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**ABUNDÂNCIA ESTRUTURA INTERAÇÕES DE CONTATO  
COM CORAIS EM RECIFES BRASILEIROS**

Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Mestre em Ecologia.

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Por

**Ana Carolina Grillo Monteiro**

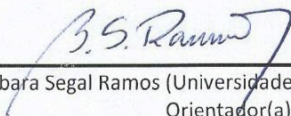
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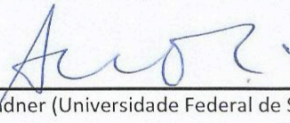
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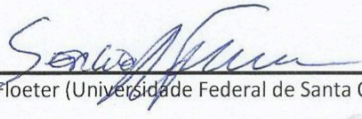
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Florianópolis, 22 de Março de 2016.



À mamãe e ao papai, por toda a dedicação.



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*Doch der Haiſch lebt im Wasser  
So die Tränen sieht man nicht  
(Mas o tubarão vive na água  
então ninguém vê suas lágrimas)  
(Rammstein)*



## RESUMO

Interações ecológicas entre as espécies de um ecossistema desempenham um importante papel na estrutura e funcionamento de comunidades. Portanto, uma das questões centrais em ecologia é compreender os mecanismos que afetam as interações ecológicas em diferentes ecossistemas. Os ambientes recifais apresentam uma das maiores riquezas de espécies e de interações ecológicas. Nesses ecossistemas, o substrato é densamente ocupado por organismos bentônicos, que frequentemente se contatam fisicamente e interagem entre si. O tipo de interação estabelecida pode favorecer o contato físico entre as espécies envolvidas, no caso de mutualismos, ou desfavorecer esse contato, no caso de interações antagonísticas. No Brasil, ecossistemas recifais são principalmente representados por recifes biogênicos marginais e por recifes rochosos. Apesar de ecossistemas semelhantes a esses ocorrerem em todo o mundo, a maior parte dos estudos sobre interações ecológicas entre organismos bentônicos, sobretudo em ecossistemas tropicais, foi feita em recifes de corais. Nesse estudo, avaliamos as interações de contato físico entre corais pétreos e outros organismos bentônicos em quatro áreas ao longo da costa brasileira, duas no leste e duas do sul, investigando se as interações ocorreram de acordo com a abundância das categorias de organismos envolvidos. Ainda, utilizamos a abordagem de redes complexas para examinar a estrutura das interações das três áreas de estudo mais ao norte. O número de espécies de corais e outras categorias de organismos bentônicos foi maior em recifes do leste do que do sul, assim como o número de categorias nas interações de contato com corais. Nos quatro locais de estudo, a abundância das categorias diretamente determinou a abundância das interações de contato entre organismos bentônicos, independente da identidade ou riqueza das categorias ou das características físicas dos recifes. Em todas as áreas de estudo, as espécies de corais interagiram mais com o grupo bentônico mais abundante: a matriz de algas epilíticas. Essa grande importância da abundância das espécies nas interações estudadas pode ser explicada pelas condições particulares dos recifes brasileiros, conhecidos por suas altas taxas de sedimentação e, mais ao sul, baixas temperaturas, comparados a regiões onde recifes de corais geralmente ocorrem. Nas três redes de interações obtidas, os organismos mais abundantes interagiram mais entre eles, enquanto organismos menos abundantes interagiram menos entre si. As redes de interação apresentaram alto aninhamento e conectância, mas baixa modularidade. Esses padrões

sugerem uma baixa especificidade das interações estudadas e reforçam o papel da abundância na estrutura das interações de contato entre organismos sésseis em diferentes recifes ao longo da costa brasileira.

**Palavras-chave:** Comunidade bentônica. Comunidades coralíneas não construtoras. Interações biológicas. Redes de interações. Scleractinia.

## ABSTRACT

Ecological interactions among species within an ecosystem can play an important role in the structure and functioning of natural communities. Therefore, one of the central questions in ecology is to understand the mechanisms shaping ecological interactions in different ecosystems. Reef environments present some of the highest known levels of species richness and ecological interactions. In these ecosystems, the substrate is densely occupied by sessile organisms, which frequently contact physically and interact mutually. The type of interaction may favor physical contact among the interacting species, as in the case of mutualisms, or reduce these contacts, as in the case of antagonistic interactions. In Brazil, reef ecosystems are mostly represented by biogenic marginal reefs and by rocky reefs. Although systems such as these occur worldwide, most studies on ecological interactions among benthic organisms, especially in the tropics, were conducted on coral reefs. In this study, we evaluated physical contact interactions among hard corals and other benthic organisms in four areas along the Brazilian coast, two in the eastern and two in the southern region, by assessing whether interactions occurred as expected from the abundance of the categories of organisms involved. We also used complex network approaches to examine the structure of interactions in the three northernmost study areas. The number of coral species and other categories of benthic organisms was larger on eastern reefs, as was the number of categories of contact interactions with corals. In all four study areas, the abundance of the categories directly influenced the abundance of contact interactions among the benthic organisms, regardless of the identity or richness of the categories or the physical characteristics of the reef. In all study areas, coral species interacted more with the most abundant benthic group: the epilithic algal matrix. This substantial importance of species abundance in the studied interactions may be explained by the particular conditions of Brazilian reefs, known for their high sediment rates and, further south, low temperatures. Additionally, in the three networks obtained, the abundant organisms interacted more among themselves, whereas few interactions occurred among less abundant groups. The 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 the contacts among sessile organisms along the Brazilian coast.

**Keywords:** Benthic community. Biological interactions. Interaction networks. Non-reef-building coral communities. Scleractinia.

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## 1 INTRODUÇÃO GERAL

O estudo das relações de organismos entre si e com o meio ambiente, chamadas de interações ecológicas, é um dos temas frequentes desde os primórdios da Ecologia (e.g., Paine 1980, Tansley 1917). Como consequência, hoje sabe-se que a identidade das espécies em um dado ecossistema, bem como as condições ambientais, são fatores determinantes na estruturação das interações ecológicas em uma comunidade (Bertness e Callaway 1994, Paine 1974). Por outro lado, as interações ecológicas têm um papel fundamental na distribuição e abundância de espécies de um determinado sistema (Christian 2001, Dayton 1971). Portanto, entender os mecanismos moduladores das interações é um desafio na Ecologia que pode ajudar, por exemplo, a identificar os fatores que mantêm as interações em diferentes ambientes.

Os ecossistemas recifais estão entre os mais ricos em número de espécies e complexidade estrutural (Spalding et al. 2001). A variedade de formas e cores se confunde diante da diversidade de espécies, e a alta densidade de espécies por unidade de área promove uma grande variedade de interações ecológicas entre os organismos. Entre essas interações, observam-se desde aquelas que beneficiam ambas as espécies envolvidas (e.g., mutualismo) a interações que afetam negativamente uma (e.g., predação, parasitismo) ou ambas as espécies participantes das associações (e.g., competição), e até interações que beneficiam ou desfavorecem uma das espécies, sem afetar a outra espécie envolvida (e.g., comensalismo e amensalismo, respectivamente). Esses diversos tipos de interações também permitem a coexistência do grande número de espécies nos recifes e, em alguns casos, podem levar à redução e à exclusão de algumas espécies (Spalding et al. 2001).

Na segunda metade do século XX, interações desarmônicas entre espécies, como competição e predação, foram as mais estudadas em vários tipos de ambientes (e.g., Chase et al. 2002, Kaye e Hart 1997). No caso dos organismos marinhos sésseis, como o espaço para sua fixação no substrato consolidado é um recurso limitante, a competição é comum e intensa (Dayton 1971). Na região entremarés, por exemplo, estudos clássicos demonstraram a importância destas interações desarmônicas na estruturação das comunidades (Connell 1961, Dayton 1971, Paine 1974). De maneira semelhante, em ambientes recifais, estudos demonstram que a competição pode ter efeitos bastante significativos na abundância e distribuição de espécies (Bonaldo e Hay 2014, Lapid e Chadwick 2006, McCook et al. 2001).

Em ambientes marinhos, a competição pode ocorrer de diferentes formas. Em alguns casos, a competição pode ocorrer à distância, quando metabólitos secundários denominados aleloquímicos são empregados e liberados no ambiente por pelo menos uma das espécies da interação. Essas substâncias aleloquímicas podem, entre outros efeitos, inibir o desenvolvimento e o assentamento de larvas e causar lesão tecidual da espécie adjacente (Hellio et al. 2005, Jompa e McCook 2003). Esse mecanismo é conhecido em corais pétreos (e.g., Koh e Sweatman 2000), mas mais comumente em corais moles (e.g., Maida et al. 2001), zoantídeos (e.g., Hines e Pawlik 2012), esponjas (e.g., Pawlik et al. 2007) e algas (e.g., Rasher et al. 2011, Rasher e Hay 2014). Mecanismos envolvendo contato físico entre organismos também desempenham um importante papel na competição pelo espaço no substrato recifal. Alguns corais pétreos, assim como coralimorfários, podem utilizar tentáculos varredores, outros tentáculos especializados ou filamentos mesentéricos para agredir organismos em contato, garantindo áreas maiores para seu crescimento (e.g., Bruno e Witman 1996, Chadwick 1991, Lapid et al. 2004). Além disso, as altas taxas de crescimento de alguns grupos, como ascídias, zoantídeos, esponjas e macroalgas, permitem que estes cresçam sobre competidores inferiores e ganhem espaço no substrato (e.g., Aerts 1998, Lirman 2001, Rabelo et al. 2013).

A forma de crescimento dos organismos bentônicos também pode representar uma vantagem competitiva em determinadas situações. Formas arborescentes, por exemplo, dependem menos do substrato do que as incrustantes, e podem sombrear outros organismos e desfavorecê-los caso estes dependam da luz para seu crescimento e sobrevivência (Jackson 1979, McCook et al. 2001). Consequentemente, é difícil estabelecer uma hierarquia linear de dominância competitiva em organismos sésseis recifais (Chornesky 1989). Uma grande diversidade de estratégias evoluiu em função da alta competitividade e, assim, o resultado da competição é variável e depende, dentre outros fatores, dos mecanismos utilizados e das condições abióticas (Aerts 2000, Bak et al. 1982). Perturbações de intensidade e tamanho intermediário, aliadas a uma variedade de mecanismos competitivos por parte dos organismos, impedem a dominância por uma ou poucas espécies na comunidade, permitindo assim que uma alta riqueza e diversidade seja mantida em ambientes marinhos (Connell 1978, Paine 1974, Russ 1982).

Embora haja menor número de estudos sobre interações harmônicas em comparação a interações desarmônicas em ambientes bentônicos, o papel de interações como mutualismo e facilitação na estruturação de comunidades é amplamente aceito (Bruno e Bertness

2000). Em recifes de corais, além da estrutura tridimensional, que gera diversos tipos de habitats para milhares de organismos, e da própria simbiose que ocorre entre corais e algas zooxantelas, alguns trabalhos demonstraram relações harmônicas entre outras espécies e grupos bentônicos. Associações entre diferentes espécies de esponjas, por exemplo, podem ser benéficas ao aumentar as taxas de crescimento das espécies associadas e sua resistência a más condições ambientais, além de diminuir sua predação (Wulff 1997, Wulff 2008). Também, há evidências de efeitos positivos de algumas espécies de algas em corais, como o aumento do recrutamento de larvas e de sua metamorfose mediados por macroalgas, algas calcárias incrustantes e emaranhado de algas filamentosas (Birrell et al. 2008, Gleason 1996). Ainda, algumas espécies de macroalgas podem diminuir o branqueamento dos corais, devido ao sombreamento (Jompa e McCook 1998). Portanto, há grande variedade de interações entre organismos marinhos, bem como dos efeitos causados por essas interações.

Fatores abióticos, ao influenciarem diretamente a sobrevivência e a aptidão dos organismos, também podem alterar o resultado, intensidade e natureza das interações ecológicas (Bertness e Callaway 1994). Estas conclusões vieram de estudos em costões rochosos, ambientes caracterizados por variações abióticas (i.e., temperatura e umidade) em pequena escala (i.e., poucos metros de distância), sobretudo nas zonas superiores. Pesquisadores observaram que, nas zonas inferiores dos costões, que passam a maior parte do tempo submersas, as condições físicas são ótimas para a maioria dos organismos, já que há menor variação de temperatura e umidade. Assim, nestas áreas, as interações bióticas desarmônicas, como de competição e predação, afetam mais as espécies do que as variáveis ambientais. Já, nas zonas superiores dos costões, onde as condições abióticas sofrem altas variações de temperaturas e dissecação, a tolerância dos organismos ao ambiente é mais forte em determinar a estrutura da comunidade (Connell 1961, Menge e Sutherland 1987). Além disso, a facilitação desempenha importante papel na sobrevivência das espécies nestas zonas superiores, já que espécies diferentes podem se agrupar para minimizar condições severas de dissecação, diminuindo assim sua perda de água (Bertness e Leonard 1997).

Além das interações bióticas e das condições ambientais, outros fatores atuam na estruturação das comunidades, como processos históricos e evolutivos, dispersão de espécies e distúrbios ambientais; e suas intensidades variam de acordo com as comunidades e com a escala espacial (Jackson et al. 2001, Leibold 2004). Assim, uma gama de

variáveis é responsável pelo resultado final de um sistema ecológico, cuja estrutura é alvo constante de mudança (Magurran et al. 2010).

Em recifes de corais, variações no nível ótimo de alguns fatores, como temperatura, salinidade, nutrientes, luminosidade e saturação de aragonita, podem afetar o desenvolvimento dos recifes e originar ambientes com características diferentes (Kleypas et al. 1999). Essas variações no desenvolvimento incluem recifes marginais e comunidades coralíneas não construtoras (Kleypas et al. 1999, Perry e Larcombe 2003). Em termos de bioconstrução, os recifes marginais são sistemas com menores níveis ou áreas de acreção de carbonato de cálcio quando comparados a recifes de corais não marginais (Perry e Larcombe 2003). Já comunidades coralíneas não construtoras são caracterizadas pela ocorrência isolada de colônias de corais que não formam recifes. Assim, os corais se desenvolvem sobre costões ou recifes rochosos (Perry e Larcombe 2003). No Brasil, os ambientes recifais possuem algumas características particulares, como altas taxas de sedimentação e de aporte de nutrientes, que tornam a água muito turva, o que pode restringir o desenvolvimento da estrutura recifal e originar recifes marginais (Segal e Castro 2011). Assim, espécies nativas de corais do Brasil estão adaptadas a essas condições e são consideradas resistentes a elas (Leão et al. 2003). Ainda, nas regiões com condições físicas mais limítrofes, temos a presença de colônias de corais espalhadas sobre a matriz rochosa (Castro e Pires 2001). Embora os recifes marginais, assim como os recifes rochosos, estejam distribuídos por todo o mundo (Kleypas et al. 1999, Perry e Larcombe 2003), a maioria dos estudos sobre a biologia e ecologia de espécies recifais tropicais está limitada a recifes de corais não marginais do Caribe e Indo Pacífico. Dadas as diferenças na estrutura física e nos fatores ambientais entre recifes de corais e recifes marginais e rochosos, é possível que a estrutura e a dinâmica das interações biológicas entre esses ambientes também difira. Dessa forma, um próximo passo no estudo da ecologia de ambientes recifais tropicais seria uma melhor compreensão sobre a biologia das espécies e interações entre elas em ambientes distintos dos recifes de corais mais amplamente estudados.

Para compreender melhor a estrutura e dinâmica de interações ecológicas, ferramentas derivadas da teoria de redes complexas têm sido cada vez mais utilizadas (e.g., Araújo et al. 2008, Bascompte et al. 2003, Dáttilo et al. 2014). Nessa abordagem, interações entre organismos são representadas graficamente, de tal forma que os “nós” numa rede de interações representam indivíduos, espécies, grupos morfológicos, etc., e linhas entre os nós representam as interações (Bascompte 2007, 2009).



Assim, a abordagem de redes ressalta o padrão de interações encontrado, permite comparações no espaço e no tempo e gera novas questões sobre a ecologia e evolução das interações multiespecíficas (Bascompte 2009).

Redes de interações em sistemas terrestres, como polinização, têm sido amplamente estudadas (e.g., Olesen et al. 2007, Vázquez et al. 2009). Contudo, estudos sobre redes ecológicas em ecossistemas marinhos são relativamente raros, sobretudo considerando interações entre espécies bentônicas. Nós utilizamos aqui, pela primeira vez, ferramentas de redes complexas no estudo de interações entre organismos sésseis em ambientes recifais. A partir da construção das redes, foi possível comparar os padrões de interação de contato de borda entre corais pétreos e outros organismos sésseis entre diferentes recifes brasileiros. Espera-se que o presente trabalho abra as portas para outros estudos em comunidades bentônicas incorporando métodos de redes e ambientes marginais, e assim logre-se compreender melhor alguns aspectos, como o papel das interações na manutenção da comunidade frente a diferentes condições físicas e biológicas.

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## 2 CAPÍTULO ÚNICO

(formatado para submissão ao periódico *Oikos*)

### **Abundance drives physical contact interactions with scleractinian corals in marginal and rocky reefs**

#### 2.1 ABSTRACT

A central question in ecology is to understand the mechanisms shaping ecological interactions in different ecosystems, as they can play important roles in the structure of communities. In reef ecosystems, the substrate is densely occupied by sessile organisms, which frequently contact physically and interact mutually. The type of interaction may favor or reduce physical contact among the interacting species, as in the case of mutualisms or antagonisms. In Brazil, reef ecosystems are represented by biogenic marginal reefs and by rocky reefs. Although systems such as these occur worldwide, most studies on ecological interactions among tropical benthic organisms were conducted on coral reefs. In this study, we evaluated physical contact interactions among hard corals and other benthic organisms in four areas along the Brazilian coast, two in the eastern and two in the southern region, by assessing whether interactions occurred as expected from the abundance of the categories of organisms involved. We also used complex network approaches to examine the structure of interactions in the three northernmost study areas. In all four study areas, the abundance of the categories directly influenced the abundance of interactions among the benthic organisms, regardless of the identity or richness of the categories or the physical characteristics of the reef. All coral species interacted more with the most abundant benthic group: the epilithic algal matrix. This importance of species abundance in the studied interactions may be explained by the particular conditions of Brazilian reefs, known for their high sediment rates and, further south, low temperatures. The 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 the contacts among sessile organisms along the Brazilian coast.

**Keywords:** Benthic community. Biological interactions. Interaction networks. Non-reef-building coral communities.

## 2.2 INTRODUCTION

Ecological interactions are pervasive in nature and may have a range of implications for the fitness, distribution and survival of the interacting species. While some interactions seem to have little influence on some of the interacting species, others may evolve into interdependence of the participating organisms (e.g., Blackall et al. 2015, Selosse et al. 2004). Along with other factors, e.g., abiotic conditions, disturbances, evolutionary processes and species dispersal, ecological interactions may play key roles in the structure of communities and in the dynamics of the ecosystem as a whole, as they may affect, for example, the diversity and richness of species (Bertness and Leonard 1997, Christian 2001, Dayton 1971, Paine 1974).

Because of the importance of ecological interactions in the structure and dynamics of some natural communities, different techniques and perspectives have been applied to characterize these interactions. For instance, 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 et al. 2003, Dáttilo et al. 2014). In this method, 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 formalism 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 driven by species abundance (e.g., Canard et al. 2014, Dupont et al. 2003, Krishna et al. 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 (Krishna et al. 2008, Vázquez et al. 2005, 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 and Aizen 2004, Vázquez et al. 2005). Moreover, when considering quantitative data on interactions among organisms (i.e., quantitative networks), usually only a small proportion of all interactions is strong enough to ecologically influence the abundant species, and weak interactions could represent a



minor effect on them (Vázquez and Aizen 2004, Vázquez and Simberloff 2002). In this sense, species abundance can significantly affect ecological interactions by determining which organisms have a higher frequency and abundance of interactions with other organisms in the network.

Reef ecosystems are one of the most diverse habitats, as they present some of the highest levels of species richness and densities of species per unit area (Spalding et al. 2001). These ecosystems are also characterized for their high diversity of ecological interactions, which mediates coexistence 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 and Negri 1999, Morse et al. 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 and Witman 1996). Therefore, interactions among sessile species, related to physical contact between them, may directly influence their fitness and survival. In turn, these survival and fitness effects of species interactions may directly influence the patterns of distribution and abundance of benthic species (e.g., Foster et al. 2008, Lapid and 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 et al. 2004, Nugues et al. 2004, Richardson et al. 1979). Among the different groups of scleractinian corals, Mussidae and Montastraeidae are two of the most aggressive, as they frequently damage outcompeting corals (Chornesky and 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 and Williams 1983, Lang 1973, Logan 1984, Richardson et al. 1979).

Not only biological interactions and other factors but also abiotic conditions affect the structure of natural communities (Done 1999, Dunson and Travis 1991). On marginal reefs, the abiotic conditions are

considered to be near the threshold for the development of the coral reef ecosystem (Kleypas et al. 1999). On these reefs, levels above or below the optimal range of physical parameters, such as temperature, salinity, luminosity and aragonite saturation, can reduce the process of accretion of the framework (Perry and Larcombe 2003). Under further limiting conditions, non-reef-building coral communities develop over rocky reefs. Despite the clear differences among coral reefs, marginal reefs and non-reef-building coral environments, and the wide distribution of marginal and rocky reefs worldwide (Kleypas et al. 1999, Perry and Larcombe 2003), few studies have focused on the biology of species in these systems. Indeed, most studies on ecological interactions in the benthos on tropical reefs have been conducted on more diverse coral reefs in the Indo-Pacific and Caribbean (but see Cruz et al. 2016, Miranda et al. 2016). Therefore, a further step in the understanding of ecological interactions in the benthic community in tropical reefs would be to evaluate the structure of these interactions in tropical marginal and rocky reefs.

The Brazilian coast shows high rates of sedimentation and nutrient input (Leão et al. 2003, Segal and Castro 2011). These conditions restrict the development of coral reefs in this region (Segal and Castro 2011). Moreover, along the southern coast of Brazil (Leão et al. 2003), corals do not form reef frameworks, as only scattered coral colonies occur over rocky reefs. Consequently, Brazilian benthic environments also present high rates of endemism of a number of reef clades, with species adapted to the particular conditions in this region (Leão et al. 2003). Because of the particular environmental conditions of the Brazilian coast and the uniqueness of the local fauna, the region offers a good scenario for testing hypotheses on the ecology of marine species on tropical marginal and rocky reefs.

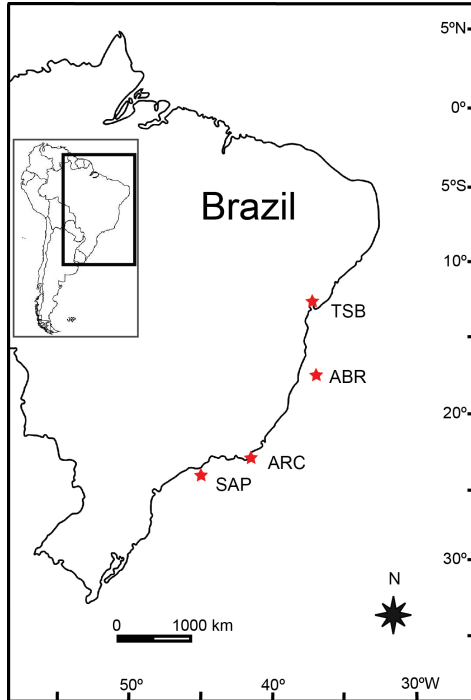
In this study, we first assessed the structure of physical contact interactions between corals and other sessile organisms on marginal reefs and rocky reefs along the Brazilian coast. For it, we used, for the first time, complex network approaches to describe the structure of the studied interactions in different reef systems across the broad studied latitudinal range. Thereafter, we asked the following two questions: (1) Do interactions of corals with benthic organisms occur as expected by the abundance of the organisms in each area? (2) Do more aggressive corals (e.g., *Mussidae* and *Montastraeidae*) interact less with other organisms?

## 2.3 MATERIAL AND METHODS

### 2.3.1 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) (Fig. 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 et al. 2003). Within the Brazilian coast, true coral reefs are only found in this region, along with rocky formations. 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 et al. 2010). The average sea surface temperature in ABR is 25.4°C, varying from 23.4° to 27.5°C (Collins et al. 2008). TSB is the second largest Brazilian Bay, with an area of approximately 1000 km<sup>2</sup> (Lessa et al. 2000) and an average sea surface temperature of 26°C, varying from 24.2° to 27.8°C (Collins et al. 2008). Although human development around the bay, primarily subsequent to the 1950's, 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 et al. 2006).

ARC (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 the tropical and subtropical regions. The reef matrix in these areas is composed of rocks and has a lower structural complexity than reefs of the eastern region. Although there is a decrease in coral cover from northern to southern Brazilian reefs (Leão et al. 2003), the special hydrodynamic regimes of ARC sustain a rich reef community and a high level of coral cover (Castro et al. 1995, Lima and Coutinho 2016, Oigman-Pszczol et al. 2004), with an average sea surface temperature of 23.9°C, varying from 21.8° to 26.2°C (Collins et al. 2008). SAP has an average sea surface temperature of 24.1°C, varying from 21.5° to 27°C (Collins et al. 2008), and the poorest coral species richness among the four study areas, with only two species of zooxanthellate scleractinian corals (Amaral and 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).



**Figure 1.** Study areas on the Brazilian coast: TSB = Todos os Santos Bay; ABR = Abrolhos; ARC = Arraial do Cabo; SAP = São Paulo.

### 2.3.2 Data collection

Physical contact interactions (hereafter termed interactions) among hard corals and neighboring sessile organisms were surveyed through photoquadrats in the four study areas. Photographs were taken 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 study area, three or four sites were sampled (total of 14 sampled sites). Within each sampled site, approximately 25 zones of 2 m<sup>2</sup> (here termed plots) were haphazardly delimited. In these plots, between 5 and 10 photoquadrats, each 25 cm x 25 cm (625 cm<sup>2</sup>) in surface area, were haphazardly taken (i.e., 77–413 photos per site; 2628 photos in total). Photos used were taken from the image bank of Project SISBIOTA–Mar.

The abundance of sessile organisms was assessed using a subsample of 15–20 of the plots with the best photographic quality in each area. The photoquadrats within these plots were analyzed to obtain the percent cover in each area using the software photoQuad v1.3 (Trygonis and Sini 2012). For this measurement, 50 random points were placed over each photo, and the organism immediately under each point was 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. Scleractinian corals, hydrozoans and anemones 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 and Barnes 2001) and algae were identified to morpho-functional categories (modified from Steneck and Dethier 1994). Among the algae, the "epilithic algal matrix" (EAM) refers to algal assemblages composed of calcareous and filamentous species, with associated organic matter, fauna and trapped sediments (Wilson et al. 2003). Abundance 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. Colonies of three species were not considered for this assessment: the mushroom-like form of *Mussismilia braziliensis* and phaceloid morphology of *Mussismilia harttii* did not allow visualizing 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 1.48v software (Schneider et al. 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 described above. The measurements of colonies and contact areas were all done by one person (ACGM), thus providing a better standardization of the method. In some cases, corals did not contact other organisms but contacted sediment; therefore, this category was included as one of the neighboring organisms. 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). However, 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. Within the interacting borders of the coral colonies and neighboring organisms, we searched for tissue lesion marks such as bleaching. We considered *Mussismilia hispida* and *Favia gravida* as members of Mussidae, and *Montastraea cavernosa* as a Montastraeidae (following Budd et al. 2012).

### 2.3.3 Interaction networks

Tools derived from complex network theory were used to provide a better visualization of the studied interactions and to analyze 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 and Nepusz 2006) in R version 3.1.3 for Mac OS X (R Core Team 2015). We were unable to construct a network for SAP, as we only recorded one species of coral in this area.

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 network: degree for each interacting category and network average degree, 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. Accordingly, degree represents the generalization level of each category (Bascompte and Jordano 2007). Average degree ( $k_{med}$ ) is the mean degree of all network nodes (Costa et al. 2007), and connectance indicates the proportion of possible interactions actually observed in the network, ranging from 0 to 1 (Jordano 1987). This metric indicates the percentage of all possible connections that are observed in the network. 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 interaction in which less connected species are subsets of highly connected ones (Bascompte et

al. 2003). This metric was obtained using the NODF index (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al. 2008) in the software ANINHADO (Guimarães Jr and 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 null model approach. 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 et al. 2007). 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 and Girvan 2004) and a simulated annealing optimization procedure (Guimerà and Amaral 2005), with the software MODULAR (Marquitti et al. 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 among 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 and Paul 2001, Lang 1973, McCook et al. 2001, Miranda et al. 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).

#### **2.3.4 Statistical analyses**

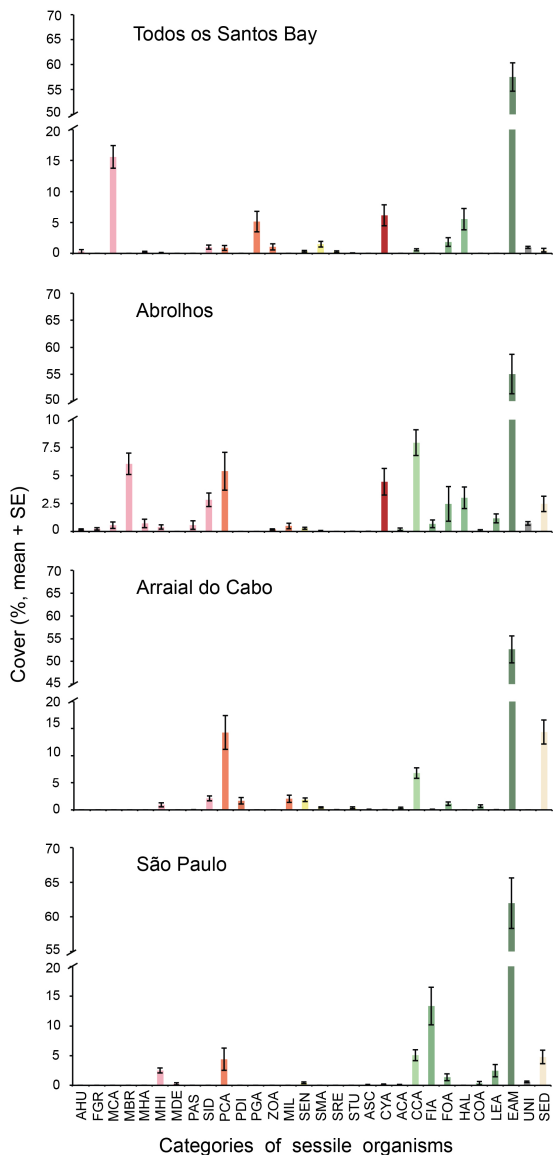
To investigate whether the interactions of corals with neighboring organisms occurred as expected from the abundances of each species or category considered, and whether more aggressive corals (Mussidae and Montastraeidae) interacted less with other organisms than expected by

their abundances, for each study area we compared the interaction abundance of each coral-neighboring organism pair with the abundance (mean % cover) of each species or category. Interaction abundance of each coral species vs. neighboring organism was considered to represent a measure of the mean perimeter of the contact between a given coral species with each neighboring organism. Subsequently, G tests for goodness-of-fit were calculated to compare the observed interaction abundance of each coral-neighboring organism pair in the four study areas with the expected interaction abundances of the same interacting pair (modified from Bonaldo and Hay 2014). The expected interaction abundance for each coral-neighboring organism 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 et al. 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). Furthermore, to test the relationship between categories abundances and interaction abundances across all coral species and organisms within each area, a correlation was performed between the abundances of neighboring organisms (mean % cover) and interaction abundance of all coral species with each neighboring organism (percentage).

## 2.4 RESULTS

In the four reef areas studied, the cover of most scleractinian coral species was lower than 3%, with the exception of *Mussismilia braziliensis* in ABR ( $6\% \pm 0.9$ , mean  $\pm$  SE) and *Montastraea cavernosa* in TSB ( $16\% \pm 1.8$ , mean  $\pm$  SE) (Fig. 2, Supplementary Table 1). 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 number of coral species (TSB: 5, ABR: 8, ARC: 3, SAP: 2), as well as of all benthic categories combined (TSB: 18, ABR: 25, ARC: 20, SAP: 15).





**Figure 2.** Benthic cover (% mean  $\pm$  SE) of sessile organisms in four study areas along the Brazilian coast. Color shades indicate the categories for the benthic organisms: 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.

The total number of categories (i.e., considering corals and neighboring organisms) in physical contact interactions 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.

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* 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 comprised algae, EAM, cyanobacteria, sponges, ascidians, hydrozoans 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 a larger number of categories of neighboring organisms in all study areas. Additionally, the most abundant neighboring category (EAM for all study areas) interacted with all coral species (Fig. 3, Supplementary Table 2). In general, all coral species had higher interaction abundance with more abundant neighboring organisms. The most abundant coral species in each area were also recorded interacting with a larger number of coral colonies, although the interaction abundance between corals was very low in all four study areas (TSB:  $1.87\% \pm 0.35$ , ABR:  $1.42\% \pm 0.15$ , ARC:  $0.44\% \pm 0.16$ , SAP:  $1.1\% \pm 0.34$ ; mean %  $\pm$  SE). 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 (Fig. 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 ( $p \leq 0.01$ ), but no significant differences were found from the

network nestedness in ARC ( $p = 0.09$ ). 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 ( $p \geq 0.14$  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 the coral family ( $p > 0.90$  for all interacting coral species in all areas). We also searched for tissue lesions on the borders of the interacting organisms. Only 18 coral colonies showed signs of bleaching on the contacting border across all study areas. Of these, only one pair of contacts included a Mussidae as the possible aggressor. Additionally, significant positive correlations were found between the abundance of each neighboring category and their interaction abundance with coral species in all study areas (TSB  $r = 0.953$ ,  $p < 0.001$ ; ABR  $r = 0.986$ ,  $p < 0.001$ ; ARC  $r = 0.964$ ,  $p < 0.001$ ; SAP  $r = 0.995$ ,  $p < 0.001$ ; Supplementary Fig. 1).

**Table 1.** Acronyms for coral species and categories of neighboring organisms.

<b>Coral species</b>	<b>Acronyms</b>
<i>Agaricia humilis</i>	AHU
<i>Favia gravida</i>	FGR
<i>Montastraea cavernosa</i>	MCA
<i>Mussismilia hispida</i>	MHI
<i>Porites astreoides</i>	PAS
<i>Porites branneri</i>	PBR
<i>Siderastrea</i> sp.	SID
<b>Categories of neighboring organisms</b>	
Articulated coralline algae	ACA
Corticated algae	COA
Crustose coralline algae	CCA
Epilithic algal matrix	EAM
Filamentous algae	FIA
Foliose algae	FOA
<i>Halimeda</i> sp.	HAL
Leathery algae	LEA
Cyanobacteria	CYA
Encrusting sponge	SEN
Massive sponge	SMA
Repent sponge	SRE
Tubular sponge	STU
<i>Millepora</i> spp.	MIL
<i>Lebrunia danae</i>	LDA
<i>Palythoa caribaeorum</i>	PCA
<i>Palythoa grandiflora</i>	PGA
Zoanthid (other)	ZOA
<i>Agaricia humilis</i>	AHU
<i>Favia gravida</i>	FGR
<i>Madracis decactis</i>	MDE*
<i>Mussismilia braziliensis</i>	MBR
<i>Montastraea cavernosa</i>	MCA
<i>Mussismilia hispida</i>	MHI
<i>Mussismilia harttii</i>	MHA

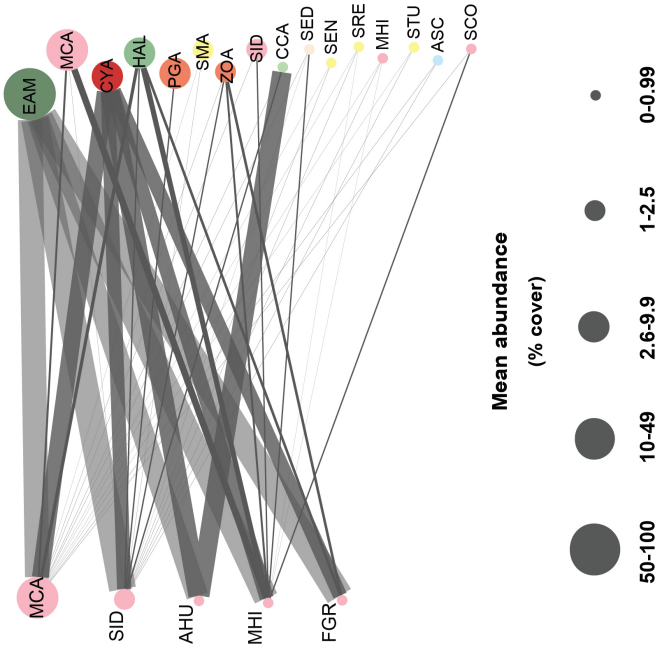
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<i>Porites astreoides</i>	PAS
<i>Porites branneri</i>	PBR
<i>Scolymia</i> sp.	SCO
<i>Siderastrea</i> sp.	SID
<i>Phyllogorgia dilatata</i>	PDI*
Ascidian	ASC
Unidentified organisms	UNI*
Sediment	SED

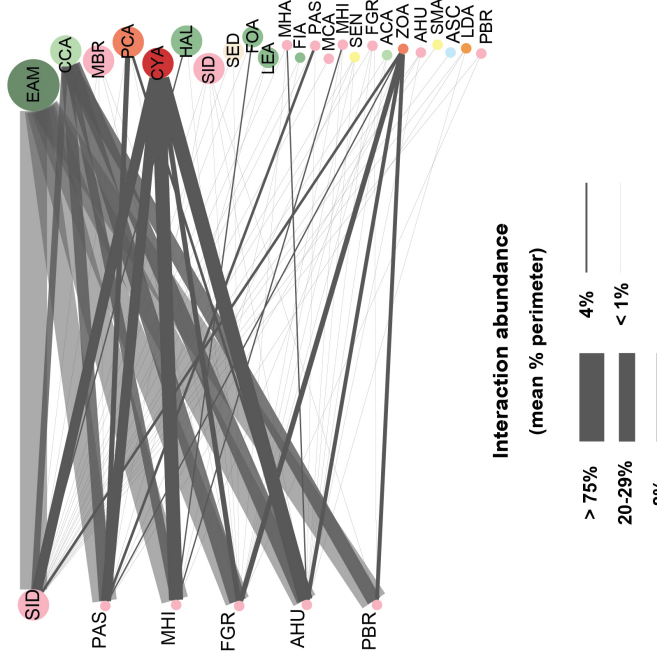
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\* Organisms that do not occur in the interaction networks

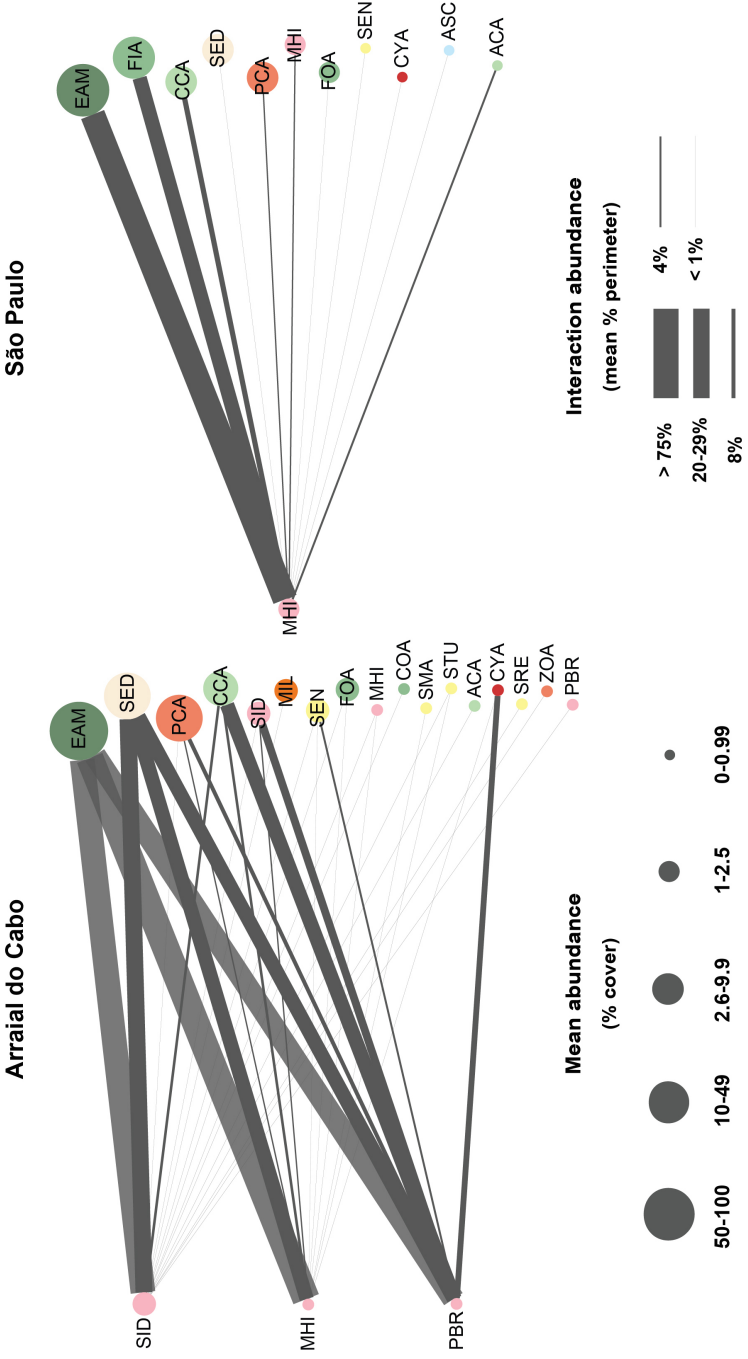
Todos os Santos Bay



Abrolhos



**Figure 3.** Networks for physical contact interactions between corals and other benthic organisms in four areas along the coast of Brazil. Circles on the left represent coral species, circles on the right the neighboring organisms. Color shades of circles indicate the categories for the benthic organisms: 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.



**Figure 3 (cont).** Networks for physical contact interactions between corals and other benthic organisms in four areas along the coast of Brazil. Circles on the left represent coral species, circles on the right the neighboring organisms. Color shades of circles indicate the categories for the benthic organisms: 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.

## 2.5 DISCUSSION

Our results elucidate the importance of the abundance of marine sessile organisms in the composition of physical contact interactions with scleractinian corals in marginal and rocky reefs in Brazil. These results are particularly relevant considering that our study encompassed reefs with different features along the Brazilian coast: marginal and rocky reefs in the eastern region (TSB and ABR), including the richest reefs in the South Atlantic, and less diverse rocky reefs in the South (ARC and SAP). Although corals interacted with more categories of neighboring organisms in the eastern study areas, in all four study areas, each coral species interacted more with few, but abundant, neighboring organisms, which resulted in highly connected and nested interaction networks with low modularity. Thus, despite physical (e.g., water temperature) and biotic (e.g., species richness) differences among the four areas, abundance was an important driver of physical contact interactions with corals throughout the studied range.

In the present study, the importance of the abundance of organisms was emphasized by the fact that physical contacts with all coral species occurred as expected by the abundances of the interacting pair. Likewise, studies on mutualistic (i.e., pollination; Dupont et al. 2003, Vázquez and Aizen 2004, Vázquez et al. 2007) and antagonistic interactions (i.e., host-parasite; Canard et al. 2014, Vázquez et al. 2007) have shown the elevated contribution of the species abundance distribution in the structure that is usually observed in these interactions. However, the influence of biological mechanisms in shaping the interactions in the present study cannot be discarded. In TSB, for example, the interaction abundance of *Agaricia humilis* with crustose coralline red algae (CCA) was relatively high considering the low abundances of both categories. CCA is considered an important inducer for coral settlement and metamorphosis (Hadfield and Paul 2001), with some experiments performed specifically with *A. humilis* and CCA species (Morse et al. 1988, Morse and Morse 1991). 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 here observed between them. Therefore, in addition to the abundance of species and other categories, ecological interactions among benthic organisms may play a role in shaping the distribution of benthic groups in Brazilian reefs.

In addition to positive interactions among benthic organisms, these species have evolved numerous competitive mechanisms to settle



and persist in the limited space on the substrate of tropical reefs (reviewed by Chadwick and Morrow 2011). Some of these competitive mechanisms have been shown to influence interactions with corals in different coral reefs (e.g., Bonaldo and Hay 2014, Lapid and 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 expected interactions with Mussidae and Montastraeidae corals to occur less frequently than expected given the abundance of the categories in our study, but interaction abundance with these species was primarily driven by the abundance of the interacting organisms, as found for other coral clades. Nevertheless, we excluded from our samples two species of Mussidae (*Mussismilia braziliensis* and *M. harttii*; the former highly abundant in ABR) because their morphology did not allow us to analyze 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 *M. hispida* suffered from necrosis, but *M. cavernosa* did show a strong resistance against the alien coral (e.g., Miranda et al. 2016, Santos et al. 2013). However, both *M. hispida* and *M. cavernosa* suffered tissue lesion and overgrowth when competing with the zoanthid *P. variabilis* in a previous study in TSB (Cruz et al. 2016). Despite the presence of mesenterial filaments (Cruz et al. 2016, Santos et al. 2013) and belonging to the Mussidae family, these evidences suggest that *M. hispida* could be a weak competitor also when contacting other corals, unlike *M. cavernosa* and Caribbean mussids (Lang 1973, Logan 1984). *M. hispida* is an endemic species, which evolved in the particular scenario of Brazilian reefs, with high sediment loads 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 other coral species that thrive in the high diversity and competitive coral reef communities. According to our results, interactions seemed to rely predominantly on a probabilistic process, which masked possible biological mechanisms behind the assessed contact interactions. However, it is probable that some coral species can influence aggressive interactions in Brazilian reefs. Nevertheless, more information on the

biology of coral species in Brazil is still needed, especially regarding their competitive abilities against other organisms.

Although we could not identify the ecological interactions behind the physical contacts, they probably included different types of interactions, such as facilitative, neutral and antagonistic. For example, competition for space among sessile organisms is one of the central interactions in the marine benthos (Dayton 1971, Paine 1974). Among several competitive mechanisms, spatial interference competition often results in aggressive physical interactions, such as overgrowth (e.g., Bruno and Witman 1996, Engel and Pawlik 2005). Numerous studies tried to uncover algal interactions with corals, often considered antagonistic (Miller and Hay 1996, Tanner 1995). However, some macroalgal species can have neutral and positive effects on corals (reviewed by McCook et al. 2001), with effects also depending on coral species (Bonaldo and Hay 2014, Rasher et al. 2011). In contrast, zoanthids are usually superior competitors to corals, as due to their rapid growth and variable shape, they can easily overgrow and damage tissue in several coral species (Cruz et al. 2016, Rabelo et al. 2013, Suchanek and Green 1981). Further studies on the biology of the studied species are thus necessary to verify the nature of the studied interactions and their extent in structuring Brazilian coastal reef communities.

Different from our findings, a previous study in Fiji found that contacts between corals and allelopathic algae occurred less than expected from the abundances of the species pair (Bonaldo and Hay 2014). This previous study suggests that antagonistic interactions influence the distribution and, hence, the abundance of coral-algal contacts. In contrast, on coral reefs in Colombia, sponge-coral contact interactions were primarily related to sponge and coral cover (Aerts and Van Soest 1997), a pattern similar to our findings. The importance of the abundance of species and other categories in structuring physical contact interactions shown by our study could be due to the unusual reef environment for corals in Brazil. Brazilian reefs are either marginal or rocky reefs, as they present abiotic characteristics near or beyond the limit for the development of coral reef ecosystems (Kleypas et al. 1999, Perry and Larcombe 2003, Rogers 1990). High sedimentation rates and nutrient input, resulting in turbid waters in several regions along the Brazilian coast (Castro et al. 2012, Leão et al. 2003, Segal and Castro 2011), and low winter sea temperatures in the South (Maida and Ferreira 1997) act as an environmental filter for the establishment and survivorship of corals. Therefore, coral species in Brazil are considered stress tolerant or highly resistant to local abiotic characteristics (Darling

et al. 2012, Leão et al. 2003); consequently, their tolerance to physical conditions may be more relevant than biotic interactions in shaping physical contacts. The studied interactions, however, require further investigation before taking general conclusions, especially as the biology of benthic organisms in Brazil remains largely unknown. However, even in coral reefs, species abundance may be a determining factor in shaping benthic interactions, as evidenced by other ecological associations in different environments (e.g., Dupont et al. 2003, Floeter et al. 2007, Vázquez et al. 2007), but biological interactions might be relatively more important than in marginal systems.

In our physical contact interaction networks, the most abundant corals interacted with more categories of neighboring organisms. Nevertheless, the majority of these interactions represented a small amount of the interacting border of the coral colonies, and only few interactions represented most of its borders, as described for other natural communities (e.g., Vázquez and Simberloff 2002). Because the strongest interactions with all corals in all our four study areas were with the EAM, this category could play an important role in shaping the community of corals. As the EAM comprises organic matter, fauna, trapped sediments and a wide variety of algal species (Wilson et al. 2003), interactions with corals may largely differ according to the EAM composition. Indeed, a large array of effects of the EAM on corals has been observed, including positive, neutral, and negative interactions (Jompa and McCook 2003, McCook et al. 2001). Therefore, 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 in our study.

In the three interaction networks in the present study, nestedness was high; thus, the interactions of the nodes with few links did form a subset of the interactions of the nodes with many links. The highest nestedness value reported for ABR, compared to the other two networks, is expected because more complex networks, i.e., higher number of interacting categories, tend to be more nested (Bascompte et al. 2003). On the other hand, two of three networks were more nested than expected by the null model, suggesting the contribution of other, non-casual, mechanisms (e.g., biological) to generate the observed pattern (Rezende et al. 2007, Vázquez et al. 2007, 2009, Vizentin-Bugoni et al. 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 and Lewinsohn 2004), such as host specificity (e.g., Fonseca and Ganade 1996). Therefore, the low modularity detected in our networks, as well as the high connectance, reinforce the low specificity of the studied associations and, again, the role of factors other than biological interactions (e.g., abundance) as an important driver of the contacts among sessile organisms along the Brazilian coast.

In summary, we found that the abundance of benthic organisms is an important factor in shaping physical contact interactions in marginal reefs and rocky reefs along the Brazilian coast. We hypothesize that this high importance of abundance is probably related to the particular conditions of marginal and rocky reefs in Brazil, which directly influence the adaptation of organisms and their abundances. Therefore, some caution is warranted when making any generalizations about reef species based solely on studies in the Indo Pacific and the Caribbean, where most studies on tropical reef ecology have been conducted. As shown by the present study, it is possible that the environmental conditions of marginal and rocky reefs impose particular pressures on their unique fauna, with direct consequences on the biology of these species and on the ecological interactions among them. Still, there is evidence that biological mechanisms can affect interactions in these ecosystems but possibly to a lesser degree in Brazilian reefs. Future studies on the biology of species in marginal and rocky reefs, focused on interspecific interactions, may help comprehend to what extent biotic interactions influence the fitness and distribution of species in these reefs.

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### 3 CONCLUSÃO GERAL

Este estudo é pioneiro em considerar a importância da abundância das espécies nas interações de contato entre organismos sésseis marinhos em diferentes ambientes recifais. Ainda, é o primeiro a utilizar a abordagem de redes complexas para caracterizar a estrutura de interações de contato físico entre organismos bentônicos em ecossistemas marinhos. Nosso estudo mostrou que a abundância das interações de contato com corais pétreos está diretamente relacionada à abundância dos organismos em quatro recifes (incluindo recifes biogênicos marginais e recifes rochosos) ao longo da costa brasileira, independente da riqueza de espécies presentes no recife e de suas condições abióticas. Em nosso sistema de estudo, relações biológicas podem não exercer uma influência tão forte nas interações de contato com corais quanto a abundância. Portanto, pode ser que, nas áreas estudadas, a tolerância das espécies frente às condições ambientais tenha um papel mais relevante do que interações biológicas na comunidade.

Apesar das redes de interação estudadas serem principalmente estruturadas pela abundância dos organismos, em alguns casos organismos pouco abundantes apresentaram intensidade de interação relativamente alta. Logo, a influência das interações bióticas não deve ser negligenciada, já que ela pode explicar uma parcela das interações que ocorrem no ambiente. Essa contribuição de mecanismos biológicos em interações de contato entre organismos bentônicos é evidenciada por estudos anteriores na costa brasileira, em que interações de contato tiveram efeitos significativos no crescimento e sobrevivência de corais (e.g., Cruz et al. 2016, Miranda et al. 2016, Santos et al. 2013).

A estrutura geológica dos recifes brasileiros é única, assim como a fauna local, caracterizada pela presença de espécies endêmicas. Porém, ainda há poucos estudos sobre biologia e ecologia das espécies bentônicas locais, principalmente endêmicas, o que dificulta compreender as interações bióticas entre essas espécies (mas veja Cruz et al. 2016, Miranda et al. 2016, Segal e Castro 2011). Devido à falta dessas informações, em alguns casos o conhecimento sobre sistemas mais estudados, como o Caribe e o Indo-Pacífico, são extrapolados para espécies brasileiras. Tais generalizações devem ser feitas com cuidado, sobretudo considerando as particularidades da fauna e da estrutura dos recifes do Brasil, que podem refletir no funcionamento do sistema todo. Estudos em recifes brasileiros, e outros recifes marginais e rochosos, são fundamentais para a compreensão da ecologia das espécies locais, e do

papel de interações ecológicas na sobrevivência e distribuição de espécies nesses ecossistemas.

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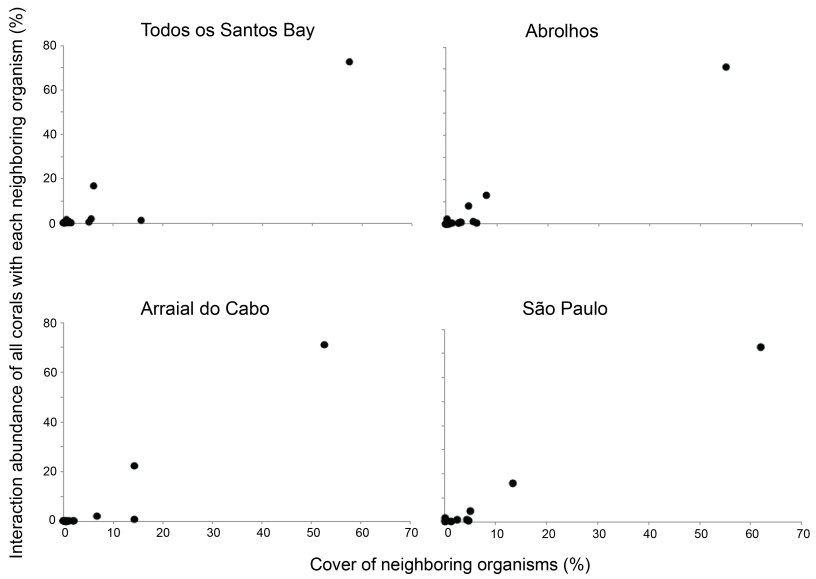
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## APÊNDICES



**Supplementary Figure 1.** Correlation between the abundance of each neighboring organism category and their interaction abundance with all coral species in four study areas along the Brazilian coast.

**Supplementary Table 1.** Benthic cover (% mean  $\pm$  SE) of categories of sessile 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 species and categories are defined in Table 1.

Species or Categories	Study Areas			
	TSB	ABR	ARC	SAP
AHU	0.31 $\pm$ 0.3	0.18 $\pm$ 0.07	-	-
FGR	-	0.24 $\pm$ 0.11	-	-
MCA	15.57 $\pm$ 1.84	0.56 $\pm$ 0.30	-	-
MBR	-	6.04 $\pm$ 0.95	-	-
MHA	0.25 $\pm$ 0.11	0.72 $\pm$ 0.39	-	-
MHI	0.09 $\pm$ 0.06	0.40 $\pm$ 0.19	0.95 $\pm$ 0.39	2.50 $\pm$ 0.41
MDE	-	-	-	2.25 $\pm$ 1.17
PAS	-	0.57 $\pm$ 0.37	0.01 $\pm$ 0.01	-
SID	1 $\pm$ 0.33	2.84 $\pm$ 0.60	2.11 $\pm$ 0.44	-
PCA	0.89 $\pm$ 0.41	5.40 $\pm$ 1.70	14.27 $\pm$ 3.11	4.39 $\pm$ 1.86
PDI	-	-	1.67 $\pm$ 0.60	-
PGA	5.14 $\pm$ 1.66	-	-	-
ZOA	1.05 $\pm$ 0.5	0.19 $\pm$ 0.06	-	-
MIL	-	0.50 $\pm$ 0.25	2.07 $\pm$ 0.68	-
SEN	0.34 $\pm$ 0.12	0.28 $\pm$ 0.09	1.87 $\pm$ 0.36	0.43 $\pm$ 0.12
SMA	1.48 $\pm$ 0.46	0.05 $\pm$ 0.05	0.43 $\pm$ 0.11	0.03 $\pm$ 0.02
SRE	0.26 $\pm$ 0.13	-	0.02 $\pm$ 0.02	-
STU	0.05 $\pm$ 0.04	0.01 $\pm$ 0.01	0.39 $\pm$ 0.17	-
ASC	-	0.02 $\pm$ 0.01	0.08 $\pm$ 0.07	0.11 $\pm$ 0.04
CYA	6.14 $\pm$ 1.7	4.44 $\pm$ 1.19	0.03 $\pm$ 0.03	0.16 $\pm$ 0.09
ACA	-	0.20 $\pm$ 0.10	0.34 $\pm$ 0.17	0.11 $\pm$ 0.05
CCA	0.57 $\pm$ 0.17	7.94 $\pm$ 1.15	6.79 $\pm$ 0.97	5.08 $\pm$ 0.92
FIA	-	0.68 $\pm$ 0.35	0.09 $\pm$ 0.05	13.35 $\pm$ 3.16
FOA	1.83 $\pm$ 0.69	2.46 $\pm$ 1.56	1.15 $\pm$ 0.33	1.37 $\pm$ 0.58
HAL	5.54 $\pm$ 1.74	3.01 $\pm$ 0.97	-	-
COA	-	0.09 $\pm$ 0.07	0.69 $\pm$ 0.26	0.36 $\pm$ 0.30
LEA	-	1.17 $\pm$ 0.41	0.02 $\pm$ 0.01	2.46 $\pm$ 1.05
EAM	57.50 $\pm$ 2.88	55.01 $\pm$ 3.64	52.66 $\pm$ 2.98	61.97 $\pm$ 3.65
UNI	0.96 $\pm$ 0.15	0.72 $\pm$ 0.15	-	0.59 $\pm$ 0.13
SED	0.54 $\pm$ 0.30	2.47 $\pm$ 0.7	14.36 $\pm$ 2.20	4.76 $\pm$ 1.12



**Supplementary Table 2.** The number of links (k, degrees) for corals and neighboring organisms in networks of physical contact interactions 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 species and categories are defined in Table 1. K-values for categories that occurred as corals are indicated as (c) and for categories that occurred as neighboring organisms are indicated as (n).

Species or Categories	Study Areas			
	TSB	ABR	ARC	SAP
AHU	3(c)	15(c); 3(n)	-	-
FGR	4(c)	15(c); 4(n)	-	-
MCA	15(c); 3(n)	1(n)	-	-
MBR	-	4(n)	-	-
MHA	-	3(n)	-	-
MHI	10(c); 3(n)	7(c); 3(n)	11(c); 2(n)	11(c); 1(n)
PAS	-	12(c); 3(n)	-	-
PBR	-	5(c); 2(n)	7(c); 1(n)	-
SCO	2(n)	-	-	-
SID	14(c); 2(n)	23(c); 5(n)	15(c); 3(n)	-
LDA	-	3(n)	-	-
PCA	-	4(n)	3(n)	1(n)
PGA	1(n)	-	-	-
ZOA	4(n)	6(n)	1(n)	-
MIL	-	-	1(n)	-
SEN	2(n)	4(n)	3(n)	1(n)
SMA	2(n)	1(n)	1(n)	-
SRE	3(n)	-	1(n)	-
STU	2(n)	-	2(n)	-
ASC	2(n)	1(n)	-	1(n)
CYA	5(n)	5(n)	2(n)	1(n)
ACA	-	3(n)	1(n)	1(n)
CCA	3(n)	6(n)	3(n)	1(n)
FIA	-	2(n)	-	1(n)
FOA	-	2(n)	2(n)	1(n)
HAL	4(n)	2(n)	-	-
COA	-	-	1(n)	-
LEA	-	2(n)	-	-
EAM	5(n)	6(n)	3(n)	1(n)
SED	3(n)	2(n)	3(n)	1(n)