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Padrões de distribuição de macroinvertebrados bentônicos em estuários tropicais: perspectiva para o entendimento taxonômico e funcional de comunidades

Belém
2020

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Doutor(a) em Ecologia.
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Se as coisas são inatingíveis... ora!
Não é motivo para não querê-las...
Que tristes os caminhos, se não fora
A presença distante das estrelas!

Mario Quintana

Padrões de distribuição de macroinvertebrados bentônicos em estuários tropicais: perspectiva para o entendimento taxonômico e funcional de comunidades

RESUMO

A compreensão dos padrões de diversidade em escalas espaciais e temporais, e dos processos que direcionam a composição e diversidade funcional das comunidades biológicas, proporciona um melhor entendimento sobre a dinâmica dos ecossistemas. Nesse contexto, os ecossistemas estuarinos são modelos ideais para o estudo de padrões biodiversidade, devido à sua condição de interface entre ecossistemas continentais e marinhos, o que possibilita o estudo da diversidade ao longo de gradientes ambientais. Assim, o objetivo geral desta tese foi explorar os padrões de distribuição taxonômica e funcional das comunidades de macroinvertebrados bentônicos de estuários tropicais. O estudo foi realizado em seis estuários, sendo três localizados em uma região tropical típica (Paraíba do Norte, Mamanguape e Passos) e três localizados em uma região semiárida (Tubarão, Galinhos e Casqueira). Em cada estuário, foram amostrados doze pontos distribuídos em quatro zonas estuarinas (ZI, ZII, ZIII e ZIV). Em cada ponto foram coletadas três sub-amostras. A amostragem foi realizada em um período de seca e um de chuva. Esta tese é composta por três seções. Na primeira seção, nosso objetivo foi avaliar o particionamento aditivo da diversidade taxonômica dos estuários tropicais típicos e semiáridos nos componentes α, β e γ. Além disso, a diversidade beta foi dissociada em seus componentes de substituição e diferença de riqueza/abundância utilizando dados de presença e ausência (índice de Jaccard) e abundância relativa (índice de Ružicka). Os resultados deste trabalho demostraram maiores proporções de diversidade β nas maiores escalas espaciais (entre estuários e entre zonas estuarinas). Nos estuários semiáridos, os componentes de diferença de riqueza e substituição de espécies mostraram maior importância relativa nos períodos de chuva e seca, respectivamente. Quando considerados dados de abundância, no geral o componente de diferença de abundância mostrou maior importância relativa em ambos os conjuntos de estuários e períodos sazonais. Não foi observado um padrão claro nos estuários tropicais típicos. Na segunda sessão, nós comparamos o particionamento da diversidade α, β e γ funcional e taxonômico das comunidades de moluscos e poliquetas entre os estuários tropicais típicos e semiáridos. A diversidade beta contribuiu mais para a diversidade gama taxonômica e a diversidade alfa contribuiu mais para a diversidade gama funcional, em ambos os tipos de estuários. Na terceira sessão, avaliamos o aninhamento funcional (traitNODF) da comunidade de poliquetas em função do gradiente de salinidade. Foram considerados apenas os estuários Paraíba do Norte e Mamanguape, e analisados padrões sazonais. Os resultados demonstram uma tendência ao aninhamento funcional da comunidade de poliquetas em relação ao gradiente de salinidade. Os resultados obtidos na presente tese são discutidos considerando aspectos teóricos e aplicados, e podem auxiliar na elaboração de planos de manejo e gestão de estuários tropicais, promovendo a conservação da biodiversidade e de seus serviços ecossistêmicos.

Palavras-chave: Diversidade funcional. Diversidade taxonômica. Diversidade beta. Macrofauna bentônica. Partição aditiva.

Distribution patterns of benthic macroinvertebrates in tropical estuaries: perspective for taxonomic and functional understanding of communities

ABSTRACT

Understanding the patterns of diversity in spatial and temporal scales, and the processes that drives the composition and functional diversity of biological communities, provides a better understanding of the dynamics of ecosystems. In this context, estuarine ecosystems are ideal models for the study of biodiversity patterns, due to their condition of interface between continental and marine ecosystems, which makes it possible to study diversity along environmental gradients. Thus, the general objective of this thesis was to explore the patterns of taxonomic and functional distribution of benthic macroinvertebrate communities in tropical estuaries. The study was carried out in six estuaries, three located in a typical tropical region (Paraíba do Norte, Mamanguape, and Passos) and three located in a semi-arid region (Tubarão, Galinhos, and Casqueira). In each estuary, twelve sites were sampled, distributed in four estuarine zones (ZI, ZII, ZIII, and ZIV). At each site, three sub-samples were collected. Sampling was carried out in a dry and a rainy period. This thesis has three sections. In the first section, our objective was to evaluate the additive partitioning of the taxonomic diversity of typical tropical and semi-arid estuaries into components α, β, and γ. In addition, beta diversity was dissociated into its components of substitution and difference in richness/abundance using data of presence and absence (Jaccard index) and relative abundance (Ružicka index). The results of this work showed greater proportions of β diversity at the largest spatial scales (between estuaries, and estuarine zones). In the semi-arid estuaries, the components of richness difference, and species substitution showed greater relative importance in periods of rain and dry, respectively. When considering abundance data, in general, the difference in abundance component showed greater relative importance in both sets of estuaries and seasonal periods. There was no clear pattern in typical tropical estuaries. In the second session, we compare the partitioning of the functional, and taxonomic α, β, and γ diversity of mollusc and polychaete communities between typical and semi-arid tropical estuaries. Beta diversity contributed more to taxonomic gamma diversity and alpha diversity contributed more to functional gamma diversity, in both types of estuaries. In the third session, we evaluated the functional nestedness (traitNODF) of the polychaete community in relation to the salinity gradient. In this session, only the Paraíba do Norte and Mamanguape estuaries were considered, and seasonal patterns were analyzed. The results demonstrate a trend towards functional nestedness of the polychaete community in relation to the salinity gradient. The results obtained in the present thesis are discussed considering theoretical and applied aspects and can assist in the development of management plans for tropical estuaries, promoting the conservation of biodiversity and its ecosystem services.

Key-words: Functional diversity. Taxonomic diversity. Beta diversity. Benthic macrofauna. Additive partition.

SUMÁRIO

1 INTRODUÇÃO GERAL

O conhecimento dos processos que determinam os padrões de biodiversidade e a estruturação de comunidades em diferentes escalas espaciais e temporais é um dos principais objetivos da ecologia e é chave para que seja possível estabelecer prioridades de conservação da biodiversidade (Dolbeth et al., 2013; Little & Altermatt, 2018). Os processos que influenciam na formação e estruturação de comunidades podem ser caraterizados naqueles baseados em distribuições aleatórias de espécies (ou seja, neutralidade) e aqueles relacionados à amplitude de nicho dos indivíduos (Gaston & Chown, 2005). No primeiro caso, as espécies são consideradas como equivalentes ecologicamente, ou seja, elas não competem entre si e suas abundâncias oscilam aleatoriamente no ambiente devido a processos de imigração e extinção (Hubbell, 2001; Adler et al., 2007; Harris et al., 2017). Em contrapartida, a teoria de nicho prediz que as espécies que compõem uma comunidade se estabelecem nos locais de acordo com suas tolerâncias e requerimentos quanto às condições ambientais, e de suas interações com outras espécies (Chesson, 2000).

Seguindo a abordagem teórica de nicho, três principais processos podem explicar os padrões de diversidade de espécies: (i) limitação das espécies em alcançar locais distantes; (ii) seleção de espécies pelas condições ambientais dos habitats e (iii) interações bióticas entre as espécies (Chesson, 2000; Leibold et al., 2004; Gómez-Rodríguez & Baselga, 2018). A atuação desses processos na montagem das comunidades pode ocorrer de forma simultânea, e a comunidade científica tem se concentrado em explicar qual destes processos exercem maior importância em cada contexto e tipo de ambiente (Mouillot et al., 2007; Vergnon et al., 2009). Para isso, muitos estudos têm avaliado mudanças na composição de espécies em escalas espaciais e temporais (p.ex.: Ligeiro et al., 2010; Molozzi et al., 2013; Barros et al., 2014), assim como tem investigado a importância relativa dos mecanismos que impulsionam essas mudanças (Legendre et al., 2019).

Em uma perspectiva espacial de distribuição de espécies, Whittaker (1960; 1972) descreveu os componentes de diversidade alfa (diversidade dentro de um local; α), beta (variação na composição de espécies entre locais; β) e gama (diversidade total de uma determinada região; γ). Segundo Whittaker (1960; 1972), a diversidade total de uma área de interesse pode ser obtida através da multiplicação dos componentes da diversidade alfa e beta (isto é, método multiplicativo; $\gamma = \alpha \times \beta$). Anos depois da primeira publicação do

Whittaker, MacArthur et al. (1966) propôs a adição das diversidades alfa e beta para se obter a diversidade gama ($\gamma = \alpha + \beta$) (Veech et al., 2002). O método utilizado por MacArthur et al. (1966) foi consolidado pelo trabalho de Lande (1996), quando foi definido e formalizado o método do particionamento aditivo da diversidade. A abordagem aditiva mostra baixa dependência entre os componentes da diversidade alfa e beta e permite que todos os componentes da diversidade possam ser mensurados na mesma escala numérica, além de permitir a avaliação de padrões hierárquicos da diversidade de espécies ao longo de múltiplas escalas espaciais e temporais (Veech et al., 2002; Crist et al., 2003).

A comunidade científica começou a dar enfoque ao componente beta da diversidade somente nas últimas décadas (Anderson et al., 2011; Legendre & De Cáceres, 2013). A diversidade beta pode ser estimada através de diferentes medidas de dissimilaridade, além do particionamento aditivo e multiplicativo. As diferentes maneiras de se calcular a diversidade beta foram classificadas por Jurasinski et al. (2009) em dois principais tipos abordagens: (i) diversidade proporcional e (ii) diversidade de diferenciação. A diversidade proporcional caracteriza abordagens que consideram a riqueza de espécies ou índices de diversidade (p.ex., índices de Shannon e Simpson) em múltiplas escalas espaciais ou temporais (isto é, particionamento da diversidade aditivo e multiplicativo) (Jurasinski et al., 2009). Em contrapartida, a diversidade de diferenciação engloba as abordagens que consideram índices de dissimilaridade (p.ex., índices de Jaccard, Sørensen) para estimar a diversidade beta entre pares de amostras, em uma dada escala espacial ou temporal de interesse (Jurasinski et al., 2009).

Nas últimas décadas, tem sido reconhecido que a diversidade beta pode ser um resultado de diferentes componentes, levando-se em consideração a presença e ausência de espécies (p.ex., substituição de espécies, diferenças de riqueza, aninhamento taxonômico) ou abundância relativa de indivíduos (p.ex., substituição de abundância, diferenças de abundância) (Legendre et al., 2014). Esses componentes podem ser estimados através de diferentes medidas de dissimilaridade (p.ex., índices de Jaccard, Sørensen e Ružicka). Embora utilizadas com menor frequência, as medidas baseadas na abundância relativa dos indivíduos para avaliar os componentes da diversidade beta taxonômica tem sido incentivadas, uma vez que a biodiversidade é um conceito multifacetado que inclui aspectos como identidade, raridade e dominância das espécies (Hillebrand et al., 2018).

Além de aspectos taxonômicos, a consideração de abordagens funcionais também auxilia na obtenção de respostas mais abrangentes sobre os padrões de distribuição das comunidades. Abordagens baseadas em características funcionais podem ser utilizadas de forma complementar ao estudo dos aspectos taxonômicos, uma vez que elas podem responder de maneiras diferentes a variações ambientais naturais ou antrópicas (Kuzmanovic et al., 2017). As características (ou "*traits*") funcionais das espécies, como modo de alimentação e tamanho corporal, representam as adaptações das espécies de uma comunidade às condições ambientais, no sentido de maximizar sua sobrevivência e sucesso reprodutivo. Assim, as diferentes espécies atuam de forma diferenciada nos diversos processos ecossistêmicos, como o fluxo de energia e ciclagem de nutrientes (Bremner et al., 2006; Laureto et al., 2015). Mudanças nas características funcionais das espécies de uma comunidade podem indicar os efeitos diretos de estresses ambientais naturais ou antrópicos no funcionamento ecológico dos ecossistemas (Bremner et al., 2006; Darr et al., 2014). A variabilidade de papéis ecológicos que as espécies de uma comunidade desempenham em um determinado ecossistema (isto é, diversidade funcional; DF) pode ser estimada através da categorização das espécies em grupos funcionais (Heino, 2005). A redundância funcional refere-se ao oposto disso, e ocorre quando as espécies que compõem uma comunidade desempenham papéis ecológicos semelhantes (Laureto et al., 2015).

Diante o reconhecimento da importância do aspecto funcional das comunidades, o conceito de particionamento da diversidade alfa, beta e gama, bem como a dissociação dos componentes da diversidade beta, tem sido extrapolado, considerando também características funcionais das espécies (Ricotta, 2005). Nesse caso, a diversidade alfa corresponde a variabilidade de características funcionais entre indivíduos dentro de um local (diversidade alfa), entre locais (diversidade beta) ou dentro de uma paisagem ou região (diversidade gama) (De Bello et al., 2009; De Bello et al., 2010). Recentemente, estudos tem particionado a diversidade funcional e taxonômica em múltiplas escalas espaciais simultaneamente (p.ex., Dolbeth et al., 2013; Nunes et al., 2016). Esses estudos tem fornecido importantes informações sobre os mecanismos que impulsionam a montagem das comunidades considerando múltiplas facetas da diversidade.

Abordagens baseadas em características funcionais em ambientes estuarinos ainda são incipientes (Bremner et al., 2008), principalmente em estuários localizados em regiões tropicais. Esses ecossistemas são modelos ideais para o estudo de padrões de biodiversidade e mecanismos subjacentes à montagem das comunidades. Isso deve-se a esses locais serem ambientes de transição entre os ecossistemas continentais e marinhos, sujeitos a estresses naturais e antropogênicos, altamente variáveis e dinâmicos no espaço e no tempo (Elliott & Quintino, 2007). Em estuários tropicais típicos, mudanças ambientais graduais ocorrem da direção da drenagem continental para o mar (ou seja, de montante para jusante), tornando possível o estudo dos padrões de biodiversidade ao longo de gradientes ambientais (Telesh & Khlebovich, 2010). A descarga de água da drenagem continental é um aspecto chave desses ecossistemas, pois favorece a variação progressiva da salinidade ao longo dos estuários. Além disso, outros fatores como a geomorfologia do sistema, a influência das ondas e a amplitude das marés, também podem alterar as condições ambientais ao longo dos ecossistemas estuarinos (p.ex., salinidade, composição dos sedimentos e a matéria orgânica) (Bernardino et al., 2015; Francisco & Netto 2020).

Embora os estuários tropicais típicos sejam caracterizados por mudanças ambientais longitudinais graduais, as condições climáticas das regiões onde os estuários estão inseridos, em conjunto com alterações no influxo de água da drenagem continental e das marés, podem alterar a dinâmica desses ecossistemas. Em regiões áridas e semiáridas, eventos como escassez de chuvas e elevadas temperaturas conferem condições ambientais particulares aos estuários (Elliott & Whitfield, 2011). Nestes ecossistemas, os períodos de seca prolongada causam uma maior evaporação da água e um baixo influxo de água doce no estuário (geralmente de origem subterrânea), fazendo com que a salinidade aumente de forma inversa, ou seja, no sentido de jusante para a montante, e por esse motivo esses ambientes são caracterizados como estuários inversos ou negativos (Pritchard, 1952; Duarte et al., 2020).

Entre as comunidades estuarinas, a macrofauna bentônica é frequentemente utilizada em estudos ecológicos por integrar aspectos físicos, químicos e biológicos dos ecossistemas (Barros et al., 2012; Bernardino et al., 2015; Van der Linden et al., 2017). Esses organismos são caracterizados por habitar o sistema bentônico, e em estuários, essa comunidade é principalmente representada por poliquetas, moluscos e dípteras. Além disso, os macroinvertebrados bentônicos estão envolvidos em processos ecossistêmicos fundamentais, como a ciclagem de nutrientes e o fluxo de energia, sendo importantes itens alimentares de peixes e aves (Tomiyama et al., 2008).

Embora exista um número considerável de estudos em estuários temperados que investigue os padrões de distribuição de espécies da macrofauna bentônica e os mecanismos subjacentes, nos estuários tropicais esses padrões ainda são pouco conhecidos (p.ex., Barros et al., 2012; Medeiros et al., 2016; Van der Linden et al., 2017) principalmente os localizados em regiões tropicais semiáridas. É necessário o desenvolvimento de mais estudos voltados a compreensão das relações existentes entre as espécies e seus ambientes, pois essas informações podem auxiliar no desenvolvimento de estratégias apropriadas para a conservação da diversidade de espécies e dos papeis funcionais desempenhados por elas (Bremner et al., 2008).

Na presente tese, associamos abordagens taxonômicas (presença/ausência de espécies e abundância relativa dos indivíduos) e funcionais (características funcionais das espécies) para compreender melhor os padrões de distribuição das comunidades de macroinvertebrados bentônicos em estuários que estão inseridos em regiões com diferentes condições climáticas. A estrutura da tese é composta por três seçoes. A primeira teve como principais objetivos avaliar o particionamento aditivo da diversidade taxonômica das comunidades de macroinvertebrados bentônicos nos componentes α, β e γ em estuários semiáridos e tropicais típicos. Nós também investigamos quais componentes da diversidade beta, substituição de espécies ou diferença de riqueza (dados de presença e ausência das espécies) e substituição de abundância ou diferença de abundância (dados de abundancia relativa), tiveram maior importância relativa na estruturação da composição da macrofauna bentônica. Este artigo está publicado na revista *Limnology and Oceanography* (A1). Na segunda seção, avaliamos a relação entre o particionamento funcional e taxonômico das comunidades de poliquetas e moluscos em estuários semiáridos e tropicais típicos. Este manuscrito será submetido ao periódico *Hydrobiologia* (A1). Finalmente, a terceira seção da tese, teve como objetivo central avaliar o aninhamento funcional (traitNODF) da comunidade de poliquetas ao longo do gradiente de salinidade em estuários tropicais típicos, e avaliar o efeito dos períodos sazonais nesse padrão. Esse artigo está publicado na revista *Estuarine, Coastal and Shelf Sciense* (A1).

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Spatial scale drives diversity patterns of benthic macroinvertebrate communities in tropical estuaries

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2 SPATIAL SCALE DRIVES DIVERSITY PATTERNS OF BENTHIC MACROINVERTEBRATE COMMUNITIES IN TROPICAL ESTUARIES

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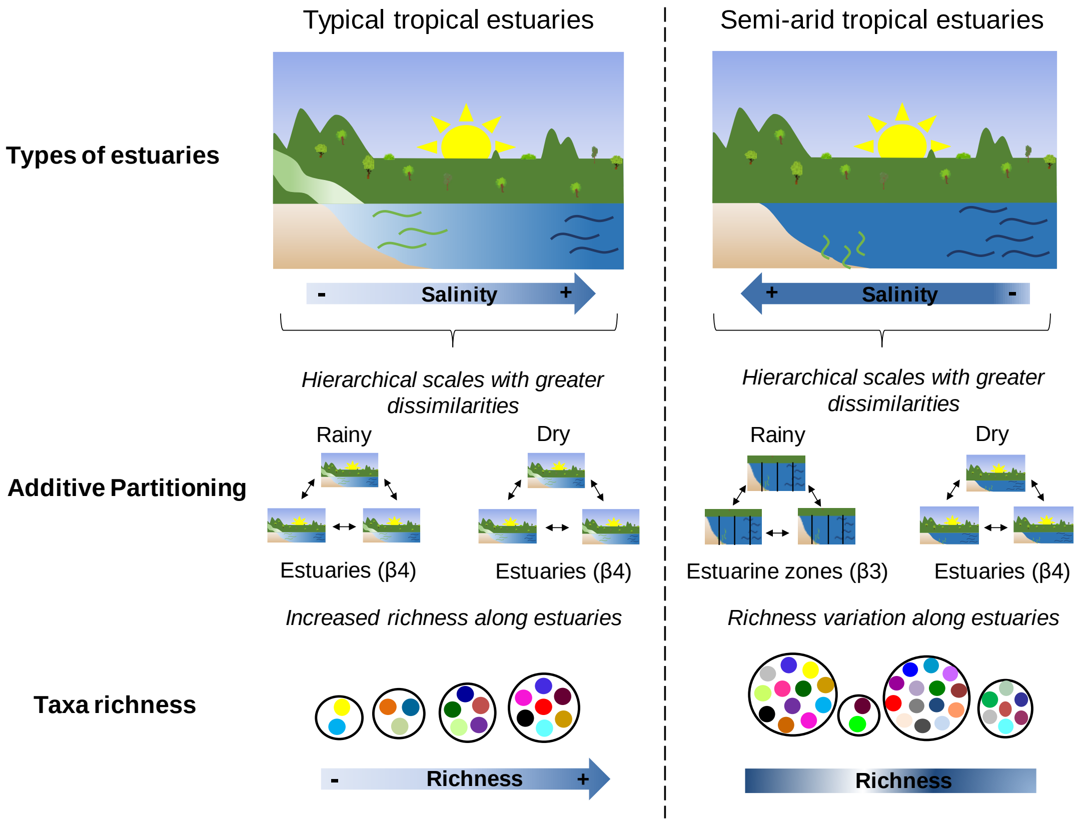
Running head: Diversity patterns of benthic macrofauna

Keywords: abundance/species replacement; abundance/richness difference; additive partitioning; benthic macrofauna; environmental filtering.

Graphical abstract:



ABSTRACT

Identifying the hierarchical spatial levels that show the greatest dissimilarities between communities and how these patterns are generated is essential to provide insights into the monitoring and protection of biodiversity. In this study, we additively partitioned diversity of macroinvertebrates into alpha, beta and gamma diversity across multiple scales in typical and semi-arid tropical estuaries. We also determined which components of the total beta diversity, in terms of species replacement or richness difference (presence-absence data) and abundance difference (relative abundance data), had the greatest relative importance in structuring the composition of benthic macrofauna. In typical and semi-arid tropical estuaries, a non-random spatial pattern was observed in additive partitioning of diversity, with higher values of beta diversity obtained at the largest scales analyzed. When considering the presence-absence data, in general there was no clear trend which components of beta diversity had greater relative importance in typical estuaries. In the semi-arid tropical estuaries, the richness difference component showed greater relative importance in the rainy season, whereas the species replacement presented greater proportions in the dry season. When considering abundance data, in general the abundance difference component showed greater relative importance in typical and semi-arid tropical estuaries in the two seasonal periods. Approaches based on the presence/absence and on the relative abundance of species provided complementary answers about the distribution patterns of benthic macroinvertebrate communities. We demonstrated that environmental filtering and dispersal limitation may affect the patterns of distribution of benthic macrofauna in estuaries located in regions with different climatic conditions.

2.1 INTRODUCTION

In the current scenario of accelerated environmental change and difficulties in implementing conservation strategies, understanding spatial patterns of biodiversity and how biological dissimilarity is generated are some of the main challenges in ecology (Gómez-Rodríguez et al. 2015; Heino et al. 2019). In this sense, describing how local communities interact with each other can contribute to the establishment of efficient conservation strategies (Leibold et al. 2004; Socolar et al. 2016).

As proposed by Whittaker (1960), the total diversity of a given region (gamma diversity; γ) can be dissociated into alpha (diversity of a given site; α) and beta (variation of diversity between sites; β) diversities. Beta diversity is a measure of compositional dissimilarity between sites, since it takes into consideration patterns of co-occurrence of species between localities (Whittaker 1960; Baselga 2010; Gómez-Rodríguez and Baselga 2018).

Emerging beta diversity among communities can result from different components (e.g., species replacement, abundance replacement, richness differences, abundance differences) (Schmera and Podani 2011; Carvalho et al. 2012; Podani et al. 2013). Species replacement and abundance replacement occur due to changes in species identity or number of individuals from one site to another, respectively (Podani 2013; Legendre 2014). Differences in species richness occur due to loss (or gain) of species between sites, while abundance differences refer to the dissimilarity in the number of individuals between sites (Carvalho et al. 2012; Legendre 2014). The relative contributions of each of these components to beta diversity may be related to the ecological tolerance and niche breadth of the species that make up a community in response to environmental variation (Carvalho et al. 2012).

In the past few decades, dissimilarity coefficients that differ in their mathematical properties have been used to decompose the total beta diversity into its components (e.g., Jaccard, Sørensen and Ružicka indices) (Baselga 2010; Schmera and Podani 2011; Podani et al. 2013). Traditionally, studies that decompose the total beta diversity into its components in estuarine ecosystems have only used presence-absence data (e.g., Barros et al. 2014; Medeiros et al. 2016a; Menegotto et al. 2019). However, it has been shown that considering only the identity of the species may not represent adequately patterns of biodiversity since these measures disregard important aspects of a community, such as the dominance and rarity of the species (Hillebrand et al. 2018). In this case, indices that consider relative abundances can provide more refined information to differentiate between communities (Legendre 2014).

Knowing the mechanisms underlying beta diversity patterns helps us understand how local communities interact with each other in metacommunities at different spatial scales (Wilson 1992; Leibold et al. 2004; Heino and Tolonen 2017). Estuarine ecosystems are ideal models for studying beta diversity patterns, since these ecosystems are naturally dynamic and highly spatially variable. The classical definition of estuaries considers these ecosystems as transition zones, where gradual longitudinal changes (e.g., water quality, depth, and sediment composition) occur in the upstream-downstream direction (i.e., from the continental drainage towards the sea), mainly in terms of salinity, that acts as an environmental filter in these ecosystems (Attrill and Rundle 2002). These gradual changes favor the existence of an estuarine gradient and a high spatial variability that shapes the distribution of benthic macrofauna, acting as "ecophysiological filters" (Remane 1934). Thus, since environmental conditions vary along estuaries, only species with the ability to perform osmoregulation persist in each environment, while others are not able to colonize and persist at a site (Remane 1934; Little et al. 2017). Estuarine benthic communities are predominantly marine and, therefore, a high richness and abundance of macroinvertebrates occurs in areas close to the sea, with a gradual decay towards areas closer to continental drainage (Alves et al. 2020).

The classical concept of estuaries as transitional environments between continental freshwater and marine ecosystems defines well most of the estuarine ecosystems of temperate and tropical regions, but not all. In the last few decades, a redefinition of the concept of estuaries has been proposed to also include those that exhibit some particularities that do not fit the classical concept (Potter et al. 2010; Nebra et al. 2016). Some estuaries, mainly those situated in regions with high temperatures and low precipitation (e.g., semi-arid regions), are little influenced by continental drainage, and may have continuous or periodic connection with the sea (Potter et al. 2010). In these cases, there are no clear longitudinal environmental patterns, but the salinity of these ecosystems shows a subtle decrease near the sea, being characterized as *negative* or *inverse estuaries* (Potter et al. 2010). The high salinity throughout the ecosystem contributes to the establishment of favorable habitats for the benthic macrofauna longitudinally, thus allowing high species richness and abundances at both ends of the estuaries.

In addition to spatial variation, estuaries are also subject to temporal variations related to the seasonally-regulated discharge of water from continental drainage and to their connection with the ocean regulated by the tides (Gobler et al. 2005; Telesh and Khlebovich 2010). Seasonality changes physical, chemical and morphological factors of estuarine ecosystems (e.g., input of nutrients and sediments, and modifications in water quality) and shapes the structure of biological communities (Gobler et al. 2005; Schallenberg et al. 2010; Netto et al. 2012).

In typical tropical estuaries (i.e., those presenting clear environmental gradients), during periods of greater rainfall greater continental drainage may cause a decrease in estuarine salinity as well as favor passive dispersal of benthic macrofauna. On the other hand, during periods of drought the salinity of the estuaries tends to increase due to the lower discharge of water from the continental drainage, and the species tend to present less passive dispersal. In contrast, in estuaries located in semi-arid regions, due to the absence of a direct entry of water from the continental drainage, the salinity changes irregularly along the estuary during the dry and rainy seasons. However, in rainy periods the salinity of the estuary decreases due to the greater precipitation and groundwater input in this seasonal period. Consequently, the community structure of the benthic macrofauna also varies irregularly in these estuaries.

In this study, we evaluated (i) the diversity patterns of benthic macroinvertebrate communities of estuaries located in typical and semi-arid tropical regions at multiple spatial scales and in different seasonal periods. We also focused on (ii) the components of beta diversity that show greater relative importance considering presence-absence and relative abundance data of the benthic macrofauna of typical and semi-arid tropical estuaries in different seasonal periods. Our intention here was not to describe a temporal pattern, but only to evaluate if sampling in different seasonal periods can influence the spatial patterns analyzed. Our hypotheses were: (i) the alpha diversity of the benthic macrofauna in both typical and semi-arid tropical estuaries is driven both by the seasonal periods and the estuarine longitudinal gradient (estuarine “zones”). We expected to observe a greater richness in areas with higher salinity and during the rainy period; (ii) higher values of beta diversity of estuarine benthic macrofauna occur at higher spatial scales (in our study, between estuarine zones and between estuaries), in both typical and semi-arid tropical estuaries and seasonal periods sampled; and (iii) the predominant components of total beta diversity are different between typical and semi-arid tropical estuaries, being mainly associated with species replacement and abundance replacement in semi-arid tropical estuaries. This should be due to irregular environmental variations along these ecosystems, and owing to differences in richness/abundance in typical tropical estuaries resulting from the gradual environmental changes exhibited by these environments.

2.2 MATERIAL AND METHODS

2.2.1 Study area

The study was carried out in six tropical estuarine ecosystems, of which three were typical of tropical (Paraíba do Norte, Mamanguape and Passos) and three were typical of semi-arid tropical (Tubarão, Galinhos and Casqueira) climatic conditions (Fig. 1; Table 1). All estuaries are located in northeastern Brazil. The typical tropical estuaries are located in the "As" climate (Alvares et al. 2013), i.e., hot and humid tropics, and the semi-arid tropical estuaries are situated in a semi-arid climate of the "BSh" type, with little precipitation and high evaporation rates (Alvares et al. 2013). The climatic conditions in northeastern Brazil (i.e., low precipitation and high temperatures) favor the existence of only two well-defined climatic periods in the region, dry and rainy (Santos et al. 2017). The rainy season typically occurs from June to August and the dry season from December to March (CPTEC, www.cptec.inpe.br, accessed in December 2018).

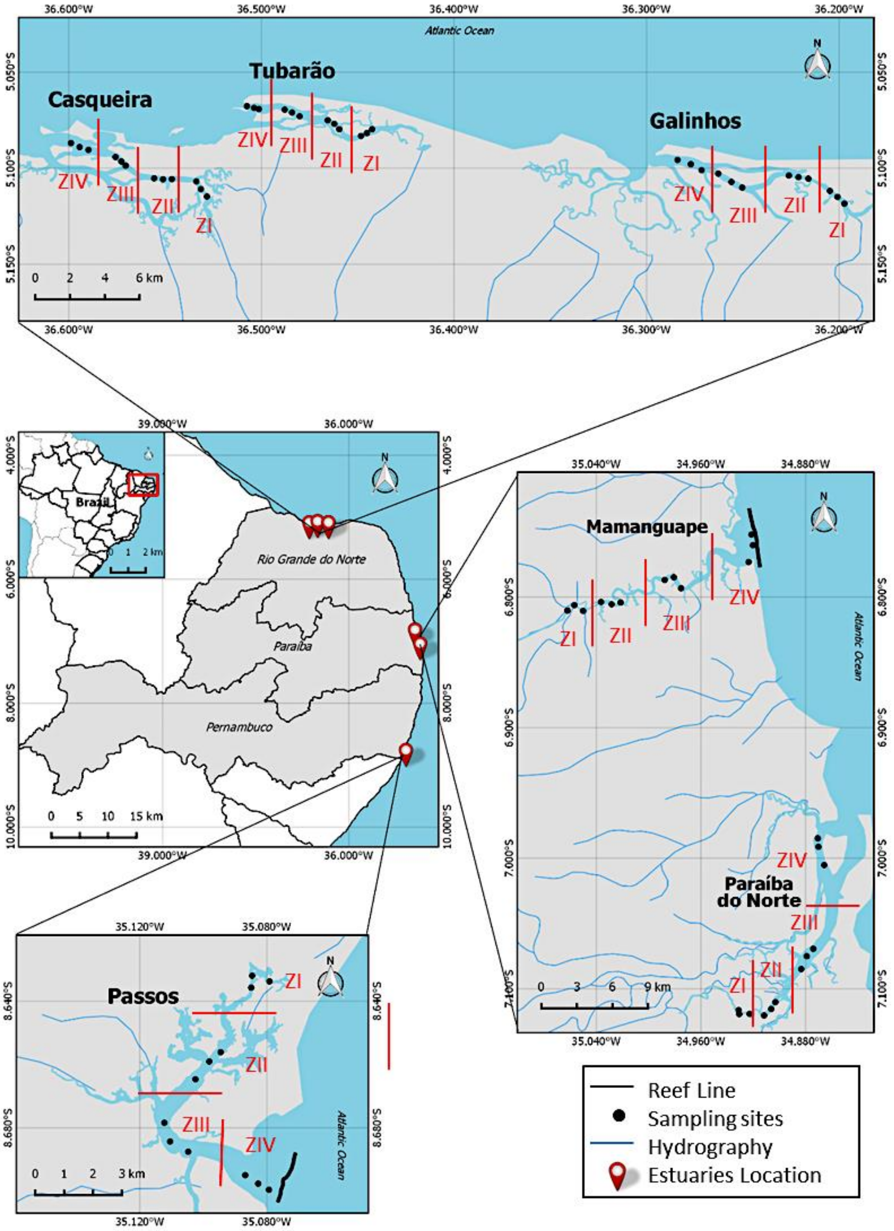


Figure 1. Geographic location of the typical (Paraíba do Norte, Mamanguape and Passos) and semi-arid (Tubarão, Casqueira and Galinhos) tropical estuaries in the states of Rio Grande do Norte, Paraíba and Pernambuco, presenting the sampling sites. Zone I (sites 1 to 3), Zone II (sites 4 to 6), Zone III (sites 7 to 9) and Zone IV (sites 10 to 12). Zone I is closest to continental drainage (upstream) and zone IV is closest to the sea (downstream).

Table 1. Characteristics of typical (Paraíba do Norte, Mamanguape and Passos) and semi-arid (Tubarão, Casqueira and Galinhos) tropical estuaries.

Characteristics	**Semi-arid tropical**			**Typical tropical**		
	Tubarão	**Galinhos**	**Casqueira**	**Mamanguape**	**Paraíba**	**Passos**
Mean annual rainfall (mm)	500	500	500	1200	1200	2000
Longitudinal extensions (km)	10	15	15	24	22	12
Location (state)	Rio Grande do Norte	Rio Grande do Norte	Rio Grande do Norte	Paraiba	Paraíba	Pernambuco
Inserted in a protection area	Yes	No	No	Yes	No	Yes

2.2.1.1 Typical tropical estuaries

The estuaries of Paraíba do Norte, Passos and Mamanguape include extensive areas of mangrove vegetation and, close to the estuaries, there is intensive sugarcane cultivation (Alves and Nishida 2003; Silva et al. 2004; Santana et al. 2018) (Table 1). Leisure, tourism and recreation activities are carried out in these ecosystems, with greater intensity in the Paraíba do Norte estuary (Alves and Nishida 2003; Marcelino et al. 2005). The Passos estuary is part of the estuarine complex of the Formoso River, along with the Ariquindá, Formoso and União rivers. This complex is strongly influenced by the sea because it is situated in a meso-tide estuarine complex (i.e., with tides ranging from 2 to 4 m), receiving a very low continental water supply (Figueirêdo et al. 2014).

2.2.1.2 Semi-arid tropical estuaries

Anthropogenic influences can be identified along the Tubarão, Casqueira and Galinhos ecosystems, although these ecosystems still exhibit characteristics of preserved environments, mainly the Tubarão estuary (Table 1). In this estuary, there are traditional human communities (Indigenous and others) that make sustainable use of the natural resources (Sales et al. 2016). In the Galinhos and Casqueira estuaries there are areas of salt production and shrimp farming.

2.2.2 Sampling design and collection of benthic macrofauna

Due to the high spatial variation in the environmental characteristics and ecological dynamics of estuarine ecosystems, a specific sampling design was devised for capturing the longitudinal environmental variations. In each estuary, four estuarine zones were established a priori with the aid of satellite images, defined as ZI, ZII, ZIII and ZIV, from upstream (continental drainage) to downstream (sea). In each zone, three equidistant sites were sampled (Fig. 1). Sediment composition and salinity were surveyed, and the longitudinal variations of these variables were used to define the estuarine gradient. We used a salinity refractometer (Model VX100SG) to determine the salinity of water at each site. To evaluate the sediment composition at each sampling site, an extra sediment sample was collected with a van Veen dredge (500 cm^2). Using a mechanical sieving, the sediment was classified into six grain size classes: clay (<38 μm), silt (38-63 μm), fine sand (63-250 μm), medium sand (250-500 μm), coarse sand (500-1000 μm), and gravel (>1000 μm). The zonation employed covered well the variation of environmental characteristics, mainly in terms of salinity levels (supplementary material I, II, and III).

At each site, three benthic macroinvertebrate subsamples were collected in the subtidal region, always during low tide, with a van Veen dredge (500 cm^2). Samples were washed in situ in 0.5-mm sieves. Only Mollusca, Polychaeta and Diptera were considered in this study, given the high representativeness of these groups in estuarine benthic communities (>90% of the individuals collected) and because these organisms could be identified to the genus level. The macroinvertebrate identification was performed in the laboratory with the aid of specialized taxonomic keys to mollusks (Rios 1985; Mikkelsen and Bieler 2008; Tunnell et al. 2010), polychaetes (Amaral and Nonato 1996) and dipterans (Trivinho-Strixino 2011).

The three taxonomic groups were combined to perform statistical analysis because our objective was to assess general biodiversity patterns of estuarine benthic macrofauna. We also conducted the analyses for each group separately, which showed little differences compared with the general pattern (Supplementary material IV and V). Therefore, we focused on the results of the whole community, emphasizing the generality of our conclusions.

The field collections were conducted during two periods: dry season (in December 2016 in semi-arid tropical estuaries and in February 2017 in tropical estuaries) and rainy season (in June in semi-arid tropical estuaries and in August in tropical estuaries, both in 2016), covering the typical climatic variation of the region.

2.2.3 Data analyses

2.2.3.1 Alpha diversity of benthic macroinvertebrates

To evaluate the influence of zones and periods on the alpha diversity of benthic macroinvertebrates, a Permutational Analysis of Variance (PERMANOVA) was performed for each set of estuaries (typical and semi-arid tropical), using 9999 permutations ($\alpha=0.05$) (Anderson et al. 2008). Euclidean distance was used as the dissimilarity measure between sites. As a measurement of α diversity, we considered the rarefied richness observed in the zones of each estuary, thereby minimizing the effect of the numbers of individuals on the sampled richness (individual-based rarefaction) (Hurlbert 1971; Gotelli and Colwell 2001). The abundance values used for the rarefaction procedures were 119 and 69 for the typical and semi-arid tropical estuaries, respectively, because these were the minimum abundances found in each group of sites. For each set of estuaries, three categorical factors were considered: period (two fixed levels: rainy and dry), estuarine zone (four fixed levels: ZI, ZII, ZIII and ZIV) and estuary (three random levels: Paraíba do Norte, Mamanguape and Passos or Tubarão, Casqueira and Galinhos).

2.2.3.2 Additive partitioning of diversity of benthic macrofauna

To partition the benthic macrofaunal diversity of the typical and semi-arid tropical estuaries at multiple spatial scales in the dry and rainy periods we used the additive partitioning method. This method enables all components of diversity to be measured on the same numerical scale, and thus these can be directly compared (Veech et al. 2002; Crist et al. 2003). In addition, this method shows low dependence between the alpha and beta components of diversity (Veech and Crist 2010). For these reasons, the additive partitioning of diversity is considered the most suitable for studying the variations of species diversity at different spatial scales.

We considered four nested spatial levels to perform additive partitioning of diversity. They corresponded to the diversity observed within the subsamples (α_1), the variation in diversity between subsamples (β_1), the variation in diversity between sites (β_2), the variation in diversity between estuarine zones (β_3) and the variation in diversity between estuaries (β_4). The beta diversity of each level was obtained from the difference between the average alpha diversity of the hierarchical level considered and the average alpha diversity observed at the next higher level ($\beta_i=\alpha_{i+1} - \alpha_i$) (Crist et al. 2003). The total diversity (γ) was then obtained through the sum of α_1 diversity (average alpha diversity of the lowest spatial level) and all components of beta diversity ($\gamma=\alpha_1+\beta_1+\beta_2+\beta_3+\beta_4$) (Josefson 2009) (Fig. 2). An individual-based null model (type I, according to Crist et al. 2003) was used to determine whether the observed components of diversity differed from a situation in which individuals were randomly distributed between subsamples, thus removing the effect of any aggregation of genera that might have occurred along all the spatial scales analyzed (Crist et al. 2003). The significance of differences between observed and expected values under null models at each hierarchical level was obtained considering the proportion of times that the null models obtained results higher than the observed pattern, using 9999 randomizations (Crist et al. 2003). In this case, a high proportion of expected values higher than observed values ($Prop_{exp>obs} > 0.975$) indicates that the observed values were significantly lower than those expected at random, whereas low proportions ($Prop_{exp>obs} < 0.025$) indicate that the observed values were significantly higher than those expected at random (Crist et al. 2003).

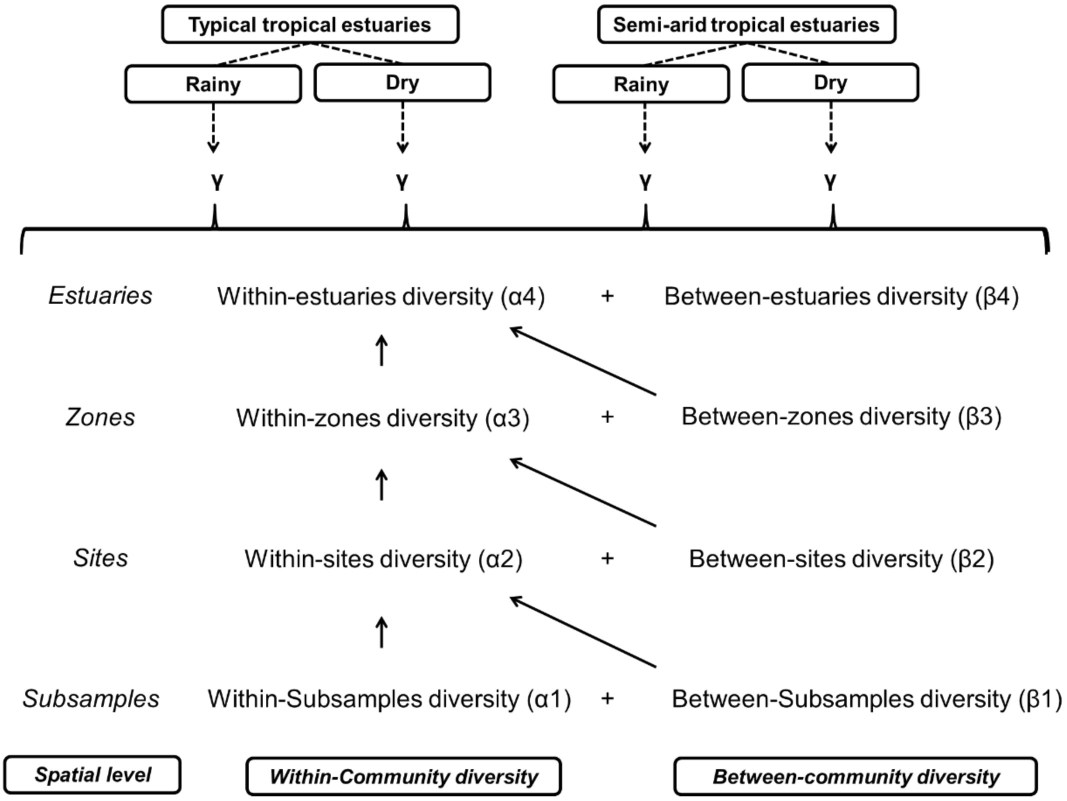


Figure 2. A scheme of the nested hierarchical spatial model applied in the typical and semi-arid tropical estuaries sampled in the dry and rainy periods. α1 is the diversity within subsamples, α2 is the diversity within sites, α3 is the diversity within zones, α4 is the diversity within estuaries, β1 is the diversity between subsamples, β2 is the diversity between sampling sites, β3 is the diversity between estuarine zones, and β4 is the diversity between estuaries. The total diversity of the typical and semi-arid tropical estuaries, in each period, is represented by the diversity γ, obtained by the sum of the components α1 and β ($\gamma = \alpha1 + \beta1 + \beta2 + \beta3 + \beta4$).

2.2.3.3 Components of total beta diversity

To decompose the total beta diversity (i.e., average dissimilarity between sites) considering the composition of the benthic macroinvertebrate communities based on replacement ($\beta repl_J$) and richness difference ($\beta rich_J$) (Schmera and Podani 2011; Carvalho et al. 2012) or replacement ($\beta repl_R$) and abundance difference ($AbDiff_R$) components (Podani 2013), we used the Jaccard dissimilarity coefficient (presence/absence data) and Ružicka dissimilarity coefficient (abundance data), respectively. For these analyses, we considered the macroinvertebrate communities of the sampling sites (i.e., summing the subsamples) at each estuary and at each sampling period (dry and rainy). Our interest was to quantify the components of total beta diversity of the regional species pool sampled within each estuarine ecosystem. For this analysis, we considered the pairwise dissimilarity between sites. The βtotal value varies from 0 to 1 and corresponds to the sum of βrepl and βrich/AbDiff$_R$ (βtotal = βrepl + βrich/AbDiff$_R$). The closer to the βtotal values, the greater the contribution of replacement or richness/abundance difference to beta diversity.

PERMANOVA analyses were performed in the statistical program PRIMER + PERMANOVA 6.1 (Systat Software, Cranes Software International Ltd., Anderson et al. 2008). The additive partitioning of diversity was performed in the software Partition 3.0 (Veech and Crist 2009). The decomposition of the Jaccard and Ružicka indices was performed in the software R (R CORE TEAM 2018), using the “BAT” package (Cardoso et al. 2015).

2.3 RESULTS

2.3.1 Composition of benthic macroinvertebrate communities

The polychaetes, mollusks and dipterans totaled 26,339 individuals collected. Of these, 13,008 were collected in the rainy season and 13,331 in the dry season. Polychaetes and mollusks were usually found in all estuaries and zones, while dipterans showed the lowest taxonomic richness, and were collected only in two typical tropical estuaries, mainly in upstream zones.

In the rainy season, we gathered 2,017 polychaetes, 1,984 mollusks and 521 dipterans in the typical tropical estuaries. The most representative genera were the polychaete *Laeonereis* and the dipteran *Polypedilum*, both in the Mamanguape estuary, and the mollusk *Caecum* in the Passos estuary (Supplementary material VI). In semi-arid tropical estuaries, only polychaetes and mollusks were collected, with an abundance of 4,936 and 3,550 individuals, respectively (Supplementary material VI). The most representative genera of polychaetes and mollusks in the semi-arid estuaries in the rainy season were *Exogone* (in the Casqueira estuary) and *Nucula* (in the Galinhos estuary). During the dry season, 1,276 polychaetes, 2,554 mollusks and 941 dipterans were collected in the typical tropical estuaries. The dominant genera were *Laeonereis* (in the Mamanguape estuary), *Polypedilum* (in the Mamanguape estuary) and *Caecum* (in the Passos estuary), representing polychaetes, dipterans and mollusks, respectively (Supplementary material VII). In semi-arid tropical estuaries, the benthic macrofauna was represented by 4,054 polychaetes and 4,506 mollusks. The genera *Laonice* (in the Casqueira estuary) and *Nucula* (in the Galinhos estuary) exhibited the greatest abundances (Supplementary material VII).

2.3.2 Alpha diversity of benthic macroinvertebrates

Rarefied richness was significantly different between zones of the typical tropical estuaries and showed a decay towards the areas of lower salinity (Table 2 and Fig. 3). This trend is less evident in the Passos estuary (Fig. 3). Differences in rarefied richness were not observed between zones of semi-arid tropical estuaries, nor between periods in either type of estuaries (Table 2; Fig. 3). The interactions between zones and seasonal periods were also not significant for typical and semi-arid tropical estuaries (Table 2).

Table 2. Results of the PERMANOVA comparing the rarefied richness of the estuarine zones of the benthic macroinvertebrate communities, considering the estuarine zones (fixed factor), seasonal periods (fixed factor) and estuaries (random factor). df = Degrees of freedom. SS = Sum of squares. MS = Medium squares (SS/Df). Pseudo-F = Statistic of the analysis.

	Semi-arid tropical					Typical tropical				
Source	**df**	**SS**	**MS**	**Pseudo-F**	***p*(perm)**	**df**	**SS**	**MS**	**Pseudo-F**	***p*(perm)**
Zones	3	31.356	10.452	0.23565	0.8609	3	795.18	265.06	5.6939	0.0418
Periods	1	2.7839	2.7839	8.7956	0.8139	1	28.722	28.722	0.65067	0.505
Zones x Periods	3	3.4741	1.158	9.9032	0.9512	3	64.548	21.516	0.91392	0.4838
Estuaries	2	206.16	103.08	8.815	0.0178	2	345.09	172.55	7.3291	0.0251
Zones x Estuaries	6	266.12	44.353	3.7929	0.0736	6	279.31	46.552	1.9773	0.219
Periods x Estuaries	2	63.302	31.651	2.7067	0.1452	2	88.284	44.142	1.875	0.2292
Total	23					23				

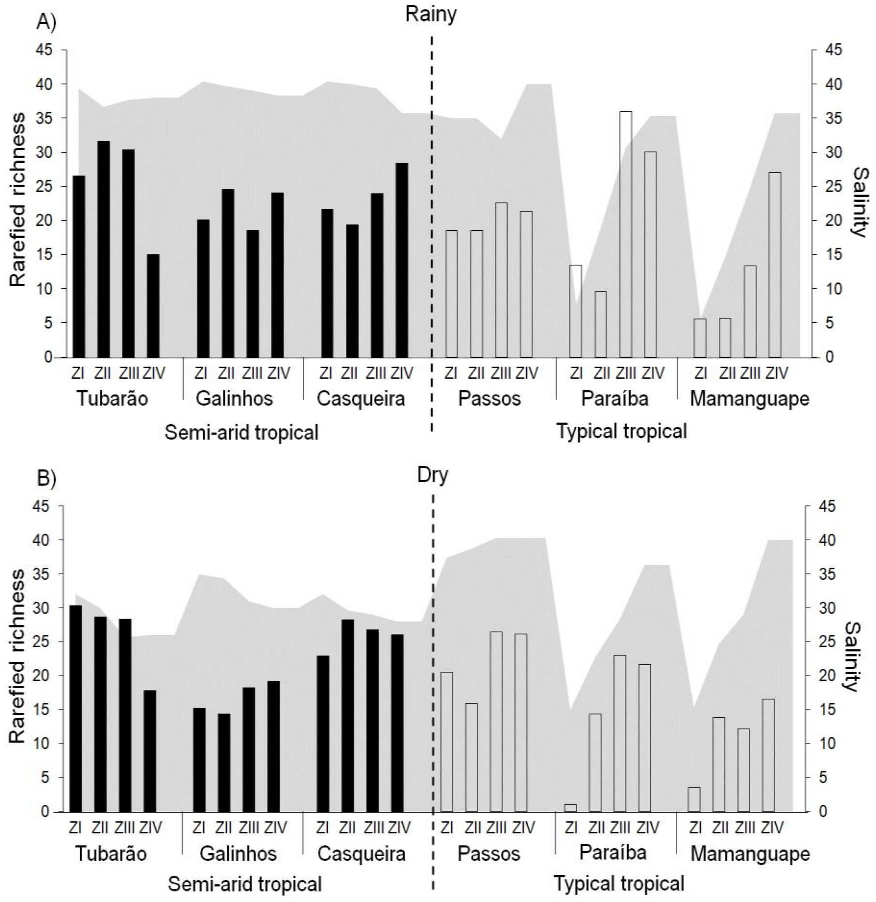


Figure 3. Rarefied taxonomic richness of the benthic macroinvertebrate communities observed in estuarine zones (ZI, ZII, ZIII and ZIV) in the semi-arid and typical tropical estuaries, during the rainy (A) and dry (B) periods. The gray shading shows the mean values of the salinity levels in the zones (see supplementary material I).

2.3.3 Additive partitioning of diversity of benthic macrofauna

Semi-arid tropical estuaries had a higher total richness of macroinvertebrate genera (gamma diversity) than typical tropical estuaries in both seasonal periods (rainy: semi-arid tropical =144, typical tropical =111; dry: semi-arid tropical =134, typical tropical =92) (Fig. 4). A non-random pattern was observed in the spatial distribution of taxa along the hierarchical levels considered in this study (Fig. 4). The highest proportions of beta diversity occurred at the largest spatial scales (between estuaries and estuarine zones) in typical tropical (rainy season: β4=40.45%, β3=32.66%; dry season: β4=43.80%, β3=29.85%) and semi-arid estuaries (rainy season: β4=24.72%, β3=30.71%; dry season: β4=31.65%, β3=27.05%), with observed values being higher than those expected at random ($\text{Prop}_{\text{exp>obs}} < 0.001$) (Fig. 4). The lowest values of beta diversity occurred between the subsamples and between the sampling sites in the semi-arid tropical (rainy period: β_1=9.48%, β_2=15.17%; dry period: β_1=9.92%, β_2=15.31%) and typical tropical estuaries (rainy period: β_1=6.34%, β_2=11.57%; dry period: β_1=5.98%, β_2=10.99%). In both periods, the observed values were significantly lower than those expected at random for β_1 in the semi-arid tropical estuaries in dry season, and for β_1 and β_2 in the typical tropical estuaries ($\text{Prop}_{\text{exp>obs}} > 0.999$). The β_2 value observed at the semi-arid tropical estuaries (β_2=14.14%) was statistically non-significant in the rainy period (Fig. 4).

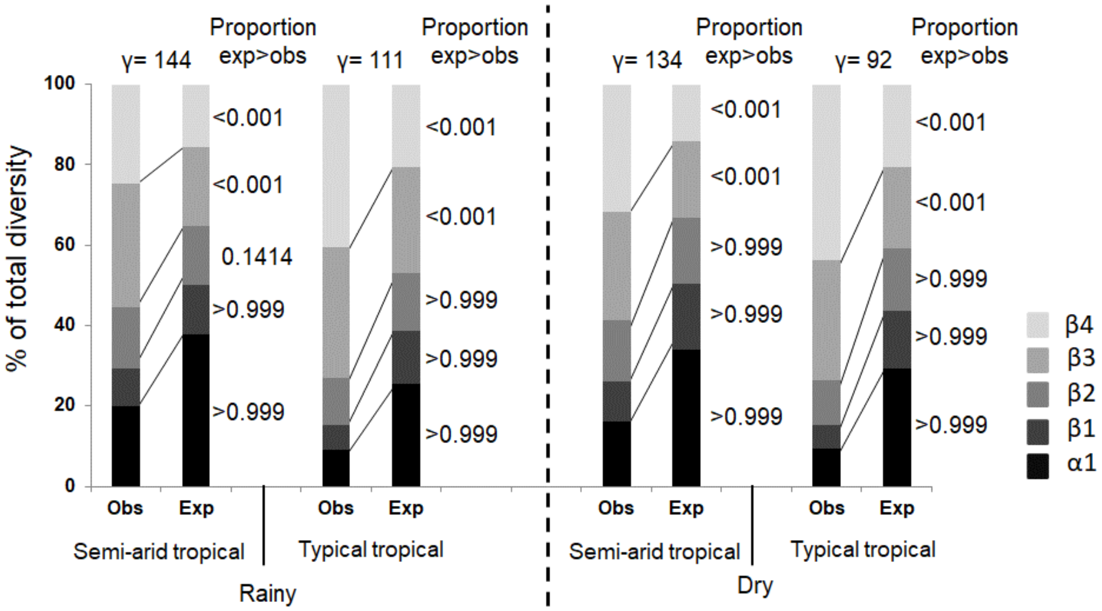


Figure 4. Proportions of values observed (Obs) and expected under null models (Exp) of the additive partitioning of the benthic macroinvertebrate diversity in the semi-arid and typical tropical estuaries during rainy and dry periods. The components of diversity are: α1 (diversity within subsamples), β1 (variation between subsamples), β2 (variation between sampling sites), β3 (variation between zones) and β4 (variation between estuaries).

2.3.4 Components of total beta diversity

Mean values of total beta diversity (βtotal) between sampling sites measured using the Jaccard and Ružicka indices varied subtly between the typical and semi-arid tropical estuaries in both seasonal periods (Table 3). In general, when considering the Jaccard index, there was no clear trend in which of the components had greater relative importance in typical estuaries (Table 3). On the other hand, in the semi-arid tropical estuaries, the richness difference component presented greater relative importance in the rainy season, whereas the species replacement presented greater proportions in the dry season (Table 3). When beta diversity was partitioned with the Ružicka index, in general the abundance difference component showed greater relative importance in the typical and semi-arid tropical estuaries in the two seasonal periods, except in the Passos and Tubarão estuaries in the rainy and dry periods, respectively (Table 3).

Table 3. Mean values of Jaccard dissimilarities (presence and absence data) and Ružicka (abundance data) of the benthic macroinvertebrate communities of the sampling sites (i.e., summing the subsamples) of each estuary in the rainy and dry periods, decomposed into species replacement (βrepl_J) and richness difference (βrich_J) components, and abundance replacement (βrepl_R) and abundance difference (AbDiff_R) components.

	Rainy						**Dry**					
	Semi-arid tropical			**Typical tropical**			**Semi-arid tropical**			**Typical tropical**		
	Tubarão	**Galinhos**	**Casqueira**	**Mamanguape**	**Paraíba**	**Passos**	**Tubarão**	**Galinhos**	**Casqueira**	**Mamanguape**	**Paraíba**	**Passos**
Jaccard												
Btotal$_J$	0.80	0.74	0.79	0.84	0.82	0.78	0.80	0.77	0.73	0.83	0.85	0.79
Brepl$_J$	0.34	0.32	0.46	0.44	0.28	0.49	0.41	0.41	0.43	0.45	0.27	0.50
Brich$_J$	0.46	0.42	0.33	0.40	0.54	0.29	0.39	0.36	0.30	0.38	0.58	0.29
Ružicka												
Btotal$_R$	0.90	0.87	0.90	0.92	0.92	0.86	0.91	0.89	0.88	0.90	0.91	0.90
Brepl$_R$	0.33	0.29	0.35	0.36	0.39	0.56	0.55	0.31	0.40	0.36	0.20	0.41
AbDiff$_R$	0.57	0.58	0.55	0.56	0.53	0.30	0.36	0.58	0.48	0.54	0.71	0.49

2.4 DISCUSSION

The taxonomic alpha diversity of benthic macroinvertebrate communities varied throughout the zones in the semi-arid and typical tropical estuaries, but in different directions. In the typical tropical estuaries, an increase in taxonomic alpha diversity was observed in the upstream-downstream direction, which is in agreement with other studies (e.g., Bleich et al. 2011; Medeiros et al. 2016a; Little et al. 2017). Several studies have shown that, in these ecosystems, salinity is the main factor shaping taxonomic richness variation along the estuarine longitudinal gradient (Gilberto et al. 2007; Telesh and Khlebovich 2010; Barros et al. 2014). Although we expected that the richness difference component would be of greater relative importance for beta diversity in typical tropical estuaries, the influence of salinity as an environmental filter for this community may explain the relative importance of both components. As the environmental conditions of the estuaries change from upstream to downstream, the number and identity of species that inhabit each estuarine zone varies due to environmental filtering owing to salinity, thereby generating a richness difference as well as a species replacement gradient. Our results generally corroborated those of Menegotto et al. (2019), who decomposed the beta diversity patterns of the estuarine benthic macrofauna in the turnover and nestedness components (*sensu* Baselga 2010). They observed that salinity was the factor driving species replacement along the estuary at larger spatial scales. Nestedness is a special case of richness difference, where poorer communities are subsets of richer communities (Baselga 2010). Therefore, it is not directly comparable to the richness difference component we used in this study.

The zones with lower salinity are recognized as ecophysiological barriers, favoring the persistence of species that are adapted to low salinity levels. This may be related to the colonization of euryhaline species (e.g., *Laeonereis*; Supplementary material VIII), which have morphological and physiological adaptations to regulate internal ion concentrations and persist at lower levels of salinity (Cartier et al. 2011). As salinity increases, there is a progressive increase in the species richness of marine taxa along the estuary (Medeiros et al. 2016a). Accordingly, species that accidentally disperse, but do not have adaptations to persist outside their salinity limits, are replaced along the longitudinal gradient of estuaries, as was evident for the dipterans present in the Mamanguape estuary, especially during the dry season (Supplementary material VII).

A clear pattern in the taxonomic richness of the benthic macroinvertebrate communities along the semi-arid tropical estuaries zones was not observed in our study. This finding is in line with the results of Nebra et al. (2016), who also analyzed the distribution of benthic macrofauna in an estuarine environment that did not show a defined salinity gradient. This may be related to the absence of a direct supply of water from the continental drainage and the extreme environmental conditions of a semi-arid climate to which these estuaries are subjected (i.e., high temperature and low precipitation). However, these conditions do not generate a gradual change in environmental conditions, as occurs along typical tropical estuaries. The substantial salt incursion into these ecosystems, together with a reduced continental influence, favors the establishment and survival of marine species throughout the entire ecosystems, which explains the higher diversity observed along all zones in these estuaries. In semi-arid tropical estuaries, benthic organisms are adapted to abrupt environmental variations, not only in terms of salinity, but in relation to other environmental parameters (e.g., sediment type, pH, temperature, redox potential) (Medeiros et al. 2016b; Nebra et al. 2016). Due to the absence of a clear longitudinal environmental gradient in these ecosystems, seasonal environmental variations seemed to have a greater effect on the structuring of the total beta diversity of estuarine macrobenthic communities, changing the relative importance of species replacement (drought period) and richness difference (rainy season) components.

The higher proportions of beta diversity observed at larger spatial scales may be explained by the restricted ability of species to disperse, or due to the increase of environmental factors that limit colonization (e.g., salinity), resulting in more aggregate communities (Josefson 2009). The lack of morphological and functional abilities of the estuarine benthic macrofauna (mainly polychaetes and mollusks) to disperse to more distant sites may be a key structuring factor at larger spatial scales, as these organisms are mostly sedentary in benthic habitats and mainly passively dispersed (Medeiros et al. 2016a).

In estuarine ecosystems, tidal variations and the discharge of water from the continental drainage are factors that affect the passive dispersal of the benthic species through drift mechanisms (Josefson and Hansen 2004). The greater diversity of genera observed in zone I compared to zone II in the tropical estuaries Paraíba do Norte and Mamanguape during the rainy season (Fig. 3) reinforced this idea. Probably, many taxa present in zone I may have been supported by mass effects during the rainy season. Species typical of continental drainage and areas of higher salinity (habitat source) emigrate by passive dispersal to zone I (habitat sink), which may have compensated for the naturally low richness of these areas. This suggests that mass effects occurring in this seasonal period may have allowed partial homogenization of the community structure between adjacent zones and, consequently, decreased beta diversity (Leibold et al. 2004; Heino et al. 2015). Such potentially high dispersal rates may also explain the presence of dipterans in downstream areas of the Mamanguape estuary during the rainy season.

In the dry season, we observed that, as a consequence of the environmental changes related to seasonal climatic variation (i.e., low discharge of freshwater in estuaries and high temperatures), many macroinvertebrate genera that were present in zone I of the typical tropical estuaries disappeared from that zone (e.g., *Chironomus* and *Hemipodia;* Supplementary material VIII). This environmental filtering of genera might have occurred due to the significant increase in salinity levels in zone I in the dry period when compared to the rainy season (supplementary material I). In this case, the environmental characteristics of the dry period may have acted as a dispersal barrier that prevented species migration between estuarine zones (Heino et al. 2015). Thus, the species that migrated to zone I during the rainy season may not have the ability to persist to the new environmental conditions of drought periods and, consequently, presented decreased survival rates, resulting in communities that only persist in habitats with particular environmental characteristics (Harrison et al. 1992; Kawecki 2008). This pattern was not observed in the Passos estuary because this ecosystem is strongly influenced by saline incursions and has a very low inflow of continental freshwater drainage, maintaining high salinity throughout the estuary and consequently showing little variation in taxonomic richness between estuarine zones (Figueirêdo et al. 2014).

The results of additive partitioning analysis were similar to those obtained in studies of estuaries of temperate regions, which also showed greater dissimilarities at the larger spatial scales, i.e., between different salinity zones (e.g., Josefson 2009; Josefson and Göke 2013). In our study, we considered one additional spatial level, corresponding to the diversity between estuaries. Our results showed that at larger spatial scales, the spatial distances (in this study represented by the geographic separation between the estuaries at the β_4 scale) and environmental filtering were likely to be the factors that most influenced the dissimilarity of the benthic macroinvertebrate communities, except in the semi-arid tropical estuaries in the rainy season.

The results of decomposing the total beta diversity based on the quantitative differences (i.e., Ružicka dissimilarity coefficient) showed that the abundance difference component had greater relative importance than the replacement component. These results suggest that in estuaries located in the typical and semi-arid tropical region there was generally a low replacement of abundance of benthic macroinvertebrates throughout the estuaries. However, the difference in the number of individuals that occurred between the sites was high. Thus, our results suggest that as the environmental conditions of typical and semi-arid tropical estuaries change along the longitudinal gradient there is considerable variation in the number of rare and dominant species, affecting both the identity of the species and their relative abundances.

When presence-absence data was considered, community structure was different between typical and semi-arid estuaries. On the other hand, when indices that account for relative abundances were used, the benthic macrofauna was patterned in similar ways between estuaries. Therefore, in highly variable and dynamic environments such as estuarine ecosystems, the use of approaches that consider both the presence-absence data and relative abundances simultaneously can provide complementary views about the distribution patterns of the biota. These results are important since, in some cases, the identity of species between locations may remain the same although the dominance of species may change and cause potential changes in ecosystem functioning.

We considered only the taxonomic diversity of the benthic macrofauna. Thus, we propose that future studies should investigate how the functional diversity of the benthic macrofauna is shaped according to the environmental conditions of typical and semi-arid tropical estuaries. A functional approach would help filling knowledge gaps about the structuring of the biotic communities and the functional dynamics of these ecosystems.

In the face of constant global environmental change, our results showed that during periods of drought, benthic macroinvertebrate communities tended to become more patchily distributed and tied to the environmental conditions of each estuarine zone. In addition, during drought periods species adapted to areas of lower salinity are eliminated from this environment due to unfavorable conditions and low passive dispersal rates. Therefore, prolonged periods of drought can cause a decline in the biodiversity of benthic macrofauna, with consequent changes in the dynamics and functioning of estuarine ecosystems. Such changes are likely to occur in any other ecosystem which shows similarly strong environmental gradients and seasonally-driven dispersal limitation.

In conclusion, we observed that the environmental conditions of estuaries located in regions with different climatic conditions contributed to distinct distribution patterns of the benthic macrofauna. However, the relative abundances of macroinvertebrate genera were structured in similar ways between typical and semi-arid estuaries. Environmental variations and dispersal barriers likely affected community composition at multiple spatial scales and during different seasonal periods. Therefore, all these factors should be considered when trying to understand metacommunity organization and the effects of anthropogenic alterations on estuarine environments. In addition, we suggest that approaches aimed to understand the distribution patterns of estuarine communities should consider not only species identity but also their relative abundances, as a simultaneous consideration of both approaches provides more comprehensive and complementary views of biodiversity.

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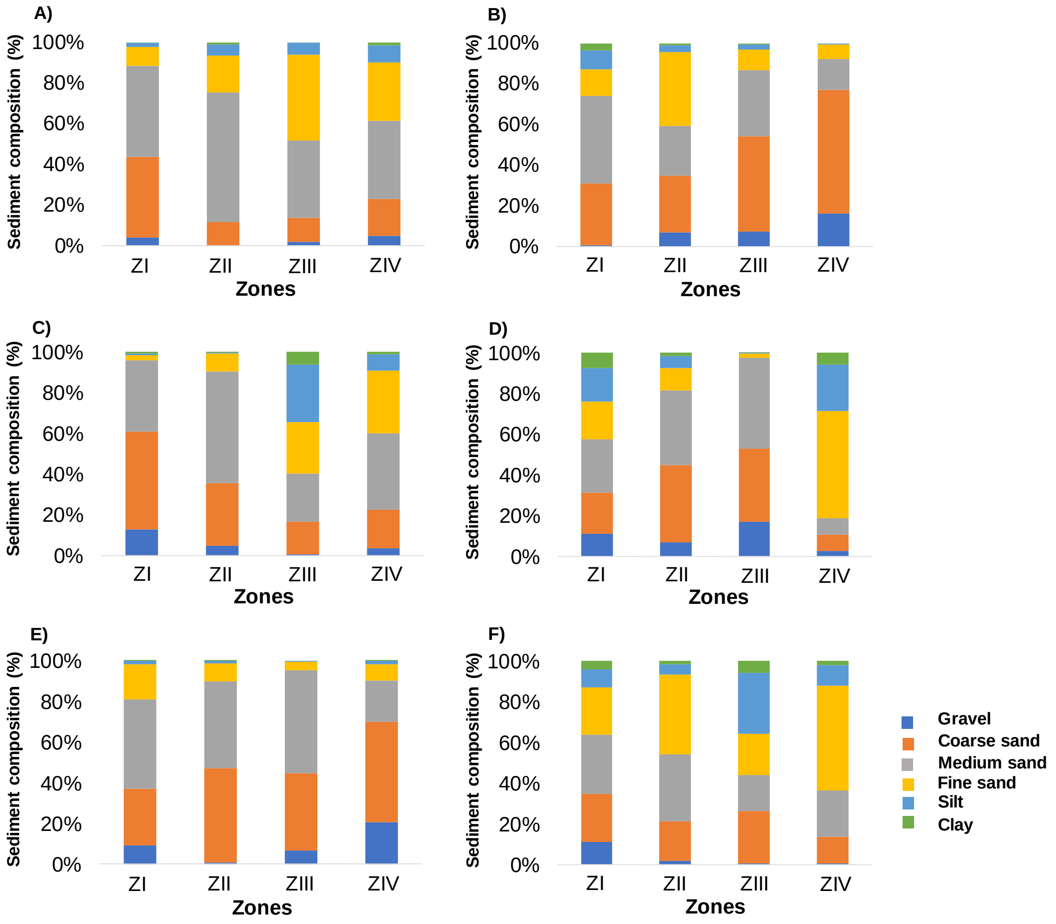
Conflict of interest

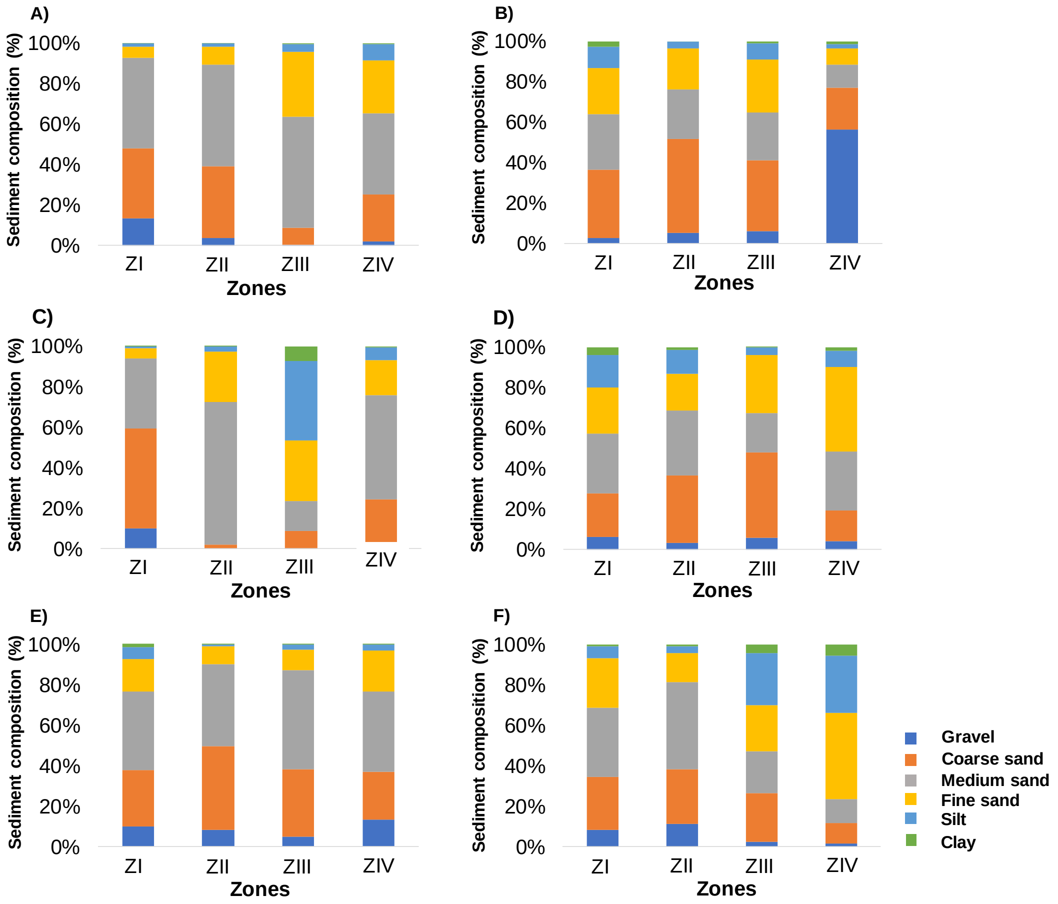
No conflict of interest

Supplementary material I. Mean values and standard deviation of the salinity measurements at the sites of each estuarine zone (ZI, ZII, ZII and ZIV) of the typical (Mamanguape, Paraíba do Norte and Passos) and semi-arid (Tubarão, Galinhos and Casqueira) tropical estuaries in the rainy and dry periods.

	Rainy period					
	Typical tropical			**Semi-arid tropical**		
	Mamanguape	**Paraíba**	**Passos**	**Tubarão**	**Galinhos**	**Casqueira**
ZI	5.66 ± 2.51	7.66 ± 5.68	35.00 ± 0.00	39.33 ± 1.52	40.33 ± 0.58	40.33 ± 0.58
ZII	14.66 ± 1.15	19.00 ± 2.00	35.00 ± 0.00	36.66 ± 2.88	39.67 ± 0.58	40.00 ± 0.00
ZIII	24.66 ± 0.57	30.66 ± 3.05	32.00 ± 6.08	37.66 ± 1.52	39.00 ± 0.00	39.33 ± 0.58
ZIV	35.66 ± 4.93	35.33 ± 0.57	40.00 ± 0.00	38.00 ± 0.00	38.33 ± 1.15	35.67 ± 0.58
	Dry period					
	Typical tropical			**Semi-arid tropical**		
	Mamanguape	**Paraíba**	**Passos**	**Tubarão**	**Galinhos**	**Casqueira**
ZI	15.33 ± 4.72	15.00 ± 5.00	37.33 ± 5.51	32.00 ± 0.00	35.00 ± 0.00	32.00 ± 0.00
ZII	24.67 ± 0.58	22.68 ± 2.52	38.67 ± 4.04	30.00 ± 2.00	34.33 ± 0.57	29.68 ± 0,58
ZIII	29.00 ± 2.64	28.33 ± 0.58	40.33 ± 0.58	25.68 ± 1.15	31.00 ± 0.00	29.00 ± 1.00
ZIV	40.00 ± 0.00	36.33 ± 1.53	40.33 ± 0.58	26.00 ± 0.00	30.00 ± 0.00	28.00 ± 1.53



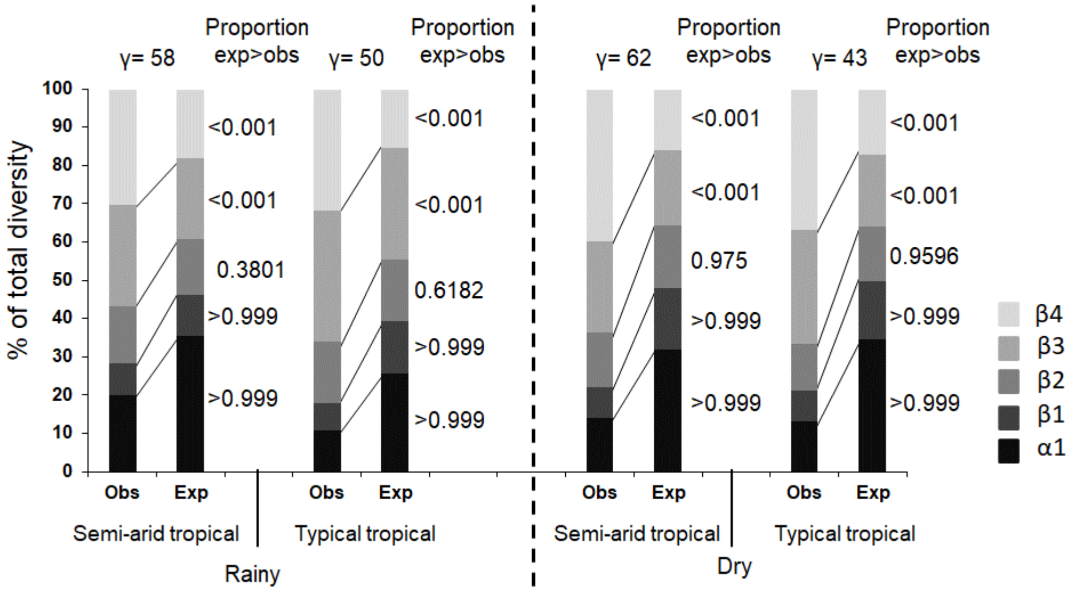
Supplementary material II. Proportion of clay, silt, fine sand, medium sand, coarse sand and gravel along the zones in the typical estuaries Paraíba do Norte (A), Mamanguape (C) and Passos (E), and semi-arid tropical estuaries Tubarão (B), Casqueira (D) and Galinhos (F) in the rainy season.



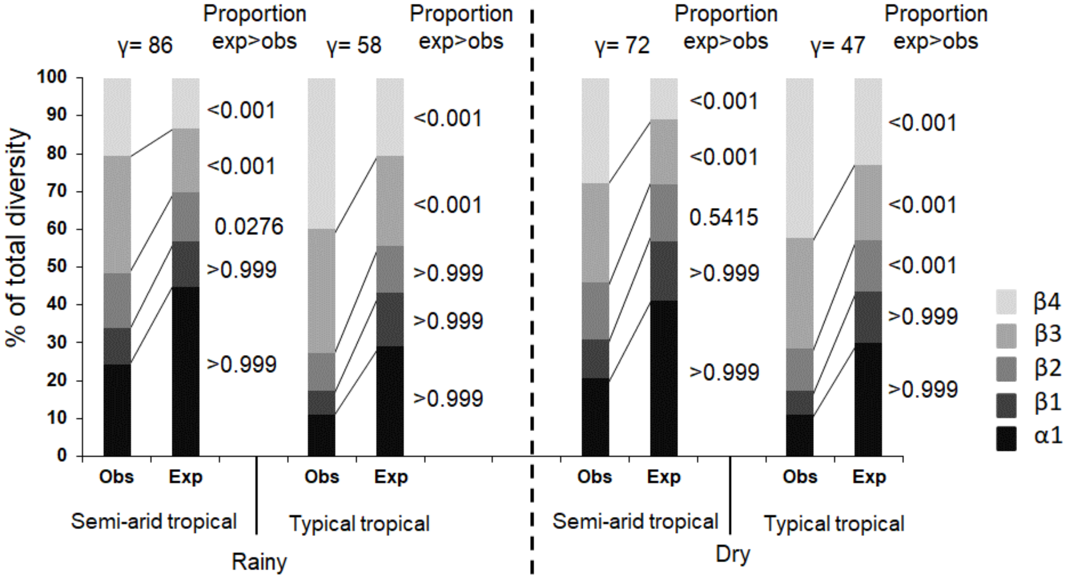
Supplementary material III. Proportion of clay, silt, fine sand, medium sand, coarse sand and gravel along the zones in the typical estuaries Paraíba do Norte (A), Mamanguape (C) and Passos (E), and semi-arid tropical estuaries Tubarão (B), Casqueira (D) and Galinhos (F) in the dry season.

Supplementary material lV. Proportions of values observed (Obs) and expected under null models (Exp) of the additive partitioning of the mollusks (A) and polychaetes (B) in the semi-arid and typical tropical estuaries during rainy and dry periods. The components of diversity are: α1 (diversity within subsamples), β1 (variation between subsamples), β2 (variation between sampling sites), β3 (variation between zones) and β4 (variation between estuaries).

A) Mollusks

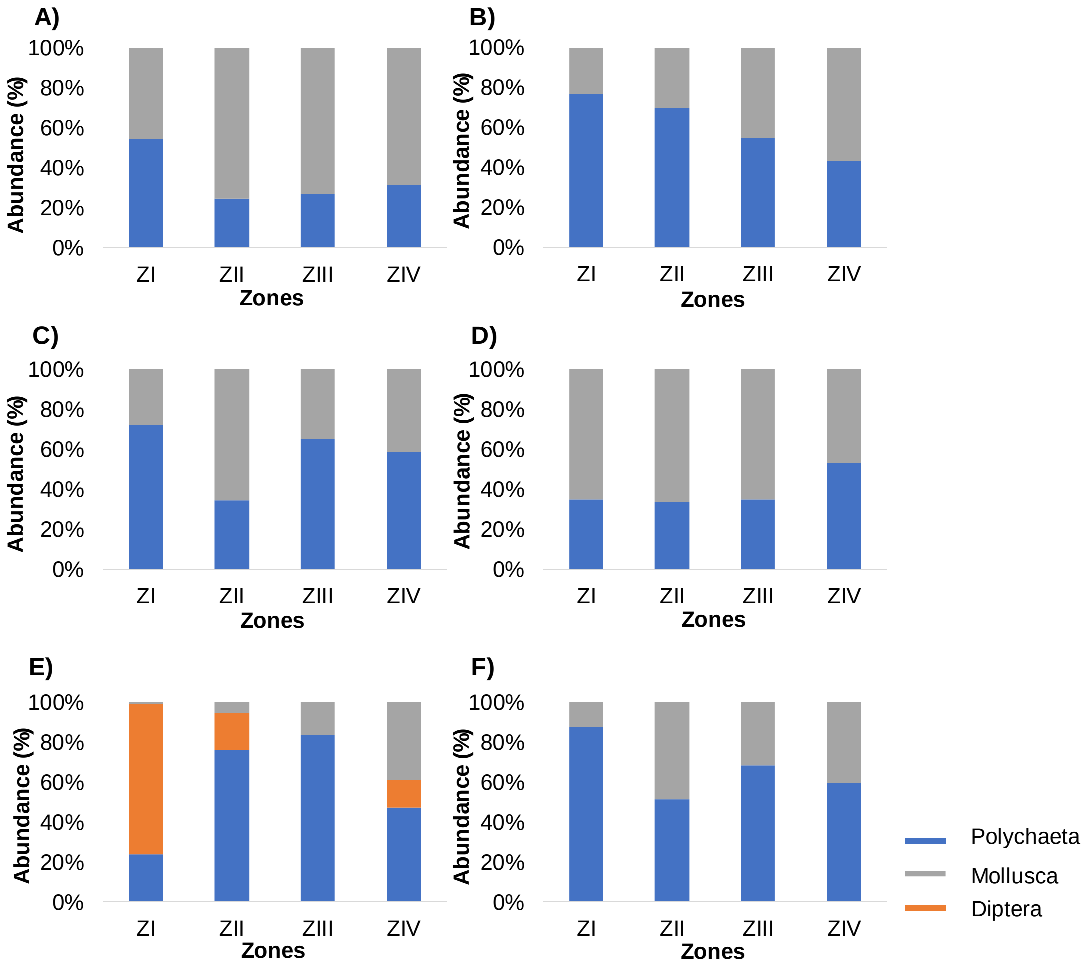


B) Polychaetes

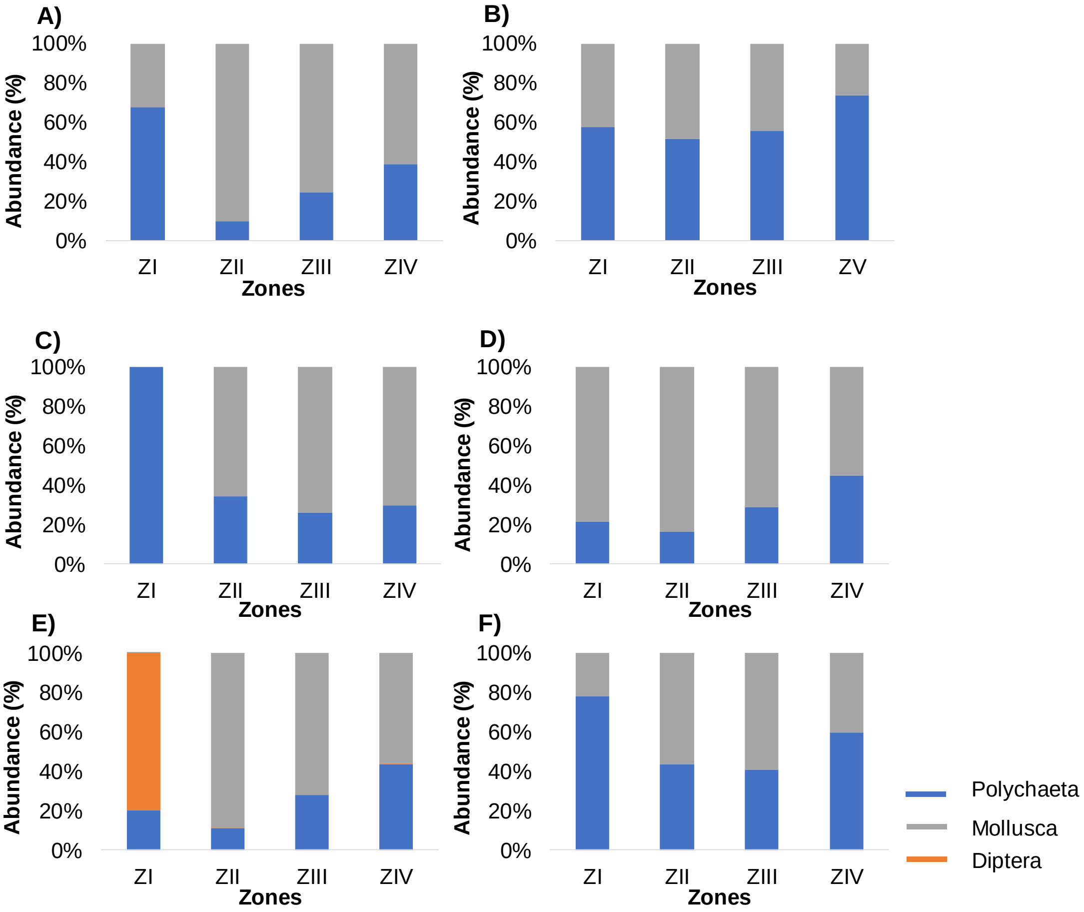


Supplementary material V. Mean values of Jaccard dissimilarities (presence and absence data) and Ružicka (abundance data) of the mollusks and polychaetes of the semi-arid and typical tropical estuaries sampled in the rainy and dry periods, decomposed into species replacement ($\beta repl_J$) and richness difference ($\beta rich_J$) components, and replacement ($\beta repl_R$) and abundance difference ($\beta AbDiff_R$) components.

	Rainy						**Dry**					
	Semi-arid tropical			**Typical tropical**			**Semi-arid tropical**			**Typical tropical**		
	Tubarão	**Galinhos**	**Casqueira**	**Mamanguape**	**Paraíba**	**Passos**	**Tubarão**	**Galinhos**	**Casqueira**	**Mamanguape**	**Paraíba**	**Passos**
Mollusks												
Btotal$_J$	0.80	0.68	0.80	0.86	0.76	0.75	0.79	0.73	0.77	0.80	0.84	0.74
Brepl$_J$	0.35	0.25	0.46	0.20	0.23	0.37	0.38	0.28	0.46	0.17	0.20	0.42
Brich$_J$	0.45	0.43	0.34	0.66	0.53	0.38	0.41	0.45	0.31	0.63	0.64	0.32
Btotal$_R$	0.89	0.86	0.89	0.90	0.87	0.85	0.91	0.88	0.86	0.88	0.90	0.89
Brepl$_R$	0.40	0.25	0.31	0.20	0.36	0.42	0.48	0.21	0.40	0.14	0.15	0.28
BAbDiff$_R$	0.49	0.61	0.58	0.70	0.51	0.43	0.43	0.67	0.46	0.74	0.75	0.61
Polychaetes												
Btotal$_J$	0.79	0.78	0.78	0.82	0.85	0.76	0.80	0.79	0.71	0.85	0.86	0.84
Brepl$_J$	0.31	0.29	0.42	0.41	0.29	0.46	0.41	0.38	0.36	0.51	0.23	0.44
Brich$_J$	0.48	0.49	0.36	0.41	0.56	0.30	0.39	0.41	0.35	0.34	0.63	0.40
Btotal$_R$	0.90	0.87	0.90	0.90	0.94	0.90	0.90	0.91	0.89	0.93	0.93	0.92
Brepl$_R$	0.26	0.30	0.32	0.32	0.31	0.38	0.43	0.36	0.31	0.33	0.21	0.30
BAbDiff$_R$	0.64	0.57	0.58	0.58	0.63	0.52	0.47	0.55	0.58	0.60	0.72	0.62



Supplementary material VI. Percentage of abundance of main taxonomic groups (Polychaeta, Mollusca and Diptera) in the typical tropical estuaries Passos (A), Paraiba do Norte (C) and Mamanguape (E) and in the semi-arid tropical estuaries Tubarão (B), Galinhos (D) and Casqueira (F) in the rainy season.



Supplementary material VII. Percentage of abundance of main taxonomic groups (Polychaeta, Mollusca and Diptera) in the typical tropical estuaries Passos (A), Paraiba do Norte (C) and Mamanguape (E), and in the semi-arid tropical estuaries Tubarão (B), Galinhos (D) and Casqueira (F) in the dry season.

Supplementary material VIII. Abundance of each genera, total abundance and richness of the benthic macroinvertebrate community sampled in typical (Mamanguape, Paraiba do Norte, and Passos) and semi-arid (Tubarão, Galinhos, and Casqueira) tropical estuaries in dry and rainy seasons.

	Typically tropical						**Semi-arid tropical**					
	Mamanguape		**Paraíba**		**Passos**		**Tubarão**		**Galinhos**		**Casqueira**	
	Rainy	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**
Polychaeta												
Arabella	0	0	0	0	0	0	2	0	0	0	10	3
Acromegalomma	6	1	18	24	11	6	0	21	1	18	3	14
Allita	0	0	16	0	4	1	0	2	0	0	0	0
Amphictene	0	0	3	0	0	0	0	0	0	1	0	0
Aricidea	7	0	1	0	0	3	78	32	31	19	85	178
Armandia	14	26	1	0	3	14	12	34	11	19	26	0
Boccardia	0	0	6	0	0	1	0	0	0	5	1	0
Branchiomma	0	0	0	0	0	0	0	12	1	0	3	0
Branchiosyllis	0	0	0	0	0	0	0	0	0	0	1	0
Cabira	0	0	6	0	5	0	2	0	2	5	4	0
Capitella	2	0	3	0	31	15	8	0	15	55	16	24
Caulleriella	0	0	0	0	0	0	2	0	0	0	0	0
Ceratonereis	0	0	0	0	2	2	7	20	4	3	6	55
Chaetacanthus	0	0	0	0	0	0	1	0	2	0	1	0
Chone	0	0	0	0	3	0	0	2	1	1	5	152
Chrysopetalum	0	0	0	0	0	0	0	0	0	0	2	4
Cirrophorus	0	0	0	0	0	0	1	15	32	5	141	86
Clymenella	0	0	1	0	2	1	23	0	5	0	39	0
Cossura	0	1	2	0	0	0	0	0	4	30	1	0
Diopatra	0	0	29	8	6	28	1	6	4	1	2	19
Dispio	0	0	0	0	0	0	1	6	15	2	1	0
Dorvillea	0	0	16	5	49	42	112	55	27	13	32	29
Drilonereis	0	0	0	0	1	0	0	0	0	0	6	0
Eteone	0	0	5	0	0	0	5	7	0	0	3	1
Euclymene	5	0	41	4	0	0	6	29	66	83	30	82
Eumida	0	1	0	0	0	0	1	1	10	1	89	48
Euphionella	3	0	0	0	0	0	0	4	1	0	29	3
Exogone	1	0	3	0	142	27	24	30	147	24	677	210
Glycera	1	25	7	9	4	5	2	8	10	7	9	4
Glycinde	11	75	65	17	50	14	32	22	165	55	41	52
Goniada	1	0	0	0	1	0	13	3	0	0	0	6
Goniadides	0	5	3	23	34	9	21	126	1	1	16	4
Grubeulepis	1	0	0	0	0	3	0	2	10	3	9	43
Gymnonereis	0	0	0	0	0	0	50	17	18	90	58	142
Hemipodia	2	0	35	5	2	9	17	25	1	11	7	1
Hermundura	0	0	0	0	0	0	0	1	14	3	4	5
Hesione	0	0	0	0	0	0	0	0	0	0	2	4

Heteromastus	4	1	61	2	10	56	8	0	7	12	3	0
Heteropodarke	0	0	0	0	1	0	0	0	0	0	0	0
Hydroides	0	0	0	0	0	0	0	0	0	3	0	0
Isolda	0	0	16	3	3	6	3	3	3	8	3	0
Kinbergonuphis	6	0	7	8	17	18	14	26	54	36	15	33
Labrorostratus	0	0	0	0	0	0	0	0	0	0	1	0
Laeonereis	284	166	73	7	47	33	0	0	0	0	1	2
Laonice	0	0	0	0	0	0	90	101	52	6	107	312
Lumbrineris	170	89	41	70	0	1	17	9	13	34	9	27
Lysarete	0	0	0	3	0	0	0	0	0	0	0	1
Lysidice	1	0	0	2	43	50	48	17	3	5	23	31
Magelona	16	0	31	0	13	0	55	0	33	0	33	0
Marphysa	0	0	0	0	0	1	0	0	0	1	0	0
Mediomastus	27	2	30	0	10	10	31	2	47	40	95	5
Melinna	0	0	0	0	0	0	4	2	0	3	0	0
Mexieulepis	0	0	0	0	0	0	0	0	0	0	1	0
Micronereides	0	0	0	0	0	0	1	0	0	0	2	0
Myrianida	0	0	1	0	0	0	0	0	0	0	0	0
Naineris	0	0	0	0	0	0	1	0	0	0	1	0
Neanthes	0	0	15	0	0	0	0	0	0	0	0	0
Nereis	0	0	0	7	0	0	0	0	0	0	0	0
Nicolea	0	0	3	5	0	1	37	31	17	63	199	163
Nothria	0	0	1	1	1	0	0	0	0	0	0	0
Notomastus	0	1	3	2	0	11	32	35	61	44	169	84
Odontosyllis	0	0	0	0	3	0	0	6	2	1	54	31
Owenia	1	0	46	19	0	2	7	22	32	6	9	4
Oxydromus	0	0	0	0	0	1	4	16	7	4	75	52
Paradoneis	0	0	0	0	9	12	0	0	0	0	11	16
Paraonis	13	0	0	0	0	0	26	0	3	2	4	4
Paraprionospio	0	0	0	0	0	0	0	0	0	0	4	0
Pectinaria	0	0	3	1	0	0	0	0	28	4	4	4
Periboea	0	0	1	0	0	0	0	0	1	0	1	0
Pettiboneia	0	0	0	0	1	0	3	7	15	0	8	2
Pherusa	0	0	0	0	0	0	2	1	2	0	25	5
Pholoe	0	0	0	0	0	0	0	0	0	1	0	2
Phyllodoce	0	2	0	0	3	0	1	0	0	0	0	0
Pionosyllis	0	0	0	0	0	1	3	18	11	0	58	4
Pisionidens	0	0	0	0	0	0	0	0	0	0	7	0
Poecilochaetus	0	0	1	0	1	0	2	1	1	0	1	1
Polycirrus	0	0	4	0	0	1	1	2	0	0	0	0
Prionospio	2	0	1	0	0	0	0	1	0	3	22	3
Protoaricia	0	0	0	0	0	0	0	1	0	0	1	0
Pseudostreblosoma	0	0	0	0	0	0	0	0	2	0	0	0
Sabella	0	0	3	0	0	0	4	0	7	2	104	0
Sabellaria	0	0	0	4	0	0	0	1	0	0	4	0
Salvatoria	0	0	0	0	0	0	1	0	0	8	4	17

Scolelepis	0	0	1	0	2	0	2	0	1	1	15	0
Scoloplos	21	16	40	13	43	35	98	87	4	36	46	75
Sigambra	4	2	13	28	74	133	20	3	4	0	1	5
Sphaerosyllis	0	0	0	0	0	5	15	0	2	0	4	0
Spio	0	0	0	0	0	0	9	3	43	36	7	10
Spiochaetopterus	0	0	0	0	0	0	0	0	8	4	1	0
Spiophanes	0	0	12	0	0	2	2	1	4	40	0	1
Sternaspis	6	0	9	0	4	0	89	5	0	0	48	64
Sthenelanella	0	0	0	2	0	0	0	0	10	0	0	0
Streblosoma	0	0	0	0	0	0	6	0	2	0	133	14
Syllis	0	1	4	3	91	26	32	10	20	15	67	71
Synelmis	0	0	0	0	1	0	0	0	0	0	1	0
Terebellides	0	1	0	1	0	0	3	21	0	0	6	57
Trochochaeta	0	0	0	0	0	0	0	0	0	0	1	0
Total abundance	609	415	681	276	727	585	1092	912	1097	873	2747	2269
Richness	25	17	44	27	37	36	57	50	58	51	76	54
Insecta												
Aedokritus	0	3	0	0	0	0	0	0	0	0	0	0
Chironomus	144	0	0	0	1	0	0	0	0	0	0	0
Polypedilum	375	938	0	0	0	0	0	0	0	0	0	0
Tanytarsus	1	0	0	0	0	0	0	0	0	0	0	0
Total abundance	520	941	0	0	1	0	0	0	0	0	0	0
Richness	3	2	0	0	1	0	0	0	0	0	0	0
Mollusca												
Abra	2	3	4	0	6	0	7	27	5	16	3	24
Acrosterigma	0	0	1	0	0	0	0	1	1	1	0	1
Acteocina	6	2	4	7	30	19	27	10	21	10	28	44
Alaba	0	0	0	0	3	2	4	25	0	0	0	11
Amygdalum	0	0	0	0	0	0	0	0	4	0	3	1
Anadara	0	0	1	0	2	0	0	0	0	8	22	16
Angulus	0	0	3	0	0	0	0	0	0	0	1	0
Anomalocardia	35	117	81	67	77	132	61	112	166	148	9	116
Arca	0	0	0	0	0	0	0	0	0	0	2	0
Assiminea	0	5	0	5	0	43	0	2	0	0	0	4
Astarte	0	0	0	0	0	0	0	0	0	0	1	0
Atys	0	0	0	0	1	0	0	0	0	0	0	1
Bittiolum	0	0	0	0	95	1	1	5	0	2	10	3
Boonea	1	0	0	3	3	5	4	6	17	3	108	46
Bostrycapulus	0	0	0	0	0	0	0	1	0	0	0	0
Brachidontes	2	0	0	6	0	0	0	0	1	0	0	0
Bulla	0	0	0	0	0	0	3	17	5	0	1	11
Caecum	24	0	0	1	814	915	58	75	4	0	576	221
Callista	4	5	57	267	0	7	7	7	25	10	2	11
Calyptraea	0	0	0	0	5	9	0	2	0	0	0	0
Caryocorbula	1	2	63	38	8	19	19	40	47	41	55	150
Cerithiopsis	0	0	0	0	1	0	0	0	0	0	0	0

Cerithium	0	0	0	0	0	0	0	0	0	4	0	0
Conus	0	0	0	0	0	0	2	0	0	0	1	9
Costoanachis	2	0	0	8	0	6	0	11	0	0	0	8
Crassinella	0	0	0	0	22	3	0	4	2	1	4	18
Ctena	0	0	0	0	0	0	2	0	0	0	3	0
Cumingia	0	0	0	0	0	0	0	0	0	0	1	0
Cylichnella	15	202	27	79	2	0	21	7	125	68	45	41
Dallocardia	0	0	0	0	0	0	0	3	0	0	0	0
Diplodonta	0	0	0	0	2	35	0	0	2	0	1	0
Epitonium	0	0	1	0	1	0	0	0	1	0	0	1
Ervilia	0	0	0	0	4	22	0	0	0	0	0	1
Eulimastoma	0	0	5	5	2	2	0	1	0	0	5	4
Eulimella	0	0	0	0	0	1	0	0	0	0	0	6
Eulithidium	0	0	0	0	3	0	0	2	0	0	0	0
Fargoa	0	0	0	0	0	0	0	0	0	0	8	4
Glycymeris	0	0	0	0	0	0	0	1	0	0	0	0
Gouldia	4	14	0	1	7	27	57	16	100	65	18	7
Gregariella	0	0	0	0	0	0	0	0	0	0	1	0
Haminoea	2	0	0	0	0	0	2	26	0	0	0	1
Iselica	0	0	1	0	3	7	1	2	7	12	0	0
Kurtziella	0	0	0	0	0	0	0	0	1	0	0	0
Lioberus	0	0	57	0	0	0	0	4	0	1	0	5
Lucinella	0	0	0	0	0	1	0	0	0	1	0	1
Lucinoma	0	0	0	0	9	6	3	0	1	0	0	0
Lunarca	0	0	0	0	0	0	0	0	0	0	1	0
Lyonsia	0	0	1	0	3	2	1	4	1	6	3	10
Macoma	37	31	65	5	185	63	8	20	9	7	33	53
Melanella	0	0	0	0	0	0	0	0	0	0	2	3
Modiolus	0	1	0	0	0	0	0	0	0	0	0	0
Mytella	0	0	0	0	1	0	0	0	0	0	0	0
Nassarius	1	0	2	2	0	0	0	0	0	0	0	0
Natica	0	0	0	0	2	2	16	12	17	8	14	9
Neritina	0	0	0	1	5	3	13	6	0	0	0	18
Nucinella	0	0	0	0	0	0	0	0	0	1	0	2
Nucula	0	0	2	1	10	0	19	33	784	1686	209	374
Odostomia	0	64	5	64	3	0	0	0	3	0	4	0
Oliva	0	0	0	0	0	0	0	0	0	0	0	1
Olivella	6	0	4	0	3	16	73	48	34	31	1	0
Parvanachis	3	0	13	2	7	0	21	3	4	0	9	0
Parvilucina	0	4	0	4	0	1	6	0	1	0	3	6
Phacoides	0	0	0	0	0	1	4	3	1	0	0	25
Pitar	0	0	0	0	3	28	0	34	1	3	2	0
Pteria	0	0	0	0	0	0	0	0	0	0	1	0
Radiolucina	0	0	0	0	0	0	0	5	0	0	0	0
Scaphopoda	0	0	10	33	0	1	1	14	292	340	74	55
Schwartziella	2	0	1	0	7	0	0	0	0	0	0	2

Solariorbis	0	0	1	0	0	6	0	0	0	1	0	1
Sphenia	0	0	0	0	0	0	7	0	23	0	5	1
Spisula	0	0	0	0	3	0	0	0	0	0	0	0
Tagelus	2	0	2	0	53	47	1	11	3	5	3	7
Teinostoma	0	1	1	0	0	2	1	0	0	0	3	2
Tellina	2	22	0	5	3	0	0	7	0	2	9	4
Tenaturris	0	0	0	0	0	0	0	1	0	0	1	2
Texadina	0	0	0	0	1	0	0	0	0	0	0	0
Thracia	0	0	0	0	0	0	0	0	2	0	3	0
Trachycardium	0	0	0	1	0	0	1	0	2	0	1	0
Transennella	0	0	0	0	0	0	18	25	4	0	7	0
Turbonilla	4	2	15	26	11	14	7	7	6	3	23	28
Volvarina	0	0	0	0	0	0	3	0	0	2	30	10
Volvulella	0	0	0	0	0	0	0	1	0	0	0	0
Zafrona	0	0	2	0	0	0	0	0	0	0	0	0
Total abundance	155	475	429	631	1400	1448	479	641	1722	2486	1349	1379
Richness	20	14	27	23	38	33	34	42	36	29	45	48

Tropical estuarine gradient drives opposite patterns in the functional and taxonomic diversity of polychaetes and molluscs

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3 TROPICAL ESTUARINE GRADIENT DRIVES OPPOSITE PATTERNS IN THE FUNCTIONAL AND TAXONOMIC DIVERSITY OF POLYCHAETES AND MOLLUSCS

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ABSTRACT

The determination of the processes that act in the assembly of the communities is a theme of growing interest among ecologists. Different processes (e.g., environmental filtering and biotic interactions) can shape the structure of communities depending on the spatial scale analyzed. In this study, we partitioned the functional and taxonomic diversities of polychaete and mollusc communities of typical and semi-arid tropical estuaries into the alpha, beta, and gamma components. The communities of polychaetes and mollusks were sampled in three typical tropical estuaries (Paraíba do Norte, Mamanguape and Passos) and three semi-arid estuaries (Galinhos, Tubarão and Casqueira) once in each period (dry and rainy). To partition the functional and taxonomic diversity we used Rao's quadratic entropy and Simpson's index, respectively. Our results demonstrated that alpha functional diversity had a greater contribution to gamma diversity. When considering taxonomic diversity, beta diversity showed greater contributions to gamma diversity. These results indicate that different processes act in the assembly of the functional and taxonomic diversity of mollusks and polychaetes at different spatial scales. More specifically, biotic interactions seem to be more important in the assembly of functional diversity while environmental filtering seems to have a greater effect on taxonomic diversity. Therefore, functional and taxonomic approaches provided complimentary results on the distribution patterns of estuarine communities at spatial scales.

Key-words: Estuaries. Spatial scales. Environmental filtration. Biotic interactions.

3.1 INTRODUCTION

The relative roles of processes (e.g., environmental filtering and biotic interactions) that act in the assembly of communities at local and regional scales it is a central research topic in biogeography, ecology, and conservation biology (Mouillot et al., 2007; Heino et al., 2019). The processes that influence the formation and structuring of communities can vary depending on the particular dynamics of ecosystems that can influence, for example, passive dispersal or the existence of barriers for dispersal (De Bello et al., 2012; Münkemüller et al., 2012; Heino et al., 2015).

Typical estuaries are transition environments (Francisco & Netto, 2020), where energy and material transfers take place between freshwater habitats and the adjacent ocean (Berthelsen et al., 2020). Due to this condition of interface between the continental and marine ecosystems, the environmental conditions (e.g., salinity, sediment composition) of the estuaries tend to change longitudinally (Attrill & Rundle, 2002). Variations in the longitudinal environmental conditions of typical tropical estuaries, mainly salinity, act as an environmental filter and cause a decline in the diversity of the benthic macrofauna from areas closest to the sea towards continental drainage, structuring communities spatially (Remane, 1934; Alves et al., 2020).

In estuaries located in semi-arid regions, these ecosystems are influenced by factors such as high temperatures, low rainfall, and low continental drainage of mainly underground origin (Duarte et al., 2020). In these cases, the environmental conditions tend to be less spatially variable along these ecosystems (Potter et al., 2010). In estuaries that environmental conditions tend to be more spatially constant, communities are adapted to persist and survive in different environmental conditions and do not show a gradual decline in the composition of species longitudinally (Medeiros et al., 2020). In this way, factors operating on a local scale may have greater relative importance in the structuring of communities.

Seasonal environmental changes also influence the estuarine dynamics. Dry and rainy periods alter the discharges of water from the continental drainage, saline incursion, and water evaporation rates (Netto et al., 2012; Francisco & Netto, 2020). These changes alter the discharge of nutrients and sediments, as well as they can increase (dry periods) or decrease (rainy periods) the salinity levels of the estuaries (Teske & Wooldridge, 2001).

Thus, spatial (estuarine gradient) and temporal (seasonal changes) factors can directly influence the observed distribution patterns of estuarine benthic communities (Alves et al., 2020; Francisco & Netto, 2020). The additive partitioning of diversity has been widely used to understand spatial distribution patterns and the factors that operate at spatial scales in the assembly of communities (e.g., Josefson et al., 2009; Ligeiro et al., 2010; Ferreira et al., 2017). In this approach, the total diversity of a defined geographic area (γ diversity) is composed of the sum of the diversity observed within a given location (α diversity) and the dissimilarity in the composition of species between different locations (β diversity) (i.e., $\gamma = \alpha + \beta$; Lande, 1996).

Recently, diversity partitioning has been carried out considering multiple facets of biodiversity (e.g., taxonomic and functional diversity) (De Bello et al., 2009; De Bello et al., 2010). Although taxonomic approaches can explain the distribution of species among sites, the occurrence of individuals in particular habitat types is closely linked to their functional traits (Bremner et al., 2006). Functional traits (e.g., morphological, physiological, and life history) reflect the way organisms respond to biotic and abiotic interactions and are related to the performance of species to adapt, develop and reproduce under certain environmental conditions (Violle et al., 2007; Van der Linden et al., 2016;

Egres et al., 2019). Consequently, the functional traits are related to the functioning of ecosystems (Bremner, 2008).

Understanding the patterns of taxonomic and functional distribution of macroinvertebrate communities in tropical estuarine ecosystems can provide important insights to improve the ecological quality and functioning of these ecosystems. Benthic macroinvertebrates, including mollusks and polychaetes, play vital ecological roles in estuaries, including participation in nutrient cycling and energy flow to higher trophic levels (Pennifold & Davis, 2001). Among estuarine macroinvertebrates, mollusc and polychaete communities are among the most frequent and abundant taxonomic groups (e.g., Zhong et al., 2020), and are constantly used in studies that investigate community distribution in estuaries (e.g., Medeiros et al., 2016a; Van der Linden et al., 2017).

This study helps to understand an existing knowledge gap on the mechanisms underlying the assembly of the benthic macrofauna of estuaries located in regions with different climatic conditions, considering multiple facets of diversity. We evaluated the relationship between the functional and taxonomic distribution patterns of polychaete and mollusc communities along environmental gradients of typical and semi-arid tropical estuaries in a dry and in a rainy period. For this, we partitioned the taxonomic and functional gamma diversity in their alpha and beta components. We hypothesize that the functional and taxonomic beta diversity of molluscs and polychaetes contribute with greater proportions to the gamma diversity in the typical tropical estuaries due to the strong environmental gradient observed at these estuaries. In contrast, the taxonomic and functional alpha diversity contribute with greater proportions of gamma diversity in semi-arid estuaries due to the more homogeneous environmental conditions throughout these ecosystems. We expect this to happen regardless of the seasonal period analyzed.

3.2 MATERIAL AND METHODS

3.2.1 Study area

The present study was conducted in six tropical estuaries located in northeastern Brazil, three located in a typical tropical region (Paraíba do Norte, Mamanguape, and Passos), and three located in a semi-arid region (Tubarão, Galinhos, and Casqueira) (Fig. 1). The northeast region of Brazil is marked by low rainfall and high temperatures. Thus, only dry (from December to March) and rainy (from June to August) periods are recognized in the region (Santos et al., 2017; CPTEC, www.cptec.inpe.br, accessed in December 2018). Typical tropical estuaries are located in a hot and humid climate, and semi-arid tropical estuaries are located in a semi-arid climate, characterized by little precipitation and high evaporation rates (Alvares et al., 2013).

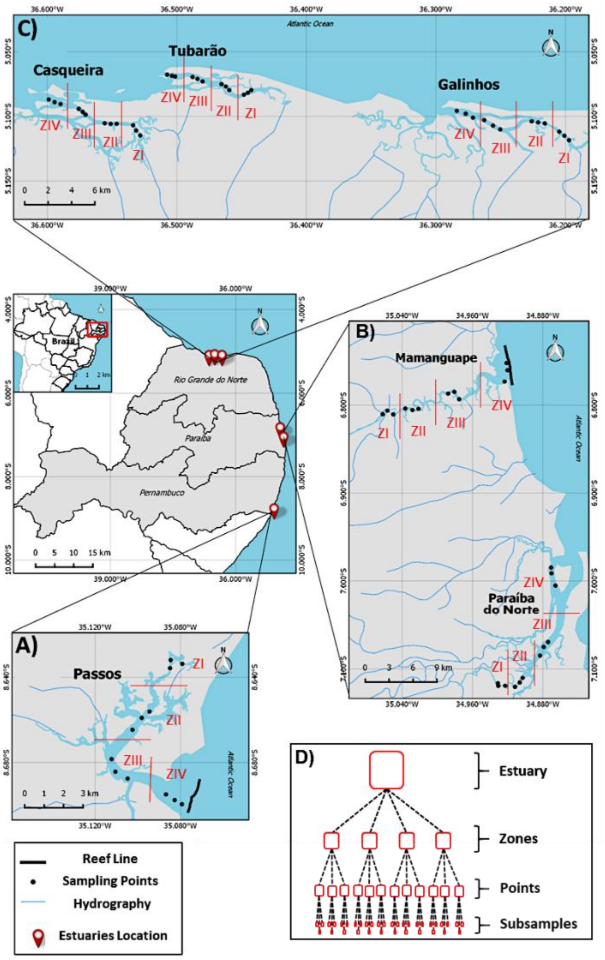

Fig. 1 Map showing the distribution of the sampled sites in the typical (A and B) and semi-arid tropical (C) estuaries located in northeastern Brazil and the sample design of the study (D). Sites 1 to 3 (zone I), sites 4 to 6 (zone II), sites 7 to 9 (zone III), and sites 10 to 12 (zone IV).

3.2.1.1 Typical tropical estuaries

The Paraíba do Norte, Mamanguape, and Passos estuaries are 22, 24, and 12 km long, respectively. In the surroundings of these ecosystems, there are extensive areas of mangrove vegetation. Leisure activities, fishing, and intensive sugarcane cultivation are identified in these ecosystems, mainly in the Paraíba do Norte estuary (Santana et al., 2018). The Mamanguape and Passos estuaries are located within protected areas (Barra do Rio Mamanguape and Guadalupe Environmental Protection Area, respectively). The Passos estuary is part of the estuary complex of the Formoso River, which is strongly influenced by the sea and receives a low supply of continental water (Figueirêdo et al., 2014).

3.2.1.2 Semi-arid tropical estuaries

The Tubarão, Casqueira, and Galinhos estuaries are 10, 15, and 15 km long, respectively. These estuarine ecosystems are classified as inverse, or negative, and have characteristics of preserved ecosystems although anthropogenic influences can still be identified around them (Medeiros et al., 2016b; Duarte et al., 2020). The Tubarão estuary is inserted in a protected area that sustainably uses its resources (Ponta do Tubarão Sustainable Development Reserve) (Sales et al., 2016). Areas intended for salt production and shrimp farming are identified in the Galinhos and Casqueira estuaries (Duarte, 2020).

3.2.2 Sampling design and collection of benthic macrofauna

To capture the ecological dynamics of estuarine ecosystems and their longitudinal environmental variations, we sampled the entire extent of the estuaries. In each estuary, twelve sampling sites were established from the continental drainage (upstream) towards the sea (downstream) (Fig. 1). These sampling sites were subdivided into four estuarine zones: Sites 1 to 3 (zone I), sites 4 to 6 (zone II), sites 7 to 9 (zone III), and sites 10 to 12 (zone IV) (Fig. 1). At each site, three subsamples were collected (Fig. 1D), and salinity was determined with the aid of a salinity refractometer (Model VX100SG). This sample design was able to capture the estuarine longitudinal environmental variations, mainly in terms of salinity (Fig. 2; for more details see Medeiros et al., 2020).

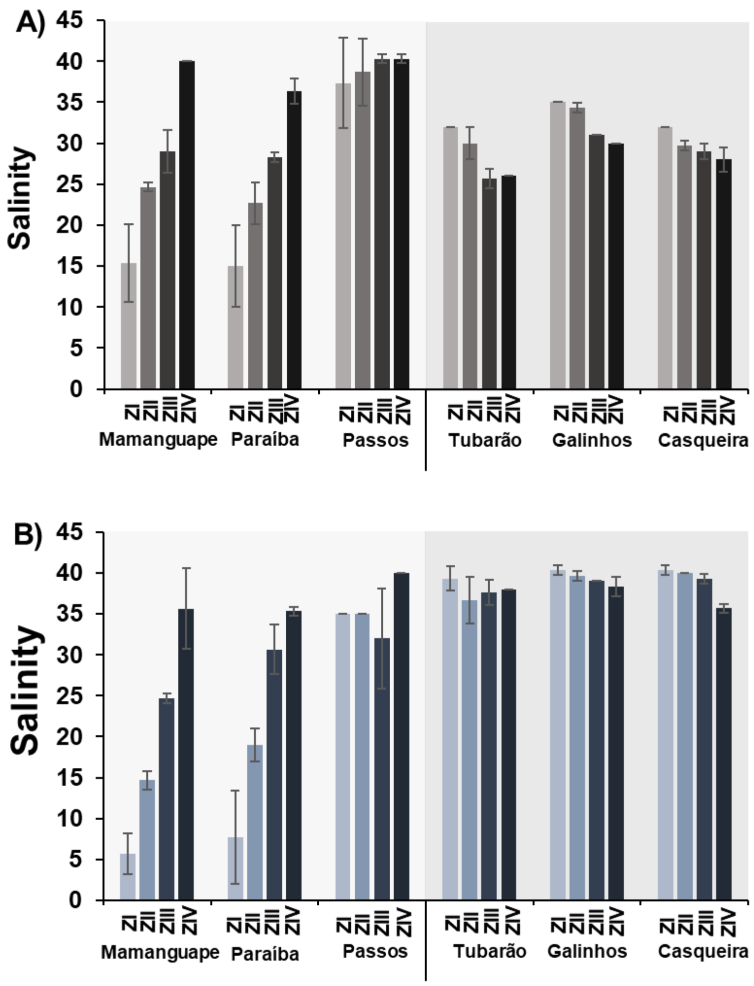

Fig. 2 Mean and standard deviation of the salinity sampled at the zones of the typical and semi-arid tropical estuaries in the periods of drought (A) and rain (B).

The samples were collected in the subtidal region during low tide, with a van Veen dredge (500 cm²). The collected material was washed *in situ* in 0.5 mm sieves and conserved in 70% alcohol. The identification of molluscs and polychaetes was carried out in the laboratory at the taxonomic level of genera with the aid of a microscope and specialized taxonomic keys for molluscs (Rios, 1985; Mikkesen & Bieler, 2008; Tunnell et al., 2010) and polychaetes (Amaral & Nonato, 1996). To carry out the data analyses, we combined the two communities. The results presented by the communities separately were similar to those obtained with the communities together (Supplementary material I, II, III and IV), so we preferred to present only the general pattern.

This study was carried out in a dry and in a rainy period, covering the yearly climatic variation of northeastern Brazil. The collections of the dry period occurred in December 2016 in semi-arid estuaries and in February 2017 in typical tropical estuaries. The collections of the rainy period occurred in June and August 2016, in the typical and semi-arid tropical estuaries, respectively.

3.2.3 Functional traits

The polychaete and mollusc communities were analyzed with six categorical functional traits that reflect the potential of the communities to express the environmental changes along the tropical estuarine gradients and their sensitivity to environmental perturbations (Bremner et al., 2006; Van der Linden et al., 2017; Egres et al., 2019): Maximum body size, Feeding strategy, Living habitat, Life-span, Larval-development, and Fecundity (Table 1). Under conditions of environmental stress, smaller organisms, deposit feeders, tube and burrow dwellers, with short life span, high dispersion capacity (Planktotrophic) and with high fecundity are expected (Pearson & Rosenberg, 1978; Webb et al., 2009; Veríssimo et al., 2012; Van der Linden et al., 2017). The functional traits considered in this study can also contribute to a better understanding of estuarine ecosystems functioning, because they reflect important aspects such as life history and potential trophic interactions (Maximum body size), population dynamics (Life-span), community growth or decline (Fecundity), flow of energy and cycling of matter in food chains (Feeding strategy), dispersal capacity of species (Larval-development) and bioturbation (living habitat) (Pearson & Rosenberg, 1978; Webb et al., 2009; Veríssimo et al., 2012; Van der Linden et al., 2017). Information on the functional traits of polychaetes and mollusc were obtained from published papers and online databases (Polytraits, Faulwetter et al., 2014; Biological Traits Information Catalogue – BIOTIC, MarLIN, 2006; Van der Linden et al., 2017). Some information on the functional traits of the molluscs was not found in online databases and published articles. In these cases, the information was attributed according to the specialized knowledge of one of the authors (Luiz Ricardo L. Simone).

Table 1 Functional traits of communities of polychaetes and molluscs, their respective categories and codes used for each category.

Traits	Categories	Codes
Maximum body size	Very small (<1 cm)	BS_V
	Small (1.1-3 cm)	BS_S
	Medium (3.1-6 cm)	BS_M
	Large (>6.1 cm)	BS_L
Life-span	Short (<1 year)	LS_S
	Medium (1-3 years)	LS_M
	Longe (>3 years)	LS_L
Fecundity	Low (1-2500 eggs)	FE_L
	Medium (2500-100.000 eggs)	FE_M
	High (>100.000 eggs)	FE_H
Feeding strategy	Predator	FS_P
	Scavenger	FS_SC
	Grazer	FS_G
	Deposit	FS_D
	Suspension	FS_S
Living habitat*	Tube dwelling	LH_T
	Burrow dwelling	LH_B
	Surface dwelling	LH_S
Larval-development	Direct	LD_D
	Lecithotrophic	LD_L
	Planktotrophic	LD_P

*Only the polychaete community has the category "burrow dwelling".

3.2.4 Data analyses

To evaluate the distribution of the functional traits of polychaetes and molluscs along the estuarine gradient, community-weighted mean (CWM) of traits were performed for each estuarine ecosystem and seasonal period. To obtain a better visualization of the dominance distribution of the functional traits along the longitudinal extension of the estuaries, we combined the samples from each estuarine zone. As traits are categorical, the CWM values ranged from 0 to 1 and allowed to determine the dominant trait categories in the community weighted by abundance (Ricotta & Moretti, 2011). Permutational multivariate analysis of variance (PERMANOVA; 9999 permutations) were performed to evaluate the spatial and seasonal differences in composition and CWM values in the typical and semi-arid tropical estuaries (Anderson et al., 2008). For each set of estuaries (typical and semi-arid), we considered a sample design with three factors: estuaries (random factor with three levels: Mamanguape, Passos, and Paraíba or Tubarão, Galinhos, and Casqueira), zones (fixed factor with four levels: ZI, ZII, ZIII, and ZIV), and period (fixed factor with two levels: drought and rain). The distribution of abundance and CWM results were explored using Principal Coordinates Analysis (PCoA), with vector overlap considering Spearman's correlation (Anderson et al., 2008). To perform the PERMANOVA and PCoA analyses, the abundance and CWM matrices were initially square root transformed and Bray-Curtis dissimilarity matrices computed.

We assumed an additive relationship to partitioning of taxonomic and functional diversity in the alpha (α), beta (β), and gamma (γ) components ($\gamma = \alpha + \beta$, Lande, 1996; Veech et al., 2002). When functional diversity is considered, alpha and beta diversity correspond respectively to the variability between pairs of species within each site (alpha diversity; α) and between sites (beta diversity; β). We computed the Simpson index and Rao quadratic entropy index, as mathematical equivalents for the taxonomical and functional diversity, and converted them into their α, β, and γ components following De Bello et al. (2009) and De Bello et al. (2010). Rao index was calculated based on the Gower distance. Additionally, we used Jost's correction to the Rao and Simpson indices (Jost, 2007; De Bello et al., 2010). This correction resolves the dependency between the α and β components of diversity and is indicated to avoid a possible underestimation of the observed beta diversity (Jost, 2007; De Bello et al., 2010).

PERMANOVA and PCoA analyses were performed using PRIMER + PERMANOVA 6.1 software (Systat Software, Cranes Software International Ltd., Anderson et al., 2008). Community weighted mean trait values (CWM) were performed in the R environment, using "dbFD" function of the DF package. The taxonomic and functional diversity partitioning were also performed in the R environment, with the "Rao" function of De Bello et al. (2010).

3.3 RESULTS

3.3.1 Distribution of composition and functional traits along the longitudinal gradient of the estuaries

The communities of polychaetes and molluscs showed a total abundance of 22,808 individuals, of which 10,817 were polychaetes (68 genres) and 11,991 molluscs (62 genres). The mollusc community totaled 4,318 individuals collected in typical tropical (dry = 2,424; rainy = 1,894) and 7,673 in semi-arid estuaries (dry = 4,323; rainy = 3,350). When considering the polychaete community, a total abundance of 3,045 individuals was collected in typical tropical estuaries (dry = 1,176; rainy = 1,869) and 7,772 in semi-arid estuaries (dry = 3,519; rainy = 4,253).

The composition of molluscs and polychaetes was significantly different between the zones of typical tropical estuaries (*p*(perm) = 0.007; Table 2). The polychaete *Leonereis* presented greater representativeness in zone I of the typical tropical estuaries in both seasonal periods (Fig. 3A and B). In zones II, III and IV there was a greater abundance of molluscs *Cylichnella* and *Tellina* in the dry period and *Caryocorbula* in the rainy period. The Passos estuary differed from the other typical tropical estuaries, with greater proportions of the molluscs *Acteocina* and *Caecum* and the polychaete *Exogone* in all estuarine zones, in both seasonal periods. In semi-arid tropical estuaries, there was no clear trend in the representativeness of abundance along estuarine zones. In general, the polychaete *Dorvillea* showed greater representativeness in zone I of all estuaries during the dry period. In the other zones of the semi-arid estuaries, the abundance of polychaetes and molluscs varied between the estuaries in both seasonal periods.

Table 2 Results of PERMANOVA analyzes of the composition and dominance of the functional traits of the mollusc and polychaete communities between estuarine zones (fixed factor), seasonal periods (fixed factor) and estuaries (random factor). df = Degrees of freedom. Pseudo-F = Statistic of the analysis.

	Typical tropical estuaries			
Dependent variable	**Significant terms**	**d.f.**	**Pseudo-F**	***p*(perm)**
Abundance	Zones	3	1.9599	0.007
	Estuaries	2	7.6984	0.0001
	Periods	1	0.913	0.531
	Estuaries x zones	6	2.8494	0.0001
	Estuaries x periods	2	2.1913	0.0006
	Periods x zones	3	0.7923	0.754
Functional traits	Zones	3	3.2497	0.0203
	Estuaries	2	5.9134	0.0012
	Periods	1	0.854	0.5304
	Estuaries x zones	6	1.979	0.06
	Estuaries x periods	2	2.296	0.06
	Periods x zones	3	1.7032	0.1372
	Semi-arid estuaries			
Abundance	Zones	3	1.398	0.141
	Estuaries	2	5.9776	0.0001
	Periods	1	1.842	0.168
	Estuaries x zones	6	3.0779	0.0001
	Estuaries x periods	2	1.336	0.104
	Periods x zones	3	0.917	0.584
Functional traits	Zones	3	1.074	0.393
	Estuaries	2	10.949	0.0001
	Periods	1	1.005	0.44
	Estuaries x zones	6	4.0469	0.0001
	Estuaries x periods	2	5.5347	0.0001
	Periods x zones	3	0.685	0.829

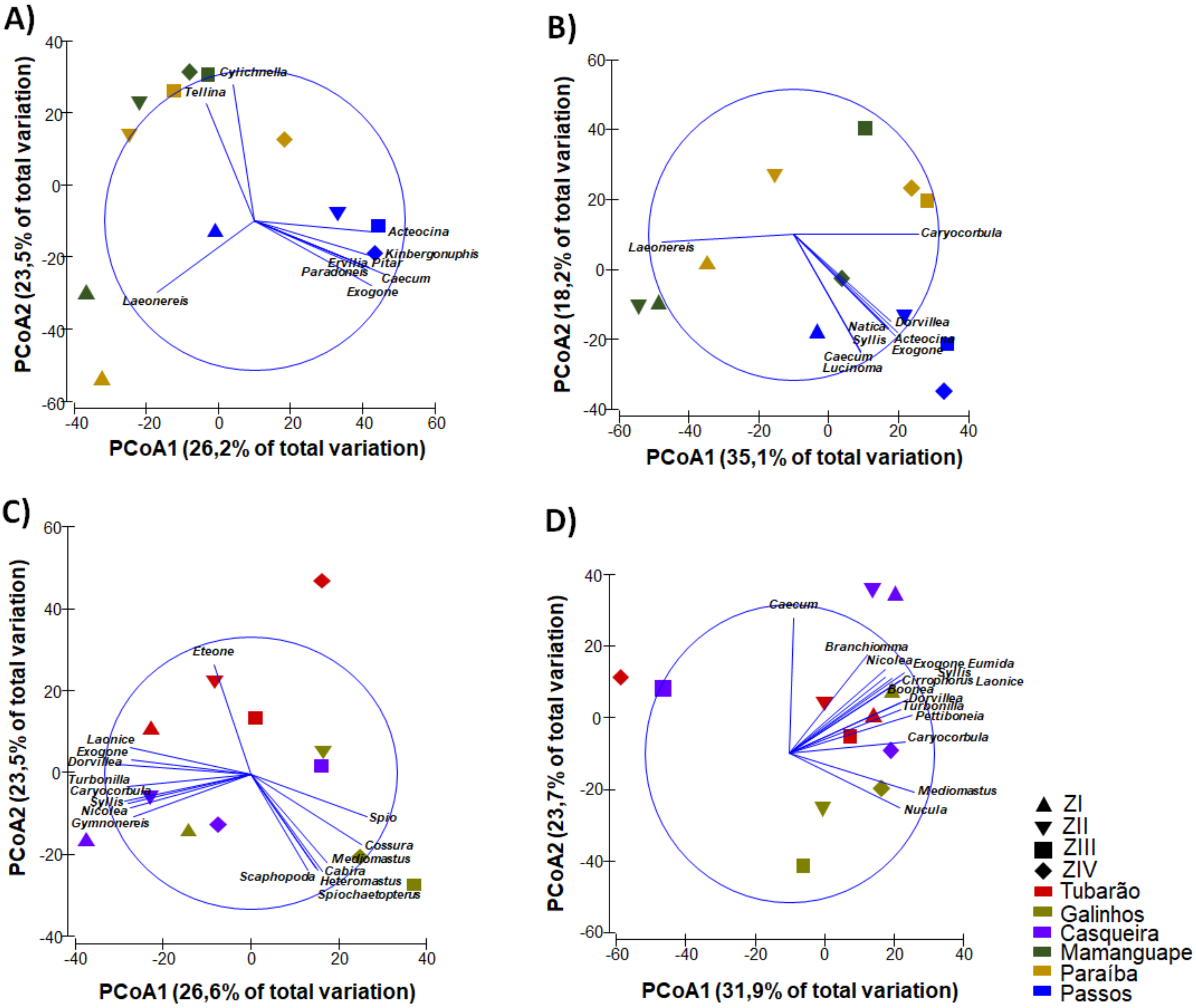

Figure 3 Principal Coordinates Analyses (PCoA) using Bray-Curtis dissimilarity showing differences between the zones of the typical (A and B) and semi-arid (C and D) tropical estuaries in the dry (A and C) and rainy (B and D) periods. The relationships between the relative abundances of the genera and the PCoA axes are indicated by the length and direction of the vectors. Only vectors with Spearman correlation > 0.8 with PCoA1 or PCoA2 were represented.

The dominance of the functional traits of the mollusc and polychaete communities differed significantly between the zones of typical tropical estuaries (*p*(perm) <0.05; Table 2), without presenting significant differences in the semi-arid estuaries. Significant differences were observed in the interaction between estuaries x zones and estuaries x periods of the semi-arid tropical estuaries (*p*(perm) <0.05; Table 2). In general, in the zone closest to the continental drainage (ZI) of typical tropical estuaries it was observed a greater proportion of organisms that shared predator/scavenger/deposit feeding strategies, and larger sized and medium life span organisms, in both seasonal periods (Fig. 4A and 4B; Supplementary material V and VI). In the dry period, organisms that presented a scavenger/grazer and suspension feeding strategy, surface/burrow dwellers, low life span and lecithotropic larval development showed greater dominance in the zones of higher salinity of the typical tropical estuaries (Fig. 4A; Supplementary material V). In the rainy period, in the areas closest to the sea it was observed an increase in the dominance of small organisms, with low life span, direct larval development, that shared scavenger/grazer/deposit feeding strategies and with low fecundity (Fig. 4B; Supplementary material VI). These trends were less evident in the Passos estuary. In semi-arid estuaries, there was no clear trend in the variation of dominance of functional traits along the longitudinal extent of the estuaries and between estuaries, as occurred in typical tropical estuaries (Fig. 4C and 4D; Supplementary material VII and VIII).

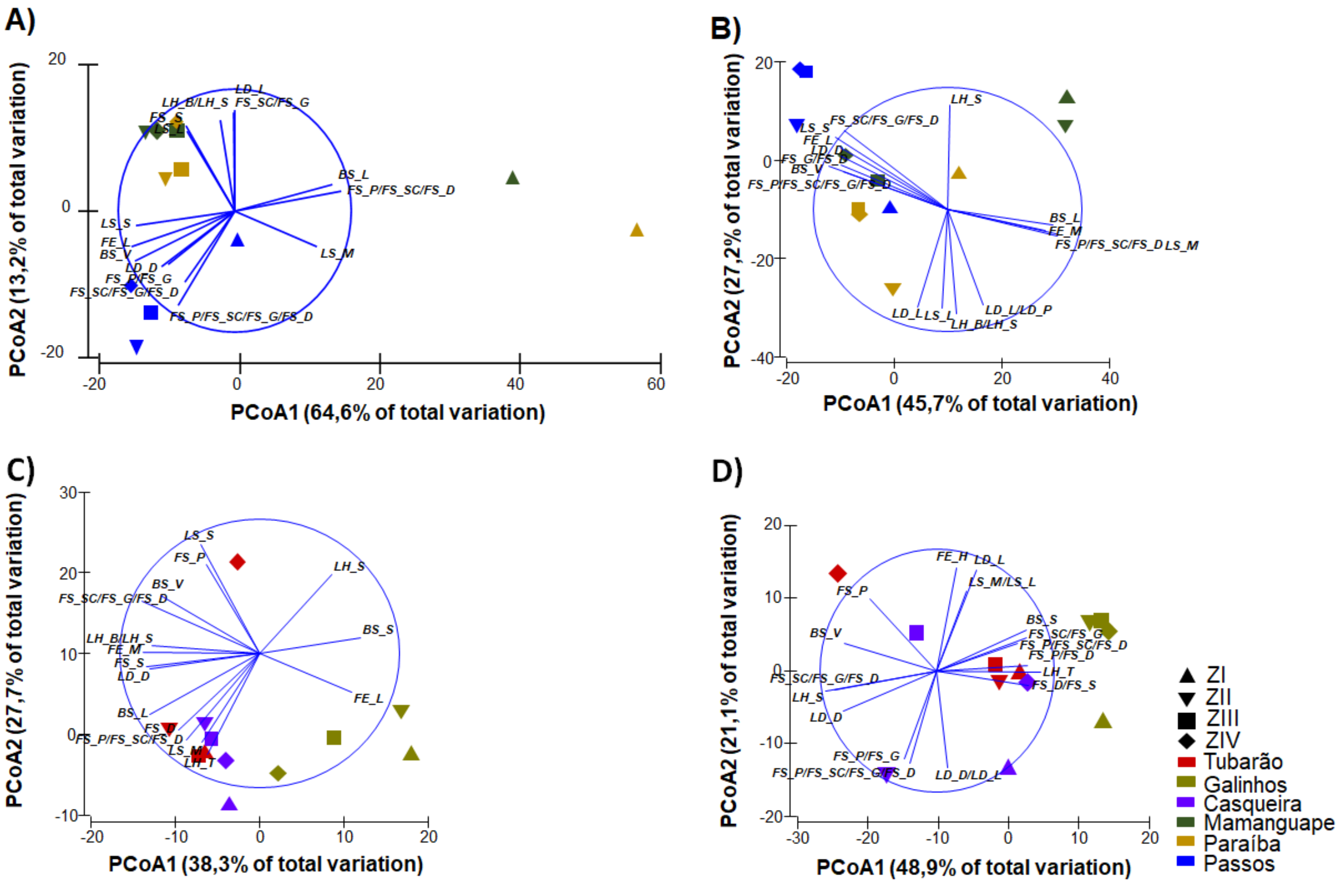

Figure 4. Principal Coordinates Analyses (PCoA) using Bray-Curtis dissimilarity showing differences between the zones of the typical (A and B) and semi-arid (C and D) tropical estuaries in the dry (A and C) and rainy (B and D) periods. The relationships between the CWM values and the PCoA axes are indicated by the length and direction of the vectors. Only vectors with Spearman correlation > 0.7 with PCoA1 or PCoA2 were represented. The codes of the categories of the functional traits can be seen in table 1.

3.3.2 Additive partitioning of taxonomic and functional diversity

When the taxonomic diversity was partitioned, the highest proportions of diversity occurred between sites (β; dissimilarity of species pairs between sites) (Fig. 5). The average values of beta diversity obtained in typical tropical estuaries were 6.31 (± 1.04) in the dry period and 5.41 (± 4.31) in the rainy period (Fig. 5). In the semi-arid estuaries, the average values of beta diversity obtained in the dry and rainy periods were 12.83 (± 7.33) and 12.87 (± 3.56), respectively (Fig. 5). When considering the functional diversity of the mollusc and polychaete communities, the alpha diversity (α; dissimilarity between traits pairs within each site) contributed with greater proportions to the gamma diversity (Fig. 5). The average alpha functional diversity of typical tropical estuaries was 1.77 (± 0.25) in the dry period and 1.81 (± 0.20) in the rainy period. In the semi-arid estuaries, the average alpha diversity observed in the dry and rainy periods was 2.44 (± 0.43) and 2.47 (± 0.18), respectively (Fig. 5). This pattern in the partitioning of functional and taxonomic diversity was observed in all estuaries (typical and semi-arid tropical) and seasonal periods (dry and rainy) (Fig. 5).

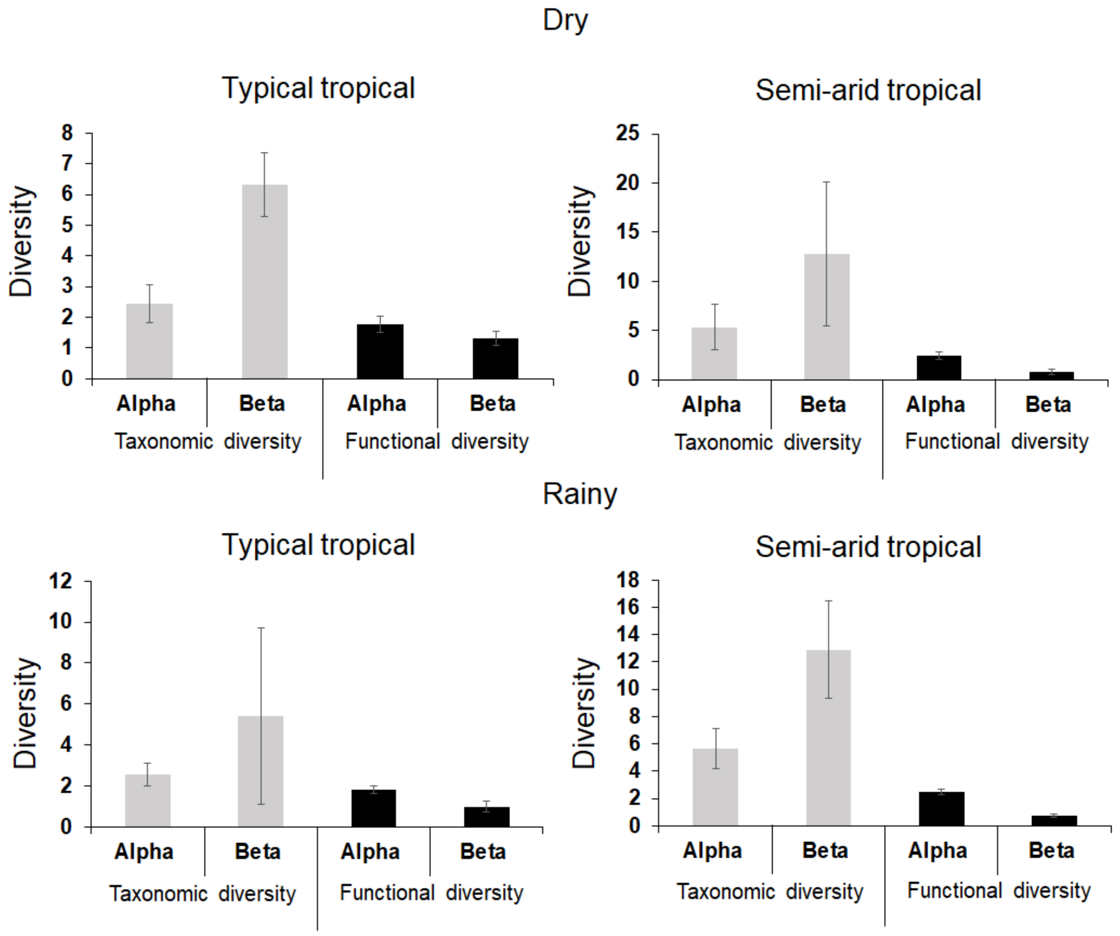

Figure 5 Average (± standard deviation) alpha and beta taxonomic and functional diversity of the communities of polychaetes and molluscs from typical (Mamanguape, Passos, and Paraíba do Norte) and semi-arid (Tubarão, Galinhos, and Casqueira) tropical estuaries during dry and rainy periods.

3.4 DISCUSSION

The partitioning of the functional and taxonomic diversity of polychaetes and molluscs responded in a similar way in typical and semi-arid tropical estuaries, contrary to our expectations. In both types of estuaries, taxonomic diversity had higher values of beta diversity, although when considering functional diversity, the highest proportions of diversity occurred on the local scale (alpha diversity). These results indicate that different mechanisms (e.g., environmental filtering, biotic interactions) act in the assembly of the functional and taxonomic diversity of polychaetes and mollusks.

Values of functional alpha diversity greater than beta diversity indicate that there is a high functional diversity within the sampling sites (alpha diversity), i.e., higher variation among the functional traits of the individuals within the sites, compared to the dissimilarity between the sampling sites (beta diversity). The high alpha functional diversity may be related to a greater relative importance of biotic interactions between species at this spatial scale, resulting in the coexistence of species with different functional traits within the sites (Wilson, 2007; Chesson, 2000). Thus, biotic interactions favor the persistence of a set of species with less niche overlap and consequently greater functional divergence (Dolbeth et al., 2013). On the other hand, the lower proportions of functional beta diversity indicate a functional redundancy (Petchey et al., 2007) between sites at each estuary, as shown in other studies (e.g., De Bello et al., 2009; Nunes et al., 2016). That is, the communities that persist in the sampling sites perform the same functions along the estuaries (Nunes et al., 2016), and there is a similarity in the functional traits of the polychaetes and mollusks along the sampling sites. This can also be observed in the distribution of the dominance of the traits throughout the estuarine ecosystems (Supplementary material V, VI, VII, and VIII).

Previous studies have partitioned the taxonomic diversity of estuarine benthic macroinvertebrate communities in estuaries presenting a strong environmental gradient (e.g., Josefson & Goke, 2013; Medeiros et al., 2016a). The results of these studies corroborate our results, showing that taxonomic beta diversity contributed with greater proportions to gamma diversity. These results are attributed to the selection of species according to the longitudinal environmental variations of the estuaries, mainly salinity, that acts as an environmental filter (Menegotto et al., 2019). Taxonomic trends observed in semi-arid estuaries were contrary to our expectations. We expected that in these types of ecosystems, due to the more homogenous longitudinal environmental conditions, taxonomic diversity would be structured mainly on smaller spatial scales. However, we attribute the highest proportions of beta diversity in these ecosystems due to limited dispersal of organisms (Leibold et al., 2004; Mouillot et al., 2007) in these estuaries. In this case, the low inflow of water from the continental drainage may be limiting the passive dispersion of these organisms and generating taxonomically aggregated communities along the longitudinal extent of the estuaries. Thus, our results also demonstrated that although the typical and semi-arid tropical estuaries have different dynamics, the patterns of community distribution are similar.

The values of functional beta diversity were higher in typical estuaries than in semi-arid estuaries. This result demonstrates that although the dispersal limitation may be acting in the assembly of taxonomic diversity between sites (beta diversity) in semi-arid estuaries, environmental filtering has a greater effect on the structuring of communities in typical tropical estuaries on this spatial scale. This was also indicated by the significant differences in abundance and functional traits between zones of typical tropical estuaries.

Our results suggest that although taxonomic diversity is structured mainly on the largest spatial scales, this does not occur for functional diversity. Contrary to other studies that have shown a functional change along the longitudinal dimension of the estuaries (e.g., Van der Linden et al., 2017; Darr et al., 2014), our results indicate that, although the identity of the species changed, similar functions were performed along the estuaries. This longitudinal functional redundancy of the polychaetes and mollusks indicate that even when stressful conditions cause the elimination of species in certain areas of the estuaries these functions will still be exercised in other areas. Thus, the functional distribution of communities may be related to nested patterns. That is, places with less functional diversity can be subsets of sites where the greatest functional diversity, as observed by Bender et al. (2017). Therefore, we suggest that future studies may evaluate the existence of functional nested patterns in tropical estuarine ecosystems.

In conclusion, we demonstrated that the functional and taxonomic diversity of benthic macroinvertebrate communities present a similar pattern in estuaries with different dynamics. However, functional diversity is mainly governed by factors acting on smaller spatial scales and taxonomic diversity by factor operating at larger scales. These results indicate a greater relative importance of environmental filtering and dispersal limitation in the structuring of taxonomic diversity, but interactions between species having a greater effect on functional diversity. Thus, the joint use of taxonomic and functional approaches delivers more comprehensive answers about the dynamics and functioning of communities. Future studies should consider both facets of diversity to obtain more refined answers about the assembly of communities.

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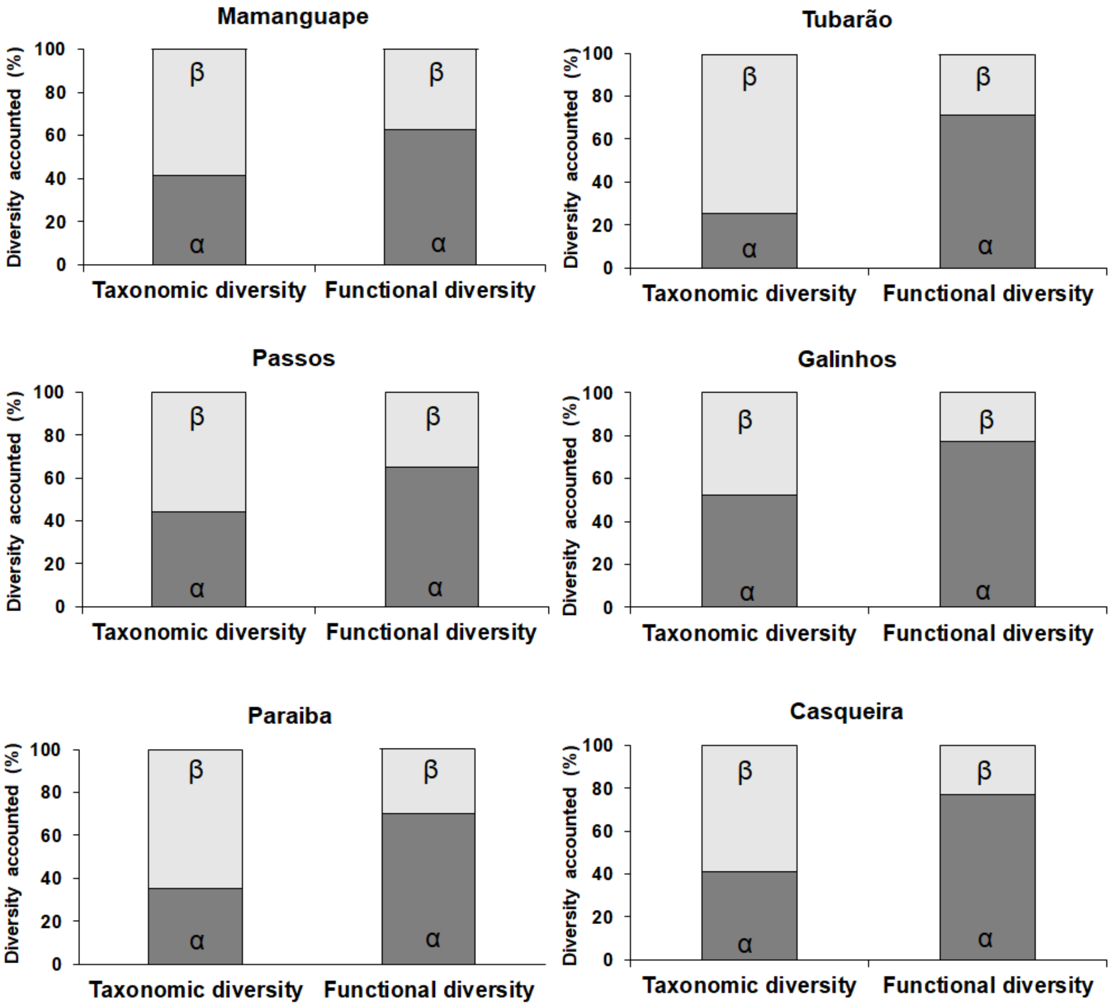
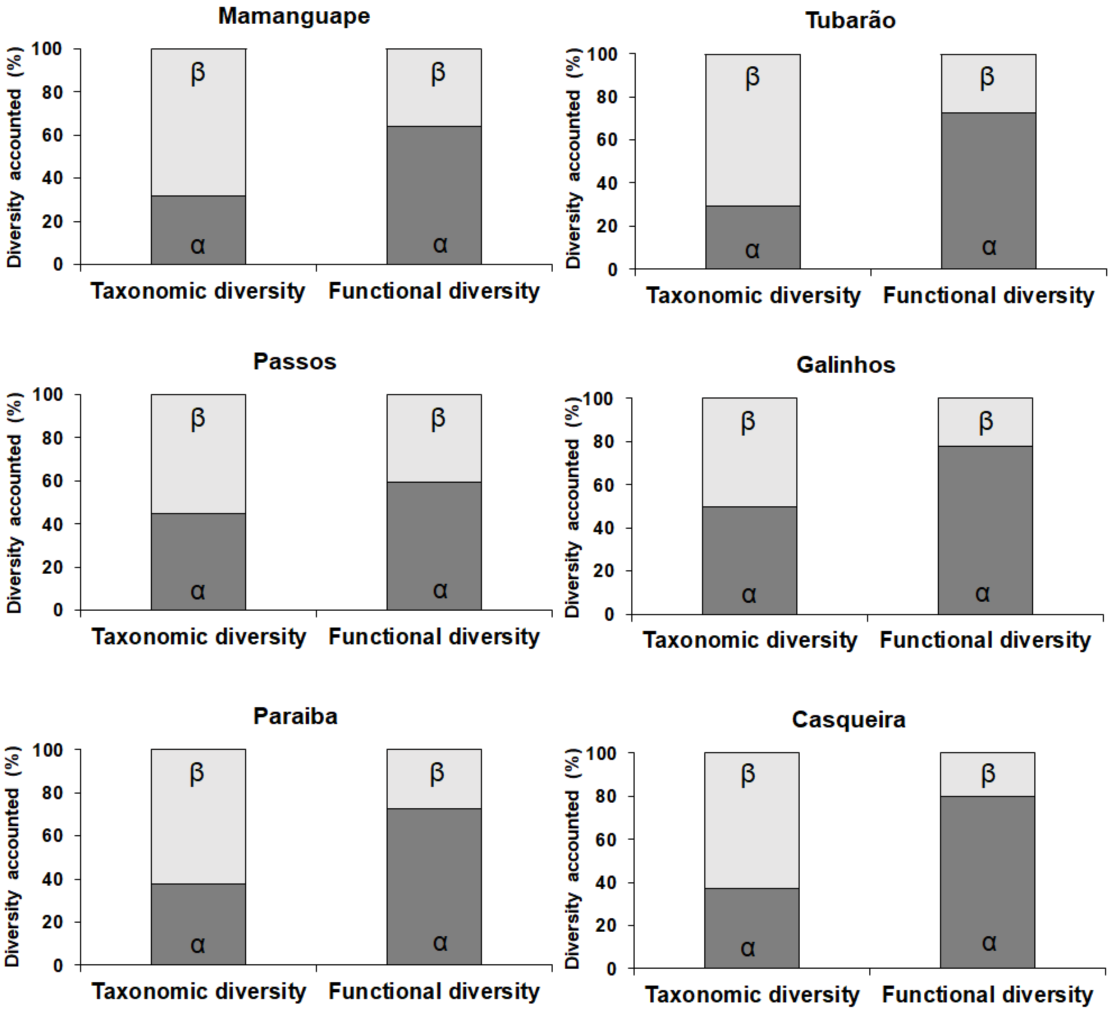
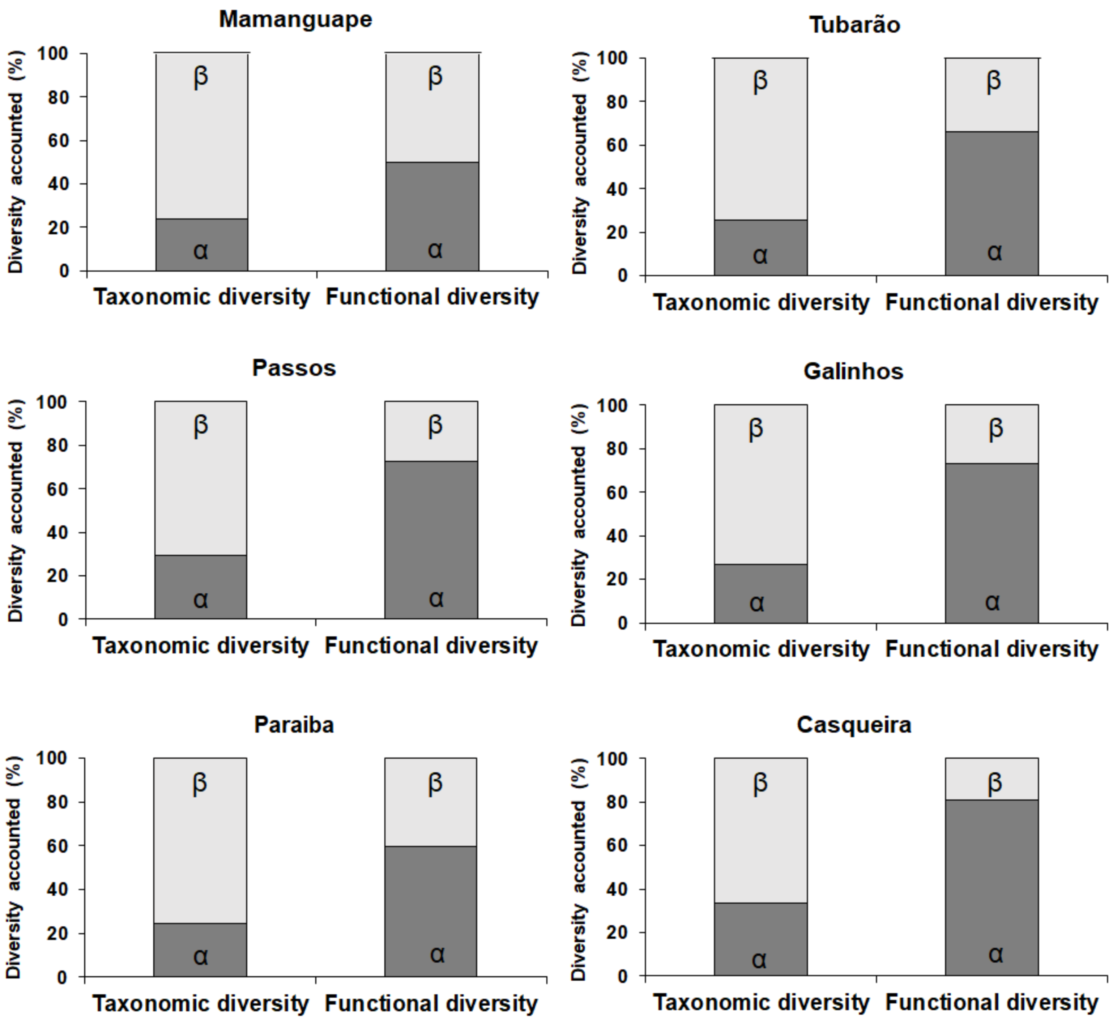
Supplementary material



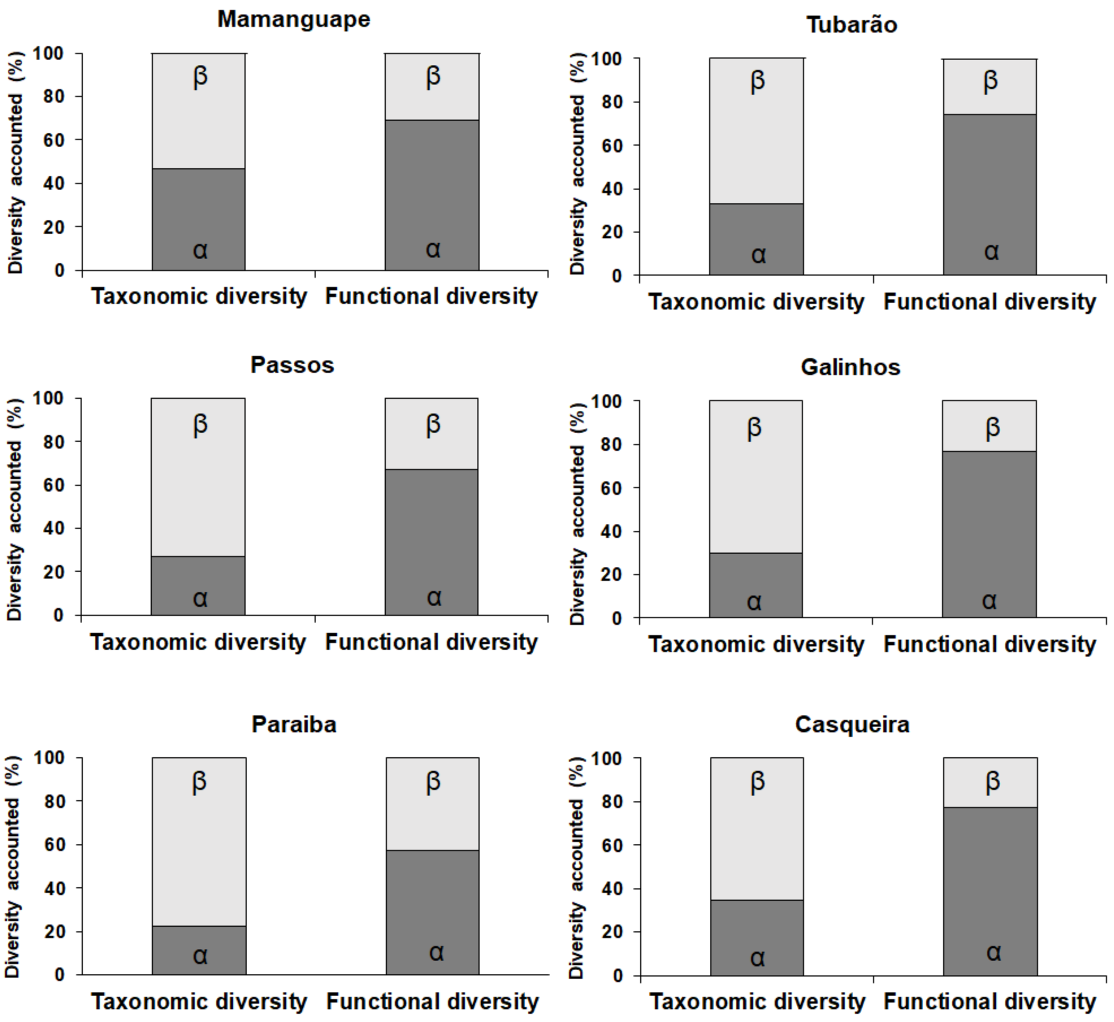
Supplementary material I. Observed (Obs) and expected (Exp) proportions of alpha and beta diversity of taxonomic and functional diversity of mollusc community in typical tropical (Mamanguape, Passos and Paraíba do Norte) and semi-arid (Tubarão, Galinhos and Casqueira) estuaries during the dry period.



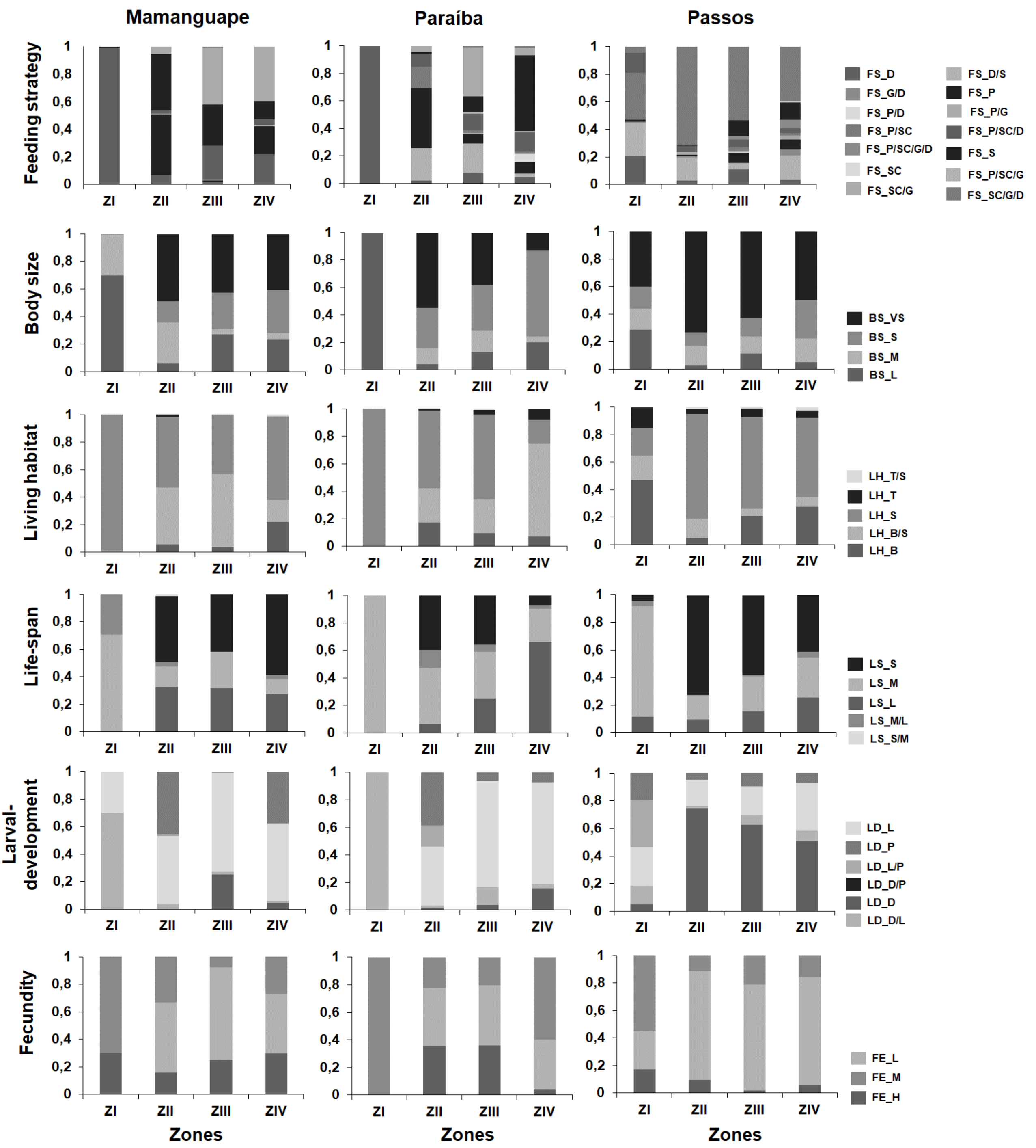
Supplementary material II. Observed (Obs) and expected (Exp) proportions of alpha and beta diversity of taxonomic and functional diversity of mollusc community in typical tropical (Mamanguape, Passos and Paraíba do Norte) and semi-arid (Tubarão, Galinhos and Casqueira) estuaries during the rainy period.



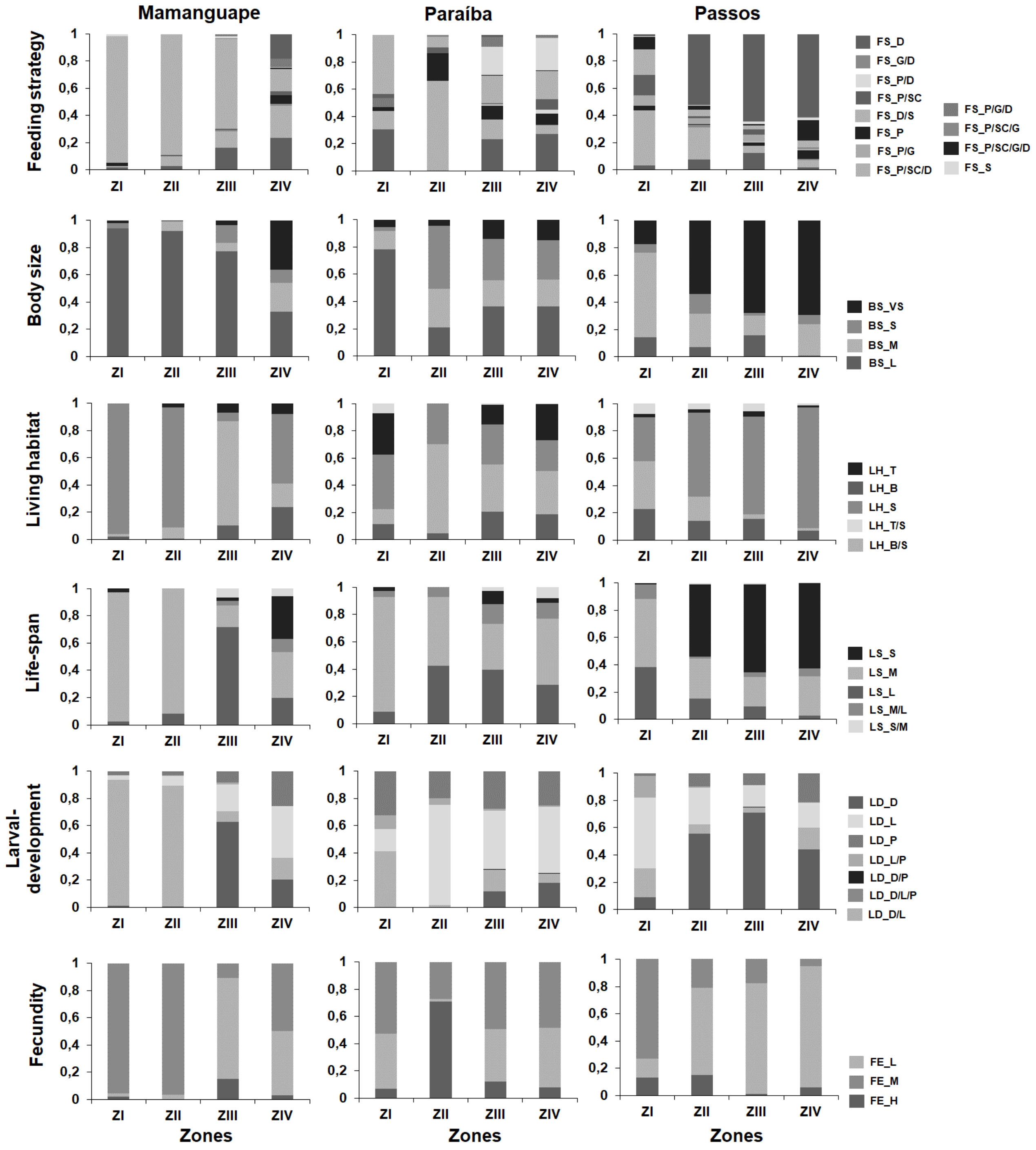
Supplementary material III. Observed (Obs) and expected (Exp) proportions of alpha and beta diversity of taxonomic and functional diversity of polychaete community in typical tropical (Mamanguape, Passos and Paraíba do Norte) and semi-arid (Tubarão, Galinhos and Casqueira) estuaries during the dry period.



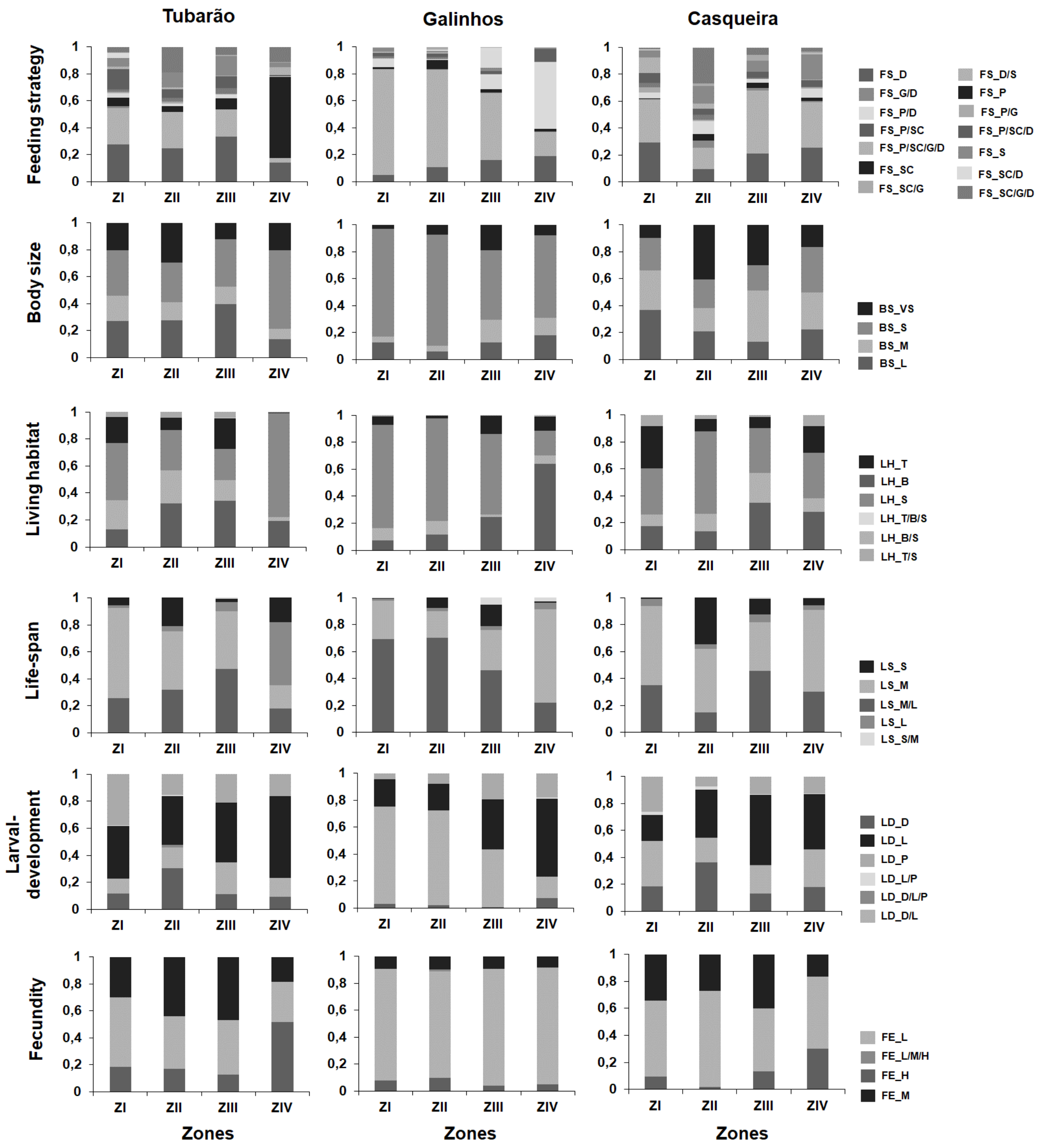
Supplementary material IV. Observed (Obs) and expected (Exp) proportions of alpha and beta diversity of taxonomic and functional diversity of polychaete community in typical tropical (Mamanguape, Passos and Paraíba do Norte) and semi-arid (Tubarão, Galinhos and Casqueira) estuaries during the rainy period.



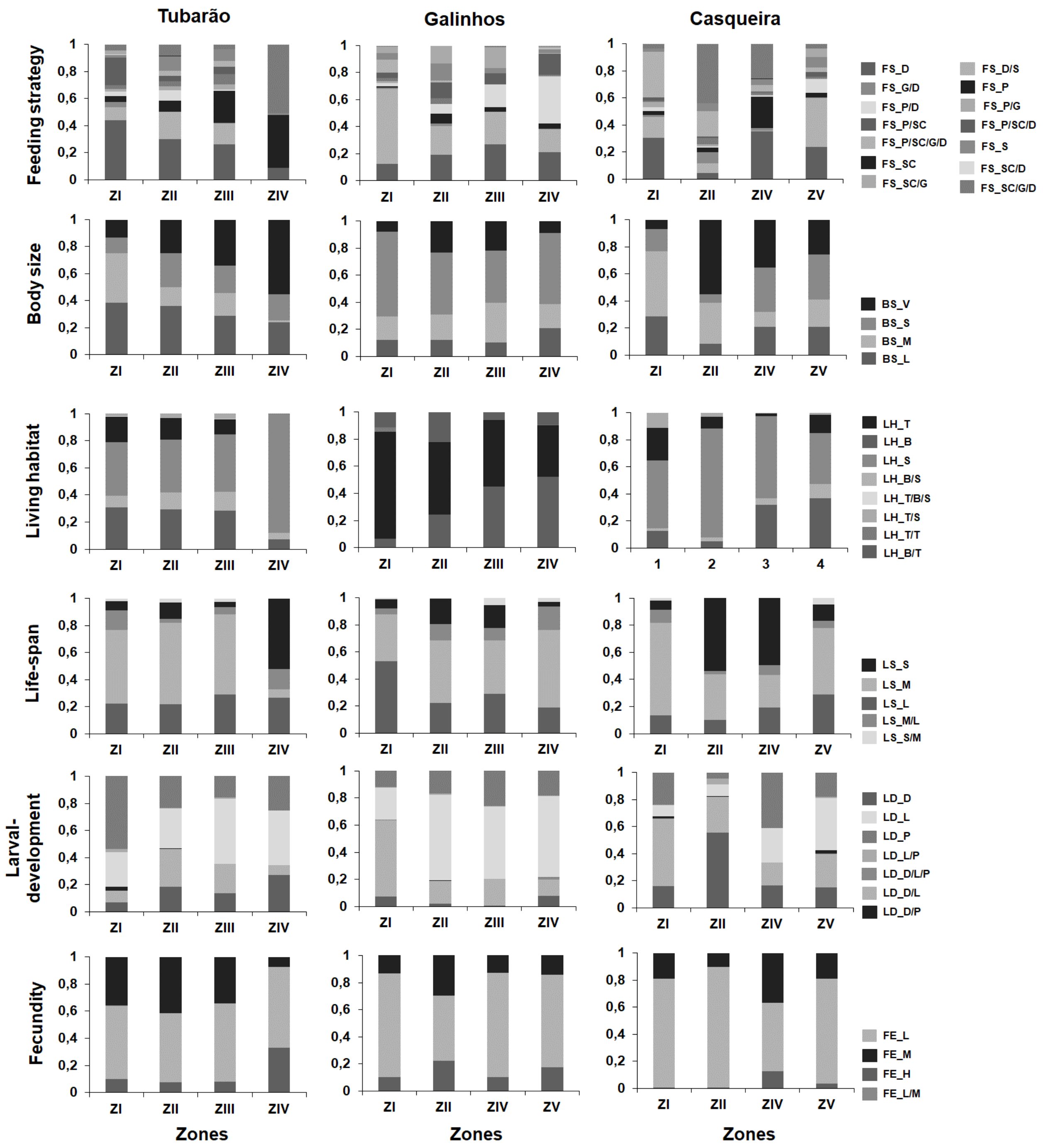
Supplementary material V. Variation of community weighted mean (CWM) trait category of the mollusc and polychaete communities along the zones of the typical tropical estuaries (Mamanguape, Paraíba and Passos) during the dry period. The codes that indicate the categories of the functional traits are available in table 1.



Supplementary material VI. Variation of community weighted mean (CWM) trait category of the mollusc and polychaete communities along the zones of the typical tropical estuaries (Mamanguape, Paraíba and Passos) during the rainy period. The codes that indicate the categories of the functional traits are available in table 1.



Supplementary material VII. Variation of community weighted mean (CWM) trait category of the mollusc and polychaete communities along the zones of the semi-arid estuaries (Tubarão, Galinhos and Casqueira) during the dry period. The codes that indicate the categories of the functional traits are available in table 1.



Supplementary material VIII. Variation of community weighted mean (CWM) trait category of the mollusc and polychaete communities along the zones of the semi-arid estuaries (Tubarão, Galinhos and Casqueira) during the rainy period. The codes that indicate the categories of the functional traits are available in table 1.

Saline gradient drives functional nestedness of polychaete communities in tropical estuaries

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4 SALINE GRADIENT DRIVES FUNCTIONAL NESTEDNESS OF POLYCHAETE COMMUNITIES IN TROPICAL ESTUARIES

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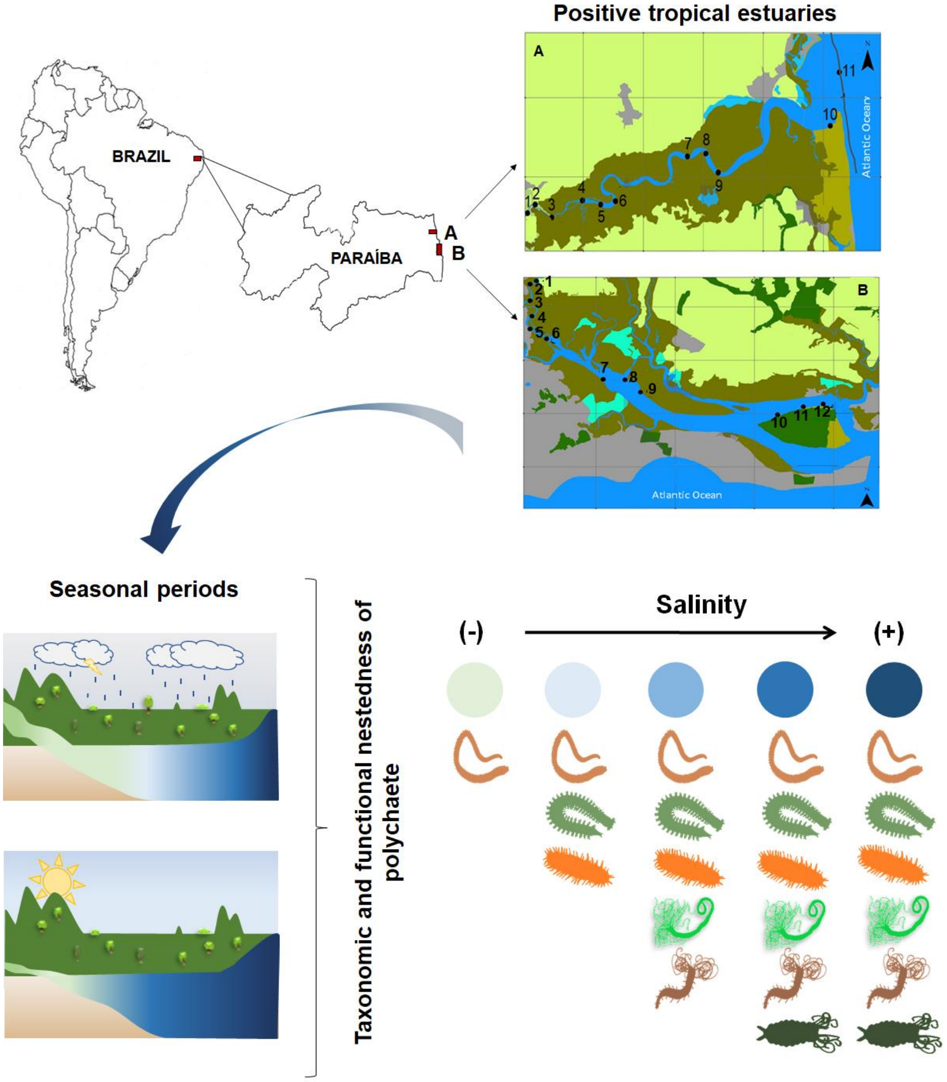
Graphical abstract



ABSTRACT

Estuarine environmental gradients are strong drivers structuring aquatic metacommunities and may cause an orderly loss or gain of species across sites. Locations with milder environmental conditions may allow the establishment of different species with different functional traits, while stressful sites may restrict the occurrence of a reduced set of species with specific functional traits. This can generate a functional nestedness pattern, where the sets of functional traits present at sites with low functional diversity are subsets of the functional traits present at sites with higher functional diversity. In this study, we evaluated the functional nestedness of polychaete communities along salinity gradients of tropical estuaries, and the effects of seasonal periods on the distribution pattern. Two tropical estuarine ecosystems (Mamanguape and Paraíba do Norte) were sampled for two years. Three functional characteristics were considered due to their potential to reflect the species responses to the salinity gradient: maximum body size, life span and fecundity. Functional nestedness was estimated with the traitNODF metric. Subsequently, we used a permutation test to assess whether the nestedness observed along the salinity gradient was distinct from the expected at random. Our results demonstrated that the polychaete communities presented a tendency to functional nestedness along the salinity gradient of estuaries, with observed statistics higher than expected in six of the eight tests performed (2 estuaries * 2 years * 2 seasons). Therefore, the functional diversity of polychaete genera present in the low salinity sites in general were nested subsets of the diversity at high salinity sites. Our results suggest that salinity acted as a strong environmental filter in estuarine ecosystems, causing an orderly loss in the functional characteristics of polychaete genera along the longitudinal extension of the estuaries. Our results advance in the understanding on how environmental gradients structure polychaete communities and can support future studies aimed to develop concrete conservation strategies for estuarine ecosystems located throughout the world.

Key-words: Biological traits, salinity gradient, benthic macrofauna, estuarine dynamics

4.1 INTRODUCTION

Several factors may drive the organization of metacommunities (e.g., environmental filtering and dispersion limitation) (Leibold et al., 2004; Heino et al., 2015). In transition ecosystems with strong environmental gradients, the establishment of different longitudinal abiotic conditions can cause environmental filtering to exercise greater relative importance than dispersal limitation and interactions between species in the assembly of communities (Alves et al., 2020). In this situation, only species that have functional attributes to persist under specific environmental conditions are selected at each location (Kraft et al., 2015).

The interface condition of estuaries between continental and marine ecosystems favors gradual environmental changes along their longitudinal dimension, especially in salinity levels (Quinlan and Phlips, 2007; Telesh and Khlebovich, 2010). The salinity gradient in estuaries makes these ecosystems highly spatially and temporally variable, shaping the biodiversity of their communities (Attrill and Rundle, 2002; Elliott and Quintino, 2007; Telesh et al., 2013). The existence of longitudinal patterns in the distribution of benthic macroinvertebrate diversity of estuaries mediated by the saline conditions is well documented in the literature, considering mainly taxonomic data (e.g., Remane, 1934; Telesh et al., 2013). These studies have observed a decrease in species richness and change in species composition as the estuarine salinity decreases (e.g., Barros et al., 2014; Medeiros et al., 2016).

The occurrence of species along a gradient is closely linked to their biological and ecological traits, which make them tolerant to a limited range of environmental conditions. The estuarine benthic macrofauna is predominantly marine and the areas of lower salinity in estuaries constitute a physiological barrier for species (e.g., polychaete communities), being a natural stress (Elliott and Quintino, 2007; Telesh and Khlebovich,

2010) for those that do not have functional attributes to persist in these conditions (Darr et al., 2014). Considering marine species, the mildest locations of the salinity gradient (i.e., locations with high salinity, closer to the sea) may allow the establishment of species with different functional traits, while stressful locations (low salinity) restrict the occurrence of marine species in locations closer to the continental drainage. In this case, the species that make up the community in stressful locations tend to have specific categories of functional traits, that is, small size, short life span, and high reproduction (Odum, 1985; Llodra, 2002). These species are recognized as strategists and tolerant species to cope with environmental stresses because they allocate energy to strategies that maintain their survival and reproduction (Odum, 1985; Llodra, 2002). Although the persistence of strategist species has been mainly related to stresses of anthropic origin, Elliott and Quintino (2007) suggested that this can be extended to estuarine environments, where natural environmental stress occurs mainly due to variations in salinity. This can generate a functional nestedness gradient, where the sets of functional traits of species present at stressful sites, containing lower functional diversity, are subsets of the functional traits present at sites with higher functional diversity (Bender et al., 2017). In this case, nestedness occurs due to the persistence of species adapted to stressful environmental conditions throughout the ecosystem (Gutiérrez-Cánovas et al., 2013).

The differences of rainfall between seasonal periods and the influence of the tides change the salinity threshold longitudinally in the estuaries. In periods of high rainfall, strong continental drainage into the estuary favors a decrease in water salinity (Medeiros et al., 2020). During dry periods estuaries are subjected to a greater influence of saline incursion and higher evaporation of water due to higher air temperatures. These seasonal climatic conditions affect environmental conditions across estuaries and make certain salinity levels inhospitable for species that lack the ability to regulate internal ion concentrations. Consequently, the structure of estuarine communities also varies throughout the year, due to changes in the saline gradient (Gobler et al., 2005; Netto et al., 2012).

Previous studies have assessed taxonomic nestedness of benthic macrofauna communities in tropical and temperate estuaries using dissimilarity indices (e.g., Barros et al., 2014; Medeiros et al., 2016; Menegotto et al., 2019). In estuaries subject to high intensities of anthropic influences, Barros et al. (2014) and Medeiros et al. (2016) observed that the benthic macroinvertebrate communities tend to present nestedness. Menegotto et al. (2019) identified that the sediment composition in smaller spatial scales generated a taxonomic nestedness of the benthic macrofauna. However, depending on the objectives of the study, taxonomic data may be less explanatory if environment selects the species not for their identity but for their functional traits (Melo et al., 2014). When only taxonomic composition is taken into account, species are considered functionally equivalent to each other, which are very unlikely (Melo et al., 2014). Thus, considering taxonomic and functional aspects simultaneously can provide more refined and complementary answers on the structuring of communities.

Studies evaluating functional nestedness are recent and usually involve island or fragments and their connection to the regional species pool. For example, Melo et al. (2014) identified functional nestedness of Caribbean bats in relation to the size of oceanic islands, while Bender et al. (2017) detected the same pattern in fish assemblages considering the area and isolation of tropical reefs. Also, there are records of functional nestedness of birds in relation to forest fragment area (Matthews et al., 2015), and for climbing plant assemblages in relation to the size and area of the tree vegetation islands in a grassland matrix (Seger et al., 2017). Nonetheless, functional nestedness records on environmental gradients (not area or degree of isolation) seems to be rare.

Polychaetes have been used widely as a biological model in several ecological studies in estuarine ecosystems due to their high species richness and occurrence under various environmental conditions, reflecting general patterns of the estuarine benthic macrofauna (Olsgard and Somerfield, 2000; Schüller et al., 2009). Polychaetes present traits (e.g., are relatively sedentary organisms and have life cycles that can last from weeks to years) (Giangrande, 1997), which make them sensitive to the environmental conditions of the habitats (Del-Pilar-Ruso et al., 2009).

In this study, we evaluated the functional nestedness of polychaete communities along salinity gradients of tropical estuaries and the effects of seasonal periods on this pattern. Our hypotheses were i) that polychaete communities in sites farther from the ocean (more stressful sites) are taxonomically and functionally nested in relation to those closer to the ocean (milder salinity conditions) (Fig. 1), and ii) that the degree of nestedness varies throughout the year, with larger effect sizes during the rainy season. We expect to observe higher functional nestedness in the rainy season because in this seasonal period the salinity of the upstream zones decreases due to greater continental drainage in this period, making the salinity levels more stressful for polychaetes, mostly adapted to higher levels of salinity. This would result in a restricted set of strategist polychaetes in these zones, with a gradual increase of organisms towards the estuarine zones of greater salinity. Joint assessment of taxonomic and functional nestedness patterns can provide a broader and more accurate understanding of the mechanisms that drive community assembly in estuarine ecosystems, thereby allowing for more effective management and conservation measures.

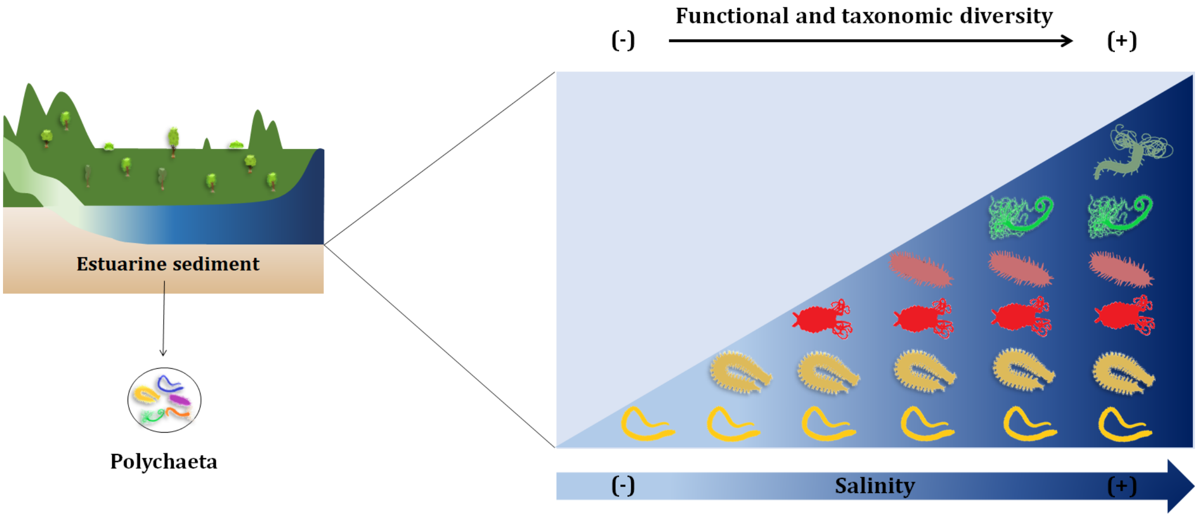


Fig. 1. Representation of the hypothesis tested in this study. The salinity gradient of the estuaries generates taxonomic nestedness (represented by the different body shapes of the organisms) and functional nestedness (represented by the different colors of the organisms) of the polychaete communities.

4.2 MATERIAL AND METHODS

4.2.1 Study area

We studied two estuaries, Paraíba do Norte (6°54’14” - 7°07’36”S; 34°58’16” - 34°49’31”W) e Mamanguape (6°43’02” - 6°51’54”S; 35°67’46” - 34°54’04”W) (Fig. 2). They are located in the tropical region of Northeastern Brazil, which is characterized by a hot and humid tropical climate of type “As” (Alvares et al., 2013). The average annual rainfall of the region is 1200 mm and has two well defined climatic periods: dry and rainy. The period of greatest rainfall occurs from June to August and the dry one between December and March (CPTEC, 2018). The intermediate months to these two seasonal periods have transitional climatic conditions.

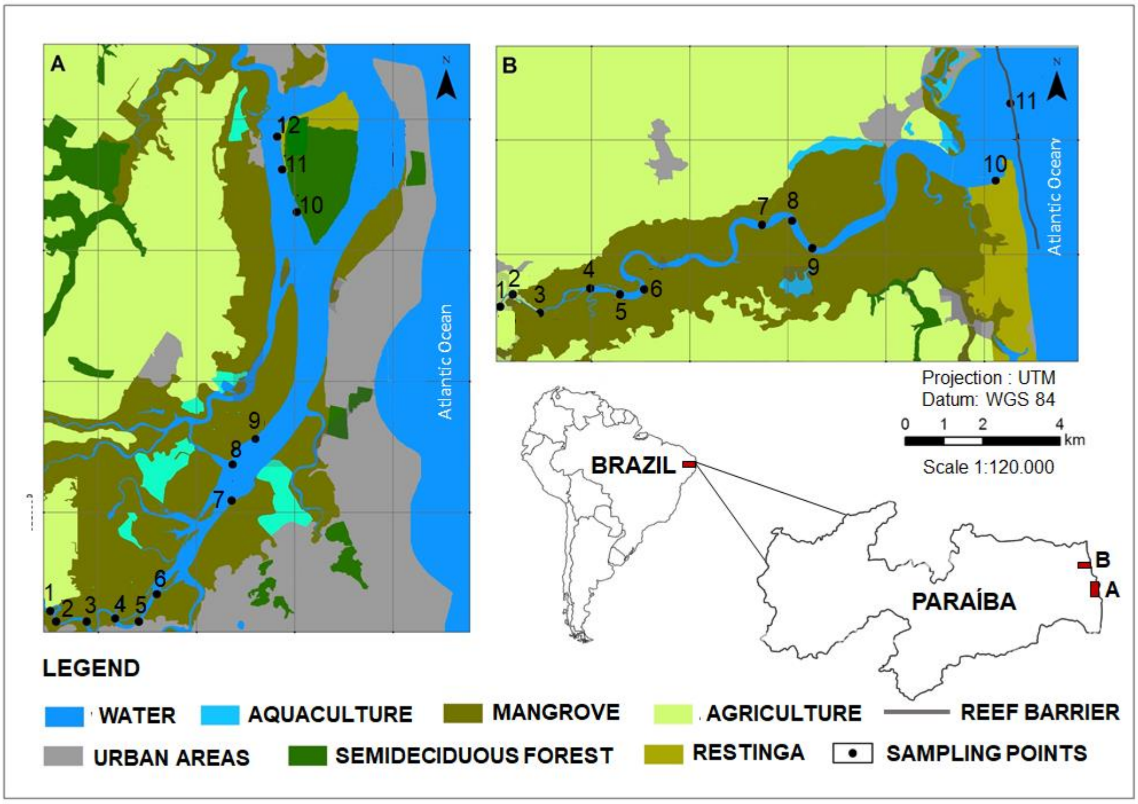


Fig. 2. Locations of the Paraíba do Norte (A) and Mamanguape (B) estuaries, located in Paraíba State, Brazil.

The Paraíba do Norte estuary is approximately 3012 ha (Santana et al., 2018), about 22 km long and surrounded by a population of nearly 1,100,000 inhabitants. It receives direct influence from the Atlantic Ocean due to its free connection to the sea. The Mamanguape estuary extends over 690 ha (Santana et al., 2018), with a length of 24 km. A population of about 66,000 inhabitants resides near the estuary (Van der Linden et al., 2017). At the mouth of the estuary, parallel to the shoreline, a reef barrier extends 8.5 km in length (Santana et al., 2018). The Mamanguape estuary is located in an environmental protection area and has well-preserved mangrove areas (Santana et al., 2018). Despite this, shrimp farms and the cultivation of sugarcane are present in areas close to this ecosystem (Van der Linden et al., 2017; Medeiros et al., 2016). The Paraíba do Norte estuary is located in an urbanized region, which exerts potential anthropic activities in this ecosystem (e.g., leisure, fishing, disposal of domestic and industrial waste, sugarcane cultivation) (Van der Linden et al., 2017).

4.2.2 Saline gradient and sample design

Samples were collected in two years, sampling two periods of drought (in 2013 and 2017) and two periods of rain (in 2014 and 2016) in order to evaluate how climatic variation of the region shapes the estuarine dynamics and benthic community structure. We selected 11 sampling sites in Mamanguape and 12 sampling sites in Paraíba do Norte estuary, which reflect the longitudinal environmental changes in the estuaries, mainly in terms of salinity (Fig. 2). Although other factors also vary along the estuaries (e.g., sediment composition), those variations do not occur progressively and predictably like salinity. For this reason, only salinity was considered in this study. The sites were sampled from the continental drainage towards the sea. The salinity at each sampling site was estimated using a salinity refractometer, and results varied widely among sites (Table 1). We obtained three sample units at each site and later combined the sample units for data analyses.

Table 1. Salinity at sampling sites of the Paraíba do Norte and Mamanguape estuaries during the dry and rainy periods in the two years of study. Sites are ordered from the upstream (continental drainage) to the downstream (near the sea) portions of the estuaries.

	2013-2014				**2016-2017**			
	Dry (2013)		**Rainy (2014)**		**Rainy (2016)**		**Dry (2017)**	
Sites	**Mamanguape**	**Paraíba**	**Mamanguape**	**Paraíba**	**Mamanguape**	**Paraíba**	**Mamanguape**	**Paraíba**
1	14	3	0	1	8	3	10	10
2	15	6	0	1	5	6	17	15
3	16	8	0	3	6	14	19	20
4	19	9	1	6	14	17	25	20
5	21	10	4	8	14	19	24	23
6	22	12	5	10	16	21	25	25
7	29	21	12	17	24	28	26	28
8	30	21	14	18	25	30	30	28
9	30	20	14	20	25	34	31	29
10	36	34	36	28	30	35	40	35
11	36	35	32	28	39	35	40	36
12	-	35	-	33	-	36	-	38

4.2.3 Field sampling

The polychaete communities were sampled during low tide and in the subtidal region with a van Veen dredge (area of 0.1 m² in 2013 and 2014 and an area of 0.05 m² in 2016 and 2017). Due to the different areas of the samplers, the results of the taxonomic composition of the polychaete communities were represented in terms of density (number of individuals/area). The sampled sediment was washed *in situ* in 0.5 mm mesh sieves. In the laboratory, the polychaetes were selected and preserved in 70% alcohol. All organisms were identified at the taxonomic level of genera using specialized taxonomic keys (Amaral and Nonato, 1996; Amaral et al., 2006).

4.2.4 Functional traits

Three functional traits were selected based on the literature and each one presented three levels (Table 2): maximum body size, life span, and fecundity. These functional traits are recognized as important for strategists and tolerant species to cope with environmental stresses (Odum, 1985; Llodra, 2002), and have been evaluated (Darr et al., 2014) and reported (Elliott and Quintino 2007) as meaningful for the evaluation of estuarine salinity gradients (Table 2). Information of the functional traits of polychaetes were obtained from online databases MarLIN (MarLIN, 2006) and Polytraits (Faulwetter et al., 2014) and in published papers (Van der Linden et al., 2017).

Table 2. Functional traits of the polychaete communities with their respective categories and the importance of each characteristic in relation to the salinity gradient.

Traits	Categories	Importance
Maximum body size	Small (<21 mm) Medium (21-100 mm) Large (>100 mm)	Determinant of general life history and the structuring of trophic interactions (Webb et al., 2009). Small species are more adapted to areas with low salinity (Darr et al., 2014).
Life span	Short (<1 year) Medium (1-3 years) Long (>3 years)	Reflects the movement of matter in the benthic system (Veríssimo et al., 2012). Short-lived organisms are better adapted to areas with low salinity (Darr et al., 2014).
Fecundity	Low (1-2500 eggs) Medium (2500-100,000 eggs) High (>100,000 eggs)	Characteristic that indicates population growth potential. Species with high fecundity are favored under environmental stress (e.g., areas with low salinity) (Llodra, 2002; Van der Linden et al., 2017).

To the species were assigned values that ranged from 1 to 3 in relation to body size, corresponding to the categories “small”, “medium” and “large” and for fecundity the values from 1 to 4 that represented fecundity “low”, “medium”, “low/medium” and “high”, respectively. For life span, values 1, 3 and 5 were assigned to taxa that had exclusively “short”, “medium”, and “long” life span. The taxa that had life spans that encompassed more than one category were assigned values 2 and 4, which represented the organisms with short to medium or medium to long life spans, respectively.

4.2.5 Data analysis

We used the treeNODF metric to evaluate the functional nestedness of the estuarine polychaete communities along the salinity gradients in the different seasonal periods. This metric evaluates nestedness by considering the resemblance among species in terms of functional traits (traitNODF) or phylogenetic relatedness (phyloNODF) (Melo et al., 2014). TreeNODF is a direct extension of the NODF index (*Nestedness Based on Overlap and Decreasing Fill*; Almeida-Neto et al., 2008), which is based on the taxonomic composition of species. Therefore, in NODF, the underlying diversity measure is species richness. In the other hand, in traitNODF, the functional diversity used is given by the sum of the branch lengths of tree-like objects that unites species in a community (e.g., a functional dendrogram; Petchey and Gaston, 2002) (Melo et al., 2014). The metric traitNODF has two components: S.fraction corresponds to nestedness in terms of species composition, while topoNODF corresponds to the proportion of traitNODF value that is due to functional similarity of species or functional tree topology (Melo et al., 2014).

The functional similarity between the polychaete genera of each estuary and at each seasonal period was estimated from dendrograms obtained with the functional traits of the genera. Dendrograms were obtained using the Gower distance and UPGMA (*Unweighted Pair Group Method with Arithmetic mean*; Petchey and Gaston, 2002) clustering algorithm. Functional nestedness (traitNODF) is calculated in two steps. In the first step, for each pair of sites it is evaluated whether the functional diversity of the supposedly species-richer community (sites with higher salinity) is in fact greater than the functional diversity of the supposedly species-poorer community (sites with lower salinity). If not, nestedness is zero. If so, nestedness corresponds to the proportion of the branches present in the functionally-poorer community that are also present in the richer community (Melo et al., 2014). For each comparison, the maximum traitNODF value is 100 and occurs when the functional diversity of the poorer community is a perfect subset of the community with higher functional diversity (Melo et al., 2014). Following this procedure, one nestedness value is generated for each pair of sites at each estuary. In the second step, traitNODF for each estuary is then obtained calculating the average nestedness between all pair of sites (Melo et al., 2014).

To test our hypothesis that communities in low salinity locations are nested in those with higher salinity we constructed matrices of presence or absence of polychaete genera (columns) by sites (rows). The ordering of the rows was given by decreasing of salinity, that is, from downstream to upstream sites. This ordering determined the pairwise comparisons of the supposedly functionally-richer sites (those closest to the ocean) and the functionally-poorer ones (those farthest to the ocean). Salinity values in estuaries are highly dynamic throughout the day, and due to the impossibility of taking salinity measurements at all sampled sites simultaneously, we used the position of the sampling sites in the longitudinal gradient as a salinity proxy. A matrix row permutation test was used to assess whether the observed nestedness was greater than expected in a situation where polychaete communities were randomly distributed along the gradient. Species composition and functional traits within communities were not randomized. The randomization test based on permutation of rows is indicated in cases where sites are ordered according to an a priori hypothesis (in our case, which the saline gradient drives the taxonomic and functional nestedness of polychaete communities). This ordering of the matrix accordingly to an independent factor is not possible using the dissimilarity metric popularized by Baselga (2010) that assess nestedness or, more properly, species richness differences (Almeida-Neto et al., 2012).

We carried eight tests, one for each combination of estuary, season and year (2 * 2 * 2 = 8). Sampling effort differed between years (0.1 m^2 in 2013 and 2014 and 0.05 m^2 in 2016 and 2017). However, analyses were done separately for each dataset and thus comparisons included pairs of samples obtained with the same effort. The tests were performed considering 9999 permutations. TraitNODF analyses were performed in the R environment using the ‘treeNodf’ function of the ‘CommEcol’ package (Melo, 2013).

4.3 RESULTS

4.3.1 Taxonomic composition of the polychaete communities

Samples included 9916 individuals of the two estuaries during all four sampling periods. In the Mamanguape estuary, the polychaete community presented an average density of 27.33 ± 22.69 individuals/m^2 in the rainy season and 72.32 ± 121.22 individuals/m^2 in the dry season of the first year of collection (2013/2014). In the second year of collection (2016/2017), an average density of 51.96 ± 48.47 individuals/m^2 was sampled in the rainy season and 41.48 ± 47.74 individuals/m^2 in the dry season. The genera that presented higher densities in the Mamanguape estuary were *Lumbrineris* (27.06%), *Spiochaetopterus* (16.05%) and *Kinbergonuphis* (13.07%) in the 2014 rainy season and *Laeonereis* (81.11%), *Timarete* (5.75%) and *Armandia* (2.14%) in the dry period of 2013 (Fig. 3). *Laeonereis* (47.70%), *Lumbrineris* (31.31%) and *Mediomastus* (4.97%) presented higher densities in the 2016 rainy season and *Laeonereis* (45.48%), *Lumbrineris* (24.38%) and *Glycinde* (20.55%) in the 2017 dry season (Fig. 3).

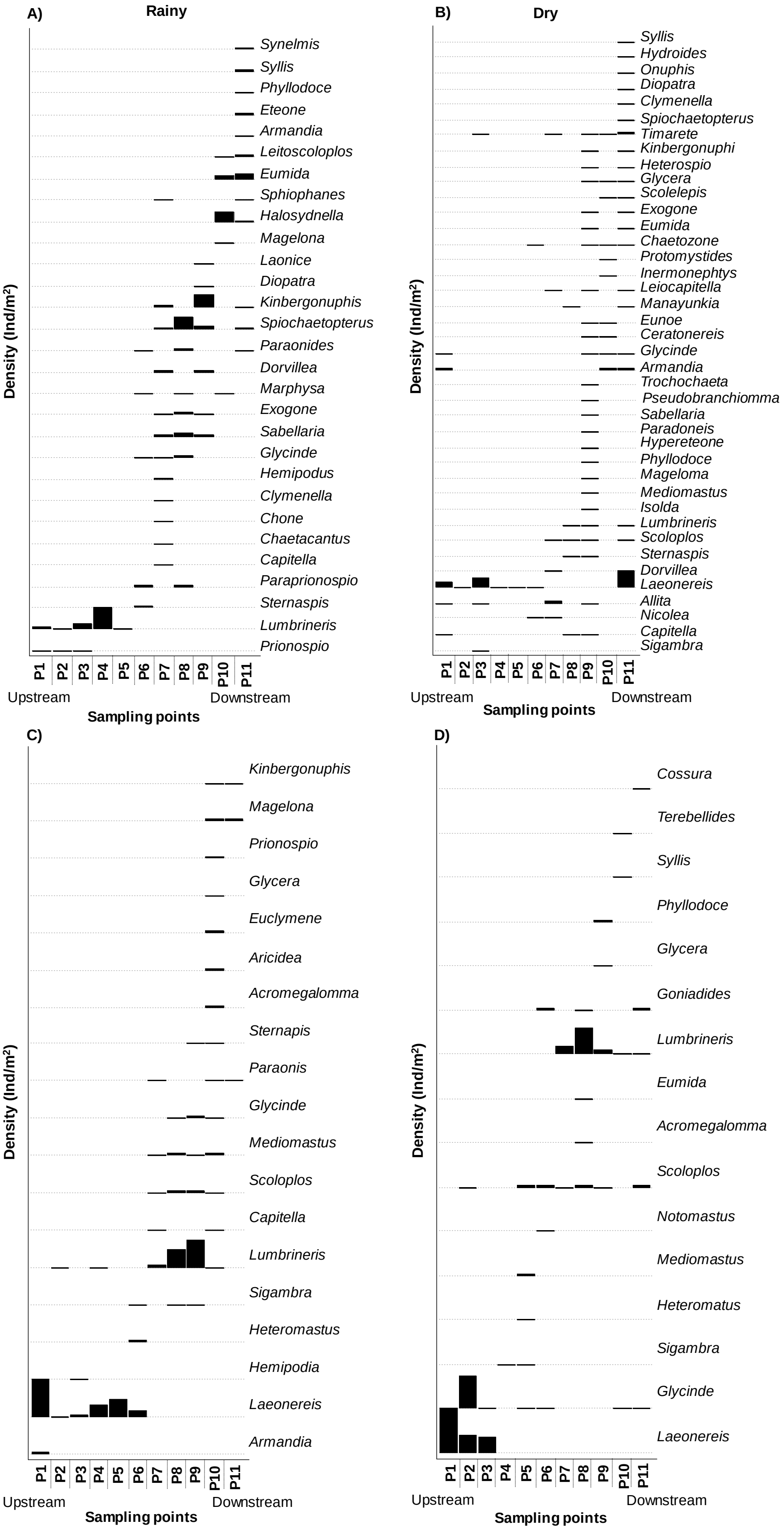


Fig. 3. Density (individuals/m^2) of polychaete genera at the Mamanguape estuary sampling sites during the rainy (A and C) and dry (B and D) periods in the first 2014/2013 (A and B) and second 2016/2017 (C and D) year of collection. The polychaete genera were ordered on the X axis according to their occurrence along the salinity gradient.

The polychaete community of the Paraiba do Norte estuary presented an average density of 27.02 ± 20.18 individuals/m^2 in the rainy season and 58.41 ± 64.71 individuals/m^2 in the dry season, both seasonal periods of the first year of collection (2013/2014). In the second year of collection (2016/2017), the average density of the polychaete community sampled in the Paraiba do Norte estuary was 25.04 individuals/m^2 ± 27.30 in the rainy season and 20.44 individuals/m^2 ± 27.29 in the dry season. The most representative polychaete genera in the first year of collection were *Laeonereis* (38.45%), *Heteromastus* (11.31%) and *Kinbergonuphis* (4.87%) in the 2014 rainy season and *Laeonereis* (48.99%), *Leiocapitella* (4.21%) and *Sabellaria* (4.05%) in the 2013 dry season (Fig. 4). In the second year of collection, *Laeonereis* (12.78%), *Heteromastus* (10.68%) and *Lumbrineris* (7.18%) presented higher densities in the rainy season, while in the dry season *Lumbrineris* (25.36%), *Sigambra* (10.14%) and *Acromegalomma* (8.69%) were the most representative genera (Fig. 4). No specimen was found in samples of sites 3 and 7 of the Paraíba do Norte estuary in the dry period of the second year of collection (Fig. 4D).

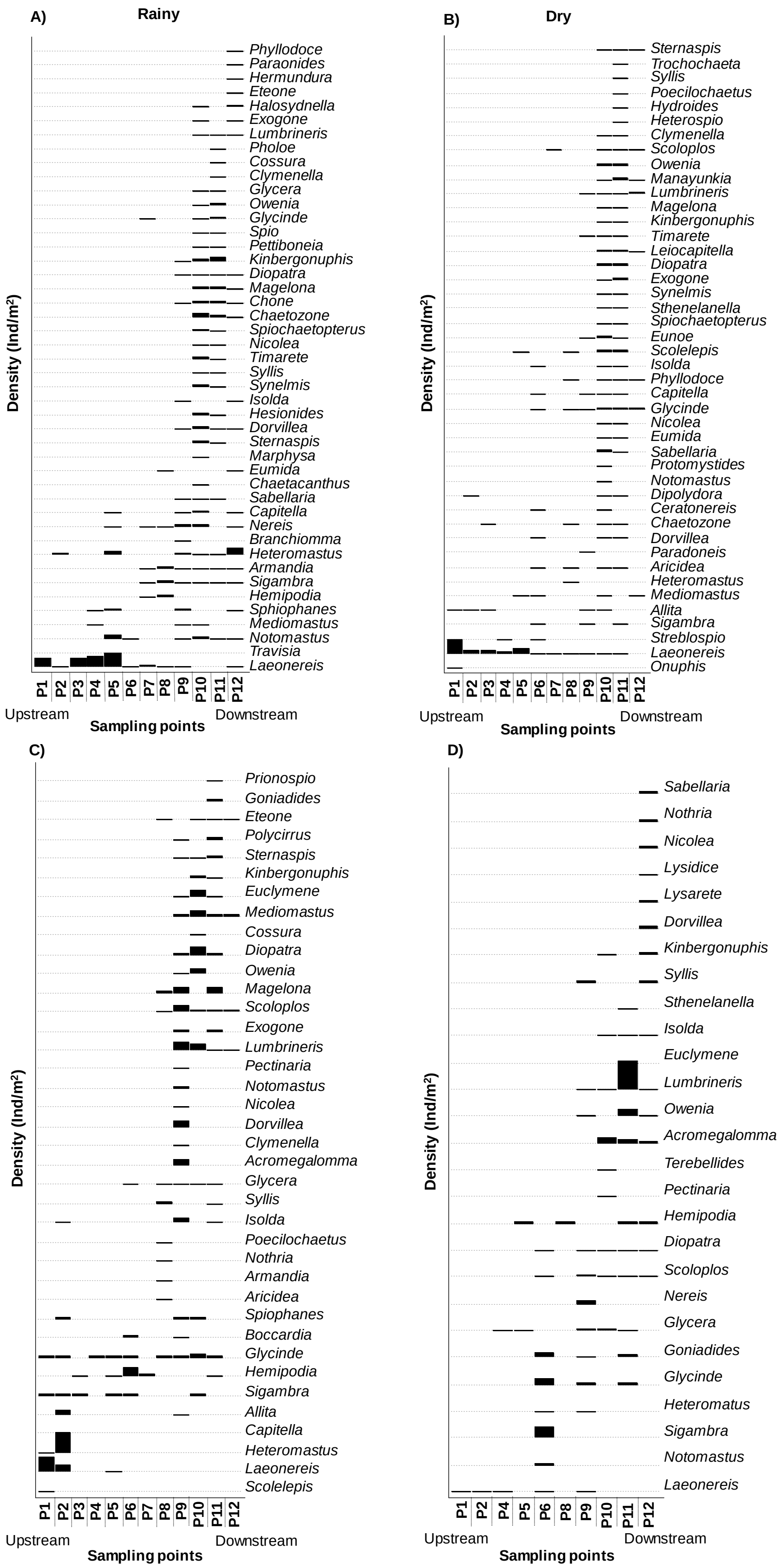


Fig. 4. Density (individuals/m^2) of polychaete genera at the Paraiba do Norte estuary sampling sites during the rainy (A and C) and dry (B and D) periods in the first 2014/2013 (A and B) and second 2016/2017 (C and D) year of collection. The polychaete genera were ordered on the X axis according to their occurrence along the salinity gradient.

4.3.2 Functional diversity of the polychaete communities

The polychaete community showed a tendency of increase in the number of categories of functional traits along the salinity gradient of the Mamanguape and Paraiba do Norte estuaries, although a seasonal pattern was not observed (Figs 5 and 6). Overall, a restricted set of categories of functional traits present in the sites with highest salinity were found in the sites closest to the continental drainage (Figs 5 and 6).

In the Mamanguape estuary, the functional traits of polychaete genera present in the lowest salinity sites was similar to the highest salinity sites for the functional characteristics maximum body size (in the dry period of 2013 and of the rainy of 2017; Figs 5A and 5B), life span (in the dry period of 2017; Fig. 5D), and fecundity (in the dry period of 2013; Fig. 5E). In the Paraiba do Norte estuary, the same occurred only for the functional trait maximum body size, and fecundity, in the dry period of 2013 (Fig. 6A) and rainy period of 2016 (Fig. 6F), respectively.

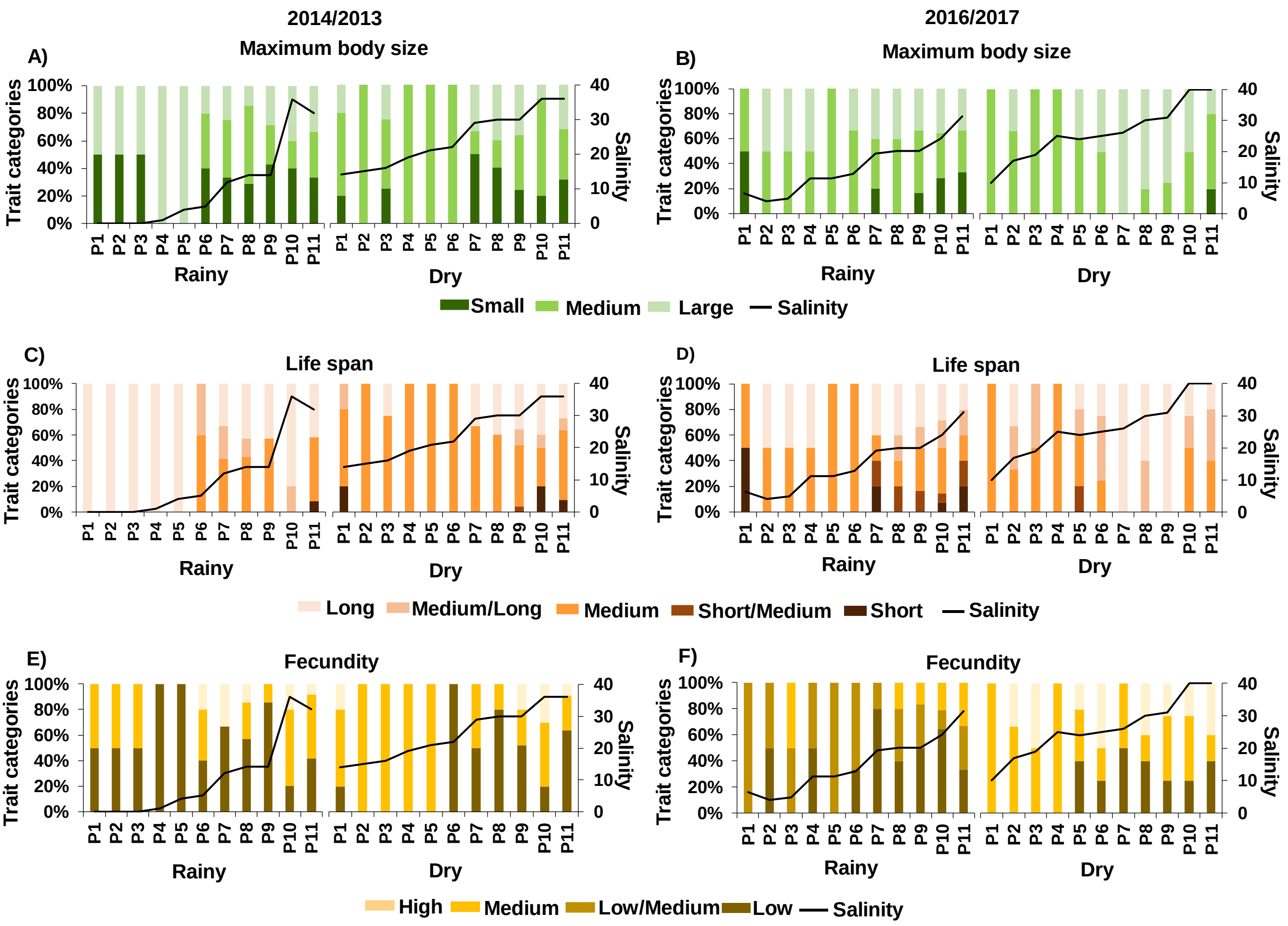


Fig. 5. Percentage (%) of the categories of the maximum body size (A and B), life span (C and D) and fecundity (E and F) traits of the polychaetes genera along the salinity gradient of the Mamanguape estuary in the first (A, C and E) and second (B, D and F) years of collection.

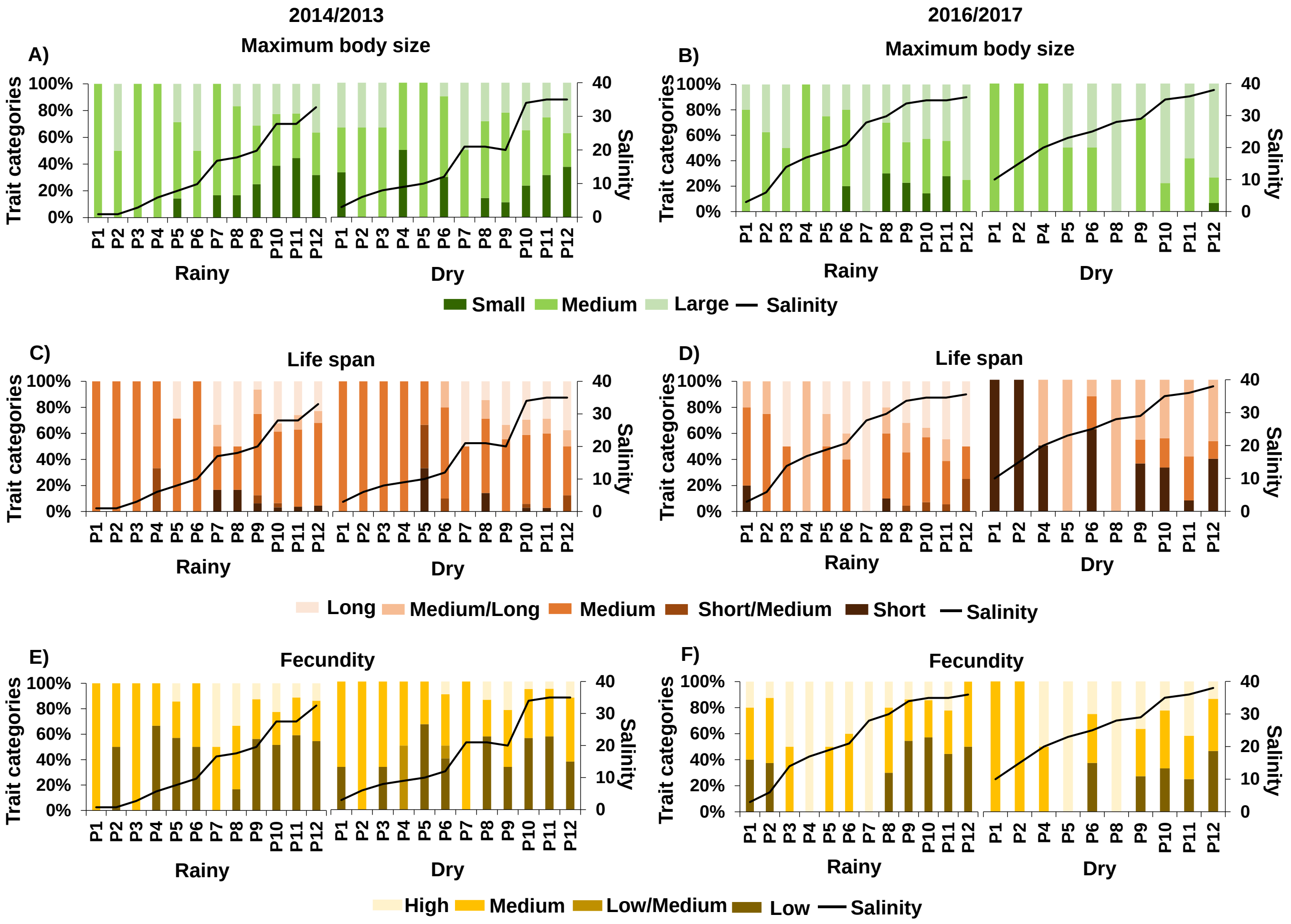


Fig. 6. Percentage (%) of the categories of the maximum body size (A and B), life span (C and D) and fecundity (E and F) traits of the polychaetes genera along the salinity gradient of the Paraiba do Norte estuary in the first (A, C and E) and second (B, D and F) years of collection.

4.3.3. Functional nestedness of the polychaete communities

The polychaete communities showed a tendency to be functionally nested along the salinity gradient of the estuaries (Table 3). The functional diversity of polychaete genera present in the lower salinity sites tended to be subsets of the higher salinity sites. Six out of the eight tests performed (2 estuaries * 2 times of the year * 2 years of study) indicated a functional nestedness greater than the expected by chance (Table 3). The two non-significant tests refer to the Mamanguape estuary during the dry period of 2017 and to the Paraiba do Norte estuary during the rainy season of 2016 (Table 3). For the latter case, although the overall traitNODF was not significant (p = 0.080), its topoNODF component was higher than the expected by chance (p = 0.027).

Table 3. Functional nestedness analysis of the polychaete communities in relation to the salinity gradient of the Paraíba do Norte and Mamanguape estuaries partitioned into their components S.fraction (nestedness in relation to community composition) and topoNODF (nestedness in relation to tree topology). Mean = average of the values obtained from the null distribution (9999 permutations). SD = Null distribution standard deviation. Z = Effect Size ([Observed– Mean]/SD). Negative effect sizes (Z-scores) indicate that observed values were smaller than expected at random.

	Mamanguape									
	Rainy					**Dry**				
Metric	Observed	Mean	SD	Z	*P*	Observed	Mean	SD	Z	*P*
	2014					**2013**				
traitNODF	49.87	33.60	8.56	1.90	0.027	60.22	39.11	10.17	2.07	0.018
S.fraction	5.37	9.50	3.60	-1.15	0.860	29.01	21.06	6.13	1.30	0.103
topoNODF	44.50	24.10	7.44	2.74	<0.001	31.21	18.05	5.59	2.35	0.004
	2016					**2017**				
traitNODF	53.83	35.88	9.20	1.95	0.023	26.87	30.77	9.19	-0.42	0.659
S.fraction	20.90	17.44	4.66	0.74	0.241	15.76	14.01	4.51	0.39	0.357
topoNODF	32.93	18.44	6.11	2.37	0.006	11.11	16.76	5.23	-1.08	0.852
	Paraíba do Norte									
	Rainy					**Dry**				
Metric	Observed	Mean	SD	Z	*P*	Observed	Mean	SD	Z	*P*
	2014					**2013**				
traitNODF	80.49	44.71	10.62	3.37	<0.001	67.28	41.31	9.95	2.61	0.003
S.fraction	58.09	32.44	7.67	3.34	<0.001	40.85	25.72	6.81	2.22	0.009
topoNODF	22.40	12.27	4.23	2.39	0.001	26.43	15.59	4.13	2.62	0.002
	2016					**2017**				
traitNODF	52.89	39.84	9.30	1.40	0.080	64.98	35.55	9.58	3.07	<0.001
S.fraction	30.32	24.75	6.14	0.91	0.192	40.27	21.79	5.81	3.18	<0.001
topoNODF	22.57	15.09	4.00	1.86	0.028	24.71	13.76	4.55	2.40	0.003

In the Mamanguape estuary, when traitNODF values were significant, only the functional composition (topoNODF) of polychaete genera was significantly nested, with larger effect sizes (Table 3). In the Paraiba do Norte estuary, the taxonomic (S.fraction) and functional (topoNODF) composition of the polychaete communities were significantly nested (Table 3).

4 DISCUSSION

The salinity gradient drove the categories of functional traits of the polychaete community of the tropical estuaries studied, corroborating our first hypothesis. The categories of functional traits of the upstream areas (lower salinity zones) generally were nested subsets of the functional traits of the downstream sites (higher salinity zones). When traitNODF was partitioned into its components, in the Mamanguape estuary the values of the topoNODF were higher than those of the S.fraction. In the Paraíba do Norte estuary, both components of traitNODF (S.fraction and topoNODF) were similar. Contrary to our second hypothesis, we did not observe larger effect sizes during the rainy periods.

Several studies have shown that salinity acts as an environmental filter by selecting the species composition according to the salinity levels (Remane, 1934; Gilberto et al., 2007; Telesh and Khlebovich, 2010; Menegotto et al., 2019). Our results showed that the salinity gradient of tropical estuaries not only selected species longitudinally (in the Paraíba do Norte estuary), but also caused a non-random loss of functional traits of polychaete genera. Even when S.fraction values were not significant (Mamanguape estuary) functional nestedness was higher than expected by chance. Thus, our results demonstrated that the functional distribution (topoNODF values) of polychaetes along the studied estuaries was more strongly structured by the salinity gradient than the taxonomic distribution (S.fraction values). The functional nestedness observed in the Paraíba do Norte and Mamanguape estuaries is supported by the habitat templet concept (Southwood, 1977), which predicts that throughout evolutionary history, habitat conditions shape the functional traits of species to ensure its persistence and reproductive success. In this sense, a set of species with adequate functional traits persist in the environment and when stressful environmental conditions begin to emerge, the less adapted species are lost. Thus, only species with functional traits that confer abiotic tolerance can survive, develop and reproduce in the environment (Richmond and Woodin, 1999).

Our hypotheses dealt with nestedness and we showed that polychaete assemblages in areas far from the ocean presented not only reduced functional diversity but that this diversity was a subset of that present in areas closer to the ocean. This result does not indicate that turnover was unimportant. In fact, both nestedness and turnover are usually present in gradients, although one of them may be preponderant (Baselga 2010). Indeed, in a previous study in the two estuaries studied here, Medeiros et al. (2016) partitioned the beta diversity of a larger set of organisms (mollusks and dipterans in addition to polychaetes) through a dissimilarity index and found communities presented important turnover in the estuaries. It is important to note, however, that Medeiros et al. (2016) considered other communities in addition to polychaetes and it is possible that part of their overall result were produced by opposing responses of the organisms, for instance, with polychaetes presenting higher functional diversity toward the ocean and Diptera presenting the reverse pattern.

Our results showed that only a set of polychaete genera with few categories of functional traits were observed in the estuarine areas with lower salinity. This result was also observed by Van der Linden et al. (2017), who assessed the functional diversity of polychaetes and mollusks along spatial gradients, using a larger set of functional traits. This suggests that in these areas the polychaete genera present similar functional traits and, consequently, the communities share a large proportion of the branch length of the functional dendrogram (Matthews et al., 2015). This low functional diversity can be explained by the fact that the energy expenditure for the individuals to regulate their internal ion concentrations and to perform the osmoregulation can be very costly (Rivera-Ingraham and Lignot, 2017). Additionally, salinity stress can cause other physiological changes, such as altering metabolic rates and causing changes in oxygen consumption (Richmond and Woodin, 1999). The greatest diversity of categories of functional traits found in higher salinity areas can be explained by the appropriate salinity conditions for polychaetes to develop their vital activities and persist in the environment.

Our results did not show a trend in the variation of effect sizes between dry and rainy periods, as we hypothesized. Recently, Francisco and Netto (2020) showed that temporal environmental variations altered the hydrodynamics estuaries and structured the benthic communities. When considering the functional nestedness of polychaete communities, our results showed that the salinity gradient drove nested patterns throughout all the year, regardless of the seasonal period analyzed.

Although functional nestedness was identified in the tropical estuaries studied, the distribution of the categories of functional traits across the estuaries did not show a clear pattern. As suggested by Medeiros et al. (2016), some individuals from the benthic macrofauna may be found in certain salinity zones not because the habitat is suitable for their persistence but because the dynamics of the ecosystem may have caused a passive dispersal of these organisms. Thus, the absence of a strong pattern may be related to the high estuarine dynamics and spatial variability, since the salinity values changed between the two estuaries and between sampling periods. Therefore, our results suggest that, when functional nestedness in environmental gradients (not area or isolation) is evaluated, the dynamics of the ecosystem directly influence the observed patterns. Other studies have also highlighted the difficulty of identifying patterns and isolate factors that shape the distribution of benthic macrofauna in estuarine ecosystems due to their high spatial and temporal variability (e.g., Elliott and Quintino, 2007; Darr et al., 2014). Assessing the functional composition of benthic macroinvertebrates along salinity gradients, Darr et al. (2014) also recognized that, in addition to salinity, other factors also vary across estuaries (e.g., sediment composition), but that these variations are not as gradual and predictable as salinity.

In this study, we considered only the salinity gradient of the estuaries. Thus, future studies should investigate the functional nestedness of the polychaete community along other gradients, including gradients of anthropogenic stress. Understanding nested patterns in relation to anthropogenic stress would help to understand whether these activities cause the formation of species subsets, as occurred in the case of the salinity gradient. These studies would fill an existing knowledge gap on the effects of anthropogenic activities on the functional distribution patterns of estuarine communities.

In conclusion, salinity acted as a determining factor of the functional nestedness of the polychaete community. In the lower salinity sites, the polychaete community presented sets of functional traits that generally were nested subsets of the higher salinity zones, where a greater range of categories of functional traits was observed. Our results advance in the understanding on how environmental gradients structure polychaete communities of tropical estuaries and can support future studies aimed at the development of concrete conservation strategies for these ecosystems (e.g., prioritize the protection of areas with higher salinity). The salinity gradient was a stronger environmental filter for functional diversity than for taxonomic diversity. Therefore, effective conservation policies for estuarine ecosystems worldwide should prioritize functional diversity as an ecological indicator.

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5 CONCLUSÃO GERAL

Os resultados obtidos na presente tese forneceram importantes entendimentos sobre os padrões de diversidade funcional e taxonômico de macroinvertebrados bentônicos estuarinos, em múltiplas escalas espaciais e temporais. Nós abordamos os efeitos de gradientes estuarinos, principalmente de salinidade, sobre a montagem das comunidades de macroinvertebrados bentônicos. A estruturação das comunidades de macroinvertebrados bentônicos foram exploradas em diferentes tipos de estuários e nós observamos os efeitos das diferentes dinâmicas estuarinas sobre a organização das comunidades da macrofauna bentônica.

Mais especificamente, avaliando padrões de diversidade espacialmente e a importância relativa dos componentes da diversidade beta (levando-se em consideração abundância relativa e incidência da macrofauna bentônica), nós observamos que diferentes mecanismos estruturam a diversidade das comunidades em diferentes escalas espaciais e períodos sazonais. Ainda, vimos que a filtragem ambiental e barreiras de dispersão foram identificados como os processos mais importantes, gerando maiores dissimilaridades nas maiores escalas espaciais analisadas. Quando comparamos os padrões funcionais e taxonômicos em múltiplas escalas espaciais, encontramos que as interações bióticas exerceram um importante papel na montagem da diversidade funcional das comunidades, com maiores proporções de diversidade nas menores escalas analisadas (diversidade alfa) em ambos os tipos de estuários estudados. Também observamos uma redundância funcional ao longo da dimensão longitudinal dos estuários semiáridos e tropicais típicos. Analisando os padrões de distribuição de poliquetas ao longo de estuários típicos tropicais, observamos que as comunidades apresentam padrões aninhados de espécies em períodos de seca e de chuva, devido a variações graduais de salinidade. Ou seja, a diversidade funcional de locais com menor salinidade são subconjuntos da diversidade funcional de locais com maior salinidade. Assim, o gradiente longitudinal de salinidade dos estuários tropicais típicos causa uma perda ordenada de categorias de características funcionais.

Considerando a elevada variabilidade ambiental dos ecossistemas estuarinos, nossos resultados auxiliaram na compreensão da organização dos macroinvertebrados bentônicos estuarinos tropicais, principalmente os estuários semiáridos que são poucos compreendidos e estudados. Embora os estuários semiáridos sejam menos variáveis longitudinalmente em relação aos estuários tropicais típicos, esses ecossistemas demonstraram uma elevada biodiversidade e a organização das comunidades mostraram-se tão complexa quanto a dos estuários típicos. Ainda, nós sugerimos que embora alguns padrões sejam semelhantes entre os dois tipos de estuários, os mecanismos subjacentes a montagem das comunidades parece não ser os mesmos. Por exemplo, em estuários tropicais típicos, filtros ambientais atuam na montagem das comunidades espacialmente, enquanto que nos estuários semiáridos a limitação de dispersão parece exercer maior importância relativa.

O conhecimento sobre a dinâmica dos ecossistemas e como suas comunidades respondem a variações ambientais dos habitats é um dos primeiros passos para que medidas de conservação possam ser adotadas. Neste sentido, a presente tese apresentou importantes *insights* voltados a descrição de padrões de biodiversidade e propomos que i) múltiplos aspectos taxonômicos (abundância e riqueza) forneceram repostas complementares sobre os padrões de distribuição das comunidades em estuários localizados em regiões com diferentes condições ambientais; ii) abordagens taxonômica e funcional responderam de maneiras distintas às variações ambientais dos estuários tropicais e devem ser analisadas simultaneamente para a obtenção de respostas mais abrangentes e iii) quando o objetivo de estratégias de conservação é priorizar locais com maior diversidade possível, locais de maior salinidade devem ser considerados no caso dos estuários típicos tropicais. Nos estuários semiáridos, devido as variações de salinidade mais homogêneas longitudinalmente, vários locais devem ser considerados.

6 ARTIGOS PUBLICADOS DURANTE O DOUTORADO

Desde o início do doutorado (dezembro de 2016), foram publicados cinco artigos em revistas de qualis A1, A2 e B2.

(i) VAN DER LINDEN, PIETER; MARCHINI, A.; SMITH, C.J.; DOLBETH, M.; SIMONE, L.R.L.; MARQUES, J.C.; MOLOZZI, J.; **MEDEIROS, C.R.**; PATRÍCIO, J. Functional changes in polychaete and mollusc communities in two tropical estuaries. Estuarine, Coastal and Shelf Science, v. 187, p. 62-73, 2017.

(ii) **MEDEIROS, C.R.;** AZEVÊDO, E.L.; BARBOSA, J.E.L.; MOLOZZI, J. Effectiveness of abundance and biomass curves in detecting environmental alterations in semi-arid region reservoirs. Biota Neotropica, v. 18, p. 1, 2018.

(iii) AZEVÊDO, E.L.; **MEDEIROS, C.R.**; GOMES, W.I.A.; AZEVÊDO, D.J.S.; ALVES, R.R.N.; DIAS, T.L.P.; MOLOZZI, J. The use of Risk Incidence and Diversity Indices to evaluate water quality of semi-arid reservoirs. Ecological Indicators, v. 90, p. 90-100, 2018.

(iv) PAIVA, F.F.; GOMES, W.I.A.; **MEDEIROS, C.R.**; ÁLVARO, E.L.F.; RIBEIRO, I.M.S.; MOLOZZI, J. Environmental factors influencing the occurrence of alien mollusks in semi-arid reservoirs. Limnetica, v. 2, p. 187, 2018.

(v) **MEDEIROS, C.R.**; HEINO, J.; SANTOS, P.J.P.; MOLOZZI, J.; LIGEIRO, R. Spatial scale drives diversity patterns of benthic macroinvertebrate communities in tropical estuaries. limnology and Oceanography, p. l-13, 2020.

(vi) **MEDEIROS, C.R.**; PAIVA, F.F.; LIGEIRO, R.; MOLOZZI, J.; MELO, A.S. Saline gradient drives functional nestedness of polychaete communities in tropical estuaries. Estuarine Coastal and Shelf Science, p. 107185, 2021.