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BIOGEOGRAFIA MARINHA BRASILEIRA: UMA ABORDAGEM MULTI-TÁXON PARA DELINEAR A SETORIZAÇÃO DE SUB-PROVÍNCIAS

Florianópolis
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Orientador: Prof. Sergio R. Floeter, Dr.

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O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Prof. Paulo Antunes Horta, Dr.
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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestra em Ecologia.

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“Natura simplicitatem amat” [A natureza ama a simplicidade].

(KEPLER, 1619)

RESUMO

Padrões de distribuição das espécies têm sido extensivamente debatidos sob a ótica de suas relações com fatores históricos, ecológicos e ambientais. Inicialmente, estudos biogeográficos utilizaram condições abióticas e taxas de endemismo para propor que a região entre o deságue do Rio Amazonas (latitude 0°) e o Estado de Santa Catarina (28°) seja denominada Província Biogeográfica Marinha Brasileira (PMB). Esta área engloba uma das maiores extensões litorâneas tipicamente tropicais do mundo, estendendo-se por cerca de 8.000 quilômetros com distintos ambientes marinhos. Apesar de existirem estudos realizados com diferentes táxons buscando setorizar a PMB, até o presente momento, esta Província carece de uma abordagem multi-táxon para investigar possíveis distinções bióticas e o papel de fatores ambientais na determinação de seus padrões biogeográficos. Neste estudo, utilizamos análises de agrupamento de cinco fatores ambientais para dividir a PMB em intervalos geográficos. Em seguida, investigamos os agrupamentos em relação a similaridades bióticas de nove grupos taxonômicos (2.412 espécies) e também a beta-diversidade dentre as sub-províncias. Utilizamos uma análise de redundância baseada em distâncias (db-RDA) para investigar relações entre os padrões biogeográficos das espécies e as similaridades ambientais entre os intervalos geográficos. Encontramos oito intervalos geográficos distintos considerando as variáveis ambientais, e cinco considerando a similaridade biótica (sendo estes cinco as sub-províncias). Observamos um gradiente latitudinal de riqueza para a maioria dos táxons, com alguns apresentando um padrão no formato de “mid-domain”. A beta-diversidade foi baixa entre as sub-províncias e o componente “aninhamento” foi o mais importante, indicando uma alta conectividade ao longo da PMB. A db-RDA indicou que as variáveis ambientais explicaram os padrões de agrupamento das espécies em 64% e que temperatura da superfície oceânica, turbidez da água e velocidade das correntes descrevem o agrupamento da costa Nordeste do Brasil. As sub-províncias Banco dos Abrolhos e Norte foram as mais distintas em ambos agrupamentos (ambientais e bióticos). Não há áreas costeiras contínuas de substrato consolidado nestas sub-províncias, mas sim recifes com características de “mid-shelf” em plataformas rasas e extensas. Ademais, há uma significativa influência da pluma do Amazonas no Norte. Uma abordagem multi-táxon é ideal para o entendimento de padrões biogeográficos, assim como sua resposta aos fatores históricos e ambientais.

Palavras-chave: Filtros ecológicos. Biogeografia marinha. Ambientes recifais. Distribuição de espécies.

ABSTRACT

Species distribution patterns are extensively debated in the light of their environmental dependence and historical factors. Early biogeographical studies focused on abiotic factors and endemism rates to propose the Marine Biogeographical Brazilian Province (BMP), which extends from the Amazon River mouth (latitude 0°) to the Santa Catarina State (28°). This area encompasses one of the world's largest tropical coasts, extending for 8,000 km and presenting different marine environments. To date, no study ever used a multi-taxa approach to investigate possible biotic distinctions in the BMP and the role of environmental factors in determining biogeographical patterns. Here, we used cluster analysis of five environmental factors to divide the BMP in geographical bins. We investigated how nine taxonomic groups (2,412 species) are clustered and calculated beta diversity indexes among sub-provinces. We used a distance-based redundancy analysis (db-RDA) to understand how species biogeographical patterns are explained by the environmental similarities among bins. We found eight different geographical bins considering the environmental factors, while five considering species biogeography. We also observed a latitudinal gradient of species richness for most taxa, some presenting a "mid-domain" shape pattern. Beta diversity among sub-provinces was low, and the nestedness component more important, indicating high connectivity along the BMP. The db-RDA indicated that environmental variables explained 64% of species clustering patterns, with sea surface temperature, water turbidity and current velocity explaining the biotic clustering of the Brazilian northeastern coast. Sub-provinces North and Abrolhos Bank were the most distinct areas regarding environmental and biotic data. Both regions do not present continuous consolidated benthic substratum but instead are characterized by mid-shelf reefs in shallow extensive shelfs. Moreover, the influence of the Amazon River plume on the North is significant. Our multi-taxa approach is ideal for understanding biogeographical patterns, as well as its response to environmental and historical factors.

Keywords: Ecological filters. Marine biogeography. Reef environments. Species distribution.

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INTRODUÇÃO GERAL

A distribuição das espécies no globo e seus padrões de riqueza são temas amplamente debatidos (e.g. DARWIN, 1859; EKMAN, 1953; McGILL & COLLINS, 2003; TITTENSOR *et al*., 2010), assim como a influência de diversos fatores bióticos e abióticos nestas variáveis (RICKLEFS, 2008). Sintetizando aspectos de diversos ramos das ciências (e.g. ecologia, geologia e paleontologia), a biogeografia busca realizar o delineamento de regiões do globo para entender as forças históricas e evolutivas que moldam os padrões de biodiversidade (FLOETER *et al*., 2009). Por muitas vezes trabalhar com escalas espaciais e temporais muito extensas, estudos biogeográficos não costumam ser experimentais, mas sim comparativos, baseados em observações. Nestes estudos, as teorias são desenvolvidas com base nos padrões observados, com subsequente teste de hipóteses e possíveis predições de como acontecimentos futuros podem afetar os ecossistemas (PEREIRA & SOARES-GOMES, 2009).

Há séculos o ser humano busca uma forma de setorizar o ambiente marinho. Historicamente, acreditava-se que a distribuição dos animais nos oceanos era determinada por três fatores: clima, composição da água do mar e profundidade (FORBES, 1844). Neste período, as regiões biogeográficas do ambiente marinho eram delimitadas com base na temperatura da água e no grau de isolamento em relação aos continentes (DANA, 1853; WOODWARD, 1856). Ekman (1953) foi o primeiro a definir regiões biogeográficas marinhas baseando-se em características zoogeográficas, barreiras ambientais e níveis de endemismo. De forma semelhante, Briggs (1974) sintetizou e atualizou esta classificação. Em seu trabalho, Briggs classificou áreas com taxas de endemismo maiores que 10% como "Províncias". Ainda hoje alguns trabalhos de biogeografia marinha utilizam taxas de endemismo da fauna para subdividir as regiões, chamando-as "áreas de endemismo" (*e.g*. FLOETER *et al*., 2008).

Em sua primeira classificação, Briggs (1974) sugeriu que a Província Biogeográfica Marinha Brasileira (PMB) tinha sua origem às margens do Delta do Orinoco (Venezuela, ~08°N) e terminava na região de Cabo Frio (Rio de Janeiro, Brasil, ~23°S). Esta extensão advém do fato de que Briggs supôs (erroneamente) que o final da distribuição dos manguezais brasileiros dava-se na região de Cabo Frio, e a ocorrência deste ecossistema é comumente utilizada como um *proxy* para distribuição de biotas tropicais. Baseando-se nos padrões de distribuição de peixes recifais, descritos por Floeter *et al*. (2008), Briggs e Bowen (2012) atualizaram a descrição dos limites da PMB, a qual estende-se por cerca de 8.000 quilômetros ao longo do Oceano Atlântico Sul, englobando uma das maiores zonas costeiras tropicais do mundo (BARROSO *et al*., 2016).

Ao Norte, a PMB é delimitada pela pluma do Amazonas (latitude ~0°), que a separa da Provincia Caribenha. Seu limite sul é mais comumente reconhecido como o estado de Santa Catarina, local onde termina a ocorrência contínua de recifes rochosos, havendo então substituição por substratos inconsolidados ao sul do Cabo de Santa Marta (latitude ~28°S). A PMB engloba uma ampla variedade de ecossistemas marinhos, tendo recifes como um importante aspecto fisiográfico em pelo menos um terço de sua extensão (MAGRIS *et al*., 2021). Ao longo desta vasta e ecologicamente diversa província, múltiplas condições oceanográficas e fatores ambientais podem ser considerados como promotores de padrões de distribuição das espécies (FLOETER *et al*., 2001).

Além do conceito de endemismo, outros fatores são utilizados na idealização de delineamentos e estudos biogeográficos, como variáveis oceanográficas (SPALDING *et al*., 2007), similaridade entre a composição da biota (FLOETER *et al*., 2008; BARROSO *et al*., 2016; TARGINO & GOMES, 2020) e presença de barreiras biogeográficas (LUIZ *et al*., 2012). Tratando da distribuição das espécies, há três principais barreiras que são reconhecidas como elementos determinantes na delineação da PMB: 1) a pluma do Amazonas-Orinoco –um vasto despejo de água doce que separa a PMB do Caribe (LUIZ *et al*., 2012; PAILLER *et al*., 1999); 2) a barreira do Atlântico –3.500 quilômetros de águas profundas e oligotróficas separando a América Equatorial da costa Oriental Africana (BOEHM *et al*., 2013; NUNES *et al*., 2011); e 3) a pluma do Rio da Prata –águas frias provindas do segundo maior rio da América do Sul, que limitam a distribuição de diversas espécies tropicais (AUED *et al*., 2018; PIOLA *et al*., 2005). Estas são as principais barreiras biogeográficas que contornam as fronteiras da PMB, entretanto a área por elas delimitada não é homogênea (Figura 1).

Diversos filtros ecológicos agem sobre a biota da PMB (FLOETER *et al.*, 2001), dentre os quais destacam-se: o deságue de diversos rios (*e.g.* Rio São Francisco, Rio Doce e mais notavelmente o Rio Amazonas, que agregam dinamismo a fatores como turbidez e salinidade); o gradiente de temperatura, e a desconformidade dos substratos ao longo da costa, os quais variam de costões rochosos mais ao Sul (FLOETER *et al*., 2001) até uma considerável cobertura de corais no Nordeste (LEÃO *et al*., 2019). Estes filtros ecológicos estabelecem diferentes graus de influência em cada táxon, dependendo de sua aptidão para ultrapassá-los, de acordo com suas características biológicas intrínsecas.

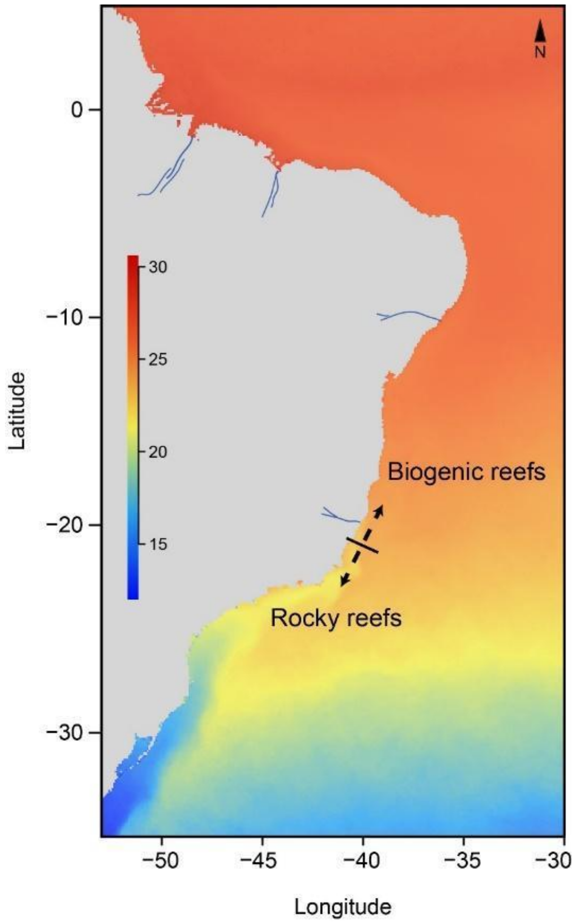

Figure 1: Mapa esquemático demonstrando alguns dos fatores ambientais que sofrem alterações ao longo da PMB. Escala de temperatura representando as temperaturas mínimas em uma escala temporal de 10 anos, advindas de dados de satélite do Bio-Oracle (TYBERGEIN *et al.*, 2012).

Tais fatores ambientais agem influenciando a distribuição das espécies em diferentes padrões ao longo da costa brasileira, o que torna possível realizar subdivisões entre áreas menores e mais similares, como sub-províncias. Embora alguns estudos já tenham considerado variáveis oceanográficas e barreiras biogeográficas para investigar divisões da PMB (Figura 2), estes são em sua maioria focados em um único grupo taxonômico (*e.g.* PALÁCIO, 1982; FLOETER & SOARES-GOMES, 1999; FLOETER *et al.*, 2001; BARROSO *et al.*, 2016; ZELINDA *et al.*, 2019), carecendo uma abordagem integrada, incorporando diferentes táxons no mesmo estudo.

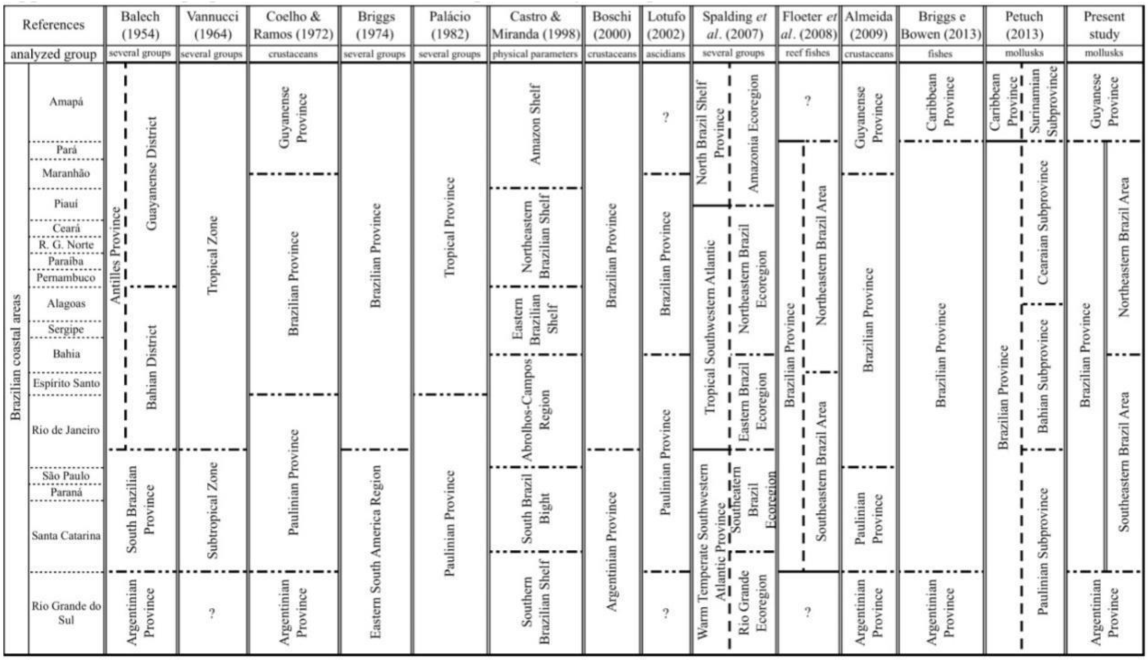

Figure 2: Propostas de delimitação da Província Marinha Brasileira, com seus limites e subdivisões. Fonte: Barroso et al., 2016 (Material suplementar).

Seguindo o princípio de que cada grupo taxonômico possui características próprias, intrínsecas de sua ecologia e fisiologia e associadas à história evolutiva das espécies, estes podem responder de formas distintas às variáveis oceanográficas, barreiras biogeográficas e filtros ecológicos. Desta forma, obter dados quantitativos consistentes sobre a biodiversidade dos locais é essencial, pois possibilita testar hipóteses sobre a distribuição dos organismos (KULBICKI *et al*., 2013). Nós agora temos a oportunidade de utilizar uma robusta matriz multi-táxon para delinear sub-províncias inclusas na PMB, o que nos permite obter resultados provindos de uma gama maior de variáveis bióticas e usufruir das diferenças intrínsecas entre os grupos para melhor demarcar os limites das sub-províncias. No atual cenário de interferências antrópicas ao ambiente marinho, dentre elas as aceleradas mudanças climáticas (BERNARDO-MADRID *et al*., 2019), limites biogeográficos podem tornar-se mais dinâmicos. Neste contexto, estudos como este são importantes para embasar futuras comparações (WORM, 2006; BARROSO *et al*., 2016), além de priorizar ações baseadas na composição das assembleias das espécies (KULBICKI *et al*., 2013).

Neste trabalho, almejamos delimitar sub-províncias incorporadas à PMB e averiguar como variáveis ambientais e barreiras biogeográficas estão relacionadas à distribuição dos organismos recifais. Nós hipotetizamos que os grupos taxonômicos reagiriam de formas distintas às variáveis ambientais, dado sua variedade de características intrínsecas, resultando em diferentes padrões de distribuição. Ademais, acreditamos que certos filtros se manifestariam de forma mais intensa, afetando visivelmente todos os grupos. Para investigar essas hipóteses, nós compilamos dados de distribuição de 2.412 espécies, advindos de *checklists* de nove grupos taxonômicos distintos e rigorosamente supervisionados por especialistas.

Nós então exploramos a similaridade das espécies ao longo de oito intervalos geográficos pré-delimitados, com características ambientais heterogêneas, o que resultou numa divisão da PMB em cinco sub-províncias. Utilizando dados oceanográficos de longo prazo em conjunto com nossa matriz biológica multi-táxon, nós investigamos como filtros ecológicos e barreiras biogeográficas se relacionam à divisão das sub-províncias. Ainda, encontramos padrões distintos de distribuição de espécies, influenciados por barreiras biogeográficas proeminentes.

OBJETIVOS

Objetivo Geral

Explorar subdivisões internas na Província Biogeográfica Marinha Brasileira (PMB) e relacionar tais classificações a fatores ambientais e barreiras biogeográficas presentes na costa do Brasil.

Objetivos Específicos

- Delinear sub-províncias da PMB utilizando as semelhanças entre padrões de distribuição de nove grupos taxonômicos recifais.
- Relacionar a setorização das sub-províncias com fatores ambientais (temperatura da superfície oceânica, salinidade, velocidade das correntes, turbidez da água e tipo de formação recifal) e barreiras biogeográficas presentes (disponibilidade de substrato, deságue de rios caudalosos).
- Averiguar se há ou não uniformidade nos padrões de distribuição dos organismos recifais, e explorar como as variáveis ambientais e barreiras biogeográficas afetam tais padrões.
- Comparar os resultados obtidos com esta abordagem multi-táxon a trabalhos prévios.

CAPÍTULO ÚNICO: Brazilian marine biogeography: a multi-taxa approach for outlining sectorization

To be submitted to Journal of Biogeography

Brazilian marine biogeography: a multi-taxa approach for outlining sectorization

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Abstract

Species distribution patterns are extensively debated in the light of their environmental dependence and historical factors. Early biogeographical studies accounted for abiotic factors and endemism rates to propose the Marine Biogeographical Brazilian Province (BMP), which extends from the Amazon River mouth (latitude 0°) to the Santa Catarina State (28°S). This area encompasses one of the world's largest tropical coasts, stretching for 8,000 km and presenting distinct marine environments. Nevertheless, no study to date introduces a multi-taxa approach to investigate possible biotic distinctions and the role of environmental factors in determining biogeographical patterns in the BMP. Here, we used cluster analysis of five environmental factors to divide the BMP in distinct geographical bins. Thereon, we investigated how nine taxonomic groups (2,412 species) are clustered and calculated beta diversity indexes among sub-provinces. We used a distance-based redundancy analysis (db-RDA) to understand how biogeographical patterns are explained by the environmental similarities among bins. We found eight different geographical bins based on environmental factors, and five intervals considering species composition similarities, which we considered as "sub-provinces". We also observed a latitudinal gradient of species richness for most taxa, some presenting a "mid-domain" shape pattern. Beta diversity among sub-provinces was low, and the nestedness component more important, indicating high connectivity along the BMP. The db-RDA indicated that environmental variables explained 64% of species clustering patterns, with sea surface temperature, water turbidity and current velocity explaining the biotic grouping of the Brazilian Northeast coast. Sub-provinces North and Abrolhos Bank were the most disparate areas regarding both environmental and biotic data. Both regions do not present continuous consolidated benthic substrate but instead have mid-shelf reefs in extensive shallow continental shelves. Moreover, the influence of the Amazon River plume on the North is significant. A multi-taxa approach is a robust model for the understanding of overall biogeographical patterns, as well as its responses to environmental and historical factors.

Keywords: Ecological filters. Marine biogeography. Reef environments. Species distribution.

Introduction

Species diversity and distribution patterns are extensively debated in the light of ecological and environmental aspects (e.g. Ricklefs, 1987; Darwin, 1859; McGill & Collins, 2003; Spalding et al., 2007; Tittensor et al., 2010). Biogeographical studies aim to outline the effect of these processes, as well as historical and evolutionary forces driving biodiversity patterns (Wiens & Donoghue, 2004). Historically, studies linked organisms' distribution and abiotic variables, such as seawater temperature, depth and mainland distance (isolation). Based on these variables, biogeographers primarily divided the marine environment in zones with similar characteristics (Forbes, 1844; Dana, 1853). Ekman (1953) was the first to propose a division of marine regions by using zoogeographical variables, such as endemism and biogeographical filters. Later, Briggs (1974) updated the existing classifications and established marine regions, considering endemism rates as the metric to describe “Provinces”. This is still a valuable concept used in biogeographical studies, often referred to as “areas of endemism” (Floeter et al., 2008).

On his first classification, Briggs (1974) suggested the existence of a Biogeographical Brazilian Marine Province (BMP) extending from the Orinoco Delta (Venezuela, ~08°N) to Cabo Frio (Brazil, ~23°S), where he wrongly assumed was the final distribution of Brazilian mangrove ecosystems (a proxy for the whole tropical biota distribution). Based on reef fish distributions derived from Floeter et al. (2008), Briggs and Bowen (2012) updated the BMP’s limits, which extends for about 8,000 km alongside the South Atlantic Ocean, encompassing one of the world’s largest tropical coastlines (Barroso et al., 2016). The updated BMP is northerly separated from the Caribbean by the Amazon River’s plume and stretches southwards until the rocky reefs of Santa Catarina state (latitude 28°S). The BMP encompasses a wide variety of marine environments throughout its extension, where reefs represent an important physiographic feature in at least a third of the coast (Magris et al., 2021), and many oceanographical conditions can be regarded as drivers for species distribution (Floeter et al., 2001).

Besides the endemism standard, scientists also render biogeographical delimitations based on oceanographical variables (Spalding et al., 2007), species composition (Floeter et al., 2008; Barroso et al., 2016; Targino & Gomes, 2020), and biogeographical barriers (Luiz et al., 2012). Regarding species dispersal, three major biogeographical barriers are recognized to be of greater importance delineating the BMP: 1) the Amazon-Orinoco plume - a vast freshwater discharge which separates the Brazilian Province from the Caribbean (Luiz et al., 2012; Pailler et al., 1999); 2) the deep waters of the Mid-Atlantic Barrier forming a 3,500 km long stretch between equatorial America and the eastern African coast (Boehm et al., 2013; Nunes et al., 2011); and 3) the Plata River's plume - cold waters issuing from the second largest river in South America, which limits the southern distribution of several tropical species (Aued et al., 2018; Piola et al., 2005). These biogeographical barriers outline the BMP, where a large set of environmental variables drive species distributions into different patterns feasible to divide into smaller, more similar areas, like sub-provinces. Although a few studies have already considered oceanographical variables, along with biogeographical barriers, to investigate divisions within the BMP, they are mostly focused on single taxonomic groups.

Because each taxonomic group possesses their own set of biological characteristics and distinct evolutionary histories, they can respond differently to distinct oceanographical variables, biogeographical filters and barriers. Hence, it is important to obtain consistent quantitative data on the local biota in order to better understand its distribution (Kulbicki et al., 2013). We now have the opportunity to utilize a robust multi-taxa matrix to delineate sub-provinces' limits, which allows us to obtain results with a larger selection of biotic variables. Biotic variables of different taxonomic groups also present distinct characteristics, which is important to help better delineate sub-provinces limits. Anthropic activities have been aggregating elements of dynamism to biogeographical limits, because of effects on environmental characteristics and species distributions (Bernardo-Madrid et al., 2019; Worm et al., 2006). In this context, multi-taxa studies are crucial in order to establish future comparisons between distribution patterns (Barroso et al., 2016).

In this study we aimed to delineate sub-provinces within the BMP and assess how environmental variables and known biogeographical barriers relate to the distribution of reef organisms. Each taxonomic group possesses a wide array of intrinsic characteristics which might produce distinct ecological and physiological responses. Consequently, we hypothesized that taxonomic groups would react differently to environmental variables, resulting in distinct distribution patterns. We anticipate that some filters will strongly affect all organisms, sturdily driving the biogeography of the entire Brazilian marine biota.

To investigate such propositions, we compiled the largest distributional multi-taxa dataset ever created in the southern Atlantic, comprising 2,412 shallow reef species (up to 50 m), belonging to nine different taxonomic groups (algae, anemones, corals, anomurans, true crabs, lobsters, prosobranchs, elasmobranchs and reef fish). We then investigated species similarity patterns along pre-delimited geographical bins with distinct environmental variables, which resulted in five sub-provinces. By using long-term abiotic data along with our multi-taxa dataset, we assessed how ecological filters and biogeographical barriers relate to our five sub-provinces. Moreover, we revealed distinct patterns of species distributions influenced by prominent biogeographical filters.

Materials and methods

Geographical bins delineation

We divided the Brazilian Province in eight different geographical bins according to their environmental similarities (Fig. 1). Although, geopolitically, the Brazilian coast extends until latitude 33°45’03", we established the Santa Catarina state (28°S) as the southern limit of our study area due to the subsequent substitution of rocky reefs by unconsolidated substrate south of this region. To divide the MBP, we used long-term continuous data of five environmental variables obtained from Bio-Oracle (Tyberghein et al., 2012) on a temporal scale of 10 years: sea surface temperature (minimal SST in °C), minimal diffuse attenuation (proxy for water turbidity/m), salinity (minimal ppm), current velocity (maximal; m/s) and primary production (as maximum carbon phytoplankton biomass; ¾mol/mŸ). Besides these continuous variables, we categorized the reef environments as “Biogenic/Sandstone” or “Rocky” according to primary substrate formation; coastal shelf width (km) was estimated for each biogeographical bin based on a mean value of three haphazardly chosen distances from the coastal line to the shelf slope (i.e. ~200 m deep). To avoid oceanographical interferences and lack of sampling in deeper habitats we considered marine environmental data representative of depths between 10 to 200 m deep (Fig. 1). Environmental variables were chosen based on their capacity to explain marine biodiversity patterns and processes as well as their influence on organisms physiology and ecology (e.g. Ellis et al,. 2019; Targino & Gomes, 2020; Coles & Jokiel, 1992; Barroso et al., 2016; Hochberg et al., 2020; Harvey et al., 2013; Curry, 2020). All variables were previously submitted to correlation tests to avoid high correlation.

Although the four Brazilian oceanic islands belong to the Brazilian Province (Barroso et al., 2016; Floeter et al., 2008; Pinheiro et al., 2018), we excluded them from our analysis due to their small size, high isolation and lack of biotic data for some of the taxonomic groups.

Multi-taxa clustering

For each geographical bin we gathered presence (1) or absence (0) data for nine major taxonomic groups, encompassing 2,412 reef species, by researching published papers (e.g. Barroso et al., 2016; Targino & Gomes, 2020; Pinheiro et al., 2018), regional checklists (e.g. Dutra et al., 2006; Torrano-Silva & Oliveira, 2013) and "grey literature" (unpublished thesis and other academic sources strictly and previously validated by us), double-checked with online databases. The nine taxa (algae, anemones, corals, anomurans, true crabs, lobsters, prosobranchs, elasmobranchs and reef fish) were chosen based on their close dependence on reef environments and well-established taxonomy. Here, we consider as "reef associated taxa" species that possess a known direct or indirect relationship to hard substrates. Depth range of all species distributional records varied between 0 and 50 m. Invasive, introduced and cryptogenic species were not included in our dataset. All matrices resulting from such compilations (see Supplementary Material 1) were revised by specialist researchers on each of the taxonomic groups.

Statistical analysis

To delineate the geographical bins according to their mean environmental variables we used bootstrapped cluster analyses (999 replications), performed with Euclidean distance matrix and UPGMA. Data were transformed by standardization to decrease data dispersion. To verify the similarities among geographical bins based on the distribution of all taxa, as well as for each of the taxonomic groups separately, we also performed bootstrapped cluster analyses (999 replications) with Sørensen similarity coefficient and UPGMA. We calculated biotic dissimilarities between sub-provinces as the change in species composition between places (see Baselga, 2010; Mittelbach & McGill, 2019) using the two components of beta diversity partitioning (i.e. turnover and nestedness) with the package "*betapart*" (Baselga et al., 2020). To understand the influence of environmental variables on species distribution across the Brazilian geographical bins, we performed a distance-based redundancy analysis (dbRDA), using the Kulczynski distance matrix. We tested environmental variables collinearity though the *vif* function. Subsequently, we used analyses of variance (ANOVA) to test for significance of the general effect, the canonical axes (999 replications), and the environmental variables (999 replications). All analyses and graphics were performed in the R software (R Core Team, 2020) using the packages: "*pvclust*" (Suzuki & Shimodaira, 2006), "*ggplot2*" (Wickham, 2011), "*raster*" (Hijmas, 2020), "*sdmpredictors*" (Boch, 2020) and "*vegan*" (Dixon, 2003).

Results

Geographical bins delineation

We identified eight different geographical bins along the BMP, considering the environmental variables, each encompassing about 2 degrees of latitude (Fig. 1). The northernmost bin (N_NE), which initiates on the Amazon's River mouth, is characterized by an extensive continental shelf (mean 114.49 km) and high sea surface temperatures (averaging 27.3 °C). The three subsequent bins (NE1, NE2 and Bah) possess a shorter coastal platform (mean widths 53.79, 50.8 and 19.57 km respectively), warm waters (averaging 26 °C) and shallow reefs built by sandstone covered by biogenic elements (i.e. "Biogenic/ Sandstone reefs") such as bryozoans, coralline algae and vermetids (Leão et al., 2016; Testa & Bosence, 1999). The São Francisco River mouth separates the bins NE2 and Bah.

Another important brazilian river, Rio Doce, is located between the Abr and SE bins. The Abr bin is composed of the biogenic reefs of the Abrolhos Bank, where the BMP reaches its maximum shelf widths (mean 164 km). Abrolhos' waters are warm (24.64 °C) and shallow, and represent the only site in Brazil where biogenic reefs are mainly constructed by bryozoans and cnidarians (Leão & Kikuchi, 2001). The Vitoria-Trindade seamount chain, which potentially shifts the Brazilian Current's course (Napolitano et al., 2020), is another prominent oceanographic feature South of the Abrolhos Bank, also encompassing the northern portion of the next bin, SE.

The SE coastal platform shortens (58.9 km) after the enlargement observed in the Abrolhos Bank, and there's the seasonal influence of upwelling events, which bring colder waters to the surface (Valentin, 2001), averaging 22.37 °C during the winter. The SE bin is also characterized by a substantial reduction of biogenic/sandstone reefs and the absolute dominance of rocky reefs (Floeter et al., 2001). The SE_S bin is composed solely of rocky reefs with slightly lower sea surface temperatures (21 °C) and a coastal platform that is ~100 km wider than the platform observed in the SE bin. The continental shelf in the southernmost bin, S, is in average 92.28 km wide. It represents the final occurrence of rocky reefs in Brazil, with the lowest absolute minimal sea surface temperatures predominant during the winter (17.5 °C).

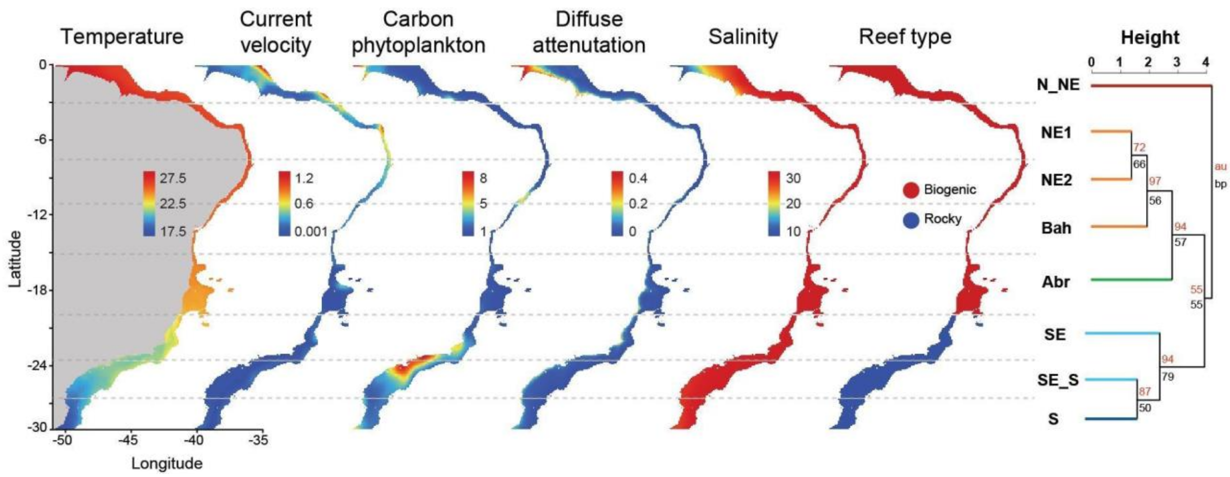

Figure 1: Large scale oceanographic and environmental features along the Brazilian Marine Province: minimal sea surface temperature (°C), maximal current velocity (m/s), maximum carbon phytoplankton biomass (¾mol/mŸ), minimal diffuse attenuation (/m), minimal salinity (ppm), and reef type. Bootstrapped cluster analyses showing no significant grouping among the geographical bins. Red numbers represent approximately unbiased *p*-values ("au"), black numbers show the bootstrap probability value ("bp") for each cluster. Dendrogram branches are colored according to the species similarity results (see Fig. 2). Acronyms in the dendrogram refer to the eight environmentally distinct geographical bins: North/ Northeast (N_NE); Northeast 1 (NE1); Northeast 2 (NE2); Bahia State (Bah); Abrolhos Bank (Abr); Southeast (SE); Southeast/ South (SE_SE) and South (S).

Biotic affinities

We found five sub-provinces grouped according to the multi-taxa clustering. The NE1, NE2 and Bah geographical bins formed one single sub-province (the Northeast sub-province), as well as SE with SE_S (the Southeast sub-province; Fig. 2). The remaining three geographical bins (N_NE, Abr, and S) remained as unique sub-provinces (North, Abrolhos Bank, and South sub-provinces, respectively). Species richness varied considerably among biogeographical bins, but a cohesive proportion of contribution is maintained to each taxonomic group, as represented by the colors in the bar plot. Highest values of species richness are found between the states of Bahia (southern limit of Northeast sub-province) and Rio de Janeiro (center of Southeast sub-province; Fig. 2).

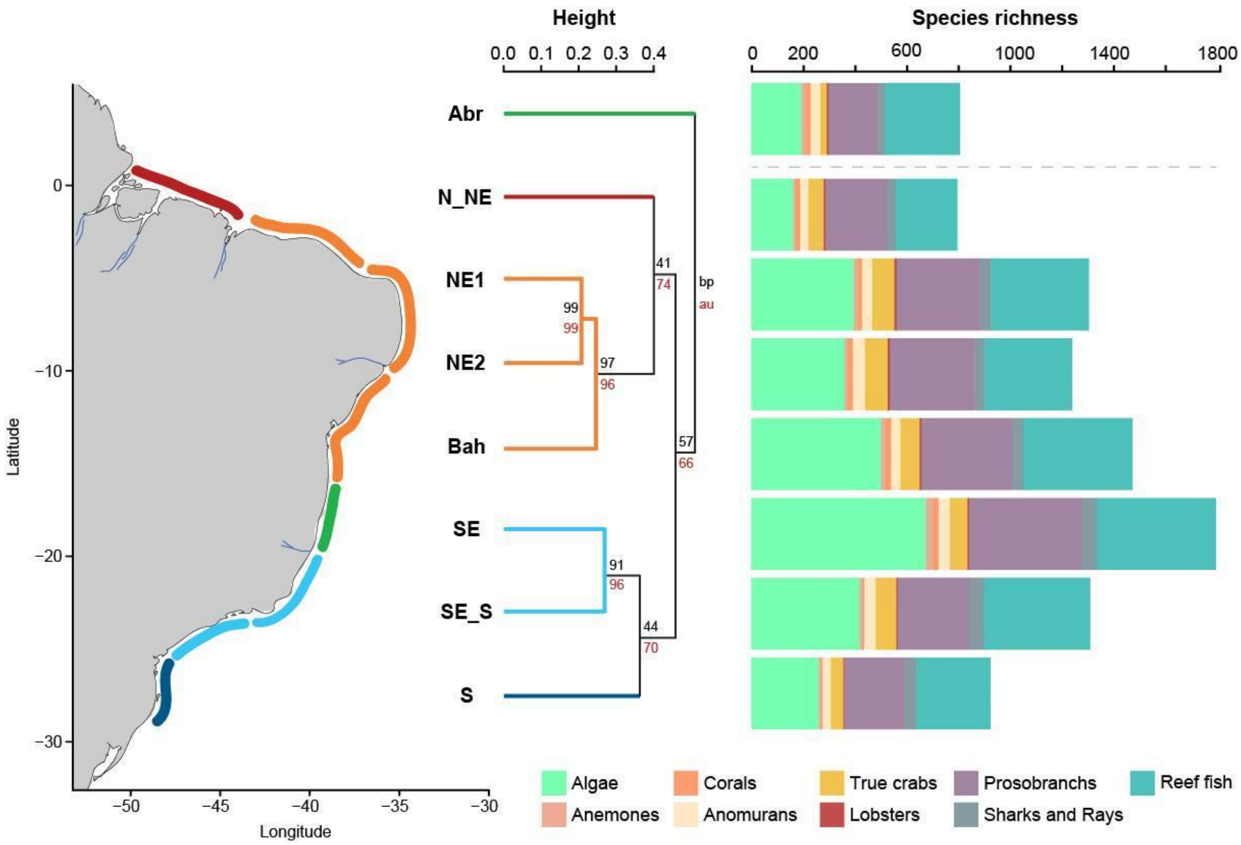

Figure 2: Bootstrapped cluster analyses, using Sørensen dissimilarity ("Height") and UPGMA, showing species grouping considering geographical bins. Map and dendrogram branches are colored according to sub-provinces (significant groups). Red numbers represent approximately unbiased *p*-values ("au"), black numbers show the bootstrap probability value ("bp") for each cluster. Acronyms in the dendrogram refer to the eight environmentally distinct geographical bins: North/ Northeast (N_NE); Northeast 1 (NE1); Northeast 2 (NE2); Bahia State (Bah); Abrolhos Bank (Abr); Southeast (SE); Southeast/ South (SE_SE) and South (S). Bar plot for taxonomic richness showing the contribution of each taxon to the absolute number of species recorded on each geographical bin. Species richness in the Abrolhos Bank (Abr) is shown out of its geographical position to match the respective dendrogram branch.

Neighboring sub-provinces displayed low dissimilarity, with nestedness being the major component of beta diversity along the BMP (Fig. 2). The highest levels of turnover occurred between the Abrolhos Bank and Southeast sub-provinces.

Cluster analysis of each taxonomic group presented similar results to the multi-taxa approach (Fig. 2). Sharks & Rays, Lobsters, Corals and Prosobranchs showed a clear division between colder and warmer sea surface temperatures.

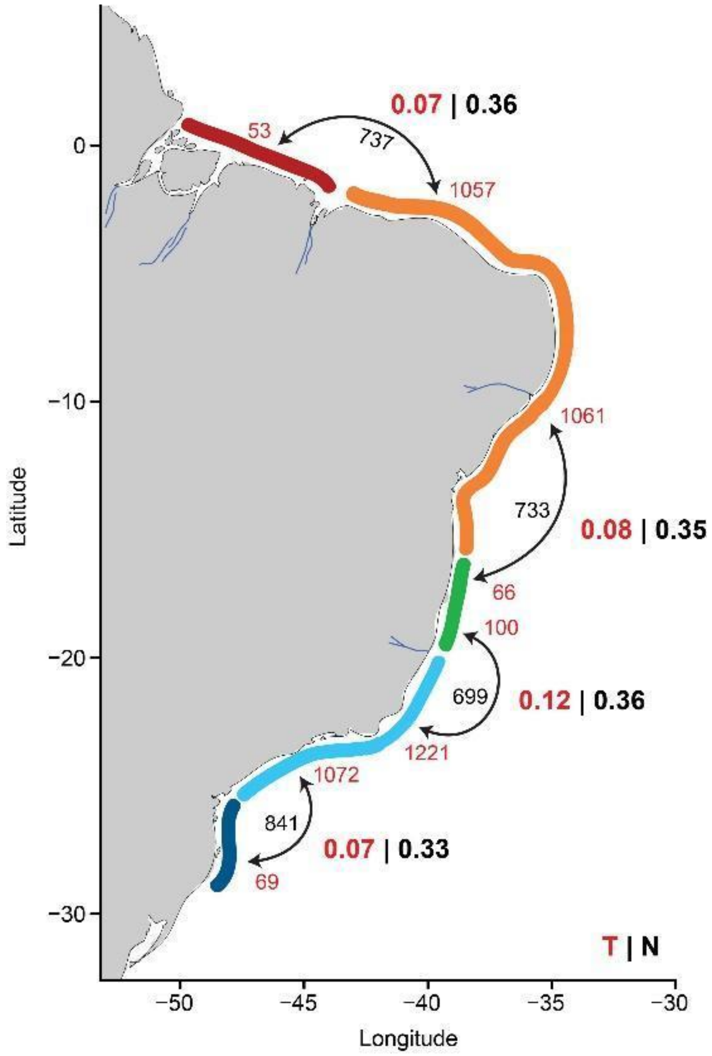

Figure 3: Dissimilarity components among Brazilian marine sub-provinces. Three Northeastern geographical bins (NE1, NE2 and Bah) and two Southeastern bins (SE and SE_S) are merged forming two sub-provinces according to the multi-taxa cluster results (see Fig. 2). Red and black bold numbers indicate species turnover and nestedness, respectively. Red numbers close to the arrowheads represent the number of unique species (i.e. species present in a sub province that are absent in its neighbor). Black numbers under the arches represent the shared number of species between adjacent sub-provinces.

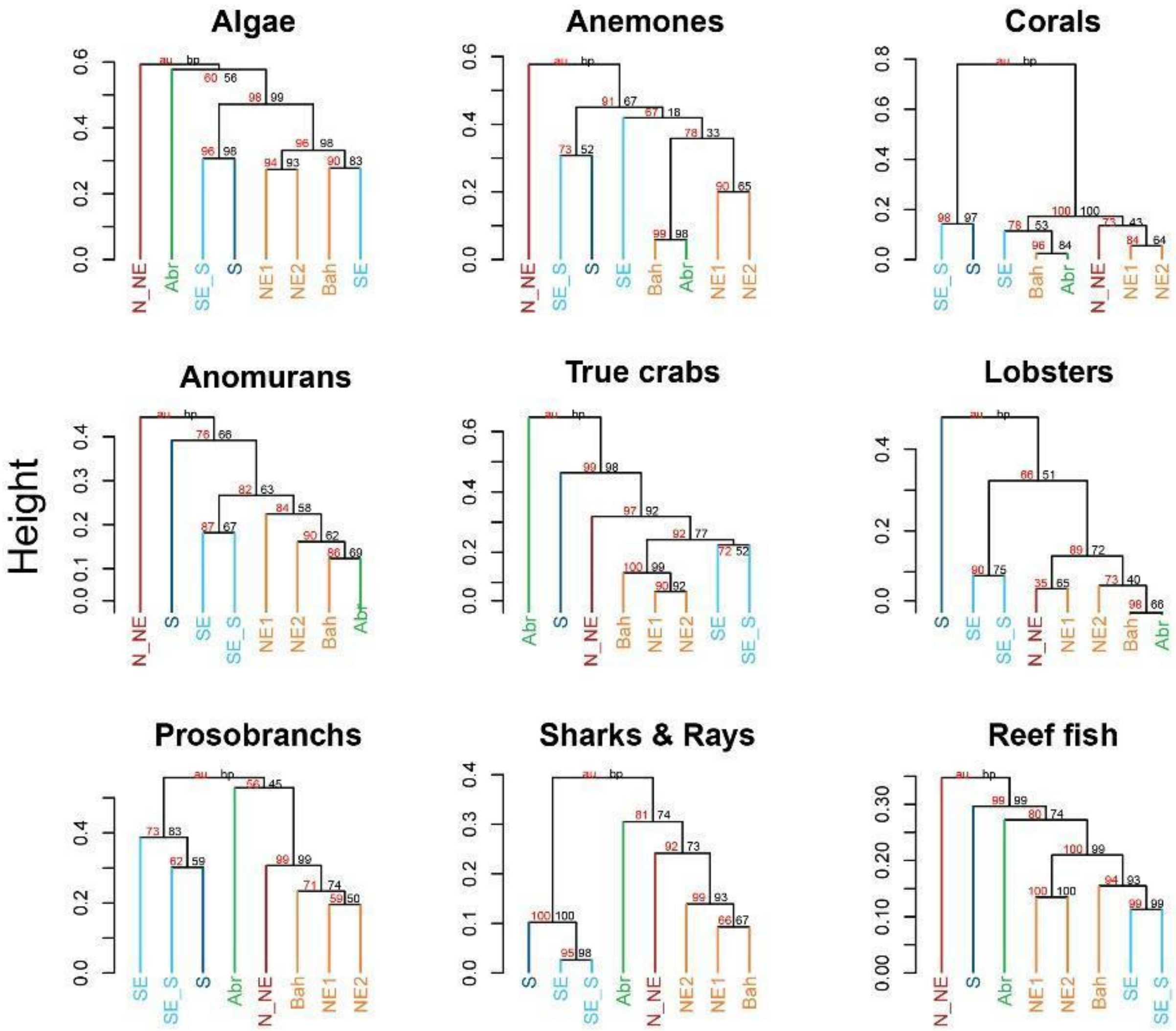

Figure 4: Cluster analyses for each Brazilian marine taxonomic group according Sørensen dissimilarity "Height" (UPGMA clustering algorithm). Colors represent the sub-provinces found using all taxonomic groups together (see Fig. 2). Acronyms in the dendrogram refer to the eight environmentally distinct geographical bins: North/ Northeast (N_NE); Northeast 1 (NE1); Northeast 2 (NE2); Bahia State (Bah); Abrolhos Bank (Abr); Southeast (SE); Southeast/ South (SE_SE) and South (S).

The environmental variables current velocity (CV), sea surface temperature (SST) and diffuse attenuation (DA) were significant in explaining the species and sub-provinces grouping ($R^2 = 0.64$). Reef type and shelf width were collinear and consequently excluded from the db-

RDA analyses, while salinity and phytoplankton biomass (PHYTO) were not significant (Fig. 5).

We also found a significant explanatory power for the first canonical axis (db-RDA axis 1), revealing a more prominent division between North/Northeast and South/Southeast. Observing the taxonomic groups individually, we identified a higher richness in the region encompassing Bahia and Rio de Janeiro states (Fig. 5). Most groups were well distributed across all sub-provinces, but Corals and Lobsters showed a classical tropical pattern, highly influenced by sea surface temperature. Anemones reached peak diversity in the Southeast sub-province.

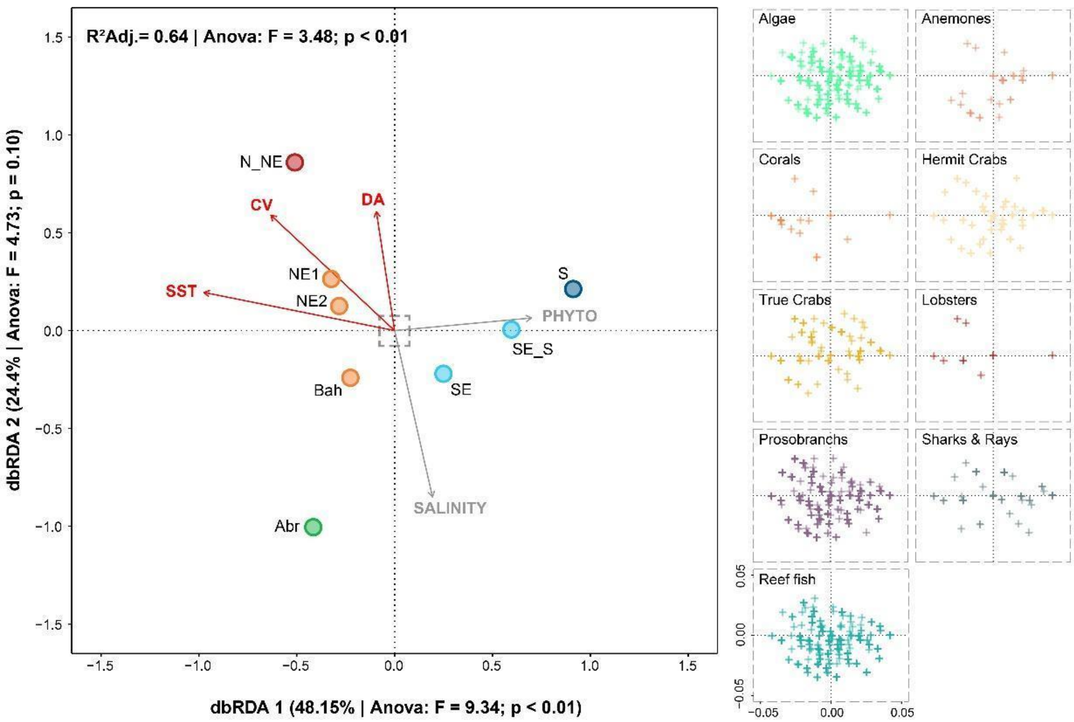

Figure 5: Distance based redundancy analysis (db-RDA) showing environmental variables (CV = current velocity; SST = sea surface temperature; DA = diffuse attenuation; PHY = phytoplanktonic biomass; SALINITY= salinity) influence over the Brazilian sub-provinces. Red arrows show statistically significant variables (p <0.05), while grey arrows were not significant when explaining species distributions along the BMP. Acronyms along with colored circles refer to the eight environmentally distinct geographical bins: North/ Northeast (N_NE); Northeast 1 (NE1); Northeast 2 (NE2); Bahia State (Bah); Abrolhos Bank (Abr); Southeast (SE); Southeast/ South (SE_SE) and South (S). Dashed squares on the right represent the db-RDA species score for each taxonomic group separately. The dashed square in the center of the db-RDA corresponds to the scale in which the species scores are presented.

Discussion

Considering our multi-taxa approach, the BMP is divided into five sub-provinces: North, Northeast, Abrolhos Bank, Southeast and South. Species distribution across these sub-provinces are influenced by sea surface temperature, current velocity and water turbidity, which were the main environmental forces driving this sectorization. Besides these variables, other historical, evolutionary and ecological forces can also play a role in shaping species distribution along the BMP, like the three main biogeographical barriers which separate this Province from other oceanic areas (the Amazon River, the Mid-Atlantic Barrier and the Plata River).

Sea surface temperature is the main factor accounting for marine biota regionalization recognized since Dana (1853), and it outstandingly influenced all our studied taxonomic groups. The latitudinal gradient of richness is one of the most well-known large-scale biodiversity patterns (Willig et al., 2003), being largely influenced by temperature for several taxa (Kerswell, 2006; Macpherson 2002; Parravicini et al., 2013). For example, many species show distributions restricted to the tropical areas of BMP, like the fish *Haemulon squamipinna*, the fire-coral *Millepora braziliensis*, the hermit-crab *Dardanus fucosus* as well as the gastropods *Lebrunia neglecta* and *Conus mauricioi*. This pattern can also be noted in taxa not included in our study, like the endemic sponges *Aplysina solangeae* (Pinheiro et al., 2007) and *Sigmaxinella cearense* (Salani et al., 2006), both occurring exclusively in the warmer waters of North and Northeast sub-provinces.

Despite some species showing typically tropical distributions, our multi-taxa results point to an inverse pattern of increasing species richness from tropical to subtropical regions. Latitudinal gradients are known to be influenced mainly by three non-exclusive aspects: ecological, evolutionary and historical processes, as discussed in Cruz-Motta et al. (2020), and a few other studies have shown similar patterns to what we unrevealed here (e.g. Chaudhary et al. (2016) in a global scale, and Aued et al. (2018) for Brazilian benthic communities). We found the highest values for species diversity among the intermediate latitudes of Bahia and Rio de Janeiro (geographical bins “Bah” and “SE”; Fig. 2). This area, encompassed by the southern limit of Northeast and north of Southeast sub-provinces, function as an ecotone, sharing great diversity and heterogeneity of habitats, which is related to a greater species richness (Bell et al., 1991). The aforementioned regions present many embayments, with continuous fractal shore lines. Also, between these sub-provinces, sea surface temperature allows an overlap of typically tropical and subtropical organisms, thus increasing diversity. The

North and South sub-provinces present a higher endemism rate, compared to mid-latitudes, perhaps indicating a "mid-domain effect" in the BMP.

Ocean circulation patterns may also support the accumulation of species around mid-latitudes (i.e. "Bah" and "SE" bins) due to the influence of the South-Equatorial Current (SEC; Floeter et al., 2001). The SEC splits into two branches between 5 and 10° S before running southwards as the Brazilian Current (BC; Araújo et al., 2020). The joining of the warm waters of the BC and cold waters, subjected to the influence of upwelling events in the SE, may allow the coexistence of tropical and subtropical species. Currents can also be important drivers for species dispersal during their pelagic larvae stage (Bowen, 2006, Cowen & Sponaugle, 2009). Some pelagic larvae lack swimming abilities and might be driven into a barrier, like a river, which might hinder dispersion with an input of brackish water, or simply an increase in turbidity (Mulder & Syvitski, 1995). Water turbidity was shown to be another key element on species distributions along the BMP, which relates to the presence of many large streams like the São Francisco and Rio Doce rivers.

Freshwater discharges from rivers can affect salinity levels and are known sources of nutrients and sediment for coastal reefs (van Dam et al., 2011). These elements can constrain marine species dispersion, especially during pelagic larval stages, when some organisms decrease survival when exposed to brackish water (Sastry & Bliss, 1983; Sheppard et al., 2018). We observed a general break among geographical bins "NE2" and "Bah" for Anemones, Lobster, Anomurans and Corals (Fig. 2), what could perhaps be a signal of the São Francisco River acting as a filter for species dispersal (Peluso et al., 2018, Souza et al., 2017) since this river's mouth is bounded by these two geographical bins. Water turbidity is a determinant agent for many other benthic organisms (Uthicke et al., 2010), and benthic composition can also be important in determining the presence or absence of other organisms since there are many close relations observed (e.g. interactions between fish and the benthos; Bellwood et al., 2014).

In addition to these environmental variables and biogeographic barriers, the coastal areas of North and Abrolhos Bank sub-provinces are dominated by mangroves, with the absence of suitable consolidated substratum (biogenic or rocky reefs) can hinder dispersal, limiting the connectivity between areas (Scheltema, 1968, 1995). The lack of shallow continuous coastal reef formations can explain the low richness we found for all taxonomic groups in the North sub-province, composed mostly of mesophotic reefs with the presence of a parcel with mid-shelf characteristics (Cordeiro et al., 2015) and also in the Abrolhos Bank (Fig. 2). Contrastingly to our study, the latter is commonly perceived as a rich site for many benthic organisms (with the occurrence of essentially all Brazilian coral species), perhaps because Abrolhos reefs are structurally complex, mainly built by bryozoans and cnidarians (Bastos et al., 2018; Miloslavich et al., 2011). Rhodolith beds (i.e. aggregations of unattached calcareous nodules composed of crustose, benthic marine red algae) are the main contributors to the "flora" of Abrolhos (Brasileiro et al., 2016). Such environments are dynamic given the mobility of Rhodolits (Foster, 2001), which can present some difficulties for colonization for macro and megafauna, reducing overall richness in these environments in comparison to other vast stretches of rocky bottoms.

Large, continuous, consolidated coastal environments harbor a large algal diversity (Kerswell, 2006). Macroalgal assemblages have an effect on other levels of communities (Lubchenco & Gaines, 1981), both as primary producers and habitat constructors for a diverse benthic fauna (Santelices et al., 2009), which may also be related to the availability of smaller scale spatial refuges within the reef (Poray & Carpenter, 2014; Charton & Ruzafa, 1998). Differently from richer areas (Northeast and Southeast sub-provinces), the Abrolhos Bank's platform is shallow and wide, being where the BMP reaches its maximum shelf widths (245 km; Floeter et al., 2001), creating a relatively impoverished habitat seascape, which links to a depletion in species richness (Bell et al., 1991). Additionally, the combination of Abrolhos sedimentation (i.e. siltation; Segal & Castro, 2011), which causes anoxic soft bottoms that intertwine the coral pinnacles; and a large continuously shallow platform (i.e. lacking upwelling intrusions) makes for a less suitable environment for a great portion of reef biota. Also, the highest turnover contribution to the beta diversity indicates lower connectivity between the Abrolhos Bank and the adjacent, richer, sub-provinces (Fig. 3).

In the last 16,000 years, sea levels had relevant oscillations in orders of more than 130 m below present stands (Milliman & Emery, 1968). During glacial periods a portion of ocean waters is retained in polar caps, which reflects in sea level regressions (Lambeck et al., 2014) and may alter the availability of reef habitats, especially shallow ones. The majority of the Abrolhos Bank's wide and shallow platform was above ocean level during glacial periods (Passos et al., 2001), this scenario could suggest a decline in habitable reef areas and populations, leading to local extinctions of many reef groups (Smith & Monk, 2001) contributing to the richness patterns found in this study. With shorter coastal platforms the Northeast sub-province (formed by the "NE1", "NE2" and "Bah" geographical bins), could have had a better resilience during glacial events. These bins also share similar reef formations and sea surface temperatures year-round.

The rocky reef formations and lower mean temperatures are the most important features of the Southeast sub-province. The influence of colder waters during upwelling events brings up large amounts of nutrients (Valentin, 2001), related to the higher average phytoplanktonic biomass found in this area (see Fig. 1). Apart from seasonal upwelling events, the prevailing colder temperatures are found in the South sub-province during winter, which marks the transition of a more tropical to a sub-tropical regime. The South marks the southern limit of distribution for typical mangrove ecosystems (Ximenes et al., 2018), as well as widely distributed corals (Capel et al., 2012) and many other tropical organisms in the Atlantic Ocean (e.g. Anderson et al., 2015; Giraldes & Freire, 2015; Padula et al., 2011). In agreement with our results, we observe that all taxonomic groups present examples of species with distributions restricted to the subtropical sub-provinces (Southeast and South), like the gastropod *Caecum eliezere,* the anemone *Bunodosoma caissarum*, the hermit-crab *Paguristes pauciparus* and the reef fish *Paraclinus spectator*. The sponges *Aplysina caissara* (Pinheiro & Hajdu, 2001) and *Petromica citrina* (Monteiro & Muricy, 2004) and nudibranchs *Tambja brasiliensis* and *Roboastra ernsti* (Pola et al., 2014) also occur exclusively in these sub-provinces, indicating the patterns we found in this study could also extend to other taxonomic groups.

Along the BMP, an area bounded by the latitudes 0° and 28° S (Briggs & Bowen, 2012), composed of a combination of tropical and subtropical biotas (Aued et al., 2018; Bouzon & Freire, 2007), biogeographical filters act as barriers with different effectiveness to the distribution of distinct taxonomic groups (e.g. Barroso et al., 2016; Mandai et al., 2018; Pinheiro et al., 2018; Peres & Mantelatto, 2020; Targino & Gomes, 2020). Although physiological and ecological discrepancies between taxa were expected to bring a certain divergence among distribution patterns, we were still able to discover a consistent, statistically supported, pattern when analyzing all groups simultaneously. Our delineation of subdivisions within the BMP is concordant with Castro & Miranda (1998) oceanographical study, based on physical variables. These authors nominated fewer distinct areas within the BMP, but with overall similar limits to the sub-provinces we presented here. Several previous studies also proposed comparable divisions based on singular taxa (e.g. Almeida, 2009; Barroso et al., 2016; Floeter et al., 2008; Garcia et al., 2007; Petuch, 2013). Noticeably, a significant number of propositions show a division close to the latitudes around Rio de Janeiro (where the upwelling influence begins), essentially separating the Brazilian coast in more typically tropical and subtropical areas (e.g. Almeida, 2009; Balech, 1954; Floeter & Soares-Gomes, 1999; Vannucci, 1964)

Spalding et al. (2007) included the BMP in their global study where "Ecoregions" are defined as areas of relatively homogeneous species composition, conceptually comparable to our sub-provinces. The aforementioned study portrays the areas corresponding to Southeast and South sub-provinces as "Warm Temperate Southwestern Atlantic". Based on our results and specific literature for each taxon, which shows warm temperate biotas differ from the BPM (e.g. Barroso et al., 2016; Pinheiro et al., 2018; Targino & Gomes, 2020), we suggest these two sub-provinces belong to a subtropical region and are not analogues to the Argentinian Province. In addition to the clear distinctions observed in the biotas, intrinsic differences in environmental factors such as sea surface temperature and substrate availability (Boschi, 1979, 2000) also differ between the areas presented in our study and the Argentinian Province.

Our work highlights the importance of describing more consistent and reliable species distributions instead of blindly grabbing information from extensive, but many times inaccurate, online sources (Robertson, 2008). In addition, we argue in favor of combined multi- and representative taxon analysis as a consistent baseline to support biogeographical proposals. This is essential to discover concomitant patterns, allowing us to identify processes that might have generated them. Such data is obtained throughout the years by the means of checklists and supported by taxonomists and museum collections (McNeely, 2002). Advancing this knowledge is of the most importance, as it lays the foundation for studies in varied scientific disciplines, such as ecology and biogeography (Stork & Samways, 1996). The amount of available biotic data varies considerably among regions and taxonomic groups (Garcia et al., 2007) which can pose a barrier for multi-taxa and broad-scale studies (which generally differs in their sampling approaches).

We were able to overtake such difficulties by forming a solid network of collaborators and relying on previous compilations of species distributions and temporal environmental data, which is also crucial when working towards a broader understanding of marine biota assemblies. Without such collaborations and precursory information, it would not be feasible for us to perform this study in its current biogeographic and taxonomic proportion.

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Data availability statement

Data and R codes will be publicly available at the Zenodo platform after publication, but, upon the Editor's request, we would be glad to share the data privately with reviewers during the peer-review process.

Conflict of interest

We declare that there is no conflict of interest.

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CONCLUSÃO GERAL

Considerando nossa abordagem multi-táxon em águas rasas e recifais, a BMP divide-se em cinco sub-províncias: Norte, Nordeste, Banco dos Abrolhos, Sudeste e Sul. A distribuição das espécies dentre as sub-províncias é influenciada principalmente pela temperatura da superfície oceânica, velocidade das correntes e turbidez da água. Além disso, outras forças históricas e evolutivas desempenham importantes papéis como motoras da distribuição da biota da BMP, como as três principais barreiras biogeográficas que delimitam esta Província (Rio Amazonas, Barreira do Atlântico e Rio Da Prata).

A temperatura, um fator reconhecido desde os primórdios das tentativas de setorização do ambiente marinho (DANA, 1853), foi o principal fator que influenciou os grupos taxonômicos estudados. Algumas espécies possuem distribuições restritas a áreas de águas mais quentes, e isso pode ser visto em algumas análises multivariadas realizadas individualmente entre os grupos (Figura 6). Lagostas, prosobrânquios e elasmobrânquios, por exemplo, mostram claras divisões entre intervalos geográficos de águas mais frias e mais quentes. Observamos também uma “quebra” de distribuição entre os intervalos “NE2” e “Bah” para Anêmonas, Lagostas, Anomuros e Corais (Fig. 2 e Fig. 6), o que pode indicar que o Rio São Francisco age historicamente como um filtro para a dispersão destes organismos (PELUSO *et al*., 2018, SOUZA *et al*., 2017), pois este rio deságua na divisa entre estes intervalos geográficos.

O Banco de Abrolhos, região mais rica em corais na PMB (MILOSLAVICH *et al*., 2011), mostrou-se frequentemente isolado nas análises de agrupamento e com baixa riqueza geral. Formou assim singularmente uma sub-província com características próprias notáveis, dentre as quais: rodolitos como principais componentes de sua “flora” (BRASILEIRO *et al*., 2016), sedimento anóxico que intermeia os pináculos recifais (SEGAL & CASTRO, 2011) e uma plataforma rasa e com a maior extensão dentre a costa brasileira (245 km; Floeter et al., 2001), o que influencia na ausência de ressurgência na região. A sub-província Norte também demonstrou possuir baixa riqueza, o que pode estar relacionado a algumas características por ela compartilhadas com o Banco dos Abrolhos: recifes com características de “*mid-shelf*”, ou seja, ausência de recifes costeiros e depleção de substrato consolidado.

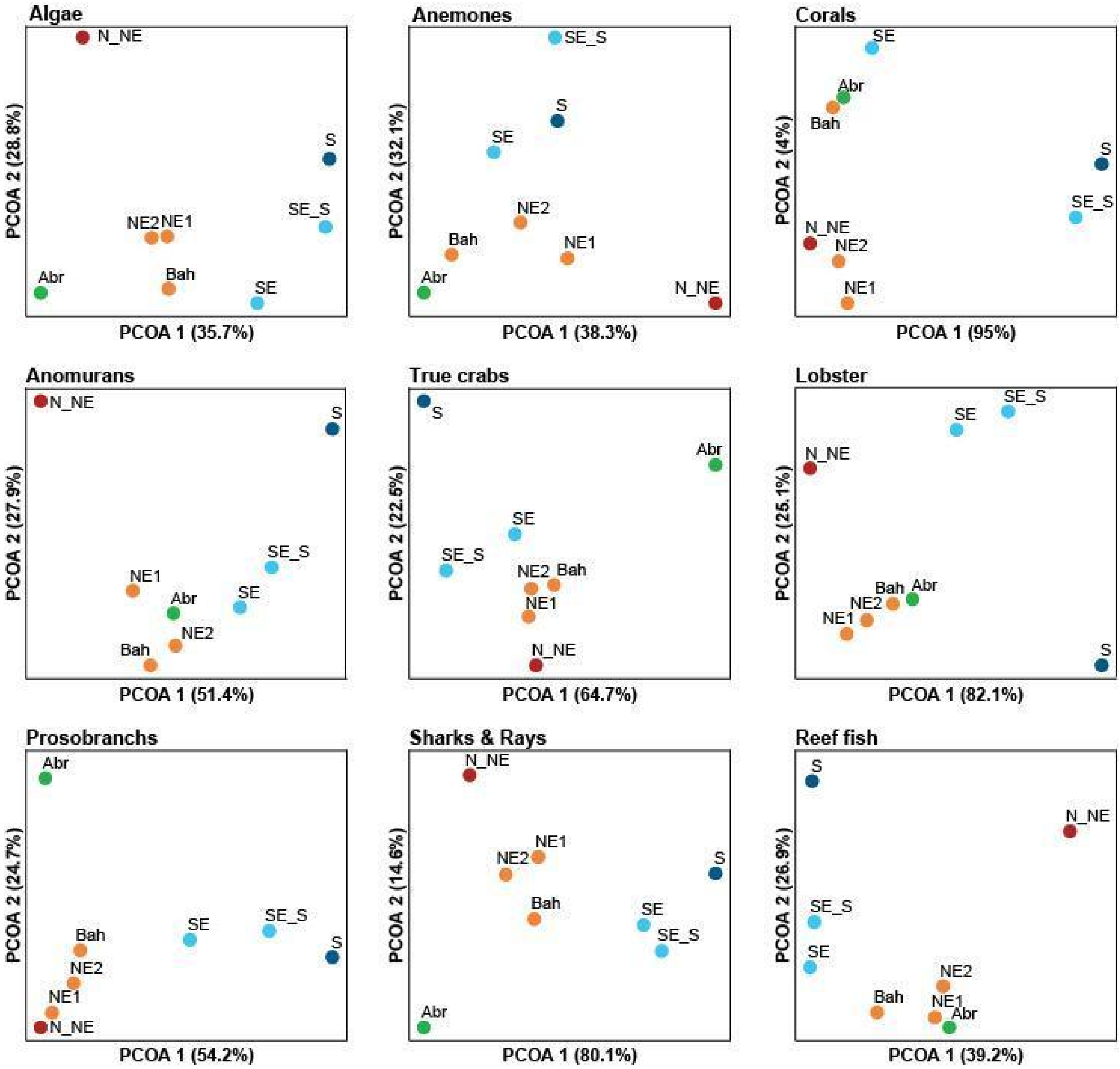

Figure 3: Análise de coordenadas principais (índice de dissimilaridade de Sørensen) demonstrando os agrupamentos dos intervalos geográficos em relação à similaridade de espécies. Cores dos intervalos representam as sub-províncias às quais estes pertencem.

A maior riqueza foi observada entre os Estados da Bahia e do Rio de Janeiro, o que pode ser consequência de diversos fatores que juntos tornam esta área ideal para uma sobreposição de faunas tipicamente tropicais e subtropicais. A sub-província Sul é o limite de distribuição de diversas espécies tropicais pois possui a menor média de temperaturas durante o inverno, um fator limitante.

Apesar das diferenças fisiológicas e ecológicas dentro dos grupos taxonômicos, neste estudo encontramos padrões consistentes, estatisticamente comprovados, que nos levaram a definir estas cinco sub-províncias. Nossa delineação está de acordo com o trabalho de Castro & Miranda (1998), baseado em variáveis físicas, e também se assemelha aos resultados de diversos autores que utilizaram grupos taxonômicos singulares (*e.g.* ALMEIDA, 2009; BARROSO *et al*., 2016; FLOETER *et al*., 2008; GARCIA *et al*., 2007; PETUCH, 2013). Embora o estudo global de Spalding et al. (2007) tenha enquadrado boa parte da PMB em uma zona "temperada quente", nossos estudos, assim como a literatura específica de cada grupo taxonômico, não suportam tal classificação. Além de diferenças ambientais intrínsecas (como temperatura da água e tipo de substrato disponível), as biotas de zonas "temperadas quentes" (Província Argentina) são comprovadamente distintas do encontrado na PMB (BARROSO *et al*., 2016; TARGINO & GOMES, 2020).

Nosso trabalho destaca a importância de estudos taxonômicos, assim como a contínua obtenção de dados de distribuição de espécies para o descobrimento de reais padrões concomitantes, o que nos permite identificar os processos que podem tê-los gerado.

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