

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

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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

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1. INTRODUCTION

Mangrove research has historically focused on evaluating short-term and small-scale spatial forest structure and associated aquatic biodiversity (Rivera-Monroy 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 eco-geomorphology 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 character-

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istics 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

2.1. 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.

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*, *Rhi-*

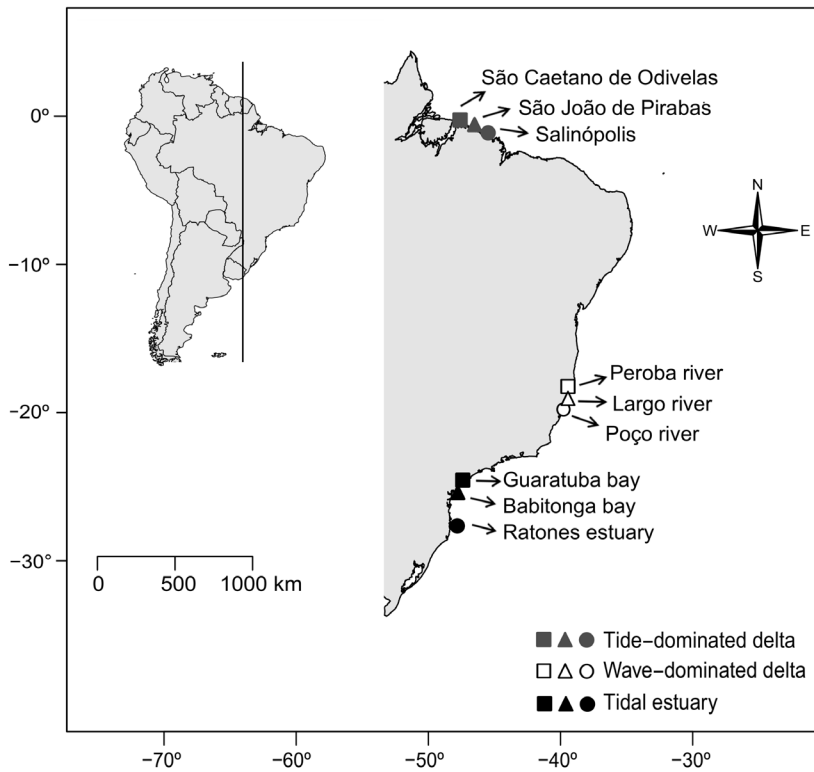


Fig. 1. Study area, showing the sampled coastal settings (tide-dominated delta, wave-dominated delta, tidal estuary) and sites within each coastal setting

zophora mangle, *R. racemosa*, *R. harrisonii*, and *Laguncularia racemosa*.

Wave-dominated delta occupies an extensive area of the central coast of Brazil. These habitats are char-

acterized 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 at www.int-res.com/articles/suppl/m638p025_supp.pdf).

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 |
| Climate and geophysical | | | |
| 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 yr ⁻¹) | 3000 | 1400 | 1500 |
| Main discharge | Amazon River | Several rivers | Few rivers |
| Tidal regime | Macrotidal | Mesotidal | Microtidal |
| Mangrove forest | | | |
| 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>A. schaueriana</i> <i>Laguncularia racemosa</i> <i>Rhizophora harrisonii</i> <i>R. mangle</i> <i>R. racemosa</i> | <i>A. germinans</i> <i>A. schaueriana</i> <i>L. racemosa</i> <i>R. mangle</i> | <i>A. schaueriana</i> <i>L. racemosa</i> <i>R. mangle</i> |

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.

2.2. 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 (mm yr^{-1}) were retrieved from the WordClim database (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° (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° resolution. Average annual potential evapotranspiration (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° 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 $K1 + O1$ or semidiurnal amplitude $M2 + S2$) on a grid of 0.0625° 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.'

2.3. 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°C until constant weight was achieved. Soil bulk density was determined by dividing the dry mass of each sample by its total volume (g cm^{-3} ; SCS-USDA 1972). Total soil phosphorus (mg cm^{-3}) was obtained with 1 N HCl for 16 h after combustion in a furnace at 550°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; mg cm^{-3}), soil nitrogen (N; 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°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^{-1}) at each site using the following equation (Cannell 1984, Rovai et al. 2016):

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

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 ($\text{m}^2 \text{ha}^{-1}$); H is height (m); and WSG is wood specific gravity ($\text{g dry mass cm}^{-3}$). We used previously estimated values of $F = 0.7$ (Roberts & Ruara 1967, Kairo et al. 2002, Bundotich et al. 2009) and $\text{WSG} = 0.77$ 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 (≤ 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^2). 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 dif-

fered 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*, *Laeonereis* 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.

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

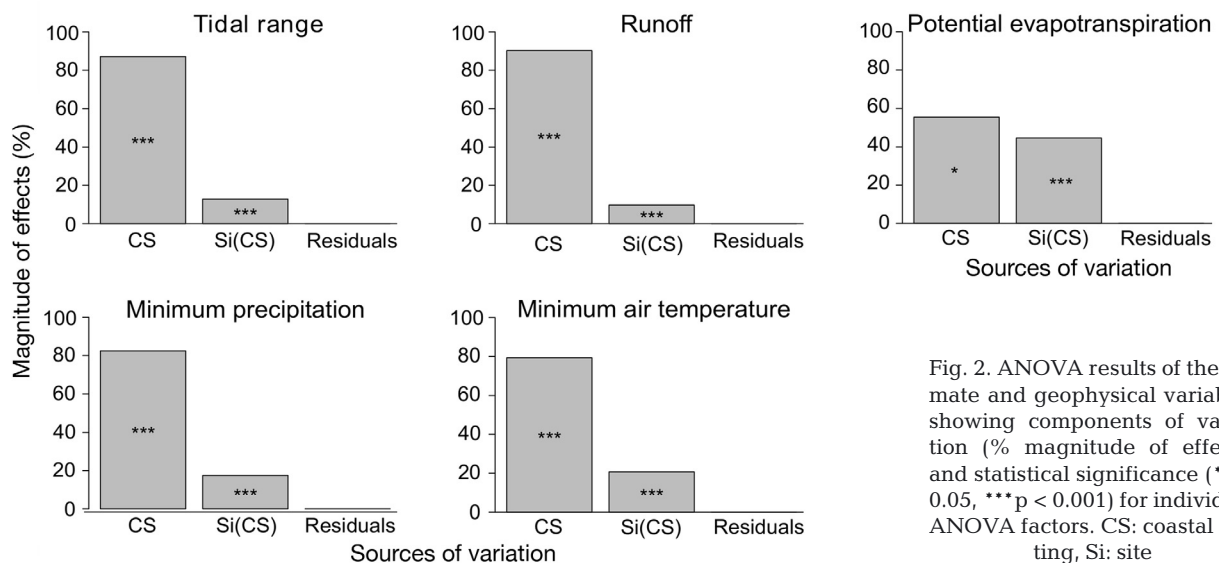


Fig. 2. ANOVA results of the climate and geophysical variables showing components of variation (% magnitude of effects) and statistical significance (* $p < 0.05$, *** $p < 0.001$) for individual ANOVA factors. CS: coastal setting, Si: site

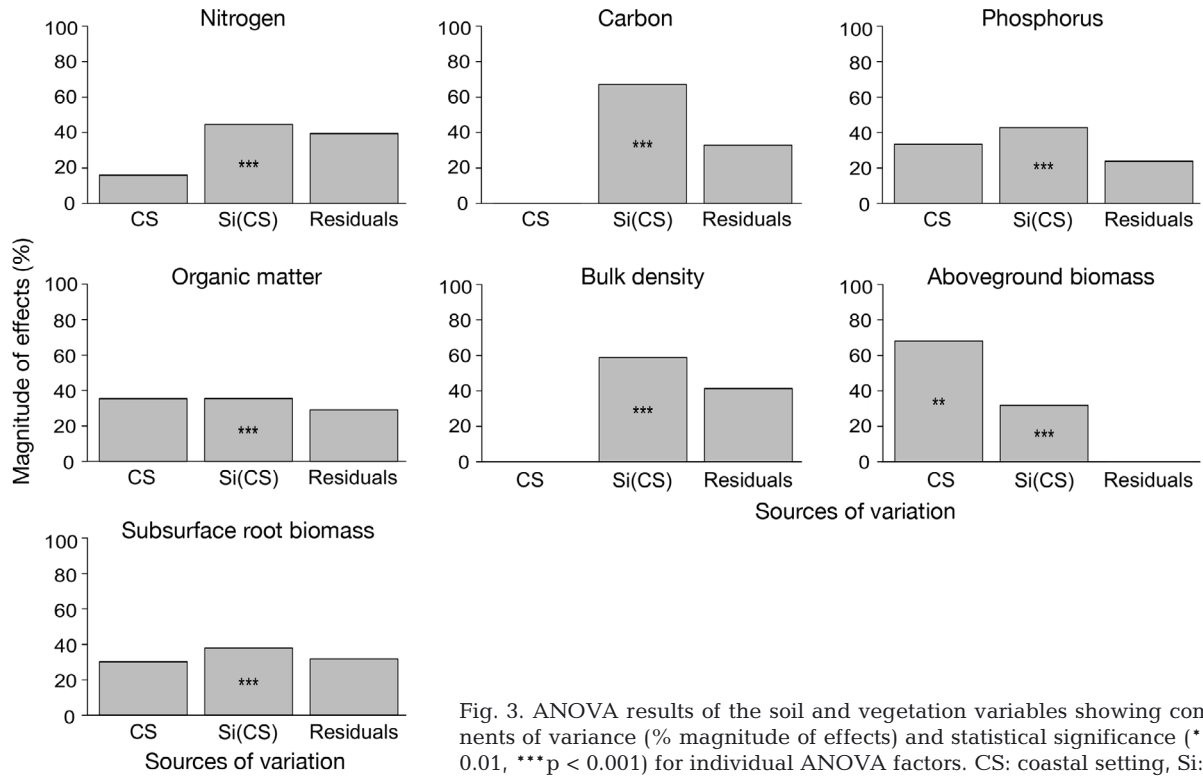


Fig. 3. ANOVA results of the soil and vegetation variables showing components of variance (% magnitude of effects) and statistical significance (**p < 0.01, ***p < 0.001) for individual ANOVA factors. CS: coastal setting, Si: site

polychaetes *I. pulchella*, *Manayunkia brasiliensis*, *C. capitata*, *Laeonereis* spp., *Heteromastus similis*, *Alitta succinea*, and *Dipolydora socialis*, and oligocha-

etes 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 para-

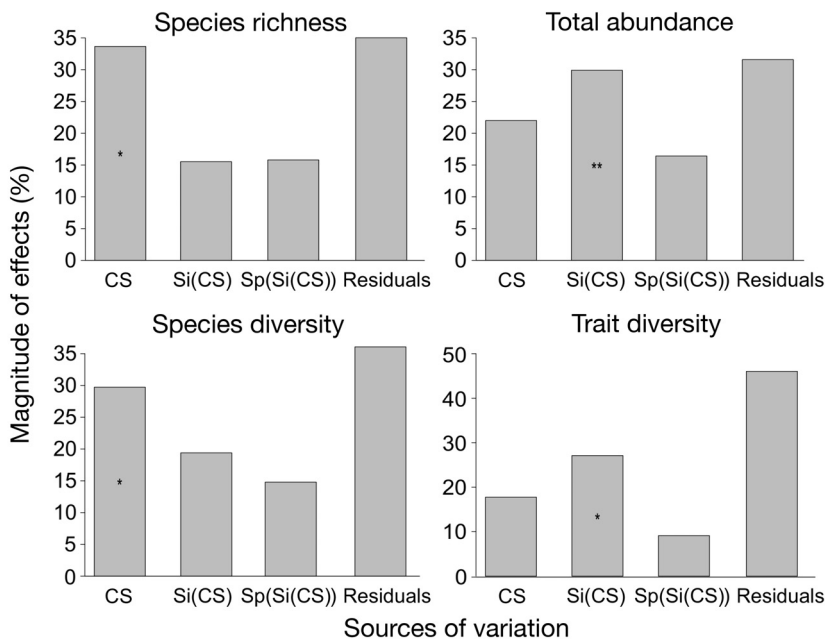


Fig. 4. ANOVA results of the macrofauna community variables showing components of variation (% magnitude of effects) and statistical significance (*p < 0.05, **p < 0.01) for individual ANOVA factors. CS: coastal setting, Si: site, Sp: sampling points

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 |
| Macrofauna community | | | |
| Species richness (ind. 0.05 m ⁻²) | 6.04 \pm 0.67 | 3.77 \pm 0.34 | 8.44 \pm 0.63 |
| Total abundance (ind. 0.05 m ⁻²) | 23.92 \pm 3.21 | 24.09 \pm 4.03 | 97.78 \pm 18.79 |
| Species diversity (ind. 0.05 m ⁻²) | 1.39 \pm 0.09 | 1.00 \pm 0.07 | 1.47 \pm 0.07 |
| Trait diversity (ind. 0.05 m ⁻²) | 3.52 \pm 0.70 | 1.41 \pm 0.42 | 5.58 \pm 1.14 |
| Climate and Geophysical | | | |
| Tidal range (m) | 4.55 \pm 0.10 | 2.54 \pm 0.01 | 0.99 \pm 0.10 |
| Runoff (m ³ s ⁻¹) | 1461.01 \pm 11.82 | 482.70 \pm 0.39 | 775.57 \pm 9.20 |
| Potential evapotranspiration (mm yr ⁻¹) | 2135.71 \pm 36.29 | 2320.09 \pm 16.08 | 1920.63 \pm 7.08 |
| Minimum precipitation (mm yr ⁻¹) | 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 |
| Vegetation and soil | | | |
| Aboveground biomass (t ha ⁻¹) | 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 ⁻³) | 0.18 \pm 0.02 | 0.39 \pm 0.10 | 0.24 \pm 0.04 |
| Soil carbon (mg cm ⁻³) | 2.65 \pm 0.28 | 4.82 \pm 1.04 | 3.49 \pm 0.59 |
| Soil phosphorus (mg cm ⁻³) | 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 ⁻³) | 0.71 \pm 0.06 | 0.54 \pm 0.07 | 0.60 \pm 0.06 |

podia with similar rami tended to be more associated with higher site aboveground biomass, soil bulk density, and potential evapotranspiration.

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 envi-

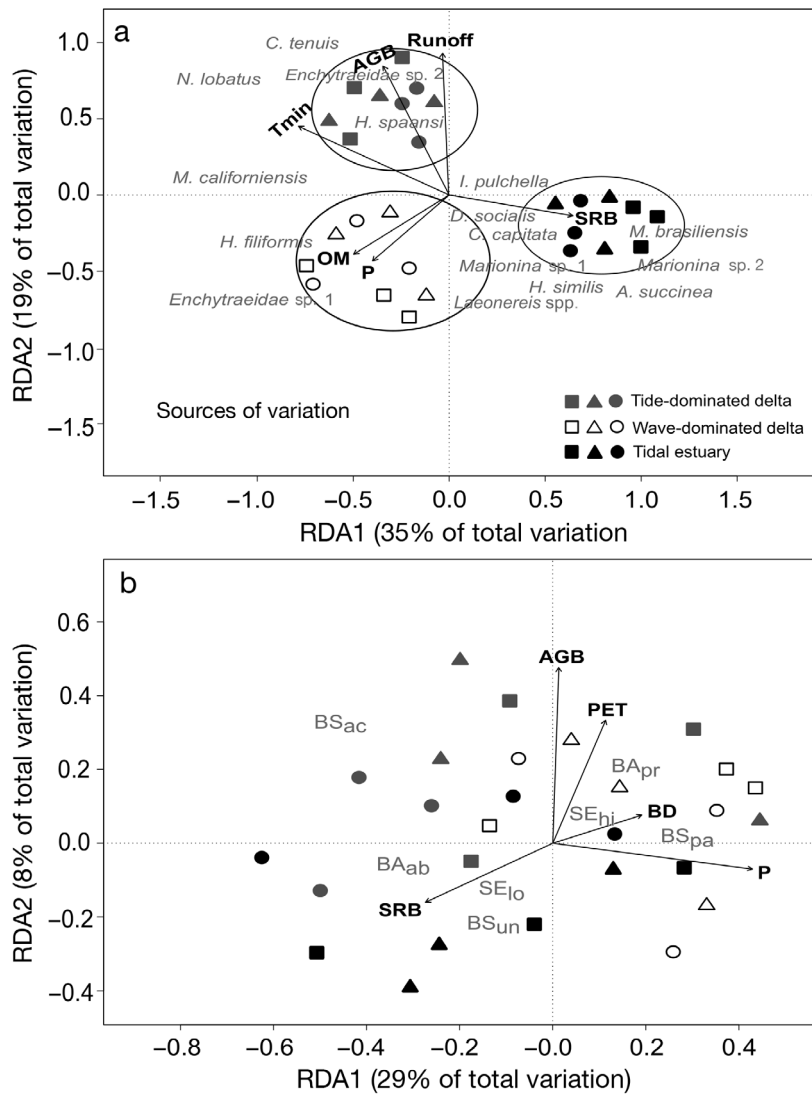


Fig. 5. Redundancy analyses (RDA) of the relationships among (a) the most abundant macrofauna taxa (see Section 3 for full species names) and (b) annelid assemblage functional traits with selected vegetation (AGB: aboveground biomass, SRB: subsurface root biomass), soil (P: total phosphorus, BD: bulk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

ronments (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 desicca-

tion 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 mor-

phological 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 modi-

fications 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 small-scale 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

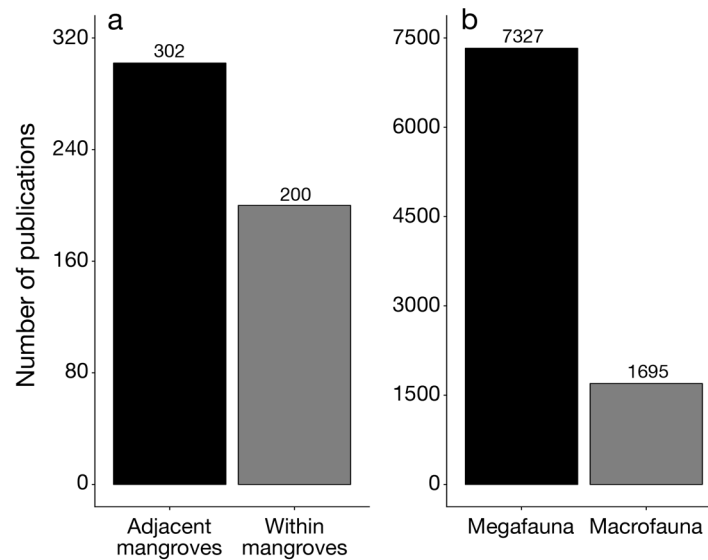


Fig. A1. (a) Number of publications macrofaunal community studies carried out in areas adjacent and within mangrove forests. The queries were: 'mangrove' (in Title) versus 'macrofauna,' or 'benth*,' 'epifauna,' or 'infauna' (in Title/Abstract/Keyword). (b) Number of publications on macrofauna and megafauna in mangroves. The queries were separated to macrofauna ('mangrove'—in Title—versus 'isopod*,' 'nemert*,' 'annelid*,' 'polychaet*,' 'bivalv*,' 'oligochaet*,' '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