



Co-occurring morphologically distinct algae support a diverse associated fauna in the intertidal zone of Araçá Bay, Brazil

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Abstract: Species diversity is regulated by historical, neutral and niche processes, with species tolerance, dispersal and productivity guiding diversity at larger scales, while habitat heterogeneity and biotic interactions acts in smaller scales. In rocky shores, several organisms provide secondary substrates for mobile fauna, with macroalgae being the most abundant and diverse ones. The patchiness promoted by different macroalgae hosts enhances small-scale heterogeneity and may increase and maintain the diversity of the mobile organisms, since there is a close relationship between the associated fauna and its hosts. In this study we selected three morphologically different macroalgae that coexist in the same rocky shore height in the Araçá Bay, an area under the threat of the nearby harbor expansion, and evaluated the fauna associated to each algal host. Even under similar abiotic pressure (same rocky shore height), the associated fauna of each algal host varied in number and composition, revealing a close relationship. The poorly branched foliose *Ulva lactuca* sustained a lower density of organisms and was dominated by isopods, while the heavily branched turf and Bostrychietum community showed a high density of organisms, with a dominance of peracarid crustaceans and annelids on the turf and more resistant groups, such as bivalves, acarids and terrestrial insects on the Bostrychietum. Previous studies in the Araçá Bay already revealed a large spatial heterogeneity in the processes and sessile organisms distribution, and here we highlight that this heterogeneity can be observed in an even smaller scale, with different algal hosts mediating the turnover of species in a scale of centimeters and meters, resulting in diversity maintenance of the associated fauna. Since the harbor expansion may prevent the occurrence of macroalgae as a result of light limitation by suspended platforms, we may expect not only a decrease in algal cover but also in the total diversity of the associated fauna in the Araçá Bay.

Keywords: rocky shore, phytal, peracarids, structural complexity, spatial heterogeneity

Algas co-ocorrentes e morfologicamente distintas suportam uma diversa fauna associada na zona entremarés na Baía do Araçá, Brasil

Resumo: A diversidade de espécies é regulada por processos históricos, neutros e de nicho, com a tolerância das espécies, dispersão e produtividade do sistema guiando a diversidade em grandes escalas, enquanto a heterogeneidade do habitat e as interações bióticas atuam em escalas menores. Em costões rochosos uma série de organismos funciona como substrato secundário para a fauna móvel, sendo macroalgas o tipo mais abundante e diverso de substrato. O mosaico formado pelas diferentes macroalgas hospedeiras aumenta a heterogeneidade em pequena escala e pode aumentar e manter a diversidade dos organismos móveis, uma vez que existe uma relação próxima entre a fauna associada e seus hospedeiros. Neste estudo nós selecionamos três macroalgas diferentes morfologicamente e que coexistem na mesma altura no costão rochoso na Baía do Araçá, uma área sob a ameaça de expansão do porto que fica nas proximidades, e analisamos a fauna associada a cada alga hospedeira. Mesmo sob pressões abióticas similares (mesma altura no costão rochoso), a fauna associada a cada alga variou em número e composição, revelando de fato uma relação próxima entre fauna e alga. *Ulva lactuca*, uma alga foliosa com pouca ramificação, apresentou uma baixa densidade de organismos e foi dominada por isópodes, enquanto que o turf e o Bostrychietum, algas altamente ramificadas e mais complexas, apresentaram uma alta densidade de organismos, com uma dominância de crustáceos peracáridos e anelídeos no turf e grupos mais resistentes como bivalves, ácaros e insetos terrestres no Bostrychietum. Estudos anteriores conduzidos na Baía do Araçá já mostraram uma grande heterogeneidade espacial nos processos ecológicos e na distribuição dos

organismos sésseis, e aqui nós ressaltamos que esta heterogeneidade pode ser observada numa escala ainda menor, com as diferentes algas mediando o turnover de espécies numa escala de centímetros a metros, resultando na manutenção da diversidade da fauna associada. Como a expansão do porto pode impedir a ocorrência das macroalgas devido à limitação de luz que será imposta pelas plataformas flutuantes, nós podemos esperar não apenas uma diminuição da cobertura de macroalgas mas também da diversidade total da fauna associada na Baía do Araçá.

Palavras-chave: *costão rochoso, fital, peracáridos, complexidade estrutural, heterogeneidade espacial*

Introduction

The diversity of species in an ecosystem is determined by historical, neutral and niche processes acting on both large and small spatial scales, which combined will determine the biodiversity patterns in a global scale (Ricklefs 1987, Huston 1999, Shurin & Allen 2001, Navarrete et al. 2005). While in large-scale, diversity is usually regulated by species tolerances, dispersal and productivity (Menge & Olson 1990, Whittaker et al. 2001, Hawkins et al. 2004), in small-scale, habitat heterogeneity and biotic interactions, such as predation, competition and facilitation seems to be the main drivers of diversity (Menge & Sutherland 1976, Menge & Olson 1990, Hewitt et al. 2005, Wiens 2011, Wisz et al. 2012). Although macroscale investigations on species diversity have been recognized as of major importance in a changing world (e.g. climate change: Brown et al. 2000, Harley et al. 2006; bioinvasion: Molnar et al. 2008), understanding how diversity is shaped in smaller scales may contribute to its maintenance, but is still poorly explored.

Rocky shores are dynamic coastal habitats under periodically tidal variation, and represent a transition zone between terrestrial and marine environments, which are under contrasting physical conditions (Ewel et al. 2001, Wall et al. 2001). As a result, organisms are distributed across the shore in horizontal bands according to its resistance to air exposure and competitive ability (Stephenson & Stephenson 1972, Chappuis et al. 2014). However, studies looking at the processes affecting the diversity of benthic communities in the intertidal zone showed that besides the well-known drivers of zonation, variation in biological interactions and habitat heterogeneity at a scale of few centimeters or meters may play also an important role in the patterns of diversity (McGuinness & Underwood 1986, Shurin & Allen 2001, Fraschetti et al. 2005, Le Hir & Hily 2005, Gingold et al. 2010, Valdivia et al. 2014).

A wide array of organisms acting as secondary substrate inhabit the rocky intertidal and this mosaic of hosts may help increasing diversity locally, since communities may change among the different hosts in a scale of a few meters (e.g. Parker et al. 2001, Kelly et al. 2008). Intertidal macroalgae are among the most abundant and diverse secondary substrate in rocky shores. They vary in color and shape, range from subtidal areas to the upper midlittoral, and can harbor diverse assemblages, providing both shelter and food for the associated fauna (Christie et al. 2009). The tridimensional complexity may create micro-habitats that protect associated organisms against predators (Duffy & Hay 1991), wave action (Sotka 2007) and desiccation (Davenport et al. 1999), and may also trap sediments (Airold & Virgilio 1998), which may favor deposit feeder species (Prathey et al. 2003). Besides, the alga itself and the epiphytic assemblage supported by it may be used as food by associated animals (Viejo 1999), and differences in diet preferences and algal palatability may favor different faunas (Duffy & Hay 1991, Zamzow et al. 2010, Tavares et al. 2013, Machado et al. 2017). Thus, variation in both algal host attributes, and associated fauna needs in terms of habitat and food, results on species-specific interactions and, consequently, on a taxonomic diversity of associated organisms among coexisting macroalgae in the shore (Engelen et al. 2013, Best et al. 2014). In this way, the spatial heterogeneity of hosts and the algal identity may play a crucial role in maintaining the biodiversity in intertidal areas, reinforcing

the idea that conservation efforts should take into account different spatial scales (Thompson et al. 2002).

Coastal areas are among the ecosystems deeply affected by human activity, since most of the world's population inhabits coastlines (Dafforn et al. 2015). The introduction of man-made structures, such as harbors, piers, marinas and breakwaters (Bulleri & Chapman 2010, Mineur et al. 2012), and also the increased discharge of pollutants (Addison et al. 2008, Piola et al. 2009) are leading to a severe modification of coastal ecosystem functioning, mainly resulting in a loss of biodiversity (Airoldi et al. 2008, Magurran et al. 2015, Bianchelli et al. 2016). The Araçá Bay in the São Sebastião Channel, São Paulo – Brazil, is an area under intense anthropogenic influence as a result of São Sebastião Harbor proximity, which leads to frequent sewage discharges and oil spills for decades. However, the area still holds a high biodiversity and has socio-economic importance for the local fisherman community that conduct artisanal fishery and shellfish harvesting in the area (Amaral et al. 2010). Recently, the Araçá Bay system has been threatened by the plan of expansion of São Sebastião Harbor (for details check Pardal-Souza et al. 2017), which would lead to irreversible damages to this ecosystem. Although the plan consists in covering the bay with suspended platforms, a recent study conducted in the area has shown that the limitation of light imposed by the platforms may lead to significant changes in the structure of sessile and mobile community, reducing the occurrence of macroalgae (Pardal-Souza et al. 2017).

Since heterogeneous micro-habitats can sustain a variable community, our goal was to verify if coexisting macroalgal hosts support different communities, contributing to the maintenance of biodiversity in the Araçá Bay. We selected three distinct macroalgae occurring at the same zone in the shore and compared the associated community to understand the importance of the algal identity on setting the patterns of diversity of associated fauna. We expected to find distinct patterns of abundance of organisms, richness, evenness and diversity of groups, and community structures among hosts, reinforcing the idea that heterogeneity at small scales may help maintaining biodiversity in intertidal systems.

Material and Methods

1. Study Area

Sampling was conducted in the rocky shores of Pernambuco Island (23°48'54.9"S, 45°24'24.6"W), inside the Araçá Bay in the São Sebastião Channel, São Paulo – Brazil (for details check Amaral et al. 2010, Dias et al. in press). The Araçá Bay is a shallow bay that includes sandy and rocky shores, mud flats and mangroves (Dias et al. in press), sustaining a high biodiversity (Amaral et al. 2010). The rocky shore is composed by both platforms and variable sized boulders, which creates a heterogeneous and complex habitat (Amaral et al. 2016).

2. Sampling Procedure

To evaluate how the identity of co-occurring macroalgae can affect the associated fauna living on it, we selected three distinct algae: *Ulva lactuca* (Linnaeus 1753) – an ephemeral green alga with poorly branched foliose

fronds; *Bostrychietum* community – a group of red algae with heavily branched fronds, dominated by *Bostrychia* sp. (Montagne 1842) and that normally occurs on the upper portions of the intertidal zone (García et al. 2016); algal turf – dominated by the red filamentous algae *Gracilaria* sp. (Greville 1830) that mostly occurs in the intertidal fringe.

The samples consisted of 30 cores (10 for each alga) with an area of 36 cm² scraped along 20 m of a uniform rocky shore during a spring tide in July 2013. *Bostrychietum* beds extend from the supralittoral to the midlittoral while *Ulva* and turf beds extends from the midlittoral to the sublittoral fringe, so any difference in the associated fauna could be the result of habitat-specific traits or caused by the height of the algae on the shore. Because we were interested in the differences among associated fauna caused by the identity and the complexity created by secondary substrata, and not by differences in shore height, all samples were randomly collected in the midlittoral, where species distributions overlapped. Scraped samples were individually kept in alcohol 70% and then, in the laboratory, all organisms were separated and classified in major taxonomic groups. After separating the organisms, we quantified the volume of each sample in order to standardize the variables measured; however, since the volume did not differ among the three different algae ($F_{2,27} = 1.60$; $p = 0.221$), we decided to use the raw data, with no volume standardization.

3. Data Analyses

We compared the richness of taxonomic groups, evenness, Shannon diversity and total abundance of organisms with one-way ANOVA considering alga identity as a fixed factor. In order to achieve normality and homoscedasticity, abundance data was log transformed. For significant effects, we performed Tukey's test *a posteriori* for pairwise comparisons. Additionally, we performed separate analysis comparing the abundance of the most abundant groups among the algal species using the same ANOVA model.

To evaluate how the algal identity affects the structure of the associated fauna community, we used the abundances of all taxonomic groups in a multivariate approach, building a resemblance matrix using Bray-Curtis distance. The resemblance matrix was used in a PERMANOVA test with 999 unrestricted permutations of the raw data (Anderson 2001) using the same model explained above, and to build an n-MDS plot to better visualize groups relationship (Clark 1993). For significant factors, we performed a pairwise comparison (Anderson 2001) and then a SIMPER test to obtain the groups that most contributed to such significant effects (Clark 1993).

Results

We recorded 13,689 individuals of the following taxonomic groups: Amphipoda, Tanaidacea, Isopoda, Ostracoda, Cirripedia, Copepoda, Bivalvia, Gastropoda, Hydrozoa, Polychaeta, Oligochaeta, Nematoda, Rhabditophora, Ascidiacea, Bryozoa, Acari, Pycnogonida, Collembola, Diptera, Coleoptera and Lepidoptera. Amphipoda was the most abundant group, with 135±43 individuals per sample, followed by Bivalvia, with 85±18 individuals per sample, and Acari, with 60±22 individuals per sample.

Algal identity did not affect richness of groups, evenness and Shannon diversity, but influenced total abundance, with more individuals being observed on turf and *Bostrychietum* when compared to *Ulva* (Figure 1, Table 1). Each algal species also showed a specific community structure for the associated fauna, clustering separately in the n-MDS plot (Figure 2, Table 1). The groups that most contributed to the differences among algal species were Amphipoda, Tanaidacea, Oligochaeta and Polychaeta, more abundant on turf; Isopoda, more abundant on turf and *Ulva*; Nematoda, with similar abundance on the three algae; Bivalvia, more abundant on turf and *Bostrychietum*; and Acari and Diptera, more abundant on *Bostrychietum* (Figure 3, Table 2 and 3).

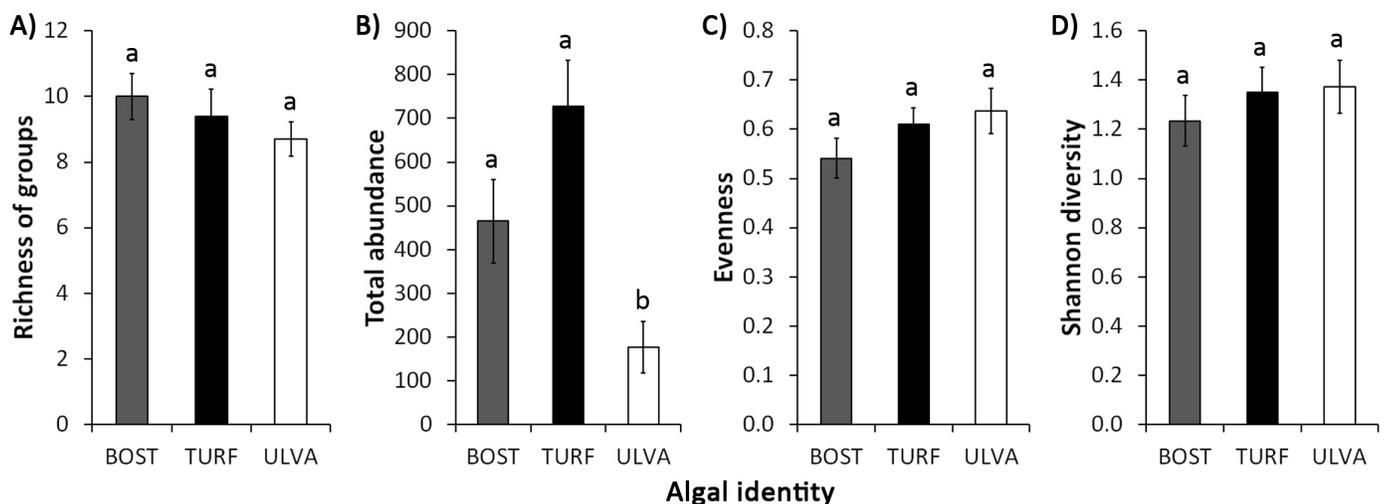


Figure 1. Mean (\pm SE) A) richness of groups, B) total abundance, C) evenness and D) Shannon diversity of faunal community associated to *Bostrychietum* (BOST), algal turf (TURF) and *Ulva lactuca* (ULVA) in the intertidal fringe of Araçá Bay. For each variable, differences between algae sharing a single letter are not significant ($p > 0.05$).

Table 1. Summary results of ANOVAs for richness of groups, total abundance, evenness and Shannon diversity, and PERMANOVA for community structure, comparing these attributes of associated fauna among *Bostrychietum*, algal turf and *Ulva lactuca*. 'ns' – non-significant; '***' – $p < 0.001$.

Source	Richness of Groups				Total Abundance			Evenness			Shannon Diversity			Community Structure		
	DF	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	Pseudo-F	P
Algal Identity	2	4.23	0.89	ns	6.25	13.8	***	0.024	1.5	ns	0.055	0.5	ns	8733	12.6	***
Error	27	4.76			0.45			0.016			0.107			695		

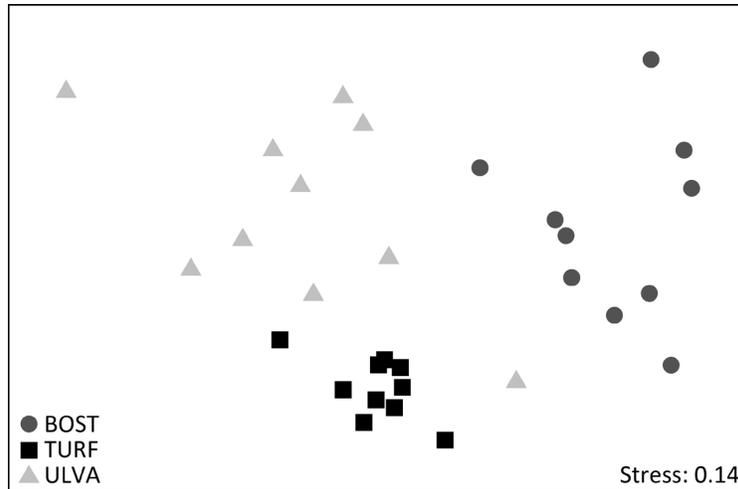


Figure 2. nMDS plot of abundance of all taxonomic groups of faunal communities associated to Bostrychietum (BOST – dark gray circles), algal turf (TURF – black squares) and *Ulva lactuca* (ULVA – light gray triangles) in the intertidal fringe of Araçá Bay.

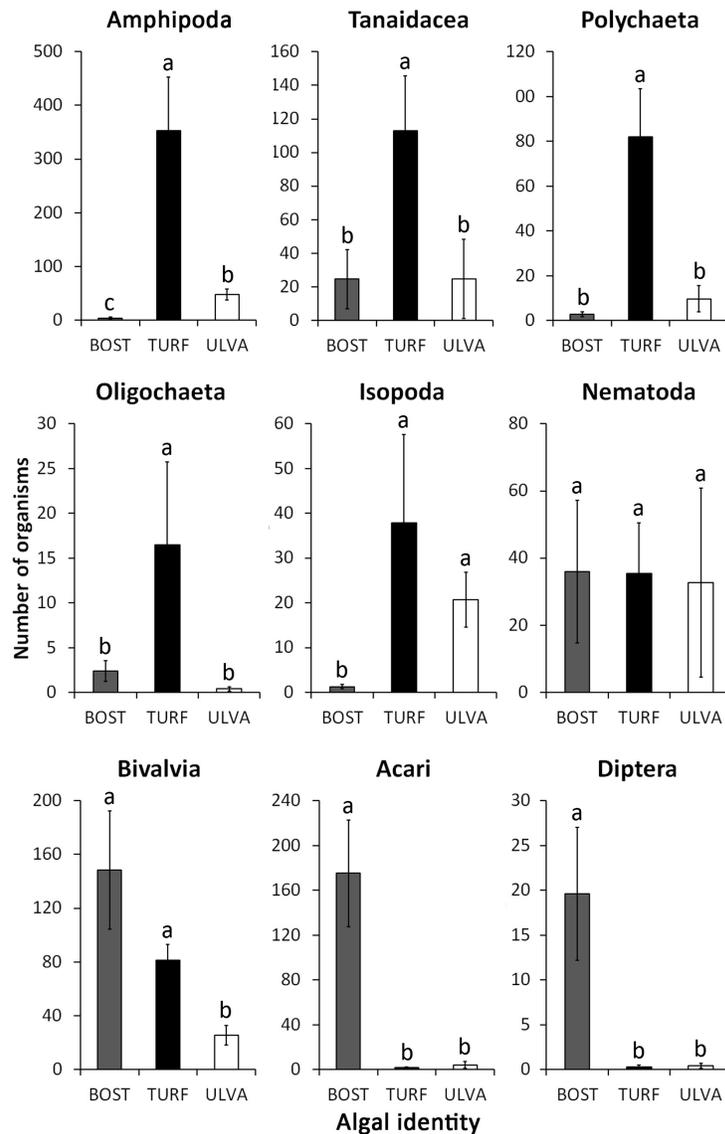


Figure 3. Mean abundance (\pm SE) of the most abundant groups of faunal communities associated to Bostrychietum (BOST – dark gray), algal turf (TURF – black) and *Ulva lactuca* (ULVA – light gray) in the intertidal fringe of Araçá Bay. For each taxonomic group, differences between algae sharing a single letter are not significant ($p > 0.05$).

Table 2. SIMPER results showing the relative contribution (%) of the five taxonomic groups that most contributed to significant differences among associated fauna of Bostrychietum (B), algal turf (T) and *Ulva lactuca* (U). Abbreviations in front of each taxa stand for the alga in which the group was more abundant.

<i>B x T</i>		<i>B x U</i>		<i>T x U</i>	
Group	(%)	Group	(%)	Group	(%)
Amphipoda (T)	15.16	Acari (B)	16.61	Tanaidacea (T)	17.48
Acari (B)	14.95	Amphipoda (U)	11.70	Polychaeta (T)	12.55
Polychaeta (T)	11.43	Diptera (B)	8.62	Nematoda (T)	9.66
Tanaidacea (T)	10.34	Bivalvia (B)	8.41	Amphipoda (T)	8.75
Diptera (B)	7.62	Isopoda (U)	8.26	Oligochaeta (T)	8.42

Table 3. Summary results of ANOVAs comparing the abundance of the most abundant groups of associated fauna among Bostrychietum, algal turf and *Ulva lactuca*. 'ns' – non-significant; '***' – $p < 0.01$; '****' – $p < 0.001$.

Source	<i>Amphipoda</i>				<i>Tanaidacea</i>			<i>Isopoda</i>		
	DF	MS	F	P	MS	F	P	MS	F	P
Algal Identity	2	8.87	35.8	***	5.77	12.98	***	2.19	7.13	**
Error	27	0.25			0.45			0.31		
Source	<i>Oligochaeta</i>				<i>Polychaeta</i>			<i>Nematoda</i>		
	DF	MS	F	P	MS	F	P	MS	F	P
Algal Identity	2	1.49	7.50	**	5.48	26.90	***	0.74	1.57	ns
Error	27	0.20			0.20			0.47		
Source	<i>Bivalvia</i>				<i>Acari</i>			<i>Diptera</i>		
	DF	MS	F	P	MS	F	P	MS	F	P
Algal Identity	2	1.83	10.06	***	10.30	54.80	***	2.91	21.55	***
Error	27	0.18			0.19			0.14		

Discussion

We show that even under similar abiotic pressure (same rocky shore height), different coexisting algae influenced the fauna associated to them. Although we did not observe the effect of algal identity on all community metrics, the abundance of organisms and the community structure were particular for each algal host, showing a strong taxon-specificity between host and associated fauna, in a way that the coexisting algae increase the turnover and total diversity of animals in the Araçá Bay. Besides, more complex algae (Bostrychietum and turf) sustained higher abundances, reinforcing the idea that complexity creates an array of micro-habitats in different scales that supports more individuals.

Habitat complexity has been recognized as of major importance on characterizing the spatial distribution of species from intertidal areas (Beck 1998, 2000). Complex substrates are expected to provide several resources, allowing the maintenance of more abundant and diverse assemblages with different survival requirements (e.g. Hicks 1977). Within the macroalgae, higher branching can support higher faunal abundances by supplying additional surface for attachment (Hacker & Steneck 1990) or by offering higher interstitial volume (Bueno et al. 2017). In our study, the highly branched turf and Bostrychietum hosted higher abundances of faunal groups, while the smooth sheet-like blades of *Ulva* supported less individuals, both accounting for the total as well as for the most abundant groups (Amphipoda, Bivalvia and Acari). The lower number of individuals on *Ulva* may be an effect of the reduced surface rugosity, demanding much effort for animals to keep anchored, as observed for amphipods (Hacker & Steneck 1990). Besides, it does not provide as many refuges as intricate canopies (Zamzow et al. 2010), resulting in a very specific fauna inhabiting *Ulva* blades (Corte et al. 2012). Habitat selection on macroalgae can be size-dependent (Hacker and Steneck 1990), and the spaces between the overlapping blades of *Ulva* could be sufficient as shelter from predation for small, but not for large species (Holmlund et al. 1990).

The turf, mainly composed by *Gracilaria* in our study, hosted the highest abundances of most faunal groups, especially the peracarid crustaceans (Amphipoda, Tanaidacea and Isopoda) and annelids (Polychaeta and Oligochaeta). In shores from the Northwestern Atlantic Ocean, patches of *Gracilaria vermiculophylla* (Papenfuss 1967) are effective shelters for the amphipod *Gammarus mucronatus* (Say 1818) regarding both desiccation and predation risks (Wright et al. 2014). Turfs intricate canopy can retain water and ameliorate conditions during periods of air exposure (Bertness et al. 1999), enhancing the survivorship of *G. mucronatus* during low tides (Wright et al. 2014). During high tides, *G. mucronatus* on algal turf, similar to the studied here, were less prone to be detected by predators (Wright et al. 2014). We believe that such algal attributes would work for most of the groups found on the algal turf in Araçá Bay, representing then a suitable refuge from biotic and abiotic pressures.

Algae belonging to the Bostrychietum community are frequently found on upper intertidal areas on both rocky shores and mangroves. Since this region is under high abiotic stress (Connell 1972), it is expected that Bostrychietum species living in such region show adaptations to deal with emersion periods, as observed to *Bostreyhia radicans* (Montagne 1842), which sustained maximum photosynthetic rates, constant respiratory rates and a fast recovery after relatively long periods of desiccation (Mann & Steinke, 1988). Since the spatial distribution of macroalgae associated fauna can be related to host identity and vertical position on the shore (Bueno et al. 2017), faunal assemblages could develop a close relation with their host and occupy different levels on the shore. Mites (Acari), for example, use Bostrychietum as habitat and source of food and their spatial distribution on rocky shores is closely related to the host position (Pfungstl 2013). As previously observed for Bostrychietum covering mangrove pneumatophores in the same area (García et al. 2016), the rocky shore Bostrychietum in our study showed the presence of more resistant organisms like bivalves, acaris, and typically terrestrial animals, such as insects. The occurrence of these organisms in the lower limit of

Bostrychietum bed in the midlittoral zone may reflect a close algal-fauna association and, in turn, a side-effect of insects using the algae as a proxy of the height in the shore.

While the turf and Bostrychietum are more perennial algae, *Ulva* is an ephemeral species that commonly increases the occurrence or abundance after nutrient input (Chávez-Sánchez et al. 2017, Dias et al. in press). The variation in abundance and occurrence of ephemeral algal species may contribute to promote temporal heterogeneity that was not explored here. The temporal variability of host coupled with the spatial heterogeneity imposed by perennial hosts may enhance diversity maintenance (Chesson 2000). Although we do not know if the differences of associated fauna composition observed among the three algal hosts sampled here will be maintained through time, the alternation between higher discrepancy and higher similarity among the associated fauna of different algal hosts will also impose temporal variation and does contribute to heterogeneity in such scale, maintaining diversity (Menge & Sutherland 1976).

Benthic communities in the entrance of the Araçá Bay are more dynamic and controlled by oceanic processes operating at the São Sebastião Channel, while those at the inner portion of the bay are under the influence of Mãe Isabel River (Corte et al. 2017, Gorman et al. 2017, Dias et al. in press). As a consequence of this variable influence, the bay becomes shallower and richer in organic matter (Corte et al. 2017), and also receives a higher nitrogen input (Gorman et al. 2017) towards the inner portion. This environmental gradient spatially affects population dynamic of barnacles (Dias et al. in press) and also the community structure of sessile species in spatial and temporal scales (Kitazawa et al. in prep.). Here we show that the heterogeneity in the Araçá Bay is also observed in an even smaller scale, being mediated by the patchiness promoted by different algal hosts to the associated fauna. While the maintenance of such small-scale heterogeneity is important to guarantee refuges, acting as reservoirs to rare species (Hewitt et al. 2005, 2010), the maintenance of variation in a larger scale is also crucial, since local diversity does not depend solely on ecological processes, but is linked to the regional pool of species in marine communities, which highlights the importance of protecting larger areas (Witman et al. 2004) such as the Araçá Bay.

Our results corroborate the idea that community organization, in terms of abundance and community structure here, can vary in a considerable small-scale in the intertidal system (algal patches within the same rocky shore height) and, in our study, this is related to the heterogeneity promoted by different algal host holding specific associated faunas. Although we did not observe differences of richness, evenness and Shannon diversity, we believe that increasing the taxonomic resolution would result in differences in such metrics too. This is crucial to diversity maintenance not only in the local scale (among patches), but also in larger scales (regional diversity), with broad implications to conservation, especially today with the anthropogenic threat that most coastal systems have been facing, such as the Araçá Bay. The expansion of São Sebastião Harbor may lead not only to a homogenization of conditions, which may result on the survivorship of only few resistant species, but will also preclude algae survivorship through light limitation caused by the suspended platforms (Pardal-Souza et al. 2017). As a consequence, following the decrease of diversity of macroalgae species, we may also expect a great loss of diversity of associated organisms, since they are closely related to their hosts.

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Authors' Contributions

HRF and GMD substantially contributed in the concept and design of the study and to data collection.

EAV, HRF and GMD contributed to data analysis and interpretation.

EAV, HRF, MB, FPPL and GMD contributed to manuscript preparation and critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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