

Taxonomic and functional β -diversity patterns reveal random assembly rules in nearshore fish assemblages

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ABSTRACT: Evaluating β -diversity provides ecologists with a greater understanding of the processes that drive compositional variation of biological communities in ecosystems. The decomposition of taxonomic and functional β -diversity into their components of turnover (species replacement) and nestedness (species loss) was conducted for nearshore fish assemblages in 4 areas with different habitat characteristics on the southeastern Brazilian coast. We hypothesized that the environmental filtering process is occurring along a gradient of wave exposure, anthropogenic influences, sediment types and water physicochemical variables, inducing high taxonomic and functional β -diversity. Higher functional β -diversity compared to taxonomic β -diversity was found, which suggests that different species tend to play different functions, indicating taxonomically and functionally distinct assemblages. Taxonomic and functional turnover presented similar values and were both comparatively higher than nestedness, indicating the predominance of species replacement over species loss. β -diversity did not differ significantly from the null expectations of randomness, suggesting no influence of environmental filtering in the assemblages. The high nestedness in the area where anthropogenic activities are more intense suggests that only fish with the ability to tolerate harsh conditions can potentially settle there. We conclude that there is an environmental gradient that partially explains the differences in the components of functional β -diversity. However, the large unexplained part of the variation suggests that species are functionally distinct and organized at random with no influences of environmental filtering. This study helps to assess the impact of natural and human activities on the functional facets of biodiversity at the local scale.

KEY WORDS: Environmental filtering · Fish assemblages · Estuarine ecosystem · Nestedness · Null models · Spatial turnover · Soft-bottom habitats

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1. INTRODUCTION

Analysing the different β -diversity patterns and their respective components of turnover and nestedness that reflect biological phenomena is essential for understanding the processes underlying biodiversity patterns. β -diversity is the variability in the specific composition of a biological community among sites/

habitats within an area (Whittaker 1972, Magurran 2004, Anderson et al. 2011). Baselga (2010) proposed a framework for the assessment of β -diversity, disentangling the contributions of the spatial turnover and nestedness components, which results from 2 anti-thetic processes, namely species replacement and species loss, respectively. The author suggested that a high level of β -diversity may have 2 different impli-

cations. It can reflect a low proportion of shared species between 2 communities having a similar number of species, that is, a high contribution of the turnover component and low nestedness. Conversely, when the biotas of sites with fewer species are subsets of the biotas of richer sites, it can reflect a high contribution of the nestedness component and low turnover.

β -diversity has frequently been expressed in terms of the taxonomic aspect of biodiversity. However, it is widely acknowledged that the evaluation of taxonomy is not sufficient to understand the effects of assemblages on ecosystem functioning without considering the functional facet of biodiversity (Petchey & Gaston 2006, Laureto et al. 2015). Functional diversity is an important metric in biodiversity studies because it relates the roles that organisms play within ecosystems, including mechanisms of ecological interactions (Mason et al. 2005, Mouchet et al. 2013, Stuart-Smith et al. 2013). Villéger et al. (2012) suggested that taxonomic and functional β -diversity deserve to be quantified simultaneously and that differences between these 2 facets of biodiversity can help to understand community assembly rules. Two communities with few species in common (high taxonomic β -diversity) would show low functional β -diversity if their respective species are functionally similar. In addition, if functional β -diversity is lower than taxonomic β -diversity, such differences can be driven by a lower functional turnover compared with taxonomic turnover, while the nestedness-resultant component is similar for taxonomic and functional β -diversity. Villéger et al. (2013) decomposed functional β -diversity, the dissimilarity in functional composition among communities, into functional turnover and functional nestedness-resultant components for European fish assemblages. They found that fish faunas with different species tend to share functional attributes. The predominance of turnover can indicate that sites differ in environmental heterogeneity by selecting different species, whereas the predominance of nestedness can indicate species loss because environmental filtering favours certain species over others, and only fish with the ability to tolerate the abiotic conditions (e.g. generalists or resistant species) can potentially occupy the sites.

Species loss and species replacement can reflect processes structuring communities, such as stochastic and deterministic assembly. The deterministic factors include selection imposed by the abiotic environment (environmental filtering) and species interactions. In contrast, the stochastic factors include

unpredictable disturbance, probabilistic dispersal and random birth/death events (Chase & Myers 2011, Ford & Roberts 2018, Mori et al. 2018). Null models have been used for testing these predictions of ecological theory, comparing observed statistical patterns to those expected in the absence of a particular assembly mechanism (Gotelli 2000, Ulrich & Gotelli 2007). Simulated fish assemblages under the assembly processes of random (stochastic) and selective extinction (deterministic process of environmental filtering) can be used to test the strength of the correlations between functional and taxonomic β -diversity and these components, representing one approach for connecting statistical patterns to assembly mechanisms (Si et al. 2016).

The biodiversity of fishes in coastal ecosystems changes according to habitat variations (e.g. type, quality, area), seascape composition (e.g. habitat context, diversity, connectivity) and exposure to both natural and anthropogenic disturbances (Pittman & McAlpine 2003, Nagelkerken 2009, Sheaves et al. 2015), sediment contamination, wave activity and grain size (McKinley et al. 2011, Oliveira & Pessanha 2014). Transitional habitats, where abiotic conditions may vary to form environmental gradients, are important to evaluate to detect possible trends in the processes that determine the structuring of communities and to assess the effects of environmental and biotic variables (Mouillot et al. 2007, Henriques et al. 2017b). The substitution of fish species in shallow coastal areas has been related to changes in peaks of recruitment (Mariani 2001, Favero & Dias 2015, Macura et al. 2016), or to the interaction between species and environmental variables (Benazza et al. 2015, Pereira et al. 2015), such as the degree of exposure to waves, availability of habitats and natural resources, among other factors, including human influences (Vargas-Fonseca et al. 2016, Borland et al. 2017, Olds et al. 2018). In this sense, shallow areas located along a gradient of wave exposure, different sediment type and habitat availability offer interesting scenarios to test variations in β -diversity.

On the southern coast of the state of Rio de Janeiro, Brazil, there are large bays with adjacent unprotected sandy beaches that form a gradient of exposure to waves and of habitat diversity. In general, oceanic beaches are more exposed to waves and offer limited habitat diversity, while beaches within bays offer a gradient of exposure to waves and greater habitat diversity. The latter beach type varies from the innermost part, which is generally the most protected but more subject to changes caused by anthropogenic activities, to the more external areas,

where the conditions near the connection with the sea have the opposite characteristics. This is the case in the study area, where the innermost part of a large bay is more altered by anthropogenic activities, whereas the outermost part is less influenced by such activities and has more habitat diversity (Cunha et al. 2006, Leal Neto et al. 2006, Molisani et al. 2006, Araújo et al. 2016). Therefore, the unprotected ocean beaches and the relatively protected beaches within bays may provide an appropriate scenario for addressing the decomposition of taxonomic and functional β -diversity.

In this study, we focussed on decomposing taxonomic and functional β -diversity into their turnover and nestedness components to uncover underlying patterns in the communities of heterogeneous habitats. In the marine environment, habitats, even those in close proximity to one another, may have very different fish species compositions and abundances, with these differences being strongly driven by feeding habits and resource availability (Whitfield & Patrick 2015). Four areas with different habitat characteristics, 1 in an unprotected zone and 3 along a gradient of wave exposure and anthropogenic influences from the inner to the outer zones, and with different sediment types in a tropical bay in southeastern Brazil, were assessed. We hypothesized that the environmental filtering process is occurring along a gradient of wave exposure and anthropogenic influences, different sediment types and water physico-chemical variables, inducing high taxonomic and functional β -diversity. Our expectation is that there is a pool of fish species in the coastal area (inner platform) that select and are associated with different types of habitats, indicating the effects of environmental heterogeneity on β -diversity.

2. MATERIALS AND METHODS

2.1. Study area

The southern coast of Rio de Janeiro state is located in a transition area between the tropical and subtropical regions (22–23° S), and is characterized by the presence of large bays adjacent to unprotected oceanic sandy beaches. Four coastal areas along a coastline of approximately 150 km in southeastern Brazil were studied (Fig. 1). One area is located in an unprotected zone (oceanic beaches, OC), and 3 within a large

bay (Sepetiba Bay). The latter experience an increasing degree of wave exposure and marine influences and decreasing anthropogenic influences from the inner to the outer zones (B1: inner, B2: intermediate, B3: outer) and have different types of substrate. B1 is the most altered locality, with the heaviest influence of anthropogenic activities because of its proximity (1 km) to the major effluent discharge point source. A large amount of domestic wastewater and industrial effluent from the outskirts of the city of Rio de Janeiro is discharged at this point source, contributing to a homogeneous clay and muddy substratum at B1, whereas B2 and B3 have more diverse sediment types (Leal Neto et al. 2006, Araújo et al. 2016). Each of the sites/beaches within the areas has a shoreline length of approximately 1000 m, and the areas are approximately 10–80 km apart.

The waters within Sepetiba Bay are saline (ca. 28–31) and with variable transparency (Secchi depth 0.2–2 m). The substratum is mainly muddy in the inner zone, and predominantly sandy in the outer zone (Araújo et al. 2002, 2016). The mean tidal range is from 0.5 m (neap tides) to 1.3 m (spring tides). Small rivers and streams drain into the bay, contributing to decreases in salinity and increases in turbidity in the inner bay areas. In the last decade, this coastal system has suffered growing environmental degradation due to increases in industrial and municipal effluents brought into the bay from the outskirts of the city of Rio de Janeiro (Leal Neto et al. 2006, Araújo et al. 2016).

The oceanic beaches in the zone adjacent to Sepetiba Bay (OC) are characterized as reflective beaches. These beaches are interspersed with rocky reefs located below low hills and are located in an unprotected coastal area where the wave action is

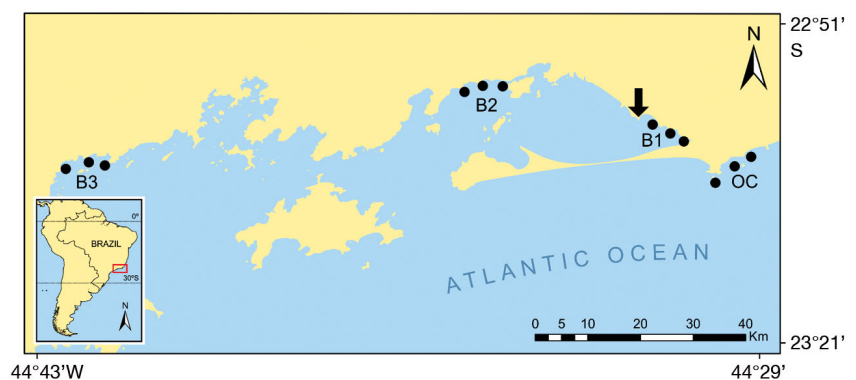


Fig. 1. Study area with indication of the sampling localities; OC: oceanic beaches; B1: innermost area within the Sepetiba Bay; B2: intermediate area; B3: outermost area. Point source of effluents indicated by the arrow

strongest. These beaches are characterized by medium to coarse sand, with mean grain size of 0.43 mm, tidal range of approximately 1 m and intertidal beach slope varying from 1/5.29 to 1/17.82 m (Veloso et al. 2006). These beaches have low-amplitude semidiurnal tides with a mean variation of 0.7 m and a maximum tidal range of 1.5 m. The mean water temperature ranges from 20.6°C (winter) to 26.1°C (summer), and the mean salinity ranges from 34 to 35.

The sediment granulometric fractions change among the areas. Silt and clay predominate at B1. The proportion of very fine sand is higher at B2, whereas the proportions of coarse and medium sand are higher at B3; OC has a predominance of granules and very coarse sand (Veloso et al. 2006, Silva-Camacho et al. 2017).

2.2. Sampling design

Quarterly surveys were carried out in March, June, September and December of 2014 and 2015 at 3 sites in each of the 4 areas with 4 replicates. For each area and each sampling time, all fish from the 3 sites and 4 replicates were pooled. In total, we obtained 32 samples (4 areas × 4 seasons × 2 years). The fish assemblages were sampled using a beach seine (12 × 2.5 m; 5 mm mesh size). Samplings were carried out during the day (between 10:00 and 16:00 h) at high tide. The net was fitted with 2 hauling ropes (30 m each) and was set perpendicular to the shore at a depth of approximately 1.5 m. Seine hauls were performed by 2 persons, one at each end of the rope, covering a sampling length of approximately 30 m. The hauls lasted an average of 15 min, and the distance seined and the time required for each haul was standardized, thus allowing comparisons among samplings. The total sampled area was considered to be the distance the net was moved offshore multiplied by the mean width of the haul, resulting in an effective fishing area of approximately 300 m².

Immediately after collection, all fish were anaesthetized in benzocaine hydrochloride (50 mg l⁻¹). After euthanasia, the fish were fixed in 10% formalin and then preserved in 70% ethanol after 48 h. This project received a permanent license for the collection of zoological material (SISBIO number 10707/ Normative Instruction ICMBio no. 03/2014) and followed the ethics rules applicable to the use of animals in teaching and/or research based on the provisions of Brazilian law (Federal Law 11.794 of 8 October 2008). All fish were identified to species

level, counted, measured (total length in mm) and weighed (g).

2.3. Environmental characterization

2.3.1. Physicochemical variables

On each sampling occasion, the environmental variables of sub-superficial water temperature (°C), salinity, turbidity (NTU), dissolved oxygen (mg l⁻¹) and pH were measured using a multiprobe (Horiba W-23; Horiba Trading). Transparency was measured using a Secchi disk, and depth was recorded with a digital sounder (Speedtech model SM-5).

2.3.2. Sediment granulometric and nutrient analysis

For the granulometric and nutrient analysis, sediment samples were collected using a PVC corer (10 cm in diameter and 50 cm in length) in a collecting area of 0.00785 m² at a depth of 15 cm using 4 replicates. The collected sediment was placed in plastic bags, weighed (precision of 0.01 g) and dried at 80°C in an oven. A portion of the sediment (300 g) was used in the granulometric analyses, and another part (150 g) was used in the nutrient analyses.

The determination of the granulometric fractions was obtained using the method proposed by Suguio (1973) with the aid of a screening apparatus for 15 min. The granulometric parameters were calculated according to Folk & Ward (1957) and classified according to Shepard (1954). Grain sizes were classified in accordance with Wentworth (1922), with corresponding values of phi. The mean granule size was determined from each granulometric fraction weight retained in each sieve using the software SysGran 3.0 (Camargo 2006). The silt and clay fractions were grouped together.

The following nutrients in the sediment were analysed: organic matter content (g dm⁻³), carbon (g kg⁻¹), total nitrogen (%TN) and total phosphorus (mg dm⁻³). Organic matter and carbon were determined using the method of Walkley & Black (1934) and modified by Frattini & Kalckmann (1967). The %TN in the sediment was determined using the Kjeldahl nitrogen method with a diffusion camera (Bremner 1960). The total phosphorus was determined using a spectrophotometer after digestion with HNO₃-HCl (3:1, V/V) at 200°C. The phosphorus contained in the sulfuric extract represents the total concentration of this element (Bowman 1988).

2.3.3. Morpho-dynamism

The degree of wave exposure was calculated followed the methodology proposed by McLachlan (1980), which is based on the sum of the scores assigned for the following parameters (Table S1 in the Supplement at www.int-res.com/articles/suppl/m627p109_supp.pdf): (1) wave action, (2) surf zone width, (3) presence/absence of holes or shallow depressions produced in the substratum by the macrofauna, (4) percent of sand grains that are 62–125 μm in size, (5) depth of sediment layers in which reduction is evident, (6) mean diameter of the sediment particles and (7) slope of the intertidal zone. Based on these results, the degree of exposure of the beach was defined in the following intervals: 1–5, very sheltered; 6–10, sheltered; 11–15, exposed; 16–20, very exposed.

The morpho-dynamic state of each beach was assessed using the dimensionless Dean parameter, Ω (Short & Wright 1983), which was determined according to the following equation: $\Omega = Hb/(Ws \times T)$, where Hb is the mean wave height (cm); Ws is the velocity of the settling sediment (cm s^{-1}), which is obtained using the mean sediment diameter considering a density of 2.65 and a temperature of 22°C (Gibbs et al. 1971); and T is the time interval (period, in seconds) between 2 consecutive waves. Wave height was estimated by measuring the height of the waves with graduated poles against the horizon. The wave period (T) was estimated with a chronometer and corresponded to 1/10 of the real time between 11 consecutive wave crests from a fixed point in the surf zone. Three replicates were performed to obtain an average measurement. Thus, reflective beaches have $\Omega < 2$, intermediate beaches have $2 < \Omega < 5$, and dissipative beaches have $\Omega > 5$.

2.4. Data analyses

2.4.1. Functional traits

The traits were chosen to encompass diverse attributes that influence functional roles in fish assemblages, including vertical distribution in the water column, life history strategy, trophic levels, body transversal shape and maximum body size (Wine-miller et al. 2015, Villéger et al. 2017). Trait information (Table 1) was obtained directly from the collected species, from the FishBase dataset (www.fishbase.org) and from our combined knowledge (Tables S2 & S3).

2.4.2. Measuring taxonomic and functional β -diversity

Fish data, expressed as the total number of individuals of each species from each locality and each sampling occasion, were used to calculate the taxonomic and functional β -diversity and their decomposition into a turnover and a nestedness-resultant component. Taxonomic β -diversity and its decomposition were calculated using the beta.pair function (incidence-based pairwise dissimilarities), which computes 3 distance matrices accounting for the (1) turnover (replacement), (2) nestedness and (3) total dissimilarity (i.e. the sum of the 2 components) (Baselga 2010). The fish data matrix was combined with the matrix of traits for calculating the functional β -diversity and their decomposition into a turnover and a nestedness-resultant component. Functional dissimilarities were based on the volume of the convex hull intersections in a multidimensional functional space using the functional.beta.pair function (x , index.family = 'multidim'), where x is the data frame, sites are the rows, and species are the columns (Villéger et al. 2013). The data frame had 32 sites (rows) (4 localities \times 4 seasons \times 2 years). The function returns a list with 3 dissimilarity matrices: (1) turnover – replacement, (2) nestedness and (3) total dissimilarity (i.e. the sum of both components). Each dissimilarity matrix present 496 pairwise combinations (32 \times 32 sites).

2.5. Statistical analyses

The physicochemical variables, granulometric sediment percentage, sediment nutrients and morpho-dynamism variables were compared among the 4 localities (fixed factors) using a permutational analysis of variance (PERMANOVA). Pairwise PERMANOVA comparisons were performed to assess differences in environmental variables among the localities. These analyses were conducted in Primer 6.1 and PERMANOVA+ software (Clarke & Gorley 2006).

The variations in the functional β -diversity and its components were assessed based on the means and standard error of functional β -diversity and its components at each locality for the following 7 pairs of seasons during the 2 yr period: summer vs. autumn 2014, autumn vs. winter 2014, winter vs. spring 2014, spring 2014 vs. summer 2015, summer vs. autumn 2015, autumn vs. winter 2015, winter vs. spring 2015. The aim was to assess for each locality possible vari-

Table 1. Functional trait categories with indication of the rationale for the trait selection

Trait	Categories/quantitative values	Trait selection rationale
Life history strategy	Amphidromous Semi-anadromous Semi-catadromous Non-migratory Oceanodromous	Quantifies habitat importance to fish populations at various life stages and habitat requirements of fish populations (Costello et al. 2015, Ladds et al. 2018)
Vertical distribution	Benthopelagic Benthic Pelagic	The level in the water column occupied by fish is critical for determining their ecological niches, as it influences the set of potential prey available and fish impacts on nutrient transfer between vertical strata (Costello et al. 2015, Ladds et al. 2018)
Trophic levels (TLs)	Varied from 2 to 4.5 in this study. Values between 2.0 and 2.19 represent primary consumers, which feed mainly on plants/detritus (herbivores). Values between 2.2 and 2.79 represent omnivores, which consume plants/detritus and animals (Froese & Pauly 2017). Values ≥ 2.8 refer to secondary and tertiary consumers which feed mainly on animals (carnivores)	TLs express where fish and other organisms tend to operate in their respective food webs. TLs are not attributes of the organisms for which feeding is being categorized, but of their interactions with other organisms. Thus, to estimate the TLs of fish, we must consider both their diet composition, and the TLs of their food item(s). $TL = 1 + \text{mean TL of the food items}$, where the mean is weighted by the contribution of the different food items (Froese & Pauly 2017)
Transverse body shape	Varied from 0.13 to 6.33 in this study	Related to the vertical position in the water column and hydrodynamic ability of fish. Transverse body shape = Bd/Bw , where Bd is body depth and Bw is body width. Values varied from fishes laterally compressed (>2.5) to flatfishes (<0.5) (Watson & Balon 1984)
Maximum body size	Varied from 2.3 to 42.8 cm in this study	Body size determines energy needs through the amount of energy required per unit of body mass and constrains prey–predator relationships. Size also influences growth rate, with small fishes growing faster than larger ones. Mortality rate tends to be higher for smaller fishes (Watson & Balon 1984)

ations in β -diversity and its components over time (seasons).

The correlations between taxonomic and functional β -diversity as well as between their respective components were tested using Mantel permutational tests. Partial Mantel tests were also carried out to account for the geographical distance between localities and for differences in species richness. To test the strength of the correlations between functional and taxonomic β -diversity, we obtained simulated fish assemblages under the assembly processes of random and selective extinction following Si et al. (2016). The random assembly algorithm randomly subsampled species without replacement from the regional pool by maintaining the observed species richness at each locality (i.e. fixed-row random-column algorithm, or the 'r0' algorithm; rows are localities, and columns are species). We also simulated another 2 null models under the process of random extinction for the localities: (1) maintaining species occupancy but randomizing species richness (i.e.

random-row, fixed-column algorithm, or the 'c0' algorithm) and (2) maintaining both species occupancy and species richness (i.e. fixed-row, fixed-column algorithm, or the 'quasiswap' algorithm) (Jonsson 2001, Miklós & Podani 2004). 'Selective extinction', the deterministic process of environmental filtering, was also simulated by randomly choosing an 'optimal' species and then selecting the nearest species (e.g. the species with the lowest Gower's distance) to this optimal species until the target local species richness was reached for each site. Each simulation was run 100 times. According to Si et al. (2016), if 'selective extinction' is the major process driving community assembly, the observed correlation coefficient (Pearson's r) is outside the 95th quantiles of the null distributions obtained under the random extinction scenario. In contrast, if random extinction predominantly drives the process of community assembly, we expect the observed correlation coefficients to be in the 5th and 95th quantiles of the null distributions obtained under the random extinc-

tion scenario but to be outside the 5th quantiles of the null distributions obtained under the 'selective extinction' scenario. The R scripts for computing taxonomic and functional β -diversity, their respective turnover and nestedness-resultant components, and graphics followed the script 'multidimFbetaD' (<http://villeger.sebastien.free.fr>). The R scripts for randomization tests simulating the processes of random and selective extinction were used following Si et al. (2016) in R version 3.5.1 (R Core Team 2018) using the packages 'betapart' (Baselga & Orme 2012), 'FD' (Laliberté & Legendre 2010) and 'vegan' (Oksanen et al. 2013).

We used multiple regression models to examine the relationships between the Gower distance of β -diversity and its turnover and nestedness-resultant components (response variables) and the Euclidean distance matrices of the environmental physicochemical, granulometry, sediment nutrient and morpho-dynamism variables (predictors). When redundant variables, i.e. those that correlated with one another with an r -value >0.8 , were identified, only 1 of those variables was considered in the analysis. Only the variables of organic matter and carbon were redundant ($r > 0.8$), and we only included carbon in the multiple regression analysis. Prior to the analysis, the environmental variables were standardized to mean of 0 and SD of 1, and a Euclidean similarity matrix was calculated for each variable. These analyses were performed using the software STATISTICA version 10 (StatSoft Inc. 2011).

3. RESULTS

3.1. Environmental variables

All water physicochemical variables presented significant differences among the localities (Figs. S1–S4). The water temperature was significantly higher at the sheltered beaches (B1, B2 and B3) compared with the oceanic beaches (OC), whereas salinity and dissolved oxygen were significantly higher at OC compared with B1, B2 and B3. The turbidity was significantly higher at B1, followed by B2, and lower at B3 and OC. The pH presented a lower value at B1 compared to B2, B3 and OC (Fig. S1).

B1 showed higher concentrations of organic matter and carbon compared with B2, B3 and OC (Fig. S2). Total nitrogen was higher at B1 and B2 and

lower at B3 and OC, whereas total phosphorus was higher at B2 compared with B1, B3 and OC.

The distribution of the granulometric sand fractions in the sediment was heterogeneous, with a low degree of selection (poorly selected). The granulometric composition varied significantly among the localities, with very coarse and coarse fractions of sediments predominating to a greater degree at B2, B3 and OC compared with B1 (Fig. S3). In relation to fine sediment, B1 presented a significantly higher proportion compared to B2, B3 and OC. In relation to the clay and silt fractions, B1 presented a significantly higher proportion compared to B2, B3 and OC.

The oceanic beaches (OC) were classified as exposed and/or reflective and were characterized by moderate to strong waves and high dynamism. On the other hand, the beaches within bays (B1 and B2) were classified as sheltered or dissipative, whereas the B3 beaches were classified as intermediate and sheltered (Fig. S4). The bay beaches showed an increase in the degree of wave exposure and marine influence from B1 to B3.

3.2. Taxonomic and functional β -diversity

A total of 71 fish species in 35 families were recorded in the 3 systems (Table S4). The taxonomic β -diversity ranged from 0.16 to 0.84, with an average value of 0.57 ± 0.005 (SE). The turnover average (0.49) was higher than the nestedness-resultant component (0.07) and contributed 86% of the taxonomic β -diversity, whereas the nestedness component contributed 14% (Table 2).

Functional β -diversity ranged from 0.23 to 0.94, with an average value of 0.75 ± 0.004 . On average, the turnover (0.54) was higher than the nestedness-resultant component (0.21) and contributed 72% of the functional β -diversity, whereas the nestedness contributed 28% of the functional β -diversity (Table 2). The functional β -diversity was significantly correlated with the taxonomic β -diversity (Mantel test, $r = 0.501$, $p < 0.001$) (Fig. 2). In addition, the

Table 2. Average \pm SE (range in brackets) of taxonomic and functional β -diversity and its components of turnover and nestedness for the nearshore fish community in coastal areas of the southeastern Brazilian coast

	Taxonomic	Functional
β -diversity	0.57 ± 0.005 (0.16–0.84)	0.75 ± 0.004 (0.23–0.94)
Turnover	0.49 ± 0.006 (0.0–0.83)	0.54 ± 0.009 (0.0–0.94)
Nestedness	0.07 ± 0.002 (0.0–0.38)	0.21 ± 0.008 (0.0–0.7)

functional turnover and taxonomic turnover were also significantly correlated ($r = 0.387$, $p < 0.001$). Although the functional nestedness was almost 3 times greater than the taxonomic nestedness, they were also significantly correlated ($r = 0.452$, $p < 0.001$). Turnover predominated in both the taxonomic and functional β -diversity (Fig. 2).

When the effect of the geographic distance and the difference in the number of species between the areas was removed, the partial Mantel tests also indicated significant correlations (Table 3). The functional β -diversity was significantly correlated with

the taxonomic β -diversity regardless of the geographical distance ($r = 0.470$, $p < 0.001$) and difference in species richness ($r = 0.498$, $p < 0.001$). The correlations between taxonomic turnover ($r = 0.364$, $p < 0.001$) and functional turnover ($r = 0.301$, $p < 0.001$) were also significant. However, the correlation between taxonomic nestedness and functional nestedness was lower when the effect of the difference in the number of fish species was removed ($r = 0.187$, $p < 0.001$) than when the effect of geographical distance was removed ($r = 0.462$, $p < 0.001$) (Table 3).

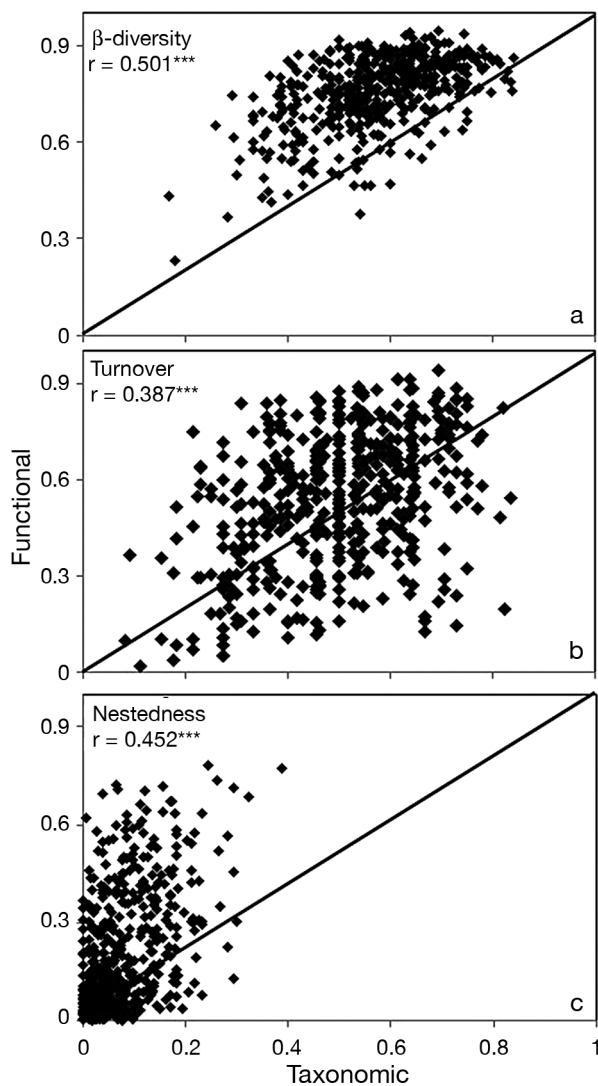


Fig. 2. Correlations between taxonomic and functional β -diversity for the fish assemblage of coastal areas on the southeastern Brazilian coast. (a) β -diversity and its respective (b) turnover and (c) nestedness components. Values above each panel are Pearson's correlation coefficients and associated Mantel test p -values (** $p < 0.001$)

3.3. Null model of β -diversity correlation coefficients

The observed correlation coefficients between taxonomic and functional β -diversity and their components were within the 95th quantiles of the null distributions, indicating that the observed patterns were not significantly different from the null expectations of random extinction when using the 'r0', 'c0' and 'quasiswap' algorithms (Fig. 3). The only exception was found for the 'r0' algorithm (β -diversity) and for the turnover component when using the 'quasiswap' algorithm. When using the 'selective extinction' algorithm, the observed correlation coefficients were outside the 5th and 95th quantiles of the null distributions, indicating that observed patterns were significantly different from the null expectations (Fig. 3). 'Selective extinction' was not the process driving the community assembly of fishes in our study system because the observed correlation coefficients were outside the 95th quantiles of the null distributions obtained under the selective extinction scenario. Therefore, random extinction seems to be the process driving community assembly in the present study.

3.4. Temporal functional β -diversity

A differentiated spatial pattern was observed when functional β -diversity and its components were analysed separately within each locality (among pairs of seasons). High functional β -diversity was observed in all 4 localities, with the highest values at OC and the lowest at B1 (pseudo- $F = 3.18$; $p = 0.03$) (Fig. 4a). The functional turnover was higher at B2, B3 and OC compared with B1 (pseudo- $F = 3.67$; $p = 0.03$), whereas the functional nestedness was higher at B1 compared with B2, B3 and OC (pseudo- $F = 3.47$;

$p = 0.03$) (Fig. 4a). The locality B1 is the nearest to the effluent discharges from the major point source, whereas B3 is the farthest (Fig. 4b). Although OC is

at an intermediate distance, it is not influenced by the point source because it is located outside the bay on an exposed beach.

Table 3. Mantel tests between taxonomic and functional β -diversity and their components. Partial Mantel tests account for differences in species richness and geographical distance between sites. Values are Pearson's correlation coefficients and associated Mantel test p -values (** $p < 0.001$)

	Mantel test	Partial Mantel test	
		Geographic distance	Difference in species richness
Taxonomic vs. functional β -diversity	0.501***	0.470***	0.498***
Taxonomic vs. functional turnover	0.387***	0.364***	0.301***
Taxonomic vs. functional nestedness	0.452***	0.462***	0.187***

Most of the convex-hull diagrams on the trait space of functional β -diversity and its components (Fig. S5) showed a predominance of nestedness at B1 and turnover at B2, B3 and OC. The low overlap between fish assemblage in the functional space can explain the higher level of functional β -diversity observed in this study, with frequent species replacement occurring among species that are functionally distinct, including those with the combinations of extreme traits, i.e. species located near the borders of the functional space (Fig. S5).

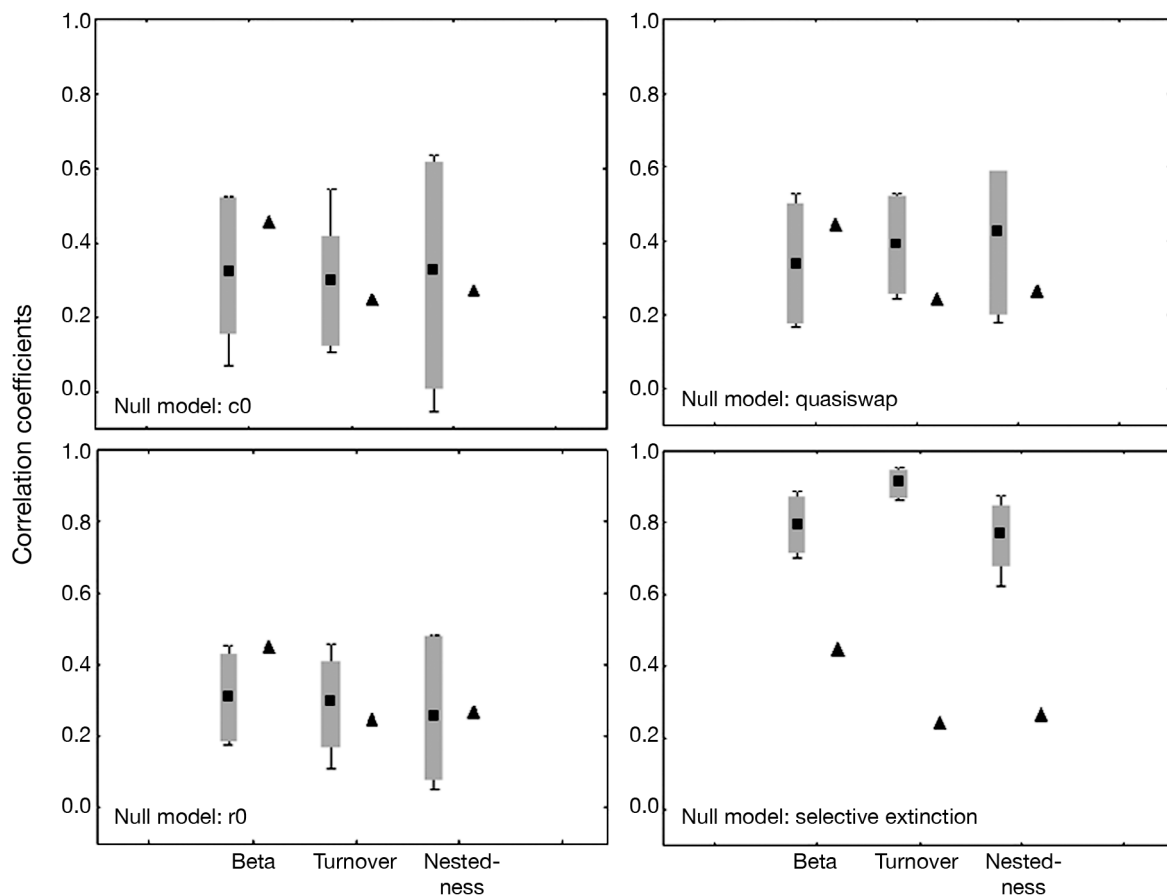


Fig. 3. Results of randomization tests. Null model 'c0' (random-row, fixed-column; maintains species occupancy). Null model 'r0' (fixed-row, random-column; maintains species richness). Null model 'quasiswap' (fixed-row, fixed-column; maintains both). Null model 'selective extinction' in the processes of environmental filtering (randomly select an 'optimal' species). The black triangles are the observed correlation coefficients between taxonomic and functional diversities and their components. The black squares in boxes are the median values of the null distributions. The lower and upper hinges (boundaries of boxes) are the 5th and 95th quantiles of the null distributions. The lower and upper adjacent values (whiskers below and above box plots) are the minimum and maximum of the null distributions

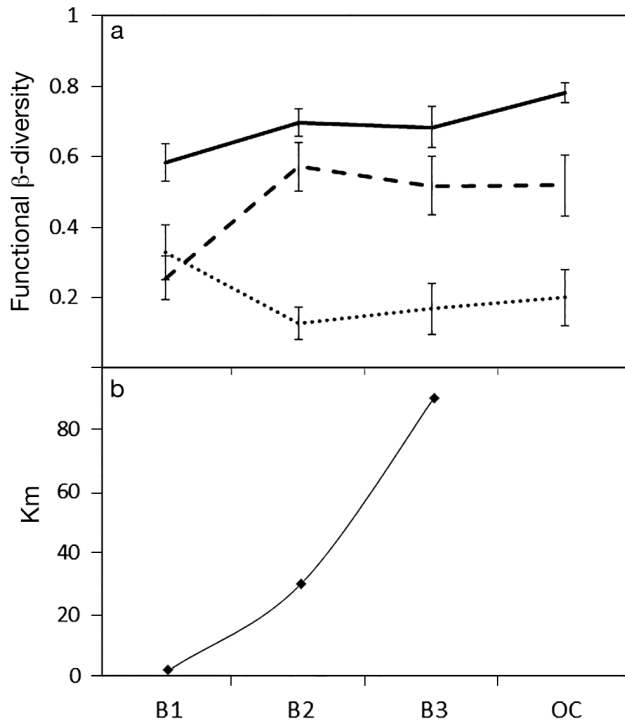


Fig. 4. (a) Mean and SE of functional β -diversity and its components in each locality among pairs of adjacent seasons. Solid line: functional β -diversity; dashed line: turnover; dotted line: nestedness. (b) Distance of the localities from the point source of the effluent discharges into the bay

3.5. Environmental influences on functional β -diversity

The strength of the relationships between the environmental variables and the functional β -diversity and its turnover and nestedness components was comparatively higher for the β -diversity ($R^2 = 0.19$) and the turnover ($R^2 = 0.20$) components than for nestedness ($R^2 = 0.15$) (Table 4). In addition, different environmental variables (physicochemical variables, granulometry, sediment nutrients, morpho-dynamism) had different degrees of influence on the functional β -diversity and its components. Water temperature, salinity, total nitrogen in the sediment and very coarse and coarse grain sizes directly influenced β -diversity, whereas the dissolved oxygen and very fine sand had the opposite effect (Table 4). Water temperature, salinity, total nitrogen in the sediment and coarse and fine grains had a positive effect on the turnover, whereas carbon in the sediment, very fine sand grains and clay and silt had a negative effect. On the other hand, clay and silt had a positive effect on the nestedness, whereas the total nitrogen and coarse and fine grains had a negative effect (Table 4).

4. DISCUSSION

Our results showed higher values of functional β -diversity compared to taxonomic β -diversity for the fish assemblage of coastal areas in southeastern Brazil, which suggests that different species tend to play different functional roles. Contrary to our findings, Villéger et al. (2012) found extremely low functional β -diversity values despite high dissimilarity in the taxonomic structure of tropical estuarine fish communities in the southern Gulf of Mexico. Such high taxonomic β -diversity may be associated with marked environmental gradients where a similar functional structure over space occurs, despite the strong dissimilarity in taxonomic structure along environmental gradients. Indeed, 2 communities can be very dissimilar in terms of species composition but very similar in terms of biological composition regarding trophic levels (Villéger et al. 2008), morphological traits (Irz et al. 2007) or phylogenetic lineages (Bryant et al. 2008). High functional β -diversity found in our study indicates replacement of functionally distinct species occurring among fish assemblages of the coastal areas, with those having specialized traits playing a key role by shaping the functional space. The functional β -diversity was higher due to the greater contribution of nestedness, a pattern that was also observed by Trindade-Santos et al. (2018), simulating shifts in taxonomic and functional β -diversity of ray-finned fishes.

In the present study, taxonomic and functional turnover presented similar values, and both were comparatively higher than the nestedness-resultant component. Some evidence indicates that species turnover is consistently the larger component of total β -diversity (Soininen et al. 2018), and this also suggests that a difference in richness often plays a smaller role in the generation of β -diversity patterns (Viana et al. 2016, Hill et al. 2017). Species turnover may reflect species sorting by the environment or dispersal processes, whereas nestedness is often related to ordered extinction–colonization dynamics (Si et al. 2016). Moreover, functional nestedness was higher than taxonomic nestedness, suggesting that the loss of functional attributes is greater than the loss of species. Taxonomic diversity losses could affect functional diversity, depending on the position of each species in the functional space. A decrease in the functional space of the community can be expected if a species that has extreme combinations of functional characteristics is eliminated (Mouillot et al. 2013). Differentiated patterns of nestedness between taxonomic and functional β -diversity may sug-

Table 4. Results of the multiple regression models for the functional β -diversity and its turnover and nestedness components (dependent variables) and the environmental variables (predictors). Significant coefficients (b , slopes) and their p -values are highlighted in **bold**

	β -diversity $R^2 = 0.19$; $F_{16, 479} = 7.1$ $p < 0.00001$		Turnover $R^2 = 0.20$; $F_{16, 479} = 7.6$ $p < 0.00001$		Nestedness $R^2 = 0.15$; $F_{16, 479} = 5.5$ $p < 0.00001$	
	b	p	b	p	b	p
Intercept	0.665	0.001	0.406	0.001	0.258	0.001
Temperature ($^{\circ}\text{C}$)	0.020	0.001	0.027	0.014	-0.007	0.470
Salinity	0.016	0.003	0.020	0.050	-0.004	0.680
Dissolved oxygen (mg l^{-1})	-0.018	0.004	-0.023	0.050	-0.005	0.656
Turbidity (NTU)	-0.001	0.812	-0.001	0.924	-0.000	0.972
pH	-0.001	0.850	0.012	0.262	-0.013	0.185
Carbon (g dm^{-3})	-0.011	0.153	-0.035	0.020	0.023	0.088
Total nitrogen (%)	0.011	0.010	0.031	0.001	-0.020	0.015
Total phosphorus (mg dm^{-3})	0.005	0.396	0.000	0.966	0.004	0.656
% Very coarse sand	0.020	0.018	0.019	0.200	-0.000	0.973
% Coarse sand	0.051	0.001	0.100	0.001	-0.049	0.016
% Medium sand	0.001	0.756	-0.005	0.632	0.007	0.484
% Fine sand	0.005	0.589	0.049	0.008	-0.044	0.011
% Very fine sand	-0.022	0.003	-0.030	0.034	0.007	0.555
% Clay and silt	0.004	0.670	-0.079	0.001	0.084	0.001
Wave exposure	0.002	0.692	0.013	0.2890	-0.011	0.355
Dean parameter (Ω)	-0.000	0.592	0.002	0.2199	-0.002	0.100

gest that the few species with extreme combinations of treatments were lost, leaving behind species with combinations of common traits. This emphasizes that modifications in taxonomic diversity provide only a limited picture of the ecological implications of changing biodiversity. The changes extend far beyond just numerical losses or species additions, but carry significant ecological consequences, with an increase in the functional similarity between assemblages. The contrasting nestedness-resultant components of taxonomic and functional β -diversity demonstrate the importance of considering the multifaceted nature of biodiversity when examining community assemblages.

The test of randomness indicated that the correlations between taxonomic and functional β -diversity and their components did not significantly differ from the null expectations of randomness, suggesting that there is no evidence of influences of niche filtering in the assemblages for the traits used in the analysis. However, the predominance of turnover can indicate that the localities differ in environmental heterogeneity by selecting different species. Therefore, it can be concluded that fish assemblages may have substituted species with different functional attributes in the different localities, with these species being functionally distinct and organized at random.

When we removed the effect of the geographic distance between sites, there were no differences in the

correlations between functional β -diversity and taxonomic β -diversity or between their components, indicating that the distances between the localities did not influence the β -diversity in this study, which was carried out at the local scale. This is not in accordance with the general pattern that the similarity in species composition between 2 sites typically decreases as the distance between them increases, since nearby sites tend to be more similar in their environmental conditions than more distant sites (Rouquette et al. 2013). However, the correlation between taxonomic nestedness and functional nestedness was lower when the effect of the difference in the number of fish species was removed, indicating that the difference in the number of species influences the nestedness component. Other studies (e.g. Leprieur et al. 2009, Baselga et al. 2012, Loiseau et al. 2017) have also confirmed the influence of the number of species on the nestedness component of β -diversity.

In general, β -diversity increases with habitat heterogeneity and fragmentation, and therefore lower β -diversity is expected in marine ecosystems than in terrestrial and freshwater ecosystems (Soininen et al. 2007, Henriques et al. 2017b). Changes in species diversity may be common in ecosystems that are composed of a mosaic of different habitats. Such differences in habitats within ecosystems can facilitate each other through structural complementarity and

through exchange of material and energy across habitats (Alsterberg et al. 2017). In relation to the fish assemblage of coastal areas, bays tend to provide shallow sheltered habitats for juvenile fishes in a fluctuating physicochemical environment, whereas oceanic beaches usually provide high energy but stable physicochemical habitats for small fishes that can withstand turbulent waters (Azevedo et al. 2017).

A differentiated spatial pattern was observed when analysing the variations in the mean functional β -diversity and its decomposition with respect to the sampling periods at each location. A predominance of functional turnover was found at B2, B3 and OC, whereas functional nestedness predominated at B1. Differences in the environmental conditions at the 4 localities seem to have resulted in differences in functional β -diversity, although the explanation of the relationship with environmental variables was low for functional β -diversity ($R^2 = 0.19$) and its turnover ($R^2 = 0.20$) and nestedness ($R^2 = 0.15$) components. Some environmental variables related to functional turnover may indicate a weak but significant relationship between this component and the environmental variables (e.g. temperature, salinity, carbon, total nitrogen, % coarse, fine and very fine sand, and % clay and silt). The low explanation of environmental variables may suggest multiple factors influencing the differentiated spatial pattern observed in the functional β -diversity (Henriques et al. 2017a,b). In this sense, Teichert et al. (2018) provided evidence that estuarine characteristics and biogeographic, hydroclimatic and land cover conditions also influence β -diversity patterns.

Environmental stress or disturbance in this coastal system can favour the formation of communities with a combination of common characteristics, and functional diversity has been used to determine how diversity may be affected (Araújo et al. 2016, Dolbeth et al. 2016, Azevedo et al. 2017). Anthropogenic activities in Sepetiba Bay, which are more intense at B1, where a large number of species may become unable to survive without being replaced by other species, may be one of the explanations for the predominance of functional nestedness at this locality, reflecting a process of functional attribute loss as a consequence of any factor that promotes the orderly disaggregation of assemblages. Nestedness of species assemblages occurs when the biotas at sites with smaller numbers of species are subsets of the biotas at richer sites (Wright & Reeves 1992, Gaston & Blackburn 2000, Ulrich & Gotelli 2007). Thus, fish with certain traits that are sensitive to particular environmental conditions locally disappear, but

generalist/resistant species can still exist, leading to a dominant nestedness component in functional β -diversity.

Decomposing β -diversity into turnover and nestedness helped to identify the processes behind the variation in assemblages. This was necessary because β -diversity indices are unable to distinguish patterns of species substitution and loss (Baselga 2010, 2012, Baselga & Leprieur 2015). However, the causes of nestedness or spatial turnover and their biological implications of species loss or species replacement are always completely different because each case can be caused by different historical or environmental factors. Linking the causes and consequences of biodiversity change is complex because species assemblages are simultaneously shaped by many factors, including disturbance, environmental heterogeneity, deterministic niche factors and stochasticity (Mori et al. 2018). The occurrence of another factor affecting functional turnover at sites B2, B3 and OC may mean that the assemblages host different functional strategies derived from seascape connectivity based on the proximity between juvenile and adult habitat patches (see also Nagelkerken 2009, Sheaves 2009, Olds et al. 2018). Baselga et al. (2012) suggested that nested patterns are caused by species losses caused by physiological constraints, whereas turnover seems to be associated with speciation, concluding that the new threshold-based view may help reveal the role of historical factors in shaping β -diversity patterns. In tropical seascapes, links between habitats are particularly important for mobile organisms, such as fish, which move among habitats to spawn, disperse, feed and seek refuge from predators (e.g. Nagelkerken 2009, Sheaves 2009, Igulu et al. 2014). These connections also promote an increase in functional attributes due to the presence of occasional species, which are species with a low frequency of occurrence and low abundance, using the environment occasionally and coming from adjacent areas.

The fish assemblages on the south coast of Rio de Janeiro may show the predominance of species substitution from site to site, being functionally distinct and organized at random, with no selective environmental filtering of species. We might conclude that there is an environmental pattern that may partially explain the differences in the components of functional β -diversity but that there is no evidence of influences of environmental filtering in the assemblages for the traits used in the analysis. There is a large unexplained part of the data variation that may be due to chance, biotic interactions or other unmeasured factors.

Our study is a step forward in understanding functional β -diversity in nearshore fish communities along the southeastern Atlantic coast. Estuarine areas, such as bays, tend to provide shallow sheltered habitats for juvenile fishes in a fluctuating physicochemical environment, whereas oceanic beaches usually provide high energy but stable physicochemical habitats for small fishes that can withstand turbulent waters (Araújo et al. 2016, Borland et al. 2017). There is an urgent need for the further exploration of the dynamics between trait-based functional diversity and ecosystem functioning. The conservation of coastal and marine habitats has been driven in part by mediating the effects of habitat loss on declines in species richness; however, such actions are often insufficient. Several coastal fish populations have undergone declines in abundance and diversity during recent decades (Araújo et al. 2016). Management of these systems requires the protection of different habitats, and conservation measures should support the heterogeneity of biological assemblages. This research helps to assess the assembly rules on the functional facets of biodiversity and advances our understanding of species responses to environmental variation at the local scale, which is important for ecosystem-based management of coastal fishes.

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