

The Bostrychietum community of pneumatophores in Araçá Bay: an analysis of the diversity of macrofauna

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A mangrove forest can harbour several macroalgal assemblages growing on pneumatophores, roots, stems and other hard substrates. These algae belong to various genera, most typically Bostrychia, and form a community called the Bostrychietum. This study describes the fauna associated with the Bostrychietum and the effect of emersion time on the community. Seasonal samples were collected from pneumatophores on an island in Araçá Bay in 2012, in two areas, one on the border of the island and one inland. Each pneumatophore was considered a sample. The border samples, with a shorter emersion time, contained a richer algal flora associated with pneumatophores, and fauna with species of varied dietary habits. The inland samples, with a longer emersion time, contained only two algal genera and fauna species comprised mostly of omnivorous amphipods and desiccation-resistant detritivorous species. Macrofauna diversity and richness varied over time and were lower in spring. Therefore, the emersion time of the Bostrychietum and the period of the year affect the community structure, for both the macroalgae and the associated fauna.

Keywords: Mangrove, pneumatophores, faunal variations, algal composition, habitat complexity

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INTRODUCTION

The mangrove forest environment is restricted to tropical and subtropical coastal strips of land, often in sheltered areas, and provides favourable conditions for nourishment, protection and reproduction of many animal species. Pneumatophores are essential gas-exchange structures of mangrove trees, such as *Avicennia schaueriana*, which can reach a height of 35 cm in saturated soils (Gwyther, 2000). Macroalgae grow on the mangrove pneumatophores, roots, stems and other hard substrates (Melville & Pulkownik, 2007).

Algae associated with pneumatophores are exposed to abrupt gradients of temperature, salinity, light and nutrient availability, and to emersion and submersion during the tidal cycles. They are important primary producers in the estuarine ecosystem, through their production of organic matter and contribution to nutrient cycling (Yokoya *et al.*, 1999; Melville & Pulkownik, 2007).

The Bostrychietum community (Post, 1936) is composed of red algae of the genera *Bostrychia*, *Caloglossa*, *Catenella* and *Murrayella* (West, 1991; Yokoya *et al.*, 1999), and green algae such as *Ulva* and *Cladophora* (Fontes *et al.*, 2007). These communities show seasonal alterations influenced by nutrient availability, related to high temperatures and increased light intensity that stimulate algae growth (West, 1991; Yokoya *et al.*, 1999). Since the stems and pneumatophores colonized by the algal community are restricted to the upper range of the spring tides (Rützler & Feller, 1999), the Bostrychietum community in mangrove forests

indicates the tide level, since the algal biomass shrinks as the exposure time increases (Melville & Pulkownik, 2007).

Molluscs, amphipods and insect larvae, in addition to meiofaunal nematodes and copepods (Gee & Somerfield, 1997; Proches *et al.*, 2001; Proches & Marshall, 2002) dominate the fauna of the Bostrychietum community. Both algae and fauna are adapted to an environment that is periodically exposed to air during tidal fluctuations (Robles, 1982; Gee & Somerfield, 1997). Flora and fauna composition and abundance differ from those of nearby non-vegetated benthic sediments (Proches *et al.*, 2001). Neotropical and subtropical Bostrychietum communities have been studied in regard to biomass and coverage (West, 1991; Yokoya *et al.*, 1999; Fontes *et al.*, 2007) and spatial and temporal variations (Yokoya *et al.*, 1999), but there are no records concerning faunal composition and density.

The daily and temporal variations in emersion to which the Bostrychietum is subjected alter the composition of the flora and fauna; it is expected that areas with longer emersion times would contain fewer species, and also that the community would show differences over time. In this study, we analysed the temporal variation in the abundance, richness and diversity of the Bostrychietum community present on pneumatophores of *Avicennia schaueriana*, in two areas with different emersion periods.

MATERIALS AND METHODS

Study area

Araçá Bay, located on the continental side of the São Sebastião Channel on the south-east coast of Brazil (Figure 1), was

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formed during the construction of the São Sebastião harbour. The bay is limited by rocky flanks and bordered by four beaches. It features two small islands (Pernambuco and Pedroso), three main mangrove centres, and an extensive soft-bottom plain, entirely uncovered during spring-tide periods. This configuration protects the area from the direct effects of hydrodynamic factors outside the São Sebastião Channel; the hydrodynamics are dominated by the tides, but also feature low-amplitude waves (Amaral *et al.*, 2010). The bay is up to 10 m deep in its outer end, and becomes narrower and shallower inland. The bottom is gently sloping, with large areas uncovered during low tides. Tides vary between average levels of + 2.06 m (maximum), + 1.15 m (mean) and + 0.80 m (minimum), with the maximum and minimum amplitudes being the average values of spring tides, and neap-tide levels closer to the overall mean. The sediment composition ranges from dense silt to medium sand, and from very poorly to poorly sorted (Gubitoso *et al.*, 2008).

The vegetation and fauna are typical of mangrove forests (Amaral *et al.*, 2010). The dominant species in the mangrove enclaves are *Avicennia schaueriana* (black mangrove) and *Laguncularia racemosa* (white mangrove). These trees have pneumatophores (aerial roots) that are colonized by epiphytic algae.

The sampling was conducted on Pernambuco Island (Figure 1), which has a grove formed mainly by *A. schaueriana*, and some rocky outcrops around the island, and is populated by many invertebrates, chiefly gastropods, polychaetes and hermit crabs (Amaral *et al.*, 2010). During low-tide periods, the pneumatophores are completely emerged, and during high tides, only the tree trunks are exposed.

Sampling procedure

Samples were collected on four occasions in 2012: summer (January), autumn (April), winter (August) and spring

(November), on the side of Pernambuco Island facing the continent. In each period, 40 pneumatophores were randomly collected, 20 in the border area, which is close to the low-tide limit during spring tides, and 20 in the grove inner area, where pneumatophores are emerged for longer periods of time. Each pneumatophore was considered a sample. The structures were cut with scissors, placed in individual plastic bags, and frozen for later screening in the laboratory.

The algae were separated from the pneumatophores in the laboratory, washed in trays to remove the retained sediment, and identified to the genus level. The water from the trays, containing sediment and fauna, was filtered in 200 μm -mesh bags over a container to retain the water. The filtered material plus the sediment retained by the bags were again filtered on filter paper and then oven-dried. The fauna retained during the process was counted and identified.

Adults of Malacostraca, Gastropoda, Bivalvia and Polychaeta were identified to species or genus. The juveniles of these taxonomic groups, chironomid larvae, and trombiculid mites were not identified to species level due to the difficulty of identification, but they were counted. Both the algae and the sediment retained in the samples were dried in an oven for 48 h and weighed on a 0.01 g semi-analytical precision balance.

Data analysis

The weights of algae and retained sediment were compared across the samples through an analysis of variance (ANOVA) of two factors: season and sampled area, followed by an *a posteriori* SNK test to determine where the most significant differences occurred. Before the analyses, the homogeneity of the data was tested through the Cochran test, and to satisfy the homogeneity premise, data were appropriately transformed when necessary (Underwood, 1997).



Fig. 1. Araçá Bay, São Sebastião, state of São Paulo. Collection site, Pernambuco Island, circled (figure adapted from Amaral *et al.*, 2010).

A PERMANOVA analysis was conducted to evaluate the differences in the densities of the major groups Crustacea, Mollusca, Polychaeta, Diptera and Acari between areas and among seasons (Anderson, 2001). This test results in the *pseudo-F*, which is a multivariate analogue of Fisher's *F*, calculated from a dissimilarity matrix and *P* values obtained through permutation tests, and an *a posteriori* paired *t*-test, to determine which seasons contributed most to the variation. The Bray–Curtis index was used to evaluate the similarity between the border and inland communities, followed by non-metric multidimensional scaling (nMDS) in order to visually represent the sample ordering. SIMPER was done to evaluate the species that contributed most to the similarities between samples of the same group, as well as those that contributed most to the difference between groups, using the Primer 6.0 software (Clarke & Gorley, 2006).

The density of individuals of each macrofauna taxon was obtained by dividing their total number by the dry weight of the sample [total abundance (N)/sample weight (dry weight of algae + sediment)]. The Shannon diversity index (*H'*) and Margalef richness index (α) were calculated, based on the numerical distribution of individuals of different species as a proportion of the total number of individuals in the sample, for the individuals identified to species level. Diversity and richness of macrofauna were compared across the samples through the same ANOVA design mentioned above, as were the densities of the dominant species.

RESULTS

The Bostrychietum from pneumatophores of *Avicennia schaueriana* was composed of six algal genera, of which *Bostrychia* and *Catenella* (Rhodophyta) were dominant and also the only genera present in the inland samples. Border samples also included the red algae *Ceramium* and *Hypnea*, as well as the green algae *Ulva* and *Cladophora*. Algal occurrence varied seasonally, with *Ulva* and *Hypnea* occurring only in some seasons, while *Ceramium* and *Cladophora* were frequent and abundant year-round. Algal dry weight differed among seasons and between areas (Table 1). The dry weight was highest in summer and lowest in winter. Algal dry weight was consistently higher in inland areas, except during autumn (Figure 2A).

Table 1. ANOVA results for the weight of algae and sediment in the samples from border and inland areas through the seasons. Significant values in bold.

| Source | d.f. | MS | F | P |
|--|------|------|-------|--------|
| Algal dry weight | | | | |
| Season | 3 | 5.28 | 56.97 | <0.001 |
| Area | 1 | 2.44 | 26.31 | <0.001 |
| Season × area | 3 | 0.39 | 4.18 | 0.01 |
| Residuals | 152 | 0.09 | | |
| Ln(x + 1), Cochran's test C = 0.2702, P < 0.01 | | | | |
| Sediment weight | | | | |
| Season | 3 | 2.03 | 13.89 | <0.001 |
| Area | 1 | 0.22 | 1.53 | 0.219 |
| Season × area | 3 | 1.41 | 9.65 | <0.001 |
| Residuals | 152 | | | |
| Ln(x + 1), Cochran's test C = 0.3123, P < 0.01 | | | | |

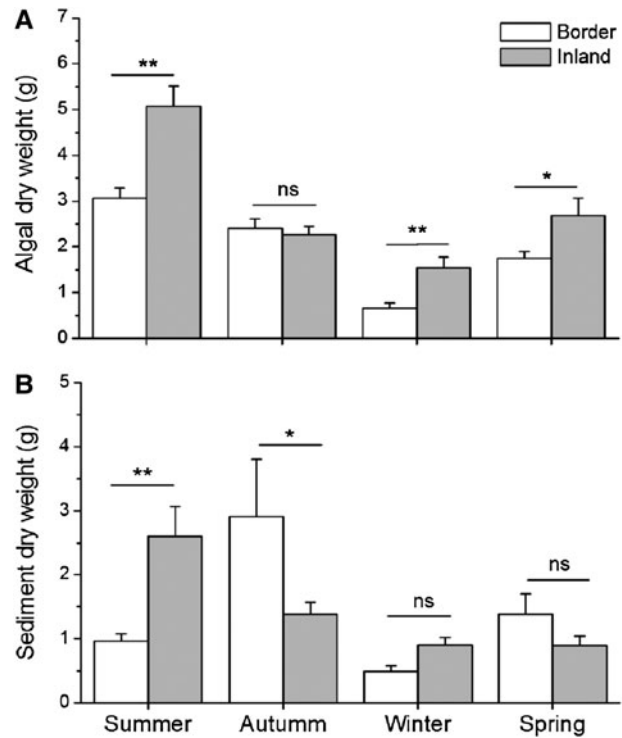


Fig. 2. Mean change (± standard error) in the weight of the samples during the seasons for the two sites sampled on Pernambuco Island. (A) algal weight; (B) sediment weight. SNK test (**P* < 0.01; ***P* < 0.001; ns: non-significant).

The weight of the sediment in the algae differed among seasons, and the interaction of the factors season × area best explained the results (Table 1). The amount of sediment retained on the pneumatophores was higher in the border area in autumn, while the inland samples contained more sediment during summer. During winter and spring, sediment retention was similar between areas (Figure 2B).

A total of 2578 adult macrofauna individuals were found in the samples collected on the border of the island, and 2925 in the inland samples, including crustaceans, molluscs and polychaetes. Chironomid larvae (Diptera) and trombiculid mites (Acari) were also present, totalling 626 individuals in the border samples and 1004 in the inland samples.

The season × area interaction most affected the distribution of Crustacea, Mollusca, Polychaeta, Diptera and Acari (Table 2). Border and inland areas were similar during summer (*t* = 1.32, *P* = 0.16) and autumn (*t* = 1.40, *P* = 0.12), and differed during winter (*t* = 4.89, *P* = 0.01) and spring (*t* = 2.87, *P* = 0.01). Within areas, no differences occurred between summer and autumn for the border areas (*t* = 1.09 and *P* = 0.31). The remaining comparisons for border samples and all comparisons for inland samples were significant. The nMDS analysis indicated two distinct groups of sampling areas. By season, the summer and autumn samples formed groups (Figure 3), in agreement with the pairwise test results mentioned above. The dissimilarity percentage (SIMPER) between the border and inland samples was 56.04%, to which Crustacea contributed most (53.8%), followed by Diptera (25.2%).

The mean density of Crustacea was higher in the border than in the inland samples (*F* = 20.4; d.f. = 1; *P* < 0.001). Peracarid crustaceans, including the gammarideans *Chelorchestia darwini* and *Parhyale hawaiiensis*, the tanaid

Table 2. PERMANOVA results comparing the density of the major groups Crustacea, Mollusca, Polychaeta, Diptera and Acari found in the Bostrychietum between border and inland areas through the seasons. Significant values in bold.

| Source | d.f. | MS | Pseudo-F | P |
|---------------|------|--------|----------|--------------|
| Season | 3 | 10,469 | 8.29 | 0.001 |
| Area | 1 | 21,079 | 16.68 | 0.001 |
| Season × area | 3 | 9294 | 7.36 | 0.001 |
| Residuals | 152 | | | |

Zeuxo coralensis and the isopod *Dynoides castroi*, dominated all samples. The ANOVA results showed significant values for the interaction season × area for *C. darwini*, *P. hawaiiensis* and *Z. coralensis*; while the results for *D. castroi* indicated differences between areas (Table 3). *Chelorchestia darwini* showed consistently higher densities in the inland samples throughout the year, with a peak in summer. *Parhyale hawaiiensis* occurred in higher densities in the border area year-round, but the differences were significant only for winter and spring. The density of *Z. coralensis* was similar in the border and inland areas during all seasons, except for winter, when the density was higher in the border. *Dynoides castroi* was absent during winter and spring inland, and occurred in higher densities during summer, winter and spring in the border area (Figure 4).

The Diptera group, represented by chironomid larvae, was present in both the border and inland areas, once significant results were observed only to the factor season (Table 4). Their densities were higher during summer and winter and lowest in spring (Figure 5). The interaction between season and area was significant for trombiculid mites (Table 4). In border areas, higher densities were observed in summer and autumn and mites were absent in spring. In inland samples, these mites were denser in summer when compared with other seasons (Figure 6).

The Bostrychietum harbours a wide array of species with different feeding strategies. The most abundant species are shown in Table 5. The overall density varied between areas and among seasons (Table 6). During summer and autumn, densities were similar in border and inland areas (Table 7, SNK test, $P > 0.05$), and lower in inland areas in winter and spring (Table 7, SKN test, $P < 0.01$). Macrofauna diversity

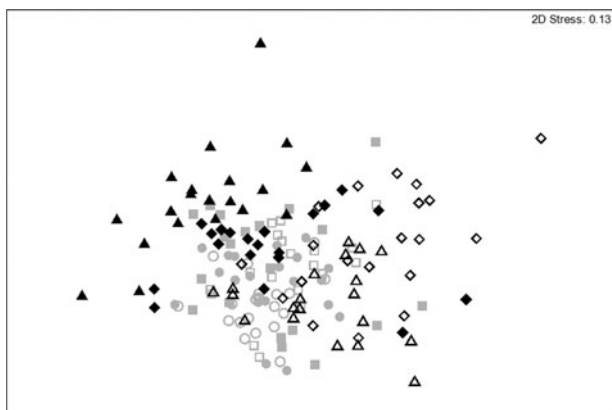


Fig. 3. nMDS plot for density values of the major groups for each site sampled during the four seasons. Filled symbols = Border; empty symbols = Inland. Circle: Summer; square: Autumn; triangle: Winter; rhombus: Spring. Grey symbols indicate summer and autumn group formation.

Table 3. ANOVA results for the density of dominant species from the Bostrychietum of Araçá Bay between border and inland areas through the seasons. Significant values in bold.

| Source of variation | d.f. | MS | F | P |
|---|------|--------|-------|------------------|
| <i>Chelorchestia darwini</i> | | | | |
| Season | 3 | 29.92 | 9.03 | <0.001 |
| Area | 1 | 117.13 | 35.34 | <0.001 |
| Season × area | 3 | 12.55 | 3.79 | 0.012 |
| Error | 152 | 3.31 | | |
| No transformation; Cochran's test $C = 0.4452$, $P < 0.01$ | | | | |
| <i>Parhyale hawaiiensis</i> | | | | |
| Season | 3 | 1.59 | 2.51 | 0.061 |
| Area | 1 | 22.25 | 35.09 | <0.001 |
| Season × area | 3 | 6.41 | 10.10 | <0.001 |
| Error | 152 | 0.63 | | |
| Ln(x + 1); Cochran's test $C = 0.1889$, $P > 0.05$ | | | | |
| <i>Zeuxo coralensis</i> | | | | |
| Season | 3 | 135.44 | 5.47 | 0.001 |
| Area | 1 | 181.00 | 7.31 | 0.008 |
| Season × area | 3 | 134.03 | 5.42 | 0.001 |
| Error | 152 | 24.75 | | |
| No transformation; Cochran's test $C = 0.8921$, $P < 0.01$ | | | | |
| <i>Dynoides castroi</i> | | | | |
| Season | 3 | 1.48 | 0.77 | 0.511 |
| Area | 1 | 29.00 | 15.17 | <0.001 |
| Season × area | 3 | 3.05 | 1.59 | 0.193 |
| Error | 152 | 1.91 | | |
| No transformation; Cochran's test $C = 0.6067$, $P < 0.01$ | | | | |

and richness varied over time (Table 6). Spring samples contributed most to these differences, since they showed the lowest values for both Shannon (Table 7, SNK test, $P < 0.01$) and Margalef indexes (Table 7, SNK test, $P < 0.01$).

DISCUSSION

The composition of the Bostrychietum community of Araçá Bay showed significant temporal variation and was similar in summer and autumn between border and inland areas. Crustaceans and chironomid larvae dominated and contributed most to differentiate the sampled areas. Macrofauna diversity and richness varied over time and were lowest in spring.

The fauna associated with the Bostrychietum is determined, among other factors, by the algae that form the community; the presence of sediment retained on the fronds, which increases the water content of the substrate; and the presence of organic matter (Proches & Marshall, 2002). Higher richness of associated algae increases the buildup of sediment and water content on the pneumatophores, which favours their colonization by fauna (Proches *et al.*, 2001; Proches & Marshall, 2002). More-ramified algae, or those bearing more epiphytes, host a more-diverse fauna with differing dietary habits (Chemello & Milazzo, 2002). Differences in species diversity over time can also be explained by the reproductive cycles of the species, in addition to algal biomass, since life-history characteristics and niche availability are fundamental for species establishment.

The high diversity of Bostrychietum algae on pneumatophores, with *Bostrychia* and *Catenella* predominating, was similar to that observed in previous studies (Melville & Pulkownik, 2007; Fontes *et al.*, 2007). Several genera found on pneumatophores in the Bostrychietum, such as

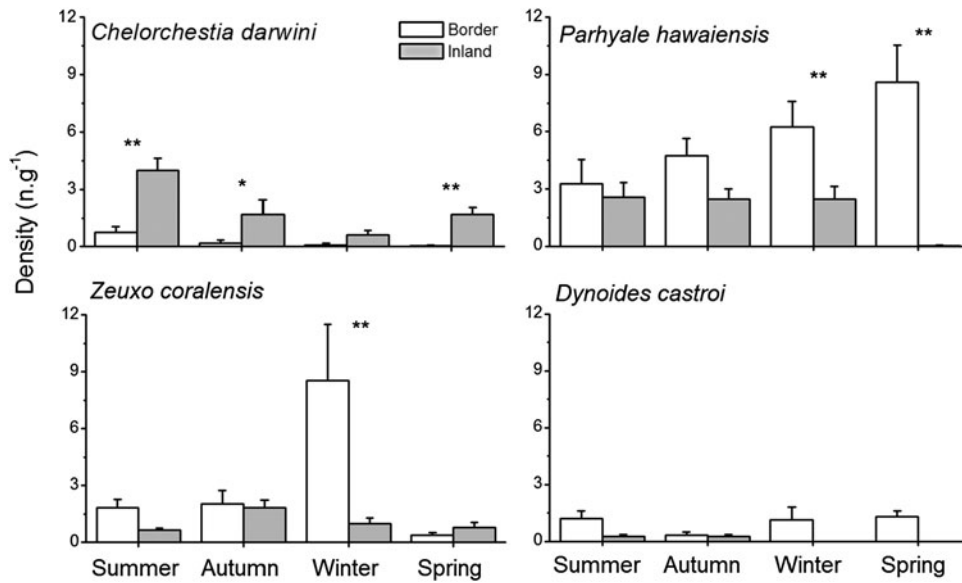


Fig. 4. Densities (number of individuals per g of sample) of the most common peracarid crustaceans found in inland and border areas through the seasons. Bars represent standard error. SNK test (* $P < 0.01$; ** $P < 0.001$).

Ceramium and *Amphiroa*, are also common on rocky shores (e.g. Amado-Filho *et al.*, 2006). Overall algal dry weight was higher during summer and lower during winter, probably in response to their reproductive cycles, availability of nutrients, and moisture. The presence of *Hypnea* only in the winter samples can be explained by the timing of the reproductive cycle of members of this genus, which occurs in the drier seasons (autumn and winter) in south-eastern Brazil (Caires *et al.*, 2013). *Ulva* was abundant in the border areas in autumn. This genus comprises ephemeral algae that can exploit nutrient enrichment resulting from anthropogenic activities (Fujita, 1985; Mackenzie, 2000). The green algae *Ulva* and *Cladophora* depend on nitrate and phosphate for their growth, and hence their presence may indicate a higher organic-matter input (Taouil & Yoneshigue-Valentin, 2002). These algae attach themselves to pneumatophores in the lowest zone, since they are more sensitive to desiccation (Taouil & Yoneshigue-Valentin, 2002). *Bostrychia* and *Catenella* occurred in both areas, and were dominant on the inland pneumatophores. These algae, unlike green algae,

have mechanisms to resist desiccation, with a reduced respiration rate in warmer periods and a return to normal photosynthesis and respiration rates after periods of extreme desiccation (Yokoya *et al.*, 1999); they also tolerate high levels of solar irradiation. This may explain why only these algae were present in the inland areas.

Pneumatophore algal cover may enhance the substrate complexity, forming an intricate habitat that facilitates sediment trapping (Proches & Marshall, 2002). Sediment deposition patterns may vary temporally and spatially. Annual cycles for sediment accumulation, with more intense deposition during winter months, were reported in coastal areas, in response to rough weather and increased local turbulence (Airoldi *et al.*, 1996). The higher sediment accumulation during summer and autumn in Araçá Bay is probably related to algal cover, since in this protected bay the hydrodynamics are mostly governed by tides (Amaral *et al.*, 2010). The effects of sediment on macrofauna associated with pneumatophores vary widely, depending on the spatial scale and the requirements of the individual species (Chapman & Tolhurst, 2007).

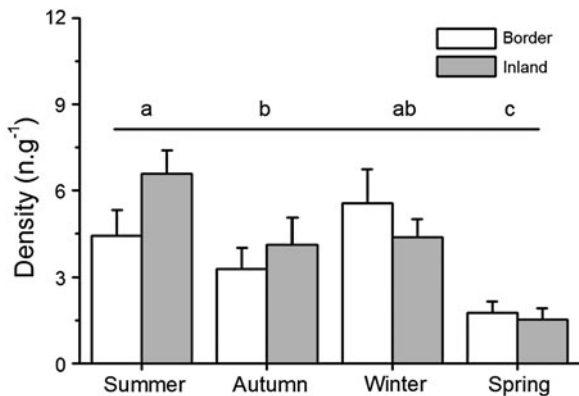


Fig. 5. Density (number of individuals per g of sample) of chironomid larvae found in inland and border areas through the seasons. Bars represent standard error. SNK test (different letters indicate $P < 0.01$; same letters indicate $P > 0.05$).

Table 4. ANOVA results for the density of chironomid larvae and trombiculid mites from the Bostrychietum of Araçá Bay between border and inland areas through the seasons. Significant values in bold.

| Source of variation | d.f. | MS | F | P |
|--|------|-------|-------|------------------|
| Chironomidae | | | | |
| Season | 3 | 6.37 | 13.19 | <0.001 |
| Area | 1 | 0.82 | 1.69 | 0.196 |
| Season × area | 3 | 0.57 | 1.19 | 0.317 |
| Error | 152 | 0.48 | | |
| Ln(x + 1); Cochran's test $C = 0.2362, P > 0.05$ | | | | |
| Trombiculidae | | | | |
| Season | 3 | 39.28 | 34.69 | <0.001 |
| Area | 1 | 3.90 | 3.44 | 0.067 |
| Season × area | 3 | 5.74 | 5.08 | 0.002 |
| Error | 152 | 1.13 | | |
| No transformation; Cochran's test $C = 0.3288, P < 0.01$ | | | | |

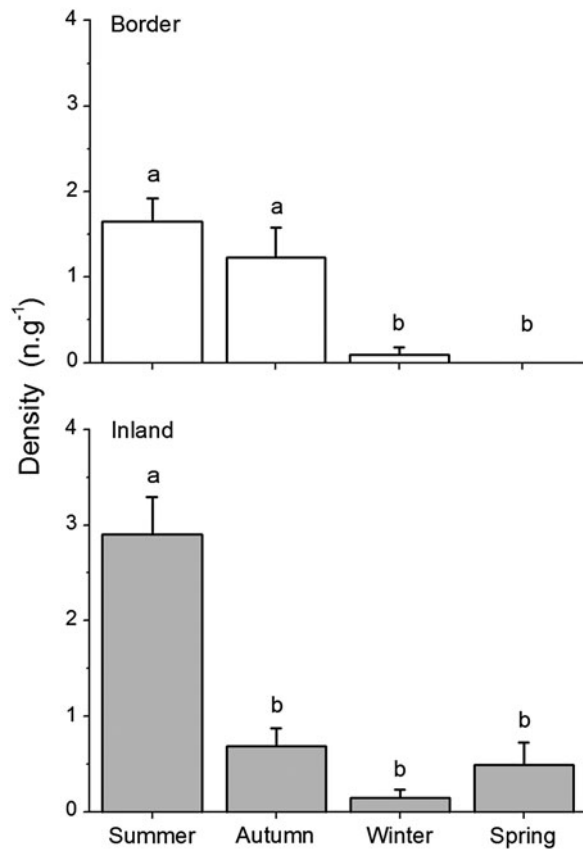


Fig. 6. Density (number of individuals per g of sample) of trombiculid mites found in border and inland areas through the seasons. Bars represent standard error. SNK test (different letters indicate $P < 0.01$; same letters indicate $P > 0.05$).

Among the major groups (Crustacea, Mollusca, Polychaeta, Diptera and Acari), Crustacea was responsible for differentiating the border and inland areas. The most abundant crustaceans were the gammaridean amphipods *Parhyale hawaiiensis* and *Chelorchestia darwini*. *Parhyale hawaiiensis* commonly occurs on biological substrates in the mesolittoral zone of rocky shores (Leite *et al.*, 2011), tolerating long periods of exposure. It feeds mainly on fragments of green and red algae, which support abundant populations in the Bostrychietum environment (Poovachiranon *et al.*, 1986; Pereira *et al.*, 2000). The high algal content in the diet of *P. hawaiiensis* probably explains their occurrence mostly in the border areas. The talitrid *C. darwini* is found in mangroves and estuarine areas along the Brazilian coast, inhabiting mud or vegetation (Serejo, 2004), and has been collected in Bostrychietum communities in locations near Araçá Bay (Souza *et al.*, 2013). Lopes (2011) suggested that *C. darwini* prefers lower-salinity habitats, and found higher abundances in edge areas, in contrast to the results of the present study. The proximity to water, favouring transport through the tidal currents may explain those results (Lopes, 2011).

Contrary to expectation, the density of chironomid larvae was similar in both areas. The longer emersion time was expected to promote the dominance of these animals in the inland samples, when there would be a higher possibility of oviposition. Females prefer to lay eggs in places with less wave action, and on rocky shores, these highly specialized larvae are found in pools or among algal fronds and lichens

Table 5. The most abundant species inhabiting the Bostrychietum of Araçá Bay, and their respective feeding habits.

| Species (n) | Order | Feeding | References |
|---------------------------------------|-----------------|---------|--------------------------------------|
| <i>Parhyale hawaiiensis</i> (1853) | Amphipoda | D | Shoemaker (1956) |
| <i>Chelorchestia darwini</i> (854) | | D | Lowry (2015) |
| <i>Amphioe ramondi</i> (75) | | H | Jacobucci (2005) |
| <i>Apothyale media</i> (17) | | H | Tavares <i>et al.</i> (2013) |
| <i>Monocorophium</i> sp. (17) | | D | Icely & Nott (1985) |
| <i>Zeuxo coralensis</i> (683) | Tanaidacea | D | Anderson (2015) |
| <i>Leptochelia savignyi</i> (16) | | D | Odum & Heald (1972) |
| <i>Pachygrapsus transversus</i> (81) | Decapoda | O | Christofolletti <i>et al.</i> (2010) |
| <i>Dynoides castroi</i> (237) | Isopoda | H | Pires-Vanin (1981) |
| <i>Perinereis</i> sp. (54) | Phyllodocida | O | Fauchald & Jumars (1979) |
| <i>Littorina flava</i> (96) | Caenogastropoda | H | Longo <i>et al.</i> (2014) |
| <i>Echinolittorina lineolata</i> (35) | | H | Longo <i>et al.</i> (2014) |

in the mesolittoral and supralittoral, where they feed on fungal hyphae and algae (Garbary *et al.*, 2009). The density of chironomid larvae varied among seasons, and was lowest in spring. The temporal variation of chironomid larvae could be related to the presence of predators, since the mottled crab *Pachygrapsus transversus* is a potential predator of these larvae (Robles, 1982) and was found in the Bostrychietum fauna. However, *Pachygrapsus* was more abundant in summer in the inland samples and in autumn in the

Table 6. ANOVA results relating the factors area and season to the community descriptor indexes (Density, Shannon and Margalef). Significant values in bold.

| Source | d.f. | MS | F | P |
|--|------|-------|-------|------------------|
| Density (d) | | | | |
| Season | 3 | 1.63 | 3.73 | 0.013 |
| Area | 1 | 10.97 | 25.07 | <0.001 |
| Season × area | 3 | 3.46 | 7.91 | <0.001 |
| Residuals | 152 | 0.44 | | |
| Ln(x + 1), Cochran's test C = 0.2000, P > 0.05 | | | | |
| Shannon (H') | | | | |
| Season | 3 | 1.86 | 14.32 | <0.001 |
| Area | 1 | 0.24 | 1.85 | 0.175 |
| Season × area | 3 | 0.12 | 0.96 | 0.415 |
| Residuals | 152 | 0.13 | | |
| No transformation, Cochran's test C = 0.1874, P > 0.05 | | | | |
| Margalef (α) | | | | |
| Season | 3 | 2.05 | 9.08 | <0.001 |
| Area | 1 | 0.40 | 1.75 | 0.188 |
| Season × area | 3 | 0.59 | 2.62 | 0.053 |
| Residuals | 152 | 0.23 | | |
| No transformation, Cochran's test C = 0.2186, P > 0.05 | | | | |

Table 7. Mean values (\pm standard error) of community descriptor indexes (Density, Shannon and Margalef) in border and inland areas through the seasons.

| | Summer | Autumn | Winter | Spring |
|-----------------------|--------------------|--------------------|---------------------|---------------------|
| Density (d) | | | | |
| Border | 8.06 (\pm 1.46) | 8.73 (\pm 1.41) | 18.59 (\pm 4.66) | 10.58 (\pm 2.21) |
| Inland | 7.89 (\pm 1.18) | 6.63 (\pm 0.92) | 4.98 (\pm 1.00) | 2.70 (\pm 0.57) |
| Shannon (H') | | | | |
| Border | 1.06 (\pm 0.09) | 1.02 (\pm 0.08) | 0.89 (\pm 0.06) | 0.557 (\pm 0.06) |
| Inland | 1.02 (\pm 0.08) | 0.78 (\pm 0.08) | 0.91 (\pm 0.09) | 0.517 (0.10) |
| Margalef (α) | | | | |
| Border | 1.19 (\pm 0.11) | 1.24 (\pm 0.12) | 0.90 (\pm 0.11) | 0.62 (\pm 0.06) |
| Inland | 1.14 (\pm 0.09) | 0.79 (\pm 0.08) | 0.99 (\pm 0.12) | 0.64 (\pm 0.14) |

border areas, which suggests that any predation did not affect the dipteran larvae. Reproductive synchronization with environmental factors is widely reported for Chironomidae, since adults are short-lived and the larval development period is relatively long (Cheng & Frank, 1993), and decoupling from exogenous cycles could explain the lower densities observed in spring. However, replicated seasonal sampling would be necessary to evaluate whether an annual cycle of chironomid larvae reproduction exists.

Macrofaunal species density varied both spatially and temporally. Border and inland densities were similar in summer and autumn, whereas in winter and spring, densities were lower inland. Diversity and richness varied over time, and were lowest in spring. Macrofaunal richness was higher in the border samples, coinciding with the higher richness of algae, which probably increased the habitat complexity. *Dynoides castroi*, *Ampithoe ramondi* and *Perinereis* sp. occurred mostly on the border of the island. The crustaceans *D. castroi* and *A. ramondi* are herbivores, feeding preferentially on green algae such as *Cladophora* and *Ulva* (Pires-Vanin, 1981), and on *Sargassum* in the infralittoral zones of rocky shores (Jacobucci, 2005; Machado, 2013), as well as on filamentous algae such as *Hypnea*, *Ceramium* and *Cladophora* (Brawley & Adey, 1981; Machado, 2013). The abundance of these algae in the border area possibly favoured the presence of these crustaceans. Members of *Perinereis* are omnivorous polychaetes that feed on small crustaceans, larvae and filamentous green algae (Fauchald & Jumars, 1979). Their presence in the border area may be related to the wider variety of prey items compared with inland areas.

The composition and density variations of the Bostrychietum fauna of pneumatophores differ from observations on rocky-shore communities (Garcia & Leite, in preparation). The lower diversity and richness of species found in Araçá Bay, in both the border and inland areas, spatially and temporally, are probably due to differences in environmental conditions. The present results showed that the Bostrychietum microsystem features microscale variations in community composition, varying between areas with different emersion times and over time. This is a dynamic community of great importance for diversity in mangrove forests.

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