



# Multiscale mechanisms underpin the ecological uniqueness of local fish assemblages in tropical coastal seascapes

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Received: 12 April 2021 / Accepted: 9 December 2021 / Published online: 29 December 2021  
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## Abstract

Multiscale processes through dynamic boundaries drive the local contributions (LCBD; uniqueness in species composition and abundance) and species contributions (SCBD; individual species abundance variation) to fish beta diversity in coastal seascapes. We partitioned LCBD into  $LCBD_{Repl}$  (replacement) and  $LCBD_{AbDiff}$  (abundance difference), and used model-based approaches to investigate whether seascape size influences environmental and spatial drivers of LCBD, and effects of species (distribution, prevalence, and coastal dependence) on SCBD. Three large bays (bay level) and three zones per bay (zone level), southeastern Brazil, were seascape models during 1 year. At the bay level, more locations had higher LCBD, related to species composition, lower water transparency, and much less to flood/high tides and higher number of estuaries.  $LCBD_{Repl}$  was also prevalent and stronger positive effects of transparency and mangrove cover reinforced the importance of environmental filtering and alternative habitats driving local contributions to replacement processes in larger seascapes. Species richness influenced positively LCBD primarily at the zone level, and negative effects of vegetal cover and primarily human settlements suggested species loss under lower heterogeneity. Also, more similar  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  evidenced the increasing local contributions to abundance differences in smaller species pools. At both levels, larger- and finer-scale spatial effects evidenced possible influences of dispersal and biotic interactions, respectively, on  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$ . SCBD was positively related to species prevalence at locations and distribution at both levels. Therefore, multiscale mechanisms dependent and irrespective of seascape size support the critical importance of habitat availability, complexity, and variety to beta diversity of coastal fishes.

**Keywords** Beta diversity · Scale dependence · Coastal fish · Assembly processes · Spatial heterogeneity · Multiscale environmental gradients

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Responsible Editor: W. Figueira.

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## Introduction

Coastal ecosystems (e.g., estuaries, mangroves, seagrass beds, and coral reefs) are critical components of seascapes, spatially heterogeneous areas with complex arrangements of marine and brackish habitat patches, highly connected by ecological processes at multiple spatial and temporal scales (Boström et al. 2011). High structural complexity and resource availability provide high-quality areas for feeding, spawning, and nursery, rendering coastal ecosystems an imperative for the life cycles of numerous species (Whitfield 2017; van Lier et al. 2018). Coastal ecosystems also deliver several other necessary services, such as coastal protection, ocean nourishment, and fishery resources and recreation for humans (Liquete et al. 2013). Consequently, most coastal areas worldwide accumulate human impacts

primarily related to land-based pollution, frequently consumed in mesopelagic food webs or deposited thousands of kilometers away, besides structural changes along the shoreline, overfishing, and ship/boat traffic (Baztan et al. 2014; Hilborn 2016; Schulz et al. 2020). Therefore, the management of coastal resources must consider multiscale ecological processes driving local contributions to biodiversity patterns and ecosystem functions and services within seascapes (Cardinale et al. 2012; Annis et al. 2017).

Highly dynamic boundaries and features support the intense energy flow and exchange of species, nutrients, and other materials between coastal habitats, whereas the static location favors land-based processes (Sheaves 2009; Hazen et al. 2013). Therefore, the spatial and temporal contexts of marine and freshwater influences may be more relevant to shape biodiversity patterns in coastal seascapes than habitat type (Neves et al. 2016; Bradley et al. 2019). The seascape composition (i.e., the abundance and variety of habitat patches) and configuration (i.e., the spatial arrangement of patch types), in turn, are stronger drivers of biodiversity in areas with exceptionally high spatial heterogeneity (Henderson et al. 2017; Camara et al. 2019). These areas include large tropical bays, complex ecosystems under gradients of riverine vs. marine influences that harbor a great variety of habitats (e.g., estuaries, mangroves, and sandy beaches) (Kjerfve et al. 1997). In this scenario, biodiversity is a primary result of ecological processes associated with local environmental conditions and the connectivity between alternative habitats (van Lier et al. 2018; Rodil et al. 2021). These relationships are also dependent on the spatial and temporal scales in which key ecological processes (e.g., species movement and nutrients flow) operate (Sheaves 2009; Camara et al. 2021). Disentangling the spatial and temporal scales and contexts in which environmental changes impact biodiversity components is, therefore, an essential step to set conservation aims based on the structural complexity of habitats and seascapes.

Fishes can connect food webs in different ecosystems depending on specific dispersion capabilities and habitat requirements associated with the life cycles of individuals (Vinagre et al. 2011). Some fish species complete their life cycles at a given habitat patch, whereas others spend only particular stages in coastal ecosystems, performing ontogenetic and seasonal migrations between the coast and the ocean (Potter et al. 2015; Andrade-Tubino et al. 2020). The highly dynamic boundaries in pelagic systems favor otherwise the occurrence of numerous rare marine-origin species, which may lead to the prevalence of random assembly processes (Ford and Roberts 2018; Araújo et al. 2019). Therefore, specific differences in the habitat use modulate the effects of local habitat quality and availability of alternative habitats on fish diversity (Vargas-Fonseca et al. 2016; Henderson et al. 2020). In this sense, convergences in

environmental tolerances, habitat requirements, and dispersal capabilities of fish species sharing the habitat use may reveal multiscale mechanisms related to the contributions of local assemblages to spatial and temporal diversity patterns in seascapes (Potter et al. 2015; Camara et al. 2020).

Beta diversity measures are a result of joint contributions of assemblages in localities and/or temporal intervals, and individual species to the overall variation (Anderson et al. 2011). Mechanisms promoting beta diversity patterns in seascapes can, therefore, be assessed by local contribution (LCBD) and species contribution to beta diversity (SCBD) (Legendre and Cáceres 2013). LCBD expresses the uniqueness of habitat patches in terms of species composition (and abundance), and may be indicative of local contributions to species replacement and richness/abundance differences (Legendre 2014). SCBD, in turn, expresses the occurrence/abundance variation of individual species within the seascape (Legendre and Cáceres 2013). This approach is especially interesting in the face of increasing processes of homogenization, with human-related environmental changes (e.g., habitat degradation, Gomes-Gonçalves et al. 2020; urbanization and landscape transformation, Henderson et al. 2020; rising ocean temperatures, Magurran et al. 2015; and changes in upwelling regimes, Wang et al. 2015) reducing differences between coastal fish assemblages in multiple spatial and temporal scales. Beta diversity in coastal seascapes is also influenced by natural processes that promote spatial and temporal heterogeneity, such as environmental gradients (e.g., Chin et al. 2018), population processes (e.g., Krueck et al. 2020), and biotic interactions (e.g., Mouchet et al. 2013). These multiple influences frequently produce spatial and temporal structures due to the non-random organization of local assemblages arising from unaccounted ecological processes at multiple scales (Dray et al. 2006; Dornelas et al. 2014). Therefore, disentangling multiscale environmental, spatial and temporal effects on both LCBD and SCBD may reveal critical mechanisms driving fish diversity patterns in coastal seascapes.

We assessed multiscale environmental and spatial drivers of LCBD and SCBD in tropical coastal seascapes using three large bays in southeastern Brazil as models during 1-year period. Beta diversity was partitioned into LCBD and SCBD at the bay and zone levels (i.e., within each bay and each zone per bay, respectively) (Legendre and Cáceres 2013). For each hierarchical level, we also partitioned beta diversity into abundance-based replacement and abundance difference components, and assessed LCBDs for each assembly process (Legendre 2014). Besides differences in spatial extents (seascape size), the two hierarchical levels include marked gradients of conservation and marine vs. freshwater influences (Camara et al. 2019, 2020). We considered that larger seascapes encompass higher environmental heterogeneity, providing more alternative habitats and niche opportunities

for different species (Messmer et al. 2011; Massicotte et al. 2015). Furthermore, hierarchical environmental gradients gradually select species from the regional pool to local assemblages, whereas the interplay between landscape processes and local environmental conditions, including biotic processes at fine spatial scales, shape diversity patterns from local to larger scales (Mouchet et al. 2013; Camara et al. 2020). We, therefore, hypothesized that (1) more locations and species have higher overall LCBD and SCBD, respectively, at the bay level. Also, (2) climate and ocean conditions and spatial structures at larger scales influence LCBD indices primarily at the bay level, whereas landscape features, local habitat quality, spatial structures from intermediate to finer scales, and spatial and temporal variation in fish assemblage structure influence LCBD indices primarily at the zone level. Considering the largely shared regional pool of fish species in the study area (Reis et al. 2016; Araújo et al. 2018), we also hypothesized (3) higher local contributions to abundance differences than replacement at both levels, and (4) higher SCBD for species more dependent on coastal habitats and more widespread. This study aimed at identifying multiscale mechanisms supporting critical

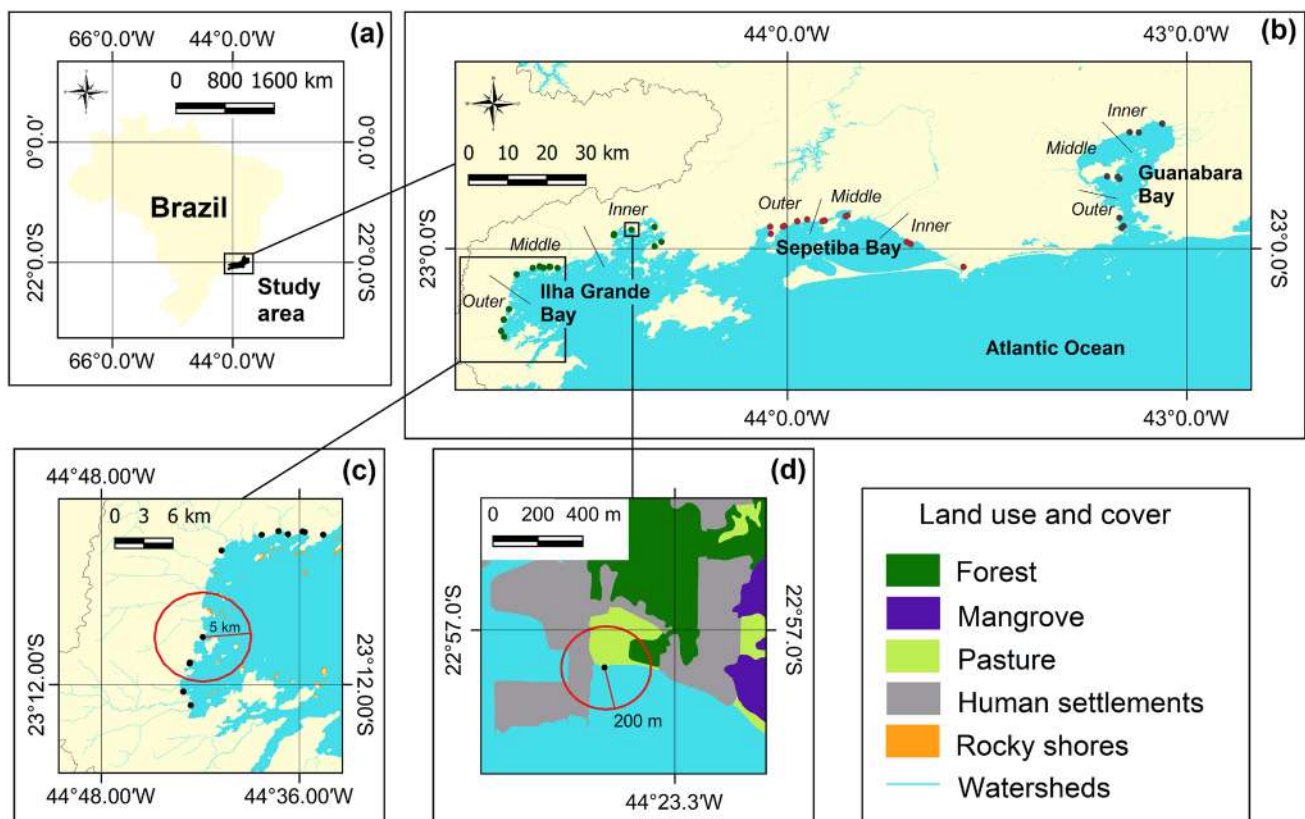
contributions of locations and species to fish diversity in tropical coastal seascaapes.

## Materials and methods

### Study area

The Ilha Grande, Sepetiba, and Guanabara bays are three large tropical seascaapes sequentially distributed over a 150 km extent on the coast of the Rio de Janeiro state, southeastern Brazil (Fig. 1a, b). The average annual temperature is 22 °C and total annual rainfall ranges from 1000 to 1600 mm, peaking from October to March (Alvares et al. 2013). Spring (September–November) and summer (December–February) constitute wet seasons, whereas autumn (March–May) and winter (June–August) are primarily dry seasons (CPTEC/INPE 2020).

Ilha Grande bay is a largely open system with approximately 1150 km<sup>2</sup> of surface area, and a highly jagged shoreline and numerous islands that protect some areas from the open sea (Fig. 1b). These features most likely support the



**Fig. 1** Location of (a) the tropical seascaapes in the Rio de Janeiro State, southeastern Brazil, and (b) sampling locations (circles) in the Inner, Middle, and Outer zones of Ilha Grande (dark green), Sepetiba (brown), and Guanabara (dark gray) bays. The buffer areas consid-

ered for each sampling location to obtain the metrics representative of (c) hydrological features (5 km radius buffer) and (d) land use and cover (200 m radius buffer)

slight variation in the marine influence in this bay, also characterized by extensive native forest cover and several conservation areas (Camara et al. 2020). The input of domestic sewage is primarily restricted to localities near summerhouse settlements, but the bay is surrounded by a nuclear power plant, private marinas, a port area, and a large oil terminal (Teixeira-Neves et al. 2015). The riverine input consists of several small watersheds due to the predominance of coastal mountains that reach the coastline (Guerra and Soares 2009). Consequently, sand bottoms associated with rocky shores and shallow waters (< 8 m) are the main physiographic features (Teixeira-Neves et al. 2015).

Sepetiba bay is a semi-enclosed ecosystem with about 545 km<sup>2</sup> of surface area and a narrow sandy barrier in its southern portion (Fig. 1b). The system is connected to the open sea by a 12 km wide channel in the west, and much less in the east, by a small inlet, shallow and with extremely reduced water flow going through mangrove forests (Fig. 1b; Molisani et al. 2004). The bay has also other types of native forest, and primarily both mud and sand flats, and to a lesser extent rocky shore habitats (Camara et al. 2020). In the last century, structural changes in large rivers have increased sedimentation rates in the bay, and the fast growth of urban, industrial, and cultivation areas has increased loads of organic and industrial effluents primarily in the last decades (Molisani et al. 2004, 2006). More recently, the inner portions of the bay (east side) suffered large structural changes in the shoreline to harbor a large cargo port terminal, a steel company, and a terminal for submarines (Araújo et al. 2016). Temporal decreases in species richness and abundance also evidence impacts of overfishing (Araújo et al. 2016).

Guanabara bay constitutes an iconic landscape in the Rio de Janeiro state, with high-density human settlements over a stunning scenario of escarpments, hills, fluvial and marine coastal plains, beaches, and coastal lagoons (Soares-Gomes et al. 2016). This highly industrialized metropolitan area has gas and oil terminals, and two large ports (Fistarol et al. 2015). A large highway bridge crosses the bay, which harbors navy bases and the heavy traffic of ferries, fishing boats, and yachts (Kjerfve et al. 1997). The bay has approximately 405 km<sup>2</sup> of surface area, the innermost location is 35 km distant from the open sea, and the inner portion is much wider (19 km mean wide) than the middle-outer portion (10 km mean wide) (Fig. 1). This gradual tapering results in a narrow entrance (1.6 km wide) and shallow depths (< 10 m), which limit water circulation and enhance influences of tides and winds, especially in the inner portions (Kjerfve et al. 1997). Consequently, the fluvial and marine sediments are not evenly distributed, and the sandy substrate is abruptly replaced by muddy substrate from areas closer to the sea to intermediate-inner portions (Baptista-Neto et al. 2006). Water quality is also lower primarily in these portions due to the dense drainage basin with numerous rivers, streams,

and channels highly polluted with industrial and domestic effluents (Fistarol et al. 2015). Regardless of intense human pressures, the bay still harbors extensive mangrove areas and smaller patches of native forest (Camara et al. 2020).

Decreasing degrees of conservation and marine influence, and increasing human impacts and freshwater influence are observed primarily from the Ilha Grande to the Guanabara bay, but also between different zones within the bays (Camara et al. 2019; 2020). We, therefore, considered three major zones in each bay, as follows: (1) Inner zone, area more protected from the open sea and under higher land-based influences (e.g., riverine input, pollution, and changes in the coastal landscape); (2) Middle zone, a transition area less sheltered from the open sea, but still under high land-based influences; and (3) Outer zone, area closer to the open sea and under higher marine influence (e.g., ocean currents, waves, and euhaline ranges of salinity).

### Fish sampling

Sampling was performed bimonthly during seven periods between September 2017 and September 2018 in the Ilha Grande, Sepetiba, and Guanabara bays (Fig. 1b). For each bay and period, sampling was performed at three locations per zone (i.e., Inner, Middle, and Outer) (Fig. 1b). However, different sets of locations were sampled in each period to better consider the environmental heterogeneity intrinsic to each seascape and identify critical locations for fish diversity. Therefore, we sampled 17 locations in the Ilha Grande bay and 15 locations in the Sepetiba bay. In the Guanabara bay, for logistic reasons, sampling was always carried out at the same locations. A total of 191 samples were obtained at the sampling locations (3 locations × 3 zones × 3 bays × 7 periods + 2 locations). The two additional locations are situated in the Ilha Grande bay, and one was sampled in November 2017 and another in March 2018.

Each sample included three replicates per location. For each replicate, fishes were collected on the shore (< 1.5 m) with a beach seine net (12 × 2.5 m; 5 mm mesh size) dragging perpendicular to the shoreline (30-m long), and covering a swept area of about 300 m<sup>2</sup>. Fishes were fixed in 10% formalin, and after 48 h preserved in 70% ethanol. All fishes were identified to the species level as described in Araújo et al. (2018), and voucher specimens were deposited in the Ichthyological Collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro.

### Local habitat quality

Habitat quality included physicochemical parameters and substrate measures recorded at each location concurrently

with fish sampling. Salinity, pH, and temperature ( $^{\circ}\text{C}$ ) were obtained with a HANNA HI 9829 multiprobe (HANNA Instruments, São Paulo, Brazil), and depth (cm) was measured with a Speedtech model SM-5 digital probe (Speedtech Instruments, Great Falls, Virginia). Transparency (%) was measured with a Secchi disk and calculated as a percentage of Secchi depth/depth. Substrate type was classified considering the occurrence of clay + silt, fine sand, medium sand, coarse sand, gravel, and rocky bottom, estimated by visual census at three sampling points (1 m and 0.5 m depth, and at the spread washing zone) within the area of approximately 300 m<sup>2</sup> covered by the fish sampling. The classification was based on the scale defined by the granulometric analysis described in Camara et al. (2019). Substrate type was scored from 1 (clay + silt) to 6 (rocky bottom) and calculated as the mean value per location.

### Ocean and climate conditions

The tide variation was observed during the sampling procedures at each location, and classified as flood, high, ebb, or low tide. Tidal phase was then scored from 1 (flood/high tide) to 2 (ebb/low tide). Likewise, the moon phase was firstly classified as third quarter, new, first quarter, and full, and then scored as 1 (first/third quarter) and 2 (new/full), considering its weaker and stronger influences on the intensity of tidal regimes, respectively.

The accumulated rainfall (mm) expressed the rainfall amounts observed 15 days before fish sampling at each location and period. We considered this interval due to the large differences in the water renewal time between the three systems, which may vary from weeks to months in the different areas of the Guanabara bay, and be relatively rapid in the other bays, especially in the outermost areas (Pinto et al. 2017; Andrade et al. 2019). The accumulated rainfall values were obtained from the Instituto Nacional de Meteorologia website, considering the nearest weather stations to the sampling locations (INMET 2020). In the Ilha Grande bay, accumulated rainfall was obtained at the Angra dos Reis station and the Paraty station, about 1.3 km and 2.1 km from the coastline, for locations in the Inner and Outer zones, respectively. For locations in the Middle zone, accumulated rainfall was the mean values recorded at the two stations. In the Sepetiba bay, accumulated rainfall was obtained at the Marambaia station, about 2 km from the coastline in the Inner zone and 46 km from the most distant location in the Outer zone. In the Guanabara bay, accumulated rainfall was obtained at the Niteroi station, about 1 km from the coastline, for locations in the Inner and Middle zones, and the Copacabana station, about 4.5 km from the coastline, for locations in the Outer zone.

### Landscape and seascape features

Metrics representative of landscape features and seascape configuration were obtained using a geographic information system (QGIS Development Team 2018). The geoprocessing procedures used vectorial layers of hydrography and land use/cover (1: 25,000 scale; 2018) provided by a partnership between the Instituto Brasileiro de Geografia e Estatística (IBGE) and the Secretaria de Estado do Ambiente do Estado do Rio de Janeiro (SEA-RJ) (Portal GeoINEA 2020).

For each location, geographical coordinates were obtained during field sampling with a handheld GPS Garmin eTrex 10 (Garmin International, Inc., Olathe, Kansas, USA). Metrics of land use/cover were firstly obtained as the areas (km<sup>2</sup>) of native forest cover, pasture cover, and human settlements within a 200 m radius buffer from the GPS coordinates of each location, and then calculated as a percentage of the buffer area (Fig. 1d). In the three bays, the distance of 200 m separate most locations within the same zone, including those locations sampled in different periods. Furthermore, previous studies revealed important effects of landscape metrics obtained within this radius on the fish assemblage structure in the studied systems (Camara et al. 2019, 2020). We, therefore, considered 200 m buffers to assess the landscape heterogeneity primarily related to each location.

Drainage density (km<sup>-1</sup>) was calculated as the total length of streams and rivers (km) within a 5 km radius buffer from the GPS coordinates of each location (Fig. 1c). The distance of 5 km corresponds to approximately the shorter distance between locations in different zones within the same bay, and we considered this radius to assess the major effects related to the marine and freshwater gradients that distinguish zones (Araújo et al. 2002, 2017).

Metrics of seascape configuration were representative of the availability of alternative habitats for local assemblages. We considered metrics within 5 km radius buffers for estuaries and rocky shores, habitats largely distributed and strongly associated with the levels of marine vs. freshwater influences that distinguish zones (Camara et al. 2020). For each location, nearby estuaries were considered as the total number of estuaries within a 5 km buffer, whereas the availability of rocky shores was calculated as a percentage of the total area of rocky shores (km<sup>2</sup>) by the buffer area. Mangroves provide more complex habitats and resources for fish refuge (Whitfield 2017), but have more restricted extent and distribution due to the specific environmental conditions required to develop and heavy human pressures (Giri et al. 2011). Therefore, to assess the influence of mangroves on the ecological uniqueness of each location, we obtained the total area (km<sup>2</sup>) within a 200 m radius buffer, and calculated the mangrove cover as a percentage of the buffer area.

## Spatial structures

Multiscale spatial variables were obtained by a principal coordinates of neighbor matrices analysis (PCNM; Borcard and Legendre 2002; Borcard et al. 2004). Spatial variables explaining the local contribution to beta diversity in further analyses were representative of spatial structures expressing the strength of the spatial autocorrelation in the response, i.e., how much localities close together are ecologically similar due to unmeasured intrinsic processes of communities, such as biotic interactions (finer scales) and dispersion (larger scales) (Dray et al. 2006). The PCNM used a distance matrix based on pairwise aquatic distances between the 41 sampling locations to decompose the original distances in eigenvectors that represent new independent spatial variables (Borcard et al. 2004). Only PCNM eigenvectors with positive eigenvalues were considered as possible proxies of spatial structures over the spatial range included in the data set (Borcard and Legendre 2002). The first PCNM axis (S1) represents the spatial structure at the broader spatial scale and the last one (S25) the finest spatial scale. Therefore, each spatial variable may be indicative of unmeasured processes structuring local fish assemblages at a given spatial scale. We then arbitrarily defined the ranges of spatial scales encompassing the spatial variables: larger scales (S1–S8), intermediate scales (S9–S16), and finer scales (S17–S25). The analysis was performed in the R environment (version 3.6.3; R Core Team 2020) using the package ‘vegan’ (version 2.5–6; Oksanen et al. 2019).

## Fish assemblage metrics

The spatial and temporal variations in the abundances of individual species between samples were assessed and controlled by model-based Bayesian ordinations using latent variable models (Hui et al. 2015). Model-based approaches are regarded as multivariate extensions of generalized linear (mixed) models (Hui et al. 2015; Warton et al. 2015). The method can handle to non-normal distributions and explicitly model the strong mean–variance relationship typical of count data, controlling for confounding effects of location (mean abundance) and dispersal (variance) (Bolker et al. 2009; Warton et al. 2012). Therefore, the model-based ordination allows disentangling of species-level from assemblage-level effects.

We fitted two pure latent variable models in the R environment (version 3.6.3; R Core Team 2020) using the package ‘boral’ (version 1.9; Hui 2016, 2020). Modeling was performed on the  $n \times p$  species data ( $p = 127$  species and  $n = 191$  samples), where rows  $i = 1, \dots, n$  are samples and columns  $j = 1, \dots, p$  are species, assuming Poisson counts for species, and including two latent variables ( $z_i$ ) and a fixed row effect ( $\alpha_i$ ) (Hui 2016). For each sample, the latent variables are a pair

of coordinates representing the position of the sample in the two-dimensional ordination (Hui et al. 2015). The row effect allows to construct an ordination in terms of species composition rather than sample total abundance (Hui et al. 2015). In our study, each sample was obtained at a single location per period, and different periods may represent a same season. We then included row effects for location and season due to their stronger influences on the occurrence and abundance of individual species (Andrade-Tubino et al. 2020). Therefore, we performed two independent unconstrained analysis, with a fixed row effect for location or season, to obtain latent variables representative of the residual variation after controlling for these spatial and temporal influences, respectively, as follows:

$$\log(\mu_{ij}) = \alpha_{\text{fixed}[i]} + \theta_{0j} + z_{i1} \times \theta_{j1} + z_{i2} \times \theta_{j2} = \alpha_{\text{fixed}[i]} + \theta_{0j} + z_i^T \theta_j,$$

where  $\mu_{ij}$  is the mean response at sample  $i$  for species  $j$ ,  $\alpha_{\text{fixed}[i]}$  is a vector denoting the fixed row effect (location or season) applied to the sample  $i$ ,  $\theta_{0j}$  is the species-specific intercept,  $z_i = (z_{i1}, z_{i2})^T$  is a vector of two latent variables, and  $\theta_j = (\theta_{j1}, \theta_{j2})^T$  are the corresponding species-specific coefficients (Hui 2016). The means of the posterior distributions of the latent variables were included in the following analyses as proxies of species composition in assemblages after controlling for the effects of localities (LV1(Lo), LV2(Lo)) and seasons (LV1(Se), LV2(Se)). Likewise, the species-specific coefficients were included as proxies of the unconstrained distributions of individual species after controlling for the effects of localities (Sp\_c1(Lo), Sp\_c2(Lo)) and seasons (Sp\_c1(Se), Sp\_c2(Se)). We used the default methods described in Hui (2016), with the estimations for both models performed using a Bayesian Markov Chain Monte Carlo (MCMC) method via JAGS (version 4.3.0; Plummer 2003). We ran a single chain with 40,000 iterations, a burn in of 10,000, and a thinning factor of 30, and used weakly informative priors to stabilize the MCMC sampling and prevent it from sampling excessively large coefficients (Hui 2016).

Species richness was calculated as the number of species per sampling unit (i.e., location per period), and used as a surrogate for species diversity to reduce the influence of spatial and temporal variations in the relative abundance on the species prevalence. The calculation was performed in the R environment (version 3.6.3; R Core Team 2020) using the package ‘vegan’ (version 2.5–6; Oksanen et al., 2019). We also calculated the prevalence of individual species in the seascape as the number of locations in which each species occurred per zone and bay during the sampling periods.

## Habitat use groups

The coastal habitats in our study have environmental differences primarily related to gradients of marine vs. freshwater

influence (Camara et al. 2020). Species were then assigned to estuarine habitat use groups based on the functional guilds proposed by Potter et al. (2015), complemented by specific information for the study area (Araújo et al. 2016; Andrade-Tubino et al. 2020). We, therefore, used ecological information primarily at the family level to classify species into seven habitat use groups expressing the degree of dependence on estuarine habitats (Table S1). Very high dependence: (1) estuarine group, species that spend the life cycle entirely or primarily in estuaries; and (2) marine estuarine-dependent group, marine species that require estuarine habitats during the juvenile life. High dependence: (3) semi-anadromous group, species that spend most of the life cycle in the sea and migrate to the upper portions of estuaries to spawn; and (4) semi-catadromous group, species that spend most of the life cycle in freshwater and migrate to the lower portions of estuaries to spawn. Intermediate dependence: (5) marine estuarine-opportunist group, marine species typically euryhaline that frequently enter estuaries in large numbers, especially in the juvenile life, but use coastal marine areas as alternative nursery areas. Low dependence: (6) marine straggler group, species that are stenohaline and occur in low numbers in estuaries; and (7) freshwater species, species that occur in low to high numbers in upper estuarine areas, but may spend the entire life cycles in freshwater environments.

### Localities and species contributions to beta diversity

Beta diversity expressed a non-directional variation between sampling units at the zone and bay levels (Anderson et al. 2011). Considering that each sampling unit was a single location in a given period and different sets of locations were sampled in each period, we calculated beta diversity separately for the seven periods per bay (bay level) and zone within bay (zone level) to obtain balanced estimates. Therefore, for each period, we first Hellinger-transformed the location-by-species abundance matrix, and then calculated the total beta diversity, the local contribution to beta diversity (LCBD), and the species contribution to beta diversity (SCBD) as proposed by Legendre and De Cárceres (2013). We also assessed the LCBD based on the contributions of the abundance-based replacement ( $LCBD_{Repl}$ ) and abundance difference ( $LCBD_{AbDiff}$ ) components of beta diversity (Legendre and De Cárceres 2013; Legendre 2014). Likewise, for each period at the bay and zone levels, we first calculated the pairwise total beta diversity and the replacement and abundance difference components, based on the abundance-based Sørensen index, as described in Legendre (2014). The abundance-based replacement expressed the replacement of individuals of some species by the same number of individuals of different species between pairs of locations, whereas

the abundance difference referred to the individuals that are not involved in replacement (Legendre 2014).

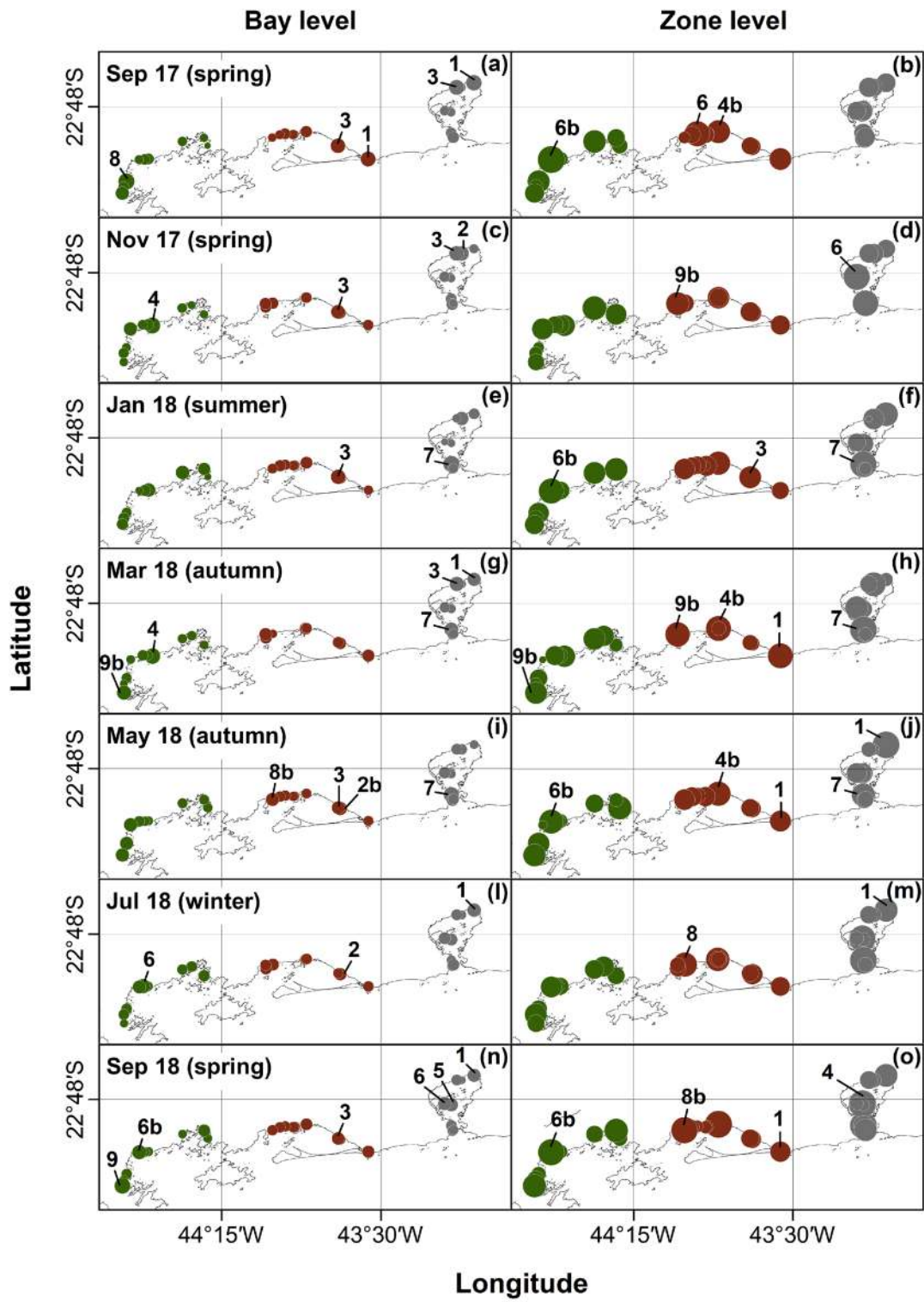
$LCBD$ ,  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  values expressed the ecological uniqueness of individual locations per period in terms of species composition and abundance, abundance-based replacement and abundance difference, respectively (Legendre and De Cárceres 2013; Legendre 2014). Large  $LCBD$  values may be indicative of high-diversity or extremely species-poor locations, and thus concomitant assessment of  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  allows to elucidate how different assembly processes contribute to the local uniqueness (Legendre 2014). All  $LCBD$  indices vary from 0 to 1, for locations that contribute less and more than the mean to the overall variation (i.e., beta diversity), respectively (Legendre and De Cárceres 2013).  $SCBD$  values, in turn, expressed the degree of variation in the abundances of individual species in the set of sampling locations per period, varying from 0 to 1, for species that have smaller and larger contributions to beta diversity, respectively (Legendre and De Cárceres 2013). All calculations were performed in the R package ‘adespatial’ (version 0.3–8; Dray et al. 2020), following the mathematical procedures described in Legendre and De Cárceres (2013).

### Statistical modeling

For each period, the strength of the overall  $LCBD$  patterns at the bay and zone levels was tested separately within each bay and zone per bay, respectively, by independent permutations within the columns of the location-by-species abundance matrix, while preserving the species abundance distributions (Legendre and De Cárceres 2013).  $P$  values  $< 0.05$  were indicative of non-random patterns.

We modeled the responses of  $LCBD$ ,  $LCBD_{Repl}$ ,  $LCBD_{AbDiff}$ , and  $SCBD$ , at the bay and zone levels, to multiscale environmental effects and spatial and temporal structures using beta regression (BR) and generalized linear mixed models (GLMMs) specifying the Beta distribution for the response variables (Cribari-Neto and Zeileis 2010; Brooks et al. 2017). Beta distribution can accommodate several shapes and is therefore flexible to model continuous variables ranging between 0 and 1, which are typically heteroskedastic and asymmetric (Ferrari and Cribari-Neto 2004). Both BRs and GLMMs used a logit-link function to relate the expected values of responses to linear predictors (Gelman and Hill 2007; Bolker et al. 2009).

Prior to models fitting, the environmental variables were centered and standardized to improve the parameter estimates and for fitting comparable models (Schielzeth 2010). The habitat use was included as a dummy variable with the estuarine group as the reference level. For  $LCBD$  indices and  $SCBD$ , at each hierarchical level, we calculated the variance inflation factor (VIF) for each predictor variable in





**Fig. 2** Local contribution to beta diversity (LCBD) per bay (left panel) and zone (right panel) of sampling locations in the Ilha Grande (dark green), Sepetiba (brown), and Guanabara (dark gray) bays. Numbered locations in the Inner (1–3b), Middle (4–6b), and Outer (7–9b) zones of the bays have higher LCBD and stronger evidence for non-random patterns based on the permutation tests

full models (i.e., including all predictors; Table S2) to avoid multicollinearity (Zuur et al. 2010). For all cases, almost all variables had  $VIF < 2$ , and none had  $VIF > 4$ , which is indicative of negligible multicollinearity (Zuur et al. 2010). We then performed a variable selection using a forward stepwise procedure based on the corrected Akaike information criterion (AICc) (Li et al. 2020). At each step, the procedure fits a least square regression for each possible combination of all predictors and add a variable to the final model based on the lowest AICc value. The selection stops when the number of parameters increases and no information is added. For LCBD indices, all procedures were performed separately for models including only environmental effects and models including both environmental and spatial effects, resulting in two final models per hierarchical level. For SCBD, the procedures were performed once for each hierarchical level and included metrics representative of the species dependence on coastal habitats, the spatial and temporal distribution of individual species, and their prevalence in the seascape.

All selected variables were included as fixed effects in full GLMMs, with models specified for responses of LCBD indices and SCBD including random effects to control for possible influences of the hierarchical structure (i.e., locations, zones, bays, and nested effects of locations within zones and bays, and zones within bays) and season, and species identity, respectively (Bolker et al. 2009). First, we applied a model selection procedure based on the AICc to compare full models with different combinations of random effects and select the optimum random structure for the responses of LCBD,  $LCBD_{Repl}$ ,  $LCBD_{AbDiff}$ , and SCBD at each hierarchical level (Burnham and Anderson 2002). For LCBD indices, each candidate GLMM included a possible combination of random effects (i.e., hierarchical structure and/or season). The full GLMMs explaining the responses of SCBD included a random effect for species identity at both the bay and zone levels. For all cases, the set of candidate models also included full BR models (i.e., models with no random effects).

In a second step of the model selection, an automated procedure using the best full model (i.e., GLMM or BR) as a start point was used to obtain the submodels with the most parsimonious combinations of fixed effects (Bartoń 2020). In all steps, candidate models were ranked according to the AICc weight ( $w_i$ ) and all models with  $\Delta AICc < 2$  were selected for interpretation (Burnham and Anderson 2002; Wagenmakers and Farrell 2004). The goodness-of-fit

of each selected model was indicated by the squared correlation between the response and the predicted value based only on the fixed effects included in the model ( $r^2_f$ ), and both the fixed and random effects included in the model ( $r^2_{f+r}$ ).

We used model averaging to obtain inferences across the selected models to explain LCBD indices and SCBD by model-averaged parameter estimates and the associated confidence intervals (Burnham and Anderson 2002). Therefore, the approach estimated the strength of environmental and spatial effects based on their contributions to the average model. A parameter was informative if the 95% confidence interval did not overlap zero. The relative variable importance (RVI) for the parameter estimates in the average model was calculated by summing the  $w_i$  of the selected models recalculated without the other candidate models (Burnham and Anderson 2002).

All analyses were performed in the R environment (version 3.6.3; R Core Team 2020) with the packages ‘adespatial’ (version 0.3–8; Dray et al. 2020), ‘car’ (version 3.0–10; Fox and Weisberg 2019), ‘lme4’ (version 1.1–26; Bates et al. 2015), ‘betareg’ (version 3.1–3; Cribari-Neto and Zeileis 2010), ‘glmmTMB’ (version 1.0.2.1; Brooks et al. 2017), ‘StepReg’ (version 1.4.1; Li et al. 2020), ‘MuMIn’ (version 1.43.17; Bartoń 2020), and ‘ggcorrplot’ (version 0.1.3; Kasambara 2019).

## Results

### Scale-dependent patterns of LCBD

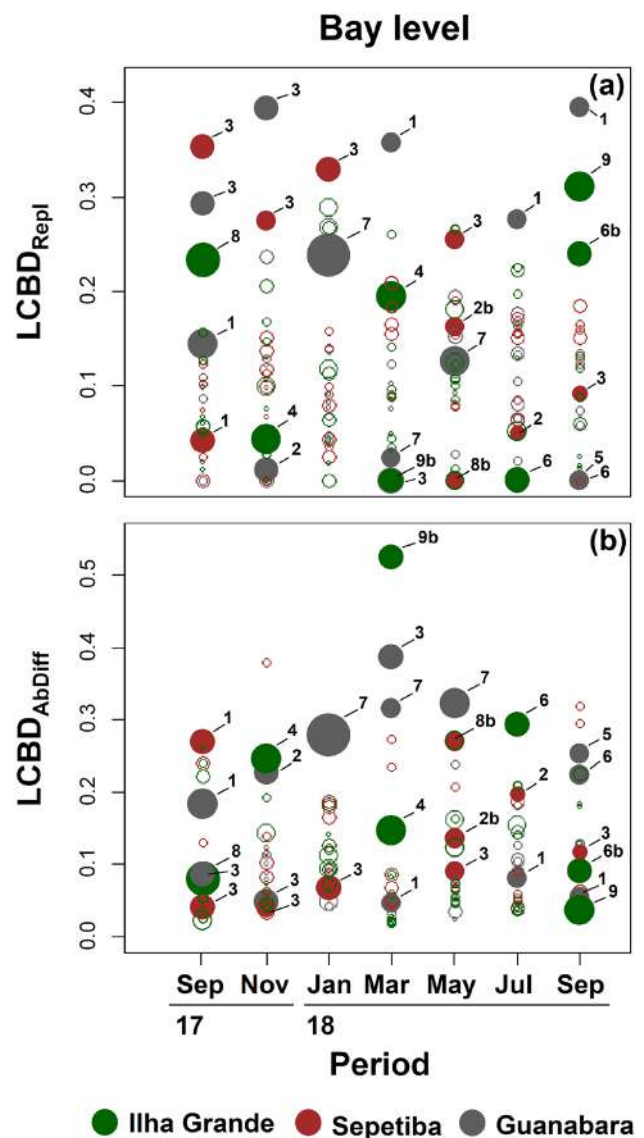
LCBD varied between the sampling periods at both the bay and zone levels (Fig. 2a–o). In the Ilha Grande bay, based on the permutation tests per bay and zone in each bay, more locations had non-random LCBD values higher than most locations at the bay level, whereas one location in the Middle zone and another in the Outer zone had higher values at both hierarchical levels ( $p$  values  $< 0.05$ ; Fig. 2a–o). The opposite was observed in the Sepetiba bay, with more locations exhibiting higher non-random LCBD at the zone level ( $p$  values  $< 0.05$ ; Fig. 2a–o). Three locations in the Sepetiba bay, two of them in the Inner and one in the Outer zone, had higher LCBD than most locations at both hierarchical levels ( $p$  values  $< 0.05$ ; Fig. 2a–o). In the Guanabara bay, more locations had higher non-random LCBD at the bay level, and three locations, one in each zone, had higher values at both hierarchical levels ( $p$  values  $< 0.05$ ; Fig. 2a–o). Therefore, in all bays, the non-random contributions of some locations to beta diversity, primarily in the Outer zone, was not dependent on the seascape size. Likewise, marked differences between bays were primarily related to LCBD values in their respective zones.

At the bay level, also considering the non-random patterns, LCBD was generally higher in the Guanabara bay, followed by the Sepetiba and Ilha Grande bays (Fig. 2, left panel). In the Guanabara bay, the highest LCBD varied over time between a set of six locations, primarily in the Inner zone, but also in the Middle and Outer zones (Fig. 2, left panel). The highest LCBD also varied between a set of five locations primarily in the Inner zone of the Sepetiba bay (Fig. 2, left panel). Only one location had higher LCBD during one sampling period (autumn) in the Outer zone of the Sepetiba bay, whereas one location in the Inner zone had higher LCBD over almost the entire annual cycle (Fig. 2, left panel). In the Ilha Grande bay, the highest LCBD also varied between a set of six locations, but in the Middle and Outer zones, with values slightly higher in the former zone (Fig. 2, left panel).

Based on the non-random patterns, at the zone level, LCBD was higher in the Sepetiba bay than the Guanabara and Ilha Grande bays (Fig. 2, right panel). The highest LCBD varied between sets of seven, four and two locations in the Sepetiba, Guanabara, and Ilha Grande bays, respectively (Fig. 2, right panel). In the Sepetiba bay, these locations were more equally distributed between zones compared with the other bays (Fig. 2, right panel). A similar trend was observed in the Guanabara bay, but the highest LCBD occurred primarily in the Outer zone and to a lesser extent the Inner zone (Fig. 2; right panel). Only locations in the Middle and Outer zones had the highest LCBD in the Ilha Grande bay, one location in the former zone in most sampling periods and one location in the Outer zone only in one period (autumn) (Fig. 2, right panel).

### Assembly processes supporting LCBD

At the bay level, more locations with higher non-random LCBD had also higher local contributions than other locations to the abundance-based replacement ( $LCBD_{Repl}$ ) (Fig. 3a). However, other several locations with higher non-random LCBD had higher local contributions than other locations based on the abundance difference ( $LCBD_{AbDiff}$ ) (Fig. 3b). Major differences regarding the assembly processes leading to more unique local assemblages were observed in the Sepetiba bay, with the prevalence of  $LCBD_{Repl}$  in most locations with higher non-random LCBD (Fig. 3a, b). A temporal decrease in  $LCBD_{Repl}$  values was also observed in the Sepetiba bay, which was followed by a quite slight increase in  $LCBD_{AbDiff}$  values (Fig. 3a, b). In the Guanabara bay, also considering locations with higher non-random LCBD values, regardless of the highest  $LCBD_{Repl}$  values observed for some locations, most of locations had higher  $LCBD_{AbDiff}$  (Fig. 3a, b). A gradual increase in  $LCBD_{AbDiff}$  from September 2017 to March 2018 (wet season), followed by a gradual decrease to September 2018 (dry



**Fig. 3** Local contribution to beta diversity based on abundance replacement ( $LCBD_{Repl}$ ) and abundance difference ( $LCBD_{AbDiff}$ ) at sampling locations per bay (Ilha Grande, Sepetiba, and Guanabara). Circle areas are proportional to the overall LCBD. Filled circles indicate locations in the Inner (1-3b), Middle (4-6b), and Outer (7-9b) zones of the bays with higher overall LCBD per bay and stronger evidence for non-random patterns based on the permutation tests

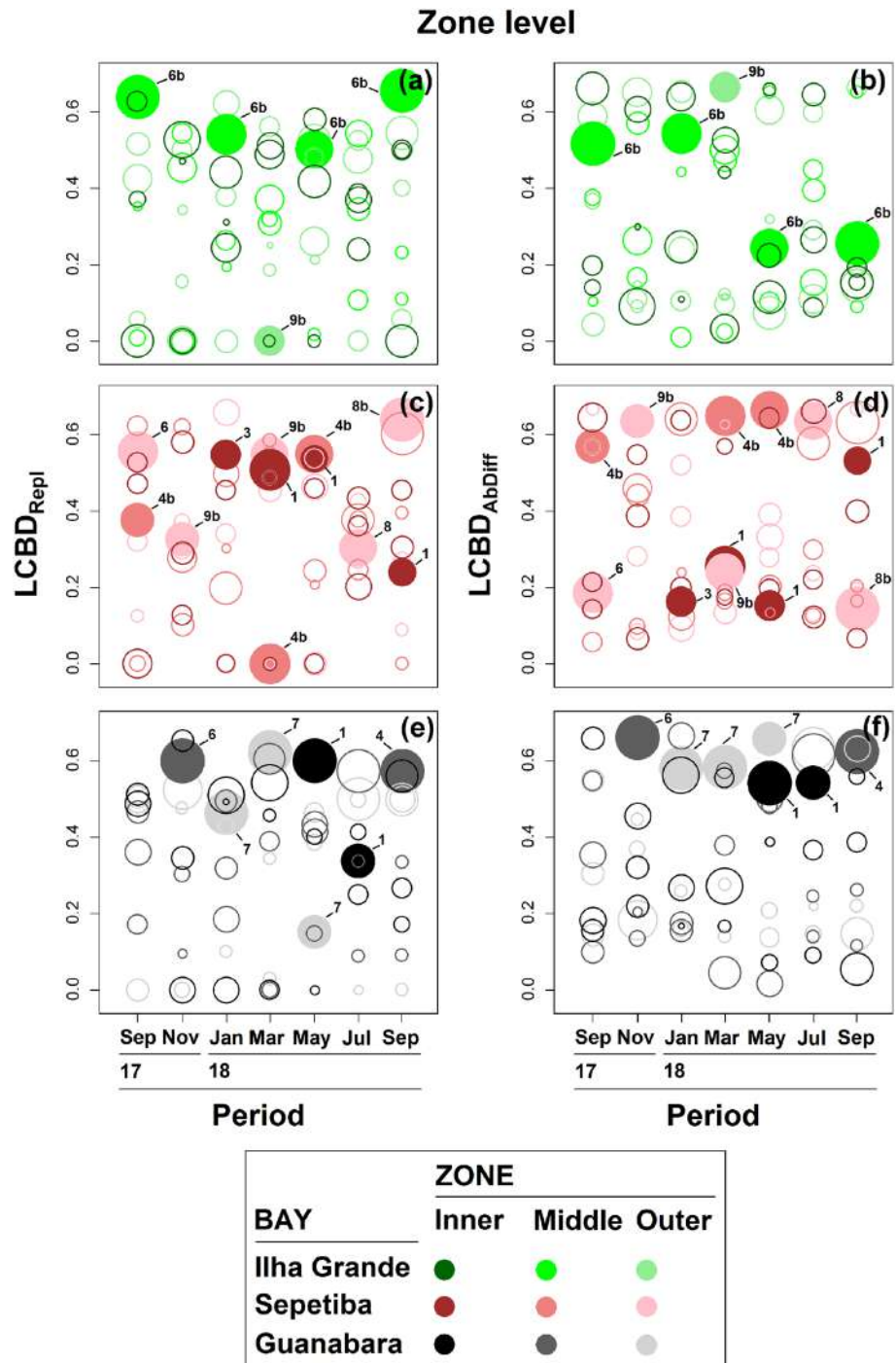
season) was also observed in the Guanabara bay (Fig. 3b). On the other hand, no clear temporal trends were observed for  $LCBD_{Repl}$  in the Guanabara bay (Fig. 3a). Similar values of  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  and no clear temporal or spatial trends were indicative of proportional local contributions of both assembly processes to beta diversity in the Ilha Grande bay (Fig. 3a, b).

Considering locations with higher non-random LCBD at the zone level, differences in the assembly processes supporting more unique locations were more marked between

bays, and to a lesser extent zone per bay (Fig. 4a–f). In the Ilha Grande bay, higher  $LCBD_{Repl}$  in the Middle zone contrasted with higher  $LCBD_{AbDiff}$  in the Outer zone (Fig. 4a–b). However, this trend was supported by one location in each zone, and only the location in the Middle zone had higher  $LCBD_{Repl}$  during most periods (Fig. 4a). Differences between zones were even more slight in the Guanabara bay, where highest values of both  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  were observed for most locations with higher non-random

$LCBD$  (Fig. 4e, f). Considering the sampling periods, higher  $LCBD_{AbDiff}$  was prevalent in the Guanabara bay, but the lower values of  $LCBD_{Repl}$  observed in some sampling periods were not enough to support differences between zones (Fig. 4e, f). In the Sepetiba bay,  $LCBD_{Repl}$  was primarily higher in the Inner and Outer zones, whereas higher  $LCBD_{AbDiff}$  was prevalent in the Middle zone (Fig. 4c, d). For all zones and  $LCBD$  indices, the trend was supported by several locations, evidencing stronger differences in the

**Fig. 4** Local contribution to beta diversity based on abundance replacement ( $LCBD_{Repl}$ ) and abundance difference ( $LCBD_{AbDiff}$ ) at sampling locations per zone (Inner, Middle, and Outer) in the Ilha Grande, Sepetiba, and Guanabara bays. Circle areas are proportional to the overall  $LCBD$ . Filled circles indicate locations in the Inner (1-3b), Middle (4-6b), and Outer (7-9b) zones of the bays with higher overall  $LCBD$  per zone and stronger evidence for non-random patterns based on the permutation tests



primary assembly processes between zones in the Sepetiba bay compared with the other bays (Fig. 4c, d).

### Environmental, assemblage-based and spatial sources of variation

For models including only environmental effects, variables selected to explain LCBD at the bay level included metrics representative of local habitat quality, ocean conditions, seascape configuration, and assemblage structure (Table S3). At the zone level, variables selected to explain LCBD were primarily landscape features, besides seascape configuration and assemblage metrics (Table S3). Metrics of seascape configuration representative of the availability of alternative habitats were nearby estuaries and mangrove cover at the bay level and mangrove cover at the zone level (Tables S3). Regarding assemblage metrics, species richness was selected to explain LCBD at both hierarchical levels, whereas variables selected for the full models exclusively at the bay and zone levels were latent variables representative of the variation in species composition after controlling for effects of season (LV1(Se)) and location (LV2(Lo)), respectively (Table S3). Considering the LCBD indices based on different assembly processes, environmental models explained only  $LCBD_{Repl}$  at the bay level, and the selected variables included transparency, mangrove cover, and nearby estuaries (Table S4). For all LCBD indices, at both hierarchical

levels, only spatial variables were selected for the models considering both environmental and spatial effects (Tables S3, S4). Models explaining LCBD included spatial variables representative of spatial structures from larger to finer spatial scales, but the range of spatial scales was slightly wider at the zone level (Table S3). Spatial structures from larger to finer scales also explained  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  at both hierarchical levels (Table S4). However,  $LCBD_{Repl}$  was primarily explained by spatial structures at larger scales, whereas spatial structures at finer scales were the primary drivers of  $LCBD_{AbDiff}$  (Table S4).

Local habitat quality distinguished bays in terms of a much higher water transparency in the Ilha Grande bay and lower in the Sepetiba bay (Table 1). Tidal phase, in turn, was primarily characterized by ebb/low tides in the Guanabara bay and flood/high tides in the other bays (Table 1). However, differences between locations in different bays were mostly supported by landscape metrics (Table 1). Forest cover was much higher in the Ilha Grande bay, followed by the Guanabara bay, where higher values were observed at some locations, regardless of the prevalent low values (Table 1). Pasture cover was also much higher in the Ilha Grande bay, very reduced in the Sepetiba bay and quite negligible in the Guanabara bay (Table 1). Contrary to the observed for forest and pasture covers, human settlements were higher in the Guanabara bay and decreased to the Ilha Grande bay (Table 1). Regardless of quite lower and

**Table 1** Environmental variables selected to explain the local contribution to beta diversity

Variable	Ilha Grande bay			Sepetiba bay			Guanabara bay		
	Median	Quartiles		Median	Quartiles		Median	Quartiles	
		Lower	Upper		Lower	Upper		Lower	Upper
<b>Local habitat quality</b>									
Transparency (% depth)	100.00	50.00	100.00	50.23	36.81	76.94	63.10	40.42	87.30
<b>Ocean-related variables</b>									
Tidal phase	1.00	1.00	2.00	1.00	1.00	2.00	2.00	1.00	2.00
<b>Landscape metrics</b>									
Forest cover (%)	12.30	2.76	22.78	0.00	0.00	0.21	0.30	0.00	9.78
Pasture cover (%)	10.00	0.00	25.98	0.00	0.00	2.60	0.00	0.00	0.00
Human settlements (%)	34.74	0.00	42.75	48.37	21.72	49.51	50.25	25.25	55.17
<b>Seascape configuration</b>									
Number of nearby estuaries	8	6	9	4	3	5	3	0	7
Mangrove cover (%)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Rocky shores (%)	0.09	0.02	0.13	0.02	0.00	0.05	0.03	0.01	0.85
<b>Assemblage-based metrics</b>									
Species richness	8	6	11	9	7	11	10	7	12
Latent variable 1 (season)	- 0.13	- 0.63	0.53	- 0.18	- 0.48	0.83	0.37	- 0.24	1.82
Latent variable 2 (location)	0.28	- 0.37	1.24	0.76	- 0.75	1.46	0.30	- 0.46	1.37

Median, lower and upper quartiles of the samples obtained at locations during seven two-month intervals through 1-year period in the Ilha Grande, Sepetiba, and Guanabara bays. Variables representative of local habitat quality, ocean and climate conditions, landscape features, seascape configuration, and assemblage structure



### Multiscale environmental and spatial drivers of LCBD

All environmental models selected to explain LCBD at both hierarchical levels included location as random effect, which shared a large fraction of the explained variation with environmental effects (Tables 2, S5). Model selection applied to both environmental and spatial effects, in turn, resulted in spatial models with no random structure (Tables 2, S5). Environmental models explaining LCBD<sub>Repl</sub> also included location as a random effect, which had a slighter influence on the response to environmental effects compared with environmental models for LCBD (Tables 3, S6). Spatial models selected to explain LCBD<sub>Repl</sub> at the bay level also included a random effect for location, but its influence on the response variation was negligible (Tables 3, S6). At the zone level, spatial models including only location and both location and

season as random effects were selected to explain LCBD<sub>Repl</sub>, and in all cases the influence of the random structure on the response variation was also slight (Tables 3, S6). At both hierarchical levels, spatial models selected to explain LCBD<sub>AbDiff</sub> had no random structure (Tables 3, S6).

At the bay level, more models included the negative effects of transparency and LV1(Se) on LCBD (Table 2). The negative effect of LV1(Se) was primarily indicative of higher LCBD associated with species composition in the Ilha Grande, followed by the Sepetiba bay, and lower LCBD in the Guanabara bay (Fig. 5a). The negative effect of transparency on LCBD contrasted with a stronger positive effect on LCBD<sub>Repl</sub>, indicative of higher abundance-based replacement under increasing transparency (Tables 2, 3). Mangrove cover had an even stronger positive influence on LCBD<sub>Repl</sub> at the bay level (Table 3). LCBD, in turn, was also positively related to nearby estuaries and species richness, and

**Table 2** Parameter estimates (95% confidence intervals) and relative variable importance (RVI) based on the averages of beta regression and generalized linear mixed models better explaining ( $\Delta AICc < 2$ ) the local contributions to beta diversity at the bay and zone levels

Parameter	Bay level Estimate	RVI	Zone level Estimate	RVI
Env	Random effect: Lo		Random effect: Lo	
Intercept	- 2.076 (- 2.170, - 1.982)		- 0.737 (- 0.843, - 0.630)	
Transparency	<b>- 0.251 (- 0.443, - 0.058)</b>	1.00 (7)		
Species richness	0.113 (- 0.011, 0.339)	0.69 (4)	<b>0.218 (0.050, 0.386)</b>	1.00 (6)
LV1_Se	<b>- 0.110 (- 0.196, - 0.024)</b>	1.00 (7)		
LV2_Lo			0.021 (- 0.017, 0.105)	0.48 (3)
Tidal phase	- 0.048 (- 0.273, 0.047)	0.43 (3)		
Nearby estuaries	0.097 (- 0.027, 0.354)	0.59 (4)		
Mangrove			- 0.039 (- 0.494, 0.154)	0.23 (3)
Forest cover			<b>- 0.297 (- 0.561, - 0.034)</b>	1.00 (6)
Pasture cover			- 0.143 (- 0.511, 0.058)	0.63 (4)
Settlements			<b>- 0.405 (- 0.792, - 0.017)</b>	1.00 (6)
Env + S				
Intercept	- 2.124 (- 2.203, - 2.045)		- 0.744 (- 0.822, - 0.667)	
S2			<b>- 0.505 (- 0.996, - 0.014)</b>	1.00 (3)
S6	<b>- 0.670 (- 1.192, - 0.146)</b>	1.00 (3)		
S8	<b>0.684 (0.215, 1.153)</b>	1.00 (3)		
S9	<b>- 0.394 (- 0.763, - 0.024)</b>	1.00 (3)	<b>- 0.434 (- 0.824, - 0.052)</b>	1.00 (3)
S10			- 0.399 (- 1.003, 0.000)	0.80 (2)
S11			- 0.196 (- 0.706, 0.079)	0.62 (2)
S12	<b>0.727 (0.209, 1.244)</b>	1.00 (3)		
S14	0.238 (- 0.109, 0.894)	0.61 (2)	<b>- 0.527 (- 1.038, - 0.016)</b>	1.00 (3)
S15	<b>0.415 (0.005, 1.016)</b>	0.81 (2)	<b>0.869 (0.352, 1.386)</b>	1.00 (3)
S16	<b>0.590 (0.188, 0.992)</b>	1.00 (3)		
S17	<b>- 0.654 (- 1.190, - 0.118)</b>	1.00 (3)		
S19	<b>- 0.689 (- 1.294, - 0.084)</b>	1.00 (3)	<b>- 0.887 (- 1.492, - 0.282)</b>	1.00 (3)
S20	<b>0.496 (0.103, 0.888)</b>	1.00 (3)	<b>0.474 (0.077, 0.870)</b>	1.00 (3)
S21			<b>- 0.710 (- 1.216, - 0.205)</b>	1.00 (3)

Model selection based on environmental (Env) and spatial effects (S). The number of models including each parameter in parenthesis. Location (Lo) as random effect. Estimates with confidence intervals that do not overlap zero in bold

**Table 3** Parameter estimates (95% confidence intervals) and relative variable importance (RVI) based on the averages of beta regression and generalized linear mixed models better explaining ( $\Delta AIC_c < 2$ ) the local contributions to beta diversity of abundance-based replacement ( $LCBD_{Repl}$ ) and abundance difference ( $LCBD_{AbDiff}$ ) at the bay and zone levels

Parameter	$LCBD_{Repl}$ Estimate	RVI	$LCBD_{AbDiff}$ Estimate	RVI
<b>Bay level</b>				
Env	Random effect: Lo			
Intercept	- 2.338 (- 2.607, - 2.069)			
Transparency	<b>0.400 (0.022, 0.778)</b>	1.00 (2)		
Mangrove cover	<b>0.525 (0.042, 1.008)</b>	1.00 (2)		
Nearby estuaries	0.067 (- 0.267, 0.671)	0.33 (1)		
Env + S	Random effect: Lo			
Intercept	- 2.332 (- 2.586, - 2.078)		- 2.092 (- 2.200, - 1.984)	
S5	<b>1.193 (0.043, 2.343)</b>	1.00 (2)		
S6			- 0.094 (- 1.034, 0.326)	0.27 (2)
S8	<b>2.123 (0.830, 3.416)</b>	1.00 (2)	- 0.115 (- 1.045, 0.274)	0.30 (2)
S16			<b>0.660 (0.139, 1.180)</b>	1.00 (6)
S20			<b>0.552 (0.035, 1.068)</b>	1.00 (6)
S25	- 0.476 (- 2.278, 0.351)	0.49 (1)	0.246 (- 0.195, 1.208)	0.49 (3)
<b>Zone level</b>				
Env + S	Random effects: Lo			
Intercept	- 1.279 (- 1.578, - 0.979)		- 0.734 (- 0.858, - 0.610)	
S2	- 1.323 (- 3.415, 0.047)	0.79 (2)		
S9			- 0.333 (- 1.148, 0.095)	0.63 (4)
S18	- 0.358 (- 2.864, 0.686)	0.33 (1)	<b>1.296 (0.488, 2.103)</b>	1.00 (7)
S20			0.397 (- 0.049, 1.215)	0.68 (4)
S25			0.354 (- 0.233, 1.507)	0.56 (4)
	Random effects: Lo, Se			
Intercept	- 1.232 (- 1.593, - 0.872)			
S2	- <b>1.754 (- 3.500, - 0.008)</b>	1.00 (3)		
S15	0.164 (- 1.097, 2.609)	0.22 (1)		
S18	- 0.357 (- 2.883, 0.691)	0.33 (1)		

Model selection based on environmental (Env) and spatial effects (S). Location (Lo) and season (Se) as random effects. The number of models including each parameter in parenthesis. Estimates with confidence intervals that do not overlap zero in bold

negatively related to tidal phase, but these variables were included in fewer models and, according to the model averaging, had negligible effects (Table 2).

Considering the spatial models at the bay level,  $LCBD$  was slightly more related to spatial structures at intermediate scales, but also at finer and larger scales (Table 2). Therefore, there were relevant effects on  $LCBD$  not accounted for at scales most likely comparable to zones within each bay and small groups of locations.  $LCBD_{Repl}$ , in turn, was more related to the spatial structure at larger scales, whereas  $LCBD_{AbDiff}$  was primarily influenced by spatial structures at finer scales (Table 3).

Forest cover, human settlements, and species richness were included in more models at the zone level, with the landscape metrics and species richness negatively and positively related to  $LCBD$ , respectively (Table 2). Human settlements had stronger effects than the other variables, whereas mangrove and pasture cover, and  $LV2(Lo)$  were

included in fewer models and had negligible averaged effects (Table 2). Mangrove and pasture cover were also negatively related to  $LCBD$ , whereas  $LV2(Lo)$  had a positive effect indicative of slight seasonal increases in  $LCBD$  following composition changes from the spring to the winter (Table 2; Fig. 5b).

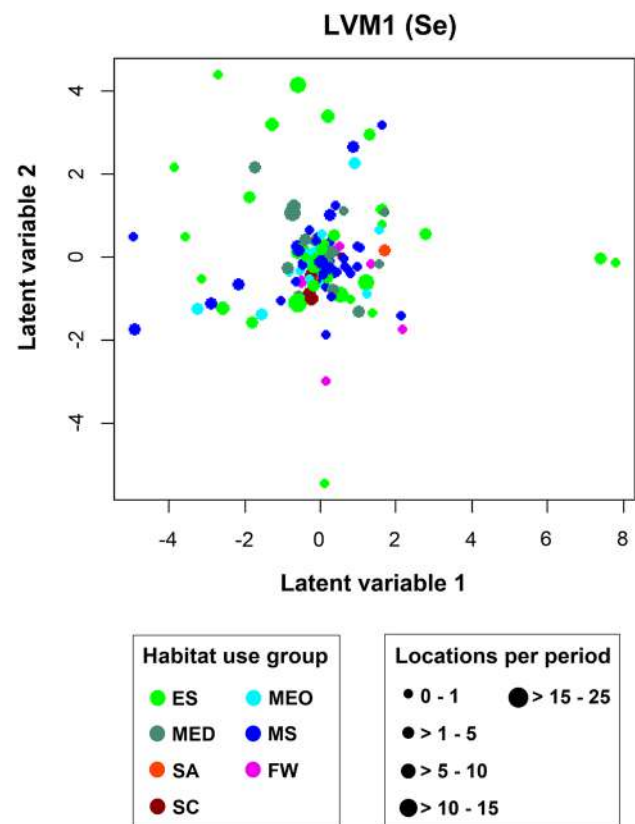
According to the model averaging at the zone level,  $LCBD$  was more related to spatial structures at intermediate to finer scales, and to a lesser extent to the spatial structure at a much larger scale (Table 2). This large-scale spatial structure was most likely representative of areas larger than individual bays and also influenced  $LCBD_{Repl}$ , whereas  $LCBD_{AbDiff}$  was primarily associated with the spatial structure at a finer spatial scale (Table 3). These relationships evidenced the importance of unaccounted effects at larger and finer spatial scales for assembly processes supporting  $LCBD$  patterns at the zone level.

## Assemblage- and species-level patterns in SCBD

In all bays, SCBD was much higher for estuarine species at both the bay and zone levels (Table S7). *Atherinella brasiliensis* and *Anchoa* sp. had higher SCBD at both hierarchical levels, whereas *Anchoa januaria* contributed more to beta diversity only at the bay level, and *Harengula clupeiola* (larvae) and *Odontesthes bonariensis* only at the zone level (Table S7). At the bay level, to a lesser extent, SCBD was also higher for other 20 estuarine species, followed by 17 marine stragglers, six marine estuarine-dependent species, three semi-anadromous and one semi-catadromous species, four marine estuarine-opportunists, and three freshwater species (Table S7). A similar trend was observed at the zone level, with intermediate SCBD observed for 29 marine stragglers, followed by 26 other estuarine species, 10 marine estuarine-opportunists, eight marine estuarine-dependent, two semi-anadromous and three semi-catadromous species, and four freshwater species (Table S7). Several species also had intermediate values of SCBD at both hierarchical levels, mostly estuarine and marine straggler species, 16 and 15, respectively, followed by six marine estuarine-dependent species, four marine estuarine-opportunists, two semi-anadromous and one semi-catadromous species, and three freshwater species (Table S7). Therefore, estuarine and marine straggler species generally contributed more to beta diversity, whereas marine estuarine-dependent, semi-anadromous and semi-catadromous species had intermediate contributions, and freshwater species contributed less. For marine estuarine-opportunists, in turn, more species had higher SCBD at the zone level.

Variables selected to explain SCBD at both hierarchical levels were the number of locations in which each species occurred, species-specific coefficients representative of the unconstrained distributions of individual species after controlling for season effect,  $Sp\_c1(Se)$  and  $Sp\_c2(Se)$ , and habitat use (Table S3). Therefore, spatial effects were more important to explain SCBD than seasonal effects. Four estuarine species and only one marine estuarine-dependent species occurred at more than 10 locations per period (Fig. 6). Likewise, more estuarine species occurred at five to < 10 locations per period, whereas only three species of other habitat use groups (i.e., marine estuarine-dependent, semi-catadromous, and marine straggler) occurred in this interval of locations per period (Fig. 6). Most species occurred at less than five locations per period, most of them marine stragglers, followed by estuarine species, marine estuarine-opportunist and dependent species, and many less freshwater, semi-catadromous and semi-anadromous species (Fig. 6).

According to the ordination of the latent variable species-specific coefficients expressing the unconstrained distribution of individual species after controlling for season effect, most species were not widespread in the spatial gradients



**Fig. 6** Model-based unconstrained Bayesian ordination using the posterior mean estimates for the fish species composition at sampling locations in the Ilha Grande, Sepetiba, and Guanabara bays, after controlling for season effect (Se). Means of the posterior distributions of the latent variable species-specific coefficients selected to explain the species contribution to beta diversity are shown for each species according to their habitat use groups (estuarine, ES; marine estuarine dependent, MED; semi-anadromous, SA; semi-catadromous, SC; marine estuarine opportunist, MEO; marine straggler, MS; and freshwater, FW) and the mean number of locations where they occur per sampling period

(Fig. 6).  $Sp\_c1(Se)$  was primarily indicative of the occurrence of less marine stragglers, and to a lesser extent marine estuarine-opportunist species, from negative to positive scores, whereas two freshwater species and one semi-anadromous species had positive scores (Fig. 6). Estuarine and to a much lesser extent marine estuarine-dependent species were more widespread over the spatial gradient (Fig. 6). Likewise, regardless of their prevalent negative scores, marine stragglers were also widely distributed in the spatial gradient associated with the latent variable 1 (Fig. 6).  $Sp\_c2(Se)$  expressed primarily the gradient of species occurring in increasing numbers of locations per period from negative (primarily freshwater species) to positive scores (primarily estuarine and to a lesser extent marine estuarine-dependent species) (Fig. 6). This gradient was only slightly related to habitat use, but most species with positive scores were



estuarine and to a lesser degree marine estuarine-dependent, whereas freshwater species had intermediated to negative scores (Fig. 6).

Habitat use was not included in the models better explaining SCBD, and based on the model averaging, Sp\_c2(Se) had a negligible effect on SCBD (Table 4). SCBD was positively related primarily to the prevalence at locations and less to Sp\_c1(Se) at both hierarchical levels (Table 4). SCBD was therefore primarily higher for species occurring at more locations per zone and bay. Likewise, SCBD was primarily lower for some marine straggler species and to a lesser extent some marine estuarine-opportunist species, and higher for a few freshwater and semi-anadromous species, and primarily estuarine species. However, species with different habitat uses, including marine straggler and estuarine species, had lower and higher SCBD. Also, a large fraction of the variation in the response of SBCD was associated with species identity at both hierarchical levels (Table S5).

### Discussion

Multiscale mechanisms dependent on the seascape size drive the contributions of individual locations to beta diversity of coastal fishes in tropical seascapes. The effect of LV1(Se) on local contribution to beta diversity (LCBD) at the bay level evidenced that differences in species composition between locations (after controlling for the season effect) may be more relevant in larger seascapes. This possibility was confirmed by higher contributions of locations with higher LCBD to abundance-based replacement (LCBD<sub>Repl</sub>) than abundance differences (LCBD<sub>AbDiff</sub>) between local habitats at the bay level. Furthermore, the effects of spatial structures primarily at larger scales on LCBD<sub>Repl</sub> at both the bay and zone levels were indicative of unaccounted processes driving the contributions of local assemblages to abundance-based replacement in spatial extents most likely larger than individual bays. These findings reinforce the prevalence of large-scale mechanisms supporting replacement processes in nearshore assemblages over increasing spatial extents

(e.g., from regional to continental scale, Viana et al. 2016; from estuarine sectors to the entire estuary, Menegotto et al. 2019).

At the zone level, a stronger relationship between species richness and LCBD suggested that the contributions of local assemblages to beta diversity in smaller seascapes are primarily related to species loss (or gain) between locations. Based on an analogous process whereby individuals of all species are equally lost, a larger number of more unique local assemblages with higher LCBD<sub>AbDiff</sub> emphasized the importance of richness differences between locations (Legendre 2014). Higher LCBD<sub>AbDiff</sub> at the zone than the bay level also evidenced the importance of even more shared species pool to promote primarily abundance differences between locations in smaller seascapes (Reis et al. 2016; Araújo et al. 2018). Also, the increasing importance of biotic processes generating abundance differences in smaller spatial extents was supported by stronger fine-scale spatial effects on LCBD<sub>AbDiff</sub> at both hierarchical levels (Munsch et al. 2016; Yeager et al. 2017). To a much lesser degree, the slight effect of LV2(Lo) on LCBD suggested that the local uniqueness in smaller seascapes may be influenced by seasonal changes in species composition (after controlling for the location effect), which was reinforced by the random structures associated with location and season in models explaining LCBD<sub>Repl</sub>. Therefore, local uniqueness is a primary result of replacement processes in larger tropical seascapes, and a more balanced result of different assembly processes in smaller spatial extents. At both hierarchical levels, marked differences between individual seascapes in LCBD indices and spatially structured patterns evidenced prevailing spatial processes driving fish beta diversity, as supported by previous short-term studies using metrics based on both species richness and composition in different coastal ecosystems (e.g., bays, oceanic beaches, and coastal lagoons, Camara et al. 2019; coastal lagoons, Camara et al. 2021).

The prevalence of multiscale environmental effects on LCBD and LCBD<sub>Repl</sub> at the bay level suggested that the ecological uniqueness of locations is a primary product of environmental filtering processes selecting species with different

**Table 4** Parameter estimates (95% confidence intervals) and relative variable importance (RVI) based on the averages of generalized linear mixed models better explaining ( $\Delta AICc < 2$ ) the species contributions to beta diversity at the bay and zone levels

Parameter	Bay level Estimate	RVI	Zone level Estimate	RVI
	Random effect: species		Random effect: species	
Intercept	- 4.679 (- 4.852, - 4.506)		- 3.566 (- 3.739, - 3.393)	
Number of locations	<b>0.286 (0.252, 0.320)</b>	1.00 (2)	<b>0.304 (0.228, 0.380)</b>	1.00 (2)
Sp_c1(Se)	<b>0.058 (0.009, 0.106)</b>	1.00 (2)	<b>0.055 (0.012, 0.099)</b>	1.00 (2)
Sp_c2(Se)	0.038 (- 0.001, 0.117)	0.67 (1)	0.032 (- 0.002, 0.101)	0.66 (1)

Models included the number of locations where each species occurred per sampling period and the species-specific coefficients (Sp\_c1 and Sp\_c2) after controlling season effect (Se). The number of models including each parameter in parenthesis. Species identity as random effect. Estimates with confidence intervals that do not overlap zero in bold

traits to local fish assemblages in larger seascapes (Mouchet et al. 2013; Yeager et al. 2017). Environmental effects representative from local to regional conditions evidenced the importance marine and freshwater influences for fish beta diversity at the bay level. Transparency was the variable better explaining LCBD, and despite representative of local conditions, expressed strong differences between bays. Therefore, transparency is an important regional driver of the ecological uniqueness of local assemblages in larger seascapes. The positive effect of transparency (higher marine influence) in accordance with larger-scale spatial effects on  $LCBD_{Repl}$  provided further evidence for the influence of transparency at scales most likely larger than individual bays. To a lesser extent, tidal phase reinforced the importance of regional gradients, with higher values of LCBD under flood/high tide (higher marine influence) and lower transparency (lower marine influence) expressing the mutual roles of marine and freshwater influences. The slight positive effects of nearby estuaries on LCBD and  $LCBD_{Repl}$ , and stronger positive effect of mangrove cover on  $LCBD_{Repl}$ , in turn, evidenced the importance of estuarine habitats to promote higher local contributions to abundance-based replacement. Therefore, our study confirmed the importance of environmental context (estuarine vs. marine conditions) and seascape configuration for coastal fish biodiversity (van Lier et al. 2018; Bradley et al. 2019; Camara et al. 2020), while revealing environmental filtering as a primary mechanism driving fish beta diversity in more heterogeneous seascapes based on the contributions of coastal localities to abundance-based replacement processes.

The slight influences of most environmental factors at the bay level are most likely related to marked differences in the marine vs. freshwater balance between systems and zones (Tables 1, S2; Camara et al. 2020). The generally higher  $LCBD_{Repl}$  in the Sepetiba bay coincident with lower transparency and high number of nearby estuaries supported the importance of the estuarine context to fish beta diversity. In the Guanabara bay, the absence of nearby estuaries to some locations and higher variation in transparency values between zones most likely supported wider ranges of  $LCBD_{Repl}$ . In the Ilha Grande bay, regardless of a higher number of nearby estuaries, the prevalence of small watersheds associated with the largely opened connection to the open sea most likely leads to higher water transparency (Guerra and Soares 2009). Therefore, the similar values of  $LCBD_{Repl}$  and  $LCBD_{AbDiff}$  in the Ilha Grande bay, with no clear spatial and temporal trends, may be explained by smoother environmental gradients. The marine context enable marine-origin species to have a quite similar chance of being selected from the regional pool for different local assemblages. At the same time, a large number of rare marine species most likely support the random temporal variation in LCBD values primarily in the outermost areas

(Tables S1, S7), reinforcing the primary importance of rare marine species for fish diversity patterns in coastal ecosystems under higher marine influence (da Silva and Fabr e 2019; Camara et al. 2021). These relationships are also in accordance with previous studies that support strong influences of random processes on fish beta diversity in coastal areas (e.g., Ford and Roberts 2018; Ara ujo et al. 2019). At the zone level, the prevalence of spatial effects and more marked differences in LCBD indices between bays and zones were indicative of multiscale unaccounted processes generating differences in the local contributions to assembly processes primarily between smaller tropical seascapes (Vasconcelos et al. 2014; Krueck et al. 2020).

Land-based processes and availability of alternative habitats are critical drivers of fish diversity patterns in coastal seascapes (van Lier et al. 2018; Henderson et al. 2020). In our study, the exclusive selection of landscape and seascape metrics for environmental models explaining LCBD at the zone level supported the primary influence of landscape-scale processes on fish beta diversity in smaller tropical seascapes. Areas with larger vegetal cover generally provide more complex habitats and feeding resources based on the input of wood debris and organic matter (Crook and Robertson 1999; Whitfield 2017). Therefore, the negative effect of forest cover on LCBD in accordance with intermediate- to fine-scale structures associated with LCBD, primarily due to fine-scale effects on  $LCBD_{AbDiff}$ , is most likely a result of a higher similarity between local assemblages in high-quality habitats provided by small groups of localities in more forested areas. At the same time, much higher forest cover in the Ilha Grande bay, characterized by greater marine influence, may favor environmental filtering processes selecting the same marine-origin species, which also culminate in lower LCBD. Further evidence in this sense was provided by the large-scale structure associated with  $LCBD_{Repl}$ , indicative of unaccounted processes establishing the species pool at scales much larger than zones based on the contributions of local assemblages to abundance-based replacement.

The negative effect of human settlements on LCBD at the zone level was stronger most likely as a result of homogenization processes related to habitat loss and human pressures under higher levels of urbanization (Massicotte et al. 2015; Gomes-Gon alves et al. 2020). Considering the percentage of human settlements much higher in the Guanabara bay, which has limited marine influence and much lower species richness primarily related to a lower number of marine-origin species (Table S1), the opposite effects of species richness and human settlements on LCBD reinforce the possibility of species loss producing less unique local assemblages in more urbanized areas. A lower relevance of this process in smaller seascapes harboring more complex habitat structures was supported by a lower negative effect of forest cover, besides the slight averaged effects of mangrove cover and

pasture cover on LCBD. Therefore, opposite mechanisms support more unique assemblages at species-richer locations and less unique local assemblages in more urbanized areas, and to a lesser extent in more vegetated areas, most likely due to more niche opportunities for different fish species (Messmer et al. 2011; Whitfield 2017). In this sense, considering the reduced span of mangrove cover and the distribution largely restricted to a few locations, its positive and stronger effect on  $LCBD_{Repl}$  at the bay level evidenced the critical importance of the availability of more complex habitats for fish beta diversity primarily in larger seascapes, but also regardless of the seascape size.

The contributions of individual species to beta diversity (SCBD) generally irrespective of the seascape size testified the importance of the largely shared species pool for assembly processes driving fish beta diversity. Habitat use group was not included in the models better explaining SCBD, but more restricted distributions of semi-anadromous, semi-cataadromous and freshwater groups most likely explain their small numbers of species with higher SBCD as a result of more specific conditions required for their occurrences (i.e., presence of estuaries) (Elliott et al. 2007; Reis et al. 2016). Estuarine species and to a lesser extent marine estuarine-dependent species, in turn, can establish populations across a larger number of alternative habitats, but may be much less abundant under higher marine influence due to the high dependence on estuarine conditions (Potter et al. 2015; Camara et al. 2020). This may explain much higher SCBD observed for a few estuarine species and intermediate values observed for other several species of the group, besides more marine estuarine-dependent species with higher SCBD at the zone than the bay level. The large number of marine straggler species with higher SCBD may be related to their typically rare occurrences at several locations due to their sporadic and random dispersal in coastal seascapes (Elliott et al. 2007; Araújo et al. 2016). In this sense, slightly larger numbers of marine straggler and marine estuarine-opportunist species with higher contribution to beta diversity at the zone level, and their higher frequencies primarily in the Middle–Outer zones reinforced the primary relevance of random assembly processes at locations across a marine context and in smaller seascapes (Table S7). These relationships confirm the strong influences of intrinsic features of individual systems on beta diversity patterns, and the strength of scale-dependent patterns of LCBD. Also, the variance in SCBD largely associated with species identity was indicative of other important ecological attributes of individual species influencing their contributions to beta diversity regardless of the seascape size.

The prevalence of spatial trends in SCBD and the overall concordance between bays and zones, based on the responses to effects of species-specific coefficients representative of the distribution of individual species after

controlling for season effect ( $Sp\_c1(Se)$ ), reinforced the primary relevance of processes generating spatial structures to assembly patterns in tropical seascapes. The primary contribution of more widespread species to fish beta diversity in coastal seascapes with different sizes was evidenced by stronger positive relationships between the number of locations in which each species occurred and SBCD. Especially considering that the positive effect of  $Sp\_c1(Se)$  supported very slight increases in SCBD from marine straggler and marine estuarine-opportunist species to freshwater and semi-anadromous species, the contributions of individual species to beta diversity are primarily related to their prevalence in the seascapes. More widespread species may promote the seascape connectivity, reducing impacts of urbanization on coastal biodiversity (Vargas-Fonseca et al. 2016; Henderson et al. 2017), whereas species with restricted distribution require specific environmental contexts (Potter et al. 2015; Andrade-Tubino et al. 2020). Therefore, our results testified the importance of habitat complexity, connectivity between habitat patches, and spatial arrangement of seascape mosaic in coastal conservation planning (Henderson et al. 2017; Ortodossi et al. 2019; Rodil et al. 2021).

Conservation actions designed to protect coastal fish biodiversity in tropical seascapes must consider multiscale habitat–species relationships driving scale-dependent roles of more diverse local assemblages in fish beta diversity. More locations with higher LCBD at the bay level evidenced the primary importance of a greater environmental heterogeneity to beta diversity in larger seascapes. The environmental mechanisms supporting primarily  $LCBD_{Repl}$  evidenced that restoring and/or protecting habitat heterogeneity in larger tropical seascapes implies to prioritize the availability of high-complexity alternative habitats in estuarine and marine contexts. These relationships are especially critical considering that nearshore fish assemblages include primarily juvenile fishes with different levels of estuarine dependence (Elliott et al. 2007; Araújo et al. 2016), and different environmental contexts may support independent seascape nurseries in small spatial extents (Munsch et al. 2016; Bradley et al. 2019).

Regardless of the primary importance of species richness at the zone level, a slighter positive effect on LCBD at the bay level evidenced that higher contributions of species-richer local assemblages to fish beta diversity are not completely dependent on the seascape size. The higher environmental heterogeneity may, therefore, explain the lower importance of differences in species richness driving LCBD in larger seascapes. These results have critical consequences for conservation aims, considering that declines in species richness are strongly associated with processes of environmental homogenization in coastal seascapes increasingly subjected to human impacts (Massicotte et al. 2015; Araújo et al. 2016). For the studied seascapes, these consequences

may be even more threatening given the reduction in species richness from Ilha Grande to Guanabara bay (Table S1), following decreasing degrees of conservation and increasing human impacts. These findings highlight the importance of small-scale conservation actions focused on the maintenance of species-rich local assemblages primarily in seascapes encompassing a lower variety of habitat patches, and reinforce the need for conservation prioritization of high-complexity habitats irrespective of the seascape size.

Our study showed that larger seascapes are indeed more heterogeneous areas that support more local assemblages with higher contributions to fish beta diversity. Higher values of LCBD and primarily  $LCBD_{Repl}$  related to gradients of marine vs. freshwater influence and availability of high-complexity habitats evidenced that environmental filtering is a primary mechanism driving fish beta diversity by means of local contributions to abundance-based replacement in larger seascapes. Spatial effects indicative of unaccounted processes influencing the uniqueness of local assemblages at scales larger than individual bays reinforced the importance of large-scale replacement processes in more heterogeneous seascapes. A stronger positive relationship between species richness and LCBD, and higher  $LCBD_{AbDiff}$  at the zone level, besides fine-scale spatial effects on  $LCBD_{AbDiff}$ , provided substantial evidence for more critical decreases in fish beta diversity related to species loss in smaller seascapes. The negative effect of human settlements on LCBD was strongly indicative of species loss between localities in less heterogeneous areas as the primary landscape process driving fish beta diversity in smaller seascapes. Besides confirming the primary importance of landscape-scale processes at the zone level, slighter negative effects of vegetal cover and availability of alternative habitats (mangrove cover) on LCBD evidenced a damping effect of more complex habitats on species loss in smaller seascapes.

The positive relationship between SCBD and the number of locations in which individual species occurred evidenced that fish species able to colonize and establish populations in a larger number of alternative coastal habitats play a central role in beta diversity patterns. Regardless of highly species-specific responses, most species with higher SCBD were estuarine, evidencing the importance of species more dependent on coastal habitats to fish beta diversity irrespective to the seascape size. A concurrent higher contribution of several marine straggler species reinforced the importance of the environmental context (estuarine vs. marine conditions) to fish beta diversity in larger seascapes. Also, considering that the same rare marine straggler species occurred at least in two bays, their higher SCBD are most likely mediated by random dispersal processes between habitats in the marine context. These relationships highlight the importance of the maintenance of seascape connectivity by means of the availability of high-quality estuarine and marine habitat patches. Future investigations including

information on individual species traits related to feeding, reproduction, and/or dispersal capability, besides environmental effects primarily at finer and larger spatial scales, and larger temporal intervals, may better clarify the mechanisms herein described and provide further support for the maintenance of fish beta diversity in tropical coastal seascapes.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-04007-6>.

**Acknowledgements** We are grateful to several students at the Laboratório de Ecologia de Peixes (UFRRJ) for field sampling and fish identification, especially to Rafaela de Sousa Gomes-Gonçalves, Fernanda Silva de Aguiar, Tailan Moretti Mattos and Wagner Uehara. We also thank the Instituto Brasileiro de Geografia e Estatística (IBGE), the Secretaria de Estado do Ambiente do Estado do Rio de Janeiro (SEA-RJ), and the Instituto Estadual do Ambiente do Estado do Rio de Janeiro (INEA) for providing the vectorial layers for GIS analyses. We thank the reviewers.

**Author contributions** EMC and FGA conceived the study and defined the relevant data set. EMC performed the statistical analyses and wrote the paper. MFA, TPF, LMN and LNS performed and/or coordinated sampling and laboratory procedures. All authors approved the final manuscript for publication.

**Funding** This work was supported by a compensatory measure established by the Term of Adjustment of Conduct of responsibility of PetroRio, conducted by the Ministério Público Federal-MPF/RJ, with implementation of the Fundo Brasileiro para a Biodiversidade-FUNBIO (Grant #16/2017 to FGA). Grants for EMC were provided by the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro – FAPERJ (PDR10 E-26/201.929/2020 and E-26/201.930/2020).

**Availability of data and material** All relevant data are available in the paper and its Supplementary Information. Additional data are available from the corresponding author on reasonable request.

**Code availability** Not applicable.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

**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). This research was conducted under SISBIO Collection of Species Permit number 10707 issued by ICMBio, Brazilian Environmental Agency.

**Consent to participate.** Not applicable.

**Consent for publication** Not applicable.

## References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JDM, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22(6):711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL et al (2011) Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14(1):19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Andrade VS, Rosman PCC, Azevedo JPS (2019) Evaluation of baroclinic effects on mean water levels in Guanabara Bay. *RBRH* 24:e48. <https://doi.org/10.1590/2318-0331.241920180112>
- Andrade-Tubino MF, Azevedo MCC, Franco TP, Araújo FG (2020) How are fish assemblages and feeding guilds organized in different tropical coastal systems? Comparisons among oceanic beaches, bays and coastal lagoons. *Hydrobiologia* 847(2):403–419. <https://doi.org/10.1007/s10750-019-04101-3>
- Annis GM, Pearsall DR, Kahl KJ, Washburn EL, May CA, Taylor RF et al (2017) Designing coastal conservation to deliver ecosystem and human well-being benefits. *PLoS ONE* 12(2):e0172458. <https://doi.org/10.1371/journal.pone.0172458>
- Araújo FG, Azevedo MCC, de Araújo SM, Pessanha ALM, Gomes ID, da Cruz-Filho AG (2002) Environmental influences on the demersal fish assemblages in the Sepetiba Bay. *Brazil Estuaries* 25(3):441–450. <https://doi.org/10.1007/BF02695986>
- Araújo FG, Azevedo MCC, Guedes APP (2016) Inter-decadal changes in fish communities of a tropical bay in southeastern Brazil. *Reg Stud Mar Sci* 3:107–118. <https://doi.org/10.1016/j.rsma.2015.06.001>
- Araújo FG, Pinto SM, Neves LM, Azevedo MCC (2017) Inter-annual changes in fish communities of a tropical bay in southeastern Brazil: What can be inferred from anthropogenic activities? *Mar Pollut Bull* 114(1):102–113. <https://doi.org/10.1016/j.marpolbul.2016.08.063>
- Araújo FG, Rodrigues FL, Teixeira-Neves TP, Vieira JP, Azevedo MCC, Guedes APP et al (2018) Regional patterns in species richness and taxonomic diversity of the nearshore fish community in the Brazilian coast. *Estuar Coast Shelf Sci* 208:9–22. <https://doi.org/10.1016/j.ecss.2018.04.027>
- Araújo FG, Azevedo MCC, de Sousa G-G, Guedes APP (2019) Taxonomic and functional  $\beta$ -diversity patterns reveal random assembly rules in nearshore fish assemblages. *Mar Ecol Prog Ser* 627:109–123. <https://doi.org/10.3354/meps13081>
- Baptista-Neto JA, Gingele FX, Leipe T, Brehme I (2006) Spatial distribution of heavy metals in surficial sediments from Guanabara Bay: Rio de Janeiro, Brazil. *Environ Geol* 49:1051–1063. <https://doi.org/10.1007/s00254-005-0149-1>
- Bartoń K (2020) MuMIn: multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baztan J, Carrasco A, Chouinard O, Cleaud M, Gabaldon JE, Huck T et al (2014) Protected areas in the Atlantic facing the hazards of micro-plastic pollution: first diagnosis of three islands in the Canary Current. *Mar Pollut Bull* 80(1–2):302–311. <https://doi.org/10.1016/j.marpolbul.2013.12.052>
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH et al (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24(3):127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153(1–2):51–68. [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4)
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85(7):1826–1832. <https://doi.org/10.1890/03-3111>
- Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Mar Ecol Prog Ser* 427:191–217. <https://doi.org/10.3354/meps9051>
- Bradley M, Baker R, Nagelkerken I, Sheaves M (2019) Context is more important than habitat type in determining use by juvenile fish. *Landscape Ecol* 34(2):427–442. <https://doi.org/10.1007/s10980-019-00781-3>
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9(2):378–400. <https://doi.org/10.3929/ethz-b-000240890>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York
- Camara EM, Azevedo MCC, Franco TP, Araújo FG (2019) Hierarchical partitioning of fish diversity and scale-dependent environmental effects in tropical coastal ecosystems. *Mar Environ Res* 148:26–38. <https://doi.org/10.1016/j.marenvres.2019.05.006>
- Camara EM, Andrade-Tubino MF, Franco TP, Araújo FG (2020) Multilevel decomposition of spatial and environmental effects on nearshore fish assemblages in tropical semi-enclosed ecosystems. *Estuar Coast Shelf Sci* 237:106691. <https://doi.org/10.1016/j.ecss.2020.106691>
- Camara EM, Andrade-Tubino MF, Franco TP, Santos LN, Santos AFGN, Araújo FG (2021) Scale sensitivity of environmental effects on the temporal beta diversity of fishes in tropical coastal lagoons. *Mar Ecol Prog Ser* 658:195–217. <https://doi.org/10.3354/meps13571>
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P et al (2012) Biodiversity loss and its impact on humanity. *Nature* 486(7401):59–67. <https://doi.org/10.1038/nature11148>
- Chin ATM, Linke J, Boudreau M, Thériault MH, Courtenay SC, Cormier R et al (2018) Beta diversity changes in estuarine fish communities due to environmental change. *Mar Ecol Prog Ser* 603:161–173. <https://doi.org/10.3354/meps12683>
- CPTEC/INPE (2020) Centro de Previsão de Tempo e Estudos Climáticos/Instituto Nacional de Pesquisas Espaciais, previsão oceânica. <http://ondas.cptec.inpe.br/>. Accessed 10 April 2020
- Cribari-Neto F, Zeileis A (2010) Beta regression in R. *J Stat Softw* 34(2):1–24. <https://doi.org/10.18637/jss.v034.i02>
- Crook DA, Robertson AI (1999) Relationships between riverine fish and woody debris: implications for lowland rivers. *Mar Freshw Res* 50(8):941–953. <https://doi.org/10.1071/MF99072>
- da Silva VEL, Fabr e NN (2019) Rare species enhance niche differentiation among tropical estuarine fish species. *Estuar Coasts* 42:890–899. <https://doi.org/10.1007/s12237-019-00524-2>
- Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344(6181):296–299. <https://doi.org/10.1126/science.1248484>
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Modelling* 196(3–4):483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>
- Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guenard G et al (2020) Adespatial: multivariate multiscale spatial analysis. R package version 0.3–8. <https://CRAN.R-project.org/package=adespatial>
- Elliott M, Whitfield AK, Potter IC, Blaber SJ, Cyrus DP, Nordlie FG et al (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish Fish* 8(3):241–268. <https://doi.org/10.1111/j.1467-2679.2007.00253.x>

- Ferrari S, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. *J Appl Stat* 31(7):799–815. <https://doi.org/10.1080/0266476042000214501>
- Fistarol GO, Coutinho FH, Moreira APB, Venas T, Cánovas A, de Paula Jr SE et al (2015) Environmental and sanitary conditions of Guanabara Bay, Rio de Janeiro. *Front Microbiol* 6:1232. <https://doi.org/10.3389/fmicb.2015.01232>
- Ford BM, Roberts JD (2018) Latitudinal gradients of dispersal and niche processes mediating neutral assembly of marine fish communities. *Mar Biol* 165:94. <https://doi.org/10.1007/s00227-018-3356-5>
- Fox J, Weisberg S (2019) *An R companion to applied regression*, 3rd edn. Sage Publications, Thousand Oaks
- Gelman A, Hill J (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge
- Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T et al (2011) Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob Ecol Biogeogr* 20(1):154–159. <https://doi.org/10.1111/j.1466-8238.2010.00584.x>
- Gomes-Gonçalves RS, Aguiar FS, Azevedo MCC, Araújo FG (2020) Functional stability despite anthropogenic influences on the ichthyofauna of a tropical bay. *Mar Environ Res* 159:105016. <https://doi.org/10.1016/j.marenvres.2020.105016>
- Guerra JV, Soares FLM (2009) Circulation and flux of suspended particulate matter in Ilha Grande Bay, SE Brazil. *J Coast Res* 56:1350–1354
- Hazen EL, Suryan RM, Santora JA, Bograd SJ, Watanuki Y, Wilson RP (2013) Scales and mechanisms of marine hotspot formation. *Mar Ecol Prog Ser* 487:177–183. <https://doi.org/10.3354/meps1047>
- Henderson CJ, Gilby BL, Lee SY, Stevens T (2017) Contrasting effects of habitat complexity and connectivity on biodiversity in sea-grass meadows. *Mar Biol* 164(5):117. <https://doi.org/10.1007/s00227-017-3149-2>
- Henderson CJ, Gilby BL, Schlacher TA, Connolly RM, Sheaves M, Maxwell PS et al (2020) Landscape transformation alters functional diversity in coastal seascapes. *Ecography* 43(1):138–148. <https://doi.org/10.1111/ecog.04504>
- Hilborn R (2016) Policy: marine biodiversity needs more than protection. *Nature* 535(7611):224–226. <https://doi.org/10.1038/535224a>
- Hui FKC (2016) Boral–Bayesian ordination and regression analysis of multivariate abundance data in R. *Methods Ecol Evol* 7(6):744–750. <https://doi.org/10.1111/2041-210X.12514>
- Hui FKC (2020) boral: Bayesian ordination and regression analysis. R package version 1.9. <https://CRAN.R-project.org/package=boral>
- Hui FKC, Taskinen S, Pledger S, Foster SD, Warton DI (2015) Model-based approaches to unconstrained ordination. *Methods Ecol Evol* 6(4):399–411. <https://doi.org/10.1111/2041-210X.12236>
- INMET (2020) Instituto Nacional de Meteorologia, estações automáticas—gráficos. [http://www.inmet.gov.br/porta1/index.php?r=home/page&page=rede\\_estacoes\\_auto\\_graf](http://www.inmet.gov.br/porta1/index.php?r=home/page&page=rede_estacoes_auto_graf). Accessed 15 Apr 2020
- Kassambara A (2019) ggcorrplot: visualization of a correlation matrix using 'ggplot2'. R package version 0.1.3. <https://CRAN.R-project.org/package=ggcorrplot>
- Kjerfve B, Ribeiro CHA, Dias GTM, Filippo AM, Quaresma VS (1997) Oceanographic characteristics of an impacted coastal bay: Baía de Guanabara, Rio de Janeiro. *Brazil Cont Shelf Res* 17(13):1609–1643. [https://doi.org/10.1016/S0278-4343\(97\)00028-9](https://doi.org/10.1016/S0278-4343(97)00028-9)
- Krueck NC, Treml EA, Innes DJ, Ovenden JR (2020) Ocean currents and the population genetic signature of fish migrations. *Ecology* 101(3):e02967. <https://doi.org/10.1002/ecy.2967>
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Glob Ecol Biogeogr* 23(11):1324–1334. <https://doi.org/10.1111/geb.12207>
- Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol Lett* 16(8):951–963. <https://doi.org/10.1111/ele.12141>
- Li J, Lu X, Cheng K, Liu W (2020) StepReg: Stepwise Regression Analysis. R package version 1.4.1. <https://CRAN.R-project.org/package=StepReg>
- Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A et al (2013) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS ONE* 8(7):1–15. <https://doi.org/10.1371/journal.pone.0067737>
- Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B (2015) Rapid biotic homogenization of marine fish assemblages. *Nat Commun* 6(1):1–5. <https://doi.org/10.1038/ncomms9405>
- Massicotte P, Proulx R, Cabana G, Rodríguez MA (2015) Testing the influence of environmental heterogeneity on fish species richness in two biogeographic provinces. *PeerJ* 3:e760. <https://doi.org/10.7717/peerj.760>
- Menegotto A, Dambros CS, Netto SA (2019) The scale-dependent effect of environmental filters on species turnover and nestedness in an estuarine benthic community. *Ecology* 100(7):e02721. <https://doi.org/10.1002/ecy.2721>
- Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* 92(12):2285–2298. <https://doi.org/10.1890/11-0037.1>
- Molisani MM, Marins RV, Machado W, Paraquetti HHM, Bidone ED, Lacerda LD (2004) Environmental changes in Sepetiba bay. *SE Brazil Reg Environ Change* 4(1):17–27. <https://doi.org/10.1007/s10113-003-0060>
- Molisani MM, Kjerfve B, Silva AP, Lacerda LD (2006) Water discharge and sediment load to Sepetiba Bay from an anthropogenically-altered drainage basin. *SE Brazil J Hydrol* 331(3–4):425–433. <https://doi.org/10.1016/j.jhydrol.2006.05.038>
- Mouchet MA, Burns MD, Garcia AM, Vieira JP, Mouillot D (2013) Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion. *Oikos* 122(2):247–257. <https://doi.org/10.1111/j.1600-0706.2012.20411.x>
- Munsch SH, Cordell JR, Toft JD (2016) Fine-scale habitat use and behavior of a nearshore fish community: nursery functions, predation avoidance, and spatiotemporal habitat partitioning. *Mar Ecol Prog Ser* 557:1–15. <https://doi.org/10.3354/meps11862>
- Neves LM, Teixeira-Neves TP, Pereira-Filho GH, Araújo FG (2016) The farther the better: effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. *PLoS ONE* 11(12):e0166679. <https://doi.org/10.1371/journal.pone.0166679>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D et al (2019) *Vegan: community ecology package*. R package version 2.5–6. <https://CRAN.R-project.org/package=vegan>
- Ortodossi NL, Gilby BL, Schlacher TA, Connolly RM, Yabsley NA, Henderson CJ, Olds AD (2019) Effects of seascape connectivity on reserve performance along exposed coastlines. *Conserv Biol* 33(3):580–589. <https://doi.org/10.1111/cobi.13237>
- Pinto AFS, Martins MVA, Fonseca MCM, Pereira E, Terroso DL, Rocha F, Rodrigues MAC (2017) Holocene closure of a barrier beach in Sepetiba bay and its environmental impact (Rio de Janeiro, Brazil). *J Sediment Environ* 2(1):65–80. <https://doi.org/10.12957/jse.2017.28215>
- Plummer M (2003) JAGS: A program for analysis of Bayesian Graphical Models using Gibbs Sampling. In: Hornik K, Leisch F, Zeileis A (eds) *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*. Vienna, Austria, pp 1–8. <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Proceedings/>

- Portal GeoINEA (2020) Base de dados geoespaciais. <http://www.inea.rj.gov.br/portaigeoinea>. Accessed 15 October 2020
- Potter IC, Tweedley JR, Elliott M, Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish Fish* 16(2):230–239. <https://doi.org/10.1111/faf.120>
- QGIS Development Team (2018) QGIS Geographic Information System (version 3.4.14). Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- R Core Team (2020) R: A language and environment for statistical computing (version 3.6.3). R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA (2016) Fish biodiversity and conservation in South America. *J Fish Biol* 89:12–14. <https://doi.org/10.1111/jfb.13016>
- Rodil IF, Lohrer AM, Attard KM, Hewitt JE, Thrush SF, Norkko A (2021) Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. *Biodivers Conserv* 30(11):3023–3043. <https://doi.org/10.1007/s10531-021-02234-3>
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113. <https://doi.org/10.1111/j.2041-10X.2010.00012.x>
- Schulz K, Stevens PW, Hill JE, Trotter AA, Ritch JL, Tuckett QM et al (2020) Coastal restoration evaluated using dominant habitat characteristics and associated fish communities. *PLoS ONE* 15(10):e0240623. <https://doi.org/10.1371/journal.pone.0240623>
- Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar Ecol Prog Ser* 391:107–115. <https://doi.org/10.3354/meps08121>
- Soares-Gomes A, Da Gama BAP, Neto JB, Freire DG, Cordeiro RC, Machado W et al (2016) An environmental overview of Guanabara Bay, Rio de Janeiro. *Reg Stud Mar Sci* 8:319–330. <https://doi.org/10.1016/j.rsma.2016.01.009>
- Teixeira-Neves TP, Neves LM, Araújo FG (2015) Hierarchizing biological, physical and anthropogenic factors influencing the structure of fish assemblages along tropical rocky shores in Brazil. *Environ Biol Fish* 98:1645–1657. <https://doi.org/10.1007/s10641-015-0390-8>
- van Lier JR, Wilson SK, Depczynski M, Wenger LN, Fulton CJ (2018) Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows. *Landsc Ecol* 33(8):1287–1300. <https://doi.org/10.1007/s10980-018-0682-4>
- Vargas-Fonseca E, Olds AD, Gilby BL, Connolly RM, Schoeman DS, Huijbers CM et al (2016) Combined effects of urbanization and connectivity on iconic coastal fishes. *Divers Distrib* 22(12):1328–1341. <https://doi.org/10.1111/ddi.12495>
- Vasconcelos RP, Eggleston DB, Le Pape O, Tulp I (2014) Patterns and processes of habitat-specific demographic variability in exploited marine species. *ICES J Mar Sci* 71(3):638–647. <https://doi.org/10.1093/icesjms/fst136>
- Viana DS, Figuerola J, Schwenk K, Manca M, Hobæk A, Mjelde M et al (2016) Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography* 39(3):281–288. <https://doi.org/10.1111/ecog.01231>
- Vinagre C, Salgado J, Cabral HN, Costa MJ (2011) Food web structure and habitat connectivity in fish estuarine nurseries—impact of river flow. *Estuar Coasts* 34(4):663–674. <https://doi.org/10.1007/s12237-010-9315-0>
- Wagenmakers EJ, Farrell S (2004) AIC model selection using Akaike weights. *Psychon Bull Rev* 11:192–196. <https://doi.org/10.3758/BF03206482>
- Wang D, Gouhier TC, Menge BA, Ganguly AR (2015) Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518:390–394. <https://doi.org/10.1038/nature14235>
- Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol Evol* 3(1):89–101. <https://doi.org/10.1111/j.2041-210X.2011.00127.x>
- Warton DI, Foster SD, Death G, Stoklosa J, Dunstan PK (2015) Model-based thinking for community ecology. *Plant Ecol* 216(5):669–682. <https://doi.org/10.1007/s11258-014-0366-3>
- Whitfield AK (2017) The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Rev Fish Biol Fish* 27(1):75–110. <https://doi.org/10.1007/s11160-016-9454-x>
- Yeager LA, Deith MC, McPherson JM, Williams ID, Baum JK (2017) Scale dependence of environmental controls on the functional diversity of coral reef fish communities. *Global Ecol Biogeogr* 26(10):1177–1189. <https://doi.org/10.1111/geb.12628>
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1(1):3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

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