Received: 6 September 2020 | Revised: 25 August 2021 | Accepted: 3 September 2021

DOI: 10.1111/geb.13415

Global Ecology and Biogeography | A Journal of Macroecology | WILEY

RESEARCH ARTICLE

Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning

Jan Steger[1] | Marija Bošnjak[1,2] | Jonathan Belmaker[3,4] | Bella S. Galil[4] | Martin Zuschin[1] | Paolo G. Albano[1,5]

[1]Department of Palaeontology, University of Vienna, Vienna, Austria

[2]Croatian Natural History Museum, Zagreb, Croatia

[3]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

[4]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

[5]Department of Animal Conservation and Public Engagement, Stazione Zoologica Anton Dohrn, Naples, Italy

Correspondence
Jan Steger, Department of Palaeontology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria.
Email: jan.steger@univie.ac.at

Funding information
Austrian Science Fund, Grant/Award Number: P28983-B29; OeAD-GmbH, Grant/Award Number: Ernst Mach fellowship

Handling Editor: Janne Soininen

Abstract

Aim: A large body of ecological theory predicts that non-indigenous species (NIS) are successful invaders if their niches overlap little with native taxa. Native–non-indigenous trait dissimilarity, however, may also be observed if NIS have outcompeted ecologically similar native species. Discriminating these scenarios is essential for assessing invasion impacts but requires baseline assemblage data that are frequently unavailable. We overcome this impediment by analysing death assemblages – identifiable organism remains in the seafloor – which are natural community archives. Focusing on molluscs from the heavily invaded Eastern Mediterranean, we gain insights into the contentious role of competitive displacement by NIS as the primary driver of the massive regional declines of native populations, and their potential to alter ecosystem functioning.

Location: Israel/Eastern Mediterranean.

Time period: Pre-Lessepsian invasion (pre-1869) to contemporary.

Major taxa studied: Mollusca.

Methods: We sampled molluscan living and death assemblages from various substrates on the Israeli shelf and compiled trait information on all constituent species. We then compared the abundance-weighted trait composition and functional diversity of native and non-indigenous assemblage components. Death assemblage time-coverage was quantified radiometrically.

Results: Native and non-indigenous assemblage components consistently differed in trait composition, both in present-day (i.e., living) and historical (i.e., death) assemblages, irrespective of habitat conditions. Furthermore, present-day non-indigenous assemblage components had a different trait composition than historical native assemblages. These findings suggest that the increasing NIS dominance has considerably altered the functional properties of shallow-water molluscan assemblages.

Main conclusions: By utilizing death assemblages, we show that native and non-indigenous assemblage components have differed in trait composition since the

onset of the invasion, suggesting that competition was unlikely the primary driver of the regional-scale native biodiversity loss. Our findings, however, also imply that NIS cannot functionally compensate for native species disappearance. Instead, the transition towards increasingly NIS-dominated assemblages has profoundly altered ecosystem functioning, with unknown consequences.

KEYWORDS

biological invasions, competition, death assemblages, ecosystem functioning, historical baselines, Lessepsian invasion, marine molluscs, non-indigenous species, traits

1 | INTRODUCTION

In today's globalized world, introductions of non-indigenous species (NIS) occur at unprecedented rates (Seebens et al., 2017), with often profound impacts on native biodiversity and ecosystem functioning (e.g., Pyšek et al., 2020; Strayer, 2012). Assessing the potential for such impacts requires knowledge on how the traits of NIS relate to those of native species, as species' functional attributes are important determinants of biotic interactions and ecosystem processes (e.g., Engelhardt et al., 2009; Hooper et al., 2005; McGill et al., 2006; Pearson et al., 2012).

To successfully establish and increase in abundance, NIS do not only require traits that allow them to cope with the local abiotic conditions, but also to acquire sufficient resources to sustain growth and reproduction (e.g., Byers, 2000; Gallien & Carboni, 2017). While some NIS may achieve the latter by being superior competitors compared to functionally similar native species (e.g., Byers, 2000), a large and influential body of ecological theory suggests that niche differences to native species are key determinants of invasion success (see Catford et al., 2009 for a review). Such differences may enable NIS to effectively exploit available resource opportunities (sensu Shea & Chesson, 2002) and alleviate direct competition with resident species, as predicted by concepts such as limiting similarity (MacArthur & Levins, 1967), Darwin's naturalization hypothesis (Darwin, 1859), the 'empty niche' hypothesis (Hierro et al., 2005), and related theoretical frameworks (see Catford et al., 2009 for a review). While aiming at mechanistic explanations of invasions success, these hypotheses also yield two major predictions regarding the impact of biological invasions: first, due to complementary resource use, NIS are unlikely to competitively displace native species; second, biological invasions should cause major functional shifts at the ecosystem scale because successful (i.e., abundant) NIS will substantially alter the trait structure of recipient assemblages (Pearson et al., 2012).

Studies exploring the functional dissimilarity between NIS and native species – either directly via traits or indirectly via phylogenetic distances – have produced contradictory results (e.g., Diez et al., 2008). However, this may largely reflect differences in the conceptual frameworks and spatial scales involved (Thuiller et al., 2010). Indeed, considering that resource partitioning and competition are most relevant at small spatial scales and advanced stages of the invasion process (e.g., Schaefer et al., 2011), several recent empirical works found that abundant or invasive NIS often tend to differ either phylogenetically, ecologically and/or morphologically from native species (Azzurro et al., 2014; Diez et al., 2008; Divíšek et al., 2018; Pearson et al., 2012).

Such findings, however, can be confounded by the lack of a historical perspective on community dynamics in systems with long invasion histories. In such systems, any differences in the trait composition of present-day native and non-indigenous components of local assemblages could represent the outcome of two contrasting scenarios. First, abundant NIS may indeed be those whose niches overlap little with native species; hence, trait dissimilarity was present since the onset of their introduction. Second, present-day trait patterns may represent 'shifted baselines' (Pauly, 1995): successful NIS have outcompeted native species with similar traits in recipient assemblages, resulting in the trait segregation observed today. In this latter scenario, non-indigenous assemblage components should share high trait similarity with historical native assemblages.

The limited temporal coverage of observational data for many ecosystems relative to their invasion history, particularly in the marine realm (Ojaveer et al., 2018), therefore poses a major limitation to the interpretation of empirically observed trait patterns (Thuiller et al., 2010) and unbiased assessments of invasion impacts. Death assemblages – the accumulations of taxonomically identifiable organism remains encountered in a landscape or seafloor – are faithful natural archives of community composition that can help overcome this impediment (see Kidwell & Tomasovych, 2013 for a review). Due to the durability of skeletal elements such as molluscan shells, foraminifera tests and fish otoliths, and generally low sedimentation rates in open shelf environments, remains of multiple generations accumulate in death assemblages over time-scales of decades to millennia (Kidwell & Tomasovych, 2013). This extensive temporal mixing ('time-averaging') renders death assemblages compositionally inert to any recent directional change in living communities, and underlies their ability to record long-term ecological baselines and pre-impact assemblage composition. Capitalizing on these properties, death assemblages have successfully been exploited to reveal unrecorded shifts in taxonomic composition in habitats with long histories of anthropogenic alteration (e.g., Tomašových & Kidwell, 2017), and can

also provide invaluable information on the trait composition of past assemblages (Miller et al., 2014).

In this study, we combine present-day and geohistorical data from living and death assemblages, respectively, to assess the impacts of the so-called Lessepsian invasion (Por, 1978) – among the largest and longest-lasting biological invasions (Rilov & Galil, 2009) – on the native biota and ecosystem functioning in the Eastern Mediterranean Sea: following the opening of the Suez Canal in 1869, hundreds of tropical Red Sea species established populations in the basin in the course of this largely unidirectional process, and have become dominant components of local communities (e.g., Edelist et al., 2012; Galil et al., 2021; Rilov et al., 2018). Concurrent with this development, massive regional-scale population collapses of formerly common native Mediterranean species have been reported and suspected to primarily represent the outcome of competitive interactions with NIS (e.g., Edelist et al., 2012; Galil, 2007). However, scientific evidence supporting this interpretation has remained scarce (but see e.g., Safriel & Sasson-Frostig, 1988; Steger et al., 2021; Yeruham et al., 2020) and, indeed, several declines concerned native species without apparent non-indigenous competitors (Rilov, 2016). This suggests that other drivers, particularly regionally rapid seawater warming, might play a more significant role in native species' demise than previously thought (Albano et al., 2021; Givan et al., 2018; Rilov, 2016). Recent studies on Lessepsian fishes further support the secondary role of competitive displacement (Buba & Belmaker, 2019; Buba et al., 2017; Givan et al., 2018) and suggested that NIS indeed tend to occupy 'empty niches' (Azzurro et al., 2014; Givan et al., 2017), but none involved pre-invasion assemblage data.

We here test the hypothesis that native and non-indigenous components of benthic assemblages from the shallow Israeli Mediterranean shelf have differed in their trait composition since the onset of the Lessepsian invasion. We focus on molluscs, the largest and taxonomically and functionally most diverse group of Lessepsian invaders, whose shells provide rich death assemblages that enable reconstructing baselines. This extended temporal perspective, combined with a unique multi-assemblage dataset covering a wide range of shallow subtidal soft and hard substrates, allowed us to gain important insights into general patterns of native versus non-indigenous trait structure, functional diversity, and the potential of the Lessepsian invasion to impact Eastern Mediterranean ecosystem functioning.

2 | METHODS

2.1 | Field sampling and sample treatment

We analysed molluscan assemblages from 72 samples collected at 10 stations along the *c.* 200-km-long Israeli Mediterranean shelf between 2016 and 2018 (see Supporting Information Appendix S1, Figure S1.1 for a map). We collected 48 van Veen grab samples from subtidal soft substrates (10–41 m depth) and twenty-four 1-m^2 airlift suction samples from subtidal hard substrates (11–28 m depth). Our analysis is based on the resulting 45,414 living individuals and 12,041 shells representing 360 species (274 native taxa and 86 NIS). Sampling was conducted in both spring and autumn to capture seasonal variation. Detailed information on sampling stations and samples is available from Supporting Information Table S1.1. Bulk samples were sieved on a 0.5-mm mesh, the retained material fixed in ethanol and subsequently picked for molluscan individuals in the lab. For the analysis of death assemblages, quantitative splits of air-dried sample residues were picked until approximately 1,000 shell elements per station had been obtained. Only shell fragments constituting at least half of the shell, with either the apex or aperture (in gastropods) or the hinge (in bivalves) preserved, and retaining enough morphological characters to enable reliable taxonomic identification were considered. To obtain abundances comparable to living individuals, the abundance of skeletal elements was corrected for the number of elements present in living individuals, that is, dividing the raw counts of loose bivalve valves by 2, and those of polyplacophoran plates by 8 (Kowalewski et al., 2003). Shells of pelagic gastropods and non-marine taxa transported into the sampling sites were excluded from the dataset (Supporting Information Appendix S2).

To enable a rigorous temporal interpretation of the ecological information extracted from time-averaged death assemblages, we quantified their shell age distributions by radiocarbon dating (see Albano et al., 2021). At each station, we dated 10 to 15 valves of common native bivalve species that were also recorded alive in our samples (see Supporting Information Table S1.2 for further details and a list of dated species), using accelerator mass spectrometry (AMS) of powdered carbonate targets (Bright et al., 2021; Bush et al., 2013). Ages are reported in calendar years before the year of sample collection. Detailed descriptions of sample treatment, radiocarbon analysis, calibration of ages, and individual shell age data are available from Albano et al. (2021, supplementary material).

2.2 | Trait dataset

To functionally characterize the molluscan species in our samples, we collected information on five ecologically important traits – maximum adult body size, feeding habit, environmental position, substrate affinity and host association – using published literature, online databases and/or observations on our specimens (see Supporting Information Appendix S3 for a list of references). We chose these traits because (a) they capture several important aspects of molluscan ecology, (b) reliable information is available for the great majority of species covered in this study, and (c) they have been successfully used in studies focusing on invasion success in Lessepsian bivalves (Nawrot et al., 2015) and on native versus non-indigenous niche overlap in Eastern Mediterranean rocky intertidal molluscs (Steger et al., 2021). Details on the ecological relevance of the selected traits and the number of scored modalities (i.e., the different categories of a trait) are provided in Supporting Information Table S1.3.

As many species exhibit affinities to more than one modality per trait, we used a fuzzy-coding procedure (Chevenet et al., 1994) to generate the species × traits matrix. This approach allows scoring of trait modality affinity in a flexible, semi-quantitative way, providing a more realistic representation of species' functional roles in ecosystems. Following recommendations by Degen et al. (2018), we adopted the widely used numeric scoring system ranging from 0 to 3, where 0 corresponds to 'no affinity' to a given modality, 1 to 'low affinity', 2 to 'high affinity' and 3 to 'exclusive affinity'. If two or more modalities are expressed to a similar degree, each was scored with '2' by convention. In the rare case that information on a particular trait was not available for a species (concerning seven species, or 2% of taxa), all its modalities were scored with '0', so the profile would not bias subsequent analyses (Chevenet et al., 1994). After collecting trait information, raw modality scores of each trait were converted to proportions adding up to unity (e.g., Oug et al., 2012); in this way, all species and traits were weighted equally in the analyses, irrespective of the number of modalities per trait. This standardized trait matrix is provided in Supporting Information Appendix S4.

2.3 | Data analysis

2.3.1 | Trait composition of native versus non-indigenous assemblage components

Patterns of multivariate trait composition for native and non-indigenous assemblage components within stations were assessed by fuzzy correspondence analysis (FCA; Chevenet et al., 1994), an extension of multiple correspondence analysis designed for fuzzy-coded data. To calculate assemblage component trait profiles, we weighted standardized modality scores of species (modalities × species table) by their relative abundances (species relative abundance × assemblage component table) using matrix multiplication (see Oug et al., 2012; Steger et al., 2021); this takes into account that ecosystem functioning is mainly driven by dominant species (e.g., Gaston et al., 2018; Winfree et al., 2015). Assemblage component replicates with < 5 individuals were excluded from the analysis, including all spring-season non-indigenous components of station SG10, and station NG10 (no non-indigenous components of sufficient sample size were available). We further excluded trait modalities not represented at a given station (i.e., zero-only columns; see Supporting Information Table S1.4). FCA was performed using the 'ade4' package (v. 1.7–13; Dray & Dufour, 2007) in the statistical programming environment R (v. 3.5.2; R Core Team, 2018). Correlation ratios (Chevenet et al., 1994) were used to assess the relevance of the different traits for separating native and non-indigenous assemblage components. Differences in FCA scores of present-day native and non-indigenous assemblage components on the first three axes were tested by permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), using Euclidean distances and 9,999 permutations. For death assemblage components, the significance of the native versus non-indigenous separation was assessed by running PERMANOVA on ordination scores calculated for sets of 30 analytical replicates per station, obtained by a resampling procedure (see Supporting Information Appendix S1, section 1.5 for details). Finally, we used PERMANOVA (Bray–Curtis distances, 9,999 permutations) to test for native versus non-indigenous differences in the abundance-weighted modality composition of individual traits; to control for the influence of local environmental conditions on modality composition, sampling stations were defined as strata in this across-sites analysis. PERMANOVA was conducted using the 'vegan' R package (v. 2.5–4; Oksanen et al., 2019).

2.3.2 | Functional diversity

We assessed the functional diversity of native and non-indigenous assemblage components at the different stations to gain further insights into their trait structure and diversity. Functional diversity was measured based on the arrangement of species and their abundances in functional space, a multidimensional coordinate system in which species are positioned according to their trait (dis)similarity (Villéger et al., 2008). To build this space, we first grouped the 360 partially redundant species trait profiles into 151 unique functional entities (i.e., distinct trait combinations, see e.g., Villéger et al., 2011). We then calculated a functional distance matrix for these entities, using the generalized Gower dissimilarity measure (Pavoine et al., 2009), which can handle mixed variable types, including fuzzy-coded variables (Pavoine et al., 2009). The distance matrix was subsequently converted into Euclidean functional space using principal coordinates analysis (PCoA; see Legendre & Legendre, 2012). Functional spaces with up to 10 dimensions were built and their quality assessed using an updated and modified version of the 'quality_funct_space' R function (Maire et al., 2015), available from Villéger (2017). The selected 4-dimensional functional space had a mean squared deviation of 0.0147 between the Gower and Euclidean distances – confirming that it faithfully represents the original functional relationships (see Maire et al., 2015) – and was the best compromise between retaining information and enabling the calculation of functional diversity indices (see below) even for the most species-poor assemblage components. To test the sensitivity of our analysis to the choice of traits, we calculated Gower distances based on all different combinations of four out of five traits (cf. Toussaint et al., 2016). The correlation between these matrices and the distance matrix based on all five traits was assessed by Mantel tests and found to be robust against trait omission (Mantel $r > .87$, all $p = 10^{-4}$; Supporting Information Table S1.5).

We assessed the functional alpha diversity of present-day assemblage components using three complementary indices: functional richness, functional divergence and functional evenness (Villéger et al., 2008). As the latter two incorporate information on species relative abundances, these indices were calculated after assigning to all species the coordinates of their respective functional entities. Functional richness measures the amount of functional space occupied by an assemblage, that is, the volume of the minimum

TABLE 1 Median ages (in calendar years before sample collection) of native death assemblages from the Israeli Mediterranean shelf (from Albano et al., 2021) and percentages of shells pre-dating the opening of the Suez Canal in AD 1869 (pre-Lessepsian shells), determined by radiocarbon dating

	Soft substrates						Hard substrates			
	NG10	NG30	SG10	SG20	SG30	SG40	Ashqelon −12 m	Ashqelon −25 m	Achziv −12 m	Achziv −20 m
Number of dated valves	15	15	15	15	15	15	10	10	10	10
Median age (years)	24	53	763	769	1,461	125	56	26	55	33
Share of pre-Lessepsian shells (%)	6.7	40	53.3	66.7	93.3	53.3	0	10	0	0

convex hull including all constituent species, and thus reflects the range of trait values present (Villéger et al., 2008). This index does not consider species abundances and has no theoretical upper limit. Functional divergence measures how species abundances are distributed in assemblage trait space, and can be regarded as a proxy of functional niche differentiation (Mouchet et al., 2010); it represents the deviation of species abundances from the mean distance to the assemblage centroid (Mouchet et al., 2010; Villéger et al., 2008). Functional divergence is independent of species richness and takes high values if species with extreme trait profiles have high relative abundances in the assemblage (Villéger et al., 2008). Functional evenness measures the regularity of species' distribution and their relative abundances in assemblage functional space, based on the minimum-spanning tree connecting all constituent species. This index therefore takes low values if abundances are clustered in certain parts of the assemblage functional space (Mouchet et al., 2010). Finally, to explore the degree of functional differentiation between corresponding native and non-indigenous assemblage components independent of species' relative abundances, we calculated their functional beta diversity, using the Jaccard-like dissimilarity index proposed by Villéger et al. (2013). This index, ranging between 0 and 1, can be decomposed into additive turnover and nestedness-resultant components. The turnover component takes high values if assemblage components show little overlap in functional space, whereas the nestedness-resultant component does so if one of the assemblage components occupies a small portion of the functional space filled by the other (i.e., is nested within the latter; Villéger et al., 2013).

All functional diversity indices were calculated for present-day native and non-indigenous assemblage components at the station scale, that is, based on pooled replicate data. Pooling allowed us to level out the small-scale patchiness and seasonality typical of living populations, so indices would most faithfully reflect the actual functional diversity hosted by the various stations. Calculations were performed using the 'multidimFD' and 'multidimFbetaD' R functions, available from Villéger (2017). Evidence for systematic patterns in the relative functional alpha diversity of native versus non-indigenous assemblage components within soft and hard substrate habitats was assessed using a dual approach. First, we calculated log-ratios of index values as $\text{Ratio}_{\text{Index}} = \log_{10}(\text{Index}_{\text{native component}}/\text{Index}_{\text{non-indigenous component}})$, where 'Index' corresponds to either functional richness, divergence, or evenness. These ratios enable summarizing and comparing information on native versus non-indigenous relative functional diversity across sampling sites that differ in abiotic conditions, species richness, and trait distributions; they take positive values if the native component has a greater value for the functional diversity index under consideration, and negative values vice versa. Second, we conducted paired-samples Wilcoxon signed rank tests to assess any significant differences in functional diversity index values between native and non-indigenous assemblage components; due to the limited number of hard substrate stations ($n = 4$), signed rank tests were not conducted for this habitat. Finally, we also tested for habitat-specific differences in the values of alpha functional diversity ratios, as well as of functional beta diversity indices, by comparing soft and hard substrate stations with Wilcoxon rank sum tests.

3 | RESULTS

3.1 | Time range of historical baselines

Death assemblages from the different stations had median ages ranging from 24 years (at NG10) to 1,461 years (at SG30, Table 1; see also Albano et al. (2021)). The oldest median ages were observed at soft substrate stations off southern Israel (SG10, SG20, SG30 and SG40), where death assemblages contained at least 53% of pre-Lessepsian (i.e., pre-AD 1869) shells (Table 1). At stations SG20 and SG30, this share was 67 and 93%, respectively, suggesting that these death assemblages constitute good pre-invasion baselines (see also Supporting Information Figure S1.2). In contrast, death assemblages from soft substrates off northern Israel (stations NG10 and NG30), and those collected on hard substrates, were much younger (Supporting Information Figure S1.2), and had decadal-scale median ages (Table 1). Overall, there was a significant correlation between death assemblage median age and the proportion of pre-Lessepsian shells (Spearman's rho = .70, $p = .02$).

3.2 | Trait composition of assemblages

Native and non-indigenous components of present-day (i.e., living) assemblages consistently differed in their multivariate trait composition, forming well-defined clusters in ordination space (FCA: Figure 1; PERMANOVA: all $p < .05$, R^2 range: .32–.89, Table 2). This segregation was independent of occasionally pronounced seasonal variation in trait composition within groups, and mostly occurred along FCA axis 1 (i.e., the axis explaining the greatest amount of variance in the data), except for stations SG40 and Ashqelon −25 m, which separated along axis 2 (Figure 1). At SG40 (Figure 1e), axis 1 corresponded to seasonal differences in present-day assemblage

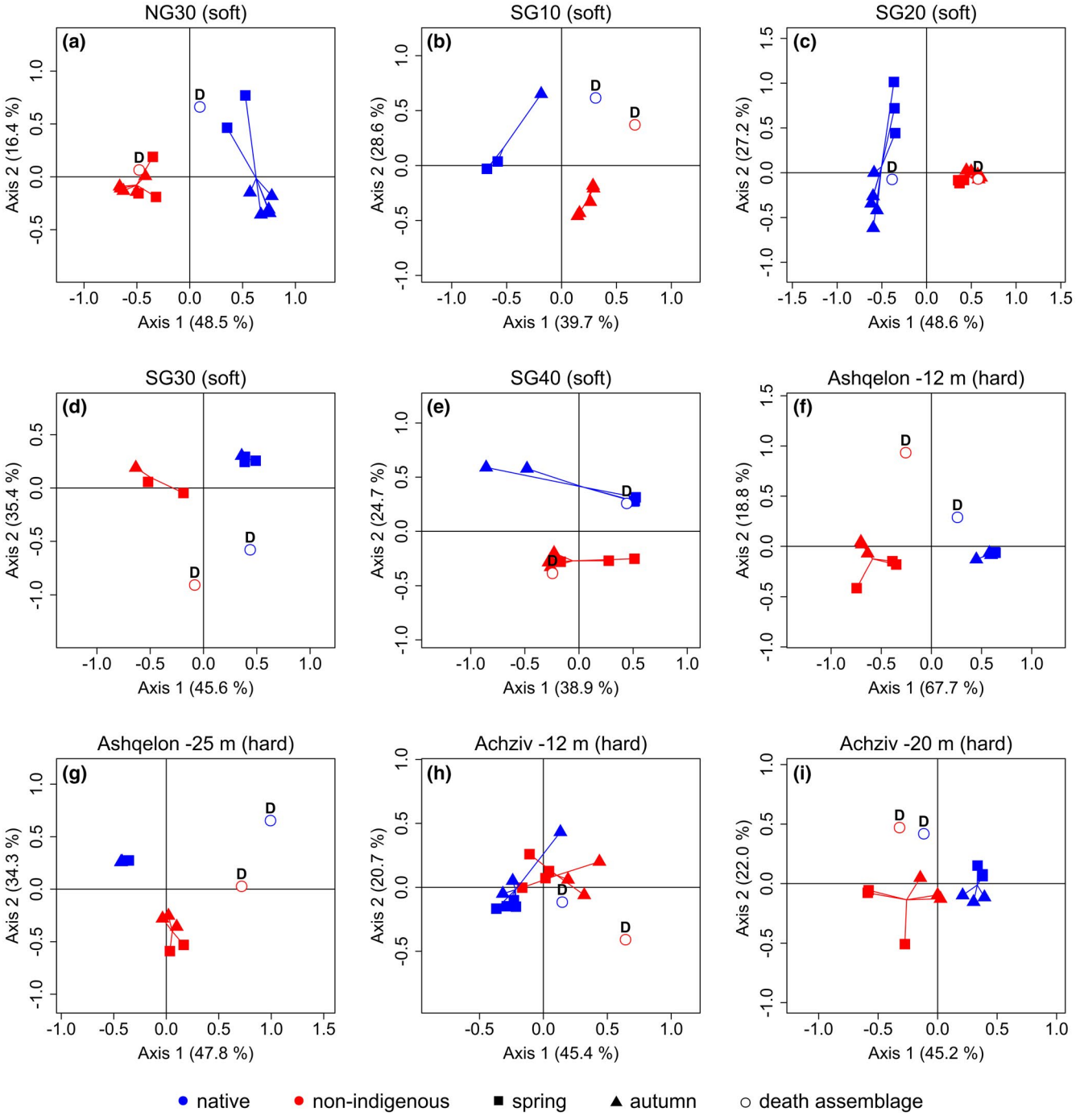

FIGURE 1 Fuzzy correspondence analysis (FCA) ordination plots (first two axes) of present-day and historical trait profiles of native (blue) and non-indigenous (red) molluscan assemblage components from the Israeli Mediterranean shelf. (a) to (e) correspond to soft, (f) to (i) to hard substrate stations. Historical (i.e., death assemblage) trait profiles are indicated by open circles and marked with a 'D' for visibility. Lines connect native and non-indigenous assemblage component profiles to their centroids. Native and non-indigenous components were significantly separated at all stations (permutational multivariate analysis of variance (PERMANOVA) of FCA axis 1–3 scores, all $p < .05$, Table 2)

TABLE 2 Results of permutational multivariate analysis of variance (PERMANOVA) conducted on fuzzy correspondence analysis (FCA) axis 1–3 scores of present-day molluscan assemblage components from the Israeli Mediterranean shelf, using the factor 'native versus non-indigenous'

Station	*n* (native)	*n* (non-indigenous)	R^2	Pseudo-*F*	*p*-value
NG30	7	8	.658	25.000	.0003
SG10	4	5	.745	20.469	.0087
SG20	8	8	.530	15.764	.0002
SG30	4	4	.886	46.790	.0283
SG40	5	7	.316	4.630	.0097
Ashqelon −12 m	6	6	.855	59.054	.0027
Ashqelon −25 m	5	5	.745	23.322	.0081
Achziv −12 m	7	7	.364	6.874	.0022
Achziv −20 m	6	6	.577	13.642	.0029

Note: *n*, number of replicates.

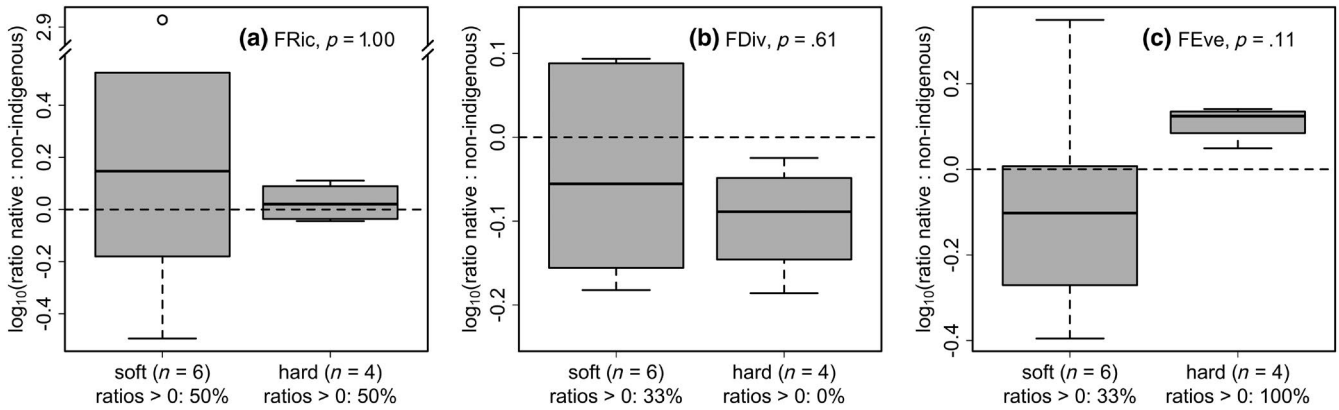

FIGURE 2 Functional diversity index ratios (native versus non-indigenous components, $\log_{10}$-scale) for present-day molluscan assemblages from soft and hard substrates on the Israeli Mediterranean shelf. The percentage of ratios > 0 (i.e., greater index values of the native component) is provided below each boxplot. Neither assemblage component consistently had a greater functional richness (FRic, panel a), whereas native components on hard substrates always had a lower functional divergence (FDiv, panel b, all ratios < 0), but greater functional evenness (FEve, panel c, all ratios > 0) than their non-indigenous counterparts. For all indices, absolute values of index ratios did not differ significantly between soft and hard substrates (Wilcoxon tests, $W \leq 15$, *p*-values as indicated on panels). Note the discontinuous *y* axis in (a); the dashed line marks index value equality of assemblage components

trait composition, whereas at Ashqelon −25 m (Figure 1g), this axis reflected differences between corresponding present-day and historical (i.e., death) assemblage components.

Similar to present-day assemblages, a strong trait segregation was apparent between native and non-indigenous components of almost all historical assemblages (Figure 1; PERMANOVA: all $p = 10^{-4}$, R^2 range: .97–1.00, Supporting Information Table S1.6), irrespective of the amount of time that they captured (correlation analysis between the proportion of variance explained by the factor 'native versus non-indigenous' (PERMANOVA R^2) and death assemblage median age: Spearman's rho = .35, $p = .35$). In contrast to the clear native versus non-indigenous separation, corresponding present-day and historical assemblage components often functionally overlapped or were separated along a direction roughly perpendicular to the segregation of present-day native and non-indigenous assemblage components (Figure 1).

Traits that repeatedly had the highest correlation ratio for axis 1 were 'maximum adult body size' (SI; 56% of the nine stations) and 'environmental position' (EP; 22% of stations), whereas 'feeding habit' (FH) had the second highest correlation ratio in 89% of stations (Supporting Information Table S1.7). Considering axis 2, 'maximum adult body size' and 'feeding habit' had the highest correlation ratio in 56 and 33% of stations, respectively (Supporting Information Table S1.7). A comparison of the trait modality distribution between present-day native and non-indigenous assemblage components revealed significant differences for all five traits (PERMANOVA, all $p <$ .001, R^2 range: .03–.26, Supporting Information Table S1.8), but complex station-specific patterns (Supporting Information Figures S1.3–S1.7). However, non-indigenous components from most stations had a greater proportion of both very small (size classes > 1 to 2 mm and > 2 to 4 mm) and rather large-sized taxa (> 32 to 64 mm) compared to their native counterparts, whereas among the latter, medium-sized taxa (> 8 to 16 mm, and to a lesser extent > 16 to 32 mm) were usually better represented than in non-indigenous components (Supporting Information Figure S1.3). Additionally, non-indigenous components

were often characterized by a greater prevalence of surface deposit feeders and, particularly on hard substrates, fewer suspension feeders (Supporting Information Figure S1.4). Non-indigenous components from hard substrates were further richer in browsing carnivores/ectoparasites and had a higher prevalence of host-associated taxa. On soft substrates, non-indigenous components had a greater share of epifaunal but fewer host-associated taxa than native components (Supporting Information Figures S1.5 and S1.7, respectively). Trait modalities exclusively present in native assemblage components were the feeding types 'subsurface deposit feeder' and 'scavenger', but they were extremely rare (Supporting Information Figure S1.4). Similarly, chemosymbiotic molluscs were mostly restricted to native assemblage components, and usually found in very low proportions.

3.3 | Native versus non-indigenous functional diversity

Log-ratios of functional richness for native versus non-indigenous components of present-day soft substrate assemblages ranged from −0.50 to 2.93 (median: 0.15; Figure 2a; see Supporting Information Table S1.9 for index values). These ratios were less variable in hard substrates, ranging from −0.04 to 0.11 (median: 0.02). Neither assemblage component consistently had a greater functional richness (Figure 2a: 50% of ratios > 0 for both habitats; Wilcoxon signed rank test for soft substrate stations: $V = 12$, $p = .84$). Considering stations with a greater functional richness of the native component (i.e., ratios > 0), greater ratio values were observed in soft than hard substrate assemblages, despite a similar species richness of corresponding native and non-indigenous components of the former (Supporting Information Table S1.9). Native components of hard substrate assemblages always had a lower functional divergence than corresponding non-indigenous components (ratio range: −0.19 to −0.02, median: −0.09), that is, a smaller proportion of native abundance was contributed by species with extreme trait values. In contrast, no differences were found for soft substrate assemblages (ratio range: −0.18 to 0.09, median: −0.06; signed rank test, $V = 7$, $p = .56$; Figure 2b), similar to functional richness. Native components had a greater functional evenness in all studied hard substrate assemblages (ratio range: 0.05 to 0.14, median: 0.12; Figure 2c), suggesting a more even distribution of taxa and their abundances in assemblage trait space. Again, no differences were found for soft substrate assemblages (range of ratios: −0.40 to 0.35, median: −0.10; signed rank test, $V = 6$, $p = .44$; Figure 2c). Absolute values of log-ratios did not differ between soft and hard substrates for any of the three alpha-diversity indices (Wilcoxon rank sum test, W range: 4–15, all $p > .05$; Figure 2).

Mean (± *SD*) functional beta diversity of corresponding native versus non-indigenous assemblage components was .75 (± .22), with assemblage components from soft substrate stations (.92 ± .10) having significantly greater index values than those from hard substrates (.51 ± .03; Wilcoxon rank sum test, $W = 24$, $p = .01$; Figure 3a, Supporting Information Table S1.9). Considering all stations, on average 90% of functional beta diversity was contributed by the turnover component (soft substrates: 91%, rocky substrates: 89%; Figure 3b, Supporting Information Table S1.9), suggesting that even when species' relative abundances are factored out, present-day native and non-indigenous assemblage components occupy largely distinct portions of trait space. In contrast, the nestedness-resultant component was small (.07 ± .07) and did not significantly differ between soft and hard substrates (.08 ± .09 versus .06 ± .03, respectively; rank sum test, $W = 11$, $p = .91$; Figure 3c, Supporting Information Table S1.9).

4 | DISCUSSION

4.1 | Interpreting present-day trait patterns with a historical perspective

Native and non-indigenous trait profiles were consistently segregated in the ordinations, indicating that abundant NIS have traits

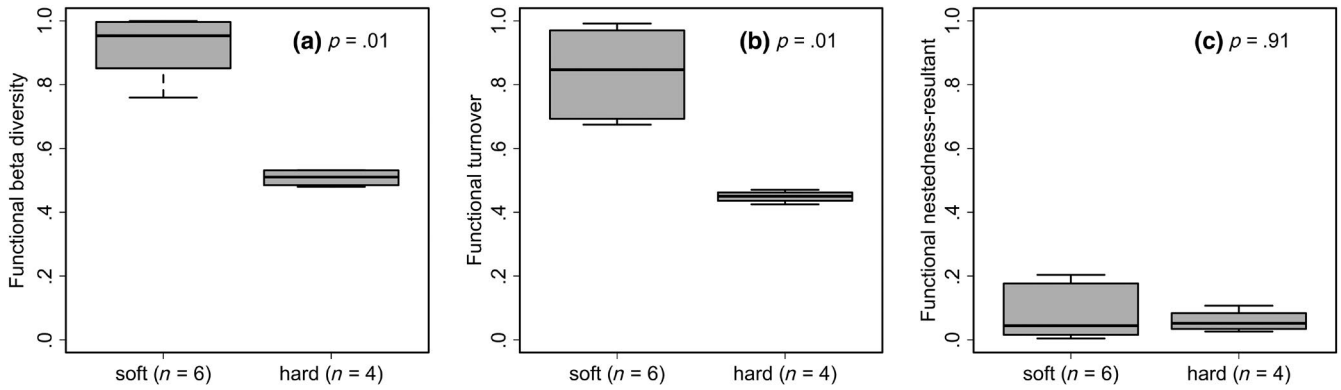

FIGURE 3 Functional beta diversity of native versus non-indigenous components of present-day molluscan assemblages from the Israeli Mediterranean shelf (a), and its decomposition into turnover (b) and nestedness-resultant (c) components. In both substrate types, beta diversity was mainly related to functional turnover. Soft substrate assemblages had significantly greater index values for total beta diversity and functional turnover than those from hard substrates (Wilcoxon tests, both $W = 24$, $p = .01$), whereas no such difference was found for the nestedness-resultant component ($W = 11$, $p = .91$)

dissimilar from dominant native taxa. This result applies not only to present-day assemblages, but also to historical (i.e., death) ones, suggesting that Lessepsian invaders have occupied 'empty' niches since the onset of the invasion. Indeed, if the present-day pattern were the outcome of functional segregation over time, then we should have observed overlap between non-indigenous assemblage components and native death assemblages. This, however, was not the case: at almost all stations, historical trait profiles either overlapped with their corresponding present-day ones (Figure 1a,c and e), or showed an offset along roughly the same direction (Figure 1b,d,f and g). This offset therefore reflects factors similarly affecting the trait composition of native and non-indigenous assemblage components, such as taphonomic bias (e.g., the selective loss of fragile shells or shell transport away from/into the sampling site), recent changes in local environmental conditions that modified both assemblage components, or a combination of both (Kidwell, 2013). In contrast, the accumulation of rare species, typical of time-averaged death assemblages (Kidwell, 2013), is unlikely to notably decrease functional live-dead fidelity as (a) abundance-weighting emphasizes the traits of dominant species, reducing the influence of rare taxa, even if they had distinct functional properties; (b) the number of scored trait modalities is limited (23 in this study) and therefore less sensitive to the effects of time-averaging than taxonomic richness; and (c) the offset occurs in both highly (e.g., station SG30) and minimally time-averaged (e.g., hard substrate stations) death assemblages (Supporting Information Figure S1.2). This reasoning is supported by findings of high fidelity in feeding guild structure even for death assemblages whose taxonomic richness was greatly inflated compared to corresponding living assemblages (García-Ramos et al., 2016).

Importantly, the clear separation of native and non-indigenous trait profiles not only occurred across sampling sites with very different habitat conditions, but was also independent of the age of local death assemblages: for example, the ordination pattern obtained for station SG30 (Figure 1d), where the death assemblage was almost entirely (93%) pre-Lessepsian – and thus constitutes an ideal baseline (Table 1, Supporting Information Figure S1.2) – mirrored those for most hard substrate sites (e.g., Figure 1f,g and i) whose death assemblages generally encompassed only the last few decades. Notwithstanding their young age, such death assemblages still retain a very strong signature of diverse native assemblages because they mostly pre-date the collapse of native species and the onset of the massive increase in NIS prevalence that took place only during the most recent decades (Albano et al., 2021; Edelist et al., 2012; Galil et al., 2021; Rilov, 2016). Thus, by adopting an extended temporal perspective utilizing death assemblages, we demonstrated that the Lessepsian invasion has followed a pattern consistent with concepts like limiting similarity (MacArthur & Levins, 1967), Darwin's naturalization hypothesis (Darwin, 1859), or the 'empty niche' hypothesis (Hierro et al., 2005; see Catford et al., 2009 for a review), and that present-day trait differences indeed do not represent 'shifted baselines' (Pauly, 1995).

4.2 | The role of NIS in the collapse of native species

The consistent differences in trait composition, particularly the lack of overlap between non-indigenous trait profiles and historical native ones, suggest that native assemblages on the shallow Israeli Mediterranean shelf have not been functionally displaced by NIS. Our findings for molluscs corroborate studies on modern fish assemblages that found a low potential for direct competition between native and non-indigenous species in the Eastern Mediterranean Sea (Arndt et al., 2018; Buba & Belmaker, 2019; Givan et al., 2018). We here extend observations to another ecologically important phylum, a diverse range of shallow subtidal soft and hard substrates and, most importantly, across a long temporal perspective. Although none of the above-mentioned fish studies had data on native assemblages before the onset of the Lessepsian invasion, they analysed temporal trends using trawl datasets from two distinct time periods (1990–1994 versus 2008–2011) that saw a major turnover in the local fish communities: a marked increase in both the number and relative abundance of non-indigenous fishes, and a strong decline of several native species (Edelist et al., 2012). Together, fishes and molluscs account for 54% of the 452 multi-cellular NIS recorded in Israel to date (Galil et al., 2021), suggesting that these findings might be of general validity, although a broader coverage of Lessepsian phyla is required to draw final conclusions.

We emphasize that our assemblage-scale results must not be interpreted as dismissing the potential for significant negative interactions. For example, NIS can affect native assemblages through various direct and indirect interactions other than competition, such as predation (e.g., Green et al., 2012) or habitat modification by ecosystem engineers (e.g., Crooks, 2002). Nevertheless, it seems improbable that these factors can explain the massive (88–95% in the shallow subtidal) loss of native molluscan diversity observed at all stations covered by this study (see Albano et al., 2021). While non-indigenous predators can severely decimate vulnerable native species (e.g., Chiba & Sato, 2013; Hadfield et al., 1993), it is unlikely that they could drive to (near) extirpation most representatives of a taxonomically, ecologically and morphologically highly diversified group such as Mediterranean molluscs, in both soft and hard substrates. For example, the formerly abundant large-sized shallow-water predatory whelk *Stramonita haemastoma* (Linnaeus, 1767) has undergone a major collapse along the Israeli shore in recent decades despite the absence of known non-indigenous predators or potential competitors (Rilov, 2016). This is surprising, considering that this species was shown to prefer the abundant Lessepsian mussel *Brachidontes pharaonis* (P. Fischer, 1870) as prey over smaller native mussels and barnacles, and therefore should even have energetically benefited from the invasion (Rilov, 2016; Rilov et al., 2002). Similar to non-indigenous predators, NIS known to be ecosystem engineers, such as the Indo-Pacific rabbitfishes *Siganus rivulatus* Forsskål & Niebuhr, 1775 and *Siganus luridus* (Rüppell, 1829) (Vergés et al., 2014; Yeruham et al., 2020), the shrub-like macroalga *Galaxaura rugosa* (J. Ellis & Solander) J. V. Lamouroux, 1816 (Peleg et al., 2020), and the bivalves *Chama pacifica* Broderip, 1835 and *B. pharaonis* (Nawrot

et al., 2015) are restricted to particular habitat types and depth intervals, whereas native biodiversity loss invariably occurred across all studied habitats (Albano et al., 2021). Furthermore, several native components of soft-bottom molluscan assemblages apparently have not changed functionally over time (Figure 1a,c and e) as would have been expected under modified local habitat conditions (see e.g., Kidwell, 2009). Together, these findings imply that regional-scale changes in abiotic conditions that broadly affect species across stations, such as warming seawater temperatures (Ozer et al., 2017), likely play a major role as driver of the massive native biodiversity loss in shallow subtidal habitats along the Israeli coast (see Albano et al., 2021; Givan et al., 2018; Rilov, 2016). Warming acts on such a broad spatial scale that as conditions become unsuitable for many native species, those with more restricted ranges may eventually go globally extinct as a small geographical range is among the best predictors of extinction risk (Chichorro et al., 2019).

4.3 | A 'novel ecosystem' in the Eastern Mediterranean

Given the distinct trait profiles of native and non-indigenous assemblage components, the faunal transition towards increasingly NIS-dominated systems (e.g., Rilov, 2016; Rilov et al., 2018) has considerably altered key functional properties of shallow-water molluscan assemblages on the Israeli Mediterranean shelf, which today has all the characteristics of a 'novel ecosystem' (sensu Hobbs et al., 2013a). Such ecosystems emerge through direct or indirect human agency that has resulted in an irreversible departure from historical baseline conditions (e.g., due to alterations related to climate warming and biological invasions); in addition, they are characterized by novel combinations of species and/or functional properties, with ramifications for important ecosystem processes (Hobbs et al., 2013b).

Our results therefore suggest that non-indigenous assemblage components cannot maintain or restore the functions lost due to the massive regional collapse of native populations (e.g., Albano et al., 2021; Rilov, 2016), despite their often considerable functional richness, which was on par with that of their native counterparts in all hard substrate assemblages, and even exceeded it at 50% of the soft substrate stations. This interpretation was further supported by the analysis of native versus non-indigenous functional beta diversity: at all stations, beta diversity was high (mean value: .75) and mainly related to functional turnover, which – on average – contributed 90% to the Jaccard-like dissimilarity index. In addition to these general patterns, native versus non-indigenous trait space occupation also showed habitat-specific differences: on hard substrates, non-indigenous molluscs always had a greater functional divergence (log-index ratios < 0) and lower functional evenness (log-ratios > 0). This may indicate a greater degree of niche differentiation and a patchier distribution of species and abundances in trait space, respectively (Mouchet et al., 2010; Mouillot et al., 2013; Villéger et al., 2008). On the other hand, functional turnover, and hence overall beta diversity, was significantly greater in soft versus hard substrates. Our results for molluscs thus corroborate recent evidence for functional differences between dwindling native brown algal forests and non-indigenous red algal assemblages on infralittoral reefs off Israel, the latter being characterized by an inverted (heterotrophic) net carbon balance and lower habitat-provisioning capacity, in terms of biomass, for macrozoobenthic assemblages (Peleg et al., 2020).

Our ordinations identified 'maximum adult body size', 'feeding habit' and 'environmental position' as important traits distinguishing native and non-indigenous assemblage components; similar results were obtained by PERMANOVA analyses of single-trait modality composition: the amount of variance explained by the factor 'native versus non-indigenous' was greatest for 'body size' ($R^2 = .26$), followed by 'feeding habit', 'host association' and 'environmental position' ($R^2 = .07$ to $.08$), and least for 'substrate affinity' ($R^2 = .03$), though all comparisons were statistically significant. Body size is a synthetic trait related to species' metabolic rates, life history characteristics and trophic interactions, thereby influencing multiple aspects of ecosystem functioning (Woodward et al., 2005; Yvon-Durocher & Allen, 2012). Across different soft and hard substrate types, non-indigenous components were characterized by an often greater proportion of both very small and rather large individuals compared to their native counterparts, whereas intermediate size classes were better represented among native components. The greater share of small size classes in non-indigenous assemblage components matches the finding that climate warming favours small individuals and species, potentially due to physiological advantages of small body size at warm temperatures (Daufresne et al., 2009; Lurgi et al., 2012). However, massive biological invasions can also modify such selection-driven size trends if NIS are sourced from species pools with a greater median body size, as recently demonstrated for Lessepsian bivalves (Nawrot et al., 2017); this likely contributes to the observed greater share also of large-sized species among non-indigenous components.

Lessepsian molluscs also directly affect trophic networks in the Eastern Mediterranean by modifying feeding guild composition. Non-indigenous assemblage components across subtidal habitats were often characterized by a greater share of surface deposit feeders, whereas suspension feeders were better represented among native components from hard substrates. The relative abundance of these functional groups can have important implications for pelagic–benthic coupling, sediment stability and biogeochemical fluxes at the sediment–water interface (Griffiths et al., 2017; Rhoads & Young, 1970; Snelgrove, 1997). Among higher-order consumers, a greater proportion of ectoparasites/browsing carnivores (and consequently host-associated individuals) was found among non-indigenous molluscan components from hard substrates. A surprisingly large number of parasitic gastropods, particularly of the family Pyramidellidae, has been introduced to the Mediterranean Sea (Oliverio & Taviani, 2003), but hardly anything is known about their hosts. While parasites may be co-introduced with their original

hosts (Boussellaa et al., 2018; Galil, 2007), it has been observed that Indo-Pacific pyramidellids also feed on native Mediterranean molluscs (so-called 'parasite spillover'; Oliverio, 1994), with unknown implications for the population dynamics of these new hosts. Last but not least, we found a greater importance of epifaunal lifestyle for non-indigenous assemblage components in most soft-bottom habitats, suggesting potential implications for the vulnerability to predation, sediment oxygenation and biogeochemical processes, for example via changing rates of bioturbation (de Moura Queirós et al., 2011; Kristensen et al., 2012; Vermeij, 1987).

With ongoing warming, thermophilic NIS will clearly be the winners in the future Eastern Mediterranean (Givan et al., 2018), likely further increasing the functional deviation of shallow water assemblages from their historical baselines. The interplay of massively declining native biota, booming non-indigenous populations and constant novel introductions through the Suez Canal suggests that the composition of local benthic assemblages will likely continue to evolve rapidly, with potentially profound but little understood consequences for ecosystem services.

ACKNOWLEDGMENTS

This research was conducted in the framework of the project 'Historical ecology of Lessepsian migration' funded by the Austrian Science Fund (FWF) P28983-B29 (PI: P.G.A.). M.B. was supported by an Ernst Mach fellowship of the OeAD (Österreichischer Austauschdienst). We are indebted to the captain and crew of R/V 'Mediterranean Explorer' (EcoOcean), Shahar Malamud, Angelina Ivkić, Martina Stockinger, Justina Givens, Karolina Czechowska, Ivo Gallmetzer and Patrick Bukenberger for help in the field. Beata Dunne, Verena Gareis, Alexander Heidenbauer, Anna Hinterplattner, Nadja Loferer and Denny Morchner helped with sorting the samples in the lab. Sample preparation for radiocarbon dating was conducted by Darrell Kaufman's team at Northern Arizona University and sample analysis at the University of California at Irvine Keck AMS Lab. Quan Hua helped with the calibration of radiocarbon ages. We further acknowledge Sébastien Villéger, Stéphane Dray, Sandrine Pavoine, Aurélie Siberchicot, Johann Hohenegger, Michał Kowalewski, Renate Degen, Rafał Nawrot, Stefan Dullinger and Barbara Mähnert for helpful discussions, and Michael Stachowitsch for proofreading. P. Graham Oliver and Henk Mienis provided access to molluscan literature. The Israel Nature and Parks Authority kindly granted permit 41928 for field sampling.

AUTHOR CONTRIBUTIONS

J.S. and P.G.A. conceptualized the study. J.S., P.G.A., M.Z., M.B. and B.S.G. contributed to fieldwork and/or data acquisition. J.S. conceived and performed the statistical analyses with input from J.B. and P.G.A. J.S. and P.G.A. wrote the initial draft. All authors contributed to the interpretation of the results and manuscript writing.

DATA AVAILABILITY STATEMENT

Raw data and R scripts are available from the figshare repository: https://doi.org/10.6084/m9.figshare.c.5574813.

ORCID

Jan Steger https://orcid.org/0000-0001-7021-810X
Marija Bošnjak https://orcid.org/0000-0002-1851-1031
Jonathan Belmaker https://orcid.org/0000-0002-5618-7359
Bella S. Galil https://orcid.org/0000-0002-9268-7211
Martin Zuschin https://orcid.org/0000-0002-5235-0198
Paolo G. Albano https://orcid.org/0000-0001-9876-1024

REFERENCES

Albano, P. G., Steger, J., Bošnjak, M., Dunne, B., Guifarro, Z., Turapova, E., Hua, Q., Kaufman, D. S., Rilov, G., & Zuschin, M. (2021). Native biodiversity collapse in the Eastern Mediterranean. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20202469. https://doi.org/10.1098/rspb.2020.2469

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

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*(2), 19. https://doi.org/10.3390/fishes3020019

Azzurro, E., Tuset, V. M., Lombarte, A., Maynou, F., Simberloff, D., Rodríguez-Pérez, A., & Solé, R. V. (2014). External morphology explains the success of biological invasions. *Ecology Letters*, *17*(11), 1455–1463. https://doi.org/10.1111/ele.12351

Boussellaa, W., Neifar, L., Goedknegt, M. A., & Thieltges, D. W. (2018). Lessepsian migration and parasitism: Richness, prevalence and intensity of parasites in the invasive fish *Sphyraena chrysotaenia* compared to its native congener *Sphyraena sphyraena* in Tunisian coastal waters. *PeerJ*, *6*, e5558. https://doi.org/10.7717/peerj.5558

Bright, J., Ebert, C., Kosnik, M. A., Southon, J. R., Whitacre, K., Albano, P. G., Flores, C., Frazer, T. K., Hua, Q., Kowalewski, M., & Martinelli, J. C. (2021). Comparing direct carbonate and standard graphite ^{14}C determinations of biogenic carbonates. *Radiocarbon*, *63*(2), 387–403. https://doi.org/10.1017/RDC.2020.131

Buba, Y., & Belmaker, J. (2019). Native-exotic diversity relationships for Eastern Mediterranean fishes reveal a weak pattern of interactions. *Marine Ecology Progress Series*, *611*, 215–220. https://doi.org/10.3354/meps12871

Buba, Y., van Rijn, I., Blowes, S. A., Sonin, O., Edelist, D., DeLong, J. P., & Belmaker, J. (2017). Remarkable size-spectra stability in a marine system undergoing massive invasion. *Biology Letters*, *13*(7), 20170159. https://doi.org/10.1098/rsbl.2017.0159

Bush, S. L., Santos, G. M., Xu, X., Southon, J. R., Thiagarajan, N., Hines, S. K., & Adkins, J. F. (2013). Simple, rapid, and cost effective: A screening method for ^{14}C analysis of small carbonate samples. *Radiocarbon*, *55*(2–3), 631–640. https://doi.org/10.1017/s0033822200057787

Byers, J. E. (2000). Competition between two estuarine snails: Implications for invasions of exotic species. *Ecology*, *81*(5), 1225–1239.

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Chevenet, F., Dolédec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, *31*, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Chiba, T., & Sato, S. (2013). Invasion of *Laguncula pulchella* (Gastropoda: Naticidae) and predator–prey interactions with bivalves on the Tona coast, Miyagi prefecture, northern Japan. *Biological Invasions*, *15*(3), 587–598. https://doi.org/10.1007/s10530-012-0310-1

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229. https://doi.org/10.1016/j.biocon.2019.07.001

Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos*, *97*(2), 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Darwin, C. (1859). *On the origin of species*. John Murray.

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences USA*, *106*(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106

de Moura Queirós, A., Hiddink, J. G., Johnson, G., Cabral, H. N., & Kaiser, M. J. (2011). Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions*, *13*(5), 1059–1075. https://doi.org/10.1007/s10530-011-9948-3

Degen, R., Aune, M., Bluhm, B. A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczuk, M., Zhulay, I., Albano, P. G., Bremner, J., Grebmeier, J. M., Link, H., Morata, N., Nordström, M. C., Shojaei, M. G., Sutton, L., & Zuschin, M. (2018). Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. *Ecological Indicators*, *91*, 722–736. https://doi.org/10.1016/j.ecolind.2018.04.050

Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G., & Duncan, R. P. (2008). Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecology Letters*, *11*(7), 674–681. https://doi.org/10.1111/j.1461-0248.2008.01178.x

Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N. J., Lososová, Z., Pyšek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nature Communications*, *9*(1), 4631. https://doi.org/10.1038/s41467-018-06995-4

Dray, S., & Dufour, A.-B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*(4), 1–20. https://doi.org/10.18637/jss.v022.i04

Edelist, D., Rilov, G., Golani, D., Carlton, J. T., & Spanier, E. (2012). Restructuring the sea: Profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions*, *19*(1), 69–77. https://doi.org/10.1111/ddi.12002

Engelhardt, K., Symstad, A., Prieur-Richard, A.-H., Thomas, M., & Bunker, D. E. (2009). Opening communities to colonization - the impacts of invaders on biodiversity and ecosystem functioning. In S. Naeem, D. E. Bunker, A. Hector, M. Loreau, & C. Perrings (Eds.), *Biodiversity, ecosystem functioning, and human wellbeing: An ecological and economic perspective* (pp. 217–229). Oxford University Press.

Galil, B. S. (2007). Seeing Red: Alien species along the Mediterranean coast of Israel. *Aquatic Invasions*, *2*(4), 281–312. https://doi.org/10.3391/ai.2007.2.4.2

Galil, B. S., Mienis, H. K., Hoffman, R., & Goren, M. (2021). Non-indigenous species along the Israeli Mediterranean coast: Tally, policy, outlook. *Hydrobiologia*, *848*, 2011–2029. https://doi.org/10.1007/s10750-020-04420-w

Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, *40*(2), 335–352. https://doi.org/10.1111/ecog.02446

García-Ramos, D. A., Albano, P. G., Harzhauser, M., Piller, W. E., & Zuschin, M. (2016). High dead-live mismatch in richness of molluscan assemblages from carbonate tidal flats in the Persian (Arabian) Gulf. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *457*, 98–108. https://doi.org/10.1016/j.palaeo.2016.06.006

Gaston, K. J., Cox, D. T. C., Canavelli, S. B., García, D., Hughes, B., Maas, B., Martínez, D., Ogada, D., & Inger, R. (2018). Population abundance and ecosystem service provision: The case of birds. *BioScience*, *68*(4), 264–272. https://doi.org/10.1093/biosci/biy005

Givan, O., Edelist, D., Sonin, O., & Belmaker, J. (2018). Thermal affinity as the dominant factor changing Mediterranean fish abundances. *Global Change Biology*, *24*(1), e80–e89. https://doi.org/10.1111/gcb.13835

Givan, O., Parravicini, V., Kulbicki, M., & Belmaker, J. (2017). Trait structure reveals the processes underlying fish establishment in the Mediterranean. *Global Ecology and Biogeography*, *26*(2), 142–153. https://doi.org/10.1111/geb.12523

Green, S. J., Akins, J. L., Maljković, A., & Côté, I. M. (2012). Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE*, *7*(3), e32596. https://doi.org/10.1371/journal.pone.0032596

Griffiths, J. R., Kadin, M., Nascimento, F. J. A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M. C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., & Winder, M. (2017). The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*, *23*(6), 2179–2196. https://doi.org/10.1111/gcb.13642

Hadfield, M. G., Miller, S. E., & Carwile, A. H. (1993). The decimation of endemic Hawai'ian tree snails by alien predators. *American Zoologist*, *33*(6), 610–622. https://doi.org/10.1093/icb/33.6.610

Hierro, J. L., Maron, J. L., & Callaway, R. M. (2005). A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology*, *93*(1), 5–15. https://doi.org/10.1111/j.0022-0477.2004.00953.x

Hobbs, R. J., Higgs, E. S., & Hall, C. M. (2013a). Defining novel ecosystems. In R. J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel ecosystems: Intervening in the new ecological world order* (pp. 58–60). Wiley-Blackwell.

Hobbs, R. J., Higgs, E. S., & Hall, C. M. (2013b). *Novel ecosystems: Intervening in the new ecological world order*. Wiley-Blackwell.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Kidwell, S. M. (2009). Evaluating human modification of shallow marine ecosystems: Mismatch in composition of molluscan living and time-averaged death assemblages. In G. P. Dietl & K. W. Flessa (Eds.), *Conservation paleobiology: Using the past to manage for the future*. The Paleontological Society Papers (Vol. *15*., pp. 113–139). The Paleontological Society.

Kidwell, S. M. (2013). Time-averaging and fidelity of modern death assemblages: Building a taphonomic foundation for conservation palaeobiology. *Palaeontology*, *56*(3), 487–522. https://doi.org/10.1111/pala.12042

Kidwell, S. M., & Tomasovych, A. (2013). Implications of time-averaged death assemblages for ecology and conservation biology. *Annual Review of Ecology, Evolution and Systematics*, *44*, 539–563. https://doi.org/10.1146/annurev-ecolsys-110512-135838

Kowalewski, M., Carroll, M., Casazza, L., Gupta, N. S., Hannisdal, B., Hendy, A., Krause, R. A. Jr., LaBarbera, M., Lazo, D. G., Messina, C., Puchalski, S., Rothfus, T. A., Sälgeback, J., Stempien, J., Terry, R. C., & Tomašových, A. (2003). Quantitative fidelity of brachiopod-mollusk assemblages from modern subtidal environments of San Juan Islands, USA. *Journal of Taphonomy*, *1*(1), 43–66.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., & Banta, G. T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, *446*, 285–302. https://doi.org/10.3354/meps09506

Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd ed.). Elsevier.

Lurgi, M., López, B. C., & Montoya, J. M. (2012). Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2913–2922. https://doi.org/10.1098/rstb.2012.0238

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*(921), 377–385. https://doi.org/10.1086/282505

Maire, E., Grenouillet, G., Brosse, S., & Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography*, *24*(6), 728–740. https://doi.org/10.1111/geb.12299

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Miller, J. H., Behrensmeyer, A. K., Du, A., Lyons, S. K., Patterson, D., Tóth, A., Villaseñor, A., Kanga, E., & Reed, D. (2014). Ecological fidelity of functional traits based on species presence-absence in a modern mammalian bone assemblage (Amboseli, Kenya). *Paleobiology*, *40*(4), 560–583. https://doi.org/10.1666/13062

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Nawrot, R., Albano, P. G., Chattopadhyay, D., & Zuschin, M. (2017). Climate change and body size shift in Mediterranean bivalve assemblages: unexpected role of biological invasions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1860), 20170357. https://doi.org/10.1098/rspb.2017.0357

Nawrot, R., Chattopadhyay, D., & Zuschin, M. (2015). What guides invasion success? Ecological correlates of arrival, establishment and spread of Red Sea bivalves in the Mediterranean Sea. *Diversity and Distributions*, *21*(9), 1075–1086. https://doi.org/10.1111/ddi.12348

Ojaveer, H., Galil, B. S., Carlton, J. T., Alleway, H., Goulletquer, P., Lehtiniemi, M., Marchini, A., Miller, W., Occhipinti-Ambrogi, A., Peharda, M., Ruiz, G. M., Williams, S. L., & Zaiko, A. (2018). Historical baselines in marine bioinvasions: Implications for policy and management. *PLoS ONE*, *13*(8), e0202383. https://doi.org/10.1371/journal.pone.0202383

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community ecology package*. R package version 2.5-4. https://CRAN.R-project.org/package=vegan

Oliverio, M. (1994). On the record of a living Lessepsian pyramidellid from Turkey (Heterobranchia, Heterostropha). *Notiziario del Centro Italiano di Studi Malacologici (C.I.S.MA.)*, *15*, 79–82.

Oliverio, M., & Taviani, M. (2003). The Eastern Mediterranean Sea: Tropical invasions and niche opportunities in a "Godot Basin". *Biogeographia*, *24*, 313–318. https://doi.org/10.21426/B6110004

Oug, E., Fleddum, A., Rygg, B., & Olsgard, F. (2012). Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. *Journal of Experimental Marine Biology and Ecology*, *432–433*, 94–105. https://doi.org/10.1016/j.jembe.2012.07.019

Ozer, T., Gertman, I., Kress, N., Silverman, J., & Herut, B. (2017). Interannual thermohaline (1979–2014) and nutrient (2002–2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. *Global and Planetary Change*, *151*, 60–67. https://doi.org/10.1016/j.gloplacha.2016.04.001

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, *10*(10), 430. https://doi.org/10.1016/S0169-5347(00)89171-5

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, *118*(3), 391–402. https://doi.org/10.1111/j.1600-0706.2008.16668.x

Pearson, D. E., Ortega, Y. K., & Sears, S. J. (2012). Darwin's naturalization hypothesis up-close: Intermountain grassland invaders differ morphologically and phenologically from native community dominants. *Biological Invasions*, *14*(4), 901–913. https://doi.org/10.1007/s10530-011-0126-4

Peleg, O., Guy-Haim, T., Yeruham, E., Silverman, J., & Rilov, G. (2020). Tropicalization may invert trophic state and carbon budget of shallow temperate rocky reefs. *Journal of Ecology*, *108*(3), 844–854. https://doi.org/10.1111/1365-2745.13329

Por, F. D. (1978). *Lessepsian migration - the influx of Red Sea biota into the Mediterranean by way of the Suez Canal*. Springer.

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rhoads, D. C., & Young, D. K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research*, *28*(2), 150–178.

Rilov, G. (2016). Multi-species collapses at the warm edge of a warming sea. *Scientific Reports*, *6*, 36897. https://doi.org/10.1038/srep36897

Rilov, G., & Galil, B. (2009). Marine bioinvasions in the Mediterranean Sea – history, distribution and ecology. In G. Rilov & J. A. Crooks (Eds.), *Biological invasions in marine ecosystems: Ecological, management, and geographic perspectives* (pp. 549–575). Springer.

Rilov, G., Gasith, A., & Benayahu, Y. (2002). Effect of an exotic prey on the feeding pattern of a predatory snail. *Marine Environmental Research*, *54*(1), 85–98. https://doi.org/10.1016/S0141-1136(02)00096-X

Rilov, G., Peleg, O., Yeruham, E., Garval, T., Vichik, A., & Raveh, O. (2018). Alien turf: Overfishing, overgrazing and invader domination in south-eastern Levant reef ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(2), 351–369. https://doi.org/10.1002/aqc.2862

Safriel, U. N., & Sasson-Frostig, Z. (1988). Can colonizing mussel outcompete indigenous mussel? *Journal of Experimental Marine Biology and Ecology*, *117*, 211–226. https://doi.org/10.1016/0022-0981(88)90058-5

Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., & Savolainen, V. (2011). Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters*, *14*(4), 389–396. https://doi.org/10.1111/j.1461-0248.2011.01600.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, *17*(4), 170–176. https://doi.org/10.1016/s0169-5347(02)02495-3

Snelgrove, P. V. R. (1997). The importance of marine sediment biodiversity in ecosystem processes. *Ambio*, *26*(8), 578–583.

Steger, J., Dunne, B., Zuschin, M., & Albano, P. G. (2021). Bad neighbors? Niche overlap and asymmetric competition between native and Lessepsian limpets in the Eastern Mediterranean rocky intertidal. *Marine Pollution Bulletin*, *171*, 112703. https://doi.org/10.1016/j.marpolbul.2021.112703

Strayer, D. L. (2012). Eight questions about invasions and ecosystem functioning. *Ecology Letters*, *15*(10), 1199–1210. https://doi.org/10.1111/j.1461-0248.2012.01817.x

Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization

conundrum: A quest for evidence. *Diversity and Distributions*, *16*(3), 461–475. https://doi.org/10.1111/j.1472-4642.2010.00645.x

Tomašových, A., & Kidwell, S. M. (2017). Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856), 20170328. https://doi.org/10.1098/rspb.2017.0328

Toussaint, A., Charpin, N., Brosse, S., & Villéger, S. (2016). Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific Reports*, *6*(1), 22125. https://doi.org/10.1038/srep22125

Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinos, P., Karamanlidis, A. A., Spiegel, D., & Sala, E. (2014). Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology*, *102*(6), 1518–1527. https://doi.org/10.1111/1365-2745.12324

Vermeij, G. J. (1987). *Evolution & escalation. An ecological history of life*. Princeton University Press.

Villéger, S. (2017). *Computing functional diversity indices*. Retrieved 2 August 2019 from http://villeger.sebastien.free.fr/Rscripts.html

Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, *22*(6), 671–681. https://doi.org/10.1111/geb.12021

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Villéger, S., Novack-Gottshall, P. M., & Mouillot, D. (2011). The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters*, *14*(6), 561–568. https://doi.org/10.1111/j.1461-0248.2011.01618.x

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635. https://doi.org/10.1111/ele.12424

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology and Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Yeruham, E., Shpigel, M., Abelson, A., & Rilov, G. (2020). Ocean warming and tropical invaders erode the performance of a key herbivore. *Ecology*, *101*(2), e02925. https://doi.org/10.1002/ecy.2925

Yvon-Durocher, G., & Allen, A. P. (2012). Linking community size structure and ecosystem functioning using metabolic theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2998–3007. https://doi.org/10.1098/rstb.2012.0246

BIOSKETCHES

Jan Steger is a marine biologist interested in benthic biodiversity, functional ecology, and biogeography. His current work focuses on assessing the impacts of non-indigenous species on recipient ecosystems, based on the integration of ecological and actuopalaeontological data.

Paolo G. Albano explores marine biodiversity over multiple spatial and temporal scales, with a particular interest in the drivers of its demise.

The author team consists of ecologists and palaeontologists with a shared interest in the study of biological invasions, a major component of global change.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Steger, J., Bošnjak M., Belmaker J., Galil B. S., Zuschin M., & Albano P. G. (2021). Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. *Global Ecology and Biogeography*, 00, 1–14. https://doi.org/10.1111/geb.13415