



Environmental filtering and spatial structure drive nestedness–turnover dynamics in bivalve mollusk metacommunities in the Atlantic continental margin of South America, Brazil

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Abstract

Species distributions along environmental gradients may exhibit nestedness, turnover, or clumping patterns. In environments subject to strong environmental variability, such as continental shelves, environmental filters exert a decisive influence on community composition, which may alternate across seasonal periods, leading to temporal variations in the structure and diversity of marine communities. This study aimed to investigate the organizational patterns of the metacommunity at small (north, central, and south sectors) and large spatial scales (continental margin) during two seasonal periods along a depth gradient on the northeastern Brazilian continental margin. Taxonomic α -diversity was higher in the southern sector and during the rainy periods. β -Diversity did not differ among sectors, but species composition exhibited high dissimilarity, particularly between the northern–southern and central–southern sectors, reflecting stronger species turnover during the rainy season, whereas richness differences predominated in the dry period. The metacommunity structure along the environmental gradient was predominantly Gleasonian at smaller spatial scales, with individualistic species responses and gradual shifts in composition, whereas quasi-Clementsian patterns emerged at broader scales, revealing groups of species with similar distributional limits and abrupt compositional changes. The metacommunity was primarily structured by environmental filters, with depth and gravel as the main predictors. Spatial processes had a limited influence and were associated with dispersal limitation, whereas most of the variation remained unexplained by the measured variables. Overall, the results indicate that environmental filtering (depth and gravel) constitutes the primary structuring mechanism, acting in conjunction with large-scale spatial effects associated with dispersal limitation and mass effects acting at smaller-scales.

Keywords Dispersal limitation · Mollusca · Northeastern Brazil · Species sorting

Introduction

Benthic communities play a fundamental ecological role in marine and coastal ecosystems, contributing to nutrient cycling, sediment structuring, and trophic dynamics. The distribution of benthic species along environmental gradients (such as depth, salinity, substrate type, and organic matter availability) reflects the interactions among environmental filters, dispersal, and biotic interactions (Levin et al. 2001; Corte et al. 2018). Distribution patterns may vary continuously or discretely along these gradients, revealing structural arrangements, such as nestedness, species turnover, or clumping. In areas subject to strong environmental gradients, such as continental shelves, estuaries, and transition zones between marine and freshwater environments, community structuring often reflects intense environmental

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filtering (Chase and Leibold 2003; Muehe and Garcez 2005; Heino et al. 2015; Souza et al. 2025). Depth gradients directly influence factors such as pressure, light availability, temperature, and sediment grain size, thereby affecting the spatial distribution of benthic organisms (Rex and Etter 2010; Young et al. 2022). In addition to spatial variation, the distribution of benthic species is shaped by seasonal fluctuations, particularly those associated with rainfall dynamics in tropical regions (Checon et al. 2023). The alternation between dry and rainy seasons modifies physical processes, such as turbidity, nutrient input, and sediment transport, which can alter community composition and structure (Alongi 1990).

The bivalves constitute a pivotal component of benthic ecosystems, functioning as suspension feeders that mediate organic-matter fluxes, engineer habitat structure, and support trophic dynamics (Newell and Koch 2004; Soares-Gomes and Pires-Vanin 2005; Nascimento and Rosso 2007; McKeon et al. 2015; Santos et al. 2020). Their shells provide hard substrata in otherwise soft-sediment environments, increasing habitat complexity and fostering the biodiversity. The spatial distribution of bivalve assemblages is strongly modulated by environmental filters. Salinity gradients, for example, often exert the principal influence on estuarine bivalve communities, superseding sediment type, turbidity, and temperature (McKeon et al. 2015). Salinity, temperature, and food supply also structure bivalve morphology and community composition, with distinct morphological assemblages among these environmental gradients (Telesca et al. 2018). Moreover, large-scale gradients, such as depth, dissolved oxygen, light penetration, and nutrient availability, have been shown to explain the occurrence patterns of bivalve fauna across marine benthic zones (Saeedi et al. 2022). Spatial processes, including limited dispersal and connectivity, further shape bivalve metacommunities by interacting with environmental heterogeneity; consequently, bivalve distributions reflect the joint action of local abiotic constraints and regional spatial dynamics (D'Alessandro et al. 2025).

In this context, metacommunity theory has been widely applied to understand how environmental and spatial factors shape species distributions (Leibold et al. 2004; Presley et al. 2010). This theoretical framework provides a robust conceptual basis for integrating multiple dimensions of ecological structuring, positing that local communities are interconnected through species dispersal and are organized by the interaction between local and regional processes (Leibold and Mikkelsen 2002; Leibold et al. 2004). Applications of metacommunity models have revealed recurring structural patterns, such as nestedness, species turnover, and clumped species distributions, each reflecting distinct ecological mechanisms (Soininen et al. 2007; Presley et al. 2010; Alves et al. 2020). Nested structures often indicate strong environmental filtering,

whereas high turnover suggests environmental heterogeneity. Thus, metacommunity theory represents a powerful framework for understanding the factors that shape biodiversity in both tropical and temperate aquatic systems, enabling integrative analyses of the spatial and temporal structuring of benthic fauna (Winegardner et al. 2012; Alves et al. 2020).

These patterns are also affected by spatial processes, such as habitat connectivity and dispersal limitation, which regulate organismal flow and colonization potential among sites (Palmer et al. 1996; Li et al. 2022). This perspective is particularly relevant in benthic marine systems, where many taxa exhibit low mobility and high dependence on specific environmental conditions (Heino et al. 2015; Corte et al. 2018), especially in continental shelf habitats characterized by pronounced spatial heterogeneity and habitat diversification (Souza et al. 2025). Moreover, seasonal fluctuations are one of the primary climatic factors modulating the dynamics of coastal and marine ecosystems, especially in tropical regions where rainfall regimes are highly seasonal (Corte et al. 2018; Checon et al. 2023). Precipitation events directly influence coastal hydrodynamics, freshwater inflows, and sediment and nutrient loads delivered to marine systems from adjacent river basins (Alongi 1998).

Therefore, this study aimed to investigate the metacommunity organization patterns of bivalve mollusks at both small (north, central, and south sectors) and large (continental margin) scales across two seasonal periods (dry and rainy) on the northeastern Brazilian continental margin. Considering that seasonal events, such as increased rainfall and freshwater discharge, modify the sediment distribution and salinity on the shelf, we propose the following hypotheses (Fig. 1):

Hypothesis 1 (H_1): Seasonal α -diversity of bivalve communities will decrease during the rainy season compared with the dry season, due to increased sediment homogenization and reduced salinity. Conversely, spatial α -diversity will remain constant among sectors during the rainy period owing to homogeneous spatial environmental conditions across sectors under greater hydrological influence (rainfall) throughout the continental shelf. In contrast, during the dry period, higher α -diversity will occur in the northern and southern sectors due to greater environmental heterogeneity associated with gravelly sediments in these areas.

Hypothesis 2 (H_2): During the dry season, spatial β -diversity will increase, particularly in the northern sector, which is associated with higher environmental heterogeneity linked to the carbonate–terrigenous facies of southern Alagoas.

Hypothesis 3 (H_3): At larger spatial scales (e.g., continental margins), Clementsian metacommunity structures will prevail because of species sorting and dispersal limitations, whereas at smaller scales (e.g., sectors), communities will

Fig. 1 Map of the study area showing sampling stations and transects on the continental shelf between the southern portion of the state of Alagoas (AL) and the state of Sergipe (SE) during oceanographic campaigns conducted in February and July 2011 (map of the study area modified from Carneiro and Arguelho 2018). A–H are transects. Hypothesis 1 (H1)–hypothesis 3 (H3) represent the hypotheses and predictions described in the “Introduction” section

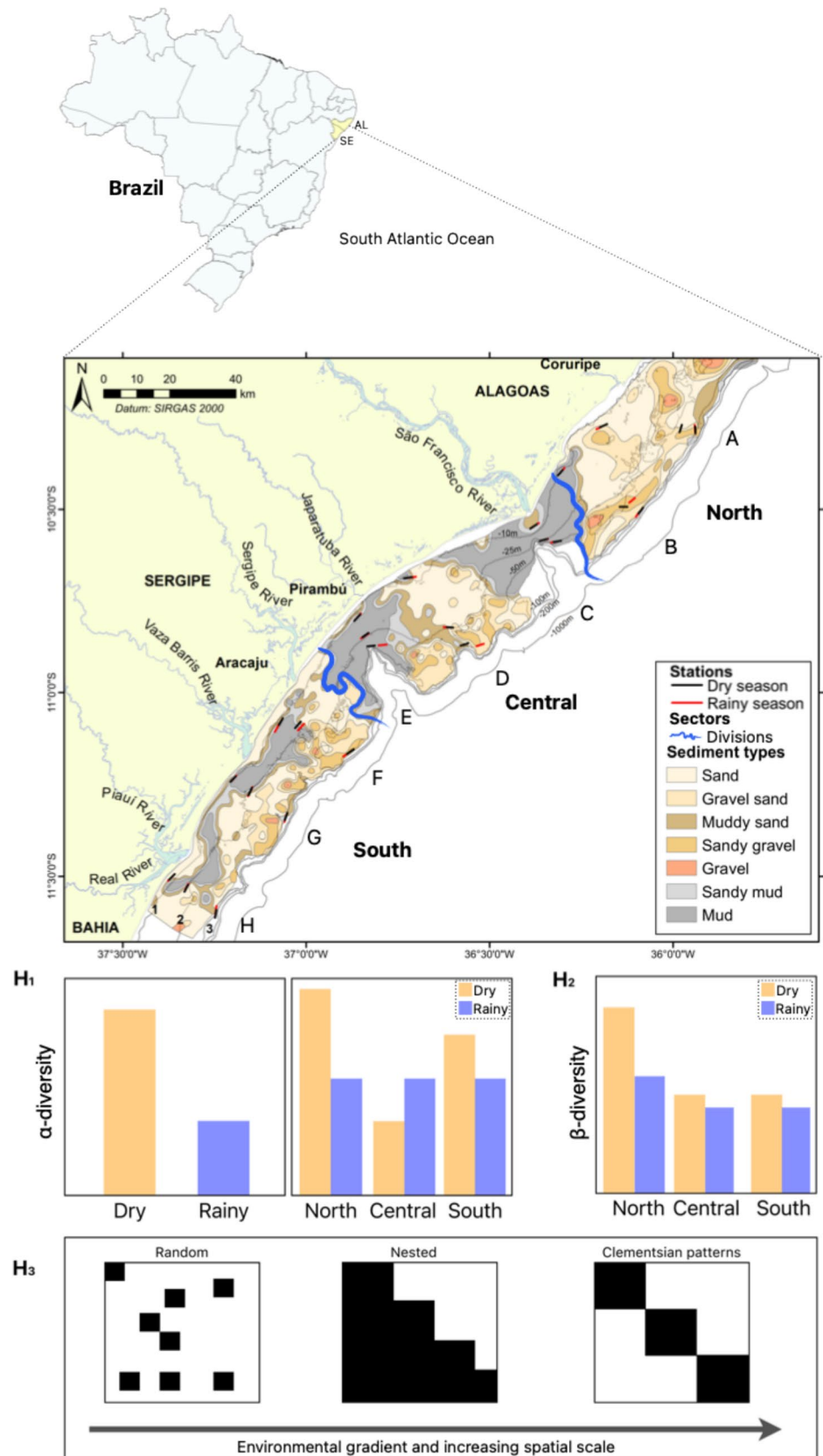


exhibit random distributions driven by mass effects at fine spatial resolutions.

Materials and methods

Study area

The study area encompasses a portion of the continental shelf off northeastern Brazil, located along the Sergipe–Alagoas (SEAL) continental margin (Fig. 1). This shelf lies within the Tertiary Coast of eastern Brazil, characterized by the Barreiras Formation on the continent, and forms a part of the broader northeastern region. However, it represents a transitional zone between the carbonate shelf dominated by calcareous algae typical of the Northeast and a well-defined sector exhibiting distinct physiographic and biogeochemical characteristics compared with adjacent regions (Knoppers et al. 2018). The Alagoas continental shelf displays an irregular and heterogeneous relief composed of various sedimentary environments, including fluvial deposits, Holocene and Pleistocene marine terraces, carbonate sediments, calcareous sands, mud, algal and coral reefs, and sandstones (Fontes et al. 2017). In contrast, the Sergipe shelf is strongly influenced by fluvial inputs, particularly from the São Francisco River estuary to the north and the Japarutuba, Sergipe, Vaza-Barris, and Piauí–Fundo–Real river systems to the south (Guimarães 2010; Knoppers et al. 2018). The seabed is predominantly composed of fine terrigenous sediments, with sandy bottoms in coastal areas and increasing gravel content in deeper zones (Guimarães 2010; Fontes et al. 2017). Based on an integrated analysis of geomorphological (seafloor morphology, bathymetry, and slope), sedimentological (texture, composition, and bioclasts), and carbonate content data, Fontes et al. (2017) categorized this portion of the northeastern Brazilian continental margin into five provinces. Following this framework, the present study divided the Sergipe–Alagoas continental margin into three sectors: north (carbonate–terrigenous and muddy–terrigenous [sand predominance]), central (muddy–terrigenous and terrigenous–carbonate [mud predominance from the São Francisco and Japarutuba river with a muddy sand patch toward the central]), and south (terrigenous–carbonate [sand predominance, with patches of gravelly sand and gravel in more distant coastal areas]) (Fig. 1).

Sampling design and sample processing

For sample collection, eight transects perpendicular to the coastline (A–H) and 24 sampling stations were established along a depth gradient (10–55 m) (grouped into three depth categories 10, 25, and 50 m to represent different depth zones), covering three sectors (north, central, and

south) of the Sergipe–Alagoas continental margin (Fig. 1; Table S1). Samples were obtained during two oceanographic surveys conducted in the dry (February 2011) and rainy seasons (July 2011). At each sampling station, a single bottom trawl was performed (totaling 24 samples per seasonal period) using fishing vessels equipped with nets of different dimensions and mesh sizes: 50 mm in the wings, 40 mm in the body, and 26 mm in the cod end (Carneiro and Arguelho 2018). Trawls were conducted during daylight hours and lasted approximately 30 min each, at speeds between 2 and 2.5 knots, and were oriented opposite to the prevailing marine current. The coordinates provided (Table S1) represent the midpoints between the start and end of each trawling.

Samples were initially examined visually to remove macroalgae-associated organisms. Subsequently, the organisms were sorted into major taxonomic groups under a stereomicroscope and preserved in 70% ethanol. Mollusks were separated from the remaining fauna and examined using a Leica EZ4 stereomicroscope. Bivalvia specimens were isolated from other mollusks and identified to the lowest possible taxonomic level based on specialized literature (Mikkelsen and Bieler 2008; Rios 2009). Only complete individuals (i.e., those with shells and soft parts) were considered in this study. The taxonomic nomenclature of the identified species was updated according to the World Register of Marine Species (<https://www.marinespecies.org>). All identified materials were deposited in the Zoological Collection of the Federal University of Sergipe (CZUFS) (see voucher numbers in Santos et al. 2020).

During faunal sampling, sediment samples were also collected using two different devices because of the wide facies variability observed on the continental shelf of the Sergipe–Alagoas continental margin. The collected sediment was used to determine the grain-size composition (mud, sand, and gravel contents). Thus, on bottoms dominated by coarse fractions or covered by rhodoliths, a modified van Veen grab with dimensions of 92 × 80 × 40 cm was employed, whereas in bottoms dominated by fine fractions, a box corer measuring 50 × 50 × 50 cm was used. The samples were bagged and preserved on ice until laboratory processing. At the end of each sediment sampling, an oceanographic conductivity, temperature, and depth (CTD) profiler mounted on a rosette was deployed for in situ measurements of temperature, salinity, and depth.

In the laboratory, sediment samples were desalinized and oven-dried at 60 °C. Subsequently, they were subjected to dry sieving for the sand and gravel fractions (> 63 µm) and pipette analysis for the mud fraction (< 63 µm) (Suguio 1973). The results of the granulometric analyses were processed using the SYSGRAM software (Camargo 2005), which applies the formulations of Folk and Ward (1957) in Suguio (1973) to obtain sediment statistical parameters,

including mean grain size (Φ), standard deviation, skewness, and kurtosis.

Data analysis

Environmental characterization

Initially, to assess the differences in environmental variables among sectors, seasonal periods, and depth categories, we applied a permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance matrices calculated from the values of each environmental variable. PERMANOVA statistically tests whether the centroids of each group (seasonal period, sectors, and depth categories) in multivariate space differ significantly ($p < 0.05$), using p -values obtained through 9999 permutations with the function *adonis2* (Anderson et al. 2006; Oksanen et al. 2025). Subsequently, principal component analysis (PCA) was performed to visualize the influence of environmental variables across depth categories, sectors, and seasonal periods, as well as habitat diversity along the Alagoas–Sergipe continental shelf. Using the same matrix, we conducted a permutational analysis of multivariate dispersions (PERMDISP; Anderson et al. 2006) to determine whether dispersion (or variability) among groups was homogeneous, employing the function *betadisper*. Multivariate dispersion was represented by box plots of distances to group centroids.

These analyses were performed using the *vegan* package (Oksanen et al. 2025), *FactoMineR* (Le et al. 2008), and *factoextra* (Kassambara and Mundt 2020), and graphical representations were generated using the *ggplot2* package (Wickham 2016), all within the R software environment (R Core Team 2025).

Spatio-temporal patterns of α -diversity and β -diversity

To test the hypothesis (H_1) that the taxonomic α -diversity of bivalve communities decreases during the rainy season compared with the dry season and is higher in the northern and southern sectors during the dry period, species richness was estimated for each sampling site. Differences between seasonal periods (dry versus rainy) and among sectors within each period (north, central, and south) were assessed using generalized linear models (GLMs) with a quasi-Poisson distribution. These models were employed to evaluate both seasonal and spatial variation, specifically comparing the dry and rainy seasons, as well as the sectors within each respective season. Model-adjusted richness estimates were visualized using log-transformed box plots for each season and sector. Samples with zero total abundance were removed from the analyses.

To test the hypothesis (H_2) that β -diversity would be higher during the dry season and in the northern sector, a

species abundance matrix was used to perform a permutational multivariate dispersion (PERMDISP) analysis (Anderson et al. 2006) via the “*betadisper*” function in the *vegan* package. From this analysis, both multivariate dispersion and the average distance to the centroid were calculated for each group (sectors and seasonal periods) using the Bray–Curtis dissimilarity metric. Differences in distances to centroids ($p < 0.05$) among groups were assessed using the “*permutest*” function from the *vegan* package. In these analyses, higher or lower dispersion was interpreted as indicative of greater or lesser diversity, respectively. Additionally, variation in species composition was investigated by partitioning diversity into two components—richness difference (β_{rich}) and species replacement (β_{repl})—using the “*beta*” function, with Bray–Curtis dissimilarity applied to the species abundance data. This partitioning was performed separately for each seasonal period to estimate the relative contribution of each component to the total β -diversity (β_{total}) among sectors.

Elements metacommunity structure

To test the hypothesis (H_3) that Gleasonian metacommunity structures would emerge at broader spatial scales (i.e., continental margin) and random structures at finer spatial scales (i.e., sectors) during the dry season, we employed the analytical framework originally proposed by Leibold and Mikkelsen (2002) and later refined by Presley et al. (2010). This framework integrates three core metrics (coherence, species turnover, and boundary clumping) to identify non-random distributional patterns among species and infer the ecological processes underlying metacommunity organization (Fig. 2).

Coherence was first assessed by quantifying the number of embedded absences (unexpected gaps in species distribution) in a site-by-species incidence matrix ordered using reciprocal averaging. Statistical significance was evaluated against a null distribution generated from 1000 randomized matrices based on the “*r1*” null model, which preserved both site richness (row sums) and species occupancy (column totals), as recommended by Presley et al. (2010). A significantly lower number of embedded absences than expected under the null model indicated positive coherence, suggesting that species distributions are structured along shared environmental or spatial gradients.

When coherence was significant, we evaluated species turnover, defined as the number of direct substitutions of one species for another between adjacent sites in the ordered matrix. Significant turnover reflects a nonrandom variation in community composition along the gradient. Boundary clumping was subsequently examined to assess whether species’ range limits were aggregated, randomly distributed, or evenly spaced. Morisita’s index (MI) was used to quantify

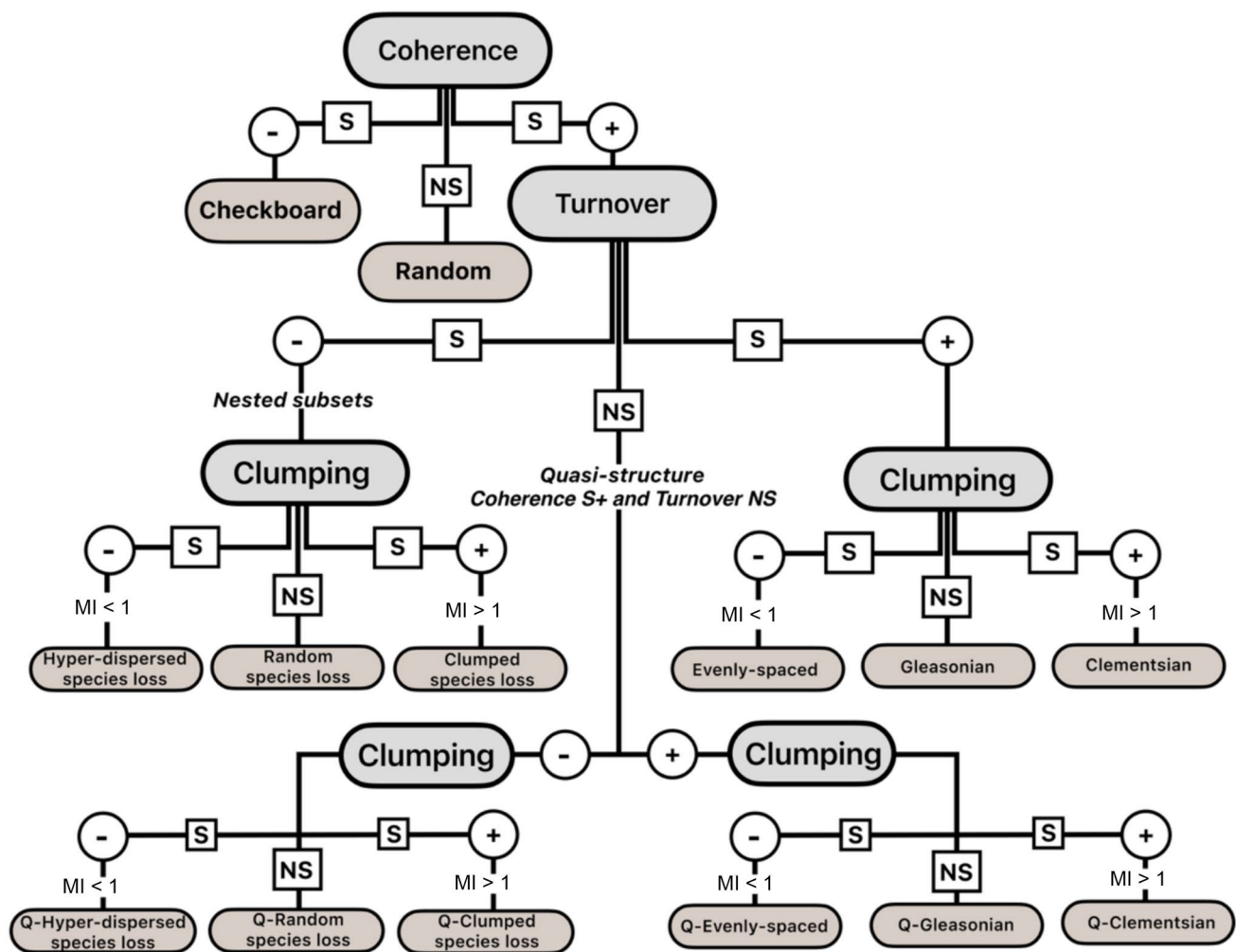


Fig. 2 Schematic representation used to examine how Elements of Metacommunity Structure (EMS; i.e., coherence, turnover, and boundary clumping) results in six main metacommunity structures (i.e., checkerboards, random, nested, evenly spaced, Gleasonian, and Clementsian) and quasi-structures (when coherence is positive

and significant but turnover is nonsignificant). A plus sign (+) indicates positive, and a minus sign (−) indicates negative. MI, Morisita's index value; S, significant; NS, nonsignificant. Modified from Leibold and Mikkelsen (2002) and Presley et al. (2010)

this pattern, where $MI > 1$ indicates clumped boundaries (Clementsian structure), $MI \approx 1$ suggests random distributions (Gleasonian structure), and $MI < 1$ denotes evenly spaced boundaries. The significance of the MI values was tested against a null model.

The integration of these three metrics allowed the classification of metacommunity structures into distinct idealized types, following Presley et al. (2010): Clementsian (positive coherence, positive and significant turnover, $MI > 1$), evenly spaced boundaries (positive coherence, negative and significant turnover, $MI < 1$), Gleasonian (positive coherence, positive and significant turnover, nonsignificant MI), nested (positive coherence, negative and significant turnover), random (nonsignificant coherence), and checkerboard (negative coherence) (Fig. 2). All analyses were conducted using the *Metacommunity* function in the *metacom* package

(Dallas 2020) with 1000 permutations for null model testing. Abundance data were converted to binary presence–absence matrices (presence = 1; absence = 0) to meet analytical assumptions, and data processing was performed using the *tidyverse* and *vegan* packages (Oksanen et al. 2025).

All analyses were conducted in R using the *vegan* (Oksanen et al. 2025) and *bipartite* (Dormann et al. 2009) packages.

Environmental and spatial predictors

To address the last part of our third hypothesis (H_3), which predicted large-scale environmental filtering (continental margin [CM]) while at smaller spatial scales (e.g., sectors), communities would be driven by mass effects, a redundancy analysis (RDA) was conducted. Distinct sets

of environmental and spatial predictors were constructed. Environmental variables included in situ measurements of physicochemical parameters (e.g., salinity and temperature) and habitat descriptors (e.g., sediment grain size and organic matter content), all of which were standardized using z-transformation to mitigate scale-related biases. Spatial predictors were derived from the geographic coordinates of the sampling sites using distance-based Moran's eigenvector maps (dbMEM), a method that captures spatial structures across multiple scales based on spatial autocorrelation (Borcard and Legendre 2002). A truncated Euclidean distance matrix was initially computed from the site coordinates, and dbMEM eigenvectors representing spatial patterns from broad to fine scales were generated using the *dbmem* function from the *adespatial* package in R (Dray et al. 2025). Only positive eigenvectors exhibiting significant positive spatial autocorrelation (Moran's $I > 0$) were retained for further analysis. Temporal predictors were represented by the seasonal period (dry and rainy seasons), which was treated as a categorical factor to account for cyclical variations in community structure. To reduce model complexity and prevent overfitting, a forward selection procedure (*forward.sel* function) was used to identify the most informative spatial variables.

The relative influence of environmental, spatial, and temporal predictors on species composition was quantified using variation partitioning based on RDA, as described by Borcard et al. (1992) and Peres-Neto et al. (2006). This method decomposes the total variation in the community matrix into distinct fractions explained exclusively by environmental variables (E), spatial variables (S), and seasonal factors (T), as well as their shared variations (e.g., $[E \cap S]$, $[E \cap T]$, $[S \cap T]$, and $[E \cap S \cap T]$) and the unexplained residual fraction (R). Species composition data were Hellinger-transformed using the *decostand* function in *vegan*, which is appropriate for community data with many zeros. This framework allows the testing of ecological hypotheses regarding the predominance of environmental filtering, spatial structuring, seasonality, or their joint influence on community composition. All RDAs and variation partitioning

analyses were conducted using the *rda* and *varpart* functions from the *vegan* package in R (Oksanen et al. 2025).

Results

Environmental characterization

The sediment composition along the SEAL continental margin revealed a predominance of muddy and sandy sediments, with a low occurrence of gravel. Mud content exhibited wide variation, with the highest concentrations observed at depths of 10 m (58.1%) and 50 m (49.9%) during the dry season, and at depths of 10 m (61.9%) and 25 m (49.5%) during the rainy season. Higher mud proportions were also recorded in the central and southern sectors across both seasonal periods, whereas gravel content was predominant in the northern and southern sectors during the dry and rainy seasons, respectively (Table 1).

Distinct environmental characteristics were observed along the SEAL continental margin, leading to environmental stratification based on the physicochemical properties of the sediments. Significant differences in environmental variables were detected among the depth categories (PERMANOVA; pseudo- $F = 3.82$; $p = 0.02$) and sectors (PERMANOVA, pseudo- $F = 3.92$; $p = 0.02$) (Table S2). This variation between groups in PERMANOVA was associated with multivariate dispersion effects (PERMDISP; $p < 0.05$). Additionally, no significant environmental variation was observed between the seasonal periods (dry and rainy). Based on the first two axes of the PCA, principal component (PC) 1 explained 49.1% of the total variance in the data, and PC2 accounted for 27.9%. A clear separation among the depth category was observed, with the 50 m depth being more strongly influenced by higher levels of salinity and gravel content. In contrast, the 10 m depth was more closely associated with high temperature values, mainly in the northern portion, and mud in the southern and central sectors. The 25 m depth categories showed a high concentration of mud in the central sector and gravel in northern sector (Fig. 3).

Table 1 Environmental variables measured during oceanographic campaigns conducted on the Sergipe–Alagoas continental margin, NE Brazil, to sample bivalve mollusks

Factor	Dry				Rainy			
	Temp	Sal	Mud	Gravel	Temp	Sal	Mud	Gravel
10 m	27.6 ± 0.6	37.0 ± 0.1	58.1 ± 41.5	4.75 ± 13.4	26.6 ± 0.1	36.4 ± 0.2	61.9 ± 46.0	0.0 ± 0.1
25 m	27.0 ± 0.6	37.1 ± 0.0	39.0 ± 46.2	14.3 ± 23.4	26.5 ± 0.0	37.1 ± 0.0	49.5 ± 40.7	8.5 ± 17.5
50 m	26.1 ± 1.0	37.2 ± 0.0	49.9 ± 43.5	17.3 ± 20.4	25.9 ± 0.4	37.3 ± 0.1	36.1 ± 42.6	24.9 ± 33.5
North	27.7 ± 1.2	37.1 ± 0.1	34.6 ± 42.1	26.7 ± 23.8	26.6 ± 0.4	37.1 ± 0.6	1.9 ± 45.3	3.6 ± 31.7
Central	26.8 ± 1.1	37.1 ± 0.0	64.3 ± 43.3	6.0 ± 13.9	26.2 ± 0.5	37.0 ± 0.3	70.8 ± 39.3	4.5 ± 12.8
South	26.6 ± 0.6	37.1 ± 0.1	42.8 ± 41.6	9.85 ± 19.0	26.4 ± 0.1	36.9 ± 0.3	37.1 ± 39.6	11.0 ± 26.7

Values represent mean ± standard deviation. Temperature is in celcius (°C); salinity in ppm; mud in percentage (%); gravel in percentage (%). SP, seasonal period; Temp, temperature; Sal, salinity

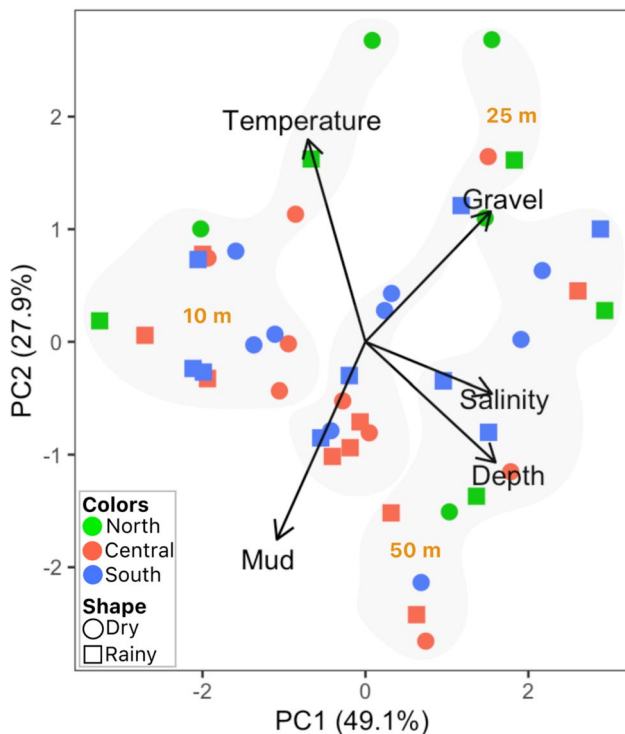


Fig. 3 Principal component analysis (PCA) based on environmental variables of bottom water and sediment between sectors (north, central, and south), depth category (10, 25, and 50 m), and seasonal periods (dry and rainy) on the Sergipe–Alagoas continental shelf, NE Brazil. The data were then transformed by $\log_{(x+1)}$. PC1, principal component 1; PC2, principal component 2

Analyses of dispersion effects, which reflect environmental heterogeneity within each depth category and sector, revealed that the 50 m depth (PERMDISP, pseudo- $F = 2.25$; $p = 0.001$) and central and southern sectors in the dry seasonal period and the northern sector in the rainy period (PERMDISP, pseudo- $F = 2.29$; $p = 0.04$) exhibited the highest multivariate dispersions, indicating greater environmental heterogeneity in these areas (Fig. 4). The dispersion effect between seasonal periods did not show significant variation (Fig. S1; Table S3).

Spatiotemporal patterns of α -diversity and β -diversity

The fauna of bivalve mollusks comprise 1384 individuals and 45 species; 276 individuals were recorded during the dry period, and 1108 during the rainy period. The southern sector presented the highest abundance (Table 2; Fig. S2). Taxonomic α -diversity of bivalve mollusks did not differ among the northern, central, and southern sectors during the dry season (GLM; $p = 0.64$; Fig. 5a; Table S4). However, during the rainy season, the southern sector exhibited higher α -diversity (GLM; $p = 0.04$; Fig. 5b; Table S4). Seasonally,

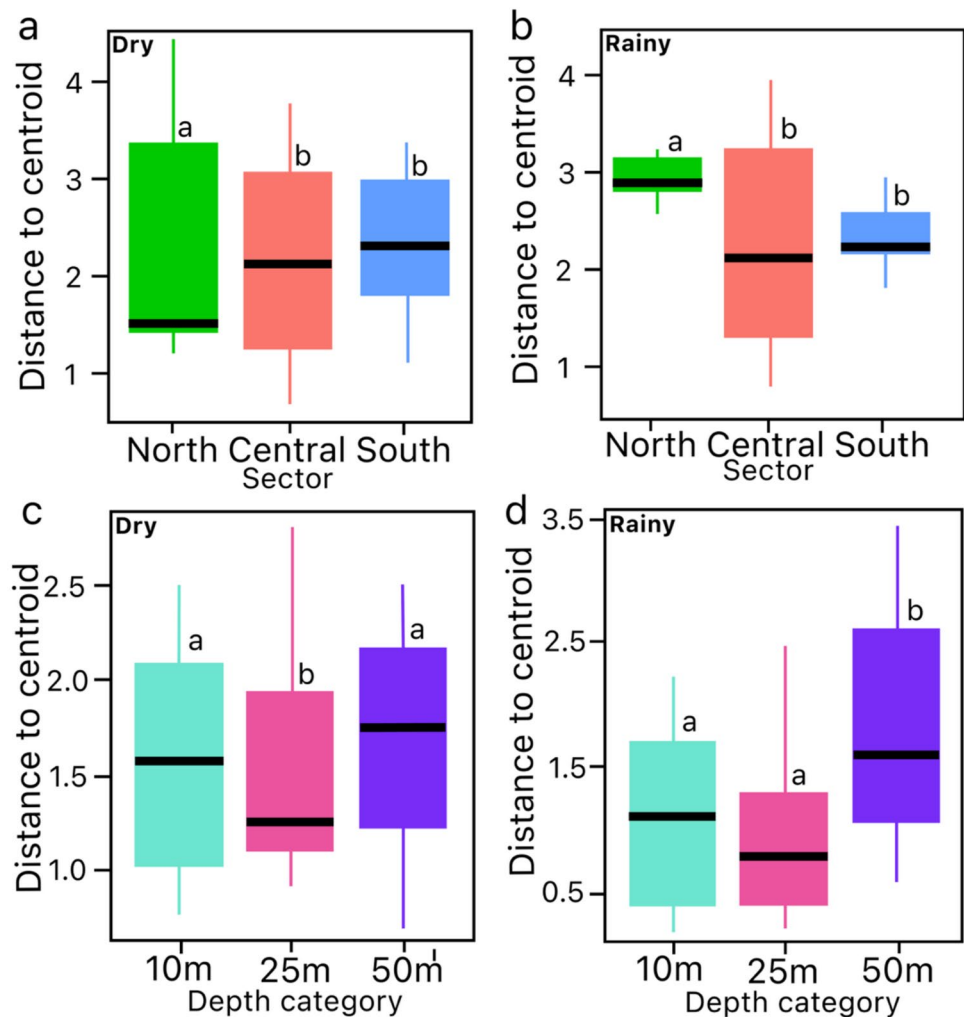
α -diversity was higher during the rainy period (Fig. 5c; Table S4).

The magnitude of β -diversity did not differ significantly among sectors or between seasonal periods, revealing similar amplitudes in internal variation rates across groups (PERMDISP; $p > 0.05$; Fig. 5d–f; Table S5). However, species composition among the sectors showed high total dissimilarity, revealing differences between sectors based on pairwise comparisons (Table 3). During the dry period, β -diversity among sectors was high, with the greatest dissimilarity observed between the north–south sectors ($\beta_{\text{total}} = 0.93$). Partitioning of β -diversity revealed that differences between the north–central sectors were mainly attributed to species turnover ($\beta_{\text{repl}} = 0.62$), whereas differences between the north–south ($\beta_{\text{rich}} = 0.60$) and central–south ($\beta_{\text{rich}} = 0.74$) sectors were more related to variations in species richness (Table 3). During the rainy period, the greatest dissimilarity was observed between the central–south sectors ($\beta_{\text{total}} = 0.92$), followed by the north–central ($\beta_{\text{total}} = 0.87$) and north–south ($\beta_{\text{total}} = 0.79$) sectors. This variation was mainly explained by species turnover ($\beta_{\text{repl}} = 0.91$ between central and south), indicating marked changes in species composition along the spatial gradient. In contrast, the difference between the north and south sectors was more closely related to variations in species richness ($\beta_{\text{rich}} = 0.64$), reflecting a nestedness pattern (Table 3).

Elements metacommunity structure

The metacommunity structure of bivalve mollusks exhibited consistent patterns across the dry and rainy seasons, although the intensity of the structural signals varied. Based on the Elements of Metacommunity Structure (EMS) framework, four idealized patterns were identified (Table 4; Fig. 6). Among these, the most frequent metacommunity structure observed along the SEAL continental margin was Gleasonian ($N = 3$), followed by quasi-Clementsian ($N = 2$), nested with clumped species loss ($N = 2$), and Clementsian ($N = 1$) structures (Table 4; Figs. S3–S4). In all communities, species distributions were positively coherent (Coh $Z < 0$; $p < 0.001$), indicating that the number of embedded absences (EmbAbs) was significantly lower than expected by chance (Table 4), likely in response to underlying environmental gradients. Furthermore, the second stage of the EMS analysis (Fig. 2) showed that turnover was significant ($p < 0.05$) in 50% of the cases (four out of eight), indicating that, along the environmental or spatial gradient, species disappeared and others appeared; turnover was predominantly positive, meaning that species replacement was greater than expected by chance (Table 4). The third stage of the analysis, concerning boundary clumping (Fig. 2), revealed that the Morisita index was significant ($p < 0.005$), greater than 1 in most cases (5), suggesting positively clumped

Fig. 4 Spatial environmental heterogeneity for sectors (north, central, and south) and depth category (10, 25, and 50 m) during the dry (a and c) and rainy (b and d) seasonal periods on the Sergipe–Alagoas continental margin, NE Brazil. Plots a, c, and e represent principal coordinates analysis (PCoA) based on Euclidean distances. Box plots b, d, and f show the distances of the samples to the centroid of each sector (PERMDISP). The data were then transformed by $\log_{(x+1)}$



species distributions, which are typical of Gleasonian, Clementsian, and quasi-Clementsian structures (Figs. S3–S4). Overall, these patterns fluctuated among the sectors and seasonal periods. During the dry season, EMS patterns were *Q*-nested in the northern sector, Gleasonian in the central sector, and Clementsian in the southern sector, whereas the continental margin exhibited a quasi-Clementsian pattern (Table 4). During the rainy season, a partial shift in patterns was observed, with the northern and central sectors exhibiting Gleasonian structures and the southern sector displaying a quasi-nested structure. The quasi-Clementsian pattern persisted along the continental margin (Table 4; Fig. 6).

Environmental and spatial filtering

Redundancy analysis (RDA) applied to the global spatial model were statistically significant (RDA; $p < 0.05$). The environmental component also demonstrated statistical significance (RDA; $p < 0.05$) (Table S6). Variance partitioning among environmental, spatial, and seasonal components revealed that the environmental fraction was the most

substantial ($[E] = 0.14$), highlighting the direct influence of environmental filters on metacommunity structure. In contrast, the shared fraction between the environmental and spatial components was minimal ($[E \cap S] = 0.03$), indicating that only a small portion of the environmental effect was spatially structured (Fig. 7). Nevertheless, the majority of the variation remained unexplained (78%), suggesting the influence of stochastic processes or unmeasured variables (Fig. 7). The purely spatial fraction accounted for 4% ($[S] = 0.04$), implying that autonomous spatial processes, such as mass effects or environmental homogenization, exert a limited influence on species distribution.

Depth ($F = 3.52$; $p = 0.002$; adjusted $R^2 = 0.15$) and gravel content ($F = 5.33$; $p = 0.001$; adjusted $R^2 = 0.11$) were identified as the main environmental predictors of variation in bivalve metacommunity composition, indicating that bathymetric and sedimentary gradients act as strong environmental filters that shape local assemblages. In addition, the spatial components dbMEM4 ($F = 3.34$; $p = 0.002$) and dbMEM5 ($F = 2.46$; $p = 0.013$) were significant, revealing spatial autocorrelation in

Table 2 List of recorded bivalve mollusk species and number of individuals for the northern, central, and southern regions during the dry and rainy seasons along the Sergipe–Alagoas continental margin, NE Brazil

	Dry			Rainy			Number (N)
	North	Central	South	North	Central	South	
<i>Arca zebra</i>	2	9	102	24	364	48	549
<i>Anadara</i> sp. 1	0	0	0	0	1	310	311
<i>Pinctada imbricata</i>	16	3	3	31	1	63	117
<i>Cratis antillensis</i>	1	1	0	5	48	0	55
<i>Corbula operculata</i>	0	3	42	3	0	2	50
<i>Dacrydium vitreum</i>	0	0	3	6	29	5	43
<i>Barbatia domingensis</i>	0	0	8	0	21	0	29
<i>Musculus lateralis</i>	2	0	7	1	6	8	24
<i>Sphenia fragilis</i>	1	0	0	0	0	18	19
Ostreidae sp. 1	0	0	0	0	0	15	15
Mytilidae sp. 2	0	0	0	0	0	13	13
<i>Crenella decussata</i>	2	7	1	1	0	1	12
<i>Spathochlamys benedicti</i>	1	1	4	3	1	1	11
<i>Anadara</i> aff. <i>notabilis</i>	0	4	0	0	2	2	8
Ungulinidae sp. 1	0	0	8	0	0	0	8
<i>Caryocorbula chittyana</i>	0	1	5	0	0	0	6
<i>Anadara</i> sp. 2	0	0	0	3	1	2	6
<i>Pteria colymbus</i>	0	0	0	2	4	0	6
<i>Cratis</i> sp. 1	0	1	5	0	0	0	6
<i>Crassinella lunulata</i>	0	0	1	1	1	3	6
<i>Arcopsis adamsi</i>	0	0	0	4	1	1	6
<i>Leptopecten bavayi</i>	1	0	2	0	0	2	5
<i>Gouldia cerina</i>	1	0	0	0	2	2	5
Limidae sp. 1	0	0	0	2	1	0	3
<i>Caryocorbula contracta</i>	0	1	1	0	0	0	2
<i>Caryocorbula swiftiana</i>	0	0	1	0	1	0	2
<i>Amygdalum sagittatum</i>	0	0	0	0	0	2	2
Mytilidae sp. 1	0	0	0	0	0	2	2
<i>Lindapecten</i> sp. 1	0	0	2	0	0	0	2
<i>Nuculana concentrica</i>	0	1	0	0	1	0	2
<i>Lamychaena hians</i>	0	0	0	1	0	1	2
Limidae sp. 2	0	0	0	0	2	0	2
<i>Corbula</i> sp. 1	0	1	0	0	0	0	1
<i>Barbatia</i> aff. <i>candida</i>	1	0	0	0	0	0	1
<i>Fugleria tenera</i>	0	0	0	0	1	0	1
<i>Botula fusca</i>	0	0	1	0	0	0	1
<i>Cyclinella</i> sp. 1	0	1	0	0	0	0	1
Veneridae sp. 1	1	0	0	0	0	0	1
<i>Lyonsia</i> sp. 1	0	1	0	0	0	0	1
<i>Cumingia lamellosa</i>	0	1	0	0	0	0	1
<i>Parvamussium pourtalesianum</i>	0	1	0	0	0	0	1
Gastrochaenidae sp. 1	0	0	0	1	0	0	1
Crassostrea sp. 1	1	0	0	0	0	0	1
Chamidae sp. 1	0	0	0	0	0	1	1
Spondylidae sp. 1	0	0	0	0	1	0	1
NI	4	3	6	10	10	9	42
N	34	40	202	98	499	511	1384

N indicates the total abundance. NI, not identified

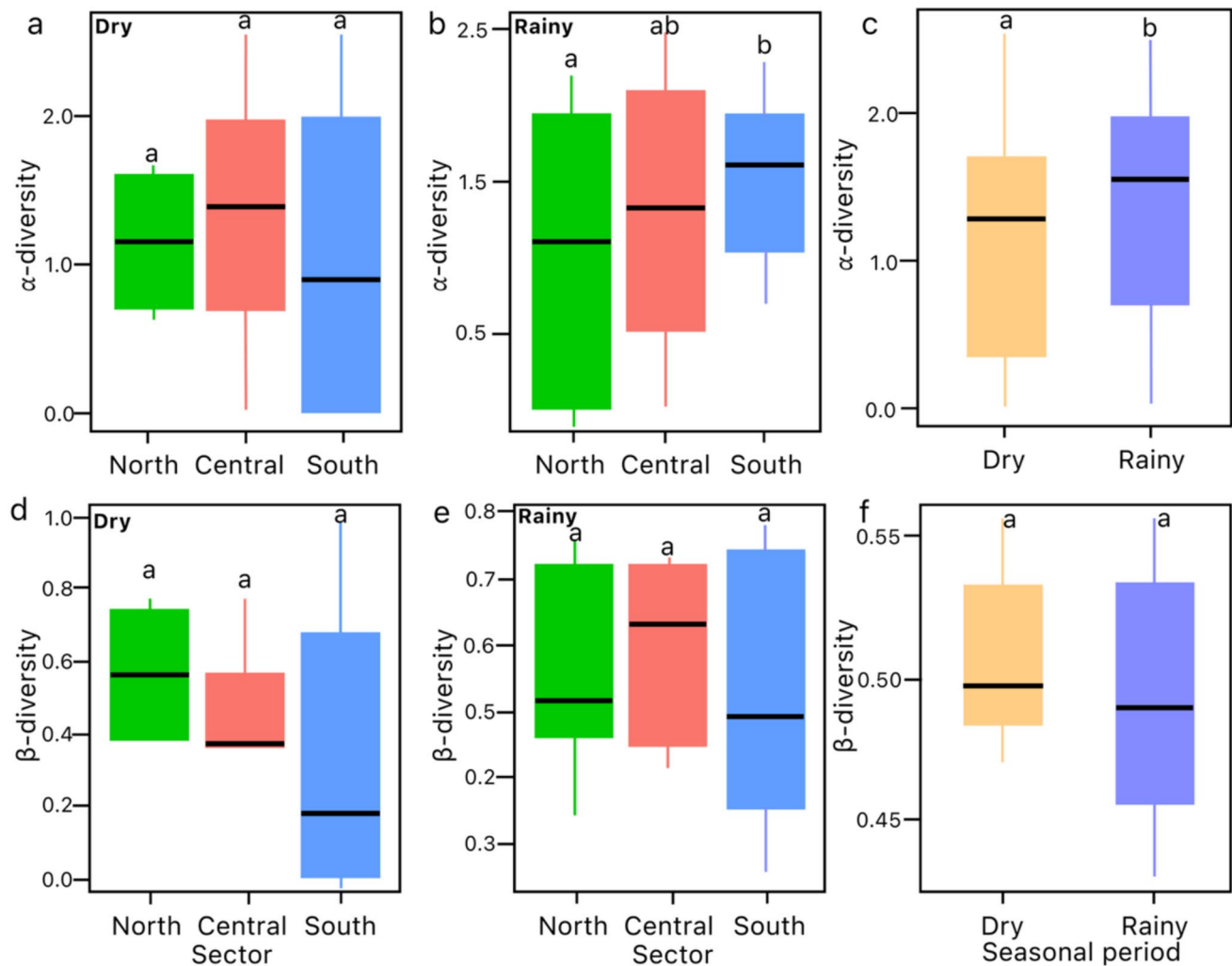


Fig. 5 Taxonomic α -diversity and β -diversity of mollusks bivalves between north, central, and south sectors during dry (a and d) and rainy (b and e) seasons, and between the seasonal periods (c, f) of the Sergipe–Alagoas continental margin, NE Brazil. α -Diversity values

(a–c) are log-transformed. Different letters in α -diversity represent significant differences identified by the GLM, while different letters in β -diversity represent significant differences in the mean centroid among groups, as identified by PERMDISP

species composition that could not be fully explained by environmental variables alone. Because dbMEM4 and dbMEM5 correspond to broad-scale spatial structures (i.e.,

high-eigenvalue eigenfunctions), these results suggest that the spatial signal is primarily associated with dispersal limitation rather than mass effects (Table S6). This pattern indicates that restricted dispersal among sites likely constrains species distribution across the continental shelf, leading to compositional differentiation among sectors. Therefore, the metacommunity structure of bivalves along the SEAL margin appears to be governed predominantly by environmental filtering (i.e., species sorting), with large-scale spatial processes reflecting dispersal constraints that modulate species turnover across the gradient (that is, the communities located in different sectors of the platform are not fully connected, and the range of dispersion of the species is insufficient to homogenize the composition throughout the sampled area).

Table 3 Partitioning of β -diversity (β_{total}) into its components of turnover (β_{repl}) and richness differences (β_{rich}) among sectors on the Sergipe–Alagoas continental margin, NE Brazil

Seasonal period	Category	β_{total}	β_{repl}	β_{rich}
Dry	North versus central	0.84	0.62	0.21
	Central versus south	0.90	0.16	0.74
	North versus south	0.93	0.33	0.60
Rainy	North versus central	0.86	0.27	0.59
	Central versus south	0.92	0.91	0.01
	North versus south	0.78	0.14	0.64

Table 4 Elements of metacommunity structure of bivalve mollusks on the continental shelf during dry and rainy seasons (SP) on the Sergipe-Alagoas continental margin, NE Brazil

Scale SP	Coherence			Turnover			Boundary clumping			
	embAbs	CohZ	P-Value	Tur	TurZ	p-Value	MI	p-Value	df	Structure
CM dry	680	−5.7	<0.001	760	1.43	0.15	1.92	<0.001	8.0	Q-Clementsian
North dry	0.0	−4.2	<0.001	57	−0.32	0.74	1.34	0.03	1.0	Q-nested*
Central dry	0.0	−3.6	<0.001	3.90	5.63	<0.001	1.00	1.0	0.0	Gleasonian
South dry	0.0	−5.5	<0.001	5.60	5.71	<0.001	2.00	<0.001	1.0	Clementsian
CM rainy	120	−6.5	<0.001	2713	0.38	0.69	1.72	<0.001	1.3	Q-Clementsian
North rainy	9.0	−2.5	0.01	6.50	−3.54	<0.001	1.08	0.12	2.0	Gleasonian
Central rainy	0.0	−4.5	<0.001	10.9	5.04	<0.001	1.05	0.08	1.0	Gleasonian
South rainy	6.0	−7.99	<0.001	317	−0.81	0.41	2.22	<0.001	4.0	Q-nested*

These results were based on a fixed-proportional ($r1$) null model. Interpretations were conducted following Leibold and Mikkelsen (2002) and Presley et al. (2010). Significant p -values are indicated by bold text. SP, seasonal periods; embAbs, embedded absences; CohZ, Z-value of coherence; Tur, Turnover test; TurZ, Z-value of turnover; MI, Morisita index; df , degree of freedom; Q, quasi; CM, continental margin

*Nested clumped species loss; the Sergipe–Alagoas continental margin

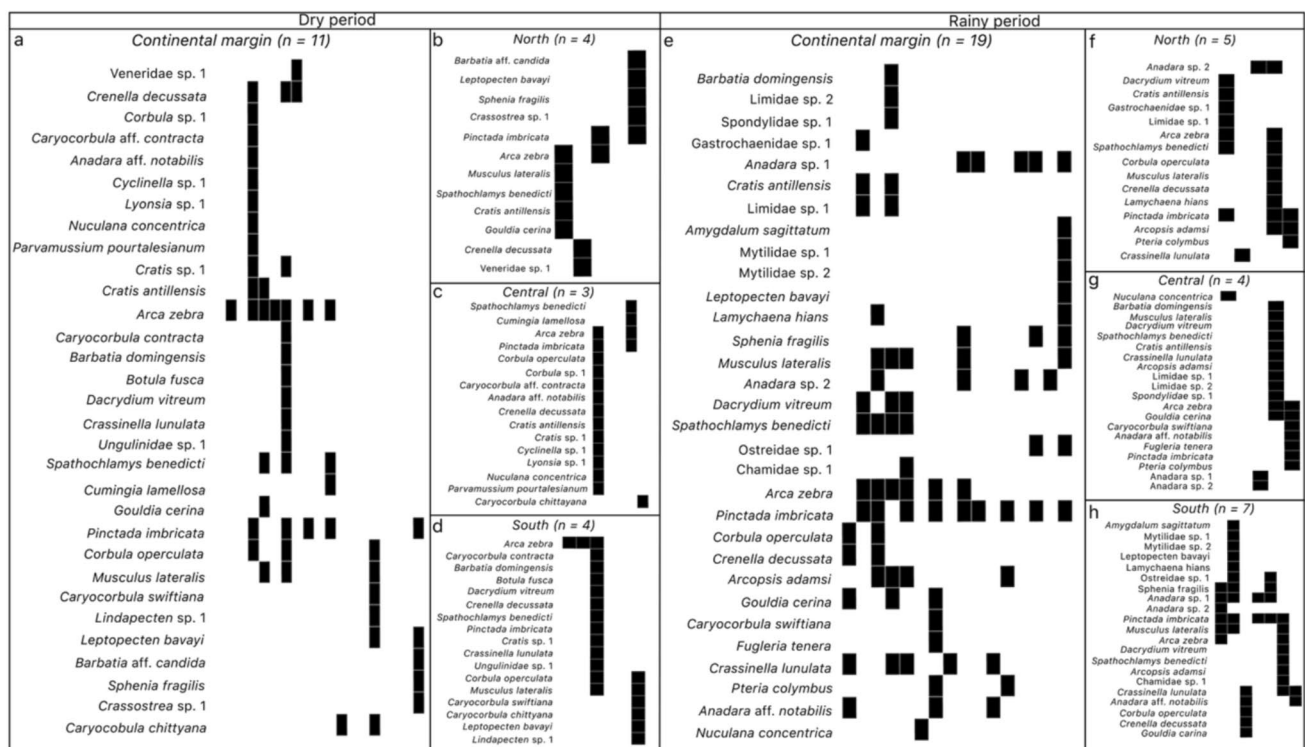


Fig. 6 Taxa of bivalve mollusks versus sites, incidence matrices along the depth gradient at the sampled stations during dry (a–d) and rainy (e–h) seasons in the north (b, f), central (c, g), and south (d, h) sectors of the Sergipe–Alagoas continental margin (a, e). Rows represent species, and columns represent local communities arranged in

decreasing order along the environmental depth gradient (i.e., from left to right, from 10 to 55 m). Black squares indicate the presence of a taxa, while white squares indicate the absence of a taxon along the gradient. n indicates the number of local communities or samples

Discussion

Our results revealed distinct spatial and seasonal patterns in the structure of bivalve mollusk communities along the

Sergipe–Alagoas continental margin, reflecting the interplay between environmental filters and spatial processes in shaping community structure. Taxonomic α -diversity was higher during the rainy season and remained spatially homogeneous among sectors during the dry period but

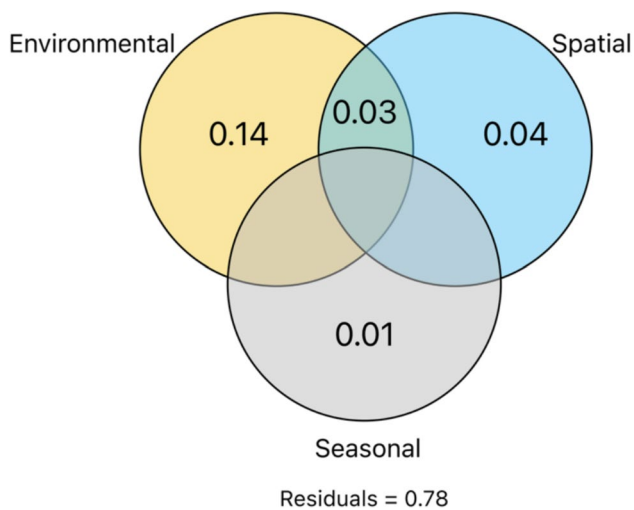


Fig. 7 Variation partitioning for the influence of environmental, spatial, and seasonal factors on the distribution of bivalve metacommunity on the continental margin of Northeastern Brazil. Values=0 are not shown

showed a marked increase in the southern sector during the rainy season. This pattern indicates that seasonality influences local richness (possibly through increased organic matter and greater resource availability) and contradicts our first hypothesis. β -diversity did not differ between seasons or sectors; however, it exhibited high compositional dissimilarity among sectors, particularly between the north–south and central–south. This suggests that, although the three sectors display equivalent levels of β -diversity, their species composition differs due to turnover, which was more pronounced during the rainy season. These findings indicate the reorganization of local communities under varying environmental conditions, partially supporting our second hypothesis. Moreover, metacommunity organization along the environmental gradient was predominantly Gleasonian at smaller spatial scales, with species showing individualistic responses that produced a continuous pattern of gradually shifting composition, and quasi-Clementsian at broader spatial scales. This indicates that environmental filtering (depth and gravel content) acts as the primary structuring mechanism, in conjunction with broad-scale spatial effects (dbMEM4 and dbMEM5), which reflect processes related to large-scale dispersal limitation, thereby supporting our third hypothesis.

Environmental heterogeneity and physicochemical stratification are key drivers of the structure and composition of benthic communities across continental shelves. Along the Sergipe–Alagoas margin, significant differences in environmental variables among depth categories and sectors revealed clear environmental structuring, with depth and sediment composition acting as the dominant gradients. The 50 m depth category, characterized by higher salinity

and gravel content, contrasted with shallower depths (10 and 25 m), which were dominated by finer sediments and higher temperatures, particularly in the northern and central sectors. These spatial environmental patterns appear to be a marked feature of the Sergipe continental shelf, as Souza et al. (2025) reported similar patterns between the 10 and 30 m depth categories. In addition, the significant effects of dispersion multivariate indicated that differences among depth categories and sectors are driven not only by mean environmental conditions but also by within-group heterogeneity. Higher multivariate dispersion observed at the 50 m depth category and in the central and southern sectors during the dry season and the north in the rainy season suggests greater environmental variability within these regions. In the central and southern sectors, this variability may be associated with the heterogeneous composition of sedimentary grains derived from multiple continental and marine sources (Fontes et al. 2017; Concentino et al. 2018). In the northern sector, environmental heterogeneity may also be enhanced by the carbonate–terrigenous facies of southern Alagoas, which represents a transitional sedimentary system combining biogenic carbonates and terrigenous inputs (Fontes et al. 2017; Concentino et al. 2018).

In addition, the greater heterogeneity observed in the central and southern regions during the dry season may be associated with reduced rainfall, which is recognized as a homogenizing factor of environmental characteristics (Corte et al. 2018; Checon et al. 2023) and oceanographic dynamics of Sergipe–Alagoas continental shelf (Manso et al. 1997). Although Souza et al. (2025) reported an increase in heterogeneity in the southern sector between 2001 and 2003, our study revealed that patterns of spatial heterogeneity are seasonally dependent, as a decrease in heterogeneity was evident in these sectors during the rainy season. On the SEAL continental shelf, the sediment plume derived from the São Francisco River (intensified by increased rainfall) moves southward across the shelf under the influence of the North Brazil Current and prevailing northeasterly surface winds (Guimarães 2010; Souza et al. 2025). This plume reaches the central and southern regions of the SEAL continental margin, consequently reducing environmental heterogeneity in these sectors during the rainy season. In contrast, the northern sector remains unaffected by the sediment plume because of the direction of the North Brazil Current and winds (Manso et al. 1997; Coutinho 2000). The lack of significant environmental differences between seasonal periods (dry versus rainy) suggests that seasonal variation is not driven by large-scale physicochemical shifts in sediments but rather by hydrological processes that occur at smaller spatial–temporal scales (e.g., sectors).

The observed spatial and seasonal patterns in the α - and β -diversity of bivalve mollusks along the Sergipe–Alagoas continental shelf were consistent with previous studies of

benthic invertebrate assemblages on continental margins (Quiroz-Martínez et al. 2022; Souza et al. 2025; Mendes et al. 2025). The higher α -diversity recorded during the rainy season, particularly in the southern sector, likely reflects the increased input of organic matter during periods of enhanced fluvial discharge, which promotes greater resource diversity for benthic species. Similar seasonal increases in local diversity have been reported for bivalves and other invertebrates in tropical shelves, where hydrological variation enhances primary productivity (Alongi 1990; Checon et al. 2023; Souza et al. 2025; Dantas et al. 2025). These patterns may also be related to the fact that, during the rainy season and in the southern sector of the continental shelf Sergipe-Alagoas, the highest biomass of calcareous algae was found, whereas in the central sector (which also exhibited high α -diversity), there was a predominance of Ochrophyta algae (Concettino et al. 2018), which may indicate a stronger association of bivalves with this type of resource/substrate and available calcium carbonate. Moreover, these changes in species composition, which were more pronounced during the rainy season, may have contributed to the increase in taxonomic α -diversity during this period. Dantas et al. (2025) reported similar patterns for the benthic fauna of the Alagoas continental shelf, where, in addition to recording more intense variations in species composition during the rainy season, the authors revealed that such changes led to an increase in both taxonomic and functional diversity in fishing areas of the region.

The lack of increase in β -diversity among sectors and between seasons, despite high compositional dissimilarity, suggests that regional-scale environmental gradients act as broad filters structuring assemblages, whereas turnover and richness variation operate complementarily across the continental shelf. Comparable findings have been described by Egilsdóttir et al. (2019) in the North Atlantic and Suárez-Mozo et al. (2021) in the Gulf of Mexico, where it was shown that, while differences among sectors during the dry season were primarily associated with variation in species richness, turnover predominated during the rainy season, suggesting a reorganization of the fauna in response to seasonal precipitation events. Thus, the predominance of species turnover between the central and southern sectors during the rainy season in the present study indicates dynamic species replacement along the spatial gradient, possibly driven by sedimentary differentiation, suggesting that environmental filtering is the primary driver of community assembly in continental shelf bivalves. Such stratification aligns with patterns observed in other continental shelf systems, where bathymetric variation and sediment granulometry jointly govern the spatial distribution and diversity of benthic communities (Rex and Etter 2010; Heino et al. 2015; Santos et al. 2020; Suárez-Mozo et al. 2021; Souza et al. 2025; Dantas et al. 2025). Hydrological fluctuations

can amplify environmental gradients and increase species turnover, fostering novel assemblages across spatial scales and enhancing regional β -diversity (Presley et al. 2010; Wingardner et al. 2012; Dantas et al. 2025). In bivalve assemblages, sediment texture strongly influences species sorting by controlling microhabitat availability, feeding modes, and larval settlement, generating compositional differentiation even over short spatial distances (Gray 2002; Rex and Etter 2010) owing to environmental filtering.

The predominance of Gleasonian and quasi-Clementsian structures in the metacommunity of bivalve mollusks along the Sergipe–Alagoas continental margin suggests that species respond individually to underlying environmental gradients, whereas subsets of species form co-occurring groups in which ecological conditions converge. Gleasonian structures are typically associated with gradual, continuous environmental gradients that promote species replacement along depth, sediment, or salinity (Presley et al. 2010; Heino et al. 2015). Similar patterns have been observed in marine benthic assemblages, where environmental sorting dominates and turnover arises from niche differentiation rather than spatial segregation (Valanko et al. 2015; Josefson et al. 2018). In contrast, quasi-Clementsian patterns (detected in both CM seasons) imply partial compartmentalization of assemblages, probably reflecting abrupt transitions in substrate or hydrodynamic regimes that delineate discrete species groups (Presley et al. 2010; Heino et al. 2015; Alves et al. 2020; Li et al. 2022). Thus, the coexistence of both Gleasonian and quasi-Clementsian patterns indicates that bivalve communities in this shelf system are organized primarily by environmental filtering but also exhibit localized community clustering, where environmental discontinuities occur.

The predominance of species turnover in 50% of cases, together with high total dissimilarity among sectors, indicates that compositional variation arises mainly from species replacement along environmental gradients rather than the nested loss of taxa. In continental shelf ecosystems, turnover tends to dominate when strong bathymetric or granulometric gradients create distinct niche environments (Egilsdóttir et al. 2019; Suárez-Mozo et al. 2021; Souza et al. 2025). Studies of bivalves and other benthic invertebrates have shown that as sediment texture, organic matter, or depth varies regionally, species adapted to specific conditions replace one another instead of forming nested subsets of tolerant taxa (Valanko et al. 2015; Josefson et al. 2018).

The occurrence of significant boundary clumping (Morisita's index > 1) in several sectors supports the existence of ecological compartments within the metacommunity, where groups of taxa share similar environmental tolerances or dispersal capacities. Positive boundary clumping is a hallmark of Clementsian and quasi-Clementsian structures and has been documented in marine benthic metacommunities

exposed to heterogeneous sediments or discontinuous hydrodynamic conditions (Presley et al. 2010; Valanko et al. 2015). Such spatially clumped patterns may arise when species assemblages are constrained by patchy environmental mosaics, for example, when coarse-grained habitats alternate with fine sediments or when current regimes create physically distinct microhabitats (Josefson et al. 2018). Thus, the patterns observed at both large and small scales on the SEAL continental shelf appear to respond to the gradient formed by bathymetry and the extensive sedimentary variability among sectors, with the northern sector exhibiting a predominance of sand, the central sector characterized by a predominance of mud with a muddy sand patch toward the south, and the southern sector dominated by mud interspersed with patches of gravelly sand and gravel, delineating well-defined sedimentary regions that harbor species with distinct ecological requirements.

It is also worth noting that, in certain small-scale cases (for instance, in the northern sector during the dry season and in the southern sector during the rainy season), quasi-nested patterns with clustered species losses prevailed. This indicates that local communities under a less pronounced environmental gradient were organized into subsets of richer assemblages. This configuration may be associated with the fact that, under conditions of more intense environmental filtering and greater spatial homogeneity (shorter distances), species with broad ecological tolerance tend to persist, whereas more sensitive taxa are selectively excluded from groups, resulting in a nested organization connected by mass effects of a few species (Presley et al. 2010; Alves et al. 2020; Li et al. 2022). Therefore, the combination of positive coherence, significant turnover, and clumped boundaries indicates that environmental heterogeneity at large scales acts as an important driver of community structure.

Integrating these EMS outcomes with the RDA and dbMEM results from this study suggests that environmental filtering, particularly related to depth and sediment composition, remains the dominant mechanism structuring bivalve communities, whereas spatial components (e.g., dbMEM4–5) reveal large-scale dispersal limitation modulating community organization (Heino et al. 2015; Li et al. 2022). These findings highlight that bivalve metacommunities on tropical continental shelves are shaped by the combined effects of species sorting across environmental gradients and spatially constrained dispersal, the relative influence of which varies seasonally with hydrological dynamics. The joint occurrence of significant spatial structuring and low dispersion supports the predominance of species sorting along environmental gradients, modulated by dispersal limitation and habitat heterogeneity on a large scale and mass effects on a lower scale. Stratification associated with depth and sediment texture acts as a strong environmental filter, structuring distinct bivalve assemblages

across depth categories. In contrast, the presence of heterogeneous sediment mosaics, particularly at approximately 50 m depth and within the central and southern shelf sectors, promotes fine-scale variability in species composition and supports microhabitat specialization. Similar interactions between environmental filtering and small-scale dispersal have been described for marine bivalves and polychaetes in shelf systems globally (Heino et al. 2015; Valanko et al. 2015; Josefson et al. 2018).

Furthermore, our findings showed that nested structures associated with clumped species loss were more likely to emerge at smaller spatial scales. This pattern suggests that such structures arise when connectivity among habitat patches increases, driven by mass-effect processes (by the few species that manage to inhabit patches under suboptimal conditions) operating over short distances (Li et al. 2022). This mechanism may have been present in the metacommunity analyzed here, given that large-scale spatial filters were linked to dispersal limitation and species sorting, whereas mass effects appeared to play a secondary role at finer scales. However, these patterns are not static in nature. Turnover mediated structures with stronger boundary clumping can also develop at small spatial scales over time as environmental gradients intensify during certain periods of the year (e.g., dry and rainy seasons). Such fluctuations can selectively filter species locally, generating Gleasonian distribution patterns, as observed in the southern sector during the rainy season in our study. This temporal variability (shifting among nested, Clementsian, or quasi-Clementsian structures) has been documented elsewhere and highlights both the ecological plasticity of natural systems and the rapid response of communities to environmental change (Li et al. 2022). Together, these findings emphasize that the structure of continental shelf bivalve communities emerges from the combined influence of environmental filtering and spatial processes associated with dispersal limitation, the relative importance of which varies with spatial scale and environmental complexity.

As the first comprehensive assessment of the metacommunity structure of bivalves associated with macroalgae in northeastern Brazil, this study revealed that community organization is driven by the combined effects of environmental gradients, spatial processes, and seasonal variability. Our results indicate that environmental filters (particularly those associated with increasing gravel content and depth) play a dominant role in structuring communities along the Sergipe–Alagoas continental margin. In parallel, EMS analyses revealed the predominance of a Gleasonian pattern at smaller spatial scales and a quasi-Clementsian species distribution pattern at broader spatial scales. However, the significant influence of broad-scale spatial components (dbMEM 4 and dbMEM 5) demonstrates that local environmental gradients alone cannot account for community

organization in the study area. Instead, these findings suggest that spatial processes operating over large extents (such as hydrodynamic connectivity, habitat continuity, and regionally structured spatial patterns) interact with environmental filtering to shape species composition. Although β -diversity did not vary significantly among sectors or seasons, the pronounced compositional dissimilarity observed indicates that both species turnover and richness variation complementarily structure the bivalve metacommunities. In a broader context, our findings indicate that the structure of bivalve metacommunities on the SEAL continental shelf arises from the interaction between pronounced environmental gradients and spatial processes operating at different scales. This perspective underscores that the benthic communities in tropical marine environments cannot be adequately explained by local diversity patterns alone, as their organization reflects the hierarchical mechanisms that govern both population persistence and regional connectivity. Understanding how environmental filters, spatial dynamics, and seasonal variability jointly shape species distribution and turnover provides a critical foundation for predicting macrofaunal responses to escalating natural and anthropogenic disturbances. Furthermore, these insights offer valuable support for management and conservation strategies by informing monitoring programs for continental shelf ecosystems that are increasingly exposed to the cumulative impacts of climate change, hydrological alterations, and intensifying coastal pressure.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-026-01325-z>.

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Data availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval This study was conducted in strict accordance with the recommendations of the ethics committee of the Federal University of Sergipe (UFS) (Contract 0050.0058681.10.2 among PETROBRAS/UFS/FAPESE). All sampling complied with Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) Biodiversity Authorization and Information System (SISBIO).

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