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Assessing Fish Community Structure and Diversity Across Environmental Gradients in a Tropical Bay

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ABSTRACT

Understanding the relationship between species distribution and the environment across spatial gradients is crucial for biodiversity evaluation. We surveyed fish populations in a tropical bay, covering a spatial gradient from the outer zone with favorable marine conditions to the inner zone affected by human activities. The tested hypothesis is that natural environmental gradients (e.g., temperature, salinity, turbidity) and anthropogenic influences (e.g., pollution, organic enrichment) affect fish communities and that environmental filters reduce taxonomic and functional diversity in more impacted zones. Species richness increased, while fish abundance and biomass decreased from the inner to the outer zone. Only functional divergence changed spatially, being higher in the outer zone. This suggests changes in species but the maintenance of most functions. Fourteen functional groups were identified based on locomotion and food acquisition traits. Higher taxonomic diversity and functional divergence in the outer zone likely stem from greater resource utilization differentiation and more favorable environmental conditions near the sea, fostering species with distinct functional attributes. Conversely, the inner zone, burdened by high organic and pollutant loads, favors species highly tolerant of harsh environmental conditions, such as marine catfishes. Fish communities exhibited spatial changes due to environmental gradients and anthropogenic influences. Environmental filters altered taxonomic indices, while functional indices remained stable, except for functional divergence, which was lower in the most impacted area, partially confirming our hypothesis. These findings advance our understanding of environmental influences on species distribution along spatial gradients in coastal systems, proving to be a promising and increasingly utilized tool for ecological assessment.

1 | Introduction

Estuarine ecosystems support diverse fish assemblages that play crucial ecological roles for human populations (Villéger et al. 2017; Borland et al. 2022). These dynamic environments experience noticeable fluctuations in abiotic conditions, such as salinity and turbidity, influenced by tides and freshwater inflows, which transport nutrients into these areas (Elliott and McLusky 2002; Onabule et al. 2020; Wolanski et al. 2004; Cloern et al. 2017). Furthermore, these ecosystems are increasingly impacted by industrial and urban development in adjacent coastal areas, which affect the distribution and functions of fish species (Gomes-Gonçalves et al. 2020; Borland et al. 2022). The environmental conditions in these areas have significantly deteriorated in recent decades, underscoring the urgent need to study local biodiversity to preserve living resources (Lotze et al. 2006). Understanding these transformations is essential for identifying conservation measures that safeguard biodiversity and its relationships with the environment, ultimately aiming for environmental protection and conservation.

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Estuarine areas are crucial for biodiversity due to their high productivity, which supports various species at different life stages (Stuart-Smith et al. 2013; Silva-Júnior et al. 2017). This is remarkable given the challenging conditions imposed by tidal influences and continental drainage (Islam et al. 2006; Macário et al. 2021). The predominant ichthyofauna in these areas mainly comprises marine species, including permanent residents and those that use estuaries at specific times in their life cycles, either as seasonal visitors or as transit areas between marine and freshwater environments.

Semi-enclosed estuarine areas, like bays, commonly feature natural environmental gradients characterized by decreasing salinity, rising temperatures, and increased turbidity as one moves from the sea toward inland areas, primarily influenced by the continent (Martino and Able 2003; McKinley et al. 2011; Onabule et al. 2020). This gradient poses physiological challenges to species, requiring them to tolerate these fluctuations (Whitfield 1999; Teichert et al. 2018; Vanalderweireldt et al. 2020). Consequently, while some species can occupy the entire estuarine area, others are adapted to specific ranges of environmental conditions, leading to variations in faunal composition across different zones (Martino and Able 2003; Laurino et al. 2021). For coastal marine fishes, the diversity of life history strategies significantly decreases from euryhaline to oligohaline areas and along a gradient of human disturbances (Henriques et al. 2017; Lai et al. 2022). These trends are associated with a convergence of species traits towards generalized feeding habits, supporting continuous environmental changes (Elliott et al. 2007; Williams et al. 2017). Habitat filtering occurs when only species with specific traits can survive in a particular habitat, leading to trait convergence among co-occurring species (Mouillot et al. 2007; Götzenberger et al. 2016). Additionally, environmental filters shape the trait distribution of species by restricting the establishment and persistence of organisms based on the suitability of their traits (Ford and Roberts 2020; Harrison and Whitfield 2024).

Functional diversity is a promising tool for studying estuarine fish assemblages because it is directly linked to the functions performed by species in ecosystems (Flynn et al. 2011; Mouillot et al. 2011). While related to taxonomic diversity, functional diversity provides an additional perspective on community function and has been applied in assessing fish communities (Villéger et al. 2008; Mouillot et al. 2013; Dolbeth et al. 2016; Gomes-Gonçalves et al. 2020; Kuang et al. 2021). This approach, when complemented with taxonomic information, can enhance our understanding of species' roles in ecosystems and inform conservation measures. There are several functional diversity indices (e.g., richness, evenness, divergence, dispersion, uniqueness, and specialization) each one associated with a specific aspect of a species role in ecosystems. These indices can reveal the relationships between species and how they cope with environmental constraints (Mouillot et al. 2007). Environmental changes in estuaries can alter the composition and function of the fish community, impacting overall ecosystem function, which can be reflected in the functional characteristics of species (Whitfield and Elliott 2002; Dias et al. 2013; Fontrodona-Eslava et al. 2021). In inner estuarine environments, which are more susceptible to changes due to continental run-off and human

activities (Araújo et al. 2016), certain attributes may be filtered, resulting in communities with lower taxonomic and functional diversity (Gomes-Gonçalves et al. 2020), indicating a prevalence of environmental filtering processes. Conversely, communities with high functional diversity may suggest competition among species, reflecting the limiting similarity theory, which predicts that coexisting species should possess distinct characteristics, reducing interspecific competition (Mouillot et al. 2007).

Sepetiba Bay, situated in the southeastern region of Brazil, encompasses various habitats, including mangroves, coastal dunes, and small estuarine areas. It boasts a rich ichthyofauna and serves as a nursery for several coastal species (Araújo et al. 2018; Gomes-Gonçalves and Araújo 2023). However, the bay's watershed area has been experiencing escalating degradation caused by organic and industrial pollution, which has adversely impacted both habitat and water quality (Castelo et al. 2021; Gomes-Gonçalves et al. 2022; Damasceno et al. 2024). These changes have been occurring over the past four decades, primarily due to urbanization and industrial development in the vicinity, including chemical and metallurgical factories (Barcellos and Lacerda 1994; Molisani et al. 2006; Castelo et al. 2021). A previous study by Araújo et al. (2016) already highlighted significant differences in the composition of the bay's ichthyofauna over three decades, indicating a decline in fish richness, abundance, and biomass over time. This study identified a strong correlation between fish composition and richness across distinct bay zones, ranging from more favorable environmental conditions near the marine influence to more challenging conditions in the inner bay areas affected by organic and industrial waste and habitat degradation.

Our study aims to assess the taxonomic and functional diversity of the ichthyofauna in Sepetiba Bay and evaluate the impact of spatial and seasonal environmental variations on fish community composition and functional diversity. Our hypothesis posits that the varying environmental conditions along the spatial gradient-from the area closest to marine influence to the innermost area-affect both the taxonomic and functional diversity of fish communities due to environmental filters. This gradient encompasses natural factors, such as salinity, depth, and turbidity, which vary from the outer to the inner zone (Araújo et al. 2016, 2017), as well as anthropogenic influences, including pollutant and nutrient discharge in the inner zone (Leal Neto et al. 2006; Molisani et al. 2006). These factors collectively contribute to a decline in water quality along the gradient. It is expected that the outer zone, closer to the sea connection, will exhibit higher taxonomic and functional diversity compared to the inner zone. In the inner zone, the negative effect of filtering on certain attributes may occur due to the more stressful conditions resulting from continental drainage and closer proximity to anthropogenic pressures.

2 | Materials and Methods

2.1 | Study Area

Sepetiba Bay $(22^{\circ}54'-23^{\circ}04' \text{ S}; 43^{\circ}34'-44^{\circ}10' \text{ W})$ is a semienclosed coastal marine system spanning approximately 450 km^2 (Figure 1). The bay has a narrow connection to the



FIGURE 1 | Study area map of Sepetiba Bay, Rio de Janeiro, Brazil, showing sampling locations across three zones (inner, middle, and outer). The color range represents the 2020 Human Influence Index (Sanderson et al. 2022), indicating areas of varying impact.

sea in the east and a wide connection in the west. It receives waters from small rivers that flow into it, carrying domestic and industrial effluents from the mainland. The contributing watershed covers 2654 km^2 . The main river contributes an average discharge of $120-190 \text{ m}^3$ /s (Leal Neto et al. 2006), while the others have smaller discharges and primarily serve as drainage channels for industries or residential areas (Leal Neto et al. 2006).

In recent decades, Sepetiba Bay has undergone significant industrial and urban development, currently hosting over 400 industries in its vicinity (Molisani et al. 2004). Approximately two million people inhabit the Sepetiba Bay watershed, primarily in the northeastern zone, as a result of industrial development in that region (Molisani et al. 2004; Carvalho et al. 2022). The initial developments included the construction of the Sepetiba Port in the 1970s, followed by the establishment of metallurgical, petrochemical, and pyrometallurgical companies (Barcellos and Lacerda 1994; Molisani et al. 2004). Additionally, there was also the expansion of the Sepetiba Port, involving dredging the access channel to a depth of 20 m, enabling the accommodation of ships weighing up to 150,000 tons (Azevedo et al. 2007). Furthermore, the construction of a large steel mill in the 2000s and the establishment of a submarine construction terminal in the late 2010s (Gomes-Gonçalves et al. 2020) represented recent changes in the vicinity of the Bay. The most recent change in the area was the placement of 4 floating power plants in the inner area of the bay at the end of 2022. These power plants use natural gas and diesel oil and have an installed generation capacity of 560 MW, causing increases in water temperature due to the cooling of the machines in a flow of 8.6 m³ per second (INEA 2022). This will cause additional disturbances not only for the fish but for the entire aquatic biota. All these developments have contributed to the degradation of the coastal habitat and an increase in pollutant discharges, directly impacting the water quality of the Bay.

This coastal system can be divided into three sampling zones (Figure 1), which are geographically continuous but differ in depth, salinity, and anthropogenic influence (Araújo et al. 2002; Azevedo et al. 2006). The inner zone, located in the innermost part of the Bay (near the coast) and adjacent to mangrove formations, is influenced by industrial and urban effluents discharged into the Bay via rivers, streams, and drainage channels. Additionally, river discharges contribute to elevated temperature and turbidity while decreasing salinity. This zone is the most altered due to its proximity to industrial development and other human activities (Cunha et al. 2006; Leal Neto et al. 2006). The outer zone, closer to the main connection with the sea, has comparatively lower temperature and turbidity than the inner zone and higher salinity (Araújo et al. 2017). It experiences relatively fewer anthropogenic influences and more stable environmental conditions (Araújo et al. 2017). Additionally, the outer zone includes several islands in the western part of the Bay. The middle zone exhibits environmental conditions that are intermediate between the inner and outer zones.

2.2 | Data Collection and Processing

Fish samples and measurements of environmental variables were conducted seasonally from June 2019 to February 2021. Collections were carried out in autumn (June), winter (September) and spring (October) in 2019, with the final collection taking place in the summer (February) of 2021 due to the COVID-19 pandemic. On each collection occasion, three bottom trawls were conducted in different zones, totaling 36 samples (4 periods \times 3 zones \times 3 locations). The trawls utilized a net with a length of 12 m, equipped with doors, featuring a mesh size of 25 mm between consecutive knots in the wings and 12 mm in the cod end region. The length of the lead line was 8 m, and the buoy line was 7 m. For each sample, the swept area

(A) was estimated using the formula: $A = D \times h \times X2$, where *D* is the length of the trawl, *h* is the length of the buoy line, and X2 is the fraction of the buoy line length that covers the width of the path traveled by the trawl net (Sparre and Venema 1995). The samples were taken at speeds ranging from 2 to 2.5 knots over a 20-min period, covering an approximate stretch of 1.5 km. It was assumed that X2=0.6, with the swept area corresponding to approximately 6000 m².

After capture, the fish were immediately anesthetized with benzocaine hydrochloride (50 mg/L), then placed in coolers with ice, transported to the laboratory, and stored in freezers for preservation. Due to the high abundance of catfish, subsampling was conducted for this group, retaining a portion and returning the excess to the environment. In this process, biomass and abundance were estimated, and these values were proportionally distributed among the catfish species found in the samples. Each fish was identified to the species level, weighed with a precision of 0.001 g on a digital scale, photographed with a CANON EOS Rebel T6 digital camera, and measured using ImageJ software. Scientific names and classifications were verified using FishBase (Froese and Pauly 2024) and the World Register of Marine Species (WoRMS 2024). None of the species were listed on the IUCN Red List of Threatened Species. The research was conducted under the Species Collection License from SISBIO, number 10707, issued by ICMBio, and all applicable guidelines for the care and use of animals were followed (CEUA UFRRJ/ ICBS Protocol 11874).

The physical and chemical variables of the water, as well as the type of substrate at each location, were recorded. Temperature (°C), pH, ORP (mV), salinity, and turbidity (formazin nephelometric units—FNU) were recorded using a HANNA HI9828 multiparameter probe. Depth (cm) was measured with a Speedtech EcoSonde model SM-5, and transparency (cm) was assessed using a Secchi disk. The substrate was sampled using a Van Veen dredge, and the type of bottom was visually determined and classified based on thickness, ranging from finer to coarser: mud, sand, and gravel.

2.3 | Morphological Measurements and Functional Attributes

Seventeen morphological measurements were taken (Figure S1 and Table S1). Body width (Bw), mouth depth (Md), mouth width (Mw), and gill raker length (GRl) were measured using a digital caliper with a precision of 0.01 mm. The remaining morphological measurements were determined using ImageJ software (Schneider et al. 2012).

Morphological measurements were utilized to determine 14 functional attributes, encompassing five related to feeding and nine related to locomotion (Table S2). In ecology, both food acquisition and locomotion are deemed crucial functions (Villéger et al. 2010). Describing them with only one functional attribute is not feasible due to the complexity of these processes (Mason et al. 2007; Villéger et al. 2010).

In some cases, fish exhibited peculiar morphologies, such as the absence of a caudal fin or dorsoventral flattening. This made

it impossible to measure certain morphological characteristics and, consequently, determine specific functional attributes. To address these exceptions, we followed the guidelines established by Villéger et al. (2010, 2017) and Brosse et al. (2021). For species without a clearly defined caudal fin, such as Cynoglossidae and Trichiuridae, we used "Caudal peduncle throttling" (CPt) with a value of 1, assuming that the depth of the caudal fin is equal to the depth of the caudal peduncle. In the case of Pleuronectiformes, body depth (Bd) and width (BW), mouth depth (Md) and width (Mw), and eye position (Ep) were measured relative to the fish's orientation in the environment. We assumed that these fish are functionally more similar to dorsoventrally flattened fish than laterally compressed fish. Since flatfish have both eyes on the same side of the head on top, we calculated the eve position using the formula: $2 \times Ed/Hd$. Considering that flatfish pectoral fins are considered non-functional (Villéger et al. 2010), Pectoral fin position (PFp) and Aspect ratio of the pectoral fin (PFa) were set to 0. Likewise, for species without a clearly defined caudal fin, such as Symphurus tessellatus (Quoy & Gaimard, 1824) and Trichiurus lepturus Linnaeus, 1758, we established the Aspect Ratio of the caudal fin (CFa) and Fins Surface ratio (FSr) as 0.

Five to six individuals, predominantly adults, were measured per species when available. If a species had fewer than five individuals, all of them were measured. From these individual measurements, an average value of the functional attributes was calculated for each species, assuming that intra-specific variations are smaller than inter-specific variations (Dumay et al. 2004; Villéger et al. 2010). Subsequently, each functional attribute was standardized to a mean of 0 and a standard deviation of 1, making all attributes equally weighted and dimensionless.

2.4 | Taxonomic and Functional Diversity

Three indices of taxonomic diversity were calculated: the Shannon Diversity Index (H'), the Simpson Dominance (SI), and Pielou's Evenness (J). The first two are based on two community attributes, namely species richness and evenness, and are widely used in assessing taxonomic diversity (Mendes et al. 2008). The main difference between these indices lies in the weighting of rare species. In the Shannon Index, an intermediate weight is assigned to balance the importance of both attributes. In contrast, in Simpson's Dominance, rare species have a lower weight, making it an effective indicator for assessing dominance (Magurran 2004; Melo 2008; Mendes et al. 2008). Pielou's Evenness (Pielou 1975), like the previously mentioned indices, quantifies diversity by considering both species richness and the distribution of abundance in the community. Its value ranges from 0 to 1, with 1 representing a community where all species have the same abundance. The combined analysis of evenness with the Shannon and Simpson indices provides a comprehensive description of taxonomic diversity in the species community.

Six functional diversity indices were calculated: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al. 2008), functional dispersion (FDis) (Laliberté and Legendre 2010), functional originality (FOri) (Mouillot et al. 2008), and functional specialization (FSpe) (Bellwood et al. 2006). FRic corresponds to the volume (convex hull) generated by the distribution of species' traits in an

n-dimensional trait space. Functional evenness (FEve) quantifies the regularity of species' occupation of the functional trait space, weighted by abundance (Villéger et al. 2008, 2010). According to Villéger et al. (2008), this index reaches higher values when abundance is distributed proportionally among species or when the distance between species in the functional trait space is uniform. FDiv reflects how abundances are distributed within the volume of the functional traits occupied by species. Functional divergence is low when the most abundant species have functional traits close to the center of trait variation among all species. Conversely, when the most abundant species have extreme functional traits, functional divergence is high (Villéger et al. 2008; Mouillot et al. 2013).

Functional dispersion (FDis) measures the average distance of each species from the centroid of all species within the multidimensional functional trait space, which is shifted toward the most abundant species (Laliberté and Legendre 2010). FOri reflects the degree of "exclusivity" (opposite of redundancy) of functional traits in the community (Mouillot et al. 2013) and is expressed as the average distance between each species and its nearest neighbor in the functional trait space (Leitão et al. 2018). FSpe represents the "distinctiveness" of functional trait characteristics in the assembly, expressed as the average distance between each species and the mean position of all species in the functional trait space (Bellwood et al. 2006; Leitão 2015).

The calculation of all indices was performed in the R environment (R Development Core Team 2022). Taxonomic diversity indices were calculated using the "diversity" function from the "vegan" package, while the functional diversity indices were calculated using the "mFD" package (Magneville et al. 2022). The script for calculating and plotting the mentioned indices was created based on the tutorial provided by Camille Magneville, which is accessible at (https://cmlmagneville.github.io/mFD/).

2.5 | Statistical Treatment

The environmental data were standardized (centered by mean and scaled by standard deviation) before being used in multivariate analyses. This process removes the influences of different measurement scales and renders the data dimensionless. Subsequently, each environmental variable underwent a permutational analysis of variance (PERMANOVA), utilizing the "adonis2" function from the "vegan" package based on the Euclidean distance matrix (Anderson et al. 2011). This analysis treated zones (three levels: inner, middle, and outer) and seasons (four levels: autumn, winter, spring, and summer) as fixed factors. All PERMANOVAs involved 999 permutations to calculate *p*-values, and followed the same design, with the sampling locations nested within the zones. In case of significant differences (p < 0.01), pairwise comparisons between groups were conducted using the "pairwise.adonis" function in the "pairwiseAdonis" package. Additionally, to identify spatial patterns of the environmental variables, a principal component analysis (PCA) was performed.

Species richness, abundance, and biomass were compared among the zones using a permutational analysis of variance (PERMANOVA) on a Bray-Curtis similarity matrix. The permutations and the design of PERMANOVA followed the same procedure as the environmental analyses. Before the analyses, abundance and biomass data were subjected to a log (x + 1) transformation to reduce the impact of more abundant species. When significant differences were identified (p < 0.05), pairwise comparisons between groups were conducted.

To analyze spatial patterns in fish composition, non-metric multidimensional scaling (nMDS) ordination was employed using a Bray-Curtis distance matrix. To determine if any species were associated with a particular zone, the Indicator Value Index (IndVal, Cáceres and Legendre 2009) was calculated using the "multipatt" function from the "indicspecies" package. The calculation of IndVal for each species was based on specificity (relative abundance in each zone) and fidelity (relative frequency in each zone), following the formula: IndValij = $Aij \times Bij \times 100$, where $\sqrt{\text{IndValij}}$ represents the indicator value of species i in zone j, Aij is the relative abundance of species i in zone j. If the species occurs only in samples from the site it indicates, then A would be equal to 1 (Specificity) Bij is the relative frequency of species i in zone j. If the species is present in all samples from the group it indicates, then B will be equal to 1 (Fidelity). Components A and B range from 0 to 1 each. Component A indicates the probability of a species being restricted to a particular zone, while component B indicates the probability of that species being present in all samples from a given zone. After multiplying the two components, the square root of the product is taken to obtain Stat (IndVal), ensuring that both components have a proportional impact on the final index.

To construct the functional space, we used principal coordinates analysis (PCoA) on a Euclidean distance matrix derived from the attributes × species matrix. Taxonomic diversity indices (Shannon Diversity, Simpson Dominance, and Pielou's Evenness) and functional diversity indices (FRic, FEve, FDiv, FDis, FOri, and FSpe) were compared between zones and seasons using PERMANOVA based on Euclidean distance. We employed 999 permutations, following the same design as the environmental variables. Significant differences between the indices (p < 0.05) were followed by pairwise comparisons. To assess associations between diversity indices and environmental variables, we utilized non-parametric Spearman correlation tests Multiple regression modeling (using the "lm" function in the "stats" package in R) was then applied to estimate the influences of environmental variables on each index. The explained variation of predictors in diversity indices was indicated by the coefficient of determination of the model (R2). All statistical analyses were conducted in an R environment (R Development Core Team 2022).

3 | Results

3.1 | Environmental Conditions

Environmental conditions in Sepetiba Bay varied significantly among different zones (F=19.09, p=0.001) and seasons (Pseudo-F=19.89, p=0.001). There was also a significant interaction between zones and seasons (Pseudo-F=2.76, p=0.001), albeit with relatively low F-values. Transparency (F=26.75) and depth (F=19.19) were higher in the outer zone compared to the inner zone, while salinity exhibited an ascending trend from the inner to the outer zone (Table S3). In contrast, temperature (F = 1.96) did not vary among the zones.

Seasonally, pH (F=126.35, p=0.001), salinity (F=53.19, p=0.001), and temperature (F=42.49, p=0.001) showed significant differences. Salinity (31.3±3.2) and temperature (26.5°C±0.8°C) were higher in summer, while pH (6.8±0.03) was lower in winter. Regarding the substrate, mud predominated in the inner zone, the middle zone featured both mud and gravel, and the outer zone comprised sand and gravel. Given the lack of substantial interactions between zones and seasons, this study prioritized spatial variations, recognizing that fish composition tends to vary more among zones than seasons (Azevedo et al. 2007).

A clear spatial pattern in the environmental conditions of the bay was identified through principal component analysis (Figure 2). The first two PCA axes collectively explained 61.62% of the data variation. The first axis, accounting for 34.29% of the variation, showed positive associations with transparency (0.49), depth (0.44), and coarser substrate (0.35) (Table 1). These characteristics were more prevalent in samples from the outer zone. In contrast, samples from the inner zone were associated with higher turbidity and temperature, correlating negatively with the first axis. Samples from the middle zone exhibited intermediate values for these variables, positioning themselves more centrally along the first axis. The second axis demonstrated a positive association with ORP (0.35) and negative associations with salinity (-0.55) and temperature (-0.41).

3.2 | Ichthyofauna

A total of 39,582 individuals were collected, representing 62 species, 47 genera, 25 families, and 15 orders (Table S4). Significant differences were found between the zones in terms of species richness (F=4.87, p=0.021), abundance (F=5.12, p=0.001), and biomass (F=2.95, p=0.001). An increase in species richness and a corresponding decrease in abundance and fish biomass were

0.25 -Zone ORP Inner Middle Outer PC2 (27.33%) 0.00 turb transr depth subs -0.25 temp -0.50 -0.25 0.00 0.25 PC1 (34.29%)

FIGURE 2 | Diagram of the first two axes of the principal component analysis (PCA) on environmental variables in Sepetiba Bay, State of Rio de Janeiro, Brazil. Variable codes are described in Table 1.

TABLE 1 Correlation of the first two axes of principal component analysis (PCA) with environmental variables in Sepetiba Bay, State of Rio de Janeiro, Brazil.

Environmental variables	Code	PC1	PC2
Substrate	subs	0.35	-0.36
pH	ph	-0.12	-0.30
Redox potential	ORP	0.17	0.35
Salinity	sal	-0.17	-0.55
Turbidity	turb	-0.48	-0.11
Temperature	temp	-0.37	-0.41
Transparency	transp	0.49	-0.27
Depth	prof	0.44	-0.32
Explanation of variance (%)		34.29	27.33

observed from the inner zone to the outer zone (Table S5). The inner zone recorded the highest fish abundance, with a total of 30,102 individuals and 34 species. Notably, 95.83% of this number belonged to the single species, the catfish *Cathorops spixii* (Agassiz, 1829). In the middle zone, 6852 individuals were found, distributed among 40 species, with *C. spixii* comprising 81.68% of the total abundance. The outer zone had the lowest abundance (2628 individuals) but the highest species richness (45 species) (Tables S4 and S5). In this zone, *Stellifer brasiliensis* (Schultz, 1945) (26.90%), *C. spixii* (17.39%), and *Ctenosciaena gracilicirrhus* (Metzelaar, 1919) (14.8%) accounted for more than half of the total abundance. In terms of biomass, *C. spixii* dominated in all three zones, contributing 86.98%, 78.62%, and 56.12% of the biomass in the inner, middle, and outer zones, respectively (Tables S4).

Fish assemblages structure changed across the three zones. The inner zone differed significantly from the outer zone, with the middle zone exhibiting an intermediate structure, displaying characteristics of both the inner and the outer zones (Figure 3). Some species were found exclusively in a specific zone: (1) the inner zone had seven exclusive species: Caranx crysos (Mitchill, 1815), Centropomus parallelus Poey, 1860, Cynoscion acoupa (Lacepède, 1801), Etropus longimanus Norman, 1933, Selene setapinnis (Mitchill, 1815), Selene vomer (Linnaeus, 1758), Sphoeroides greelevi Gilbert, 1900; (2) the middle zone had eight exclusive species: Achirus lineatus (Linnaeus, 1758), Anchoa januaria (Steindachner, 1879), Dactylopterus volitans (Linnaeus, 1758), Genyatremus luteus (Bloch, 1790), Gobionellus oceanicus (Pallas, 1770), Stephanolepis hispida (Linnaeus, 1766), Trachurus lathami Nichols, 1920, and Trichiurus lepturus; and (3) the outer zone had 15 exclusive species: Anchoa tricolor (Spix & Agassiz, 1829), Caranx latus Agassiz, 1831, Conodon nobilis (Linnaeus, 1758), Ctenosciaena gracilicirrhus, Cynoscion leiarchus (Cuvier, 1830), Dules auriga Cuvier, 1829, Isopisthus parvipinnis (Cuvier, 1830), Orthopristis ruber (Cuvier, 1830), Pomadasys ramosus (Poey, 1860), Scorpaena isthmensis Meek & Hildebrand, 1928, Stellifer brasiliensis, Syngnathus folletti Herald, 1942, Synodus foetens (Linnaeus, 1766), Syacium micrurum Ranzani, 1842, and Upeneus parvus Poey, 1852.

Several fish species were identified as indicators of specific zones, as determined by the Indicator Value (IndVal) index



FIGURE 3 | Non-metric multidimensional scaling (nMDS) ordination diagram based on species abundance, with samples categorized by zones (inner, middle, and outer) in Sepetiba Bay, State of Rio de Janeiro, Brazil. Species codes are described in Table S4.

TABLE 2 | Indicator values (Stat) and *p* values and their respective A (Specificity) and B (Fidelity) components for fish species in the zones of Sepetiba Bay.

Zone/species	A	В	Stat	р
Inner + Middle				
Cathorops spixii	0.986	1	0.993	0.005
Outer				
Anchoa tricolor	1	0.417	0.645	0.01
Upeneus parvus	1	0.417	0.645	0.005
Larimus breviceps	0.989	0.417	0.642	0.005
Menticirrhus americanus	0.844	0.417	0.593	0.04
Paralonchurus brasiliensis	0.967	0.333	0.568	0.025
Ctenosciaena gracilicirrhus	1	0.250	0.500	0.050

Note: The Stat (test statistic) represents the association between a particular species and a specific zone.

(Table 2). The catfish *C. spixii* (stat = 0.99, p = 0.005) was identified as an indicator species of the inner and middle zones. This species had a high probability of being restricted to these zones (IndVal component A = 0.98) and was found in all samples (IndVal component B = 1). For the outer zone, six indicator species were identified. Among them, *Anchoa tricolor, Upeneus parvus*, and *Ctenosciaena gracilicirrhus* were strictly associated with this zone (IndVal component A = 1), while *Larimus*

breviceps, Menticirrhus americanus, and *Paralonchurus brasiliensis* had a high probability of occurrence. According to IndVal component B, these six species had a probability ranging from 25% to 41.6% of occurring in the outer zone.

3.3 | Taxonomic and Functional Composition

The principal coordinates analysis (PCoA) on functional traits (Figure 4) revealed that 49.7% of the total variation was explained by the first axis (PCO 1) and 17.7% by the second axis (PCO 2). This analysis identified 14 distinct functional groups.

Group I consisted of benthic species characterized by their proximity to the substrate, low mobility, and laterally flattened, asymmetrical bodies, such as the flatfishes *Achirus lineatus* and *Citharichthys spilopterus*. In contrast, Group II consisted of a single pelagic species, the cutlassfish *Trichiurus lepturus*, with an elongated, laterally compressed body, indicating an adaptation for rapid swimming in open waters. Group III included the pipefish *Syngnathus folletti*, characterized by a cylindrical body with a tubular mouth and low mobility, adapted for a specialized feeding strategy, while Group IV comprised pufferfish species such as *Sphoeroides testudineus* and *Chilomycterus spinosus*, featuring robust and rounded bodies adapted for benthic life on complex substrates.

Group V was composed of the flying gurnard *Dactylopterus volitans* and the searobin *Prionotus punctatus* (Bloch, 1793). These are essentially demersal fish with cylindrical bodies that live just above the sediment layer, possessing notably large pectoral fins. Group VI consisted of benthic scorpionfish such as *Scorpaena brasiliensis*, adapted for life on complex consolidated substrates.



FIGURE 4 | Functional groups derived from principal coordinates analysis based on the functional traits of species in Sepetiba Bay. Species codes are listed in Table S4.

The seventh group (VII) included the marine catfish of the Ariidae family: *Aspistor luniscutis* (Valenciennes, 1840), *Cathorops spixii*, *Genidens barbus* (Lacepède, 1803), and *Genidens genidens* (Cuvier, 1829). These are benthic omnivorous species with dorsoventrally compressed bodies. They are adapted to live in muddy or sandy bottoms and feature prominent sensory barbels.

Benthic and demersal species found in coastal and estuarine bottoms were grouped in Group VIII, highlighting the importance of these habitats for fish diversity. The species in this group have elongated to moderately laterally compressed bodies, including the croakers *Menticirrhus americanus* (Linnaeus, 1758), *Micropogonias furnieri* (Desmarest, 1823), *Cynoscion leiarchus* (Cuvier, 1830), among others. On the other hand, Group IX comprised demersal and pelagic species with fusiform bodies, moderately laterally compressed. They are active predators, hunting a variety of prey, including fishes of the family Gerreidae and others.

Group X was formed by pelagic species of the Carangidae family, characterized by highly laterally compressed bodies adapted for rapid swimming. It includes *Selene vomer, Selene setapinnis*, and *Chloroscombrus chrysurus*. Group XI is composed of pelagic species with elongated bodies, high mobility, filter feeding, and planktivorous habits. It includes engraulid species such as *Anchoa januaria, Anchoa tricolor* (Spix & Agassiz, 1829), and *Cetengraulis edentulus* (Cuvier, 1829), as well as the species *Harengula clupeola* (Cuvier, 1829). The last groups were composed of a single species with specific morphological characteristics. Group XII was composed of the goby *Gobionellus oceanicus* with an elongated cylindrical body and eyes in a superior position. Meanwhile, Group XIII consisted of the lizardfish *Synodus foetens*, which presents dorsoventral flattening of the body and head, and a wide mouth. Group XIV, on the other hand, comprised the filefish *Stephanolepis hispidus*. It is a benthic species with a laterally flattened and tall body, large eyes, small mouth, and cryptic habits in reef areas and hard substrates.

The taxonomic diversity indices showed significant differences between zones (F=7.15, p=0.010), but no significant differences were found in taxonomic and functional indices between seasons (Table S6). No significant interactions were found between zones and seasons. Paired comparisons

TABLE 3 | Mean ± standard deviation of the taxonomic and functional indices in fish assemblages of Sepetiba Bay, Brazil.

	Zone				
Index	Inner Middle		Outer	F	
Taxonomic diversity					
Shannon	0.75 ± 0.65^{a}	1.06 ± 0.65^{a}	1.69 ± 0.49^{b}	7.81	**
Simpson	0.65 ± 0.31^{a}	0.54 ± 0.28^{ab}	$0.29\pm0.17^{\rm b}$	5.70	*
Pielou	0.35 ± 0.30^{a}	0.45 ± 0.26^{a}	0.69 ± 0.19^{b}	5.24	*
Functional diversity					
Richness	0.01 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	0.76	ns
Evenness	0.63 ± 0.11	0.59 ± 0.09	0.66 ± 0.07	2.63	ns
Divergence	$0.55\pm0.11^{\rm a}$	0.61 ± 0.06^{ab}	0.67 ± 0.05^b	7.12	**
Dispersion	0.25 ± 0.07	0.25 ± 0.07	0.27 ± 0.03	0.38	ns
Originality	0.12 ± 0.03	0.12 ± 0.03	0.11 ± 0.01	0.67	ns
Specialization	0.19 ± 0.04	0.18 ± 0.03	0.17 ± 0.03	1.02	ns

Note: Pseudo-*F* and significance of the comparisons are also shown. $p \le 0.05$; $p \le 0.01$. Superscript letters indicate significant differences. Abbreviation: ns, not significant.

Abbreviation: ns, not significal

revealed significant differences (p < 0.05) in the Shannon Diversity and Pielou Equitability indices among the zones (Table 3). These indices were lower in the inner zone, with increasing values in the middle and outer zones, indicating higher diversity and evenness in the latter. Conversely, the Simpson's Dominance index followed an opposite pattern compared to the other two taxonomic diversity indices, being higher in the inner zone.

Among the six functional diversity indices, only FDiv differed significantly among the zones (F = 7.12, p = 0.005), with higher values in the outer zone and lower values in the inner zone (Table 3). Figure 5 depicts the functional space of species, with each species positioned according to its attributes. In the inner zone, species like C. spixii and A. luniscutis, which are very abundant, exhibited less distinct functional attributes (closer to the center of gravity). In the middle zone, there was a decrease in the abundance of C. spixii and A. luniscutis, with an increase in the abundance of other species such as G. genidens, Eucinostomus argenteus Baird & Girard, 1855, Micropogonias furnieri (Desmarest, 1823), and Chloroscombrus chrysurus (Linnaeus, 1766) (Table S4). In the outer zone, S. brasiliensis was the most abundant species, followed by C. spixii. This zone appears to have a more equitable distribution of abundance among species. Overall, most of the functional indices were higher in the outer zone, except for FOri and FSpe.

Spearman's correlation analysis revealed significant positive correlations between Richness, Shannon, and Pielou's Equitability indices and substrate type (higher in coarse substrate), transparency, and depth (Figure 6), while the Simpson index showed a negative relationship with these environmental variables. Pielou's Equitability index also exhibited a significant positive correlation with salinity. Regarding functional diversity indices (FRic, FEve, FDiv, and FSpe), they were significantly correlated with certain environmental variables. FRic showed positive correlations with substrate and water transparency, while FEve displayed a negative correlation with temperature. FDiv exhibited positive correlations with substrate type (more abundant in coarse substrate) and salinity, while FSpe had a negative correlation with water transparency and depth. Compared to the functional diversity indices (except for FDiv), the taxonomic diversity indices showed a strong correlation with the environmental variables (Figure 6).

4 | Discussion

One of the most important findings of this work was the identification of a pronounced spatial gradient in Sepetiba Bay. This gradient was evident in both environmental conditions and fish assemblages, which varied notably between the outer zone, near the sea connection, and the inner zone. The outer zone exhibited more favorable environmental conditions than the inner zone, with more stable physical and chemical variables influenced primarily by its high connection to the ocean. In contrast, the inner zone experiences greater environmental stress and receives a higher organic load from continental drainage (Molisani et al. 2004, 2006; Pérez et al. 2020; Damasceno et al. 2024). Rivers and drainage channels introduce nutrients and pollutants into the bay, leading to decreased water quality, reduced salinity, increased turbidity, and raising temperature. These changes demand rapid adaptation, limiting species persistence (Menon et al. 2023; Scherer 1992). In contrast, the outer zone, with less continental influence, has more stable conditions, supporting higher fish richness and diversity. While the outer zone demonstrated higher species richness and diversity, the inner zone showed greater abundance and biomass, primarily due to marine catfishes highly adapted to the stressful conditions typical of inner estuarine areas, particularly bays (Araújo et al. 2016; Gomes-Goncalves and Araújo 2022). It is expected that fish assemblage will undergo changes along the primary spatial/longitudinal axis of estuaries, with salinity



FIGURE 5 | Functional divergence (FDiv) plot for the three sampled zones in Sepetiba Bay, State of Rio de Janeiro, Brazil. The circles represent the species present in each assemblage, with their diameter proportional to their abundance. The black rhombus indicates the position of the center of gravity of the species in the functional space. The small plus symbols represent species absent in the indicated zone but present in other zones. Species codes are described in Table S4.

explaining variability in species richness (França et al. 2011). Jaureguizar et al. (2003), in their study of the Rio de la Plata estuary, found that fish assemblages mirror the local pattern of habitat heterogeneity. However, this phenomenon is less evident in bays or embayment areas. Furthermore, a general shift in habitat utilization is more prone to occur during summer in temperate estuarine areas, as observed by Love and May (2007) in their study of Maryland's coastal bays. Our data also lend support to these observations that temperature influences changes in fish assemblage structure of coastal bays. Depth, followed by salinity, explains the majority of the variability in the abundance of dominant species and plays a significant role in shaping assemblages in subtropical estuaries (Vilar et al. 2011). This pattern was confirmed in the present study, since the outer zone consistently exhibits higher salinity, transparency, and depth, while the inner zone had higher turbidity and temperature. This environmental gradient likely contributes to consistent differences in fish assemblage structure and diversity.

Higher FDiv values were observed in the outer zone. This indicates distinct functional roles and resource utilization patterns, which reflect a high degree of niche differentiation (Mason et al. 2005; Mouillot et al. 2013; Dolbeth et al. 2016). FDiv also tends to increase when species abundance is more evenly distributed, as observed in the outer zone. In contrast, the inner zone displayed lower FDiv values, suggesting that the most abundant species share similar functional traits, reflecting a convergence of characteristics favored by local environmental conditions. Species adapted to stressful conditions benefit from the high availability of organic inputs that support the trophic web (Elliott and Quintino 2007; Castelo et al. 2021). As a result, marine catfishes such as Cathorops spixii and Aspistor luniscutis, which are tolerant of these environments (Araújo 1988; Azevedo et al. 1999), dominate the inner zone. Although these species possess specific traits, their convergent functional traits and high abundance lower functional divergence (FDiv), reducing niche diversification. However, the remaining functional indices did not vary spatially, suggesting that while species composition differs among zones, most functional roles are maintained.

Marine catfishes emerged as the most abundant functional group in both number and biomass. These species are characterized by their demersal nature, featuring dorsoventrally flattened bodies, relatively large subterminal mouths, a brood-guarding behavior, and a generalist feeding habit, which includes the ingestion of large quantities of Polychaetes, Copepods, and Ostracods (Araújo 1984, 1988; Gomes and Araújo 2004; Guedes et al. 2015). Several characteristics of the inner zone favor their presence, including estuarine beach substrates that provide natural hiding spots, reducing egg predation risk (Beck et al. 2001; Barletta et al. 2005). In brackish areas, demersal positioning and egg-carrying behavior help fish find suitable egg sites, enhancing survival chances for both adults and offspring in these dynamic ecosystems (Keck et al. 2014; Whitfield and Pattrick 2015). Moreover, the



FIGURE 6 | Spearman's correlation analysis between environmental variables and diversity indices in Sepetiba Bay, RJ. Blue indicates positive correlation, while red indicates negative correlation. The bar chart illustrates the contribution of environmental variables to diversity indices.

dominance of marine catfishes *Cathorops spixii* and *Aspistor luniscutis* in the inner zone is primarily due to their tolerance of low salinity, high turbidity, and their ability to thrive in eutrophic environments (Araújo et al. 2017). Their reproductive strategy, involving parental care through oral incubation of eggs, enhances juvenile survival (Araújo 1988; Azevedo et al. 1999). Combined with their generalist feeding habits and demersal behavior, these traits lead to a fish assemblage dominated by a few functionally similar species, resulting in lower FDiv in the inner zone.

In contrast, a broader group of species with different functional traits, encompassing a wide range of body sizes (significant variation in the Bsu-body transversal surface) and other functional attributes, predominated in the outer zone. These groups are predominantly pelagic, exhibiting robust swimming abilities and a wide variety of food options. These adaptive characteristics can be beneficial, enabling better exploitation of available food sources and the ability to escape from adverse conditions at specific times and locations (Dolbeth et al. 2016; Ford and Roberts 2020). Many of these low-abundance marine stragglers (e.g., Caranx latus, Synodus foetens, Scorpaena isthmensis) contribute to increased niche differentiation. Similarly, Souto-Vieira et al. (2023) found that the loss of rare species in a tropical estuary led to decreased niche differentiation, supporting our findings regarding the role of marine stragglers in enhancing niche differentiation in the outer zone. da Silva and Fabré (2019) and da Silva et al. (2019) found that niche differentiation is crucial for maintaining functional redundancy in estuarine systems, allowing species to effectively exploit available resources. In this context, we should not underestimate the role of rare species in the outer bay, as they are essential for maintaining ecological functions.

The higher Simpson dominance in the inner zone can be attributed to the strong presence of C. spixii, due to which it also had a higher Indicator Value (IndVal) in the inner and middle zones. Previous findings had attributed the highest abundances to the ariid G. genidens, with C. spixii ranking in the second position (Araújo et al. 2016; Gomes-Goncalves and Araújo 2022). Marine catfishes of the Ariidae family are typically one of the most common fish groups in the inner zones of tropical bays (Azevedo et al. 1999). This pattern aligns with their reproductive strategy, as they spawn in low-salinity waters, such as the river mouths and coastal lagoons (Gomes et al. 1999). The significant contribution of rivers and streams into the bay's inner zone favors the development of marine catfish, while also introducing greater quantities of nutrients, which directly support those species or strengthen the local food web (Ford and Roberts 2020; Harrison and Whitfield 2024). The increased nutrient input in the inner zone is a recognized factor, as this area receives greater inflow from rivers and drainage channels carrying nutrients and organic and inorganic loads (Molisani et al. 2004; Castelo et al. 2021; Damasceno et al. 2024). This nutrient enrichment, particularly of phosphorus (P), can stimulate primary productivity within the bay (Loureiro et al. 2005; Castelo et al. 2021),

potentially influencing the availability of food resources for the fish community.

The absence of significant differences in taxonomic and functional diversity among seasons supports previous studies that emphasize spatial variation as a more influential factor in ichthyofauna compared to seasonal variation (Araújo et al. 2016; Camara et al. 2019). Species richness estimated by rarefaction curves also indicated minimal seasonal effects in Sepetiba Bay (Gomes-Goncalves and Araújo 2022; Camara et al. 2019). The inner zone, characterized by greater anthropogenic influence and higher nutrient and pollutant inputs (Pereira et al. 2015; Gomes-Gonçalves et al. 2020; Gomes-Goncalves and Araújo 2022), exhibited lower taxonomic diversity. This can be attributed to alterations in the environment, which hinder species dispersal, promote population isolation, and establish a degree of stability in assemblage composition (Moreno and Halffter 2001; Gomes-Gonçalves et al. 2020). This phenomenon may result in the filtering of certain species or attributes that do not find favorable conditions in this zone. On the other hand, species that have managed to adapt to these stressful conditions, such as catfish, drumfish, and croakers, have benefited from greater resource availability, resulting in high abundance and biomass.

Unlike tropical estuaries, where the rainy season drives productivity by altering salinity and creating physiological filters that affect functional diversity (Neto et al. 2015; Passos et al. 2016; da Silva et al. 2021), bays highly connected to the sea, as Sepetiba Bay, are more resilient to this type of seasonal variation (Araújo et al. 2017). Souto-Vieira et al. (2023) found that sandy beaches in tropical estuaries subject to distinct rainy periods have their functions enhanced by rainfall. They also observed that environmental variations can influence species rearrangement in these areas, affecting functional diversity due to species movements across the coastal mosaic in response to environmental variability and ontogenetic migration. In environments such as bays, the larger water volume and marine influence confer greater resilience to this type of seasonal variation, with more spatially defined environmental gradients along the inner bayocean connection axis (Allen et al. 2007; Hylkema et al. 2015; Cloern et al. 2017). Our findings align with previous studies (Villéger et al. 2012; Dolbeth et al. 2016; Teichert et al. 2018), indicating that while taxonomic composition shifts significantly along spatial estuarine gradients, functional dissimilarity remains relatively low due to the dominance of a few species with similar ecological traits.

Fourteen functional groups were identified, with some groups containing only one species, raising concerns about the potential loss of ecosystem functions in response to ongoing environmental changes. In contrast, a broader group of species (Group VIII), encompassing a wide range of body sizes, predominated in the outer zone. This group is predominantly demersal, exhibiting robust swimming abilities and a wide variety of food options. These adaptive characteristics are beneficial for coping with disturbances, allowing for better exploitation of available food sources and the ability to escape toxic conditions at specific times and locations (Dolbeth et al. 2016). The inner zone exhibited the lowest diversity of functional groups, with only eight groups recorded, compared to 12 and 11 groups observed in the

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central and outer zones, respectively. Although some functional groups formed by a single species are exclusive to a particular zone, most groups were present in all three zones. This pattern reinforces the importance of protecting multiple areas to preserve greater species diversity and, consequently, maintain ecosystem functionality.

The more consistent environmental conditions, resembling those of the marine environment, may favor the presence of species more sensitive to environmental fluctuations in the outer zone. Additionally, fish exhibit greater mobility, allowing them to enter and exit the bay more easily depending on conditions, due to increased connectivity with the ocean. The presence of various islands and diversified sediment types in the outer zone also contributes to habitat complexity, allowing for greater trophic diversity in fish assemblages (Azevedo et al. 2007). Species abundance is more evenly distributed, both among species and among functional traits. In this region, species such as C. gracilicirrhus, Cynoscion jamaicensis, Diapterus rhombeus, E. crossotus, L. breviceps, M. americanus, S. brasiliensis, and Stellifer rastrifer are more abundant, primarily feeding on benthic macrofauna, smaller fish, and other items (Azevedo et al. 2007; Guedes et al. 2015). This pattern may be related to the spatial characteristics of the transition zone between the marine environment and the bay, which favors a wide distribution of species.

Management measures are essential for environments like Sepetiba Bay, which are experiencing increasing disturbance levels. To enhance conservation and management, prioritizing heavily impacted areas is crucial. In Sepetiba Bay, particularly the inner zone where nutrient and pollutant inputs are higher, mitigating human impacts from industrial and populated regions is vital. Protecting critical habitats, such as river mouths and drainage channels that serve as ecological corridors for fish communities, should be a priority. Since the 1990s, increased discharge of untreated domestic effluent into Sepetiba Bay has led to higher total organic carbon accumulation in its inner region, associated with fine sediments and eutrophication (Pérez et al. 2020; Damasceno et al. 2024). Many urban centers around the bay still lack sewage treatment, making it essential to expand sewage networks and direct waste to treatment plants to mitigate environmental impacts (Copeland et al. 2003; Araújo et al. 2017). Leal Neto et al. (2006) developed a water drainage management model for Sepetiba Bay that incorporates the watershed's dynamics, simulating various economic and demographic growth scenarios to aid in identifying investment priorities and policy analysis. Additionally, establishing and effectively managing marine protected areas is a crucial conservation strategy. Teixeira-Leite and Vianna (2023) found that areas near conservation units in Guanabara Bay have higher fish diversity, highlighting their role in mitigating human impacts. Implementing similar measures in Sepetiba Bay, especially in high-value ecological zones, could enhance habitat resilience and preserve fish diversity. Ongoing monitoring of environmental quality and fish communities is essential to evaluate the effectiveness of these protection strategies in the bay's inner regions.

Environmental gradients in tropical semi-enclosed coastal areas determine the taxonomic and functional diversity of fish, with traits being filtered at a local scale (Hylkema et al. 2015; Cloern et al. 2017). In our study, taxonomic diversity decreased in the

more impacted inner zone, while functional indices remained stable, except for functional divergence, which varied spatially. This suggests species composition changes without significant loss of functional roles, partially confirming our hypothesis. These findings align with previous research indicating that environmental gradients and anthropogenic influences can differentially affect taxonomic and functional diversity in fish communities. It is still not clear how environmental variations can determine community structure and functional diversity, although it has been observed that changes in fish functional diversity may also be related to local conditions (Brandl et al. 2016; Leitão et al. 2018). We found that underlying processes shape species distribution, tied to environmental and anthropogenic constraints in semi-enclosed transitional coastal environments. It is an important step to be further examined in studies aiming to untangle these complex relationships.

Author Contributions

Leonardo Almeida Freitas: writing – original draft, visualization, validation, software, conceptualization, methodology, investigation, formal analysis, data curation. **Francisco Gerson Araújo:** writing – original draft, visualization, supervision, resources, funding acquisition, conceptualization, formal analysis, data curation, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available upon reasonable request to the corresponding author.

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Supporting Information

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