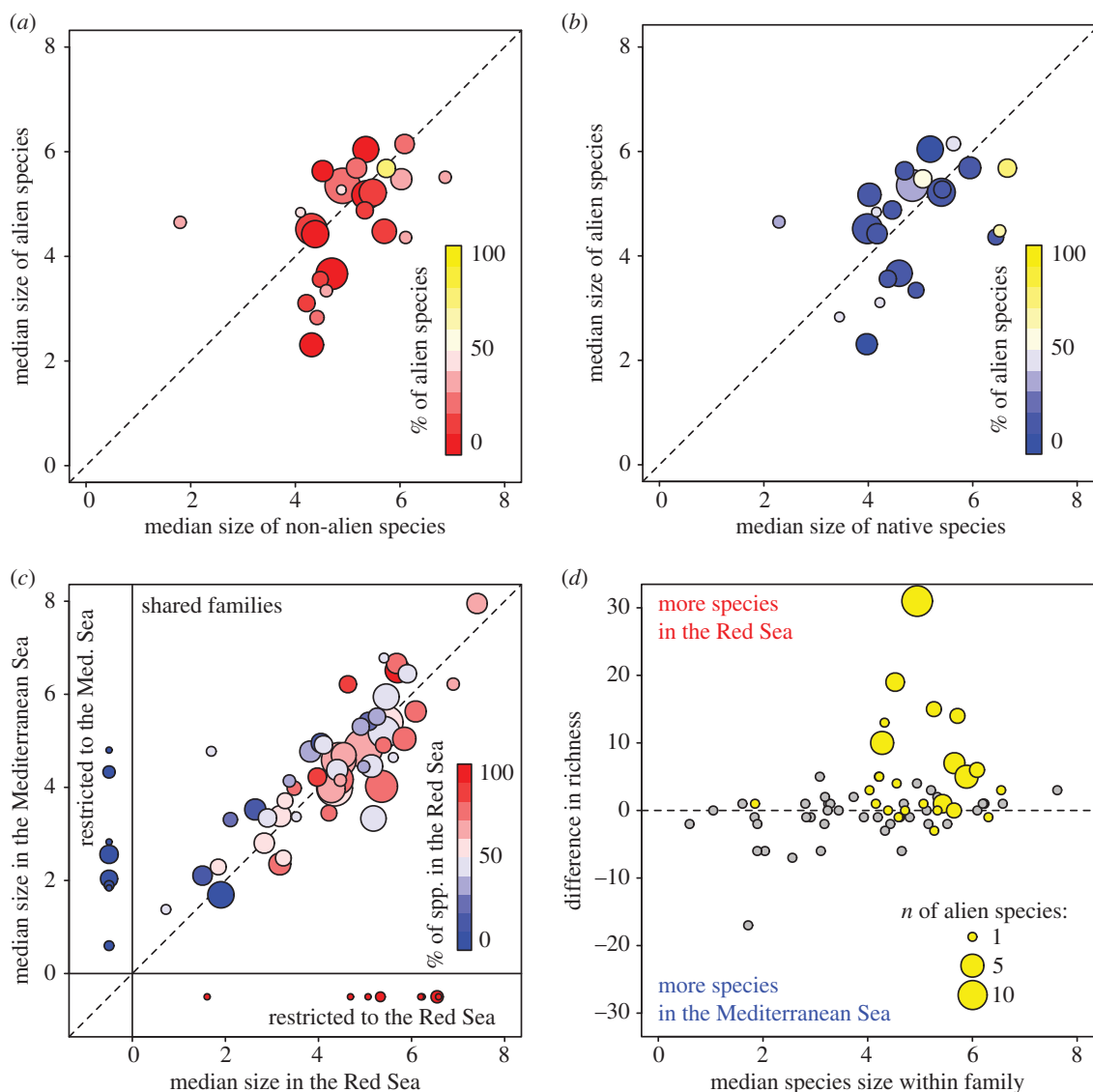
Figure 3. Body size and species richness within bivalve families. (a) Individual Red Sea families do not show consistent differences in size between alien species and those that did not invade. (b) Comparison of median size of native and alien species within Mediterranean families; alien species are not always larger than co-familial native species. (c) Within individual families, Red Sea species do not show consistently larger sizes compared with Mediterranean species; families restricted to either region tend to be species-poor, thus the distinct shapes of body-size distributions in the two regions must result primarily from the differences in the species richness among the shared families. (d) Absolute difference in the number of species belonging to a given family in the Red Sea and Mediterranean Sea plotted against its median species size; large-bodied families tend to be more diverse in the Red Sea and contain the majority of alien species (marked in yellow). Each point represents a single family; the size of a bubble is proportional to the species richness of a family in the Red Sea (a), species richness in the Mediterranean Sea (b), total richness in both regions (c) and the number of alien species (d). Dashed diagonal lines in (a–c) are 1 : 1 lines.

the proportion of large-bodied species in the Mediterranean bivalve fauna.

The magnitude of the assemblage-level size increase documented here at the scale of the whole Mediterranean Sea should be viewed as a very conservative estimate. Far more dramatic changes are likely to be taking place in its south-eastern part, the Levantine Sea, due to its proximity to both the Suez Canal and a restricted pool of native species [22,27,29]. The progressive spread of alien species along the southeast Mediterranean coasts coincides with population collapses and range contraction of native species [27,28,50]. In epifaunal assemblages inhabiting intertidal and shallow subtidal rocky habitats, Lessepsian species have already almost completely replaced native species [28,50,51]. Because the size difference between alien and native species is much stronger among epifaunal suspension feeders compared with the rest of the bivalve fauna, this turnover in species composition is causing a pronounced shift in the size

structure of hard-substrate communities. Given the important role that suspension-feeding bivalves play in benthic–pelagic coupling and nutrient cycling in coastal ecosystems [52,53], ecosystem functioning in these habitats may also be affected. Growing dominance of large-bodied alien species should lead to slower turnover rates and higher standing biomass among primary consumers, reducing rates of energy and matter fluxes.

(b) Mechanism of the size shift

In contrast to the predictions of the size-biased invasion model (figure 1b), the median size of aliens is indistinguishable from that of a random sample of the Red Sea species, suggesting that their arrival to the Mediterranean Sea is independent of species body size. The lack of consistent size differences between alien and native species within individual families indicates that the difference observed in the

total assemblage arises mostly as a consequence of family-level composition of alien species. In other words, alien species are not necessarily larger than co-familial native species, but they tend to belong to large-bodied lineages. These clades are also more diverse in the Red Sea and only a weak taxonomic bias can be detected in the invasion process. Together with the lack of strong size-selectivity, this points to the distinct taxonomic composition and shapes of body-size distributions of the Red Sea and Mediterranean species pools (i.e. source-pool effect, figure 1a) as the primary driver of the observed patterns.

These regional differences cannot be explained by sampling biases alone; although small-bodied and cryptic species may be undersampled in the Red Sea and among alien species, exclusion of such problematic groups has little effect on the results (electronic supplementary material, figure S5). The observed patterns in body size are also unlikely to be a simple expression of current environmental conditions. Interspecific latitudinal trends in body size are common within bivalve families, but they vary considerably in strength and direction across lineages and geographical regions, and along environmental gradients [42]. Our results suggest that the distinct shapes of body-size distributions in the Red Sea and Mediterranean arise as a consequence of the differences in relative diversity of families, which group species from different parts of the size spectrum (figure 3c,d). Such large-scale patterns in species richness and body size are ultimately shaped by region- and clade-specific histories of origination, extinction and immigration dynamics [41,54,55].

Although we did not find support for the correlation between body size and successful arrival of alien species into the Mediterranean Sea, such a relationship can still occur during the later stages of the invasion. Traits associated with large body size, like higher fecundity, competitive abilities or predator avoidance [14,17], may be more important during subsequent establishment and spread of alien species, especially if interactions with incumbent species limit population expansion and growth [30]. Indeed, large body size separates invasive species (i.e. those that are widespread and have a strong impact on native communities) from the rest of established Lessepsian bivalves [31].

Increase in size following the establishment in a new region (post-invasion size shift; figure 1c) is another mechanism potentially affecting size structure of recipient communities. Larger size in the invaded range compared with the native one has been demonstrated for a number of marine and estuarine invertebrate species [20,56,57], although the evidence from terrestrial organisms is more equivocal [58]. Apart from differences in latitude and abiotic conditions [20], potential mechanisms responsible for this pattern include founder effects, propagule bias, release from coevolved parasites, predators and competitors, and rapid life-history evolution in range-expanding populations (reviewed in [59,60]).

A paucity of comparative data from the native range of alien species severely limits our ability to evaluate the importance of post-invasion size shifts among Lessepsian bivalves—a problem often faced by invasion biologists [58]. We could identify only two species for which data from multiple native populations are available: *B. pharaonis* attained larger shell size in the Suez Canal and Mediterranean Sea relative to its native range, but no significant differences could be detected for *P. imbricata radiata*. Although based on more spatially restricted sampling, larger body size in alien populations has been previously shown for the Lessepsian bivalve *Spondylus spinosus* [61] and the solitary ascidian *Herdmania momus* [62]. The maximum globally observed size of several Indo-Pacific fish species was recorded from their alien populations in the Levantine Sea [63]. Further research is necessary to test the generality of these observations, but they suggest that at least some Lessepsian species can exhibit larger sizes in the Mediterranean Sea relative to their source populations.

5. Conclusions

As human-mediated dispersal of species redefines modern biographic patterns [10], our ability to use simple ecogeographic rules to develop broadly applicable predictions on the structure of the novel ecosystems may be severely limited. Due to strong human preference towards introduction of large-bodied species, alien species have already become a major driver of body-size changes in freshwater fish assemblages on a global scale [16]. We show that even in the absence of such strong, directional selection, biological invasions can result in significant alteration of the distribution of body sizes in recipient communities. Our results demonstrate the importance of the source-pool effect, and thus suggest that the biogeographic origin of alien species can determine the direction and magnitude of functional shifts in strongly invaded ecosystems. More importantly, the complex interactions between climate change and species invasions can result in unexpected outcomes, which are opposite to the predictions based on the general temperature–size relationships in marine ectotherms: continued warming of the eastern Mediterranean Sea will increase the average body size in bivalve assemblages because it facilitates the replacement of native species by larger-bodied thermophilic aliens.

It remains a major challenge to understand how these regional patterns will translate into changes in size spectra at the community scale, which in turn may affect food web structure and ecosystem functioning [2,3]. Alteration of size structure of recipient communities can result not only from a simple numerical addition of alien species, but also from their effects on diversity, abundance, population size structure and growth rates of native species [25,64,65]. As rates of spread of aliens are much higher compared with range-shifting native species [66], changes resulting from invasions may progress more rapidly than the expected responses of native communities to global warming. Therefore, the predictions on the future shifts in community size structure and related ecosystem properties need to take into account the context-dependent nature of the invasion process and its multiple interactions with other types of anthropogenic impacts.

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