NOTE

Native–exotic diversity relationships for Eastern Mediterranean fishes reveal a weak pattern of interactions

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ABSTRACT: A critical question in invasion ecology is how the native species community and the exotic species affect one another. It is commonly postulated that exotics negatively impact the native community's biodiversity, and that a rich native community can inhibit the establishment of exotics. This hypothesis can be examined using the native–exotic richness relationship (NERR), where negative impacts would be reflected by negative correlations. We examined this hypothesis in the Mediterranean Sea, which is subject to an influx of Red Sea species, making it an invasion hotspot. We tested the potentially important, yet neglected, temporal dynamics of the NERR associated with increases in the richness of exotics over time. We used data from fish bottom trawl surveys conducted in the Eastern Mediterranean over 2 time periods, spanning 2 decades, characterized by a considerable increase in numbers of exotic species. While exotic richness in the first time period was uncorrelated to that of natives, a negative NERR was observed in the second time period. However, this pattern disappeared once we controlled for depth. Results did not change when we used a diversity index instead of richness alone or changed the scale of the analyses. Together, these results suggest that for fish communities over soft substrates, native species diversity does not strongly affect exotic species diversity, which hints at weak interactions between natives and exotics.

KEY WORDS: Native–exotic richness relationship · Biological invasions · Mediterranean Sea · Lessepsian migration · Fish · Native Mediterranean fish

1. INTRODUCTION

Biologic invasions occur in a wide variety of ecosystems and are considered one of the major drivers of biodiversity loss (Simberloff et al. 2013). Elton (1958) proposed that native species richness is key to invasibility, with rich habitats being less susceptible to invasion (biotic resistance). By plotting exotic richness in a habitat against native richness, biotic resistance can be observed as a negative native–exotic richness relationship (NERR). A similar negative NERR can also be formed by the ex-clusion of native species by exotics. Due to its simplicity, NERR is a popular method to assess the impact of exotics and to assess the strength of biotic resistance imposed by the native community (Stohlgren et al. 2003, Davies et al. 2005, Fridley et al. 2007). However, the vast majority of NERR studies have focused on a single temporal snapshot (Guo 2017), which provides limited insight into the processes underlying exotic establishment (Fridley et al. 2007). Additionally, most studies have focused on terrestrial plants (e.g. Stohlgren et al. 2003, Davies et al. 2005, Fridley et al. 2007, Guo 2017), and the

shape of the NERR has not, to our knowledge, been assessed in marine systems.

As rates of invasions are rapidly increasing, it is important to understand temporal trends in both native and exotic species richness (Guo 2017). An ongoing invasion is expected to produce a temporal-dynamic NERR corresponding to the underlying invasion processes. The NERR coefficient could become more negative through time if the invasion follows Elton's hypothesis of biotic resistance due to a gradual establishment of exotics in native-poor habitats, or due to wide-scale exclusion of natives by exotics. Alternately, it could become less negative if exotics gradually become established in favorable, and thus species-rich, habitats without excluding natives (Stohlgren et al. 2003). Lastly, the slope could remain constant, indicating that the establishment of exotics is independent of native richness.

The temporal dimension also makes it is possible to examine whether change in native richness is correlated with change in exotic richness. A negative relationship across sites implies that exotic establishment leads to a decrease in native richness. However, a nonsignificant relationship may indicate that exotics simply favor species-poor habitat, as an increase in exotic richness does not result in native richness declines. Further examination of temporal trends in NERR could thus provide vital information regarding the native community's response to ongoing invasions.

The Mediterranean Sea is an invasion hotspot, with an unparalleled number of exotic species, including hundreds of Red Sea species from various taxa (Lejeusne et al. 2010, Zenetos et al. 2012, Galil et al. 2018). Over 100 introduced fish species have been documented, more than in any other marine ecosystem (Golani et al. 2002, Belmaker et al. 2013, Edelist et al. 2013). The abundance of these exotic species is expected to increase with increasing sea temperatures (Belmaker et al. 2013, Tsikliras & Stergiou 2014). However, the impact of these exotic species on native species is not clear. On the one hand, several species have caused devastating effects on the invaded environment. For example, 2 exotic rabbitfish species, *Siganus rivulatus* and *S. luridus*, have caused a significant depletion of algal growth by overgrazing (Sala et al. 2011). On the other hand, relative biomass of native species has not decreased in relation to the increased biomass of exotics (Buba et al. 2017). Moreover, trait-based analyses show that competition with exotic species is not likely to drive changes in native species abundances (Givan et al. 2017, Arndt et al. 2018). Consequently, both the commu-

nity-level impact of exotics, and the possibility of biotic resistance by native species to the spread of exotics, remain unclear.

Here we examined the native–exotic diversity relationship using data of bottom trawl surveys from 2 time periods spanning 20 yr. By using 2 time periods, we can observe the temporal trends in NERR and understand the processes by which exotic species establish and interact with the native community. Because NERR exhibits different patterns with the increase in scale (Fridley et al. 2007), we further investigated the NERR scale-dependence. Understanding the trend in the native–exotic relationships can shed light on the community-level processes behind the largest marine invasion of our time, and improve our understanding of possible future consequence of invasion to other marine ecosystems.

2. MATERIALS AND METHODS

We used bottom trawl surveys in the eastern Mediterranean Sea conducted in the years 1990–1994 and 2008–2012, using the same methods (Dornelas et al. 2018). The 2 time periods are defined by an increase in the proportion of exotic abundance from 29 to 54% of the catch (Edelist et al. 2013). Data from 1990–1994 consisted of 231 hauls, and data from 2008–2012 of 253 hauls. One box from each haul, representative of the total catch, was sampled, the fish in it were identified to the species level and counted. Altogether, the dataset contains 127 805 individual fish of 168 species.

Each haul was separated into 2 groups of species according to whether they were of Mediterranean (native) or Red Sea (exotic) origin. Biomass of each species was calculated based on the fish lengths using standard fish length–weight associations. For each group, we calculated the numerical proportion and biomass proportion of each species in the sample. Using these proportions, we calculated the Shannon entropy index to describe each group's diversity, from which we then calculated the effective number of species (Jost 2006). We calculated Shannon entropy of native and exotic species separately, to avoid the inherent negative relationship which stems from the sum of proportions equaling one. After initial examination of the NERR, additional comparisons were made between NERR in different depth groups: shallow (15–37 m), medium (38–82 m), and deep (>83 m) (Givan et al. 2018).

We tested the relationship between native and exotic species using both sampled richness (i.e. num-

ber of native and exotic species in a sample) and Shannon diversity. Linear regression was used to test for the magnitude of the native–exotic relationship as expressed by the regression slope. This was done at 5 different temporal scales: haul, day, month, season, and year. As sample size, in terms of the number of hauls, may differ across days, months, seasons, and years, we used sample-based rarefaction to make samples comparable (Gotelli & Colwell 2001). We rarefied to 2 hauls for each sampling day (retaining 70% of the sampling dates), 4 hauls for each month (retaining 70% of sampled months), 21 hauls for each season (retaining 68% of seasons), and 49 hauls for each year (retaining 70% of the years). For each rarefied sample, we calculated the average richness or diversity over 100 random samples and used this value for the calculation of the NERR. We note that total sample size decreases considerably with scale and goes down from 484 at the scale of hauls to 7 at the scale of years.

We tested for changes in the slope of the native–exotic relationship using general linear models with exotics as the response and natives as the predictor along with both period (1990–1994 vs. 2008–2012) and depth (shallow, medium, or deep). An interaction between natives and period would indicate that the native–exotic relationship has changed over time. To examine the possibility that this interaction is depth-dependent, we additionally tested for a 3-way interaction between natives, period, and depth.

We further examined whether exotics potentially favor species-poor habitats, or exclude natives, by examining the change, across time, in exotic richness with that of natives. For this, we considered combinations of season (2 categories), depth (3 categories), and spatial locations (70 categories). We then examined the change in richness across time in exotic and native species for each of the 49 season–depth–location combinations which were sampled in both periods. To account for different sampling effort, we rarefied to the lowest number of individuals sampled within the season–depth–location combinations. We used a linear model to test for the relationship between change in natives and exotics.

3. RESULTS

When using species richness, native and exotic species showed no relationship at the haul scale in the first time period and a negative relationship in the second time period (slope $p = 0.46$ for the first time period and $p < 0.001$ for the second time period;

Fig. 1A,B). The shift to a negative NERR might suggest that exotics either favor species-poor habitats or that they exclude natives. However, when we examined depth-specific NERR, a change in the NERR over time was only observed in the deep habitats, with a positive relationship becoming non-significant (Fig. S1A in the Supplement at www.int-res.com/articles/suppl/m611p215_supp.pdf; results of a 3-way interaction presented in Table S1). Further inspection of depth-specific NERR showed that shallow and medium depths did not differ between time periods in their NERR (Fig. S1A). Using Shannon entropy, we observed no significant relationship between native and exotic diversity at the haul scale within both time periods (Fig. 1C,D). This was consistent across the 3 depth groups, except for the deep habitats in 2008–2012, where a positive relationship was observed (Fig. S1B, Table S2).

When observing how the NERR changes across temporal scales, no pattern of increase was detected (Fig. 2A), suggesting that the lack of both a negative NERR and its temporal trend is scale independent. Similarly, using both biomass and abundance to calculate Shannon entropy showed no significant trend with any scale (expect for the year scale; Fig. 2B,C).

When we examined change across time in native richness against change in exotic richness, we found no significant relationship ($p = 0.84$; Fig. S2). Similarly, we found no significant pattern when examining this relationship at each depth separately ($p > 0.1$ for all 3 depth groups).

4. DISCUSSION

For more than a century, the Eastern Mediterranean Sea has been subject to an ongoing invasion through the Suez Canal. With an already high number of established exotic species and an increasing rate of invasion detections (Belmaker et al. 2009), the Eastern Mediterranean Sea serves as a unique system to examine the impact of exotic species on native communities. To understand if exotics can exclude native species, or if the native community can resist invasion, we examined the shape of the NERR. We examined for the first time how this relationship changed over a 20 yr time period during which the proportion of exotics increased from 29 to 54% of the catch. We found that the depth-specific native–exotic relationship did not change over the 2 decades examined, both when using species richness and Shannon entropy, despite the continuous increase of exotic species richness. This suggests that, at the community level, exotic
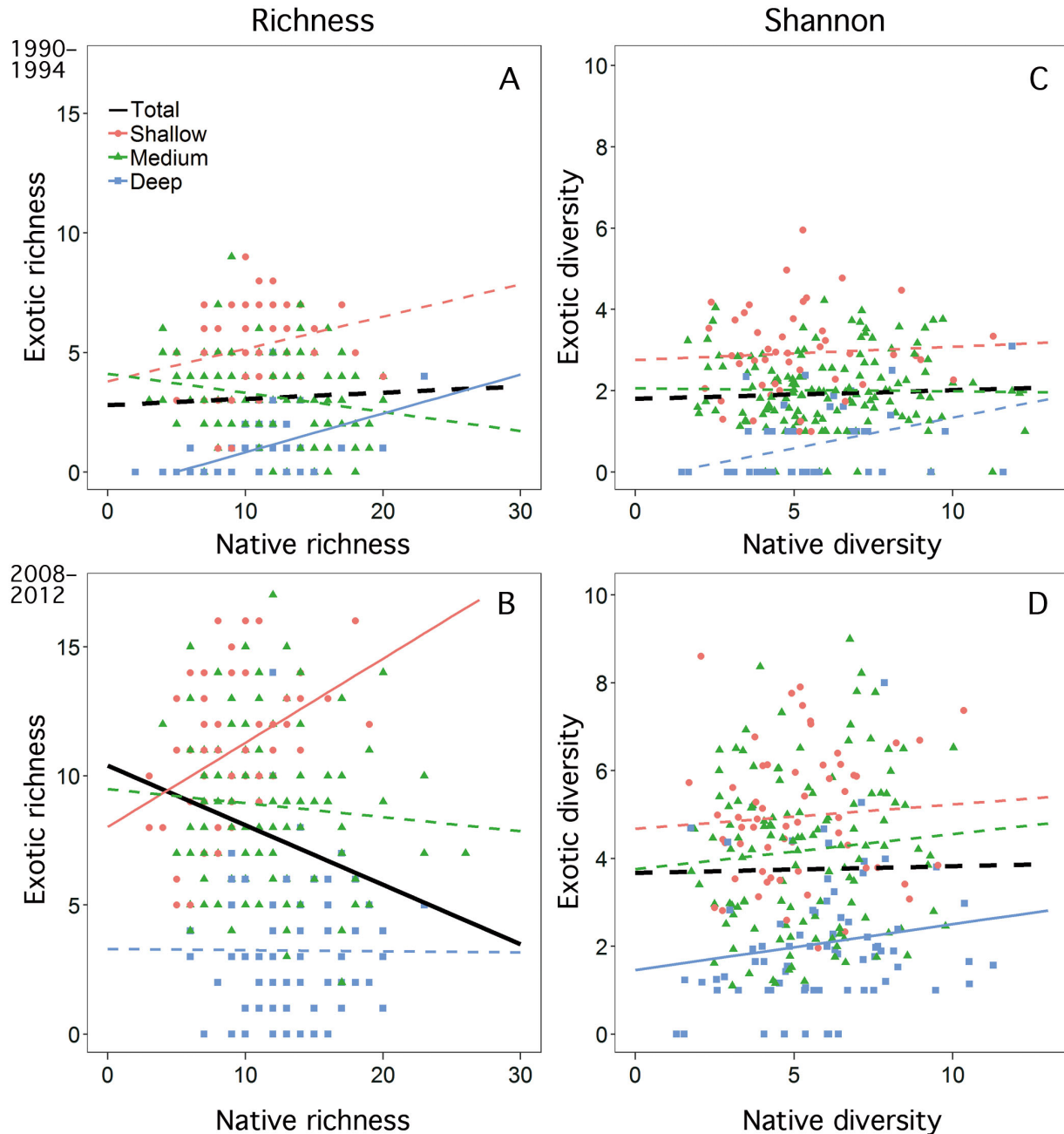
Fig. 1. Native–exotic relationship in the years (A,C) 1990–1994 and (B,D) 2008–2012 using richness (A,B) and Shannon en-tropy (effective number of species transformation; C,D) calculated based on species abundances. Red circles = shallow habitat, green triangles = medium-depth habitat, blue squares = deep habitat. Black line denotes the overall native–exotic relationship estimated using linear regression. Colored lines denote depth-specific native–exotic relationships. Solid and dashed lines: significant and non-significant slopes, respectively

establishment is not strongly limited by native rich-ness and that exotics do not exclude natives.

A prevailing hypothesis in invasion biology states that species-poor communities are also characterized by weaker biological interactions — interactions which are necessary to inhibit establishment of exotic spe-cies (Elton 1958). According to this hypothesis, as

new species colonize species-poor environments, an already negative NERR may become steeper. We found that native and exotic richness were uncorre-lated in the first time period, and that while they became negatively correlated in the second time period, this was only an artifact of more exotics enter-ing shallow depths (Goren et al. 2016). Once we con-
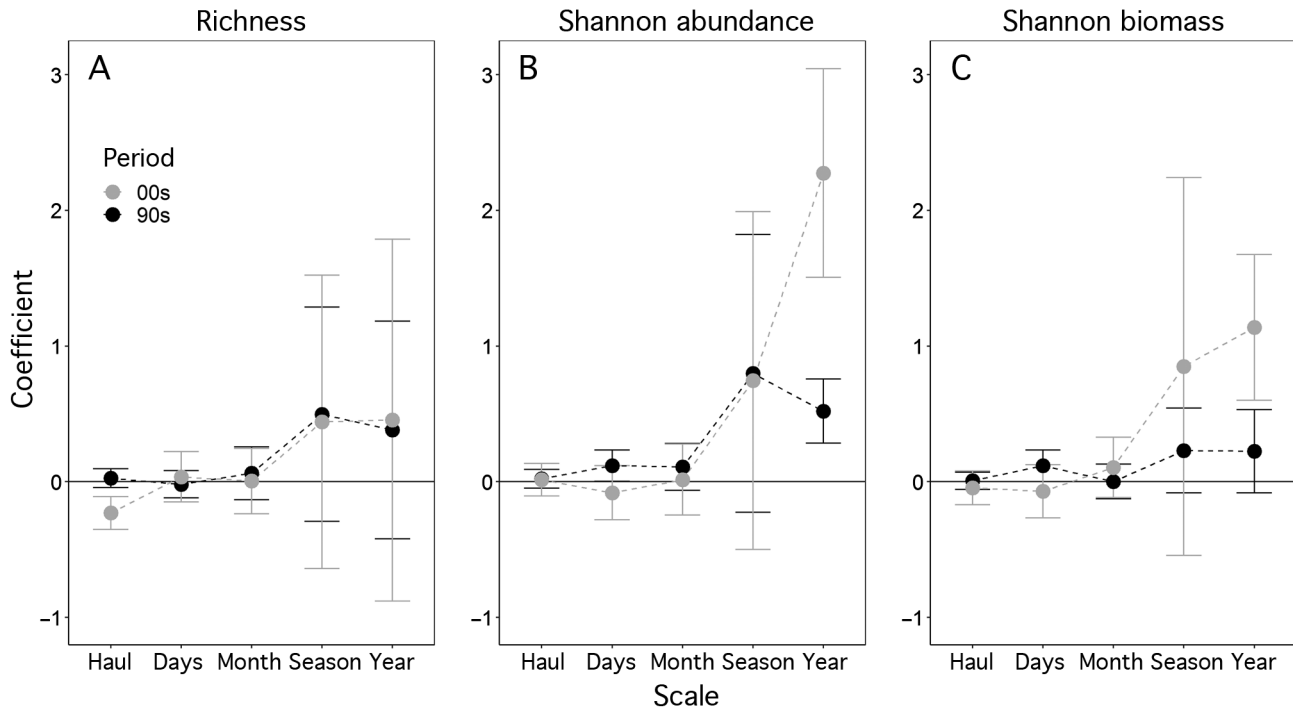
Fig. 2. Regression slope coefficients from linear regressions of exotics versus natives across temporal scales, using (A) richness and (B,C) Shannon entropy, based on species abundance (B) and biomass (C). Grey: 1990–1994, black: 2008–2012. Error bars denote 95% confidence intervals

trolled for depth, no change in the NERR was observed. This stability implies that establishment of exotics is indifferent to native richness, as the number of exotic species increased uniformly throughout a native richness gradient within a specific depth. Additionally, we found no significant relationship between the change in site-specific native and exotic richness (Fig. S2), further corroborating our finding that exotic establishment did not correspond with a decrease in native richness. These findings echo previous studies on soft-bottom fish communities in the Eastern Mediterranean which indicate weak competition between exotics and natives (Buba et al. 2017, Arndt et al. 2018, Givan et al. 2018).

The NERR is hypothesized to be greatly affected by scale, with the pattern shifting to a positive NERR at large scales (Fridley et al. 2007). It is believed that the shift to a positive NERR is due to the weakening of biotic interactions, such as competition, which dominates small scales, as well as the increase in environmental heterogeneity (Davies et al. 2005, Fridley et al. 2007). To understand how NERR changes with scale, we examined increasingly larger temporal scales which likely increases both the total number of individual samples and the heterogeneity of the samples in terms of habitats, time of day, and season. We found that the NERR did not change consis-

tently with increasing scale over both time periods. This hints that natives and exotics do not respond similarly to temporal gradients, such as daytime vs. nighttime, which would produce a positive NERR. However, we did find some evidence for a positive NERR across years, which would suggest that natives and exotics respond similarly to large-scale yearly fluctuations in resources or environment.

We examined the NERR using both richness and Shannon entropy (the effective number transformation of the Shannon index). Although diversity indices are seldom examined in the context of NERR, they may be more informative ecologically. This is because we would expect the impact of exotics or, conversely, resistance of the native community, to be mediated by species abundances, not by mere presence or absence. Hence, by focusing on species presence or absence when calculating richness, a great deal of vital information regarding species impact is lost. However, we found no clear relationship between native and exotic diversity, which further corroborates our findings that, at the community scale, exotic establishment is not determined by native species, and that natives are not excluded by exotics.

It is important to note that we focused on an open, soft-bottom habitat. Soft-bottom habitats are defined by low environmental complexity and lack of physi-

cal barriers that would otherwise inhibit the movement of fish. As a result, physical space may not be a limiting factor in these systems. It is unclear whether the lack of a negative NERR observed here would hold over hard substrate and more complex habitats, where physical space is expected to be more of a limiting resource. Additionally, we note that the geographical extent of the study is limited, focusing on Israel's continental shelf. While our findings are expected to apply to other regions of the Mediterranean, additional studies are needed to fully understand how the rapid influx of Red Sea species affects the Mediterranean fish community at larger scales. This study focused on interspecific interactions of a single taxonomic group to examine the impact of exotic species. Exotic species may still affect the invaded ecosystem by other mechanisms, such as the devastating overgrazing documented for the invasive rabbitfishes (Sala et al. 2011), or through their impact on other taxa not examined here.

In conclusion, we show that for soft-bottom fish communities in the Eastern Mediterranean, competitive exclusion of natives by exotics is likely not widespread. Similar results were found using species-specific traits (Givan et al. 2017, Arndt et al. 2018) and using total biomass (i.e. size spectra; Buba et al. 2017). In our study, we examined a different aspect of the community and tested whether exotic community diversity (richness and Shannon entropy) is affected by natives. Together, these studies provide multiple lines of evidence for overall weak interactions between natives and exotics. However, as more exotic species are established in the Eastern Mediterranean, it is still unclear what the future holds for the native fish community.

LITERATURE CITED

Arndt E, Givan O, Edelist D, Sonin O, Belmaker J (2018) Shifts in Eastern Mediterranean fish communities: abundance changes, trait overlap, and possible competition between native and non-native species. Fishes 3:19

Belmaker J, Brokovich E, China V, Golani D, Kifawi M (2009) Estimating the rate of biological introductions: Lessepsian fishes in the Mediterranean. Ecology 90:1134–1141

Belmaker J, Parravicini V, Kulbicki M (2013) Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean. Glob Chang Biol 19:1373–1382

Buba Y, van Rijn I, Blowes SA, Sonin O, Edelist D, DeLong JP, Belmaker J (2017) Remarkable size-spectra stability in a marine system undergoing massive invasion. Biol Lett 13:20170159

Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. Ecology 86:1602–1610

Dornelas M, Antao LH, Moyes F, Bates AE and others (2018) BioTIME: a database of biodiversity time series for the Anthropocene. Glob Ecol Biogeogr 27:760–786

Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: profound shifts in the world's most invaded marine ecosystem. Divers Distrib 19:69–77

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago, IL

Fridley JD, Stachowicz JJ, Naeem S, Sax DF and others (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17

Galil BS, Marchini A, Occhipinti-Ambrogi A (2018) East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. Estuar Coast Shelf Sci 201:7–16

Givan O, Parravicini V, Kulbicki M, Belmaker J (2017) Trait structure reveals the processes underlying fish establishment in the Mediterranean. Glob Ecol Biogeogr 26:142–153

Givan O, Edelist D, Sonin O, Belmaker J (2018) Thermal affinity as the dominant factor changing Mediterranean fish abundances. Glob Chang Biol 24:e80–e89

Golani D, Orsi-Relini L, Massutí E, Quignard JP (2002) CIESM Atlas of exotic species in the Mediterranean, Vol 1: Fishes. CIESM, Monaco

Goren M, Galil BS, Diamant A, Stern N, Levitt-Barmats Y (2016) Invading up the food web? Invasive fish in the southeastern Mediterranean Sea. Mar Biol 163:180

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Guo Q (2017) Temporal changes in native-exotic richness correlations during early post-fire succession. Acta Oecol 80:47–50

Jost L (2006) Entropy and diversity. Oikos 113:363–375

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Pérez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol Evol 25:250–260

Sala E, Kizilkaya Z, Yildirim D, Ballesteros E (2011) Alien marine fishes deplete algal biomass in the Eastern Mediterranean. PLOS ONE 6:e17356

Simberloff D, Martin JL, Genovesi P, Maris V and others (2013) Impacts of biological invasions: What's what and the way forward. Trends Ecol Evol 28:58–66

Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. Front Ecol Environ 1:11–14

Tsikliras AC, Stergiou KI (2014) Mean temperature of the catch increases quickly in the Mediterranean Sea. Mar Ecol Prog Ser 515:281–284

Zenetos A, Gofas S, Morri C, Rosso A and others (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). 2. Introduction trends and pathways. Mediterr Mar Sci 13:328–352