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Physical contact interactions with scleractinian corals in hard substrate communities

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Abstract

Shallow reefs are among the most diverse ecosystems, and their substrate is densely occupied by sessile organisms that frequently contact physically and interact mutually. Nevertheless, the relative importance of species abundance in shaping physical contacts in these ecosystems remains largely unknown. The aim of this study was to evaluate physical contact interactions, by using tools derived from the complex network theory, between hard corals and other benthic organisms in four areas along the Brazilian coast comprising coral reefs and rocky shores with different physical and biotic structures. It was also investigated whether interactions with corals occurred as expected by the abundance of the benthic organisms in each area, and whether corals belonging to families known as more aggressive interacted less with other organisms. In all areas, the abundance of both corals and contacting organisms directly influenced the abundance of interactions between benthic organisms, regardless of the physical or biological characteristics of the habitat and of the interacting organisms. In addition, coral species interacted more with the most abundant benthic group, the epilithic algal matrix, in all areas. Nevertheless, some evidence was found about biological mechanisms helping to explain the structure of the studied interactions, although to a lesser extent. The obtained networks presented high nestedness and connectance, but low modularity. These patterns indicate the low specificity of the studied interactions and reinforce the role of abundance as an important driver of contacts between sessile organisms in shallow hard bottom ecosystems.

KEYWORDS

benthic community, biological interactions, coral reef, interaction networks, rocky reef, South Atlantic

1 | INTRODUCTION

Shallow reefs are one of the most diverse and productive ecosystems, as they have some of the highest levels of species richness and densities of species per unit area (Coutinho et al., 2016; Spalding, Ravilious, & Green, 2001). These hard substrate ecosystems are also characterized by their high diversity of ecological interactions, which mediates co-existence among numerous organisms within the same habitat (Spalding et al., 2001). For sessile organisms, space on the reef substrate is a limiting resource (Dayton, 1971). As a result, they frequently interact physically. These physical contact interactions can be related to biotic interactions, e.g., facilitation and competition, between species. Some species of crustose coralline algae, for example, can induce the settlement and metamorphosis of coral larvae by chemical means (Heyward & Negri, 1999; Morse, Hooker, Morse, & Jensen, 1988), resulting in contact between them. In contrast, when competing for space, sessile individuals or colonies can overgrow others and even kill the subordinate organism (Aerts, 1998; Bruno & Witman, 1996). Therefore, interactions among sessile species, related to physical contact between them, may directly influence their fitness and survival,

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which, in turn, can affect the patterns of distribution and abundance of benthic species (e.g., Foster, Box, & Mumby, 2008; Lapid & Chadwick, 2006).

As a mechanism to avoid interference competition, i.e., competition for space in which competitors interact physically, e.g., by overgrowth, some species have evolved defense mechanisms. In the case of scleractinian corals, mesenterial filaments or sweeper tentacles, for example, can damage the tissue of competitors and thus increase the distance between them (Lang, 1971; Lapid, Wielgus, & Chadwick-Furman, 2004; Nugues, Delvoye, & Bak, 2004; Richardson, Dustan, & Lang, 1979). Among the different groups of zooxanthellate scleractinian corals, Mussidae and Montastraeidae are two of the most aggressive, as they frequently damage outcompeting corals (Chornesky & Williams, 1983; Lang, 1973; Logan, 1984). Corals in these families may increase their distance to other organisms in this way, thus gaining more space for their own growth on the substrate (Chornesky & Williams, 1983; Lang, 1973; Logan, 1984; Richardson et al., 1979).

Because of the importance of ecological interactions in the structure and dynamics of some natural communities, different techniques have been applied to characterize them. In this sense, studies on ecological interactions have increasingly used tools derived from complex network theory to understand the structure and dynamics of interactions (e.g., Araújo et al., 2008; Bascompte, Jordano, Melian, & Olesen, 2003; Dáttilo, Marquitti, Guimarães, & Izzo, 2014). In this approach, the interacting organisms are graphically represented by nodes connected by links that represent the interactions (Bascompte, 2007). By highlighting the connections among organisms, rather than the organisms themselves, this method allows comparisons of different types of interactions in space and time (Bascompte, 2007, 2009).

Studies on ecological interactions have shown that the structure of mutualistic and antagonistic interaction networks can be primarily driven by species abundance (e.g., Canard et al., 2014; Dupont, Hansen, & Olesen, 2003; Krishna, Guimarães, Jordano, & Bascompte, 2008; Vázquez et al., 2007). This importance of the abundance of species in network structure characterizes the neutrality hypothesis, in which individuals interact randomly, regardless of their biological traits, so that the frequency of interaction between abundant species is higher than that of rarer species (Krishna et al., 2008; Vázquez, Poulin, Krasnov, & Shenbrot, 2005; Vázquez et al., 2007). The uneven distribution of species abundance may lead to an asymmetric topology of the network in terms of number of links per species so that most rare species interact with abundant species and few interactions occur within rare species (Bascompte et al., 2003; Vázquez & Aizen, 2004; Vázquez et al., 2005). In this sense, species abundance can significantly affect ecological interactions by determining which organisms have a higher frequency and abundance of interaction with other organisms in the network.

Apart from the species abundance and the biotic interactions between/among species, abiotic factors can also influence the structure of communities (e.g., Bauman, Feary, Heron, Pratchett, & Burt, 2013; Dumas, Kulbicki, Chifflet, Fichez, & Ferraris, 2007). Moreover, some studies have highlighted the influence of physical conditions on the interactions between species (Bertness & Callaway, 1994; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). In benthic environments, the type of matrix or substrate is related to the organisms that settle over it, as well as influencing the heterogeneity and structural complexity of the habitat, and thus, species diversity (Cordeiro, Harborne, & Ferreira, 2014; Kostylev, Erlandsson, Ming, & Williams, 2005; Pratchett et al., 2008).

Despite the high diversity of species and interactions in coral reef and rocky shore ecosystems, no study, to our knowledge, has used tools from the complex network theory to analyse the relative importance of species abundance and to assess physical contact interactions in benthic communities. This is the first time such an approach has been used to investigate interactions in marine hard substrate communities at a broad geographic scale. Thus, the aim of this work was to evaluate physical contact interactions between corals and other sessile organisms in four areas along the Brazilian coast, which present differences in their biological and geological frameworks. We first assessed the benthic community in the four hard substrate areas through the percent cover of organisms. Thereafter, we analysed the structure of physical contact interactions between corals and neighboring sessile organisms in each area by using tools from the complex network theory. Furthermore, we addressed the following questions: (i) do interactions of corals with benthic organisms occur as expected by the abundance of the organisms in each area?; (ii) do biological features, such as aggressiveness in some corals (e.g., Mussidae and Montastraeidae), influence physical interaction patterns by reducing the number of contacts between corals and other groups of organisms?

2 | MATERIAL AND METHODS

2.1 | Study areas

This study was conducted in four areas along the Brazilian coast, Southwestern Atlantic: Todos os Santos Bay (TSB), Abrolhos (ABR), Arraial do Cabo (ARC) and São Paulo (SAP) (Figure 1). TSB (12°S, 38°W) and ABR (17°S, 38°W) are located in the state of Bahia, on the tropical Eastern Brazilian coast (Leão, Kikuchi, & Testa, 2003), which is the largest coral reef area in Brazil (Leão et al., 2016). TSB is the second largest Brazilian bay, with an area of approximately 1,000 km^2 (Lessa, Bittencourt, Brichta, & Dominguez, 2000) and an average sea surface temperature of 27.5°C, varying from 24.4 to 30.6°C (Selig, Casey, & Bruno, 2010). Although human development around the bay, primarily subsequent to the 1950s, has strongly affected the reef community and diminished coral abundance in this area, these reefs still sustain some of the highest levels of coral cover in Brazil (Dutra, Kikuchi, & Leão, 2006). ABR, located approximately 60 km off the coast, represents the largest and richest coral reef system in the South Atlantic (Leão et al., 2003). It harbors almost all Brazilian scleractinian coral species identified to date (Leão et al., 2003; Neves, da Silveira, Pichon, & Johnsson, 2010). The mean sea surface temperature in ABR is 26.5°C, and ranges from 23.5 to 29.6°C (Selig et al., 2010).

Arraial do Cabo (22°S, 41°W), in the state of Rio de Janeiro, and SAP (24°S, 45°W), in the state of São Paulo, are on the Southern Brazilian coast (Leão et al., 2003), in the transitional zone between

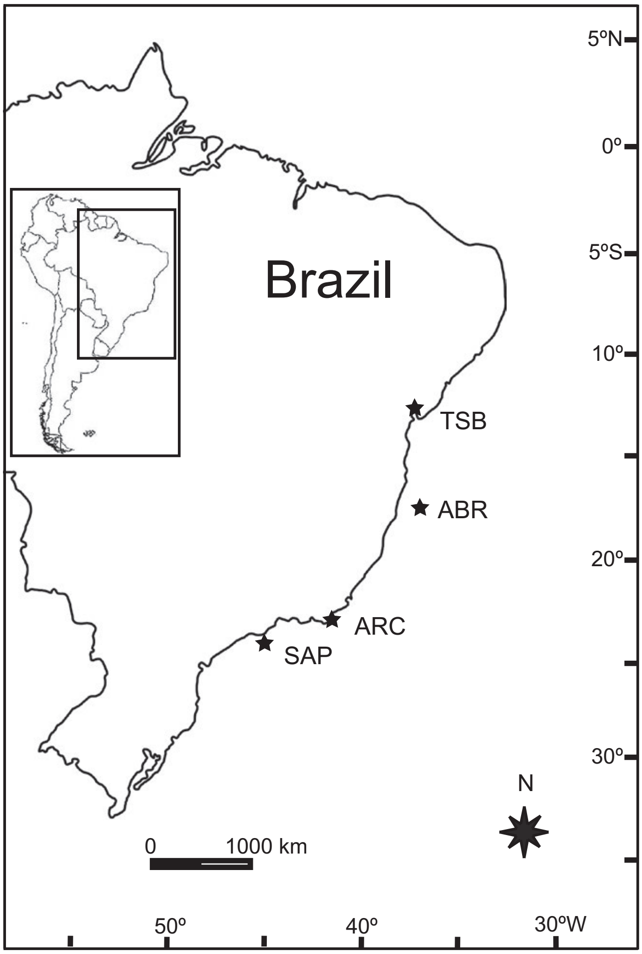

FIGURE 1 Study areas on the Brazilian coast. TSB, Todos os Santos Bay; ABR, Abrolhos; ARC, Arraial do Cabo; SAP, São Paulo

the tropical and subtropical regions. This area is considered as a marginal environment, which limits the development of coral reef ecosystems (Kleypas, McManus, & Meñez, 1999; Leão et al., 2003; Perry & Larcombe, 2003). From this area to the south, corals do not form reef frameworks as only scattered coral colonies occur over rocks, which represent the most extensive rocky shores in the Brazilian coast (Coutinho et al., 2016). Also, due to their framework, these habitats present lower structural complexity than eastern reefs. Although coral cover decreases from Northeastern to Southern Brazilian reefs (Leão et al., 2003), the occurrence of upwelling phenomena in ARC sustain a relatively richer benthic community and higher coral cover when compared to other marginal Brazilian sites (Castro, Echeverría, Pires, Mascarenhas, & Freitas, 1995; Lima & Coutinho, 2016; Oigman-Pszczol, Figueiredo, & Creed, 2004). Average sea surface temperature in this region is 23.6°C, varying from 20.6 to 26.7°C (Selig et al., 2010). SAP has an average sea surface temperature of 23.5°C, varying from 20.1 to 26.9°C (Selig et al., 2010), and the poorest coral species richness among the four study areas, with two species of zooxanthellate scleractinian corals (Amaral & Nallin, 2011). In this area, corals generally occur as isolated communities on bedrock. The sites sampled in SAP are located on the archipelagos of Alcatrazes (36 km off the coast) and Ilhabela (2.5 km off the coast).

2.2 | Data collection

Physical contact interactions (hereafter termed interactions) between hard corals and neighboring sessile organisms were surveyed through photoquadrats in the four study areas. Photographs were taken from a superior angle at horizontal reef tops, avoiding vertical walls, between 2 and 11 m deep. Sampling was conducted during the austral summers of 2010 to 2013 (December to March in each sampled year). In each study area, three or four sites were sampled (total of 13 sampled sites). Within each sampled site, approximately 25 zones of 2 m^2 (here termed plots) were haphazardly delimited. In these plots, between 5 and 12 photoquadrats, each 25 × 25 cm (625 cm^2) in surface area, were haphazardly taken (i.e., 77–413 photos per site; 2,628 photos in total). The number of plots delimited and of photoquadrats taken varied according to the sites because of the extension of the reefs and rocky shores. Photos used were taken from the image bank of Project SISBIOTA–Mar (www.sisbiota.ufsc.br).

The abundance of sessile organisms was assessed using a subsample of 14–22 of the plots (five photos each) with the best photographic quality in each site. The photoquadrats within these plots were analysed to obtain the percent cover in each area using the software PHOTOQUAD v. 1.3 (Trygonis & Sini, 2012). Percent cover was used as an estimate for abundance of sessile organisms in the present study (following Spalding, Foster, & Heine, 2003; Oigman-Pszczol et al., 2004) because of the difficulty in counting individuals for modular organisms such as corals. For this measurement, 50 random points were placed over each photo, and the organism immediately under each point was visually identified to the lowest taxonomic level possible. In some cases, organisms were assigned to morpho-functional categories (hereafter termed categories) due to limitations in identifying organisms using photos. Anemones, scleractinian and hydrozoan corals were identified to species or genus. Some zoanthids were identified to species, whereas others were identified to a single broad category. Ascidians and cyanobacteria were also each placed into single major categories. Sponges were identified to morphological categories (following Bell & Barnes, 2001) and algae were identified to morpho-functional categories (modified from Steneck & Dethier, 1994; some categories were adjusted according to the level of identification we could obtain with our methodology). Among the algae, the 'epilithic algal matrix' (EAM) refers to algal assemblages composed of a mixture of calcareous and filamentous species, with associated organic matter, fauna and trapped sediments (Wilson, Bellwood, Choat, & Furnas, 2003). Percent cover data used were taken from the database of Project SISBIOTA–Mar.

To assess interactions with scleractinian corals, only those photographs containing entire coral colonies were selected from all the photographs available, resulting in a total of 2,182 colonies being examined. Contact interactions could be relatively well assessed with photographs mostly because of the predominance of small, massive colonies in our study, and by the low three-dimensionality of Brazilian reef surfaces. Still, colonies of three species were not considered for this assessment. First, the mushroom-like form of *Mussismilia braziliensis* and phaceloid morphology of *Mussismilia harttii*, apart from their large sizes, did not allow the visualization of all contacts with the borders of their colonies solely with photographs that were taken from a superior angle. Also, as *Madracis decactis* generally inhabits shaded areas, most neighboring organisms contacting colonies of this species could not be clearly distinguished. In each of these photographs, the visible perimeter of each colony was traced and calculated with IMAGEJ v. 1.48 software (Schneider, Rasband, & Eliceiri, 2012). The perimeter of the colony contacting each different neighboring organism was then calculated to obtain quantitative data on the interaction, and the organisms involved in the interaction were identified into the same categories as described above. The interaction abundance of each coral species versus each neighboring organism category was considered as the mean perimeter of the contact between a given coral species with each neighboring organism.

The measurements of colonies and contact areas were all conducted by one person (A.C.G.) to provide a better standardization of the method than using more than one person. In some cases corals did not contact other organisms but contacted sediment, the only non-living category recorded. We only considered a contact interaction when the borders of the organisms were in touch, although it is known that mesenterial filaments and sweeper tentacles of some corals can contact organisms as far as 5 cm or more (Nugues et al., 2004; Richardson et al., 1979). Because our methodology was based on photographs, we could not confirm the extrusion of mesenterial filaments or the presence of sweeper tentacles in the colonies assessed. We considered *Mussismilia hispida* and *Favia gravida* as members of Mussidae, and *Montastraea cavernosa* as a Montastraeidae (following Budd, Fukami, Smith, & Knowlton, 2012).

2.3 | Interaction networks

Tools derived from complex network theory were used to provide a visualization of the studied interactions and to analyse and describe the structure of interactions. For each area, a bipartite network was built to represent the physical contact interaction (links) between corals and neighboring sessile organisms (nodes). Networks were built using quantitative interaction data (i.e., interaction abundance) and the *igraph* package (Csardi & Nepusz, 2006) in R version 3.1.3 for Mac OS X (R Core Team, 2015, 2017). We were unable to construct a network for SAP as we only assessed contact interactions with one coral species. The other species surveyed in this area (*Madracis decactis*) could not be analysed through photographs due to its cryptic habitat.

To characterize and compare network topologies among the three remaining study areas, we used metrics based on the presence and absence of interactions (i.e., unweighted links). The following metrics were calculated for each qualitative network: degree for each interacting category, connectance, nestedness and modularity. Degree (k) refers to the number of links per node, i.e., the number of categories interacting with a certain category. Therefore, degree represents how generalist an organism is in terms of interaction (Bascompte & Jordano, 2007). Connectance indicates the proportion of all possible interactions actually observed in the network, ranging from 0 to 1 (Jordano, 1987). A high connectance suggests a high level of interaction among all the organisms in the network, which corresponds to a low specificity of interaction. For a fully connected network, $C = 1$; for a random network, $C = \langle k \rangle / N$, where $\langle k \rangle$ is the average number of links per node and N is the total number of nodes in the web. The clustering coefficient relates to the local 'cliqueness' in a web and can represent a type of modularity index. In a random graph, the clustering coefficient is equal to the connectance.

Nestedness refers to a pattern of network interactions in which specialist nodes interact with a subset of the nodes interacting with generalist nodes (Bascompte et al., 2003). A nested network results in a core of highly connected species, which can lead to functional redundancy in the system, and in asymmetric interactions, i.e., specialists interacting with the most generalist species, which can support the survival of rare specialists (Bascompte et al., 2003; Jordano, 1987). This metric was obtained using the Nestedness metric based on Overlap and Decreasing Fill (NODF) index (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008) in the software ANINHADO (Guimarães & Guimarães, 2006). NODF ranges from 0 to 100, with higher values representing a more nested network. The significance of nestedness was tested for each network by generating 1,000 replicates using the Ce model, or null model 2, approach (see Guimarães & Guimarães, 2006).

Modularity describes the formation of modules within the network. These modules correspond to nodes that are more highly connected to each other than they are to other nodes in the network (Olesen, Bascompte, Dupont, & Jordano, 2007). The presence of modules can result from affinity among organisms due to biological or ecological traits (Olesen et al., 2007; Prado & Lewinsohn, 2004). This metric ranges from 0 to 1, with increasing values indicating more isolated modules. Modularity (M) was estimated using the Newman and Girvan's Q metric (Newman & Girvan, 2004) and a simulated annealing optimization procedure (Guimerà & Amaral, 2005), with the software MODULAR (Marquitti, Guimarães, Pires, & Bittencourt, 2014). The significance of M was tested for each network using a null model approach in which 1,000 theoretical networks, of equal richness of categories and similar heterogeneity concerning interactions among categories, were generated. M values were calculated for each network, and they were compared to the observed M value of the empirical network to assess whether this was higher than expected for the theoretical networks (Null Model II; Bascompte et al., 2003).

Studies have highlighted that interaction types might determine specific architectures of networks. In this study, we could not define the type of interaction between benthic organisms given the limited information on the biology and natural history of most species in the studied areas and because we could not identify all the organisms to the species level. Considering some previous studies (e.g., Hadfield & Paul, 2001; Lang, 1973; McCook, Jompa, & Diaz-Pulido, 2001; Miranda, Cruz, & Barros, 2016), our networks certainly included several types of ecological interactions (e.g., mutualistic, neutral and antagonistic), combined into one physical contact interaction network. Thus, we were merging different types of ecological interactions, an approach that has been encouraged because it offers a more faithful representation of natural communities (Fontaine et al., 2011).

2.4 | Statistical analyses

To analyse differences in the percent cover of each benthic category between the four study areas we performed Kruskal–Wallis non-parametric analyses of variance (ANOVAs) in R version 3.3.3 for Mac OS X (R Core Team, 2015, 2017). We did not test for unidentified organisms and sediment. For significant categories, a post-hoc Nemenyi test was applied for individual pairwise comparisons to show which areas presented statistically different percent covers.

To investigate whether the interactions of corals with neighboring organisms occurred as expected from their abundances, or whether more aggressive corals (Mussidae and Montastraeidae) interacted less than expected by their abundances with other organisms, we compared the interaction abundance of coral–neighboring organism pairs with their abundance (mean % cover) in each study area. G-tests for goodness-of-fit were calculated to compare the observed interaction abundance of coral–neighboring organism pairs with the expected interaction abundances of the same interacting pair (modified from Bonaldo & Hay, 2014). The expected interaction abundance for each coral–neighboring organism pair was calculated by the product of the abundance (mean % cover) of the given coral species and the abundance (mean % cover) of the neighboring organism in each study area (following Blüthgen, Fründ, Vázquez, & Menzel, 2008). This value was then multiplied by the mean colony perimeter of the coral species. Because of the low frequency of occurrence of some interactions, *p*-values were obtained by comparing the obtained G-value with those from non-parametric randomization tests (1,000 repetitions; Manly, 1997). We could not test the corals *Porites branneri* in ABR and ARC or *Favia gravida* in ABR as they were not found during the species abundance assessments.

3 | RESULTS

Percent cover of all categories of sessile organisms differed between the four benthic communities studied ($p < .05$), with the exceptions of the coral species *Madracis decactis* (Kruskal–Wallis ANOVA, $p = .06$, $n = 223$) and foliose algae (Kruskal–Wallis ANOVA, $p = .19$, $n = 223$) (Figure 2; Tables S1 and S2). The highest coral covers were found in TSB (*Montastraea cavernosa*, mean ± SE = 15.65 ± 1.85%, $n = 59$) and in ABR (*Mussismilia braziliensis*, mean ± SE = 6.26 ± 0.98%, $n = 45$) (Figure 2; Table S1). Across the four study areas, the highest benthic cover was represented by the EAM, which ranged between 50% and 60% of the total cover. ABR was the richest area in terms of number of coral species (TSB: five, ABR: eight, ARC: three, SAP: two), as well as of all benthic categories combined (TSB: 18, ABR: 25, ARC: 20, SAP: 15).

The total number of categories (i.e., considering corals and neighboring organisms) interacting physically was 24 in ABR, 18 in TSB, 17 in ARC and 11 in SAP, with a clear decrease from the most to least diverse area. Not all organisms identified during the benthic assessments were observed in the networks of physical contact interactions. The percentage of categories recorded within each location that interacted with corals was 88% in ABR, 83.33% in TSB, 75% in ARC and 73.33% in SAP.

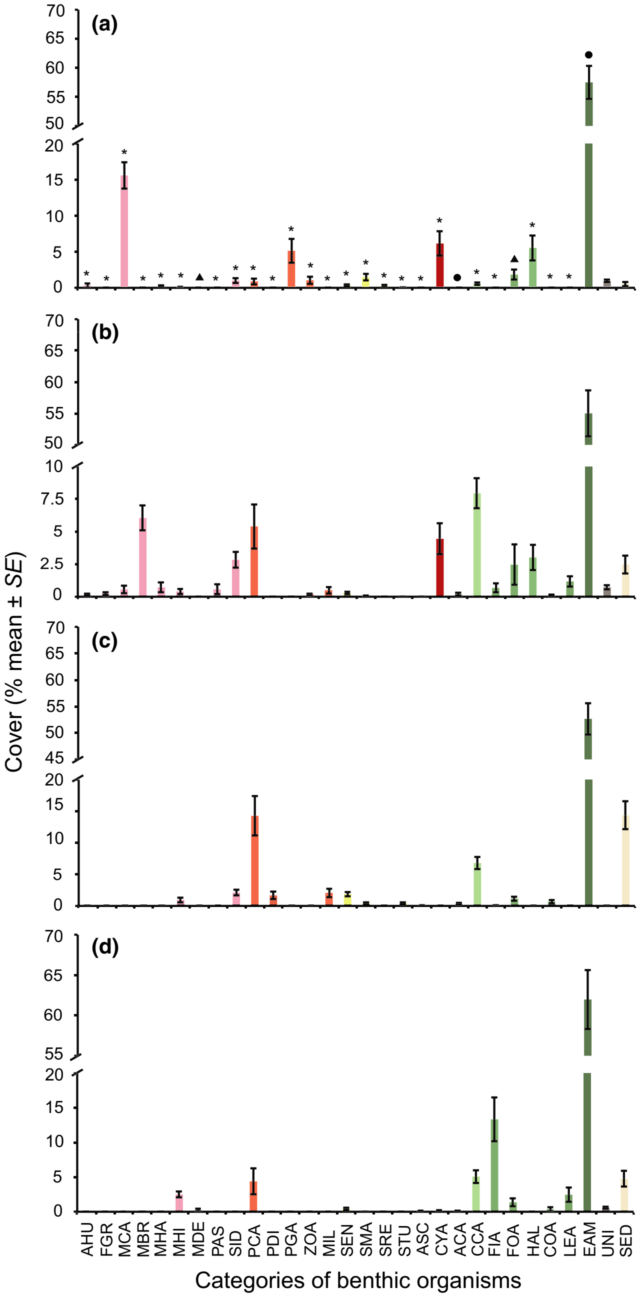

FIGURE 2 Benthic cover (% mean ± SE) of organisms in four study areas along the Brazilian coast. (a): Todos os Santos Bay ($n = 59$), (b): Abrolhos ($n = 45$), (c): Arraial do Cabo ($n = 53$) and (d): São Paulo ($n = 66$). Color shades indicate the categories for the benthic organisms and sediment: light pink = corals; orange = other cnidarians; green = algae; red = cyanobacteria; yellow = sponges; gray = unidentified organisms; beige = sediment. The acronyms of species and categories are defined in Table 1. *$p < .01$, circle = $p < .05$, triangle = $p > .05$ (Kruskal–Wallis test)

A total of 2,182 scleractinian coral colonies belonging to the following seven species were examined for the analyses of contact interactions: *Agaricia humilis*, *Favia gravida*, *Montastraea cavernosa*, *Mussismilia hispida*, *Porites astreoides*, *Porites branneri* and *Siderastrea*

TABLE 1 Acronyms for coral species and categories of neighboring organisms

Scleractinian coral species	Acronyms
Agaricia humilis	AHU
Favia gravida	FGR
Montastraea cavernosa	MCA
Mussismilia hispida	MHI
Porites astreoides	PAS
Porites branneri	PBR
Siderastrea sp.	SID
Categories of neighboring organisms	
Algae	
Articulated coralline algae	ACA
Corticated algae	COA
Crustose coralline algae	CCA
Epilithic algal matrix	EAM
Filamentous algae	FIA
Foliose algae	FOA
Halimeda sp.	HAL
Leathery algae	LEA
Cyanobacteria	CYA
Sponge	
Encrusting sponge	SEN
Massive sponge	SMA
Repent sponge	SRE
Tubular sponge	STU
Hydrozoan	
Millepora spp.	MIL
Anemone	
Lebrunia danae	LDA
Zoanthid	
Palythoa caribaeorum	PCA
Palythoa grandiflora	PGA
Zoanthid – other	ZOA
Scleractinian	
Agaricia humilis	AHU
Favia gravida	FGR
Madracis decactis	MDE[a]
Mussismilia braziliensis	MBR
Montastraea cavernosa	MCA
Mussismilia hispida	MHI
Mussismilia harttii	MHA
Porites astreoides	PAS
Porites branneri	PBR
Scolymia sp.	SCO
Siderastrea sp.	SID
Gorgonian	
Phillogorgia dilatata	PDI[a]
Ascidian	ASC
Unidentified organisms	UNI[a]
Sediment	SED[b]

[a] Organisms that do not occur in the interaction network.
[b] Not an organism.

sp. All coral species observed in physical contact interactions were found during the benthic cover assessments, with the exception of *P. branneri*, probably because of its small size, low abundance and preference for shaded areas. Neighboring organisms interacting with corals were placed into 30 categories. These categories included algae, EAM, cyanobacteria, sponges, ascidians, hydrocorals and anthozoans (the latter including anemones, zoanthids and scleractinians; Table 1).

The identity of the organisms in the interaction networks varied among areas. However, the most abundant coral species in each study area interacted with more categories of neighboring organisms in all study areas. Additionally, the most abundant neighboring category (EAM for all study areas) interacted with all coral species (Figure 3; Table S3). In general, all coral species had higher interaction abundance with more abundant neighboring organisms than with rarer ones. Nevertheless, some exceptions included interactions between *A. humilis* and crustose coralline red algae (CCA) in TSB. The most abundant coral species in each area were also recorded interacting with a larger number of coral colonies than did the less abundant species, although the interaction abundance between corals was very low in all four study areas (mean ± SE = TSB: 1.87 ± 0.35%, *n* = 302; ABR: 1.41 ± 0.15%, *n* = 1,285; ARC: 0.44 ± 0.16%, *n* = 415; SAP: 1.1 ± 0.34%, *n* = 180). Therefore, corals interacted more with more abundant neighboring organisms and, in the four areas, each coral species considered interacted more with the EAM than with any other neighboring organism (Figure 3).

The network connectance value was relatively high and similar for the three study areas (TSB: 0.57, ABR: 0.53, ARC: 0.65). Network nestedness (NODF) was high and decreased from eastern to southern areas (TSB: 75.69, ABR: 75.36, ARC: 65.23). In ABR and TSB, nestedness significantly differed from the values expected from the null model ($p \leq .01$), but no significant differences were found from the network nestedness in ARC ($p = .11$). Modularity was low for all three networks (TSB: 0.17, ABR: 0.16, ARC: 0.18), with no significant differences from the values expected from the null model ($p \geq .14$ for all networks).

The interaction abundance of corals with neighboring organisms was as expected from the abundance of each interacting pair of scleractinian coral and neighboring organism, regardless of the coral family ($p \geq .9$ for all interacting coral species in all areas; Table 2).

4 | DISCUSSION

Our results reveal the importance of the abundance of marine sessile organisms in the composition of physical contact interactions with scleractinian corals. This was emphasized by the fact that physical contacts with all coral species occurred as expected by the abundances of the benthic organisms. The results are particularly relevant considering that our study encompassed hard bottom habitats with different features along the Brazilian coast. Eastern areas (TSB and ABR) are characterized as coral reefs, with biogenic carbonates composing their structure, and they contain the richest reefs in the South Atlantic as well as all Brazilian reef-building coral species (Leão et al., 2003). Southern areas (ARC and SAP), in contrast, present a rocky framework and a less diverse hermatypic coral fauna (Leão et al.,

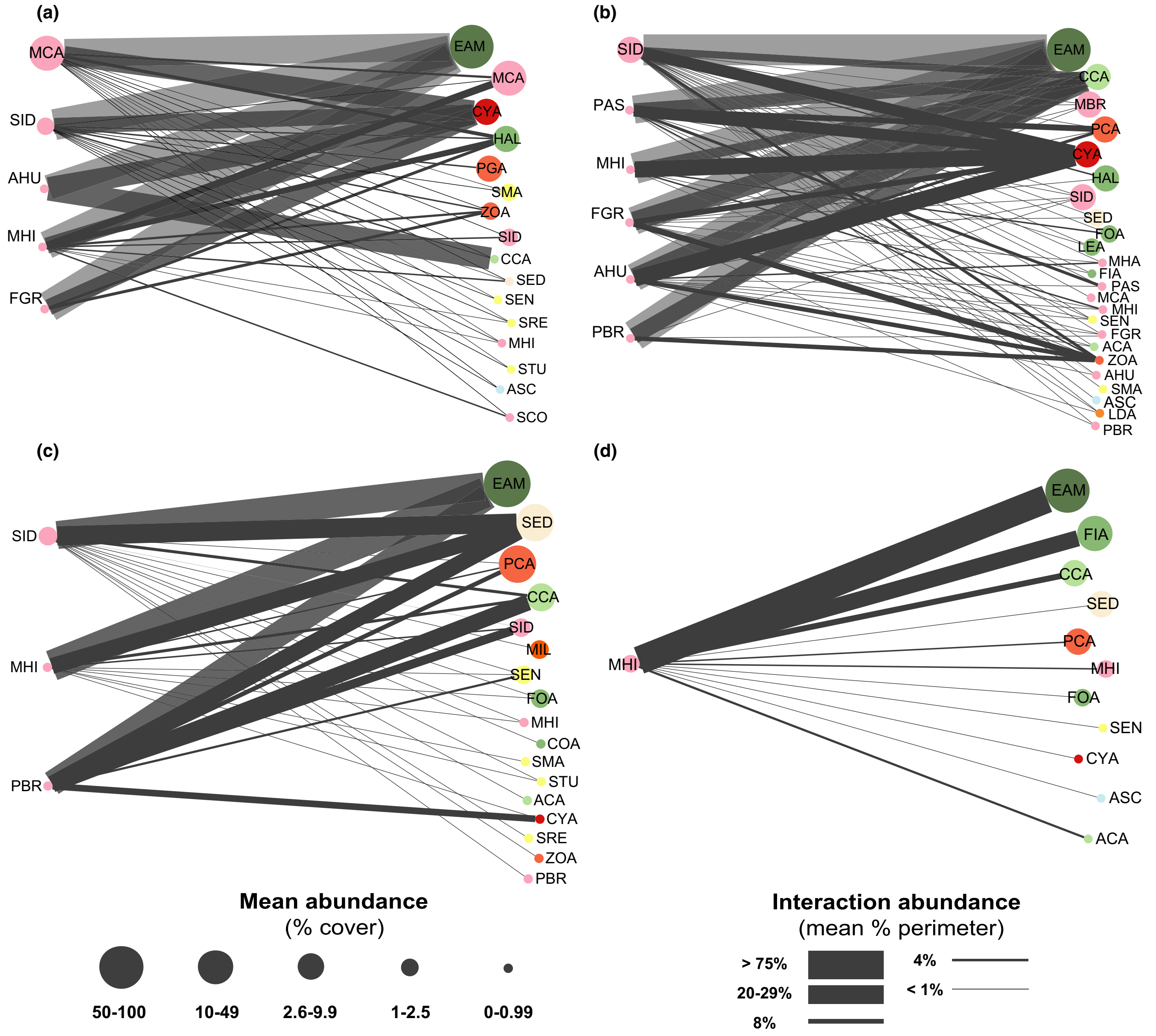

FIGURE 3 Quantitative networks for physical contact interactions between corals and other benthic organisms in four areas along the coast of Brazil. (a): Todos os Santos Bay, (b): Abrolhos, (c): Arraial do Cabo and (d): São Paulo. Circles on the left represent coral species, circles on the right the neighboring organisms and sediment. Color shades of circles indicate the categories for the benthic organisms and sediment: light pink = corals; orange = other cnidarians; green = algae; red = cyanobacteria; yellow = sponges; blue = ascidian; beige = sediment. The acronyms of species and categories are defined in Table 1

2003, 2016). Although corals interacted with more categories of neighboring organisms in the eastern study areas than in the southern areas, in all four areas each coral species interacted more with few, but abundant, neighboring organisms than with rarer ones. Likewise, studies on mutualistic (i.e., pollination; Dupont et al., 2003; Vázquez & Aizen, 2004; Vázquez et al., 2007) and antagonistic interactions (i.e., host–parasite; Vázquez et al., 2007; Canard et al., 2014) have shown the high contribution of species abundance to the structure of these interactions. Thus, despite physical (e.g., geological framework) and biotic (e.g., community composition) differences among the four areas, abundance was an important driver of contact interactions with corals in the present study.

The three interaction networks analysed presented high connectance values, which demonstrates that most organisms interacted with each other with no restrictions. Furthermore, this result also indicates that the environmental characteristics of the study areas did not determine the outcome of interactions. Nestedness was also high in all networks; thus, the interactions of the nodes with few links formed a subset of the interactions of the nodes with many links. TSB and ABR presented the highest nestedness values, as more complex

TABLE 2 G- and *p*-values for G-tests of comparisons between observed and expected interaction abundances of each coral species tested and its neighboring organisms in each study area along the Brazilian coast: TSB, Todos os Santos Bay; ABR, Abrolhos; ARC, Arraial do Cabo; SAP, São Paulo. The acronyms of coral species are defined in Table 1

Area	Coral	G-value	*p*-Value
TSB	AHU	0.17	.90
	MCA	0.05	.97
	MHI	0.03	1.00
	SID	0.07	.96
ABR	AHU	0.04	.98
	FGR	0.04	.96
	MHI	0.06	.98
	PAS	0.02	.99
	SID	0.05	.96
ARC	MHI	0.66	.93
	SID	0.75	.94
SAP	MHI	0.00	1

networks, i.e., networks with higher numbers of interacting categories, tend to be more nested (Bascompte et al., 2003). By contrast, two of the three networks were more nested than expected by the null model, suggesting the contribution of other, non-casual, mechanisms (e.g., biological) to generating the observed pattern (Rezende, Lavabre, Guimaraes, Jordano, & Bascompte, 2007; Vázquez, Chacoff, & Cagnolo, 2009; Vázquez et al., 2007; Vizentin-Bugoni, Maruyama, & Sazima, 2014). Nested networks, in turn, also mean an asymmetric topology. Furthermore, this structure can be explained by differences in abundance among groups of organisms (Dupont et al., 2003; Vázquez et al., 2005), once more corroborating the role of abundance in physical contact interaction networks among the studied sites.

In contrast to nestedness, modularity was low for all three studied networks. The presence of modularity indicates that species sharing specific ecological traits are arranged into modules within the network and that species form groups due to some type of affinity among them (Olesen et al., 2007; Prado & Lewinsohn, 2004), such as host specificity (e.g., Fonseca & Ganade, 1996). Therefore, the low modularity detected in our networks, as well as the high connectance, reinforces the low specificity of the studied associations and, again, the role of factors others than biological as drivers of the contacts analysed.

Apart from physically distinct, the marine benthic community of the four study areas, and therefore the abundance and identity of organisms involved in the interactions, also differed. To settle and persist in the limited space on the substrate, sessile organisms have evolved numerous mechanisms (reviewed by Chadwick & Morrow, 2011). Some competitive mechanisms, for instance, have been shown to influence interactions with corals in different reefs (e.g., Bonaldo & Hay, 2014; Lapid & Chadwick, 2006). Species of Mussidae and Montastraeidae, for example, are considered highly aggressive when competing against other corals, as they use defensive mesenterial filaments and sweeper tentacles, respectively, to damage the tissue of neighboring subordinates. For this reason, we hypothesized that interactions with Mussidae and Montastraeidae corals would occur less frequently than expected given the abundance of the categories. By contrast, the abundance of interactions involving these species was primarily driven by the abundance of the interacting organisms, as found for other coral clades. However, it should be noted that we excluded from our samples two species of Mussidae (*Mussismilia braziliensis* and *Mussismilia harttii*; the former highly abundant in ABR) because their tridimensional morphology did not allow us to analyse their borders in the photographs. The relative importance of abundance in physical interactions of benthic components with these species thus depends on future investigations.

Recent studies in Brazil on aggressive contacts between Brazilian and alien corals (*Tubastraea* spp.) found that the native *Mussismilia hispida* suffered from necrosis, but *Montastraea cavernosa* showed a strong resistance against the alien coral (e.g., Miranda et al., 2016; dos Santos, Ribeiro, & Creed, 2013). However, both *M. hispida* and *M. cavernosa* suffered tissue lesions and overgrowth when competing with the zoanthid *Palythoa variabilis* in a previous study in TSB (Cruz, Meira, Kikuchi, & Creed, 2016). Despite the presence of mesenterial filaments (Cruz et al., 2016; dos Santos et al., 2013) and belonging to the Mussidae family, this evidence suggests that *M. hispida* may also be a weak competitor when contacting other corals, unlike *M. cavernosa* and Caribbean mussids (Lang, 1973; Logan, 1984). *Mussismilia hispida* is an endemic species, which evolved in the particular scenario of Brazilian reefs, with high sediment load and turbid waters. It has been suggested that these distinct physical conditions have shaped the endemic coral fauna (Leão et al., 2003). Thus, we hypothesize that this particular evolutionary scenario could have led to distinct adaptations and towards a diminished aggressiveness compared to species of coral reef communities in other locations.

A few of our results point to a biotic component influencing the benthic interactions, although we expected that biological features would have a more significant role. In TSB, the interaction abundance of *Agaricia humilis* with CCA was relatively high considering the low abundances of both categories. CCA is considered an important inducer for coral settlement and metamorphosis (Hadfield & Paul, 2001), with some experiments showing this relationship specifically for *A. humilis* and CCA species (Morse & Morse, 1991; Morse et al., 1988). Based on these studies, we suggest that CCA chemical cues and their interactions facilitating the settlement of agariciid corals may have led to the high level of physical contact interaction observed between them here. Moreover, also in TSB, interaction abundance between most coral species and *Montastraea cavernosa*, the second most abundant benthic organism in this area, was very low, which could indicate an avoidance of contact with this species. Ecological interactions, to a minor degree, may therefore help explain the observed network structures and the distribution of benthic groups on the substrate.

In our interaction networks, the most abundant corals interacted with more categories of neighboring organisms than did the rarer corals. Nevertheless, the majority of these interactions represented a small amount of the interacting border of the coral colonies, and only a few interactions represented most of its borders, as described for other natural communities (e.g., Vázquez & Simberloff, 2002). Because the strongest interactions with all corals in all our four study areas were with EAM, this category may play an important role in shaping the benthic community. As EAM comprises organic matter, fauna, trapped sediments and a wide variety of algal species (Wilson et al., 2003), interactions with corals may differ greatly depending upon the EAM composition. Numerous studies have tried to uncover algal interactions with corals, which are often considered to be antagonistic (e.g., Miller & Hay, 1996; Tanner, 1995). However, some macroalgal species can have neutral and positive effects on corals (reviewed by McCook et al., 2001; Jompa & McCook, 2003), with effects also depending on the coral species (Bonaldo & Hay, 2014; Rasher, Stout, Engel, Kubanek, & Hay, 2011). Consequently, the outcome of this interaction remains to be investigated, as we were unable to identify the prevailing algal species in the EAM in the observed contacts.

Differing from our findings, a previous study in Fiji found that contacts between corals and allelopathic algae occurred less than expected from the abundance of the species pair (Bonaldo & Hay, 2014). This earlier study suggests that antagonistic interactions influence the distribution and, hence, the abundance of coral–algal contacts. The differences between the results of Bonaldo and Hay (2014) and those of our study may have been caused by their different focus, as the former study considered only some specific coral–macroalgal pairs, while the latter considered the entire benthic community. Additionally, the differences may be influenced by the lower taxonomic resolution of our study in comparison to Bonaldo & Hay's, in which most organisms were identified to genus or species level. However, the importance of the abundance of organisms in structuring physical contact interactions in our study could also be due to the particular environment for corals in Brazil. High sedimentation rates and nutrient input, resulting in turbid waters in several regions along the Brazilian coast (Castro, Segal, Negrão, & Calderon, 2012; Leão et al., 2003; Segal & Castro, 2011), and low winter sea temperatures in the south (Maida & Ferreira, 1997) act as environmental filters for the establishment and survivorship of corals. Therefore, coral species in Brazil are considered stress tolerant or highly resistant to local abiotic characteristics (Darling, Alvarez-Filip, Oliver, McClanahan, & Cote, 2012; Leão et al., 2003). Consequently, their tolerance to physical conditions may be more important than biotic interactions in shaping the benthic community and, thus, physical contacts among organisms.

5 | SUMMARY

The abundance of benthic organisms was an important factor in shaping physical contact interactions in marine consolidated substrate communities along the Brazilian coast. This pattern suggests that, as in other systems, interactions are highly mediated by the abundance of species (e.g., Dupont et al., 2003; Floeter, Vázquez, & Grutter, 2007; Vázquez et al., 2007), independently of the physical and biological features of the habitat and of the interacting organisms. Nevertheless, biological mechanisms may still help explain some of the interaction structures observed, although to a lesser extent. Thus, future studies combining photographic and in situ assessments of the benthic community, in addition to experimental approaches, may help to comprehend the outcome of ecological interactions and their influence upon the fitness and distribution of species in the particular environments of South Atlantic reefs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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