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Beta diversity and regionalization of the western Atlantic marine biota

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Abstract

Aim: Understanding the factors determining marine community variations is important for biogeography and conservation. Beta diversity is a metric for mapping species composition variations between communities and regionalizing biota. Ecoregions are commonly used for regionalization, but their empirical testing has been limited. Our aim is to map marine species composition variations in the Western Atlantic, identify variables related to these variations, and regionalize areas based on community distribution. Additionally, we test whether currently proposed ecoregions represent unique biota units and specific environmental conditions.

Location: Western Atlantic Ocean.

Taxon: Vertebrates, invertebrates and algae.

Methods: We constructed a large marine biodiversity database, including vertebrates, invertebrates, and algae, totalling over 4 million records. We used the generalized dissimilarity model (GDM) to identify variables most related to species composition variations and map beta-diversity variations. We employed an unsupervised classifier for community regionalization. To test if the ecoregion regionalization boundaries are corroborated by species distribution data, we used the Sørensen index. To assess if ecoregions correspond to environmental units, we checked if areas had distinct environmental conditions using a PCA of 134 marine environmental variables.

Results: The GDM explained a high variation in species composition, 61% in the complete database. Analysing vertebrates, invertebrates and algae separately also yielded relatively high results: 46%, 54%, and 33%, respectively. Coastal areas differed from open sea areas in composition. Environmental variables combined better explained beta diversity than isolated variables. The regionalization based on GDM was not congruent with ecoregion boundaries. Moreover, ecoregions showed no distinction in species composition or environmental conditions.

Main Conclusions: This study's regionalization is crucial for marine biodiversity conservation, focusing on understanding species composition patterns between coastal and open sea areas to develop tailored conservation strategies. Despite sampling limitations, the study advances marine biogeography knowledge by analysing over 4 million species records and 134 environmental variables. This comprehensive approach enhances understanding marine species distribution and diversity and aiding the development of effective conservation measures.

1 | INTRODUCTION

The ocean, often perceived as an extensive and homogeneous environment, is a complex mosaic of diverse habitats and ecosystems (Angel, 1993; Rothstein et al., 2006). In this intricate environment, marine species tend to cluster in specific areas, forming distinct communities with unique characteristics (Beaugrand et al., 2014; Daru et al., 2017). This distribution is influenced by a series of environmental factors such as temperature, salinity, ocean currents and ocean depth (Beaugrand et al., 2014; Burrows et al., 2019; García Molinos et al., 2022; Hays, 2017). Understanding these factors is essential to fully appreciate the complexity and diversity of the marine environment and the communities that reside within it, offering a more accurate view of ocean dynamics and biodiversity. The depth of the water column plays a crucial role in segmenting marine habitats, establishing distinct ecological gradients (Heyns et al., 2016; White et al., 2011). Environmental factors such as temperature, pressure and light availability have direct impacts on the composition and distribution of species (Beaugrand et al., 2014; Burrows et al., 2019; García Molinos et al., 2022; Hays, 2017). The marine habitats, often overlapping and interconnected, form complex biological mosaics that illustrate the adaptation and evolution of species over time (Boström et al., 2011; Yamakita & Miyashita, 2014). In addition, elements such as ocean currents and biological interactions work in an integrated manner, shaping the patterns of species dispersal and colonization in the marine environment (David & Loveday, 2018; Snead et al., 2023).

Biogeographical barriers, despite not always being visibly evident in marine environments, play a fundamental role in the distribution of species jand formation of marine communities (Antich et al., 2023; Bribiesca-Contreras et al., 2019; Hirschfeld et al., 2021).

These natural barriers restrict the dispersal of a wide range of species, establishing specific distribution patterns and exerting significant influence on ecological interactions and evolutionary processes (Sexton et al., 2009). Understanding the location and impact of these barriers is, therefore, crucial for research in marine biology and for the effectiveness of conservation strategies and management of marine resources.

Although the marine environment is diverse and vast, biogeographical and macroecological studies are less frequent in these environments compared to terrestrial ecosystems (Munguia & Ojanguren, 2015) despite the large increase in the number of these studies in the last decade. This limitation in oceanic research may be attributed to logistical challenges, such as difficult access to deep and remote areas, and the high cost of field activities in marine environments (Ramírez et al., 2022). However, it is essential to recognize the importance of the oceans, which play vital ecological, economic, and climatic roles on the planet (Mendler de Suarez et al., 2014). With increasing anthropogenic pressures, including overfishing and climate change, the need to intensify marine research becomes even more urgent (Halpern et al., 2015). A deeper understanding of the oceans will not only enrich the biogeographical perspective but also provide the basis for more effective conservation strategies, contributing to the long-term maintenance of marine ecosystems and adaptations on the scenario of climate changes.

Ecoregions, widely recognized as one of the main forms of ecological regionalization, represent terrestrial and aquatic areas with distinct ecological and climatic characteristics (Spalding et al., 2007). This practice of regionalization is commonly employed across numerous studies, including those concentrating on conservation, biogeography, and landscape ecology (Alfaro-Lucas et al., 2023; Hadiyanto et al., 2023; Novi et al., 2021; Petrov, 2022). Despite its widespread

use, there is still a lack of robust, statistically based, multi-taxa research that empirically validates this regionalization, particularly regarding the correlation of ecoregion boundaries with the actual distribution of biota. Various studies focusing on specific groups aim for such validation (Barroso et al., 2016; Veron et al., 2015). And some multi-taxa approaches have been made for certain regions but with a limited number of groups (Cord et al., 2022). However, a comprehensive and multi-taxa approach that integrates the general patterns of marine biota is still necessary, mainly because the ecoregions proposal was based only on key species (Spalding et al., 2007), without testing whether other taxa would have the same regionalization pattern. Investigating whether the proposed ecoregions accurately reflect species distribution is fundamental to ensure the effectiveness of conservation strategies and to better understand biogeographical patterns. Such an understanding is inherently linked to the concept of beta diversity, which focuses on variation in species composition and is a key element in defining ecoregions. Thus, contributing to more robust and informed strategies for environmental management and biodiversity conservation.

Beta diversity, a metric of variation in species composition between different areas, plays a crucial role in biogeographical studies (Shengbin et al., 2010). This metric is essential for identifying biogeographical barriers that limit species dispersal, directly influencing the evolution and ecology of marine communities (Antonelli, 2017). Understanding species composition patterns is essential for developing effective conservation strategies (Chen & Kishino, 2015; Sankaran, 2009; Socolar et al., 2016). These patterns help identify regions with similar biotas, indicating shared evolutionary histories or similar ecological conditions (Graham & Fine, 2008). By highlighting these areas, it is possible to direct resources and efforts more efficiently towards the preservation of marine biodiversity, contributing to the protection and sustainable management of marine ecosystems.

Thus, our objective is to map the patterns of marine species composition of vertebrates, invertebrates and algae, and identify the environmental factors related to these patterns in the Western Atlantic. Additionally, use this mapping to generate a regionalization of the marine biota, to identify areas with unique biota, and test the limits of marine ecoregions (Spalding et al., 2007) through the mapped species composition data.

2 | MATERIALS AND METHODS

2.1 | Species occurrence database

To compile the data, we carried out searches in online databases such as GBIF (Global Biodiversity Information Facility) (https://doi.org/10.15468/dl.thtnur) and OBIS (Ocean Biodiversity Information System) (https://obis.org/) and personal databases of Brazilian specialists, from collection data and collections not available online. For the online database searches, data were filtered by selecting countries in Latin America and states in the USA located below the latitude 57° south to 40° north in the Atlantic, within a limit of up to 1500 km from the coast. Additionally, we filtered the following organism groups: Annelida, Ascidiacea, Brachiopoda, Branchiopoda, Bryozoa, Cnidaria, Ctenophora, Echinodermata, Malacostraca, Maxillopoda, Mollusca, Nemertea, Nematoda, Ostracoda, Platyhelminthes, Porifera, Sipuncula, Cetacea, fish from the Tetraodontiformes and Perciformes groups, and the algal groups Chlorophyta and Rhodophyta. Data were filtered to remove records located on the continental surface or in the Pacific Ocean. In cases of non-georeferenced data, we attempted to georeferenced them by cross-referencing the locality description with the general data in the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/) to obtain coordinates. To ensure the taxonomic validity of species names, data were cross-referenced with the WoRMS (World Register of Marine Species) database (https://www.marinespecies.org/) and reviewed by experts in each taxonomic group. The database compiled a total of 4,132,448 occurrences and 22,811 species, with 20,055 being invertebrates (88%), 1618 vertebrates (7%), and 1138 algae (5%), of which 77% were from GBIF, 22% from OBIS, and 1% from the Brazilian experts databases. All data are available at https://zenodo.org/records/10779140.

2.2 | Environmental variables

To characterize the marine environmental heterogeneity in the study area, we used data from the Bio-Oracle Marine data layers for ecological modelling platform (https://www.bio-oracle.org/), which includes surface variables and benthic data with minimum, mean, maximum, and range values. The variables include temperature, salinity, current velocity, ice concentration, nutrients (nitrate, phosphate, silicate), dissolved oxygen, iron, chlorophyll, phytoplankton, primary productivity, calcite, pH, photosynthetic radiation, diffuse attenuation and cloud coverage. Additionally, we also used bioclimatic variables from the Climatologies at high resolution for the earth's land surface areas—CHELSA platform (https://chelsa-climate.org/), encompassing aspects such as mean annual temperature, temperature mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month and annual temperature range. The bathymetric data were obtained from the National Oceanic and Atmospheric Administration—NOAA (https://www.noaa.gov/). In total, 134 layers of environmental variables (Appendix S1) were used to describe the marine environmental heterogeneity in the study area, which were adjusted to the defined limits of the research area. All variables were used at a spatial resolution of 5 km per pixel. Due to the extensive availability of data, it was necessary to reduce the number of variables to reduce multicollinearity among the variables and prevent overfitting. To achieve this, we performed a spatialized principal component analysis (PCA). This analysis synthesizes the variables, combining them through their intrinsic correlations and generating axes (vectors) of values that represent all variables in a summarized way. Thus, it is possible to interpret the environmental

conditions without the need to analyse each variable individually. The PCA provided a comprehensive view of the environmental conditions and contributed to the understanding of the spatial heterogeneity in the study area. The significant axes of the PCA were used to represent the environmental characteristics of the study area. To test if the samples show any type of environmental bias, all records (regardless of taxonomic identification) were spatially cross-referenced with the significant PCA axes to obtain the distribution of environmental conditions observed in the biodiversity samples. The distribution of environmental conditions for the study area was used as predictor variables in GDM analysis. The BioDinamica package (Oliveira et al., 2019) was used to generate the PCA maps. The three first axes (the only significant ones) of the PCA represent 99.8% of the observed variation in environmental variables. To identify the isolated effect of variables 1—Climatic, 2—Chemical, 3—Physical and 4—Productivity in the following analyses, we also performed PCA for each set of these variables (Appendix S1).

2.3 | Species composition model

We employed the generalized dissimilarity model (GDM) (Ferrier et al., 2007) to map species composition patterns in our study area. This method discerns spatial patterns in species composition changes, tests their relationship with predictive variables, and uses them to forecast beta-diversity in un-sampled areas. Since our data do not come from systematic collections in standardized areas, we had to create post hoc sampling units. For this, we generated a grid of equal-area hexagons with a 100 km radius to create a presence-absence matrix from the species occurrence data. We used this matrix to calculate the Sørensen beta-diversity index (Bray & Curtis, 1957). We excluded from the analysis hexagons with fewer than 20 samples to avoid artificially inflating the similarity measured by the Sørensen index. We chose this index because it does not consider species abundance (data not available) and does not account for species absences in the index calculation. To train the model, we used curve fitting with three I-splines and included geographic distance as a predictive variable, along with the first three PCA axes of environmental variables. All analyses were conducted for the complete database, encompassing all groups, and for comparative purposes, we also performed analyses separately for vertebrates, invertebrates and algae, as these groups differ in sampling intensity and types. We also compared the results of each group with the outcome for all groups through map correlation, to ascertain which group might best indicate overall group beta-diversity. To determine the isolated predictive capacity of each type of predictor variable (climatic, chemical, physical or productivity), we performed GDM analyses on the species data sets using each set of variables separately. We conducted individualized GDM analyses for each taxonomic group, including Annelida, Ascidiacea, Brachiopoda, Branchiopoda, Bryozoa, Cnidaria, Ctenophora, Echinodermata, Crustacea, Nemertea, Nematoda, Platyhelminthes, Porifera, Sipuncula, as well as Cetacea and fish (Tetraodontiformes

and Perciformes). The aim was to compare the spatial beta diversity patterns of each taxonomic group with those derived from the comprehensive database analysis, which includes all mentioned groups, to identify consistencies or divergences in spatial beta diversity patterns. To conduct a comparison between the maps generated for each taxonomic group and the map resulting from the analysis that incorporates all the data, we employed a clustering analysis methodology. This involved assessing the average Euclidean distance between the GDM results for each individual group and the results obtained from the analysis with the entire database. This approach allowed us to quantify the similarities between the distribution maps of each group in relation to the overall observed pattern.

2.4 | Testing the limits of ecoregions as biogeographic units

To identify regions with the most significant breaks in species composition, we used an unsupervised classification to pinpoint the 10 areas with the most internally uniform composition and the greatest differences in composition between areas. The classification method employed was clustering for large applications (CLARA) (Kaufman & Rousseeuw, 1990), an unsupervised classification approach that has shown effective results in categorizing large datasets. We used this classification to compare the results from the generalized dissimilarity model (GDM) with the boundaries of marine ecoregions (Spalding et al., 2007) to check if they align with the observed species composition variation in the data. Given the significant influence of depth on beta diversity patterns and in order to reduce variability, we employed a strategy to define the boundaries of coastal areas. An unsupervised classification was applied solely to regions with depths less than 150 m. This approach aimed to prevent the extensive variation in species composition observed between continental shelf areas and deep-water zones from obscuring the species composition differences in coastal areas. To determine the optimal number of natural coastal regions, we conducted classifications on the complete database (including all groups), dividing the GDM-generated map into a progressively increasing number of parts. This process was continued until we reached a point of stability in the larger areas, where subsequent classifications did not yield the identification of new significant areas. Furthermore, to test whether the boundaries of the classified regions are supported by different organism groups, we performed the same classification for each of the groups separately, specifically for the coastal region. Subsequently, we identified the area in which the boundaries between different groups coincide with the boundaries obtained in the comprehensive classification, which included all groups (complete data). To test if species composition is distinct among ecoregions, we transformed the Sørensen similarity matrix into a vector using non-metric multidimensional scaling (NMDS) (Rabinowitz, 1975) for the hexagonal sampling units. This was done to visualize if there is an overlap of species composition among the ecoregions. The NMDS was conducted with 10,000 searches for the best solution. As ecoregions are also supposed to

represent unique environmental units of ecosystems, we also utilized the axes of the environmental PCA (described above) to see if there is environmental overlap among the ecoregions. It is expected that if ecoregions represent biota regionalization units, they should exhibit distinct species compositions between areas, thus showing little or no overlap in the Sørensen similarity NMDS scatter plot. Similarly, if ecoregions represent environmental units, they should exhibit distinct environmental conditions between areas, that is, have little or no overlap in the environmental PCA scatter plot. The BioDinamica package (Oliveira et al., 2019) was utilized for all analyses.

3 | RESULTS

3.1 | Species composition model

The species composition displayed a relatively high explanation percentage for the predictor variables in the GDM analysis, with 61.13% for the analysis involving all groups (Figure 1a). The GDM for each type of variable showed explanation percentages with chemical and climatic variables very close to each other (38.24% and 37.65%, respectively) (Figure 1a). Physical variables accounted for 34.31% of the explanation, and productivity variables for 28.95%. Group analysis indicated that invertebrates have the highest explanation percentage of variation (54.41%) and exhibit species composition patterns most like those observed for all groups in the GDM analysis ($r = 0.98$) (Figure 2). Climatic and chemical variables showed the highest explanatory power for invertebrates, at 31.84% and 30.83%, respectively (Figure 2). Physical and productivity variables accounted for 26.32% and 23.80%, respectively. The GDM for vertebrates also showed a high explanation of variation (46.03%) and a relatively high similarity with the species composition patterns of all groups ($r = 0.8$) (Figure 2). Climatic variables showed the highest explanation for species composition in vertebrates, 42.47%, closely matching the value obtained with all variables. Chemical variables accounted for 38.63%, physical 34.55% and productivity 31.85% (Figure 2). Algae showed the lowest explanation for species composition variation (33.03%) and the least similarity with results for all groups ($r = 0.66$) (Figure 2). Climatic variables showed the highest isolated explanation percentage, 24.27%. The other isolated variables showed
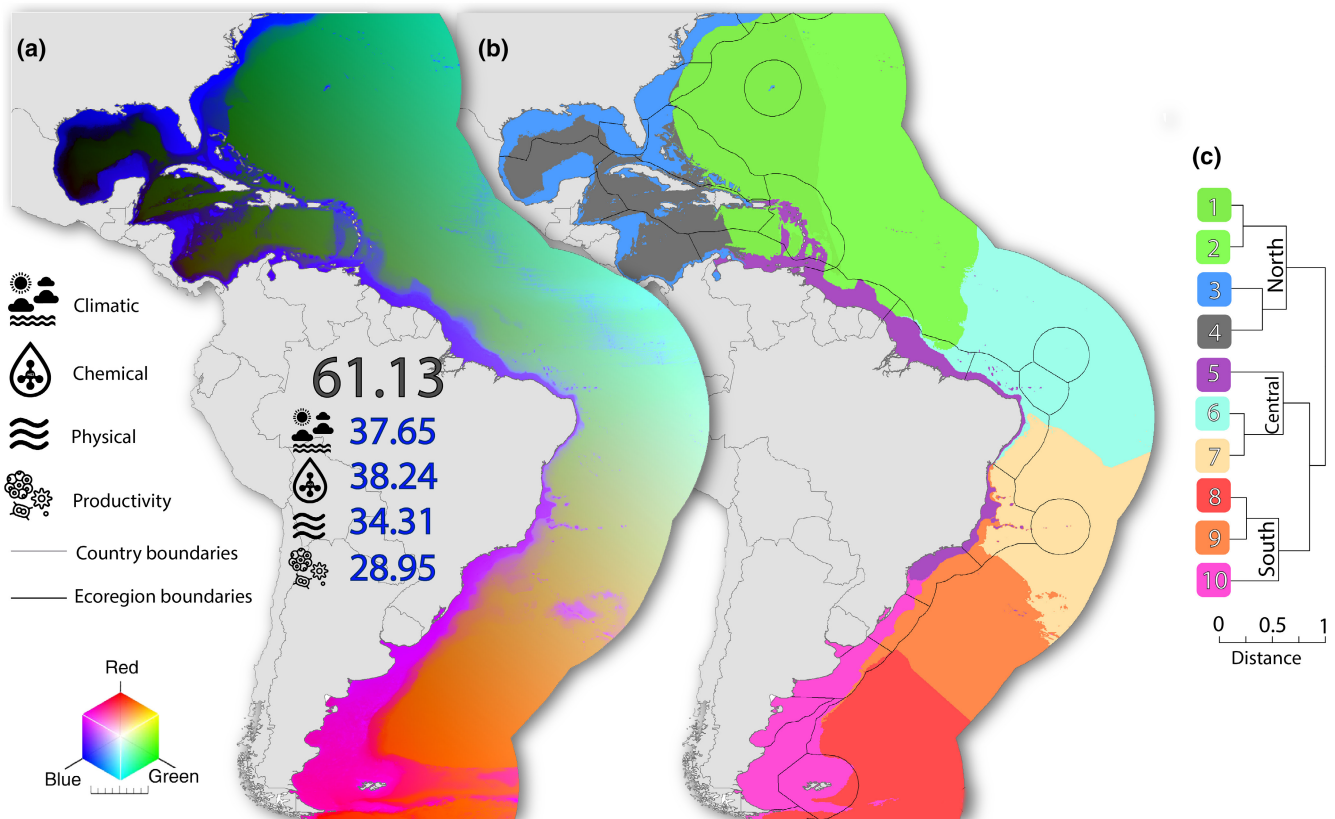
FIGURE 1 Species composition estimated by GDM for all groups of organisms. (a) RGB map of the composition, similar colours in the spectrum indicate similar species composition, grey number indicates the percentage of explanation by GDM, blue numbers indicate the percentage of explanation by GDM for each set of environmental variables. (b) Unsupervised classification of ten areas identified by the CLARA classification based on species composition and estimated by GDM, each colour indicates a region in the classification, black lines indicate the limits of the ecoregions (Spalding et al., 2007). (c) Species composition distance between the areas identified by the CLARA classification of the GDM model, colours indicate the areas of the map (b) and the numbers indicate the areas: 1—Bermuda, 2—North Atlantic, 3—North Coast, 4—Gulf of Mexico, 5—Central Coast, 6—High seas of Northeast Brazil, 7—High seas of eastern Brazil, 8—Argentine High Seas, 9—High seas of Southern Brazil, 10—Southern Coast.
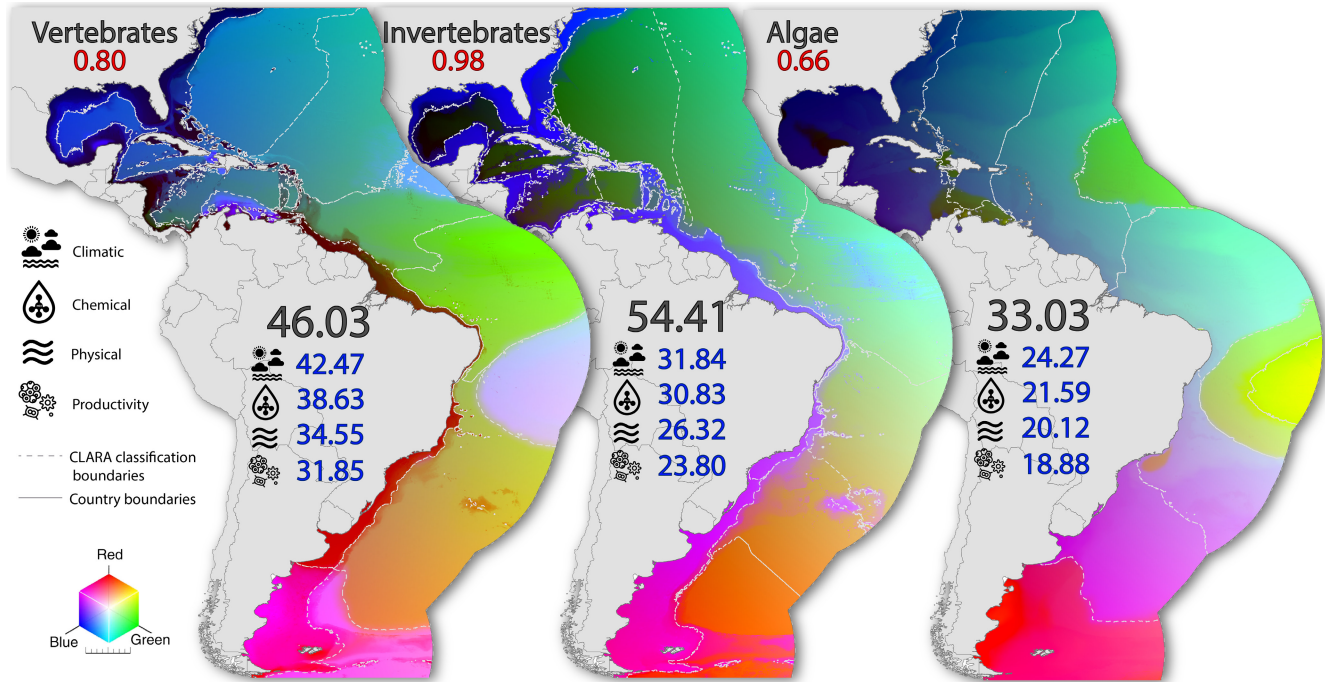
FIGURE 2 Species composition estimated by GDM for vertebrates, invertebrates and algae. In a RGB map of the composition, similar colours in the spectrum indicate similar species compositions, grey number indicates the percentage of explanation by GDM, blue numbers indicate the percentage of explanation by GDM for each set of environmental variables, the red numbers indicate the correlation between the GDM for each group and the GDM for all species groups.

similar results: chemical 21.59, physical 20.12% and productivity 18.88%. In all GDM analyses, geographical distance and environmental variables had a strong relationship with species composition variation, usually with the first axis of the PCA as the most relevant environmental variable (Appendix S1). The GDM analysis with all groups, invertebrates, and vertebrates indicated a clear distinction in composition between coastal areas and open sea areas (Figures 1 and 2). Algae showed a less clear distinction between the coast and the open sea areas. A north–south gradient of composition change was marked in all GDM analyses (Figures 1 and 2). The patterns of species composition variation are almost identical between the analysis with all groups and just invertebrates ($r=0.98$). The GDM for all groups indicated a gradual change in composition from the open sea areas in the north to the south and along the continental shelf (Figure 1a). The 10-class classification of the CLARA analysis indicated three major divisions in species composition change (Figure 1b,c). One of these divisions is in the north, including coastal areas of the Caribbean and the North Atlantic, the open sea areas of the Gulf of Mexico, Bermuda, and the North Atlantic (Figure 1b,c). Another major division in the central part of the study area includes the North Coast of South America, the southern Antilles, the open seas of northeastern Brazil, and the open sea areas of eastern Brazil (Figure 1b,c). Finally, a southern region includes the coastal areas of southern Brazil, Uruguay, and Argentina, as well as the open sea territories found in the southern and southeastern regions of Brazil and Argentina (Figure 1b,c). The open sea areas of each of the three major regions (north, central, and south) show more similarity in species composition to each other than to the coastal areas (Figure 1c).

These divisions are incongruent with the boundaries of the marine ecoregions (Spalding et al., 2007) (Figure 1b).

The GDM results for vertebrates showed some differences in species composition variation compared to the analysis with all groups ($r=0.8$). The North Coast and the Caribbean Coast exhibited the same composition similarity pattern observed in the analysis for all groups (Figure 2). The South American coast shows greater similarity along almost its entire extent from Venezuela to the coast of Uruguay, while the Argentine coast differs from these areas (Figure 2). The open sea of the north shows great similarity in the composition variation pattern observed in the data for all groups (Figure 2). Similarly, the open sea of the south show patterns very similar to those of the results with all groups (Figure 2). In the central portion, the greatest difference in the results is observed in the open sea, as these show more drastic composition changes in their central and northern parts (Figure 2). The GDM results for algae were the least like the results for all groups ($r=0.66$). The composition variation of algae differs from the other groups analysed as it does not have a clear division between the composition of coastal and open sea areas (Figure 2). The composition variation is a gradient of smooth changes, from the North, on the coast of the USA to the region of northeastern Brazil (Figure 2). In this region, there is an abrupt change in composition in open sea (Figure 2). The coast of Argentina also shows a more distinct composition than the areas of the coast of Uruguay and Brazil (Figure 2).

The analysis conducted for each taxonomic group revealed a striking distinction in species composition between continental shelf zones and deep-water areas (Figures 1 to 13 in Appendix S2). For

most groups, a gradual transition in species composition from north to south was observed, though some regions exhibited more abrupt changes along the coast (Figures 1 to 13, Appendix S2). Invertebrate groups, such as Porifera, Echinodermata, Mollusca, Crustacea and Nematoda, showed species composition patterns that closely resemble those identified in the analysis that included all groups (Figure 15 in Appendix S2). Among vertebrates, fish were found to be the group whose composition patterns were most similar to those observed in the analysis encompassing all vertebrates (Figures 12 and 15 in Appendix S2). The GDM analysis could not be carried out for the groups Brachiopoda, Branchiopoda, Ctenophora, Nemertea and Sipuncula, due to a lack of sufficient samples in terms of number and spatial distribution, preventing their independent execution.

3.2 | Testing the Limits of Ecoregions as Biogeographic Units

The ecoregions (Spalding et al., 2007) showed low congruence with the boundaries of the regions delineated by the CLARA method based on species composition in the entire study area (Figure 1). The ecoregions also did not show a distinction in species composition between areas, as shown by the direct analysis of the Sørensen index vectorised by NMDS (Figure 3). There is complete overlap in compositions between areas, preventing the distinction of any of the ecoregions in terms of their species composition.

Similarly, no environmental distinction separating the ecoregions by distinct environmental characteristics was observed (Figure 3) through the two axes of the PCA representing 99.49% of the environmental variation of the 134 environmental variables used in this study.

The coastal areas were categorized into 15 distinct regions, a result achieved following the stabilization process observed in the tests of unsupervised classification. This number reflects the optimal clustering point identified by the analysis. The classification of coastal areas revealed greater congruence with the boundaries of the ecoregions, for example the areas Southern Gulf of Mexico, Northern Gulf of Mexico, Floridian, Southeastern Brazil, Rio Grande (Figure 4). However, a distinction is observed in the boundaries between the classified areas compared to those of the ecoregions in most of the regions analysed (Figure 4). The most significant discrepancies were identified in the south and north of South America, as well as the Caribbean (Figure 4). On the Brazilian coast, although some areas show greater congruence, the boundaries between the classified regions are generally misaligned with those of the established ecoregions. Most of the boundaries of the areas defined by the CLARA method in the analysis of the coastal region, using the complete database, were congruent with those identified in the classifications of specific taxonomic groups (Figure 4 and Figures 19 to 32 in Appendix S2). Among the 14 established boundaries between the 15 areas, 10 showed consistency with the classification results of more than 5 individual groups (Figure 4).
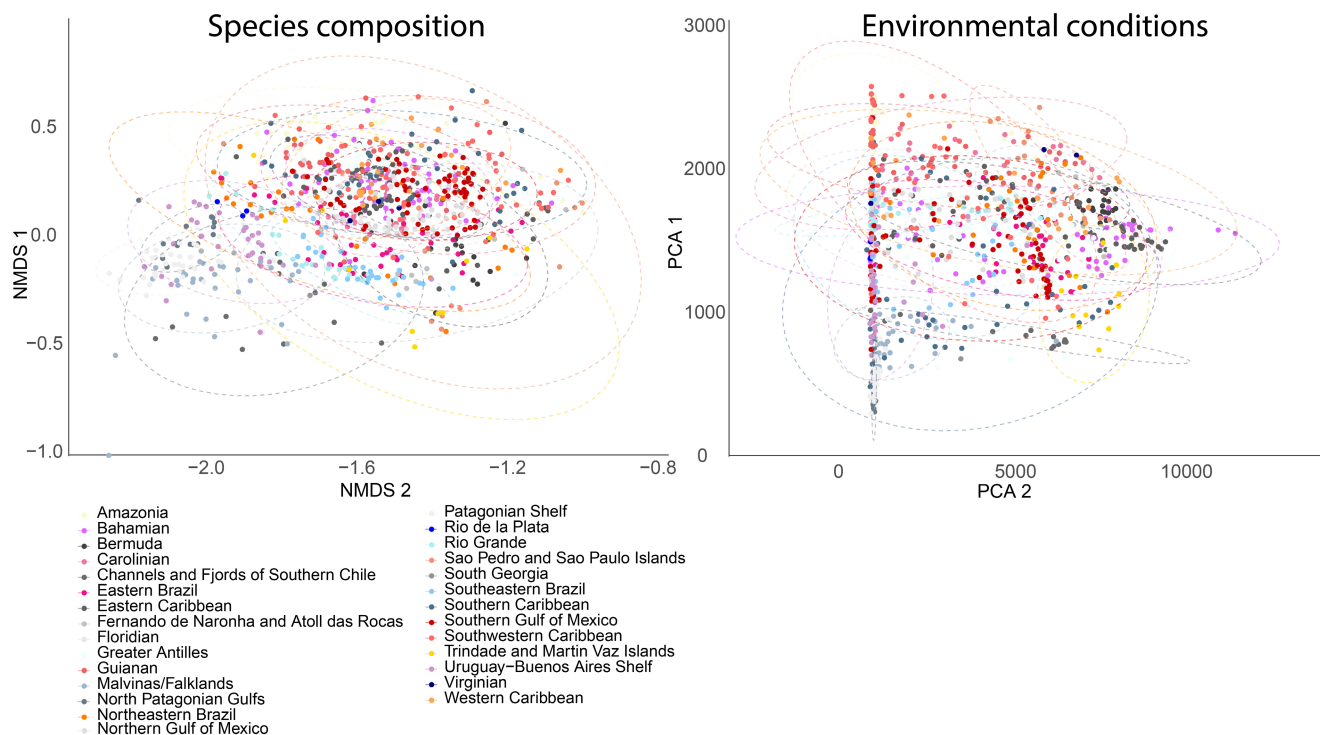
FIGURE 3 Variation in species composition and environmental conditions among ecoregions, with points representing sampling hexagons, colours indicating each ecoregion, and lines outlining the surrounding data limits of each ecoregion. On the left, the species composition estimated by Sørensen and transformed into vectors by NMDS, and on the right, the environmental variation estimated by PCA of 134 environmental variables.
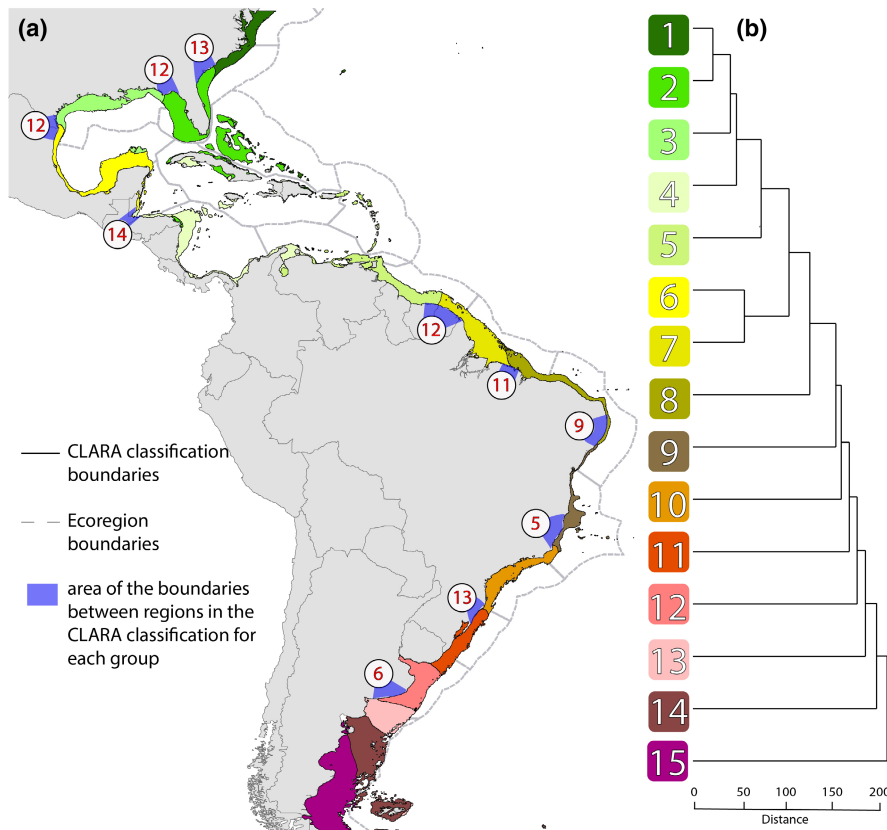
FIGURE 4 Continental shelf regionalization based on the unsupervised CLARA classification of species composition from the GDM, for all organism groups. (a) Map of the 15 regions defined by the CLARA method, with the numbers in red indicating the number of organism groups that share similar regionalization boundaries in these areas. The blue zones mark the extensions along the coast where these coincident boundaries occur among the groups. The dashed lines denote the limits of the ecoregions. (b) Dendrogram illustrating the relationships of species composition similarity between the regions demarcated by CLARA. The dendrogram numbers indicate the areas, and the colours correspond to them on the map, being: 1—Virginian, 2—Floridian, 3—Northern Gulf of Mexico, 4—South Caribbean, 5—Guianan, 6—Southern Gulf of Mexico, 7—Amazonia, 8—Northeastern Brazil, 9—Eastern Brazil, 10—Southeastern Brazil, 11–Rio Grande, 12—Uruguay-Buenos Aires Shelf, 13—North Patagonian Gulfs, 14—North Patagonian Shelf, 15—South Patagonian Shelf. The vector map (shapefile) is available in Appendix S3.

4 | DISCUSSION

The generalized dissimilarity model (GDM) demonstrated a remarkable ability to explain the variation in marine species composition, reaching 61.13%, a significant value compared to what has been presented in other studies, as already shown in reviews (Mokany et al., 2022). This result suggests that dispersal is a determining factor in the identified beta-diversity patterns. The model's high efficacy is attributed to the use of a combination of climatic, chemical, physical, and marine productivity variables, as none of these variable sets alone provided an explanation close to the model with all variables. The factors determining the structure of different marine communities are thus an interaction of various environmental variables, as long-term studies have shown (Lin et al., 2022; Sand-Jensen, 1989). These results also indicate that marine species distribution models should consider this diversity of environmental factors to capture the underlying mechanisms of species distribution in the marine ecosystem.

The comparative analysis across various taxonomic groups unveiled that invertebrates align more closely with the overall trends in marine biodiversity, diverging from the distinct patterns observed in vertebrates and algae. This finding suggests the potential suitability of invertebrates as indicators of marine biodiversity. However, caution is needed in interpreting these results, as it is important to consider that this congruence might be influenced by the larger number of invertebrate species compared to algae and vertebrates. Further investigations focused on specific invertebrate groups to accurately assess their value as indicators are essential. The observed variations among taxonomic groups highlight the diversity in species distribution patterns, which can be attributed to different influencing factors in each group. This finding underscores the complexity of ecological interactions in marine ecosystems and the importance of differentiated approaches to understanding marine biodiversity.

The most significant changes in species composition were detected in transitions between continental shelves and open

sea, indicating that this boundary might function as a geographic barrier for various species. This observation, confirmed in analyses including invertebrates and vertebrates, is likely linked to the marked differences between these ecosystems (Fujiwara & Kon, 2020a; Galéron, 2014; Woolley et al., 2016; Zheng & Klemas, 2018). The continental shelves, differing from open sea in aspects like light and substrate, seem to play a selective role in the evolution of species in these habitats (Fujiwara & Kon, 2020b; Kitchel et al., 2022). A gradual latitudinal variation in species composition was also observed in all studied groups, both in coastal zones and open sea. This variation is likely caused by climatic changes, essential factors for species diversification (Antão et al., 2020; Chaudhary et al., 2016; Rombouts et al., 2009). The continental shelf, noted for its rich species diversity and variety of benthic environments like coral reefs and rocky formations, is particularly prominent in terms of marine biodiversity (Bonecker et al., 2014; de Juan et al., 2023). The variations observed along the coasts emphasize the importance of this region for the conservation of marine biodiversity (Ayyam et al., 2019; Lotze, 2021), especially given its greater impact from human activities (Allan et al., 2023). In contrast, algae showed a smoother variation in composition along the north–south gradient and less pronounced differentiation between coastal and open sea zones, a pattern that might be influenced by the smaller quantity of algae samples in the database and the limited number of species, affecting the beta-diversity metrics.

The analysis with the generalized dissimilarity model (GDM) revealed a notable discrepancy between the spatial distribution of marine species and the established limits of ecoregions, as demonstrated by NMDS (Spalding et al., 2007). The application of the Sørensen index did not show a typical biota or a clear distinction between ecoregions, indicating that the current boundaries might not adequately represent species distribution. This can be primarily attributed to the boundaries defined for coastal ecoregions, set as a buffer along the coast, without adequately considering the natural contour of the continental shelf. Such an approach results in the inclusion of areas with variable depths, both deep and shallow regions, within each defined ecoregion. On the other hand, the boundaries defined among the ecoregions proved to be relatively similar when compared to the boundaries obtained from the analysis restricted to the continental shelf, despite there being differences in the exact location of these boundaries between areas (Figure 4). The boundaries from the regionalization analysis of the continental shelf areas remained even after the detailed analysis of different taxonomic groups individually, revealing a significant congruence in the patterns of species composition distribution, even among groups with little evolutionary relationship. Some of these boundaries are also in line with delineations proposed in previous studies for specific groups (Barroso et al., 2016) and even in approaches involving multiple taxa (Cord et al., 2022). The differences observed between our results and the ecoregions may be due to the methodology employed in the delineation of ecoregions, which typically uses only selected species, without

considering the majority of marine biota (Spalding et al., 2007). The analysis did not find a significant environmental differentiation between ecoregions, contradicting the expectation of distinct ecosystems with unique environmental characteristics (Spalding et al., 2007). Possibly, this observation can also be attributed to the striking environmental differences between the continental shelf and the deeper areas (Figure 33 in Appendix S2). Thus, the use of a coastal buffer in delineating the oceanic edges of the ecoregions (Spalding et al., 2007) may have resulted in an expansion of environmental variation within the regions, leading to the observed overlap between points in the analysis. This finding indicates that the ecoregion boundaries should be adjusted to more accurately reflect the actual variations of marine biodiversity and environmental conditions. These results point to the need for a critical review of ecoregion boundaries, aligning them more closely with the actual distributions of marine biota. This incongruence is particularly important in biodiversity conservation, biogeography, and macroecology, where ecoregion boundaries are commonly used for analyses and decision-making (Beck & Odaya, 2001; Miclat et al., 2006; Wang et al., 2021). A crucial aspect for conservation is the need to adjust the marine boundaries of the ecoregions so that they align with the contours of the continental shelf. This is because regions beyond this limit harbour distinct sets of species, thereby requiring specific conservation policies. The study highlights the necessity of a more detailed and evidence-based approach in defining ecoregions, ensuring they more faithfully represent the diversity and complexity of marine ecosystems.

The regionalization proposed in this study is relevant for developing strategies for marine biodiversity conservation. A critical step in selecting areas for conservation is the precise definition of biogeographic units. Understanding the patterns of species composition in detail, especially the differences between coastal zones and open sea oceans, is essential for creating appropriate management and conservation methods. These strategies should be tailored to each specific environment, considering the unique characteristics of each marine ecosystem. A thorough understanding of these patterns enables the implementation of more effective conservation measures that recognize and protect the diversity of marine habitats. This study marks a significant advance in understanding marine biogeography, despite limitations due to sampling gaps. It is essential to recognize that the biogeographic units identified in this study, given their geographic scale and data resolution, might not have captured more subtle variations in local species composition. Therefore, additional surveys of the biota are necessary for a more detailed analysis of these variations. The growing availability of environmental and biodiversity data, coupled with the current capability to process large volumes of data, enables the performance of analytical regionalization based directly on available databases. In this study, we analysed over 4 million species occurrence records and 134 environmental variables at a resolution of $5\,km^2$, providing a comprehensive view of the marine biota of the Western Atlantic. This approach is crucial for enhancing knowledge about the distribution and diversity of

marine species, significantly contributing to the advancement of marine conservation and biogeography.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.