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Exploring local and species contributions to beta diversity in a bay fish community: A baseline assessment of the Ubatumirim Bay

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ABSTRACT

The organization of fish communities into habitat use groups facilitates a replicable understanding of species distribution due to the distinctive characteristics and ecological roles of these groups. Partitioning beta diversity and assessing both species contribution to beta diversity (SCBD) and local contribution to beta diversity (LCBD) can evaluate the ecological importance of each group and measure the uniqueness of each site. This study aimed to comprehend how different habitat groups within the marine fish assemblage in the Ubatumirim Bay contribute to beta diversity and to correlate the uniqueness of each sampling site to their attributes to better understand the importance of habitat use groups and the community composition variation in the bay. We sampled ichthyofauna at six locations within the bay, employing a shrimp trawl net at varying depths. We categorized the 95 identified species into five distinct habitat groups: reef-associated, pelagic-neritic, demersal, benthopelagic, and pelagic-oceanic, each with different ecological characteristics and preferences. However, no significant differences were detected in SCBD among these groups. An increase in LCBD values was observed with the decrease in mean sediment diameter, indicating a higher environmental complexity, possibly acting as an environmental filter. One of the sampled sites, Couves Island, stood out with a significantly higher LCBD value, which underscores the importance of such diverse environments in maintaining regional biodiversity. These findings can serve as a valuable baseline reference in conservation planning and management, particularly in assessing the effectiveness of the recently established Marine Environment Protection Area. For instance, comparing the current observations with future surveys could quantify the impact of this protection initiative, thus providing evidence of management efficacy and showing the potential effects of impacts (such as predatory tourism) in the Ubatumirim Bay area.

Keywords: Spatial scale; Environmental filtering; Assemblage vulnerability; Marine Protected Area; Couves Island

INTRODUCTION

Beta diversity, the component of total diversity that reflects the strength of compositional differences between local communities (Socolar et al., 2016), holds special significance in applied ecology and conservation. This concept enables us to delve deeper into the drivers of regional diversity either by the dissection of alpha and gamma diversity components (Jost, 2007) or by species turnover and species addition (Baselga, 2010; Legendre 2014). Furthermore, a unique

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perspective has been offered by Legendre and Cáceres (2013), wherein beta diversity is seen as a variance component that can be additively decomposed into the local contribution to beta diversity (LCBD) and the species contribution to beta diversity (SCBD). Herein, LCBD measures the degree of uniqueness of each sample unit, whereas SCBD quantifies the degree of contribution of each species from the community to total beta diversity.

This methodology makes it practicable to construct a profile of community variation in a region to pinpoint priority sites based on community composition (Vilmi et al., 2017). This becomes an essential step toward conservation since species distribution and assemblage composition variations can be directly impacted by local extinctions and anthropogenic influences such as habitat loss (Santos et al., 2021). Furthermore, it draws attention to the necessity of understanding these communities prior to any specific impact or ecological change. LCBD values, in this context, can be a crucial tool as high LCBD measurements often indicate sites with an uncommon species combination, showing high conservation value or even a degraded environment necessitating immediate restoration. This facilitates the protection of sites hosting contrasting communities on a regional level (Hill et al., 2021). On the other hand, SCBD values may be high when a species shows substantial variations in abundance across locations (Legendre and Cáceres, 2013), and these values can be visualized within each group if added.

This brings us to a key point: the clustering of species. Over the years, the practice of grouping species has been leveraged in ecological research toward a better understanding of how ecosystem processes influence community structure (Korňan and Kropil, 2014; Malaterre et al., 2019). Exemplifying this strategy in action, in their study on Marine Protected Area reefs, Honda et al. (2013) grouped species by habitat use to comprehend which species were related to which environments. Similarly, Munsch et al. (2016) classified fish species in nearshore waters by underwater surveys according to their behavior-based habitat preferences. Also, Camara et al. (2023) elaborated on community distinct groups such as trophic guilds, reproductive guilds, habitat use, and others, enabling the identification of major functional groups of fish species in bays and coastal lagoons. Thus, grouping species per habitat can accurately portray local ecological dynamics and help to identify habitat-specific threats, thus enabling more targeted conservation strategies. Additionally, this simplifies communication with non-experts and decision makers regarding the effects of environmental management to defend an ecological block perspective over exclusive focus on the species level. Thus, species grouping can be a flexible tool for conservation efforts, enabling predictions of ecological change and assessments of human impacts (Simberloff and Dayan, 1991; Wilson, 1999; Benoit et al., 2021).

Therefore, this approach not only demarcates sample place heterogeneity, but also underscores the significance of species and groups in a regional context. Studies have attempted to unravel the determinants of LCBD and SCBD in diverse habitats such as freshwater environments (Lopes et al., 2014; Kong et al., 2017), forests (Qiao et al., 2015; Tan et al., 2019; Santos et al., 2021), and others (Silva et al., 2018; Hill et al., 2021). However, few have endeavored to comprehend the patterns of SCBD and LCBD in marine environments (Cionek et al., 2022), underscoring the need for continued research to infer these patterns across various ecosystems and regions.

In response to this need, this study aims to measure the LCBD and SCBD values associated with the ichthyofauna in the Ubatumirim Bay. Data from the region of Ubatumirim and nearby islands, such as Couves Island, were sampled before its inclusion into the Marine Environment Protection Area of São Paulo North Coast (Decree-law 66823/22). We predicted that sites within the Bay may harbor species with distinct contributions to total beta diversity, potentially influenced by the environmental characteristics of each site. In particular, we expected that areas with greater environmental complexity, such as rocky shores and islands, would show higher LCBD values since it could be positively related to habitat structure (Hill et al., 2021).

METHODS

STUDY AREA AND SAMPLING

This study was carried out in the Ubatumirim Bay (23º20’ – 23º26’S e 44º50’ – 44º56’W), which belongs to the municipality of Ubatuba in the north coast of São Paulo State. The Bay is formed by several small islands, of which the Couves Island is the largest. The islands of the region constitute Marine Protected Areas (state law 149/69 and 13,426/79), showing unique terrestrial and marine ecosystems. The ichthyofauna was sampled by trawling in all four seasons (spring, summer, autumn, and winter) in 2000. A shrimp trawl equipped with two double-rig nets (mesh size 20 and 15 mm in the cod end) was employed for this purpose.

Throughout the four seasons of the year, six transects in distinct environments in the Ubatumirim Bay were sampled. These included a transect running parallel to the Ubatumirim Beach at a depth of 2 m, a sheltered rocky shore at 5 m, an exposed rocky shore at 7 m, two transects parallel to the mainland, one located more interior within the bay at 10 m and another situated more externally at 15 m, as well as a transect parallel to the rocky shores of Couves Island at 16 m (Figure 1), with a sample size of 24 transects and four transects per site. Each transect was subjected to a 30-minute haul.

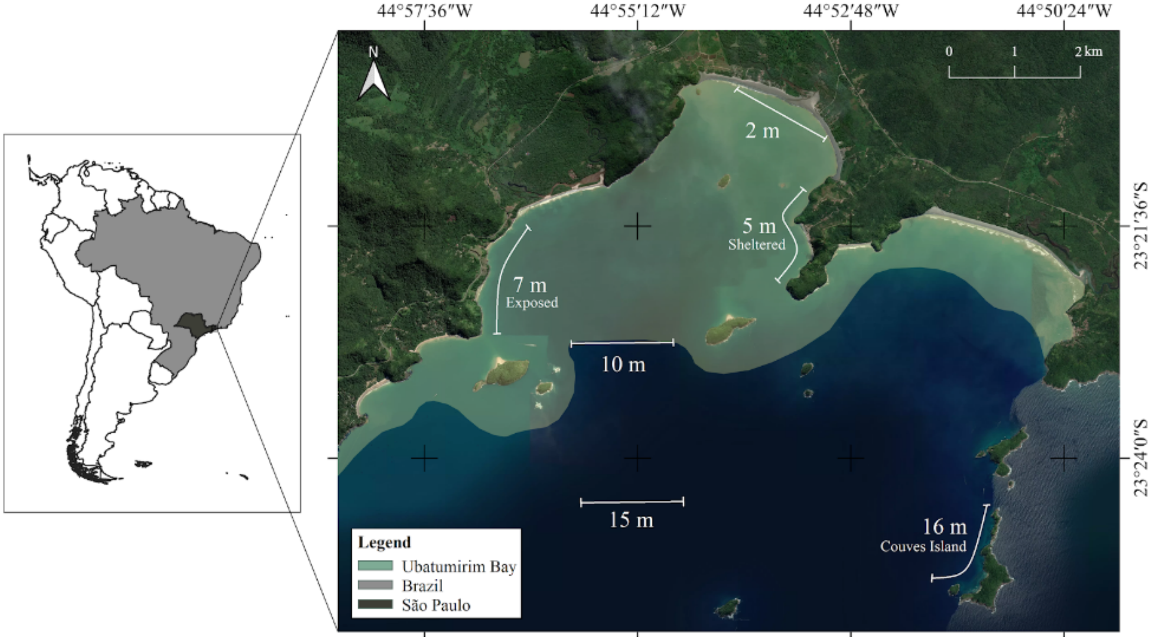

Figure 1. Map of the studied area in the Ubatumirim Bay with the marking of the six sampling points and their respective depths.

Bottom salinity and temperature were sampled in each transect using a Nansen bottle — measured by a refractometer and thermometer — and depths were measured by an echo sounder coupled with a GPS. Sediment samples were collected by a transect with a Van Veen-type sediment catcher, covering a bottom area of 0.06 m^2, from which the values of mean sediment diameter (phi) were calculated. Procedures for sediment analysis followed Håkanson and Jansson (1983) and Tucker (1988).

The fish were fixed in 10% formalin and identified at species level according to the specialized literature (Figueiredo and Menezes, 1978; Menezes and Figueiredo 1980, 1985; Cervigón et al., 1992). Specimens were deposited in the fish collection are of the Laboratory of Zoology at the University of Taubaté (IAM/CCILZU).

SPECIES GROUPING AND DATA ANALYSIS

Species were categorized based on their habitat usage into five groups, detailed in the Supplementary Material (Table S1). Classification was conducted according to information available at https://www.fishbase.se/search.php (Froese and Pauly, 2000). The five groups include demersal species, which inhabit the water column and primarily consume bottom-dwelling organisms; benthopelagic species, known for their feeding habits across the bottom, the water column, and the surface; pelagic-neritic species, typically occupying only the water column in close proximity to the continent, usually in shallower waters; pelagic-oceanic species that reside in the water column but are found in deeper waters away from the coast; and reef-associated species, related with consolidated substrates such as coral and rocky reefs (Froese and Pauly, 2000).

Total beta diversity (β_{Total}) was measured by the variance of the Hellinger transformed data table containing abundance values, with species as columns and sample units as rows (Legendre and Cáceres, 2013). To obtain the species contribution to beta diversity (SCBD) and local contribution to beta diversity (LCBD) values, the *adespatial* package was used (Dray et al., 2021). A Kruskal-Wallis test was conducted to examine significant differences of SCBD values according to habitat use group type. Habitat use group and total length in centimeters were used to calculate functional richness on the *FD* R package (Froese and Pauly, 2000; Laliberté and Legendre, 2010; Laliberté et al., 2014).

A beta regression was used to model SCBD and LCBD values since the response variables can only take values from 0 to 1, assuming a beta-distributed dependent variable. Prior to beta regression modelling, predictors were assessed for their variance inflation factor (VIF), only incorporating variables with VIF < 3. For SCBD values, a regression considering relative abundance of each species (raised to the power of two) and species occupancy was performed. Species occupancy was measured by the number of samples in which the species were found. For LCBD, two regressions were made, one with community metrics: species richness, functional richness, and relative abundance per transect, and one with environmental variables: bottom temperature, bottom salinity, and mean sediment diameter. All analyses were performed on R (R Core Team, 2022).

RESULTS

A total of 13,055 individuals were sampled, representing 95 species that were distributed into five habitat groups, each harboring their following richness: 43 species in the demersal group, 32 in the reef-associated one, nine in both the benthopelagic and pelagic-neritic ones, and two species in the pelagic-oceanic one. Subsequently, total beta diversity was measured (β_{Total} = 0.61). No significant differences were found between the five habitat groups (Chi-squared = 4.69, df = 4, p = 0.31) (Fig. 2), with the ten species with higher SCBD values detailed in Figure 2. SCBD showed a positive relation with the total relative abundance of species (Figure 3a, Table 1), with the same happening for the number of sites in which the species occurred (Figure 3b).

The LCBD values ranged from 0.025 to 0.075. Functional richness, species richness, and relative abundance of the site were considered poor predictors of LCBD (Table 1; Figure 4). LCBD values showed a significant and negative relation with mean sediment diameter, with the lower values of mean sediment diameter occurring on Couves Island (16 m transect), harboring higher contributions to beta diversity (Figure 4, Table 1).

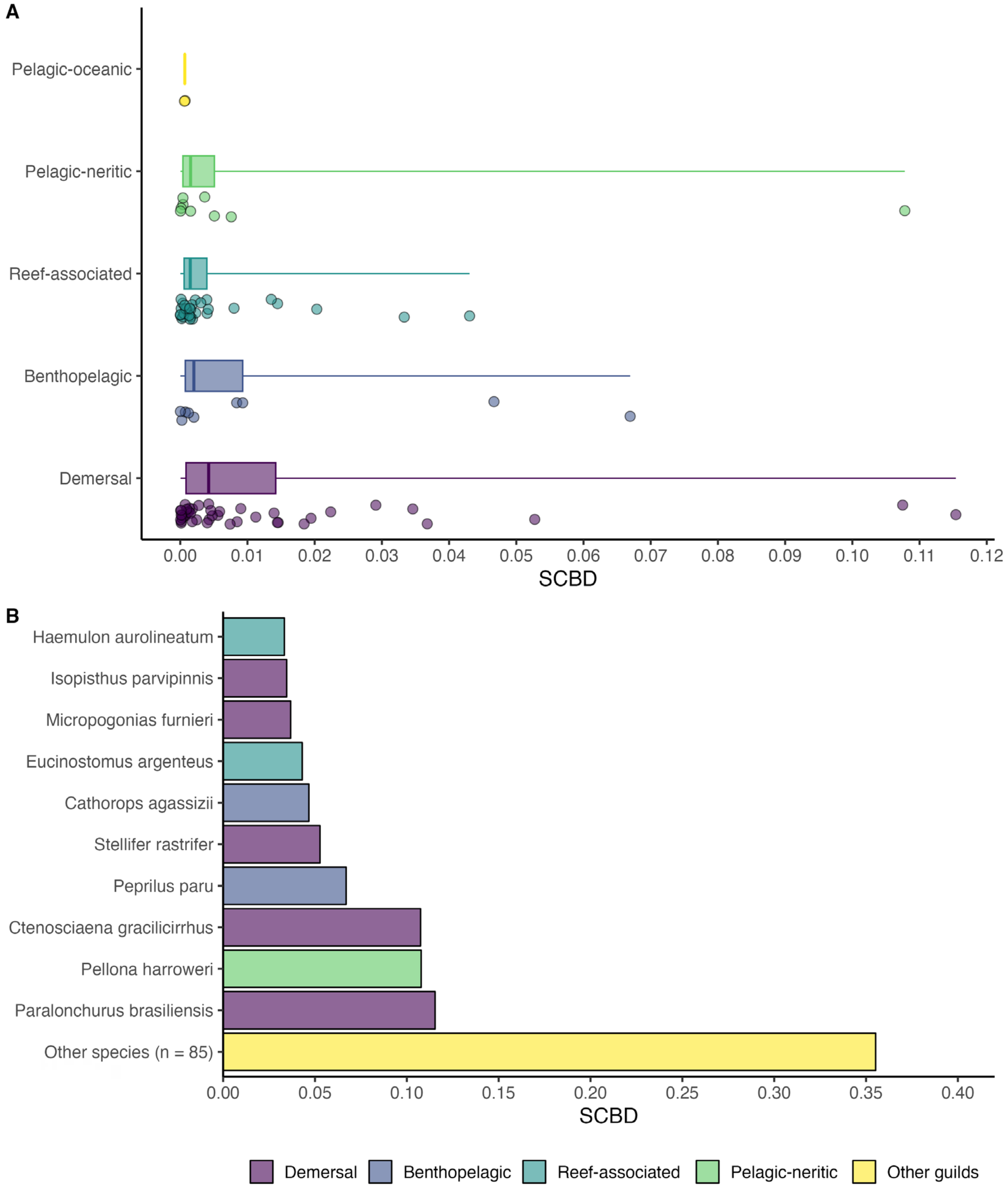

Figure 2. Boxplot and points representing the SCBD values per habitat use groups of the marine fish assemblage in the Ubatumirim Bay (A). Barplot of the species contribution to beta diversity (SCBD), discriminating the ten species with higher SCBD values and all other 85 species values summed by habitat use groups of each species (B).

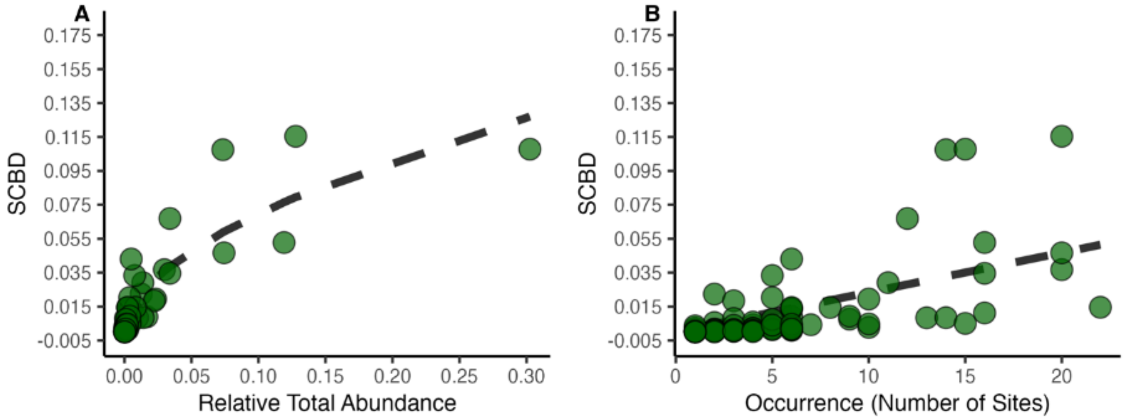

Figure 3. Relation between the relative total abundance of species and their contribution to beta diversity (SCBD) (A). Relation between species occurrence and their contribution to beta diversity (SCBD) within the sampled community in the Ubatumirim Bay (B).

Table 1. Beta regression with species contribution to beta diversity (a) and local contribution to beta diversity (b, c) as response variables. LCBD values were explained by community metrics (b) and environmental variables (c). No. of sites: number of sites in which each species occurred. Rel. abundance: relative abundance of each species raised to the power of two in the model to capture the power relation. F. richness: functional richness for each sample. Rel. Abund.: relative abundance for each sample. BT: bottom temperature. BS: bottom salinity. phi: mean sediment diameter. Std. Error: standard error. p: probability associated with z. Asterisks representing significant variables.

	Estimate	**Std. Error**	**z value**	**p**	**Pseudo R^2**
(a) SCBD					
Intercept	−5.683	0.177	−32.081	< 0.01*	0.518
N. of sites	0.131	0.013	9.648	< 0.01*	
Rel. abundance	19.358	3.690	5.530	< 0.01*	
(b) LCBD					
Intercept	−3.1203	0.2593	−13.031	< 0.01	0.095
F. richness	−0.001	0.0001	−1.027	0.304	
Richness	0.0041	0.0137	0.0305	0.760	
Rel. Abund.	−2.0073	1.8842	−1.065	0.287	
(c) LCBD					
Intercept	−3.153	1.311	−2.405	0.016	0.291
BT	0.037	0.022	1.671	0.094	
BS	0.009	0.028	0.337	0.736	
phi	−0.255	0.075	−3.386	<0.01*	

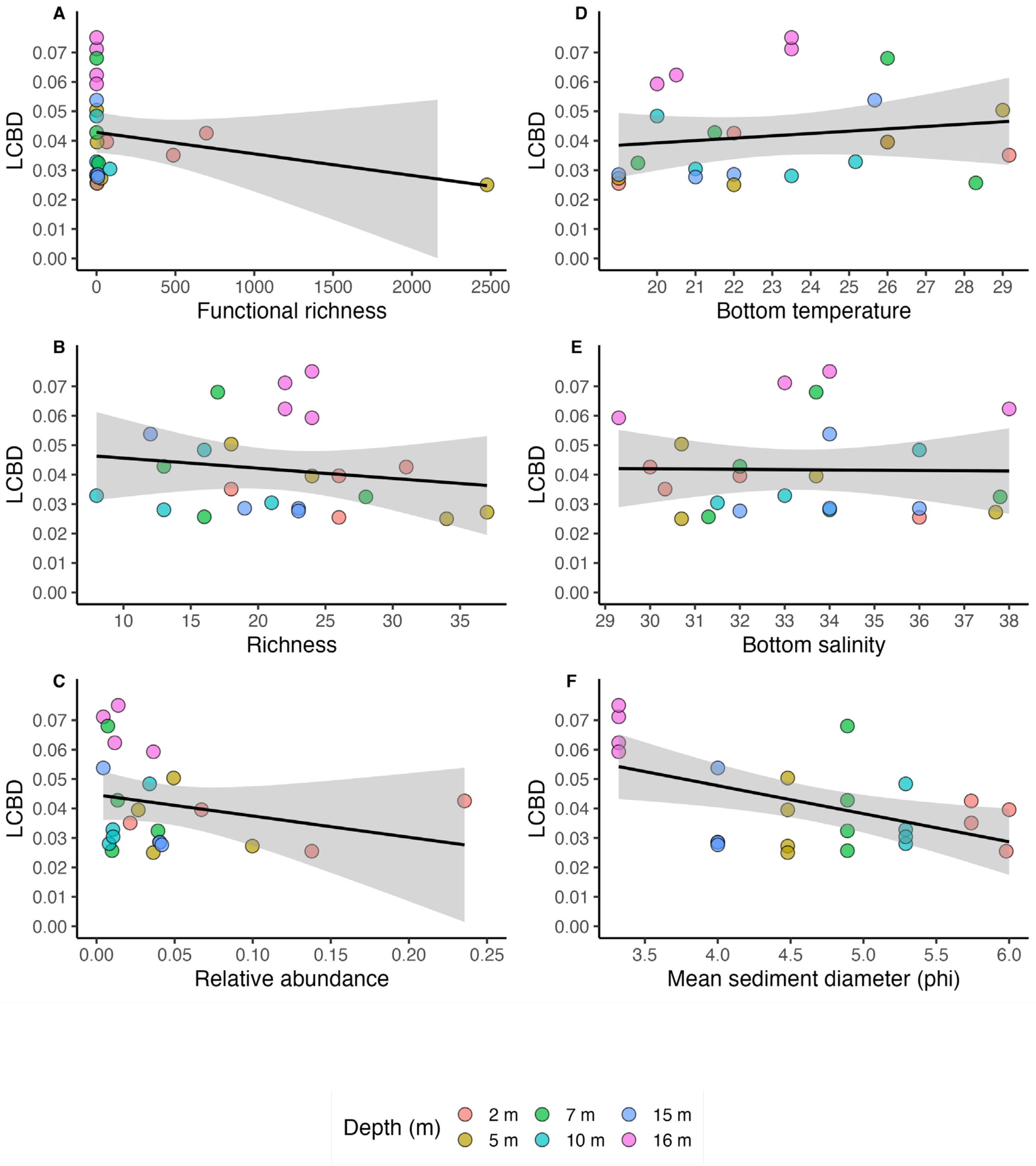

Figure 4. Relation of the community metrics: Functional richness (A), Richness (B), Relative abundance (C); and environmental variables: Bottom temperature (D), Bottom salinity (E), Mean sediment diameter (F); with measurements of local contribution to beta diversity (LCBD) of the sampled units in the Ubatumirim Bay.

DISCUSSION

We observed that species with higher abundance and wider distribution tended to make greater contributions to regional beta diversity. This relation was evinced by the positive relationship between SCBD values, relative abundances, and species occupancies. This corroborates previous findings (Tan et al., 2019; Santos et al., 2021), suggesting that biodiversity maintenance at regional levels may depend on guaranteeing that most species can find suitable conditions to maintain widespread and abundant populations. This may involve some degree of community-dependency as the unimodal relationship has also been described in literature (Heino and Grönroos, 2017).

Meanwhile, habitat use groups showed no significant difference in SCBD values. Investigating riverine fish, Xia et al. (2022) noted the absence of significant correlations between traits and SCBD values, including trophic guild among these traits. Similarly, Silva et al. (2018) also found a notable correlation between SCBD and both abundance and occurrence, but not with functional traits such as trophic guild. This suggests that SCBD seems to be primarily influenced by variations in species abundance rather than previously considered specific traits, with only niche position showing significant values (Silva et al., 2018). In this context, we aimed to elucidate similar patterns within fish communities in marine environments. Nevertheless, these relations failed to seem markedly distinct from those in other habitats (Heino and Grönroos, 2017; Xia et al., 2022). It is conceivable that most of the variation is driven by species-specific factors. Therefore, we encourage the exploration of different traits at group levels and across various spatial scales to ascertain whether these patterns are confined to local contexts or independent of marine environment traits.

Nevertheless, the demersal group contributed more to the samples, partially due to the chosen sampling method as trawling may favor species associated with the substrate (Lowe-McConnell, 1987). In total, five of the 10 species with the highest contribution belong to the demersal group, more specifically to the Sciaenidae family, namely: *Paralonchurus brasiliensis* (Steindachner, 1875), *Ctenosciaena gracilicirrhus* (Metzelaar, 1919), *Stellifer rastrifer* (Jordan, 1889), *Micropogonias furnieri* (Desmarest, 1823), and *Isopisthus parvipinnis* (Cuvier, 1830).

The Sciaenidae family is generally found in unconsolidated substrate and shallow waters, making it an important resource for fisheries on the Brazilian continental shelf. It is considered the most important family in the demersal fish community in Southeastern and Southern Brazil (Menezes and Figueiredo, 1980; Soares and Vazzoler, 2001). Moreover, the biomass of Sciaenidae fishes and Penaeoida shrimp show a relation in the Ubatuba region that is influenced by the coastal water (CW) entrance in the winter. This entrance brings about high temperatures and low salinity, thereby favoring the establishment of shrimp species that serve as an important dietary resource for the fish (Souza et al., 2008).

The importance of Sciaenidae for regional beta diversity has also been found elsewhere (Cionel et al., 2022) with *P. brasiliensis* and *S. rastrifer* attaining higher values. *Paralonchurus brasiliensis,* the species with the highest SCBD value, is indeed recognized for its extensive distribution and demersal habits (Robert et al., 2007). Similarly, *C. gracilicirrhus* shows high abundance in coastal regions in Southeastern Brazil (Araújo et al., 2002); it possesses low commercial value and is often discarded as bycatch—a trait that contrasts with the typical characteristics of most of its family members (Pombo et al., 2013). Another species with a high SCBD value and belonging to the same family refers to *S. rastrifer*, also part of an abundant genus in coastal and shallow waters. Another pattern found for this beta diversity partitioning was seen for a species of the pelagic-neritic group, *Pellona harroweri* (Fowler, 1917), which was the second species with the higher value of contribution to beta diversity since a high value of SCBD can be related to abundance oscillation (Santos et al., 2021), a typical feature of *P. harroweri* due to its habit of forming schools as animals that inhabit open areas count on safety in numbers (Krause et al., 2010).

Regarding the values of local contribution to beta diversity, the negative relationship between LCBD values and species richness is habitual (Heino and Grönroos, 2017; Tan et al., 2019; Santos et al., 2021) but, although a common pattern, it fails to constitute a rule (Silva et al., 2018) since this relationship may relate to the simple fact that sites with greater taxonomic richness can show low values of contribution to beta diversity due to the natural greater chance of sharing species with other sites in the region (Hill et al., 2021). On the other hand, marine environments have shown that sites with high LCBD fail to necessarily represent sites with low richness but heterogeneous sites acting on the community with different environmental filters (Cionek et al., 2022). When using abundance data, Heino and Grönroos (2017) also found no significant relationship between LCBD and taxonomic richness. Similarly, functional richness showed no significant relationship with LCBD for mammalian communities (Santos et al., 2021). Our findings align with this observation, indicating the insignificant relationship between local contribution to beta diversity and functional richness. This suggests that, for fish assemblages in marine environments, the extent to which species fill the functional space within a community may fail to correlate with LCBD values.

Considering environmental variables as predictors of the LCBD values, the Couves Island stood out in all samples, harboring a unique fish composition that may be related to its heterogeneous trait acting as an environmental filter selecting different species (Peláez et al., 2017). Island heterogeneity can be observed by distinct mean sediment diameters (phi), showed by the beta regression, which reflects a measure of structural complexity, characterized by a thicker sediment, or at least reflecting the spatial differentiation in the region. Islands such as Couves Island are known for their rocky reefs that may be acting as an environmental filter, harboring community structures similar to coral reefs. However, the management and conservation of the former is often placed in the background, which highlights the need to better understand the occurrence of that group and the environment in which they occur (Rolim et al., 2017; Vieira et al., 2021).

For that reason, the distinctiveness of Couves Island fish composition was evinced, and this diversity profile of local contribution to beta diversity can be preserved over time if this heterogeneous environment and fauna keeps its features (Peláez et al., 2017). The preservation of such characteristics seems to be provided by its island rocky reefs filtering different species, especially from the reef-associated group, with their distinct structural complexity and sheltering reflected on the sediment diameter. This is highly relevant to biodiversity conservation as the rocky reefs of these islands were classified as environments with high environmental sensitivity, which are still targeted by anthropic effects such as predatory tourism (Poletto and Batista, 2008).

Our study makes it possible to explore future comparisons that seek to understand whether the heterogeneity of the region will be preserved if future surveys are conducted. This is because protected island environments can act as a refuge for feeding and reproduction (Rolim et al., 2017). Species and local contribution to beta diversity are suitable indices to be applied in such comparisons as they reflect both local species distribution and abundance as local environmental heterogeneity proves to be important tools to understand the functionality of these ecosystems.

Understanding these patterns for SCBD and LCBD are essential for conservation and ecological knowledge as it enables identifying which places have priority regarding the need to protect their faunal heterogeneity. A possible relationship of LCBD values with the greater structural complexity of rocky reefs is noted when compared to other environments in the region, highlighting the importance of studies that seek to understand how species and sites contribute to local diversity and how the difference in faunal composition can offer a conservation tool on a regional scale, enabling the adequate management of these sites. Such findings directly contribute to the ecological knowledge of marine fish assemblages, acting as predictors or even encouragers of the conservation process of species and of local characteristics. We recommend that future studies apply a new methodology that can measure structural complexity per site. The measurements in this work, if compared with new measurements after the region became part of a Marine Environmental Protection Area, will offer a better uptake of the management effectiveness and predatory tourism impact in the Ubatumirim Bay area.

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AUTHOR CONTRIBUTIONS

J.H.A.C.: Conceptualization; Investigation; Formal Analysis; Writing – Original Draft.

I.A.M.: Methodology; Funding Acquisition; Writing – Review & Editing.

M.C.: Investigation; Writing – Review & Editing.

F.C.F.: Conceptualization; Investigation; Writing – Review & Editing.

U.P.S.: Supervision; Conceptualization; Investigation; Writing – Review & Editing.

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