#### **ORIGINAL PAPER**



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

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#### Abstract

Species distribution patterns in the Brazilian Marine Province (BMP) are extensively debated, nevertheless no study used a multi-taxa approach to investigate possible biotic distinctions and the role of environmental factors in determining biogeographical patterns in this province. Here, we compiled the largest distributional multi-taxa dataset in the southern Atlantic (2412 reef species) to address the following: (1) similarities among areas accounting for species composition and environmental characteristics; (2) the absolute species richness of nine taxonomic groups among geographical bins; and (3) how species biogeographical patterns are explained by the environmental similarities. We hypothesized sub-provinces' limits will be strongly correlated to environmental delimitations, being sea surface temperature a central component influencing biotic subdivision on the BMP. We found eight different geographical bins considering the environmental factors, while five considering species distributions. 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. Using a db-RDA, we demonstrated 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. Our study highlights the importance of using a multi-taxa approach to understand the relationship between biogeographical patterns, as well as its response to environmental and historical factors.

Keywords Ecological filters · Marine biogeography · Reef environments · Species distributions · Latitudinal gradients

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# Introduction

Species diversity and distribution patterns are extensively debated in the light of ecological and environmental aspects (e.g. Darwin 1859; Ricklefs 1987; McGill and 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 and Donoghue 2004). Historically, studies linked organisms' distribution to 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 (i.e. geological or ecological processes which limit organisms dispersal between areas). 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, ~ $08^{\circ}$ N) to Cabo Frio (Brazil, ~ $23^{\circ}$ 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 8000 km alongside the South Atlantic Ocean, encompassing one of the world's largest tropical coastlines (Barroso et al. 2016). The updated BMP is separated from the Caribbean in the north by the Amazon River's plume and stretches southwards until the end of 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 and Gomes 2020), and biogeographical barriers (Luiz et al. 2012). Regarding species dispersal, three 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 (Pailler et al. 1999; Tosetto et al. 2022); (2) the deep waters of the Mid-Atlantic Barrier forming a 3500 km long stretch between Equatorial America and the Western African coast (Nunes et al. 2011; Boehm et al. 2013); 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 (Piola et al. 2005; Aued et al. 2018). These major 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 considered oceanographical variables, along with biogeographical barriers, to investigate divisions within the BMP (e.g. Spalding et al. 2007; Souza et al. 2017; Aued et al. 2018), they are mostly focused on single taxonomic groups. Because each taxonomic group possesses their own set of biological characteristics and distinctive evolutionary histories, they can respond differently to distinct oceanographical features, biogeographical filters and barriers. 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. Human activity is altering these limits (Capinha et al. 2015), aggregating elements of dynamism to biogeographical breaks, causing changes on environmental features and species distributions (Worm et al. 2006; Bernardo-Madrid et al. 2019). In this context, multi-taxa studies are crucial to establish future comparisons between distribution patterns (Barroso et al. 2016).

In this study, we aimed to delineate sub-provinces within the BMP by asking how environmental features and known biogeographical barriers relate to the distribution of reef organisms. Despite such distinctions, we anticipate that some filters will strongly affect all organisms, sturdily driving the biogeography of the entire Brazilian marine biota. We hypothesized sub-provinces' geographical limits will be strongly correlated to the delimitations found for environmental features, being sea surface temperature a central component influencing biotic subdivisions on the BMP. Despite such relation to temperature, each taxonomic group possesses intrinsic characteristics which might produce distinct ecological and physiological responses. We believe taxonomic groups could react differently to environmental variables, resulting in distinct distribution patterns. Thus, the regions nearest to the Equator (i.e. North and Northeastern latitudinal bins) should concentrate the largest number of species, based on the well-known latitudinal gradient of richness.

To investigate such propositions, we compiled the largest distributional multi-taxa dataset ever created in the southern Atlantic, comprising 2,412 shallow (down to 50 m) reef species, belonging to nine different taxonomic groups (macroalgae, anemones, corals, anomurans, crabs, lobsters, prosobranch gastropods, elasmobranchs and reef fish). Using these taxons, we assessed (1) the existence of a latitudinal gradient for species richness, and its relation to filters and barriers present on the BMP; (2) the influence of ecological filters and biogeographical barriers on the distribution and richness of Brazilian reef organisms and (3) how the species composition changes between sub-provinces (beta diversity).

## Materials and methods

## **Geographical bins delineation**

We divided the Brazilian Province in eight different geographical bins of approximately 3 degrees of latitude 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 BMP, 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; <sup>3</sup>/<sub>4</sub> mol/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.  $\sim 200 \text{ m deep}$ ). To avoid oceanographical interferences and lack of sampling in deeper habitats we considered marine environmental data representative of depths between 10 and 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. Coles and Jokiel 1992; Harvey et al. 2013; Barroso et al. 2016; Ellis et al. 2019; Curry 2020; Hochberg et al. 2020; Targino and Gomes 2020). All variables were previously submitted to correlation tests to avoid high correlation, which could influence the analyses. Although the four Brazilian oceanic islands belong to the Brazilian Province (Floeter et al. 2008; Barroso et al. 2016; 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 2412 reef species, by researching published papers (e.g. Barroso et al. 2016; Pinheiro et al. 2018; Targino and Gomes 2020), regional checklists



**Fig. 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 ( $\frac{1}{100}$ , 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 coloured 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\_S) and South (S)

(e.g. Dutra et al. 2006; Torrano-Silva and 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 (macroalgae, anemones, corals, anomurans, crabs, lobsters, prosobranch gastropods, 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 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 as the clustering method. Data were transformed by standardization to decrease data dispersion. To verify the similarities among geographical bins based on species 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. To preclude possible bias related to species miss-identification and difference on the sampling effort among the bins, we performed the same cluster analyses using genus distribution (please refer to Fig. S1 in Supporting Information). We calculated biotic dissimilarities between sub-provinces as the change in species composition between locations (see Baselga 2010; Mittelbach and McGill 2019) using the two components of beta diversity partitioning (i.e. turnover and nestedness) through 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 (db-RDA), 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 2021) using the packages: "pvclust" (Suzuki and Shimodaira 2006), "ggplot2" (Wickham 2011), "raster" (Hijmans 2020), "sdmpredictors" (Bosch 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 3 degrees of latitude (Fig. 1). The northernmost bin North/Northeast (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 Northeast 1 (NE1), Northeast 2 (NE2) and Bahia State (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 Abrolhos Bank (Abr) and Southwest (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 (averaging 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 (~19°–21°S), which potentially shifts the Brazilian Current's course (Napolitano et al. 2021), 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 Southwest/South (SE\_S) bin is composed solely of rocky reefs with slightly lower sea surface temperatures (averaging 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, South (S), is on 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). For further details on geographical bins features, please refer to Table S1 in Supporting Information.

# **Biotic affinities**

We found five sub-provinces grouped according to the multitaxa clustering. The NE1, NE2 and Bah geographical bins



Fig. 2 Bootstrapped cluster analyses, using Sørensen dissimilarity and UPGMA, showing species grouping on the eight geographical bins along the Brazilian Marine Province. Map and dendrogram branches are coloured 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 envi-

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 (Fig. 2). 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).

Neighboring sub-provinces displayed low dissimilarity, with nestedness being the major component of beta diversity along the BMP (Fig. 3). The highest levels of turnover (0.12) occurred between the Abrolhos Bank and Southeast sub-provinces.

Cluster analysis of each taxonomic group presented similar results to the multi-taxa approach (Fig. 4). Sharks

ronmentally distinct geographical bins: North/Northeast (N\_NE); Northeast 1 (NE1); Northeast 2 (NE2); Bahia State (Bah); Abrolhos Bank (Abr); Southeast (SE); Southeast/South (SE\_S) and South (S). Barplot for taxonomic richness shows 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

and Rays, Lobsters, Corals and Prosobranchs showed a clear division between colder and warmer sea surface temperatures.

The environmental variables current velocity (CV), sea surface temperature (SST) and diffuse attenuation (DA) were significant in explaining the species and subprovinces 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. 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.



Fig. 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 subprovinces 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

# 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 subprovinces 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 biogeographical areas (i.e. the Amazon River, the Mid-Atlantic Barrier and the influence of the northbound Plata River plume).

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 (Macpherson 2002; Kerswell 2006; 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 gastropod 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 revealed herein (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 acts 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 et al. 2006; Cowen and 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 and Syvitski 1995;





**Fig. 4** Cluster analyses for each Brazilian marine taxonomic group following Sørensen dissimilarity "Sørensen" (UPGMA clustering method). Colors represent the five sub-provinces found within the Brazilian Marine Province, using all taxonomic groups together (see Fig. 2). 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\_S) and South (S)

Tosetto et al. 2022). Water turbidity was shown to be another key element on species distributions along the BMP, which relates to the temporal presence of many large rivers such as 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). All these elements can constrain the dispersal of marine species, especially during pelagic larval stages, by decreasing the survival of some organisms exposed to brackish water (Sastry 1983; Sheppard et al. 2018). This could be observed between the NE2 and Bah geographical bins for the taxons anemones, lobster, anomurans and corals (Fig. 2), perhaps the result of the São Francisco River mouth acting as a filter for species dispersal (Souza et al. 2017; Peluso et al. 2018). 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 features and biogeographic barriers, the impoverished coastal areas of both the North and the Abrolhos Bank sub-provinces are dominated



**Fig. 5** Distance based redundancy analysis (db-RDA) showing environmental variables (*CV* current velocity, *SST* sea surface temperature, *DA* diffuse attenuation, *PHY* phytoplanktonic biomass, *SAL* sea surface 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 coloured circles refer to the

by mangroves and show, in both cases, absence of suitable consolidated substratum near the coast (biogenic or rocky reefs). Whereas this may hinder dispersal of reef organisms, limiting the connectivity between areas (Scheltema 1968, 1995), it also indicates that the lack of shallow coastal reef formations might explain the comparatively low richness we found for nearly all taxonomic groups in these two areas (Fig. 2). In contrast to our study, however, the Abrolhos Bank is generally perceived as a rich site for many benthic organisms, due to the occurrence of nearly all Brazilian reef coral species and the presence of structurally complex reefs in the mid shelf, mainly built by bryozoans and cnidarians (Miloslavich et al. 2011; Bastos et al. 2018). Our results indicate that this perception may be misleading. 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

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\_S) 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

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 macroalgal diversity (Kerswell 2006). Macroalgal assemblages have an effect on other levels of communities (Lubchenco and Gaines 1981), both as primary producers and habitat constructors for a diverse benthic fauna (Santelices et al. 2009). This may also be related to the availability of smaller scale spatial refuges within the reef (Charton and Ruzafa 1998; Poray and Carpenter 2014). Differently from richer areas, the Abrolhos Bank is formed by a large shallow platform, the widest in BMP (~245 km from coastline to slope at 200 m deep; Floeter et al. 2001). The absence of coastal reefs and the long distance to deeper mesophotic reefs creates a relatively impoverished seascape within a homogeneous depth profile. This may decrease habitat heterogeneity and availability, which can directly affect species richness (Bell et al. 1991). Additionally, the combination of Abrolhos sedimentation (i.e. siltation; Segal and 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 and 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 et al. 2001) contributing to the observed lower richness patterns found in this study.

The rocky reef formations and lower mean temperatures are the most important features of the Southeast subprovince. 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 subtropical 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 and Freire 2015; Padula et al. 2011). In agreement with our results, we observed 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 and Hajdu 2001) and Petromica citrina (Monteiro and 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  $0^{\circ}$  and  $28^{\circ}$  S (Briggs and Bowen 2012), composed of a combination of tropical and subtropical biotas (Bouzon and Freire 2007; Aued et al. 2018), 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 and Mantelatto 2020; Targino and Gomes 2020; Tosetto et al. 2022). 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 and 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 single taxa (e.g. Garcia et al. 2007; Floeter et al. 2008; Almeida 2009; Petuch 2013; Barroso et al. 2016; Sissini et al. 2021). 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. Balech 1954; Vannucci 1964; Floeter and Soares-Gomes 1999; Almeida 2009).

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 and 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 are 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 et al. 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. 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 assemblages.

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Author contributions IC, LTN and SRF conceived the ideas and designed the study; IC and LTN performed statistical analyses; IC led the writing; all the authors contributed to the writing and discussions. All authors gave final approval for publication.

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**Data/code availability** The data that support the findings of this study are openly available in Zenodo: https://doi.org/10.5281/zenodo.55073 90.

#### Declarations

Conflict of interest The authors declare no conflicts of interest.

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