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Global Coastal Biogeographic Boundaries: Unveiling the Nature of Processes Shaping the Distribution of Marine Biodiversity

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ABSTRACT

Aim: Identify biogeographic boundaries that delineate the distribution of species assemblages along global non-insular coastlines, characterise the potential barriers responsible for biogeographic boundaries and realign coastal biogeographic provinces.

Location: Global.

Time Period: Not applied.

Major Taxa Studied: Animalia.

Methods: Global databases of marine animals were used to define biogeographic boundaries as regions that concentrate species range limits. To mitigate sampling bias inherent in uneven presence records in biodiversity databases, we applied a resampling methodology. We used the identified dispersal barriers to divide the study area into ecoregions in order to realign coastal biogeographic provinces. These ecoregions were then clustered into biogeographic provinces based on the similarity of their biodiversity.

Results: We identified 24 biogeographic boundaries along the coastlines of the Americas and 27 along Afro-Eurasia. The 52 ecoregions delimited by the biogeographic boundaries were classified into 23 biogeographic provinces. In most cases, the proportion of exclusive species within each province was higher than 25%. When comparing the proportion of exclusive species to the previous classifications of biogeographic provinces, a higher proportion was found. Of the 21 boundaries of the new biogeographic provinces, nine are aligned with and six are close to previous boundaries between the biogeographic provinces or realms defined in previous studies. Our analysis revealed the presence of 6 additional subdivisions and significant realignments within the marine biogeographic provinces.

Main Conclusions: The objective data-driven approach was effective to identify biogeographic boundaries and realign biogeographic provinces. Most boundaries were associated with strong thermohaline gradients, which typically occur along water-mass fronts due to converging currents, upwelling or river discharge. Such processes, in conjunction with geomorphology and

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circulation patterns, interact to restrict the dispersal of marine organisms by restricting movement and filtering species according to their ecological niches.

1 | Introduction

Understanding patterns in the distribution of biological diversity is crucial in ecology and biogeography, particularly in light of the challenges posed by climate change and global biodiversity decline. In this context, the delineation of biogeographic regions that harbour similar biota plays a pivotal role in macroecological and evolutionary research, as well as in shaping large-scale conservation initiatives (Calatayud et al. 2019; Montalvo-Mancheno et al. 2020). Within the marine realm, Ekman (1953) and Briggs (1974) conducted pioneering studies that comprehensively divided the world's continental shelves into large biogeographic provinces. Briggs (1974) defined provinces based on a given level (10%) of endemism, relying on climate patterns and an extensive literature review of the regional distribution of marine fauna, with a primary focus on fish species due to their historically higher data availability. Subsequent realignments were proposed for these provinces (Briggs 1995; Briggs and Bowen 2012, 2013) and synthesised by Toonen et al. (2016). In parallel, Spalding et al. (2007), also relying on the existing literature, proposed a hierarchical biogeographic classification for the world's coastal and shelf areas where finer scale ecoregions were nested within biogeographic provinces and realms.

However, these studies did not have a unified criterion for defining province boundaries. They were rooted in regional studies with different animal assemblages, methodologies and spatiotemporal scales. Recently, a more objective approach, based on the clustering of a global dataset of species distribution, was proposed for a global ocean subdivision into biogeographic realms (Costello et al. 2017). This approach considered the global ocean as a whole in the analyses, resulting in large realms that combined coastal zones and the vast open ocean. As a result, the complexities of coastal biogeographic patterns, which typically reflect processes occurring on smaller scales, were not properly assessed or discussed (Costello et al. 2017). Therefore, no attempt was made to relate the boundaries of their results to previous coastal biogeographic classifications (Briggs and Bowen 2012; Spalding et al. 2007; Toonen et al. 2016).

The existence of biogeographic boundaries separating marine provinces arises from both contemporary and historical barriers and environmental filters that limit species dispersal and consequently their geographic range. These barriers and filters play a crucial role in partially isolating biological communities, thereby fostering increased speciation and endemism within provinces. Consequently, the delineation of biogeographic province boundaries should ideally align with them. However, identifying such features poses a significant challenge in the marine realm. Marine dispersal is generally more extensive compared to terrestrial dispersal due to the prevalence of at least one planktonic life stage in most marine organisms. Beyond the active movement of adult organisms, these stages facilitate passive transport by ocean currents, enabling dispersal over long distances with minimal energy expenditure (Burgess et al. 2016; Sardet 2015). Hence, identifying dispersal barriers is challenging in such a dynamic environment where a combination of oceanic features can hinder both active and passive species dispersal across the seascape.

Therefore, dispersal barriers along continental shelves have mostly been identified indirectly by (i) identifying regions that concentrate the geographic range limits of large groups of species, such regions are typically referred to as biogeographic boundaries (Gaines et al. 2009; Pappalardo et al. 2015); (ii) by comparing biodiversity on either side of hypothesised barriers (Mironov and Dilman 2010; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022) or (iii) by examining genetic divergence within specific taxa (Araujo et al. 2022; Rocha et al. 2005; Teske et al. 2008). However, such barriers have only been studied at regional scales. A comprehensive, global-scale approach, to identify biogeographic boundaries along continental shelves, and the potential processes acting as barriers and filters to species dispersal at these boundaries, remains to be undertaken.

The emergence of global platforms that integrate species distribution data from various sources has created new opportunities for studying marine life diversity and distribution (Costello et al. 2017; Saeedi et al. 2019; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022). These platforms allow researchers to implement integrative approaches and apply objective criteria to identify biogeographic boundaries. This shift promises to improve our understanding of where dispersal barriers and filters restrict the distribution ranges of marine organisms globally, contributing to a more comprehensive perspective on marine biogeography. However, utilising large multisource databases can introduce biases in the results and compromise the reliability of the findings, particularly in undersampled regions where data scarcity is an issue (Leles et al. 2019; Robertson 2008).

In this study, we use animal occurrence data from the Ocean Biodiversity Information System (OBIS 2024) and the Global Biodiversity Information Facility (GBIF 2024) to identify biogeographic boundaries. These are defined as regions with clumped species range limits (Pappalardo et al. 2015) that shape the distribution of species assemblages along non-insular coastlines worldwide (Americas and Afro-Eurasia). For that, we propose a new methodology that accounts for sampling bias associated with uneven presence records in large databases. We then characterise these boundaries based on the primary oceanographic processes that potentially act as dispersal barriers and filters restricting species distribution within these boundaries. The biogeographic boundaries are then used to define coastal ecoregions (similar to the definition of Spalding et al. 2007), which are then grouped together to redefine coastal biogeographic provinces housing similar fauna. The resulting reorganisation is compared with the most recent and widely used subdivisions of coastal biogeography proposed in existing literature (Briggs and Bowen 2012; Spalding et al. 2007; Toonen et al. 2016) in terms of presence of exclusive species. This integrative approach provides valuable insights into the factors influencing species distributions and helps refine our understanding of coastal biogeography.

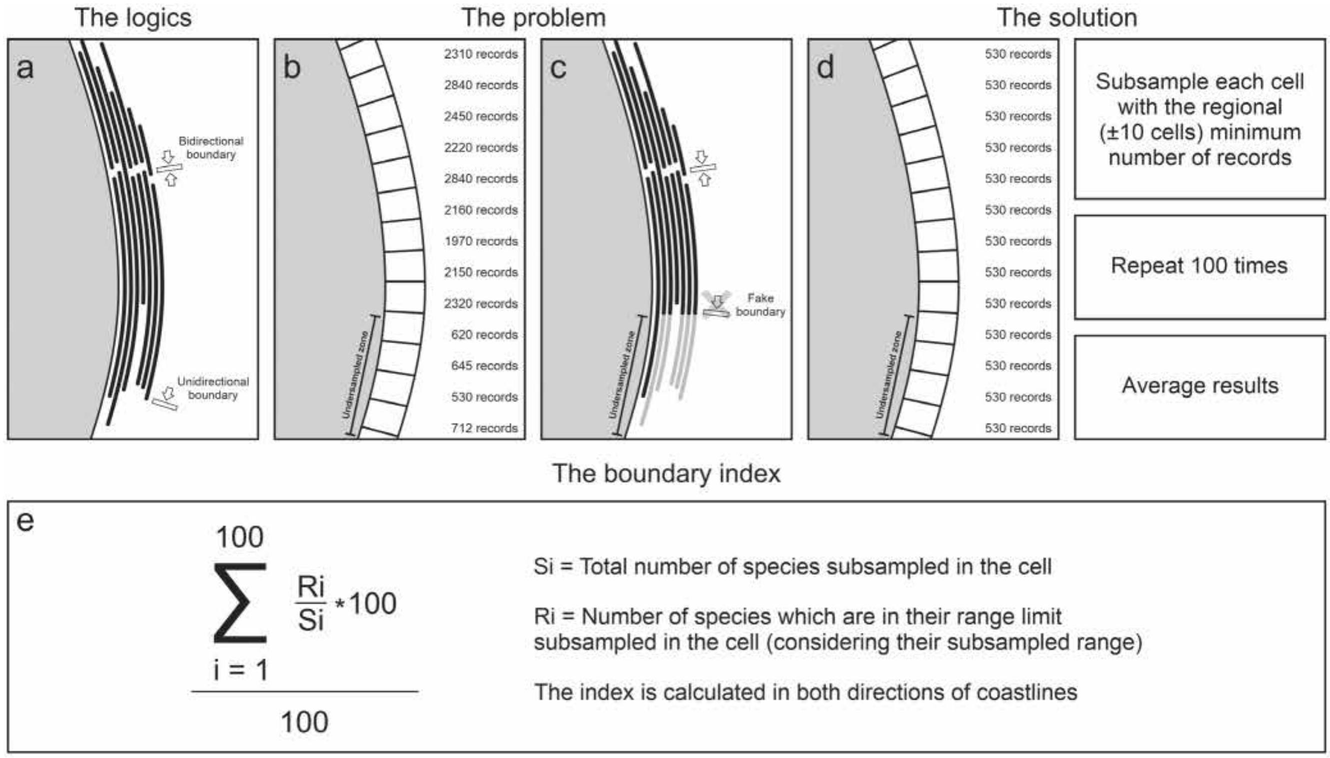

FIGURE 1 | Schematic representation of the method used to define biogeographic boundaries. (a) Biogeographic boundaries are defined as the zones where the range limits of extensive sets of species are concentrated relative to other zones in the region. In the scheme, each black line represents the range of a species. (b) The number of species records varies along the cells, with some zones being undersampled. (c) Undersampling in certain zones can lead to the artefact concentration of species' range boundaries in the vicinity of well-sampled zones. (d) Summary of the strategy to deal with data scarcity. (e) Mathematical formulation of the boundary index.

2 | Methods

2.1 | Biodiversity Data Acquisition, Processing and Analysis

OBIS and GBIF serve as the most comprehensive platforms for aggregating marine species observation datasets (GBIF 2024; OBIS 2024). We extracted the global dataset of animal species presence records from OBIS using the *robis* package in R 4.1.0 in March 2024. For better computational performance, the data was downloaded in bands of 1 degree of longitude. To obtain data from GBIF, we downloaded all non-bird (to reduce the amount of data) animal records contained in four polygons surrounding the zone of interest (Figure S1) using the *rgbif* package in R 4.1.0 in March 2024 (DOI: 10.15468/dl.s7n6sp, 10.15468/dl.su4e27, 10.15468/dl.d9epnm and 10.15468/dl.a633gy).

To process the data, for each downloaded band or polygon, we excluded records below the species level. We then intersected the spatial coordinates of the records with a polygon shapefile consisting of 600 cells of similar size distributed along the coasts (2° width) of the landmasses, as shown in Figure S1. These cells were arranged from the east to the west, based on the global configuration of coastlines, facilitating consistent spatial analysis and comparisons. The intersection was performed using the *st_join* function from the *sf* package in R. For each species retained in the intersection, we then checked for taxonomic validation by matching the species Aphia ID with its status in the World Register of Marine Species (WoRMS; Ahyong et al. 2024) using the *wormsbyid* function from the *worms* package in R. Species names were replaced with the current valid name in the case of synonyms and taxonomic changes, and all invalid and doubtful species were excluded from the dataset. All species classified as terrestrial in WoRMS were also excluded from the dataset, even if they were also classified as marine (e.g., marine birds). Finally, duplicate records (same species, latitude and longitude) were excluded using the *unique* function in R. The processing resulted in 8,060,353 unique records of marine animals.

To delineate the distribution of biogeographic boundaries, we identified regions that concentrate the range limits of extensive sets of species relative to other zones in the region (Figure 1a; Gaines et al. 2009; Pappalardo et al. 2015). However, the use of large multisource databases, such as OBIS and GBIF, poses challenges in addressing data scarcity in undersampled regions (Chaudhary and JohnCostello 2023; Costello et al. 2017; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022). These data limitations can introduce bias into large-scale analyses, potentially compromising the reliability of the findings (Leles et al. 2019; Robertson 2008). In our case, the lack of data in certain regions would lead to a concentration of species' range limits in the well-sampled neighbouring areas (Figure 1b,c).

To mitigate this issue, we implemented a random resampling procedure that equalised sampling effort across cells along the coastlines, ensuring a consistent sampling effort across all cells in the region (±10 cells; Figure 1d). For each landmass (Americas and Afro-Eurasia), we then determined the westernmost and easternmost cell along the coastline where each subsampled species was observed. Species with a distribution restricted to a single cell were not considered because their distribution is likely restricted to processes on scales smaller than those considered here or are rare species for which the records in the database are unlikely to represent their real range. We quantified the proportion of westernmost and easternmost boundaries relative to the total number of subsampled species in each cell. This process was repeated 100 times and the results were averaged to obtain a boundary index for each cell and direction (Figure 1d,e). This rigorous methodology increases the robustness of our results and provides a more accurate representation of the species distribution patterns along the studied coastlines. Cells with a boundary index greater than 22% (75th percentile) in total and greater than 30% above the average values of the neighbouring cells (±2 cells) were considered as biogeographic boundaries. Adjacent boundaries (up to 3 cells away) were interpreted as one.

To determine the relevance of the most representative animal phylum to define boundaries, we calculated the proportion of species range limits (considering the sum of both directions) at the boundary cell (for consecutive boundaries interpreted as one, we calculated the average between all cells). Boundaries were then classified by hierarchical clustering using the Ward method using the *hclust* function from the *stats* package in R, according to a Bray–Curtis similarity matrix generated based on the relative number of species range limits in each phylum using the *vegdist* function from the *vegan* package in R.

After, the identified biogeographic boundaries were used to divide the study area into ecoregions. Ecoregions are smaller scale biogeographic regions constrained by different oceanographic regimes and dispersal barriers (Spalding et al. 2007). The species occurrence dataset was classified according to the ecoregions, and they were then clustered based on the similarity of their biodiversity to establish biogeographic provinces. To do this, we subsampled the species records within each ecoregion, considering the lowest number of records present in an ecoregion (1056). A Sørensen similarity matrix was then generated based on the presence and absence of species using the *vegdist* function from the *vegan* package in R. This entire process was repeated 100 times, and the resulting similarity matrices were averaged. The final similarity matrix was subjected to hierarchical clustering using the Ward method. Hierarchical cluster analysis was performed using the *hclust* function from the *stats* package in R. To compare the biodiversity patterns of our realignment with the most recent and widely used subdivisions of coastal biogeography proposed in existing literature (Briggs and Bowen 2012; Costello et al. 2017; Spalding et al. 2007; Toonen et al. 2016), we examined the relative number of exclusive species (species unique to the province in the processed dataset) in relation to the number of cells within each province.

To gain insight into the oceanographic factors likely responsible for limiting species distribution at each boundary, we used datasets encompassing seafloor relief from the General Bathymetric Chart of the Oceans (GEBCO Bathymetric Compilation Group 2020) and surface temperature, salinity and oceanic circulation from the Global Ocean Physics Reanalysis (GLORYS12V1, 2019 data integrated; Mercator Ocean International 2024). To assess temperature and salinity changes along coastlines, we averaged the data within each cell of the grid (Figure S1) and compared it to the adjacent cells in both directions. All data analyses were performed using R 4.1.0 (R Core Team 2020). Maps were generated using QGIS 3.16 (QGIS Development Team 2024).

3 | Results and Discussion

3.1 | Biogeographic Boundaries

Applying our novel approach to 8,060,353 presence records representing 55,792 animal species from the OBIS and GBIF databases, we successfully identified 51 biogeographic boundaries (Figures 2–4). We applied the same methodology to a grid with three times wider cells to test whether the boundary index was stable in a dataset with reduced sampling bias (e.g., Kulbicki et al. 2013), and a similar distribution of the boundary index was obtained (Figure S2). Of the biogeographic boundaries, 24 were located along the coastlines of the Americas (Figure 2; Table 1; Box 1) and 27 along Afro-Eurasia (Figures 3 and 4; Table 1; Box 1). Unidirectional boundaries predominated in both landmasses (19 in the Americas and 17 in Afro-Eurasia), but bidirectional boundaries were also common in Afro-Eurasia (10 boundaries). Unidirectional boundaries are typically associated with hydrodynamic barriers that restrict species dispersal in only one direction (Byers and Pringle 2006; Gaines et al. 2009). While this was indeed the case for some of the unidirectional boundaries we observed here, in most cases unidirectional boundaries were identified at the transition from a species-rich to a species-poor region. Thus, although a potential barrier or environmental filter at these boundaries would actually restrict species in both directions, the low number of species in the poorest region did not result in a detectable boundary in that direction.

Such a circumstance has previously been hypothesised to be the reason for the predominance of unidirectional, poleward biogeographic boundaries along the east coast of North America (Pappalardo et al. 2015). Here, we confirm the pattern along coastlines across the continent, which are generally meridionally oriented, with most unidirectional boundaries restricting species towards the poles. This pattern is likely due to the higher species richness observed in tropical regions. The latitudinal gradient of species richness, with the highest levels of biodiversity typically found in tropical regions and decreasing towards higher latitudes, is one of the best documented biodiversity patterns on both land and sea (Chaudhary et al. 2017; Clarke and Crame 1997; Hayden and Dolan 1976; Hutchins 1947; Miloslavich et al. 2011).

Of the 51 boundaries identified, 9 (2, 6, 10, 13, 18, 25, 32, 46 and 50) are located very close to the boundaries of the biogeographic realms defined in Costello et al. (2017; Figure 5). The agreement between observations in both works is to be expected, as both analyses are partly based on OBIS animal occurrence data, and the strongest coastal boundaries are also likely to contribute to major changes in global marine biodiversity. However, by focusing specifically on coastal areas, we are able to identify

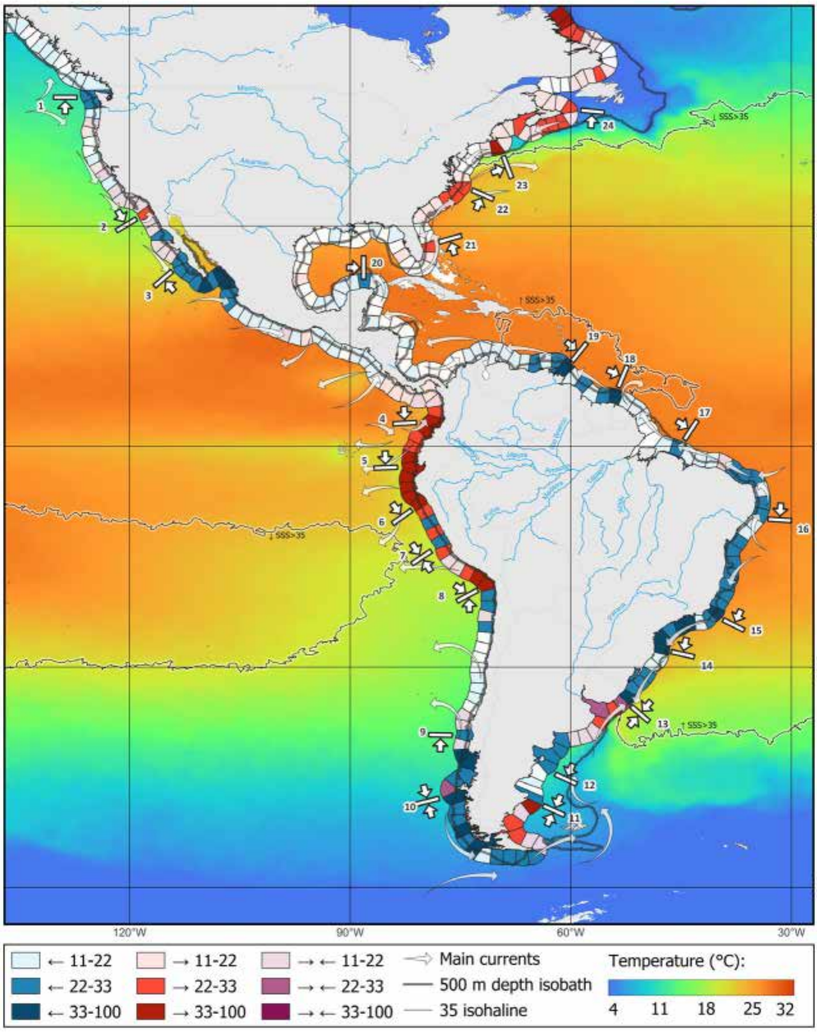

FIGURE 2 | Distribution of the boundary index along both directions of the coastlines (colour in the cells) in the Americas. The position and direction of the boundaries are indicated by white bars with one or two arrows for unidirectional and bidirectional boundaries, respectively. The sea surface temperature is shown as a colour gradient. Main currents are indicated (grey arrows), as well as the 35 salinity isohaline (black fin line) and the 500 m depth isobath (thick grey line).

complexities in coastal biogeographic patterns that typically reflect processes occurring at smaller scales and are masked when aggregated across the vast open ocean.

The biogeographic boundaries we identified also coincided with or were close to 13 boundaries (2, 5, 10, 12, 21, 22, 25, 29, 32, 34, 41, 50 and 51) of coastal biogeographic provinces (Briggs and Bowen 2012; Toonen et al. 2016) and to 31 boundaries (3, 7, 9, 10, 12, 13, 14, 15, 18, 19, 20, 21, 22, 23, 24, 25, 27, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 44, 46, 47 and 51) of coastal ecoregions (Spalding et al. 2007; Figure 5). To date, these are the most widely used biogeographic classifications of neritic habitats, and the former is based on several realignments of the seminal classification provided by Briggs (1974). In contrast to our approach based on a global species occurrence database, these studies were based on extensive literature reviews of the regional distribution of marine fauna. The use of biodiversity databases is often placed in doubt due to the issues inherent to these methods, such as sampling biases and taxonomic errors (Leles et al. 2019; Robertson 2008). However, the high agreement between our results and the distribution of boundaries well established in the empirical literature provides further validation of the biogeographic boundaries identified by our objective and sampling bias corrected approach. This also shows that our quantitative analysis independently corroborates previous biogeographic classifications, including the Spalding et al. (2007) ecoregions and the provincial scheme of Briggs and Bowen (2012), Toonen et al. (2016), thereby strengthening both the conclusions of this study and the value of these widely used systems. In addition, several of the boundaries we identified were located within previous provinces. Particularly, for regions or animal groups where information is limited, the identification of these new boundaries is an important contribution to guiding future fieldwork.

While our approach was intended to be integrative, considering the entire animal kingdom to define biogeographic boundaries, we must recognise that the patterns we observed are still mainly driven by the most diverse taxonomic groups present in each cell of the grid. Such higher diversity may be due both to natural differences between taxa and to regional taxonomic biases, not accounted for by our sampling correction procedure. To gain insight into the taxonomic relevance at each boundary, we

TABLE 1 | Alongshore biogeographic boundaries.

Biogeographic boundary	Dir	Biogeographic Province	Oceanographic features
Northeast Pacific			
Vancouver Island (**1**)	N	NE Pacific	GEO ● TEMP ● DIV
Southern California Bight (**2**)	S	NE Pacific | California	GEO ● TEMP ● UW ● ED
Magdalena Bay (**3**)	N	California | Tropical E Pacific	TEMP ● SAL ● CUR
Southeast Pacific			
Esmeraldas (**4**)	S	Tropical E Pacific	TEMP ● SAL ● CUR
Gulf of Guayaquil (**5**)	S	Tropical E Pacific |Peruvian	TEMP ● SAL ● UW ● RIV
Malabrigo (**6**)	S	Peruvian	GEO ● TEMP ● UW
Paracas Peninsula (**7**)	Bi	Peruvian	GEO ● TEMP ● UW
Arica Bend (**8**)	Bi	Peruvian | Chilean	TEMP
Valdivian coast (**9**)	N	Chilean	GEO ● TEMP ● SAL● RIV
Taitao Peninsula (**10**)	Bi	Chilean | Southern America	GEO ● TEMP ● SAL● RIV
Southwest Atlantic			
Puerto Deseado (**11**)	Bi	Southern America	TEMP ● SAL● RIV
Valdés Peninsula (**12**)	S	Southern America	TEMP ● SAL● RIV
Brazil–Malvinas Confluence (**13**)	Bi	S. America | Southern Brazil	TEMP ● SAL ● FT ● RIV ● CONV ● ED
South Brazil Bight (**14**)	S	Southern Brazil	TEMP ● SAL ● RIV
Cabo Frio upwelling (**15**)	S	S Brazil | T Brazil	TEMP ● UW
NBUC system (**16**)	S	Tropical Brazil	CUR
Maranhense Gulf (**17**)	SE	Tropical Brazil | Amazonian	GEO ● SAL● RIV ● CUR
Northwest Atlantic			
AORP: NBC retroflexion (**18**)	E	Amazonian	SAL ● RIV ● CUR
AORP: Orinoco River (**19**)	E	Amazonian | Gulf-Caribbean	SAL ● RIV ● CUR
Yucatán Peninsula (**20**)	E	Gulf-Caribbean	GEO ● CUR
Palm Beach (**21**)	N	Caribbean | Eastern USA	GEO ● TEMP ● UW ● FT ● CONV
Cape Hatteras (**22**)	N	Eastern USA	TEMP ● SAL ● FT ● CONV
Cape Cod (**23**)	N	Eastern USA | NW Atlantic	TEMP
Cape Breton (**24**)	N	NW Atlantic	TEMP
Northeast Atlantic			
English Channel (**25**)	S	NE Atlantic	TEMP ● CUR
Bay of Biscay (**26**)	Bi	NE Atlantic | Lusitania	GEO ● TEMP ● SAL ● RIV
Gulf of Cadiz (**27, 28**)	Bi	Lusitania	GEO ● TEMP ● FT ● UW
Canary (**29**)	Bi	Lusitania | Tropical EA	TEMP ● FT ● UW ● CONV
Cap-Vert Peninsula (**30**)	N	Tropical EA	SAL ● RIV ● UW ● DIV
Southeast Atlantic			
Congo River Mouth (**31**)	**S**	Tropical EA	SAL ● RIV
Angola–Benguela Front (**32**)	Bi	Tropical EA | S Africa	TEMP ● FT ● UW ● CONV ● OMZ
Lüderitz Upwelling Cell (**33**)	N	Southern Africa	TEMP ● UW ● OMZ

(Continues)

TABLE 1 | (Continued)

Biogeographic boundary	Dir	Biogeographic Province	Oceanographic features
Cape of Good Hope (**34**)	N	Southern Africa	UW
West Indian			
Delagoa Bight (**35**)	Bi	Southern Africa | W Indian	GEO ● CUR ● ED
Indian SEC bifurcation (**36, 37**)	Bi	W Indian | Arabian	DIV ● UW
Gulf of Aden (**38, 39**)	Bi	Arabian	GEO ● SAL
Gulf of Oman (**40, 41**)	Bi	Arabian | N Indian	GEO ● SAL ● OMZ
Indo-Pacific			
Karnataka Coast (**42**)	SE	Northern Indian	SAL
Krishna River Mouth (**43**)	NE	Northern Indian	SAL ● RIV
Ganges River Mouth (**44**)	E	Northern Indian	SAL ● RIV
Irrawaddy River Delta (**45**)	SE	N Indian | SE Asia	SAL ● RIV
Northwest Pacific			
Beibu Gulf (**46**)	N	SE Asia | Chinese	GEO ● TEMP ● SAL ● RIV ● CONV
Yangtze River plume (**47**)	N	Chinese | Korean	TEMP ● SAL ● RIV
Korea Bay (**48**)		Korean	TEMP ● SAL ● RIV
Musu Dan (**49**)	Bi	Korean | NW Pacific	GEO ● TEMP
Hokkaido (**50**)	Bi	Northwestern Pacific	GEO ● TEMP
Nevelskoy Strait (**51**)	Bi	Northwestern Pacific	GEO ● TEMP

Note: Direction species are restricted (Dir). Biogeographic province the boundary shapes the limit or is included within limits. Oceanographic features potentially behind the boundary.
Abbreviations: CONV, Currents convergence; CUR, Strong currents; DIV, Currents divergence; ED, Eddy; FT, Water masses front; GEO, Geomorphologic changes; OMZ, Oxygen minimum zone; RIV, Large river discharge; SAL, Strong salinity gradient; TEMP, Strong temperature gradient; UW, Changes in upwelling pattern.

classified them according to the relative importance of phyla in defining the boundary index. Three groups of boundaries were observed (Figure S3). In group 1, boundaries were mainly defined by Arthropoda (crustaceans), and Chordata (mostly fish) had a relatively low importance, which was similar to other popular taxa (Mollusca, Annelida, Cnidaria and Echinodermata, Figure S4). In group 2, range limits of both crustaceans and fishes were the most relevant, but Mollusca, Annelida, Cnidaria and Echinodermata also contributed to boundaries definition (Figure S4). Finally, in group 3, boundaries were mostly defined by the range limits of fish species (Figure S4). No patterns were observed in the spatial distribution of each group or its direction (Figure S3).

Although the boundaries were primarily driven by the most diverse taxonomic groups present in each grid cell, in most cases, a higher proportion of range limits relative to the total number of species was typically observed in cells within biogeographic boundaries, even among the less diverse phyla. Such circumstances were observed when comparing the three boundary groups with cells not classified as biogeographic boundaries (Figure S4b). The results show that the boundaries we identified generally correspond to changes in biodiversity across all animal taxa. Note that these differences were not significant (high standard deviation; Figure S4b) because the boundary index was interpreted in its regional context. Therefore, cells with a higher boundary index were not defined as boundaries in regions with widely high values (e.g., south-eastern coast of Asia; Figure 4).

3.2 | Potential Dispersal Barriers and Environmental Filters Associated With Biogeographic Boundaries

To gain insight into the oceanographic factors likely responsible for limiting species distribution at each biogeographic boundary, we used datasets that included seafloor relief, surface temperature, salinity, ocean circulation and referenced descriptions of regional oceanography (Figures 2–4; Table 1; Box 1). In most cases, the boundaries were shaped by a confluence of factors acting in concert to impede species dispersal. In particular, strong temperature gradients emerged as a prominent and recurring feature associated with most biogeographic boundaries. These temperature gradients were observed in 79% of the boundaries along the American coast and 44% along the Afro-Eurasian coast. Many of these boundaries are unidirectional towards the poles and are more prevalent along the American coastline, which is generally oriented in a meridional direction. Such pronounced temperature gradients result from various oceanographic processes or latitudinal climate variations. It is well documented that latitudinal variations and climate patterns play an important role in shaping

BOX 1 | Details of biogeographic boundaries.

Northeast Pacific

Vancouver Island (1)A unidirectional biogeographic boundary establishing the northern limit of species distribution was detected in the south of Vancouver Island. This boundary lies in the transition region between subtropical and temperate climates, with an annual mean surface temperature around 11°C. The predominant factor restricting the northward extension of species is likely the strong thermal gradient, which poses a challenge for species intolerant to colder waters. Additionally, the bifurcation of the North Pacific Current, leading to the northward Alaska Current and the southward California Current (Checkley Jr. and Barth 2009), may also contribute to this dispersal limitation.

Southern California Bight (2)A unidirectional biogeographic boundary establishing the southern limit of species distribution was detected in the Southern California Bight. North of the bight, Point Conception was historically reported as a biogeographic barrier in the Northeastern Pacific (Toonen et al. 2016). However, recent studies observed that many marine animals could cross that point, and a transition zone was recognised between Oregon and California biogeographic provinces, along the Southern California Bight (Toonen et al. 2016). In accordance, the boundary we detected is located in the southern limit of this transition zone. A set of noteworthy oceanographic features characterises this location. Below the surface, the headland of Point Conception extends towards Baja California, and south of this point, the continental shelf/slope is quite deeper. South of the boundary, coastal upwelling is reduced. These factors contribute to the establishment of a strong temperature gradient observed in epipelagic waters, with annual mean temperatures increasing from ~15°C in the north to ~18°C in the south. Additionally, in this region, the Southern California Countercurrent flows northward along the coast, as opposed to the southward California Current, generating the strong Catalina Eddy (Checkley Jr. and Barth 2009). The combined influence of changes in geomorphology and temperature, upwelling and diverging current patterns is likely to be responsible for this strong biogeographic boundary.

Magdalena Bay (3)A unidirectional biogeographic boundary establishing the northern limit of species distribution was detected north of the entrance of the Gulf of California, in Magdalena Bay. This boundary lies in the transition zone between subtropical and tropical climates, with annual mean surface temperatures increasing from less than 20°C to more than 27°C. Additionally, the California Current flows strongly southwards along the coast (Checkley Jr. and Barth 2009), in opposition to the direction of the boundary. Waters emerging from the Gulf are slightly saltier than the surrounding seawater, and the entrance of the Gulf itself breaks the connectivity of the continental shelf. The combination of these characteristics is likely responsible for hindering the dispersal of tropical species northwards.

Southeastern Pacific

Esmeraldas (4), Gulf of Guayaquil (5), Malabrigo (6) and Paracas Peninsula (7)A set of unidirectional biogeographic boundaries establishing the southern limits of species distribution (4, 5 and 6) and a bidirectional biogeographic boundary (7) were detected along a wide portion of the northwestern coast of South America. The entire region lies in a dynamic region characterised by surface and sub-surface currents from the Humboldt Current system flowing in distinct directions (Chaigneau et al. 2013). To the north of the boundaries, the region is characterised by surface equatorial and tropical water masses. As opposed to the south, particularly south of the Gulf of Guayaquil, coastal upwelling is strong, and the cold, nutrient-rich coastal water prevails over the continental shelf (Swartzman et al. 2008). As a consequence of the high productivity, a shallow oxygen minimum layer compressing the epipelagic habitat is present throughout this region, with a much higher intensity south of the boundary (Bertrand et al. 2010). Both circulation and upwelling patterns in this area exhibit large seasonal and interannual (regulated by ENSO) variability (Chaigneau et al. 2013; Chavez et al. 2008; Swartzman et al. 2008). Such variability is likely responsible for the presence of several biogeographic boundaries in the region. Additionally, strong changes in the width of the continental shelf are observed at both Malabrigo and Paracas Peninsula. These geomorphological differences further limit habitat availability for species settlement, imposing additional challenges for dispersal in the region.

Arica Bend (8)A bidirectional biogeographic boundary was detected at the Arica bend. At this boundary, there is a change in the coastline orientation, weakening eastward currents. As a consequence, coastal upwelling and productivity are reduced. Such conditions contrast sharply with those found in the north and south, particularly the northern Humboldt Current system in the north, where cold coastal waters with high productivity and a shallow oxygen minimum layer prevail (Bertrand et al. 2016; Demarcq 2009; Montecino and Lange 2009).

Valdivian Coast (9) and Taitao Peninsula (10)A unidirectional biogeographic boundary establishing the northern limit of species distribution (9) and a bidirectional biogeographic boundary (10) were detected along the southern coast of Chile. This region lies in the transition between temperate and subtropical climate patterns exhibiting a strong surface temperature gradient. In addition, the region marks the northern limit of the complex Chilean Fjords system and the southern limit of the Humboldt Current system. These boundaries are thus likely associated with the distribution limits of species inhabiting cold estuarine systems (Brattström and Johanssen 1983; S. Palma et al. 2017, 2018).

Southwestern Atlantic

Magellan Strait Plume: Puerto Deseado (11) and Valdés Peninsula (12) Two biogeographic boundaries were detected in the zone of influence of the cold and low-salinity plume emerging from the Magellan Strait over the Patagonian continental shelf (Palma and Matano 2012). Porto Deseado (11) is bidirectional and is located north of the Atlantic entrance of the Magellan Strait.

(Continues)

The Valdés Peninsula (12) was unidirectional, establishing the southern limit of species distribution. South of Porto Deseado, the influence of the plume is notably strong, with significant impacts on primary production (Gil et al. 2019; Palma and Matano 2012). North of this region, the influence of the plume weakens, but extends up to the Valdés Peninsula (Palma and Matano 2012), where the second boundary was observed. Consequently, both boundaries exhibit strong gradients in temperature and salinity.

Brazil–Malvinas Confluence Zone/La Plata River Plume (13)A bidirectional biogeographic boundary was detected along the Brazil–Malvinas Confluence Zone, where also lies the mouth of the large La Plata River. In this region, the strong Malvinas/Falkland Current approaches the coast, flowing northward along the coast and carrying cold and low-salinity waters from both the Southern Ocean and the La Plata River towards the Brazil–Malvinas Confluence Zone. Within this highly energetic zone, the Malvinas Current converges with the warmer and southward Brazilian Current, causing a strong thermohaline gradient and generating eddies (Jullion et al. 2010). The combination of a large river plume, converging currents and strong environmental gradients likely contributes to this multifaceted biogeographic boundary.

South Brazil Bight (14) and Cabo Frio Upwelling (15) Unidirectional biogeographic boundaries establishing the southern limit of species distribution were detected along a wide portion of the South/Eastern Brazilian Coast, extending from the coast of Santa Catarina State to Todos os Santos Bay. The South Brazil Bight (14) experiences local upwelling and lies within the transition zone between tropical and subtropical climates, characterised by strong temperature and salinity gradients due to higher river discharge (Castro et al. 2006). The second one lies north of Cabo Frio (15). This area features intense local coastal upwelling, resulting in a strong surface temperature cooling (Castro et al. 2006).

North Brazilian Undercurrent System (16)A unidirectional biogeographic boundary establishing the southern limit of species distribution was detected along the northeast coast of Brazil, under the influence of the North Brazilian Undercurrent system. The barrier appointed to isolate the Caribbean and Brazilian provinces is the Amazon–Orinoco Rivers plume. However, recent studies have shown that the strong westward currents along the north and northeast Brazilian coasts potentially act as a unidirectional barrier preventing the dispersal of Caribbean species to Brazil and enhancing dispersal towards the Caribbean Sea (Luiz et al. 2013; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022). The boundary we identified herein is associated with strong currents, supporting this hypothesis. The North Brazilian Undercurrent originates where the southern core of the South Equatorial Current (sSEC) reaches the Brazilian coast and bifurcates into two branches (Dossa et al. 2021; Stramma and England 1999). Additionally, along this region, at the convex coastline of the Touros Bend, two strong currents, the North Brazilian Undercurrent and the central core of the South Equatorial Current, converge and bottleneck, forming the North Brazilian Current (Dossa et al. 2021; Stramma and England 1999), likely contributing to limiting the southward species dispersal.

Maranhense Gulf (17)A unidirectional biogeographic boundary establishing the eastern limit of species distribution was detected at the Maranhense Gulf. West of this boundary, complex estuarine systems are present. Beyond the presence of these distinct habitats, the discharge of the estuaries connects with Amazon and Orinoco Plumes, producing a large low-salinity and highly productive coastal system. In opposition, the region to the east is dominated by tropical oligotrophic waters where complex reef systems are present (Carneiro et al. 2022). Additionally, this boundary is under the influence of the strong westward North Brazilian Current (Stramma and England 1999), likely contributing to limiting the eastward species dispersal.

Amazon–Orinoco Plume: NBC Retroflexion (18), Orinoco River Mouth (19) Two unidirectional biogeographic boundaries establishing the southeastern limit of species distribution were detected along the region under the influence of the large surface plume of low-salinity and high concentration of the suspended material caused by the Amazon and Orinoco rivers runoff (Lentz and Limeburner 1995). The Amazon–Orinoco plume was reported as a boundary between the Brazilian and Caribbean biogeographic provinces (Rocha 2003; Toonen et al. 2016; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022), but until now, the exact spots where biodiversity changes were never identified. The westernmost biogeographic boundary is located off the Orinoco River mouth, where the influence of the plume gets stronger. In the new classification, this boundary separates the Amazonian and Gulf of Mexico and Caribbean biogeographic provinces. The second boundary is located in the region where part of the North Brazilian Current is seasonally retroflexed, creating a highly energetic system characterised by strong currents, eddies and a strong influence from the Amazon River Plume (Johns et al. 1990).

Northwestern Atlantic

Yucatán Peninsula (20)A unidirectional biogeographic boundary establishing the southern limit of species distribution was detected at the Yucatán Peninsula, at the boundary between the Gulf of Mexico and Caribbean Sea. In this region with a curved coastline, the strong Yucatán current flows through the channel formed between the mainland and the main island of Cuba, heading towards the Gulf of Mexico (Alvera-Azcárate et al. 2009). This strong current likely hampers the dispersal of gulf species against its flow.

Palm Beach (21), Cape Hatteras (22), Cape Cod (23) and Cape Breton (24) Four unidirectional biogeographic boundaries establishing the northern limit of species distribution were detected along the east coast of North America. The first one is in the channel between Palm Beach (21) in the east of Florida Peninsula and Little Bahama Island. Although this region is influenced by the warm and northward-flowing Florida Current and Gulf Stream, local upwelling and coastal currents carry colder northern waters, likely lowering temperatures to the levels outside the tolerance range of warm-water tropical species (Walker and Gilliam 2013). The second biogeographic boundary lies at Cape Hatteras (22). In this region, the Gulf Stream shifts farther away from the coast and the southward currents derived from the Labrador Current flow alongshore, carrying colder temperate and less saline waters (< 18°C and < 35 in annual mean). The third biogeographic boundary lies in Cape Cod (23), at the entrance of

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the Gulf of Maine. In this region, colder waters from the Gulf, transported by southward currents, reduce average annual temperatures from 12°C to less than 8°C. The fourth biogeographic boundary lies in Cape Breton (24), at the entrance of the Gulf of St. Laurence. Parallel to the previous boundary, in this region, colder waters from the Gulf, transported by southward currents, reduce average annual temperatures from 7°C to less than 5°C.

Northeastern Atlantic

English Channel (25)A unidirectional biogeographic boundary establishing the southern limit of species distribution was detected in the south entrance of the English Channel. In addition to the presence of warmer subtropical surface waters in the south, the flux of seawater entering the channel through its southern entrance and flowing northwards potentially hinders dispersal of northern species to the south.

Bay of Biscay (26)A bidirectional biogeographic boundary was detected in the Bay of Biscay. Apart from the expected latitudinal temperature changes, this boundary exhibits strong variations in the seascape (Lezama-Ochoa et al. 2015). In the northern part, the continental shelf is much wider and continental runoff is markedly larger, resulting in a surface freshening reaching less than 35 annually. In consequence, primary production is much larger in the northern part of the Bay (Lezama-Ochoa et al. 2015). Such differences in the seascape were already associated with differences in microzooplankton and fish distribution (Lezama-Ochoa et al. 2015).

Gulf of Cadiz (27, 28) Unidirectional biogeographic boundaries were detected at both sides of the Gulf of Cadiz, the zone of connection between the Mediterranean Sea and the Atlantic Ocean. This region is located along the transition zone between temperate and subtropical climates and is associated with the warmer waters flowing out of the Mediterranean Sea. Thus, surface water rapidly warms from an annual mean of less than 15°C to over 18°C.

Canary (29) and Cap-Vert Peninsula (30)A bidirectional (29) and a unidirectional (30, establishing the northern limit of species distribution) biogeographic boundary were detected along the northwest coast of Africa. Along this region, the confluence between the southward-flowing Canary Current and the northward-flowing Mauritanian Current (Arístegui et al. 2009) isolates two distinct water masses and oceanographic processes occurring in the north (Canary Current System) and in the south (Mauritanian Current System), likely leading to intense biodiversity turnover in the region of Cape Blanc. The Canary system in the north features colder North Atlantic Central Water and intermittent upwelling throughout the year. Conversely, the Mauritanian System to the south transports warmer South Atlantic Central Water, with seasonal upwelling during winter (Arístegui et al. 2009). Differences in continental runoff, influenced by the desertic Saharan landscapes in the Canary system and higher runoff in the Mauritanian System, may further contribute to biodiversity turnover in this region. The Cap-Vert Peninsula biogeographic boundary (30) is established along the path of the North Equatorial Countercurrent as it approaches the African coast. Here, the Countercurrent splits into two branches: the Mauritanian Current in the north and the Guinea Current in the south/east (Arístegui et al. 2009). In contrast to the Mauritanian system, the Guinea/Angola Current System experiences reduced upwelling, with great effects on primary production (Alory et al. 2021). Additionally, the tropical rainforests and large rivers along the Guinea/Angola System's mainland greatly reduce regional sea surface salinity.

Congo River Mouth (31)A unidirectional biogeographic boundary establishing the southern limit of species distribution was detected close to the Congo River Mouth. Over the continent, the Congo River matches with the transition between the tropical rainforests to the north and the savannas to the south. In consequence, such a transition is reflected in the coastal salinity along the Guinea/Angola System, which is quite lower to the north of this boundary.

Southern Africa

Angola–Benguela Front (32)A bidirectional biogeographic boundary was detected in the confluence between the Angola and Benguela currents. The confluence of these two currents promotes a strong front isolating two distinct marine systems, expected to lead to significant changes in their biodiversity (Kirkman et al. 2016). To the North, the Angola Current flows southwards, transporting warm tropical water. In the northern region (the Guinea/Angola System), as previously discussed, upwelling is reduced and river runoff is high (Alory et al. 2021). Contrastingly, the Benguela Current carries cold southern waters and is associated with strong coastal upwelling. This upwelling brings cold, nutrient-rich and low-salinity waters to the surface, drastically reducing surface temperature and increasing primary production there. These distinct environmental characteristics create a strong thermal and ecological gradient in the area where the Angola and Benguela currents converge (Kirkman et al. 2016).

Lüderitz Upwelling Cell (33)A unidirectional biogeographic boundary establishing the northern limit of species distribution was detected in the region of the Lüderitz Upwelling Cell. The Lüderitz Cell is renowned as the world's most intense upwelling area, and it effectively divides the Benguela System into two distinct subsystems characterised by different hydrodynamic regimes and geomorphology (Kirkman et al. 2016). The Northern Benguela subsystem experiences continuous upwelling and high productivity, leading to strong oxygen depletion. In contrast, the Southern Benguela subsystem exhibits weaker and seasonally variable upwelling. Additionally, it features a wider and well-oxygenated continental shelf in the Southern subsystem (Kirkman et al. 2016).

Cape of Good Hope (34)A unidirectional biogeographic boundary establishing the northern limit of species distribution was detected at the Cape of Good Hope. At this spot, the strong Agulhas current has often been appointed a hydrodynamic barrier, hindering the dispersal of Atlantic species in the direction of the Indian Ocean. However, the boundary we observed herein establishes species distribution limits in the opposite direction. Therefore, the changes in species composition at this spot are likely due to the changes in the upwelling regime, which is quite stronger to the north of the boundary (Kirkman et al. 2016).

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Delagoa Bight (35)A bidirectional biogeographic boundary was detected at Delagoa Bight along the eastern section of the Agulhas Current. As mentioned in the previous boundary, the Agulhas Current, a powerful oceanic flow that moves westward along the southern corner of Africa, is renowned as a biogeographic barrier preventing Atlantic species from entering the Indian Ocean. However, the spot with most restriction seems to lie along the region of this boundary instead of the Cape of Good Hope, as previously appointed. This region is highly dynamic, featuring the formation of numerous eddies (Goschen et al. 2015; Lamont et al. 2010). Apart from their potential to disrupt local circulation, which can hinder species' passive dispersal, these eddies also contribute to the coastal upwelling in the southwestern coast of Africa, creating a strong thermal front (Goschen et al. 2015). In addition, the stretch of the coast to the south of the boundary exhibits a considerably thinner continental shelf compared to the larger banks to the south (Agulhas Bank) and north (Delagoa Bight). These geomorphological differences further limit habitat availability for species settlement, imposing additional challenges for dispersal in the region.

Indo-Pacific

Indian SEC Bifurcation (36, 37) Two unidirectional biogeographic boundaries were detected along the region of the bifurcation of the Indian South Equatorial Current, north of the island of Madagascar. Along this region, the Indian South Equatorial Current, locally referred to as Northeast Madagascar Current, reaches the East African Coast where it splits into two branches. The southern branch, known as the Mozambique Current, flows through the Mozambique Channel, where we detected the southern boundary (**36**), featuring several topographically induced eddies with potential to hinder species dispersal (Schott et al. 2009). Meanwhile, the northern boundary (**37**) is marked by a strong change in the production regime. To the south, along the East African Coastal Current, a typical western boundary system, with oligotrophic waters being adverted over the continental shelf, is observed. Distinctly, to the north, during the southwest monsoon season, neritic waters are transported offshore, upwelling nutrient-rich deeper waters and supporting enhanced primary production (Chatterjee et al. 2019).

Gulf of Aden (38, 39) Unidirectional biogeographic boundaries were detected at both margins of the Gulf of Aden entrance in the western Arabian Sea. The break in the continental shelf at the Gulf entrance, hampering benthic species dispersal, is likely behind this biogeographic boundary.

Gulf of Oman (40, 41) Unidirectional biogeographic boundaries were detected at both margins of the Gulf of Oman entrance in the north of the Arabian Sea. Beyond the break in the continental shelf at the Gulf entrance, which hampers benthic species dispersal, surface waters in the region exhibit higher salinity compared to the rest of the Arabian Sea. Moreover, there is a large minimum oxygen zone in this area (Paulmier and Ruiz-Pino 2009). These environmental factors have the potential to concentrate niche limits or a large group of species.

Karnataka Coast (42), Krishna River Mouth (43), Ganges River Mouth (44) and Irrawaddy River Delta (45) Several unidirectional biogeographic boundaries establishing the eastern limit of species distribution were detected along the coast of the North Indian Ocean and Bay of Bengal. At the northern end of the Bay of Bengal, the outflow of several large rivers results in a drop in surface salinity from more than 36 in the northern Arabian Sea to less than 32 in the northeastern Bay of Bengal and Andaman Sea. Interestingly, throughout this entire region, we did not identify boundaries operating in the opposite direction, indicating that the rich biodiversity of Southeast Asian Seas extends broadly up to the coast of India. This aligns with the distribution of previous biogeographic provinces, which encompass the entire Indo-Pacific within a single province. We hypothesise that the prevailing westward circulation along the Indo-Pacific plays a significant role in the westward spread of organisms from the Southeast Asian Seas, effectively overcoming potential barriers present along the coasts. Starting in the west, within the South China Sea, a strong western boundary current flows southwards towards the Sunda Shelf. This current compels seawater and potentially its associated fauna to outflow into the Indian Ocean through various straits in the area, including the Malacca Strait, which opens into the Andaman Sea (Qu et al. 2009). Once in the Indian Ocean, equatorial westward currents (Schott et al. 2009) have the potential to transport planktonic stages directly to the Southern coast of India, effectively bypassing the low salinity barriers present in the northern Bay of Bengal.

Beibu Gulf (46)A bidirectional biogeographic boundary was detected along the Beibu Gulf. Along this stretch of coastline, there is a huge geomorphologic change, transitioning from the wide Sunda Shelf in the South to a much narrower shelf along the coast of Vietnam and again to a shallow sea in the Beibu Gulf to the north of this boundary. It is worthy of noticing that all along the Sunda Shelf, we observe high rates of the eastern limits of species distribution. This large continental shelf interconnects the Islands of Southeast Asia to the mainland and was above sea level during past low sea-level periods, effectively acting as a physical barrier separating the Indian and Pacific realms. Presently, the shelf is characterised by several shallow-water seas, straits and bays that harbour unique habitats, supporting the highest biodiversity within the global ocean. In terms of currents and water masses, while the circulation in the South China Sea predominantly flows southward (Qu et al. 2009), northward coastal currents induced by seasonal monsoon winds can reach this region (Chen et al. 2012). The convergence of these currents creates a front between the low salinity plume originating from the Beibu Gulf and the Mekong and other rivers discharging to the south and the higher salinity waters of the South China Sea.

Northwestern Pacific

Yangtze River Plume (47) and Korea Bay (48)A bidirectional (48) and a unidirectional (7, establishing the northern limit of species distribution) biogeographic boundary were detected along the coast of the Yellow Sea. The Yangtze is the third largest

(Continues)

BOX 1 | (Continued)

river in the world and, coupled with other rivers from the Yellow Sea, its discharge produces a surface plume of low salinity and suspended material that spreads over the entire continental shelf in the East China Sea (Gomes et al. 2018). In addition to the biogeochemical changes induced by the river discharge, waters in the north of the Yellow Sea exhibit lower temperatures, likely contributing to preventing the dispersal of tropical and subtropical species.

Musu Dan (49) and Hokkaido (50). Two bidirectional biogeographic boundaries were detected at the Sea of Japan, one around Musu Dan (49), a headland at the northern point of the East Korea Bay and the other between the Japanese island of Hokkaido (50) and the coast of Russia. The Sea of Japan is a deep-water sea (up to 3700 m) surrounded by large continental shelfs and both boundaries are located at the beginning of the slope of these shelfs. Beyond the huge geomorphological changes, strong thermal gradients are observed along both boundaries, with a potential to limit species distribution.

Nevelskoy Strait (51)A bidirectional biogeographic boundary was detected along the Nevelskoy Strait. The Nevelskoy Strait is a narrow (7–40 km) and shallow (7–10 m depth) channel connecting the Sea of Okhotsk to the Sea of Japan in the northern entrance of the strait of Tartary (Ponomarev et al. 2018). Apart from this geomorphological barrier, the strait freezes during winter (Ponomarev et al. 2018), completely blocking species dispersal during this season.

terrestrial and marine biodiversity, with the highest levels of biodiversity typically found in tropical areas and decreasing towards higher latitudes (Chaudhary et al. 2017; Clarke and Crame 1997; Hayden and Dolan 1976; Hutchins 1947; Miloslavich et al. 2011).

Strong boundaries are also formed by the convergence of ocean currents, as observed in Brazil–Malvinas Confluence (13), Angola–Benguela Front (32) and Beibu Gulf (46, Table 1). In regions of convergence, distinct water masses meet, resulting in the formation of a pronounced thermohaline gradient front, which is particularly prominent in subtropical areas. These fronts can be overwhelming obstacles for many marine species (Clarke 1993; Gaylord and Gaines 2000), creating bidirectional boundaries. Conversely, diverging currents often result in the isolation of distinct marine systems that typically lack the pronounced fronts observed in converging currents. Consequently, these boundaries tend to be unidirectional and generally weaker than those associated with converging currents, as observed in Vancouver Island (1), Cap-Vert Peninsula (30) and Indian SEC bifurcation (36, 37; Table 1). In addition to affecting species changes, divergent currents also contribute to the transport of planktonic organisms, including larval stages, in opposite directions (Gaylord and Gaines 2000). Based on this premise, a recent work used dispersal modelling to split global coastlines into regions of high connectivity (Legrand et al. 2024). The simulations were performed considering the planktonic stage duration of distinct groups. Interestingly, when considering corals, fish and crustaceans, several of the boundaries of these hydrodynamic regions coincide with the biogeographic boundaries defined here (54% of the total: 1, 3, 5, 7, 8, 10, 11, 13, 16, 18, 19, 21, 23, 24, 25, 27, 28, 33, 36, 37, 40, 44, 45, 46, 47, 48, 49, 51). Such concordant observations reinforce the key role of ocean circulation and passive dispersal in shaping marine biodiversity (Legrand et al. 2024; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022).

Thirteen biogeographic boundaries are influenced by changes in upwelling regime and intensity, often triggered by changes in current direction or coastline orientation (Table 1). The most intense upwelling-related boundaries are found predominantly along the eastern margins of ocean basins, where they serve as distinctive features. However, their strength can be influenced by local circulation patterns in specific regions, such as in the Gulf of Guayaquil (5), the Arica Bend (8), the Canarias (29), the Angola–Benguela Front (32), the Lüderitz Upwelling Cell (33) and the Cape of Good Hope (34). Additionally, local upwelling can also occur along the western margins, and certain boundaries are associated with these systems, including the Cabo Frio upwelling (15), Palm Beach (21) and the Indian SEC bifurcation (36, 37). Upwelling induces significant changes in marine biogeochemistry, which can impede species dispersal between different systems (Fenberg et al. 2015; Teske et al. 2008; Thiede and Jünger 1992). The cold waters brought to the surface generate strong thermal gradients, which are particularly pronounced in tropical and subtropical regions where the surrounding surface waters are warmer (Fenberg et al. 2015). These upwelled waters transport substantial nutrient inputs into the photic zone, stimulating primary productivity. The availability of resources supports greater biodiversity (Gagné et al. 2020). Moreover, changes in nutrient supply can favour particular primary producers, such as diatoms, dinoflagellates or cyanobacteria, which in turn serve as prey for particular animal foragers, leading to variations in biodiversity across the food web (Sommer et al. 2002). Finally, because of their high productivity, upwelling regions often exhibit oxygen minimum zones. These zones compress the epipelagic habitat into a shallow surface layer, posing challenges for species with high metabolic requirements to traverse (Bertrand et al. 2010, 2011; Hauss et al. 2016; Tosetto et al. 2023).

Four major river outflows, the Amazon (18, 19), La Plata (13), Congo (31) and Yangtze (47), are associated with biogeographic boundaries. Additionally, the presence of several rivers reducing salinity in the northern Bay of Bengal, including the Ganges River, is associated with the boundaries depicted in the region (43, 44, 45). Freshwater discharge from large rivers induces significant changes in salinity, oxygen content, primary production and species composition at the base of the continental shelf's food web (Coles et al. 2013; Gomes et al. 2018), which can limit species dispersal. Among these, the Amazon and La Plata river plumes have previously been recognised as biogeographic barriers (Briggs 1974; Rocha 2003; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022).

The biogeographic boundaries observed in Southern California Bight (2), Malabrigo (6), Paracas Peninsula (7), Yucatan

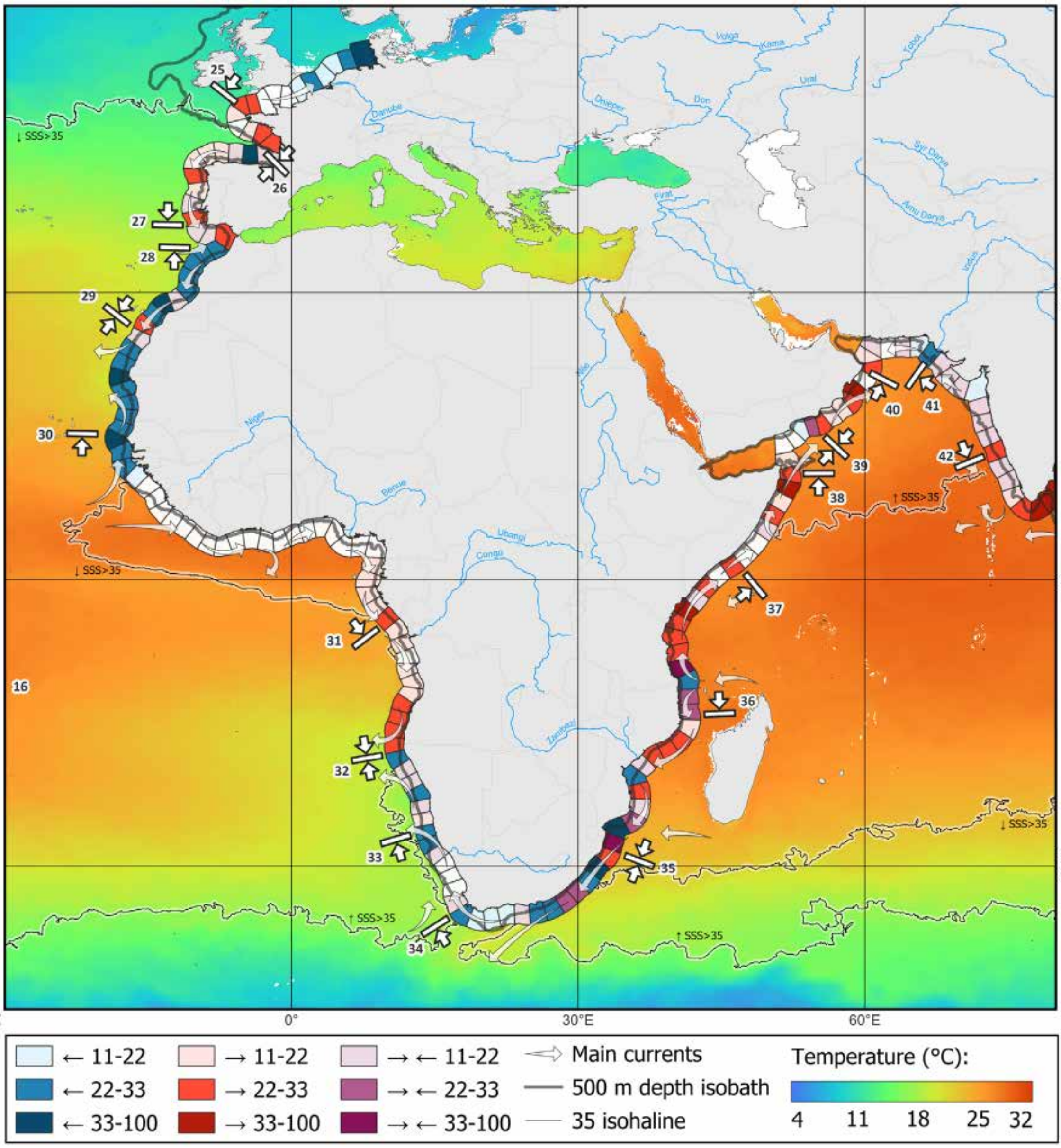

FIGURE 3 | Distribution of the boundary index along both directions of the coastlines (colour in the cells) in Europa and Africa. The position and direction of the boundaries are indicated by white bars with one or two arrows for unidirectional and bidirectional boundaries, respectively. The sea surface temperature is shown as a colour gradient. Main currents are indicated (grey arrows), as well as the 35 salinity isohaline (black fin line) and the 500 m depth isobath (thick grey line).

Peninsula (20), Palm Beach (21), Bay of Biscay (26), Delagoa Bight (35), Beibu Gulf (46), Musu Dan (49) and Hokkaido (50) are related to variations in continental shelf width and depth. A reduction in the extent of the continental shelf has the effect of limiting the habitat available for species settlement, while species adapted to deeper waters may not survive on shallow shelves (Kitchel et al. 2022). Consequently, these habitat barriers have the potential to limit dispersal in both directions. Similarly, disruptions in continental shelf connectivity caused by the Gulf of California (3), Gulf of Cadiz (27, 28), Gulf of Aden (38, 39) and Gulf of Oman (40, 41) are also associated with biogeographic boundaries. While long distances in the open ocean are known to be impassable for many coastal species (Floeter et al. 2008), our results underline that even relatively short distances that break continental shelf connectivity can affect dispersal. Large nearshore islands can hinder the dispersal of coastal species by restricting movement to the straits between the islands and the mainland. These narrow channels can limit dispersal, particularly in the face of strong currents as observed in the Yucatán Peninsula (20) and English Channel (25); periods of seafloor exposure during glacial periods of low sea level as observed along the Sunda Shelf (45 to 46), and seasonal freezing as in the Nevelskoy Strait (51).

The strong thermohaline gradients that were associated with many biogeographic boundaries occur mostly along water-mass fronts as a result of converging currents, upwelling or river discharge. Such processes interact with geomorphology and circulation patterns, interplaying to limit the dispersal of marine organisms, both by restricting movement and by filtering

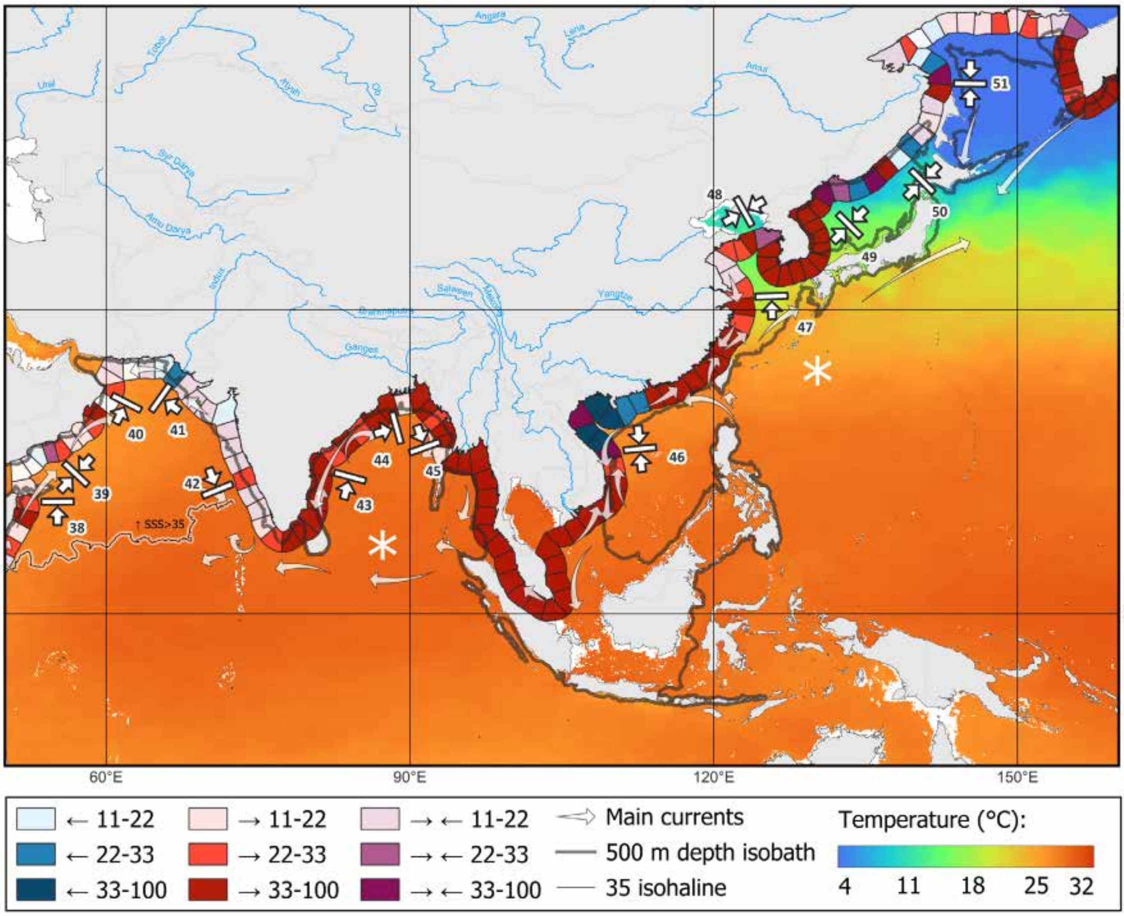

FIGURE 4 | Distribution of the boundary index along both directions of the coastlines (colour in the cells) in Asia. The position and direction of the boundaries are indicated by white bars with one or two arrows for unidirectional and bidirectional boundaries, respectively. The sea surface temperature is shown as a colour gradient. Main currents are indicated (grey arrows), as well as the 35 salinity isohaline (black fin line) and the 500 m depth isobath (thick grey line). *Indicates zones with high seasonal variability in ocean circulation.

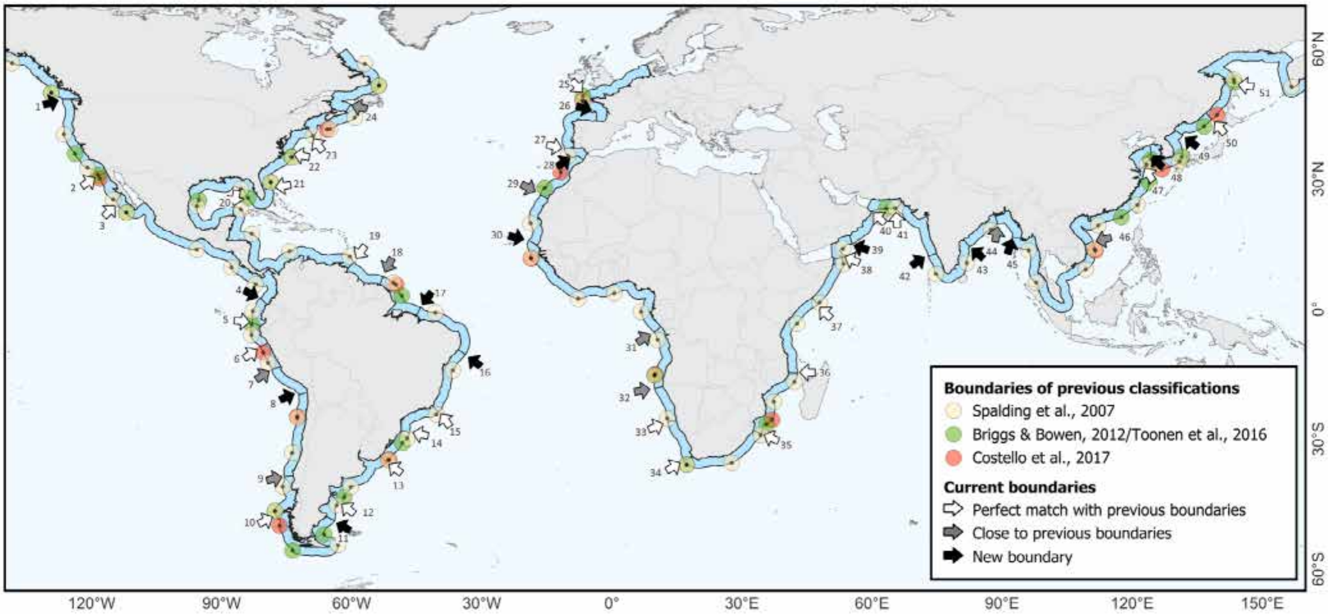

FIGURE 5 | Relation of biogeographic boundaries identified in this study to the boundaries of previous biogeographic classifications (Briggs and Bowen 2012; Costello et al. 2017; Spalding et al. 2007; Toonen et al. 2016).

species through their ecological niches. In the face of recent climate change, strong changes in the global ocean are expected (Bijma et al. 2013). Predicting biodiversity responses to this scenario, including changes in dispersal barriers and the extent and direction of species range shifts, is a major challenge for scientists and resource managers. Making such predictions is not straightforward due to the diverse nature of the mechanisms that constrain species distributions at the boundaries we observe. Most recent studies report a prevalence of poleward range shifts as a consequence of warming sea surface temperatures (Poloczanska et al. 2013; Walther et al. 2002). However, beyond temperature, changes in ocean circulation, river discharge, upwelling intensity and deoxygenation are expected to interact with climate change (Bijma et al. 2013). As we have seen, these features promote stronger fronts that create many of the coastal biogeographic boundaries. Therefore, a first step in making confident predictions about the future distribution of coastal biodiversity should ideally consider these issues.

3.3 | Redefining Coastal Biogeographic Provinces

The identified biogeographic boundaries isolate the biota of 53 ecoregions along the coastlines of the Americas and Afro-Eurasia. These systems are generally smaller and exhibit lower levels of endemism than are typically expected for biogeographical provinces. The occurrence of biodiversity turnover at such smaller scales is an expected result, since within each province there are different oceanographic regimes and dispersal barriers that may constrain species distribution. We therefore considered this primary classification as ecoregions to be nested within biogeographic provinces. While biogeographic provinces were defined as primary units in Briggs and Bowen (2012) and Toonen et al. (2016), Spalding et al. (2007) proposed a nested system, where ecoregions were grouped within provinces and realms based on the published literature and author expertise.

Although relevant for defining the biogeographic boundaries, the boundary index used in our approach is not suitable as an objective criterion for defining larger biogeographic provinces in which ecoregions are nested (i.e., a lower value to define ecoregions and a higher value to define provinces), as it is relative to the number of species subsampled, which varies greatly depending on the regional context. Instead, to define biogeographic provinces, we used a clustering method based on the similarity of biodiversity between ecoregions. This resulted in the identification of 23 provinces (Figure 6, shapefile in File S5 and S6).

Of the 21 biogeographic boundaries delineating the new biogeographic provinces, nine are aligned with and six are close to previous boundaries between the biogeographic provinces or realms defined in Briggs and Bowen (2012), Toonen et al. (2016), Spalding et al. (2007) and Costello et al. (2017). The slight deviations between some of our boundaries and the previous boundaries of the biogeographic provinces are likely due to our integrative approach, which was able to detect boundaries more precisely. Furthermore, our analysis has revealed the presence of additional subdivisions and major realignments of coastal biogeographic provinces, guided by 6 additional boundaries.

Compared to the subdivision of Briggs and Bowen (2012), and Toonen et al. (2016), in which our biogeographic provinces presented higher resemblance in terms of shared boundaries, we propose the following subdivisions or major realignments. Along the western coast of South America, we propose the Peru-Chilean biogeographic province be split into the Peruvian and Chilean provinces, with the division occurring at the **Arica Bend (8)**. On the eastern coast of South America, our analysis suggests a split of the Argentinean province at the **Brazil–Malvinas Confluence (13)**, which is also a realm boundary in Costello et al. (2017) and an ecoregion boundary in Spalding et al. (2007). While this region was previously considered as a boundary between biogeographic provinces in Briggs (1974), it has been excluded in their recent realignments (Briggs and Bowen 2012; Toonen et al. 2016). The boundary between the Brazilian and Argentinean provinces was established at the Santa Catarina Bight, where we also found a unidirectional boundary. However, our analysis reveals a higher biodiversity transition in the **Cabo Frio upwelling** region **(15)**, which is also a province boundary in Spalding et al. (2007). The Amazon–Orinoco river plume has long been recognised as a dispersal barrier between the Tropical Brazilian Coast and the Caribbean Sea (Rocha 2003; Toonen et al. 2016; Tosetto, Bertrand, Neumann-Leitão, and Nogueira Júnior 2022). However, specific locations of biodiversity shifts within this region have not been adequately identified. Accordingly, we portray the Amazonian region as a biogeographic province isolated from the Caribbean province by the region with the stronger influence of the **Amazon–Orinoco plume (19)** and from the Tropical Brazil province at the **Maranhense Gulf (17)**, both of which are also province boundaries in Spalding et al. (2007).

In the previous classifications of the Atlantic coast of North America, the Carolina province was divided into two sections isolated by the tip of Florida, which was included in the Caribbean province (Briggs and Bowen 2012; Toonen et al. 2016). This is not an expected result for a biogeographic province, which is typically characterised by uniform regions. In our new classification, this inaccuracy has been resolved by including the western part of the Carolina province in the Gulf of Mexico and Caribbean province. At the other extreme, the boundary between the Carolina and Western Atlantic provinces was previously established at Cape Hatteras, where we also detected a unidirectional biogeographic boundary. However, our analysis reveals a higher biodiversity transition at **Cape Cod (25)**, which is also an ecoregion boundary in Spalding et al. (2007) and here isolates the Eastern USA and Northwestern Atlantic provinces. Across the Atlantic Ocean, the boundary between the Eastern Atlantic and Lusitanian provinces was established at the English Channel, where we also detected a unidirectional boundary. However, our analysis reveals a higher biodiversity transition in the **Bay of Biscay (25)**, which here isolates the Eastern USA and Northwestern Atlantic provinces.

Moving to the Indian Ocean, we propose to divide the Western Indian Ocean biogeographic province into the Southwestern Indian and Arabian provinces, with the division occurring at the northern part of the **Indian SEC bifurcation (37)**, which is also an ecoregion boundary in Spalding et al. (2007). In South Asia, the Indo-Polynesian was previously recognised as the largest biogeographic province defined in the literature, extending

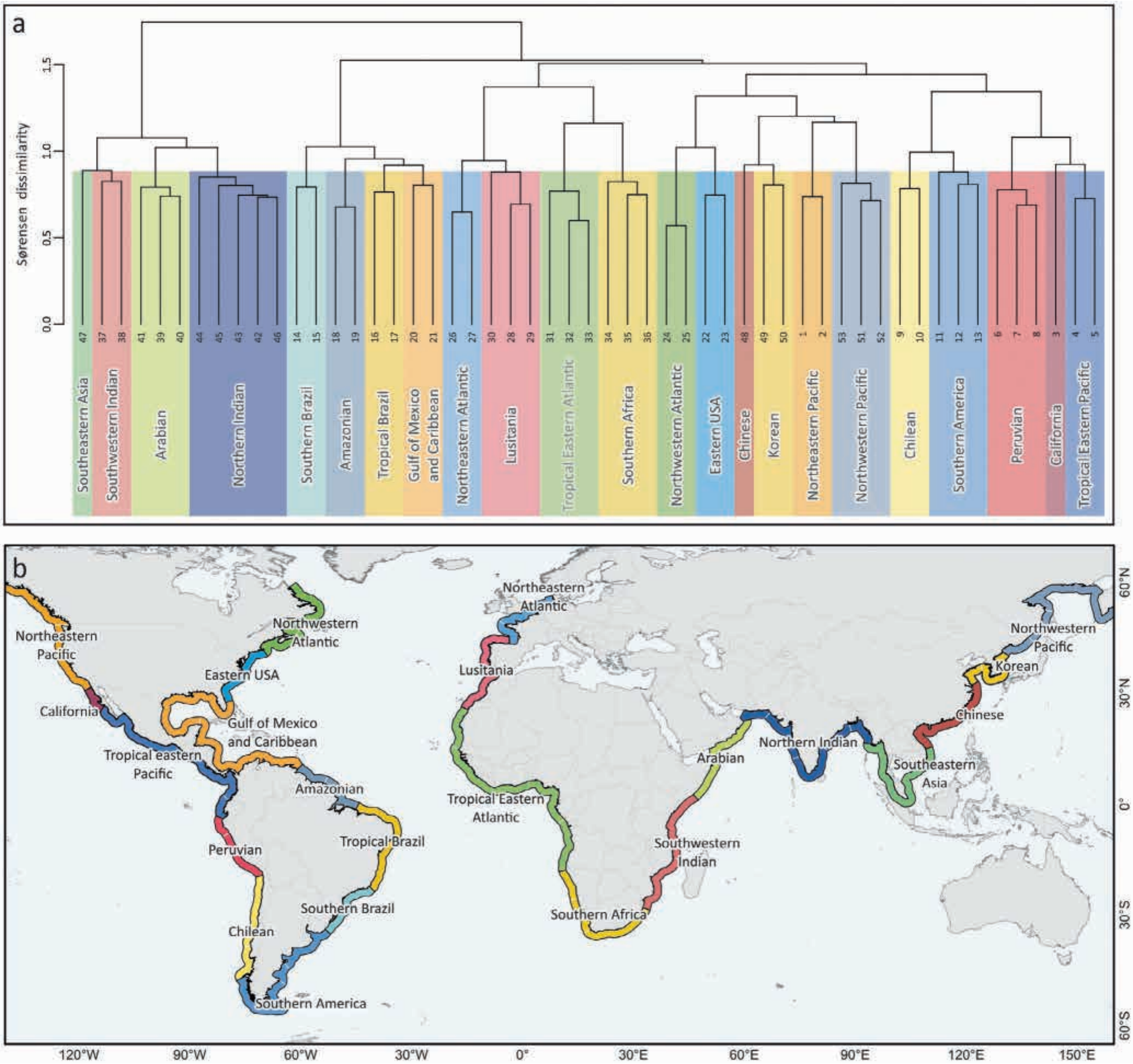

FIGURE 6 | (a) Cluster analysis dendrogram classifying 52 ecoregions in 23 biogeographic provinces. (b) Distribution of coastal biogeographic provinces.

from the west coast of India to the coast of China. However, our analysis revealed the presence of multiple unidirectional boundaries within this region, consistent with a previous study suggesting subdivisions within the province (Kulbicki et al. 2013). The most significant changes in the biodiversity in this region are in the **Irrawaddy River Delta (45)**. On the northwestern Pacific coast, we were unable to detect the previously defined boundary between the Indo-Polynesian and Sino-Japanese provinces south of Taiwan Island. Instead, we identified a robust bidirectional boundary with multiple interacting oceanographic features located to the south, specifically in **Beibu Gulf (46)**, which is close to a realm boundary in Costello et al. (2017) and a province boundary in Spalding et al. (2007) and here serves as the boundary between Southeastern Asia and Chinese provinces. Finally, in the previous classification (Briggs and Bowen 2012; Toonen et al. 2016), the Oriental province was isolated in several sections. In our new classification, this has been resolved by the creation of the new Korean province, which is isolated from the Chinese province at **Musu Dan (49)**.

Traditionally, biogeographic provinces have been defined based on a specified level of endemism, often requiring a minimum of 10% (Briggs 1974; Briggs and Bowen 2012). To assess the level of endemism within the newly defined biogeographic provinces resulting from our classification, we calculated the proportion of exclusive species within each province when considering all marine animals and the most representative phyla in terms of total species number (Figure 7a). It is important to note, however, that this measure is not a strict measure of endemism, as it does not take into account the possibility that species are present in regions of the world ocean other than the grid of cells considered in our study. The proportion of exclusive species was in most

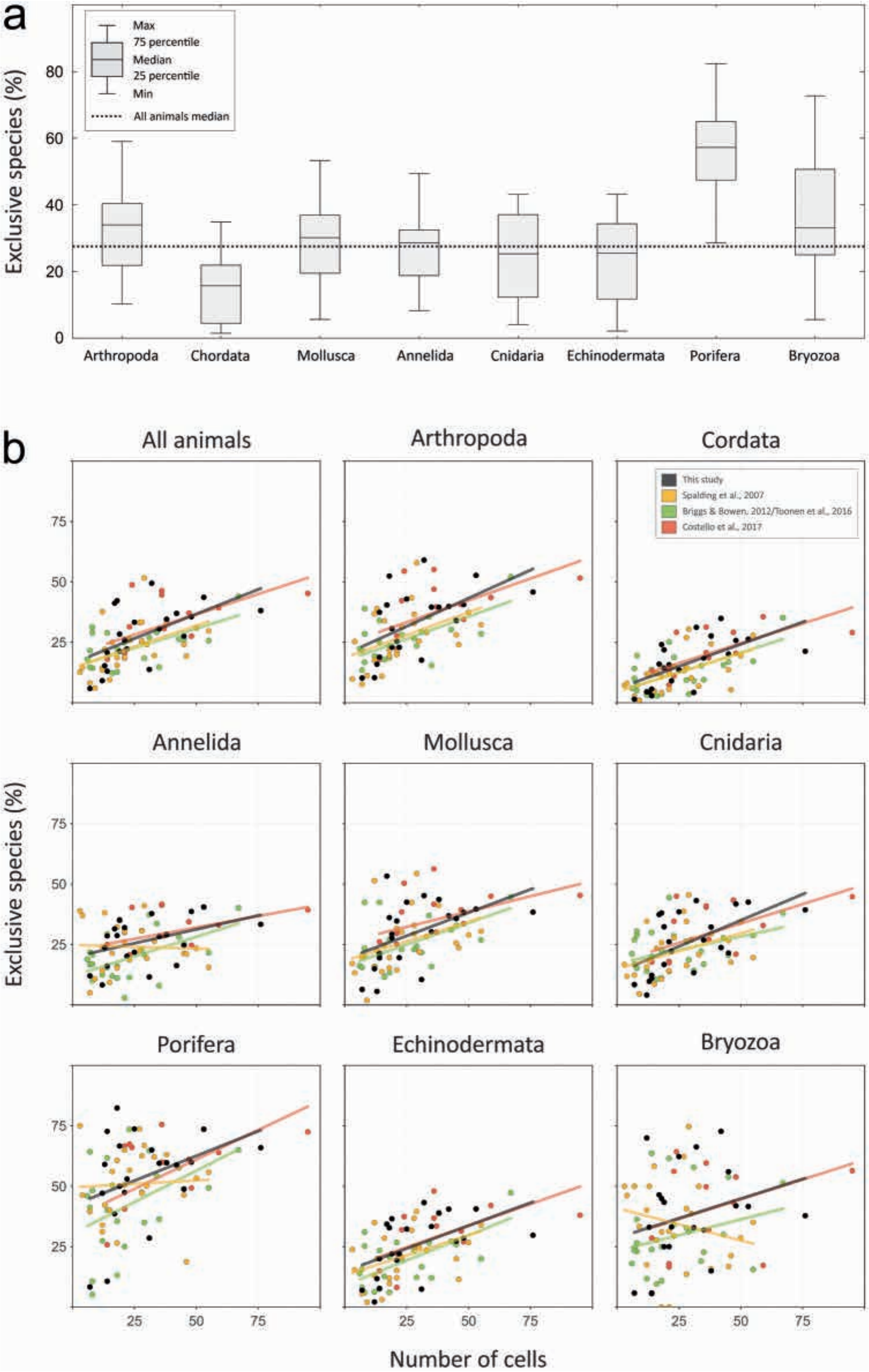

FIGURE 7 | (a) Proportion of exclusive species among the most representative phyla in the new realignment of biogeographic provinces. (b) Comparison of the proportion of exclusive species relative to the number of cells in each province from this study and previous biogeographic classifications (Briggs and Bowen 2012; Costello et al. 2017; Spalding et al. 2007; Toonen et al. 2016) considering the entire set of marine animals and the most representative phyla.

cases higher than 25% (median for all marine animals = 27.6%). Among the most representative phyla, the number of exclusive species within provinces was higher in Porifera and Bryozoa (Figure 7a). These two phyla have limited dispersal since they are composed of predominantly sessile organisms with very short planktonic larval durations (Bradbury et al. 2008). Thus, the higher endemism among them would be expected. On the other hand, the lower number of exclusive species was observed in the Chordata (Figure 7a), which is mainly composed of mobile fish with long planktonic larval durations (Bradbury et al. 2008).

To ensure a fair comparison with the previous classification of coastal biogeographic provinces and realms (Briggs and Bowen 2012; Costello et al. 2017; Spalding et al. 2007; Toonen et al. 2016), we repeated the calculation within the same coastal areas and dataset, split at the points of the boundaries of previous classifications (note that provinces and their extensions outside the grid of our study were not considered). We then compared the proportion of exclusive species relative to the number of cells in each province (Figure 7b). The results revealed that, for both the full set of marine animals and the most representative phyla, our new realignment yielded a higher proportion of exclusive species when compared to the provinces Briggs and Bowen (2012), Toonen et al. (2016) and Spalding et al. (2007; Figure 7b). The number of exclusive species in our realignment was also similar to that observed in Costello et al. (2017; Figure 7b). However, the realms within their work were in general larger than the provinces depicted here and the number of exclusive species is area dependent (i.e., one single zone encompassing the whole dataset would consist entirely of exclusive species). Since larger areas tend to encompass more exclusive species, our more spatially refined realignment provides a more robust and meaningful biogeographic delineation. This finding suggests that subdividing provinces based on the identified biogeographic boundaries results in a greater degree of biogeographic isolation.

4 | Conclusions

This study uses an objective methodology to provide a comprehensive reassessment of coastal biogeographic provinces, their associated boundaries, and the oceanographic factors that shape marine biodiversity. Through the identification of 51 biogeographic boundaries along the coastlines of the Americas and Afro-Eurasia, and the subsequent clustering of ecoregions, we have refined the classification to include 23 coastal biogeographic provinces. This innovative approach, based on objective criteria and an integrative analysis of global species distribution data, has significantly improved the accuracy and robustness of the province boundaries compared to previous methodologies. Historically, the delineation of boundaries between ecoregions and provinces has lacked a standardised methodology and relied primarily on local knowledge of biodiversity distribution (Briggs 1974, 1995; Briggs and Bowen 2012). Therefore, the use of large-scale databases of species occurrences to identify biogeographic boundaries and their use as reference points for separating neighbouring provinces represents a significant advance in our understanding of biodiversity patterns in marine systems. Of the biogeographic boundaries identified and retained as province boundaries, nine coincide with the previous boundaries, and six are located in close proximity to them. Additionally, we have proposed six new subdivisions of biogeographic provinces in regions where literature data is limited. The remaining boundaries delineate finer-scale ecoregions.

Despite our efforts to minimise the effects of sampling bias, it is important to acknowledge the potential impact of data scarcity, particularly in undersampled and poorly studied areas. However, there is reason for optimism as marine science has advanced in less developed countries, leading to an increase in marine biodiversity studies in recent years (e.g., Eduardo et al. 2022; Tosetto, Bertrand, et al. 2022; Tosetto, Neumann-Leitão et al. 2022). It is therefore crucial to include distribution data from these regions in the databases. Doing so will not only confirm our findings but also have the potential to uncover new biogeographic boundaries and provide deeper insights into the distribution of marine life across the world's oceans.

The potential dispersal barriers and environmental filters associated with the biogeographic boundaries identified in this study were characterised by diverse oceanic features, with strong temperature gradients emerging as a prominent factor influencing biodiversity patterns. Additionally, converging currents and upwelling played a key role in shaping such patterns. Variations in continental shelf width and disruptions in connectivity also contributed to the formation of potential dispersal barriers. Given the ongoing effects of climate change on oceanic conditions (Bijma et al. 2013), accurate predictions of species range shifts are essential, particularly for conservation efforts. The comprehensive assessment of oceanographic factors presented in this study provides valuable insights into the mechanisms influencing species distributions. By incorporating these factors into their analysis, resource managers and scientists can improve their ability to predict how coastal biodiversity will respond to changing environmental conditions. Armed with this knowledge, they can develop more effective conservation strategies to safeguard marine ecosystems under changing environmental conditions.

Author Contributions

Everton Giachini Tosetto and Arnaud Bertrand conceptualized the study. All authors contributed to methodology, formal analysis, and investigation. Everton Giachini Tosetto, Matthieu Lengaigne, and Arnaud Bertrand wrote the original draft, and all authors contributed to review and editing of the manuscript.

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Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the article and its Supporting Information.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70083.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Grid of cells considered in the analyses. **Figure S2:** Results of the boundary index (see methods) when considering a grid of three times larger cells to perform the analyses. **Figure S3:** Biogeographic boundaries classified in three groups according to the relative importance of phyla (arrows) and relative importance of most representative phyla in each boundary. **Figure S4:** (a) Mean and standard deviation of the relative importance of most representative phyla in each group of boundaries. (b) Average proportion of species in their range limit in relation to the total number of species in each phyla in each group of boundaries and in cells not considered boundaries (out). **File S5:** Occurrence data of Animal species underlying our results. **File S6:** Shape file of ecoregions and realigned biogeographic provinces.