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RESEARCH PAPER

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The stability of coastal benthic biogeography over the last 10 million years

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Abstract

Aim: We demarcate marine benthic global bioregions based on fossil and recent occurrence data. Our main goal is to compare past and present biogeography and to extract major abiotic drivers of biogeographical patterns. We specifically test the hypothesis that global biogeography has changed markedly after the climatic fluctuations of the past 10 Myr.

Location: Worldwide.

Time period: Recent; late Miocene–Pleistocene interval.

Major taxa studied: Benthic taxa with a rich fossil record: Bivalvia, Brachiopoda, Bryozoa, Gastropoda, Echinodermata, Decapoda and reef corals.

Methods: We use occurrence data from the Ocean Biogeographic Information System (OBIS) and the Paleobiology Database to construct compositional networks and outline objective marine bioregions of benthic marine invertebrates using the "infomap" community detection algorithm. We assess the association of modern bioregions with a variety of environmental parameters by applying multivariate statistical analyses, such as principal components analysis, random forests and multiple logistic regressions.

Results: Recent first-order bioregions for the coastal ocean are, in general, consistent across all taxa. Seawater temperature surpasses nutrients, primary production and salinity as a predictor of modern bioregion distributions. Despite substantial climatic variations, late Cenozoic biogeographical patterns recorded in fossils are very similar to modern ones.

Main conclusions: Biogeographical boundaries within oceans are strongly controlled by temperature gradients, but open oceanic and continental barriers determine the global biogeographical structure. The joint structure of a landmass distribution, deep ocean basins and the latitudinal temperature gradient defines bioregionalization of the benthic marine habitat, which did not change substantially over the past 10 Myr.

KEYWORDS
global, invertebrates, marine, networks, palaeobiogeography, recent biogeography, temperature

1 | INTRODUCTION

We know intricate details about the geographical distribution of life in both terrestrial and marine habitats, but much less about the drivers of the macroscale structure. Plate tectonics and climate shape the principal biogeographical patterns on land (Ficetola, Mazel, & Thuiller, 2017), and similar processes are sometimes invoked for the marine realm (Costello et al., 2017; Spalding et al., 2007). A rigorous and quantitative assessment of benthic marine biogeography is still lacking, although revealing these factors and the stability of global structure would greatly aid the success of broad-scale conservation strategies (Lourie & Vincent, 2004) and sustainable resource management (Lourie & Vincent, 2004; Olson & Dinerstein, 1998) in the face of anthropogenic climate change (Perry, Low, Ellis, & Reynolds, 2005). Understanding the determinants of biogeography is also important for a suite of fundamental research questions in ecology and evolution about speciation processes (Briggs & Bowen, 2013; Heads, 2005; Stigall, 2013) and taxonomic richness patterns (Beaugrand, Rombouts, & Kirby, 2013; Chaudhary, Saeedi, & Costello, 2016; Tittensor et al., 2010).

1.1 | Determinants of biogeography

Deep oceanic basins and landmasses form obvious barriers to species dispersion that are ultimately controlled by plate tectonic processes. Therefore, shallow-water biogeography and continent configuration are likely to be connected closely. Such a connection is suggested, but not explicitly explored, by the association between past global marine biodiversity and the fragmentation of continents (Zaffos, Finnegan, & Peters, 2017). Longitudinal (i.e., north–south) coastlines are split into chains of bioregions (Valentine, Foin, & Peart, 1978), implying that variables with latitudinal gradients play a major role in shaping the realm-level pattern. These include the direct effect of ambient temperature and dissolved oxygen concentration on species distribution patterns (Pörtner & Knust, 2007; Sunday, Bates, & Dulvy, 2012), but changes in primary production and nutrient concentrations are also associated with boundaries of marine bioregions (Longhurst, 2007). Finally, different preferences of seawater salinity are also expected to influence biogeographical patterns (Costello et al., 2017). Revealing the history of biogeography by using phylogeography (Briggs & Bowen, 2013) or fossil distribution patterns, and by analysing the distribution of present-day bioregions, is expected to contribute to our understanding of their determinants.

1.2 | Past conditions

Most extant marine invertebrate species have been present for the last 10 Myr and should thus enable a comparison between recent and fossil biogeographical patterns. There are indications for the long-term stability of pelagic ecosystems at the level of oceanic gyres (Sibert, Norris, Cuevas, & Graves, 2016), but there are no studies on the stability of benthic marine biogeography.

Environmental conditions have varied greatly since the late Miocene, potentially affecting global oceanic biogeography. Progressive cooling (Raymo & Ruddiman, 1992), cold snaps in the late Miocene (Herbert et al., 2016) and a warmer interval in the Pliocene (Brierley et al., 2009; Fedorov et al., 2006) preceded the Pleistocene ice age. The habitable area changed owing to the intermittent sea-level rises and falls driven by glacial–interglacial cycles (Ludt & Rocha, 2015). The resulting environmental changes could have had notable effects on global bioregionalization by changing patterns of nutrient supply, primary production, salinity and ambient temperature.

1.3 | Approaches to revealing biogeographical structure

The discipline of marine biogeography has yet to embrace organism occurrence data, which have contributed to a more objective delineation of terrestrial bioregions and to a better understanding of abiotic controls without circular reasoning (Ficetola et al., 2017; Holt et al., 2013; Kreft & Jetz, 2010; Vilhena & Antonelli, 2015). In the modern ocean, most of the traditional global partitioning schemes are semi-quantitative and incorporate several abiotic variables (Ekman, 1953; Longhurst, Sathyendranath, Platt, & Caverhill, 1995; Spalding et al., 2007; Spalding, Agostini, Rice, & Grant, 2012; Watling, Guinotte, Clark, & Smith, 2013) or have been limited to a few higher taxa (Briggs & Bowen, 2012; Kulbicki et al., 2013). Establishing biogeographical patterns from fossils suffers from the same problems, relying either on subjective criteria (e.g., Westermann, 2000) or on taxon-specific analyses (Harper et al., 2013; Rojas, Patarroyo, Mao, Bengtson, & Kowalewski, 2017; Vilhena et al., 2013).

A robust partitioning approach should handle taxon occurrence (and, if available, phylogenetic) information in an automatic and reproducible way (Kreft & Jetz, 2010). It should also be independent from abiotic variables and should be applicable to occurrences of any kind, for instance to fossils. Owing to the potential plasticity of biogeographical boundaries in the marine realm (Briggs, 1995; Costello et al., 2017; Ekman, 1953), there might not be a single solution to the problem of biogeographical partitioning (Kreft & Jetz, 2010). Although recent advancements (Costello et al., 2017) towards a completely quantitative global structuring bring us closer to this goal, the applicability of a taxonomically synoptic approach in fossil contexts and the comparability of its results are yet to be tested. This last step is essential to assess the stability of large-scale biogeographical structures in the face of environmental changes.

1.4 | Objectives

Our primary objective is to assess the long-term stability of shallow marine biogeographical structure. To test our key hypothesis that the global biogeographical structure changed considerably in response to environmental change, we first outline and characterize objective marine biogeographical units by applying community detection methods (Rosvall & Bergstrom, 2008) on compositional networks (Vilhena & Antonelli, 2015). We choose our focus to be on shallow-water benthic invertebrate groups that have a good fossil record. In this way, we can assess the applicability of the best partitioning method for fossil occurrences, whilst keeping fossil and recent data comparable. Secondly, we evaluate the role of abiotic predictors in shaping benthic biogeography. We hypothesize that continental configuration governs the distribution of bioregions via landmass and open ocean barriers, whereas the latitudinal gradient of seawater temperature sets the locations of their contacting boundaries. We expect that temperature has smaller effects on the faunal composition of bioregions than landmasses and open-ocean boundaries because it is more temporally dynamic. Thirdly, we compare modern and fossil biogeographical schemes from the past 10 Myr, which we expect to show different patterns. Despite the considerable changes in the abiotic environment, we find that bioregions have remained remarkably stable over the past 10 Myr.

2 | METHODS

2.1 | Data

We downloaded point occurrence data of extant marine species from the Ocean Biogeographic Information System (OBIS) database (https://www.iobis.org) on 2 June 2017. The queried taxa comprise the mollusc classes Bivalvia and Gastropoda, the phyla Brachiopoda and Echinodermata, and the orders Decapoda (Crustacea) and Scleractinia (Cnidaria). Occurrence data were cross-referenced with the World Register of Marine Species (WoRMS) database (https://www.worms.org/, downloaded on 14 September 2015) for taxonomic corrections and for homogenizing suprageneric taxonomic information. Using the "z3" resolution coastlines and land polygons of the OpenStreetMapData inventory (https://openstreetmapdata.com/), we identified occurrences that fell on land and were not within 100 km (error margin based on the possible rounding of decimal input data in degrees) distance from coastlines and omitted them from all analyses. To restrict our analysis to benthic fauna, the gastropod superorder Pteropoda was omitted, and the decapod group is represented only by the benthic Achelata, Anomura, Astacidea, Brachyura, Gebiidea and Polycheilda infraorders. As the data focus on shallow-water environments, the generally deep-water azooxanthellate and apozooxanthellate stony corals were also omitted (Cairns, 2007). The genus list of Kiessling and Kocsis (2015) was used to filter non-zooxanthellate corals (https://datadryad.org/resource/doi:10.5061/dryad.mv32t).

Environmental data included a global bathymetry model (ETOPO1; Amante & Eakins, 2009) downloaded from the National Geophysical Data Center at a resolution of 0.125°. We downloaded additional environmental variables from the Bio-Oracle v2.0 dataset (Assis et al., 2018; Tyberghein et al., 2012) that represent conditions between 2000 and 2014 to use as predictors for the bioregion distributions. The variables include annual mean sea bottom temperature (SBT) and its range, mean dissolved O_2 concentration and salinity at the bottom, and sea surface SiO_4^{4-}, NO_3^{2-} and PO_4^{3-} concentrations. Sea surface temperature approximates shallow-cell bottom temperature very well ($\rho = 0.95$), therefore it was not considered in the analysis. We also included primary productivity at both the surface and the bottom as potential predictors of global biogeographical patterns (see Supporting Information Appendix S1).

OBIS does not provide information on the spatial extent of samples, so we aggregated the point occurrence data to hexagonal grid cells, forming a tessellated icosahedral grid handled in the R package "icosa" (Kocsis, 2017). This approach has the advantage that gridded cells are nearly uniform over the surface of Earth in terms of cell size and shape. We implemented multiple grid resolutions to assess the influence of geographical grid resolution on the patterns of bioregions. We base our key results on an intermediate-level resolution grid [with a cell area of *c.* 65,000 km^2, using the tessellation vector (4, 7)], as this resolution is representative of a wider range of geographical resolutions (see Results). Abiotic variables were also binned to the same grids by averaging raster points in a cell that represented environments shallower than 200 m.

Random noise is expected to have a large effect on the biogeographical partitioning where the number of occurrences is low in grid cells. Therefore, we introduced a minimum occurrence quota per geographical cell. If not mentioned explicitly, this threshold was set to 20 occurrences, balancing geographical cell retention with removal of low-information cells (Supporting Information Appendix S1). For this occurrence quota, we treated multiple entries of a species within a cell as different occurrences.

To be consistent with earlier partitioning schemes, we separate "shallow" and "deep" environments at a depth of 200 m (Briggs & Bowen, 2012; Longhurst et al., 1995; Spalding et al., 2007). Both the depth and the coordinate entries in OBIS contain errors; therefore, the ETOPO1 bathymetric map was used to assess the likely depth of occurrences. Given that shallow water is more likely to be sampled, we chose to assign cells to the shallow environment if there was at least one 0.125° × 0.125° pixel of "shallow" environment in the cell. After filtering, 3,679,862 occurrences could be assigned to the shallow environment and were used in biogeographical analyses (Supporting Information Figure S1.1 and Table S1.1).

For fossil occurrence data, we mined the Paleobiology Database (PBDB; https://www.paleobiodb.org) on 7 July 2017. The downloaded occurrences comprised the same groups as in the modern dataset. We matched collections with the dynamic time-scale of the Fossilworks portal (https://www.fossilworks.com), then analysed the last, late Miocene–Pleistocene time slice. Fossil biogeography is based on considerably time-averaged data. Nevertheless, we argue that the use of this coarse temporal resolution is justified by the lack of major extinctions in the marine realm from this interval. Taxa that were registered to be freshwater or terrestrial in WoRMS were omitted from both the recent and the fossil datasets. Owing to the lower data density, fossil occurrences were binned to a coarser grid than the recent ones [cell area *c.* 354,000 km^2, with the tessellation vector (4, 3)]. After filtering occurrences that were not identified to species level, 62,176 fossil occurrences remained in the dataset for analysis.

2.2 | Biogeographical partitioning using network analysis

We transformed the species/grid cell contingency table (adjacency matrix) to a bipartite occurrence network (Vilhena & Antonelli, 2015) using the R package "igraph" (Csárdi & Nepusz, 2006). This network comprises nodes that represent grid cells and, separately, the species that occur in them, and the edges (linking the grid cell and species nodes) indicate whether a species in question occurs in a grid cell or not. This network is bipartite in nature because nodes representing species can connect only with nodes representing grid cells, and vice versa.

To extract bioregions from the occurrence data, we ran community detection algorithms (Fortunato & Hric, 2016) on both the bipartite graphs and their grid cell projections (Supporting Information Figure S1.2). The edge weights in the projected, unipartite graphs (containing only nodes that represent geographical cells) were set according to the number of shared species between two nodes. However, to incorporate changes in sampling intensity, we adopted the "connection strength" (CS) of Rojas et al. (2017) as edge weights in the unipartite graph:

$$\mathrm{CS}_{kl} = \frac{\Gamma(k) \cap \Gamma(l)}{\mathrm{C}(k) + \mathrm{C}(l)}, k \neq l, \tag{1}$$

where k and l indicate different geographical cell nodes, $\Gamma(k)$ denotes the neighbours of k (species nodes) in the bipartite graph, and $\mathrm{C}(k)$ indicates the number of collections in the cell k, as a proxy for sampling intensity. We used the number of occurrences in grid cells as proxies for sampling, and in those cases $\mathrm{C}(k)$ denotes the number of occurrences in cell k. The effect of this correction is minor (Supporting Information Figure S1.3), but it prevents the inflation of the number of shared species between two nodes when sampling intensity is above average.

Amongst the plethora of community detection methods, the "infomap" (Rosvall & Bergstrom, 2008) algorithm was favoured because of its validation in previous biogeographical analyses (the procedure is also referred to as "map equation"; Bloomfield, Knerr, & Encinas-Viso, 2017; Rojas et al., 2017; Vilhena & Antonelli, 2015; Vilhena et al., 2013). The approach has its roots in information theory and is based on the information quantity accumulated by random walkers on the network. We also tested other algorithms, but "infomap" performed best, based primarily on the low spatial overlap amongst inferred bioregions. We calculated spatial overlap by computing the spherical characteristic hulls of bioregions (see Supporting Information Appendix S1). Spatial overlap is the proportion of the total overlapping area (number of cells) and the area covered by at least one bioregion. We applied the same partitioning scheme to the different subsets of occurrence data.

We also partitioned the fossil occurrences after dividing the data into three geological time bins. In other words, data from a single cell (D_j) were divided into age-specific subsets (D_j^i) that represent the same geographical locality (cell j) but different geological ages (age i). The partitioning algorithm was repeated for each of the three geological ages in the last 10 Myr (late Miocene, Pliocene and Pleistocene). Partitioning these spatiotemporal containers (k_j^i) in a single network with the same methods resulted in units that have almost the same geographical extent, but are traceable through time (Kiel, 2017; Kocsis, Reddin, & Kiessling, 2018).

As point occurrence data do not represent complete geographical ranges, we tested the effects of absent records. We iteratively reran the main partitioning algorithm on randomly selected (bootstrapped) occurrence records to assess the sensitivity of results (i.e., bioregion robustness). In order to contrast the output similarity of diverse partitionings, we calculated the adjusted mutual information (AMI; Vinh, Epps, & Bailey, 2009) between the overlapping parts of two partitionings (U and V). This metric behaves in a similar manner to a correlation coefficient, but it cannot be negative, varying only between zero and one; AMI is zero when the association between U and V is completely random, and it is one if the two partitionings are identical.

2.3 | Abiotic parameters and bioregion assignment

To display variation in the environmental variables, we applied principal components analysis (PCA) to the geographical cell means of environmental variables. In order to show more between-bioregion variation, the PCA eigenvectors were calculated only with the centroids of the bioregions, before we projected the individual cells into the rotated space. The variables were standardized to a mean of zero and unit variance before analysis. To link changes of environmental variables to bioregion assignments, we tabulated the vectors between their centroids in the rotated space. To characterize which environmental variables drive the bioregion transitions, the angles between the transition vectors and the vectors of the environmental variables were calculated and rotated to the [0°, 90°] quadrant. This allows a numerical assessment of their degree of association, with lower values (equivalent to more parallel vectors) meaning a closer relationship, and higher values meaning a more distant one. The median angle for each environmental vector was computed.

As an alternative assessment of the influence of environmental variables on the membership of cells to bioregions, we also applied random forests of 2,000 classification trees (Finnegan, Heim, Peters, & Fischer, 2012; Prasad, Iverson, & Liaw, 2006). The advantage of this machine-learning approach is that it does not assume a pre-defined relationship between the predictor and explanatory variables; therefore, it can uncover hidden structure in the data. The importance of variables was calculated using the R packages "party" (Strobl, Boulesteix, Zeileis, & Hothorn, 2007) and "randomForest" (Liaw & Wiener, 2002). In "party", we used the function "cforest()", which builds a random forest using conditional inference trees. This step avoids biased variable selection in the "randomForest()" procedure (Strobl et al., 2007). To limit the effect of collinear variables, we compared random forests including all variables with results excluding the variables that resulted in correlations of $\rho \geq 0.7$ between variables. Known causal relationships (e.g., the determination of dissolved oxygen by water temperature) aided the identification of variables to drop.

We tested the effect of changes in environmental variables and shortest water distance on bioregion boundaries using a multiple logistic regression model. In this framework, pairs of sampled cells can represent either the same or different bioregions, defining a binary response variable, zero (same bioregion) or one (different bioregion). This response (zero or one) was modelled using the absolute differences in the abiotic explanatory variables and the shortest water distances between the respective pair of cells (i.e., given large changes in an abiotic parameter from one cell to another cell, is the probability higher that the bioregion assignment will change?). Cell pairs were selected based on the following criteria: (a) the two cells must be connected by seawater without entering a third bioregion; and (b) if the two cells belong to a different bioregion, at least one of them has to be on the boundary of the bioregion to which it is assigned. Cell pairs in which both cells came from the internal parts of different bioregions were not considered. As an exhaustive look-up of all cell pairs was not feasible owing to the complex spatial configuration and high number of sampled geographical cells, we sampled the pool of eligible cell pairs with random walkers. We generated 100 independent random walks of 10^7 cell steps and extracted cell pairs that fitted the above criteria. Although not all cell pairs were recovered, the overwhelming majority were found and integrated into the model.

We used additive instead of multiplicative modelling, as the numerous interaction terms of abiotic variables are difficult to interpret. The extremely high ratio of observations to explanatory variables lends spurious significance for all variables in predicting the response parameter. Neither stepwise model selection based on the Akaike information criterion (AIC; Burnham & Anderson, 2002) nor Wald's Z-tests were effective in filtering irrelevant parameters. Therefore, the abiotic parameters were z-scored before modelling, and we relied on the magnitude of coefficient estimates and the Z statistics to rank the importance of the variables. We used the D^2 statistics (Guisan & Zimmermann, 2000) to express the total predictive capacity of the models.

2.4 | Remarks on programming and software use

Except for the "Louvain" algorithm, we ran all analyses in the R programming environment (R Development Core Team, 2017). We partitioned the network of the total dataset with both the "igraph" and the console application (https://www.mapequation.org/) implementation of "infomap". A two-level hierarchy output (bioregions and cells) is constrained in "igraph". We tried to reveal a nested structure of the biogeographical partitioning with the console application, but only traces of a multi-level hierarchy were present (see Results). We preferred "igraph" for most analyses, as it and the console application provided almost identical results, but "igraph" allowed a faster workflow. In the analytical scripts, we used functions from the namespaces of R packages listed under Supporting Information Appendix S2. Unless noted otherwise, results of iterative methods, such as resampling and certain simulations, are based on 100 trials. The plotted maps show equirectangular projections; the continent configurations are calculated with the GPlates 2.0 software with the rotation file of Matthews et al. (2016).

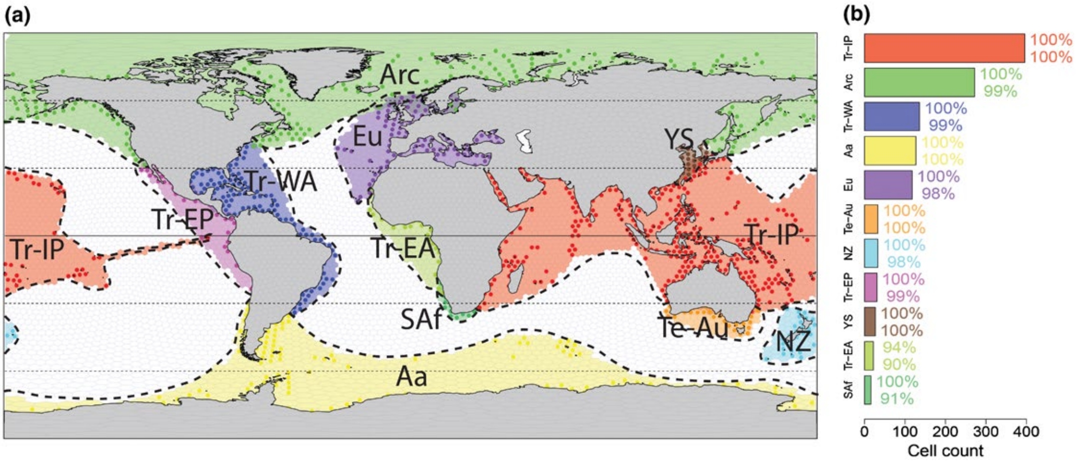

FIGURE 1 Biogeographical partitioning of the recent species-level dataset (OBIS). Data comprise occurrences of seven higher taxa (bryozoans, brachiopods, bivalves, gastropods, zooxanthellate stony corals, echinoderms and decapods). The partitioning is based on the "infomap" (Rosvall & Bergstrom, 2008) algorithm applied to a unipartite geographical cell network (Rojas et al., 2017), where each cell holds ≥20 occurrences. (a) Bioregions are indicated by colours (online version): circles denote sampled cells (above minimum occurrence quota); and background shapes represent interpolations based on spherical characteristic hulls (L = 3,500 km). The modularity of this partitioning is 0.56. Dashed lines represent the 30 and 60° latitudinal circles. (b) The bioregion areas expressed as cell counts. Percentage values indicate the stability based on bootstrap resampling (100 trials): upper values describe the partitions; and lower values indicate the mean of the individual stability of constituent cells. Abbreviations of bioregions ordered by size: Tr-IP: tropical Indo-Pacific; Arc: Arctic; Tr-WA: Western Atlantic; Aa: Antarctic; Eu: European; Te-Au: temperate Australian; NZ: New Zealandian; Tr-EP: tropical East Pacific; YS: Yellow Sea; Tr-EA: tropical East Atlantic; SAf: South African. See Supporting Information Appendix S3 for the shapefile of the partitioning [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Partitioning objective marine bioregions

3.1.1 | Modern bioregions

We establish 11 objective bioregions for shallow-water marine benthic animals (Figure 1). Alternative partitioning methods yielded different biogeographical partitionings (Supporting Information Figure S1.4), but the original, "unipartite-infomap" network approach performs best in terms of spatial overlap (Supporting Information Figure S1.5). The identified bioregions are insensitive to the effects of spatial resolutions (Supporting Information Figures S1.6 and 7). Only the Baltic Sea emerges as an additional, independent bioregion at very fine spatial resolutions. Traces of a multi-level hierarchy can be detected using such fine grains, but the only affected area is the Antarctic bioregion, which could be separated to an Antarctic *sensu stricto* and a South American subunit. No additional levels of global hierarchy are present with the best-performing "unipartite-infomap"

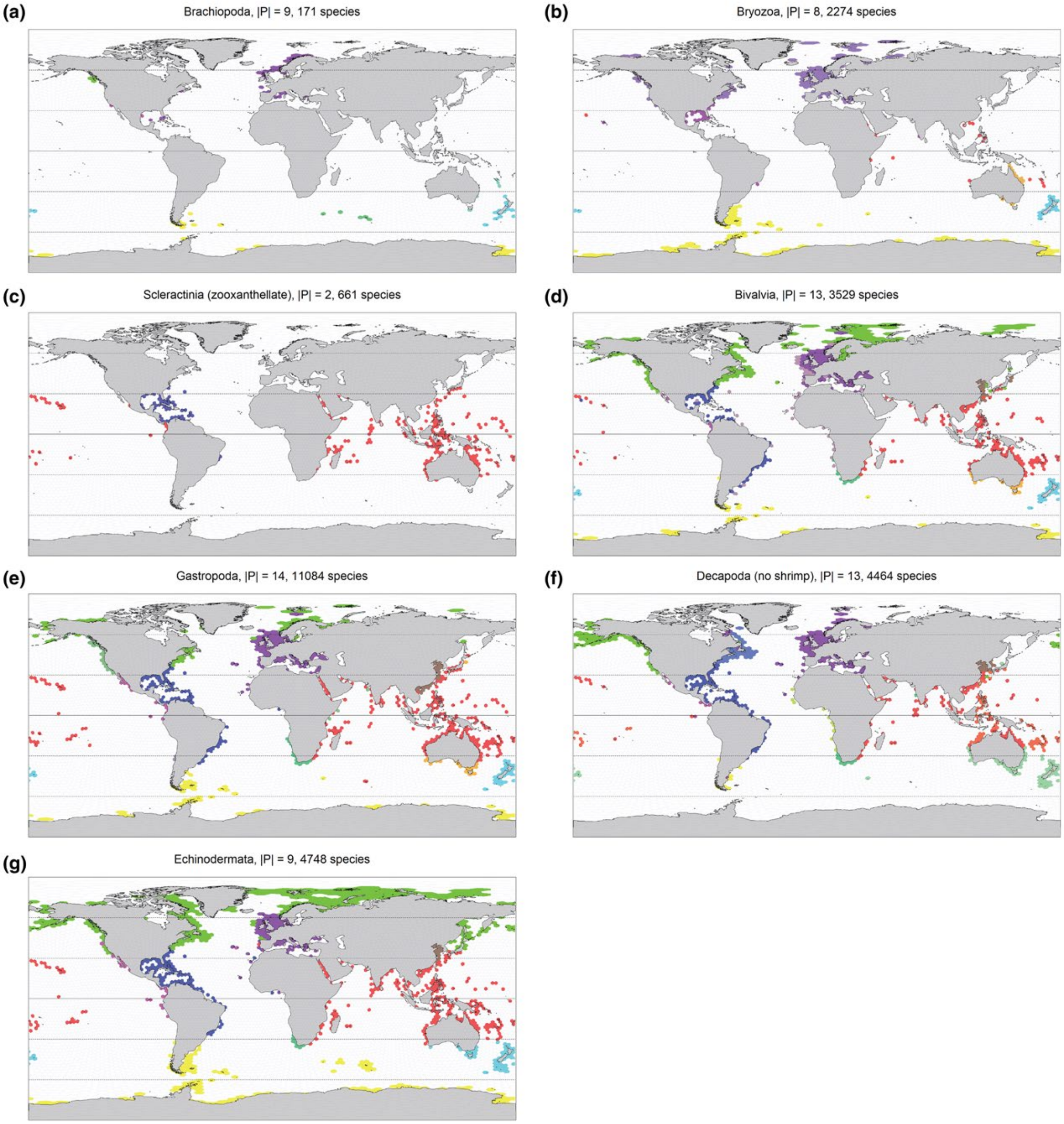

FIGURE 2 Individual partitioning results for the seven benthic taxonomic groups using the same methods as in Figure 1. Despite vast differences in sampling and diversity, the emerging units are spatially consistent and are relatively similar for the different taxa. This is also indicated by high adjusted mutual information (minimum = 0.61, decapods vs. corals). |P| denotes the number of bioregions. Colours of bioregions (online version) are calculated based on their distances to the centroids of bioregions shown in Figure 1. See Supporting Information Appendix S3 for the shapefile of the partitionings [Colour figure can be viewed at wileyonlinelibrary.com]

approach. The partitioning is also remarkably stable under changes in both within and above cell-level sampling parameters (Supporting Information Figure S1.8).

The size distribution of our bioregions is highly skewed (Figure 1b). About 80% of all species are endemic to a single bioregion, but not all bioregions are dominated by endemic species. The value of endemicity ranges between 29% and 78%, and larger bioregions tend incorporate more endemic species ($\rho = 0.67$, $p = 0.021$). Despite the high dissimilarity amongst bioregions (Supporting Information Figure S1.9, mean Jaccard distance = 0.96), patterns of community nestedness suggest that some bioregions resemble “colonies” of larger bioregions, rather than standing out as independent “mainlands” (i.e., dissimilarity attributable to species turnover). For example, the Yellow Sea (YS), the South African (SAf) and temperate Australian (Te-Au) bioregions are characterized by substantially lower endemism and also show an increased nestedness component of faunal dissimilarity in connection to the Tr-IP bioregion (Supporting Information Figure S1.9).

3.1.2 | Taxon-specific partitioning

Most features of biogeographical structure are concordant amongst taxonomic subsets (Figure 2), despite profound phylogenetic distance and different sampling patterns (Supporting Information Appendix S1). The high AMI (Supporting Information Table S1.2, average of taxon vs. total partitioning = 0.84) suggests that the partitioning is driven by the same factors. Similar to the total partitioning, the number of biogeographical units is modest in all cases.

Most taxa share a unified temperate south-American–Antarctic bioregion, which never falls into the same bioregion as the similar latitude New-Zealandian bioregion. Despite the shared general patterns, there are considerable differences amongst the taxon-specific partitionings. Only the Isthmus of Panama structures the distribution of zooxanthellate stony corals (Figure 2c), whereas the East-Pacific barrier has relatively minor effects. The Arctic and European bioregions are not separated for bryozoans. Decapods and echinoderms do not separate into a temperate Australian and a New-Zealandian bioregion.

3.2 | Determinants of biogeography

3.2.1 | Environmental variables

Bioregions are mostly delimited by land or vast distances of open ocean, which confirms the importance of plate tectonics as a main determinant of marine biogeography. Besides this primary structure, bioregions within oceans are latitudinally divided, suggesting that changes in the oceanic environmental conditions also have an influence on the bioregion distribution. Ordination (Figure 3a) and random forest analysis of environmental parameters suggest that, amongst physicochemical seawater properties, temperature plays a dominant role in defining modern biogeographical structure. Bioregions are distinguished by mean annual sea bottom temperature (SBT; Table 1). Although the temperature envelopes of some bioregions overlap (Figure 3b), bioregions within the same envelope are separated by land or deep ocean barriers.

Multiple logistic regression on cell membership via possible travelling routes suggests that bioregion transitions are more likely to be associated with mean SBT differences than with any other parameter. This model indicates that temperature is at least twice as effective in predicting bioregion transitions as water distance (Table 1), and it outperforms by far other abiotic variables, such as changes in salinity, primary production and SBT range. Translating changes of seawater temperature to distance via their effect on species compositional dissimilarity (Supporting Information Figure S1.10) shows that, on average, a change of 1°C in seawater temperature is equivalent to a spatial distance of 1,400 km, which is much more than the global average latitudinal temperature gradient of *c.* 220 km/°C. The average SBT difference between contacting bioregions (11.3°C) translates to nearly 15,000 km of spatial distance.

3.2.2 | The influence of boundary types on bioregion composition

To assess the effects of different boundary types on the faunal similarity amongst bioregions, we drafted a graph of bioregions, based on their geographical distribution (Figure 4). Out of 55 potential connections, we identify 29 direct neighbours. Neighbouring bioregions have significantly greater similarity (Wilcoxon rank sum test, $p < 0.0001$, $n = 55$) compared with more distant ones. Between the neighbouring bioregion pairs, three major types of boundaries were defined: (a) 13 latitudinal, probably temperature-related, directly contacting boundaries; (b) six open ocean boundaries; and (c) five land boundaries. We identified another five connections around the Antarctic as both latitudinal and open ocean boundaries. These were omitted from further assessment because they confounded two boundary types. We expect latitudinal (a) boundaries to be more permeable to faunal diffusion (e.g., temporary barrier breakdowns) than the oceanic (b) and landmass (c) boundaries. The faunal similarities are not dependent on boundary type (Kruskal–Wallis test with boundary types as categories and based on total Jaccard dissimilarity, $p = 0.129$). Results are the same ($p = 0.333$) when only the turnover component of dissimilarities is considered (total dissimilarity—nestedness component; Supporting Information Figure S1.9).

3.3 | Palaeontological application

3.3.1 | Similarity between the recent and the last 10 Myr

Application of the same partitioning method to fossil occurrences of the last *c.* 10 Myr (Figure 5) resulted in a remarkably similar pattern of bioregionalization to that of the modern ocean. This result is

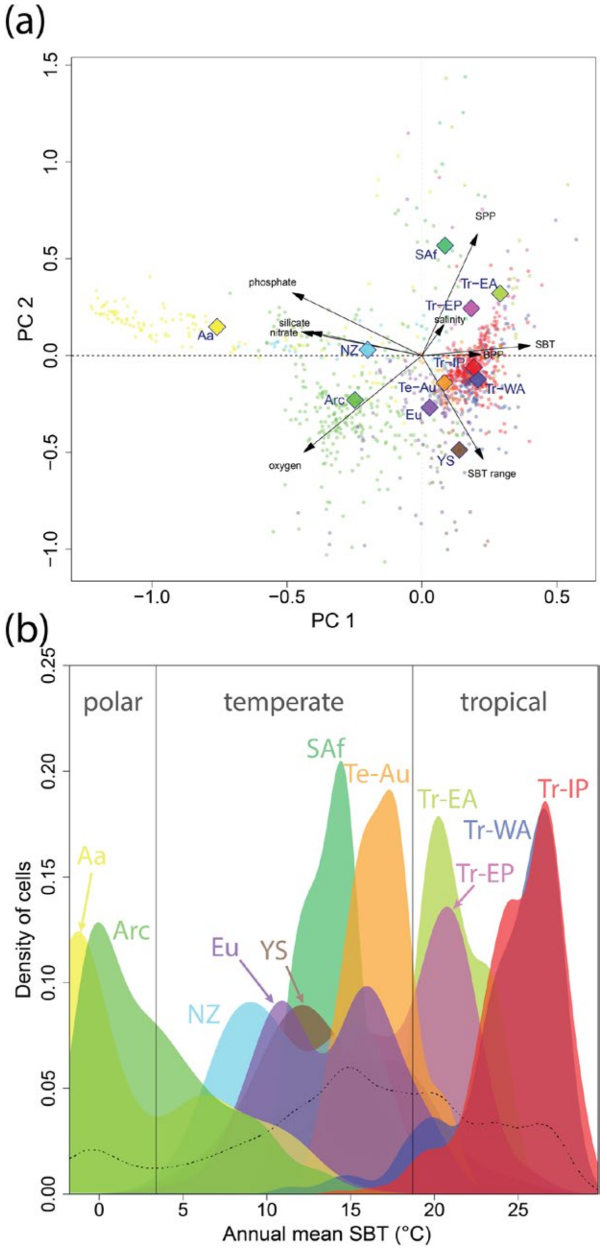

FIGURE 3 Environmental determination of benthic bioregions via the association of abiotic parameters with the partitioning shown in Figure 1. (a) Principal component analysis of geographical cells with the averages of standardized parameters from the Bio-Oracle v2.0 datasets (Assis et al., 2018; Tyberghein et al., 2012). Points indicate geographical cells, and diamonds indicate averages for the bioregions. Only the centroids were used to calculate eigenvectors. Bioregion changes are most prominent along the sea bottom temperature (SBT) vector (Table 1). The percentages of variance explained are 49.04% for principal component (PC) 1 and 29.69% for PC 2. (b) Scaled density of bioregion cells in the dimension of annual mean SBT. The dotted line indicates the mean density. Vertical lines delineate arctic, temperate and tropical bioregions and are aligned to local minima of the mean density curve (18.7 and 3.4°C). The characteristic SBT of tropical bioregions is dependent on their geographical position. The bioregions situated along the western margins of continents (Tr-EA and Tr-EP) represent the slightly colder temperatures of upwelling zones. See Figure 1 for the abbreviations of bioregions [Colour figure can be viewed at wileyonlinelibrary.com]

also reflected by the high mutual information between modern and fossil partitionings (AMI = 0.81; between Figure 5 and Supporting Information Figure S1.6a). As the number of sampled cells is different in the recent and fossil partitionings, we contrasted the number of bioregions in the jointly covered area. At this coarser geographical resolution, there are 11 and 10 bioregions in the fossil and recent partitioning, respectively. The difference between the number of bioregions in the two partitionings is not significant ($p = 0.159$, based on a bootstrap resampling of cells). Most present-day bioregions are maintained in the fossil partitioning and have similar boundaries. The relatively complex structure of the eastern Pacific, indicated by the fossil biogeography, is likely to be the result of including fossils from both before and after the closure of the Isthmus of Panama (at *c*. 3 Ma; O'Dea et al., 2016).

3.3.2 | History of biogeographical units

The present-day bioregions can be traced through time (Figure 6). The partitioning result of the simultaneous clustering of the late Cenozoic ages is remarkably similar to those that result from their individual treatment (Supporting Information Figure S1.11). Despite the profound climate change, there are no major changes in the positions of the bioregions. The similarity of ancient and current biogeographical partitionings indicates that most bioregions have been present for ≥10 Myr. Owing to the lower sampling levels, the partitionings in Figure 6 are noisier than the one outlined by the total data (Figure 5). However, the Arctic bioregion extends further south in the Pleistocene than today, and the North-eastern Pacific (NEP) and South-eastern Pacific (SEP) temperate bioregions (Figure 5) remained separate in the Pleistocene. Meanwhile, the recent data suggest a single, individual bioregion for most of the west coast of America.

4 | DISCUSSION

Benthic bioregions are not only methodologically robust, but also stable through time. We reject the hypothesis that the global biogeographical patterns changed considerably over the last 10 Myr. The observed stability of the bioregions indicates that despite the varying environmental conditions, the main determinants of biogeography remained relatively unchanged over the analysed interval.

4.1 | Biogeographical partitionings

4.1.1 | Comparison with other biogeographical partitioning schemes

The outlined bioregions resemble the realm-level partitions of the Marine Ecoregions of the World (MEOW; Spalding et al., 2007), but differences include a more distinct longitudinal pattern. For example, the Atlantic Ocean is split into western and eastern units, and New Zealand is separated from temperate Australia. In contrast, our

TABLE 1 The importance of environmental variables as predictors for the partitioning shown in Figure 1

	PCA	Random forests			Logistic regression		
Variable	Mean angle of vectors (°)	Mean decrease in accuracy (randomForest)	Mean decrease in Gini index (randomForest)	Conditional mean decrease in accuracy (party)	Coefficient estimate	*z* value	D^2
O_2	38.17	–	–	–	0.05	5.56	19.5
PO_4^{3-}	39.07	189.69	241.61	0.059	0.29	17.16	17.6
NO_3^-	40.72	–	–	–	0.419	29.05	14.1
SBT	**37.70**	**277.43**	**317.01**	**0.063**	**3.21**	**226.65**	**47.2**
SBT range	40.43	81.70	82.26	0.001	−0.09	−15.52	0.2
Bottom PP	38.01	64.61	65.12	< 0.001	−0.21	−27.89	0.1
Surface PP	41.89	75.07	60.26	0.001	0.22	25.26	1.8
Salinity	37.85	151.03	202.36	0.015	0.06	10.84	0.1
SiO_4^{4-}	41.43	–	–	–	−0.6	−47.64	9
SWD	–	–	–	–	1.09	170.17	19.5

Notes. The strongest value in each assessment type is in bold. The SBT is the most important predictor with all three approaches. The results of the vector alignment tests and random forests are based on cell means. The multiple logistic regression of bioregion cell pairs (n = 349,360) uses differences between cell means (response = 0 for the same bioregion and response = 1 for different bioregions, using the neighbouring bioregions, where at least one cell is from the boundary area of a bioregion). The D^2 values indicate the explained variance of the parameter when it is used to model the transitions on its own. Replacing the shortest distances on water (SWD) with great circle distances resulted in almost identical values. The total D^2 of the model is 57.59%. Abbreviations: PCA: principal components analysis; PP: primary production; SBT: sea bottom temperature; SWD: shortest sea water distance.

analysis lumps three MEOW realms into a single, vast bioregion comprising the tropical to subtropical Indo-Pacific (Tr-IP).

Our unipartite network solution suggests fewer and considerably coarser bioregions than the cluster-based approach of Costello et al. (2017). The coastal biogeographical units of Costello et al. (2017) are almost perfectly nested (Table 2) in our bioregions shown in Figure 1. The main differences between the partitionings probably emerge because we did not lump benthic and nektonic/planktonic organisms. We suggest that the partitioning output of the “unipartite-infomap” method represents higher-level units in the biogeographical hierarchy, perhaps at the level of realms, whereas the bioregions of Costello et al. (2017) are lower in the hierarchy, such as at the level of provinces.

4.1.2 | Robustness of biogeographical partitionings

The fact that similar patterns emerge from independent modern and fossil datasets suggests a limited impact of incomplete sampling and random error. Simulations show these factors to have only marginal effects on the precision of the partitioning output (Supporting Information Appendix S1). Given that the palaeo-partitioning is based on much fewer occurrence data than the recent partitioning scheme, we are not concerned by the somewhat noisier palaeo-patterns (e.g., around the poorly sampled Antarctic area). It is highly unlikely that the same basic pattern would emerge from the two independent datasets if they were incompatible and if the partitioning algorithm was inappropriate.

The partitioning patterns of individual taxa suggest that they share most major biogeographical boundaries. Some of the barriers allow better connectedness for specific groups, such as the oceanic barrier between New Zealand and Australia for echinoderms and decapods, but most bioregions are recognizable across the taxonomic subsets. Based on the AMIs between the partitionings, their patterns of similarity appear to be decoupled from phylogeny, ecology or larval types of the groups. The exploration of taxonomic idiosyncrasies is beyond the scope of the present study.

Meaningful bioregions can be outlined robustly without environmental information even in relatively poor sampling conditions. This is supported not only by the past partitioning but also by the similarity of the taxon-specific results. This observation is especially relevant for outlining and tracing bioregions through deep time (Kiel, 2017; Kocsis et al., 2018), when quantifiable environmental information is sparse.

4.2 | The determinants of stability

Based on our results, continent configuration and the latitudinal temperature gradient jointly define marine bioregionalization. Landmasses and open ocean boundaries outline its primary features by controlling the distribution and connectivity patterns of the shallow benthic habitat space. Seawater temperature acts as a secondary determinant, arranging bioregions latitudinally in the connected areas.

4.2.1 | Continent configuration

Plate tectonic processes have a direct effect on landmass-barrier formation, which are generally unlikely to change over a few millions of years. A major exception is the closing Isthmus of Panama

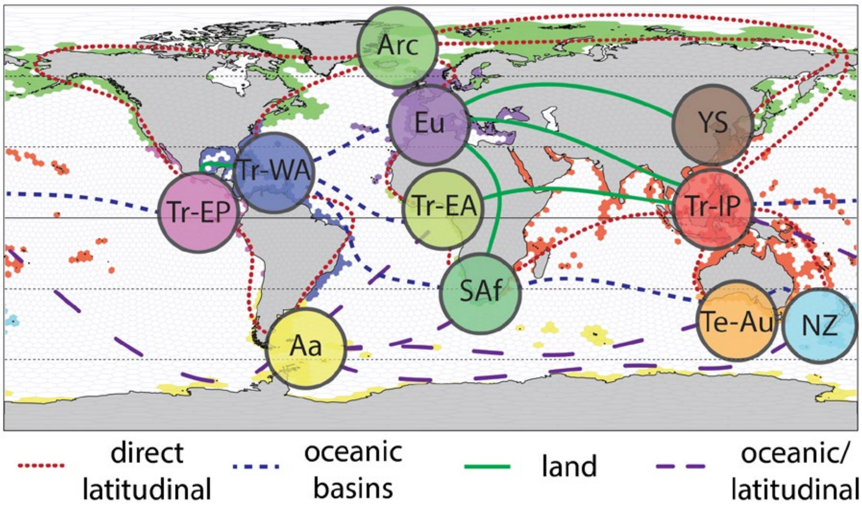

FIGURE 4 Interconnection of bioregions in terms of faunal composition and connection type. A secondary graph of the established bioregions (Figure 1) indicates the types of relationships between bioregion faunas. In total, five out of 29 connections are over land, 13 are sampled, direct latitudinal, six are longitudinal oceanic, and five are both latitudinal and oceanic. See Figure 1 for the abbreviations of bioregions [Colour figure can be viewed at wileyonlinelibrary.com]

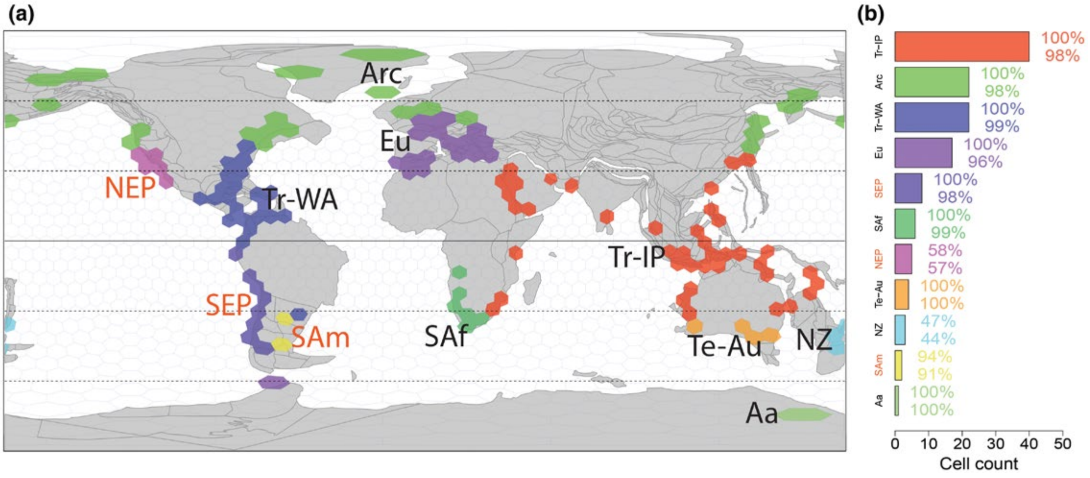

FIGURE 5 Biogeographical partitioning of the species-level fossil dataset (PBDB) from the last 10 Myr (Cenozoic 6, late Miocene–Pleistocene interval), with the same methods as Figure 1, except for a coarser spatial resolution. (a) A map of the partitioning. (b) The distribution of sampled cells with the results of bootstrapping. Bioregions with black names match unambiguously with those of the recent, thus we named them so. Bioregions with red labels indicate changes; the Tr-WP bioregion is split into two independent bioregions indicated as North-East Pacific (NEP) and South-East Pacific (SEP), and its tropical part is joined with the tropical west Atlantic (Tr-WA). The Antarctic bioregion of Figure 1 is fragmented, probably as a result of the poorer sampling of the region. We calculated the colours of the bioregions (online version) based on their distances to the centroids of the bioregions shown in Figure 1. The same spatial resolution partitioning of the recent dataset is shown in Supporting Information Figure S1.6a. See Supporting Information Appendix S3 for the shapefile of the partitioning [Colour figure can be viewed at wileyonlinelibrary.com]

in the Pliocene *c.* 2.8 Ma (O'Dea et al., 2016), with well-known biogeographical consequences (McKinney, 1998). The Pleistocene partitioning indicates that evolutionary changes of cell compositions were not substantial enough to reflect unequivocally different bioregion membership. The differences seen in the by-slice partitionings (compare Figure 5 with Supporting Information Figure S1.11) also reflect the uncertainty of bioregion assignment. This pattern of faunal distributions suggests that although a vicariance event (e.g., emergence of a landmass barrier) can interrupt gene flow in a geological instant, the faunal compositions of the resulting areas might show delayed divergence. This isthmus is now an effective barrier for all marine taxa, and it is the single dominant barrier for reef corals (cf. Veron, Stafford-Smith, DeVantier, & Turak, 2015).

The physical obstacles imposed by landmasses are more difficult to overcome for marine organisms than greater distances in water. Populations of the same species can be genetically distinct over shorter distances (300–400 km) because of historical barriers (such as during the lower sea level of the Pleistocene; Barber, Palumbi, Erdmann, & Moosa, 2000). Small-scale barriers to gene flow of individual species (Peluso et al., 2018) can be transgressed

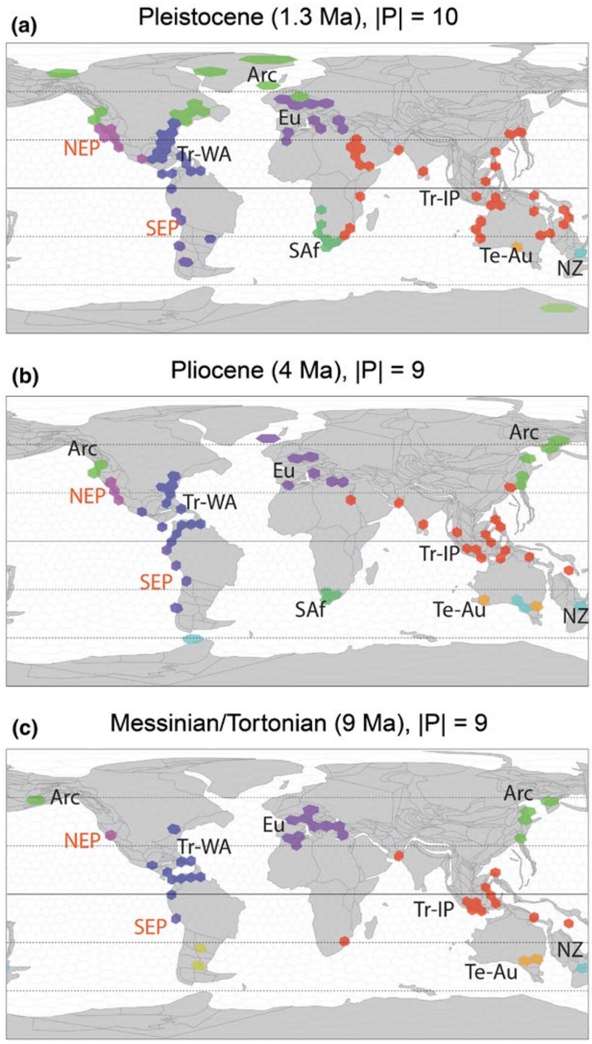

FIGURE 6 The history of global marine biogeography in the past 10 Myr at the geological age level. (a) Pleistocene age. (b) Pliocene age. (c) Messinian/Tortonian ages. Bioregions coded with the same colours are linked by the analytical method (they represent the same clusters); their exact colour (online version) values are based on their distances to the bioregions shown in Figure 1. The bioregions are stable across millions of years. Ages indicate the mean age of the time slice. See Figures 1 and 5 for the abbreviations of bioregion names [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Comparison of the outlined bioregions with those proposed by Costello et al. (2017)

Bioregions in this study	Seas group of Costello et al. (2017)	Number
Arc (B)	Inner Baltic Sea	1
Eu	Black Sea	2
Eu	NE Atlantic	3
Arc	Norwegian Sea	4
Eu	Mediterranean	5
Arc	Arctic seas	6
Arc	N Pacific	7
Arc	N American Boreal	8
–	*Mid-tropical North Pacific Ocean*	*9*
Tr-EP	*South-east Pacific*	*10*
Tr-WA	Caribbean & Gulf of Mexico	11
Tr-EP	Gulf of California	12
Tr-IP	Indo-Pacific seas & Indian Ocean	13
Tr-IP	Gulfs of Aqaba, Aden, Suez, Red Sea	14
–	*Tasman Sea*	*15*
Tr-IP	Coral Sea	16
Tr-IP	*Mid South Tropical Pacific*	*17*
Eu/Arc	*Offshore & NW North Atlantic*	*18*
Tr-IP	*Offshore Indian Ocean*	*19*
Tr-IP/Arc	*Offshore W Pacific*	*20*
Eu/Tr-WA	*Offshore S Atlantic*	*21*
–	*Offshore mid-E Pacific*	*22*
Tr-EA	Gulf of Guinea	23
Aa (Aa/SA)	Rio de La Plata	24
Aa (Aa/SA)	Chile	25
Te-Au	South Australia	26
SAf	S Africa	27
NZ	New Zealand	28
YS	NW Pacific	29
Aa (Aa/Aa)	*Southern Ocean*	*30*

Notes. Italic entries indicate dominantly offshore realms. These have a worse match with our partitioning results, probably because of the different taxonomic and depth scope of the two analyses. The Inner Baltic Sea is outlined as an independent unit in partitionings of higher spatial resolutions (Supporting Information Figure S1.6) and is therefore also indicated with (B). Likewise, the Antarctic (Aa) bioregion shows a nested structure at fine spatial resolutions. These units are indicated as "Aa/SA" (South American) and "Aa/Aa" (sensu *stricto* Antarctic) subregions. Abbreviations of bioregions ordered by size: Tr-IP: tropical Indo-Pacific; Arc: Arctic; Tr-WA: Western Atlantic; Aa: Antarctic; Eu: European; Te-Au: temperate Australian; NZ: New Zealandian; Tr-EP: tropical East Pacific; YS: Yellow Sea; Tr-EA: tropical East Atlantic; SAf: South African.

by more dispersible species that will ensure ecological and biogeographical connections. In the absence of substantial environmental change, vast distances over deep ocean are required to cause bioregion boundaries, such as those between the tropical Indo-Pacific and the Eastern Pacific (the East Pacific Barrier; Wood et al., 2016) and between the two tropical Atlantic bioregions. These boundaries are occasionally crossed by means of transoceanic rafting (Thiel & Gutow, 2005), even when dispersal is prevented by additional obstacles imposed by current systems (Fraser, Kay, Plessis, & Ryan, 2017). Bioregions thus seem to be unaffected by random invasions, but present-day warming-induced relocations of species (Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015) may meet the intensity needed for an expansion of some bioregions at the expense of others (García Molinos et al., 2016).

The importance of landmass and open ocean boundaries indicates that changing continental configuration over geological time-scales should have a direct effect on coastal bioregionalization, as already suggested by Valentine et al. (1978). This tectonic driver could explain the observed relationship between species richness and continental fragmentation (Zaffos et al., 2017). The slow drift of continents, with a potential lag of faunal response, is likely to constrain the pace of biogeographical changes, suggesting that without abrupt changes in faunal composition (i.e., a mass extinction; Kocsis et al., 2018), global biogeography should feature similar stability over geological time.

4.2.2 | Seawater temperature

Beyond the effects of continental configuration, temperature has the most important effect on bioregion boundaries. Temperature is a well-known driver of marine species distributions (Sunday et al., 2012); it has the greatest influence on marine regional diversity (Tittensor et al., 2010) and is dominant in shaping the marine latitudinal diversity gradient (Chaudhary et al., 2016). Steep temperature (and salinity) gradients in the seas are often generated by surface currents, which might act as direct dispersal barriers (Gaylord & Gaines, 2000). However, the probable resilience of the structure to invaders renders the physiological adaptation of marine organisms to specific temperature regimes (Sunday et al., 2012) a more influential determinant.

Temperature differences do not need to be great to separate bioregions, as long as differences between bioregions exceed the natural variability within them. In this framework, even the extremely large size of the Tr-IP bioregion is plausible. The lack of a longitudinal land barrier between the tropical waters of the Indian and Pacific ensures connectivity between the two ocean basins, whereas the relatively short distances between shallow habitat areas of the region (Figure 1) hinder its fragmentation into smaller units. The bioregion is centred around the East Indies Triangle (Briggs, 2005), where the high species diversity also increases the chance of range overlaps, and therefore, the integrity of the region. Range sizes of some groups are also reported to be greater in the tropics in association with similar temperatures (Tomašových, Jablonski, Berke, Krug, & Valentine, 2015), and the Tr-IP covers a relatively narrow SBT range (Figure 3). However, changes in seawater temperature might lead to the disruption of established bioregions, which, if persistent, might give way to some form of allopatric speciation (Heads, 2005). For example, the Yellow Sea (YS), temperate Australian (Te-Au) and South African (SAf) bioregions show a close connection to the Tr-IP bioregion. Weak or temporally variable boundaries could also allow the diffusion of species from Tr-IP over geological time-scales, in accordance with the "out-of-the-tropics" hypothesis (Jablonski, Roy, & Valentine, 2006). The structure of bioregionalization did not change in response to environmental conditions, but it is likely that climatic changes led to the latitudinal shift of bioregion boundaries. Demonstrating these changes, however, is limited by the density of fossil samples and thus the spatial resolution of the partitionings.

Environmental determinants seem to be more important in the marine realm than on land, where the influence of plate tectonics dominates by far (Ficetola et al., 2017). Although the configuration of continents has the greatest effect on the distribution of bioregions, the secondary role of temperature is also vital in supporting the structure of biogeography. The effects of temperature-based barriers on the faunal similarity of bioregions are similar to those of other boundaries. In theory, owing to the linked nature of shallow benthic environments of the world, the removal of temperature-related barriers could lead to a biogeographically undivided world.

4.2.3 | Implications for the future

The biogeographical patterns of the past suggest that that the primary structure of the marine habitat might not change substantially with global warming. Assuming that the structure of the ocean circulation system remains intact (Wilson & Kirkendale, 2016), the arrangement of bioregions might fundamentally be preserved, perhaps with poleward-shifted boundaries. However, the joint effects of anthropogenic climate change and our direct interference with the marine environment by pollution (Halpern et al., 2008), overexploitation (Coleman & Williams, 2002) and species introductions (Bax, Williamson, Aguero, Gonzalez, & Geeves, 2003) may have unpredictable effects on bioregionalization. The apparent homogenization of the biota (Magurran et al., 2015) and the novel interactions amongst species that migrate at different paces (García Molinos et al., 2016) may also lead to extinctions. The opening of niches and the rapid spread of opportunistic taxa may then quickly reshape the standing biogeographical patterns (Kocsis et al., 2018).

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA ACCESSIBILITY

All our analyses rely on publically available datasets. The used subset of these data and the code of the analyses have been archived in Zenodo (https://doi.org/10.5281/zenodo.1219098).

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