Anaide Wrublevski Aued

Macroecologia de comunidades bentônicas recifais do Atlântico Sul Ocidental: padrões e processos

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutora em Ecologia

Orientadora: Profa. Dra. Bárbara Segal
Coorientador: Prof. Dr. Sergio R. Floeter

Florianópolis
2018

Ficha de identificação da obra elaborada pelo autor
através do Programa de Geração Automática da Biblioteca Universitária
da UFSC.

Aued, Anaide W
Macroecologia de comunidades bentônicas recifais do Atlântico Sul Ocidental: padrões e processos / Anaide W Aued; orientadora, Bárbara Ramos Segal, coorientador, Sergio Ricardo Floeter, 2018.
115 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, Florianópolis, 2018.

Inclui referências.

1. Ecologia. I. Ramos Segal, Bárbara. II. Ricardo Floeter, Sergio. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

Anaide Wrublevski Aued

Macroecologia de comunidades bentônicas recifais do Atlântico Sul Ocidental: padrões e processos

Esta Tese foi julgada adequada para obtenção do Título de "Ecologia", e aprovada em sua forma final pelo Programa Pós-Graduação em Ecologia

Florianópolis, 28 de fevereiro de 2018.

____
Prof. Fábio Gonçalves Daura Jorge, Dr.
Coordenador do Curso

Banca Examinadora:

____
Prof.ª, Dr.ª Bárbara Segal
Orientadora
Universidade Federal de Santa Catarina

____
Prof.ª Malva Isabel Medina Hernández, Dr.ª
Universidade Federal de Santa Catarina

____
Prof. Tito Monteiro da Cruz Lotufo, Dr.
Universidade de São Paulo

____
Prof. Eduardo Hetter Giehl, Dr.
Universidade de Santa Catarina

Este trabalho é dedicado a todos os que olham a natureza e se deslumbram com sua beleza.

AGRADECIMENTOS

Agradeço, primeiramente, aos meus queridos pais, por todo o amor e por nunca medirem esforços para que eu tivesse uma boa educação e me permitirem estudar as duas coisas que mais gosto, o mar e o mundo. Obrigada também aos meus irmãos, Wladi e Nena, e a mãe "adotiva" Elizete pelo eterno apoio e por estarem sempre ao meu lado.

Um obrigada mais que especial ao meu amado marido, Bruno, pela parceria nesse momento enlouquecido de nossas vidas. Que todas as horas de dedicação ao doutorado, períodos de afastamento e estresse sejam convertidas em amadurecimentos para nós dois e fortalecimento da nossa relação. Agradeço imensamente todo o apoio e parceria que você me dá. Sem sombra de dúvidas, sem você eu não teria conseguido. Te amo meu parceiro de vida!

Agradeço muito os meus orientadores. À Bárbara Segal, pela paciência, confiança, e por me permitir crescer junto com ela e me ensinar sobre o mundo bentônico. Ao Sergio Floeter, que desde o mestrado tem me instigado com ideias malucas e me permitido entrar no mundo da macroecologia.

Um imenso obrigada ao governo brasileiro da época, que me possibilitou fazer o estágio sanduíche na Brown Univeristy e ampliar minha ideia de mundo e pesquisa. Agradeço as pessoas incríveis que conheci lá, principalmente Jon Witman, Franz Smith e Robert Lamb. Essa tese não seria a mesma sem a parceria e ajuda essencial de vocês. You're the best!

Gostaria de agradecer enormemente a toda a equipe da rede SISBIOTA-Mar e dos laboratórios LBMM e LABAR por todo aprendizado, ajuda no campo, e na identificação dos inúmeros fotoquadrados. Aprendi muito com todos vocês. Principalmente com Gui, Mari, Juan, Cadu e Davi. Sem vocês eu não teria finalizado esse sonhado doutorado.

Agradeço por fim, todos os meus amigos e pessoas que de alguma forma participaram no desenvolvimento deste doutorado. Foram inúmeros aprendizados e muito crescimento pessoal. A todos, meus sinceros agradecimentos.

RESUMO

O entendimento de como a distribuição dos seres vivos varia no espaço e no tempo é a base para estudos de macroecologia, biogeografia e ecologia. Dentre os padrões de larga escala, o gradiente latitudinal de diversidade é um dos padrões mais conhecidos, tanto em ambiente terrestre como marinho, onde a maior riqueza de espécies ocorre na região próximo ao Equador e declina em direção aos polos. Além da descrição de padrões, os estudos de ecologia moderna têm focado em entender os processos e mecanismos envolvidos na organização das comunidades e no funcionamento ecossistêmico. Os atributos das espécies são considerados respostas aos diferentes fatores bióticos e abióticos, e a abordagem funcional da diversidade tem sido cada vez mais utilizada para entender como as comunidades são organizadas, podendo inclusive, inferir sobre o funcionamento ecossistêmico. Os ambientes marinhos estão sofrendo globalmente com impactos antrópicos (*e.g.* sobrepesca, mudanças climáticas), o que tem levado a uma grande perda de diversidade marinha. Assim, estudos que avaliem os padrões de diversidade marinha e suas variações frente a fatores ambientais são essenciais para o entendimento da biodiversidade e seu funcionamento e, posteriormente, prever possíveis mudanças. A Província Brasileira possui uma grande extensão, cerca de 8 mil quilômetros da costa brasileira mais quatro ilhas oceânicas, e apresenta ambientes heterogêneos, o que a torna um bom modelo para estudos de larga escala. Esta tese aborda as duas bases da macroecologia, a descrição de padrões e a investigação dos processos que levam aos padrões observados, e se encontra dividida em dois artigos: (1) "*Large-scale patterns of benthic marine communities in the Brazilian Province*", que descreve a estrutura das comunidades e os padrões de diversidade taxonômica dos organismos bentônicos marinhos ao longo do gradiente latitudinal da Província Brasileira (2) "*Functional richness far from the classic diversity center: the case of reef benthic communities along the Brazilian Province*", que avalia a influência de filtros abióticos (*e.g.* salinidade, temperatura, ondas e nutrientes) na diversidade funcional nas comunidades bentônicas ao longo da Província Brasileira. Para isso, nós amostramos a comunidade bentônica durante o período de verão de 2011 a 2014 em dois estratos de profundidades (1 a 7 metros e 8 a 15 metros) em 40 sítios ao longo da Província Brasileira (entre as latitudes 0˚ a 27˚S), agrupados dentro de 15 localidades, através de metodologia de fotoquadrados. Ao total foram analisados 3.855 fotoquadrados e os organismos foram identificados ao menor nível taxonômico possível, posteriormente agrupados pelos seus atributos funcionais. Foi observado

que: (I) as comunidades bentônicas marinhas são dominadas por turf e macroalgas e apresentam baixa cobertura de corais; (II) não existe diferença na estrutura da comunidade entre os estratos de profundidade amostrados; (III) como padrão geral, a diversidade bentônica é menor em baixas latitudes e apresenta o pico de diversidade em latitudes intermediárias (entre 20˚S-23˚S); (IV) comunidades em latitudes maiores que 20˚S apresentam um aumento da cobertura de outros grupos bentônicos, como octocorais, organismos supensívoros e filtradores e outros invertebrados; (V) a riqueza funcional também foi baixa próximo da região do equador e maior entre as latitudes 20˚S-23˚S; (VI) a divergência funcional foi menor próxima aos limites sul e norte da Província Brasileira e maior na latitude 12˚S (Baia de Todos os Santos, BA); (VII) a equitabilidade funcional não variou ao longo do gradiente estudado; (VIII) salinidade, temperatura, ondas e nutrientes explicam 48,9% da riqueza funcional, 44,2% da divergência funcional e 5,46% da equitabilidade funcional. As condições ambientais, como a salinidade baixa proveniente do desague do rio Amazonas, baixas temperaturas e salinidade no limite sul da Província Brasileira e a influencia de ondas maiores principalmente nas ilhas oceânicas, atuam como filtros que limitam a chegada e/ou o estabelecimento dos organismos, gerando assim, baixa diversidade próximo aos limites norte e sul da Província Brasileira e nas ilhas oceânicas. As comunidades bentônicas da Baia de Todos os Santos (12˚S) apresentaram valores mais altos de divergência funcional, indicando que filtros bióticos atuam ali mais fortemente. A região entre a latitude 20˚S-23˚S corresponde à zona de transição entre águas frias, trazendo organismos subtropicais da região sul, e as águas quentes, provenientes do norte e que transportam organismos com afinidades tropicais, favorecendo assim a alta diversidade na região. Além disso, a quantidade de nutrientes - maior na região entre 20˚S-27˚S - está ligada à disponibilidade de energia e recursos alimentares, o que também influencia na diversidade e abundância dos organismos bentônicos marinhos estudados. Assim, o padrão de diversidade taxonômica e funcional atípico dos organismos de recifes rasos do Atlântico Sul Ocidental, com maiores riquezas em latitudes intermediárias (20˚S-23˚S), é resultante da influência dos fatores abióticos acima descritos. Os resultados desse estudo proporcionam o primeiro *baseline* quantitativo das comunidades bentônicas marinhas brasileiras, podendo inclusive ter implicações para conservação dos recifes rasos do Brasil.

Palavras-chave: Biodiversidade marinha 1. Larga escala 2. Gradiente latitudinal 3. Província Brasileira 4. Diversidade funcional 5. Recifes 6. turf 7. Macroalgas 8. Brasil 9.

ABSTRACT

The understanding of how the distribution of living things varies spatially is the basis for the studies of macroecology, biogeography and ecology. Within these large-scale patterns, latitudinal gradients of diversity are one of the most well-known general patterns for both terrestrial and marine environments, where highest species richness occurs near the equator and declines towards the poles. Beyond just describing such patterns, modern ecology attempts to understand how ecosystem processes and mechanisms influence community assembly and ecosystem functioning. Species' traits are a response to different biotic and abiotic factors, and functional diversity has been used to understand how communities are structured, and may provide information about ecosystem functioning. Marine environments are suffering globally from human impacts (e.g., overfishing, climate change), which is causing a large decline in marine diversity. Thus, studies that assess marine diversity patterns and its changes due to environmental factors are essential to understanding biodiversity and its functioning, and help to quantify possible changes. The Brazilian Province covers a large area, with nearly 8,000 km of coastline as well as the oceanic islands, and is characterized by heterogeneous environments, being a good model for large-scale studies. This thesis investigates the two main bases of macroecology, the description of patterns and the investigation of the processes that lead to the observed pattern, divided into two articles: (1) "Large-scale patterns of benthic marine communities in the Brazilian Province", which describes the structure of communities and the pattern of taxonomic diversity of marine benthic organisms along the latitudinal gradient of the Brazilian Province (2) "Functional richness far from the classic diversity center: the case of reef benthic communities along the Brazilian Province", which evaluates the influence of abiotic filters (e.g., salinity, temperature, wave action and nutrients) on functional diversity in benthic communities throughout the Brazilian Province. To accomplish this, we sampled during austral summer of 2011 to 2014 benthic communities in two depth strata (1-7 meters and 8-15 meters) in 40 sites along the Brazilian Province (between latitudes 0º to 27ºS), grouped into 15 localities through photoquadrats. In total, 3,855 photoquadrats were analyzed, and the benthic organisms were identified to the lowest possible taxonomic level and later grouped based on their functional traits. We observed that: (I) marine benthic communities are dominated by turf and macroalgae and are characterized by low coral cover; (II) no difference in community structure was observed between sampled depth strata; (III) as a general pattern, benthic diversity is lower in lower latitudes and peaks in mid-latitudes (between 20ºS-23ºS); (IV) benthic communities at latitudes higher than 20ºS showed an increase of other benthic groups, such as octocorals, suspension/filter-feeders organisms, and other invertebrates; (V) functional richness was also low near the equator and higher between latitudes 20ºS-23ºS; (VI) functional divergence was low near the southern and northern limits of the Brazilian Province and higher at the latitude 12ºS (Baia de Todos os Santos, BA); (VII) functional evenness did not vary along the studied gradient; (VIII) salinity, temperature, wave action and nutrients explained 48.9% of functional richness, 44.2% of functional divergence, and 5.46% of functional evenness. Environmental conditions, such as low salinity from the drainage of the Amazon River, low temperatures and salinity at the southern limit of the Brazilian Province and in the influence of higher waves in oceanic communities, act as filters that limit the arrival and/or establishment of organisms, generating low diversity near the northern and southern limits and in oceanic islands. Benthic communities in the Baia de Todos os Santos (12˚S) had higher values of functional divergence, indicating that biotic filters acted more strongly at this locality. The region between latitudes 20˚S-23˚S corresponds to a transition zone between cold waters, which bring subtropical organisms from the south region, and warm waters, which come from the north and carry organisms with tropical affinities, favoring the high diversity in the region. Moreover, the amount of nutrients - greater in the region between 20˚S-27˚S - is linked to the availability of energy and food resources, which also influence in the diversity and abundance of the marine benthic organisms studied. Thus, the taxonomic and functional diversity patterns for shallow reef organisms of the Southwestern Atlantic, with higher richness at mid-latitudes (20˚S-23˚S), is a result of the influence of the abiotic factors. The results of this study provide the first quantitative baseline of Brazilian marine benthic communities, and may even have implications for shallow reef conservation in Brazil.

Keywords: Marine biodiversity 1. Large-scale 2. Environmental gradients 3. Brazilian Province 4. Functional diversity 5. Reefs 6. Turf 7. Macroalgae 8. Brazil 9.

LISTA DE FIGURAS

INTRODUÇÃO GERAL..27

CAPÍTULO 1..50

CAPÍTULO 2..85

SUMÁRIO

APRESENTAÇÃO

A curiosidade pela variação da biodiversidade ao redor da Terra tem deslumbrado e intrigado os naturalistas desde o tempo das grandes viagens, quando importantes pensadores da natureza começaram a quantificar a distribuição da biodiversidade ao longo do planeta e a questionar o porquê dos padrões observados. Tais perguntas deram início aos estudos de biogeografia e macroecologia. Atualmente, a Terra vivencia uma perda global da biodiversidade, e em ritmo acelerado, devido aos diferentes impactos antrópicos, como por exemplo, o aumento da poluição e mudanças climáticas, inclusive no ambiente marinho. Tais ameaças demandam um maior entendimento dos padrões espaciais da biodiversidade, e dos processos e mecanismos que regulam tais padrões. Dessa forma compreendendo o funcionamento ecossistêmico, para que assim, talvez, possamos criar novas estratégias de proteção da biodiversidade e mitigação dos impactos.

As comunidades de um local são influenciadas por fatores em escalas locais e regionais, e quanto mais soubermos sobre os padrões e processos em larga escala, maior será nosso entendimento sobre a biodiversidade global. No ambiente marinho, a Província Brasileira possui uma grande extensão, cerca de 8.000 quilômetros de costa, contem diferentes habitats e condições ambientais distintas, possuindo assim um papel importante para a biodiversidade da região do Atlântico Sul Ocidental. Atualmente, sabe-se que a Província Brasileira possui uma baixa diversidade, se comparada com províncias próximas, como por exemplo a Província do Caribe, e que a maior riqueza não ocorre na região dos trópicos, como predito pelo padrão geral do gradiente latitudinal da diversidade, e sim em latitudes médias. Apesar desse padrão ser consistente para diferentes grupos taxonômicos no Atlântico Sul Ocidental, pouco se sabe a respeito dos processos e mecanismos que geram esse padrão atípico de diversidade.

Ecologia de comunidades tem ido além de descrever os padrões e tenta entender os processos e mecanismos que geram a estrutura das comunidades. Uma abordagem que tem sido cada vez mais utilizada para entender os diferentes filtros atuantes na montagem das comunidades é a diversidade funcional, já que ela leva em conta os atributos resposta das espécies para os filtros abióticos e bióticos. No ambiente marinho, essa abordagem tem sido amplamente utilizada em assembleias de peixes recifais, corais e bivalves, porém estudos com toda a comunidade bentônica ainda são relativamente escassos. Uma das razões é que é difícil uniformizar os atributos para toda uma comunidade e que, para muitas espécies bentônicas marinhas, as informações dos atributos ainda não estão disponíveis na literatura, criando assim obstáculos para o entendimento funcional dos organismos bentônicos recifais. Apesar disso, estudos em comunidades recifais tem tentado utilizar a abordagem funcional e avançar para entender como as espécies respondem aos diferentes filtros, inclusive permitindo a avaliação de impactos e mudanças em funções ecossistêmicas.

Esta tese está organizada em uma introdução geral, na qual é apresentada a base teórica utilizada para nortear o nosso estudo, a lacuna do conhecimento, nossas hipóteses, objetivos e metodologia, e posteriormente, dois capítulos, em inglês e em formato de artigo, que foram submetidos a revistas indexadas A1. No primeiro capítulo, em revisão pela revista *Plos One*, nós descrevemos o padrão latitudinal (entre 0° e 27° de latitude) de riqueza e da composição das comunidades bentônicas marinhas da Província Brasileira, fornecendo uma base para o entendimento posterior dos processos que governam a estrutura das comunidades. Pela primeira vez, foi possível realizar um *baseline* quantitativo das comunidades bentônicas marinhas brasileiras, que poderá servir de base para avaliação dos impactos nos recifes e informação para criação de novas áreas de preservação da biodiversidade. O segundo capítulo, submetido à revista *Global Ecology and Biogeography*, avalia os possíveis processos ecológicos (i.e., filtros bióticos e abióticos) que regem os padrões de diversidade de organismos bentônicos recifais ao longo da Província Brasileira. Para isso, utilizamos índices de diversidade funcional, já que são considerados melhores indicadores que a diversidade taxonômica para verificação de como os filtros ambientais e interações biológicas influenciam a estrutura das comunidades.

INTRODUÇÃO

1.1 BIODIVERSIDADE E PADRÕES DE LARGA ESCALA

Por cerca de 200 anos as diferenças geográficas da biodiversidade e sua complexidade ao redor da Terra despertam o interesse pela observação da natureza. A documentação da grande biodiversidade na região dos trópicos por pensadores das ciências naturais do século XIX, como Alexander von Humboldt (VON HUMBOLDT, 1808), Charles Darwin (DARWIN, 1859) e Alfred Russel Wallace (WALLACE, 1905), estimularam os ecólogos no mundo todo a buscar as explicações da diminuição da riqueza de espécies dos trópicos em direção ao polos. A macroecologia é uma ciência multidisciplinar, que engloba as áreas da ecologia, biogeografia e macroevolução, e pode ser definida como a investigação empírica das relações entre as espécies e o ambiente, e que tem como objetivo descrever e explicar a diversidade, distribuição e abundâncias dos organismos em larga escala (BROWN; MAURER, 1989; BROWN, 1995). Dessa forma, a descrição dos grandes padrões é considerada a base para a compreensão dos processos e mecanismos que geram as variações da biodiversidade, dinâmica e complexidade dos sistemas ecológicos (BROWN, 1995; BROWN, 1999; GASTON; BLACKBURN, 1999; UNDERWOOD; CHAPMAN; CONNELL, 2006).

Um dos padrões de larga escala mais conhecido é o gradiente latitudinal de diversidade, em que a maior diversidade (i.e., riqueza de espécies) ocorre na região próxima do equador e diminui à medida que aumentam as latitudes, é um dos padrões de larga escala mais abrangentes na Terra (BROWN, 2014; HILLEBRAND, 2004b; PIANKA, 1966; TITTENSOR et al., 2010; WILLIG; KAUFMAN; STEVENS, 2003). Esse padrão já foi descrito para diversos grupos de organismos, em diferentes partes do globo e em diferentes ambientes, como nos ecossistemas terrestres, aquáticos e marinhos (WILLIG et al., 2003; BROWN, 2014). Entretanto, apesar de ser consistente para vários organismos, esse padrão é variável de acordo com o grupo e local estudado.

Para o ambiente marinho, organismos de águas rasas têm o padrão global de diversidade com maior riqueza na região do Pacífico Ocidental e apresentam gradiente latitudinal de diversidade bem definido ao longo das regiões continentais (TITTENSOR et al., 2010; WITMAN; ROY, 2009). Grupos de organismos marinhos bem estudados e com bom conhecimento taxonômico, como peixes recifais e bivalves (TITTENSOR et al., 2010; JABLONSKI et al., 2013) apresentam maior número de espécies na região tropical. Entretanto, outros grupos marinhos não seguem o padrão latitudinal de diversidade clássico. O padrão global de riqueza para macroalgas marinhas, por exemplo, é diferente entre os distintos clados (KEITH *et al.*, 2014). A riqueza pode ser variável ainda entre os diferentes oceanos, por exemplo, a diversidade marinha no Atlântico que difere entre o hemisfério sul e norte (REX et al., 1993; CHOWN et al., 2004) e entre as margens leste e oeste (MACPHERSON, 2002). No oceano Atlântico, a diversidade de diferentes grupos taxonômicos, incluindo peixes recifais (FLOETER et al., 2001; PINHEIRO et al., 2018), gastrópodes (BARROSO *et al.*, 2016), algas, peixes e invertebrados (MILOSLAVICH *et al.*, 2011), e *Symbiodinium* (PICCIANI et al., 2016), é maior em latitudes intermediárias.

Apesar da descrição das distribuições das ocorrências das espécies em larga escala terem sido o foco da macroecologia nas últimas décadas, atualmente, o enfoque tem sido voltado para explicações dos padrões, enfatizando mais os mecanismos envolvidos na organização das comunidades (AGRAWAL et al., 2007). Várias hipóteses têm tentado explicar as variações da diversidade na Terra, incluindo explicações ecológicas, evolucionárias e biogeográficas (HILLEBRAND, 2004b; BROWN, 2014). Embora tenha-se avançado no entendimento dos possíveis processos e mecanismos, há ainda pouco consenso sobre as explicações envolvidas na organização das comunidades, seja pelo grande número de explicações, a complexidade em entender como os processos mutuamente atuam, ou a grande dificuldade em provar os mecanismos que regem as estruturas das comunidades (BROWN, 2014). Apesar do debate sobre a influência de fatores locais e regionais na regulação das ocorrências das espécies (RICKLEFS, 2008; SCHLUTER, RICKLEFS, 1993), no presente momento, entende-se que a estrutura das comunidades é um resultado de diferentes processos estocásticos e determinísticos que atuam em escalas locais e regionais sinergicamente (ZOBEL, 1997; CHASE, 2007; RICKLEFS, 2008; MCGILL, 2010).

Dentro das possíveis explicações ecológicas, a teoria dos filtros abióticos (i.e., filtros oriundos de variáveis ambientais) e a teoria dos filtros bióticos (i.e., interações entre as espécies) tentam explicar a organização das comunidades (ZOBEL, 1997; GÖTZENBERGER *et al.*, 2012; KRAFT et al., 2015). A teoria dos filtros bióticos prediz que a força das interações entre as espécies (e.g., competição, predação e facilitação) determinam a organização das espécies e suas abundâncias em uma comunidade (MACARTHUR & LEVINS, 1967; RICKLEFS, 1987), possuindo uma importância maior em escalas menores (MCGILL, 2010). Filtros bióticos podem influenciar negativamente a diversidade de uma comunidade local se as espécies existentes utilizam os mesmos tipos de recursos, como o uso de espaço ou recurso alimentar, ou, poderiam promover a diferenciação de nicho, caso estas utilizem de forma similar os recursos (MACARTHUR & LEVINS, 1967; GÖTZENBERGER et al., 2012). Por outro lado, os filtros abióticos possuem papel importante na estruturação das comunidades tanto em escalas pequenas quando grandes (MCGILL, 2010), onde condições ambientais extremas impedem e limitam a chegada e/ou estabelecimento das espécies em determinadas comunidades (KRAFT et al., 2015). De fato, em estudos de larga escala, como o padrão de diversidade ao longo do gradiente latitudinal, diversas variáveis abióticas variam com a latitude, como por exemplo a temperatura e quantidade de nutrientes (WILLIG et al., 2003; RICKLEFS, 2004), e o reconhecimento da influência dos fatores de larga escala na estrutura e na dinâmica das comunidades locais estimulou os estudos de macroecologia (GASTON; BLACKBURN, 1999; GASTON; BLACKBURN 2000).

No ambiente marinho, a organização e distribuição dos organismos das comunidades bentônicas geralmente estão associadas com variáveis ambientais como, por exemplo, a salinidade, a quantidade de nutrientes, a penetração da luz, a sedimentação e a temperatura (WITMAN & GRANGE, 1998; KLEYPAS et a*l.*, 1999; WITMAN & SMITH, 2001; MCARTHUR et al., 2010). A temperatura é considerada um dos fatores primários atuando na diversidade e distribuição dos organismos (CLARKE & GASTON, 2006), principalmente no ambiente marinho (TITTENSOR et al., 2010). A temperatura está ligada com a quantidade de energia no ambiente, favorecendo grandes populações e promovendo diferenciação de nicho (FRASER & CURRIE, 1996; EVANS et al., 2016), ou como um fator estressor, interferindo na fisiologia dos organismos e limitando a distribuição das espécies não adaptadas (CLARKE & GASTON, 2006).

Os filtros abióticos e bióticos, portanto, influenciam na ocorrência e abundância das espécies, e além disso, interferem nas características morfológicas, fisiológicas e comportamentais dos organismos, chamadas de atributos de resposta (LAVOREL & GARNIER, 2002). De fato, a ecologia de comunidade moderna tem cada vez mais utilizado a abordagem funcional para entender como os diferentes fatores influenciam as espécies, através de seus atributos, a organização das comunidades e o funcionamento ecossistêmico (MCGILL et al., 2006a; CARMONA et al., 2016).

2.1 DIVERSIDADE FUNCIONAL

À medida que os estudos de ecologia de comunidade tentam explicar os mecanismos que regem as comunidades, a diversidade funcional tem sido cada vez mais utilizada para entender os processos e o funcionamento dos ecossistemas (MCGILL et al., 2006; AGRAWAL et al., 2007). A diversidade funcional leva em consideração os atributos dos organismos, os quais podem ser características fenotípicas, comportamentais ou fisiológicas, consideradas atributos de respostas aos diferentes filtros abióticos e bióticos e que influenciam as performances dos organismos nas comunidades (NOCK; VOGT; BEISNER, 2016; MCGILL et al., 2006; TILMAN, 2001). O uso da abordagem funcional tem sido amplamente difundido em estudos de ecologia e conservação, uma vez que diversidade funcional é considerada melhor preditor que a diversidade taxonômica para avaliação de respostas da comunidade a mudanças ambientais e efeitos de distúrbio (MCGILL et al., 2006; Mouillot et al., 2013). A abordagem da diversidade funcional, inclusive, é baseada no conceito de nicho de Hutchinson (HUTCHINSON, 1957), e propõe que os valores e extensões dos atributos das espécies determinam sua posição e extensão no nicho ao longo de gradientes, e podem ser quantificados através do volume ocupado por um grupo de espécies no espaço funcional dos atributos (*functional trait space*) (VIOLLE & JIANG, 2009; LAMANNA et al., 2014).

A tentativa de medir a diversidade funcional acontece há aproximadamente 20 anos (PETCHEY & GASTON, 2006), e atualmente, existem diversas métricas funcionais para avaliação dos diferentes aspectos das comunidades (VILLÉGER et al., 2008, 2011; MOUCHET et al., 2010; Mouillot et al., 2013; Carmona et al., 2016). Porém, os três componentes primários da diversidade funcional (riqueza funcional, divergência funcional e equitabilidade funcional) continuam sendo os mais adequados para medir as diferenças entre as comunidades (MASON et al., 2005; VILLÉGER et al., 2008). Riqueza funcional (FRic) se refere ao espaço ocupado por uma comunidade no espaço funcional, ou *functional trait space*, equitabilidade funcional (FEve) mede a regularidade das distribuições das abundâncias no espaço funcional e leva em consideração a menor distância entre os pontos, ou *minimum spanning tree*, e a divergência funcional (FDiv) mede a distribuição das abundâncias entre as espécies raras e dominantes no volume funcional (VILLÉGER et al., 2008). Grupos funcionais, também chamados de entidades funcionais, são grupos de espécies que possuem os mesmos valores e extensões dos atributos funcionais, e assim são influenciados de maneira parecida pelo ambiente e interações, ou tem papel similar no funcionamento ecossistêmico (NOCK; VOGT; BEISNER, 2016; TILMAN, 2001; VIOLLE et al., 2007).

Apesar do avanço do uso da abordagem funcional no entendimento de como os processos ecológicos atuam em larga escala na diversidade e na estruturação das comunidades marinhas de águas rasas, principalmente para peixes recifais e bivalves, a aplicação desta abordagem em diferentes grupos taxonômicos ainda é incipiente, ou quase inexistente. Num momento em que os ambientes marinhos estão sofrendo ameaças mundialmente, com grande perda da diversidade marinha, faz-se importante o entendimento dos padrões e processos que regem as comunidades como um tudo, englobando diferentes grupos taxonômicos, como as comunidades bentônicas marinhas. Aliando padrões ao entendimento dos processos que geram esses padrões é possível gerar informações básicas para tomadores de decisões, e ampliar o conhecimento sobre o funcionamento dos ecossistemas recifais. Portanto, o presente estudo teve como objetivo descrever a estrutura e os padrões de diversidade em larga escala das comunidades bentônicas recifais ao longo do gradiente latitudinal da Província Brasileira e testar quais fatores abióticos atuam nos padrões observados.

3.1 OBJETIVOS

3.1.1 Objetivo Geral

Descrever o padrão de riqueza e da composição das comunidades bentônicas marinhas ao longo do gradiente latitudinal da Província Brasileira e, inferir sobre os processos ecológicos que governam tal padrão no Atlântico Sul Ocidental.

3.1.2 Objetivos Específicos

1). Apresentar o padrão de composição das comunidades bentônicas ao longo da Província Brasileira, criando assim um patamar de referência (*baseline*) para as comunidades bentônicas dos recifes brasileiros;
(Capítulo 1: “Large-scale patterns of benthic marine communities in the Brazilian Province”)

2). Descrever o padrão de diversidade das comunidades bentônicas num gradiente latitudinal (de 0˚ até 27˚S) do Atlântico Sul Ocidental;
(Capítulo 1: “Large-scale patterns of benthic marine communities in the Brazilian Province”)

3). Demonstrar a variação da diversidade funcional ao longo do gradiente latitudinal da Província Brasileira;
(Capítulo 2: “Functional diversity of reef benthic communities along a latitudinal environmental gradient”)

4). Inferir sobre os processos ecológicos (filtros abióticos e bióticos) que governam o padrão de diversidade do Atlântico Sul Ocidental;
(Capítulo 2: “Functional diversity of reef benthic communities along a latitudinal environmental gradient”)

5). Testar quanto da variação dos índices funcionais é explicada pelos filtros abióticos e inferir sobre quais possíveis mecanismos poderiam explicar o padrão latitudinal.
(Capítulo 2: “Functional diversity of reef benthic communities along a latitudinal environmental gradient”)

4.1 ÁREA DE ESTUDO

4.1.1 Província Brasileira

A Província Brasileira, denominação proposta primeiramente por Briggs (1974) e modificada posteriormente por Floeter et al. (2008), engloba os quase 8 mil quilômetros da costa brasileira e as ilhas oceânicas do Brasil, sendo elas as ilhas do arquipélago de Fernando de Noronha, do Arquipélago de São Pedro e São Paulo, da Ilha da Trindade e do Atol das Rocas (Figura 1) (BRIGGS, 1974; BOWEN, 2012; FLOETER et al., 2008). A Província Brasileira começa na boca do Rio Amazonas (0˚S) e vai até o estado de Santa Catarina (28˚S) (BRIGGS, 1974; BRIGGS, 1995; FLOETER et al., 2008). A Província é delimitada por três grandes barreiras biogeográficas: 1) a pluma do Rio Amazonas, que impede e limite o cruzamento da fauna e flora marinha da Província do Caribe para o Brasil, 1) a barreira do meio do Atlântico, que isola a Província brasileira da biodiversidade do oeste da África, e 3) as baixas temperaturas provenientes da pluma do Rio da Prata, no Uruguai, que limitam a distribuição de organismos tropicais para a região mais ao sul (FLOETER et al., 2008).

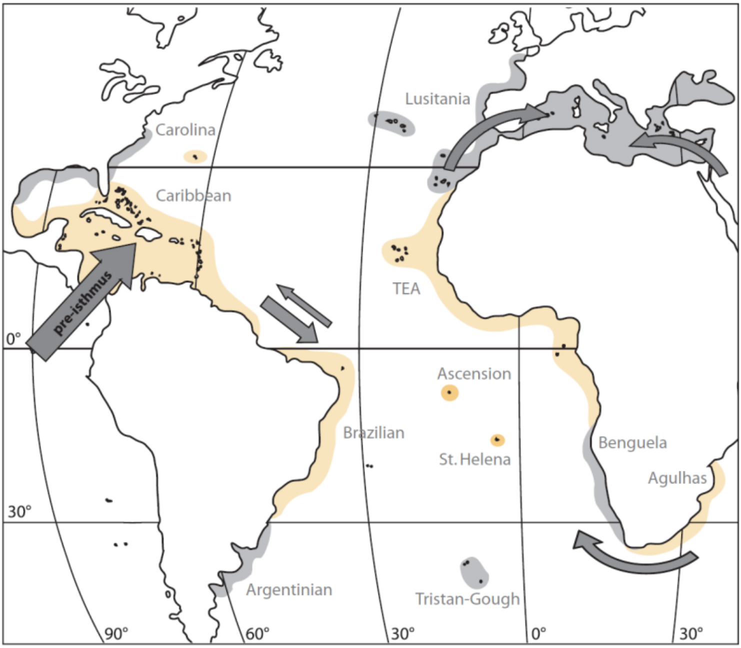

Figura 1 Mapa das províncias biogeográficas do oceano Atlântico. Retirado de Briggs & Bowen (2013).

Embora os recifes da Província Brasileira correspondam a somente 5% dos recifes do oceano Atlântico, o grau de endemismo das espécies é considerado alto, por exemplo, cerca de 34% das espécies de corais, 11% das macroalgas marinhas, e 35% das esponjas são endêmicos dessa Província (CASTRO; PIRES, 2001; FLOETER et al., 2009).

Os habitats recifais da Província Brasileira são distintos ao longo do gradiente latitudinal, por exemplo, a região nordeste e central da Província é caracterizada por afloramentos areníticos e carbonáticos, correspondendo principalmente a recifes biogênicos. Os recifes biogênicos coralíneos são encontrados principalmente na região de Abrolhos (BA). A parte sul-sudeste da Província é marcada por praias arenosas interrompidas por costões rochosos (BARROSO et al., 2016). A Província é caracterizada por forte influência de aportes oriundos de rios, principalmente na região norte e nordeste (LEÃO & GINSBURG, 1997), de ventos fortes na região norte-nordeste, e possui largura variável da plataforma continental ao longo das latitudes (MILOSLAVICH *et al.*, 2011). A Província Brasileira é ainda influenciada pelas águas quentes da Corrente do Brasil provenientes da região norte do país, com temperaturas do mar geralmente acima de 20˚C, e das águas frias, oriundas da correntes das Malvinas e da Pluma do Rio da Prata derivadas da região sul, com temperatura abaixo de 16˚C (CASTRO; MIRANDA, 1998; PALMEIRA et al., 2015).

5.1 MÉTODO

5.1.1 Comunidades bentônicas marinhas de substrato consolidado

As comunidades bentônicas marinhas de substrato consolidado, formadoras de ambientes recifais, representam um dos ecossistemas mais produtivos e diversos do planeta (WAHL, 2009) e são formadas pela presença de macroalgas, produtores primários das cadeia tróficas marinhas (ADEY, 1998), e por invertebrados móveis e sésseis. Essas comunidades possuem a capacidade de modificar o ambiente, promovendo assim complexidade estrutural tri-dimensional, e fornecem uma variedade de serviços ecossistêmicos, como o ciclo de nutrientes, abrigo e proteção, e berçário (SOARES et al. 2016; WAHL, 2009; WITMAN; DAYTON, 2001). Juntamente com as florestas tropicais, as comunidades bentônicas recifais representam o ápice de diversidade global (REAKA-KUDLA, 1997).

No Brasil, a maioria dos estudos com comunidades bentônicas recifais ao longo do gradiente latitudinal são principalmente descritivos (CASTRO; PIRES, 2001; FIGUEIREDO et al., 2008; GHILARDI; PEREIRA FILHO; BERCHEZ, 2008; LABOREL, 1970; LEÃO; KIKUCHI; TESTA, 2003; MILOSLAVICH et al., 2011) e, até o presente momento, não existe um trabalho quantitativo, com metodologia padronizada, que avalie as comunidades bentônicas recifais ao longo da costa brasileira. A falta de um estudo de base impossibilita compreender a biodiversidade e inferir mudanças na estrutura das comunidades bentônicas brasileiras. Além disso, a falta de informações básica sobre a biologia e ecologia destes organismos bentônicos (COSTELLO et al., 2015) dificulta o entendimento sobre o funcionamento dos ecossistemas reciais brasileiros

5.1.2 Amostragem das comunidades bentônicas

Este estudo analisou as comunidades bentônicas de substrato consolidado raso em 40 sítios localizados dentro de 15 localidades ao longo do gradiente latitudinal (0˚ a 27˚S) da Província Brasileira. Em cada localidade foram amostrados de um a cinco sítios, porém a maioria incluiu ao menos três sítios amostrados. Todas as coletas aconteceram no período de verão, entre 2011 a 2014. Em cada sítio, foram amostrados dois estratos de profundidade: 1-7 metros e 8-15 metros, levando em consideração as características particulares de cada local. Em cada estrato de profundidade, as comunidades bentônicas foram quantificadas através de amostragem padronizada com uso de cinco fotoquadrados (25x25 cm) aleatórios. dentro de uma área de recife relativamente plana de $2m^2$. Em cada estrato de profundidade foram amostradas seis a vinte áreas de recifes ($2m^2$). As áreas foram amostradas com distância mínima de 2 metros, sendo consideradas como amostras independentes nas análises. Ao total, foram amostradas de 8 a 30 áreas de recifes em cada sítio, resultando em no mínimo 40 e no máximo 150 fotoquadrados por sítio, assim, 3855 fotoquadrados foram analisados para este estudo.

Posteriormente, cada fotoquadrado foi analisado através do programa PhotoQuad (TRYGONIS & SINI, 2012), utilizando 50 pontos aleatórios em cada imagem, e identificando o organismo embaixo de cada ponto ao menor nível taxonômico possível. A composição da comunidade, em seu menor nível de resolução, foi utilizada para as análises de avaliação da estrutura das comunidades. Adicionalmente, os organismos foram agrupados em grupos taxonômicos e com funções reconhecidas para os ambientes recifais (e.g., coral, macroalgas, suspensívoros e filtradores, etc). Para as análises da diversidade taxonômica, o número de táxons em cada sítio, aninhado dentro das localidades, foi considerado como a riqueza local. Para a abordagem da diversidade funcional, os táxons foram agrupados de acordo com os seus valores e extensões dos atributos funcionais, após realizada uma busca pelos atributos funcionais importantes para o funcionamento dos recifes brasileiros.

5.1.3 Seleção e classificação dos atributos funcionais

Para o uso da abordagem funcional, foi necessário fazer uma ampla revisão dos atributos dos organismos bentônicos marinhos ligados às funções importantes para o funcionamento dos ecossistemas recifais. Atributos funcionais são características morfológicas, fisiológicas ou comportamentais dos organismos que podem estar ligadas ao uso de algum tipo de recurso, ou que promovam algum serviço ecossistêmico

(TILMAN, 2001; VIOLLE et al., 2007). No ambiente marinho, os principais recursos para os organismos bentônicos são a disponibilidade de nutrientes, a quantidade de luz, por exemplo para a realização da fotossíntese, e o uso do espaço, já que são em sua maioria organismos sésseis (WAHL, 2009). Já os principais serviços ecossistêmicos que as comunidades bentônicas promovem são: a complexidade estrutural, abrigo e proteção para outros animais, fornecimento de alimento para organismos de grupos tróficos mais altos, e resiliência do recife frente a distúrbios (MOBERG & FOLKE, 1999; WAHL, 2009). Nosso trabalho levou em conta atributos funcionais relacionados com o uso de recursos e com o fornecimento de serviços ecossistêmicos para as comunidades estudadas e que pudessem ser aplicados para os diferentes grupos taxonômicos que amostramos. O nosso esquema de classificação foi baseado em categorizações prévias dos organismos bentônicos (ver BELL; BARNES, 2001; BREMNER; ROGERS; FRID, 2006; COSTELLO et al., 2015; LITTLER; LITTLER, 1984; STENECK; DETHIER, 1994; WAHL, 2009).

Com base nesses estudos, nós selecionamos seis atributos considerados de resposta aos diferentes filtros bióticos e abióticos que atuam na estruturação das comunidades bentônicas locais, e consequentemente nas características destas, e com relevância ecológica para as comunidades estudadas (Tabela 1). Quando a informação do atributo não era encontrada na literatura nós consideramos o atributo dominante para níveis taxonômicos maiores, ou para o grupo em geral. Além disso, transformamos os atributos em níveis categóricos, para que pudessem ser aplicados mais facilmente para todos os organismos amostrados, pertencentes a diferentes grupos taxonômicos (Tabela 2).

Tamanho do corpo

O tamanho corporal tem uma relação direta com o uso do espaço e com as abundâncias dos organismos em uma comunidade, além disso, esse atributo está ligado indiretamente com a longevidade (WOODWARD et al., 2005). Nós selecionamos informações do tamanho corporal no sentido horizontal, que tem a ver com uso do substrato, e utilizamos informações da literatura ou ajuda de especialistas (ver informações na Tabela 2). Os tamanhos dos organismos unitários foram considerados como sendo o tamanho máximo registrado na literatura, porém, para os organismos modulares (e.g., corais) nós utilizamos o tamanho máximo das colônias, ou agregações modulares, reportado na literatura. O tamanho do corpo foi dividido em 4 níveis: S = < 10 cm; M = 10-50 cm; L = 50-400 cm e XL = > 400 cm (Tabela 1).

Tabela 1 Esquema de classificação dos atributos funcionais.

Categoria	Atributo	Níveis do atributo
Biológica	Tamanho do corpo	Pequeno (<10 cm) Médio (10-50 cm) Grande (50-400 cm) Muito grande (>400cm)
	Forma do corpo	Arborescente Incrustante Incrustante/filamentosa Filamentosa Massiva
	Grupo Trófico	Autotrófico Autotrófico/heterotrófico Carnívoro Raspador Suspensívoro/filtrador
	Modularidade	Solitário Modular
	Mobilidade	Séssil Móvel
História de vida	Tipo de reprodução	Assexuada Assexuada/sexuada Sexuada

Forma do corpo

A forma do corpo dos organismos bentônicos está diretamente ligada com a complexidade do habitat e do uso de recursos (RICHARDSON et al., 2017). Nós selecionamos cinco categorias que pudessem ser aplicadas para todas as comunidades estudadas, mesmo sabendo que existem mais formas que as cinco usadas nesse estudo. Assim, a forma do corpo foi classificada em: E = incrustante, M = massiva, B = arborescente ou com crescimento vertical, F = filamentosa e EF = incrustante/filamentosa.

Grupo trófico

Grupo trófico está diretamente ligado às interações biológicas e ao ciclo de nutrientes (HILLEBRAND, 2008; WAHL et al., 2011). Nós consideramos as categorias predominantes para os grupos de organismos. Grupo trófico foi dividido em seis categorias: A = autotrófico, S = suspensívoro/filtrador, G = raspador, C = carnívoro e AC = autotrófico/heterotrófico.

Modularidade

A modularidade está ligada a ocupação do espaço e à história de vida (reprodução) (WAHL et al., 2011). Nós a classificamos em dois níveis: S = organismos solitários e M = organismos modulares.

Mobilidade

A mobilidade é um indicativo do potencial de dispersão dos organismos e, consequentemente, tem a ver com a capacidade de resiliência (COSTELLO et al., 2015). Mobilidade também foi classificada em: S = séssil e M = móvel.

Tipo de reprodução

Os atributos ligados à história de vida dos organismos geralmente descrevem a persistência e/ou a longevidade de um indivíduo ou de uma população em um determinado local ao longo do tempo. Sendo assim, o tipo de reprodução está ligado com a capacidade de dispersão de uma espécie e pode ter relação com a habilidade de recuperação de uma população após um distúrbio (COSTELLO et al., 2015). Nós dividimos o tipo de reprodução em: S = sexuada, A = assexuada e AS = assexuada/sexuada.

Tabela 2 Classificação dos táxons segundo os atributos funcionais.

Phylum	Taxa	Tamanho do corpo	Forma do corpo	Grupo trófico	Modularidade	Mobilidade	Tipo de reprodução
Annelida	Polychaeta	S	B	S	S	S	AS
Arthropoda	Hexanauplia	S	E	S	S	S	S
	Malacostraca	S	M	C	S	M	S
Bryozoa	Schizoporella sp.	M	E	C	M	S	AS
Chlorophyta	Bryopsis pennata	L	B	A	M	S	AS
	Caulerpa racemosa	L	B	A	M	S	AS
	Caulerpa spp.	L	B	A	M	S	AS
	Caulerpa verticillata	L	B	A	M	S	AS
	Chaetomorpha sp.	S	F	A	M	S	AS
	Champia parvula	S	B	A	M	S	AS
	Codium intertextum	XL	E	A	M	S	AS
	Codium spp.	S	B	A	M	S	AS
	Halimeda spp.	XL	B	A	M	S	AS
	Udotea sp.	S	B	A	M	S	AS
	Ulvophyceae não identificada1	XL	F	A	M	S	AS
	Ulvophyceae não identificada2	XL	F	A	M	S	AS

Phylum	Taxa	Tamanho do corpo	Forma do corpo	Grupo trófico	Modularidade	Mobilidade	Tipo de reprodução
	Ventricaria ventricosa	S	M	A	M	S	AS
Chordata	Ascidia não identificada1	S	E	S	M	S	AS
	Ascidia não identificada2	S	M	S	M	S	AS
	Botrylloides nigrum	S	E	S	M	S	AS
	Didemnum perlucidum	S	E	S	M	S	AS
	Didemnum sp.	S	E	S	M	S	AS
	Phallusia nigra	S	M	S	S	S	AS
	Trididemnum sp.	S	E	S	M	S	AS
Cnidaria	Agaricia fragilis	M	E	AC	M	S	AS
	Agaricia humilis	M	E	AC	M	S	AS
	Agaricia spp.	M	E	AC	M	S	AS
	Alcyonacea	S	B	C	M	S	AS
	Anthozoa não identificado	L	M	AC	M	S	AS
	Bunodosoma caissarum	S	M	C	S	M	AS
	Carijoa riisei	L	B	C	M	S	AS
	Favia gravida	S	E	AC	M	S	AS
	Favia leptophylla	L	M	AC	M	S	AS
	Heterogorgia spp.	S	B	C	M	S	AS
	Hydrozoa	S	B	C	M	S	AS

Phylum	Taxa	Tamanho do corpo	Forma do corpo	Grupo trófico	Modularidade	Mobilidade	Tipo de reprodução
	Idiellana pristis	S	B	C	M	S	AS
	Leptogorgia spp.	S	B	C	M	S	AS
	Macrorhynchia philippina	S	B	A	M	S	AS
	Madracis decactis	L	B	C	M	S	AS
	Meandrina brasiliensis	M	M	AC	M	S	AS
	Millepora alcicornis	L	B	AC	M	S	AS
	Millepora nitida	M	M	AC	M	S	AS
	Millepora não identificada1	L	E	AC	M	S	AS
	Millepora não identificada2	L	E	AC	M	S	AS
	Montastraea cavernosa	L	M	AC	M	S	AS
	Muricea flamma	S	B	C	M	S	AS
	Muriceopsis sulphurea	S	B	AC	M	S	AS
	Mussismilia braziliensis	L	M	AC	M	S	AS
	Mussismilia harttii	L	B	AC	M	S	AS
	Mussismilia hispida	M	M	AC	M	S	AS
	Mussismilia spp.	L	E	AC	M	S	AS
	Palythoa caribaeorum	XL	E	AC	M	S	AS
	Palythoa variabilis	L	E	AC	M	S	AS
	Parazoanthus axinellae	L	E	AC	M	S	AS

Phylum	Taxa	Tamanho do corpo	Forma do corpo	Grupo trófico	Modularidade	Mobilidade	Tipo de reprodução
	Phyllogorgia dilatata	S	B	AC	M	S	AS
	Plexaurella grandiflora	S	B	AC	M	S	AS
	Plexaurella regia	S	B	AC	M	S	AS
	Porites astreoides	M	M	AC	M	S	AS
	Porites branneri	M	E	AC	M	S	AS
	Porites spp.	M	E	AC	M	S	AS
	Protopalythoa spp.	L	E	AC	M	S	AS
	Rhizangiidae	M	E	AC	M	S	AS
	Siderastrea spp.	L	M	AC	M	S	AS
	Zoanthus sociatus	XL	E	AC	M	S	AS
Cyanobacteria	Cyanobacteria	XL	EF	A	M	S	AS
Echinodermata	Asteroidea	M	M	C	S	M	S
	Echinaster	S	M	C	S	M	S
	Echinometra lucunter	M	B	G	S	M	S
	Eucidaris tribuloides	M	B	G	S	M	S
	Ophiothela mirabilis	S	E	C	S	M	S
	Tropiometra sp.	M	B	S	S	M	S
Ochrophyta	Colpomenia sinuosa	S	M	A	M	S	AS
	Dictyopteris plagiogramma	S	B	A	M	S	AS

Phylum	Taxa	Tamanho do corpo	Forma do corpo	Grupo trófico	Modularidade	Mobilidade	Tipo de reprodução
	Dictyopteris spp.	M	B	A	M	S	AS
	Dictyota spp.	M	B	A	M	S	AS
	Dictyotaceae não identificada1	L	B	A	M	S	AS
	Dictyotaceae não identificada2	S	B	A	M	S	AS
	Lobophora variegata	XL	B	A	M	S	AS
	Padina sp.	L	B	A	M	S	AS
	Sargassum spp.	S	B	A	M	S	AS
	Stypopodium spp.	S	B	A	M	S	AS
Porifera	Demospongiae arborescente	S	B	S	S	S	AS
	Demospongiae globular	M	M	S	S	S	AS
	Demospongiae incrustante	M	E	S	S	S	AS
	Demospongiae massiva	M	M	S	S	S	AS
	Demospongiae papilada	M	E	S	S	S	AS
	Demospongiae tubular	S	B	S	S	S	AS
Rhodophyta	Corallinales	XL	E	A	M	S	S
	Corallinaceae não identificada1	L	B	A	M	S	AS
	Corallinaceae não identificada2	L	B	A	M	S	AS

Phylum	**Taxa**	**Tamanho do corpo**	**Forma do corpo**	**Grupo trófico**	**Modularidade**	**Mobilidade**	**Tipo de reprodução**
	Coralline turf	XL	EF	A	M	S	AS
	Digenea simplex	XL	B	A	M	S	AS
	Galaxaura spp.	S	B	A	M	S	AS
	Gelidiella acerosa	XL	B	A	M	S	AS
	Gelidiopsis spp.	L	B	A	M	S	AS
	Gelidium floridanum	L	B	A	M	S	AS
	Gigartinacea	XL	B	A	M	S	AS
	Hypnea musciformis	XL	B	A	M	S	AS
	Laurencia spp.	L	B	A	M	S	AS
	Ochtodes secundiramea	S	B	A	M	S	AS
	Peyssonnelia sp.	XL	B	A	M	S	AS
	Tricleocarpa cylindrica	S	B	A	M	S	AS
	Wrangelia sp.	L	B	A	M	S	AS

REFERÊNCIAS

Adey, W.H. (1998) Review-Coral Reefs: Algal Structured and Mediated Ecosystems in Shallow, Turbulent, Alkaline Waters. Journal of Phycology, 34, 393–406.

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M.G. & Werner, E. (2007) Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment, 5, 145–152.

Barroso, C.X., Lotufo, T.M. da C. & Matthews-Cascon, H. (2016) Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships. Journal of Biogeography, 43, 2477–2488.

Bell, J.J. & Barnes, D.K. (2001) Sponge morphological diversity: A qualitative predictor of species diversity? Aquatic Conservation: Marine and Freshwater Ecosystems, 11, 109–121.

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecological Indicators, 6, 609–622.

Briggs, J.C. & Bowen, B.W. (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. 39, 12–30.

Briggs, J.C. (1974) Marine zoogeography. McGraw-Hill, New York.

Briggs, J.C. (1995) Global biogeography. Elsevier, Amsterdam.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: The division of food and space among species on continents. Progress in Physical Geography, 243, 1145–1150.

Brown, J.H. (1995) Macroecology. The university of Chicago press, Chicago.

Brown, J.H. (1999) Macroecology: progress and prospect. Oikos, 87, 3-14.

Brown, J.H. (2014) Why are there so many species in the tropics? Journal of Biogeography, 41, 8–22.

Carmona, C.P., de Bello, F., Mason, N.W.H. & Lepš, J. (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. Trends in Ecology and Evolution, 31, 382–394.

Castro, B.M. & Miranda, L.B. (1998) Physical Oceanography of the western Atlantic Continental shelf located between 4oN and 34oS, coastal segment (4W). The Sea, 11: 209–251.

Castro, C.B. & Pires, D.O. (2001) Brazilian coral reefs: what we already know and what is still missing. Bulletin of Marine Science, 69, 357–371.

Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences, 104, 17430–17434.

Chown, S.L., Sinclair, B.J., Leinaas, H.P. & Gaston, K.J. (2004) Hemispheric asymmetries in biodiversity - A serious matter for ecology. PLoS Biology, 2.

Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. Proceedings of the Royal Society B: Biological Sciences, 273, 2257–2266.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, É.Ó., Lear, D. & Tyler-Walters, H. (2015) Biological and ecological traits of marine species. PeerJ, 3, e1201.

Darwin, C. (1859) On the origin of species by means of natural selection, J. Murray, London.

Evans, K.L., Warren, P.H., Gaston, K.J., Evans, K.L., Warren, P.H. & Gaston, K.J. (2016) Species – energy relationships at the macroecological scale: a review of the mechanisms. 80, 1–25.

Figueiredo, M.A.O., Horta, P.A., Pedrini, A.G. & Nunes, J.M.C. (2008) Benthic Marine Algae of the Coral Reefs of Brazil: a Literature Review. Oecologia brasiliensis, 12, 258–269.

Floeter, S.R., Guimarães, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. Global Ecology and Biogeography, 10, 423–431.

Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W. & Bernardi, G. (2008) Atlantic reef fish biogeography and evolution. Journal of Biogeography, 35, 22–47.

Floeter, S.R., Soares-Gomes, A. & Hajdu, E. (2009) Biogeografia marinha. In: Biologia Marinha. Interciência, Rio de Janeiro.

Fraser, R.H. & Currie, D.J. (1996) The Species Richness-Energy Hypothesis in a System Where Historical Factors Are Thought to Prevail: Coral Reefs. The American Naturalist, 148, 138–159.

Gaston, K.J. & Blackburn, T.M. (1999) A Critique for Macroecology. Oikos, 84, 353–368.

Gaston, K.J. & Blackburn, T.M. (2000) Pattern and process in macroecology. Blackwell, Oxford.

Ghilardi, N.P., Pereira Filho, G.H. & Berchez, F. (2008) Current Knowledge status of the ecology of hard bottom benthic communities in Brazil and the need for new approaches. Oecologia Australis, 12, 197–205.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K. & Zobel, M. (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. Biological Reviews, 87, 111–127.

MaCarthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. 101, 377–385.

Macpherson, E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences, 269, 1715–1720.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos, 111, 112–118.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D. & Radke, L.C. (2010) On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine, Coastal and Shelf Science, 88, 21–32.

McGill, B.J. (2010) Matters of Scale. Science, 328, 575–576.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006a) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution, 21, 178–185.

Miloslavich, P., Klein, E., Díaz, J.M., Hernández, C.E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M. V., Díaz de Astarloa, J.M., Lewis, M., Yorio, P., Piriz, M.L., Rodríguez, D., Valentin, Y.Y., Gamboa, L. & Martín, A. (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: Knowledge and gaps. PLoS ONE, 6, 1–43.

Moberg, F.F. & Folke, C. (1999) Ecological goods and services of coral reef ecosystems. Ecological Economics, 29, 215–233.

Mouchet, M. a., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24, 867–876.

Mouillot, D., Graham, N. a J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution, 28, 167–177.

Nock, C.A., Vogt, R. J. & Beisner, B.E. (2016) Functional traits. John Wiley & Sons, Chichester.

Palmeira, A.C.P.A, Camargo, R., Palmeira, R.M.J. (2015) Relação entre a temperatura da superfície do mar e a camada de mistura oceânica sob a passagem de ciclones extratropicais no Atlântico Sudoeste. Revista Brasileira de Meteorologia. 30: 89-100.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: Back to basics and looking forward. Ecology Letters, 9, 741–758.

Pianka, E.R. (1966) Latitudinal Gradients in Species Diversity: A Review of Concepts. The American Naturalist, 100, 33–46.

Picciani, N., Seiblitz, I.G. de L., Paiva, P.C., Castro, C.B. & Zilberberg, C. (2016) Geographic patterns of *Symbiodinium* diversity associated with the coral *Mussismilia hispida* (Cnidaria, Scleractinia) correlate with major reef regions in the Southwestern Atlantic Ocean. Marine Biology, 163, 1–11.

Pinheiro, H.T., Rocha, L.A., Macieira, R.M., Carvalho-Filho, A., Anderson, A., Bender, M.G., DiDario, F., Ferreira, C.E.L., Figueiredo-Filho, J., Francini-Filho, R., Gasparini, J.L., Joyeux, J.C., Luiz, O.J., Mincarone, M., Moura, R.L., Nunes, J., Quimbayo, J.P., Rosa, R., Sampaio, C., Sazima, I., Simon, T., Vila-Nova, D.A. & Floeter, S.R. (2018) Southwestern Atlantic reef fishes: zoogeographic patterns and ecological drivers reveal a secondary biodiversity center in the Atlantic Ocean. Diversity and Distributions.

Reaka-Kudla, M.L. (1997) The global biodiversity of coral reefs: a comparison with rain forests. In: Biodiveristy II: Understanding and protecting our biological resources. Joseph Henry Press, Washington.

Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L. & Wilson, G.D.F. (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature, 365, 636–639.

Richardson, L.E., Graham, N.A.J. & Hoey, A.S. (2017) Cross-scale habitat structure driven by coral species composition on tropical reefs. Scientific Reports, 1–11.

Ricklefs, R.E. (1987) Community Diversity: Relative Roles of and Regional Processes. Science, 235, 167–171.

Ricklefs, R.E. (2008) Disintegration of the Ecological Community. The American Naturalist, 172, 741–750.

Schluter, D. & Ricklefs, R.E. (1993) Species diversity: an introduction to the problem. In: Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Soares, M.O., Lotufo, T.M.C., Vieira, L.M., Salani, S., Hadju, E., Matthews-Cascon, H., Leão, Z.M.A.N., Kikuchi, R.K.P. (2016) Brazilian marine animal forest: a new world to discover in the Southwestern Atlantic. Springer International Publishing, Switzerland.

Steneck, R.S. & Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities. Oikos, 69, 476–498.

Tilman, D. (2001) Functional diversity. Encyclopedia of Biodiversity, 3, 109–120.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E. Vanden & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. Nature, 466, 1098–1101.

Trygonis, V. & Sini, M. (2012) PhotoQuad: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. Journal of Experimental Marine Biology and Ecology, 424–425, 99–108.

Underwood, A.J., Chapman, M.G. & Connell, S.D. (2006) Observations in ecology: you can’t make progress on processes without understanding the patterns. 250, 97–115.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89, 2290–2301.

Villéger, S., Novack-Gottshall, P.M. & Mouillot, D. (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecology Letters, 14, 561–568.

Violle, C. & Jiang, L. (2009) Towards a trait-based quantification of species niche. Journal of Plant Ecology, 2, 87–93.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! Oikos, 116, 882–892.

Wahl, M. (2009) Marine Hard Bottom Communities Studies Volume 206, Springer Berlin Heidelberg, Berlin.

Wallace, A.R. (1905) My life: a record of events and opinions. Chapmam and Hall, London.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution, and Systematics, 34, 273–309.

Witman, J.D. & Dayton, P.K. (2001) Rocky subtidal communities. In: Marine community ecology. Sunderland, Massachussetts.

Witman, J.D. & Grange, K.R. (1998) Links between rain, salinity, and predation in a rocky subtidal community. Ecology, 79, 2429–2447.

Witman, J.D. & Roy, K. (2009) Marine macroecology. The University of Chicago Press, Chicago and London.

Witman, J.D., Etter, R.J. & Smith, F. (2004) The relationship between regional and local species diversity in marine benthic communities: A global perspective. Proceedings of the National Academy of Sciences, 101, 15664–15669.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. Trends in Ecology and Evolution, 20, 402–409.

Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? TREE, 12, 266–269.

CAPÍTULO 1

Large-scale patterns of benthic marine communities in the Brazilian Province

(artigo em revisão no periódico Plos One)
formatação de acordo com as regras da revista

Large-scale patterns of benthic marine communities in the Brazilian Province

Short-title**: Benthic marine communities in the Brazilian Province**

Anaide W. Aued[1,2,3,4*], Franz Smith[4], Juan P. Quimbayo[1,2], Davi V. Cândido[3], Guilherme O. Longo[5], Carlos E. L. Ferreira[6], Jon D. Witman[4], Sergio R. Floeter[1,2] & Bárbara Segal[1,3]

1 Programa de Pós-Graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil,
2 Marine Macroecology and Biogeography Lab, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil,
3 Laboratório de Ecologia de Ambientes Recifais, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil,
4 The Witman Lab, Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, United States of America,
5 Marine Ecology Lab, Department of Oceanography and Limnology, Universidade Federal do Rio Grande do Norte, Natal, Brazil,
6 Reef Systems Ecology and Conservation Lab, Universidade Federal Fluminense, Niterói, RJ, Brazil

* Corresponding author: anaidewru@gmail.com

ABSTRACT

As marine ecosystems are influenced by global and regional processes, standardized information on community structure has become crucial for assessing broad-scale responses to natural and anthropogenic disturbances. Extensive biogeographic provinces, such as the Brazilian Province in the southwest Atlantic, present numerous theoretical and methodological challenges for understanding community patterns on a macroecological scale. In particular, the Brazilian Province is composed of a complex system of heterogeneous reefs and few offshore islands, with contrasting histories and geophysical-chemical environments. Despite the large extension of the Brazilian Province (almost 8,000 thousand kilometers), most studies of shallow benthic communities are qualitative surveys and/or have been geographically restricted. We quantified community structure of shallow reef habitats from 0˚ to 27˚S latitude using a standard photographic quadrat technique. Percent cover data showed benthic communities of Brazilian reefs were dominated by algal turfs and frondose macroalgae, with low percent cover of reef-building corals. Community composition differed significantly among localities, mostly because of their macroalgal abundance, despite reef type or geographic region, with no evident latitudinal pattern. Benthic diversity was lower in the tropics, contrary to the general latitudinal diversity gradient pattern. Richness peaked at mid-latitudes, between 20˚S to 23˚S latitude, where it was ~3.5-fold higher than the poorest richness. This study provides the first large-scale description of benthic communities along the southwestern Atlantic, providing a baseline for macroecological comparisons and evaluation of futures impacts. Moreover, the new understanding of richness distribution along the Brazilian reefs will contribute to conservation planning efforts, such as management strategies and the spatial prioritization for the creation of new marine protected areas.

Keywords: Latitudinal gradient, Brazil, baseline, benthic cover, turf, macroalgae, reef ecosystem, hard substrate

INTRODUCTION

Understanding how marine biodiversity varies on local and regional scales serves as the foundation for studies in ecology, biogeography, and conservation [1-2]. One of the most pervasive large-scale patterns of biodiversity is the latitudinal diversity gradient, in which the highest richness commonly occurs towards the equator and declines towards higher latitudes [3-7], a pattern that has been described for many groups of organisms in terrestrial and marine environments [4,7]. Despite the existence of a relatively consistent pattern across different groups, the latitudinal diversity gradient is somewhat variable among taxa and regions [2, 6]. For example, marine diversity patterns of fish and invertebrates in the Atlantic differ between eastern and western shelves [8] and between Northern and Southern Hemisphere [9-10]. Despite these examples, we still lack a comprehensive and quantitative description of large-scale patterns of benthic communities in the Atlantic.

The Brazilian Province comprises almost 8,000 kilometers of Brazil's coastline and the offshore islands of Rocas Atoll, Fernando de Noronha, St. Paul's Rocks and Trindade [11-13]. This region exhibits a wide range of reefs habitats, ranging from the Amazon River mouth (0˚ latitude) to the state of Santa Catarina (28˚S latitude) [11-12, 14]. The region is bounded by three prominent biogeographic barriers: the Amazon Plume, that divides the marine fauna and flora of Brazil from the Caribbean Province; the Mid-Atlantic Barrier, that isolates the Brazilian Province from Western Africa; and low temperatures from the La Plata River plume that limits the distribution of tropical marine organisms southwards [12]. Despite the large extension and heterogeneity (e.g. tropical and subtropical affinities), most studies have been conducted on a few areas and small geographical scales [14-19]. Latitudinal comparisons of benthic community structure along the Brazilian coast have been based on literature reviews and qualitative work [see 20-28].

Marine biodiversity worldwide is declining due to anthropogenic impacts, including climate change [29-30]. As a result, many coral reefs lost their ability to recover after a disturbance, causing phase shifts in benthic structure, such as macroalgae dominance [31]. Many management and conservation efforts have been made worldwide to try to mitigate the threats to the marine environments. In 2010, Brazilian Government agreed to the targets of the United Nations Biodiversity Convention to protected marine and coastal biodiversity and to establish 10 % of no-take marine protected areas (MPAs) by 2020, currently, only 2% of the marine areas in Brazil are protected. Many reasons limit our ability to debate, predict and evaluate such changes in these ecosystems, for example, the absence of quantitative baselines information and the understanding of patterns through time and space for many reef systems [32]. Therefore, large-scale information of reef biodiversity of the Brazilian Province is critical to understand, help conservation targets and mitigate human impacts on these ecosystems.

In this study our aims were: 1) to provide a community-wide description of shallow benthic marine communities in the Brazilian Province, and 2) to quantify the biodiversity patterns of the benthic communities along the latitudinal gradient in the Brazilian Province. This study provides a valuable baseline for benthic communities along the Brazilian Province, allowing comparisons on how benthic communities change over time and contributes to the understanding of patterns of reef benthic communities in the Atlantic.

MATERIALS AND METHODS

Study area

The Brazilian Province has an extensive coastline and exhibits a wide range of environments. Even though reefs of the Brazilian Province correspond to 5% of Atlantic reefs, rates of endemism are high: ~34% for reef-building corals, 11% for macroalgae, and 35% for sponges [22, 33]. The northeastern and central portion of the Province are influenced by carbonatic and sandstone outcrops (mostly biogenic reefs), while the southeastern-southern part is dominated by siliciclastic bottoms on the shelf and sand beaches interrupted by crystalline rocky shores [34]. The Brazilian coast is influenced by the warmer Brazil Current flowing southwards (sea temperature above 20˚C) and the colder Brazilian Northern Current flowing northwards (sea temperature below 16˚C) 35-37]. The southeastern coast is also influenced by upwelling events, especially in Rio de Janeiro and Santa Catarina states, bringing colder and nutrient-rich waters into shallow water environments. This Province is also characterized by high terrestrial runoff from rivers [38], strong wind influences and variable shelf width [25]. Four oceanic islands belong to the Brazilian Province, three of which were included in the present study: Rocas Atoll (3˚87’S; 33˚80’W), Fernando de Noronha (3˚86’S; 32˚43’W), and Trindade Island (20˚51’S; 29˚33’W).

Ethics Statement

This study was conducted in accordance with all Brazilian government legislation. Including authorization to SISBIOTA-Mar project to assess images of the benthic communities along the Brazilian reefs, under the permits # 06/2012 (Parcel do Manuel Luis; SEMA-MA), # 29953–1 (Rocas Atoll; ICMBio/ MMA—Brazilian Ministry of Environment), # 29687-2 (Fernando de Noronha; ICMBio/ MMA—Brazilian Ministry of Environment), # 32145-1 (Costa dos Corais, ICMBio/ MMA—Brazilian Ministry of Environment), # 22637 (Abrolhos, ICMBio/ MMA—Brazilian Ministry of Environment), # 4416-1 (Trindade Island, ICMBio/ MMA—Brazilian Ministry of Environment), # 37869 (Alcatrazes, ICMBio/ MMA—Brazilian Ministry of Environment), # 21422 (Florianópolis Norte, ICMBio/ MMA—Brazilian Ministry of Environment), and for RN Maracajaú (APA dos Recifes de Corais, IDEMA-RN).

Benthic sampling

We sampled 40 sites within 15 localities from 0° to 27°S latitude along the tropical and subtropical reefs of the Brazilian Province during the Austral summer from 2011 to 2014 (Fig 1A; S1 Table). Seven localities were located on biogenic reefs, and eight were rocky reefs (S1 Table). At each locality, between one and five sites were assessed (but most of them had at least three sampled sites; S1 Table). At each site, surveys were conducted at two depth strata: 1-7 meters (shallow) and 8-15 (deep) meters, unless only one-depth strata was found. We haphazardly selected six to twenty $2m^2$ horizontal surfaces of reef area on each depth strata (S1 Table) and characterized the benthic community using a set of five 25x25 cm photoquadrats [19]. The $2m^2$ areas were at least 2 meters apart from each other, and we treated as independent samples in the analysis. Between 8 to 30 reef areas were assessed at each site, resulting in a minimum of 40 and maximum of 150 photoquadrats per site and 3,855 photoquadrats in the entire study (S1 Table).

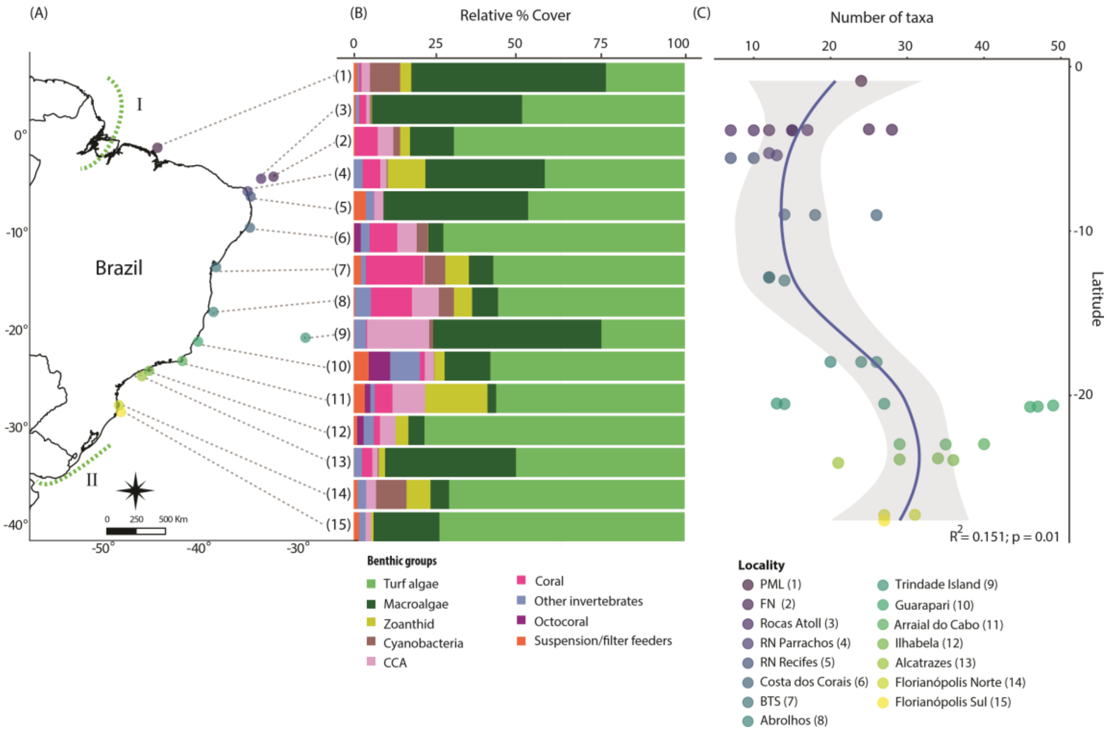

Figure 1 **Relative percent cover of benthic groups and richness along the Brazilian Province.** (A) Location of studied localities in the Brazilian Province, (B) Relative percent cover of benthic groups by localities (non-living organisms were excluded), (C) Number of taxa by sites along the Brazilian Province. The blue line represents the second-order polynomial equation. I = Amazon discharges and II = La Plata River plume. PML = Parcel do Manuel Luis, FN = Fernando de Noronha, BTS = Baia de Todos os Santos.

Photoquadrat analysis

Images obtained from the photoquadrats were analyzed using PhotoQuad software [39], by laying fifty random points on each image and identifying the organism underneath. The identification of benthic organisms simply using images may be problematic, with loss of taxonomic resolution [40], therefore all organisms were identified to the lowest taxonomic level possible (adapted from [41]). Because identification of some benthic organisms from images can be challenging, community composition was based on the lowest taxonomic level possible. This resulted in taxa identified to different hierarchical taxonomic levels, where 82% of taxa were able to be identified to Family level (Table S2). Published guides, checklists (e.g. [42-45]), and taxonomic specialists were frequently consulted during the analysis of these images to confirm accurate identification. Raw data and the classification scheme are available on the Dryad repository (doi:10.5061/dryad.f5s90).

Data analysis

Benthic structure

For benthic community composition, percent cover data (organisms classified at the lowest taxonomic level possible) was transformed by arcsine-square root, to reduce the influence of abundant and rare organisms [46]. We compared benthic community composition among localities by cluster analysis (complete linkage method) by using the function *pvclust* within the package “pvclust” [47] in R software [48]. A cophenetic correlation analysis was used to calculate the reliability of cluster branches. Additionally, we evaluated differences of community composition between depth strata by sites nested within localities by Nonmetric Multidimensional Scaling analysis (NMDS) with Bray-Curtis dissimilarity using the function *metaMDS* within package “vegan” [49]. Statistical differences in community composition were tested between depth strata, reef type (biogenic and rocky reef) and localities (only for sites with both depth strata sampled) with PERMANOVA analysis using the function *adonis* within the package “vegan” [49] in R software [48]. The statistical significance of the PERMANOVA was tested using 999 permutations under a reduced model and type II (conditional) sums of squares [50].

To analyze community structure in terms of the dominant groups of biota, worldwide studied in reef ecosystems, we also grouped the percent cover of benthic organisms into nine benthic groups: crustose coralline algae (CCA), coral, cyanobacteria, macroalgae, octocoral, other invertebrates, suspension/filter feeders, turf algae, and zoanthid, and we showed their latitudinal patterns by localities and sites by depth strata. Algal turfs are a recognized major component of reef environments and can be defined as a complex epilitical algal matrix, which includes detritus/sediment and cryptofauna associated [51-52].

Diversity patterns

We used the number of all taxa (observed) from each site to evaluate trends of diversity along the latitudinal gradient of the Brazilian Province, with sites nested within localities. Species richness estimations were calculated for the Chao metric (observed plus undetected taxa) to compare across sites with different levels of sampling intensity [53]. Species accumulation curves were built using the function *poolaccum* and *specpool* within package “vegan” [49] in R software [48]. We used the package “ggplot2” to plot the number of taxa and latitude, using the function *stat_smooth* to identify the patterns [54] and the function *poly* within package “stats” to perform regression analysis [48]. All statistical analyses were performed in the R software, version 3.4.2 [48].

RESULTS

Benthic structure

Benthic communities in the Brazilian Province were dominated by turf algae (mean cover = 52.9% ± 27.6 SD; Figs 1B and 2). The localities of Parcel do Manuel Luis (PML; 0˚latitude), and Trindade Island (20˚latitude) exhibited the lowest turf algae cover (19.20% ± 19.82 SD and 23.35% ± 23.09 SD, respectively). On the other hand, the localities of Ilhabela (23˚latitude), Florianópolis Sul (27˚latitude) and Florianópolis Norte (27˚latitude) had the highest turf algae cover (71.35% ± 25.18 SD, 68.34% ± 10.71 SD and 67.51% ± 27.70 SD, respectively; Figs 1B and 2). Frondose macroalgae were also abundant in the Brazilian Province (mean cover = 17.36% ± 24.04 SD; Fig 1B, Figs 2 and 3), but variable among localities (Trindade Island = 47.35% ± 27.18 SD (20˚latitude) to Arraial do Cabo = 2.33% ± 4.05 SD (22˚latitude)) and depth strata between sites (Fig 2). Localities distant from the coast showed the highest cover of frondose macroalgae (Trindade Island = 47.35% ± 27.18 SD (20˚latitude) and PML = 47.34% ± 22.74 SD (0˚latitude)), characterized by a high cover of *Halimeda* sp. at PML and *Caulerpa verticillata* at Trindade Island. Overall, 67.5% of the 40 sampled reefs were turf dominated (*i.e.* percent cover >50%), 12.5% of all reefs were dominated by frondose macroalgae, and 80% of the reefs were dominated by turf and frondose macroalgae (Fig 2).

Overall, the reef-building coral cover was low (mean cover = 4.38% ± 8.17 SD; Figs 1 and 2-3) and dominated by massive species, mostly colonies of the genera *Siderastrea*, *Montastraea*, and *Mussismilia*. The highest percent cover was at Baia de Todos os Santos (BTS; 12˚latitude), Abrolhos (17˚latitude) and Costa dos Corais (9˚latitude) (mean cover = 17.23% ± 15.07 SD, 12.05% ± 10.25 SD and 7.63% ± 7.46 SD, respectively; Fig 1B). Corals showed higher percent cover at 1-7 meters (Fig 2). The percent cover of reef-builders (corals and CCA) was also low in most localities. The only localities that displayed percent cover of reef-builders greater than 5% were Costa dos Corais (9˚latitude; 16.50% ± 6.67 SD), Abrolhos (17˚latitude; 9.99% ± 9.26 SD), BTS (12˚latitude; 8.90% ± 13.55 SD), Trindade Island (20˚latitude; 8.84% ± 15.33 SD), and Arraial do Cabo (22˚latitude; 6.96% ± 8.30 SD; Figs 1B and 2). At latitudes higher than 24˚S (Alcatrazes), the percent cover of reef-builders was close to zero (mean cover = 1.55% ± 3.40 SD; Figs 1B and 2).

The percent cover of octocorals, suspension/filter feeders (mostly ascidians and sponges) and other invertebrates were low overall but increased after latitude 20˚S (Guarapari; Figs 1B and 2). Octocorals and suspension/filter feeders were more abundant at 8-15 meters, while zoanthids were more abundant at 1-7 meters (Fig 2). Among all the localities, Baia de Todos os Santos (BTS; 12˚latitude), Abrolhos (17˚latitude), Guarapari (20˚latitude) and Arraial do Cabo (22˚latitude) showed approximately 50% of benthic cover not composed of turf algae or frondose macroalgae, and instead showed a more diverse benthic groups composition (Fig 1B). BTS and Abrolhos exhibited higher cover of reef-builders (mostly corals), zoanthids and cyanobacteria. In contrast, Guarapari and Arraial do Cabo showed a greater representation of zoanthids (dominated by *Palythoa caribaeorum*), reef-builders (mostly CCA), octocorals (*Phylogorgia dilatata*, *Plexaurella regia*, *Plexaurella grandiflora* and *Leptogorgia* sp.), suspension/filter feeders and other invertebrates (mostly crinoids).

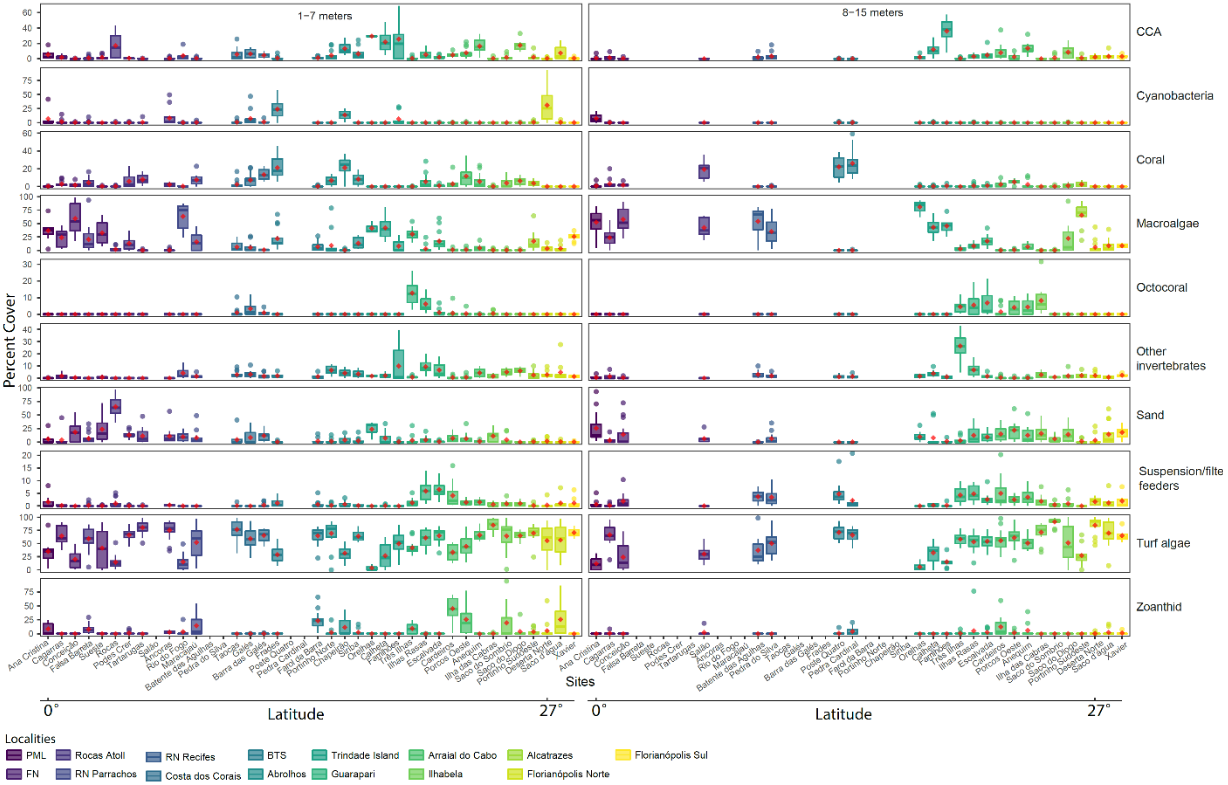

Figure 2 **Percent cover of reef surface by sites at shallow (1-7 meters) and deep strata (8-15 meters).** Bars represent the median, two hinges and two whiskers. Dots are outliers. Red dots represent the means. Sites are orientated from 0˚latitude to 27˚S latitude. Red dots represent the means. PML = Parcel do Manuel Luis, FN = Fernando de Noronha, BTS = Baia de Todos os Santos.

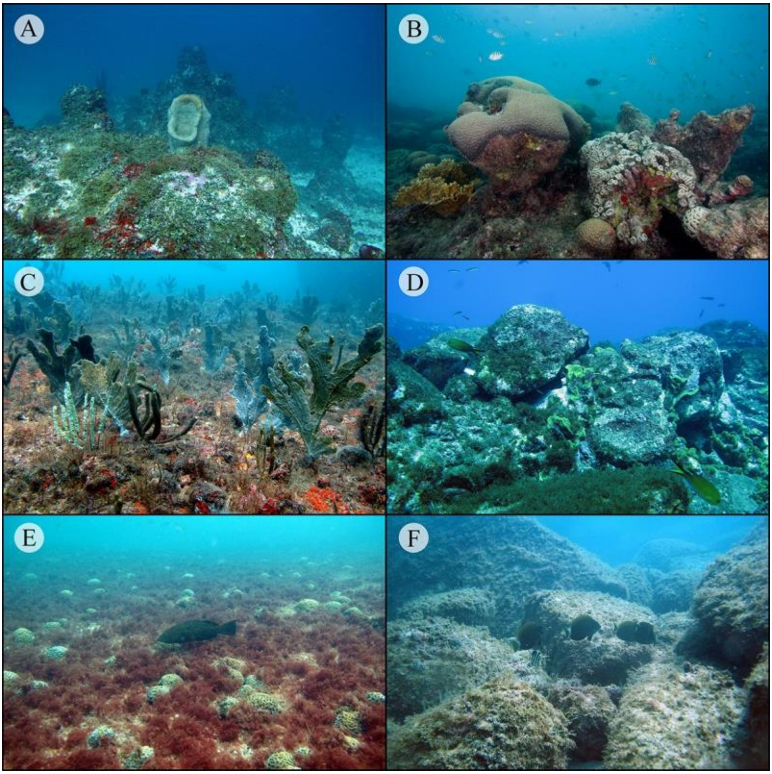

Figure 3 **The general aspect of reef benthic communities in the Brazilian Province.** (A) Parcel do Manuel Luis (PML), (B) Abrolhos, (C) Guarapari, (D) Trindade Island, (E) Alcatrazes and (F) Florianópolis Sul.

Regarding the geographic distribution of our sampled communities, the cluster analysis revealed two major clustering groups, grouped by frondose macroalgae abundance (Fig 4). The first group, with macroalgal dominance, was composed by the localities of RN Recifes (5˚latitude), RN Parrachos (5˚latitude), Fernando de Noronha (FN; 3˚latitude), PML (0˚latitude) and Trindade Island (20˚latitude). The second group, dominated by turf algae, was formed by Alcatrazes (24˚latitude), Florianópolis Sul (27˚latitude), Ilhabela (23˚latitude), Costa dos Corais (9˚latitude), Florianópolis Norte (27˚latitude), Baia de Todos os Santos (BTS, 13˚latitude), Rocas Atoll (3˚latitude), Arraial do Cabo (22˚latitude), Abrolhos (17˚latitude), and Guarapari (20˚latitude). Benthic community composition was different among localities but not between depth strata and reef type (Table 1; S1A Fig). Benthic communities of the sites belonging to Trindade Island, Parcel do Manuel Luis (PML), Guarapari and Fernando de Noronha (FN) were distinct from those at the other localities (nMDS; S1B Fig).

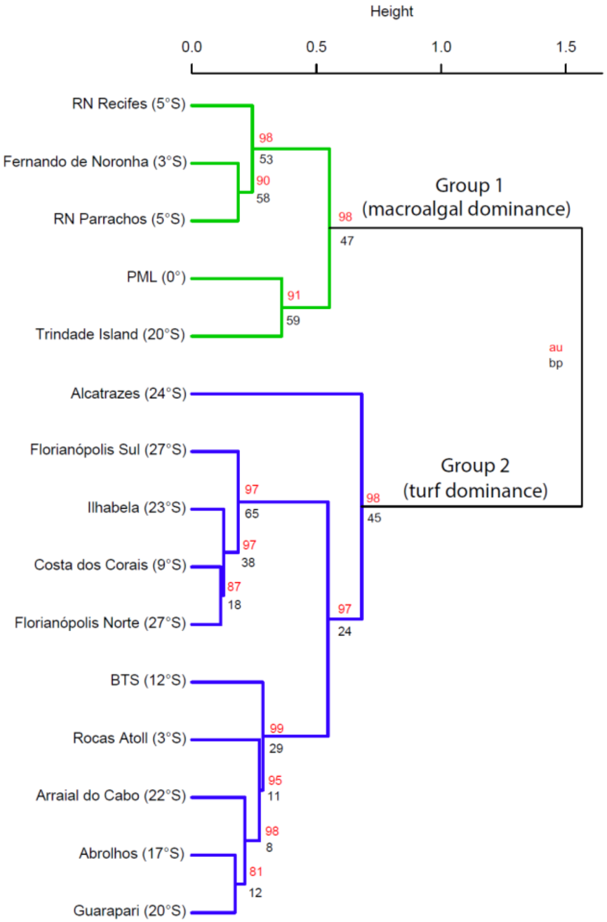

Figure 4 **Cluster analysis (complete linkage method) of benthic cover at localities sampled.** Approximated unbiased (red) and bootstrap probability (black) are the values of cophenetic correlation analysis. Green and blue show significant clades identified. PML = Parcel do Manuel Luis, BTS = Baia de Todos os Santos.

Table 3 **Results of PERMANOVA test.**

Source	**df**	**F**	**p (perm)**
Reef	1	1.6038	0.099
Locality	9	5.0275	0.001*
Depth	1	1.3302	0.198
Locality:Depth	8	0.8853	0.753
Residual	20		

Reef = reef type (biogenic and rocky reef), df = degree of freedom, F = F value, p = p value.

Diversity patterns

A total of 103 taxa were recorded across the Brazilian Province. Both observed taxa and Chao estimator showed the same patterns (S2 Fig). We found low diversity at low latitudes (at latitude 5˚S; S_{obs} = 12 and Chao = 13.43), and diversity peaked at mid-latitudes, around latitude 20˚S to 23˚S (~3.5-fold higher than lower richness; Fig 1C and S2 Fig). Among the three oceanic islands Rocas Atoll showed the highest diversity (S_{obs} = 34 and Chao = 41.92) and Trindade Island the lowest diversity (S_{obs} = 20 and Chao = 23.93) (Fig 1C and S2 Fig).

DISCUSSION

Our results provide the first broad-scale baseline and diversity patterns for shallow water benthic communities along the Brazilian coastline and oceanic islands. Reefs of the Brazilian Province have low reef-building coral cover and are dominated by algal turfs and macroalgae, even at biogenic reef systems, being this pattern consistent with coastal and oceanic reef localities. High algae cover has also been observed on reefs worldwide, but not at the same magnitude quantified in this study. For instance, macroalgae cover at Caribbean reefs is ~23.6% [55] and 1% of the reefs in the Indo-Pacific show macroalgae cover higher than 50% [56]; turf algae were the most abundant benthic group in Curaçao reefs (percent cover ranging from 20.3-41%; [57]), in the Mediterranean (percent cover ranging from 50-70%; [58]), South Australia (percent cover of 39%; [59]), and at the remote reefs of the Line Islands (36% cover; [60]), but none of these studies recorded such a high cover of algal turfs as we did in our study.

Studies worldwide have documented the decline of calcifying organisms (corals and CCA) and phase shifts to macroalgae and turf algae [29, 61-63]. Primary producers, such as macroalgae and turf algae, can benefit and become dominant when there is an increase in nutrients and sediment loads, and a reduction of herbivores [29, 57, 59, 64]. Turf algae, for example, can occupy space quickly by vegetative reproduction and become dominant under different disturbance and stress conditions [65]. In subtropical reefs of Arraial do Cabo, the ornamental collection was reported to cause loss of 50% of coral cover, mainly fire corals [66], with turf algae being the most competitive group to occupy free space. Additionally, herbivorous fishes, like parrotfishes, were reported as overfished in southeastern Brazilian reefs [67-68]. This dominance of turf and macroalgae on Brazilian reefs may occur because (1) the physicochemical conditions of Brazilian waters and low coral cover may facilitate the high cover of turf algae and macroalgae, resulting in a different stable state for the community, (2) the effect of anthropogenic activities, such as reduction of herbivores and high sedimentation/nutrients inputs caused by urban development and coastal runoff may resulted on a phase shift, or (3) a combination of physicochemical conditions and anthropogenic activities. Although studies have reported an increase of turf algae cover in the Caribbean (from 24.5% to 38%; [69]) and a moderate increase at the Abrolhos reef in Brazil [18], the lack of previous reports of Brazilian benthic structure makes it difficult to determine if turf-dominated reefs in the Brazilian Province are a result of reef degradation or part of a different stable state. Furthermore, the dynamic of Brazilian reefs may have some singularities when compared to the Pacific and Caribbean reefs.

Benthic community composition differed among the studied localities, mostly due to algae composition, but did not follow a clear latitudinal pattern. Different benthic communities are usually associated with nutrient and light availability [70-71], differences in sea temperature and salinity [72] and effects of disturbances [73]. For example, Parcel do Manuel Luis (PML; 0° latitude), Trindade Island (20°S latitude) and Fernando de Noronha (FN; 3°latitude) are distant from the coast and with clear waters, where light availability may influence the high cover of macroalgae. Arraial do Cabo, for instance, is influenced by upwelling events [74] which could influence benthic community structure [75]. Therefore, we suggest that a combination of local and context-dependent factors (*e.g.* water transparency, upwelling, urban development) may be driving the differences among the benthic communities of the studied localities.

We found low benthic diversity in the tropics, divergent to the general pattern of latitudinal diversity gradient. Although most marine taxa exhibit a global pattern of diversity peaking at the western Pacific and near the equator [6], many other studies have documented that the latitudinal patterns in the Atlantic differ from the general diversity patterns, for different groups of organisms [8, 25, 34]. The lower diversity at the tropics in the southwestern Atlantic has been attributed to a combination of extreme environmental features, such as high waves and wind exposure at the northeast part of Brazil, heterogeneous and narrow shelf width, and sedimentation and/or salinity effects from rivers [8, 38, 76]. Such factors can play an important role in the establishment and survival of reef organisms.

Instead of peaking near the equator, we found that the highest diversity (~3.5-fold than the poorest locality) of the Brazilian Province occurred at mid-latitudes, around 20˚S to 23˚S latitude. This same pattern has been described for different taxonomic groups in southwestern Atlantic, including fishes [77], algae, invertebrates and fish [25], gastropods [34], and *Symbiodinium* [78]. This mid-latitude region corresponds to a transitional zone between tropical and subtropical reefs influenced by the warm Brazil Current and the cold Brazilian Northern Current. This may allow organisms with tropical and subtropical affinities to coexist, resulting in higher diversity. Also, the heterogeneity of local habitats within this region (*e.g.* coralline communities, rocky reefs and rhodolith beds) has been suggested as a factor contributing to the greater diversity of reef organisms [34, 79-80].

Oceanic localities showed low diversity compared to coastal communities. Oceanic islands tend to display low species richness and high endemic rates as a result of their isolation and relatively shallow water zones [81]. For example, Trindade Island showed a remarkably low richness despite its latitudinal position (20˚S) and is considered one of the most species-poor oceanic islands in the world [12]. The large distance from the coast restricts immigration of species with limited dispersal abilities from the mainland. In addition, relatively narrow shallow zones, and strong oceanographic conditions (i.e. wave exposure, currents) likely account for its low richness [82].

This is the first study to provide a standardized quantitative characterization of the shallow water benthic communities of the Brazilian Province. We showed that algal turfs and macroalgae are the dominant groups across the Province, but the lack of previous quantitative baselines impairs our ability to determine if this is a natural stable state of Brazilian marine communities, a result of anthropogenic events, or a combination of both. Future experimental and observational studies are needed to properly address this issue. Our study provides baseline information of benthic community composition that can be used to macroecological studies and to evaluate impacts in Brazilian marine habitats, such as the impact from a mining dam collapse in Doce river [83] that has affected sediment and water quality at Guarapari and Abrolhos regions [84-85]. Also, our results on benthic diversity patterns can contribute to the discussion on future environmental planning and management targets. The region of Guarapari holds the highest diversity of fish [86] and we show that this region has also the highest benthic diversity. However, this region contains the least amount of marine protected areas, resulting in a general mismatch among MPAs locations and reef biodiversity. Thus, combining information of different reef organisms can help environmental managers protect reef biodiversity.

ACKNOWLEDGMENTS

We wish to thank the Marine Biodiversity Network (SISBIOTA–Mar) team for logistical and fieldwork support and Júlia Correia and Débora Ferrari for help with photoquadrats analysis. This work was funded by the project SISBIOTA–Mar: Brazilian Marine Network (P.I: S.R. Floeter - CNPq 563276/2010-0 and FAPESC 6308/2011-8). We also want to thank CAPES (“Science Without Borders”) for a scholarship from the Brazilian Government to A.W.A. Thanks to the logistical support from the following institutions (and people): ICMBio, Reserva Biológica do Atol das Rocas (Maurizélia Brito and Jarian Dantas), Parque Nacional Marinho de Fernando de Noronha, SEMA-MA, IDEMA-RN, Estação Ecológica Tupinambás, Marinha do Brasil and SECIRM (Programa PROTRINDADE). Thanks to the two anonymous reviewers for constructive criticisms that greatly improved this manuscript.

REFERENCES

1. Gaston KJ. Global patterns in biodiversity. Nature. 2000;405: 220-227. doi:10.1038/350122282. Underwood AJ, Chapman MG, Connell SD. Observations in ecology: you can’t make progress on processes without understanding the patterns. J Exp Mar Bio Ecol. 2000;250: 97-115.

3. Pianka ER. Latitudinal gradients in species diversity: a review of concepts. Am Nat. 1996;100: 33-46.
4. Willig MR, Kaufman DM, Stevens RD. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu Rev Ecol Evol Syst. 2003;34: 273-309.
5. Hillebrand H. Strength, slope and variability of marine latitudinal gradients. Mar Ecol Prog Ser. 2004; 273:251-267. doi:10.3354/meps273251
6. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, et al. Global patterns and predictors of marine biodiversity across taxa. Nature. 2010;466: 1098-1101. doi:10.1038/nature09329
7. Brown JH. Why are there so many species in the tropics? J. Biogeogr. 2014;41: 8-22. doi:10.1111/jbi.12228
8. Macpherson E. Large-scale species-richness gradients in the Atlantic Ocean. Proc R Soc Lond. 2002;269: 1715–1720. doi: 10.1098/rspb.2002.2091
9. Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature. 1993;365: 636-639.
10. Chown SL, Sinclair BJ, Hans PL, Gaston KJ. Hemispheric asymmetries in biodiversity – a serious matter for ecology. Plos Biol. 2004;2(11): e406. doi: 10.1371/journal.pbio.0020406
11. Briggs JC. Marine zoogeography. 1st ed. New York: McGraw-Hill Book Company; 1974.
12. Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, et al. Atlantic reef fish biogeography and evolution. J Biogeogr. 2008;35: 22-47. doi: 10.1111/j.1365-2699.2007.01790.x
13. Briggs JC, Bowen BW. A realignment of marine biogeographic provinces with particular reference to fish distributions. J Biogeogr. 2012;39: 12-30. doi: 10.1111/j.1365-2699.2011.02613.x
14. Briggs JC. Global biogeography. 1st ed. Amsterdam: Elsevier; 1995.
15. Villaça R, Pitombo FB. Benthic communities of shallow-water reefs of Abrolhos, Brazil. Rev Bras Oceanogr. 1997;45: 35–43.
16. Oigman-Pszczol SS, Figueiredo MAO, Creed JC. Distribution of benthic communities on the tropical rocky subtidal of Armação dos Búzios, Southeastern Brazil. Marine Ecology. 2004;25: 173-190.
17. Bruce T, Meirelles PM, Garcia G, Paranhos R, Rezende CE, Moura RL, et al. Abrolhos bank reef health evaluated by means of water quality, microbial diversity, benthic cover, and fish biomass data. PLoS ONE. 2012;7: e36687. doi:10.1371/journal.pone.0036687
18. Francini-Filho RB, Coni EOC, Meirelles PM, Amado-Filho GM, Thompson FL, Pereira-Filho GH, et al. Dynamics of coral reef benthic assemblages of the Abrolhos bank, Eastern Brazil: inferences on natural and anthropogenic drivers. PLoS ONE. 2013;8: e54260. doi:10.1371/journal.pone.0054260
19. Longo GO, Morais RA, Martins CDL, Mendes TC, Aued AW, Cândido D, et al. Between-habitat variation of benthic cover, reef fish assemblage and feeding

pressure on the benthos at the only atoll in South Atlantic: Rocas Atoll, NE Brazil. PLoS ONE. 2015;10: e0127176. doi:10.1371/journal.pone.0127176
20. Laborel J. Les peuplements de Madréporaires de côtes tropicales du Brésil. Annls Univ. Abidjan. 1970; 2: 1-260. French.
21. Maida M, Ferreira BP. Coral reefs of Brazil: an overview. Proc 8th Int Coral Reef Sym. 1997;1: 263- 274.22. Castro CB, Pires DO. Brazilian coral reefs: What we already know and what is still missing. Bull Mar Sci. 2001;69: 357-371.
23. Ghilardi NP, Pereira-Filho GH, Berchez F. Current knowledge status of the ecology of hard bottom benthic communities in Brazil and the need for new approaches. Oecol Bras. 2008;12: 197-205.
24. Figueiredo MAO, Horta PA, Pedrini AG, Nunes JMC. Benthic marine algae of the coral reefs of Brazil: a literature review. Oecol Bras. 2008;12: 258-269.
25. Miloslavich P, Klein E, Diaz JM, Hernández CE, Bigatti G, Campos L, et al. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. PLoS ONE. 2011;6: e14631. doi:10.1371/journal.pone.0014631
26. Longo LL, Amado-Filho GM. Knowledge of Brazilian benthic marine fauna throughout time. História, Ciência, Saúde. 2014; 21:1-16. doi:10.1590/S0104-59702014000300011
27. Leão ZMAN, Kikuchi RKP, Ferreira BP, Neves EG, Sovierzoski HH, Oliveira MDM, et al. Brazilian coral reefs in a period of global change: A synthesis. Braz J Oceanogr. 2016;64: 97-116. doi:10.1590/S1679-875920160916064sp2
28. Soares MO, Lotufo TMC, Vieira LM, Salani S, Hadju E, Matthews-Cascon H et al. Brazilian marine animal forests: A new world to discover in the Southwestern Atlantic. 2016; doi:10.1007/978-3-319- 17001-5_51-1
29. Hughes TP. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science. 1994;265: 1547-1551.
30. Bellwood DR, Hughes TP, Folke C, Nystrom M. Confronting the coral reef crisis. Nature. 2004;429: 827-833
31. Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L et al. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol. 2007;17: 360-365. doi:10.1016/j.cub.2006.12.049
32. Gatti G, Bianchi CN, Parravicini V, Rovere A, Peirano A, Montefalcone M, et al. Ecological change, sliding baselines and the importance of historical data: Lessons from combing observational and quantitative data on a temperate reef over 70 years. PLoS ONE. 2015; 10: e0118581. doi: 10.1371/journal.pone.0118581
33. Floeter SR, Soares-Gomes A, Hajdu E. Biogeografia marinha. In: Pereira RC, Soares-Gomes A, editors. Biologia Marinha. Rio de Janeiro: Interciência; 2009. pp 421-441. Portuguese.
34. Barroso CX, Lotufo TMC, Matthews-Cascon H. Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships. J Biogeogr. 2016; doi:10.1111/jbi.12821

35. Castro BM, Miranda LB. Physical Oceanography of the western Atlantic Continental shelf located between 4oN and 34oS, coastal segment (4W). The Sea. 1998;11: 209–251.
36. Prates AP, Lima LH, Chatwin A. Coastal and marine conservation priorities in Brazil. In: Chatwin A, editor. Priorities for coastal and marine conservation in South America. Arlington: The Nature Conservation; 2007. pp. 15-23.
37. Palmeira ACPA, Camargo R, Palmeira RMJ. Relação entre a temperatura da superfície do mar e a camada de mistura oceânica sob a passagem de ciclones extratropicais no Atlântico Sudoeste. Revista Brasileira de Meteorologia. 2015;30: 89-100. doi:10.1590/0102-778620130679 Portuguese.
38. Leão ZMAN, Ginsburg RN. Living reefs surrounded by siliciclastics sediments: the Abrolhos coastal reefs, Bahia, Brazil. Proc 8th Int Coral Reef Symp. 1997;2: 1767–1772.39. Trygonis V, Sini M. photoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. J Exp Mar Bio Ecol. 2012; doi:10.1016/j.jembe.2012.04.018
40. Preskitt LB, Vroom PS, Smith CM. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. Pac. Sci. 2004; 58: 201-209.
41. Althaus F, Hill N, Ferrari R, Edwards L, Przeslawski R, Schonberg CHL, et al. A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The CATAMI classification scheme. PLoS ONE. 2015;10: e0141039. doi:10.1371/journal.pone.0141039
42. Littler DM, Littler MM. Caribbean reef plants an identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico. 1st ed. Washington: OffShore Graphics; 2000.
43. Veron JEN. Corals of the world. Townsville: Australian Institute of Marine Science; 2000.
44. Human P, Deloach N. Reef creature identification: Florida, Caribbean, Bahamas. 2nd ed. Jacksonville: New World Publications; 2002.
45. Hetzel B, Castro CB. Corais do Sul da Bahia. 1st ed. Rio de Janeiro: Nova Fronteira; 1994. Portuguese.
46. Gotelli NJ, Ellison AM. A primer of ecological statistics. Sunderland: Sinauer Associates; 2004.
47. Suzuki R, Shimodaira H. pvclust: Hierarchical clustering with p-values via multiscale bootstrap resampling. 2015. Available from: https://CRAN.R-project.org/package=pvclust
48. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2016. Available from: https://www.R-project.org/
49. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. vegan: Community Ecology Package. R package version 2.4-3. 2017. Available from: https://CRAN.R-project.org/package=vegan
50. Anderson MJ, Gorley RN, Clarke KR. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth; 2008.

51. Littler MM, Littler DS. Algae, turf. in: Hopley D (eds) Encyclopedia of Modern Coral Reefs. Encyclopedia of Earth sciences series. Dordrecht, Springer; 2011.52. Connell SD, Foster MS, Airoldi L. What are algal turfs? Towards a better description of turfs. Mar Ecol Prog Ser. 2014; 495:299-307. doi:10.3354/meps10513
53. Chao A, Chiu CH. Species richness: Estimation and comparison. Wiley StatsRef: Statistics Reference Online. 2016; 1-26.
54. Wickham H. ggplot2: Elegant graphics for data analysis. New York: Springer-Verlag; 2009.
55. Jackson JBC, Donavan MK, Cramer KL, Lam VV. Status and trends of Caribbean coral reefs: 1970-32012. Global Coral Reef Monitoring Network, Switzerland, IUCN; 2014.
56. Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VG. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology. 2009; 90:1478-1484.
57. Vermeij MJA, Moorselaar I, Engelhard S, Hornlein C, Vonk SM, Visser PM. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS ONE. 2010; 5: e14312. doi:10.1371/journal.pone.0014312
58. Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, et al. Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser. 2001;214: 137-150.59. Gorgula SK, Connell SD. Expansive covers of turf-forming algae on human-dominated coast: The relative effects of increasing nutrient and sediment loads. Mar Biol. 2004; 145:613-619. doi: 10.1007/s00227-004-1335-5
60. Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, et al. Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE. 2008; 3:e1548. doi: 10.1371/journal.pone.0001548
61. McCook LJ. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs. 2001; 19:419-425. doi:10.1007/s003380000119
62. Mumby PJ, Hastings A, Edwards HJ. Thresholds and the resilience of Caribbean coral reefs. Nature. 2007; 450:98-101. doi:10.1038/nature06252
63. Connell SD, Russell BD. The direct effects of increasing CO2 and temperature on non-calcifying organisms: Increasing the potential for phase shifts in kelp forests. Proc R Soc B. 2010; 277:1409-1415.
64. Burkepile DE, Hay ME. Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology. 2006; 87:3128-3139.
65. Airoldi L. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology. 1998; 79:2759-2770.
66. Rogers R, Correal GO, Oliveira TC, Carvalho LL, Mazurek P, Barbosa JEF, et al. Coral health rapid assessment in marginal reef sites. Mar. Biol. Res. 2014; 10:612-624. doi:10.1080/17451000.2013.84194467. Floeter SR, Halpern BS, Ferreira CEL. Effects of fishing and protection on Brazilian reef fishes. Biol Conserv. 2006. I28: 391-402. doi:10.1016/j.biocon.2005.10.005

68. Bender MG, Machado GR, Silva PJA, Floeter SR, Monteiro-Neto C, Luiz OJ, et al. Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the southwestern Atlantic. PLoS ONE. 9(10): e110332. doi:10.1371/journal.pone.0110332
69. Bakker DM, Duyl FC, Bak RPM, Nugues MM, Nieuwland G, Meesters EH. 40 years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: The rise of slimy cyanobacterial mats. Coral Reefs. 2017; 36:355-367. doi:10.1007/s00338-016-1534-9
70. Cummings V, Thrush S, Norkko A, Andrew N, Hewitt J, Funnell G et al. Accouting for local scale variability in benthos: implications for future assessments of latitudinal trends in coastal Ross Sea. Antartic Science. 2006; 18:633-644.71. Ackleson SG. Light in shallow waters; a brief research review. Limnol. Oceanogr. 2003; 48:323-328.
72. McArthur MA, Brooke BP, Przeslawski R, Ryan DA, Lucieer VL, Nichol S, et al. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuar Coast Shelf Sci. 2010; 88:21-32.
73. Witman JD, Cusson M, Archambault P, Pershing AJ, Mieszkowska N. The relation between productivity and species diversity in temperate – Arctic marine ecosystems. Ecology. 2008; 88:S66-S80.
74. Valentin JL. The Cabo Frio Upwelling System, Brazil. In: Seeliger U, Kjerfve B. editors. Coastal Marine Ecosystems of Latin America. Ecological Studies (Analysis and Synthesis). Berlin, Heidelberg: Springer. 2001.
75. Witman JD, Smith F. Rapid community change at a tropical upwelling site in the Galápagos Marine Reserve. Biodivers Conserv. 2004; 12:25-45.
76. Barros KVS, Rocha-Barreira CA. Influence of environmental factors on a Halodule wrightii ascherson meadow in Northeastern Brazil. Braz J Aquat Sci Technol. 2014; 18:31-41.
77. Floeter SR, Guimarães RZP, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL. Geographic variation in reef-fish assemblages along the Brazilian coast. Glob Ecol Biogeogr. 2001; 10:423-431.
78. Picciani N, Seiblitz IGL, Paiva PC, Castro CB, Zilberberg C. Geographic patterns of Symbiodinium diversity associated with the coral Mussismilia hispida (Cnidaria, Scleractinia) correlate with major reef regions in the Southwestern Atlantic Ocean. Mar Biol. 2016; doi:10.1007/s00227-016-3010-z
79. Horta PA, Amancio E, Coimbra CS, Oliveira EC. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras. Hoehnea. 2001; 28:243-265. Portuguese.
80. Leão ZMAN, Kikuchi RKP, Testa V. Latin American Coral Reefs of Brazil. In: Cortes J, editor. Latin American coral reefs. Amsterdam: Elsevier Publisher; 2003. pp 09-52.
81. Whittaker RJ, Fernández-Palacios JM. Island Biogeography: Ecology, evolution, and conservation. 2nd ed. Oxford: Oxford Univ Press; 2007.
82. Pinheiro HT, Bernardi G, Simon T, Joyeux JC, Macieira RM, Gasparini et al. Island biogeography of marine organisms. Nature. 2017; doi:10.1038/nature23680

83. Escobar H. Mud tsunami wreaks ecological havoc in Brazil. Science. 2015; 350:1138-1139.
84. Mazzei EF, Bertoncini AA, Pinheiro HT, Machado LF, Vilar CC, Guabiroba HC et al. Newly discovered reefs in the Southern Abrolhos Bank, Brazil: anthropogenic impacts and urgente conservation needs. Mar Pollut Bull. 2016; 114:123-133. doi: 10.1016/j.marpolbul.2016.08.059
85. Miranda LS, Marques AC. Hidden impacts of the Samarco mining waste dam colapse to Brazilian marine fauna – an axample from the staurozoans (Cnidaria). Biota Neotropica. 2016; 16(2):e20160169. doi:10.1590/1676-0611-BN-2016-0169
86. Vila-Nova DA, Ferreira CE, Barbosa FG, Floeter SR. Reef fish hotspot as surrogates for marine conservation in the Brazilian coast. Ocean Coast Manag. 2014; 102:88-93. doi:10.1016/j.ocecoaman.2014.09.005

Supporting information

Table S1 **Summary of field effort at the sites along the Brazilian Province.** FN = Fernando de Noronha, PML = Parcel do Manuel Luis, BTS = Baia de Todos os Santos.

Locality	Site	Lat	Lon	Reef type	Month	Year	Depth (m)	N (2m^2 area)	N (photoquadrats)
Rocas Atoll	Âncoras Falsa	-3.87517	-33.8036	Biogenic	January	2012	1-7	16	80
Rocas Atoll	Barreta	-3.86035	-33.8188	Biogenic	January	2012	1-7	19	95
Rocas Atoll	Rocas	-3.86895	-33.7919	Biogenic	January	2012	1-7	20	100
Rocas Atoll	Podes Crer	-3.87296	-33.8123	Biogenic	January	2012	1-7	17	85
Rocas Atoll	Salão	-3.87473	-33.8094	Biogenic	January	2012	8-15	9	45
Rocas Atoll	Tartarugas	-3.87299	-33.8094	Biogenic	January	2012	1-7	18	90
FN	Cagarras	-3.81455	-32.3902	Rocky	October	2011	1-7	13	65
							8-15	15	75
FN	Conceição	-3.83904	-32.415	Rocky	October	2011	1-7	14	70
							8-15	15	75
FN	Sueste	-3.86684	-32.4228	Rocky	October	2011	1-7	14	70
Trindade Island	Calheta	-20.5075	-29.3103	Rocky	July	2012	1-7	11	55
							8-15	13	65
Trindade Island	Farrilhões	-20.5226	-29.4979	Rocky	July	2012	1-7	9	45
							8-15	8	40

Locality	Site	Lat	Lon	Reef type	Month	Year	Depth (m)	N (2m^2 area)	N (photoquadrats)
Trindade Island	Orelhas	-20.4925	-29.3431	Rocky	July	2012	1-7	4	20
							8-15	14	70
PML	Ana Cristina	-0.86987	-44.2643	Biogenic	April	2013	1-7	7	35
							8-15	14	70
RN Parrachos	Maracajaú	-5.39411	-35.259	Biogenic	October	2011	1-7	14	70
RN Parrachos	Rio do Fogo	-5.26212	-35.3634	Biogenic	October	2011	1-7	8	40
RN Recifes	Batente das Agulhas	-5.56435	-35.0725	Biogenic	March	2013	8-15	8	40
RN Recifes	Pedra do Silva	-5.56447	-35.0901	Biogenic	March	2013	8-15	14	70
Costa dos Corais	Barra das Galés	-9.03269	-35.1927	Biogenic	March	2012	1-7	15	75
Costa dos Corais	Galés	-9.02426	-35.1915	Biogenic	March	2012	1-7	15	75
Costa dos Corais	Taocas	-8.9985	-35.1806	Biogenic	March	2012	1-7	15	75
BTS	Farol da Barra	-13.0083	-38.5308	Biogenic	March	2012	1-7	15	75
BTS	Frades	-12.8092	-38.6264	Biogenic	March	2012	1-7	15	75
BTS	Pedra Cardinal	-12.8371	-38.5491	Biogenic	March	2012	8-15	14	70

Locality	Site	Lat	Lon	Reef type	Month	Year	Depth (m)	N (2m^2 area)	N (photoquadrats)
BTS	Poste Quatro	-12.8147	-38.5717	Biogenic	March	2012	8-15	15	75
Abrolhos	Chapeirão	-17.9628	-38.6625	Biogenic	March	2010	1-7	15	75
Abrolhos	Portinho Norte	-17.9638	-38.6936	Biogenic	March	2010	1-7	15	75
Abrolhos	Siriba	-17.9706	-38.7158	Biogenic	March	2010	1-7	15	75
Guarapari	Escalvada	-20.6996	-40.4076	Rocky	February	2014	1-7	15	75
							8-15	15	75
Guarapari	Ilhas Rasas	-20.6766	-40.3662	Rocky	February	2014	1-7	15	75
							8-15	15	75
Guarapari	Três Ilhas	-20.6123	-40.3788	Rocky	February	2014	1-7	15	75
							8-15	15	75
Arraial do Cabo	Anequim	-22.9805	-41.9845	Rocky	March	2011	1-7	14	70
							8-15	10	50
Arraial do Cabo	Cardeiros	-22.9651	-42.0017	Rocky	March	2011	1-7	16	80
							8-15	15	75
Arraial do Cabo	Porcos Oeste	-22.9657	-41.9937	Rocky	March	2011	1-7	13	65
							8-15	8	40
Ilhabela	Ilhas das Cabras	-23.8303	-45.3939	Rocky	March	2013	1-7	13	65

Locality	**Site**	**Lat**	**Lon**	**Reef type**	**Month**	**Year**	**Depth (m)**	**N (2m^2 area)**	**N (photoquadrats)**
							8-15	14	70
Ilhabela	Saco do Diogo	-23.9354	-45.2836	Rocky	March	2013	1-7	9	45
							8-15	13	65
Ilhabela	Saco do Sombrio	-23.8933	-45.244	Rocky	March	2013	1-7	11	55
							8-15	11	55
Alcatrazes	Portinho Sudoeste	-24.1052	-45.7025	Rocky	March	2013	1-7	12	60
							8-15	10	50
Florianópolis Norte	Saco d'água	-27.277	-48.3685	Rocky	April	2011	1-7	10	50
							8-15	14	70
Florianópolis Norte	Deserta Norte	-27.2645	-48.3317	Rocky	April	2011	1-7	15	75
							8-15	15	75
Florianópolis Sul	Xavier	-27.6035	-48.3876	Rocky	April	2011	1-7	8	40
							8-15	6	30
Total								**764**	**3820**

Tabela S2 **Taxa classification scheme.**

sisbiota_code	**Taxa**	**Kingdom**	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Benthic Group**
Agaricia.fragilis	*Agaricia fragilis*	Animalia	Cnidaria	Anthozoa	Scleractinia	Agariciidae	*Agaricia*	Coral
Agaricia.humilis	*Agaricia humilis*	Animalia	Cnidaria	Anthozoa	Scleractinia	Agariciidae	*Agaricia*	
Agaricia.sp	*Agaricia* spp	Animalia	Cnidaria	Anthozoa	Scleractinia	Agariciidae	*Agaricia*	Coral
Anemona	*Bunodosoma caissarum*	Animalia	Cnidaria	Anthozoa	Actiniaria	Actiniidae	*Bunodosoma*	Other invertebrates
Arborescent.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
Ascidea.colonial	Phlebobranchia	Animalia	Chordata	Ascidiacea	Phlebobranchia			Suspension/filter feeders
Astrangia.Phyllangia	Rhizangiidae	Animalia	Cnidaria	Anthozoa	Scleractinia	Rhizangiidae		Coral
Botrylloides.nigrum	*Botrylloides nigrum*	Animalia	Chordata	Ascidiacea	Stolidobranchia	Styelidae	*Botrylloides*	Suspension/filter feeders
Bryopsis.pennata	*Bryopsis pennata*	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Bryopsidaceae	*Bryopsis*	Macroalgae
Calcareous articulate algae	Corallinaceae	Plantae	Rhodophyta	Rhodophyceae	Corallinales	Corallinaceae		Macroalgae
calcareous.turf	Coralline turf	Plantae	Rhodophyta	Rhodophyceae	Corallinales	Corallinaceae		Turf
Carijoa.riisei	*Carijoa riisei*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Clavulariidae	*Carijoa*	Octocoral
Caulerpa.racemosa	*Caulerpa racemosa*	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Caulerpaceae	*Caulerpa*	Macroalgae
Caulerpa.sp	*Caulerpa* spp.	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Caulerpaceae	*Caulerpa*	Macroalgae
Caulerpa.verticillata	*Caulerpa verticillata*	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Caulerpaceae	*Caulerpa*	Macroalgae
Chaetomorpha.sp	*Chaetomorpha*	Plantae	Chlorophyta	Ulvophyceae	Cladophorales	Cladophoraceae	*Chaetomorpha*	Macroalgae
Champia.parvula	*Champia parvula*	Plantae	Chlorophyta	Florideophyceae	Rhodymeniales	Champiaceae	*Champia*	Macroalgae
Cianobacterias	Cyanobacteria	Bacteria	Cyanobacteria					Cyanobacteria

sisbiota_code	**Taxa**	**Kingdom**	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Benthic Group**
Cirripedia	Hexanauplia	Animalia	Arthropoda	Hexanauplia				Other invertebrates
Codium.intertextum	*Codium intertextum*	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Codiaceae	*Codium*	Macroalgae
Codium.spp	*Codium* spp.	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Codiaceae	*Codium*	Macroalgae
Colpomenia.sinuosa	*Colpomenia sinuosa*	Chromista	Ochrophyta	Phaeophyceae	Scytosiphonales	Scytosiphonaceae	*Colpomenia*	Macroalgae
corticated.algae	Gigartinacea	Plantae	Rhodophyta	Florideophyceae	Gigartinales	Gigartinacea		Macroalgae
Crinóide	*Tropiometra* sp.	Animalia	Echinodermata	Crinoidea	Comatulida	Tropiometridae	*Tropiometra*	Other invertebrates
crostose.coralline.algae	Corallinales	Plantae	Rhodophyta	Florideophyceae	Corallinales			CCA
Dictyopteris	*Dictyopteris* spp.	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Dictyopteris*	Macroalgae
Dictyopteris.plagiogramma	*Dictyopteris plagiogramma*	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Dictyopteris*	Macroalgae
Dictyota.sp	*Dictyota* spp.	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Dictyota*	Macroalgae
Didemnum	*Didemnum* sp.	Animalia	Chordata	Ascidiacea	Aplousobranchia	Didemnidae	*Didemnum*	Suspension/filter feeders
Didemnum.perlucidum	*Didemnum perlucidum*	Animalia	Chordata	Ascidiacea	Aplousobranchia	Didemnidae	*Didemnum*	Suspension/filter feeders
Digenea.sp.	*Digenea simplex*	Plantae	Rhodophyta	Florideophyceae	Ceramiales	Rhodomelaceae	*Digenea*	Macroalgae
Estrela	*Echinaster*	Animalia	Echinodermata	Asteroidea	Spinulosida	Echinasteridae	*Echinaster*	Other invertebrates
Favia.gravida	*Favia gravida*	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Favia*	Coral
foliaceous.algae	Dictyotaceae	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae		Macroalgae
Galaxaura.sp	*Galaxaura* spp.	Plantae	Rhodophyta	Florideophyceae	Nemaliales	Galaxauraceae	*Galaxaura*	Macroalgae
Gelidiella.acerosa	*Gelidiella acerosa*	Plantae	Rhodophyta	Florideophyceae	Gelidiales	Gelidiellaceae	*Gelidiella*	Macroalgae

sisbiota_code	**Taxa**	**Kingdom**	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Benthic Group**
Gelidiopsis	*Gelidiopsis* spp.	Plantae	Rhodophyta	Florideophyceae	Rhodymeniales	Lomentariaceae	*Gelidiopsis*	Macroalgae
Gelidium.floridanum	*Gelidium floridanum*	Plantae	Rhodophyta	Florideophyceae	Gelidiales	Gelidiaceae	*Gelidium*	Macroalgae
Globular.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
green.filamentous.algae	Ulvophyceae	Plantae	Chlorophyta	Ulvophyceae				Macroalgae
Halimeda	*Halimeda* spp.	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Halimedaceae	*Halimeda*	Macroalgae
Heterogorgia	*Heterogorgia* spp.	Animalia	Cnidaria	Anthozoa	Alcyonacea	Plexauridae	*Heterogorgia*	Octocoral
Hypnea.musciformis	*Hypnea musciformis*	Plantae	Rhodophyta	Florideophyceae	Gigartinales	Cystocloniaceae	*Hypnea*	Macroalgae
Idiellana.pristis	*Idiellana pristis*	Animalia	Cnidaria	Hydrozoa	Leptothecata	Sertulariidae	*Idiellana*	Other invertebrates
Incrusting.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
Jania.Amphiroa	Corallinaceae	Plantae	Rhodophyta	Florideophyceae	Corallinales	Corallinaceae		Macroalgae
Laurencia.sp	*Laurencia* spp.	Plantae	Rhodophyta	Florideophyceae	Ceramiales	Rhodomelaceae	*Laurencia*	Macroalgae
leathery.algae	Dictyotaceae	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae		Macroalgae
Leptogorgia.sp	*Leptogorgia* spp.	Animalia	Cnidaria	Anthozoa	Alcyonacea	Gorgoniidae	*Leptogorgia*	Octocoral
Lobophora.variegata	*Lobophora variegata*	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Lobophora*	Macroalgae
Macrorhynchia.philippina	*Macrorhynchia philippina*	Animalia	Cnidaria	Hydrozoa	Leptothecata	Aglaopheniidae	*Macrorhynchia*	Other invertebrates
Madracis.decactis	*Madracis decactis*	Animalia	Cnidaria	Anthozoa	Scleractinia	Astrocoeniidae	*Madracis*	Coral
Massive.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
Meandrina.brasiliensis	*Meandrina brasiliensis*	Animalia	Cnidaria	Anthozoa	Scleractinia	Meandrinidae	*Meandrina*	Coral

sisbiota_code	**Taxa**	**Kingdom**	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Benthic Group**
Millepora.alcicornis	*Millepora alcicornis*	Animalia	Cnidaria	Hydrozoa	Anthoathecata	Milleporidae	*Millepora*	Coral
Millepora.incrusting	*Millepora* sp.	Animalia	Cnidaria	Hydrozoa	Anthoathecata	Milleporidae	*Millepora*	Coral
Millepora.nitida	*Millepora nitida*	Animalia	Cnidaria	Hydrozoa	Anthoathecata	Milleporidae	*Millepora*	Coral
Millepora.sp	*Millepora* spp.	Animalia	Cnidaria	Hydrozoa	Anthoathecata	Milleporidae	*Millepora*	Coral
Montastraea.cavernosa	*Montastraea cavernosa*	Animalia	Cnidaria	Anthozoa	Scleractinia	Montastraeidae	*Montastraea*	Coral
Muricea.flamma	*Muricea flamma*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Plexauridae	*Muricea*	Octocoral
Muriceopsis.sulphurea	*Muriceopsis sulphurea*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Plexauridae	*Muriceopsis*	Octocoral
Mussismilia.braziliensis	*Mussismilia braziliensis*	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Mussismilia*	Coral
Mussismilia.harttii	*Mussismilia harttii*	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Mussismilia*	Coral
Mussismilia.hispida	*Mussismilia hispida*	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Mussismilia*	Coral
Mussismilia.leptophylla	*Favia leptophylla*	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Favia*	Coral
Mussismilia.spp	*Mussismilia* spp.	Animalia	Cnidaria	Anthozoa	Scleractinia	Mussidae	*Mussismilia*	Coral
Octhodes.secundiramea	*Ochtodes secundiramea*	Plantae	Rhodophyta	Florideophyceae	Gigartinales	Rhizophyllidaceae	*Ochtodes*	Macroalgae
Octocoral.another	Alcyonacea	Animalia	Cnidaria	Anthozoa	Alcyonacea			Octocoral
Ophiothela.mirabilis	*Ophiothela mirabilis*	Animalia	Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothela*	Other invertebrates
ouriço1	*Echinometra lucunter*	Animalia	Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Echinometra*	Other invertebrates
ouriço2	*Eucidaris tribuloides*	Animalia	Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Eucidaris*	Other invertebrates
Outra.ascidia	Phlebobranchia	Animalia	Chordata	Ascidiacea	Phlebobranchia			Suspension/filter feeders

sisbiota_code	**Taxa**	**Kingdom**	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Benthic Group**
Outro.anthozoa	Anthozoa	Animalia	Cnidaria	Anthozoa				Other invertebrates
Outro.crustaceo	Malacostraca	Animalia	Arthropoda	Malacostraca				Other invertebrates
Outro.echinoderma	Asteroidea	Animalia	Echinodermata	Asteroidea				Other invertebrates
Outro.hydrozoa	Hydrozoa	Animalia	Cnidaria	Hydrozoa				Other invertebrates
Padina.sp	*Padina*	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Padina*	Macroalgae
Palythoa.caribaeorum	*Palythoa caribaeorum*	Animalia	Cnidaria	Anthozoa	Zoantharia	Sphenopidae	*Palythoa*	Zoanthid
Palythoa.variabilis	*Palythoa variabilis*	Animalia	Cnidaria	Anthozoa	Zoantharia	Sphenopidae	*Palythoa*	Zoanthid
Papilate.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
Parazoanthus.cf.axinellae	*Parazoanthus axinellae*	Animalia	Cnidaria	Anthozoa	Zoantharia	Parazoanthidae	*Parazoanthus*	Zoanthid
Peyssonnelia	*Peyssonnelia* sp.	Plantae	Rhodophyta	Florideophyceae	Peyssonneliales	Peyssonneliaceae	*Peyssonnelia*	Macroalgae
Phallusia.nigra	*Phallusia nigra*	Animalia	Chordata	Ascidiacea	Phlebobranchia	Ascidiidae	*Phallusia*	Suspension/filter feeders
Phyllogorgia.dilatata	*Phyllogorgia dilatata*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Gorgoniidae	*Phyllogorgia*	Octocoral
Plexaurella.grandiflora	*Plexaurella grandiflora*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Plexauridae	*Plexaurella*	Octocoral
Plexaurella.regia	*Plexaurella regia*	Animalia	Cnidaria	Anthozoa	Alcyonacea	Plexauridae	*Plexaurella*	Octocoral
Poliqueta	Polychaeta	Animalia	Annelida	Polychaeta				Other invertebrates
Porites.astreoides	*Porites astreoides*	Animalia	Cnidaria	Anthozoa	Scleractinia	Poritidae	*Porites*	Coral
Porites.branneri	*Porites branneri*	Animalia	Cnidaria	Anthozoa	Scleractinia	Poritidae	*Porites*	Coral
Porites.sp	*Porites* spp.	Animalia	Cnidaria	Anthozoa	Scleractinia	Poritidae	*Porites*	Coral

sisbiota_code	Taxa	Kingdom	Phylum	Class	Order	Family	Genus	Benthic Group
Protopalythoa	*Protopalythoa* spp.	Animalia	Cnidaria	Anthozoa	Zoantharia	Sphenopidae	*Protopalythoa*	Zoanthid
Sargassum.sp	*Sargassum* spp.	Chromista	Ochrophyta	Phaeophyceae	Fucales	Sargassaceae	*Sargassum*	Macroalgae
Schizoporella.sp	*Schizoporella* sp.	Animalia	Bryozoa	Gymnolaemata	Cheilostomatida	Schizoporellidae	*Schizoporella*	Other invertebrates
Siderastrea.spp	*Siderastrea* spp.	Animalia	Cnidaria	Anthozoa	Scleractinia	Siderastreidae	*Siderastrea*	Coral
Stypopodium	*Stypopodium* spp.	Chromista	Ochrophyta	Phaeophyceae	Dictyotales	Dictyotaceae	*Stypopodium*	Macroalgae
Tricleocarpa.cylindrica	*Tricleocarpa cylindrica*	Plantae	Rhodophyta	Florideophyceae	Nemaliales	Galaxauraceae	*Tricleocarpa*	Macroalgae
Trididemnum	*Trididemnum* sp.	Animalia	Chordata	Ascidiacea	Aplousobranchia	Didemnidae	*Trididemnum*	Suspension/filter feeders
Tubular.sponge	Demospongiae	Animalia	Porifera	Demospongiae				Suspension/filter feeders
Udotea	*Udotea* sp.	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Udoteaceae	*Udotea*	Macroalgae
Ulvophyceae	Ulvophyceae	Plantae	Chlorophyta	Ulvophyceae				Macroalgae
Ventricaria.ventricosa	*Ventricaria ventricosa*	Plantae	Chlorophyta	Ulvophyceae	Siphonocladales	Valoniaceae	*Ventricaria*	Macroalgae
Wrangelia	*Wrangelia* sp.	Plantae	Rhodophyta	Florideophyceae	Ceramiales	Wrangeliaceae	*Wrangelia*	Macroalgae
Zoanthus.sociatus	*Zoanthus sociatus*	Animalia	Cnidaria	Anthozoa	Zoantharia	Zoanthidae	*Zoanthus*	Zoanthid

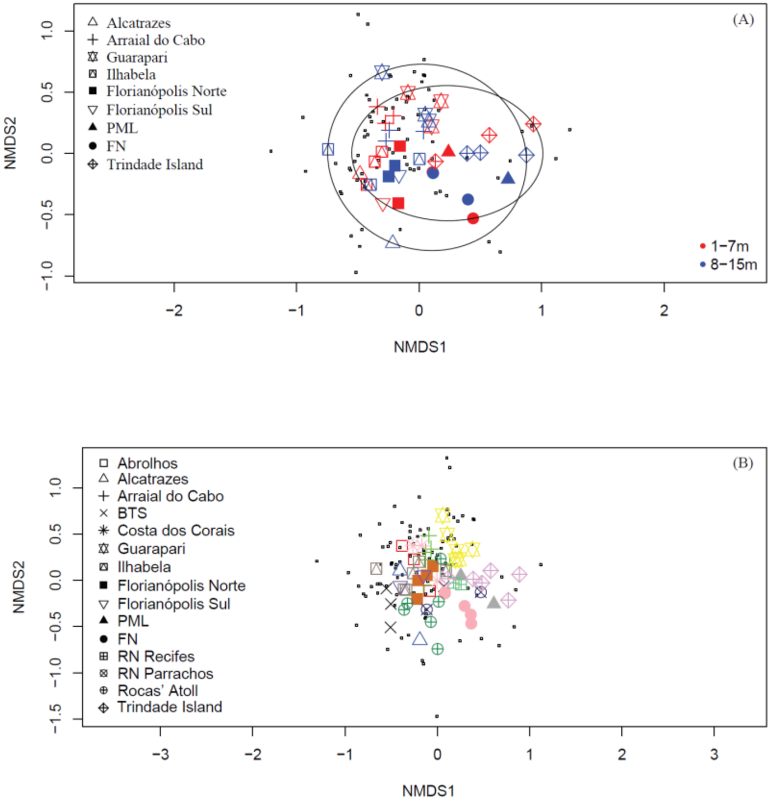

Figure S1 **nMDS ordination with the benthic community composition.** (A) sites only with both depth strata; (B) all sites surveyed. Black squares are the organisms. FN = Fernando de Noronha, PML = Parcel do Manuel Luis and BTS = Baia de Todos os Santos.

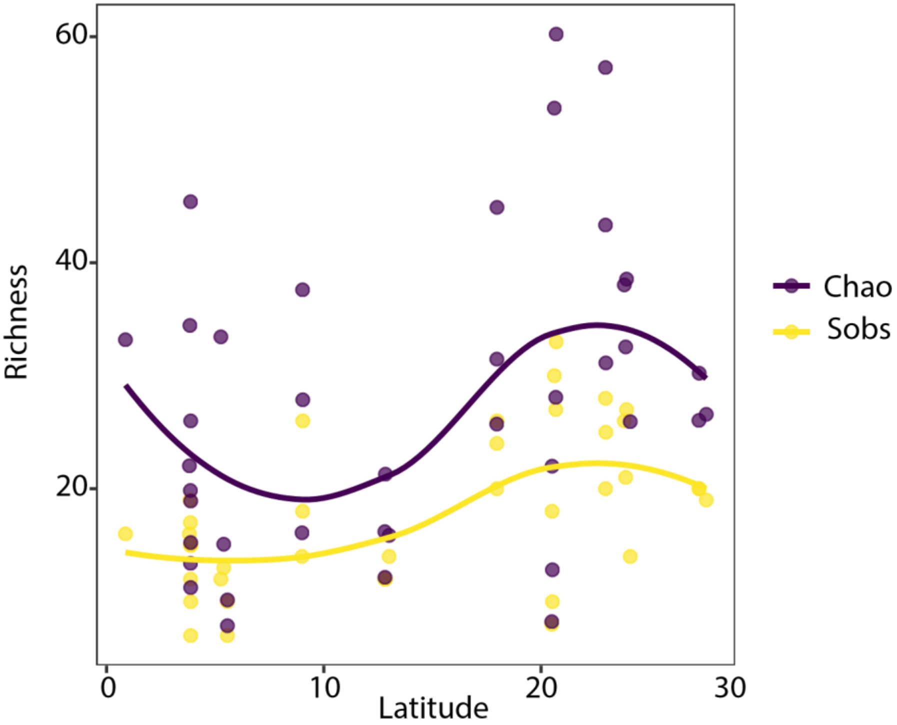

Figure S2 **Species accumulation curves using observed taxa (S_{obs}) and Chao estimator.**

CAPÍTULO 2

Functional richness far from the equator: the case of reef benthic communities along the Brazilian Province

(artigo submetido ao periódico Global Ecology and Biogeography)
formatação de acordo com as regras da revista

Functional richness far from the equator: the case of reef benthic communities along the Brazilian Province

Short title: Functional diversity of benthic communities along the Brazilian Province

Authors: Anaide W. Aued[1,3], Franz Smith[2], Guilherme O. Longo[4], Juan P. Quimbayo[3], Mariana G. Bender[5], Davi Candido[1], Carlos E. L. Ferreira[6], Jon D Witman[2], Sergio R. Floeter[3] & Bárbara Segal[1]

1 Laboratório de Ecologia de Ambientes Recifais, Department of Ecology and Zoology, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil,
2 The Witman Lab, Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, USA,
3 Marine Macroecology and Biogeography Lab, Department of Ecology and Zoology Department, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil,
4 Marine Ecology Lab, Department of Oceanography and Limnology, Universidade Federal do Rio Grande do Norte, Natal, Brazil,
5 Marine Macroecology and Conservation Lab, Department of Ecology and Evolution, Universidade Federal de Santa Maria, Santa Maria, RS, Brazil,
6 Reef Systems Ecology and Conservation Lab, Universidade Federal Fluminense, Niterói, RJ, Brazil

ABSTRACT

Aim: To assess the functional structure of benthic communities along a latitudinal gradient ranging from 0˚ to 27˚S and test the relative influence of abiotic filters in community assembly.
Location: Reef sites along the Brazilian Province.
Time period: 2011-2014.
Major taxa studied: Reef benthic communities, including macroalgae and invertebrates.
Methods: We surveyed 40 sites distributed in 15 localities along the Brazilian Province using a standardized photoquadrat technique and classified benthic organisms based on biological and life-history traits associated to body size, form, resource use and behavior. Functional diversity for each local community was assessed using indices of functional richness (FRic), evenness (FEve) and divergence (FDiv). We also tested the predictive effect of large-scale environmental filters on functional diversity components.
Results: We found lower FRic in both limits of the gradient and peaking at mid-latitudes (20˚S-23˚S), FDiv showed a hump-shaped trend along the gradient, reaching its highest value at latitude 12˚S, while FEve did not vary with latitude. Environmental variables explained 48.9% of FRic, 44.2% of FDiv and only 5.56% of FEve. The effect of abiotic filters in community structure differed across latitudes and between coastal and oceanic localities. While salinity limited FRic in the north, salinity and temperature acted in the Southern limit, and wave exposure was an important filter in oceanic islands, with reduction of core functions in these regions. Productivity was relevant at mid-latitudes, supporting greater FRic and FDiv in these communities.
Main conclusions: The unusual functional diversity gradient identified for benthic communities across the Southwestern Atlantic is caused by large-scale environmental filters. The functional approach applied herein improves the understanding of the effect of abiotic filters in community assembly and support discussions on reef ecosystems functioning.

Keywords: Biodiversity, biotic filter, latitudinal gradient, Southwestern Atlantic, environmental filtering, reef ecosystem, traits.

INTRODUCTION

Understanding the drivers of biodiversity patterns across Earth is among the greatest puzzles of ecology. Such differences in biological communities across scales result from a combination of both stochastic and deterministic processes (Chase, 2007; McGill, 2010). Several hypotheses have attempted to explain the almost ubiquitous latitudinal diversity gradient including ecological, evolutionary and biogeographic theories (Hillebrand, 2004a), yet the numerous explanations and the difficulties involved in attesting its causal mechanisms have resulted in little consensus among the possible explanatory hypotheses (Brown, 2014b). The ecological theories for the origin of biodiversity variation include the neutral theory, the myriad of biotic interactions, and the effect of environmental filtering across scales (Zobel, 1997; Götzenberger *et al.*, 2012; Kraft *et al.*, 2015). At large spatial scales, the latitudinal diversity gradient can be regulated by differences in climate and productivity conditions (Willig *et al.*, 2003; Ricklefs, 2004), along with many other environmental drivers (Willig *et al.*, 2003). Such variation in abiotic filters could prevent the establishment or persistence of species with particular traits or phenotypes through environmental filtering (Kraft *et al.*, 2015). At the local scale, biotic interactions may shape local diversity patterns by excluding coexistent species sharing similar resources, or by promoting niche differentiation (MacArthur & Wilson, 1967; Götzenberger *et al.*, 2012).

Species interact with each other and its surrounding environment through behavioral and associated biological traits, responding to biotic and abiotic filters (Lavorel & Garnier, 2002). Functional diversity is a facet of diversity and measures the values and range of organisms traits that influence ecosystems processes (Tilman, 2001). Therefore, functional diversity may offer an opportunity to measure biodiversity responses to environmental change, and is often considered a better predictor of alteration when compared to taxonomic diversity (McGill, Enquist, Weiher & Westoby, 2006; Villéger, Miranda, Hernández & Mouillot, 2010). Also, decomposing functional diversity in other metrics helps unveil the link between biodiversity and ecosystem functioning and the influence of biotic and abiotic filters on the composition of communities (Villéger, Mason & Mouillot, 2008)

Environmental filtering and biotic interactions influence different components of functional diversity (Raevel, Violle, Munoz, 2012). Environmental conditions, such as low temperatures, might influence species and their local abundances through their physiological tolerance, excluding non-adapted organisms (Clarke & Gaston, 2006). The importance of environmental filtering can be inferred by lower functional richness and functional divergence indices, which reveal the effect of filters over patterns of traits occurrence and species' abundance in a community (Botta-Dukát & Czúcz, 2016; Yeager, Deith, McPherson, Williams & Baum, 2017). Biotic filters (i.e., interactions), in their turn, can be inferred by higher functional evenness and functional divergence indices by influencing species' abundance (Botta-Dukát & Czúcz, 2016). While functional evenness measures to which extent species abundances are equally distributed across the functional space, functional divergence quantifies the proportion of abundance of the dominant species compared to rare species in such functional space (Villéger *et al.*, 2008). Therefore, through the functional diversity approach it is possible to infer how environmental and biotic filters have shaped the structure of biological communities.

Marine ecosystems harbor high diversity communities throughout a multitude of environmental filters (*e.g.*, salinity, temperature, productivity). At a global scale, marine functional diversity (i.e., bivalves) shows a peak of functional richness in the tropics and an increase functional evenness with increasing latitude (Berke, Jablonski, Krug & Valentine, 2014). For marine benthic communities, processes operating at large-scales have influenced latitudinal patterns of species diversity (Witman, Etter & Smith, 2004). Temperature parameters, for instance, may be the main drivers of functional diversity gradient in scleractinian corals (Sommer, Beger, Harrison, Babcock & Pandolfi, 2017). In the Southwestern Atlantic, the latitudinal biodiversity gradient does not conform with the general pattern of higher species richness in the tropics. Instead, species richness peaks at mid-latitudes, and that has been shown for different marine organisms (Floeter *et al.*, 2001; Miloslavich *et al.*, 2011; Barroso, Lotufo & Matthews-Cascon, 2016; Picciani, Seiblitz, Paiva, Castro & Zilberberg, 2016; Pinheiro *et al.*, 2018). Nevertheless, few studies have explored the potential explanatory variables of the processes shaping community assembly along the latitudinal gradient of the Southwestern Atlantic (but see Bender, Pie, Rezende, Mouillot & Floeter (2013)). A functional approach to the study of marine benthic communities and its distinct pattern of diversity would help understand how important are the different filters driving reef communities' assembly, and with further possible influences on ecosystem functioning. In this paper, we (i) assessed the functional structure of reef benthic communities; and (ii) explored the mechanisms associated with community assembly along the Brazilian Province, that comprises a large latitudinal gradient and has a wide range of environmental conditions (Miloslavich *et al.*, 2011). We also provide insight into the ecological processes that have shaped the observed patterns of reef benthic community structure in the studied localities, untangling the effects of environmental filtering and biotic filters. We expected functional diversity components to peak in mid-latitudes, because in the taxonomically richest regions ecological interactions are more intense and might promote niche differentiation. We also hypothesized that environmental filtering decreases functional richness patterns by excluding non-adapted species, and functional divergence due to the higher abundance of well-adapted species. Furthermore, we expected that biotic filters would increase functional divergence and functional evenness by increasing the abundances of certain organisms.

MATERIAL AND METHODS

We collected quantitative information of multiphyletic shallow benthic communities (from 1 to 15 meters depth) at 40 different sites distributed across 15 localities along the latitudinal environmental gradient (0°52'S to 27°60'S) in the Brazilian Province (Fig. 1 and see Appendix S1 in Supporting Information). All fieldwork was conducted during the Austral summer from 2011 to 2014. Benthic communities were sampled by a set of five replicate random photoquadrats (25x25cm) placed haphazardly within a $2m^2$ reef area. At each site, we sampled eight to thirty reef areas, resulting in 40 to 150 photoquadrats per site. The percent cover of each photoquadrat was quantified using photoQuad software (Trygonis & Sini, 2012) by laying 50 random points and identifying the organism underneath.

Functional traits

We considered 'functional traits' as morphological and physiological traits of a group of species that respond to environmental conditions in similar ways and define ecological functions (Costello *et al.*, 2015). For the majority of benthic organisms, most of the information regarding traits is not available in the literature. However, we selected a set of functional traits that were available in the literature and could be applied for multiphyletic benthic taxa; such traits also seemed appropriate for the broad geographic extent of our study. We classified benthic organisms according to five biological traits (maximum body size, growth form, trophic category, modularity, mobility) and one life-history trait (reproduction type) (see Costello *et al.*, 2015; see Appendix S2).

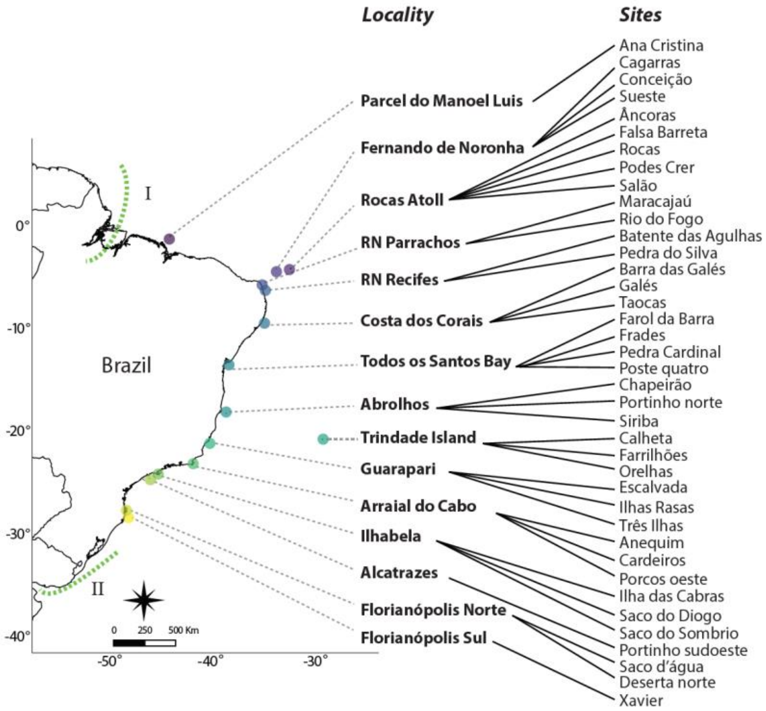

Figure 1 **Location of 40 sites within 15 localities for benthic communities along the latitudinal gradient of the Brazilian Province.** I = Amazon River mouth; II = Plata River plume.

Functional diversity metrics

Functional entities (FE) were defined as unique combinations of the six traits mentioned above. The position of FEs and their abundances on the functional trait space reflect the differences between their traits at local communities (D'agata *et al.*, 2016), and are applied in functional diversity metrics. We used three indices reflecting the multiple facets of functional diversity (functional richness, functional evenness, and functional divergence) (see Appendix S3). All indices vary between 0 and 1. Functional richness (FRic) reflects the volume inside the functional trait space occupied by the community (Villéger *et al.*, 2008). Low values of FRic indicate low niche space filled (Mason, Mouillot, Lee & Wilson, 2005). Functional evenness (FEve) measures the regularity of the distribution of abundances at the functional trait space (by the minimum spanning tree method). Low values of FEve indicate that the abundance of species are tightly packed in the functional trait space, suggesting that resource availability of niche space, while occupied, are under-utilized (Mason *et al.*, 2005; Villéger *et al.*, 2008). Functional divergence (FDiv) reflects how the abundance of dominant species is distributed within the functional trait space. FDiv values close to 1 show that the most abundant species are far from the center of the functional space when compared to rare species, indicating a high degree of niche differentiation (Mason *et al.*, 2005; Villéger, 2008). Further information and details of functional diversity indices can be accessed at Villéger *et al.* (2008).

Environmental variables

To investigate the influence of environmental parameters over the functional diversity of benthic communities, we selected the following environmental variables: photosynthetically active radiation (PAR, as a proxy for light availability), chlorophyll a (Chla, as a proxy for productivity), waves (Hsig), sea surface salinity (SSS), and, sea surface temperature (SST) (see Appendix S3). We obtained mean PAR data from Bio-Oracle at 9.2 km resolution (Tyberghein *et al.*, 2012). Mean and standard deviation of monthly Chlorophyll a was obtained from the Global Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua Satellite for the fieldwork period (NASA). Monthly mean and standard deviation of waves (significant wave height) were obtained from WAVEWATCH III (WW3) Global Wave Model at 2' resolution (Tolman, 2014). We extracted information of annual mean, monthly minimum, monthly maximum, and annual variation of SSS and SST from the MARSPEC (Sbrocco & Barber, 2013) dataset derived from the SRTM30_PLUS high resolution.

We used Pearson's correlation coefficient ($r > 0.7$) to verify the potential multicollinearity between environmental variables (see Appendix S4) and selected one variable among correlated pairs. We used mean Chla, mean Hsig, minimum monthly SSS and minimum monthly SST in generalized additive models (GAMs) to investigate the influence of productivity, waves, salinity, and cold stress on functional diversity of the shallow benthic communities.

Data analysis

We calculated functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) of the reef benthic community of 15 localities extending 27° of latitude along the Brazilian Province. The functional trait space for each local community was built based on the selected six functional traits using the Gower's distance. Using this distance matrix, a principal coordinate analysis (PCoA) was conducted on the multidimensional trait space. We plotted the distribution of species and their abundance in the functional trait space, using the first two principal axes. To explore benthic organisms' functional roles, we built a two-dimensional functional space encompassing all benthic organisms sampled in our study and their six selected ecological traits. We used Generalized Additive Models (GAMs) to explore the environmental predictors that would explain the variation of functional diversity metrics across sites. FRic, FEve, and FDiv (response variables) were modeled as a function of chlorophyll a, waves, salinity (SSS), and, SST (explanatory variables). All analysis were performed in R software (R Core Team), version 3.4.2, using the packages 'vegan' (Oksanen et al., 2017), 'ggplot2' (Wickham, 2009), 'FD' (Laliberté *et al.*, 2014), and 'mgcv' (Wood, 2017).

RESULTS

Functional diversity metrics

In our categorization scheme, we identified 103 taxa grouped within 35 functional entities (organisms with equivalent functional roles) for Brazilian reef benthic communities (Fig. 3b). Our results show that functional richness and functional divergence of Brazilian benthic communities varied along the latitudinal gradient, but that was not the case for functional evenness values (Fig. 2 and Fig. 3a). Functional richness (FRic) was lower in the tropics and peaked at mid-latitudes (Fig. 2). Overall, the volume (FRic) occupied by tropical benthic communities was smaller compared to mid-latitude communities, showing a reduction in the number of functional entities (Fig. 3a). Coastal benthic communities between latitudes 20°41'S (Guarapari) to 23°56'S (Ilhabela) filled the largest volumes of the functional space, due to a greater number of functional entities in this region (Fig. 3a). Communities at the northern and southern limit of the latitudinal gradient exhibited smaller FRic (functional volumes), indicating that core functions were missing in these regions. For example, bio-constructors, mobile invertebrates, and, suspension/filter feeders were less common or absent in these communities. Oceanic benthic communities filled a smaller proportion of the functional trait space, given the absence of small three-dimensional organisms and mobile invertebrates in these communities (Fig. 3a). In the oceanic island of Fernando de Noronha (3’50˚S latitude), for instance, the branching fire coral *Millepora alcicornis* is the unique species presenting an encrusting body form.

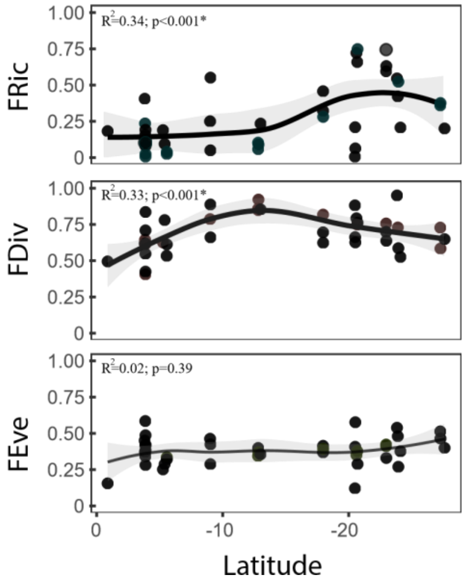

Figure 2 **Functional diversity metrics across the latitudinal gradient of the Brazilian Province.** FRic = functional richness, FDiv = functional divergence and FEve = functional evenness.

Functional divergence (FDiv) showed a significant hump-shaped relationship along the latitudinal gradient ($R^2 = 0.33$, $p<0.001$; Fig. 2). Values of FDiv peaked at mid-latitudes (12˚48’S; Todos os Santos Bay), indicating a greater niche differentiation of abundant functional entities (Fig. 2). At such mid-range latitude benthic communities exhibited greater percent cover of turf algae (~57% cover) and reef-building coral *Montastraea cavernosa* (~15% cover). In general, FDiv was comparative lower for benthic communities at the northern and southern limits of the studied gradient, indicating a higher degree of niche overlap. Functional evenness (FEve) did not vary along the latitudinal gradient ($R^2 = 0.02$, $p=0.39$; Fig. 2).

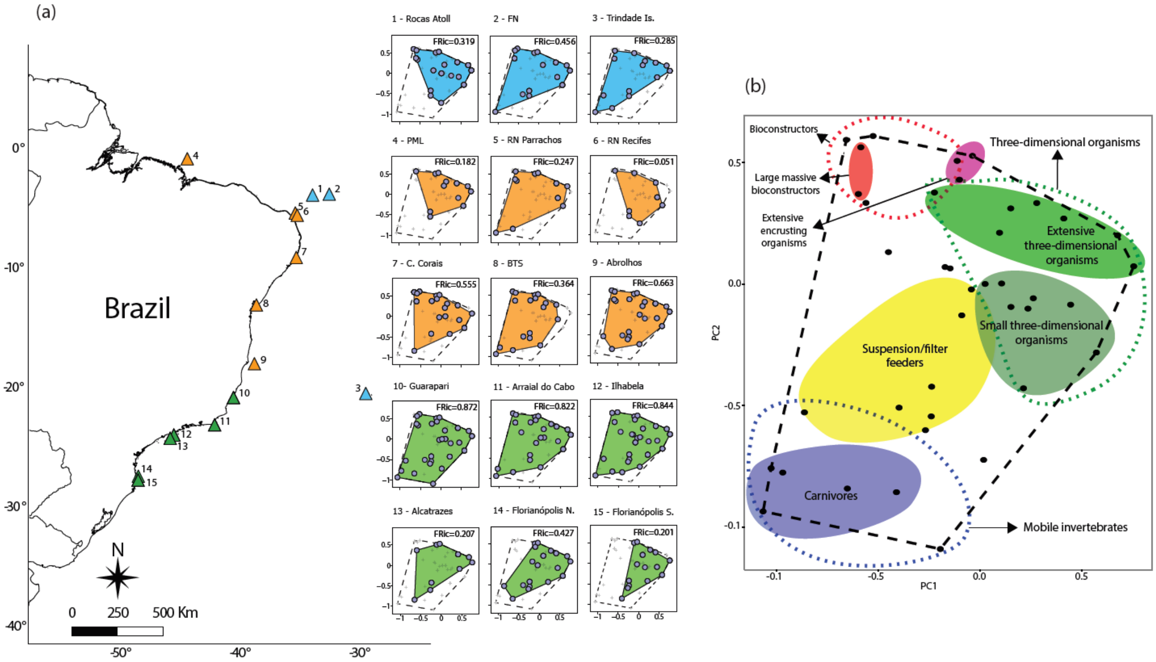

Figure 3 The functional trait space of benthic communities along the latitudinal gradient of the Brazilian Province. (a) the volume occupied by benthic communities of the 15 sampled localities. Dashed line represents the regional functional trait space. Color code: blue = oceanic communities, orange = biogenic reefs and green = rocky reefs. (b) position of all functional entities (with similar traits values) in the regional functional trait space of benthic communities.

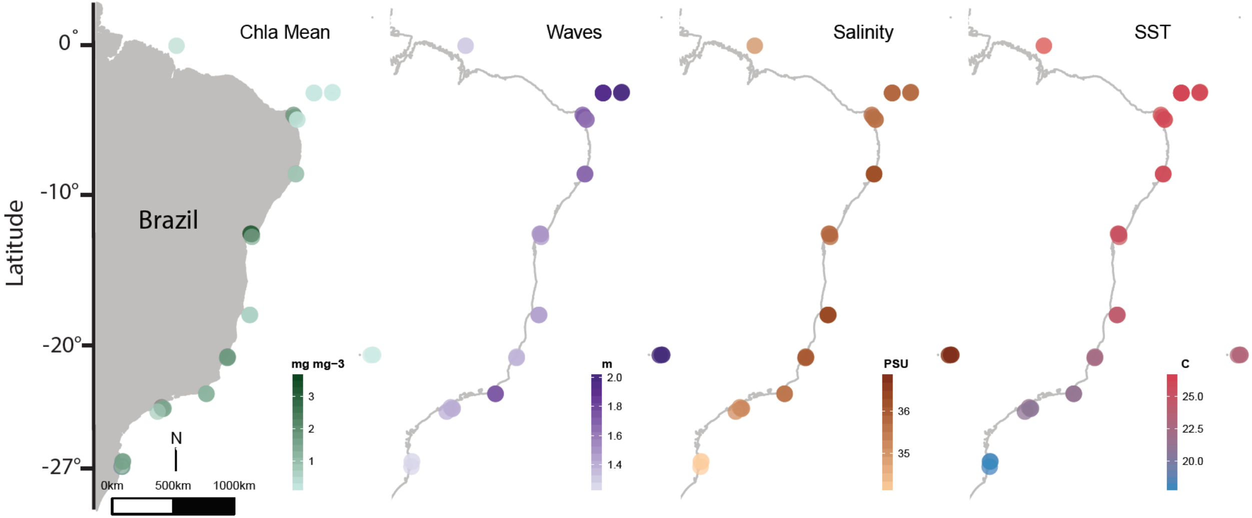

Figure 4 Variation of selected environmental variables in 15 sampled localities along the Brazilian Province.

Environmental variables and functional diversity

Chlorophyll a (Chla) was lower at oceanic islands and latitude 0˚52'S, ranging from 0.04 to 0.43 mg m-3, and peaked at 12˚48'S (Todos os Santos Bay; 3.68 mg/m3) (Fig. 4). Chla was also high at mid-latitudes, ranging from 2.18 mg/m3 (20˚41'S; Guarapari) to 1.76 mg/m3 (27˚15'S, Florianópolis Norte). Monthly mean waves height (Hsig) was highest at the oceanic sites, with waves' height close to 2 meters at the sites of Trindade Island (20˚30'S) (Fig. 4). Sites at the limits of the latitudinal gradient had the lowest influence from waves, based on smaller wave heights (Ana Cristina at Parcel do Manoel Luis to the North, and Florianópolis Norte in the South). Salinity showed a hump-shaped pattern along the latitudinal gradient, with low values at its northern and southern limits (35.20 PSU at Parcel do Manoel Luis and 34.1 PSU at Florianópolis Norte) (Fig. 4). SSS peaked at latitude 9˚1'S (Costa dos Corais), 17˚57'S (Abrolhos), 20˚41'S (Guarapari), and 20˚30'S (Trindade Island). Sea surface temperature (monthly minimum SST) declined with increasing latitude, reaching ~27˚C at low latitudes and 21˚C at higher latitudes (Fig. 4).

The model including Chla, waves, salinity, and, SST as predictor variables explained 48.9% of the variation of FRic, 44.2% of the deviance of FDiv, and 5.56% of the variation in FEve (GAM; Table 1). In the model, salinity had a slightly positive effect, and SST had a negative effect on FRic but not statistically significant (see Appendix S5). The variables had a slight positive-to-linear overall effect on FDiv and a linear effect on FEve (see Appendix S5).

Tabela 1. Results of the Generalized Additive Models (GAMs) analyzing each functional diversity metrics variation along the latitudinal gradient of the Brazilian Province. FRic = functional richness; FDiv = functional divergence; FEve = functional evenness; UBRE = Un-biased risk estimator.

	Intercept		Smooth terms		
Parameters	Estimates	p value	Adjusted R^2	UBRE	Deviance explained
FRic	-1.11	<0.001	0.49	-0.59	48.90%
FDiv	0.82	<0.05	0.38	-0.71	44.20%
FEve	-0.61	0.07	-0.05	-0.72	5.56%

DISCUSSION

Our study shows that reef benthic functional diversity along the Southwestern Atlantic does not follow the general pattern of higher richness in the tropics. Instead, functional richness (FRic) peaks at mid-latitudes (20°S to 23°S) and functional divergence (FDiv) has a hump-shaped pattern across the sampled gradient, peaking at 12°S. Our results suggest that environmental filtering (e.g., salinity and temperature) plays an important role in determining functional patterns at both ends of the latitudinal gradient, at mid-latitudes (e.g., nutrients), and in oceanic communities (e.g., waves). The low FRic and high FDiv valued for sites at latitude 12˚48'S (Todos os Santos Bay), biotic filters seem to have a greater effect in structuring community assembly in this region.

The lower FRic and FDiv values identified for communities in the northern and southern limits of the Brazilian Province, indicate that salinity and temperature are the major drivers of functional community structure in these regions. Distribution patterns of biodiversity are influenced by physiological tolerances of organisms and their ability to establish and persist in diverse environments (Kraft *et al.*, 2015). At the northern limit of the Brazilian Province, low-salinity stress derived from the Amazon River discharges (e.g., freshwater and sediment) is a major barrier for many shallow marine organisms, including sessile and mobile taxa (Miloslavich *et al.*, 2011). However, reef species with broad environmental tolerances, and ecological traits such as rafting, deep-water use, and large body sizes have greater hability to cross this barrier (Moura *et al.*, 2016). Moreover, it has been suggested that low-salinity stress can influence the diversity of marine benthic communities by excluding predators and amending competiton (Fong *et al.*, 1996; Witman & Grange, 1998). Mobile invertebrates predators, such as sea stars and sea urchins, are probably constrained by hyposaline conditions due to practically no potential of osmotic regulation.

Temperature has also been considered one of the main determinants of reef benthic communities distribution worldwide (McArthur *et al.*, 2010; Stuart-Smith *et al.*, 2017). Cold stress, for instance, can affect the metabolism and photosynthetic efficiency of reef-building corals, and temperatures below 18˚C are considered the lower limit for coral survival (Coles & Fadlalallah, 1991; Kleypas *et al.*, 1999). Likewise, temperatures might be affecting benthic communities in the southern limit (i.e., subtropical region) of the Brazilian Province. The lower FRic in this region indicates a smaller number or absence of functional entities, such as corals, important organisms of the core function of reef-building that alter habitat complexity.

At oceanic localities, lower FRic is possible related to lower species richness in those sites, which are characterized as subsets of the regional species' pool (Bender *et al.*, 2013). Moreover, this low FRic can also be associated with local conditions such as high wave action and isolation, since these regions presented the greater values for mean wave heights and are located more than 200 km off the coast, which could decrease the colonization rate of benthic organisms. Marine communities of oceanic islands are known for their low species richness, due to historical, geographic, and, climatological conditions of islands (Pinheiro *et al.*, 2017). Harsh conditions, like the physical stress from waves, can influence species growth and body form, altering building functions of reef ecosystems and well as other core functions. The endemic fire coral *Millepora alcicornis* shows only one haplotype along Brazilian populations, and two growth forms (de Souza *et al.*, 2017). The branching form is the most pervasive type among all coastal populations. Yet, at the oceanic island of Fernando de Noronha, *M. alcicornis* exhibits only an encrusting form, with scarce, short branches. The function of promoting habitat complexity by large branching hard-corals is only exerted by *M. alcicornis* in the Brazilian Province. Nevertheless, this function is missing at Fernando de Noronha.

Sites within Todos os Santos Bay (12˚48'S) showed low FRic and the highest FDiv values, indicative of the greater importance of biotic filters (e.g., competition) in shaping these communities (Botta-Dukát & Czúcz, 2016). High FDiv occurs when functional entities with extreme values of functional traits show greater abundances relative to the mean abundance in the functional space (Villéger *et al.*, 2008), suggesting greater niche differentiation and, thus, low resource competition (Mason *et al.*, 2005). Todos os Santos Bay also had the highest values of productivity (i.e., chlorophyll a) along the Brazilian Province. Although nutrients do not influence diversity directly, patterns of abundance are usually associated with resource availability in the ecosystem (Clarke & Gaston, 2006). In this region, the two dominant taxa (i.e., turf algae and coral *Montastraea cavernosa*) may compete for the same resources (i.e., substrate space, nutrients and light). A recent work documented a decline in coral cover of *M. cavernosa* over the years, suggesting that turf algae is as better competitor, and attesting the importance of biotic interactions in mediating the dynamics of reef benthic communities (Cruz, Kikuchi, Longo & Creed, 2014).

In the Southwestern Atlantic, the peak of taxonomic richness occurs at mid-latitudes (Floeter *et al.*, 2001; Miloslavich *et al.*, 2011; Barroso *et al.*, 2016; Picciani *et al.*, 2016), a transition zone between tropical and subtropical reefs. Different abiotic conditions (some form of energy such as temperature, light, and productivity) control species distribution at such transitional zones (Hawkins *et al.*, 2003; Sommer *et al.*, 2017). The higher FRic and FDiv values identified for this region suggest that both abiotic and biotic filters act in the functional composition of these communities. Productivity (i.e., chlorophyll a) also peaked at this transition zone, between 20˚S to 23˚S latitude. In accordance with the species-energy hypothesis (Clarke & Gaston, 2006), productivity in this region may affect diversity secondarily by increasing species' abundances and leading to greater niche diversification and functions. Likewise, the differences between dominant species (i.e., well adapted) with similar functions in the ecosystem may also be a result of biotic filters (i.e., competition or limiting similarity) at site-scale.

Although FRic and FDiv metrics were good predictors of the functional diversity of shallow-water benthic communities, FEve did not show a clear latitudinal pattern and we consider it not a suitable indicator for detecting biotic filtering. This may be explained by the metrics of FEve, calculated by the minimum spanning tree between neighbors' species in the functional trait space, while biotic filtering takes into account the differences in traits of the dominant species (Botta-Dukát & Czúcz, 2016).

Here we have shown that functional diversity along the Southwestern Atlantic does not conform with the classical latitudinal gradient of diversity. This is mostly related to environmental filters that act differently at northern, southern, and intermediate parts of the latitudinal gradient, as well as in oceanic localities. Temperature is generally held to be the main environmental variable in predicting diversity patterns across latitudinal gradients, but we show that other variables also contribute to community assembly along the studied gradient. For example, the low-salinity stress derived from the Amazon River act as a barrier to marine biodiversity at low latitudes. The functional diversity approach over large-scale studies provides an important tool to understand how communities are assembled and how they respond differently to distinct filters. This is particular important because environmental variables are under continued change, mostly due to anthropogenic activities, and ultimately may alter benthic communities' structure, with potential implications to reef ecosystem functioning.

Acknowledgements

We acknowledge the Brazilian Marine Biodiversity Network (SISBIOTA–Mar) team for fieldwork, photoquadrat analysis and logistical support. This work was fully funded by the project SISBIOTA–Mar: Brazilian Marine Biodiversity Network (P.I: S.R. Floeter - CNPq 563276/2010-0 and FAPESC 6308/2011-8). We also want to thank CAPES ("Science Without Borders", Brazilian Government) for a scholarship to A.W.A to study at Brown University.

REFERENCES

Barroso, C.X., Lotufo, T.M. da C. & Matthews-Cascon, H. (2016) Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships. Journal of Biogeography, **43**, 2477–2488.

Bender, M.G., Pie, M.R., Rezende, E.L., Mouillot, D. & Floeter, S.R. (2013) Biogeographic, historical and environmental influences on the taxonomic and functional structure of Atlantic reef fish assemblages. 1173–1182.

Berke, S.K., Jablonski, D., Krug, A.Z. & Valentine, J.W. (2014) Origination and immigration drive latitudinal gradients in marine functional diversity. PLoS ONE, 9.

Botta-Dukát, Z. & Czúcz, B. (2016) Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. Methods in Ecology and Evolution, **7**, 114–126.

Brown, J.H. (2014) Why are there so many species in the tropics? Journal of Biogeography, **41**, 8–22.

Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences, **104**, 17430–17434.

Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. Proceedings of the Royal Society B: Biological Sciences, **273**, 2257–2266.

Coles, S.L. & Fadlalallah, Y.H. (1991) Reef coral survival and mortality at low-temperatures in the Arabian gulf: new species-specific lower temperature limits. Coral Reefs, **9**, 231–237.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, É.Ó., Lear, D. & Tyler-Walters, H. (2015) Biological and ecological traits of marine species. PeerJ, 3, e1201.

Cruz, I.C.S., Kikuchi, R.K.P., Longo, L.L. & Creed, J.C. (2014) Evidence of a phase shift to Epizoanthus gabrieli Carlgreen, 1951 (Order Zoanthidea) and loss of coral cover on reefs in the Southwest Atlantic. Marine Ecology, 1–8.

D'agata, S., Vigliola, L., Graham, N.A.J., Wantiez, L., Parravicini, V., Villéger, S., Mou-Tham, G., Frolla, P., Friedlander, A.M., Kulbicki, M. &

Mouillot, D. (2016) Unexpected high vulnerability of functions in wilderness areas: evidence from coral reef fishes. Proceedings of the Royal Society B: Biological Sciences, **283**, 20160128.

Floeter, S.R., Guimarães, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. Global Ecology and Biogeography, **10**, 423–431.

Fong, P., Boyer, K.E., Desmond, J.S. & Zelder, J.B. (1996) Salinity stress, nitrogen competition and facilitation: what contrals seasonal succession of 2 opportunistic green macroalgae? Journal of Experimental marine biology and ecology, **206**, 203–221.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K. & Zobel, M. (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. Biological Reviews, **87**, 111–127.

Hawkins, B., Field, R., Cornell, H., Currie, D.J., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology, **84**, 3105–3117.

Hillebrand, H. (2004) On the Generality of the Latitudinal Diversity Gradient. The American Naturalist, **163**, 192–211.

Kleypas, J., McManus, J.W. & Menez, L.A.B. (1999) Environmental limits to coral reef develpment: Where do we draw the line? American Zoology, **39**, 146–159.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015) Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology, **29**, 592–599.

Laliberté, E., Legendre, P. & Shipley, B. (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisting the Holy Grail. Functional Ecology, **16**, 545–556.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos, **111**, 112–118.

MacArthur, R.H. & Wilson, E.O. (1967) The theory of Island Biogeography. Princeton, Princeton University Press.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D. & Radke, L.C. (2010) On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine, Coastal and Shelf Science, **88**, 21–32.

McGill, B.J. (2010) Matters of Scale. Science, **328**, 575–576.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution, **21**, 178–185.

Miloslavich, P., Klein, E., Díaz, J.M., Hernández, C.E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M. V., Díaz de Astarloa, J.M., Lewis, M., Yorio, P., Piriz, M.L., Rodríguez, D., Valentin, Y.Y., Gamboa, L. & Martín, A. (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: Knowledge and gaps. PLoS ONE, **6**, 1–43.

Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva, J.M., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V., Bahia, R.G., Paranhos, R.P., Dias, R.J.S., Siegle, E., Figueiredo, A.G., Pereira, R.C., Leal, C. V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitão, S., Yager, P.L., Francini-Filho, R.B., Fróes, A., Campeão, M., Silva, B.S., Moreira, A.P.B., Oliveira, L., Soares, A.C., Araujo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A.B., Thompson, C.C., Rezende, C.E. & Thompson, F.L. (2016) An extensive reef system at the Amazon River mouth. Science advances, **2**, 1–11.

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua {Chlorophyll concentration} Data; NASA OB.DAAC, Greenbelt, MD, USA.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H., Szoecs, E. & Wagner, H. (2017). vegan: Community Ecology Package. R package version 2.4-4. https://CRAN.R-project.org/package=vegan.

Picciani, N., Seiblitz, I.G. de L., Paiva, P.C., Castro, C.B. & Zilberberg, C. (2016) Geographic patterns of *Symbiodinium* diversity associated with the coral *Mussismilia hispida* (Cnidaria, Scleractinia) correlate with major reef regions in the Southwestern Atlantic Ocean. Marine Biology, **163**, 1–11.

Pinheiro, H.T., Bernardi, G., Simon, T., Joyeux, J.-C., Macieira, R.M., Gasparini, J.L., Rocha, C. & Rocha, L.A. (2017) Island biogeography of marine organisms. Nature, **549**, 82–89.

Pinheiro, H.T., Rocha, L.A., Macieira, R.M., Carvalho-Filho, A., Anderson, A., Bender, M.G., DiDario, F., Ferreira, C.E.L., Figueiredo-Filho, J., Francini-Filho, R., Gasparini, J.L., Joyeux, J.C., Luiz, O.J., Mincarone, M., Moura, R.L., Nunes, J., Quimbayo, J.P., Rosa, R., Sampaio, C., Sazima, I., Simon, T., Vila-Nova, D.A. & Floeter, S.R. (2018) Southwestern Atlantic reef fishes: zoogeographic patterns and ecological drivers reveal a secondary biodiversity center in the Atlantic Ocean. Diversity and Distributions.

R Development Core Team (2015) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for statistical Computing.

Raevel, V., Violle, C. & Munoz, F. (2012) Mechanisms of ecological succession: Insights from plant functional strategies. Oikos, **121**, 1761–1770.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters, **7**, 1–15.

Sbrocco, E.J. & Barber, P.H. (2013) MARSPEC: ocean climate layers for marine spatial ecology. Ecology, **94**, 979–979.

Sommer, B., Beger, M., Harrison, P.L., Babcock, R.C. & Pandolfi, J.M. (2017) Differential response to abiotic stress controls species distributions at biogeographic transition zones. Ecography, 1–12.

de Souza, J.N., Nunes, F.L.D., Zilberberg, C., Sanchez, J.A., Migotto, A.E., Hoeksema, B.W., Serrano, X.M., Baker, A.C. & Lindner, A. (2017) Contrasting patterns of connectivity among endemic and widespread fire coral species (Millepora spp.) in the tropical Southwestern Atlantic. Coral Reefs, **36**, 701–716.

Stuart-Smith, R.D., Edgar, G.J. & Bates, A.E. (2017) Thermal limits to the geographic distributions of shallow-water marine species. Nature Ecology and Evolution, **1**, 1846–1852.

Tilman, D. (2001) Functional diversity. Encyclopedia of Biodiversity, **3**, 109–120.

Trygonis, V. & Sini, M. (2012) PhotoQuad: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. Journal of Experimental Marine Biology and Ecology, 424–425, 99–108.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F. & De Clerck, O. (2012) Bio-ORACLE: A global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography, **21**, 272–281.

Tolman, H. L., 2014: User manual and system documentation of WAVEWATCH III version 4.18. NOAA / NWS / NCEP / MMAB Technical Note 316.

Villéger, S. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. Ecology, **89**, 2290–2301.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. Ecology, **89**, 2290–2301.

Villéger, S., Miranda, J.R., Hernández, D.F. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecological applications, **20**, 1512–1522.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution, and Systematics, **34**, 273–309.

Wickham, H. (2009) ggplot2: Elegant Graphics for Data Analysis. New York, Springer-Verlag.

Witman, J.D., Etter, R.J. & Smith, F. (2004) The relationship between regional and local species diversity in marine benthic communities: A global perspective. Proceedings of the National Academy of Sciences, **101**, 15664–15669.

Witman, J.D. & Grange, K.R. (1998) Links between rain, salinity, and predation in a rocky subtidal community. Ecology, **79**, 2429–2447.

Wood, S. (2017) Stable and Efficient Multiple Smoothing Parameter Estimation for Generalized Additive Models. Journal of the American Statistical Association, **99**, 673-686.

Yeager, L.A., Deith, M.C.M., McPherson, J.M., Williams, I.D. & Baum, J.K. (2017) Scale dependence of environmental controls on the functional diversity of coral reef fish communities. Global Ecology and Biogeography, **26**, 1177–1189.

Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? TREE, **12**, 266–269.

Data accessibility statement

All data used in our study (functional diversity metrics and extracted environmental information) can be accessed in Supporting Information Appendix S3.

Biosketch

Our research team interest is focused on large-scale patterns of marine diversity and ecosystem functioning, linking organisms' traits to ecological functions in reef systems. We are mostly interested in understanding the ecological and evolutionary processes that influence the global patterns of marine communities.

Supplementary materials

Appendix S1 Field work sampling effort.

Locality	Site	Lat	Lon	Reef type	Month	Year	Depth (m)	N (2m^2 area)	N (photoquadrats)
Rocas Atoll	Âncoras	-3.88	-33.80	Biogenic	January	2012	1-7	16	80
Rocas Atoll	Falsa Barreta	-3.86	-33.82	Biogenic	January	2012	1-7	19	95
Rocas Atoll	Rocas	-3.87	-33.79	Biogenic	January	2012	1-7	20	100
Rocas Atoll	Podes Crer	-3.87	-33.81	Biogenic	January	2012	1-7	17	85
Rocas Atoll	Salão	-3.87	-33.81	Biogenic	January	2012	8-15	9	45
Rocas Atoll	Tartarugas	-3.87	-33.81	Biogenic	January	2012	1-7	18	90
Fernando de Noronha	Cagarras	-3.81	-32.39	Rocky	October	2011	1-7 and 8-15	28	140
Fernando de Noronha	Conceição	-3.84	-32.41	Rocky	October	2011	1-7 and 8-15	29	145
Fernando de Noronha	Sueste	-3.87	-32.42	Rocky	October	2011	1-7	14	70
Trindade Island	Calheta	-20.51	-29.31	Rocky	July	2012	1-7 and 8-15	24	120
Trindade Island	Farrilhões	-20.52	-29.50	Rocky	July	2012	1-7 and 8-15	17	85
Trindade Island	Orelhas	-20.49	-29.34	Rocky	July	2012	1-7 and 8-15	18	90
PML	Ana Cristina	-0.87	-44.26	Biogenic	April	2013	1-7 and 8-15	22	110
RN Parrachos	Maracajaú	-5.39	-35.26	Biogenic	October	2011	1-7	14	70
RN Parrachos	Rio do Fogo	-5.26	-35.36	Biogenic	October	2011	1-7	8	40
RN Recifes	Batente das Agulhas	-5.56	-35.07	Biogenic	March	2013	8-15	8	40
RN Recifes	Pedra do Silva	-5.56	-35.09	Biogenic	March	2013	8-15	14	70
Costa dos Corais	Barra das Galés	-9.03	-35.19	Biogenic	March	2012	1-7	15	75
Costa dos Corais	Galés	-9.02	-35.19	Biogenic	March	2012	1-7	15	75
Costa dos Corais	Taocas	-9.00	-35.18	Biogenic	March	2012	1-7	15	75
Todos os Santos Bay	Farol da Barra	-13.01	-38.53	Biogenic	March	2012	1-7	15	75
Todos os Santos Bay	Frades	-12.81	-38.63	Biogenic	March	2012	1-7	15	75

Locality	Site	Lat	Lon	Reef type	Month	Year	Depth (m)	N (2m^2 area)	N (photoquadrats)
Todos os Santos Bay	Pedra Cardinal	-12.84	-38.55	Biogenic	March	2012	8-15	14	70
Todos os Santos Bay	Poste Quatro	-12.81	-38.57	Biogenic	March	2012	8-15	15	75
Abrolhos	Chapeirão	-17.96	-38.66	Biogenic	March	2010	1-7	15	75
Abrolhos	Portinho Norte	-17.96	-38.69	Biogenic	March	2010	1-7	15	75
Abrolhos	Siriba	-17.97	-38.72	Biogenic	March	2010	1-7	15	75
Guarapari	Escalvada	-20.70	-40.41	Rocky	February	2014	1-7 and 8-15	30	150
Guarapari	Ilhas Rasas	-20.68	-40.37	Rocky	February	2014	1-7 and 8-15	30	150
Guarapari	Três Ilhas	-20.61	-40.38	Rocky	February	2014	1-7 and 8-15	30	150
Arraial do Cabo	Anequim	-22.98	-41.98	Rocky	March	2011	1-7 and 8-15	24	120
Arraial do Cabo	Cardeiros	-22.97	-42.00	Rocky	March	2011	1-7 and 8-15	31	155
Arraial do Cabo	Porcos Oeste	-22.97	-41.99	Rocky	March	2011	1-7 and 8-15	21	105
Ilhabela	Ilhas das Cabras	-23.83	-45.39	Rocky	March	2013	1-7 and 8-15	27	135
Ilhabela	Saco do Diogo	-23.94	-45.28	Rocky	March	2013	1-7 and 8-15	22	110
Ilhabela	Saco do Sombrio	-23.89	-45.24	Rocky	March	2013	1-7 and 8-15	22	110
Alcatrazes	Portinho Sudoeste	-24.11	-45.70	Rocky	March	2013	1-7 and 8-15	22	110
Florianópolis Norte	Saco d'água	-27.28	-48.37	Rocky	April	2011	1-7 and 8-15	24	120
Florianópolis Norte	Deserta Norte	-27.26	-48.33	Rocky	April	2011	1-7 and 8-15	30	150
Florianópolis Sul	Xavier	-27.60	-48.39	Rocky	April	2011	1-7 and 8-15	14	70
Total								**771**	**3855**

Appendix S2. Description of functional traits.

We selected six traits within biological (maximum body size, growth form, trophic type, modularity, and, mobility) and life-history category (reproduction type) considered with ecological importance (Wahl, 2009). We based our classification scheme on previous categorization for benthic organisms (Littler & Littler, 1984; Steneck & Dethier, 1994; Bell & Barnes, 2001; Bremner *et al.*, 2006; Wahl, 2009; Costello *et al.*, 2015), selecting traits with ecological relevance for the studied communities (i.e., similar requirements of resources and/or provide similar services) and that could be applied to most taxa. If trait information was lacking in literature, we assumed the dominant trait from higher taxonomic levels.

Maximum body size

Body size is directly related to the use of space and abundance, and indirectly to longevity and metabolic rates resource (Woodward *et al.*, 2005). The maximum body size was divided in four ordinal categories: S = <10 cm, M = 10-50 cm, L = 50-400 cm, and, XL = >400 cm. We selected information about maximum horizontal body size from literature and/or help from specialists. For unitary organisms we consider individual size but for colonial organisms we used the maximum reported size for colony or modular aggregations.

Growth form

Benthic growth form is related to habitat complexity and resource use (Richardson *et al.*, 2017a). Growth form was classified as five categories in order to be able to compare the whole community. We divided it growth form in: E = encrusting, M = massive, B = bushy or with up-ward growth, F = filamentous, and, EF = encrusting/filamentous.

Trophic type

Trophic type is linked to competitiveness and food webs and nutrient cycling (Hillebrand, 2004a; Wahl *et al.*, 2011). Trophic type was categorized in six categories: A = autotroph, S = suspension/filter feeder, G = grazer, C = carnivore, and, AC = autotroph/carnivore.

Modularity

Modularity is related to reproduction type and the ability to occupy the substrate (Wahl *et al.*, 2011). We divided modularity as: S = solitaries and M = modular.

Mobility

Mobility is an indicative of dispersal potential of organisms (Costello *et al.*, 2015). We categorized mobility as: S = sessile or M = mobile organism.

Reproduction type

Life-history traits can describe the persistence and/or longevity of individual or populations over time. To distinguish species sexual and asexual reproduction is easily available for most taxa and can indicate the ability of a specie to disperse or recover from a disturb (Costello *et al.*, 2015). We classified reproduction type as: S = sexual, A = asexual, and, AS = asexual/sexual.

References

Bell, J.J. & Barnes, D.K. a (2001) Sponge morphological diversity: A qualitative predictor of species diversity? Aquatic Conservation: Marine and Freshwater Ecosystems, 11, 109–121.

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecological Indicators, 6, 609–622.

Costello, M.J., Claus, S., Dekeyzer, S., Vandepitte, L., Tuama, É.Ó., Lear, D. & Tyler-Walters, H. (2015) Biological and ecological traits of marine species. PeerJ, 3, e1201.

Hillebrand, H. (2004) On the Generality of the Latitudinal Diversity Gradient. The American Naturalist, 163, 192–211.

Littler, M.M. & Littler, D.S. (1984) Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. Journal of Experimental Marine Biology and Ecology, 74, 13–34.

Richardson, L.E., Graham, N.A.J. & Hoey, A.S. (2017) Cross-scale habitat structure driven by coral species composition on tropical reefs. Scientific Reports, 1–11.

Steneck, R.S. & Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities. Oikos, 69, 476–498.

Wahl, M. (2009) Marine Hard Bottom Communities Studies Volume 206, Springer Berlin Heidelberg, Berlin.

Wahl, M., Link, H., Alexandridis, N., Thomason, J.C., Cifuentes, M., Costello, M.J., da Gama, B.A.P., Hillock, K., Hobday, A.J., Kaufmann, M.J., Keller, S., Kraufvelin, P., Krüger, I., Lauterbach, L., Antunes, B.L., Molis, M., Nakaoka, M., Nyström, J., bin Radzi, Z., Stockhausen, B., Thiel, M., Vance, T., Weseloh, A., Whittle, M., Wiesmann, L., Wunderer, L., Yamakita, T. & Lenz, M. (2011) Re-structuring of marine communities exposed to environmental change: A global study on the interactive effects of species and functional richness. PLoS ONE, 6, 3–5.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. Trends in Ecology and Evolution, 20, 402–409.

Table S2.1 Organisms and functional classification scheme using the six selected traits.

Taxa	**Maximum body size**	**Growth form**	**Trophic type**	**Modularity**	**Mobility**	**Reproduction type**
Agaricia fragilis	M	E	AC	M	S	AS
Agaricia humilis	M	E	AC	M	S	AS
Agaricia spp	M	E	AC	M	S	AS
Bunodosoma caissarum	S	M	C	S	M	AS
Demospongiae	S	B	S	S	S	AS
Phlebobranchia	M	E	S	M	S	AS
Rhizangiidae	M	E	AC	M	S	AS
Botrylloides nigrum	S	E	S	M	S	AS
Bryopsis pennata	L	B	A	M	S	AS
Corallinaceae	L	B	A	M	S	AS
Coralline turf	XL	EF	A	M	S	AS
Carijoa riisei	L	B	C	M	S	AS
Caulerpa racemosa	L	B	A	M	S	AS
Caulerpa spp.	L	B	A	M	S	AS
Caulerpa verticillata	L	B	A	M	S	AS
Chaetomorpha	S	F	A	M	S	AS
Champia parvula	S	B	A	M	S	AS

Taxa	Maximum body size	Growth form	Trophic type	Modularity	Mobility	Reproduction type
Cyanobacteria	XL	EF	A	M	S	AS
Hexanauplia	S	E	S	S	S	S
Codium intertextum	XL	E	A	M	S	AS
Codium spp.	S	B	A	M	S	AS
Colpomenia sinuosa	S	M	A	M	S	AS
Gigartinacea	XL	B	A	M	S	AS
Tropiometra sp.	M	B	S	S	M	S
Corallinales	XL	E	A	M	S	S
Dictyopteris spp.	M	B	A	M	S	AS
Dictyopteris plagiogramma	S	B	A	M	S	AS
Dictyota spp.	M	B	A	M	S	AS
Didemnum sp.	S	E	S	M	S	AS
Didemnum perlucidum	S	E	S	M	S	AS
Digenea simplex	XL	B	A	M	S	AS
Echinaster	S	M	C	S	M	S
Favia gravida	S	E	AC	M	S	AS
Dictyotaceae	S	B	A	M	S	AS
Galaxaura spp.	S	B	A	M	S	AS
Gelidiella acerosa	XL	B	A	M	S	AS

Taxa	Maximum body size	Growth form	Trophic type	Modularity	Mobility	Reproduction type
Gelidiopsis spp.	L	B	A	M	S	AS
Gelidium floridanum	L	B	A	M	S	AS
Demospongiae	M	M	S	S	S	AS
Ulvophyceae	XL	F	A	M	S	AS
Halimeda spp.	XL	B	A	M	S	AS
Heterogorgia spp.	S	B	C	M	S	AS
Hypnea musciformis	XL	B	A	M	S	AS
Idiellana pristis	S	B	C	M	S	AS
Demospongiae	M	E	S	S	S	AS
Corallinaceae	L	B	A	M	S	AS
Laurencia spp.	L	B	A	M	S	AS
Dictyotaceae	L	B	A	M	S	AS
Leptogorgia spp.	S	B	C	M	S	AS
Lobophora variegata	XL	B	A	M	S	AS
Macrorhynchia philippina	S	B	A	M	S	AS
Madracis decactis	L	B	C	M	S	AS
Demospongiae	M	M	S	S	S	AS
Meandrina brasiliensis	M	M	AC	M	S	AS
Millepora alcicornis	L	B	AC	M	S	AS

Taxa	**Maximum body size**	**Growth form**	**Trophic type**	**Modularity**	**Mobility**	**Reproduction type**
Millepora sp.	L	E	AC	M	S	AS
Millepora nitida	M	M	AC	M	S	AS
Millepora spp.	L	E	AC	M	S	AS
Montastraea cavernosa	L	M	AC	M	S	AS
Muricea flamma	S	B	C	M	S	AS
Muriceopsis sulphurea	S	B	AC	M	S	AS
Mussismilia braziliensis	L	M	AC	M	S	AS
Mussismilia harttii	L	B	AC	M	S	AS
Mussismilia hispida	M	M	AC	M	S	AS
Favia leptophylla	L	M	AC	M	S	AS
Mussismilia spp.	L	E	AC	M	S	AS
Ochtodes secundiramea	S	B	A	M	S	AS
Alcyonacea	S	B	C	M	S	AS
Ophiothela mirabilis	S	E	C	S	M	S
Echinometra lucunter	M	B	G	S	M	S
Eucidaris tribuloides	M	B	G	S	M	S
Phlebobranchia	S	M	AC	M	S	AS
Anthozoa	L	M	AC	M	S	AS
Malacostraca	S	M	C	S	M	S

Taxa	**Maximum body size**	**Growth form**	**Trophic type**	**Modularity**	**Mobility**	**Reproduction type**
Asteroidea	M	M	C	S	M	S
Hydrozoa	S	B	C	M	S	AS
Padina	L	B	A	M	S	AS
Palythoa caribaeorum	XL	E	AC	M	S	AS
Palythoa variabilis	L	E	AC	M	S	AS
Demospongiae	M	E	S	S	S	AS
Parazoanthus axinellae	L	E	AC	M	S	AS
Peyssonnelia sp.	XL	B	A	M	S	AS
Phallusia nigra	S	M	S	S	S	AS
Phyllogorgia dilatata	S	B	AC	M	S	AS
Plexaurella grandiflora	S	B	AC	M	S	AS
Plexaurella regia	S	B	AC	M	S	AS
Polychaeta	S	B	S	S	S	AS
Porites astreoides	M	M	AC	M	S	AS
Porites branneri	M	E	AC	M	S	AS
Porites spp.	M	E	AC	M	S	AS
Protopalythoa spp.	L	E	AC	M	S	AS
Sargassum spp.	S	B	A	M	S	AS
Schizoporella sp.	M	E	C	M	S	AS

Taxa	Maximum body size	Growth form	Trophic type	Modularity	Mobility	Reproduction type
Siderastrea spp.	L	M	AC	M	S	AS
Stypopodium spp.	S	B	A	M	S	AS
Tricleocarpa cylindrica	S	B	A	M	S	AS
Trididemnum sp.	S	E	S	M	S	AS
Demospongiae	S	B	S	S	S	AS
Udotea sp.	S	B	A	M	S	AS
Ulvophyceae	XL	F	A	M	S	AS
Ventricaria ventricosa	S	M	A	M	S	AS
Wrangelia sp.	L	B	A	M	S	AS
Zoanthus sociatus	XL	E	AC	M	S	AS

Appendix S3 Functional diversity metrics and environmental parameters at sampled sites.

Locality	Site	Lat	Lon	FRic	FDiv	FEve	mean Chla	mean Hsig	min monthly SSS	min monthly SST
Rocas Atoll	Âncoras Falsa	-3.88	-33.80	0.103	0.618	0.487	0.12	1.94	35.78	26.34
Rocas Atoll	Barreta	-3.86	-33.82	0.156	0.614	0.585	0.11	1.94	35.78	26.34
Rocas Atoll	Rocas	-3.87	-33.79	0.191	0.548	0.416	0.11	1.94	35.78	26.34
Rocas Atoll	Podes Crer	-3.87	-33.81	0.102	0.425	0.384	0.12	1.94	35.78	26.34
Rocas Atoll	Salão	-3.87	-33.81	0.025	0.836	0.282	0.12	1.94	35.78	26.34
Rocas Atoll	Tartarugas	-3.87	-33.81	0.006	0.709	0.422	0.12	1.94	35.78	26.34
Fernando de Noronha	Cagarras	-3.81	-32.39	0.406	0.619	0.451	0.09	1.99	35.76	26.31
Fernando de Noronha	Conceição	-3.84	-32.41	0.236	0.645	0.373	0.11	1.99	35.76	26.31
Fernando de Noronha	Sueste	-3.87	-32.42	0.080	0.406	0.342	0.11	1.99	35.76	26.31
Trindade Island	Calheta	-20.51	-29.31	0.209	0.662	0.408	0.06	2.02	36.93	23.35
Trindade Island	Farrilhões	-20.52	-29.50	0.063	0.627	0.577	0.05	2.04	36.93	23.34
Trindade Island	Orelhas	-20.49	-29.34	0.006	0.882	0.121	0.05	2.02	36.93	23.37
PML	Ana Cristina	-0.87	-44.26	0.182	0.495	0.155	0.43	1.36	35.20	26.81
RN Parrachos	Maracajaú	-5.39	-35.26	0.094	0.780	0.288	1.78	1.76	35.73	26.06
RN Parrachos	Rio do Fogo	-5.26	-35.36	0.189	0.626	0.252	2.00	1.73	35.76	26.08

Locality	Site	Lat	Lon	FRic	FDiv	FEve	mean Chla	mean Hsig	min monthly SSS	min monthly SST
RN Recifes	Batente das Agulhas	-5.56	-35.07	0.025	0.612	0.336	0.22	1.65	35.69	26.25
RN Recifes	Pedra do Silva	-5.56	-35.09	0.039	0.532	0.321	0.28	1.65	35.69	26.24
Costa dos Corais	Barra das Galés	-9.03	-35.19	0.551	0.661	0.424	0.84	1.68	36.28	25.94
Costa dos Corais	Galés	-9.02	-35.19	0.050	0.888	0.288	0.84	1.68	36.28	25.93
Costa dos Corais	Taocas	-9.00	-35.18	0.250	0.787	0.463	1.20	1.68	36.27	25.42
Todos os Santos Bay	Farol da Barra	-13.01	-38.53	0.234	0.854	0.356	1.42	1.49	35.82	25.28
Todos os Santos Bay	Frades	-12.81	-38.63	0.103	0.858	0.344	3.68	1.49	35.68	25.42
Todos os Santos Bay	Pedra Cardinal	-12.84	-38.55	0.090	0.922	0.368	2.97	1.49	35.70	25.32
Todos os Santos Bay	Poste Quatro	-12.81	-38.57	0.058	0.849	0.399	3.04	1.49	35.68	25.37
Abrolhos	Chapeirão	-17.96	-38.66	0.323	0.818	0.414	0.63	1.45	36.40	24.48
Abrolhos	Portinho Norte	-17.96	-38.69	0.458	0.696	0.369	0.62	1.45	36.39	24.44
Abrolhos	Siriba	-17.97	-38.72	0.281	0.624	0.393	0.59	1.45	36.39	24.43
Guarapari	Escalvada	-20.70	-40.41	0.748	0.762	0.288	1.80	1.38	36.07	22.47
Guarapari	Ilhas Rasas	-20.68	-40.37	0.659	0.749	0.378	1.66	1.38	36.09	22.48
Guarapari	Três Ilhas	-20.61	-40.38	0.722	0.793	0.351	2.18	1.38	36.10	22.45

Locality	Site	Lat	Lon	FRic	FDiv	FEve	mean Chla	mean Hsig	min monthly SSS	min monthly SST
Arraial do Cabo	Anequim	-22.98	-41.98	0.631	0.637	0.331	1.18	1.76	35.58	21.24
Arraial do Cabo	Cardeiros	-22.97	-42.00	0.744	0.757	0.412	1.33	1.66	35.57	21.19
Arraial do Cabo	Porcos Oeste	-22.97	-41.99	0.595	0.698	0.423	1.33	1.66	35.57	21.20
Ilhabela	Ilhas das Cabras	-23.83	-45.39	0.546	0.950	0.539	1.41	1.41	35.16	21.41
Ilhabela	Saco do Diogo	-23.94	-45.28	0.523	0.586	0.270	1.60	1.41	35.26	20.54
Ilhabela	Saco do Sombrio	-23.89	-45.24	0.422	0.729	0.480	1.32	1.41	35.26	21.41
Alcatrazes	Portinho Sudoeste	-24.11	-45.70	0.207	0.526	0.376	0.75	1.41	35.14	20.93
Florianópolis Norte	Saco d'água	-27.28	-48.37	0.376	0.584	0.465	1.76	1.24	34.00	17.95
Florianópolis Norte	Deserta Norte	-27.26	-48.33	0.360	0.728	0.513	1.48	1.24	34.03	17.90
Florianópolis Sul	Xavier	-27.60	-48.39	0.201	0.649	0.400	1.55	1.26	34.08	17.75

Appendix S4 Correlation results.

Table S4.1 Pearson's correlations between environmental variables. Red values are r>0.7.

	annual var SST	max monthly SST	min monthly SST	mean annual SST	annual var SSS	max monthly SSS	min monthly SSS	mean annual SSS	sd Hsig	mean Hsig	sd Chla
mean Chla	0.27	-0.16	-0.31	-0.25	0.44	0.18	-0.3	0.07	0.29	-0.62	**0.88**
sd Chla	0.14	0.12	-0.07	0.02	0.38	0.31	-0.18	0.21	0.44	-0.41	
mean Hsig	-0.5	0.51	0.58	0.57	-0.64	-0.01	0.53	0.21	0.01		
sd Hsig	-0.08	0.17	0.03	**0.85**	-0.16	0.54	0.45	0.55			
mean annual SSS	-0.54	0.34	0.42	0.39	-0.43	**0.95**	**0.86**				
min monthly SSS	**-0.7**	0.41	0.55	0.49	**-0.79**	**0.71**					
max monthly SSS	-0.42	0.24	0.3	0.27	-0.24						
annual var SSS	**0.8**	-0.34	-0.58	-0.47							
mean annual SST	**-0.74**	**0.96**	**0.98**								
min monthly SST	**-0.86**	**0.88**									
max monthly SST	-0.55										

Appendix S5 Generalized Additive Models (GAMs).

Table S5.1 Summary of approximate significant of smooth terms of Generalized Additive Models (GAMs).

Parameters	Explanatory variables	Smooth terms			
		edf	Ref.df	Chi.sq	p-value
FRic	s(min_montly_sss)	1.348	1.572	1.91	0.352
	s(min_montly_sst)	1	1	2.129	0.145
	s(meanChla)	1.09	1.169	0.038	0.92
	s(meanHsig)	1	1	0.326	0.568
FDiv	s(min_montly_sss)	1	1	0.409	0.523
	s(min_montly_sst)	1	1	0.008	0.928
	s(meanChla)	1	1	0.659	0.417
	s(meanHsig)	1	1	0	0.986
FEve	s(min_montly_sss)	1	1	0.038	0.845
	s(min_montly_sst)	1	1	0	0.998
	s(meanChla)	1	1	0	0.99
	s(meanHsig)	1	1	0	0.999

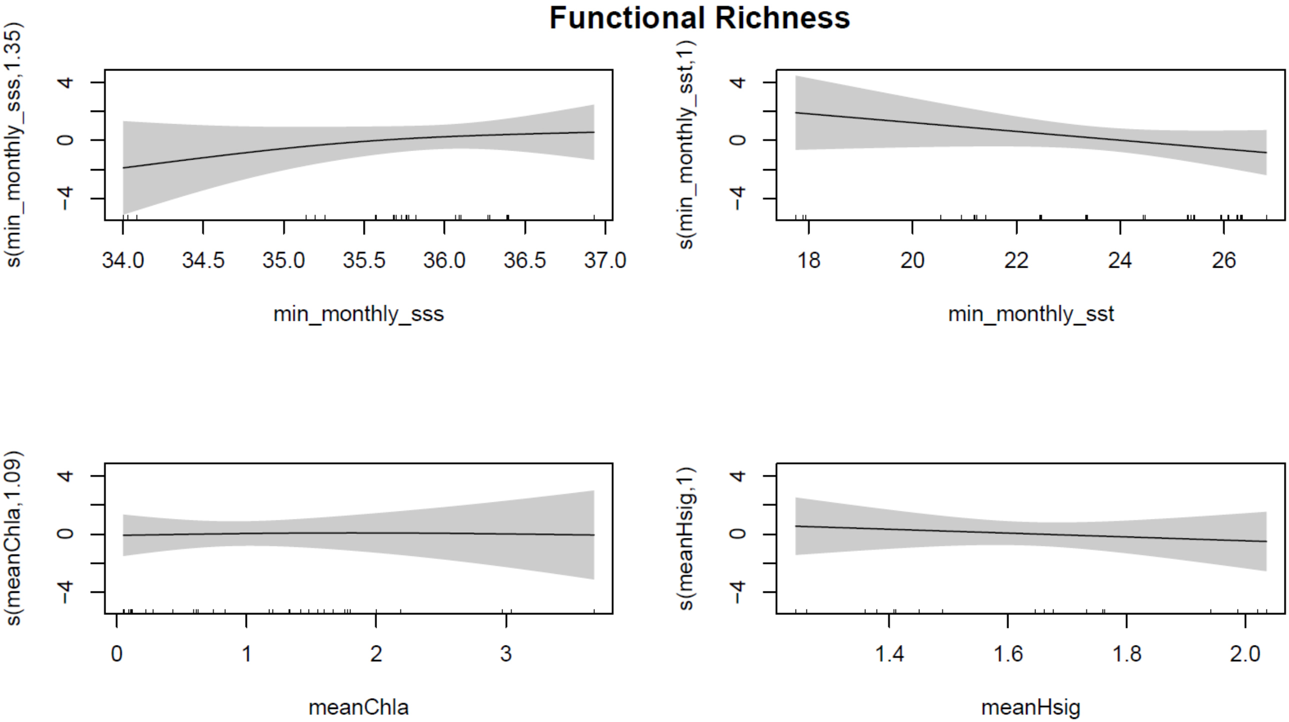

Figure S5.2 Plot with the smooth terms in the model with functional richness.

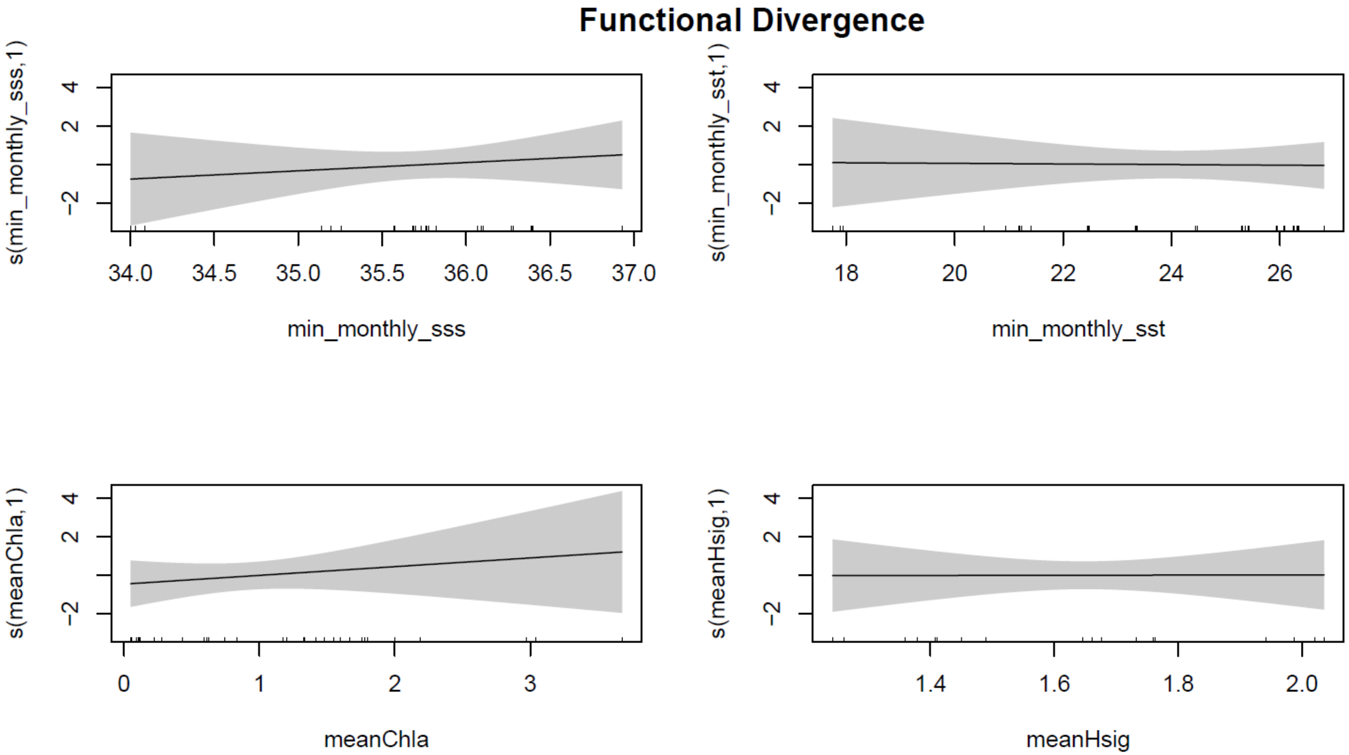

Figure S5.3 Plot with the smooth terms in the model with functional divergence.

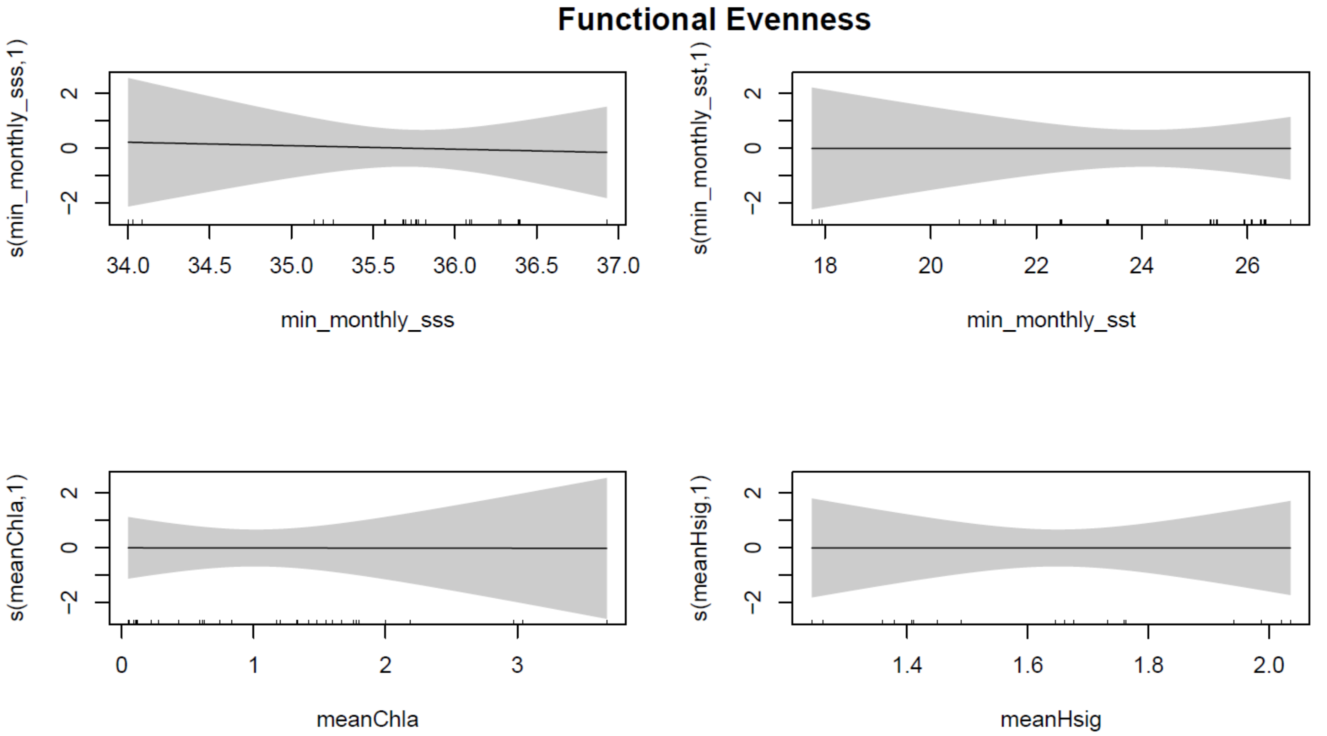

Figure S5.4 Plot with the smooth terms in the model with functional evenness.

CONCLUSÃO GERAL

Com base nos resultados apresentados neste trabalho, concluímos que as comunidades bentônicas de substrato consolidado da Província Brasileira são amplamente dominadas por *turf* e macroalgas frondosas, mesmo em locais distantes da costa e em recifes localizados em áreas marinhas protegidas. Além disso, os recifes brasileiros possuem baixa cobertura de corais construtores e a ocorrência de outros grupos de organismos é maior próximo da latitude 20˚S, região de Guarapari (ES). A estrutura das comunidades bentônicas não apresentou variação latitudinal clara entre os estratos de profundidade amostrados, porém, variou entre as localidades, indicando que fatores locais possivelmente regem a composição dessas comunidades. Adicionalmente, os resultados do primeiro capítulo proporcionam o primeiro *baseline* quantitativo das comunidades bentônicas recifais do Brasil. Tal informação pode contribuir para verificação de mudanças e respostas futuras nas comunidades bentônicas devidos à distúrbios locais, como por exemplo quantificar os efeitos do desastre do Rio Doce nas áreas recifais do Espírito Santo e Bahia. Ainda, esses resultados permitem entender a variação das mudanças nas comunidades bentônicas da Província Brasileira ao longo do tempo, como examinar se a dominância de turf e macroalgas permanece constante ao longo do tempo.

Os padrões de diversidade taxonômica e funcional analisados foram diferentes do padrão clássico de gradiente latitudinal de diversidade. No padrão clássico, a maior riqueza de espécies se encontram na região próxima à linha do equador, diferentemente do padrão encontrado no nosso estudo, onde a maior riqueza ocorre em latitudes intermediárias, entre as latitudes 20˚S e 23˚S da região costeira. Esse padrão já foi observado em outros grupos marinhos na costa sudoeste do Atlântico. Essa variação atípica da riqueza ocorre pela influencia de filtros abióticos extremos, não apenas devido à temperatura, considerado um dos fatores mais importantes nos padrões de diversidade, mas também pela ação das baixas salinidades, ondas e aporte de nutrientes ao longo do gradiente latitudinal. Além disso, as regiões de maior riqueza funcional e de espécies não estão, em sua maioria, contempladas por áreas de proteção ambiental. A região de Guarapari, no estado do Espírito Santo, apresenta a maior diversidade taxonômica e funcional de toda a costa brasileira e, ainda assim, contém poucas áreas costeiras com proteção efetiva.

Para finalizar, o nosso trabalho contribuiu para a compreensão dos diferentes processos ecológicos (e.g., filtros bióticos e abióticos) na estrutura das comunidades bentônicas recifais da região da Província Brasileira. Os dados contidos neste estudo são extremamente importantes para o nosso entendimento sobre a biodiversidade marinha do Atlântico Sul Ocidental, tal como da biodiversidade marinha global, pois podem contribuir para estudos de larga escala dos padrões e processos que regem a vida marinha da Terra.