

Multilevel decomposition of spatial and environmental effects on nearshore fish assemblages in tropical semi-enclosed ecosystems

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ABSTRACT

We investigated the effects of local- and landscape-scale environmental variables and spatial structure at three hierarchical levels (i.e. type of system, individual systems, and zones within each system) on the fish species composition and abundance in bays and coastal lagoons in southeastern Brazil. The effects were assessed at the assemblage level, and between and within habitat use groups. Exclusive and shared effects of environmental, hierarchical, and spatial variable sets were quantified by variation partitioning, and individual environmental effects were assessed by partial canonical correspondence analyses. The hierarchical and spatial structures were more relevant for habitat use groups less widespread due to the lower dependence on estuarine areas, and influenced primarily the landscape-scale environmental differences between individual systems. At the assemblage level, the exclusively environmental effects were primarily indicative of the marine (e.g., higher depth, pH, and transparency) versus continental (e.g., greater distance from the ocean and mangrove cover) influence. Estuarine, marine migrant, and marine straggler species were more widespread across these gradients, but the former species were primarily associated with greater mangrove cover and the marine stragglers with a higher marine influence. Semi-diadromous and freshwater species were less associated with greater mangrove cover and primarily restricted to coastal lagoons. The different multi-scale environmental effects within each group reinforced the relevance of intra- and inter-specific differences in environmental tolerances and requirements, and evidenced the relevance of the connectivity between alternative habitats in maintaining the structure of fish assemblages. Disentangling multilevel spatial and environmental effects, this study evidenced the critical roles of the maintenance of the environmental heterogeneity in nearby estuarine habitats for nearshore fish assemblages in different types of tropical semi-enclosed estuarine ecosystems.

1. Introduction

Coastal areas include semi-enclosed ecosystems with different levels of marine and continental influences, such as estuaries, coastal lagoons, and bays (Potter et al., 2010; Duck and da Silva, 2012; Azevedo et al., 2017). These semi-enclosed coastal ecosystems may act as alternative migration routes and shelter for fish species, providing nursery, feeding and spawning areas during their life cycles (Elliott et al., 2007; Liquete et al., 2013). Understanding the environmental drivers of the structure of fish assemblages in coastal areas is, therefore, of major relevance especially in the face of cumulative human impacts on food webs and ecosystem functioning (Halpern et al., 2015; McCauley et al., 2015). However, the effective identification of species-environment relationships is a big challenge for ecologists because many species undergo

ontogenetic changes on habitat use (Ray, 2005; Sheaves et al., 2015), and different species may present pronounced differences in the degree of dependence on estuarine areas (Able, 2005; Potter et al., 2015). Therefore, studies incorporating wide ranges of environmental conditions, such as different landscape components and ecosystems, may be helpful to elucidate the main environmental drivers of the habitat use by different coastal species (e.g., Honda et al., 2013; Baker et al., 2018).

Different physiological tolerances and degrees of dependence on estuarine areas characterize coastal fishes, with some species widely spread over coastal areas and others restricted to habitats with higher freshwater or marine influence (Elliott et al., 2007; Blaber and Barletta, 2016). Freshwater- and marine-origin species that spend their life cycle entirely or partially in estuarine habitats are expected to be more abundant in semi-enclosed ecosystems than those species that do not

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depend on estuarine habitats to complete their life cycles (Potter et al., 2015). Marine-origin species that spend only particular phases of the life cycle in estuarine habitats, in turn, are expected to be present or abundant in some periods throughout the year according to specific life-cycle requirements of their individuals (Potter et al., 2015). Therefore, the abundances of fish species in semi-enclosed ecosystems reflect the habitat suitability for specific environmental tolerances and requirements in different phases of their life cycles (Galaiduk et al., 2018). As a consequence, great changes in the species composition during annual cycles characterize the fish assemblages in semi-enclosed ecosystems (Castillo-Rivera et al., 2010; Lacerda et al., 2014).

Coastal lagoons and bays are characterized by large environmental differences primarily associated with the degree of connection with the open ocean, with the former presenting more expressive salinity gradients and lower depth due to limited connection, and the latter with a greater environmental heterogeneity associated with the higher depth, number of nearby estuaries, and susceptibility to the effects of tides, waves, and oceanic currents (Azevedo et al., 2017; Franco et al., 2019). Therefore, a better understanding of the mechanisms associated with assembly processes in these semi-enclosed ecosystems may be achieved by considering the variation in the species composition and abundance associated with species groups that have different degrees of dependence on estuarine habitats (e.g., Nicolau et al., 2010; Harvey et al., 2013; Franco and Santos, 2018). These approaches may especially benefit studies focused on the diverse tropical fish fauna (e.g., Araújo et al., 2016) and different types of coastal habitats (e.g., França et al., 2011; Honda et al., 2013).

Landscape features and then local environmental conditions act as hierarchical filters that select species for the local assemblages from the regional pool, which is previously restricted by environmental filters in larger spatial and temporal scales (Ricklefs, 2004; Leprieur et al., 2011). As a consequence, environmental effects and/or the assemblage structure are commonly scale dependent, with the observed patterns and the relevance of species-environment relationships varying between hierarchically nested spatial scales (Henriques et al., 2017; Camara et al., 2019). Likewise, as a result of processes not accounted for, surrounding localities may have correlated environmental measures (Legendre, 1993; Borcard et al., 2004). The aforementioned processes may include biotic interactions and historical contingencies, such as climate changes and sea-level oscillations that shaped coastal areas in the historical time (Macieira et al., 2015). In all cases, the observations are not independent and controlling for the hierarchical and spatial structure of data is imperative to identify effective species-environment relationships (Borcard et al., 1992; Legendre and Gauthier, 2014). Therefore, disentangling the spatial structure and environmental effects across hierarchical spatial scales may provide a better understanding of the multiple ecological factors and processes influencing the fish assemblages in different coastal ecosystems (e.g., Vilar et al., 2013; Camara et al., 2019).

We investigated environmental effects measured at the local and landscape scales and the influence of the spatial structure at three hierarchical spatial scales, herein named hierarchical levels (i.e. type of system, individual systems, and zones within each system), on the composition and abundance of fish species in two types of semi-enclosed coastal ecosystems (i.e. bays and coastal lagoons) in southeastern Brazil. The study was based on fish assemblages inhabiting shallow areas with unconsolidated substrates in the nearshore waters. Species were also classified into groups according to their habitat use to better investigate whether their degrees of dependence on estuarine areas are associated with the hierarchical structure of environmental and spatial effects. Considering that habitat use also varies between individual species, we also investigated the variation of the responses within the species groups. Based on the hierarchical organization of the environmental constraints and spatial structure, we considered the following hypotheses: (1) as higher the degree of the species dependence on estuarine areas, less spatially and hierarchically structured is the variation in species composition and abundance; (2) at the assemblage level, the

environmental effects are strongly associated with the hierarchical and spatial structures; (3) the environmental effects are less hierarchically and spatially structured within habitat use groups with higher degree of dependence on estuarine areas; (4) the exclusively environmental effects at the local scale are more relevant than those at the landscape scale to determine the within-group variation. For groups of fishes with differing habitat use we assessed the species responses to environmental variables after controlling for the hierarchical and spatial structures. This study aimed to identify the main environmental drivers of the structure of nearshore fish assemblages in tropical semi-enclosed ecosystems.

2. Materials and methods

2.1. Study area

The study area comprises semi-enclosed coastal ecosystems located along the coast of the Rio de Janeiro State, southeastern Brazil (Fig. 1a). The regional climate is tropical with the annual total rainfall (1000–1600 mm) primarily concentrated in the wet season (October to March), and annual mean temperature of 22 °C (Alvares et al., 2013). The semi-enclosed ecosystems include bays and coastal lagoons with different environmental conditions as a result of the different levels of marine and continental influences and human impacts (Camara et al., 2019).

Coastal lagoons have limited connections with the ocean and pronounced salinity gradients distinguishing zones with different levels of marine influence; while bays are more connected with the ocean and influenced by tidal regimes, and present smoother salinity gradients and greater diversity of habitats than coastal lagoons (Azevedo et al., 2017; Franco et al., 2019). Environmental differences are also supported by the reduced riverine input in the coastal lagoons, which is represented by small-size streams, most of them intermittent (Knoppers et al., 1991; Kjerfve et al., 1996), compared with the higher number of larger size estuaries flowing into the bays (Ribeiro and Kjerfve, 2002; Molisani et al., 2004). In addition to these environmental differences, coastal lagoons and bays are pooled within different portions of the study area (Fig. 1a). Therefore, there are three natural hierarchical levels, herein defined as follows: type of system, represented by the two sets of ecosystems (i.e. bays or coastal lagoons); system, represented by the individual ecosystems; and zone, the inner, middle, and outer areas of each ecosystem, which are respectively characterized by larger, intermediate, and shorter distances from the ocean (Fig. 1b).

2.2. Fish sampling

Samples were obtained in three periods during the 2017–2018 wet season (September, November, and January) in six ecosystems, three coastal lagoons (Maricá, Saquarema, and Araruama) and three bays (Guanabara, Sepetiba, and Ilha Grande) (Fig. 1a). For each of the three periods, fish sampling was performed at three sites in each of the three zones (i.e. inner, middle, and outer) of each ecosystem (Fig. 1b). For all cases, the sites were at least 200 m apart. A total of 162 samples were obtained at the sampling sites (3 sites × 3 zones × 3 periods × 6 ecosystems). In order to better characterize the environmental heterogeneity of each zone and ecosystem, sampling was performed at different sites whenever possible. For that reason, the zones were considered as the sampling units for analytical purposes, and the environmental and species data obtained at the site level were, respectively, averaged and sum up at the zone level, as described in the “2.5. Data analysis” subsection.

We sampled nearshore fish assemblages inhabiting shallow areas with unconsolidated substrates. Fishes were collected with a beach seine (12 × 2.5 m; 5-mm mesh size) set parallel to the shore at approximately 1.5-m depth, dragging for 30 m perpendicular to the shore (30-m long) and covering a swept area of about 300 m². Four replicates were obtained per site and period. The collected fishes were fixed in 10%

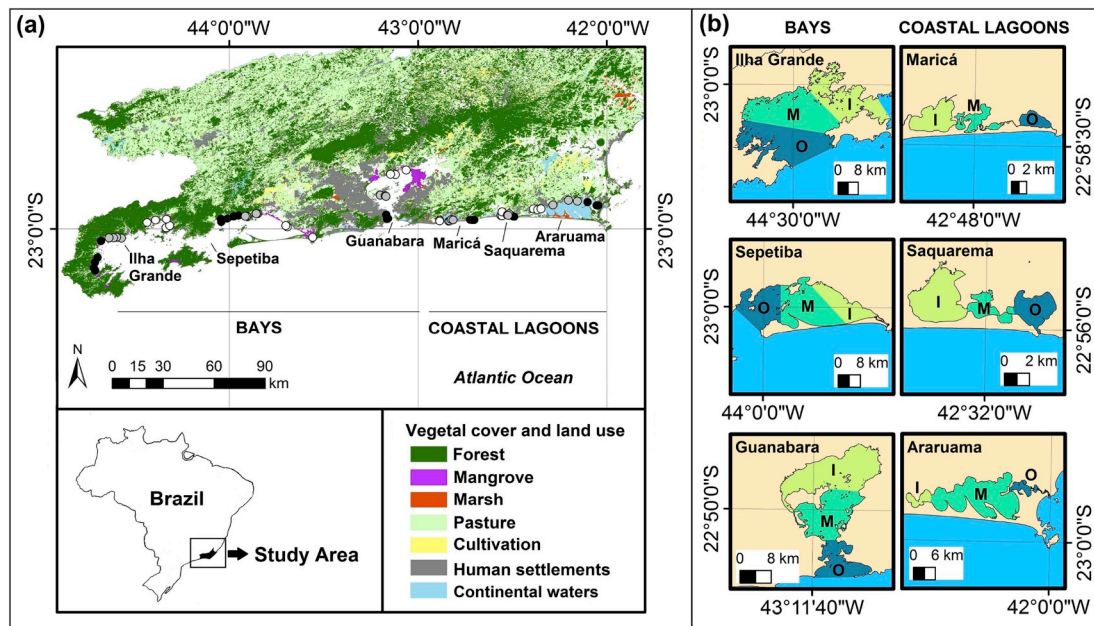


Fig. 1. Location of the (a) study area (bays and coastal lagoons) in the Rio de Janeiro State, southeastern Brazil. Sampling sites (circles) in the inner (white), middle (grey) and outer (black) zones of each ecosystem. The vegetative cover and land use types were considered for the land use metrics (within a 200-m radius buffer) for each site. Location of the (b) zones, inner (I; lime green areas), middle (M; blue-to-green areas) and outer (O; navy blue areas), in the bays (left panel; Ilha Grande, Sepetiba, and Guanabara) and coastal lagoons (right panel; Maricá, Saquarema, and Araruama). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

formalin, and after 48 h preserved in 70% ethanol. All fishes were identified at the species level, and vouchers specimens were deposited in the Ichthyological Collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro.

2.3. Environmental measures

2.3.1. Local-scale variables

At the local scale, environmental measures of water quality and substrate were recorded concurrently with the fish sampling. Salinity, pH, temperature ($^{\circ}\text{C}$), and dissolved oxygen (mg L^{-1}) were obtained with a HANNA HI 9829 multiprobe (HANNA Instruments, São Paulo, Brazil), depth (cm) was measured with a Speedtech model SM-5 digital probe (Speedtech Instruments, Great Falls, Virginia), and transparency (% Secchi depth/depth) was measured with a Secchi disk. The substrate type was classified considering the occurrence of clay + silt, fine sand, medium sand, coarse sand, gravel, and rocky bottom at three sampling points (1 m and 0.5 m depth, and at the spread washing zone). The substrate type was scored from 1 (clay + silt) to 6 (rocky bottom) and the mean value was calculated for each site.

2.3.2. Landscape-scale variables

The phases of the tide in the sampling periods were classified as flood, high, ebb, and low tide. The tidal influence was then scored from 1 (flood/high tide) to 2 (ebb/low tide). Other environmental variables at the landscape scale were metrics representative of land use and isolation obtained for each site, and morphometric features obtained for each zone using a geographical information system (ArcGIS v. 10.2; ESRI 2013). The geoprocessing procedures were based on vectorial layers of hydrography and land use (1:25,000 scale; 2015–2016) provided by a partnership between the Instituto Brasileiro de Geografia e Estatística (IBGE) and the Instituto Estadual do Ambiente do Estado do Rio de Janeiro (INEA). For each site and period, the land use metrics were obtained within a 200-m radius buffer. The limits of each zone were defined as the narrowest portions of the inlets from the outer to the inner area, and also considering the coastline entrances that represent

potential barriers for the water flow (Fig. 1b).

The land use metrics were firstly obtained as the total area (km^2) of native forest cover, mangrove cover, pasture cover, marsh cover, and human settlements within each of the 200-m radius buffers, and then calculated as percentages of the respective buffer area. Isolation measurements included the distance from the ocean (km), calculated as the distance of each site from the open ocean (i.e. the area immediately after the outer zone of the respective system; Fig. 1), and the number of nearby estuaries and the number of nearby rocky shores, calculated as the total number of estuaries and rocky shores, respectively, located within 5 km of distance from each site. The distance of 5 km was considered because it corresponds to approximately the shorter distance between sites in different zones. Morphometric features were represented by the zone area (km^2), calculated as the area covered by the water surface in each zone, and the total width of the connections between zones (km), calculated as the sum of the widths of the connections of a zone with its the adjacent zones.

2.4. Species groups

Species were classified into habitat use groups based on the functional guilds proposed by Potter et al. (2015) and, when necessary, complemented by specific information for the study area (Araújo et al., 2016; Blaber and Barletta, 2016; Petry et al., 2016). Considering the lack of ecological information for several species, we adopted a broader classification focused on the degree of dependence on estuarine areas at the family level and the main differences between the habitat use groups (Table S1). Therefore, the species were assigned to habitat use groups according to degree of dependence on estuarine areas, as follows: high dependence - (1) estuarine species, represented by species that spend the life cycle entirely or primarily in estuaries; intermediate dependence - (2) marine migrant species, corresponding to species that are frequently eurihaline and enter estuaries in large numbers typically during the juvenile life, and (3) semi-diadromous species, those species that spend one phase of the life cycle either in estuaries or the sea, and migrate between these areas for reproduction; and low dependence - (4) marine

straggler species, corresponding to species that are estenohaline and occur in low numbers in estuaries, and (5) freshwater species, represented by species that occur in low to high numbers in upper estuarine areas, but may spend the entire life cycles in freshwater environments.

2.5. Data analysis

We quantified the environmental effects at the local and landscape scales, and the influence of the spatial structure and hierarchical levels representative of ecologically relevant spatial scales on the variation in the species composition and abundance at the assemblage level and within groups of species defined according to the habitat use (i.e. estuarine, marine migrant, semi-diadromous, marine straggler, and freshwater). For each level of the species data (i.e. assemblage and habitat use groups), the spatial structure was quantified by a principal coordinates of neighbor matrices analysis (Borcard and Legendre, 2002; Borcard et al., 2004). The analysis was based on a distance matrix, calculated as the shorter aquatic distance between pairs of sites. Spatial variables were created by decomposing the original distances in eigenvectors (i.e. the new independent spatial variables). Only the PCNM eigenvectors with positive eigenvalues were used in the following analyses as proxies of dispersal processes or missing environmental variables that are spatially structured over the range of spatial scales encompassed by the sampling design (Borcard and Legendre, 2002). The analyses also included categorical variables for the hierarchical levels (i.e. type of system, system, and zone) and period. All analyses were based on the mean value of each environmental variable and the total abundance of each species per zone in each period.

Variation partitioning analyses were used to quantify the variation in the species composition and abundance at the assemblage level explained exclusively by each set of environmental variables (i.e. local- and landscape-scale variables), spatial structure, hierarchical levels or period, and the fractions explained by more than one data set (Borcard et al., 1992). Firstly, we investigated the effects of the hierarchical and spatial structure of the fish assemblages performing two types of variation partitioning: an analysis quantified the effects of each hierarchical level (i.e. type of system, system, and zone); a second analysis quantified the effects of spatial variables and non-redundant hierarchical levels in order to evaluate whether the spatial structure is associated with the ecologically relevant spatial scales represented by the hierarchical levels. Hierarchical levels without exclusive effects (i.e. those with all effects shared with the other hierarchical levels) were considered redundant, and were not included in the following analysis.

The environmental relationships were then investigated by three types of variation partitioning: an analysis quantified only the effect of the period; and independent analyses quantified the effect of the spatial structure and the additive effects of non-redundant hierarchical levels. For all cases, as the aim was to identify the exclusive and shared effects of each variable set, all environmental variables at the local and landscape scales were included in the variation partitioning. Considering that several species are restricted to a given type of system, individual system, or even zone, there is a compositional gradient characterized by null abundances varying across samples. Therefore, the variation partitioning was based on canonical correspondence analysis (CCA) that is appropriated for longer gradients resulting from expressive species replacement (Legendre and Gallagher, 2001).

The effects of individual environmental variables on the variation in the composition and abundance between of species from different habitat use groups were assessed by partial canonical correspondence analysis (pCCAs) including the spatial variables, hierarchical levels, and period as covariates to partial out their possible effects on the species-environment relationships (Legendre and Legendre, 2012). Therefore, four types of pCCA were performed: a pCCA including only the period as covariate; and pCCAs including also the spatial variables or the additive effects of non-redundant hierarchical levels as covariates. Due to the higher weights given to sites with higher total abundance in the CCA,

sites with many rare species may contribute more than sites with a few abundant species to the multiple regressions of the species on the environmental variables (Legendre and Gallagher, 2001). For that reason, in order to reduce the weight of rare species and emphasize the general responses of the groups, the pCCAs used Hellinger-transformed abundance data (Legendre and Gallagher, 2001).

Prior to running the pCCAs, we applied a variable selection using a forward stepwise procedure to identify a parsimonious subset of environmental constraints from the full CCA model (i.e. including all environmental variables). This forward procedure adds a variable at each step, and stops when the adjusted R^2 starts to decrease or overcomes the value of the full model, or the nominal p-value of 0.05 is exceeded (Blanchet et al., 2008). The same procedure was applied to identify relevant PCNM eigenvectors for modeling the spatial structure of the species data at the assemblage and group levels. The variance inflation factor (VIF) was calculated for the environmental variables selected for the final CCA model to measure the collinearity between the environmental predictors (Zuur et al., 2010). As the VIF was <2 for most variables and no variable presented $VIF >4$, the model was considered not biased by redundant environmental constraints (Zuur et al., 2010). Therefore, all the environmental variables selected for the final CCA model were included in the pCCA models.

As for the assemblage level, we also performed variation partitioning and independent pCCAs based on the species composition and abundance within each group of habitat use. The group-level variation was quantified because despite the Hellinger-transformed abundance data minimizing the influence of rare species on the CCA scores (Legendre and Gallagher, 2001), the species of some habitat use groups are generally more abundant than species of other groups. As a consequence, species from different groups contribute differentially for the analysis and the variation within groups may be captured more efficiently by removing the variation between groups. As with the assemblage-level analyses, we used Hellinger-transformed abundance data (Legendre and Gallagher, 2001) and forward stepwise procedures for variable selection (Blanchet et al., 2008), and calculated the VIF for the environmental variables selected for the final CCA models (Zuur et al., 2010). For all cases, the VIF values indicated that the models were not biased by redundant environmental constraints (Zuur et al., 2010).

In all analyses, the variation explained was expressed as values of the adjusted R^2 to provide unbiased estimates of the environmental, spatial, hierarchical, and temporal effects (Peres-Neto et al., 2006). The reliability of the fractions of the explained variation in terms of representing the variation that can be distinguished from random was estimated by permutational analysis of variance (999 permutations). For all pCCAs, the goodness of fit of the environmental variables (vectors) was measured by the squared correlation coefficient (r^2) that expresses the maximum correlation of the vectors with the ordination configuration (999 permutations; Oksanen et al., 2019). Only the environmental variables with higher correlations with the pCCA axes (considering the cut-off values of $r^2 > 0.1$ and nominal p-value < 0.05) were considered for ecological interpretation. All analyses were performed in the R environment (version 3.5.3; R Core Team, 2019) using functions contained in the *vegan* package (version 2.5–5; Oksanen et al., 2019).

3. Results

3.1. Hierarchical and spatial structure of the fish assemblages

At the assemblage level, the variation in the species composition and abundance associated with the hierarchical levels was negligible for the type of system, whereas most of the variation was exclusively associated with the system level (8%) and a smaller fraction was shared between both levels (5%; Fig. 2a). A smaller fraction was exclusively associated with the zone level (3%), followed by a fraction shared between all hierarchical levels (2%) and an even smaller fraction shared between the system and zone levels (1%; Fig. 2a). The spatial structure (i.e. the

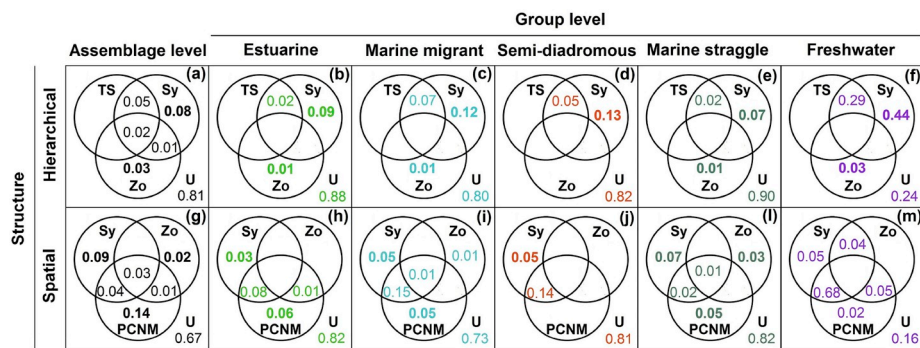


Fig. 2. Venn diagrams showing the results of variation partitioning analyses based on the species composition and abundance at the assemblage level and within the habitat use groups (estuarine, marine migrant, semi-diadromous, marine straggler, and freshwater species). Analyses performed on the exclusive and shared effects of (a–f) the hierarchical levels of type of system (TS), system (Sy), and zone (Zo), and (g–m) the spatial structure (PCNM; eigenvectors of the principal coordinates of neighbor matrices) and the hierarchical levels. Values (adjusted R^2) correspond to the fractions of explained and unexplained (U) inertia of the species data. Variation fractions with zero values not displayed. Only the hierarchical levels with non-negligible exclusive effects (i.e. adjusted $R^2 > 0$) were included in the variation partitioning analyses with the spatial structure. For the assemblage and group levels, values in bold for the testable fractions associated with the spatial structure and hierarchical levels with p-values (permutation F tests) < 0.05 .

PCNM eigenvectors) and the hierarchical levels with non-negligible exclusive effects (i.e. the system and zone levels) were associated with 33% of the variation in the species composition and abundance at the assemblage level (Fig. 2g). Most of the explained variation was exclusively associated with the spatial structure (14%), but a fraction of 9% was exclusively associated with the system level, and a smaller fraction with the zone level (2%; Fig. 2g). Considering the shared effects, larger fractions were associated with the system level and the spatial structure (Fig. 2g).

The exclusive effect of the type of system was also negligible for all habitat use groups and most of the variation was also exclusively associated with the system level, with a smaller fraction shared between both hierarchical levels (Fig. 2b–f). For all habitat use groups, an even smaller fraction, negligible for the semi-diadromous group, was exclusively associated with the zone level (Fig. 2b–f). The total variation associated with the hierarchical levels was higher for the freshwater group (76%) compared with the other habitat use groups, which had total explained variations not higher than 20% (Fig. 2b–f). A comparatively smaller fraction of the variation was associated with the spatial structure and the system and zone levels, except for the freshwater group (Fig. 2). Most of the 84% of the explained variation in the species composition and abundance within the freshwater group was shared between the system level and the spatial structure (68%; Fig. 2m). The fractions exclusively associated with the hierarchical levels and the spatial structure were negligible for this group (Fig. 2m).

A similar pattern to the freshwater group was observed for the semi-diadromous group, but only 19% of the variation in the species composition and abundance was explained and only the exclusive effect of the zone level was negligible (Fig. 2j). Most of the explained variation was also shared between the system level and the spatial structure for the estuarine, marine migrant, and marine straggler groups, but a relevant and more proportional contribution of the fractions exclusively associated with each data set was observed for these groups (Fig. 2h,i,l). The spatial structure explained more the variation than the system level only for the estuarine group (Fig. 2h), whereas the opposite was observed for the marine straggler group (Fig. 2l). The variation associated with the zone level was negligible for all habitat use groups (Fig. 2h–j,m), except for the marine stragglers (3%; Fig. 2l).

3.2. Spatial, temporal, and hierarchical environmental effects on the assemblage structure

Environmental variables at the local and landscape scales evidenced differences between bays and coastal lagoons (Table 1). At the local scale, coastal lagoons were characterized primarily by higher values of

salinity and pH, and slightly coarser substrate than bays, which, in turn, presented higher dissolved oxygen concentration, depth, and to a lesser extent transparency (Table 1). Considering the land use metrics, the greatest differences were related to the higher forest cover and pasture cover in bays and coastal lagoons, respectively (Table 1). Both types of system were characterized by higher percentages of human settlements compared with the other land use metrics. Larger environmental differences at the landscape scale were evidenced by morphometric features, with bays presenting zones with larger areas and wider connections between zones than coastal lagoons (Table 1). Differences were also evidenced by the isolation measurements, with the bays presenting higher distances from the ocean and greater number of nearby estuaries and nearby rocky shores compared with coastal lagoons (Table 1).

Landscape-scale variables explained more the variation in the composition and abundance of species (30%) than site-scale variables (16%), but a fraction of 13% was explained by both variable sets (Fig. 3a). The effect of the period was very slight and primarily associated only with the environmental effects at the landscape scale (3%; Fig. 3a). The effect of the spatial structure was mostly shared with the environmental effects (19%), with 12% of that fraction shared only with landscape-scale variables (Fig. 3b). Furthermore, the total variation associated with the spatial structure (22%) was higher than the exclusively environmental effects (14%; Fig. 3b).

The environmental effects were hierarchically structured primarily at the system level (11%; Fig. 3c), whereas the zone level added a fraction of 2% to the variation in the species composition and abundance associated with both environmental effects and hierarchical levels (Fig. 3d). The total fractions of the variation associated with the system level and the additive effect of the zone level were 16% and 19%, respectively, with smaller fractions exclusively associated each hierarchical level (Fig. 3c–d). For both cases, the pure environmental fractions were higher than the fractions associated with the hierarchical levels, and the hierarchical structure was primarily associated with the landscape-scale environmental effects (Fig. 3c–d). In all analyses, the fractions of the variation explained exclusively by the environmental effects were higher for the landscape-scale variables (Fig. 3).

3.3. Environmental determinants of the variation between habitat use groups

The constrained model resulting from the variable selection explained 23% of the total variation in the species composition and abundance, and included salinity, transparency, depth, pH, and dissolved oxygen as local-scale environmental variables, and distance from

Table 1

Environmental variables measured at the local and landscape scales. Codes, median, lower and upper quartiles of the samples obtained during the three periods in bays and coastal lagoons.

Variable	Code	Bays			Coastal lagoons		
		Quartiles			Quartiles		
		Median	Lower	Upper	Median	Lower	Upper
Local scale							
Salinity	Sa	30.5	26.6	32.5	34.3	30.1	40.9
pH	pH	8.4	8.3	8.6	8.7	8.4	9.0
Temperature (°C)	Te	26.8	24.6	27.6	26.9	25.4	27.8
Dissolved oxygen (mg L ⁻¹)	Ox	8.4	6.0	9.8	5.9	4.4	9.2
Depth (cm)	De	121.7	96.7	140.9	91.1	82.5	110.0
Transparency (%)	Tr	59	45	95	57	43	74
Type of substrate	Su	2.8	2.3	3.5	3.2	2.5	3.7
Landscape scale							
Tidal phase	TP	1.3	1.0	1.7	1.3	1.0	1.8
Land use metrics							
Forest cover (%)	FC	4	0	18	2	0	7
Mangrove cover (%)	MC	0	0	0	0	0	0
Marsh cover (%)	MrC	0	0	0	0	0	0
Pasture cover (%)	PC	1	0	7	9	8	14
Human settlements (%)	HS	32	24	43	32	16	36
Isolation measurements							
Distance from the ocean (km)	DO	31.3	25.8	32.9	9.0	3.7	21.4
Number of nearby rocky shores	RS	5	4	14	0	0	0
Number of nearby estuaries	Es	14	11	23	3	3	3
Morphometric features							
Zone area (km ²)	ZA	192.8	133.1	320.2	13.8	6.8	18.1
Total width of the connections between zones (km)	CZ	25.6	12.9	32.2	0.7	0.1	0.7

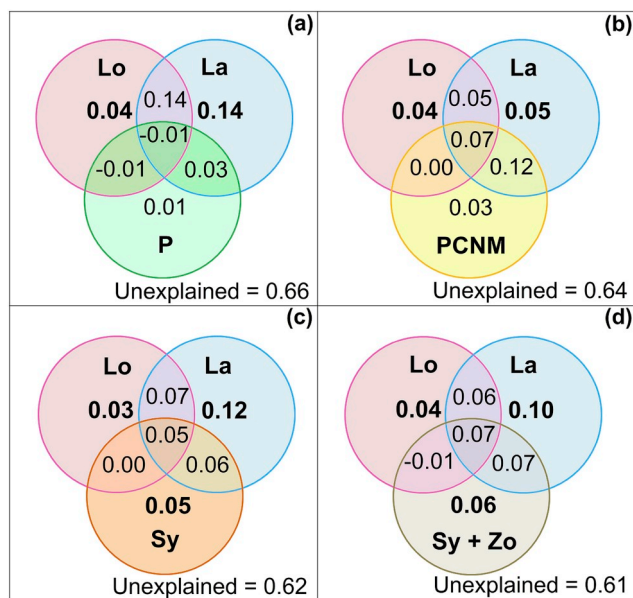


Fig. 3. Venn-diagrams showing the results of variation partitioning analyses performed on the exclusive and shared effects of the environmental variables at the local (Lo) and landscape (La) scales, and variables representative of (a) period (P) or (b) the spatial structure (PCNM; eigenvectors of the principal coordinates of neighbor matrices) or the hierarchical levels represented by (c) the system level (Sy) and the additive effect of (d) the zone level (Zo) on the composition and abundance of coastal fishes. Values (adjusted R^2) correspond to the fractions of explained and unexplained inertia of the species data. Values in bold for the testable fractions with p-values (permutation F tests) < 0.05 and < 0.01, represented by the exclusive environmental and hierarchical effects, respectively.

the ocean, number of nearby estuaries and nearby rocky shores, mangrove cover, forest cover, and total width of the connections between zones at the landscape scale (Table 2). Controlling only for the effect of the period, the pCCA model also explained 23% of the total

variation, but pH, transparency, forest cover, and mangrove cover were not relevant to explain the species-environment relationships (Fig. 4a). Wider connections between zones, higher number of nearby estuaries, distance from the ocean, and concentration of dissolved oxygen, and to a lesser extent a higher number of nearby rocky shores characterized two bays, and marine migrant species were primarily associated with these environmental conditions (Fig. 4a). Marine straggler species were also distributed across these gradients, but the most abundant and frequent species of the group were primarily associated with higher salinity and depth, which characterized other bay (Fig. 4a). The opposite gradients characterized the coastal lagoons, with freshwater species more abundant primarily in lower number of nearby rocky shores, depth, and salinity (Fig. 4a). To a lesser extent, estuarine and semi-diadromous species were also associated with the opposite gradients, but these groups were distributed across the environmental gradients and primarily associated with intermediate conditions (Fig. 4a).

The pCCA model explained 12% of the total variation after controlling also for the spatial structure (i.e. PCNM eigenvectors), and the environmental differences between different types of system were less evident (Fig. 4b). Only the number of nearby rocky shores and depth were still important compared with the analysis controlling only for the

Table 2

Local- and landscape-scale environmental variables selected for the constrained models based on the species composition and abundance at the assemblage and group levels. The values of adjusted R^2 indicate the variation explained by the set of selected variables in the canonical correspondence analyses. For variable codes see Table 1.

Species data	Selected variables		adj. R^2
	Local scale	Landscape scale	
Assemblage level	Sa, Tr, De, pH, Ox	DO, Es, RS, MC, FC, CZ	0.23
Group level			
Estuarine	Sa, Ox	DO, MC, CZ	0.14
Marine migrant	Sa, Tr, Te	DO, RS, MC, FC, PC, ZA, TP	0.24
Semi-diadromous	Sa, De, pH	DO	0.20
Marine straggler	Sa	RS, PC, ZA	0.07
Freshwater	Sa	MC, FC	0.62

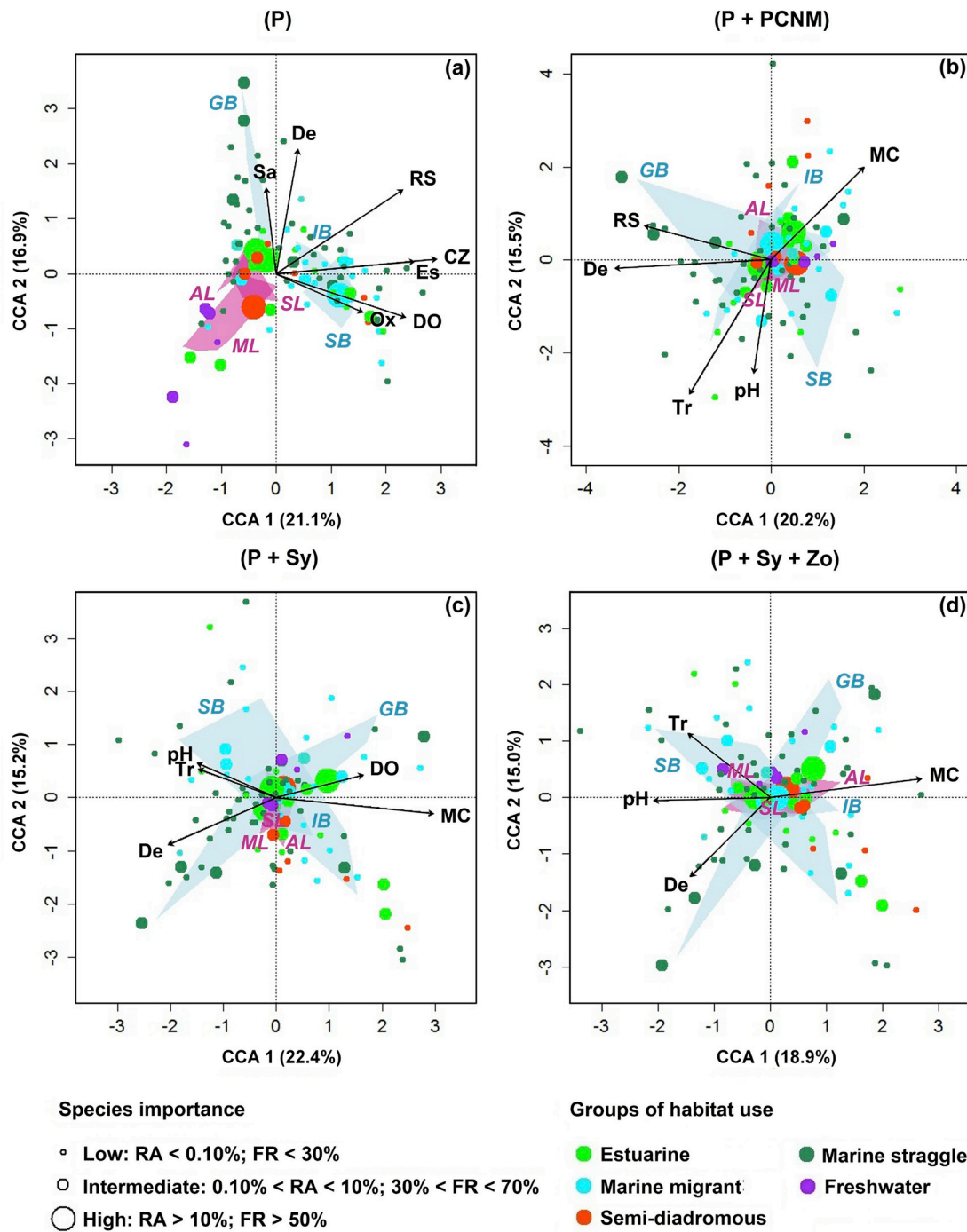


Fig. 4. Ordinations of the partial canonical correspondence analyses (pCCAs) showing the relationships between environmental variables at the site and landscape scales and species classified in groups of habitat use (estuarine, marine migrant, semi-diadromous, marine straggler, and freshwater). The pCCAs controlled for the effect of (a–d) the period (P), and the additive effects of the (b) spatial structure (PCNM; eigenvectors of the principal coordinates of neighbor matrices), or the hierarchical levels of (c) system (Sy) or (d) system and zone (Zo), and explained 23%, 12%, 12%, and 10% of the total variation, respectively. For all cases, p-values (permutation F tests) < 0.001. Arrows indicate the direction and strength of the environmental effects, with mean values at the origin. Only the environmental variables with higher correlation with the axes are displayed ($r^2 > 0.1$). The sizes of the symbols (colored circles) indicate the relative abundance (RA) and frequency (FR) of each species in the samples. Polygons represent the area covered by samples of the coastal lagoons (red-violet), Maricá (ML), Saquarema (SL), and Araruama (AL), and the bays (lightblue), Ilha Grande (IB), Sepetiba (SB), and Guanabara (GB). For variable codes see Table 1. More details regarding to the species identities and relevance presented in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

period effect (Fig. 4a–b). Higher values of these variables characterized primarily the bay previously associated with higher salinity and depth, and despite the marine straggler species had been distributed across other environmental gradients, the most abundant and frequent species of the group were still primarily associated with the that bay (Fig. 4a–b).

One of the most representative marine straggler species, as well as other less representative species, strongly associated with the mangrove cover (Fig. 4b). Freshwater species and the most frequent and abundant species of the marine migrant group were primarily associated with greater mangrove cover, but also with lower number of nearby rocky shores and

depth, and to a lesser extent lower transparency and pH (Fig. 4b). Other marine migrant species were more abundant in the opposite gradients, primarily in higher values of transparency and pH (Fig. 4b). Semi-diadromous species were also associated with higher mangrove cover and lower transparency and pH, but the most important species were primarily associated with intermediate environmental gradients (Fig. 4b). Estuarine species, in turn, were distributed across all gradients, except in higher number of nearby rocky shores and depth, but the most important species were also primarily associated with higher mangrove cover (Fig. 4b).

Controlling also for the effect of the system level in addition to the period, the pCCA model also explained 12% of the total variation, and the gradients of depth, transparency, and pH were opposite to the gradients of distance from the ocean and mangrove cover (Fig. 4c). Most marine straggler species were positively associated primarily with depth, but also transparency and pH (Fig. 4c). Some species of that group, including two of the most important, were associated with the opposite gradients and more abundant in higher values of mangrove cover and distance from the ocean (Fig. 4c). Marine migrant and estuarine species were widely distributed across all environmental gradients, but a slight increase in the importance of the positive effects of the mangrove cover and distance from the ocean was observed for both groups (Fig. 4c). The most abundant and frequent semi-diadromous species were still primarily associated with intermediate environmental gradients, and some less representative species with higher mangrove cover and lower transparency and pH (Fig. 4b). Freshwater species, in turn, were also more associated with intermediate gradients, but some species were associated with higher distances from the ocean and lower depth (Fig. 4c).

The opposite gradients of mangrove cover and pH, transparency, and depth were relevant to distinguish areas of lower and higher marine

influences, respectively, after controlling also for the effect of the zone level (Fig. 4d). The pCCA model explained 10% of the total variation and, altogether, the species of all groups, especially the marine migrant and marine straggler groups, were distributed across all gradients (Fig. 4d). Regardless of that, a slight higher importance of the positive effect of the depth, followed by transparency, was observed for most marine straggler species, and the most abundant and frequent marine migrant species were primarily associated with intermediate values of the gradients (Fig. 4d). Freshwater species were more abundant in higher transparency, whereas most estuarine and semi-diadromous species were associated with intermediate to higher values of mangrove cover, and lower transparency and pH (Fig. 4d).

3.4. Environmental effects on the within-group variation

Environmental effects at the landscape scale explained more the variation in the species composition and abundance within the habitat use groups than local-scale effects, except for the semi-diadromous group (Fig. 5). However, within all habitat use groups, almost half or most of the variation associated with the landscape-scale environmental effects was shared with the spatial structure or the hierarchical levels (Fig. 5). For all cases, the shared effects between the landscape-scale variables and the hierarchical levels, primarily the system level, were higher than the spatial effects (Fig. 5). The environmental effects at the local scale, in turn, had comparatively smaller fractions shared with the spatial and hierarchical structures, especially for the estuarine group (Fig. 5). These patterns were more evident for the variation within the freshwater group, which was highly associated with the landscape variables, strongly influenced by the spatial and hierarchical structures, and had very small fractions of the variation associated with local environmental effects (Fig. 5e). Higher fractions of the variation shared between

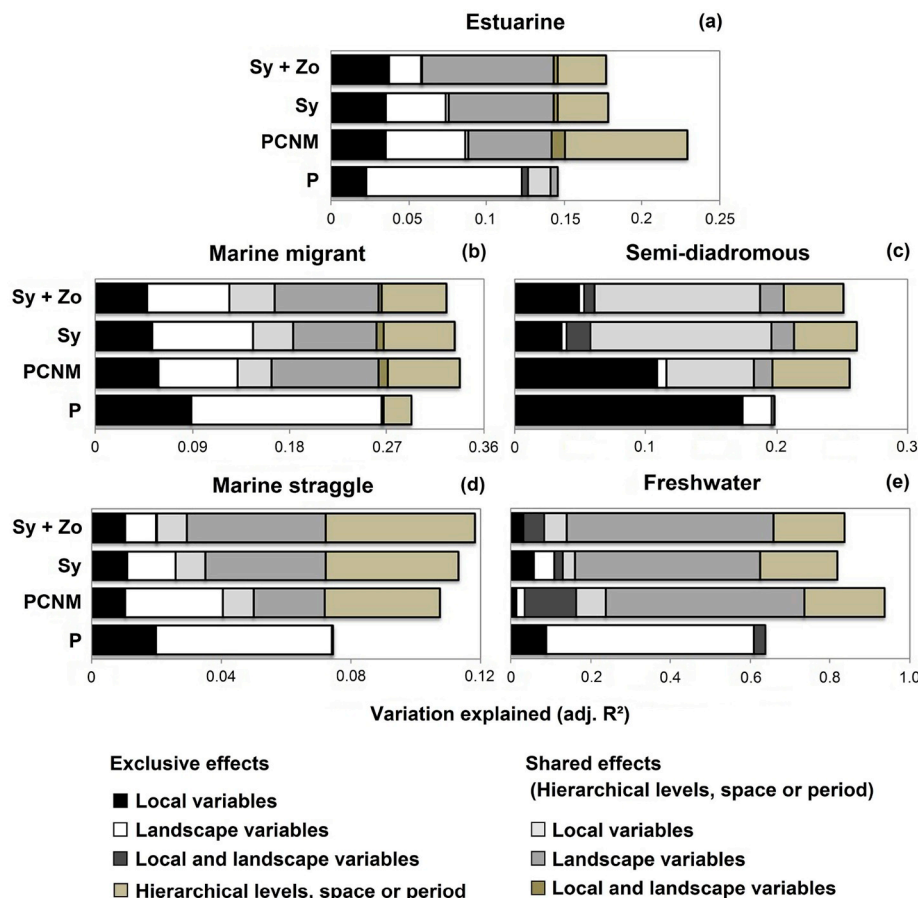


Fig. 5. Variation partitioning analyses (a–e) performed on the exclusive and shared effects of the environmental variables at the local and landscape scales, spatial structure (PCNM eigenvectors), and categorical variables representative of period (P) or the hierarchical levels of system (Sy) and zone (Zo) for the species composition and abundance within each group of habitat use (estuarine, marine migrant, semi-diadromous, marine straggler, and freshwater). The variation explained is expressed by values of adjusted R^2 . For all the testable fractions associated with environmental, spatial, and hierarchical effects, p-values (permutation F tests) < 0.05. For the fractions exclusively associated with the period, p-values (permutation F tests) < 0.01 only for the marine migrant group.

both environmental data sets were also observed within the freshwater group (Fig. 5e).

The landscape-scale effects on the variation within the semi-diadromous group, which was highly associated with the local-scale environmental effects, were very small (Fig. 5c). However, the local-scale effects were primarily shared with the hierarchical levels, especially the system level, and the spatial structure, which were strongly associated with the variation within the semi-diadromous group (Fig. 5c). The effect of the period was relevant only for the marine-migrant group, with a small fraction shared with environmental effects at the local and landscape scales and a greater fraction exclusively associated with the period (Fig. 5b).

Considering the effects of individual environmental variables, the variation in the species composition and abundance within the estuarine group was primarily associated with the mangrove cover and to a lesser extent with the distance from the ocean, salinity, and total width of the connections between zones (Fig. 6a). For all cases, the relevance of the environmental variables decreased after controlling for the spatial and hierarchical effects (Fig. 6a). The effect of the mangrove cover was primarily associated with the spatial structure, but also decreased after controlling for the effects of the hierarchical levels, primarily the system level (Fig. 6a). Among the other environmental variables, the width of the connections between zones had the highest decreases, with negligible environmental effects after controlling the spatial structure and the system effect (Fig. 6a). The effect of the salinity had proportional decreases after controlling for all spatial and hierarchical effects, whereas the effect of the distance from the ocean was primarily associated with the spatial structure and the system level (Fig. 6a).

For the marine migrant group, the variation in the species composition and abundance was explained by a greater number of local- and landscape-scale environmental variables with a proportional relevance (Fig. 6b). Stronger effects of the individual environmental variables were represented by the number of nearby rocky shores, followed by the zone area and distance from the ocean, with negligible effects observed after controlling for the spatial structure and hierarchical levels (Fig. 6b). Only for the distance from the ocean, a lower but non-negligible effect was observed after controlling for the system level, indicating that its effect was not dependent on the individual systems (Fig. 6b). The effect of the mangrove cover was slight and increased controlling for the effect of the system level, indicating that its effect was associated with the period, but not individual systems (Fig. 6b). Likewise, the increases in the effect of the tidal phase after controlling for the spatial structure and the additive effect of the zone level were indicative that its effect was influenced only by the period and individual systems

(Fig. 6b). Other environmental effects were comparatively slight and included temperature, transparency, salinity, and pasture cover (Fig. 6b). The effects of salinity and pasture cover were negligible after controlling for the spatial and hierarchical structure, whereas transparency and temperature had lower effects after controlling for the system level and the additive effect of the zone level, respectively (Fig. 6b).

Salinity, depth, and pH were the primary determinants of the variation in the species composition and abundance within the semi-diadromous group (Fig. 6c). The relevance of salinity and depth decreased after controlling for the spatial structure and especially the hierarchical effects (Fig. 6c). The zone level influenced the effect of the depth, but not salinity (Fig. 6c). The effects of pH increased controlling for the hierarchical levels, indicating that they were influenced by the period, but not by individual systems and their respective zones (Fig. 6c). The effect of the distance from the ocean on the variation within the semi-diadromous group was negligible (Fig. 6c).

The variation in the species composition and abundance within the marine straggler group was highly associated with the zone area and the number of nearby rocky shores, followed by salinity and pasture cover (Fig. 6d). The effects of the zone area and nearby rocky shores decreased strongly controlling for the spatial and especially hierarchical effects (Fig. 6d). A similar decrease was observed for the salinity effect, but it was slighter and a very small increase was observed after controlling for the additive effect of zone level (Fig. 6d). That increase was most likely indicative that the salinity effect was more influenced by the individual systems than their respective zones. The effect of the pasture cover, in turn, increased after controlling for the spatial and hierarchical effects, indicating that its effect was not spatially structured or scale dependent (Fig. 6d).

For the freshwater group, the variation in the species composition and abundance was primarily explained by the forest cover, followed by salinity and mangrove cover (Fig. 6e). The effect of the forest cover was not associated with the spatial structure, but decreased after controlling for the effects of the hierarchical levels, both the system and zone levels (Fig. 6e). The effect of the salinity was associated with the spatial structure, but it decreased more controlling for the hierarchical levels (Fig. 6e). A similar trend was observed for the effects of the mangrove cover, but with a stronger decrease and negligible effects observed after controlling for the spatial structure and the hierarchical levels, respectively (Fig. 6e).

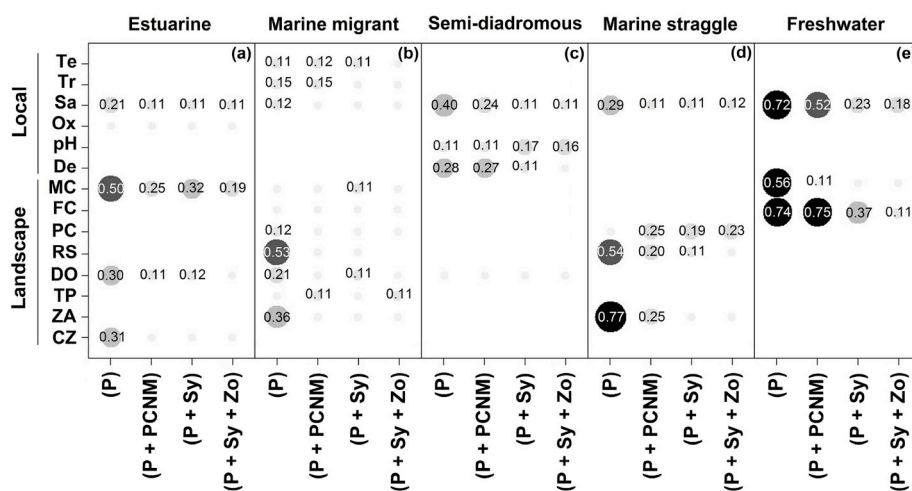


Fig. 6. Influences of individual environmental variables measured at the local and landscape scales on the variation in the composition and abundance of species within the habitat use groups. The values indicate the square of the correlation coefficient between each variable and the two first relevant axes of the ordinations of the partial canonical correspondence analyses (pCCAs). Only the values of environmental variables with higher correlation with the axes are displayed ($r^2 > 0.1$). The sizes and colors of the circles indicate the relevance of the variables to explain the variation in the species composition and abundance, with higher sizes and darker colors indicative of a greater relevance. The pCCAs controlled for the effect of the period (P), and the additive effects of the spatial structure (PCNM eigenvectors) and the hierarchical levels of system (Sy) and system and zone (Zo) on the variation within the groups of (a) estuarine, (b) marine migrant, (c) semi-diadromous, (d) marine straggler and (e) freshwater species. For variable codes see Table 1.

4. Discussion

The relevance of multilevel approaches for a better understanding of the major determinants of the structure of nearshore fish assemblages in semi-enclosed ecosystems was evidenced by the large fractions of the explained variation shared between the hierarchical levels (i.e. ecologically relevant spatial scales), the spatial structure (i.e. spatial variables), and environmental variables. The spatial structure expressed correlated environmental measures between neighbor zones (Legendre, 1993), whereas the hierarchical structure is indicative of ecological processes that, spatially structured or not, influence the assemblage patterns in the nested spatial scales (Cushman and McGarigal, 2002). Therefore, their shared fractions represent spatially-structured effects primarily within individual systems and, to a lesser extent, their respective zones. The fractions of the explained variation that were associated exclusively with the spatial structure are otherwise indicative of spatially-structured patterns resulting from multi-scale processes, such as biotic interactions, other unmeasured environmental effects, and/or stochastic processes, in other scales than the system and zone levels (Macieira et al., 2015; Ford and Roberts, 2018). For the hierarchical levels, in turn, these non-shared fractions are indicative of unmeasured environmental effects that are not spatially structured within the system and zone levels. The aforementioned relationships are most likely not primarily dependent on the type of system (i.e. bay or coastal lagoon) because its effects were totally redundant with the system and zone levels, which, in turn, had higher exclusive effects.

At the assemblage level, due to the greater importance of the non-shared effects between the hierarchical and spatial structures, their respective shared effects with the environmental variables are most likely only spatially or hierarchically structured. Therefore, most structured environmental effects, which were primarily at the landscape scale, are spatially structured at scales other than the system and zone levels, or only hierarchically structured, acting as filters primarily in the individual systems and, to a lesser extent, zones, to select species from the same regional pool of species (Henriques et al., 2017; Araújo et al., 2018). Considering the similar fractions of the variation exclusively associated with the hierarchical levels or shared with environmental variables in terms of the concept of environmental filters, it is likely that the missing environmental effects at the system and zone levels are represented primarily by variables at the landscape scale (e.g., mouth width and flow rate of estuaries) and local scale (e.g., biotic interactions), respectively (Mouchet et al., 2013; Vasconcelos et al., 2015). The large fraction of unexplained variation at the assemblage level, in turn, was most likely influenced by unmeasured factors and stochastic processes in smaller or larger spatial and temporal scales than that encompassed by the sampling design, as supported by several studies worldwide (e.g., Leprieur et al., 2011; Ford and Roberts, 2018).

For the explained variation within the habitat use groups, the fractions shared between the system level and the spatial structure, generally higher than their exclusive effects, were indicative of the selection of species by environmental filters distinguishing primarily the types of system (i.e. bays and coastal lagoons), but acting within individual systems (Table 1; Table S2). This is in accordance with the known importance of system-scale variables to explain ecological processes in estuaries and coastal lagoons, evidenced by several studies elsewhere (e.g., Pérez-Ruzafa, Mompeán, and Marcos, 2007; Sheaves and Johnston, 2009; França et al., 2011; Teichert et al., 2018). These studies highlight primarily the relevance of differences in morphometric and hydrological features, which indeed was observed especially between bays and coastal lagoons, but also between individual systems (Table 1; Table S2). As expected, the variation associated with both the spatial and hierarchical structures increased from the estuarine to the freshwater group. The habitat use groups more dependent on estuarine areas are typically able to withstand wider ranges of environmental conditions, which culminate in more widespread distributions across alternative estuarine habitats compared with the freshwater group, typically restricted to

areas under higher riverine input influences (Elliott et al., 2007; Reis et al., 2016). In this sense, the lower influence of the spatial and hierarchical structures on the variation within the marine straggler group compared with the freshwater group is most likely a result of the sporadic and random dispersal of different species of the former group across estuarine habitats (Potter et al., 2015). Furthermore, the exclusive effect of the zone level only on the marine straggler group, composed by a large number of very rare species, is most likely a result of its primary occurrence in the middle-outer zones of the systems, areas with higher marine influence.

The less hierarchically and spatially structured environmental effects within the estuarine and marine migrant groups are most likely a result of the larger environmental tolerance and the different habitat requirements associated with the high taxonomic diversity, respectively, culminating in wider distributions across the high-variability estuarine gradients (Elliott et al., 2007; Reis et al., 2016). For the semi-diadromous, in turn, the highly hierarchically structured environmental effects are most likely a result of its migrations from the sea to the upper portions of estuaries, and vice versa (Elliott et al., 2007). Therefore, despite both the semi-diadromous and the marine migrant species have intermediate dependence on estuarine areas and are subjected to ontogenetic shifts that determine expressive differences in habitat requirements during their life cycles, the former group inhabits in more specific environmental conditions than the marine migrants (Potter et al., 2015). Evidences in this sense were provided by the prevalence of the local-scale environmental effects on the variation only within the semi-diadromous group (Fig. 5c). Furthermore, the ecological range of environmental conditions suitable for the semi-diadromous group is most likely also restricted by the small number of species, taxonomic genera, and families (Ariidae, Mugilidae, Centropomidae, and Engraulidae; Table S1).

The responses of individual species to environmental variables were primarily in accordance with their habitat uses, despite the variation resulting from differences in their specific ecological requirements and the intra-specific variation associated with the phases of their life cycles (Reis-Filho et al., 2019). The responses associated with the habitat uses were primarily supported by the most abundant and frequent species of the respective groups (Fig. 4). Therefore, despite the wide distribution of several species regardless of their habitat uses, considering the most frequent and abundant species, all habitat use groups were primarily associated with environmental conditions aligned to their respective habitat requirements. In this sense, the strong influence of the spatial and hierarchical structures was evidenced by the primary association of both the marine migrant and the marine straggler species were with bays (Fig. 4a). However, the former species were primarily abundant in the two bays with a greater continental influence (i.e. higher distance from the ocean and number of nearby estuaries) and wider connections between zones, and the marine stragglers in the bay with greater marine influence (i.e. higher depth and salinity). Likewise, notably freshwater and to a lesser extent semi-diadromous species, were more abundant in coastal lagoons, primarily in lower depth, salinity, and number of nearby rocky shores (Fig. 4a). Previous studies also supported the relevance of multiple-scale differences in the habitat heterogeneity between bays and coastal lagoons to distinguish fish assemblages at the taxonomic and functional levels (Azevedo et al., 2017; Camara et al., 2019).

Despite less evident, the primary differences between bays were also supported by the species-environment relationships after controlling for the hierarchical and spatial structures (Fig. 4b–d). These differences were related to the opposite gradients of higher transparency, pH, and depth in areas under major marine influence, and greater mangrove cover in areas where the riverine outflow balance the marine influence. Although less evident, considering the most frequent and abundant species of each habitat use group, the species responses still reflected their habitat requirements. For instance, the most frequent and abundant marine migrant and marine straggler species were primarily associated with greater mangrove cover and higher marine influence,

respectively. However, the wide distribution of other marine migrant and marine straggler species across the aforementioned gradients also evidences ecologically meaningful group-level relationships. In this sense, the mangrove cover is favoring higher abundances of species with different habitat uses, including marine straggler species that randomly occupy mangrove areas, most likely by providing more complex habitats and the resources necessary for fish refuge (Whitfield, 2017; Reis-Filho and Leduc, 2018). Likewise, regardless of the higher dependence on estuarine areas, species of the marine migrant group usually spend most of their life cycles in the marine environment (Potter et al., 2015). Therefore, the less evident group-level responses for the marine straggler and marine migrant groups were most likely related to opportunistic behavior of some species occupying the mangrove areas and inter-specific differences in the prevalent phases of the life cycles of their individuals during the sampling period, respectively.

The mangrove cover was not the most extensive vegetated cover in the study area and was primarily restricted to bays, corresponding to an alternative estuarine habitat much less available compared with nearby estuaries (Table 1; Table S2). Regardless of that, most estuarine species, followed by semi-diadromous and, to a lesser extent, freshwater species, were associated with intermediate to higher values of mangrove cover. This is a pattern supported by other studies worldwide, which observed that the mangrove and nearby areas support a greater functional diversity regardless of the strong effect of the geographical position on the taxonomic composition (Hemingson and Bellwood, 2018; Reis-Filho et al., 2019). In addition, the lower transparency in mangrove areas, as observed in this study, is a result of the higher structural complexity provided by the mangrove prop roots and larger amounts of organic matter compared to non-vegetated coastal areas, environmental conditions that reduce the predation risk, providing safer breeding and/or nursery areas (Whitfield, 2017; Reis-Filho and Leduc, 2018). The less evident associations for semi-diadromous and primarily freshwater species were otherwise a result of their occurrences more restricted to coastal lagoons, whereas the mangrove cover is primarily greater near to bays.

Contrary to the mangrove cover, other alternative habitats may represent primarily the existence of non-suitable areas for the typical fish fauna of shallow areas with unconsolidated substrate. That is the case of areas with consolidated substrate represented by rocky shores, which typically harbor well-defined assemblages, with large fishes and top-predators highly associated with these habitats (Reis-Filho et al., 2019). As a consequence, species associated with rocky shores are expected to occur only sporadically in estuarine habitats and, indeed, very few species recorded in this study were also documented for nearby rocky shore habitats (Table S1; Teixeira-Neves et al., 2015). Most species were actually not associated with the number of nearby rocky shores, and the few species positively associated were primarily the marine stragglers and, to a very lesser extent, the marine migrants and estuarine species (Fig. 4a–b). Considering that all the most frequent and abundant species were marine stragglers, the positive effect of the number of rocky shores most likely reflected the presence and abundance of species less dependent on estuarine areas in the bay with higher marine influence (Fig. 4c–d; Table S2). In this sense, the greater number of number of rocky shores most likely favors the colonization of more sheltered neighbor areas, such as the studied systems and the mangrove areas, especially by juveniles of species with different habitat requirements.

At the group level, salinity was the only variable important for the variation within all habitat use groups, evidencing the limits imposed by specific physiological tolerances in the face of the balance marine *versus* riverine influence for the species composition and abundance in different estuarine habitats, which is broadly in accordance with the patterns observed in other studies (e.g., Elliott and Quintino, 2007; Camara et al., 2018; Franco et al., 2019). The effect of salinity was higher within the freshwater group, followed by the semi-diadromous, marine straggler, and estuarine groups, and especially lower for the marine migrant group. Therefore, these results are primarily in

accordance with the physiological tolerances expected for each habitat use group, but also evidence the relevance of specific habitat requirements to determine the specific responses to the salinity gradient (Potter et al., 2015; Reis et al., 2016). For instance, the greater influence of salinity within the semi-diadromous group, as well as the exclusive association of their species with local-scale environmental variables (i.e. salinity, depth, and pH; Fig. 6c), are most likely a result of the extreme habitats (i.e. the sea or the upper portions of estuaries) occupied by that group. Likewise, the comparatively lower relevance of the salinity within the marine straggler group may be explained by the greater number of rare species that may occur in areas with salinities different from the values typically observed in the sea (Table S1). However, the species within the marine straggler group are indeed primarily restricted to areas with greater marine influence, as evidenced by the effects of the zone area and the number of nearby rocky shores, which distinguish primarily bays from coastal lagoons (Table 1). The influence of the period on the effect of the pasture cover, in turn, was most likely a result of the occurrence of rare marine straggler species in coastal lagoons, where the pasture cover predominate, in periods of increased marine influence (Table 1; Fig. 6d).

The species-environment relationships within the habitat use groups generally reinforced the patterns observed at the assemblage level (Fig. 4; Fig. 6). The mangrove cover was an important driver of the variation in the species composition and abundance also within the estuarine group, reinforcing its relevance to provide more suitable environmental conditions even for species adapted to the high-variability environmental gradients that characterize estuarine habitats (Potter et al., 2015). This is supported by the great relevance of the mangrove cover for the variation within the freshwater group, with only a few species occurring in bays, but in all cases nearby from the mangrove areas. In this sense, the large and non-spatially structured effect of the forest cover within the freshwater group reinforces the relevance of more vegetated areas to provide higher complexity habitat and feeding resources for species more associated with the riverine input influence (Whitfield, 2017; Camara et al., 2019). For the variation within the marine migrant group, in turn, the effects of a larger number of environmental variables and the period was most likely a result of the great variety of habitat requirements of the different species observed during annual cycles (Castillo-Rivera et al., 2010; Lacerda et al., 2014). The influence of the period on the effects of the tidal phase and mangrove cover, and the higher effect of the mangrove cover when tidal phase was less relevant, were most likely a result of the occurrence of more marine straggler species in areas near from mangroves during periods of higher and less variable tides (Whitfield, 2017).

The differences in the species-environment relationships observed between and within groups of habitat use, as well as the hierarchical and spatial effects, evidenced the complexity inherent to the multiple drivers of the structure of nearshore fish assemblages in tropical semi-enclosed ecosystems. Regardless of that, the main patterns observed were in accordance with that expected based on the degrees of dependence on estuarine areas intrinsic to each habitat use group. The exceptions were primarily a result of the inter-specific variation associated with the richest groups, the marine migrant and marine straggler species, and stochastic processes that determine the random occurrence of a large number of rare species of the latter group. Therefore, this study provides substantial evidences that the environmental heterogeneity supported by factors at both the local and landscape scales is crucial for the structure of fish assemblages. The maintenance of greater environmental heterogeneity is primarily relevant within individual systems, where it embraces multi-scale variables representative of the balance between marine and continental (i.e. riverine input and land use) influences. Also, the relevance of the connectivity between alternative habitats was evidenced by the effects of the distance from the ocean, total width of connection between zones, and availability of less or more suitable habitats (i.e. number of rocky shores or mangrove cover) for the near-shore fish assemblages.

5. Conclusions

The explained fractions of the variation at the assemblage and group levels evidenced the critical role of disentangling spatial and multiple environmental effects over hierarchical scales to effectively understand the major determinants of the structure of nearshore fish assemblages in semi-enclosed ecosystems. In addition, more clear insights regarding the environmental mechanisms associated with assembly processes were achieved by considering the variation in the species responses within and between habitat use groups. From the assemblage to the within-group level, the effects of the hierarchical and spatial structures were of major relevance and strongly influenced environmental effects at the local and landscape scales. The shared effects between the hierarchical and spatial structures evidenced primarily the relevance of the intrinsic environmental features of individual systems and, to a lesser extent, their zones for the variation in the species responses. The redundant effect of the type of system provided further evidence regarding the greater relevance of the other hierarchical levels. As expected, the variation in the species responses was generally less spatially and hierarchically structured for habitat use groups more dependent on estuarine areas, as a consequence of their wider distributions across the estuarine gradients. However, factors such as the inter- and intra-specific variations in habitat requirements, primarily for the marine migrants, and stochastic processes determining the occurrence of a large number of very rare species, primarily for the marine stragglers, most likely also influenced the variation associated with specific differences in the habitat use groups. These factors are most likely also associated with the large fractions of unexplained variation, which reflect unmeasured factors and stochastic processes in different spatial and temporal scales than that considered in the sampling design.

Environmental effects representative of the marine (e.g., higher salinity, depth, pH, and transparency) and continental (e.g., higher distance from the ocean and vegetal cover) influences were primarily relevant to explain the assemblage variation between and within habitat use groups. The species responses in accordance with that expected for their habitat uses were primarily supported by the prevalence of the most frequent and abundant species of each group in suitable environmental conditions to their tolerances and requirements. In this sense, the estuarine and marine migrant species were associated with a wider range of environmental gradients, and the most frequent and abundant marine straggler and freshwater species primarily with higher marine and continental influences, respectively. However, only the variation within the semi-diadromous group, composed by a small number of species, was primarily associated with environmental effects at the local scale. That was most likely a consequence of the extreme habitats (i.e. the sea or the upper portions of estuaries) occupied during their life cycles. The environmental heterogeneity at both the local and the landscape scales is, therefore, determinative for the structure of the fish assemblages. The relevance of the connectivity between habitats was also evidenced by the effects of the total width of connection between zones and the availability of nearby alternative habitats. Therefore, this study provided substantial evidences to support the critical roles the conservation of the environmental heterogeneity of individual systems at the local and landscape scales, and the connectivity with alternative estuarine habitats, such as the mangrove areas and other bays and coastal lagoons, for the maintenance of nearshore fish assemblages in different types of semi-enclosed ecosystems. Future investigations based on annual cycles may better clarify these points and provide new insights regarding the environmental determinants of the structure of fish assemblages in semi-enclosed estuarine ecosystems in the tropical region.

Data availability statement

All relevant data are within the paper and its Supporting Information files. Additional data will be given as requested.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, including Universidade Federal Rural do Rio de Janeiro, Brazil, Animal Care Protocol (# 11874).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106691>.

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