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RESEARCH ARTICLE

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Global biodiversity and biogeography of rhodolith-forming species

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Abstract

Unattached nodules of calcareous red algae (Rhodophyta), known as rhodoliths, are widely reported and studied in places that extend from the tropics to polar latitudes. Factors controlling the distribution of the rhodolith-forming species remain poorly understood. A review of the global distribution of present-day rhodolith beds was undertaken, collating information on 106 rhodolith-forming species from 10 families, representing 21 genera distributed through 11 realms: 1) Arctic, 2) Temperate Northern Atlantic, 3) Temperate Northern Pacific, 4) Tropical Atlantic, 5) Western Indo-Pacific, 6) Central Indo-Pacific, 7) Eastern Indo-Pacific, 8) Tropical Eastern Pacific, 9) Temperate South America, 10) Temperate Australasia, and 11) Southern Ocean. The Central Indo-Pacific and Temperate Australasia proved to be the most diverse realms. Of 62 provinces across these realms, the Tropical Southwestern Atlantic, the Mediterranean Sea, and the Tropical East Pacific feature the highest diversity of rhodolith-forming species. A significant proportion of the 106 species (14.2%; 15 species) are endemic to a single biogeographic province. Species richness is weakly related to sampling effort (r^2=0.573) and unrelated to littoral area (r^2=0.012). Even when high latitude provinces are excluded from the analysis, no correlation between species richness and littoral was found ($r^2 = 0.0005$). A wider, evolutionary-time framework revealed that the existence of marine barriers and the geological age of their final emplacement are key elements to explaining compositional differences between the rhodoliths of former contiguous areas (e.g., Pacific versus Atlantic shores of Panama and Costa Rica, in the Central America; eastern Mediterranean Sea versus Red Sea and Gulf of Aden). Finally, we propose that the lower diversity of the rhodolith-forming species in the tropical Pacific Ocean when compared to the Atlantic Ocean (23 versus 33 spp.), may be linked to the higher abundance of corals and coral reefs in the Pacific, which act as competitors with coralline algae for space.

Highlights

- We provide an exhaustive biogeographical review of the reports on the global present-day rhodolith-forming species.
- A total of 106 rhodolith forming species, representing 21 genera, are distributed worldwide throughout 11 defined realms.
- The Tropical Southwestern Atlantic, Mediterranean Sea, and Tropical East Pacific provinces have the highest diversity of rhodolith forming-species.
- Around 14% of rhodolith-forming species are endemic to a single biogeographic province.
- The low diversity of rhodolith forming-species in the tropical Pacific Ocean may be related to the higher abundance of coral reefs, which act as competitors for space.

Keywords: biodiversity, biogeographical provinces, biogeographic realms, coralline algae, maërl, marine circulation, Rhodophyta

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Introduction

Rhodoliths are unattached nodules of varied sizes, forms, and origins formed mainly by non-geniculate coralline red algae (Bosellini and Ginsburg 1971, Bosence 1983, Aguirre et al. 2017). Included in this scenario are maërl beds *sensu stricto*, nodules formed by peyssonneliacean algae (Basso et al. 2017) and more rarely by geniculate coralline algae (Tâmega et al. 2017). Rhodoliths lie on the seafloor surface and can form huge accumulations. The accumulations denominated as rhodolith beds are well known for their widespread distribution in almost every biogeographic region, from the tropics to polar regions and from the intertidal down to ~300 m depth (Bosence 1983, Steneck 1986, Foster 2001, Matsuda and Iryu 2011, Foster et al. 2013, Riosmena-Rodríguez 2017). Although continuous growth of broken fragments is the main source of new rhodoliths in rhodolith beds and maërl, they are also initiated through recruitment from spores (Foster 2001). Rhodoliths perform a critical and understudied element of the marine diversity contributing to major ecosystem functions (Fredericq et al. 2019). They form particular ecological communities as a result of their branches and open spaces which provide living space, feeding, and nursery areas for a distinctive high diversity of plant and animal, many of commercial interest (Foster 2001, Riosmena-Rodríguez 2017).

The taxonomy of coralline algae, although of great significance, has been the subject of continuous debate since the 19th century, and is not yet resolved at any rank (Rösler et al. 2016 and references therein). Identification of coralline algae is particularly difficult and has led to confusion within ecological studies and misrepresentation of species diversity (Hind et al. 2014, Hernández-Kantún et al. 2015). Despite the publication of recent molecular phylogenetic analyses of the corallines, a considerable number of taxonomic uncertainties still exist (Hernández-Kantún et al. 2015, Rösler et al. 2016), and the overall diversity of these species remains poorly known.

Growth, subsistence, and the geographical distribution of rhodoliths are controlled mainly by hydrodynamic energy, sea bottom type, and regional current regimes (Rasser 1994, Basso et al. 2017, Riosmena-Rodríguez 2017). Albeit most species of crustose coralline algae may continue to survive unattached from hard substrates, only a few species frequently form rhodoliths or maërl (Hernández-Kantún et al. 2017). The factors controlling the geographical distribution of the various rhodolith-forming species remain largely unresolved (Foster et al. 2013). The history of the corallines' diversification since the mid-Mesozoic (early Cretaceous) to the Cenozoic, and their distinctive present-day distributions were elucidated by Aguirre et al. (2000). On the basis of the known present-day worldwide distribution of rhodolith beds, a first attempt is made, herein, to characterise the global biodiversity and biogeography of the rhodolith-forming species. Thus, the aims of this study are to: (1) investigate which region has the highest species diversity and which are the controlling factors; (2) quantify which biogeographic realms and provinces (outlined below) have the highest endemism; and (3) assess the influence of major biogeographic barriers to ocean circulation (i.e., Isthmus of Panama and Arabian Plate) that make a difference in diversity and species composition variations between otherwise adjacent regions.

Methods

Data collecting

Information on the location and geographical distribution of rhodolith-forming species was compiled through an exhaustive search of the primary literature (including reports and "grey" literature) published up to May 2020. Relevant references were carefully screeneed for each paper we found with records of rhodoliths. Reports and "grey" literature were obtained from colleagues around the world that were contacted during the course of this study. AlgaeBase (Guiry and Guiry 2019) and the World Register for Marine Species (WoRMS, Boyko et al. 2019) databases were used for assessing the current taxonomical status for each species as well as to avoid possible synonymies. A table was constructed with the geographical distribution (presence/absence) of all reported rhodolith-forming species by biogeographical provinces as defined by Spalding et al. (2007) (Supplementary Table S1). Data were hierarchically organised into 11 realms and 62 biogeographical provinces. The realms are: ARC – Arctic; TNA – Temperate Northern Atlantic; TNP – Temperate Northern Pacific; TAT Tropical Atlantic; WIP – Western Indo-Pacific; CIP – Central Indo-Pacific; EIP –Eastern Indo-Pacific; TEP – Tropical Eastern Pacific; TSA – Temperate South America; TAU – Temperate Australasia; and SOC – Southern Ocean. No information was obtained for rhodoliths from the Temperate Southern Africa (TSAF) realm of Spalding et al. (2007). A subsequent analysis of the preliminary table showed that 23 out of the 62 biogeographical provinces within the 12 realms used by Spalding et al. (2007) did not yield any rhodolith-forming species; these 23 biogeographical provinces (one realm included) were removed and the final table comprises 39 biogeographical provinces distributed among 11 realms (Supplementary Table S1).

Biogeographic analyses

Based on these data, dissimilarity indices and cluster analyses were applied to define the relationships between the different realms and biogeographical provinces. Prior to further analyses, we removed from the dataset all endemic rhodolith-forming species, i.e., those rhodolith species that occurred in a single biogeographical province. All analyses were performed on the resulting dataset that contained 44 rhodolith-forming species distributed along 37 provinces. We used R (R Core Team 2017) and the following packages: vegan (Oksanen et al. 2018), ade4 (Dray and Dufour 2007), cluster (Maechler et al. 2018), gclus (Hurley 2012), and recluster (Dapporto et al. 2015). Several classical distance metrics were utilized for analysis

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of presence/absence data, namely Jaccard (1901), Sørensen (1948), Ochiai (1957), and Simpson (1960) dissimilarities. Also, for each dissimilarity coefficient, several agglomeration methods were tested (Legendre and Legendre 1998), namely complete linkage, centroid distance, unweighted pair group method with arithmetic mean (UPGMA), and Ward's minimum variance clustering (Sokal and Michener 1958, Sokal and Sneath 1963, Ward 1963).

To determine the best combination of dissimilarity measure and agglomeration method, we calculated the cophenetic correlation value between the distance matrix and the dendrogram representation (Sokal and Rohlf 1962). The putative number of groups formed by the target realms and biogeographical provinces was estimated using both: i) the optimal number of clusters according to silhouette widths, that is Rousseeuw quality index (Rousseeuw 1987); and ii) the optimal number of clusters according to the Mantel statistic (Pearson correlation; see Legendre and Legendre 1998). For the respective implementation, we followed Borcard et al. (2011) and the hierarchical clustering approach reported by Pavão et al. (2019). These putative groups were further supported by a bootstrap validation procedure, implemented using re-cluster R package. The re-cluster package provides robust techniques to analyse patterns of similarity in species composition (Kreft and Jetz 2010, Dapporto et al. 2013, 2014, 2015[1]). Each dendrogram was targeted by a re-sampling procedure with 100 trees per iteration and a total of 1,000 iterations. All dissimilarity coefficients were re-tested using this approach, to ensure that the number of groups formed by the target realms and provinces was consistent.

The consistency of possible biogeographic relationships was further subjected to analysis through the use of discrete Bayesian Networks, using the same presence and absence data matrix, in a completely different approach, not based on similarities or dissimilarities, but on the probabilistic relationships (i.e., conditional probability tables; Scutari and Denis 2015), calculated between the target biogeographic provinces. For this analysis, all 106 rhodolith-forming species were used. We followed Scutari (2010), Nagarajan et al. (2013), Scutari and Denis (2015), and applied the bnlearn R package (Scutari 2018) to establish network structure and estimate network parameters.

Bayesian networks are a class of graphical models (Pearl 1998) that allow a concise representation of the probabilistic dependencies between a given set of random variables, as a directed acyclic graph (DAG; Nagarajan et al. 2013). Constraint-based algorithms and score-based learning algorithms were tested using the available network scores, including the Akaike Information Criterion score (AIC). Several bnlearn functions were used to calculate AIC for networks generated randomly (i.e., null models to be compared with the learned networks) and to calculate average networks resulting from a bootstrap procedure, after which, those arcs failing to pass a critical threshold were discarded (Nagarajan et al. 2013). The networks were plotted using the R package Rgraphviz (Hansen et al. 2019).

Finally, we tested for possible correlations between sampling effort (expressed as the number of papers published on rhodoliths/biogeographic province; cf. Supplementary Table S2) and species richness; and between littoral area (*sensu* Ávila et al., 2018, 2019) and species richness. Littoral area corresponds to the submarine area located between the mean sea level and a maximum depth that is taxon dependant (e.g., 50 m for gastropods and macroalgae, 200 m for fishes and echinoderms). In the case of rhodoliths, the 200-m isobath was the depth used for littoral area calculations, as records of live rhodoliths at greater depths are much less common. Littoral areas were calculated from GEBCO 2019[2] with a spatial resolution of 15 arc seconds Littoral area calculations were constrained to the biogeographical provinces of Spalding et al. (2007, their figure 2b - shapefile available at Data Basin web portal[3]). All projections are in World Mercator geographic coordinate system (WGS 84).

Ocean data are based on the Smith and Sandwell global 1-min grid between latitudes ± 81°. Higher resolution grids have been added from the LDEO Ridge Multibeam Synthesis Project, the JAMSTEC Data Site for Research Cruises, and the NGDC Coastal Relief Model. We used the World Mercator geographic coordinate system. For each biogeographic province, we calculated the total polygon area for the bathymetric range of 0–200 m. As this area included the subaerial area of possible islands/archipelagos occurring in the selected polygon, the littoral area was subsequently calculated by subtracting the total emerged area of the islands/archipelagos from the polygon total area.

Results

Biodiversity of rhodolith-forming species

The revised database includes a total of 106 rhodolith-forming species from 10 families and 21 genera that are presently reported from the 11 realms under adoption (cf. Supplementary Table S1). The families Hydrolithaceae and Mastophoroideae are the least diversified with only two species each, followed by Peyssonneliaceae and Corallinaceae with four species each, and Porolithaceae with five species. Also with a low diversity are the families Spongitaceae (10 species) and the families Mesophyllumaceae and Sporolithaceae (12 species each). Lithothamniaceae and Lithophyllaceae are the most diverse families, with 26 and 28 species, respectively. The realms ARC with two species and SOC with four are the least diverse, whereas CIP and TAU are the most diverse, respectively with 68 and 52 rhodolith-forming species. *Lithophyllum* Philippi, 1837 with 26 species, *Lithothamnion* Heydrich, 1897 (20 species), *Sporolithon* Heydrich, 1897 (13 species), and *Mesophyllum* Lemoine, 1928 (10 species) are the most diversified genera. In contrast, the genera *Amphiroa* Lamouroux, 1812, *Chamberlainium* Caragnano et al., 2018,

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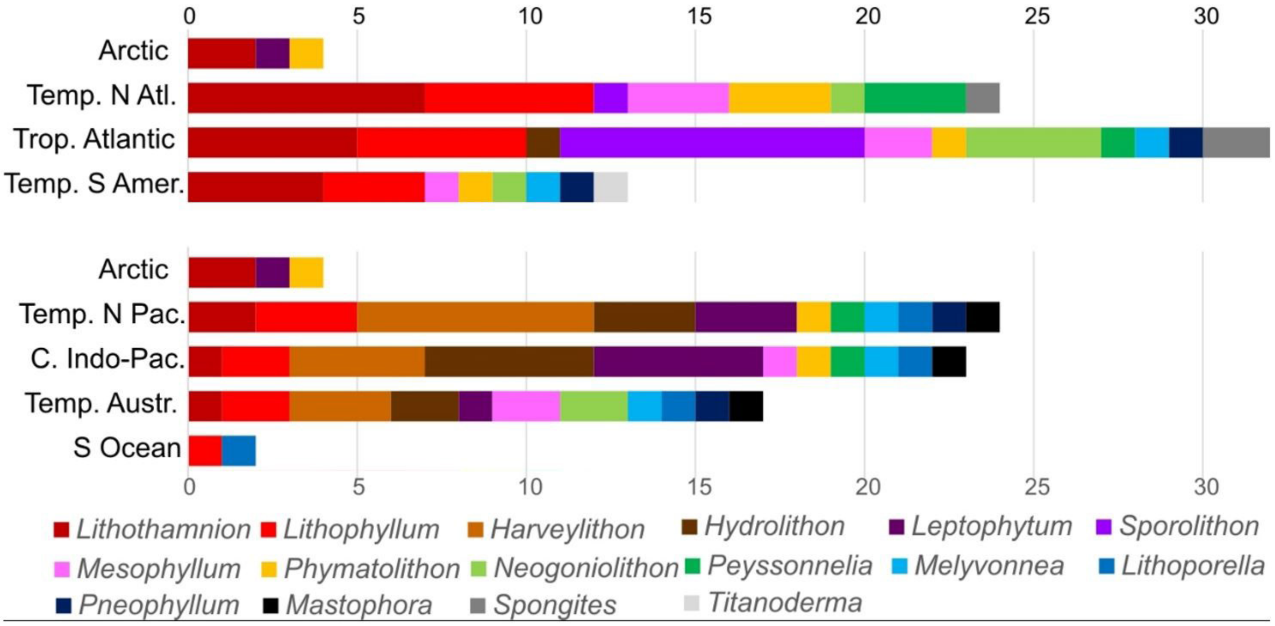

Figure 1. North-South biodiversity gradient of rhodolith-forming coralline algae for the Atlantic (above) and the western Pacific (below). Horizontal axis corresponds to the number of species. Temp.: Temperate; N: North; Atl.: Atlantic; Trop. Tropical; S: South; Amer.: America; Pac.: Pacific; Austr.: Australia.

Dawsoniolithon Caragnano et al., 2018, *Lithoporella* (Foslie) Foslie, 1909, *Mastophora* Decaisne, 1842, *Melyvonnea* Athanasiadis & Ballantine, 2014, *Pneophyllum* Kützing, 1843, *Titanoderma* Nägeli, 1858 and *Leptophytum* Adey, 1966 are all represented by a single species (Supplementary Table S1). *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason, 1943 and *Spongites fruticulosus* Kützing, 1841 are the rhodolith-forming species with widest distributional geographic ranges, being reported from five different realms.

The biogeographical provinces with highest diversity of rhodolith-forming species are TAT-14 (30 species), TEP-43 (21) and TNA-4 (19), whereas the least diverse provinces are TNA-5, TAT-13, WIP-21, CIP-36 and TSA-48, all with a single species (Table 1).

Two North-South gradients of rhodolith-forming red-algal species are shown in Fig. 1. The Atlantic gradient comprises a very low diversity in the Arctic realm with only four species, an increase in diversity towards the temperate (24 spp.) and tropical (33 spp.) realms, and then finally a decrease towards the temperate South American realm (13 spp.). The Western Pacific (excluding Indic) N-S gradient differs from the Atlantic, especially because the total number of species in the tropical Pacific realm is relatively low (23 spp.) compared to the Atlantic (33 spp.).

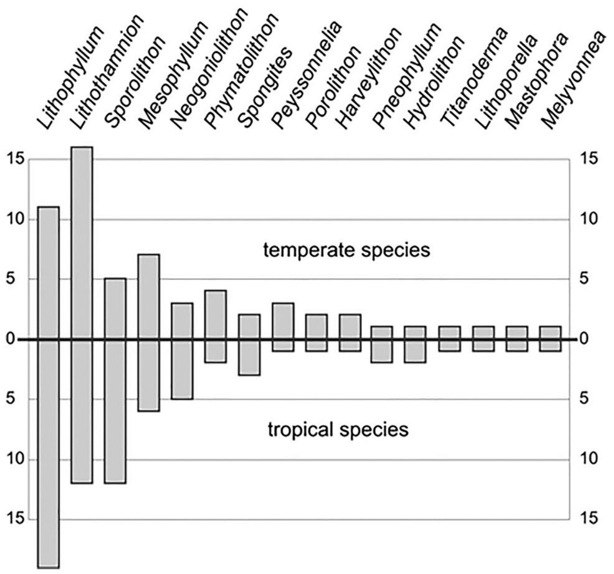

Figure 2. Biodiversity in temperate (TNA, TNP, TSA, TAU) and tropical (TAT, WIP, CIP, EIP, TEP) realms compared (Arctic and S Ocean excluded). Numbers correspond to the total number of species within the respective genera.

Comparing the diversity of the tropical and the temperate realms (excluding the Arctic and S Ocean), the difference seems limited at first sight. Both realms comprise 61 species each, and their numbers are comparable (Fig. 2). The most diverse genera are *Lithophyllum* with 26 species (7 species exclusively found in the temperate realm vs. 19 in the tropics, and 4 species in both temperate and tropics), *Lithothamnion* with 20 species (9 vs. 4, plus 8 species occurring in both temperate and tropical realms), *Sporolithon* with a total of 13 species (8 species restricted to the tropical realm) and *Mesophyllum* with 10 species (of which 3 are restricted to temperate realms and another 3 restricted to tropical realms). Finally, we advocate further research in the eastern Atlantic shores and Africa between Mauritania and South Africa to bridge the knowledge gap in these understudied areas.

Table 1. Total number of rhodolith-forming species, number and percentage of endemic rhodolith-forming species according to the realms and biogeographical provinces as defined by Spalding et al. (2007), littoral area (in km^2) and sampling effort (regarded as the total number of papers published per biogeographic province). Abbreviations for the realms: ARC – Arctic; TNA – Temperate Northern Atlantic; TNP – Temperate Northern Pacific; TAT – Tropical Atlantic; WIP – Western Indo-Pacific; CIP – Central Indo-Pacific; EIP – Eastern Indo-Pacific; TEP – Tropical Eastern Pacific; TSA – Temperate South America; TAU – Temperate Australasia; SOC – Southern Ocean.

Realm	Biogeographic Province Number	Biogeographic Province (acronym)	Total number of rhodolith-forming species	Number of endemic rhodolith-forming species	% of endemic rhodolith-forming species	Littoral area (km^2) (from 0 to -200)	Average Sea Surface Temperature (ºC)	Sampling effort (number of papers)
ARC	1	ARC-1	4	2	50.0	17204089	0.5 to 8.0	5
TNA	2	TNA-2	8	1	12.5	2478923	1.1 to 12.6	20
TNA	3	TNA-3	9	1	11.1	274426	8.1 to 17.3	14
TNA	4	TNA-4	19	10	52.6	536202	9.1 to 21.5	15
TNA	5	TNA-5	1	0	0.0	918865	1.8 to 22.9	2
TNP	8	TNP-8	4	0	0.0	1839959	1.4 to 21.4	4
TNP	9	TNP-9	12	0	0.0	577559	7.2 to 22.7	9
TNP	10	TNP-10	4	1	25.0	622747	1.8 to 12.9	3
TNP	11	TNP-11	11	5	50.0	129926	11.2 to 23.4	10
TAT	12	TAT-12	6	5	83.3	712948	15.5 to 23.5	3
TAT	13	TAT-13	1	0	0.0	375045	20.6 to 24.1	2
TAT	14	TAT-14	30	13	43.3	157173	17.6 to 22.7	32
WIP	18	WIP-18	5	4	80.0	184213	16.7 to 23.7	2
WIP	20	WIP-20	2	0	0.0	299502	17.4 to 24.6	1
WIP	21	WIP-21	1	0	0.0	308410	18.9 to 23.7	1
CIP	25	CIP-25	6	0	0.0	421289	14.7 to 24.1	1
CIP	26	CIP-26	7	0	0.0	1480046	20.3 to 25.3	1
CIP	28	CIP-28	8	0	0.0	16844	17.7 to 21.6	4
CIP	29	CIP-29	7	0	0.0	21573	17.8 to 22.8	5
CIP	30	CIP-30	16	1	6.3	576550	20.5 to 24.4	4
CIP	31	CIP-31	4	0	0.0	88136	20.5 to 23.5	2
CIP	33	CIP-33	7	0	0.0	238707	17.4 to 21.9	1
CIP	34	CIP-34	2	0	0.0	245089	18.3 to 24.2	1
CIP	35	CIP-35	11	0	0.0	93019	17.5 to 22.4	5
CIP	36	CIP-36	1	0	0.0	4278	14.6 to 17.7	1
EIP	38	EIP-38	2	0	0.0	18269	20.1 to 22.3	1
EIP	39	EIP-39	8	0	0.0	3702	19.9 to 22.4	4
EIP	40	EIP-40	9	0	0.0	12840	15.9 to 21.5	2
TEP	43	TEP-43	21	11	57.9	156765	14.4 to 23.5	8
TEP	44	TEP-44	2	2	100.0	6214	15.9 to 21.0	2
TSA	47	TSA-47	12	1	8.3	520017	8.1 to 19.9	12
TSA	48	TSA-48	1	1	100.0	1097488	2.3 to 12.9	2
TAU	53	TAU-53	10	0	0.0	39147	10.7 to 17.8	7
TAU	54	TAU-54	5	0	0.0	218759	7.8 to 14.8	3
TAU	55	TAU-55	7	0	0.0	54328	14.0 to 19.7	2
TAU	56	TAU-56	12	1	8.3	233435	8.9 to 16.2	6
TAU	57	TAU-57	11	0	0.0	310851	11.6 to 16.8	3
TAU	58	TAU-58	8	0	0.0	76240	14.4 to 19.8	3
SOC	62	SOC-62	2	0	0.0	35704	5.8 to 9.7	1

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Endemic species

From the 106 reported rhodolith-forming species, an impressive 59 species (57.3%) are geographically restricted to a single biogeographic province. However, some of these 59 rhodolith-forming species do occur in other biogeographic provinces but do not form rhodoliths; therefore, the total number of rhodolith-forming species endemic to a single biogeographic province is rather lower, just 15 species (14.2%). In addition, some biogeographic provinces exhibit a very high number of endemic species in relation to the total number of rhodolith-forming species inhabiting those areas (e.g., TAT-12, with 5 endemics out of 6 species [83.3%]; WIP-18, with 4 endemics out of 5 species [80.0%]; or TEP-44 and TSA-48, with 100% endemic species; Table 1).

Biogeography of rhodolith-forming species

The biogeographic analysis using standard clustering methods yielded 15 groups (cf. Fig. 3A), with about one quarter of those consisting of isolated biogeographical provinces: TAT-13 (group 1), CIP-36 (group 2), CIP-31 (group 8), and TAT-12 (group 15). The two largest clusters are group 7 and group 14: the first includes 6 biogeographical provinces from 2 different realms, all of them located in the Indo-Pacific area (CIP and TNP), whereas the latter includes 6 biogeographical provinces (5 of them from the TAU realm) from 2 different realms (TAU and TEP; Fig. 3A).

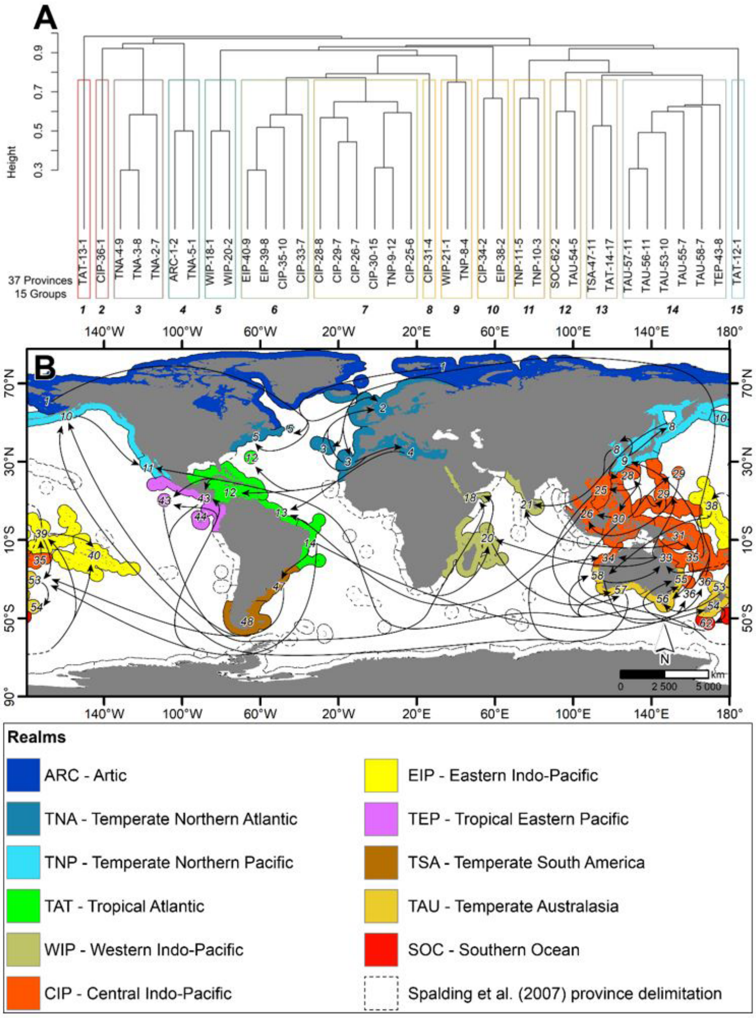

Figure 3. Rhodolith biogeographic framework, resulting from the analysis of the geographical distribution of the rhodolith-forming species over realms and biogeographical provinces (adapted from Spalding et al. [2007]; see Methods section for further explanation). (A) Results from the cluster analysis (Jaccard distance/UPGMA – the best combination of dissimilarity measure and agglomeration method, as given by the cophenetic correlation value between the distance matrix and the dendrogram representation, and confirmed using the bootstrap validation procedure) performed on the 44 rhodolith-forming species, showing a dendrogram with 15 groups depicting the relationships between the 11 realms/37 biogeographical provinces. The first three letters correspond to the acronym used for the realm, the first number that appears after the acronym refers to Spalding's biogeographical Provinces (cf. Table 1), and finally, the last number represents the number of rhodolith species present in each biogeographic province. Numbers in bold+italic placed under the main clusters highlight the 15 groups obtained. (B) Bayesian Network analysis of the possible biogeographic relationships between the 39 biogeographic provinces of Spalding et al. (2007), based on the geographic distribution of 106 rhodolith-forming species.

As usual, the pattern that emerges from the Bayesian Network analysis is rather complex (Fig. 3B). It shows a large number of arcs with significant probabilistic relationships established between several biogeographic provinces. This Bayesian Network is especially dense in the Indo-Pacific and Australasia areas. The wide geographical distribution of some rhodolith-forming species becomes apparent through the Bayesian Network analysis, which highlights significant relationships between biogeographical provinces located in different oceanic basins (e.g., TAT-14 and TAU-53; TAU-57 and TNP-10; Supplementary Figure S1). Finally, some biogeographical provinces appear to be important evolutionary areas, as they function as donors of species to other areas. The most important biogeographical provinces with such a role are TAT-14, CIP-30, CIP-35, TAU-56 and TNP-9 (Fig. 3B and Supplementary Figure S1).

Discussion

Biodiversity of rhodolith-forming species

Calcareous red algae diversity is known to be greatest in the tropical Pacific, and lowest towards the polar regions of both hemispheres (Steneck 1986). According to Steneck (1986), the diversity within the three rhodolith subfamilies shows dominance by the Mastophoroideae in the tropics and dominance by Melobesioideae at high latitudes, with the Lithophylloideae showing no biogeographic trend in diversity at all. Although recent molecular studies and revisions of the corallines have led to amendments on the status of the families and generic levels (Kato et al. 2011, Rösler et al. 2016), our results show that the Central Indo-Pacific and Temperate Australia continue to be the realms with the highest diversity.

Littoral area, as defined by Ávila et al. (2018), has been reported as the most important variable to explain species richness of a number of organisms in the marine realm (algae, molluscs, echinoderms, crustaceans, annelids, fishes; Ávila et al. 2019, Hachich et al. 2015, 2019). Littoral area is influenced by eustatic sea-level changes and submarine topography (Ávila et al. 2019). Other variables that are known to influence species richness, namely those marine organisms inhabiting insular systems, include latitude and geological age of the islands (Hachich et al. 2015, Ávila et al. 2018). We calculated the littoral area for the 39 biogeographical provinces used by Spalding et al. (2007; cf. Table 1), but, surprisingly, no correlation was found between littoral area and species richness within our data (r^2=0.012; Fig 4A). Even when high latitude biogeographical provinces affected by the last glacial episode were excluded from the analysis (e.g., ARC-1, TNA-5, TNP-10, TSA-48, SOC 62), no correlation was found (r^2=0.0005). This counter-intuitive pattern lacks explanation, and we hypothesize that the ecological conditions required by rhodolith-forming species (e.g., light exposure, type of substrate, temperature, and/or hydrodynamic conditions) are met by only a fraction of the calculated littoral areas. Unfortunately, with our current knowledge, it is not possible to calculate these restricted littoral areas, on a global scale.

Another plausible explanation for the highest diversity within the Central Indo-Pacific and Temperate Australia realms could be a sampling bias due to the greater number of studies (e.g., Steneck and Pain 1986, Verheij and Woelkerling 1992, Verheij 1994, Woelkerling 1996, Lund et al. 2000, Harvey et al. 2005, Matsuda and Iryu 2011, Neill et al. 2015, Kato et al. 2017, Nelson and Neill 2017) and the lack of or very few reports for the other realms. We checked for this, but the positive correlation found between sampling effort (number of studies) and species richness/biogeographic province proved to be weak (r^2=0.573; cf. Fig. 4B).

The North-South gradients (Fig. 1) in the Atlantic reveal a very clear pattern with an increase of diversity from the Arctic (4 spp.) over the temperate (24 spp.) to the tropics (33 spp.), and then again a decrease towards the temperate S America (13 spp.). This trend with a highest diversity in the tropics was somehow expected. However, the much lower diversity of the tropical Central Pacific (23 spp.) when compared to that of the tropical Atlantic (33 spp.) is difficult to explain. A sampling/study bias can be excluded, because all of these areas are well studied. We speculate that this condition may be

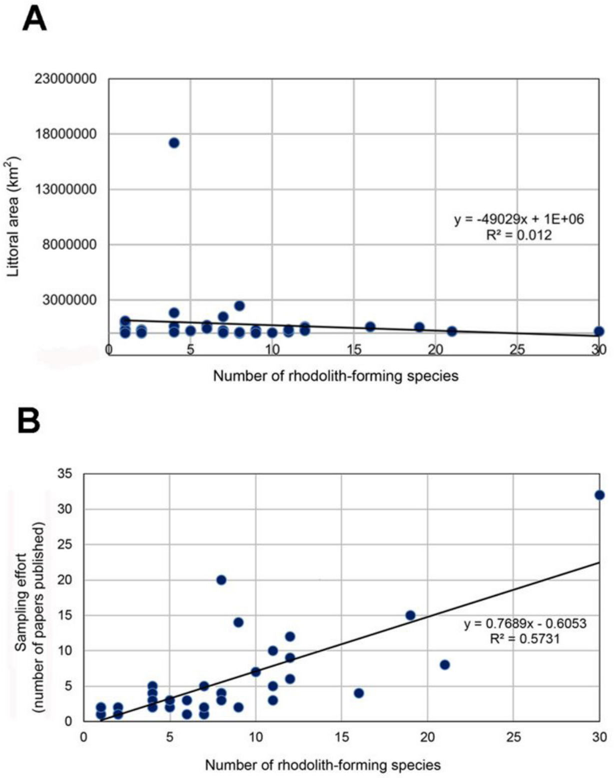

Figure 4. (A) Correlation between biogeographical provinces' littoral area (km^2) and rhodolith-forming species richness. (B) Correlation between sampling effort (expressed as number of publications/biogeographical province) and rhodolith-forming species richness.

related to the abundance of corals and coral reefs acting as competitors for space: they are much more abundant in the Pacific then in the Atlantic (beyond the Caribbean). It is well known that competition between corals and algae is common on coral reefs (e.g., Littler 1973, Littler and Littler 1994) but, as far as we know, this hypothesis has never been tested. In the few studies on coral-algal interactions dealing with the processes/mechanisms that led to (macro)algal overgrowth of corals – reviewed by McCook et al. (2001) and Chadwick and Morrow (2011) – rhodoliths have never been considered in this matter.

Another interesting observation is that both in the Atlantic and in the Pacific, the northern temperate shelves are much more diverse (24 spp./24 spp.) than the southern temperate areas (13 spp./17 spp.). This pattern is difficult to explain, and here again we are unable to exclude a sampling/study bias.

Endemic species

In general, regions that are near the edge of the effective dispersal range seem to show greater endemicity within a taxon (Mironov and Krylova 2006 and references therein). This idea is supported by the endemic patterns in the central oceanic areas: the degree of endemism is highest in small open-oceanic areas located at the periphery of great biogeographical regions; for example, Hawaii, Galapagos, Juan Fernandez, and Easter Island areas in the Pacific, South Georgia and St. Helena-Ascension areas in the Atlantic (Mironov and Krylova 2006). The same was observed by our results where the biogeographic provinces TEP-44 and TSA-48 showed a 100% rate of endemism (Table 1).

Biogeography of rhodolith-forming species and actuopalaeontological aspects

Coralline red algae as a whole, although cosmopolitan, seem to show different latitudinal and bathymetric distributions at the species level (Aguirre et al. 2002 and references therein). The bathymetric distribution was not considered in our study, as most studies do not provide information about the depth distribution of the studied taxa. However, we were able to recognize two main clusters for the biogeography of the rhodolith-forming species, with the Indo-Pacific area being the most extensive.

Considering that the coralline algae are the main carbonate producers of the Cenozoic, several attempts have been made to use them as palaeoecological proxies at a genus-level (Aguirre et al. 2000, Rasser and Piller 2004, Bassi et al. 2009), which requires a profound knowledge of their present-day ecological requirements and their geographical distribution. In their major review of biodiversity trends across deep time, Aguirre et al. (2000) summarised the results from former studies (for references see therein; suprageneric taxon names used according to those references): (1) Sporolithaceans (genus *Sporolithon*) are almost restricted to low latitudes, where they mainly thrive in deeper water; (2) Melobesioids (genera *Leptophytum, Lithothamnion, Mesophyllum, Phymatolithon*) are not latitudinally restricted; (3) Lithophylloids (genus *Lithophyllum*) are most common in shallow-water, subtropical and warm-temperate conditions; (4) Mastophoroids (genera *Hydrolithon, Lithoporella, Mastophora, Neogoniolithon, Pneophyllum, Spongites*) predominate in shallow-water tropic seas.

Our study confirms these general trends, but also reveals that the application of coralline genera as palaeoecological proxies must be very carefully done. First, *Sporolithon* is indeed more diverse in the tropics (13 spp.) than in the temperate realm (5 spp.; Fig. 2). The N-S gradients reveal, however, this is not always the case, as both in the temperate N Atlantic (7 spp.) and in the temperate N Pacific (7 spp.) this genus is more diverse than in the tropical Atlantic (5 spp.) and Pacific (4 spp.), respectively (Fig. 1). Secondly, we can also confirm that the Melobesioids are not latitudinally restricted, and yet each of the genera is far more common in temperate environments (27 spp. in total) than in the tropics (20 spp.; Fig. 2). Also from the N-S gradients (Fig. 1), it is obvious that Melobesioid genera are more diverse in the northern temperate realms than they are in the tropics. Interestingly, however, in the southern temperate realms they are even less diverse than in the tropics. Third, the trend for Lithophylloids is confirmed: they are more diverse in the subtropics. Fourth, the trend for Mastophoroid genera is confirmed as well, even though it is not very distinct (9 spp. in temperate vs. 14 spp. in tropics). And again, when considering the N-S gradients in the Atlantic and Pacific (Fig. 1), the distribution is not as clear.

The cluster analysis highlights the largest cluster (which includes groups 6, 7, 8 and 9; cf. Fig. 3A), of the large tropical areas CIP, EIP and WIP. Fig. 3A also shows that the temperate areas SOC, TAU and TSA cluster (groups 12, 13 and 14). The complex Bayesian network biogeographic analysis depicted in Fig. 3B also seems to retain ancient biogeographical patterns (e.g., a Post-Messinian Salinity Crisis re-colonization of the Mediterranean Sea by coralline algae rhodolith-forming species with an Eastern Atlantic origin – see arrow from TNA-3 to TNA-4 in Fig. 3B; cf. also Supplementary Fig. S1). Two tropical areas of the Central Indo-Pacific (CIP-31 and CIP-35; cf. Supplementary Fig. S1) seem to play a key role within the Bayesian network biogeographic analysis, probably acting (together with CIP-30) as centres of evolutionary radiation (*sensu* Briggs 1995) or as centres of redistribution (*sensu* Mironov and Krylova 2006). Interestingly, both are located in the East Indies Triangle, a comparatively small but biodiverse region within a triangle formed by the New Guinea, the Philippines, and the Malay Peninsula. We find that Bayesian network analysis appears to be a promising tool in biogeographic analysis and should be explored with larger databases (e.g., the Atlantic shallow-water molluscs or echinoderms; cf. Madeira et al. 2019, Freitas et al. 2020).

Influence of major biogeographic barriers

Isthmus of Panama

Although located at similar latitudes, there is a clear contrast in biodiversity patterns of the rhodolith-forming species from the Tropical Eastern Pacific (TEP-43, with 19 spp., 11 of them endemic; Table 1 and Fig. 2) when compared with those of the Tropical Atlantic (TAT-12, with 6 spp., 5 endemic). Moreover, from the total 25 species that are reported from both TEP-43 and TAT-12, only one rhodolith-forming species presently occurs in both areas, *Lithophyllum stictiforme* (Areschoug) Hauck (cf. Supplementary Table S1). These once contiguous areas (see Fig. 5A) are presently separated by the Isthmus of Panama (Fig. 5B), a major marine biogeographic barrier well-known to have promoted different evolutionary pathways within the shallow-water marine species of the eastern Pacific versus those inhabiting the western Atlantic (Briggs 1995, Beu 2010). The most prominent effect of such a (vicariant) barrier was to induce widespread speciation in the marine realm (Rosen 1975, Jackson et al. 2003), alongside differential extinction patterns (Vermeij and Petuch 1986). As depicted in Fig. 5A, the Pacific

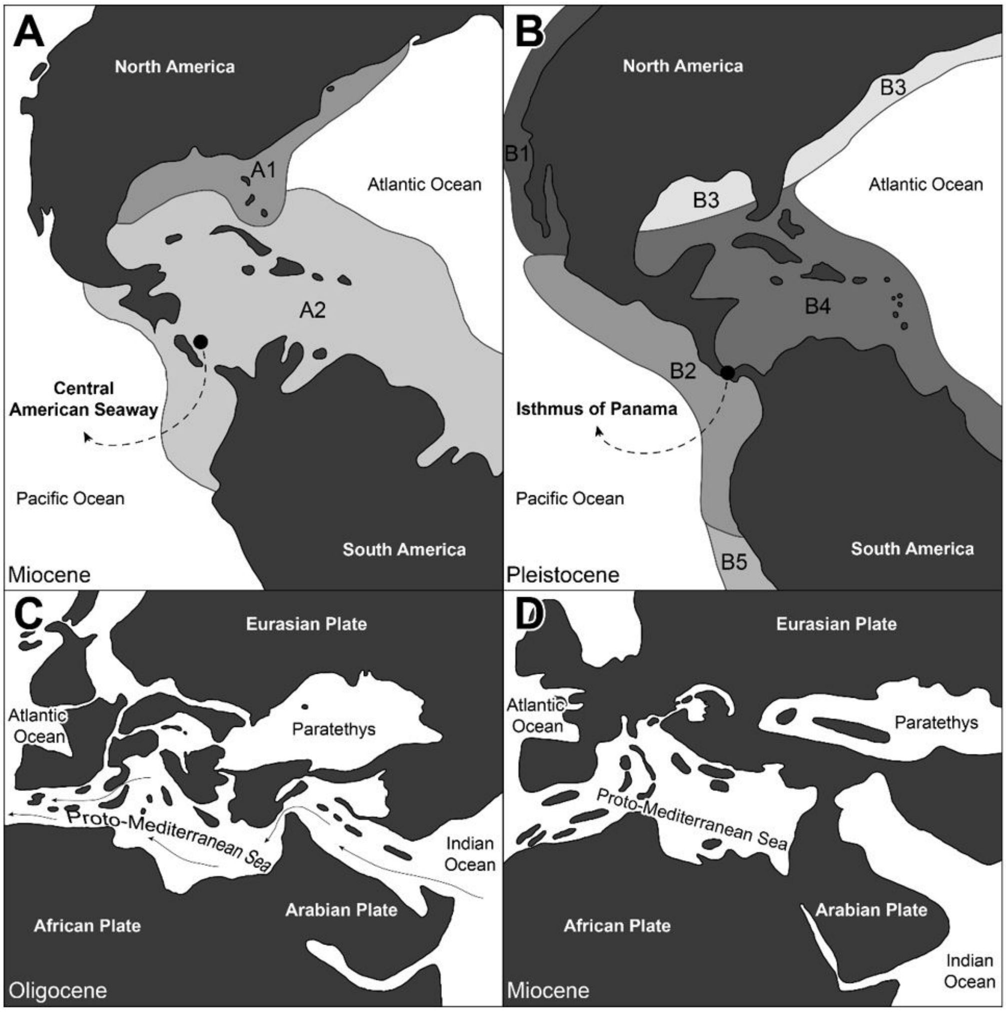

Figure 5. (A-B) Palaeogeography of the Caribbean Region during the Miocene (modified from Vermeij 2005) and the Pleistocene (modified from Spalding et al. 2007). (A) During the Miocene, the Central American Seaway (CAS) provided a pathway for the dispersal of species between the Atlantic and the Pacific Ocean. (A1) Caloosahatchian palaeobiogeographical province; (A2) Gatunian palaeobiogeographical province. (B) After the closure of the Isthmus of Panama, different faunas evolved on the Pacific and the Atlantic sides of the isthmus land barrier. (B1) Warm-temperate Northeast Pacific biogeographical province; (B2) Tropical East Pacific biogeographical Province; (B3) Warm-Temperate Northwest Atlantic biogeographical Province; (B4) Tropical North-western Atlantic biogeographical Province; (B5) Warm-Temperate Southeastern Pacific biogeographical Province. (C-D) Palaeogeography of the Western Tethys Region during the Oligocene and Early Miocene (modified from Rögl 1999 and Harzhauser et al. 2007). (C) In the Early Oligocene, the Paratethys was first isolated from the Proto Mediterranean Sea; the circulation from the Indian to the Atlantic Ocean remained open and there was a connection with the North Sea via the Rhine graben. (D) During the Miocene (Late Burdigalian), the collision of the Arabian/African Plate with the Eurasian (Iranian) Plate closed the open marine Indo-Pacific connections, thus isolating the Proto-Mediterranean Sea.

and the Atlantic oceans were connected in the past for several millions of years, sharing similar marine faunas and floras whose representatives were able to cross from the Atlantic to the Pacific Ocean through the Central American Seaway (CAS; Vermeij 2005). However, with the final emergence of the Isthmus of Panama and the consequent closure of the CAS at about 2.8 Ma (O'Dea et al. 2016; Fig. 5B), a scenario of high incidence of extinction and local disappearance events was prevalent on the Atlantic side of the former Gatunian palaeobiogeographical province, which corresponds to the present Gulf of Mexico and the Caribbean region, excluding the southern north American shores which belonged to the Caloosahatchian palaeobiogeographical province (Petuch 1982, Vermeij 2005; see Fig. 5A). These extinctions and local disappearances were caused by two extinction events that heavily affected predominantly the tropical Atlantic marine biota. The first occurred during the Late Pliocene, in the course of the transition of the Zanclean to the Piacenzian Stage, at about 3.7-3.5 Ma, thus prior to the closure of the CAS. The second occurred at the end of the Early to Middle Pleistocene, at about 1.0–0.4 Ma (Landau and Silva 2010).

Vermeij (2005) reported an extinction/local disappearance rate of 27.3% of the marine mollusc genera since the Early Pliocene, from the Atlantic side of the Gatunian palaeobiogeographical province, in contrast to just 15% for the Pacific side of the Gatunian palaeobiogeographical province. Moreover, Landau et al. (2010) demonstrated that about 50% of the subgeneric taxa of molluscs that lived around Cubagua Island (Gatunian province; Fig. 5A) during the Pliocene currently occupy more restricted geographical distributions within the eastern Pacific. These taxa correspond to the "Paciphile taxa" *sensu* Woodring (1966), i.e., taxa that were widely distributed in tropical Pacific and Atlantic regions of the Gatunian province from the Miocene up to the early Pliocene, and that nowadays are restricted to the tropical Pacific region (see also Beu 2010, Landau et al. 2016). The comparison of the species composition of fossil rhodoliths from the tropical western Atlantic with that of the recent eastern Pacific taxa may allow us to elucidate whether (similar to marine gastropods) there are also Paciphile taxa within the rhodoliths. This is a field that deserves further research.

Arabian Plate

Between the Oligocene and the Early Miocene, the Tethyan Seaway was a large marine pathway that provided a direct connection between the Indo-Pacific and the Atlantic Ocean (Fig. 5C). The Western Tethys Region *sensu* Harzhauser et al. (2007) encompassed a large area that spread from the Bay of Biscay in the west, through the modern Mediterranean Sea, ending at Pakistan and N and SW India in the far east, but also including the shores of Eastern Africa (Somalia, Kenia and Tanzania, down to Zanzibar) in the south (Harzhauser et al. 2002). This seaway first closed during the late Burdigalian, at about 19 Ma (Jones 1999), as a result of the rise of the *Gomphotherium* Landbridge (Rögl 1998). This marine biogeographic barrier resulted from the collision of the Arabian/African Plate with the Eurasian (Iranian) Plate, thus isolating the marine biota of the eastern Proto-Mediterranean Sea from that of the western Indo-Pacific Tethys (Harzhauser et al. 2007). A short, shallow marine, temporary seaway re-established the connection between the Proto-Mediterranean and the Indian Ocean during the Middle Miocene Climatic Optimum (17–14.75 Ma; Zachos et al. 2001) via the Mesopotamian Trough (Jones 1999); this seaway finally closed during the Early Serravallian (Rögl 1999; Fig. 5D). In the Late Miocene, the Messinian Salinity Crisis severely impacted the marine biota of the Mediterranean Sea (Hsü et al. 1978), causing widespread extinction of Mediterranean endemics and extirpation of marine populations. The post-Messinian Mediterranean marine biota derives from an impoverished eastern Atlantic biota (Harzhauser et al. 2002, 2007). Therefore, as a result of ~14 Ma of effective separation, it is no surprise that in present times there is not a single rhodolith-forming species in common between the Mediterranean province (TNA-4, with 19 species) and the Red Sea and Gulf of Aden province (WIP-18, with 5 species; cf. Supplementary Table S1).

Conclusions

This work is a first attempt to review the biodiversity and biogeography of the rhodolith-forming red algal species on a global scale. It reports a total of 106 rhodolith-forming species from 10 families and 21 genera, with an impressive 57.3% rate of endemic species. Rhodoliths occur in 11 out of the 12 marine realms of Spalding et al. (2007). The Central Indo-Pacific and the Temperate Australasia are the most diverse realms, whereas the Tropical Southwestern Atlantic (TAT-14, with 30 species), the Mediterranean Sea (TNA-4) and the Tropical East Pacific (TEP-43), with 19 and 20 species, respectively, are the biogeographical provinces with highest diversity of rhodolith-forming species. In a stark contrast to other studied marine groups (e.g., mollusc gastropods, other macroalgae, echinoderms, reef fishes; cf. Hachich et al. 2015, Ávila et al. 2018), littoral area does not explain the rhodolith-forming species biodiversity found in the 39 biogeographical provinces analysed.

Application of a Bayesian Network analysis highlights two major results: 1) the Tropical Southwestern Atlantic province (TAT-14), the Western Coral Triangle province (CIP-30), the Tropical Southwestern Pacific (CIP-35), the Southeast Australian Shelf (TAU-56), and the Warm Temperate Northwest Pacific (TNP-9) became important evolutionary areas because they functioned as recruitment areas of rhodolith species for other areas; and 2) the wide geographical distribution of some rhodolith-forming species, which developed as a result of significant relationships between

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biogeographical provinces located in different oceanic basins.

The existence of marine barriers and the geological age of their final emplacement are key elements to explain the disparities among the specific composition of the shallow-water marine biota of former contiguous areas (e.g., Pacific versus Atlantic shores of Panama and Costa Rica, in the Central America; eastern Mediterranean Sea versus Red Sea and Gulf of Aden). This is illustrated by the examples used in this study – the Isthmus of Panama and the *Gomphotherium* Landbridge (Arabian Plate).

Finally, we raise a hypothesis for the lower diversity of the rhodolith-forming species in the tropical Pacific Ocean when compared to the Atlantic Ocean (23 versus 33 spp.), attributing this fact to the higher abundance of corals and coral reefs in the Pacific, which act as competitors for space with rhodoliths. This hypothesis should, however, be tested in further studies.

As a final point, we recall the urgent need of systematic surveys for rhodoliths along yet unexplored extensive areas such as the eastern Atlantic shores of Africa, between Mauritania and South Africa.

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Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb

Figure S1. Raw graph depicting the results of the Bayesian Network analysis of the possible biogeographic relationships between the 39 biogeographic provinces of Spalding et al. (2007), based on the geographic distribution of 103 rhodolith-forming species.

Table S1. Checklist of the rhodolith-forming species and its geographic presence.

Table S2. Compilation of the bibliography published for each biogeographic province.

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