



Ecological uniqueness and species contribution to beta diversity differ between fishes and crustaceans' bycatch in subtropical shallow marine ecosystems

Vivian de Mello Cioneck^{1,2} · Jorge Luiz Rodrigues-Filho^{3,4} · Danielle Katharine Petsch⁵ · Joaquim Olinto Branco^{1,6}

Received: 22 July 2021 / Accepted: 20 May 2022
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2022

Abstract

We assessed the ecological uniqueness of fish and crustaceans in traditional fishing grounds from a tropical shallow marine ecosystem, where bycatch is historically high. Trimestral trawling was carried out between November 2009 and August 2010 in nine sites along 80 km of coastline in South Brazil. We investigated the local (LCBD) and species contribution to beta diversity (SCBD) using beta regression models, disentangling the influence of environmental (water, sediment characteristics) and biotic (S, abundance, diversity, dominance) parameters over LCBD; and species occurrence, total and mean local abundance association with SCBD. The shallow marine areas presented high beta diversity of fish and crustacean. We identified two ecological unique sites for fishes that occurred in colder sites, while the only unique site identified for crustaceans occurred, where crustacean species richness was lower. The ecological unique sites for both taxa were those with lower species richness and abundance, with distinct assemblages' composition, although the location of the unique sites differed between taxa. Species contribution to beta diversity was mostly driven by species with intermediary–high distribution on the region with high variability in occurrence and abundance. High biodiversity is the general rule when assessing bycatch species, and the singularity of the species composition in the unique sites stems from the occurrence of rare species, which increases the size of the species pool.

Keywords LCBD · SCBD · Incidental catch · Coastal ecosystem

Introduction

Understanding the ecological uniqueness of a site across a broad geographic extent and identifying species with large contributions to biological variability can generate important insights into the management and conservation of biodiversity (Socolar et al. 2016). This is especially true in heterogeneous systems, such as shallow marine ecosystems, that provide habitats for a highly diverse fauna including macroinvertebrates and fishes (Beck et al. 2001; Pittman and McAlpine 2003). Highly dynamic environmental conditions are generated in these ecosystems mainly due to distinct habitat configuration (Moore et al. 2010) and the interaction between water masses from the ocean and the adjacent terrestrial areas (Simpson 1981; Pereira et al. 2009), which is expected to generate natural biological variability among sites (i.e., beta diversity).

Shallow marine ecosystems are also subjected to multiple and unequal uses by local communities, for recreational

✉ Vivian de Mello Cioneck
viviancioneck@gmail.com

¹ Pós-Graduação em Ciência e Tecnologia Ambiental, Universidade do Vale do Itajaí, Itajaí, SC 88302-901, Brazil

² Departamento de Educação Científica e Tecnológica, Universidade do Estado de Santa Catarina, Florianópolis, SC 88035-901, Brazil

³ Laboratório de Ecologia Aplicada e Conservação (LEAC), Universidade do Estado de Santa Catarina, Laguna, SC 88790-000, Brazil

⁴ Programa de Pós-Graduação em Planejamento Territorial e Desenvolvimento Socioambiental (PPGPLAN)/UDESC/FAED, Florianópolis, SC 88035-901, Brazil

⁵ Departamento de Biologia, Universidade Estadual de Maringá, Maringá, PR 87020-900, Brazil

⁶ Escola do Mar, Ciência e Tecnologia, Universidade do Vale do Itajaí, Itajaí, SC 88302-901, Brazil

(Franco et al. 2016) and economic (i.e., artisanal and industrial fishing) activities. As a major economic activity in the shallow coastal areas, fisheries can negatively impact biodiversity (Lotze et al. 2006). Bottom trawling fisheries are the most widespread and impactful activity over the seabed physical structure and its associated biota (Hiddink et al. 2017; Lundquist et al. 2018). In addition, one of the main prejudices of trawling is the high incidental catches of non-target species—the bycatch (Alverson et al. 1994). Bycatch species are systematically removed from the ecosystem, with direct prejudice to energy pathways and to the food web structure (McConnaughey et al. 2000), reducing biodiversity (de Juan et al. 2020) and ultimately affecting ecosystem functioning and reducing the beta diversity of the region. Non-target species are represented by a variety of taxonomic groups, such as Echinodermata, Mollusca, Crustacea, Polychaeta and Fish (Branco et al. 2015), with important interactions that maintain a historical high diversity and abundance in distinct shallow marine areas (Rodrigues-Filho et al. 2020).

The natural variation in shallow marine ecosystems associated with the anthropogenic activities promotes ecological differences between its habitats (Blanchard et al. 2004), increasing even further the heterogeneity and beta diversity (i.e., variability among sites) in these areas (Huntington et al. 2010). The mechanisms promoting beta diversity of bycatch marine communities, and consequently their ecological uniqueness, can derive from the influence of local (e.g., environmental filtering and biotic interactions) (Pozzobom et al. 2020) and regional processes (e.g., dispersal-related processes) (Barton et al. 2013; Henriques et al. 2017). For example, depth gradients (Rodrigues-Filho et al. 2015), changes in sediment composition (Ribó et al. 2021) and pollution (Yasuhara and Yamazaki 2005) can promote environmental filtering, changing species abundances. Species and feeding interactions presented by marine aquatic communities are also important drivers of community assembly in shallow marine ecosystems (De Araujo et al. 2014).

The aforementioned spatial dynamic is enhanced by temporal variability, as in the rainy season, where higher freshwater discharge reduces water salinity, increases nutrient and riverine sediment inputs, and decreases temperature in marine shallow ecosystems (Pereira et al. 2009). Temporal influences are also important drivers of population dynamics variation (e.g., reproduction periods, short distance migration) (Rodrigues-Filho et al. 2020) and can contribute to differential responses of the aquatic fauna among seasons. Spatial, temporal and environmental influences can also promote diverging patterns of beta diversity for different taxa (e.g., crustaceans and fishes), because traits related to body size, niche width, natural history, and dispersal ability affect how organisms perceive and respond to their environment (Soininen et al. 2007; Barton et al. 2013; Clark et al.

2014). Species composition of marine invertebrates is highly related to soil granulometry and organic matter content in the sediment (Barrilli et al. 2021), while groups with wider geographical distributions, such as fishes, are especially influenced by salinity and temperature gradients (Rodrigues-Filho et al. 2015, 2020). A wide range of environmental and biological influences are expected to influence biodiversity patterns and promote community dissimilarities among shallow marine locations.

In the face of this high heterogeneity, the comprehension of the biological dissimilarity between coastal marine communities can help to identify the connections between local and regional communities (i.e., beta diversity; Anderson et al. 2011) and disentangle ecological processes that influence and maintain biodiversity of aquatic assemblages in the ecosystems, driving ecological unique locations in the seascape (Legendre and De Cáceres 2013). Ecological uniqueness can be described through local contribution to beta diversity (LCBD; Legendre and De Cáceres 2013). LCBD can indicate localities with singular species composition and high alpha biodiversity (Legendre and De Cáceres 2013; Lindegren et al. 2018; Sor et al. 2018), or represent unique localities with low alpha biodiversity due to anthropogenic pressures (e.g., overfishing and bycatch discard), which will require preservation efforts (Ruhí et al. 2017). Beta diversity can also be partitioned into species contribution to beta diversity (SCBD; Legendre and De Cáceres 2013), which identifies species with large variations (e.g., abundance or incidence) across the study area. Widespread species (i.e., generalists) that occur in most of the sites usually have lower contributions to beta diversity (i.e., low values of SCBD) than species that occur in an intermediate number of sites (i.e., high values of SCBD; Heino and Grönroos 2017; Pozzobom et al. 2020). Environmental restrictions may influence the occurrence of species into small or intermediary number of sites, while higher variation in the species composition among sites provides a broader regional species pool (Whittaker 1972).

Most studies investigated LCBD and SCBD in freshwater ecosystems (e.g., Heino and Grönroos 2017; Brito et al. 2020; Pozzobom et al. 2020). Here we assessed the ecological uniqueness of fish and crustaceans' communities from a tropical shallow marine ecosystem in traditional fishing grounds, where bycatch is historically high (see: Rodrigues-Filho et al. 2020). We investigated the local (LCBD) and species contribution to beta diversity (SCBD), disentangling the role of environmental and biotic parameters over LCBD, and species occurrence and total and mean local abundance association with SCBD. We were especially interested in understanding which sites could harbor unique assemblages (LCBD) of bycatch species. Moreover, we were interested in understanding if distinct marine assemblages subjected to bycatch (i.e.,

fish and crustaceans) respond differently to environmental constraints and if they might produce distinct ecological unique sites in traditional fishing grounds.

Methods

Study area

The study was carried out in the central-north Santa Catarina coastline, in Barra do Sul (BS), Armação Itapocoroy, in Penha (AI) and Porto Belo (PB) municipalities, in Brazil (Fig. 1). This area is highly heterogeneous, with the formation of bays and coves, and is associated with coastal lagoons and estuaries (Schettini and Carvalho 2010). It is also influenced by the interaction and mixture between Coastal, Tropical and the South Atlantic Central waters, which generates different oceanographic fronts (Pereira et al. 2009), boosting primary production (Paes and Moraes 2007) and promoting high biological abundance along the coastal area (Branco et al. 2015; Rodrigues-Filho et al. 2015). As a result of this ecological complexity, this area is also harvested for artisanal shrimp trawling fisheries (Branco et al. 2015).

Sampling

Fishes and crustaceans

Trimestral sampling was carried out between November 2009 and August 2010, in nine sites along 80 km of coastline (Fig. 1), under SISBIO license n. 324642. The sampling locations coincide with areas of traditional artisanal fishing, with the purpose of surveying demersal communities associated with fishing grounds. At each sampling site, one trawling of 20 min and 2.0 knots/hour was conducted, following the protocols used in these traditional fishing areas, that corroborates sampling sufficiency of our methods (Rodrigues-Filho et al. 2020; Barrilli et al. 2021). A vessel equipped with double trawl doors, with a mesh net of 3.0 cm and 2.0 cm, was used in the bagger.

Fish and crustacean samples were kept in ice coolers. In the laboratory, they were sorted and identified to species level according to specialized literature (Fish: Menezes et al. 2003; Crustacea: Costa et al. 2003). Crustacean species composition included those classified as target species for artisanal and industrial fisheries (*Xiphopenaeus kroyeri*, *Artemisia longinaris* and *Pleoticus muelleri*), and where not considered in the beta diversity, LCBBD and SCBD analysis, since our focus was on bycatch species. Their abundance and occurrence were used to calculate biotic indices (see “Data analysis”) that were used as explanatory variables.

Local scale environmental parameters

Before each trawl, water samples were collected with a vertical van Dorn bottle at 10 m, 20 m and 30 m, from which temperature was measured with a thermometer (0.1 °C) and salinity was measured with an optical refractometer in the field. Water samples were used to determine chlorophyll-a concentration with acetone extraction according to the methodology described in Mantoura et al. (1997). Sediment samples were collected with a Van Veen grab sampler, screened and separated according to particle size and texture, as clay, silt, sand and gravel (Folk and Ward 1957; Suguio 1973). Calcium carbonate was quantified by gravimetry (Suguio 1973), through the exposure of 100 g of a sediment sample to a solution of hydrochloric acid (HCL 10%). Organic matter content was quantified from sediment samples by loss of ignition (8 h at 800 °C).

Data analysis

We calculated beta diversity from the abundance and incidence-based matrices of fish and crustaceans according to the methods described in Legendre and De Cáceres (2013). We conducted both analyses to verify, respectively, if communities presented different patterns between quantitative and qualitative data. First, the abundance and incidence-based data of each assemblage was subjected to a Hellinger transformation. We estimated total beta diversity (BD_{total}) for the entire area along the study period to account for spatial and seasonal variation, as the total sum of squares of the species composition data. This method provides a beta diversity index that ranges between 0 and 1, that is, when all sites have entirely different species compositions, BD_{total} = 1 (Legendre and De Cáceres 2013).

BD_{total} was partitioned into local contributions of sites to beta diversity (LCBD), both for fish and crustaceans. We calculated the local contributions from the abundance (abund.) and incidence-based (incid.) data separately, totaling four distinct metrics, hereafter LCBDD_{fish.abund.}, LCBDD_{crus.abund.}, LCBDD_{fish.incid.} and LCBDD_{crus.incid.}. LCBDD represents the relative contribution of each sampling unit to beta diversity, calculated as the sum of squares of each sampling unit divided by the total sum of squares. Sites with mean local contribution significantly higher than the sites LCBDD-mean were considered unique (Legendre and De Cáceres 2013). It might represent degraded and species-poor sites or correspond to sites with special conditions that harbor higher species richness or distinct species composition among the study region (Leão et al. 2020; Pozzobom et al. 2020).

BD_{total} was partitioned into species contributions to beta diversity (SCBD), both for fish and crustaceans (from the abundance and incidence-based data separately), totaling four metrics of species contribution,

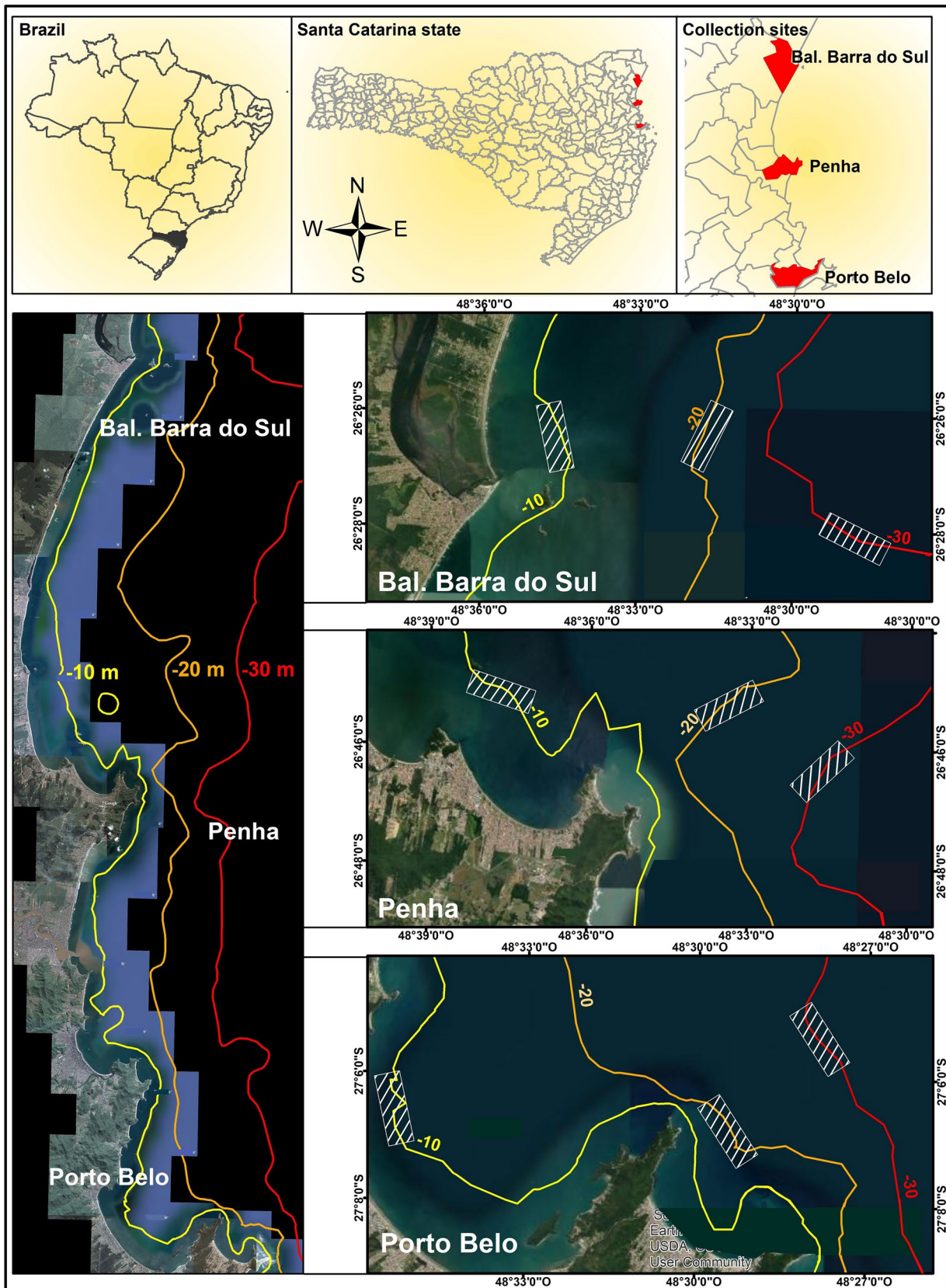


Fig. 1 Location of the sampling areas in the South coast of Brazil

hereafter $SCBD_{fish.abund}$, $SCBD_{crust.abund}$, $SCBD_{fish.incid}$ and $SCBD_{crust.incid}$. Species with SCBD higher than the average SCBD of all species pool exhibit large variations (in abundance or incidence) across the study area (Legendre and De Cáceres 2013). BDtotal, LCBD and SCBD were obtained using the *beta.div* function from 'adespatial' package (Dray et al. 2020) in R (R Core Team 2020). It is important to highlight that the species that inhabit the unique sites (LCBD) may not be the same as those with higher contribution to beta diversity (SCBD), because the LCBD metric accounts for site-specific differences, while SCBD metric accounts for species-specific contributions.

We used beta regression to model LCBD and SCBD. Beta regression is the most appropriate analysis, because it incorporates heteroskedasticity or skewness, often observed in response variables taking values from 0 to 1 (Cribari-Neto and Zeleis 2010). The beta regression model assumes that the dependent variable is beta-distributed and that the mean is related to a set of regressors through a linear predictor with unknown coefficients and a logit link function (Cribari-Neto and Zeleis 2010).

We used beta regression to identify how distinct processes contributed to local composition variation of fishes and crustaceans within shallow marine ecosystems. We analyzed which factors are related to LCBD of fish and crustaceans (abundance and incidence-based) separately with two sets of predictors (i.e., environmental and biotic). We first investigated the influence of local environmental parameters over LCBD. The environmental variables (i.e., water temperature, depth, salinity, chlorophyll-a; proportion of gravel, sand, silt, clay, carbonate and organic matter in the sediment) were previously subjected to a Pearson correlation to assess multicollinearity, using the command *rcorr.adjust* from the 'RcmdrMisc' package (Fox 2020) in R (R Core Team 2020). All sediment parameters (i.e., gravel, sand, silt, clay, carbonate and organic matter) were highly correlated to each other. We chose to retain the sand proportion in the sediment as our proxy variable, since it was consistently negatively correlated to all others (Table S1). Temperature and depth were highly correlated, and we chose to retain water temperature, since it has a clearer ecological influence over biological responses (Table S1). We ran the multiple regression with LCBD as our response variable and four initial explanatory environmental variables (water temperature, salinity, chlorophyll-a and sand). Prior to the statistical analysis, all the environmental variables were z-scores standardized (i.e., mean = 0, SD = 1), with the *decostand* function in R (R Core Team 2020). Finally, we investigated the influence of local community diversity parameters—(i) species richness, (ii) abundance ($\log(x + 1)$), (iii) Hill's numbers for taxonomic diversity ($\exp(H')$) and (iv) Simpson's diversity ($1/D$) over LCBD, in the biotic model.

We also used beta regression to understand the relation of SCBD with the number of occupied sites by the species and their total and mean local abundance. Because species occurring at an intermediate proportion of sites should be those most variable and contributing most to beta diversity (da Silva et al. 2018), we ran the beta regression on SCBD using total abundance, mean local abundance and number of sites occupied by the species to investigate for possible non-linear responses. Beta regression was conducted separately for each predictor.

We ran the beta regression with a generalized additive model (GAM) with a Beta distribution, random effects and logit link using *gam* function with family = 'betar' from the 'mgcv' package (Wood et al. 2016) for inferences about LCBD responses in the environmental and biotic model. We did that to account for both nonlinear relations between response and explanatory variables identified during data exploration (Figs. S1, S2, S3 and S4), and to account for temporal (i.e., Season) and spatial (i.e., Beach) influences over our response variable (LCBD) as random effects (Wood 2017; Pedersen et al. 2019), in R (R Core Team 2020). Random effects were inserted as smoothing parameters (i.e., $f(\text{Season}, \text{bs} = 're')$) that were constructed using random effects splines with $k = 4$ for seasons, and $k = 3$ for locations and estimated with restricted maximum likelihood estimation (REML) (Wood 2017). We ran the beta regression with GAM with Beta distribution and logit link using *gam* function with family = 'betar' from 'mgcv' package (Wood et al. 2016) for inferences about SCBD association with total abundance, mean local abundance and number of sites occupied. Model validation for all approaches was conducted by inspecting residual graphics (Cribari-Neto and Zeleis 2010; Statistics 2010; Wood 2017). Model selection was based on the *double penalty approach* by setting the argument 'select = TRUE' in the *gam* function of all models. Initial and simplified models were checked with the AICc selection criterion, and we choose the models with only significant terms, because they presented either smaller AIC values or $\Delta < 2$ compared to the initial model (Anderson 2008; Marra and Wood 2011).

Results

Total beta diversity

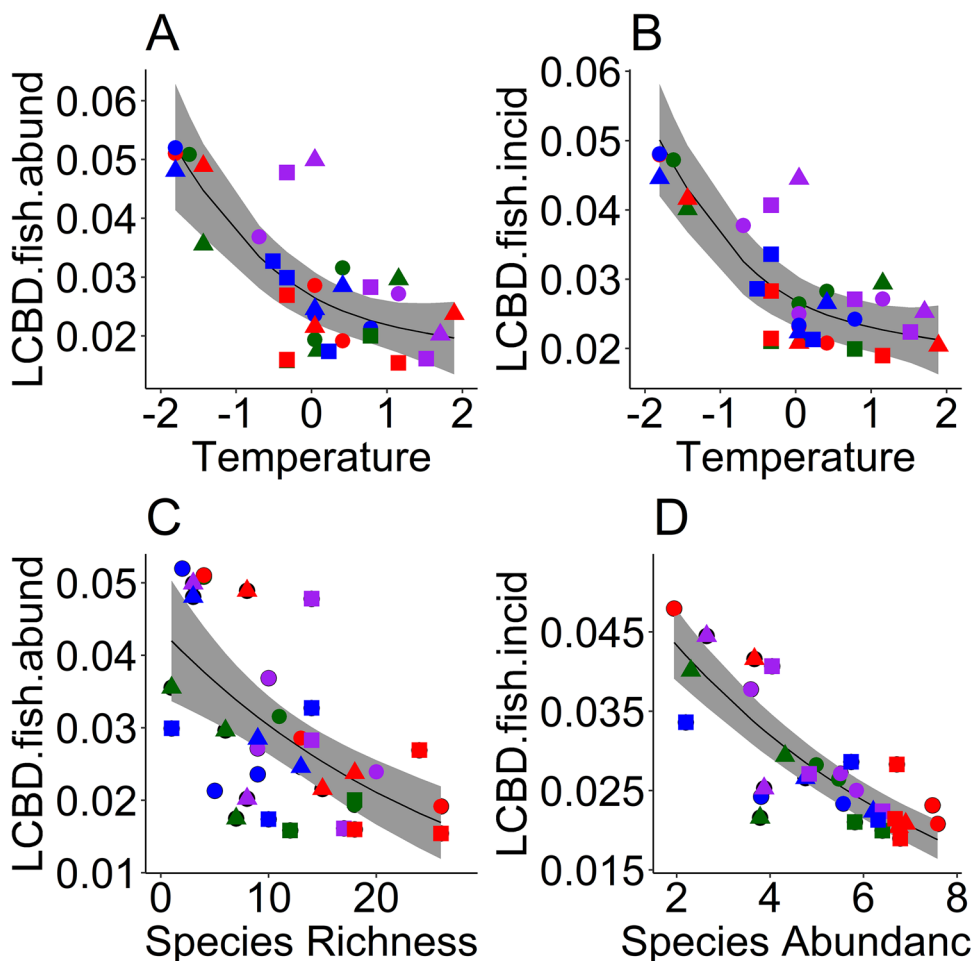
We registered 73 fish species and 12,845 individuals. Fish species richness varied from 1 to 26 per site. The total beta diversity of fishes based on abundance data was 0.71, while the beta diversity based on incidence data was 0.74. We registered 24 species of crustaceans and 5,730 individuals. Crustacean species richness varied from 1 to 13 per site. The crustacean beta diversity based on abundance data was 0.69,

Table 1 Results of the best beta regression model of the relation between Fish LCBD based in abundance data, with environmental and biotic predictors

LCBD _{fish.abund}				LCBD _{fish.abund}					
Environmental model				Biotic model					
Parametric coefficients				Parametric coefficients					
	Estimate	Std. Error	z value	Pr(> z)		Estimate	Std. Error	z value	Pr(> z)
Intercept	-3.531	0.078	-45.19	<0.001	Intercept	-3.518	0.070	-50.14	<0.001
Approximate significance of smooth terms				Approximate significance of smooth terms					
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Temp, bs='ts', k=3)	1.760	1.94	57.029	<0.001	s(S, bs='ts', k=3)	1.000	1.00	18.71	<0.001
s(Season, bs='re', k=4)	1.967	3.00	5.294	0.044	s(Season, bs='re', k=4)	1.129	3.00	1.72	0.207
s(Beach, bs='re', k=3)	0.327	2.00	0.392	0.300	s(Beach, bs='re', k=3)	0.000	2.00	0.00	0.475
R-sq.(adj)=0.635	Deviance explained=64.4%				R-sq.(adj)=0.371	Deviance explained=39.3%			
REML=-114.49	Scale est.=1			n=34	REML=-109.06	Scale est.=1			n=34

The regression models were generalized additive model with random effects for Season and Beach, using beta distribution and link=logit. n=34 sites, because two sites had no species

Fig. 2 Relationship between LCBD_{fish.abund} and predictor variables from the environmental model: **a** temperature (z-scores); and biotic model: **c** species richness of the fish assemblage. Relationship between LCBD_{fish.incid} and predictor variables from the environmental model: **b** temperature; and biotic model: **d** fish abundance (log). Abundance (log)=total fish abundance. The best models retained only one significant predictor each, that are show in the graphic. All candidate models are available in Table S4. Points color: summer (red), spring (green), winter (blue) and autumn (purple). Points shape: northern area—Barra do Sul (circle), central area—Armação do Itapocoróy (triangle), southern area—Porto Belo (square)



while beta diversity based on incidence data was 0.70. Total beta diversity was high for both taxa, since the maximum beta diversity value that can be reached with this method is $BD_{Total} = 1$.

Local contribution to beta diversity (LCBD)

$LCBD_{fish.abund}$ varied between 0.015 to 0.052, with 1 site (Barra do Sul at 30 m) contributing above average in the winter ($BS30 = 0.052$). $LCBD_{fish.incident}$ varied between 0.019

Table 2 Results of the best beta regression model of the relation between Fish LCBD incidence based, with environmental and biotic predictors

$LCBD_{fish.incident}$					$LCBD_{fish.incident}$				
Environmental model					Biotic model				
Parametric coefficients					Parametric coefficients				
	Estimate	Std. Error	z value	Pr(> z)		Estimate	Std. Error	z value	Pr(> z)
Intercept	-3.52	0.069	-50.84	<0.001	Intercept	-3.530	0.045	-77.94	<0.001
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Temperature, bs = 'ts', k = 4)	2.228	2.56	110.25	<0.001	s(Abundance(log), bs = 'ts', k = 3)	1.110	1.20	133.32	<0.001
s(Season, bs = 're')	2.537	3.00	15.34	<0.001	s(Season, bs = 're')	2.051	3.00	6.20	0.026
s(Beach, bs = 're')	0.000	2.00	0.00	0.555	s(Beach, bs = 're')	0.001	2.00	0.00	0.408
R-sq.(adj)=0.773	Deviance explained = 79%				R-sq.(adj)=0.809	Deviance explained = 80.7%			
REML = -128.38	Scale est. = 1			n = 34	REML = -132.88	Scale est. = 1			n = 34

The regression models were Generalized Additive Model with random effects for Season and Beach, using beta distribution and link=logit. Abundance was log-transformed prior to analysis. n = 34 sites, because two sites had no species found

Table 3 Results of the best beta regression model of the relation between Crustacean LCBD based in abundance data, with environmental and biotic predictors

$LCBD_{crust.abund}$					$LCBD_{crust.abund}$				
Environmental model					Biotic model				
Parametric coefficients					Parametric coefficients				
	Estimate	Std. Error	z value	Pr(> z)		Estimate	Std. Error	z value	Pr(> z)
Intercept	-3.443	0.130	-26.34	<0.001	Intercept	-3.459	0.137	-25.10	<0.001
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Sand bs = 'ts', k = 3)	1.516	1.76	2.72	0.328	s(S, bs = 'ts', k = 3)	1.000	1.00	8.706	0.003
s(Season, bs = 're')	0.000	3.00	0.00	0.495	s(Season, bs = 're')	0.000	3.00	0.000	0.656
s(Beach, bs = 're')	1.347	2.00	4.19	0.043	s(Beach, bs = 're')	1.548	2.00	7.063	0.010
R-sq.(adj)=0.135	Deviance explained = 20.9%				R-sq.(adj)=0.293	Deviance explained = 35.1%			
REML = -93	Scale est. = 1			n = 32	REML = -96.137	Scale est. = 1			n = 32

Crustacean LCBD was calculated with bycatch species. Biotic indices used in the biotic model as predictors included bycatch and target species. The regression models were Generalized Additive Model with random effects for Season and Beach, using beta distribution and link=logit. n = 32 sites, because four sites had no species found

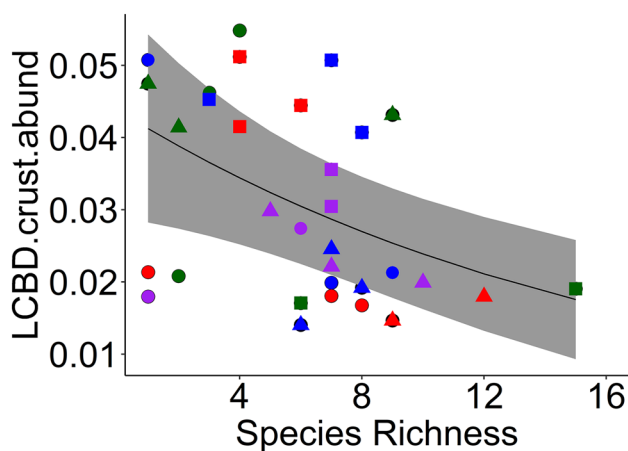


Fig. 3 Relationship between $LCBD_{crust.abund}$ and species richness of the crustacean assemblage (including the target species) from the biotic model. The best model retained only one predictor. All candidate models are available in Table S5. Points color: summer (red), spring (green), winter (blue) and autumn (purple). Points shape: northern area—Barra do Sul (circle), central area—Armação do Itapocoróy (triangle), southern area—Porto Belo (square)

to 0.049, with 2 sites (Barra do Sul and Armação Itapocoróy) contributing significantly during winter ($BS30 = 0.0049$; $AI30 = 0.0044$), autumn ($BS30 = 0.0047$), summer ($BS30 = 0.048$) and spring ($AI20 = 0.044$) (Table S2). $LCBD_{crus.abund}$ varied between 0.014 to 0.055, with 1 site (Barra do Sul at 10 m) contributing above average during autumn ($BS10 = 0.055$), and $LCBD_{crus.incid}$ varied between

0.018 to 0.051, with no sites contributing above average (Table S3).

Determinants of temporal and spatial variation in LCBD

Fish

The models that best explained $LCBD_{fish.abund}$ based on the two sets of predictors (i.e., environmental and biotic) included only one significant predictor each, that were temperature and species richness, respectively (Tables 1, S4). $LCBD_{fish.abund}$ was higher in colder sites (Fig. 2a). $LCBD_{fish.abund}$ was negatively associated with species richness, i.e., higher ecological uniqueness was registered in sites with lower species richness (Fig. 2c). The models that best explained $LCBD_{fish.incid}$ included temperature in the environmental model and total abundance in the biotic model (Tables 2, S4). $LCBD_{fish.incid}$ was higher in colder areas (Fig. 2b). $LCBD_{fish.incid}$ was higher in sites with lower total abundance (Fig. 2d).

Crustacean

$LCBD_{crus.abund}$ was not predicted by environmental variables (Tables 3, S5). $LCBD_{crus.abund}$ was predicted by species richness (S) (Fig. 3). Sites with higher crustaceans' ecological uniqueness were those with lower crustacean species richness. No site presented ecological uniqueness significantly

Table 4 Results of the best beta regression model of the relation between Crustacean LCBD based in incidence data, with environmental and biotic predictors

$LCBD_{crust.incid}$				$LCBD_{crust.incid}$					
Environmental model				Biotic model					
Parametric coefficients				Approximate significance of smooth terms					
	Estimate	Std. Error	z value	Pr(> z)		edf	Ref.edf	Chi.sq	p value
Intercept	-3.454	0.044	-76.88	<0.001	Intercept	-3.453	0.059	-57.95	<0.001
Approximate significance of smooth terms				Approximate significance of smooth terms					
s(Salinity, bs = 'ts', k = 3)	1.810	1.96	5.717	0.077	s(Exp(H), bs = 'ts', k = 3)	1.566	1.80	5.334	0.116
s(Season, bs = 're')	0.000	3.00	0.000	0.400	s(Season, bs = 're')	0.701	3.00	0.981	0.240
s(Beach, bs = 're')	0.000	2.00	0.001	0.372	s(Beach, bs = 're')	0.533	2.00	0.746	0.244
R-sq.(adj)=0.116				R-sq.(adj)=0.158					
REML = -106.95				REML = -106.96					
Deviance explained = 17.6%				Deviance explained = 22.3%					
Scale est. = 1				Scale est. = 1					
n = 32				n = 32					

Crustacean LCBD was calculated with bycatch species. Biotic indices used in the biotic model as predictors included bycatch and target species. The regression models were Generalized Additive Model with random effects for Season and Beach, using beta distribution and link=logit. $n = 32$ sites, because three sites had no species found, and 1 site was an extreme outlier and was removed from the analysis

Table 5 Results of the best beta regression model of the relation between SCBD_{fish.abund} and SCBD_{fish.incid} with total abundance (log-transformed), mean local abundance (log-transformed) and number of occupied sites

SCBD _{fish.abund}					SCBD _{fish.incid}				
Total abundance					Total abundance				
Parametric coefficients	Estimate	Std. Error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. Error	z value	Pr(> z)
Intercept	-4.965	0.090	-54.59	<0.001	Intercept	-4.458	0.061	-72.05	<0.001
SCBD _{fish.abund}					SCBD _{fish.incid}				
Total abundance					Total abundance				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Abundance(log), bs='ts', k=3)	2.359	2.936	377	<0.001	s(Abundance(log), bs='ts', k=3)	1	1	139.8	<0.001
R-sq.(adj)=0.89		Deviance explained = 83.9%			R-sq.(adj)=0.672		Deviance explained = 65.3%		
REML = -306.03		Scale est. = 1	n = 73		REML = -273.84		Scale est. = 1	n = 73	
SCBD _{fish.abund}					SCBD _{fish.incid}				
Mean local abundance					Mean local abundance				
Parametric coefficients	Estimate	Std. error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. error	z value	Pr(> z)
Intercept	-4.808	0.095	-50.39	<0.001	Intercept	-4.376	0.072	-60.52	<0.001
SCBD _{fish.abund}					SCBD _{fish.incid}				
Mean local abundance					Mean local abundance				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(MLA(log), bs='ts', k=3)	2.185	2.701	234	<0.001	s(MLA(log), bs='ts', k=3)	1.738	2.176	55.88	<0.001
R-sq.(adj)=0.8		Deviance explained = 74.8%			R-sq.(adj)=0.498		Deviance explained = 40.4%		
REML = -295.48		Scale est. = 1	n = 73		REML = -255.96		Scale est. = 1	n = 73	
SCBD _{fish.abund}					SCBD _{fish.incid}				
Number of occupied sites					Number of occupied sites				
Parametric coefficients	Estimate	Std. error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. error	z value	Pr(> z)
Intercept	-4.634	0.099	-46.59	<0.001	Intercept	-4.497	0.053	-84.56	<0.001
SCBD _{fish.abund}					SCBD _{fish.incid}				
Number of occupied sites					Number of occupied sites				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Occurrence, bs='ts', k=3)	1.367	1.646	122.5	<0.001	s(Occurrence, bs='ts', k=3)	4.616	5.529	220.5	<0.001
R-sq.(adj)=0.539		Deviance explained = 62%			R-sq.(adj)=0.71		Deviance explained = 79.8%		
REML = -287.38		Scale est. = 1	n = 73		REML = -284.49		Scale est. = 1	n = 73	

The regression models were Generalized Additive Model with random effects for Season and Beach, using beta distribution and link=logit. Regression was performed with each of the variables, separately, providing three distinct tests

higher than the average when LCBD_{crus.incid} were analyzed (Tables 4, S5), i.e., species distribution is more homogeneous with no significant species variation between sites.

LCBD_{crus.incid} was not predicted by environmental variables, nor by biotic variables (Table 4).

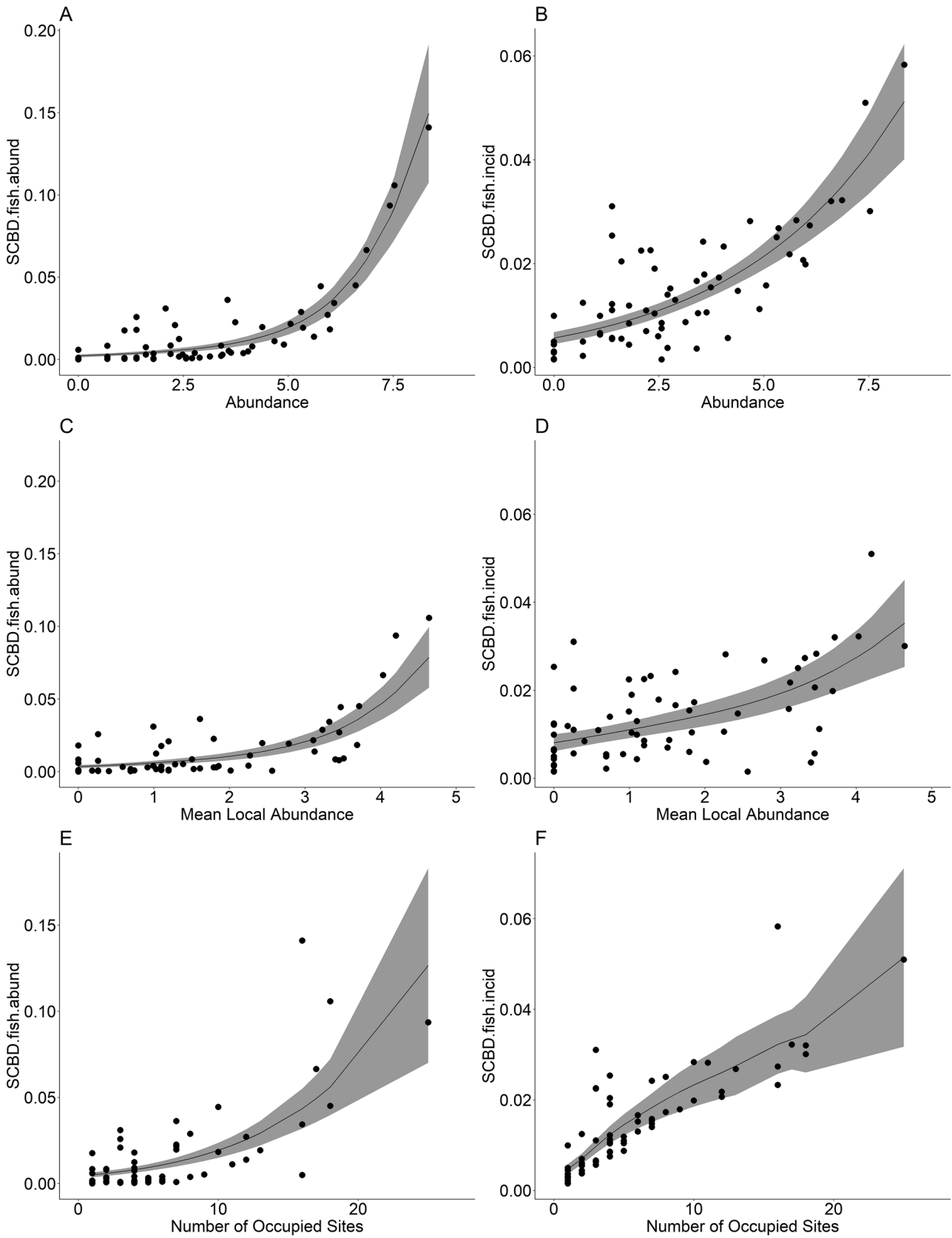


Fig. 4 Relation between $SCBD_{fish.abund}$ and $SCBD_{fish.incid}$ with total abundance (log), mean local abundance (log) and number of occupied sites by the species. $n=73$ species. The figure shows fewer points, because some species presents almost the exact numerical SCBD value and they overlap in the graphic. Points above 0.0136 represent species with SCBD higher than the mean

Species contribution to beta diversity (SCBD)

Fish

Out of 73 fish species, we registered 21 species with $SCBD_{fish.abund}$ higher than the mean (0.014). The three species with higher $SCBD_{fish.abund}$ were *Stellifer rastrifer*, *Stellifer brasiliensis* and *Paralanchurus brasiliensis* (Table S6). Higher $SCBD_{fish.abund}$ was positively related to higher total abundance (Table 5, Fig. 4a), higher mean local abundance (Table 5, Fig. 4c). $SCBD_{fish.abund}$ was higher for those species that occupied a higher number of sites (Table 5, Fig. 4e).

More species contributed to beta diversity when calculated with incidence data. Out of the 73 species, 28 species presented incidence variation higher than the mean (0.014). The three species with higher $SCBD_{fish.incid}$ were *S. rastrifer*, *P. brasiliensis* and *Cynoscion jamaicensis* (Table S6). Higher $SCBD_{fish.incid}$ was positively related to total abundance (Table 5, Fig. 4b) and mean local abundance (Table 5, Fig. 4d). $SCBD_{fish.incid}$ was higher for those that occupied higher number of sites (Table 5, Fig. 4f).

Crustaceans

Out of 24 crustacean's species, we registered 9 species with $SCBD_{crust.abund}$ higher than the mean (0.041). The three species with higher $SCBD_{crust.abund}$ were *Callinectes ornatus*, *Sicyonia dorsalis* and *Callinectes danae* (Table S7). Higher $SCBD_{crust.abund}$ was positively related with total abundance (Table 6, Fig. 5a) and mean local abundance (Table 6, Fig. 5c). $SCBD_{crust.abund}$ was higher for those species that occupied intermediary and higher number of sites (Table 6, Fig. 5e).

More crustacean's species contributed to beta diversity when calculated with incidence data. Out of the 24 species, 10 species presented incidence variation higher than the mean (0.041). The three species with higher $SCBD_{crust.incid}$ were *Portunus spinimanus*, *C. danae* and *C. ornatus* (Table S7). Higher $SCBD_{crust.incid}$ was positively related with total abundance (Table 6, Fig. 5b), but no significant relation was found with mean local abundance (Table 6, Fig. 5d). $SCBD_{crust.incid}$ was higher for those species that occupied an intermediary and higher number of sites (Table 6, Table 2).

Discussion

The shallow marine coastal areas in the South of Brazil presented high beta diversity for both fish and crustacean (bycatch) assemblages, and the ecological unique sites within our study region were those with lower species richness and abundance. These ecological unique sites were related to both local environmental and biotic features (community diversity), and it was most likely associated with the heterogeneous dynamics of this region (Rodrigues-Filho et al. 2020; Barrilli et al. 2021). The association of LCBD with the environment was mainly driven by temperature differences, but it was only significant for fishes. The local contribution to beta diversity based on crustaceans' bycatch (non-target species in fisheries) assemblages did not correlate to local environmental features; instead, it was mainly related to species richness. Beta diversity has been shown to relate to distinct socioeconomic and environmental characteristics in different sites in shallow marine ecosystems (Lazzari et al. 2020). The high diversity of both fishes and crustacean communities could be associated to the temporal and spatial variability of the water characteristics that are known to be influential over fishes (Stuart-Smith et al. 2017), while sediment variability can be more important for crustaceans because of its seasonal reproduction and feeding dynamics (Rodrigues-Filho et al. 2016). In addition, although environmental variability can be important predictor of alpha diversity patterns, it might not be high enough to drive spatial ecological uniqueness (based on beta diversity) for bycatch crustaceans in our temporal scale. The location of ecological unique sites also differed between taxa, suggesting that environmental and biotic influences might act differentially over fish and bycatch crustacean communities. It reflects the importance of wide spatial areas with low dispersal restrictions for biodiversity structuring in marine coastal areas, especially because environmental and biological interactions within these ecosystems are taxa-dependent (da Silva et al. 2020; Wu et al. 2020). The precise location of the unique site might as well change over time, because of the heterogeneous dynamics of coastal areas, and the fact that our temporal scale included a year-round investigation, may preclude temporal trends of variation in species diversity and abundance over larger periods (Carlos-Júnior et al. 2019; Rodrigues-Filho et al. 2020).

The strength and direction of association of LCBD with environmental drivers has been shown to depend on the taxonomic group analyzed, especially because it is influenced by the relation between species distribution, environmental conditions, dispersal ability and species interactions (Landeiro et al. 2018), and are especially important when assessing species that are subjected to incidental catches and discard. That is because trawling

Table 6 Results of the best beta regression model of the relation between $SCBD_{crust.abund}$ and $SCBD_{crust.incid}$ with total abundance (log-transformed), mean local abundance (log-transformed) and number of occupied sites

$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Total abundance					Total abundance				
Parametric coefficients	Estimate	Std. error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. error	z value	Pr(> z)
Intercept	-3.372	0.142	-23.69	<0.001	Intercept	-3.183	0.127	-25.03	<0.001
$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Total abundance					Total abundance				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Abundance(log), bs = 'ts', k = 3)	1.354	1.63	32.57	<0.001	s(Abundance(log), bs = 'ts', k = 3)	1	1	8.69	0.003
R-sq.(adj)=0.47			Deviance explained = 68.3%		R-sq.(adj)=0.215			Deviance explained = 29.5%	
REML = -61.423			Scale est. = 1		REML = -55.822			Scale est. = 1	
			n = 24					n = 24	
$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Mean local abundance					Mean local abundance				
Parametric coefficients	Estimate	Std. error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. error	z value	Pr(> z)
Intercept	-3.225	0.162	-19.81	<0.001	Intercept	-3.129	0.138	-22.54	<0.001
$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Mean local abundance					Mean local abundance				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(MLA(log), bs = 'ts', k = 3)	1.029	1.058	10.55	0.001	s(MLA(log), bs = 'ts', k = 3)	1	1	0.628	0.428
R-sq.(adj)=0.156			Deviance explained = 34.3%		R-sq.(adj)=-0.019			Deviance explained = 2.73%	
REML = -55.142			Scale est. = 1		REML = -52.505			Scale est. = 1	
			n = 24					n = 24	
$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Number of occupied sites					Number of occupied sites				
Parametric coefficients	Estimate	Std. error	z value	Pr(> z)	Parametric coefficients	Estimate	Std. error	z value	Pr(> z)
Intercept	-3.431	0.140	-24.44	<0.001	Intercept	3.334	0.078	-42.53	<0.001
$SCBD_{crust.abund}$					$SCBD_{crust.incid}$				
Number of occupied sites					Number of occupied sites				
Approximate significance of smooth terms					Approximate significance of smooth terms				
	edf	Ref.edf	Chi.sq	p value		edf	Ref.edf	Chi.sq	p value
s(Occurrence, bs = 'ts', k = 3)	1	1.001	54.85	<0.001	s(Occurrence, bs = 'ts', k = 3)	3.186	3.897	83.69	<0.001
R-sq.(adj)=0.73			Deviance explained = 70.8%		R-sq.(adj)=0.765			Deviance explained = 85.7%	
REML = -62.37			Scale est. = 1		REML = -68.576			Scale est. = 1	
			n = 24					n = 24	

The regression models were Generalized Additive Model with random effects for Season and Beach, using beta distribution and link=logit. Regression was performed with each of the variables, separately, providing three distinct tests

can induce chronic selectivity of resilient species (Blanchard et al. 2004), with fast-growing characteristics

(Hiddink et al. 2017), short migration fluxes (Rodrigues-Filho et al. 2015) and that benefits from the damaged or dead organisms left after a trawl pass (i.e., scavenging

macroinvertebrates) (Tillin et al. 2006), which may contribute to the historical maintenance of biodiversity in the area (Rodrigues-Filho et al. 2020). Trawling can also produce taxonomic impacts over species that are important as feeding resources for fishes and crustaceans, such as anthozoan, Malacostraca and Polychaeta (Kaiser et al. 2002), and contributes further to the selectivity of resilient species pool. Common species are usually more frequent in stressed environments (Carlos-Júnior et al. 2019). Diversity variability for distinct taxa can also be attributed to temporal dynamics of the shallow coastal areas that can shift the relative importance of water, sediment and fishing influences over communities and population organization over time (Knowlton 2004; Rodrigues-Filho et al. 2020; Barrilli et al. 2021).

Fish assemblages presented higher ecological uniqueness in colder sites, where species richness and abundances were markedly lower, especially in the northern and deeper areas of the study region (Barra do Sul—SC). This finding was consistent for both abundance and incidence of fish—LCBD. This outcome was related to the distinct fish taxonomic composition in the unique sites that were inhabited by the rarest species of our species pool. Most of these species' rest or burrow into the sandy substrate (i.e., *Syacium papillosum*, *Synodus intermedius*), or retreats into shelter when frightened (i.e., *Diplectrum formosum*). The study region does not present any physical restrictions to dispersal of fish and crustacean, especially not in our depth range, that encompass small distances (10–30 m). Even when considering the latitudinal range, which encompasses approximately 80 km, there is not any major geographical limitation to dispersal. Nevertheless, fish composition along the range of our study can change markedly, with substitution of dominant species in fishing areas (Rodrigues-Filho et al. 2015), which led us to assume that unique locations could be identified, as it was indeed. It is interesting to note that the temperature decline along the 20–30 m depth profile was most likely producing an environmental filter that precluded the occurrence of most of the fish species in some of the northern sites. Aquatic species as fishes have physiological limitations to live outside of their required temperature range (Barton et al. 2002; Mark et al. 2002). Therefore, sea surface temperature has been acknowledged as an essential environmental filter for regional and local scale studies on shallow marine ecosystems (Stuart-Smith et al. 2017). Even though the lack of geographical barriers can enable species to maintain widespread geographical distributions, environmental barriers (i.e., temperature and water masses) can provide diversity changes and dispersal restrictions to fish species (Stuart-Smith et al. 2017). The seasonal variation of abiotic characteristics can also contribute to the occurrence of distinct fish assemblages in small spatial ranges

in the south Brazilian coast (Rodrigues-Filho et al. 2015). Interestingly, most of the fishing efforts in this region are historically concentrated in shallower areas (< 20 m), where species abundance and occurrence are higher and more frequent, and might represent additional evidence of a recurrent environmental filter influence in the area.

On the other hand, bycatch crustacean's local contribution to beta diversity correlates was not consistent among abundance and incidence responses. Only one unique site was detected in a shallow site in the most northern area (Barra do Sul—SC), for abundance crustacean—LCBD. Species found in this site ($n=2$) were also rare in the region. Populations of *Exhippolysmata oplophoroides*, found in the unique site, present abundance variation during its reproductive cycle in response to rain (Santos 2018), and shows preference for colder locations (19–25 °C) (Braga 2006) in coastal areas of Brazil. The lack of influence of environmental characteristics over ecological uniqueness of bycatch crustacean assemblage disagree with our expectations, especially because the composition of the substrate differs along our study region, and it has already been acknowledged as an important and significant driver of marine macroinvertebrate community assemble in the same area (Barrilli et al. 2021), and along the Brazilian coast (Piantkoski et al. 2021). Crustacean has historically been captured in trawling in the region, with high diversity and abundance (Branco and Verani 2006; Rodrigues-Filho et al. 2016), which has been associated with the increased availability of nutrients and organic matter in the sediment (Schettini and Carvalho 2010; Branco et al. 2015; Alsaffar et al. 2019). Crustacean species are also dominant items in the diet of fish and other crustacean species, which represents an important biotic interaction and evidence of crustacean availability in the system (Branco 2005; De Araujo et al. 2014; Sabinson et al. 2015). Indeed, the only ecological unique site differed from all others due to a deviation from that pattern, with low species richness ($S=2$) and abundance ($n=14$ ind.), and it was located in the northern and shallower area of the study region. Bycatch crustacean LCBD was only (negatively) associated with species richness when calculated with abundance. This can be explained by the fact that these unique sites harbor the rarest species, as it was found for fish. Results from a temporal investigation from 1997 to 2016, conducted in the same study area (Rodrigues-Filho et al. 2020), also showed that most crustacean species caught in trawls are occasional, sometimes presenting low frequency and high abundance when caught. Only a few species (seven out of 155 spp.) were frequent and with similar abundance distribution along the study period (Rodrigues-Filho et al. 2020).

Many fish species contributed to beta diversity. Some of them were highly abundant in the region (e.g., *Stellifer rastrifer* and *Paralonchurus brasiliensis*), but presented variations in temporal and local abundance. In contrast, other fishes occurred in a

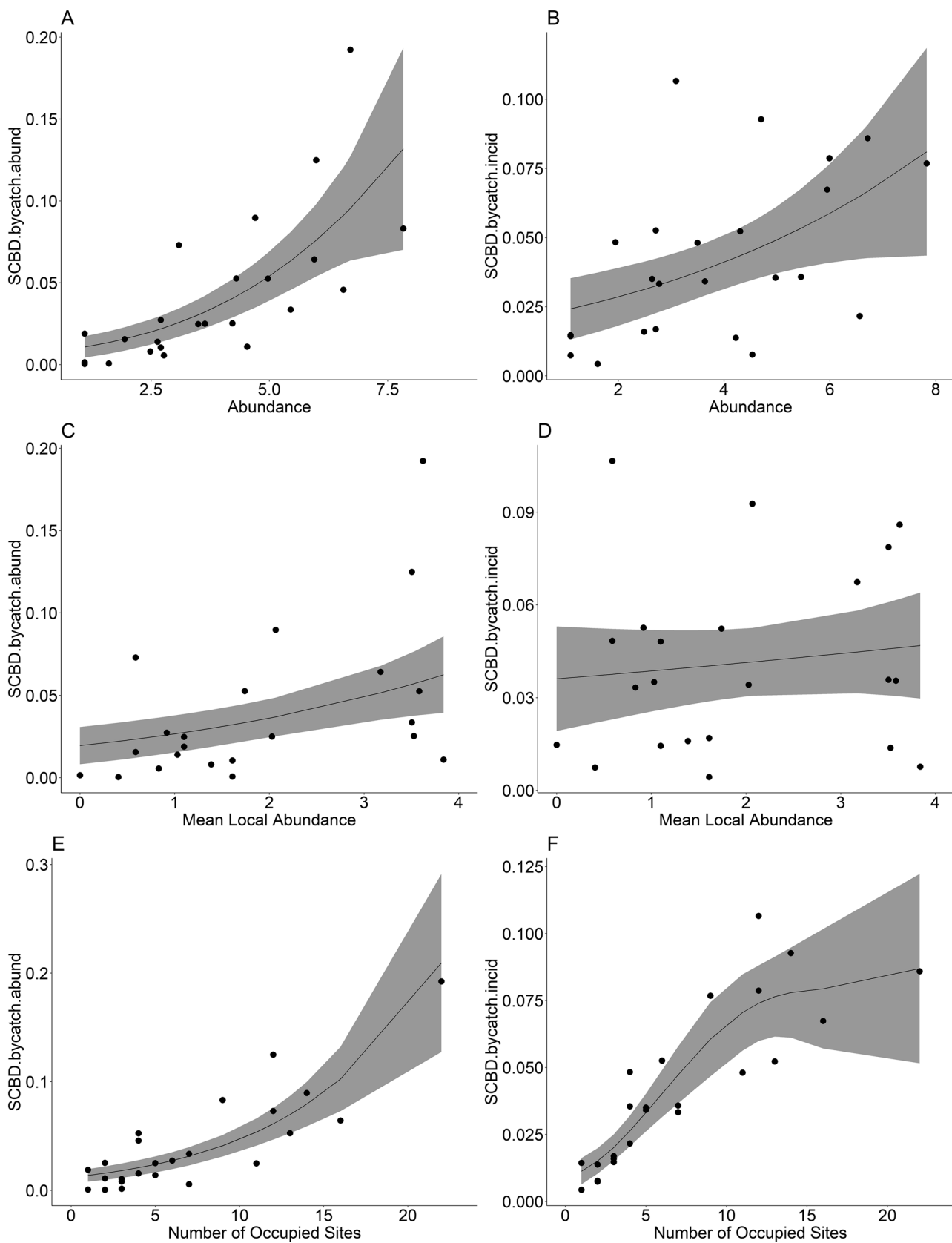


Fig. 5 Relation between SCBD_{crust.abund} and SCBD_{crust.incid} with total abundance (log), mean local abundance (log) and number of occupied sites by the species. $N=24$ species. The figure shows fewer points, because some species presents almost the exact numerical SCBD value and they overlap in the graphic. Points above 0.0416 represent species with SCBD higher than the mean

few sites with low abundances (e.g., *D. formosum* and *Xyrichtys novacula*), contributing to generating sites' ecological uniqueness. These patterns were most likely responsible for the high beta diversity in the region. As this shallow marine region is open to colonization, the maintenance of high alpha and beta diversity could be a result of the selection of species tolerant to the chronic impacts of trawling fisheries, with more general life history traits (McConnaughey et al. 2000; Magurran and Henderson 2003; Blanchard et al. 2004). Fish species with the highest contributions to beta diversity (SCBD), from abundance and incidence data, were represented mainly by Sciaenidae. *S. rastrofer* and *Stellifer brasiliensis* presented a high variation of abundance and occurrence along the year. Although they are widely distributed and abundant in the study region, their spatial and temporal distribution can vary greatly due to migration fluxes (Rodrigues-Filho et al. 2015) or fishing pressure (Rodrigues-Filho et al. 2011). This dispersal pattern can also be influenced by the movement and interaction of water masses from coastal, tropical and South Atlantic Central Water (SACW). The retraction of the SACW during winter can disturb the sediment layer, exposing some crustacean's species that are the main feeding resource of Sciaenidae in this region, attracting the fishes to new locations (Sedrez et al. 2013). Other possible explanation for their high contribution to beta diversity can be linked to their differential feeding strategies, that allows both species to consume food resources in distinct habitat compartments (i.e., benthic or pelagic) (Rodrigues-Filho et al. 2011; Sabinson et al. 2015). Generalist species with broad niches are acknowledged to contribute less to SCBD than species with small or intermediate-sized niches (Heino and Grönroos 2017). *P. brasiliensis* occurred in almost all locations along the year; however, it presented large temporal variation in abundance. This is a recurrent pattern for the species (Branco et al. 2015; Rodrigues-Filho et al. 2015), that presents large trophic spectrum and plasticity (Branco et al. 2005; Sedrez et al. 2021), and might show small scale migrations when foraging. *Cynoscion jamaicensis* was present in all sites, with large abundance variation along the year (1–243 individuals), as it was already been shown in previous studies in the region (Branco et al. 2015), which might contribute to its high contribution to beta diversity. It does not occur in sites with low temperature (< 17 °C) (Castro et al. 2002) and feed mostly of crustaceans and demersal fishes (Rondineli et al. 2007).

Almost half of the crustacean species contributed to beta diversity in the shallow marine coastal areas, which means that their occurrence and abundance are highly variable (e.g., *F. brasiliensis* and *Callinectes ornatus*), both spatial and

temporally. Crustacean species that most contributed to beta diversity were *C. ornatus* and *Callinectes danae*, which varied seasonally both in abundance and incidence. Both species occur widely along the coastal zone of Brazil (Santos et al. 2016), and present reproductive migration patterns, which might have contributed to their importance to beta diversity. *C. ornatus* presents multiple spawning periods, in which females migrate to areas with higher salinity and depth, that are more suitable to embryonic development (Branco and Lunardon-Branco 1993). Males, on the other hand, migrate from estuaries and are more abundant in the shallow coastal region during mating periods, with a preference for lower salinity. Their historical high abundance and distribution along the study region can also be attributable to their wide tolerance to salinity and they can occur all along the coast and depth ranges (Branco and Lunardon-Branco 1993). *Portunus spinimanus* presented low abundance and occurred in a small number of sites. The species occurs along all the Brazilian coast, inhabiting mostly channels and bays and feeding primarily of fish and other crustaceans (Branco and Lunardon-Branco 2002). *Sicyonia dorsalis* abundance was only higher in the winter when other species presented lower abundance, and this might be a result of temperature reduction (Piantkoski et al. 2021). Both of the rare species contributed to enhance the species diversity pool in the region.

The study region spans a meso-scale latitudinal range with areas with high contribution to beta diversity, and the occurrence of ecological unique sites with pronounced low species richness and abundance. This means that high biodiverse sites are the general rule when assessing bycatch species, and most of all, the singularity of the species composition in the unique sites stems from the occurrence of rare species which sums up to the diversity pool. LCBD in the shallow marine ecosystems are not necessarily representing sites impoverish of species, but unique locations due to environmental and biological features (or filters), that are most important to biodiversity in the region. The abundance and incidence variability of the most common fish and crustacean species, rather than species composition changes, were most important to beta diversity, and might represent a consequence of the historical trawling impacts over these assemblages, that select the most resilient species, and more detailed investigations should be explored. Most interestingly, different factors were important to explain site and species contributions to beta diversity for distinct taxa and provides an opportunity to understand biodiversity patterns and the relative importance of environmental filters and biotic interactions in structuring distinct aquatic assemblages. In addition, because unique sites are taxa-dependent, the protection of wide spatial coastal areas are necessary to attain biodiversity conservation and long-standing variation. In addition, because environmental changes and stochasticity can influence species sorting and dispersal, understanding

its main drivers can help build up strategies to biodiversity conservation and fisheries future viability in the shallow marine coastal ecosystems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-022-00872-5>.

Acknowledgements We are thankful for the logistic and economic support from Universidade do Vale do Itajaí (UNIVALI) and for all the assistance of members of the Biology Lab who conducted field collection and laboratory data analysis. V. Cionek was funded by a postdoctoral fellow (PNPD) from Coordination of Superior Level Staff Improvement (CAPES). J.L. Rodrigues-Filho thanks Foundation for Research and Innovation Support of the State of Santa Catarina (FAPESC; PAP 2021011000106) for providing the financial and infrastructure support to carry out this work. D.K Petsch would like to thank the Nacional Council for Scientific and Technological Development (CNPq) for granting a postdoctoral fellow (Process n. 163816/2020-4). J.O. Branco is thankful for the Productivity Research Grant from the Nacional Council for Scientific and Technological Development (CNPq).

Author contributions Study conception and design were performed by VMC and JLRF. Data collection was performed by JLRF and JOB. Analysis and interpretation of results was performed by VMC, JLRF and DKP. Draft manuscript preparation and critical revision was performed by all authors. All authors read and approved the final manuscript.

Funding This work was supported by a Postdoctoral (PNPD) fellow from CAPES to VMC, by a Project grant from FAPESC (PAP 2021011000106) to JLRF, by a Postdoctoral fellow (Process n. 163816/2020-4) to DKP and by a Productivity Research Grant from CNPq to JOB.

Availability of data and materials The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability The code for analysis associated with the current submission is provided in a separate file.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

References

- Alsaffar Z, Cúrdia J, Borja A et al (2019) Consistent variability in beta-diversity patterns contrasts with changes in alpha-diversity along an onshore to offshore environmental gradient: the case of Red Sea soft-bottom macrobenthos. *Mar Biodivers* 49:247–262. <https://doi.org/10.1007/s12526-017-0791-3>
- Alverson DL, Freeberg MH, Pope JG, Murawski S (1994) A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper., 339th edn. FAO, Rome
- Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York
- Anderson MJ, Crist TO, Chase JM et al (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist.

- Ecol Lett* 14:19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Barrilli GHC, Filho JLR, do Vale JG et al (2021) Role of the habitat condition in shaping of epifaunal macroinvertebrate bycatch associated with small-scale shrimp fisheries on the Southern Brazilian Coast. *Reg Stud Mar Sci* 43:101695. <https://doi.org/10.1016/j.rsma.2021.101695>
- Barton PS, Cunningham SA, Manning AD et al (2013) The spatial scaling of beta diversity. *Glob Ecol Biogeogr* 22:639–647. <https://doi.org/10.1111/geb.12031>
- Barton BA, Morgan JD, Vljayan M (2002) Physiological and condition-related indicators of environmental stress in fish. In: *Biological indicators of ecosystem stress*, pp 111–148
- Beck MW, Heck KL, Able KW et al (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)
- Blanchard F, LeLoc'h F, Hily C, Boucher J (2004) Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. *Mar Ecol Prog Ser* 280:249–260. <https://doi.org/10.3354/meps280249>
- Braga ACA (2006) *Biologia e Ecologia do camarão-espinho Biologia e Ecologia do camarão-espinho Exhippolytinae oplophoroides (Holthuis, 1948) (Caridea: Alpheoidea: Hippolytidae) na região de Ubatuba, litoral norte paulista. Universidade Estadual Paulista*
- Branco JO (2005) *Biologia e pesca do camarão sete-barbas Xiphopenaeus kroyeri (Heller) (Crustacea, Penaeidae), na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. Rev Bras Zool* 22:1050–1062. <https://doi.org/10.1590/s0101-81752005000400034>
- Branco JO, Lunardon-branco MJ (1993) Crescimento e tamanho de primeira maturação em *Callinectes ornatus* Ordway, 1863 (Decapoda, Portunidae) da região de Matinhos, Paraná, Brasil. *Arq Biol e Tecnol* 1863:497–503
- Branco JO, Lunardon-Branco MJ (2002) *Ecologia trófica de Portunus spinimanus* Latreille, 1819, na Armação do Itapocoroy, Penha, Santa Catarina. *Revta Bras Zool* 19:723–729
- Branco JO, Verani JR (2006) Análise quali-quantitativa da ictiofauna acompanhante na pesca do camarão sete-barbas, na Armação do Itapocoroy, Penha, Santa Catarina. *Rev Bras Zool* 23:381–391. <https://doi.org/10.1590/s0101-81752006000200011>
- Branco JO, Lunardon-Branco MJ, Verani JR (2005) Aspectos biológicos e pesqueiros de *Paralanchurus brasiliensis* Steindachner, (Pisces, Sciaenidae), na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. *Rev Bras Zool* 22:1063–1071. <https://doi.org/10.1590/s0101-81752005000400035>
- Branco JO, Freitas Júnior F, Christoffersen ML (2015) Bycatch fauna of seabob shrimp trawl fisheries from Santa Catarina State, southern Brazil. *Biota Neotrop* 15:1–14. <https://doi.org/10.1590/1676-06032015014314>
- Brito MTS, Heino J, Pozzobom UM, Landeiro VL (2020) Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes. *Aquat Sci* 82:43. <https://doi.org/10.1007/s00027-020-0715-3>
- Carlos-Júnior LA, Spencer M, Neves DM et al (2019) Rarity and beta diversity assessment as tools for guiding conservation strategies in marine tropical subtidal communities. *Divers Distrib* 25:743–757. <https://doi.org/10.1111/ddi.12896>
- Castro CPMG, Cergole MC, Carneiro MH et al (2002) Crescimento, mortalidade e taxa de exploração do goete, *Cynoscion jamaicensis* (Perciformes: Sciaenidae), na região Sudeste/Sul do Brasil. *Bol Do Ist Pesca* 28:141–153
- Clark MR, Rowden AA, Schlacher TA et al (2014) Identifying ecologically or biologically significant areas (EBSA): a systematic method and its application to seamounts in the South Pacific

- Ocean. *Ocean Coast Manag* 91:65–79. <https://doi.org/10.1016/j.ocecoaman.2014.01.016>
- Cribari-Neto F, Zeileis A (2010) Beta regression in R. *J Stat Softw* 34:129–150. <https://doi.org/10.1201/9781315119403-7>
- da Costa RC, Fransozo A, Melo GAS, Freire FAM (2003) Chave ilustrada para identificação dos camarões dendrobranchiata do litoral norte do estado de São Paulo, Brasil. *Biota Neotrop* 3:1–12. <https://doi.org/10.1590/s1676-06032003000100011>
- da Silva PG, Hernández MIM, Heino J (2018) Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. *Divers Distrib* 24:1674–1686. <https://doi.org/10.1111/ddi.12785>
- da Silva PG, Bogoni JA, Heino J (2020) Can taxonomic and functional metrics explain variation in the ecological uniqueness of ecologically-associated animal groups in a modified rainforest? *Sci Total Environ* 708:3. <https://doi.org/10.1016/j.scitotenv.2019.135171>
- De Araujo ME, Lunardon-Branco MJ, Verani JR et al (2014) A trophic analysis of target species of macrobenthos in a subtropical coastal community: a taxa relationship essay. *Vie Milieu Life Environ* 64:35–46
- de Juan S, Hinz H, Sartor P et al (2020) Vulnerability of demersal fish assemblages to trawling activities: a traits-based index. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2020.00044>
- Dray S, Bauman D, Blanchet G et al (2020) *adespatial*: multivariate multiscale spatial analysis. R package version 0.3-8
- Folk RL, Ward WC (1957) Brazos River Bar: a study in the significance of grain size parameters. *J Sediment Petrol* 27:3–26
- Fox J (2020) *RcmdrMisc*: R commander miscellaneous functions. R package version 2.7-1.
- Franco ACS, Ramos Chaves MCN, Castel-Branco MPB, Neves Dos Santos L (2016) Responses of fish assemblages of sandy beaches to different anthropogenic and hydrodynamic influences. *J Fish Biol* 89:921–938. <https://doi.org/10.1111/jfb.12889>
- Heino J, Grönroos M (2017) Exploring species and site contributions to beta diversity in stream insect assemblages. *Oecologia* 183:151–160. <https://doi.org/10.1007/s00442-016-3754-7>
- Henriques S, Cardoso P, Cardoso I et al (2017) Processes underpinning fish species composition patterns in estuarine ecosystems worldwide. *J Biogeogr* 44:627–639. <https://doi.org/10.1111/jbi.12824>
- Hiddink JG, Jennings S, Sciberras M et al (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci USA* 114:8301–8306. <https://doi.org/10.1073/pnas.1618858114>
- Huntington BE, Karnauskas M, Babcock EA, Lirman D (2010) Untangling natural seascape variation from marine reserve effects using a landscape approach. *PLoS ONE* 5:e12327. <https://doi.org/10.1371/journal.pone.0012327>
- Kaiser MJ, Collie JS, Hall SJ et al (2002) Modification of marine habitats by trawling activities: prognosis and solutions. *Fish Fish* 3:114–136. <https://doi.org/10.1046/j.1467-2979.2002.00079.x>
- Knowlton N (2004) Multiple “stable” states and the conservation of marine ecosystems. *Prog Oceanogr* 60:387–396. <https://doi.org/10.1016/j.pocean.2004.02.011>
- Landeiro VL, Franz B, Heino J et al (2018) Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: evidence from multiple taxonomic groups. *Divers Distrib* 24:966–977. <https://doi.org/10.1111/ddi.12734>
- Lazzari N, Martín-López B, Sanabria-Fernandez JA, Becerro MA (2020) Alpha and beta diversity across coastal marine social-ecological systems: implications for conservation. *Ecol Indic* 109:105786. <https://doi.org/10.1016/j.ecolind.2019.105786>
- Leão H, Siqueira T, Torres NR, Montag LFA (2020) Ecological uniqueness of fish communities from streams in modified landscapes of Eastern Amazonia. *Ecol Indic*. <https://doi.org/10.1016/j.ecolind.2019.106039>
- Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecol Lett* 16:951–963. <https://doi.org/10.1111/ele.12141>
- Legendre P, De Cáceres M (2013) Appendix S3—details about the properties of dissimilarity coefficients—beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol Lett* 16:1–16
- Lindgren M, Holt BG, MacKenzie BR, Rahbek C (2018) A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Sci Rep* 8:1–8. <https://doi.org/10.1038/s41598-018-22419-1>
- Lotze HK, Lenihan HS, Bourque BJ et al (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* (80-) 312:1806–1809
- Lundquist CJ, Bowden D, Cartner K et al (2018) assessing benthic responses to fishing disturbance over broad spatial scales that incorporate high environmental variation. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2018.00405>
- Magurran AE, Henderson PA (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature* 422:714–716. <https://doi.org/10.1038/nature01547>
- Mantoura FA, Jeffrey SW, Llewellyn CA et al (1997) Comparison between spectrophotometric, fluorometric and HPLC methods for chlorophyll analysis. In: Jeffrey SW, Mantoura RFC, Wright SW (eds) *Phytoplankton pigments in oceanography*. UNESCO, Paris, pp 361–380
- Mark FC, Bock C, Pörtner HO (2002) Oxygen-limited thermal tolerance in antarctic fish investigated by MRI and 31P-MRS. *Am J Physiol Regul Integr Comp Physiol* 283:1254–1262. <https://doi.org/10.1152/ajpregu.00167.2002>
- Marra G, Wood SN (2011) Practical variable selection for generalized additive models. *Comput Stat Data An* 55:2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>
- McConnaughey RA, Mier KL, Dew CB (2000) An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J Mar Sci* 57:1377–1388. <https://doi.org/10.1006/jmsc.2000.0906>
- Menezes NA, Buckup PA, De Figueiredo JL, De Moura RL (2003) *Catálogo das Espécies de Peixes Marinhos do Brasil*
- Moore CH, Harvey ES, Van Niel K (2010) The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Mar Biol* 157:2717–2729. <https://doi.org/10.1007/s00227-010-1531-4>
- Paes ET, Moraes LES (2007) A new hypothesis on the influence of the El Niño/La Niña upon the biological productivity, ecology and fisheries of the Southern Brazilian Bight. *Panam J Aquat Sci* 2:94–102
- Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ*. <https://doi.org/10.7717/peerj.6876>
- Pereira MD, Schettini CAF, Omachi CY (2009) Caracterização de feições oceanográficas na plataforma de Santa Catarina através de imagens orbitais. *Rev Bras Geofísica* 27:81–93. <https://doi.org/10.1590/s0102-261x2009000100007>
- Piantkoski EL, da Costa RC, Davanzo TM et al (2021) Which environmental factors are most relevant to the distribution of *Sicyonia dorsalis* (Penaeoidea: Sicyoniidae) in an upwelling region? *Biologia (Bratisl)* 76:1753–1762. <https://doi.org/10.2478/s11756-020-00676-8>
- Pitman SJ, McAlpine CA (2003) Movements of marine fish and decapod crustaceans: process, theory and application. In: *Advances in marine biology*, pp 205–294
- Pozzobom UM, Heino J, BritoLandeiro MTSVL (2020) Untangling the determinants of macrophyte beta diversity in tropical floodplain lakes: insights from ecological uniqueness and species contributions. *Aquat Sci*. <https://doi.org/10.1007/s00027-020-00730-2>

- R Core Team (2020) R: a language and environment for statistical computing
- Ribó M, Macdonald H, Watson SJ et al (2021) Predicting habitat suitability of filter-feeder communities in a shallow marine environment, New Zealand. *Mar Environ Res* 163:105218. <https://doi.org/10.1016/j.marenvres.2020.105218>
- Rodrigues-Filho JL, Verani JR, Peret AC et al (2011) A influência da estrutura populacional e dos aspectos reprodutivos na abundância de espécies do gênero *Stellifer* (Oken, 1817) no litoral sul Brasileiro. *Brazil J Biol* 71:991–1002. <https://doi.org/10.1590/S1519-69842011000500019>
- Rodrigues-Filho JL, Branco JO, Monteiro HS et al (2015) Seasonality of ichthyofauna bycatch in shrimp trawls from different depth strata in the southern Brazilian coast. *J Coast Res* 31:378–389. <https://doi.org/10.2112/JCOASTRES-D-13-00024.1>
- Rodrigues-Filho JL, Couto ECG, Barbieri E, Branco JO (2016) Ciclos sazonais da carcinofauna capturada na pesca do camarão-sete-barbas, *Xiphopenaeus kroyeri* no litoral de santa catarina. *Bol Do Inst Pesca* 42:648–661. <https://doi.org/10.20950/1678-2305.2016v42n3p648>
- Rodrigues-Filho LJ, Dolbeth M, Bernardes JJ et al (2020) Using an integrative approach to evaluate shrimp bycatch from subtropical data-poor fisheries. *Fish Res* 230:105587. <https://doi.org/10.1016/j.fishres.2020.105587>
- Rondineli GR, BragaTutui FMSSLS, Bastos GCC (2007) Dieta de *Menticirrhus americanus* (Linnaeus, 1758) e *Cynoscion jamaicensis* (Vaillant e Bocourt, 1883)(Pisces, Sciaenidae) no sudeste do Brasil, Estado de São Paulo. *Bol Inst Pesca* 33:221–228
- Ruhí A, Detry T, Sabo JL (2017) Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conserv Biol* 31:1459–1468. <https://doi.org/10.1111/cobi.12906>
- Sabinson L, Rodrigues-Filho J, Peret A et al (2015) Feeding habits of the congeneric species *Stellifer rastrifer* and *Stellifer brasiliensis* (Acanthopterygii: Sciaenidae) co-occurring in the coast of the state of Santa Catarina, Brazil. *Brazil J Biol* 75:423–430. <https://doi.org/10.1590/1519-6984.15813>
- Santos MCF, Port D, Fisch F et al (2016) Biologia populacional de callinectes ornatus associada à pesca do camarão-sete-barbas, rio são francisco (Alagoas e Sergipe, Brasil). *Bol do Inst Pesca* 42:449–456. <https://doi.org/10.20950/1678-2305.2016v42n2p449>
- Santos LDN (2018) Aspectos da biologia populacional de *Nematopalaemon Schmitti* (Holthuis, 1950) e *Exhippolysmata Oplophoroides* (Holthuis, 1948) no litoral sul de Pernambuco. Universidade Federal de Pernambuco
- Schettini CA, Carvalho JL (2010) Hidrodinâmica E Distribuição De Sólidos Em Suspensão No Estuário Do Rio Itajaí-Açu [Relatório]. *Brazil J Aquat Sci Technol* 2:131. <https://doi.org/10.14210/bjast.v2n1.p131-140>
- Sedrez MC, Branco JO, Júnior FF et al (2013) Ictiofauna acompanhante na pesca artesanal do camarão sete barbas (*Xiphopenaeus kroyeri*) no litoral sul do Brasil. *Biota Neotrop* 13:165–175. <https://doi.org/10.1590/S1676-06032013000100019>
- Sedrez MC, Barrilli GHC, Fragoso-moura EN et al (2021) Feeding habits of *Paralonchurus brasiliensis* (Perciformes: Scianidae) from South of Brazil. *Acta Biol Colomb* 26:333–342
- Simpson JH (1981) The shelf-sea fronts: implications of their existence and behaviour [and discussion]. *Philos Trans R Soc Lond* 302:531–546
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? *Trends Ecol Evol* 31:67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Soininen J, Lennon JJ, Hillebrand H (2007) A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88:2830–2838. <https://doi.org/10.1890/06-1730.1>
- Sor R, Legendre P, Lek S (2018) Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the Lower Mekong Basin. *Ecol Indic* 84:425–432. <https://doi.org/10.1016/j.ecolind.2017.08.038>
- Statistics A (2010) Generalized additive model selection by Alexandra Chouldechova and Trevor Hastie * Carnegie Mellon and Stanford University, pp 1–24
- Stuart-Smith RD, Edgar GJ, Bates AE (2017) Thermal limits to the geographic distributions of shallow-water marine species. *Nat Ecol Evol* 1:1846–1852. <https://doi.org/10.1038/s41559-017-0353-x>
- Suguio K (1973) Introdução à sedimentologia. Editora da USP, São Paulo
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45. <https://doi.org/10.3354/meps318031>
- Whittaker RH (1972) Evolution and Measurement of Species Diversity. *Taxon* 21:213–251
- Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. CRC Press, Bristol
- Wood SN, Pya N, Säfken B (2016) Smoothing parameter and model selection for general smooth models. *J Am Stat Assoc* 111:1548–1563. <https://doi.org/10.1080/01621459.2016.1180986>
- Wu K, Zhao W, Li M et al (2020) Taxonomic dependency of beta diversity components in benthic communities of bacteria, diatoms and chironomids along a water-depth gradient. *Sci Total Environ* 741:140462. <https://doi.org/10.1016/j.scitotenv.2020.140462>
- Yasuhara M, Yamazaki H (2005) The impact of 150 years of anthropogenic pollution on the shallow marine ostracode fauna, Osaka Bay, Japan. *Mar Micropaleontol* 55:63–74. <https://doi.org/10.1016/j.marmicro.2005.02.005>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.