

Nestedness and turnover unveil inverse spatial patterns of compositional and functional β -diversity at varying depth in marine benthos

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Editor: Andrew Barnes**Abstract**

Aim: The two additive components of β -diversity, namely turnover and nestedness, reflect the two basic mechanisms underlying the overall change in species identities across the landscape, the replacement of species or their loss, respectively. Analogously, functional turnover and nestedness express the replacement or loss of functional traits associated with variations in community composition. However, the extent to which patterns of compositional and functional nestedness and turnover may overlap, or diverge, is still uncertain in marine environments. Here, patterns of turnover and nestedness were quantified in marine benthic assemblages in order to assess their relative contribution to spatial patterns of compositional and functional β -diversity.

Location: Mediterranean Sea, NE Ionian Sea, Ionian Archipelago.

Methods: In this study, we investigated patterns of dissimilarity in species and functional trait composition in subtidal macrobenthic assemblages from Mediterranean islands in order to quantify compositional and functional β -diversity among islands, determine the relative contributions of turnover and nestedness, and compare β -diversity patterns occurring in shallow and deeper reefs.

Results: We found a complex relationship between functional and compositional β -diversity at varying depth. At 5 m, species and functional trait dissimilarity largely overlapped, with turnover being the dominant component in both cases. At 15 m, compositional β -diversity was mostly due to turnover, with a negligible contribution of nestedness, whereas the opposite occurred for functional β -diversity. Partitioning β -diversity components revealed this discrepancy and the presence of functional hotspots, which would remain unnoticed analysing the overall compositional and functional β -diversity.

Main conclusions: Our findings may have profound implications for the optimization of conservation planning, stressing the need for assessing habitat-dependent idiosyncrasies in components of functional and compositional β -diversity for a more

comprehensive picture of possible protection scenarios that, besides structure, may also allow preserving the functioning of marine communities.

KEYWORDS

distance decay, functional diversity, island biogeography, marine conservation, Mediterranean Sea, subtidal reefs, β -diversity

1 | INTRODUCTION

As originally conceived, β -diversity describes how species composition of a community changes across the landscape, thus measuring differences in species identities among spatial units within a given area (Whittaker, 1960, 1972). Since this former idea, the concept of β -diversity evolved assuming many different connotations (Anderson et al., 2011), with a proliferation of associated metrics (Tuomisto, 2010; Vellend, 2001). To date, β -diversity has become one of the most pervasive concepts in ecology, referring to the heterogeneity in the distribution of biological entities from a taxonomic, phylogenetic and functional perspective (Cardoso et al., 2014; Podani, Pavoine, & Ricotta, 2018), across space, time or any other gradient of variation (Anderson et al., 2011; Soininen, 2010).

Irrespective of which elements of biodiversity are considered, whether species, clades or functional traits, β -diversity can be partitioned in the two components of *nestedness* and *turnover*, revealing the separated contribution of two basic mechanisms causing the overall variations in the identities of elements (Baselga, 2010; Villéger, Grenouillet, & Brosse, 2013). The nestedness-resultant component relates to variations in the number of species (or functional traits, or any other type of items used to quantify diversity) due to gain or loss, so that the pools of species in less diverse assemblages appear as strict subsets of more diverse ones; on the other hand, turnover indicates replacement and occurs when the loss of species is counterbalanced by the gain of new others (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Carvalho, Cardoso, & Gomes, 2012; Wright & Reeves, 1992). Clearly, these two components imply distinct ecological processes determining biodiversity patterns. For instance, nestedness often originates from processes of ordered extinctions or colonizations along gradients, or from spatial patterns of decreasing resource or habitat availability (Bender et al., 2017; Stuart et al., 2017; Ulrich, Almeida-Neto, & Gotelli, 2009), whereas turnover in species composition may reflect species sorting by the environment or limitations to dispersal leading to selective differentiation of species pools among assemblages (Victorero, Robert, Robinson, Taylor, & Huvenne, 2018). Quantifying β -diversity and the relative contribution of its two components, therefore, is crucial to understand causes generating diversity distribution in space and time, testing general ecological theories, and to provide further insights into the dynamic of biodiversity patterns with respect to the mere analysis of α -diversity alone (Baselga, 2012; Soininen, Heino, & Wang, 2018).

If compared to freshwater and terrestrial realms, β -diversity has received limited attention in the marine systems (Gray, 2000). This is because β -diversity would be less pronounced in seas and oceans than on land, due to the lower variability of the marine environment, and the higher potential of connectivity of marine communities (Carr et al., 2003; Gaines & Bertness, 1992). Though there is evidence supporting this assumption (Soininen, Lennon, & Hillebrand, 2007), differences in patterns of β -diversity among realms are still not so clear (Soininen et al., 2018), and marine communities may exhibit lower, equal or higher β -diversity than terrestrial or freshwater ones depending on the spatial scale considered and the processes involved in species distribution and dispersal (Kinlan, Gaines, & Lester, 2005; Soininen, McDonald, & Hillebrand, 2007). Actually, exploring β -diversity patterns at a hierarchy of spatial and temporal scales could shed light on ecological processes underlying the development and persistence of marine communities (Thrush, Hewitt, Cummings, Norkko, & Chiantore, 2010), and help the understanding of links between local and regional marine biodiversity (Witman, Etter, & Smith, 2004). From a more practical perspective, measuring variations in β -diversity within or among marine communities are critical to improve regional estimates of species richness (Bevilacqua, Ugland, Plicanti, Scuderi, & Terlizzi, 2018; Terlizzi, Anderson, Bevilacqua, & Ugland, 2014) and to detect spatial homogenization in community structure related to human impacts (Bevilacqua, Plicanti, Sandulli, & Terlizzi, 2012).

Over the last two decades, intense ecological research on marine reserves as main tools to protect marine biodiversity has lent new emphasis to β -diversity (Legendre, Borcard, & Peres-Neto, 2005; Thrush et al., 2010; Winberg, Lynch, Murray, Jones, & Davis, 2007), which has been increasingly recognized as a baseline feature to inform conservation planning (Carlos-Júnior et al., 2019; Socolar, Gilroy, Kunin, & Edwards, 2016). The assessment of spatial heterogeneity in species composition in the region of interest may assist the process of siting and spacing of marine reserves, in order to insure complementarity and increase inclusiveness of regional biodiversity in protected sites (Hewitt, Thrush, Halliday, & Duffy, 2005; Neigel, 2003). Also, modelling β -diversity in relation to geographic distance or connection by currents is essential to identify relevant scales of variation in community similarity and, thus, to plan networks of marine reserves that could maximize the potential for ecological connectivity (Ratray et al., 2016; Thrush et al., 2010; Watson et al., 2011).

Conservation strategies in oceans and seas, as well as on land, have been traditionally focused on species richness, endemism and distinctiveness, or habitat diversity (Mace, 2014), thus

implying that the higher the number of species within a protected site, the higher the amount of protected functional and evolutionary features. Indeed, the relationships among compositional, phylogenetic and functional trait diversity may be not so stringent (Cumming & Child, 2009; Jarzyna & Jetz, 2018; Mazel et al., 2018) and there is mounting evidence of spatial discrepancies among these complementary facets of biodiversity for a variety of organisms (Brum et al., 2017; Devictor et al., 2010; Lindegren, Holt, MacKenzie, & Rahbek, 2017). Unravelling the relationships between compositional and functional diversity is overriding to calibrate effective management practices that may enhance dynamic properties of communities and ecosystems, such as their resilience potential (Devictor et al., 2010; Hooper et al., 2005). Given the emergent need to integrate functional diversity in spatial planning, a major relevance of disentangling patterns of nestedness and turnover can be envisaged for marine conservation (Loiseau et al., 2017). Recent advances provided theoretical and methodological basis to separate the nestedness and turnover components for compositional and functional β -diversity, allowing a better understanding of the extent to which the spatial (or temporal) distributions of species identities and associated functional traits might be aligned (Baselga, 2010; Carvalho et al., 2012; Vill  ger et al., 2013). Notwithstanding, attempts in this direction have been very rare in the marine realm (Bender et al., 2017; Loiseau et al., 2017) where the level of spatial coherence between functional and compositional β -diversity, including nestedness and turnover components, is still largely unknown. Here, a large dataset on macrobenthic assemblages from subtidal rocky reefs in six Mediterranean islands spanning over more than 300 km was used for (a) quantifying compositional and functional β -diversity of sessile fauna and flora among islands and (b) weighing the relative contributions of turnover and nestedness-resultant components, (c) modelling such variations in species composition and functional traits of assemblages at increasing geographic distance between islands, (d) assessing congruence of the observed patterns whether considering compositional or functional β -diversity and (e) at changing habitat features (i.e., depth).

2 | MATERIALS AND METHODS

2.1 | Study area and datasets

Data on macrobenthic assemblages were collected during an extensive field survey in 2001. Sessile macrobenthos was sampled at six Greek islands in the Ionian Sea (Figure 1), and namely Kerkira (KO), Paxi (PX), Lefkada (LE), Meganisi (ME), Kefalonia (KE) and Z  kynthos (ZA). At each island, four sites (100s to 1,000s m apart) were randomly selected from a set of possible sampling sites characterized by comparable environmental conditions (i.e., slope, exposure, rocky substrate) and representative of subtidal rocky assemblages on the seaward side of islands. Ten photographic samples (16 × 23 cm) of macrobenthic assemblages on sub-vertical

rocky reefs were taken in each site at 5 m and 15 m depth, for a total of 480 samples. Samples were analysed under magnification by superimposing a transparent grid of 24 equally sized squares to help the visual estimates of percentage cover of sessile organisms. A total of 67 taxa were found (see Appendix S1), most of them identified at species (80%) or genus/family (10%) level. For 10% of organisms, identification from photographic samples was possible only in terms of morphological groups. Collection of destructive samples helped the identification of difficult organisms and allowed identifying the main species included in morphological or taxonomic groups. Finally, two datasets were obtained, one for 5 m (58 taxa × 240 samples) and the other (57 taxa × 240 samples) for 15 m depth.

2.2 | Functional traits

The set of functional traits was based on previous works providing extensive analyses of biological and ecological features of marine species linked with the functioning of marine benthic ecosystems (see for details Bremner, 2008; Bremner, Rogers, & Frid, 2006) and integrated with recent reviews of functional traits for marine species (Costello et al., 2015).

A total of 48 functional traits were identified and grouped in seven main categories: (a) Morphology (e.g., *Body size*), (b) Life cycle & Growth (e.g., *Growth rate*), (c) Reproduction (e.g., *Reproductive season*), (d) Dispersal & Colonization (e.g., *Duration of larval stage*), (e) Interactions with the environment (e.g., *Maximum depth*), (f) Biological interactions (e.g., *Sociability*) and (g) Matter & Energy flow (e.g., *CaCO₃ content*). A detailed description of all selected functional traits is provided in Appendix S2 (see Supplementary Material). Data on functional traits were mined from scientific literature searching the mainstream web tools (i.e., Web of Science, Scopus, Google Scholar) and eminent online catalogues and databases (e.g., AlgaeBase). For six traits, data were available only for 1/3 of taxa or less, whereas for nine traits all taxa exhibited equal trait value. Therefore, such traits were not considered, and functional diversity analysis was based on the remaining trait matrix (67 taxa × 33 functional traits) (see Appendices S2 and S3 for full details on traits selection, values and data sources).

2.3 | Data analysis

Compositional β -diversity was measured using Jaccard dissimilarity in species composition between assemblages (Baselga & Orme, 2012; Jost, 2007). To separate the contributions to β -diversity due to species turnover and nestedness, we followed the approach proposed by Baselga (2012), which formulated the additive partitioning of Jaccard dissimilarity into these two components (Baselga, 2012; Baselga & Orme, 2012). For the simplest case of two assemblages, compositional β -diversity using Jaccard dissimilarity (β) is as follows:

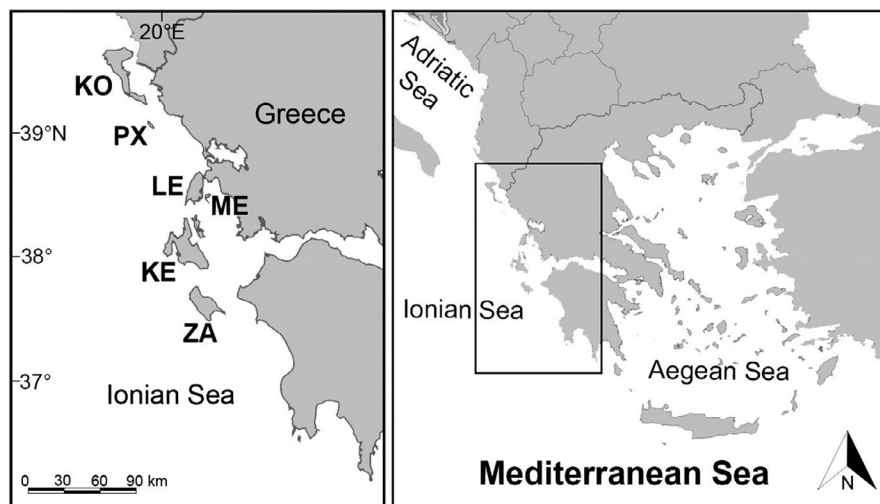


FIGURE 1 The study area included six islands of the Ionian Archipelago: Kerkira (KO), Paxi (PX), Lefkada (LE), Meganisi (ME), Kefalonia (KE), Zákynthos (ZA)

$$\beta = \frac{b+c}{a+b+c} \quad (1)$$

where a is the number of shared species, b and c the number of unique species in each of the two assemblages, respectively. When $a > 0$, besides compositional dissimilarity due to species replacement (i.e., compositional turnover component, hereafter β_{TURN}), a portion of β -diversity may be due to the different number of species between the two assemblages (i.e., compositional nestedness-resultant component, hereafter β_{NES}), and β can be partitioned into the two components as follows:

$$\beta = \frac{b+c}{a+b+c} = \left(\frac{2 \cdot \min(b,c)}{a+2 \cdot \min(b,c)} \right) + \left(\frac{|b-c|}{a+b+c} \cdot \frac{a}{a+2 \cdot \min(b,c)} \right) = \beta_{\text{TURN}} + \beta_{\text{NES}} \quad (2)$$

It is worth noting here that β_{NES} does not provide a measure of true nestedness (e.g., as NODF, Almeida-Neto et al., 2008), but rather it represents the compositional dissimilarity between nested assemblages produced by the differences in species richness. In other words, it provides the fraction of dissimilarity due to nestedness (Baselga, 2012).

Functional β -diversity was computed using the multidimensional functional space and following the method proposed by Villéger, Mason, and Moullot (2008) with its subsequent generalization to any dissimilarity measure, any number of traits and any type of traits (i.e., quantitative, semi-quantitative, qualitative) provided by Laliberté and Legendre (2010). In this framework, functional traits identify axes in the multidimensional functional space, and species are located according to their trait values. The functional space occupied by all species from a given assemblages quantifies its functional richness (FRic; Villéger et al., 2008), providing a direct measure of its functional diversity, and is calculated as the volume of the minimum polytope (convex hull) containing all species. In this case, and in analogy with compositional β -diversity between two assemblages quantified using Jaccard dissimilarity, the functional β -diversity ($F\beta$) can be defined as the ratio between functional space not shared and the functional space occupied by the two assemblages A_1 and A_2 , which is as follows:

$$F\beta = \frac{V(A_1) + V(A_2) - 2 \cdot V(A_1 \cap A_2)}{V(A_1) + V(A_2) - V(A_1 \cap A_2)} \quad (3)$$

where $V(A_1)$ and $V(A_2)$ are the volumes of the convex hulls of the two assemblages and $V(A_1 \cap A_2)$ is the volume of their intersection (Villéger et al., 2013). Since β and $F\beta$ (Equations 1, 2) are equivalent (Villéger, Novack-Gottshall, & Moullot, 2011), $F\beta$ can be partitioned in the functional nestedness-resultant ($F\beta_{\text{NES}}$) and functional turnover ($F\beta_{\text{TURN}}$) components in the same way, by substituting a , b and c in Equation 2 with $V(A_1 \cap A_2)$, $V(A_1) - V(A_1 \cap A_2)$ and $V(A_2) - V(A_1 \cap A_2)$, respectively (Villéger et al., 2013). For a full conceptual and mathematical description of compositional and functional β -diversity, partitioning for pairwise and multiple-site comparisons see Baselga (2010, 2012) and Villéger et al. (2013).

The multidimensional functional space was built by using synthetic functional axes from Principal Coordinates Analysis (PCoA) on the 33 functional traits (Appendices S2, S3). As first, a Gower dissimilarity matrix was obtained from the rectangular matrix of 67 taxa \times 33 functional traits (Appendix S3). No standardization of numeric traits was applied prior to analysis, since binary, categorical and quantitative variables are all ranged between 0 and 1 in the Gower dissimilarity. Then, the Gower dissimilarity matrix was analysed through PCoA and the resulting PCoA axes were used as the new traits to calculate functional β -diversity and its components (Laliberté & Legendre, 2010; Villéger et al., 2013). This allowed accommodating for the different types of variables and missing values in the functional trait matrix (Laliberté & Legendre, 2010; Villéger et al., 2008). Due to large computing time needed to calculate functional β -diversity and its components when the functional space is more than four-dimensional (Baselga, Orme, Villéger, De Bortoli, & Leprieur, 2018), for all analyses on functional diversity we limited the number of dimensions of the functional space to the first five PCoA axes, which, however, explained >85% of variation in the original functional trait matrix (see Appendix S4).

Functional richness (FRic, i.e., the volume occupied by the assemblage in the multidimensional functional space) of the regional species pools found at 5 m and 15 m depth was calculated to assess

functional diversity of shallower and deeper reef assemblages. FRic of assemblages in each island and depth was also calculated and Pearson's product-moment correlation was used to test relationships of FRic with species richness and area of islands.

Compositional and functional β -diversity between the whole assemblages at the two depths were quantified calculating β , $F\beta$ and their nestedness-resultant and turnover components. A distance-based test for homogeneity in multivariate dispersions (PERMDISP; Anderson, Ellingsen, & McArdle, 2006) was performed to test whether β -diversity among islands varied between 5 m and 15 m depth. In the analysis, multivariate dispersion is calculated as the average distance to the group centroid of samples (\bar{d}_{cen}) in the space defined by a resemblance matrix (Anderson et al., 2006), which represent a distance-based measure of β -diversity (Anderson et al., 2011). As first, we obtained six triangular matrices by calculating pairwise dissimilarities between assemblages at each island and each depth. Three of them were based, respectively, on the overall compositional dissimilarity and its nestedness and turnover components (i.e., β , β_{TURN} and β_{NES}), and the other three on their functional analogues (i.e., $F\beta$, $F\beta_{TURN}$ and $F\beta_{NES}$). Then, we carried out six separated PERMDISP tests (one for each of the six matrices). This allowed ascertaining whether β and $F\beta$, but also their respective components of nestedness and turnover, were consistent at the two investigated depths. All tests were based on 999 permutations. PERMDISP was done also based on dissimilarity matrices at the scale of sites to test whether there were differences β and $F\beta$ and their components among islands within depth strata and between depths for each island. Since no significant differences were detected in almost all cases (see Appendix S5), this allowed excluding that analyses at the scale of islands could have masked potential variations in β -diversity among sites within islands.

Since turnover was the dominant component underlying compositional β -diversity among islands at both depths (see Section 3), only congruence in patterns of β_{TURN} among islands between 5 m and 15 m depth was checked using Mantel test, with 999 permutations. For each depth, spatial patterns in β_{TURN} were depicted through PCoA of island centroids.

Mantel test was also used to test correlation between spatial patterns of compositional and functional turnover within depth

strata, in order to assess whether changes in species identity among islands turned into changes of assemblage functions. For assemblages at each island and depth, the corresponding convex hull was designed in the functional space identified by the first two PCoA axes, which represented >60% of variation in the original functional trait matrix (Appendix S4). PCoA bi-plots comparing convex hulls between islands were produced to exemplify prevalent spatial patterns of functional turnover and nestedness of assemblages in the region.

Finally, in equivalence to distance decay in similarity (Nekola & White, 1999), relationships of pairwise β -diversity between islands with the corresponding pairwise geographic distance were assessed at both the investigated depths by fitting negative exponential models, through GLM, of increasing compositional (β) and functional ($F\beta$) dissimilarity at increasing distance (Baselga, 2010). Geographic distance between islands were computed based on their respective geographic centre. Models of increasing β and $F\beta$ with geographic distance were compared between the two depths through a bootstrapping procedure (Baselga et al., 2018), which allowed constructing a frequency distributions ($n = 1,000$) of estimated parameters (intercept and slope). The probability of a given parameter to be larger at one depth with respect to the other was then empirically calculated by comparing the respective frequency distributions (Baselga, 2010). Models of distance decay in dissimilarity between sites within islands were also done. All analyses were done in R (R Development Core Team, 2018) using the packages "betapart" (Baselga & Orme, 2012; Baselga et al., 2018) and "vegan" (Oksanen et al., 2018).

3 | RESULTS

3.1 | Regional and local-scale compositional and functional richness at varying depth

The total functional diversity of the regional pool of species was higher at 5 m (FRic = 1.074×10^5) than at 15 m (FRic = 8.962×10^4), despite the total number of species was almost the same at the two depths (58 vs. 57 species, respectively). At 5 m, assemblages from single islands accounted, on average, for 48% ($\pm 4\%$) of the total functional diversity characterizing the whole pool of

TABLE 1 Functional richness (FRic) and species richness (SR) of rocky reef assemblages at each island and each investigated depth (5 m and 15 m)

| | 5 m | | 15 m | | Area (km ²) |
|---------|--|--------------------|--|--------------------|-------------------------|
| | FRic | SR | FRic | SR | |
| KO | 5.815×10^4 | 33 | 4.886×10^4 | 35 | 585 |
| PX | 5.040×10^4 | 35 | 4.143×10^4 | 31 | 25 |
| LE | 4.836×10^4 | 37 | 4.314×10^4 | 32 | 325 |
| ME | 4.442×10^4 | 35 | 4.566×10^4 | 35 | 22 |
| KE | 6.471×10^4 | 44 | 6.515×10^4 | 38 | 787 |
| ZA | 3.836×10^4 | 33 | 6.621×10^4 | 41 | 406 |
| Average | 5.073 (± 0.387) $\times 10^4$ | 36.2 (± 1.7) | 5.174 (± 0.453) $\times 10^4$ | 35.3 (± 1.5) | |

Note: The size of islands (km²) is also provided.

species at this depth, with higher values found at KE and KO, and the lowest value at ZA (Table 1). At 15 m, the mean functional diversity of assemblages among islands was higher, accounting for 59% ($\pm 5\%$) of the whole functional diversity of deeper reefs, with higher values reached at KE and ZA (Table 1). Values of F_{Ric} across depths were strongly correlated with the number of species ($r = 0.790$, $p = .002$) and the surface area of islands ($r = 0.664$, $p = .019$).

β -diversity between the regional pool of species at the two depths was similar whether considering species or functional trait composition ($\beta = 0.284$ and $F\beta = 0.292$, respectively). While compositional β -diversity was mostly due to species turnover ($\beta_{\text{TURN}} = 0.273$) with a negligible portion attributable to the nestedness-resultant component ($\beta_{\text{NES}} = 0.011$), the contributions of functional turnover ($F\beta_{\text{TURN}} = 0.163$) and nestedness ($F\beta_{\text{NES}} = 0.129$) were of comparable importance in determining the total functional β -diversity.

3.2 | Patterns of compositional and functional β -diversity among islands and between depths

Patterns in species turnover among islands appeared similar between 5 m and 15 m depth, although not completely overlapping (Figures 2a, 3a). At 5 m, centroids of KO and PX were clearly separated from those of the other islands, which clustered altogether (Figure 2a). At 15 m, centroids of KO-PX, LE-ME and KE-ZA formed three distinct groups (Figure 3a), closely reflecting the geographic gradient of islands (see Figure 1). A moderate correlation was found when comparing species turnover across islands between depths (Mantel test, $r = 0.501$, $p = .059$), whereas no correlation was found analysing the nestedness-resultant components (Mantel test, $r = -0.012$, $p = .488$) (see also Appendix S6). PERMDISP did not detect significant variations in compositional dissimilarity (β), and its turnover (β_{TURN}) and nestedness components (β_{NES}) between depths (Table 2). At both 5 m and 15 m depth,

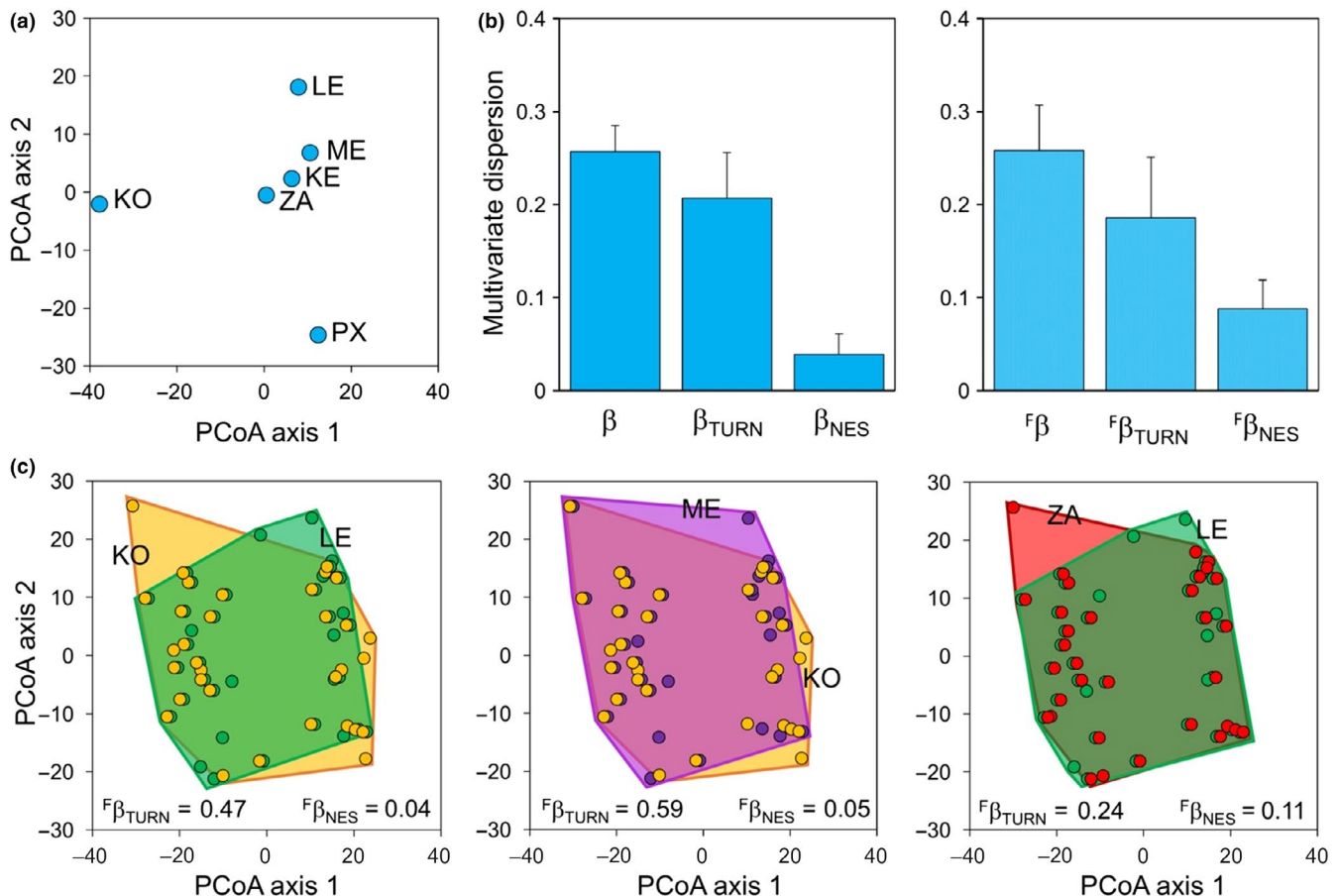


FIGURE 2 (a) PCoA ordination of centroids of island assemblages at 5 m depth (66.6% of total variation explained by axes). (b) Average distance (\pm SE) to the group centroid (\bar{d}_{cen}) of island assemblages at 5 m in the space defined by (left) compositional and (right) functional Jaccard dissimilarity matrices, and their respective turnover and nestedness-resultant components. (c) bi-plots comparing the functional space occupied by macrobenthic assemblages between islands at 5 m depth. Functional space for each island is delimited by the respective convex hull (coloured solids). The two axes represent the two synthetic functional dimensions obtained from PCoA, explaining >60% of variation in the original functional trait matrix. A subset of all possible pairwise comparisons is shown, as an example of main patterns of functional turnover and nestedness in the region. For each comparison, values of functional turnover ($F\beta_{\text{TURN}}$) and nestedness-resultant ($F\beta_{\text{NES}}$) components are also reported. Acronyms for islands are as in Figure 1

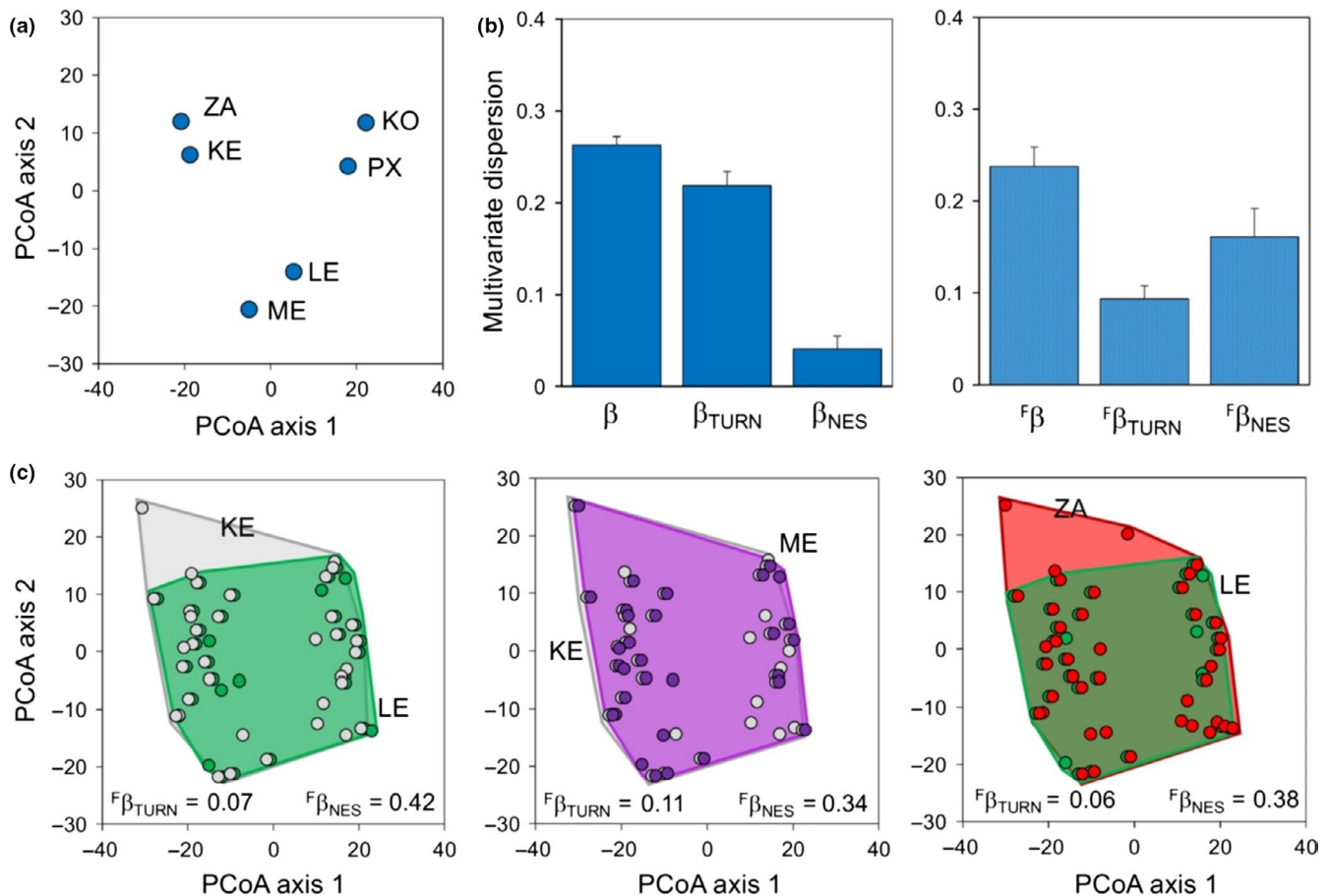


FIGURE 3 (a) PCoA ordination of centroids of island assemblages at 15 m depth (62.5% of total variation explained by axes). (b) Average distance (\pm SE) to the group centroid (\bar{d}_{cen}) of island assemblages at 15 m in the space defined by (left) compositional and (right) functional Jaccard dissimilarity matrices, and their respective turnover and nestedness-resultant components. (c) bi-plots comparing the functional space occupied by macrobenthic assemblages between islands at 5 m depth. Functional space for each island is delimited by the respective convex hull (coloured solids). The two axes represent the two synthetic functional dimensions obtained from PCoA, explaining >60% of variation in the original functional trait matrix. A subset of all possible pairwise comparisons is shown, as an example of main patterns of functional turnover and nestedness in the region. For each comparison, values of functional turnover ($F\beta_{\text{TURN}}$) and nestedness-resultant ($F\beta_{\text{NES}}$) components are also reported. Acronyms for islands are as in Figure 1

TABLE 2 Results of distance-based permutational tests on multivariate dispersion (PERMDISP) of centroids of island assemblages between the two investigated depths (5 and 15 m)

| | Compositional | | Functional | |
|----------------------|---------------|----------|------------|----------|
| | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> |
| Total dissimilarity | 0.044 | .876 | 0.132 | .880 |
| Turnover | 0.055 | .849 | 1.873 | .394 |
| Nestedness-resultant | 0.003 | .955 | 2.760 | .249 |

Note: Tests were based on compositional Jaccard dissimilarity, its turnover and nestedness-resultant components, and their functional analogues. All tests were performed with 999 permutations.

most of compositional β -diversity derived from species turnover, whereas the contribution of nestedness to the total dissimilarity was very limited (Figures 2b, 3b).

Trough PERMDISP, we also observed no significant differences between depths in functional dissimilarity ($F\beta$) and its turnover

($F\beta_{\text{TURN}}$) and nestedness-resultant ($F\beta_{\text{NES}}$) components (Table 2). However, inspection of graphs in Figures 2b, 3b showed different proportions of functional β -diversity components between depths. At 5 m, most of functional β -diversity depended on functional turnover and only a small portion was related to nestedness, whereas at 15 m the opposite occurred (Figure 3b). A further discrepancy between depths emerged when comparing their respective patterns in functional β -diversity among islands (see also Appendix S6), which were largely not correlated either considering functional turnover (Mantel test, $r = 0.274$, $p = .159$) or nestedness components (Mantel test, $r = 0.380$, $p = .097$).

Differences between depths in the contribution of functional turnover and nestedness-resultant components were clearly depicted through pairwise bi-plots of the functional space occupied by assemblages from different islands (Figures 2c, 3c). In shallower reefs, functional β -diversity between islands was mostly due to turnover so that, in most pairwise contrasts, unshared volumes of convex hulls occupied completely different portions of the whole functional

space (Figure 2c). The contribution of nestedness to functional β -diversity largely increased in deeper reefs, where assemblages of all islands were functional subsets almost completely enclosed in the functional space of KE and ZA (Figure 3c). Pairwise (between islands) values of β , β_{TURN} , β_{NES} and their functional analogues at the two investigated depths were reported in full in Supplementary Material (Appendices S7, S8).

Spatial patterns of compositional and functional turnover were strongly correlated (Mantel test, $r = 0.833$, $p = .013$) at 5 m depth, with comparable average values of β_{TURN} (0.33 ± 0.03) and $F\beta_{\text{TURN}}$ (0.28 ± 0.06) between islands. Likewise, strong correlation was found at this depth when comparing nestedness components of compositional and functional β -diversity (Mantel test, $r = 0.810$, $p = .012$). This close relationship between compositional and functional β -diversity did not extend to deeper reef assemblages. Average values of β_{TURN} (0.34 ± 0.01) and $F\beta_{\text{TURN}}$ (0.14 ± 0.02) between islands were quite different at 15 m, and the same occurred for compositional and functional nestedness-resultants (respectively, 0.07 ± 0.01 vs. 0.22 ± 0.01). At this depth, functional β -diversity reflected its compositional counterpart only in terms of nestedness (Mantel test, $r = 0.691$, $p = .016$), while compositional and functional turnover components did not show a significant correlation (Mantel test, $r = 0.157$, $p = .266$).

3.3 | Patterns of compositional and functional β -diversity versus geographic distance

The same pattern of increasing compositional β -diversity at increasing geographic distance between islands characterized assemblages at 5 and 15 m depth (Figure 4a), with no significant difference between their respective intercepts and slopes (Table 3). Model fitting, nevertheless, was significant only for deeper assemblages (Table 3). Decomposing compositional β -diversity revealed that, for assemblages at both depths, this pattern was driven by compositional turnover (Figure 4c, Table 3), whereas the nestedness-resultant component appeared independent from geographic distance (Figure 4e, Table 3). Irrespective of depth, functional β -diversity between assemblages and its turnover and nestedness components were not related to the corresponding pairwise geographic distance between islands (Table 3, Figure 4b,d,f). Comparison of models between the two depths showed equal intercepts but significantly different slopes for both functional turnover and nestedness (Table 3), indicating that spatial turnover in functional traits was higher at 5 m than at 15 m, while the opposite occurred for nestedness (Figure 4d,f). Fitting β -diversity versus geographic distance at the scale of sites showed comparable patterns (see Appendix S9).

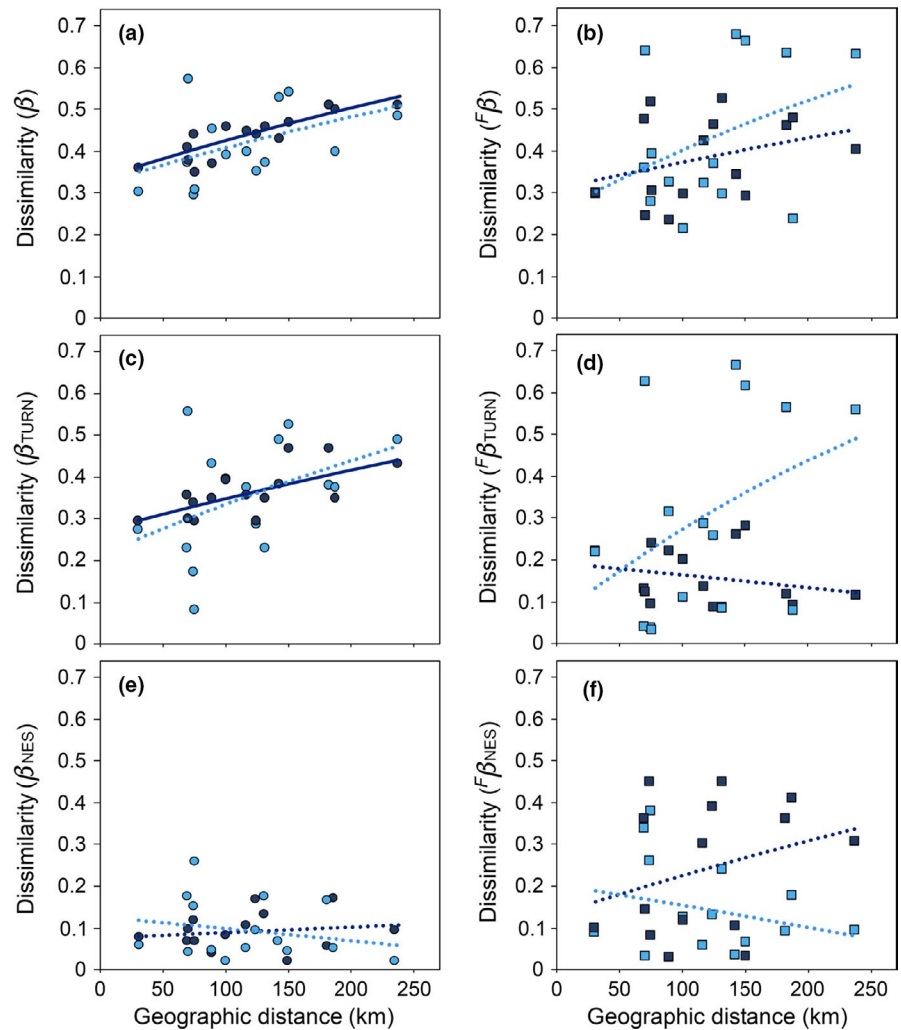
4 | DISCUSSION

The complex interplay among different factors and processes, including historical and biogeographical constraints, environmental

filtering, biological interactions and dispersal, influences species distribution in space and time (Leibold et al., 2004; McGill, 2010; Pinheiro et al., 2017), leading community composition to diverge, or resemble, from one place to another. Separating turnover and nestedness-resultant contributions to the overall β -diversity could help going through this complexity, providing further insights into mechanisms shaping community composition with respect to β -diversity as a whole. For instance, similarity in compositional β -diversity among regions or habitats could be only apparent, hiding quite different underlying patterns that might emerge only after its partitioning in fundamental components (Baselga, 2010). This study represented an emblematic example of how this issue may also concern functional β -diversity and its potential relationship with β -diversity in species composition. We found that patterns of compositional and functional β -diversity of macrobenthic assemblages were strongly correlated at 5 m depth, with turnover being the dominant components in both cases. In contrast, at 15 m depth, the contribution of nestedness was negligible only for compositional β -diversity but, on average, prevailed when analysing functional β -diversity. In other terms, at 5 m depth, changes in species composition among islands turn into changes in functional trait composition. At 15 m, instead, only a small portion of species replacement led to differentiate the functional trait spectrum among islands. In many cases, replaced species in functionally poor assemblages held traits already included in the functional space of functionally rich ones, resulting in increased functional nestedness. This discrepancy would remain unnoticed analysing the overall β -diversity, leading to the flawed conclusion that functional β -diversity among islands was similar between the two depths, and related to compositional β -diversity consistently.

The observed patterns in functional β -diversity components could derive from differences in species richness and functional redundancy of assemblages between the two investigated depths. High turnover in species composition may not correspond to high functional turnover when assemblages overlap in the functional space and species replacement between sites involves functionally redundant species (Villéger et al., 2013). On the other hand, at increasing dimensionality of the functional space, it could be unlikely that a single location may account for most of functional traits, especially in more heterogeneous environments (Mori, Isbell, & Seidl, 2018). In our case, the mean functional diversity of assemblages among islands was comparable between the two depths (see Table 1), but the functional diversity of the regional species pool at 15 m was about 17% lower than at 5 m, which implied that assemblages from single islands at 15 m were more representative of the whole functional diversity at this depth. The increased functional space at 5 m was not due to a higher species richness at this depth, as the total number of species was basically the same at 5 m and 15 m (58 vs. 57, respectively), indicating a greater redundancy of functional traits in the regional species pool of deeper assemblages. Thus, at 5 m, the lower representativeness of assemblages increased the chance for functional turnover among islands to prevail, whereas, at 15 m, the

FIGURE 4 Dissimilarity between assemblages against pairwise geographic distances at 5 m (light blue symbols) and 15 m (dark blue symbols) depth. (a) Total compositional (β) and (b) functional ($^F\beta$) dissimilarity, (c) compositional (β_{TURN}) and (d) functional ($^F\beta_{\text{TURN}}$) turnover components, (e) compositional (β_{NES}) and (f) functional ($^F\beta_{\text{NES}}$) nestedness-resultant components. Solid and dotted lines indicate significant and not significant relationships, respectively, following a negative exponential model of increasing dissimilarity at increasing distance. Coefficients are given in Table 3



higher representativeness and functional redundancy could have generated functional overlap, or embedment, of assemblages from different islands, increasing the nestedness component of functional β -diversity.

The descriptive nature of this study does not allow inferring about cause–effect relationships underlying the observed patterns, yet depth-dependent variations in habitat features might have a potential role in driving inconsistencies in the relative contributions of turnover and nestedness-resultant components between shallow and deeper assemblages. Shallow habitats are likely to be more influenced than deeper one by local environmental factors, such as, surface water temperature, exposure, natural disturbance regimes, human pressures, which increase variability in environmental conditions and lead different species to colonize different sites (Terlizzi, Benedetti-Cecchi, Fraschetti, & Anderson, 2007). Species sorting will select those organisms with functional traits that make them more prone to survive and thrive under local environmental conditions, so that turnover in species composition will correspond to functional turnover (Loiseau et al., 2017), as occurred for assemblages at 5 m depth. Deeper reefs, in contrast, are generally characterized by higher environmental homogeneity (Steneck & Dethier, 1994) and assemblages could be

structured mostly by competition rather than environmental filtering (Ballesteros, 2006; Terlizzi et al., 2007). Species with large overlap in their functional traits might be forced to occupy different sites due to competitive interactions, with functional nestedness emerging because of the presence of centres of biodiversity (Bender et al., 2017), which seemed to be represented by KE and ZA islands.

Patterns of increasing dissimilarity in species composition at increasing geographic distance virtually overlapped between at 5 m and 15 m, indicating coherence of processes influencing connectivity among islands, such as dispersal and water circulation. This is not surprising since the assemblages at the two depths shared about the 70% of species and dispersal potential should be very similar. Connectivity by currents at different depths, in addition, has been found to be quite correlated with turnover in species composition of marine benthos in the study area (Rattray et al., 2016). However, neither turnover nor the nestedness-resultant component of functional dissimilarity correlated with geographic distance between islands at the two depths, suggesting little effect of connectivity potential on functional trait configuration of assemblages. Patterns of decay in similarity at increasing distance were consistent at the

TABLE 3 Summary and parameter estimates of negative exponential models of increasing compositional and functional dissimilarities, and their respective turnover and nestedness components, at increasing geographic distance for assemblages at 5 and 15 m depth

| Dissimilarity | Depth | Intercept | Slope | R ² | p |
|---------------------------|--|-----------|---------|----------------|------|
| β | 5 m | 0.317 | 0.0013 | .228 | .073 |
| | 15 m | 0.317 | 0.0014 | .746 | .001 |
| | Intercept: 5 m = 15 m ($p = .470$); slope: 5 m = 15 m ($p = .434$) | | | | |
| β_{TURN} | 5 m | 0.208 | 0.0017 | .204 | .088 |
| | 15 m | 0.261 | 0.0011 | .458 | .002 |
| | Intercept: 5 m = 15 m ($p = .253$); slope: 5 m = 15 m ($p = .555$) | | | | |
| β_{NES} | 5 m | 0.103 | -0.0003 | .058 | .362 |
| | 15 m | 0.054 | 0.0001 | .035 | .516 |
| | Intercept: 5 m = 15 m ($p = .124$); slope: 5 m = 15 m ($p = .123$) | | | | |
| F_{β} | 5 m | 0.258 | 0.0022 | .175 | .127 |
| | 15 m | 0.299 | 0.0010 | .107 | .217 |
| | Intercept: 5 m = 15 m ($p = .345$); slope: 5 m = 15 m ($p = .199$) | | | | |
| $F_{\beta_{\text{TURN}}}$ | 5 m | 0.078 | 0.0026 | .170 | .128 |
| | 15 m | 0.171 | -0.0004 | .062 | .359 |
| | Intercept: 5 m = 15 m ($p = .225$); slope: 5 m = 15 m ($p = .042$) | | | | |
| $F_{\beta_{\text{NES}}}$ | 5 m | 0.175 | -0.0006 | .071 | .320 |
| | 15 m | 0.132 | 0.0011 | .091 | .278 |
| | Intercept: 5 m = 15 m ($p = .321$); slope: 5 m = 15 m ($p = .039$) | | | | |

Note: Pairwise comparisons of parameter estimates between models from the two depths are also provided.

scale of islands and at the scale of sites within islands, whether considering compositional or functional β -diversity and their respective components. Indeed, the relative contributions of turnover and nestedness could vary depending on the spatial scale considered and the process causing changes in community assembly (Menegotto, Dambros, & Netto, 2019). The fact that compositional and functional nestedness and turnover among sites did not vary significantly between islands, or between depths in each island, seemed to indicate that processes driving β -diversity among islands were likely to act homogeneously at the lower spatial scale.

At 15 m, all islands were functional subsets of assemblages in KE and ZA, whereas at both depths, high compositional and functional turnover distinguished KO from all the other islands. Such two main patterns were likely driving the inverse relationship in compositional and functional β -diversity components at the two depths, and provided clues that size of islands, spatial arrangement of functional hotspots, and biogeographic factors, contributed to differentiate the functional spectrum of assemblages across the region. KE and ZA were, respectively, the first and the

third island in size, located at the southeast end of the archipelago, with KE also showing the highest taxon richness at both the investigated depths. The size of islands may be strongly related to compositional and functional richness (Whittaker et al., 2014), since larger islands could provide more opportunities for species colonization and establishment from mainland and other islands than smaller ones. This could have originated an ordered spatial pattern of reduced functional richness starting from KE and ZA as centres of diversity. Same considerations may concern KO, which is the second island in size. However, in this case, turnover could have emerged as the dominant component because KO is at the transition between the South Adriatic and the North Ionian, thus hosting a quite different pool of species with respect the remaining islands which reflected the confluence of two different biogeographic regions.

Regardless of reasons behind β -diversity patterns, turnover appeared to be a major component on land (Baselga, 2010; Griffiths, 2017; Villéger et al., 2013) and sea (Brault et al., 2013; Loiseau et al., 2017; Wagstaff et al., 2014). In terrestrial and freshwater habitats, nestedness is often confined to particular conditions such as, for instance, post-glacial recolonization (Griffiths, 2017). In the marine realm, gradients in energy flux at increasing depth in deep-sea environments (Stuart et al., 2017), or the combination of size and isolation in atolls (Bender et al., 2017), have been found to originate nested patterns in community assembly. Most of these studies considered only species composition, with few attempts contrasting patterns of compositional β -diversity against their functional counterparts. Available comparative studies seem to indicate that the contribution of nestedness to the overall β -diversity tends to increase when analysing spatial distribution of functional traits (Bishop, Robertson, van Rensburg, & Parr, 2015; Matthews et al., 2015). Evidence from coral reef fish (Loiseau et al., 2017) and the present study on macrobenthic assemblages, which included algae and marine invertebrates, reflected this pattern, reinforcing the idea that functional nestedness may be considerably more common than compositional nestedness in nature, including the marine environment (Bender et al., 2017).

Our findings suggested that relationships between functional and compositional β -diversity can be even more complex than previously documented, since relatively minor changes in habitat features could reflect a substantial change in the relationships between spatial distributions of species and associated functional traits. For conservation perspectives, this stress the need for assessing intra- and inter-habitat idiosyncrasies among functional and compositional nestedness and turnover for a more comprehensive picture of possible protection scenarios, especially in shallow coastal systems where diversity and spatial heterogeneity of marine habitats is high. Habitat-specific patterns of nestedness and turnover could implicate different and conflicting conservation strategies. High compositional nestedness, for instance, would advise for the selection of few large reserves privileging nesting species-rich sites (Atman & Patterson, 1993; Wright & Reeves, 1992), while high rates of turnover would

necessarily imply a greater number of protected sites to achieve representativeness (Benedetti-Cecchi et al., 2003). Nevertheless, the inclusion of species-poor sites to complement speciose ones is often recommended, even in presence of high level of nestedness, since true nested subsets of species might be quite rare in the real world and a single large area could not ensure a comprehensive protection of the regional species pool (Fischer & Lindenmayer, 2005; Matthews et al., 2015). Adding components of functional β -diversity could complicate the matter if, for instance, high compositional turnover is associated with high functional nestedness, raising the question of whether protecting one (or a few) functional hotspots, ignoring functionally nested sites, or focusing on species identities and planning for higher numbers

of protected sites (Loiseau et al., 2017). It could be argued here that the latter strategy can be the best solution in any case, as it allows protecting many species and many functions. There is no doubt that, when conditions allow, the more is the better in terms of protected sites. However, this is nearly always impracticable in the real world (Kuempel, Adams, Possingham, & Bode, 2017), making selection of sites to protect a matter of compromise and optimization in policies of marine spatial planning (Socolar et al., 2016). In this view, partitioning β -diversity components for both species and functional trait composition could help prioritizing the choice of sites and habitats to include within protected areas, enlightening discriminating factors which could remain unseen considering a single aspect of biodiversity. High compositional

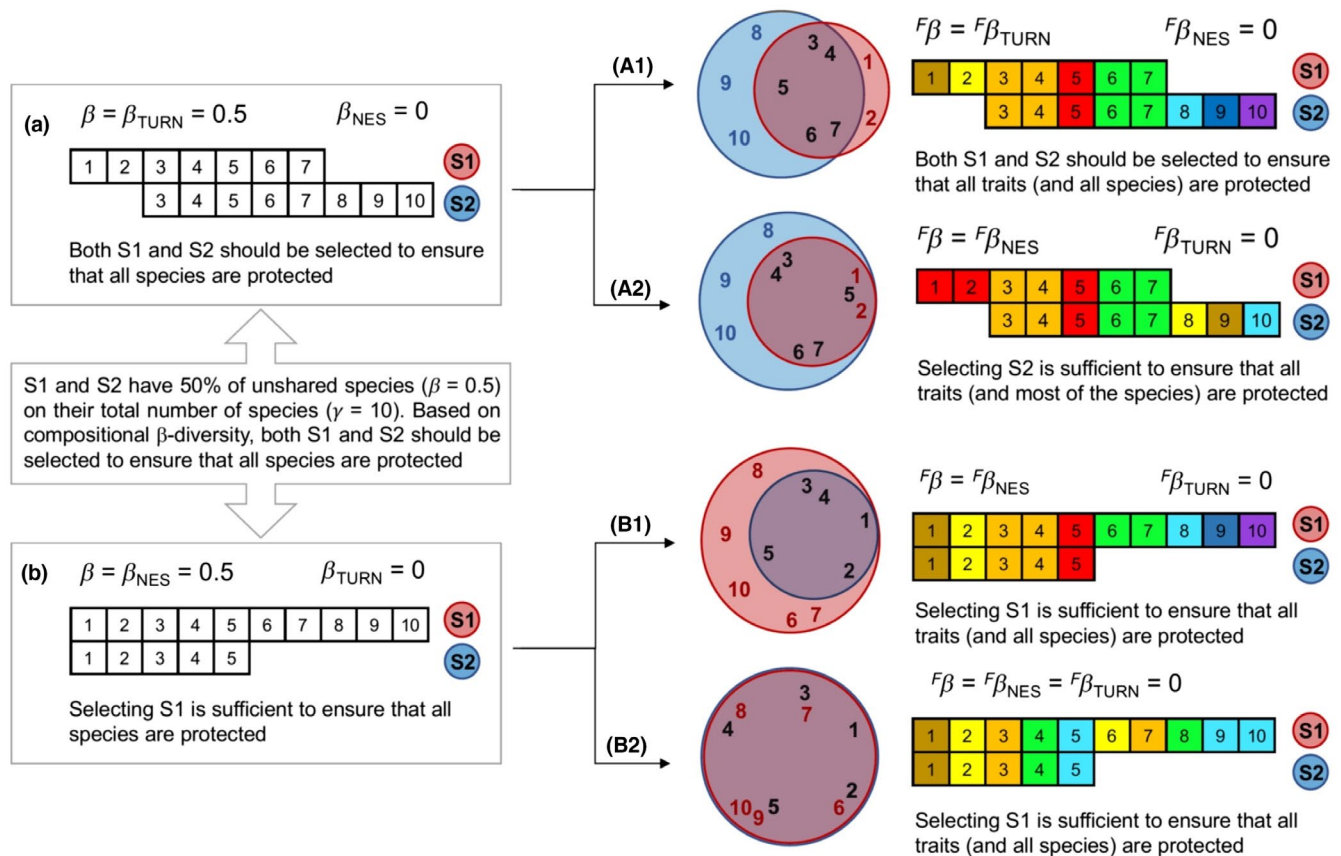


FIGURE 5 Conceptual framework for combining information on compositional and functional β -diversity components to optimize sites (or habitats) selection for protection. The simple case of two sites (or habitats) are considered (S1 and S2). Numbers in square boxes and diagrams indicate species. Same colours in boxes indicate same (or very similar) functional traits of species. Diagrams are schematic representations of the overlap between the functional space occupied by the communities in S1 and S2. In diagrams, shared species between S1 and S2 are given in black, whereas unique species in S1 and S2 are given in red and blue, respectively. Compositional β -diversity between the two hypothetical communities is $\beta = 0.5$, meaning that 50% of species on the total pool ($\gamma = 10$) is unshared. In this scenario, both S1 and S2 should be selected to protect the whole regional pool of species. If β is entirely (or mostly) due to compositional turnover (β_{TURN}), the selection of both S1 and S2 is supported (case A). If, in contrast, β is mostly due to compositional nestedness (β_{NES}), selecting only S1 is sufficient to protect all species (case B). When β_{TURN} is the dominant component, this does not necessarily imply that functional turnover ($F\beta_{\text{TURN}}$) will be the dominant component of functional β -diversity ($F\beta$). If so, the selection of both sites will be necessary to protect all species and all functions (case A.1). Otherwise, if functional nestedness ($F\beta_{\text{NES}}$) is dominant, selecting only S2 will be sufficient to protect most of the species and all functions (case A.2). When β_{NES} is dominant, also $F\beta_{\text{NES}}$ is necessarily dominant (because if the species of a given community are a subset of another one, also their functional traits will be included in the functional space of the second community). What could change is the degree of nestedness (cases B.1 and B.2). In any case, selecting only the nesting site (here S1) will ensure the protection of all species and all functions

β -diversity in a given region could strongly support the strategy of including as much sites as possible in reserve networks only when compositional turnover is the dominant component, and tightly reflects functional turnover, for an exhaustive protection of species and associate functional traits (Figure 5, case A1). Understanding whether this strategy is indispensable, or might be reasonable alternatives, is crucial, especially under reduced fund availability, reduced compliance, or other socio-economic constraints. High compositional turnover (Figure 5, case A.2) and, more generally, high β -diversity (Figure 5, cases B.1–2) might hide the dominance of compositional and functional nestedness. Unveiling these incongruences could help maximizing the protection of compositional and functional aspects of biodiversity, while reducing conservation efforts. This can be achieved, for instance, by reducing the number of sites to protect, or by calibrating reserve size to include or not different habitats according to their spatial patterns in compositional and/or functional nestedness and turnover.

The unprecedented increase of multiple human pressures is undermining the stability of marine ecosystems through the depletion of biodiversity and the erosion of their resilience potential (Conversi et al., 2015; Hughes, Bellwood, Folke, Steneck, & Wilson, 2005; Worm et al., 2006). In this context, considering only species number and composition is not sufficient for prioritizing areas deserving protection that, besides structure, may also allow preserving the functioning of communities and ecosystems (Bishop et al., 2015; Brum et al., 2017; Loiseau et al., 2017; Mazel et al., 2018). Indeed, siting of marine reserves has been rarely based on sound assessments of spatial distribution of marine resources to protect so far (Agardy et al., 2003), being often related to natural beauty or political and socio-economic opportunity. This has generated a number of “paper parks” in the rush to attain putative conservation goals, without adequate planning and resources for management (Fraschetti et al., 2009; Guidetti et al., 2008; Rife, Erisman, Sanchez, & Aburto-Oropeza, 2012). The Convention of Biological Diversity set the target of protecting 10% of seas and oceans by 2020, which could be extended to 30% by 2030 following recommendations of the World Parks Congress (Campbell & Gray, 2019). Achieving the latter objective would require an investment of 5–19 billion dollars per year, considering running costs only (Balmford, Gravestock, Hockley, McClean, & Roberts, 2004). It is clear that the future implementation of marine reserves has to follow a quite different pathway with respect to the past, relying on a careful consideration of the multiple facets of biodiversity, from species to functions, if we want not to waste resources and, above all, to insure an effective conservation of marine ecosystems.

DATA AVAILABILITY STATEMENT

Data used in the study are provided as Supplementary Material in Appendix S10.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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