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**INFLUÊNCIA DAS MÚLTIPLAS ESCALAS ESPACIAIS NA  
ESTRUTURA E FUNÇÃO DA MACROFAUNA BÊNICA DE  
MANGUEZAIS**

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Ricardo Franco Freitas

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FUNÇÃO DA MACROFAUNA BÊNICA DE MANGUEZAIS**

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Orientador: Prof. Dr. Paulo Roberto Pagliosa

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FUNÇÃO DA MACROFAUNA BÊNITICA DE MANGUEZAIS**

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutor em Ecologia.

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Coordenação do Programa de Pós-Graduação

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Prof. Dr. Paulo Roberto Pagliosa  
Orientador

Florianópolis, 14 de abril de 2020.

Este trabalho é dedicado aos meus pais e avós.

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## RESUMO

Os manguezais ocorrem ao longo de regiões tropicais e subtropicais, diferenciando em função da geomorfologia costeira, fluxo de energia, padrões de estrutura da floresta e distribuição das espécies. A comunidade bêntica macrofaunal presente nesses ambientes é influenciada pelas suas propriedades ambientais, vegetação e solo em distintas escalas espaciais. A combinação de fatores de maior escala, como a descarga de rios e amplitude de marés, é capaz de originar diferentes ambientes geomorfológicos costeiros (*coastal settings*, como os deltas e estuários e, ao mesmo tempo, podem afetar a estrutura e função macrofaunal. Apesar da árvore de mangue ser capaz de alocar uma larga proporção (~60%) de sua biomassa total para as raízes subterrâneas, pouco se sabe da sua interação com a macrofauna bêntica em escala local. Essa concentração de biomassa radicular influencia os fluxos de água, carbono e nutrientes do solo, bem como a riqueza, abundância e atributos funcionais da macrofauna de manguezais. No entanto, as contribuições relativas aos fatores de pequena e grande escala espacial na caracterização de comunidades macrofaunais ainda são pouco compreendidas. O objetivo geral da tese foi avaliar a estrutura e função da comunidade bêntica macrofaunal de manguezais em pequenas e largas escalas espaciais ao longo da costa brasileira, assim como determinar a influência de diferentes parâmetros ambientais e da vegetação de manguezais na comunidade bêntica. No primeiro capítulo, avaliamos a estrutura e função da comunidade macrofaunal em múltiplas escalas espaciais em manguezais brasileiros sob a influência de distintos ambientes geomorfológicos costeiros (estuário, delta dominado por ondas e delta dominado por marés). Os resultados demonstraram que a temperatura do ar e descarga dos rios variaram significativamente ( $p < 0,05$ ) entre os *coastal settings*, além de terem sido os fatores que mais influenciaram na riqueza (33%) e diversidade (30%) da comunidade macrofaunal em escalas espaciais maiores. Já as propriedades da vegetação e do solo de mangues estavam mais relacionadas às características funcionais dos anelídeos, contribuindo cerca de 30% em escalas espaciais menores. Os anelídeos com maior complexidade morfológica no corpo (e.g., parapódios e tentáculos bem desenvolvidos) predominaram em manguezais com baixa biomassa de raízes subsuperficiais. Por outro lado, anelídeos com corpos finos e alongados ocorreram com maior frequência em manguezais com maior densidade de raízes subsuperficiais. No segundo capítulo, avaliamos as estruturas aéreas e subterrâneas das plantas de mangues, as propriedades do sedimento e suas relações com a estrutura e função da assembleia macrofaunal em função da profundidade do solo e distância de troncos de árvores em manguezais na Ilha de Santa Catarina. Os resultados desse capítulo destacaram que a estrutura e função das assembleias macrofaunais de manguezais variaram significativamente ( $p < 0,05$ ) em função da distância dos troncos das árvores e ao longo dos estratos verticais do solo. A maior parte dos táxons faunais ocorreu nas camadas superficiais do solo (0 - 5 cm) e próximas a troncos (até 0,3 m de distância), onde tiveram uma maior proporção de raízes grossas e substratos menos coesivos, oferecendo condições favoráveis para esses organismos. A assembleia macrofaunal esteve mais associada com as alterações na complexidade dos sistemas radiculares, representadas por variações nas raízes grossas e finas de bosques de mangues. Por fim, foi verificado nessa tese que a estrutura e função da macrofauna de manguezais são altamente dependentes da escala espacial.

**Palavras-chave:** Manguezais. Macrofauna. Estrutura. Função. Escalas espaciais. Geomorfologia.



## ABSTRACT

Mangroves occur along tropical and subtropical regions, where they differ according to coastal geomorphology, energy flow, patterns of forest structure and species distribution. The benthic macrofaunal community is influenced by environmental, vegetation and soil properties in these environments at different spatial scales. The combination of larger scale factors, such as river discharge and tidal amplitude, is capable of originating different coastal settings, such as deltas and estuaries, as well as they may affect the macrofaunal structure and function. Despite the mangrove tree is able to allocate a large proportion (~ 60%) of its total biomass to the underground roots, little is known about their interaction with benthic macrofauna at local scales. This concentration of root biomass influences water, carbon and nutrients flows of the soil, as well as the richness, abundance and functional traits of the mangrove macrofauna. However, the relative contributions of factors of small- and large-spatial scale in the characterization of macrofaunal communities are still poorly understood. The main objective of this dissertation was to evaluate the structure and function of the mangrove macrofaunal community at small and large spatial scales along the Brazilian coast, as well as determining the influence of different environmental properties and mangrove vegetation on the benthic community. In the first chapter, we evaluated the structure and function of the macrofaunal community at multiple spatial scales in Brazilian mangroves under the influence of different coastal settings (estuary, wave-dominated delta and tide-dominated delta). The results showed that the air temperature and runoff varied significantly ( $p < 0.05$ ) between coastal settings, in addition to being the factors that most influenced the species richness (33%) and diversity (30%) of the macrofaunal community at larger spatial scales. The properties of mangrove vegetation and soil were more related to the functional traits of annelids, contributing about 30% at smaller spatial scales. Annelids with greater morphological complexity in the body (e.g. well developed parapodia and tentacles) predominated in mangroves with low subsurface root biomass. On the other hand, annelids with slender and cylindrical forms occurred more frequently in mangroves with higher subsurface root biomass. In the second chapter, we evaluated the above- and belowground structures of mangrove plants, sediment properties, algal cover and their relationship with the structure and function of the macrofaunal assemblage as a function of soil stratum and distance from tree trunks in mangroves on the island of Santa Catarina. The results of this chapter highlighted that the structure and function of the mangrove macrofaunal assemblages varied significantly ( $p < 0.05$ ) depending on the distance from the tree trunks and along the vertical strata of the soil. Most of the benthic taxa occurred in the upper layers of the soil (0 - 5 cm) and near trunks (up to 0.3 m away), where they had a higher proportion of fine roots and less cohesive substrate, offering favorable conditions for these organisms. The macrofaunal assemblage was more associated with changes in the complexity of root systems, represented by variations in the coarse and fine roots of mangrove forests. Finally, it was verified in this dissertation that the structure and function of the mangrove macrofauna are highly dependent on the spatial scale.

**Keywords:** Mangroves. Macrofauna. Structure. Function. Spatial scales. Geomorphology.

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## 1 INTRODUÇÃO GERAL

### 1.1 O ecossistema manguezal e a biomassa subterrânea de seus bosques

Os manguezais ocorrem ao longo de regiões tropicais e subtropicais, diferenciando em função da geomorfologia costeira, fluxo de energia, padrões de estrutura da floresta e distribuição das espécies (Schaeffer-Novelli et al. 1990; Woodroffe 1992). Esses ambientes contribuem na reciclagem de nutrientes, no balanço climático, proteção contra a erosão da costa e são considerados berçários para diversos organismos faunais e fonte inestimável de outros produtos e serviços ecossistêmicos (Bouillon et al. 2008; Nagelkerken et al. 2008). Além disso, os bosques de mangues fornecem diversos microhabitats e recursos para a biodiversidade faunal, como o sistema de raízes, troncos de árvores, camadas superficiais e internas dos solos (Lee 2008). O ecossistema manguezal é resultado de estreita relação da vegetação com a geomorfologia costeira (*coastal settings*, sensu Thom 1982), se desenvolvendo em deltas e estuários (Thom 1984). A formação desses *coastal settings* é decorrente de uma combinação de fatores globais (biogeografia e clima), regionais (geomorfologia) e locais (topografia e hidrologia). Na escala local, é determinada por três fatores ambientais: reguladores (*e.g.*; salinidade e pH), recursos (*e.g.*; nutrientes e luz) e hidroperíodo (duração e frequência de inundação por maré) (Twilley & Rivera-Monroy 2009). Todos esses fatores são determinantes nos padrões básicos da estrutura, na função das florestas e biodiversidade faunal de mangues, que serão afetados de acordo com o nível de estresse imposto pelos fatores globais, regionais e locais (Figura 1; Lee et al. 2018).

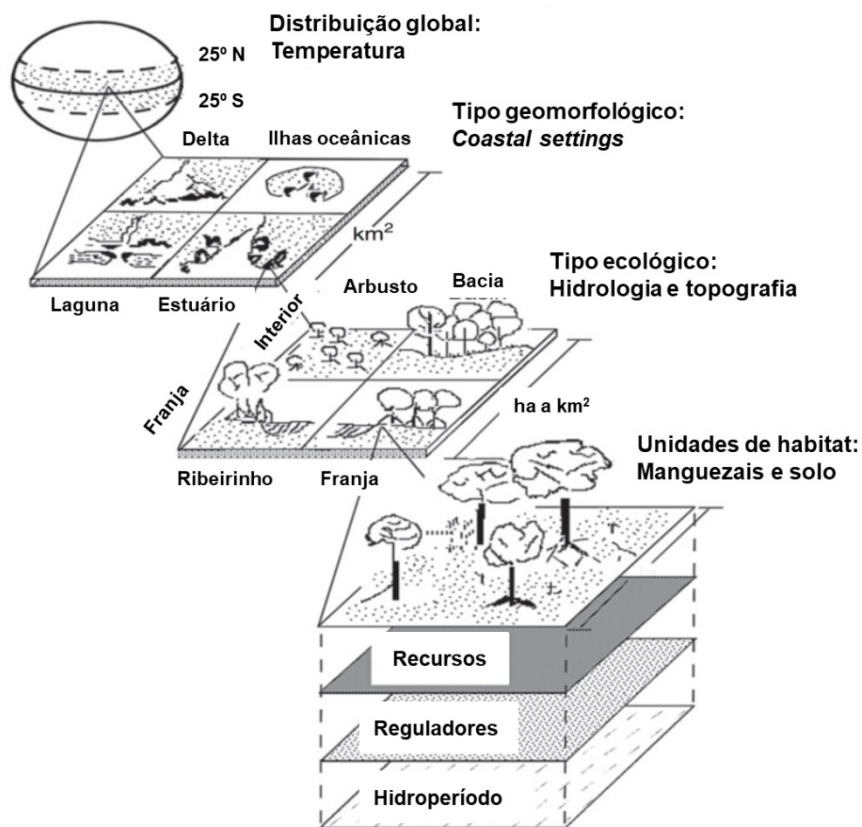


Figura 1. Classificação hierárquica usada para descrever os padrões de estrutura e função de manguezais considerando fatores globais, geomorfológicos (regionais) e ecológicos (locais) que controlam os gradientes reguladores, recursos e hidroperíodo. Extraída e modificada de Twilley & Rivera-Monroy (2009).

Os manguezais estão entre os ambientes mais produtivos do mundo (Duarte & Cebrian, 1996) e seus solos são bastante ricos em carbono (Donato et al. 2011; Kauffman et al. 2011). São também capazes de alocar uma larga proporção (~60%) de sua biomassa total para as raízes subterrâneas, principalmente em baixas durações e frequências de alagamento por maré (Castaneda-Moya et al. 2013; Khan et al. 2009). Embora o número de estudos de biomassa de raízes em manguezais tenha aumentado nos últimos 15 anos (Comley & McGuinness 2005; Tamooh et al. 2008; Castaneda-Moya et al. 2013; Robertson & Alongi 2016), ainda há uma proporção significativamente maior em pesquisas com a biomassa aérea (Rovai et al. 2016). Isso se deve principalmente às dificuldades logísticas de realizar medidas diretas da biomassa de raízes, o que faz com que elas sejam geralmente estimadas a partir de equações alométricas (Adame et al. 2017). Sendo assim, tais equações costumam ser imprecisas (Njana et al. 2015), porque a biomassa de raízes depende das características do solo (*e.g.*, nutrientes, salinidade, granulometria, temperatura), hidroperíodo, estrutura (*e.g.*,

densidade de troncos, altura da árvore) e idade da floresta, composição de espécies e métodos de amostragem (Chalermchatwilai et al. 2011; Castaneda-Moya et al. 2013; Adame et al. 2017). A biomassa e o tamanho de raízes das árvores de manguezais variam tanto verticalmente quanto horizontalmente no solo. A maioria dos estudos demonstra que uma grande proporção da biomassa de raízes grossas e finas está concentrada nas camadas superficiais do solo (até 15 cm de profundidade), em decorrência do estresse fisiológico da raiz aumentar com a profundidade (Tamooh et al. 2008; Castañeda-Moya et al. 2011; Santos et al. 2017). Horizontalmente e verticalmente, a biomassa e tamanho da raiz de mangues tendem a diminuir com a distância do tronco principal (Saintilan 1997; Komiyama et al. 2000; Tamooh et al. 2008; Adame et al. 2017). No entanto, todos esses estudos têm discussões limitadas sobre a distribuição das raízes e seu tamanho. Além disso, esses tipos de abordagens também são explicados marginalmente em florestas terrestres (Callaway et al. 1991; Millikin & Bledsoe 1999; Yanai et al. 2006; Vieira et al. 2015), nos quais se encontram resultados semelhantes aos manguezais. É também conhecido que as florestas de mangues possuem um complexo sistema de raízes (*e.g.*, pneumatóforos, raízes radiais, absorventes e âncora; Figura 2), sendo que elas podem ter diferentes origens ontogenéticas e morfoanatômicas dependendo da espécie. Esses tipos de raízes geralmente possuem diferentes diâmetros, variando desde grosso ( $> 5$  mm), médio (2 - 5 mm) e fino ( $< 2$  mm) (Castañeda-Moya et al. 2011), influenciando os fluxos de água, carbono, nutrientes no solo (Komiyama et al. 2000; Tomlinson 2016) e distribuição macrofaunal (Leung 2015a).

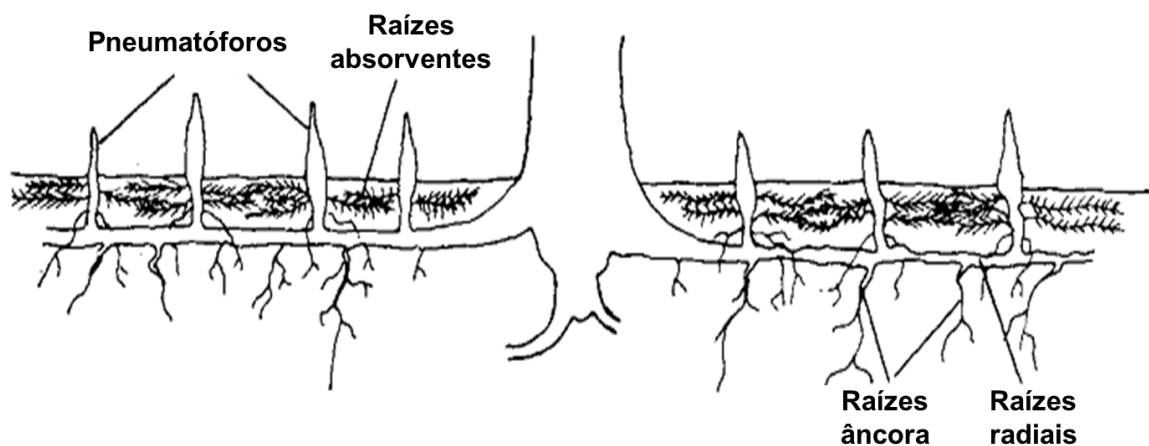


Figura 2: Desenho esquemático do sistema complexo de raízes de árvores de manguezais do gênero *Avicennia*, *Laguncularia* e *Sonneratia*. Extraída e modificada de Macnae (1968).



## 1.2 Variabilidade macrofaunal bêntica em diferentes escalas espaciais e sua relação com a vegetação de manguezal

O ecossistema manguezal possui grande influência na variabilidade espacial da estrutura e função da comunidade macrofaunal (Lee et al. 2018). A análise de distribuição espacial dos organismos macrofaunais é essencial para entender como eles interagem entre si ou com o ambiente (Underwood & Chapman 1996). Ela também facilita no entendimento dos fatores e processos que controlam a estrutura (riqueza, diversidade, abundância) e função (diversidade funcional, atributos funcionais) faunal (Underwood et al. 2000). Os padrões de distribuição da comunidade macrofaunal são afetados por fatores de diferentes escalas espaciais. Por exemplo, em largas escalas destacam-se as mudanças hidrológicas (maré e descarga de rios) e temperatura do ar, já em pequenas escalas, esses organismos podem ser influenciados pelo tipo de sedimento (granulometria, e grau de compactação) e salinidade (Kumar 2002; Saravnakumar et al. 2007). A variabilidade espacial desses organismos bênticos de manguezais podem então apresentar variações desde poucos centímetros a centenas de quilômetros (Morrisey et al. 1992, 2003). Assim, investigações em múltiplas escalas espaciais devem ser realizadas em ambientes bênticos, uma vez que essas distintas escalas podem influenciar diferentemente as características da comunidade macrofaunal (Levin 1992; Underwood & Chapman 1996).

A estrutura macrofaunal também responde à presença/ausência de espécies da flora local (Chen et al. 2015), da taxa de produtividade da serrapilheira (de Oliveira et al. 2012), idade dos bosques (Morrisey et al. 2003), densidade de pneumatóforos e tamanho da copa da árvore (Chapman and Tolhurst 2004). Em relação às funções ecológicas da macrofauna, elas podem ser avaliadas através de análises de atributos funcionais (*e.g.*, morfologia do corpo, comportamento, fisiologia) e diversidade funcional (diversidade de atributos na comunidade). Essas análises podem ser então aplicadas para uma melhor compreensão das funções do ecossistema após mudanças ambientais (Bremner 2008; van der Linden et al. 2012). Os trabalhos com essas abordagens em manguezais (Leung 2015b, Leung & Cheung 2017) demonstram que diferentes zonações, espécies e idades de árvores são capazes de diversificar as funções ecológicas da comunidade bêntica. Além disso, a diversidade funcional é considerada indicadora-chave em projetos de monitoramento nesses ambientes costeiros. Por outro lado, há ainda uma lacuna quando se relaciona o complexo sistema de raízes de manguezais com a estrutura e função macrofaunal. Os poucos trabalhos existentes são

genericamente descritivos (Wada et al. 1987; Leung 2015a,b; Checon et al. 2017), não investigando por exemplo, o efeito da distância de troncos de árvores na distribuição das raízes e da macrofauna. As raízes dos bosques de mangues são conhecidas por causarem variações na macrofauna tanto diretamente (*e.g.*, disponibilidade de alimento e de abrigo, mudanças nas taxas de deposição/erosão) quanto indiretamente (*e.g.*, mudanças nos fluxos de nutrientes) (Tolhurst & Chapman 2007; Demopoulos & Smith 2010). Como componente estrutural do sedimento, as raízes também são capazes de modificar suas propriedades, como teor de matéria orgânica e tamanho de partícula (Leung 2015a), regulando os padrões de distribuição e abundância da macrofauna. Por isso, esses componentes das raízes de mangues podem estar causando maiores influências na macrofauna do que as variações naturalmente existentes de local para local. As discrepâncias nos resultados referentes aos estudos sobre os efeitos da biomassa de raízes na macrofauna de manguezais são muito frequentes, podendo variar tanto em relação aos efeitos positivos quanto aos negativos das raízes na estrutura e função macrofaunal (Wada et al. 1987; Leung 2015a; Checon et al. 2017). Os efeitos positivos frequentemente associam uma maior biomassa de raízes ao aumento da colonização macrofaunal, por oferecerem microhabitats, matéria orgânica palatável, maior oxigenação de sedimentos e menor pressão de predação (Demopoulos & Smith 2010; Chen et al. 2015). Por outro lado, esses sistemas radiculares densos são também reconhecidos por limitar a ocorrência de organismos bênticos, oferecendo maiores dificuldades na sua alimentação e mobilidade (Sweetman et al. 2010; Leung 2015b). Dessa maneira, há a necessidade de desenvolver métodos de amostragem mais eficazes para evitar essas variações na distribuição da comunidade macrofaunal de manguezais em diferentes escalas espaciais.

## **2 OBJETIVO**

### **2.1 Objetivo geral**

O objetivo geral do trabalho foi avaliar a estrutura e função da comunidade macrobêntica macrofaunal de manguezais em pequenas e largas escalas espaciais ao longo da costa brasileira, assim como determinar a influência de diferentes parâmetros ambientais e da vegetação de manguezais na comunidade bêntica.

## 2.2 Objetivos específicos

### **Artigo I: Mangrove benthic macrofauna: drivers of community structure and functional traits at multiple spatial scales**

Objetivos: (1) Avaliar a estrutura da comunidade macrofaunal (abundância, riqueza e diversidade de espécies), atributos funcionais e diversidade de atributos da assembleia de anelídeos em múltiplas escalas espaciais (*coastal settings*, locais e pontos amostrais) em manguezais brasileiros. (2) Caracterizar a relação da macrofauna com as propriedades climáticas/geofísicas e do sedimento, biomassa aérea e subterrânea em bosques de mangue sob a influência de distintos *coastal settings* (estuário, delta dominado por ondas e delta dominado por marés).

Hipóteses: Nós hipotetizamos que o padrão de distribuição espacial da macrofauna de manguezais é mais influenciado pelas variáveis ambientais em escalas espaciais maiores do que em menores escalas; caso ocorra, a estrutura e função da comunidade macrofaunal é mais influenciada pelas forçantes climáticas e geofísicas que moldam os ambientes geomorfológicos do que pelas propriedades da vegetação e sedimento (variáveis moldadas pelos *coastal settings*); em caso negativo, a comunidade bêntica macrofaunal é mais influenciada pelas propriedades do sedimento do que pelas diferenças na vegetação de manguezais.

### **Artigo II: Changes in the vertical and horizontal distribution of complex mangrove root systems affect the benthic macrofauna**

Objetivos: Avaliar as estruturas aéreas e subterrâneas das plantas de manguezais, propriedades do sedimento e relação com a densidade, riqueza e diversidade funcional da assembleia macrofaunal em função da profundidade do solo e distância de troncos de árvores em manguezais na Ilha de Santa Catarina.

Hipóteses: Considerando que as variações na biomassa e tamanho de raízes de manguezais pode determinar a distribuição das assembleias macrofaunais, foram testadas as seguintes hipóteses: (1) Como a biomassa de raízes muda com a profundidade e distância de tronco de árvores, espera-se encontrar uma maior proporção de raízes grossas em estratos superiores do

solo e próximo às árvores de manguezais; (2) Espera-se encontrar uma maior densidade, riqueza e diversidade funcional da macrofauna em pontos distantes dos troncos de árvores e limitadas ao estrato superficial, uma vez que tendem a apresentar proporcionalmente menos biomassa radicular do que próximo dos troncos; (3) Assembleias macrofaunais são mais associadas com as raízes do que com os parâmetros do sedimento.

### **3 ARTIGO I: MANGROVE BENTHIC MACROFAUNA: DRIVERS OF COMMUNITY STRUCTURE AND FUNCTIONAL TRAITS AT MULTIPLE SPATIAL SCALES**

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## **Mangrove benthic macrofauna: drivers of community structure and functional traits at multiple spatial scales**

### **ABSTRACT**

Environmental processes acting at multiple spatial scales influence the structure and function of macrofaunal communities in marine habitats. However, the relative contributions of small- and large-scale factors in shaping faunal communities are still poorly understood. We investigated the relative contributions of climate, geophysical and soil properties, and forest structure on structural and functional characteristics of Brazilian coastal mangrove macrofauna. We found that macrofaunal community structure is mainly driven by large-scale factors, such as minimum air temperature and runoff, which significantly differed among the coastal settings investigated. Conversely, annelid assemblage functional traits were correlated with small-scale factors such as aboveground biomass, subsurface root biomass, soil bulk density, and soil phosphorus. Annelids with diversified and more complex functional traits (e.g. with respect to appendages, segments, parapodia) preferentially inhabited sites with low subsurface root biomass, while annelids with a slender body plan were more common at sites with dense root mats. Thus, while climate and geophysical conditions drive benthic macrofaunal community structure at larger spatial scales (i.e. coastal setting) in this system, vegetation and soil factors at smaller spatial scales (i.e. site) were more related to annelid functional characteristics.

**Key-words:** Coastal settings; Macrofauna; Mangrove; Spatial scales; Structure; Function

## 1. INTRODUCTION

Mangrove research has historically focused on evaluating short-term and small-scale spatial forest structure and associated aquatic biodiversity (RiveraMonroy et al. 2017). Many of these studies disregard a well-established perspective based on hypotheses connecting mangrove forest structure and function at larger spatial scales (i.e. geomorphological) with smaller-scale (i.e. ecological) factors (Thom 1982, 1984, Woodroffe 1992, Twilley et al. 1996). The ecogeomorphology model states that different types of coastal settings (CSs) are shaped by a combination of geophysical (i.e. rivers, tides, waves) and climate (i.e. precipitation, air temperature, potential evapotranspiration) drivers (Dürr et al. 2011, Steiger & Corenblit 2012, Woodroffe et al. 2016). Those factors both affect and respond to ecological and evolutionary processes, consequently impacting structural and functional characteristics of mangrove forests and the biodiversity within (Twilley 1995, Rovai et al. 2016). Merging site-specific biodiversity data with progressively larger-scale processes is therefore crucial for advancing conceptual ecological models and further elucidating potential drivers of mangrove community structure and function. However, we currently lack an integrative framework for describing mangrove macrofauna at multiple spatial scales.

Despite a considerable body of literature describing benthic fauna in mangroves (Schrijvers et al. 1998, Kumar 2002, Alfaro 2010, Leung & Cheung 2017), the interactions between mangrove characteristics and associated macrofauna is mostly biased toward specific sites and taxonomic groups. For example, a survey of the published literature (search limited to document titles) indicated that 3 out of 5 macrofaunal studies in mangrove forest focused on bare tidal flats, subtidal areas, and salt marsh areas adjacent to the mangrove forests rather than within the forest. Further, only one-sixth of these studies included macrofauna that are labor-intensive to identify, such as polychaetes, oligochaetes, insects, organisms that dwell within the sediment, or those with small body size (<1 cm) (Kennish 2016); rather, studies typically focused on highly monitored and easily handled megafauna (inaccurately referenced as macrofauna; e.g. demersal fishes, gastropods, prawns, and crabs living in holes or just above the sediment surface; organisms with body size >1 cm) (Kennish 2016) (Fig. A1 in the Appendix). Consequently, there remains a gap in knowledge concerning structural and functional aspects of macrofaunal communities within mangrove forests. Mangrove macrofauna have low mobility and high diversity in lifestyle and trophic interactions

compared to the megafauna. These characteristics suggest potential for a unique role of the macrofaunal community in mangrove ecosystem functioning.

Mangrove macrofaunal studies linking below- and aboveground vegetation data to species spatial distributions are less common than studies correlating macrofauna and soil properties (i.e. texture, composition, chemistry) (Lana et al. 1997, Kumar 2002, Thilagavathi et al. 2013). Nevertheless, there is a body of evidence suggesting that the composition and distribution of sediment-associated species are influenced more quantitatively than qualitatively by vegetation parameters, including root size and biomass (Leung 2015), pneumatophore density and crown size (Chapman & Tolhurst 2004), rate of litterfall productivity (de Oliveira et al. 2012), age of the stand (Chen et al. 2007), and zonation of tree species (Dissanayake & Chandrasekara 2014). Many of these forest traits indirectly influence the macrofauna, such as canopy shading, which regulates sediment temperature (Tolhurst & Chapman 2007), and litterfall and root productivity, which regulate sediment complexity (e.g. bulk density, grain size, carbon stock). Thus, in order to advance our understanding of the ecology of mangrove forest–macrofauna relationships, studies must address the focal habitat type (inside or outside the forest) and the targeted benthic faunal component (megafauna or macrofauna) and should also formally include soil properties and forest structural variables in the analyses.

To date, no in-depth investigations on the structure and function of mangrove macrofaunal communities have been carried out contemplating multiple spatial scales along with soil properties, vegetation, and climate-geophysical drivers. Hence, considering the established spatial hierarchy of the mangrove ecosystem (Twilley et al. 1996) and the potential influence of large-scale factors on macrofaunal taxa inhabiting other marine habitats, such as annelids (Lana & Bernardino 2018), mollusks (Reid et al. 2010), and crustaceans (Thurman et al. 2013), we hypothesized that (1) the spatial distribution pattern of the mangrove macrofauna would be more influenced by environmental variables at larger spatial scales than at smaller scales; (2) if supported, that the structure and function of the macrofaunal community would be influenced by climate and geophysical drivers shaping the CSs more than by vegetation and soil variation (features molded by the CSs); if not, the mangrove macrofaunal assemblages would be influenced more by soil properties than by differences in vegetation. To test these hypotheses, we first describe the macrofaunal community structure in terms of abundance, species richness, and species diversity. We then describe the functional characteristics of the annelid assemblages in terms of functional traits



and trait diversity at multiple spatial scales (CS, site, and sampling point) in Brazilian coastal mangroves.

## 2. MATERIALS AND METHODS

### 1.1. Study area and sampling design

The study was carried out in the 3 major coastal settings (CSs) colonized by mangrove forests along the Brazilian Atlantic coast: tide-dominated delta, wave-dominated delta, and tidal estuary (Fig. 1). The 3 CSs differ in climate and geophysical characteristics and mangrove forest structure (Table 1). It is important to note that the global distribution of CSs does not follow a latitudinal gradient, and the diversity of these settings does not often occur within the same latitudinal region.

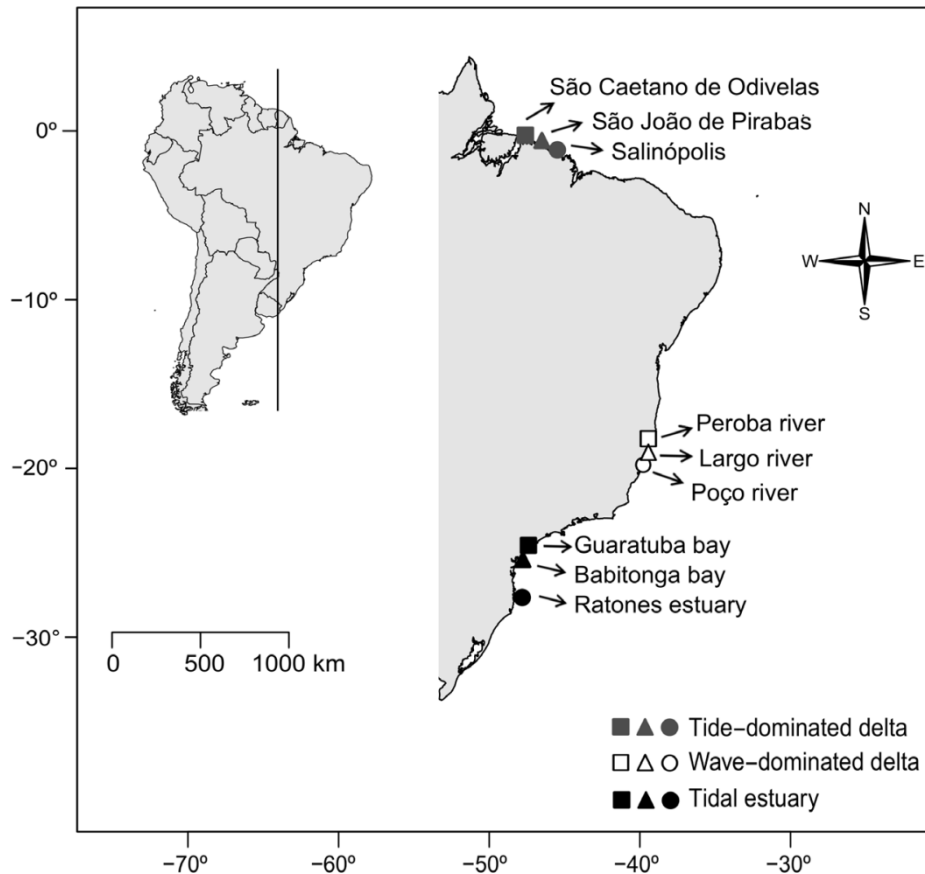


Fig. 1. Study area, showing the sampled coastal settings (tide-dominated delta, wave-dominated delta, tidal estuary) and sites within each coastal setting

Table 1. Summary of the main variables characterizing the coastal settings differences in Brazilian coast. Sources: Martorano et al. (1993), MMA (2003), Marone et al. (2004), Gomes-Sobrinho (2008), Mu et al. (2011), Rovai et al. (2012, 2016), Short & Klein (2016), ICMBio (2018)

Variables	Coastal setting		
	Tide-dominated Delta	Wave-dominated Delta	Tidal Estuary
<i>Climate and Geophysical</i>			
Latitude (° S)	~0	~15	~28
Climate	Equatorial and humid	Tropical humid	Subtropical humid
Mean air temperature (°C)	27.7	25	21
Mean annual precipitation (mm y <sup>-1</sup> )	3,000	1,400	1,500
Main discharge	Amazon River	Several rivers	Few rivers
Tidal regime	Macrotidal	Mesotidal	Microtidal
<i>Mangrove forest</i>			
Mean diameter at breast height (m)	0.40	0.20	0.14
Mean height (m)	30	15	9
Number of tree species	6	4	3
Tree species	<i>Avicennia germinans</i> <i>Avicennia schaueriana</i> <i>Laguncularia racemosa</i> <i>Rhizophora harrisonii</i> <i>Rhizophora mangle</i> <i>Rhizophora racemosa</i>	<i>Avicennia germinans</i> <i>Avicennia schaueriana</i> <i>Laguncularia racemosa</i> <i>Rhizophora mangle</i>	<i>Avicennia schaueriana</i> <i>Laguncularia racemosa</i> <i>Rhizophora mangle</i>

Sources: Martorano et al. (1993), MMA (2003), Marone et al. (2004), Gomes-Sobrinho (2008), Mu et al. (2011), Rovai et al. (2012, 2016), Short & Klein (2016), ICMBio (2018).

Tide-dominated delta is mainly influenced by Amazon River discharge and the macrotidal regime and is characterized by a pronounced seasonal rainfall pattern that ranges from dry (~70 mm) to rainy (~1900 mm) (Martorano et al. 1993). The mangroves in these settings constitute the largest continuous forest in the world, with tall and well-developed trees including *Avicennia schaueriana*, *A. germinans*, *Rhizophora mangle*, *R. racemosa*, *R. harrisonii*, and *Laguncularia racemosa*.

Wave-dominated delta occupies an extensive area of the central coast of Brazil. These habitats are characterized by rainfall that is well-distributed throughout the year, with no dry season (Gomes-Sobrinho 2008), and seasonal variation in the direction of wave propagation due to changes in wind regime (Pianca et al. 2010). These areas are influenced by a set of rivers forming typical prograding shorelines under a mesotidal regime. These forests present intermediate structural development and are composed of *A. schaueriana*, *A. germinans*, *R. mangle*, and *L. racemosa*.

Tidal estuaries are found near the geographic limit of mangrove distribution on the Brazilian coast. These mangroves are not situated in physiologically optimum habitat and are characterized by shorter trees, less developed forests, and lower tree species richness including *A. schaueriana*, *L. racemosa*, and *R. mangle*. These areas are under a microtidal regime and are characterized by having subtropical humid climate with high seasonal air temperature variability (17–25°C) (Marone et al. 2004, Short & Klein 2016).

Nine mangrove sites were selected for the study from October to December 2012, with 3 sites falling within each CS (See Fig. S1 in the supplement). The sites were positioned at the high-energy euhaline sector of each system in order to minimize variation related to local gradients in salinity, environmental energy, vegetation structure, and detritus transport. The sites were situated either in independent watersheds or within the same watershed, with a minimum distance of 50 km between sites when possible. Within each site, 3 sampling points without evident anthropogenic influence were established with a minimum distance of 50 m between sampling points and 10 m from the vegetation border. At each sampling point, we characterized (1) the macrofaunal community, (2) subsurface vegetation root biomass, and (3) nutrient and carbon stocks in the soil. We also used databases and published literature to determine, (4) vegetation aboveground biomass, (5) air temperature, (6) precipitation, (7) runoff, (8) potential evapotranspiration, and (9) tidal range.

## 1.2. Climate and geophysical drivers

The GPS coordinates of each site were recorded (Garmin eTrex 10 GPS), and the geographical position of each site was used to extract climate and geophysical data from different global databases. Data for minimum air temperature of the coldest month ( $^{\circ}\text{C}$ ) and minimum precipitation of the driest month ( $\text{mm yr}^{-1}$ ) were retrieved from the WordClim database ([www.worldclim.org](http://www.worldclim.org)). The WordClim climate charts were produced through the interpolation of data from meteorological stations from 1950–2000 at a spatial resolution of  $0.008^{\circ}$  (Hijmans et al. 2005). We extracted annual runoff data ( $\text{m}^3 \text{s}^{-1}$ ) from the Global Runoff Data Centre (Composite Runoff Fields V1.0; Fekete et al. 2002), which used a global river discharge dataset coupled with a simulated river network and a water balance model to derive a global map of runoff at  $0.5^{\circ}$  resolution. Average annual potential evapotranspiration ( $\text{mm yr}^{-1}$ ) was calculated for the period from 2000–2012 using data from MODIS that globally covers vegetated land surface area at an 8 d interval and  $0.008^{\circ}$  resolution (Mu et al. 2011). A global tidal range ( $\sim$ mean high water spring–mean low water spring, m) was calculated through the FES2012 tidal atlas of finite element solutions (Carrère et al. 2012). We chose the greatest values of the sum of the 2 major tidal constituents (i.e. diurnal amplitude  $\text{K1} + \text{O1}$  or semidiurnal amplitude  $\text{M2} + \text{S2}$ ) on a grid of  $0.0625^{\circ}$  resolution. As almost all climate and geophysical data (except runoff) were produced at a resolution higher than the distances among the sampled sites, we consider the data to be accurate for use at the scale of ‘site’.

### 1.3. Mangrove vegetation and soil features

A mangrove soil core sample (sampler = 6.35 cm i.d., 5 cm height) was taken at each sampling point to quantify soil features. The samples were oven dried at  $60^{\circ}\text{C}$  until constant weight was achieved. Soil bulk density was determined by dividing the dry mass of each sample by its total volume ( $\text{g cm}^{-3}$ ; SCS-USDA 1972). Total soil phosphorus ( $\text{mg cm}^{-3}$ ) was obtained with 1 N HCl for 16 h after combustion in a furnace at  $550^{\circ}\text{C}$  (for 2 h) and determined by colorimetric analysis through a Flow Solution IV autoanalyzer (OI Analytical; Aspila et al. 1976). Total soil organic carbon (C;  $\text{mg cm}^{-3}$ ), soil nitrogen (N;  $\text{mg cm}^{-3}$ ), and soil organic matter (%) content were determined with 2 analytical replicates of each sample via dry combustion using an ECS 4010 elemental analyzer (C, N) and loss on ignition (LOI). The soil organic matter was obtained by burning at  $550^{\circ}\text{C}$  for 4 h (Costech Analytical Technologies; Howard et al. 2014) after acid fumigation to eliminate carbonates (Harris et al. 2001).

The subsurface root biomass was measured from core samples used to describe the macrofaunal community, also taken with a core sampler (see Section 2.4). After sorting the collected faunal organisms, all remaining live and dead roots and rhizomes were separated and oven dried at 60°C until constant mass. The biomass was subsequently weighed using an analytical balance (0.001 g; Quimis Q360). We used mangrove forest structure data from previous studies near our study sites (Bastos & Lobato 1996, Silva 2001, Soares et al. 2008, Rovai et al. 2012, Carvalho 2016, Kauffman et al. 2018). The mean data from the studies were used to empirically calculate the mangrove aboveground biomass (AGB; t ha<sup>-1</sup>) at each site using the following equation (Cannell 1984, Rovai et al. 2016):

$$AGB = F \times (BA \times H) \times WSG \quad (1)$$

where F is a form factor, which is the ratio of the volume of a tree to the volume of a cylinder with the same length and cross section as the tree (Gray 1956); BA is basal area (m<sup>2</sup> ha<sup>-1</sup>); H is height (m); and WSG is wood specific gravity (g dry mass cm<sup>-3</sup>). We used previously estimated values of F = 0.7 (Roberts & Ruara 1967, Kairo et al. 2002, Bundotich et al. 2009) and WSG = 0.77 for mangrove (Rovai et al. 2016).

#### 2.4. Mangrove macrofauna

Three macrofaunal core samples (sampler = 14 cm i.d., 5 cm height) were sieved in the field using 0.5 mm mesh. All material retained was fixed in 10% buffered formalin. The faunal organisms were initially sorted under a microscope, identified to the lowest possible taxonomic level, and enumerated. The macrofaunal community was described in terms of total abundance, species richness, and species diversity (Shannon H' index). To evaluate the functional traits of mangrove macrofauna, we used only the annelid assemblages (polychaetes and oligochaetes) due to numerical dominance in the community (>80%).

We adopted a functional traits framework based on the morphological characteristics of annelids proposed by Otegui et al. (2016). We selected 3 traits related to feeding, defense, and mobility mechanisms that are functionally well-characterized for this group of organisms (Fauchald & Jumars 1979). We avoided choosing additional traits because they can be redundant in function (Faulwetter et al. 2014) and because an inappropriate range of functional traits may mask functional differences between species (Petchey et al. 2007). The selected functional traits were: (1) body appendages (presence; absence), (2) number of

segments ( $\leq 100$  segments;  $> 101$  segments), and (3) body support structures (presence of uncini; presence of parapodia with similar rami; presence of aciculae). In annelids, body appendages are related to feeding and defense (Purschke 2005), the number of segments is related to individual body size (Wilson 1975), and body support structure is ultimately related to locomotion (Beesley et al. 2000). To score functional trait types of different species, a standardized fuzzy coding approach was applied to separate these traits into categories, with scores ranging from 0 (no affinity) to 3 (total affinity) (Table S1). The functional traits within each dataset were then calculated by summing the category codes multiplied by the abundance of each annelid taxon and divided by their total abundance for each category and sample (Chevene et al. 1994).

The 3 functional traits chosen were then used to calculate the functional diversity (hereafter called ‘trait diversity’) through Rao’s quadratic entropy index (Botta-Dukát 2005). This index is a multi-trait measurement that embraces the multivariate aspects of the trait function. This measure includes information on the pairwise differences between species traits and relative abundances. It is also independent of species richness and depicts the similarity or complementarity of trait values within a community. The higher the Rao value is, the more niches the species occupy, and the more complementary are the species in the community (Laliberté & Legendre 2010).

## **2.5. Data analysis**

We first assessed the variation in climate, geophysical, soil, vegetation, and macrofaunal data (total abundance, species richness, species diversity, and trait diversity) among the different spatial scales (CS, site, and sampling point) using hierarchical nested ANOVA (Underwood 1997). The linear model used for macrofaunal data included CS (3 levels, fixed), site (3 levels, random), and sampling point (3 levels, random). For the climate, geophysical, soil, and vegetation variables, the factors used in the analysis were CS (3 levels, fixed) and site (3 levels, random). In all analyses, the site factor was nested within the CS factor, and the sampling point factor was nested within both site and CS factors where appropriate. The data were  $\log_{10}(x + 1)$  transformed and tested for homogeneity of variances using Cochran’s C-test. Furthermore, the components of variation were applied to estimate the percentage of the total variance explained by each factor and the residuals using restricted maximum likelihood estimation (Pinheiro & Bates 1996). The estimation of the components of variation is an important step in ecological ANOVA because it is not constrained by

sample size or probability-based metrics. Instead, it provides an estimate of magnitude of the effects in the ANOVA while determining the contribution of a given factor to variability in a response variable (Graham & Edwards 2001). All of the analyses were performed in the R platform version 3.3.1 (R Core Team 2018), using the ‘GAD’ (Sandrini-Neto & Camargo 2012; ANOVAs and components of variation), ‘vegan,’ and ‘FD’ packages (Oksanen et al. 2013, Laliberté et al. 2014; trait diversity).

Two redundancy analyses (RDAs) using Euclidean distance were applied separately to verify the relationships among the explanatory variables (tidal range, runoff, potential evapotranspiration, minimum precipitation, minimum air temperature, soil nitrogen, soil carbon, soil phosphorus, soil organic matter, soil bulk density, aboveground biomass, and subsurface root biomass) and the different types of faunal data (macrofaunal community structure or annelid assemblage functional traits). For macrofaunal community data, we considered only the most abundant taxa, which corresponded to 90% of the total abundance of the samples. For annelid data, we used the selected functional traits (= body appendages, number of segments, and body support structures). The Hellinger transformation was applied to each faunal data matrix for unbiased estimates of variance partitioning and to control the problem of a lack of linearity in the raw abundance data (Legendre & Gallagher 2001). All explanatory variables were square root transformed. To avoid Type I errors and overestimating the amount of explained variation, explanatory variables were selected before RDA analyses using the variance inflation factor (VIF). Variables with VIF >10 were eliminated from the model selection (Legendre & Legendre 2012). Variables that best explained the variation in each faunal data matrix were then identified by stepwise selection. The models were evaluated based on the adjusted fraction (adjusted R<sup>2</sup>). The multivariate analyses were carried out using the ‘car’ and ‘vegan’ packages (Fox & Weisberg 2011, Oksanen et al. 2013).

### **3. RESULTS**

ANOVA results indicated that all geophysical and climate variables differed significantly (all  $p < 0.05$ ) between spatial scales (CSs and site factors; Fig. 2; Table S2). The contribution of the CS factor to the variation in response variables was more than 55.5% in all cases, indicating greater influence than the site factor. Soil nutrient content (N, C, P, and organic matter) and subsurface root biomass significantly differed among sites ( $p < 0.001$ )

but did not differ among CSs (Fig. 3; Table S3). In all cases, the contributions to the total variation in response variable were higher at the site level than at the CS level. Conversely, aboveground biomass significantly differed at the CS and site levels, and the percentage of the total variance explained was mainly pronounced in CSs and not at the site level (Fig. 3). A total of 4115 individuals represented by 60 taxa were found across the studied mangroves. The dominant species were the polychaetes *Capitella cf. capitata*, *Heteromastus filiformis*, *Laonereis* spp., *Notomastus lobatus*, and *Isolda pulchella*, the bivalve *Cyclinella tenuis*, the tanaid *Halmyrapseudes spaansi*, and 2 oligochaetes (*Marionina* sp. 2 and Enchytraeidae sp. 1; Table S4). ANOVAs and the component of variation tests agreed for all macrofauna variables (Fig. 4, Table 2; Table S5). Species richness and diversity were strongly influenced by large-scale variability, which was only significant at the CS level. On the other hand, site contributed significantly to the variation in total abundance and trait diversity. As expected in multiple scale analyses, the residuals accounted for a large portion of the variation in all analyses.

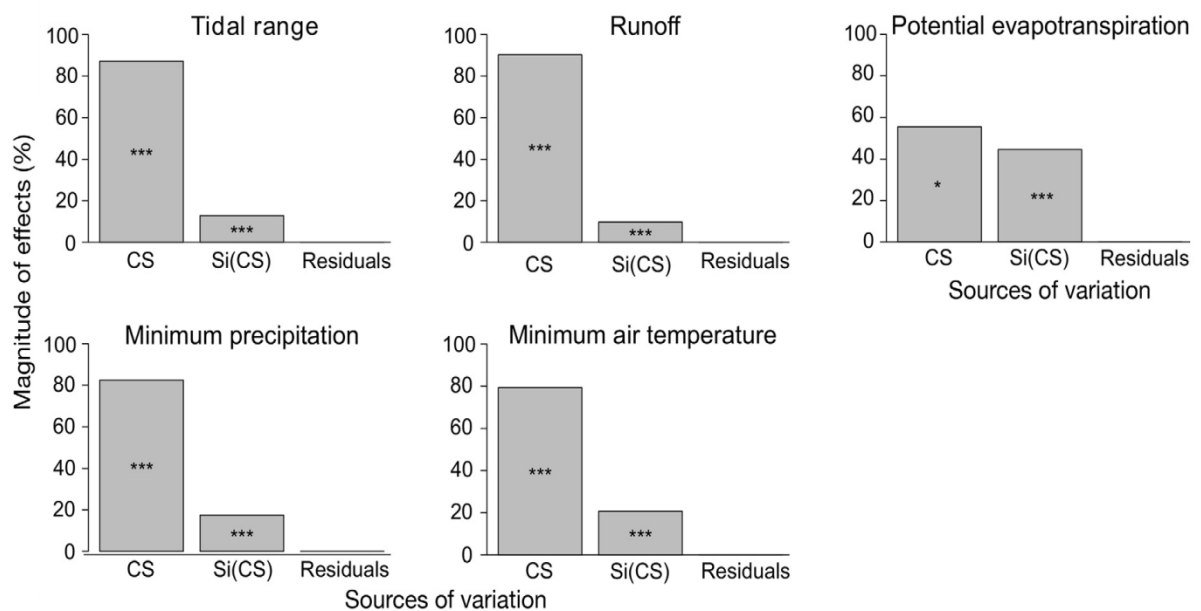


Fig. 2. ANOVA results of the climate and geophysical variables showing components of variation (% magnitude of effects) and statistical significance (\* $p < 0.05$ , \*\*\* $p < 0.001$ ) for individual ANOVA factors. CS: coastal setting, Si: site



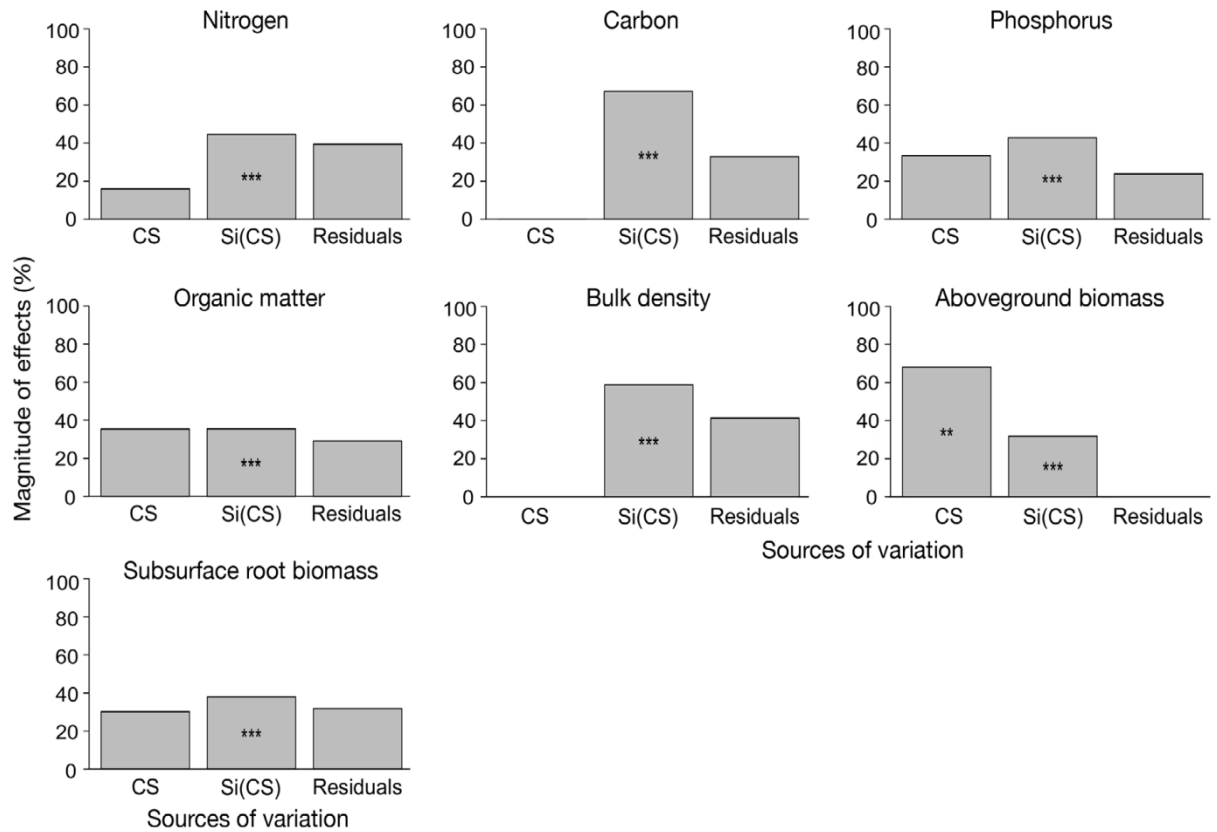


Fig. 3. ANOVA results of the soil and vegetation variables showing components of variance (% magnitude of effects) and statistical significance (\*\* $p < 0.01$ , \*\*\* $p < 0.001$ ) for individual ANOVA factors. CS: coastal setting, Si: site

Table 2. Mean values ( $\pm$ SE) of the macrofauna community, climate, geophysical, vegetation, and soil variables from the studied coastal settings

Variables	Coastal setting		
	Tide-dominated Delta	Wave-dominated Delta	Tidal Estuary
<i>Macrofauna community</i>			
Species richness (ind 0.05 m <sup>-2</sup> )	6.04 $\pm$ 0.67	3.77 $\pm$ 0.34	8.44 $\pm$ 0.63
Total abundance (ind 0.05 m <sup>-2</sup> )	23.92 $\pm$ 3.21	24.09 $\pm$ 4.03	97.78 $\pm$ 18.79
Species diversity (ind 0.05 m <sup>-2</sup> )	1.39 $\pm$ 0.09	1.00 $\pm$ 0.07	1.47 $\pm$ 0.07
Trait diversity (ind 0.05 m <sup>-2</sup> )	3.52 $\pm$ 0.70	1.41 $\pm$ 0.42	5.58 $\pm$ 1.14
<i>Climate and Geophysical</i>			
Tidal range (m)	4.55 $\pm$ 0.10	2.54 $\pm$ 0.01	0.99 $\pm$ 0.10
Runoff (m <sup>3</sup> s <sup>-1</sup> )	1461.01 $\pm$ 11.82	482.70 $\pm$ 0.39	775.57 $\pm$ 9.20
Potential evapotranspiration (mm yr <sup>-1</sup> )	2135.71 $\pm$ 36.29	2320.09 $\pm$ 16.08	1920.63 $\pm$ 7.08
Minimum precipitation (mm y <sup>-1</sup> )	15.67 $\pm$ 2.40	66.33 $\pm$ 0.24	78.67 $\pm$ 2.52
Minimum air temperature (°C)	22.35 $\pm$ 0.17	20.22 $\pm$ 0.10	16.92 $\pm$ 0.38
<i>Vegetation and soil</i>			
Aboveground biomass (t ha <sup>-1</sup> )	334.32 $\pm$ 33.8	109.75 $\pm$ 8.33	38.56 $\pm$ 2.63
Subsurface root biomass (g)	11.35 $\pm$ 1.87	11.93 $\pm$ 1.20	21.5 $\pm$ 2.34
Soil nitrogen (mg cm <sup>-3</sup> )	0.18 $\pm$ 0.02	0.39 $\pm$ 0.10	0.24 $\pm$ 0.04
Soil carbon (mg cm <sup>-3</sup> )	2.65 $\pm$ 0.28	4.82 $\pm$ 1.04	3.49 $\pm$ 0.59
Soil phosphorus (mg cm <sup>-3</sup> )	0.03 $\pm$ 0.01	0.06 $\pm$ 0.01	0.03 $\pm$ 0.01
Soil organic matter (%)	11.56 $\pm$ 1.09	21.90 $\pm$ 2.83	10.81 $\pm$ 2.18
Soil bulk density (g cm <sup>-3</sup> )	0.71 $\pm$ 0.06	0.54 $\pm$ 0.07	0.60 $\pm$ 0.06

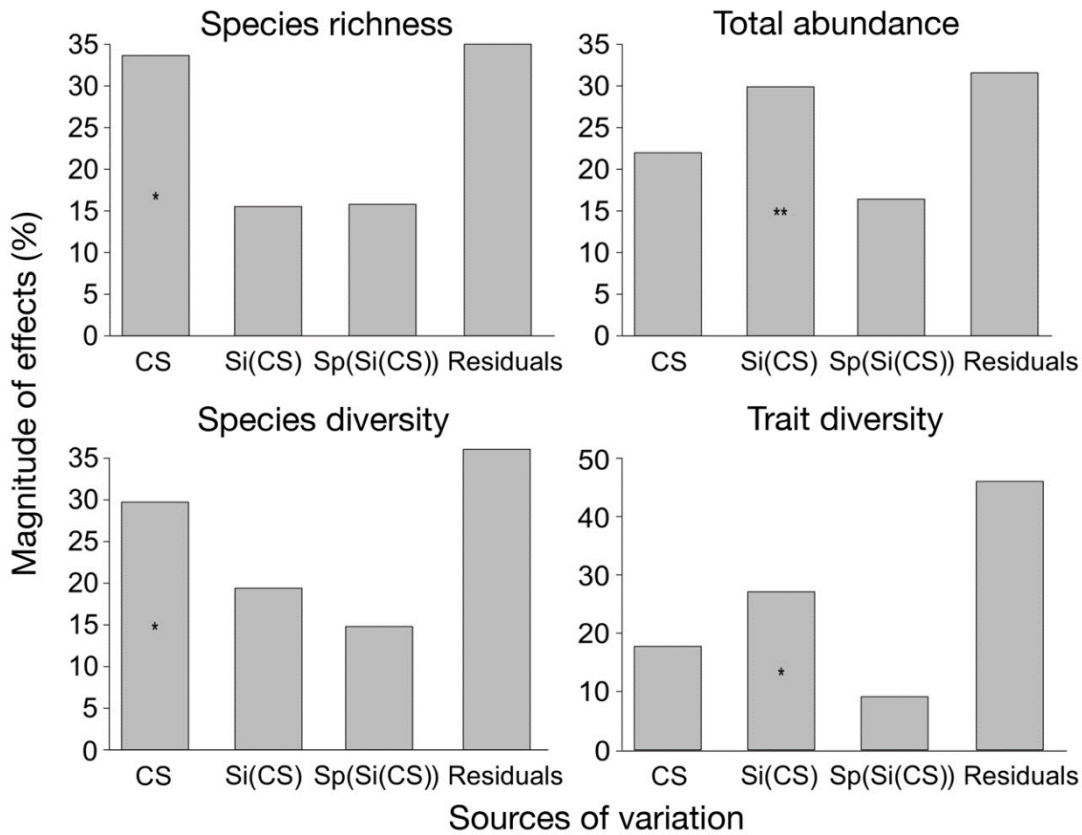


Fig. 4. ANOVA results of the macrofauna community variables showing components of variation (% magnitude of effects) and statistical significance (\* $p < 0.05$ , \*\* $p < 0.01$ ) for individual ANOVA factors. CS: coastal setting, Si: site, Sp: sampling points

RDA for macrofaunal community structure and annelid assemblage functional traits selected different sets of climate–geophysical and vegetation–soil variables (Fig. 5). RDA for abundance and composition showed that samples from the same CS were grouped and separated from the samples of the other CSs (Fig. 5a). The polychaete *H. filiformis* and the oligochaete *Enchytraeidae* sp. 1 were positively correlated with soil organic matter and total soil phosphorus in wave-dominated delta settings. The polychaetes *I. pulchella*, *Manayunkia brasiliensis*, *C. capitata*, *Laonereis* spp., *Heteromastus similis*, *Alitta succinea*, and *Dipolydora socialis*, and oligochaetes from the genus *Marionina* were associated with mangrove subsurface root biomass in the tidal estuary settings. In tide-dominated delta

settings, the annelids *Mediomastus californiensis*, Enchytraeidae sp. 2, and *Notomastus lobatus*, the bivalve *Cyclinella tenuis*, and the tanaid *Halmyrapseudes spaansi* were more associated with mangrove aboveground biomass, annual runoff, and minimum air temperature. Conversely, RDA for annelid assemblage functional traits showed that the samples were scattered and not grouped by CS (Fig. 5b; Table S6). Nevertheless, the functional trait categories of annelids were dispersed, resulting mainly from a site-related sedimentary complexity. Annelids with a slender body plan characterized by the absence of body appendages, a lower number of segments, and with aciculae mainly used for body support tended to be associated with higher site subsurface root biomass. Conversely, annelids with more complex body plan and appendages, a high number of segments, and parapodia with similar rami tended to be more associated with higher site aboveground biomass, soil bulk density, and potential evapotranspiration.

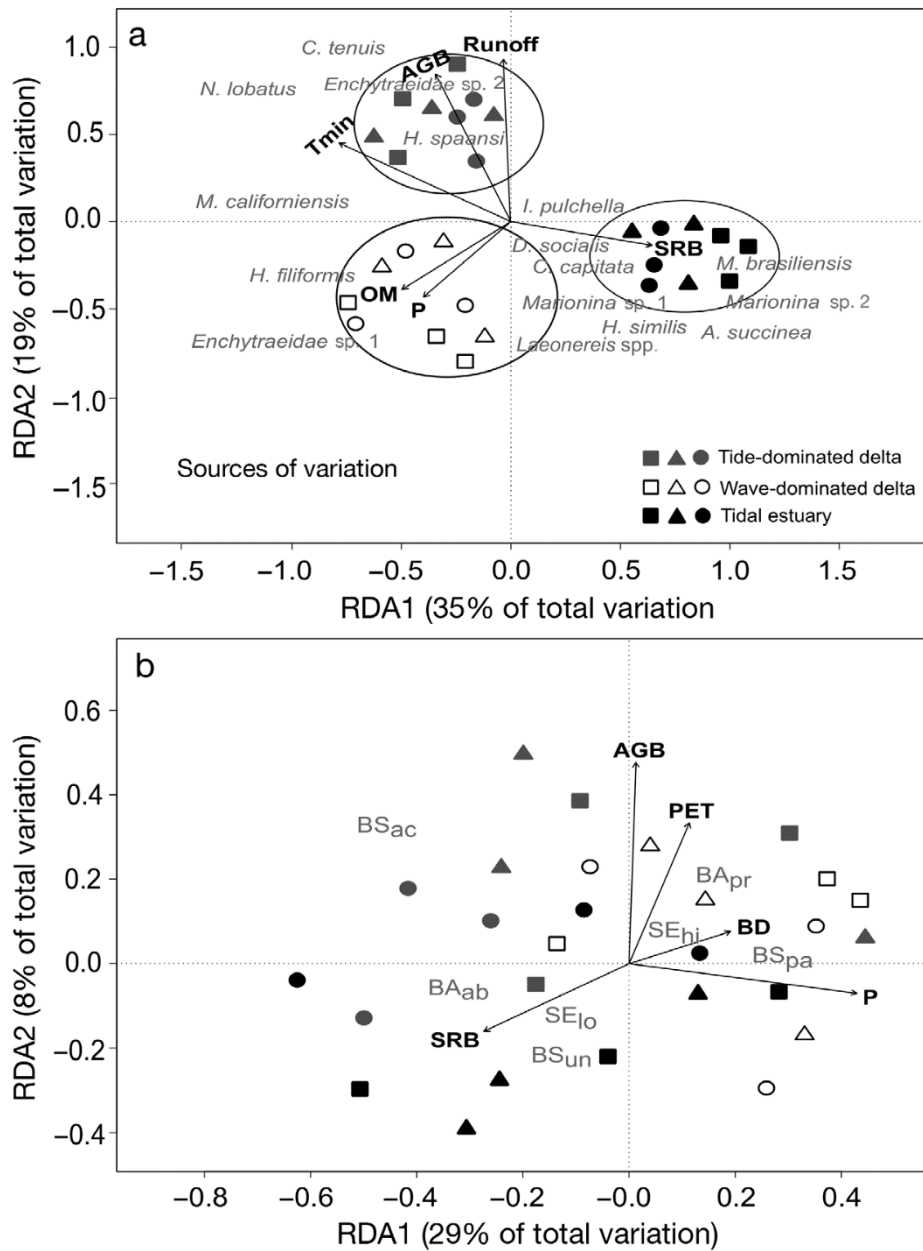


Fig. 5. Redundancy analyses (RDA) of the relationships among (a) the most abundant macrofauna taxa (see Section 3 for full species names) and (b) annelid assemblage functional traits with selected vegetation (AGB: aboveground biomass, SRB: subsurface root biomass), soil (P: total phosphorus, BD: bulk density, OM: organic matter), and climate and geophysical variables (PET: potential evapotranspiration, Tmin: minimum air temperature). BAab: absence of body appendages, BApr: presence of body appendages, SElo: lower number of segments ( $n \leq 100$ ), SEhi: higher number of segments ( $n > 101$ ), BSun: uncini, BSpa: parapodia with similar rami, BSac: aciculae

#### 4. DISCUSSION

Benthic macrofauna respond to and act in accordance with processes at multiple spatial scales in mangroves along the Brazilian coast. Macrofaunal species composition and abundance differed among spatial scales; however, explanatory factors associated with the CSs (i.e. large scale) best explained the variation. Conversely, annelid functional traits were better correlated with smaller-scale vegetation and soil properties. These patterns of species responses or trait effects at multiple scales broaden our view of species niches and functional roles. On the one hand, the boundaries of species niches were defined by environmental conditions and were mainly perceived at larger spatial scales (Grinnellian niche; Soberón 2007). On the other hand, species niche was more related to resource availability, resource partitioning, and resource competition at smaller spatial scales (Eltonian niche; Soberón 2007). Thus, while environmental conditions may drive macrofaunal community structure at larger spatial scales, biotic interactions and resource–consumer dynamics influence functional traits of annelids at smaller scales.

Although this is the first investigation to our knowledge of spatial patterns of macrofaunal communities at large scales in mangroves, our results share similarities with other studies of mangrove nematodes. The results also differ from previous studies of macrofauna in other marine environments. For example, nematode assemblage structure was found to be more driven by climate factors than by local variables (Brustolin et al. 2018). Macrofaunal community characteristics in other benthic environments also tend not to change along a spatial gradient, and macrofaunal community structure generally responds to physical conditions in sandy beaches regardless of the spatial scale of the analysis (McLachlan 1983, Defeo & McLachlan 2005). Although there are no clear patterns of community structure at larger scales, biotic interactions play important roles in shaping macrofaunal traits and food webs in rocky shores at smaller spatial scales ranging from meters to tens of kilometers (Menge et al. 1994, Cruz-Motta et al. 2010). Hence, we could say that species coexistence in mangroves is scale-mediated, and that the variety of resources or habitats used by a given species (i.e. its niche breadth) depends upon both the CS in which it lives and the functional traits it possesses.

At larger spatial scales, discrete conditions in each CS may be related to differences in macrofaunal community structure. For instance, in deltaic environments (mainly tide-dominated deltas), when the values of aboveground biomass, runoff, and air temperature were

the highest, macrofaunal species richness and diversity were lowest. Although natural dynamics as well as the intensity and frequency of the natural disturbances (i.e. sediment transport and deposition, freshwater inflow, and soil heating) may shape environmental conditions in deltaic environments, differences in metabolism (Bishop et al. 2006), colonization strategy (Ellis et al. 2004), and desiccation tolerance (Alongi 1989) among species may constrain species occurrences. Conversely, in tidal estuaries where those variables were less extreme and subsurface root biomass was higher, species richness was highest. In this case, variation in soil habitat produced by the root and rhizome architecture may have favored the diversification of species (Leung & Cheung 2017).

The pattern of distribution found in benthic macrofaunal communities at the large scale is quite different from that previously reported for benthic megafaunal communities in mangroves (Ellison 2008, Lee 2008, Lee et al. 2018). In the megabenthic species-rich mangroves of the Indo-west-Pacific, the forests are very diverse and have notably high aboveground biomass compared to the Atlantic-east-Pacific mangrove forests, where the megafauna is species-poor (Lee 2008). Thus, aboveground biomass appears to be the main factor influencing differences between megafauna and macrofauna in mangroves. For the megafauna, a higher aboveground biomass may translate to better-structured and more diversified habitats at the ground level (i.e. under trunks, branches, leaves, and aerial roots), food (i.e. flowers and litter fall), and greater protection from predators (Kon et al. 2011). For the macrofauna, lower aboveground biomass could mean increased structure in soil habitats; this is supported by the finding of lower aboveground biomass where root biomass was higher. Despite the current study only evaluating the subsurface root mat instead of ratios, trends in the relationship between root:shoot biomass show consistently lower ratios (proportionally fewer roots) in regions that are warmer (Cairns et al. 1997) or with lower salinity (Adame et al. 2017), as in the deltaic CS studied. Thus, aboveground biomass might directly increase megafaunal species richness while indirectly decreasing macrofaunal species richness.

At smaller scales, site variability was related to annelid assemblage functional traits. Annelid morphological complexity differed along an environmental gradient and was mainly driven by differences in mangrove subsurface root biomass. The presence and architecture of roots and rhizomes in tidal flats are known to enhance microhabitat diversity and influence sediment features, which in turn carries implications for annelid assemblage functional traits (Lana & Guiss 1992, Tolhurst & Chapman 2007, Demopoulos & Smith 2010). Annelids with

more complex body plans are more abundant at sites with lower root biomass and containing sediment with higher bulk density. In these habitats, the structural and physical dimensions of the sediment matrix tend to make the availability of food and shelter from predators highly unpredictable for annelids (Sueiro et al. 2011). Annelids in these habitats may use diversified structures, such as palps, lateral jaws, tentacles, and well-developed parapodia to enhance foraging radii, locomotion, burrowing, and defense (Jumars et al. 2015). These characteristics are intimately related to the variety of distinct feeding modes in annelids (e.g. selective detritus-feeders, burrowers, suspension feeders, and predators) — a necessary strategy in order to thrive in a mosaic of patchily distributed resources. This is comparable to annelid assemblages in other benthic environments such as dissipative sandy beaches, where Strong body morphological complexity is attributed to weak local hydrodynamics (Wouters et al. 2018). This diversity in functional traits increases capacity to respond to and thrive in the surrounding environment.

On the other hand, annelids with slender, cylindrical body form and lower structural complexity were more abundant at sites with higher root biomass and containing sediment with lower bulk density. This body design may enhance mobility through the dense root and rhizome mats. Their relatively low motility and limited sensory stimuli are intimately coupled with foraging behavior and success (Pagliosa 2005, Jumars et al. 2015). Reduced functionality constrains the annelids to a non-selective feeding mode, in which they use their eversible pharynges to collect food (Fauchald & Jumars 1979). Contrary to other intertidal vegetated habitats such as saltmarshes, where dense root-rhizome biomass tends to increase the microhabitat availability and promote a larger assemblage with high structural and functional diversity (Levin et al. 1998, Xingzhong et al. 2005, Braga et al. 2011), mangrove sites with high subsurface root biomass were dominated by annelids with simple body plans and lower morphological complexity. Annelid assemblages inhabiting saltmarshes are directly influenced by environmental modifications caused by plants at the surface and subsurface of the sediment (Lana & Guiss 1992, Pagliosa & Lana 2005). For example, high density of roots and stems in this ecosystem promotes increased variety of particles trapped by biogenic structures, thereby changing the sediment texture (Whitlatch 1981). Sediment texture can in turn influence annelid assemblage functional traits. In more sandy habitats, annelid assemblages presented richer and more heterogeneous functional traits, while discretely motile, small-sized, and low-sensitivity organisms are more common in muddy habitats (Otegui et al. 2016). These spatial patterns of distribution of the main functional traits in



annelid assemblages might explain differences between saltmarshes and adjacent bare tidal flats; however, they do not explain differences between mangrove sites with differing root systems.

The main structural and functional components of the root system can sometimes be attributed to tree type (Tomlinson 2016), but this did not vary among the studied CSs (i.e. *Avicennia*, *Laguncularia*, and *Rhizophora* types). Subsurface root biomass variation better explains the small-scale environmental variability in the present study. Nevertheless, the root systems of mangrove forests are recycled very slowly, and the high carbon stock found in mangrove soils are, in essence, the local dead and living roots (Rovai et al. 2018). Thus, with more root biomass, there is less soil bulk density. The distinct set of body morphological characteristics found at sites with low and high root biomasses may reflect different ecological roles of annelids in mangroves and highlights the main differences in functional traits between vegetated sedimentary habitats. While the physical presence of the salt marsh plants causes surface and subsurface modifications of sediment texture and favors the benthic habitat at the local scale, in mangroves, an increase in roots and rhizome mats seems to enhance the organic pool (i.e. dead and alive) and constrain annelid assemblage functional traits.

## 5. CONCLUSIONS

This work highlights that macrofaunal community structure and functional characteristics of annelid assemblages in mangroves depend on spatial scale. Climate–geophysical drivers were the major predictors of macrofauna community structure, while smallscale factors such as root biomass had a greater influence on annelid assemblage functional traits. Using these 2 distinct approaches at the scale of CSs is highly recommended for better interpretation of the results in mangrove benthic studies. Our work highlights the need for further investigation of mangrove macrofauna structure and function at higher hierarchical spatial scales ( $10^3$  km) between CSs.

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## APPENDIX

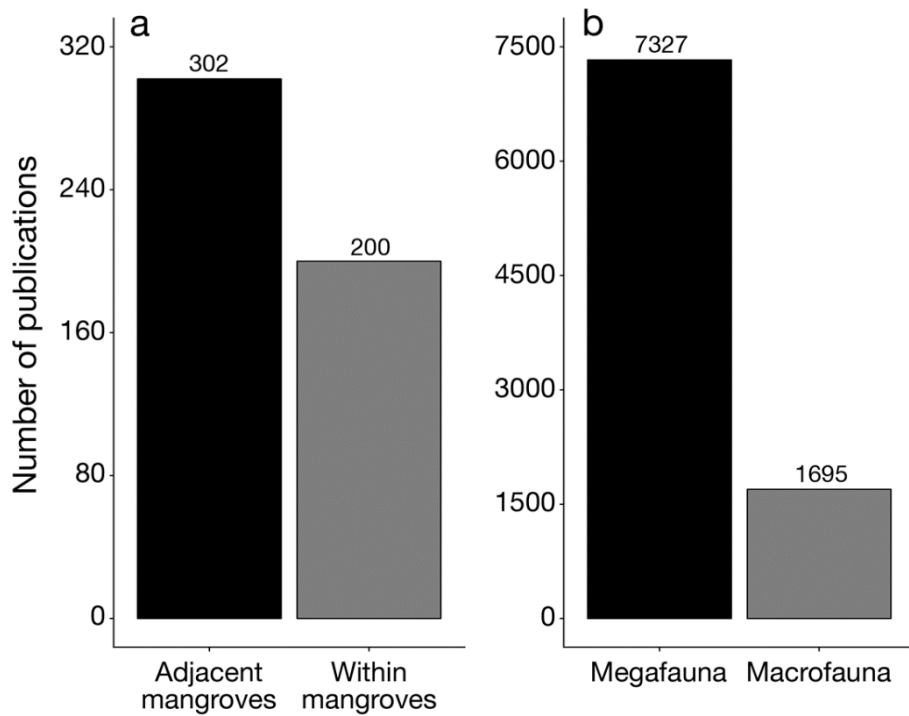


Fig. A1. (a) Number of publications macrofaunal community studies carried out in areas adjacent and within mangrove forests. The queries were: ‘mangrove’ (in Title) versus ‘macrofauna,’ or benth\*, ‘epifauna,’ or ‘infauna’ (in Title/Abstract/Keyword). (b) Number of publications on macrofauna and megafauna in mangroves. The queries were separated to macrofauna (‘mangrove’—in Title—versus ‘isopod\*,’ ‘nemert\*,’ ‘annelid\*,’ ‘polychaet\*,’ ‘bivalv\*,’ ‘oligo chaet\*,’ ‘enchytraeid\*,’ ‘tubificid\*,’ ‘clam,’ ‘capitellid\*,’ ‘tanaidac\*,’ ‘nereidid\*,’ ‘gammarid\*,’ ‘acari,’ or ‘ribbon’—in Title/Abstract/Keyword) and megafauna (‘mangrove’—in Title—versus ‘crab,’ ‘gastropod,’ ‘decapoda,’ ‘fish,’ ‘prawn,’ ‘ocypodidae,’ ‘crustacea,’ ‘gobiidae,’ ‘sponge,’ ‘ucides,’ ‘barnacle,’ ‘terebralia,’ ‘porifera,’ or ‘shrimp’—in Title/Abstract/Keyword) taxonomical groups. All bibliographic surveys were carried out online using the Scopus and Scielo databases

## SUPPLEMENT

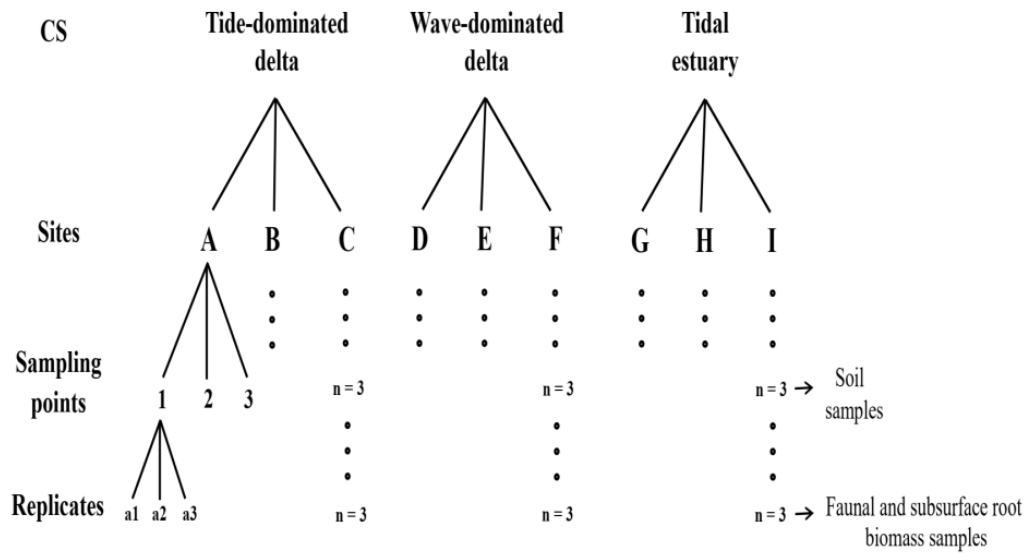


Fig. S1. Scheme of the experimental design and scales of spatial variability: CS (Tide-dominated delta, Wave-dominated delta and Tidal estuary), Sites (A, B and C), Sampling points (1, 2 and 3) and Replicates (a1, a2 and a3). CS = Coastal setting

**Table S1.** Categories of functional traits and the value given to each sub category of each annelid species. ba1: absence of body appendages, ba2: presence of body appendages, bs1: uncini, bs2: parapodia with similar rami, bs3: aciculae, s1: lower number of segments ( $n \leq 100$ ), s2: higher number of segments ( $n \geq 101$ ). Scores ranging from 0 (no affinity) to 3 (total affinity).

<b>Species</b>	<b>ba1</b>	<b>ba2</b>	<b>bs1</b>	<b>bs2</b>	<b>bs3</b>	<b>s1</b>	<b>s2</b>
Enchytraeidae	0	3	3	3	0	2	2
<i>Notomastus lobatus</i>	0	3	3	3	0	2	2
<i>Capitella cf. capitata</i>	0	3	3	3	0	2	2
<i>Heteromastus filiformis</i>	0	3	3	3	0	2	2
<i>Heteromastus similis</i>	0	3	3	3	0	2	2
<i>Mediomastus californiensis</i>	0	3	3	3	0	2	2
<i>Leitoscoloplos fragilis</i>	0	3	0	3	0	3	1
<i>Dipolydora socialis</i>	0	3	3	0	0	3	0
<i>Manayunkia brasiliensis</i>	0	3	3	0	0	2	2
<i>Streblospio</i> sp.	0	3	3	0	0	3	0
<i>Isolda pulchella</i>	3	0	3	0	0	3	0
<i>Lumbrineris</i> sp.	0	3	0	0	3	0	3
<i>Alitta succinea</i>	0	3	0	0	3	2	2
<i>Namalycastis abiuma</i>	0	3	0	0	3	2	2
<i>Laeonereis</i> spp.	0	3	0	0	3	2	2
<i>Nereis riisei</i>	0	3	0	0	3	2	2
<i>Nereis oligohalina</i>	0	3	0	0	3	2	2
<i>Namanereis pontica</i>	0	3	0	0	3	2	2
<i>Perinereis cultrifera</i>	0	3	0	0	3	2	2
<i>Ceratonereis excisa</i>	0	3	0	0	3	2	2
<i>Perinereis vancaurica</i>	0	3	0	0	3	2	2
<i>Scoletoma tetraura</i>	0	3	0	0	3	0	3
<i>Sigambra grubii</i>	0	3	0	0	3	0	3
<i>Aglaophamus verrilli</i>	0	3	0	0	3	0	3
<i>Langerhansia</i> sp.	0	3	0	0	3	2	2
<i>Nephtys fluvialis</i>	0	3	0	0	3	0	3

Table S2. Hierarchical nested analysis of variance (ANOVA) and components of variation (CV) of climate and geophysical variables. CSs: Coastal settings, Si: Sites, PET: potential evapotranspiration, Pmin: minimum precipitation, Tmin: minimum air temperature.

<b>Source</b>					
<b>Tidal range</b>	<b>d.f.</b>	<b>MS</b>	<b>F</b>	<b>p</b>	<b>CV (%)</b>
<b>CSs</b>	2	85.90	141	< 0.001	87.20
<b>Si(CSs)</b>	6	0.61	$83345 \times e^{24}$	< 0.001	12.80
<b>Residuals</b>	72	0.00			0.00
<b>Runoff</b>					
<b>CSs</b>	2	6807137	259	< 0.001	90.30
<b>Si(CSs)</b>	6	26253	$24993 \times e^{24}$	< 0.001	9.70
<b>Residuals</b>	72	0.00			0.00
<b>PET</b>					
<b>CSs</b>	2	1079223	567	0.04	55.50
<b>Si(CSs)</b>	6	190189	$79049 \times e^{24}$	< 0.001	44.50
<b>Residuals</b>	72	0.00			0.00
<b>Pmin</b>					
<b>CSs</b>	2	30097	678	< 0.001	82.50
<b>Si(CSs)</b>	6	444	$59126 \times e^{24}$	< 0.001	17.50
<b>Residuals</b>	72	0.00			0.00
<b>Tmin</b>					
<b>CSs</b>	2	202.30	448	< 0.001	79.30
<b>Si(CSs)</b>	6	4.52	$5801 \times e^{24}$	< 0.001	20.70
<b>Residuals</b>	72	0.00			0.00

Table S3. Hierarchical nested analysis of variance (ANOVA) and components of variation (CV) of soil and vegetation variables. CSs: Coastal settings, Si: Sites.

<b>Source</b>					
<b>Soil nitrogen</b>	<b>d.f.</b>	<b>MS</b>	<b>F</b>	<b>p</b>	<b>CV (%)</b>
<b>CSs</b>	2	0.31	1.35	0.33	16.00
<b>Si(CSs)</b>	6	0.23	12.59	< 0.001	44.60
<b>Residuals</b>	72	0.02			39.40
<b>Soil carbon</b>					
<b>CSs</b>	2	32.43	0.77	0.50	0.00
<b>Si(CSs)</b>	6	42.08	38.52	< 0.001	67.10
<b>Residuals</b>	72	1.09			32.90
<b>Soil phosphorus</b>					
<b>CSs</b>	2	0.005	2.77	0.14	33.40
<b>Si(CSs)</b>	6	0.001	30.07	< 0.001	42.80
<b>Residuals</b>	72	0.00006			23.80
<b>Soil organic matter</b>					
<b>CSs</b>	2	1036.55	3.78	0.09	35.40
<b>Si(CSs)</b>	6	273.69	14.32	< 0.001	35.50
<b>Residuals</b>	72	19.12			29.10
<b>Soil bulk density</b>					
<b>CSs</b>	2	0.21	0.80	0.49	0.00
<b>Si(CSs)</b>	6	0.27	19.23	< 0.001	58.70
<b>Residuals</b>	72	0.01			41.30
<b>Aboveground biomass</b>					
<b>CSs</b>	2	643425	146	0.004	68.10
<b>Si(CSs)</b>	6	43924	16965 x e <sup>-24</sup>	< 0.001	31.90

<b>Residuals</b>	72	0.00			0.00
<b>Subsurface root biomass</b>					
<b>CSs</b>	2	114.4	4.51	0.06	30.20
<b>Si(CSs)</b>	6	25.36	7.82	< 0.001	38.00
<b>Residuals</b>	72	3.24			31.80

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Table S4. Mean abundance of each species in the study site. CSs: Coastal settings, TD: Tide-dominated delta, WD: Wave-dominated delta, TE: Tidal estuary.

CSs	TD	TD	TD	TD	TD	TD
Site	A	A	A	B	B	B
Sampling point	1	2	3	1	2	3
<i>Marionina</i> spp.1	0	0	0	0	0	0
<i>Marionina</i> spp.2	0	0	0	0	0	0
Enchytraeidae 1	0	0	0	0	0	0
Enchytraeidae 2	0	4	2	1	0	9
<i>Notomastus lobatus</i>	2	2	1	3	5	1
<i>Capitella cf. capitata</i>	1	0	1	4	1	2
<i>Lumbrineris</i> sp.	0	0	0	0	0	0
<i>Alitta succinea</i>	0	0	0	4	1	2
<i>Namalycastis abiuma</i>	0	1	0	0	0	0
<i>Laeonereis</i> spp.	0	0	1	1	0	3
<i>Heteromastus filiformis</i>	0	0	0	3	2	3
<i>Heteromastus similis</i>	0	0	0	0	0	0
<i>Mediomastus californiensis</i>	0	0	1	3	0	2
<i>Leitoscoloplos fragilis</i>	0	0	0	0	0	0
<i>Dipolydora socialis</i>	0	0	0	0	0	0
<i>Streblospio</i> sp.	0	0	0	0	1	1
<i>Isolda pulchella</i>	1	0	0	1	1	1
<i>Nereis riisei</i>	0	0	0	0	0	0
<i>Nereis oligohalina</i>	0	0	1	0	0	0
<i>Namanereis pontica</i>	1	0	0	0	0	0
<i>Perinereis cultrifera</i>	0	1	0	0	0	0
<i>Ceratonereis excisa</i>	0	0	0	0	0	1
<i>Perinereis vancaurica</i>	0	0	0	0	0	0
<i>Scoletoma tetraura</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	0	1	0
<i>Aglaophamus verrilli</i>	0	0	0	1	0	1
<i>Langerhansia</i> sp.	0	0	0	0	0	1
<i>Nephtys fluvialis</i>	0	0	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	0	0	0	0	0
<i>Uca thayeri</i>	0	0	0	0	0	0
<i>Uca maracoani</i>	0	0	1	0	0	0
<i>Uca uruguayensis</i>	0	0	0	0	0	0
<i>Uca mordax</i>	0	0	0	1	0	0
<i>Uca cumulanta</i>	0	0	0	1	0	0
<i>Uca rapax</i>	0	1	0	0	0	0
<i>Uca burgersi</i>	0	1	1	0	0	0



<i>Uca leptodactyla</i>	0	0	0	0	0	0
<i>Pachygrapsus gracilis</i>	0	0	0	0	0	0
<i>Corophium</i> sp.	0	0	0	0	0	0
<i>Chelorchestia darwinii</i>	0	0	0	0	0	0
<i>Halmyrapseudes spaansi</i>	0	1	0	7	2	8
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	0
Bivalvia 1	0	0	0	0	0	0
Bivalvia 2	0	0	0	0	0	0
Bivalvia 3	1	0	1	1	0	3
<i>Lucina pectinata</i>	0	0	0	0	0	0
<i>Tellina lineata</i>	0	0	0	0	0	0
<i>Macoma constricta</i>	3	0	1	0	2	0
<i>Cyclinella tenuis</i>	0	19	3	3	4	4
<i>Melampus coffeus</i>	0	0	0	0	0	0
<i>Mytella guyanensis</i>	0	0	0	1	0	0
Acari	0	1	0	2	1	2
Tipulidae	0	0	1	0	0	0
Collembola	0	1	0	0	0	0
Chironomidae	0	0	0	0	0	0
Diptera	2	0	0	0	0	0
Tabanidae	1	0	0	0	0	0
Dolichopodidae	0	0	0	0	0	1
Ceratopogonidae	0	1	0	0	0	0
<b>CSs</b>	<b>TD</b>	<b>TD</b>	<b>TD</b>	<b>WD</b>	<b>WD</b>	<b>WD</b>
<b>Site</b>	<b>C</b>	<b>C</b>	<b>C</b>	<b>D</b>	<b>D</b>	<b>D</b>
<b>Sampling point</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>1</b>	<b>2</b>	<b>3</b>
<i>Marionina</i> spp.1	0	0	0	0	0	0
<i>Marionina</i> spp.2	0	0	0	0	0	0
Enchytraeidae 1	0	0	0	1	7	0
Enchytraeidae 2	5	0	1	0	0	0
<i>Notomastus lobatus</i>	3	9	4	2	2	5
<i>Capitella cf. capitata</i>	3	2	1	2	0	1
<i>Lumbrineris</i> sp.	0	0	0	0	0	0
<i>Alitta succinea</i>	1	0	0	0	0	0
<i>Namalycastis abiuma</i>	6	0	0	0	0	0
<i>Laeonereis</i> spp.	0	0	0	0	0	0
<i>Heteromastus filiformis</i>	0	4	1	5	2	0
<i>Heteromastus similis</i>	0	0	0	0	0	0
<i>Mediomastus californiensis</i>	0	4	0	0	0	0
<i>Leitoscoloplos fragilis</i>	0	0	0	1	0	0
<i>Dipolydora socialis</i>	0	0	0	0	0	0

<i>Streblospio</i> sp.	0	0	0	0	0	0
<i>Isolda pulchella</i>	2	0	0	1	0	0
<i>Nereis riisei</i>	0	0	0	0	0	0
<i>Nereis oligohalina</i>	0	0	0	0	0	0
<i>Namanereis pontica</i>	0	1	0	0	0	0
<i>Perinereis cultrifera</i>	0	0	0	0	0	0
<i>Ceratonereis excisa</i>	0	0	0	0	0	0
<i>Perinereis vancaurica</i>	0	0	0	0	0	0
<i>Scoletoma tetraura</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	0	0	0
<i>Aglaophamus verrilli</i>	1	0	0	0	0	0
<i>Langerhansia</i> sp.	0	0	0	0	0	0
<i>Nephtys fluvialis</i>	0	1	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	0	0	0	0	0
<i>Uca thayeri</i>	0	0	0	0	1	0
<i>Uca maracoani</i>	1	0	0	0	0	0
<i>Uca uruguayensis</i>	0	0	0	0	0	0
<i>Uca mordax</i>	0	0	0	0	0	0
<i>Uca cumulanta</i>	0	0	0	0	0	0
<i>Uca rapax</i>	0	0	0	1	1	1
<i>Uca burgersi</i>	0	0	0	0	0	0
<i>Uca leptodactyla</i>	0	0	0	0	1	0
<i>Pachygrapsus gracilis</i>	0	0	1	0	0	0
<i>Corophium</i> sp.	0	0	0	0	0	0
<i>Chelorchestia darwinii</i>	0	0	0	0	0	0
<i>Halmyrapseudes spaansi</i>	1	0	0	0	0	0
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	0
Bivalvia 1	0	0	0	0	0	0
Bivalvia 2	0	0	0	0	0	0
Bivalvia 3	0	1	0	0	0	0
<i>Lucina pectinata</i>	0	0	0	0	0	0
<i>Tellina lineata</i>	0	0	0	0	0	0
<i>Macoma constricta</i>	0	0	0	0	0	0
<i>Cyclinella tenuis</i>	0	0	1	0	0	0
<i>Melampus coffeus</i>	0	0	0	0	0	0
<i>Mytella guyanensis</i>	0	0	0	0	0	0
Acari	1	0	0	0	0	0
Tipulidae	0	0	0	0	0	0
Collembola	0	0	0	0	0	1
Chironomidae	0	0	0	0	0	0
Diptera	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	0

Dolichopodidae	1	0	0	0	0	0
Ceratopogonidae	0	0	1	0	0	0
<b>CSs</b>	<b>WD</b>	<b>WD</b>	<b>WD</b>	<b>WD</b>	<b>WD</b>	<b>WD</b>
<b>Site</b>	<b>E</b>	<b>E</b>	<b>E</b>	<b>F</b>	<b>F</b>	<b>F</b>
<b>Sampling point</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>1</b>	<b>2</b>	<b>3</b>
<i>Marionina</i> spp.1	0	0	0	0	0	0
<i>Marionina</i> spp.2	0	0	0	0	0	0
Enchytraeidae 1	29	10	14	19	7	4
Enchytraeidae 2	0	0	0	0	0	0
<i>Notomastus lobatus</i>	0	0	3	3	0	0
<i>Capitella cf. capitata</i>	5	0	1	2	1	1
<i>Lumbrineris</i> sp.	0	0	0	0	1	0
<i>Alitta succinea</i>	0	0	3	0	0	0
<i>Namalycastis abiuma</i>	0	0	0	0	0	0
<i>Laeonereis</i> spp.	2	2	0	0	0	1
<i>Heteromastus filiformis</i>	20	11	14	4	6	0
<i>Heteromastus similis</i>	0	0	0	0	0	0
<i>Mediomastus californiensis</i>	0	0	0	0	0	0
<i>Leitoscoloplos fragilis</i>	0	0	0	0	0	0
<i>Dipolydora socialis</i>	0	0	0	0	0	0
<i>Streblospio</i> sp.	0	0	0	0	0	0
<i>Isolda pulchella</i>	0	1	0	0	0	0
<i>Nereis riisei</i>	9	2	1	0	0	0
<i>Nereis oligohalina</i>	0	1	0	0	0	1
<i>Namanereis pontica</i>	0	0	0	0	0	0
<i>Perinereis cultrifera</i>	0	0	0	0	0	0
<i>Ceratonereis excisa</i>	0	0	0	0	0	0
<i>Perinereis vancaurica</i>	0	0	0	0	0	0
<i>Scoletoma tetraura</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	0	0	0
<i>Aglaophamus verrilli</i>	0	0	0	0	0	0
<i>Langerhansia</i> sp.	0	0	0	0	0	0
<i>Nephtys fluvialis</i>	0	0	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	0	0	0	0	0
<i>Uca thayeri</i>	0	0	0	0	0	1
<i>Uca maracoani</i>	0	0	1	0	0	0
<i>Uca uruguayensis</i>	0	0	0	0	0	0
<i>Uca mordax</i>	0	0	0	0	0	1
<i>Uca cumulanta</i>	0	0	0	0	1	0
<i>Uca rapax</i>	0	0	0	0	0	0
<i>Uca burgersi</i>	0	0	0	0	0	0
<i>Uca leptodactyla</i>	0	0	0	0	0	0
<i>Pachygrapsus gracilis</i>	0	0	0	0	0	0

<i>Corophium</i> sp.	0	0	1	0	0	0
<i>Chelorchestia darwinii</i>	0	0	0	0	0	0
<i>Halmyrapseudes spaansi</i>	0	0	0	0	0	0
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	0
Bivalvia 1	0	0	0	0	0	0
Bivalvia 2	0	0	1	0	0	0
Bivalvia 3	0	0	0	0	0	0
<i>Lucina pectinata</i>	0	0	0	0	0	0
<i>Tellina lineata</i>	0	0	0	0	0	0
<i>Macoma constricta</i>	0	0	0	0	0	0
<i>Cyclinella tenuis</i>	0	0	0	0	0	0
<i>Melampus coffeus</i>	0	0	0	1	0	0
<i>Mytella guyanensis</i>	0	0	0	0	0	0
Acari	0	0	0	1	0	0
Tipulidae	0	0	0	0	0	0
Collembola	0	0	0	0	0	0
Chironomidae	0	0	0	0	0	0
Diptera	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	0
Dolichopodidae	0	0	0	0	0	1
Ceratopogonidae	0	0	0	0	0	0
<b>CSs</b>	TE	TE	TE	TE	TE	TE
<b>Site</b>	G	G	G	H	H	H
<b>Sampling point</b>	1	2	3	1	2	3
<i>Marionina</i> spp.1	9	23	16	0	0	0
<i>Marionina</i> spp.2	60	86	87	3	3	21
Enchytraeidae 1	0	0	0	0	0	0
Enchytraeidae 2	0	0	0	0	0	0
<i>Notomastus lobatus</i>	0	0	0	0	0	0
<i>Capitella cf. capitata</i>	56	31	115	3	1	9
<i>Lumbrineris</i> sp.	0	0	0	1	1	1
<i>Alitta succinea</i>	1	1	1	5	3	2
<i>Namalycastis abiuma</i>	0	0	0	0	1	0
<i>Laeonereis</i> spp.	10	9	9	1	1	7
<i>Heteromastus filiformis</i>	0	0	0	0	0	0
<i>Heteromastus similis</i>	5	7	1	1	2	3
<i>Mediomastus californiensis</i>	5	0	1	0	0	0
<i>Leitoscoloplos fragilis</i>	0	0	0	0	0	0
<i>Dipolydora socialis</i>	3	16	14	0	0	7
<i>Streblospio</i> sp.	0	0	0	0	0	0
<i>Isolda pulchella</i>	0	0	0	5	9	4

<i>Nereis riisei</i>	0	0	0	0	0	0
<i>Nereis oligohalina</i>	0	0	3	2	0	0
<i>Namanereis pontica</i>	0	0	0	0	0	0
<i>Perinereis cultrifera</i>	0	0	0	0	0	0
<i>Ceratonereis excisa</i>	0	0	0	0	0	0
<i>Perinereis vancaurica</i>	0	0	0	0	0	2
<i>Scoletoma tetraura</i>	0	0	0	0	1	0
<i>Sigambra grubii</i>	0	1	2	1	0	0
<i>Aglaophamus verrilli</i>	0	0	0	0	0	0
<i>Langerhansia</i> sp.	0	0	0	0	0	0
<i>Nephtys fluvialis</i>	0	0	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	0	2	0	7	1
<i>Uca thayeri</i>	0	0	0	0	0	0
<i>Uca maracoani</i>	0	0	0	0	0	0
<i>Uca uruguayensis</i>	2	2	1	0	0	0
<i>Uca mordax</i>	0	0	1	0	0	0
<i>Uca cumulanta</i>	0	0	0	0	0	0
<i>Uca rapax</i>	0	0	0	0	0	1
<i>Uca burgersi</i>	0	0	0	0	0	0
<i>Uca leptodactyla</i>	1	1	0	0	0	0
<i>Pachygrapsus gracilis</i>	0	0	0	0	0	0
<i>Corophium</i> sp.	0	0	0	0	0	0
<i>Chelorchestia darwinii</i>	0	0	0	0	0	0
<i>Halmyrapseudes spaansi</i>	0	0	0	0	0	0
<i>Monokaliapseudes schubartii</i>	0	4	1	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	1
Bivalvia 1	0	0	1	0	0	1
Bivalvia 2	0	0	0	0	0	0
Bivalvia 3	0	0	0	0	0	0
<i>Lucina pectinata</i>	0	0	2	0	1	0
<i>Tellina lineata</i>	0	0	0	0	0	0
<i>Macoma constricta</i>	0	0	0	0	0	0
<i>Cyclinella tenuis</i>	0	0	0	0	0	0
<i>Melampus coffeus</i>	0	0	0	0	0	0
<i>Mytella guyanensis</i>	0	1	1	3	0	3
Acari	0	2	1	0	1	1
Tipulidae	0	1	0	0	0	0
Collembola	0	0	0	1	0	0
Chironomidae	0	1	0	0	0	0
Diptera	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	0
Dolichopodidae	0	0	1	0	0	1
Ceratopogonidae	0	0	0	0	0	1

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CSs	TE	TE	TE
Site	I	I	I
Sampling point	1	2	3
<i>Marionina</i> spp.1	11	0	1
<i>Marionina</i> spp.2	1	83	0
Enchytraeidae 1	0	0	0
Enchytraeidae 2	0	0	0
<i>Notomastus lobatus</i>	0	0	0
<i>Capitella</i> cf. <i>capitata</i>	5	9	4
<i>Lumbrineris</i> sp.	0	0	0
<i>Alitta succinea</i>	0	0	1
<i>Namalycastis abiuma</i>	0	0	0
<i>Laeonereis</i> spp.	2	1	1
<i>Heteromastus filiformis</i>	0	0	0
<i>Heteromastus similis</i>	0	1	1
<i>Mediomastus californiensis</i>	0	3	0
<i>Leitoscoloplos fragilis</i>	0	0	0
<i>Dipolydora socialis</i>	0	0	0
<i>Streblospio</i> sp.	0	0	0
<i>Isolda pulchella</i>	1	0	0
<i>Nereis riisei</i>	0	0	0
<i>Nereis oligohalina</i>	0	0	0
<i>Namanereis pontica</i>	0	0	0
<i>Perinereis cultrifera</i>	0	0	0
<i>Ceratonereis excisa</i>	0	0	0
<i>Perinereis vancaurica</i>	0	0	0
<i>Scoletoma tetraura</i>	4	0	0
<i>Sigambra grubii</i>	0	0	0
<i>Aglaophamus verrilli</i>	0	0	0
<i>Langerhansia</i> sp.	0	0	0
<i>Nephtys fluvialis</i>	0	0	0
<i>Manayunkia brasiliensis</i>	1	0	3
<i>Uca thayeri</i>	0	0	0
<i>Uca maracoani</i>	0	0	0
<i>Uca uruguayensis</i>	0	0	0
<i>Uca mordax</i>	0	0	0
<i>Uca cumulanta</i>	0	0	0
<i>Uca rapax</i>	1	1	0
<i>Uca burgersi</i>	0	0	0
<i>Uca leptodactyla</i>	0	1	0
<i>Pachygrapsus gracilis</i>	0	0	0
<i>Corophium</i> sp.	0	0	0
<i>Chelorchestia darwinii</i>	0	0	0

<i>Halmyrapseudes spaansi</i>	0	0	0
<i>Monokaliapseudes schubartii</i>	1	1	0
<i>Heleobia australis</i>	0	2	0
Bivalvia 1	0	1	1
Bivalvia 2	0	0	0
Bivalvia 3	0	0	0
<i>Lucina pectinata</i>	0	0	0
<i>Tellina lineata</i>	1	0	0
<i>Macoma constricta</i>	0	0	0
<i>Cyclinella tenuis</i>	0	0	0
<i>Melampus coffeus</i>	0	0	0
<i>Mytella guyanensis</i>	0	0	0
Acari	0	2	0
Tipulidae	0	0	0
Collembola	0	0	0
Chironomidae	0	1	1
Diptera	0	0	0
Tabanidae	0	0	0
Dolichopodidae	0	1	0
Ceratopogonidae	0	0	0

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Table S5. Hierarchical nested analysis of variance (ANOVA) and components of variation (CV) of macrofaunal total abundance, species richness, species diversity and trait diversity (Rao's quadratic entropy) variables. CSs: Coastal settings, Si: Sites, Sp: Sampling points.

<b>Source</b>					
<b>Total abundance</b>	<b>d.f.</b>	<b>MS</b>	<b>F</b>	<b>p</b>	<b>CV (%)</b>
CSs	2	11.31	2.27	0.18	22.00
Si(CSs)	6	4.97	5.42	0.002	29.90
Sp(Si(CSs))	18	0.92	1.79	0.06	16.42
<b>Residuals</b>	54	0.51			31.58
<b>Richness</b>					
CSs	2	140.11	8.37	0.01	33.65
Si(CSs)	6	16.74	2.09	0.11	15.53
Sp(Si(CSs))	18	7.97	1.61	0.10	15.80
<b>Residuals</b>	54	4.95			35.02
<b>Species Diversity</b>					
CSs	2	1.70	5.26	0.04	29.73
Si(CSs)	6	0.32	2.53	0.06	19.40
Sp(Si(CSs))	18	0.13	0.85	0.63	14.80
<b>Residuals</b>	54	0.15			36.07
<b>Trait diversity</b>					
CSs	2	117.81	1.95	0.22	17.78
Si(CSs)	6	60.38	3.79	0.009	27.10
Sp(Si(CSs))	18	15.92	1.12	0.36	9.12
<b>Residuals</b>	54	14.24			46.08



**Table S6.** Mean abundance of each functional trait of annelids in the study site. CSs: Coastal settings, TD: Tide-dominated delta, WD: Wave-dominated delta, TE: Tidal estuary, ba1: absence of body appendages, ba2: presence of body appendages, bs1: uncini, bs2: parapodia with similar rami, bs3: aciculae, s1: lower number of segments ( $n \leq 100$ ), s2: higher number of segments ( $n \geq 101$ ).

CSs	TD	TD	TD	TD	TD	TD	TD	TD	TD
Site	A	A	A	B	B	B	C	C	C
Sampling point	1	2	3	1	2	3	1	2	3
ba1	1.00	0.00	0.00	2.00	0.33	0.33	0.00	2.00	0.00
ba2	7.67	4.33	7.00	15.67	17.67	23.67	15.67	23.67	7.33
bs1	3.50	2.00	2.17	7.67	8.17	8.83	6.50	11.50	2.50
bs2	2.50	2.00	2.17	5.67	6.83	7.17	6.50	9.50	2.50
bs3	2.67	0.33	2.67	4.33	3.00	8.00	2.67	4.67	2.33
s1	4.67	2.17	3.33	9.83	9.33	11.83	7.33	13.50	3.50
s2	4.00	2.17	3.67	7.83	8.67	12.17	8.33	12.17	3.83
CSs	WD	WD	WD	WD	WD	WD	WD	WD	WD
Site	D	D	D	E	E	E	F	F	F
Sampling point	1	2	3	1	2	3	1	2	3
ba1	0.33	0.33	0.00	2.00	5.67	10.33	4.00	0.33	0.33
ba2	123.33	245.00	204.67	28.00	20.33	51.67	41.67	19.00	70.67
bs1	61.17	122.00	102.33	11.50	9.83	39.83	24.83	7.83	36.17
bs2	58.50	111.00	81.33	7.50	3.50	16.83	19.50	5.17	34.50
bs3	4.00	12.33	21.00	11.00	12.67	5.33	1.33	6.33	0.33
s1	62.83	126.67	112.00	16.83	15.17	37.50	24.67	8.17	35.67
s2	60.83	118.67	92.67	13.17	10.83	24.50	21.00	11.17	35.33
CSs	TE	TE	TE	TE	TE	TE	TE	TE	TE
Site	G	G	G	H	H	H	I	I	I
Sampling point	1	2	3	1	2	3	1	2	3
ba1	0.00	0.00	0.67	0.00	0.67	0.00	0.00	0.00	0.00
ba2	7.00	13.67	6.33	34.33	43.33	47.67	23.00	15.00	11.33
bs1	3.50	6.50	3.83	12.50	20.17	21.33	11.50	6.67	5.17
bs2	3.50	7.17	3.17	12.50	19.50	21.33	11.50	6.67	5.17
bs3	0.00	0.00	0.00	9.33	4.33	5.00	0.00	1.67	1.00
s1	3.50	7.00	3.83	17.17	22.33	23.83	11.50	7.00	5.67
s2	3.50	6.67	3.17	17.17	21.67	23.83	11.50	8.00	5.67

**4 ARTIGO II: CHANGES IN THE VERTICAL AND HORIZONTAL DISTRIBUTION OF COMPLEX MANGROVE ROOT SYSTEMS AFFECT THE BENTHIC MACROFAUNA**

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## **Changes in the vertical and horizontal distribution of complex mangrove root systems affect the benthic macrofauna**

### **Abstract**

Despite the mangrove tree is able to allocate a large proportion of its total biomass to the underground roots, little is known about their interaction with macrofauna. The complex root system of the mangroves is composed by different components, which they vary in their size and spatial distribution in the soil. Thus, spatial variability of the roots may affect the distribution of macrofaunal assemblages. We evaluated the above- and belowground structures of mangrove plants, sediment properties, algal cover and their relationship with macrofaunal assemblages as a function of soil strata and distance from trunks in Brazilian mangroves. We found that the structure and function of the mangrove macrofaunal assemblages vary depending on the distance from trunks and along the vertical strata of the soil. Most of the benthic taxa occurred in the upper layers (0 - 5 cm) of the soil and near trunks (~0.3 m), where they had a lower proportion of fine roots and less cohesive substrates, offering favorable conditions for these organisms. Therefore, the macrofaunal assemblages were more associated with changes in the complexity of root systems than sediment properties. Moreover, the macrofauna showed higher contribution at very small (i.e. distance from trunks and strata) than at local spatial scales (i.e. sites).

**Keywords:** Macrofaunal assemblages. Roots. Distance. Depth stratum. Spatial scales.

## Introduction

Mangroves occur along tropical and subtropical coasts, and are among the most productive and carbon-rich ecosystem in the world (Donato et al., 2011; Kauffman et al., 2011). As soft sediment inhabitants, the mangrove trees allocate a higher biomass to the belowground roots than trees in upland forests (Komiyama et al., 2008; Hutchison et al., 2014). The spatial distribution of the roots in soil varies depending on the plant life-form. Despite of that, at least a half of plant roots usually accumulate in the upper centimeters of the soil profile (Schenk and Jackson, 2002). This root biomass concentration influences the fluxes of water, carbon, and soil nutrients, as well as the distribution and activity of soil fauna.

Mangrove plants form a complex root system composed by different types of roots. The basic structural and functional components of the root system can be recognized, even though these components may have a different morphological origin in different species, as cable, anchor, pneumatophores and feeding roots (Tomlinson, 2016). Root components may influence the benthic macrofauna both directly (e.g. food, shelter, changes in deposition/erosion rates) and indirectly (e.g. shifts in nutrient flows) (Tolhurst and Chapman, 2007; Demopoulos and Smith, 2010). The development and death of roots can also change the sediment properties such as organic matter content and sediment particle sizes (Leung, 2015a), thus affecting the structure and function of macrofaunal assemblages living into the soil and among the particles. Nevertheless, there are discrepancies concerning the root system-fauna relationships (Wada et al., 1987; Demopoulos and Smith, 2010; Leung 2015a; Checon et al., 2017). Positive effects often associate a greater root biomass to an enhancement in colonization by benthic organisms, since they offer microhabitats, consumable organic matter, more sediment oxygenation and less predation pressures (Demopoulos and Smith, 2010; Chen et al., 2015). Conversely, dense root systems can inhibit infaunal development, offering greater difficulties for feeding and burrowing (Sweetman et al., 2010; Leung, 2015b; Freitas and Pagliosa, 2020).

Unravelling mangrove root system-fauna relationships may take into account the type of roots and their spatial distribution within the bi-dimensional structure of the soil. The root types usually have distinct sizes, ranging from coarse (cable roots) to medium (pneumatophores and anchor roots) and fine (feeding roots) roots (Tomlinson, 2016). Furthermore, changes in the size and biomass of mangrove roots depend on the growth direction of the each type of root. The extension of the roots tend to decrease horizontally

with the distance from the tree base (i.e. cable roots), as well as vertically, downwards with the depth in soil stratum (i.e. anchor roots) or upwards under and above the soil surface (i.e. pneumatophores) (Purnobasuki and Suzuki, 2004; Srikanth et al., 2016). Under the soil surface, horizontal and lateral roots arise from the buried pneumatophores. These feeding roots progressively branch out until finally form dense and fine root mats (Purnobasuki et al., 2017).

To date, no study has investigated the relationship between mangrove macrofaunal structure and function with the complexity of the root system, involving both vertical (depth stratum of the sediment) and horizontal (distance from tree trunks) patterns of distribution. Considering that variations in the mangrove root biomass and size can determine the distribution of the macrofaunal assemblages, we tested the following hypothesis: as the root biomass change with the depth and distance from the trunk, we hope to find a higher proportion of coarse roots in the upper strata and near mangrove tree trunks. A higher density, richness and functional diversity of the macrofauna are therefore expected to be found in areas far from tree trunks and limited to the topsoil, since these roots tend to present proportionally less biomass away than near the tree base. We also hypothesized that the macrofaunal assemblages will be more correlated with roots than sediment parameters. To test these hypotheses, we assessed the mangrove plant structures (above- and belowground), the sediment properties and the algal cover, as well as their relationship with the structure (total density, species richness) and function (functional diversity) of macrofaunal assemblages as a function of the depth stratum and distance from tree trunks in mangroves of southern Brazil.

## **Materials and Methods**

### ***Study area***

The study area is located at the southernmost latitudinal limit of the mangroves distribution on the Southwestern Atlantic coast (Island of Santa Catarina, southern Brazil; Fig. 1a). Due to the climate-geophysical conditions, the structural development of the forests is lower when compared to that of tropics, which is mainly evidenced by the mean tree height of only 8 m and mean diameter at breast height of 0.14 m (Rovai et al., 2016). The mangroves are mostly colonized by *Avicennia schaueriana*, but *Laguncularia racemosa* and *Rhizophora mangle* also occur. The interstitial salinity into the mangrove forests is around 28 (Rovai et al., 2012). The local estuaries are typically composed by small catchments (up to 500 ha)

under a semidiurnal microtidal regime, with mean amplitudes between 0.15 m on neap tides and 0.83 m on spring tides. The climate of the region is subtropical humid, with average annual temperatures of 23 °C (range of 17 – 25 °C) and well distributed precipitation throughout the year (annual average around 1,617 mm) (Netto et al., 2018).

### ***Sampling design***

The field experiment was setup in three mangrove sites located in different estuaries (Ratones, Saco Grande and Tavares Estuaries) during the austral summer 2018, always at low tides (Fig. 1a). In each site, twelve plots of 10 x 10 m were placed at least 50 m apart from each other and up to 80 m away from the border of the vegetation. The selected plots were exclusively composed by mature trees of *A. schaueriana* with limited anthropic interference, and were far from larger rivers and tidal channels. These procedures minimized the forest structural variations related to disturbances, water fluxes and vegetation type. In each site, we randomly chose six plots to accomplish each distance from the tree base, hereafter called ‘near’ and ‘far’ from trunks. At the plots ‘near’, the samples were randomly collected at distances of up to 0.3 m from any tree base, while in plots ‘far’ the samples were collected at distances between 3 and 3.5 m from any tree base. In each distance, we took triplicated soil samples at three different depth strata: 0–2.5, 2.5–5 and 5–10 cm. In each stratum we measured the root structure, sediment properties, and macrofaunal assemblage (Fig. 1b, c). Additionally, we characterized the microphytobenthos and macroalgae in both distances at the soil surface, and the aboveground forest structure in the entire plot.

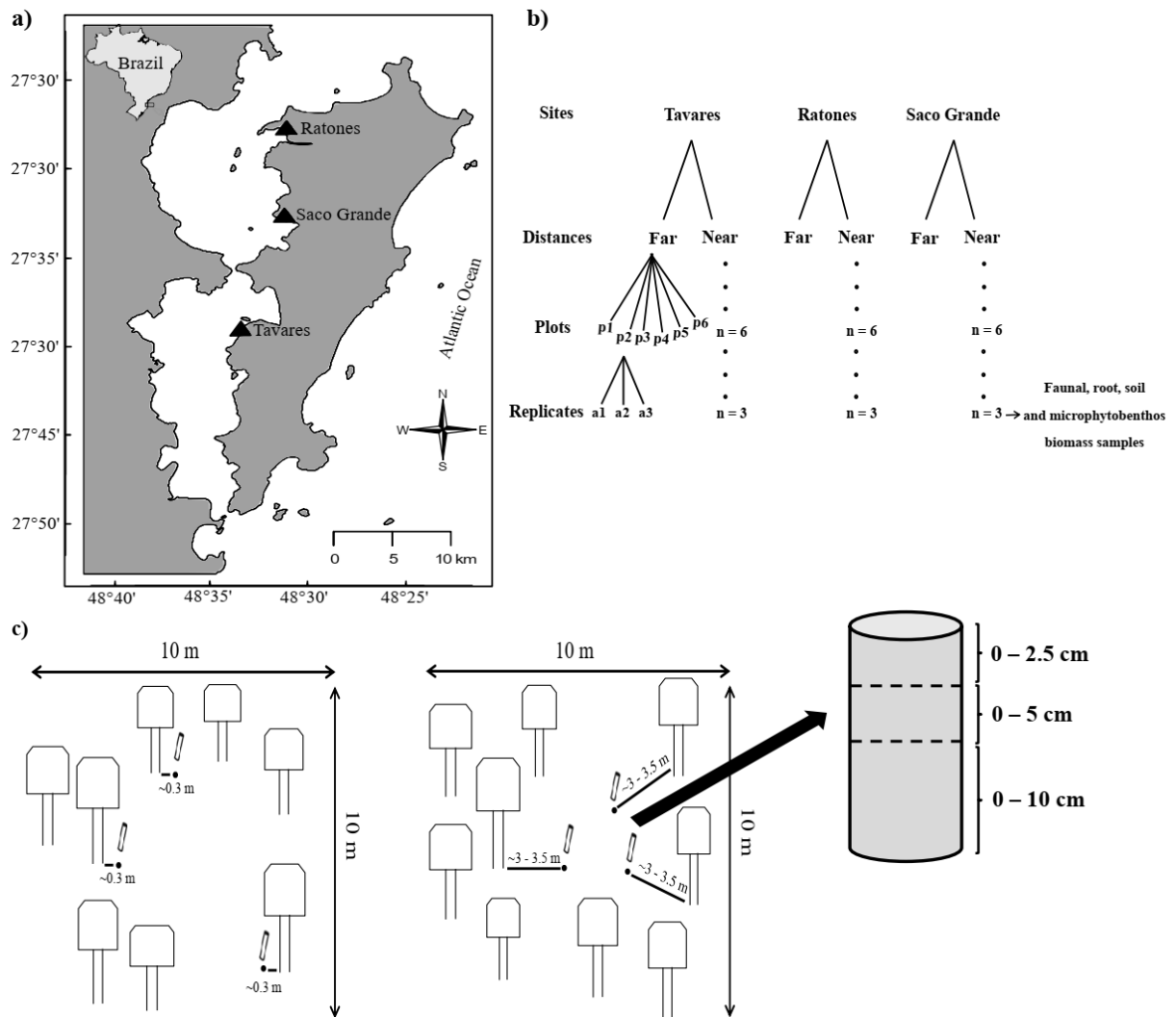


Fig. 1. a - Map of study area showing sampling sites (Tavares, Ratones, Saco Grande). b and c - Scheme of the experimental design and scales of spatial variability: Sites (Tavares, Ratones and Saco Grande), Distances (Far and Near), Plots (p1, p2, p3,p4, p5 and p6) and Replicates (a1, a2 and a3). The gray cylinder means sample core and its respective stratification.

### ***Sampling procedures for vegetation, algal and sediment parameters***

In each plot, the tree height (H; m), diameter at breast height (dbh; cm), tree density and basal area (m<sup>2</sup> ha<sup>-1</sup>) were measured (Cintrón and Schaeffer-Novelli, 1984). In each plot and distance, we also quantified the root size and biomass using three cores of 10 cm diameter and 10 cm height, stratified at 0–2.5, 2.5–5 and 5–10 cm. The samples were sieved in a 0.5 mm mesh and the remaining roots (live and dead) were separated and sorted into diameter classes: < 2 mm (fine roots), 2–5 mm (medium roots) and > 5 mm (coarse roots) (Castañeda-Moya et al., 2011). All root samples were subsequently oven dried at 60 °C (until constant mass), and the biomass (g m<sup>-2</sup>) of each diameter class was weighted in analytical scale (0.001 g; Quimis Q360).

Sample cores of 2.8 cm diameter and 11.5 cm height were carefully taken at each soil stratum used for root samples. The mud (clay + silt) fraction (%) and particle size (mm) were processed via dry sieving after homogenization of the samples (Suguo, 1973). Organic matter content (%) was measured after burning the dry soil particles in a muffle furnace at 550 °C for 4 hours (Howard et al., 2014). Bulk density (g cm<sup>-3</sup>) was calculated as the ratio between the dry mass (60 °C to a constant weight) of each sample by its total volume (SCS-USDA, 1972). In each plot and distance, three soil core samplers with an inner diameter of 1 cm and 1 cm height (~0.5 g) were collected from the soil surface for the analysis of the microphytobenthos (µg g<sup>-1</sup> sediment dry weight). The chlorophyll *a* and pheophytin were extracted from soil samples with 10 mL 100% acetone. After 24 h of darkness at -10 °C, the samples were centrifuged at 2500 rpm for 15 min, and the chlorophyll *a* and pheophytin contents were obtained using a spectrophotometer before and after acidification (1 mL of 1N of HCl; Lorenzen, 1967). In addition, three 0.6 x 0.6 m quadrat were used for the analysis of the algal cover (%).

### ***Sampling procedures for macrofauna***

In each plot and distance, three macrofaunal core samples of 10 cm diameter and 10 cm height stratified at 0–2.5, 2.5–5 and 5–10 cm were taken. These macrofaunal samples were measured from the same core samples used to describe the root size and biomass. The samples were then sieved *in situ* on 0.5 mm mesh and all material retained was fixed in 10% buffered formalin. Afterwards, the organisms were sorted and identified to the lowest possible taxonomic level under the microscope. The macrofaunal assemblage was described by the total density (ind m<sup>-2</sup>) and species richness. In order to evaluate the functional traits of the taxa, we



used Biological Traits Analysis (BTA). We chose only five traits mostly related to bioturbation and animal-mediated sediment processes. The selected traits were: feeding mode, body size (mm), bioturbation type, relative adult mobility in the sediment and depth penetration (cm). The five traits were then sub-divided into distinct categories (Supplementary Table S1) to show the existing variation of each functional trait (Jones and Frid, 2009). Standard fuzzy coding with scores ranging from 0 (no affinity) to 3 (total affinity) was applied to classify functional trait types of each taxon. Information on the selected traits were gathered from online databases Polytraits (Faulwetter et al., 2014) and BIOTIC (MarLIN, 2006), and specific literature (Jumars et al., 2015). The functional traits were calculated by the sum of the category codes multiplied by the density of each taxon and divided by their total density for each category and sample (Chevene et al., 1994). The five functional traits of the macrofauna were then used to calculate the functional diversity by the Rao's quadratic entropy index (RaoQ; Botta-Dukát, 2005). The index is a multi-trait measurement that covers the multivariate facets of the structure of the trait function. RaoQ is related to the functional differences between pairs of taxa, which is weighed by their relative abundance/density. This measure is considered robust, characterizes the similarity or complementarity of trait values within a community, and is widely used in different benthic marine environments (Laliberté and Legendre, 2010; Gusmao et al., 2016; van der Linden et al., 2017).

### ***Data analysis***

Firstly, to verify whether aboveground forest structure may be influencing the mangrove root patterns, we performed two-way analyses of variance (ANOVA) of tree height, dbh, tree density and basal area in two spatial scales: Site - random factor, with three levels (Tavares, Ratonas and Saco Grande) and Distance - fixed factor, with two levels. The aboveground forest structure analysis had the following linear model:

$$X = \mu + \text{Site} + \text{Distance} + \text{Site} \times \text{Distance} + \varepsilon,$$

where  $\mu$  is the overall mean,  $\varepsilon$  is the residual, and  $x$  is the 'crossed with' factors.

Similarly, variations in macrofaunal parameters (total density, species richness, functional diversity and selected taxa that corresponded to 85% of the total density of the samples), root (fine, medium and coarse root biomass) and sediment parameters (particle size, mud fraction, bulk density, organic matter content and microphytobenthos) were also evaluated

at distinct spatial scales in a mixed model ANOVA. The linear model included the factors: Site – random, with three levels (Tavares, Ratoles and Saco Grande); Distance – fixed, two levels (near and far from trunks); and Stratum – fixed, three levels (0–2.5, 2.5–5 and 5–10 cm). The linear model was:

$$X = \mu + \text{Site} + \text{Distance} + \text{Stratum} + \text{Site} \times \text{Distance} + \text{Distance} \times \text{Stratum} + \text{Site} \times \text{Stratum} + \text{Site} \times \text{Distance} \times \text{Stratum} + \text{Plot}(\text{Site} \times \text{Distance}) + (\text{Plot}(\text{Site} \times \text{Distance})) \times \text{Stratum} + \varepsilon.$$

where  $\mu$  is the overall mean,  $\varepsilon$  is the residual,  $\times$  is the ‘crossed with’ factors, and  $()$  is the ‘nested under’ factors.

The Stratum factor was not present in hierarchical ANOVAs of the microphytobenthos biomass (chlorophyll *a* and pheophytin) and algal cover. Thus, the linear model was:

$$X = \mu + \text{Site} + \text{Distance} + \text{Site} \times \text{Distance} + \text{Plot}(\text{Site} \times \text{Distance}) + \varepsilon.$$

where  $\mu$  is the overall mean,  $\varepsilon$  is the residual,  $\times$  is the ‘crossed with’ factors, and  $()$  is the ‘nested under’ factors.

Whenever necessary, the data were transformed (square root or  $\log(x+1)$ ) prior to analyses and tested for homogeneity of variances using Cochran’s C tests.

After assessing eventual faunal variations as a function of the stratum and the distance from the tree trunks, we analysed the relationship between the explanatory variables algal cover, root and sediment properties on the total density of the macrofauna, species richness, functional diversity and selected taxa, as response variables. We then applied Generalized Linear Mixed Models (GLMMs; Bolker et al., 2009) using the ‘lmer’ function with Gaussian distribution. The factors Site, Distance, Site  $\times$  Distance and Plot(Site  $\times$  Distance) were treated as a random effect in all GLMM analyses. Moreover, all models included the explanatory variables as a fixed effect to account for overall differences in response variables. Collinearity was checked with the variance inflation factor (VIF; Montgomery and Peck, 1992), and variables that had coefficients  $> 4$  were removed from the model (Zuur et al., 2009). A multimodel inference was then carried out to select a model that best fit our data (Burnham and Anderson, 2002). The best model was selected after running candidate models with Corrected Akaike information criterion (AICc) and AICc weights (AICcw) that were in turn used for model inference. The models with the lowest AICc values were selected and were used to get the model-averaged parameter estimates and their standard errors. We did not

conduct stepwise selection because it overestimates the effect size of significant explanatory variables and entails issues associated with model simplification (Harrison et al., 2018). In addition, the marginal  $R^2$  ( $R^2_m$ ; proportion of the variance explained only by fixed effects) and conditional  $R^2$  ( $R^2_c$ ; proportion of the variance explained by fixed and random effects) of the retained GLMMs were evaluated. Model validation was carried out through graphical observations in accordance to the protocol developed by Zuur et al. (2009). In order to equalize the size of matrices, we used in GLMMs, the average values among strata for: root biomass, particle size, mud fraction, bulk density, and organic matter in each plot.

All analyses were conducted in the R environment (R Core Team, 2019) using the ‘GAD’ (Sandrini-Neto and Camargo, 2012; ANOVAs), ‘vegan’ (Oksanen et al., 2013; functional diversity), ‘FD’ (Laliberté et al., 2014; functional diversity), ‘lme4’ (Bates et al., 2015; GLMM), ‘performance’ (Nakagawa et al., 2017; GLMM) and ‘MuMIn’ (Burnham and Anderson, 2002; GLMM) packages.

## Results

### *Spatial variability of vegetation, algal and sediment parameters*

As expected, the mangrove aboveground forest structure variables did not differ significantly (all ANOVA  $P > 0.05$ ) between sites, distances or interaction ‘Site x Distance’ (Table 1). The vegetation aboveground average values were  $8.20 \pm 1.19$  for tree height,  $0.14 \pm 0.04$  m for dbh,  $20.80 \pm 3.93$  m<sup>2</sup> ha<sup>-1</sup> for basal area and  $10.04 \pm 1.85$  for tree density.

Table 1. Summary of ANOVA for aboveground forest structure (tree height, diameter at breast height - DBH, tree density and basal area) variables.

Source	df	Tree height		DBH		Tree density		Basal area	
		MS	F	MS	F	MS	F	MS	F
<b>Site (Si)</b>	2	0.23	1.91 <sup>ns</sup>	2.28	1.15 <sup>ns</sup>	2.69	1.43 <sup>ns</sup>	32.79	1.64 <sup>ns</sup>
<b>Distance (Di)</b>	1	0.00	0.00 <sup>ns</sup>	4.47	2.25 <sup>ns</sup>	5.44	2.90 <sup>ns</sup>	0.72	0.04 <sup>ns</sup>
<b>Si x Di</b>	2	0.24	2.03 <sup>ns</sup>	0.53	0.27 <sup>ns</sup>	0.69	0.37 <sup>ns</sup>	30.09	1.51 <sup>ns</sup>
<b>Residuals</b>	30	0.12		1.99		1.88		19.97	

df = degree of freedom, MS = mean square, F= statistical value, ns = non-significant at  $p < 0.05$ .

Conversely, all other vegetation parameters varied at least in one studied spatial scale (Table 2; Fig. 2). We found considerable vertical and horizontal spatial differences for the coarse root biomass, which was significantly lower with increasing depth stratum and distance from the trunks. The fine root biomass substantially differed among distances, with the highest value in areas far from trunks. This parameter changed across sites ( $P < 0.001$ ), which reached lower values at Ratones. The fine root biomass had the greatest contribution in our study, accounting more than 80% of the total root biomass. Moreover, the medium root biomass varied significantly among strata.

Chlorophyll *a* varied significantly among distances. This parameter also showed significant differences among sites, showing higher values near trunks and in Tavares site. The algal cover and pheophytin were significantly higher at Tavares (Table 3; Fig. 3). The interaction ‘Plot(Site x Distance)’ also varied considerably for chlorophyll *a* and pheophytin. Most sediment properties (organic matter, bulk density, mud fraction and particle size) varied significantly between strata depending on the site (‘Site x Stratum’; Table 4, Fig. 4). Furthermore, organic matter, bulk density and particle size also showed significant spatial variability at the interaction ‘Site x Distance’.

Table 2. Summary of ANOVA for fine, medium and coarse root biomasses.

Source	df	Fine root		Medium root		Coarse root	
		MS	F	MS	F	MS	F
Site (Si)	2	8.54	13.44***	0.83	0.67 <sup>ns</sup>	7.3	1.8 <sup>ns</sup>
Distance (Di)	1	22.05	31.99*	0.34	0.09 <sup>ns</sup>	396.0	56.3*
Stratum (St)	2	0.07	0.30 <sup>ns</sup>	10.90	7.08*	306.5	147.4**
Si x Di	2	0.55	1.40 <sup>ns</sup>	1.71	1.19 <sup>ns</sup>	16.9	4.7 <sup>ns</sup>
Si x St	2	0.69	1.08 <sup>ns</sup>	3.68	2.98 <sup>ns</sup>	7.0	1.7 <sup>ns</sup>
Di x St	4	0.23	2.06 <sup>ns</sup>	1.54	1.51 <sup>ns</sup>	2.1	0.6 <sup>ns</sup>
Si x Di x St	4	0.39	3.47 <sup>ns</sup>	1.43	1.40 <sup>ns</sup>	3.5	1.0 <sup>ns</sup>
Pl(Si x Di)	30	0.63	4.62***	1.24	1.20 <sup>ns</sup>	4.1	0.9 <sup>ns</sup>
(Pl(Si x Di)) x St	60	0.11	0.82 <sup>ns</sup>	1.02	0.99 <sup>ns</sup>	3.5	0.8 <sup>ns</sup>
Residuals	216	0.14		1.03		4.2	

df = degree of freedom, MS = mean square, F = statistical value, Pl = Plot, ns = non-significant at \*p < 0.05, \*\*\*p < 0.001.

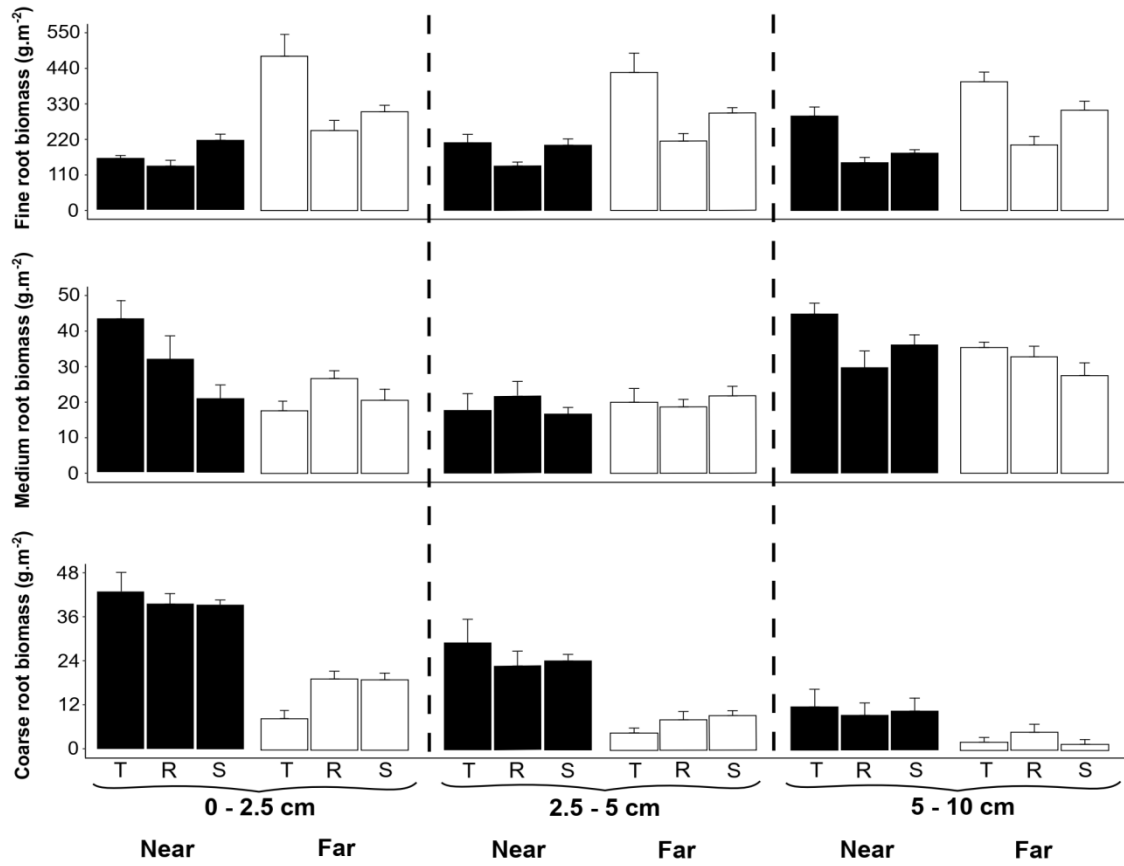


Fig. 2. Mean values ( $\pm$  SE) of the fine, medium and coarse root biomass among sites, distances and strata. T = Tavares, R = Ratones; S = Saco Grande.

Table 3. Summary of ANOVA for chlorophyll *a*, pheophytin and algal cover.

Source	df	Chlorophyll <i>a</i>		Pheophytin		Algal cover	
		MS	F	MS	F	MS	F
Site (Si)	2	130.6	57.8***	357.6	23.8***	2.7	45.7***
Distance (Di)	1	3.7	27.9*	124.6	8.6 <sup>ns</sup>	0.9	13.6 <sup>ns</sup>
Si x Di	2	0.1	0.1 <sup>ns</sup>	14.42	0.9 <sup>ns</sup>	0.1	1.2 <sup>ns</sup>
Pl(Si x Di)	30	2.3	3.4***	15.0	7.9***	0.1	1.2 <sup>ns</sup>
Residuals	72	0.7		1.9		0.1	

df = degree of freedom, MS = mean square, F = statistical value, Pl = Plot, ns = non-significant at \* $p < 0.05$ , \*\*\* $p < 0.001$ .

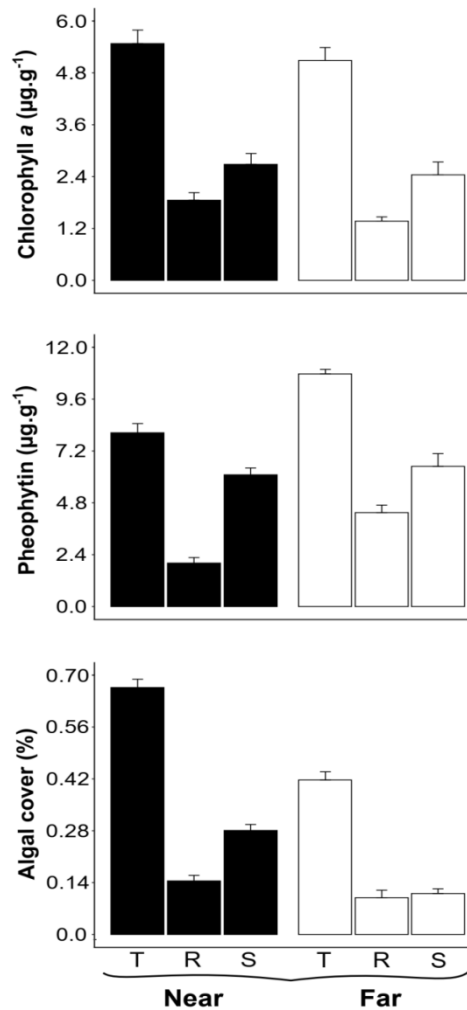


Fig. 3. Mean values ( $\pm$  SE) of the chlorophyll *a*, pheophytin and algal cover among sites and distances. T = Tavares, R = Ratonos; S = Saco Grande.

Table 4. Summary of ANOVA of organic matter, bulk density, mud fraction and particle size.

Source	df	Organic matter		Bulk density		Mud		Particle size	
		MS	F	MS	F	MS	F	MS	F
<b>Site (Si)</b>	2	3.43	71.99***	0.07	62.14***	0.18	5.98**	0.24	18.30***
<b>Distance (Di)</b>	1	2.83	9.35 <sup>ns</sup>	0.03	4.15 <sup>ns</sup>	0.001	0.03 <sup>ns</sup>	0.20	0.67 <sup>ns</sup>
<b>Stratum (St)</b>	2	0.20	4.39 <sup>ns</sup>	0.002	0.78 <sup>ns</sup>	0.06	2.39 <sup>ns</sup>	0.01	0.41 <sup>ns</sup>
<b>Si x Di</b>	2	0.30	6.37**	0.008	6.96**	0.03	1.15 <sup>ns</sup>	0.30	23.04***
<b>Si x St</b>	4	0.05	2.62*	0.002	5.54***	0.02	7.82***	0.02	5.52***
<b>Di x St</b>	2	0.12	8.24*	0.001	1.43 <sup>ns</sup>	0.004	0.98 <sup>ns</sup>	0.01	0.93 <sup>ns</sup>
<b>Si x Di x St</b>	4	0.01	0.81 <sup>ns</sup>	0.001	1.67 <sup>ns</sup>	0.004	1.13 <sup>ns</sup>	0.01	3.24 <sup>ns</sup>
<b>Pl(Si x Di)</b>	30	0.05	3.31***	0.001	4.60***	0.03	11.86***	0.01	3.43***
<b>(Pl(Si x Di)) x St</b>	60	0.02	1.22 <sup>ns</sup>	0.001	1.62**	0.003	1.36 <sup>ns</sup>	0.004	1.06**
<b>Residuals</b>	216	0.01		0.001		0.002		0.003	

df = degree of freedom, MS = mean square, F = statistical value, Pl = Plot, ns = non-significant at \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.



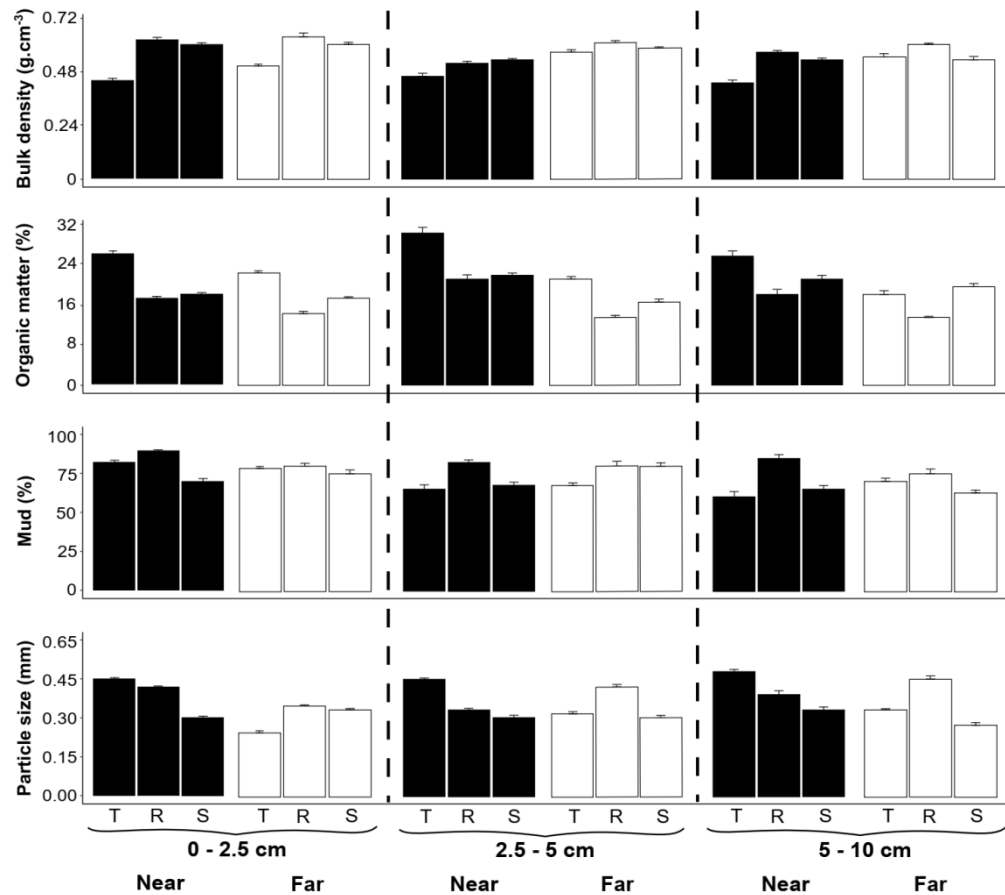


Fig. 4. Mean values ( $\pm$  SE) of the bulk density, organic matter, mud and particle size among sites, distances and strata. T = Tavares, R = Ratones; S = Saco Grande.

### *Spatial variability of macrofaunal assemblages*

The macrofaunal assemblage was only represented by 11 taxa and dominated by polychaetes (52%) and oligochaetes (45%). The dominant taxa were the polychaetes *Capitella nonatoi*, *Laeonereis acuta*, *Dipolydora socialis* and the oligochaete *Marionina* spp., corresponding to about 85% of the total density of the fauna (Supplementary Table S2). Only four taxa (*Marionina* spp., *C. nonatoi*, *L. acuta* and *D. socialis*) occurred in the deepest layer (5 - 10 cm) of the sediment. All the taxa were dominant at near trunks (all > 65%) than far from trunks.

Contrary to our hypothesis, total density, species richness and functional diversity were significantly higher near trunks (Table 5; Fig. 5). There was significant difference

among strata for functional diversity, which considerably decreased with stratum. The total density and species richness showed that differences between strata depended on the site ('Site x Stratum'). Considerable vertical spatial difference was found for the densities of *L. acuta* and *D. socialis*, which were substantially higher in upper (0 - 2.5 and 2.5 - 5 cm) than in deeper (5 - 10 cm) strata. The densities of *Marionina* spp. and *C. nonato*i were significantly higher near than far from trunks (Table 5; Fig. 6). Thus, these organisms displayed spatial variability in the distance factor. The interaction 'Site x Stratum' also differed considerably for the density of *C. nonato*i.

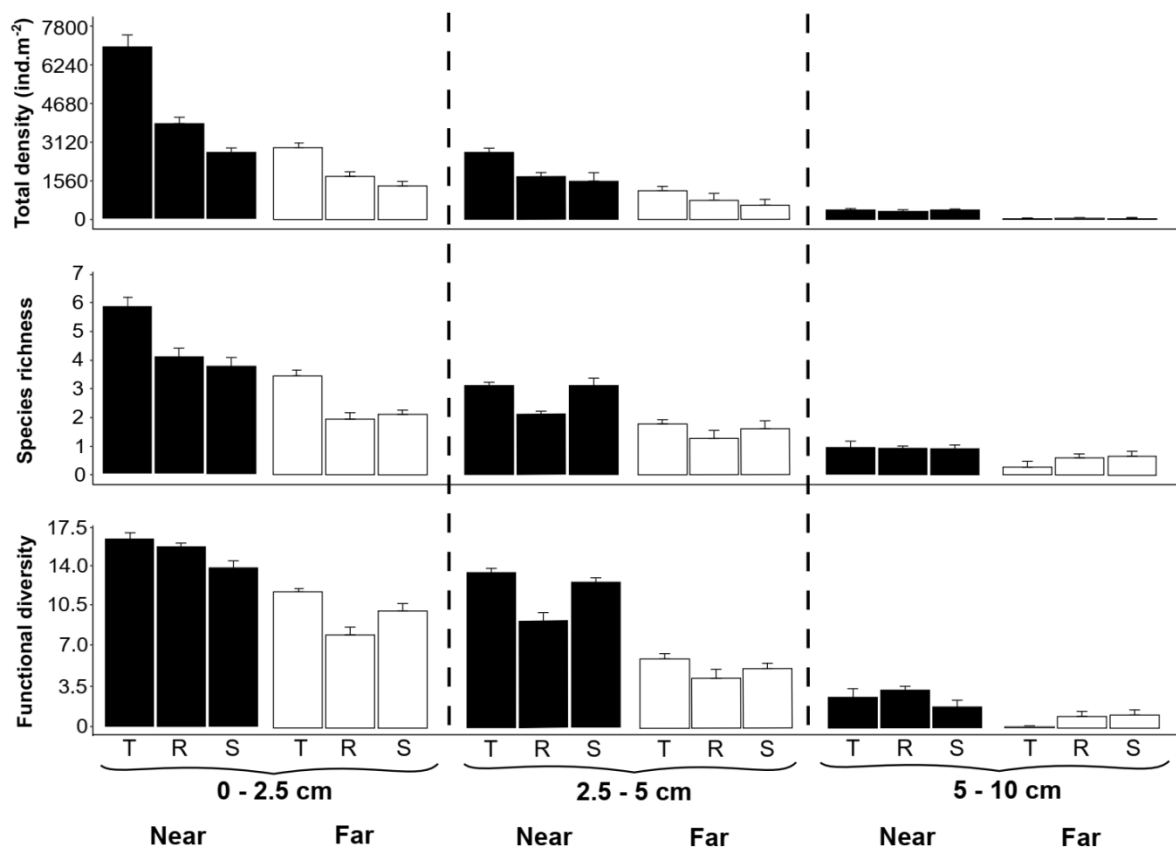


Fig. 5. Mean values ( $\pm$  SE) of the total density, species richness and functional diversity among sites, distances and strata. T = Tavares, R = Ratones; S = Saco Grande.

Table 5. Hierarchical ANOVA of total density, species richness, functional diversity, *Marionina* spp., *Capitella nonatoi*, *Laeonereis acuta* and *Dipolydora socialis*.

Source	df	Total density		Species richness		Functional diversity		<i>Marionina</i> spp.		<i>Capitella nonatoi</i>		<i>Laeonereis acuta</i>		<i>Dipolydora socialis</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Site (Si)	2	13.9	2.7 <sup>ns</sup>	1.3	3.3 <sup>ns</sup>	0.5	0.6 <sup>ns</sup>	72.0	5.6 <sup>**</sup>	35.4	3.8 <sup>*</sup>	32.4	4.5 <sup>*</sup>	6.4	0.8 <sup>ns</sup>
Distance (Di)	1	262.1	148.9 <sup>**</sup>	19.7	1141.7 <sup>***</sup>	21.8	38.2 <sup>*</sup>	99.6	46.5 <sup>*</sup>	171.5	22.7 <sup>*</sup>	150.5	9.5 <sup>ns</sup>	128.9	5.8 <sup>ns</sup>
Stratum (St)	2	557.5	57.7 <sup>**</sup>	38.1	32.2 <sup>**</sup>	51.1	49.7 <sup>**</sup>	211.8	9.7 <sup>*</sup>	545.1	15.3 <sup>*</sup>	205.5	18.9 <sup>**</sup>	105.2	18.7 <sup>**</sup>
Si x Di	2	1.8	0.3 <sup>ns</sup>	0.02	0.04 <sup>ns</sup>	0.5	0.7 <sup>ns</sup>	2.1	0.2 <sup>ns</sup>	7.5	0.8 <sup>ns</sup>	15.8	2.2 <sup>ns</sup>	22.1	2.9 <sup>ns</sup>
Si x St	4	9.7	3.4 <sup>*</sup>	1.2	5.8 <sup>**</sup>	1.0	2.3 <sup>ns</sup>	21.8	4.3 <sup>*</sup>	35.6	6.6 <sup>***</sup>	10.9	1.7 <sup>ns</sup>	5.6	1.5 <sup>ns</sup>
Di x St	2	3.5	1.4 <sup>ns</sup>	0.3	4.5 <sup>ns</sup>	1.4	2.4 <sup>ns</sup>	12.4	0.7 <sup>ns</sup>	24.8	4.2 <sup>ns</sup>	15.3	4.6 <sup>ns</sup>	18.6	1.8 <sup>ns</sup>
Si x Di x St	4	2.5	0.9 <sup>ns</sup>	0.07	0.3 <sup>ns</sup>	0.6	1.2 <sup>ns</sup>	18.1	3.5 <sup>ns</sup>	5.9	1.1 <sup>ns</sup>	3.3	0.5 <sup>ns</sup>	10.2	2.8 <sup>ns</sup>
Pl(Si x Di)	30	5.1	1.4 <sup>ns</sup>	0.4	1.9 <sup>**</sup>	0.8	2.2 <sup>***</sup>	12.8	1.7 <sup>*</sup>	9.3	1.8 <sup>*</sup>	7.2	1.3 <sup>ns</sup>	7.6	1.6 <sup>*</sup>
(Pl(Si x Di)) x St	60	2.8	0.8 <sup>ns</sup>	0.2	0.9 <sup>ns</sup>	0.4	1.2 <sup>ns</sup>	5.1	0.7 <sup>ns</sup>	5.4	1.0 <sup>ns</sup>	6.2	1.1 <sup>ns</sup>	3.7	0.8 <sup>ns</sup>
Residuals	216	3.7		0.2		0.4		7.3		5.2		5.4		4.7	

df = degree of freedom, MS = mean square, F= statistical value, Pl = Plot, ns = non-significant at \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.

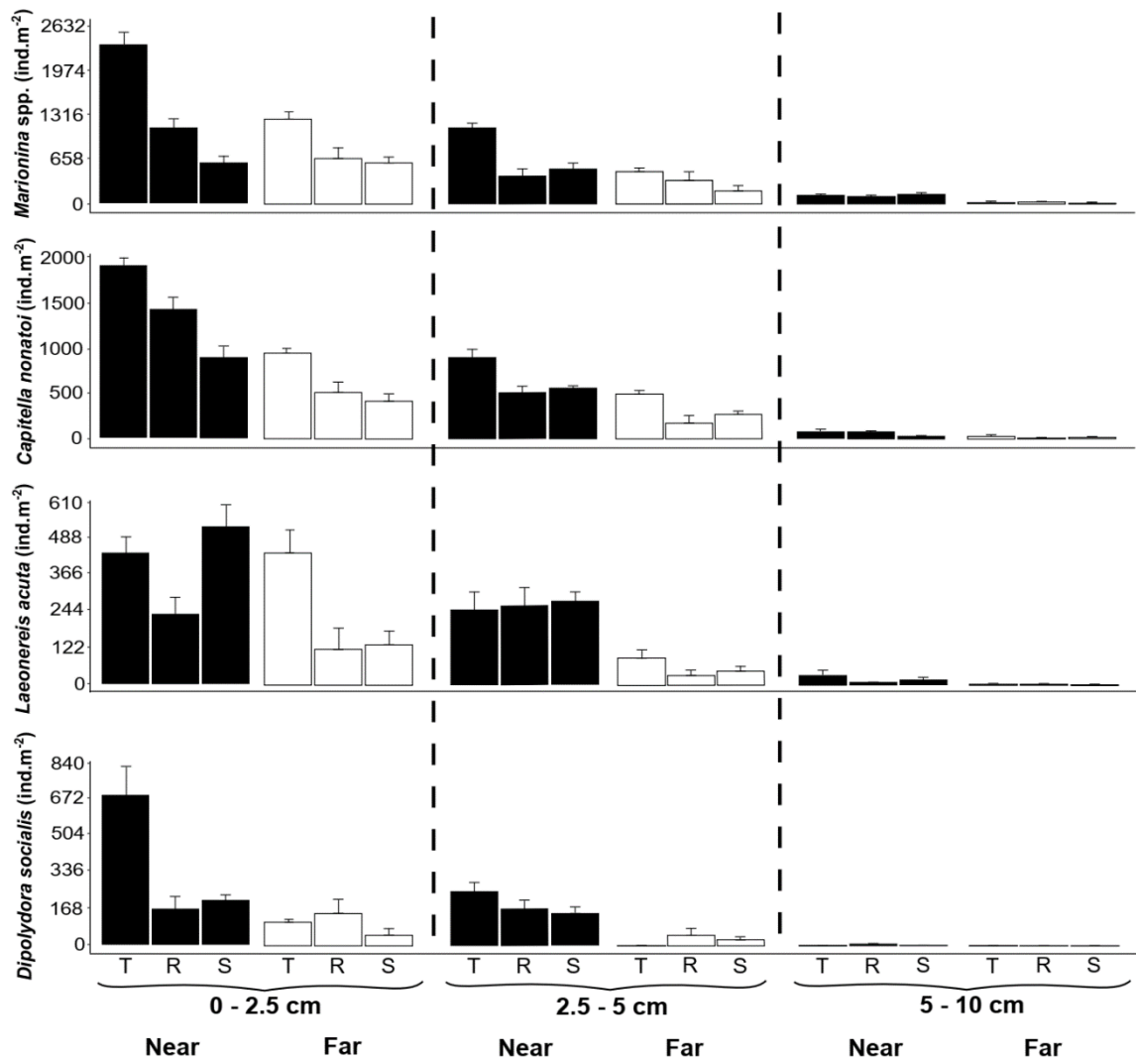


Fig. 6. Mean values ( $\pm$  SE) of the total densities of *Marionina* spp., *Capitella nonatoi*, *Laeonereis acuta* and *Dipolydora socialis* among sites, distances and strata. T = Tavares, R = Ratones; S = Saco Grande.

***Relationship between macrofaunal assemblages and algal cover, root and sediment parameters***

The GLMMs showed that root parameters (fine, medium and coarse root biomass) had more influence on all mangrove macrofaunal parameters after selection of the best models using multimodel inference (Table 6, Supplementary Table S3). The fine root biomass had the higher association with macrofauna, which this parameter appeared in all seven models of this study. The coarse root biomass also showed great influence on benthic assemblages, appearing in 5 out of 7 models. The organic matter was the only sediment parameter related with macrofaunal parameters, which appeared in 3 out of 7 models. Model-averaged parameters showed that coarse root biomass, medium root biomass and organic matter variables were positively associated with macrofaunal assemblage. On the other hand, fine root biomass had negative effects on these assemblages. The AICcw for the total density (0.46) of the macrofauna presented the highest values when compared to other models. The conditional  $R^2$  for total density of the macrofauna (0.72), species richness (0.73) and functional diversity (0.65) had the highest values in this analysis. In addition, the marginal  $R^2$  presented the greatest values for the densities of *Marionina* spp. (0.23) and *D. socialis* (0.19). Parameter estimates of most of the models showed that the fixed effects (explanatory variables) were statistically significant ( $P < 0.05$ ). Our final models indicated a normal distribution according to the model validation (Supplementary Fig. S1).

Table 6. Results of GLMM estimating selected explanatory variables on different faunal parameters. \*  $p < 0.05$ ;

Response variable	Best model	AIC <sub>c</sub>	AIC <sub>cw</sub>	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>
Total density	coarse root biomass* + (- fine root biomass)*	951.3	0.46	0.14	0.72
Species richness	coarse root biomass* + (- fine root biomass)*	403.4	0.40	0.18	0.73
Functional diversity	coarse root biomass* + (- fine root biomass) <sup>ns</sup>	503.0	0.32	0.12	0.65
<i>Marionina</i> spp	organic matter* + (-fine root biomass)* + coarse root biomass*	926.6	0.24	0.23	0.51
<i>Capitella nonatoi</i>	coarse root biomass* + (-fine root biomass)* + organic matter* + medium root biomass*	886.5	0.39	0.17	0.56
<i>Laonereis acuta</i>	coarse root biomass* + (-fine root biomass)*	860.9	0.30	0.14	0.50
<i>Dipolydora socialis</i>	(-fine root biomass)* + organic matter <sup>ns</sup>	830.7	0.23	0.19	0.43

\*  $p < 0.05$ ; - negative effect; + positive effect

## Discussion

Our results generally showed that the mangrove root parameters and associated macrofauna changed according to the distance to the tree trunks and depth stratum. The macrofaunal assemblages and coarse root biomass increased in near trunks and shallower layers, while fine root biomass was higher far from trunks and indifferent with the stratum. The higher fine root biomass away from trunks may be related to its fast growth rate and less sensitive to distance from the tree base (Komiya et al., 1987; Joslin et al., 2006). Furthermore, this pattern of increasing fine root biomass with the distance from trunks opposed previous studies (Komiya et al., 2000; Tamoo et al., 2008; Adame et al., 2017), because when away from trunks the large mass of fine roots may belong to different trees in a plot. Mature mangrove forests with higher tree density tend to display closely spaced trees (Cintrón and Schaeffer Novelli, 1984) like this study and other mangroves (Leung, 2015a; Leung and Tam, 2013), increasing both fine root biomass in the top soil layers and the difficulties of association to a specific tree (Njana et al., 2015). The massive fine root systems are mainly composed by feeding roots originated from the subterranean portion of pneumatophores and anchor roots, respectively (Tomlinson, 2016; Fig. 7). These root structures limit the habitat microspace in the sediment and affect macrofaunal assemblages due to increases in compaction (Morrisey et al., 2003; Kristensen and Kostka, 2005) and reduction in sediment moisture, temperature and microbial density (Lang'at et al., 2014; Cambi et al., 2015). The reduced interstitial space also inhibits the presence of predators and benthic organisms with more complex body plans (e.g. well-developed parapodia and tentacles; Leung, 2015b; Freitas and Pagliosa, 2020) and hampers their burrowing, locomotion, bioturbation and feeding activities (Alfaro, 2010; Sweetman et al., 2010). Thus, most species with different functional characteristics occurred near trunks, where there are reductions in fine roots, high proportions of coarse roots and a less cohesive substratum, providing more niches and microhabitats (Demopoulos and Smith, 2010). The coarse roots are mainly composed by cable roots that grow long horizontal distances in subsurface layers, from which anchor roots (similar to our medium roots; Fig. 7) originate (Tomlinson, 2016). These habitats with higher proportions of coarse roots favor the presence of benthic taxa with distinct feeding modes, such as suspension feeders, predators, deposit feeders and grazers. The diversity of niches and habitats also promotes species coexistence through higher resource partitioning and spatial segregation of potentially competing macrofaunal organisms

(Giller, 1996; Ettema and Wardle, 2002). Therefore, the discrepancies in other studies concerning the positive or negative effects of the mangrove root biomass on macrofauna (e.g. Wada et al., 1987; Leung, 2015a; Checon et al., 2017) might be a consequence of disregarding the distance from trunks in these relationships.

Despite displaying simpler body plans and cylindrical forms that could favor the occurrence within high density of fine roots, our results showed that *Marionina* spp. and *Capitella nonatoi* had their density increased in areas with lower proportions of fine root biomass (i.e. near trunks). Moreover, the high dominance of these two taxa (nearly 65% of the total density) in this study is related to their rapid growth, with ability to recruit throughout much of the year using multiple modes of reproduction (Tsutsumi et al., 1990; Giere, 2006). On the contrary, *Laeonereis acuta* and *Dipolydora socialis* showed indifferent preferences regarding the distance from tree trunks. The two faunal species are responding to other factors, such as depth strata, which they were mainly restricted to surface layers.

The topsoil may also be considered as a key component for the vertical patterns of distribution, offering favorable conditions to the structural and functional development of the mangrove macrofauna. This has been a recurrent pattern in mangroves (Wada et al., 1987; Kumar, 1997; Cheng and Chang, 1999), although not considering the effects of the distance from trunks on the macrofaunal distribution. Thus, our study has complemented that the macrofauna have higher preference to develop in surface layers of near trunks plots. In general, the more superficial, the more organisms are found. The upper stratum (0 - 2.5 cm) concentrated the higher densities for all taxa, which decreased rapidly towards lower strata (2.5 - 5 and 5 - 10 cm). Besides more oxygenated, the food availability is known to be higher in shallower than in deeper layers, with more decomposition and subsequent palatable detritus production for fauna (Alongi, 1994; Kumar, 2002). Most part of this palatable vegetative material for macrofaunal assemblages is driven by the decomposition of the fine roots, due to their high proportions in the soil and shorter lifespan compared to other root components (Joslin et al., 2006; Komiyama et al., 2008). Thus, the upper stratum generates looser packing of sediments, which provides less resistance for faunal burrowing, feeding and locomotion (Moy and Levin, 1991). These characteristics in surface sediments benefited organisms like *Laeonereis acuta* and *Dipolydora socialis*, since their distinct lifestyles and elaborate structures in the body (e.g. use their palps to select suspended food particles; Jumars et al., 2015) hamper their successful development in lower layers.



Regardless of the mangrove site, our results highlighted that the root structures had higher influence on macrofaunal patterns than sediment properties. Although Chapman and Tolhurst (2004) and Tolhurst et al. (2010) did not directly include root parameters in their analyses, they also showed similar patterns to our study, meaning that sediment properties did not influence the mangrove macrofauna. The importance of the sediment to the establishment of structural and functional patterns of mangrove macrofauna has long been recognized (Kumar, 1997, 2002; Thilagavathi et al., 2013). However, we did not find this faunal association for most sediment variables, due to the small spatial scale assumed for this study. Organic matter was the sediment parameter that most contributed to increases in the total density of mangrove fauna, and is in general positively related with food resources, which into the mangroves is mainly composed by dead fine roots (Komiyama et al., 2008; Li et al., 2017). On the other hand, excessive organic matter may decrease species richness and favor the dominance of opportunistic species, such as the capitellid *C. nonatoi* and the oligochaete *Marionina* spp., due to increases in sulfide and oxygen deficiency (Magni et al., 2015). Capitellids and oligochaetes succeed in the presence of high organic matter contents and in turn fulfill their high metabolic demands, besides being able to cope with hypoxic soils (Giere, 2006; Jumars et al., 2015). Unlike the mangrove macrofauna of our study, with horizontal and vertical distributions more directly associated to root patterns, the invertebrate communities of terrestrial environments display a higher dependence of the soil conditions. The structure and function of terrestrial invertebrates' species respond differently to distance and stratum, due to their distinct preferences for sediment properties. They may be influenced by soil acidity, aggregation, texture, moisture, heavy metals content, organic matter and temperature (Scheu and Poser, 1996; Rhoades, 1997; Józwiak et al., 2013).

We showed that the aboveground forest structure did not directly influence the structure and function of macrofaunal assemblages. This suggests that the kind of sampling design we established was well succeeded, because the mangrove forest structure parameters did not vary among sites and distances. The choice of mangrove stands with similar hydroperiod and composed only by one tree species (*A. schaueriana*) may also have reduced the discrepancies in our results. It is known that the root biomass and its size change with tree species (Tamooh et al., 2008) and frequency of tidal inundation (Castañeda-Moya et al., 2011). Each mangrove tree species has different root components, as well as their distribution in the soil (Tomlinson, 2016). For instance, *Rhizophora* trees develop some root types (e.g. prop roots) different from *Avicennia* trees, and these differences may, in turn, affect their

surrounding sediment texture and deposition (Phillips et al., 2017). Moreover, mangrove forests stands with less frequency of tidal flooding become the soil more compacted for fauna and roots (Morrisey et al., 2003; Leung, 2015a). Thus, if we had not controlled those factors, they would have contributed to variations in the distribution of roots and macrofaunal patterns among mangrove forests.

Our analyses showed the significant effects of variations along root systems at a few meters scale on the macrobenthic fauna of mangroves, a pattern commonly found in other marine benthic environments (Morrisey et al., 1992; Underwood and Chapman, 1998; Tolhurst and Chapman, 2007). This means that the structure and function of the mangrove macrofauna had higher contribution at very small (i.e. distance from the trunks and stratum) than at local spatial scales (i.e. sites). The macrofaunal differences were clearly reflected by the differences in root size and biomass distribution. Therefore, the complexity of mangrove root systems generated small-scale habitats for the macrofauna. The higher contribution of macrofaunal assemblages at these smallest spatial scales may also be caused by recruitment, dispersal, mortality, refuge from predators, food resources and sediment deposition (Chapman and Tolhurst, 2007; Tolhurst et al., 2010), which can change depending on the proportion of the root size and biomass.

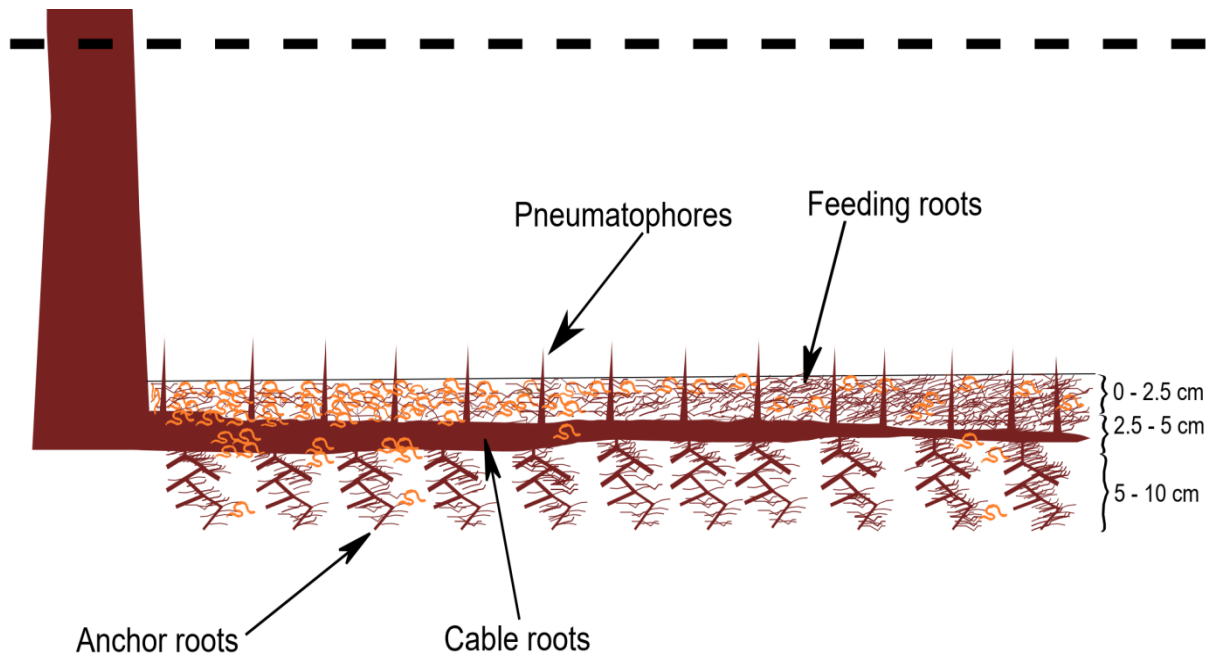


Fig. 7. Schematic representation of the distribution of the complex root system and macrofaunal assemblages occurred in this study.

## Conclusions

Our work highlights that the structure and function of macrofaunal assemblages varied both horizontally according to the distance from trunks and along the vertical strata, which were linked to changes in the complexity of root systems, represented by variations in coarse and fine roots. Future studies on near-trunk patterns of dispersion of benthic organisms are still needed to confirm if these faunal patterns apply to other mangrove forests worldwide, since this is the first study to assess the influence of the distance from trunks on the benthic fauna. We also showed that macrofaunal sampling up to 5 cm of depth stratum is sufficient within mangrove forests. Nevertheless, these findings may directly affect monitoring and conservation management strategies in mangroves, because most studies do not indicate where (near or far from the trunks) the samples are collected. For instance, the selective sampling of more easily penetrable areas to coring devices can underestimate species richness, and other structural components of the habitat. Future sampling designs should take

into consideration and incorporate the small-scale horizontal and vertical variability of the mangrove roots and associated macrofauna.

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## SUPPLEMENTS

**Supplementary Table S1.** Functional traits of the macrofaunal assemblages and associated categories.

<b>Trait</b>	<b>Number</b>	<b>Category</b>
Feeding mode	1	Deposit-feeder
	2	Suspension-feeder
	3	Oportunist/Scavenger
	4	Grazer
	5	Predator/Carnivore
Body size	1	≤ 5 mm
	2	5 - 10 mm
	3	10 - 20 mm
	4	20 - 40 mm
	5	40 - 80 mm
	6	80 - 160 mm
Bioturbation mode	1	None
	2	Biodiffuser (François et al., 1997)
	3	Gallery-difuser (Michaud et al., 2005)
	4	Upward-conveyor (François et al., 1997)
	5	Downard-conveyour (François et al., 1997)
	6	Bio-irrigator (Chennu et al., 2015)
Relative adult mobility	1	None
	2	Low
	3	Medium
	4	High
Depth in the sediment	1	Surface
	2	0 - 3 cm
	3	3 - 8 cm
	4	8 - 15 cm
	5	15- 25 cm
	6	> 25 cm

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Supplementary table S2. Mean density of each mangrove benthic taxa among sites, distances and plots.

Site	Tavares	Tavares	Tavares	Tavares	Tavares	Tavares
Distance	Near	Near	Near	Near	Near	Near
Plot	p1	p2	p3	p4	p5	p6
<i>Marionina</i> spp	3858	1678	4827	1117	3778	5628
<i>Capitella nonatoi</i>	4492	2393	4020	3012	2628	4550
<i>Alitta succinea</i>	0	513	183	187	350	0
<i>Laeonereis acuta</i>	358	550	1317	283	867	467
<i>Heteromastus similis</i>	1158	350	550	1092	700	867
<i>Dipolydora socialis</i>	803	450	1271	0	842	233
<i>Isolda pulchella</i>	117	333	67	0	0	67
<i>Manayunkia brasiliensis</i>	50	133	67	173	167	717
<i>Monokaliapseudes schubartii</i>	407	413	167	173	167	483
<i>Sigambra grubii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	0	0	0	33	0	0
Site	Tavares	Tavares	Tavares	Tavares	Tavares	Tavares
Distance	Far	Far	Far	Far	Far	Far
Plot	p1	p2	p3	p4	p5	p6
<i>Marionina</i> spp	3552	2939	2100	1450	1763	1461
<i>Capitella nonatoi</i>	1283	1217	1283	517	433	1217
<i>Alitta succinea</i>	0	325	217	117	150	67
<i>Laeonereis acuta</i>	233	142	0	123	225	117
<i>Heteromastus similis</i>	167	0	133	0	100	0
<i>Dipolydora socialis</i>	567	300	550	83	297	167
<i>Isolda pulchella</i>	0	58	50	0	147	50
<i>Manayunkia brasiliensis</i>	0	367	0	0	0	150
<i>Monokaliapseudes schubartii</i>	267	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	133	0	100
<i>Heleobia australis</i>	0	0	0	0	0	0
Sites	Ratones	Ratones	Ratones	Ratones	Ratones	Ratones
Distances	Near	Near	Near	Near	Near	Near
Plot	p1	p2	p3	p4	p5	p6
<i>Marionina</i> spp	2750	4683	4556	2333	1590	2799
<i>Capitella nonatoi</i>	1958	1200	1900	1417	600	2017
<i>Alitta succinea</i>	117	0	133	0	0	0
<i>Laeonereis acuta</i>	117	467	0	0	83	200
<i>Heteromastus similis</i>	167	300	717	267	150	0
<i>Dipolydora socialis</i>	483	567	911	0	0	0
<i>Isolda pulchella</i>	0	0	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	167	0	0	0	0

<i>Monokaliapseudes schubartii</i>	227	300	130	133	53	207
<i>Sigambra grubii</i>	0	167	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	33	0
<b>Site</b>	Ratones	Ratones	Ratones	Ratones	Ratones	Ratones
<b>Distance</b>	Far	Far	Far	Far	Far	Far
<b>Plot</b>	p1	p2	p3	p4	p5	p6
<i>Marionina spp</i>	1250	2222	1342	2638	435	344
<i>Capitella nonatoi</i>	233	305	620	950	75	399
<i>Alitta succinea</i>	67	133	0	0	0	0
<i>Laeonereis acuta</i>	179	1063	106	0	60	0
<i>Heteromastus similis</i>	100	383	450	0	0	0
<i>Dipolydora socialis</i>	0	67	0	0	0	0
<i>Isolda pulchella</i>	0	0	0	0	0	0
<i>Manayunkia brasiliensis</i>	0	0	0	0	50	0
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	33	0	0	0	0	0
<b>Site</b>	Saco Grande	Saco Grande	Saco Grande	Saco Grande	Saco Grande	Saco Grande
<b>Distance</b>	Near	Near	Near	Near	Near	Near
<b>Plot</b>	p1	p2	p3	p4	p5	p6
<i>Marionina spp</i>	1279	976	827	2194	2284	2500
<i>Capitella nonatoi</i>	1060	1168	967	967	708	1157
<i>Alitta succinea</i>	377	193	183	200	100	83
<i>Laeonereis acuta</i>	968	486	577	233	375	527
<i>Heteromastus similis</i>	100	167	350	483	150	307
<i>Dipolydora socialis</i>	371	510	800	217	200	553
<i>Isolda pulchella</i>	0	93	0	0	0	77
<i>Manayunkia brasiliensis</i>	0	227	100	0	0	222
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	123	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	0
<b>Site</b>	Saco Grande	Saco Grande	Saco Grande	Saco Grande	Saco Grande	Saco Grande
<b>Distance</b>	Far	Far	Far	Far	Far	Far
<b>Plot</b>	p1	p2	p3	p4	p5	p6
<i>Marionina spp</i>	110	213	446	1047	1196	1551
<i>Capitella nonatoi</i>	125	117	242	557	792	832
<i>Alitta succinea</i>	73	50	0	0	117	103
<i>Laeonereis acuta</i>	253	285	0	318	375	200
<i>Heteromastus similis</i>	0	0	0	0	200	97
<i>Dipolydora socialis</i>	0	167	0	138	0	63
<i>Isolda pulchella</i>	0	0	0	0	0	0

<i>Manayunkia brasiliensis</i>	73	83	167	0	0	0
<i>Monokaliapseudes schubartii</i>	0	0	0	0	0	0
<i>Sigambra grubii</i>	0	0	0	0	0	0
<i>Heleobia australis</i>	0	0	0	0	0	0

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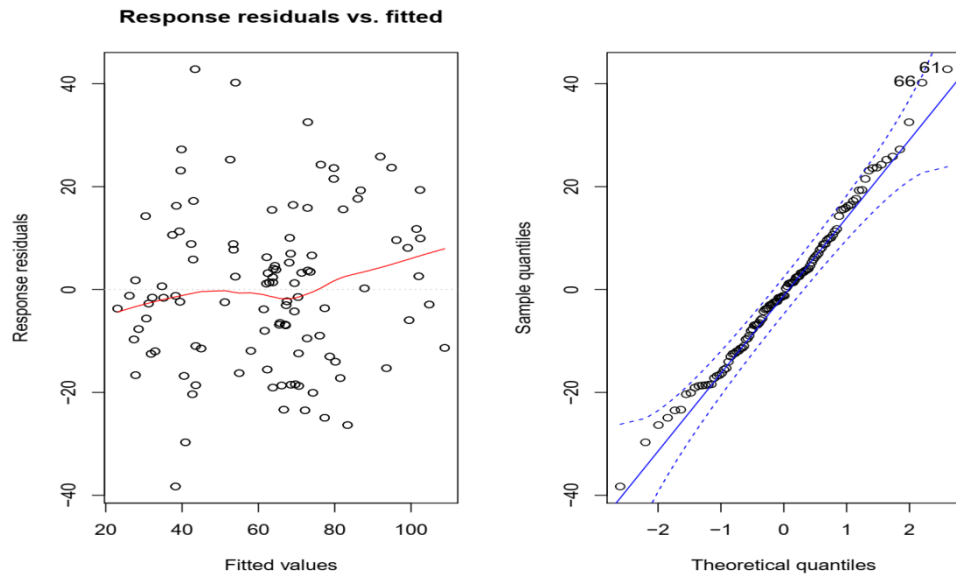
**Supplementary Table S3.** Model-averaged parameters of GLMM of each variable. Bold numbers indicate significant terms ( $p < 0.05$ ); SE = standard error; OM = organic matter, frb = fine root biomass, mrb = medium root biomass, crb = coarse root biomass. The p-values  $<0.05$  are shown in bold.

Response variable	Fixed effect	Estimate	SE	p
Total density	crb	1.25	0.92	<b>0.01</b>
	frb	-0.46	0.37	<b>0.04</b>
Species richness	crb	0.09	0.05	<b>0.01</b>
	frb	-0.03	0.02	<b>0.04</b>
Functional diversity	crb	0.20	1.20	<b>0.03</b>
	frb	-0.12	0.11	0.10
<i>Marionina</i> spp.	OM	9.89	5.27	<b>0.009</b>
	frb	-0.66	0.36	<b>0.02</b>
	crb	1.24	0.95	<b>0.01</b>
<i>Capitella nonatoi</i>	crb	3.61	4.88	<b>0.008</b>
	frb	-0.67	0.29	<b>0.001</b>
	OM	1.49	0.76	<b>0.03</b>
	mrb	1.21	0.62	<b>0.04</b>
<i>Laeonereis acuta</i>	crb	0.94	0.11	<b>0.01</b>
	frb	-0.43	0.09	<b>0.03</b>
<i>Dipolydora socialis</i>	frb	-0.82	0.44	<b>0.001</b>
	OM	2.45	1.06	0.28

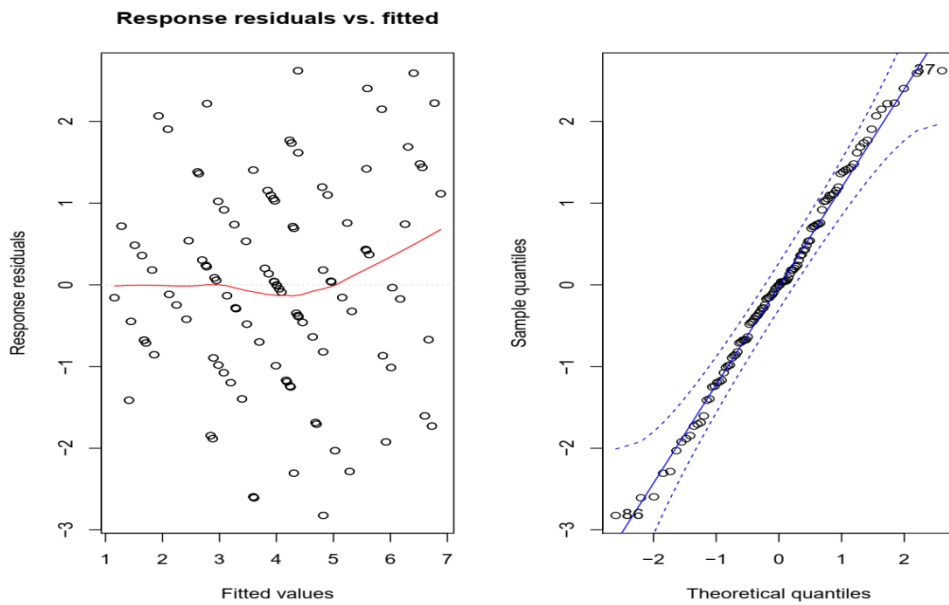


**Figure S1.** Model validation of total density (a), species richness (b), functional diversity (c), *Marionina* spp. (d), *Capitella nonatoi* (e), *Laonereis acuta* (f) and *Dipolydora socialis* (g).

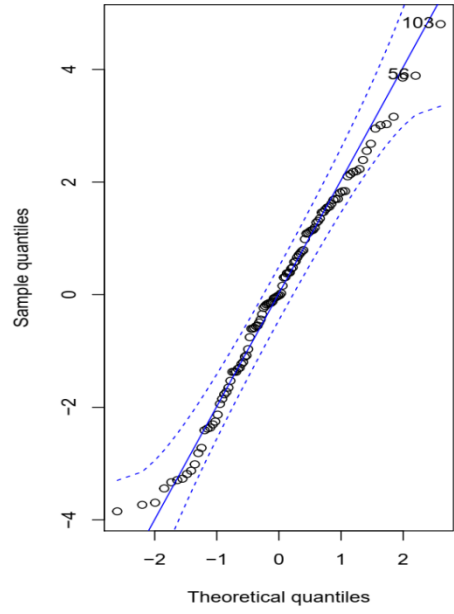
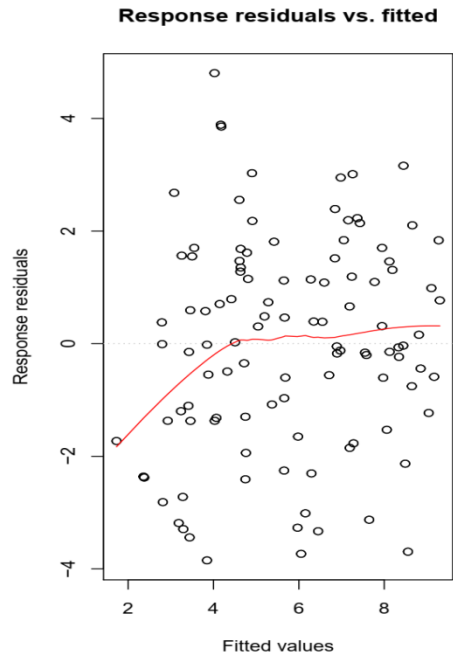
a)



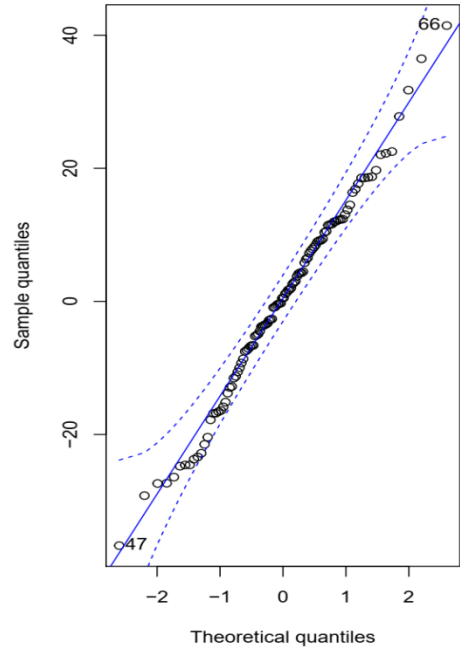
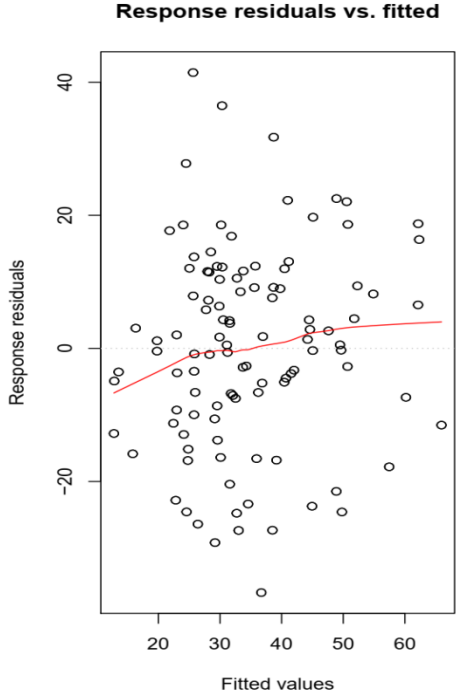
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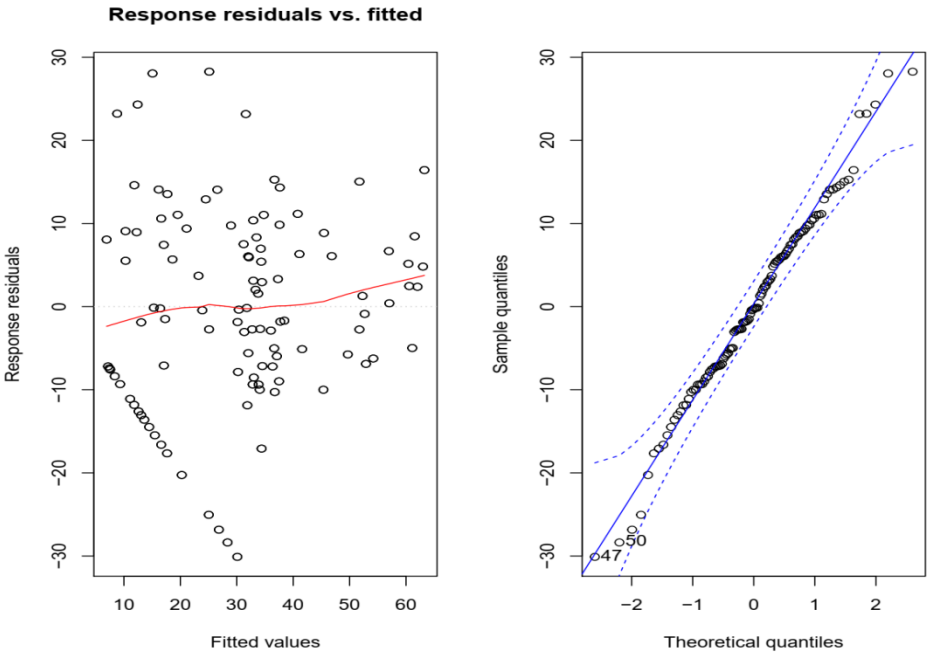
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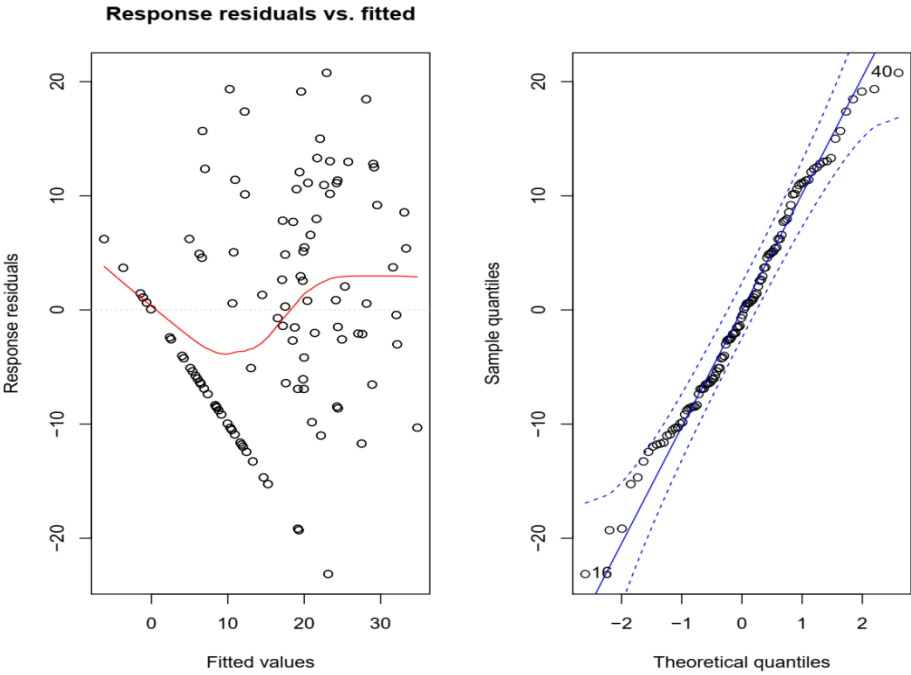
d)



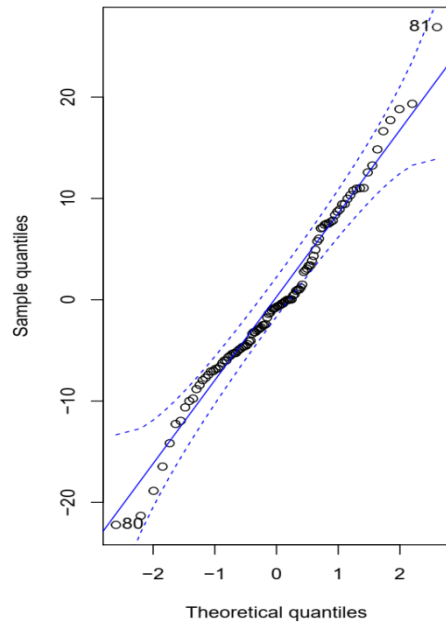
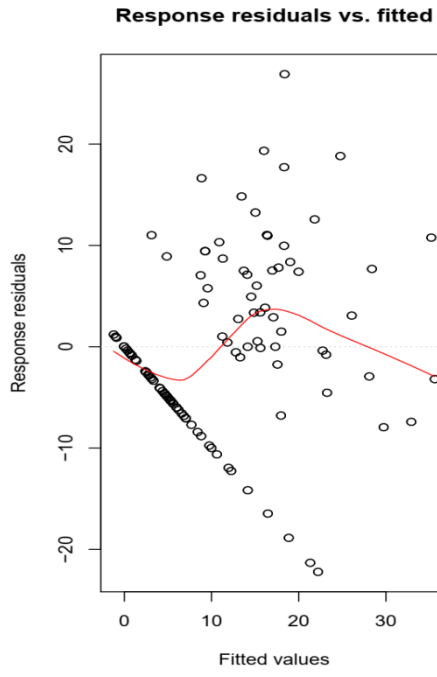
e)



f)



gg)



## 5 CONCLUSÕES GERAIS

Com base nos resultados encontrados através de experimentos de campo, podemos afirmar que a estrutura e função da comunidade macrofaunal de manguezais são altamente dependentes da escala espacial, tanto em pequenas quanto em largas escalas espaciais. Em largas escalas espaciais (centenas de quilômetros de distância), a macrofauna respondeu às propriedades climáticas e geofísicas (como a temperatura do ar e descarga dos rios), sendo também associados pelas distintas configurações geomorfológicas presentes entre manguezais da costa brasileira. Em pequenas escalas espaciais (variando de poucos centímetros até dezenas de quilômetros), os organismos macrofaunais foram principalmente influenciados pelas raízes de bosques de mangues. Nessa escala, foi demonstrado que a complexidade morfológica no corpo dos anelídeos esteve altamente relacionada com a proporção de biomassa de raízes. Além disso, as diferenças macrofaunais foram claramente refletidas pelas alterações na complexidade dos sistemas radiculares de manguezais, representadas por variações nas raízes grossas e finas em função da distância de troncos de árvores e profundidade do solo.

Nosso trabalho demonstrou que o uso de diferentes escalas espaciais é altamente recomendável para uma melhor interpretação dos resultados em estudos da macrobênticos de manguezais. É necessário que essas abordagens sejam aprofundadas, uma vez que esse é o primeiro trabalho que avaliou o efeito de múltiplas escalas espaciais em comunidades macrofaunais de manguezais. Sugerimos que futuros estudos devem também incluir escalas temporais nas análises, pois esse tipo de escala pode potencialmente influenciar a macrofauna de manguezais. Foi observada a necessidade de maiores cuidados em projetos de monitoramento e conservação de espécies em manguezais, uma vez que a maioria dos estudos não indica onde as amostras são coletadas (*e.g.*, próximo ou afastado de troncos; *coastal setting*). Por fim, recomendamos o controle de outros fatores nesses ambientes, como o hidroperíodo e composição de espécies vegetais, reduzindo, assim, possíveis discrepâncias nas variações dos padrões de distribuição da macrofauna e de raízes entre bosques de mangues.

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