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Rhodolith Beds in Brazil—A Natural Heritage in Need of Conservation

Nadine Schubert[1] | Rafael A. Magris[2] | Flávio Berchez[3,4] | Angelo F. Bernardino[5] | Carlos E. L. Ferreira[6] | Ronaldo B. Francini-Filho[7] | Tainá L. Gaspar[8,9] | Guilherme H. Pereira-Filho[10] | Sergio Rossi[11,12] | João Silva[1] | Marina N. Sissini[13] | Marcelo O. Soares[11] | Frederico T. S. Tâmega[14] | Fernando Tuya[15] | Paulo A. Horta[13]

[1]Centre of Marine Sciences (CCMAR/CIMAR LA), Campus de Gambelas, Universidade do Algarve, Faro, Portugal | [2]Chico Mendes Institute for Biodiversity Conservation, Ministry of Environment, Brasilia, Brazil | [3]Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil | [4]Cape Horn International Center, Puerto Williams, Chile | [5]Departamento de Oceanografia, Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil | [6]Laboratório de Ecologia e Conservação de Ambientes Recifais, Departamento de Biologia Marinha, Universidade Federal Fluminense, Niterói, Rio de Janeiro, Brazil | [7]Laboratório de Biodiversidade e Conservação Marinha, Centro de Biologia Marinha (CEBIMar), Universidade de São Paulo (USP), São Sebastião, Brazil | [8]Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil | [9]Laboratório de Ecologia e Ambientes Recifais, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil | [10]Laboratório de Ecologia e Conservação Marinha, Instituto do Mar, Universidade Federal de São Paulo, Santos, Brazil | [11]Instituto de Ciências do Mar (LABOMAR), Universidade Federal do Ceará, Fortaleza, Ceará, Brazil | [12]DiSTeBA, Università del Salento, Lecce, Italy | [13]Laboratório de Ficologia, Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, Brazil | [14]Instituto de Estudos do Mar Almirante Paulo Moreira, Departamento de Biotecnologia Marinha, Arraial do Cabo, Rio de Janeiro, Brazil | [15]Grupo en Biodiversidad y Conservación (IU-ECOAQUA), Universidad de Las Palmas de Gran Canaria, Telde, Spain

Correspondence: Nadine Schubert (nadine_schubert@hotmail.com) | Rafael A. Magris (rafael.magris@my.jcu.edu.au)

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The first two authors contributed equally to this article.

ABSTRACT

Aim: Brazil harbours the largest known extent of rhodolith beds (RBs) in the world, a habitat whose ecological and economic importance have been widely overlooked. This creates a dire situation that is likely to worsen with the rapidly expanding human activities, considering that less than 5% of Brazil's ocean area is fully protected. We assessed the importance of Brazilian RBs for supporting biodiversity, at a country-wide level, and identified multi-criteria hotspots that, in face of lack of protection and presence of anthropogenic threats, could safeguard conservation seascapes across Southwestern Atlantic waters.

Location: Southwestern Atlantic Ocean.

Methods: We performed a systematic review of studies on Brazilian RBs to retrieve information regarding their spatial distribution and associated biodiversity. Multi-criteria hotspots were identified based on the areas where high species diversity co-occurs with a high presence of endemic, threatened and commercially important species. Furthermore, we assessed how well RBs are covered by marine protected areas (MPAs), as well as their spatial overlap with multiple threats.

Results: Existing records for Brazilian RBs indicate > 1000 different species, mostly fish and algae, including significant numbers of endemic, threatened and commercially important species. Most of the RBs are either unprotected or only partially protected, including the majority of the biodiversity hotspots identified by our analysis. Among the main potential threats to RBs, bottom trawling ranks highest, while the expansion of seabed mining and oil and gas activities may sharply increase the risk of cumulative impacts on RBs in the near future.

Main Conclusions: Our large-scale quantitative assessment confirms the significant role of RBs as biodiversity hotspots. This information could be leveraged to help meet the twin goals of RB conservation, through the establishment of highly-protected MPAs in hotspot areas, and their sustainable use through an ecosystem-based approach that accounts for vulnerabilities of RBs to multiple threats.

1 | Introduction

Rhodolith beds (RBs) are built by free-living non-geniculate coralline algae and recognised globally as ecologically and socio-economic important yet threatened marine benthic habitats (Riosmena-Rodríguez, Nelson, and Aguirre 2017). Their importance for supporting biodiversity and facilitating other habitat-formers and foundation species, such as kelp, sponges, bivalves, is widely acknowledged (Tuya et al. 2023; Bulleri et al. 2024). Despite the large global extent of RBs, their ecological functioning and biota have been disproportionately less studied, hampering existing conservation efforts (Tuya et al. 2023). Society and decision-makers are also largely unaware of the existence of RBs. However, given the growing global and local threats to these habitats, primarily from human activity, it is crucial to recognise their value and implement effective conservation efforts globally (Tuya et al. 2023). In this context, marine biodiversity has been recognised worldwide to play an essential role in supporting a healthy planet and social well-being. Although accurately quantifying this biodiversity is complex, it is urgently needed to implement conservation and restoration measures during the United Nations Decade of the Ocean and the Decade of Ecosystem Restoration (2021–2030).

Currently, information about biodiversity associated with RBs, including threatened and endemic species, is available only on a case-by-case basis and at limited spatial scales (e.g., Moura et al. 2016; Stelzer et al. 2021; Maggio et al. 2022; Tabone et al. 2024). So far, no attempts have been made to compile a comprehensive multi-taxa biodiversity inventory at a larger spatial scale, despite its importance for emphasising the need for protective measures. In this context, Brazil offers an ideal opportunity, as RBs are one of the most prevalent megahabitats of the seascapes of the continental and insular shelves and the tops of seamounts (Pereira-Filho et al. 2012; Amado-Filho et al. 2017). In fact, Brazil has long been known to harbour the most extensive RBs in the world (Foster 2001; Amado-Filho et al. 2017). Here, suitable habitat modelling approaches estimate a total area between 167,000 and 230,000 km^2 (Carvalho et al. 2020; Santos et al. 2023), within a depth range of 2 to ~250 m depth, corresponding to 4%–6% of the global area estimate (Fragkopoulou et al. 2021). Due to this ubiquitous presence of RBs in Brazil, the associated biodiversity and other aspects of their ecology and biology are well studied in some sites within the country, including numerous reports demonstrating their ecological importance for biodiversity (e.g., Brasileiro et al. 2016; Stelzer et al. 2021; Anderson et al. 2023). Moreover, available evidence indicates that these habitats share many common species with adjacent habitats, such as coral reefs, seagrass beds and sandy bottoms (Pinheiro et al. 2015; Moura et al. 2021; Stelzer et al. 2021). They are potentially important for the ecological connectivity of fish by serving as nursery grounds for juveniles, foraging grounds for many adult species and migrations corridors between shallow and deep reefs (Moura et al. 2021; Anderson et al. 2023).

As in many other coastal marine environments, RBs are exposed to increasing pressures by multiple threats associated with anthropogenic activities. For example, bottom trawling has been identified as a major threat to RBs globally (e.g., Fragkopoulou et al. 2021; Tuya et al. 2023). Moreover, areas containing RBs are of great interest for mining companies, as they represent an important source of limestone, with Brazil being one of the top producers (Paiva et al. 2023a). However, mining activities cause habitat destruction by the removal of rhodoliths that are built by slow-growing calcareous algae (~1 mm/year) and are thus classified as non-renewable resources (Barbera et al. 2003). Mining also promotes sediment dislodgement, leading to the burial and subsequent death of rhodoliths in adjacent areas (Villas-Boas et al. 2014; Figueiredo et al. 2015; Osterloff et al. 2016). Similar to other marine benthic habitats worldwide, RBs are currently threatened by the ongoing climate change (Horta et al. 2016; Fragkopoulou et al. 2021). Although, in Brazil, there is little information on the effects of anomalous temperatures and ocean acidification on rhodolith health and diversity, only few existing studies suggest negative effects on the physiological performance of rhodoliths in face of marine heatwaves and ocean acidification conditions (Schubert et al. 2019; Koerich et al. 2021).

To address growing threats, marine protected areas (MPAs) have become a key management tool to protect diverse marine habitats and their biodiversity (IPBES 2019; United Nations 2017). This conservation approach, encompassing varying levels of restrictions, from multiple-use to no-take areas, has been widely implemented for coral reefs and mangrove habitats (Ban et al. 2011; Liao et al. 2019; Gill et al. 2024). Only a few examples of MPAs have been designated to explicitly protect RBs and their associated biodiversity (reviewed in Tuya et al. 2023). Yet, as the newly adopted Kunming-Montreal Global Biodiversity Framework calls for an urgent protection of 30% of the planet by 2030, through an ecologically representative and well-connected system of protected areas (Obura et al. 2023), the effective implementation of MPAs on RBs provides new opportunities to support the full achievement of international goals.

Previous reviews on Brazilian RBs (Amado-Filho and Pereira-Filho 2012; Horta et al. 2016; Amado-Filho et al. 2017; Paiva et al. 2023a) have addressed the qualitative importance of biodiversity associated with these habitats. However, such studies have not used quantitative spatial information to formally analyse the biodiversity associated with RBs in different ecoregions and sites (but see Lino et al. 2024) and to estimate the current coverage of RBs by MPAs. In this paper, we performed a systematic review of studies on Brazilian RBs to describe and evaluate their conservation value. We specifically aimed to (i) provide quantitative evidence for the ecological roles played by RBs in supporting biodiversity (termed hotspot) at a large spatial scale, particularly based on the co-occurrence of species of conservation/management interests (i.e., red-listed, endemic and commercially important); (ii) quantify the current coverage of RBs by MPAs across the studied region and (iii) assess the extent of anthropogenic threats to RBs in Brazil. Our results provide useful information and insights to improve conservation and management of RBs in Brazil and a first step for the implementation of a country-wide conservation planning to reconcile conservation and development needs.

2 | Methods

2.1 | Literature Search and Selection of Studies

A systematic literature search was carried out (including papers until November 2023) in the Web of Science, complemented by a search in Google Scholar (search string—'Brazil' and 'rhodolith'), to compile all the available information regarding Brazilian RBs. Following the PRISMA guidelines (O'Dea et al. 2021), only original peer-reviewed research papers were considered, while nonpeer-reviewed articles, reviews, policy papers, duplicates and those written in languages other than English were excluded. First, a systematic literature review was performed to summarise existing knowledge on Brazilian RBs, regarding the number of studies, study sites (including their geographical coordinates, when available) and topics (n = 128 studies). Second, from the studies, those reporting species inventory lists of associated fauna and/or flora were selected for a detailed analysis of the number of recorded rhodolith-bed associated species (n = 54 studies, see reference list in Supporting Information) and among those, species that are considered endemic, threatened species and/or of commercial importance were identified. Brazilian endemic species were identified, using a list provided by Correia and Sovierzoski (2012) for macrobenthic species, and the websites of Southwestern Atlantic Reef Fishes (https://swatlanticreeffishes.wordpress.com/), FishBase (https://www.fishbase.se), with updates on the Living National Treasures website (http://lntreasures.com/brazilmf.html) for marine fishes. Threatened species (vulnerable, endangered, critically endangered) were identified through the IUCN red list (IUCN 2024) and the national Brazilian red list issued by the Chico Mendes Institute for the Conservation of Biodiversity (ICMBio) (ICMBio 2022). Moreover, fish species, considered targets for fisheries, were identified as commercially important, according to Quimbayo et al. (2021).

2.2 | Rarefaction Curves

To evaluate the completeness of species inventories and to perform meaningful comparisons of species richness associated with RBs in general and with different RBs across Brazilian ecoregions, rarefaction curves (with confidence intervals) were obtained to represent how the total number of species recorded for all Brazil and in each ecoregion varied as a function of the number of sampling sites. Rarefaction was implemented in the EstimateS program (Colwell 2019).

2.3 | Conservation and Threat Assessment

We extracted spatial information on the occurrence of RBs from the compiled database, based on the literature search outlined above. The study sites (n = 1330) at which RBs have been reported were evaluated against the boundaries of MPAs, considering both no-take (i.e., considered fully protected, which refers to the IUCN categories Ia and b, II and III) and multiple-use MPAs (i.e., considered partially protected, which refers to the IUCN categories IV). Information on MPAs in Brazil was gathered and compiled from datasets held by the Brazilian Ministry of Environment (e.g., http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs). When performing this overlap, RBs were first classified into two classes, based upon their depth zones: shallow-water, for sites shallower than 30 m, and mesophotic RBs, for sites deeper than 30 m. We also assessed the RBs coverage by MPAs for each of the marine ecoregions occurring in Brazilian waters, following Spalding et al. (2007). Information on depth was extracted from the original papers, when available, or extracted from the database provided by Magris et al. (2021) otherwise.

Furthermore, a summation approach was developed to identify RB areas that could be candidates for conservation priorities, because they host a significant proportion of associated species. The approach used records for specific sites, considering the total number of species, in conjunction with the numbers of threatened species, endemic species and species of commercial interest for each site. For this step, we bound the number of species of a given RB sites to the reference range zero to one for each category and considered their respective total species number of species. This was done for 38 sites representing different sites, for which associated species occurrence records are available. Then, we ranked each site from 1 to 38, meaning that the lowest rank was assigned to the site containing the highest number of species for each category. To identify multi-criteria hotspots, i.e. sites that collectively maximised the occurrence of various aspects of biodiversity, the ranks for each category were summed and the top 10% rank values (the lowest four values) were identified. While hotspot analyses have long been considered as a starting point of the MPA planning process (e.g., Roberts et al. 2002), those would need to be combined with more refined biological information on RB ecosystems to be fully informative. Ideally, using conservation planning tools, such as Marxan or Zonation might have provided a more accurate approach to identify conservation priorities. However, this was not realistic due to the lack of standardised field data on RBs over a large spatial scale. All spatial analysis was conducted in the Geographic Information System QGIS (version 3.16.14).

We generated heatmaps, using kernel density estimation in QGIS, which indicated the density of RB sites (1330 points extracted from the reviewed papers) within a 1-km radius. The radius was set to be a good compromise between the available data and the extent of the study area. We used the heatmaps to evaluate their overlap with areas subjected to the anthropogenic threats RBs are facing. To represent human pressures on RBs, we used data for four threat categories, all known to have significant impacts on this habitat (Tuya et al. 2023): (i) destructive fisheries (fishing intensity related to vessels operating bottom trawls); (ii) land-based pollution (focusing on sediment plume delivered by rivers to the coastal waters); (iii) existing and planned oil and gas operations and (vi) existing and planned seabed mining. Based on an overlap between the RB density layer and the intensity of each threat layer, we summarised the total amount of RBs exposed to each group of threats at each marine ecoregion in Brazil. Critical RB areas in terms of threat exposure were identified by quantifying the percentage of RB heatmap at all ecoregions falling within each category of threat exposure according to tercile of values (low, medium and high). Fishing intensity was estimated based on satellite detections of Vessel Monitoring System transmission from commercial fisheries associated with bottom trawling spanning 3 years (2019–2021). Data were processed as in Magris et al. (2021). Data on oil and gas operations included both fields leased for prospecting (e.g., seismic surveys and well drilling licensed for areas planned to be explored in the near future or promising sites of potential oil fields) and leased for production, where the oil and gas industry is already extracting resources. Data were obtained from Brazil's National Agency of Petroleum, Natural Gas and Biofuels (http://app.anp.gov.br/webmaps/). Data on seabed mining were obtained from the Brazil National Department of Mineral Production (http://www.dnpm.gov.br/assuntos/ao-minerador/sigmine) and include those areas being licensed for (for further development of the activity) or already under exploration. Lastly, for land-based pollution, we used data from Magris et al. (2021).

3 | Results

3.1 | Rhodolith Beds and Their Associated Biodiversity

Our compiled database shows that biodiversity associated with Brazilian RBs was assessed in more than 50% of the compiled relevant research papers (Figure S1), demonstrating the high species richness associated with those habitats (Figure 1).

The inventory revealed a total of 1053 species records (Table S1). Among the records, macroalgae are the most representative, with 308 species (61 Chlorophyta, 42 Ochrophyta, 205 Rhodophyta), followed by macrofaunal and meiofaunal invertebrates, with 469 species, fishes (252 species) and foraminifera (24 species; Figure 2a). Noteworthy, rarefaction analysis shows that an asymptote is far from reached, indicating that the expected species richness is higher than currently known (Figure 2a inlet). Moreover, general composition of communities associated with shallow (< 30 m depth) and mesophotic RBs (> 30 m depth) does not show large differences, as most of the organism groups have been recorded in both depth strata (Figure 2b). Although, available records for zoanthid, ascidian and Sipuncula species are only available for shallow RBs, whereas nematode and bryozoan species have so far only been recorded in mesophotic beds.

The biodiversity associated with RBs varies strongly among Brazilian marine ecoregions, with the highest number of species records for Eastern Brazil ($n = 718$ species) and records for the other ecoregions varying between 116 and 201 species (Figure 3a). Even taking into account the large differences in research efforts (i.e., number of sampling sites) among ecoregions, the rarefaction curves indicate that asymptotes are far from reached in all ecoregions (Figure 3b). Furthermore, the curves suggest that RBs in some ecoregions, such as Fernando de Noronha and Rocas Atoll and Southeastern Brazil, harbour a similar species richness as Eastern Brazil, while Trindade-Martim Vaz (TMV) Islands and Northeastern Brazil exhibit higher and lower richness relative to Eastern Brazil, respectively (Figure 3b).

Among the species recorded in RBs, 4% ($n = 38$) are included in international and national red lists, categorised as endangered or vulnerable, encompassing 31 fish and 7 invertebrate species (Table S1). Similarly, 4% of all recorded species ($n = 46$) have been identified as endemic, including mostly fishes ($n = 32$), but also some invertebrates ($n = 13$) and one macroalgal species (Table S1). Across the marine ecoregions, the highest numbers of red-listed species have been recorded in Eastern Brazil, followed by TMV Islands and Amazonia, while the former two ecoregions also harbour the highest numbers of endemic species (Figure 3c). Moreover, as expected, fishes, which represent one of the most diverse groups recorded in RBs, include a large proportion of species that are of commercial interest (~15%; $n = 160$ species). The highest numbers of commercially important fishes are found in the Eastern Brazil, TMV Islands and the Amazonia ecoregions, ranging between 54 and 120 species (Figure 3c).

On a local scale, species records vary greatly among sites across ecoregions. Highest richness is reported for RBs at the Abrolhos

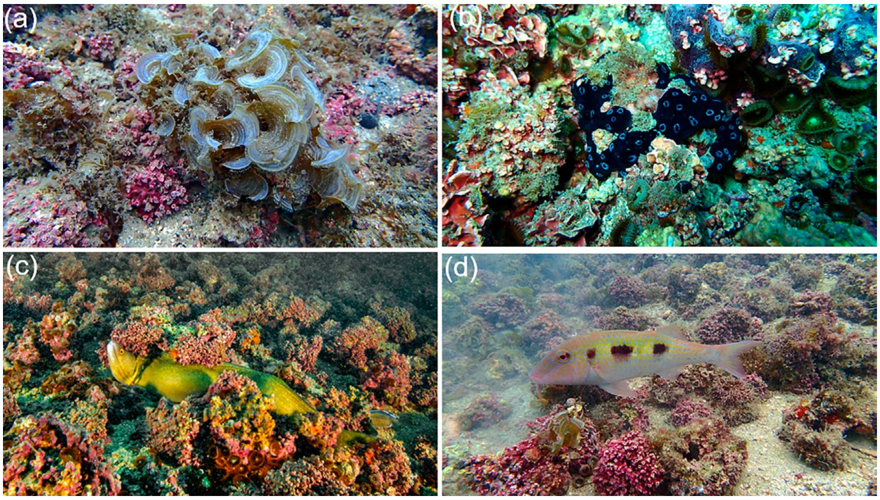

FIGURE 1 | Biodiversity associated with Brazilian rhodolith beds. Photos show (a) the brown alga *Padina gymnospora* (photo by Anonymized), (b) the ascidian *Didemnum* sp. (photo by Anonymized), (c) the purplemouth moray eel *Gymnothorax vicinus* (photo by Anonymized) and (d) the spotted goatfish *Pseudupeneus maculatus* (photo by Anonymized) in Arvoredo, SE Brazil.

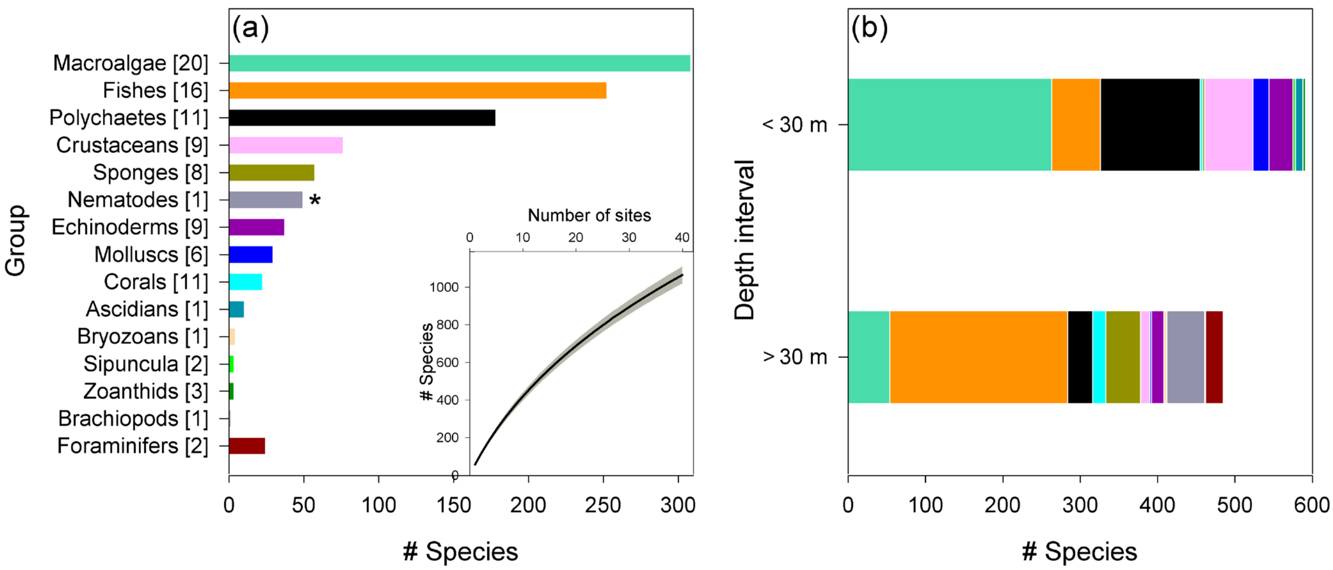

FIGURE 2 | Biodiversity associated with Brazilian rhodolith beds. (a) Recorded total species diversity (numbers in brackets indicate the number of studies for the specific taxon, *identification to the genus level only) and rarefaction curve (inlet graph), showing changes in species richness with research effort, that is, number of sampling sites, and (b) species records in shallow (< 30 m) and mesophotic depths (> 30 m). Colour coding for organism groups in panel (b) is the same as in panel (a).

Bank, encompassing 28% of the total species recorded for Brazil. Other five sites located at the Espirito Santo and Paraíba coasts, at Trindade Island and in the Amazonia shelf, stand out with 14%–18% of the total records (Figure 4a and Table S2). When considering the local biodiversity together with the occurrence of threatened, endemic and commercial species, this ranking changes, with four sites standing out as the highest-ranking hotspots: Abrolhos Bank, Trindade Island, the Great Amazon Reef System (GARS) on the Amazon shelf and Davis seamount within the Vitória-Trindade chain (Figure 4b and Table S2). Among the two highest ranking sites, the Abrolhos Bank not only exhibits the highest total species richness but also the highest number of commercially important fish species, while RBs at Trindade Island rank #2 because of their relatively high number of endemic and threatened species (Table S2 and Figure S2b,c). The GARS, which ranks #3, matches Trindade Island regarding the total species richness (15% of total records), while also hosting a large proportion of threatened and commercially valuable species (32% and 33% of total records, respectively). The Davis seamount, occupying rank #4, exhibits a lower total richness (8% of total records), but a similar number of commercial fish species as reported for the GARS, while also containing a high number of species endemic to Brazil (30% of total records). Altogether, these four hotspots collectively harbour 44% of the total number of species recorded in Brazilian RBs, as well as 87% and 83% of the threatened and endemic species, respectively.

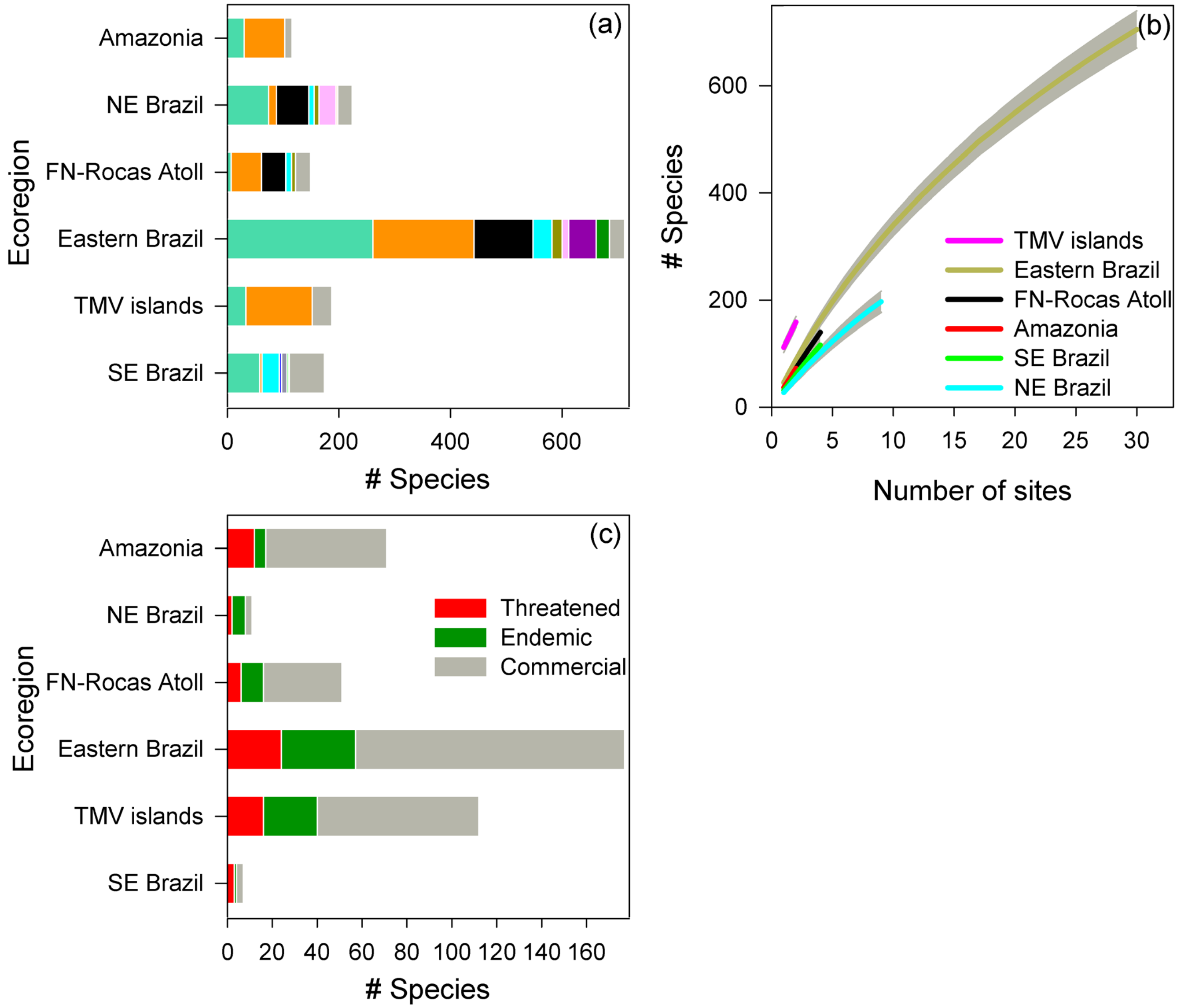

FIGURE 3 | Biodiversity associated with rhodolith beds in the different Brazilian ecoregions (*sensu* Spalding et al. 2007; FN—Fernando de Noronha, NE—Northeast, TMV—Trindade and Martim Vaz, SE—Southeast). (a) Comparison of species richness recorded in rhodolith beds across marine ecoregions, (b) rarefaction curves for each ecoregion, denoting changes in species richness with research effort, that is, number of sampling sites and (c) occurrence of threatened (vulnerable/endangered/critically endangered) and endemic species, as well as commercially important fish species across the different ecoregions. Colour coding for organism groups in panel (a) is the same as in Figure 2a.

3.2 | Current Conservation Status and Threats

In Brazil, RBs cover a wide latitudinal gradient (5° N–27° S) and encompass most of the marine Brazilian Province (*sensu* Briggs 1974) and biogeographic ecoregions (*sensu* Spalding et al. 2007), except for the Rio Grande ecoregion (south Brazil) (Figure 5a). They are especially abundant in the Amazonia, Northeastern and Eastern Brazilian ecoregions. Yet, despite their predominance in coastal and insular shelf areas, our analysis shows that currently only 15.7% of sites containing RBs fall within the boundaries of MPAs (22 of 307 encompassing the coastal and oceanic zones). Among those, only one MPA, the Costa das Algas at the Espirito Santo coast, considers RBs as a formal conservation target ('bioclastic and lithoclastic sedimentary formations'; Costa Gastão et al. 2020). The presence of RBs within the other MPAs is coincidental and opportunistic, as those are focused on protecting other habitats, such as coral and rocky reefs.

The coverage of RBs by MPAs is disproportional across Brazilian marine ecoregions. For example, our analysis shows that RBs in the FN-Rocas Atoll region have the highest coverage among ecoregions, while RBs in the Amazonia region are completely unprotected (Figure 5b). Moreover, of the 22 MPAs that include RBs, only eight are designated as no-take and should offer full protection (i.e., 2.4% of sites containing RBs and 15% of all RB sites within MPAs). In the Southeastern ecoregion, most RB sites (70%) are located within no-take MPAs. On the other hand, the vast majority of RBs covered by MPAs in the Northeastern and Eastern ecoregions are within

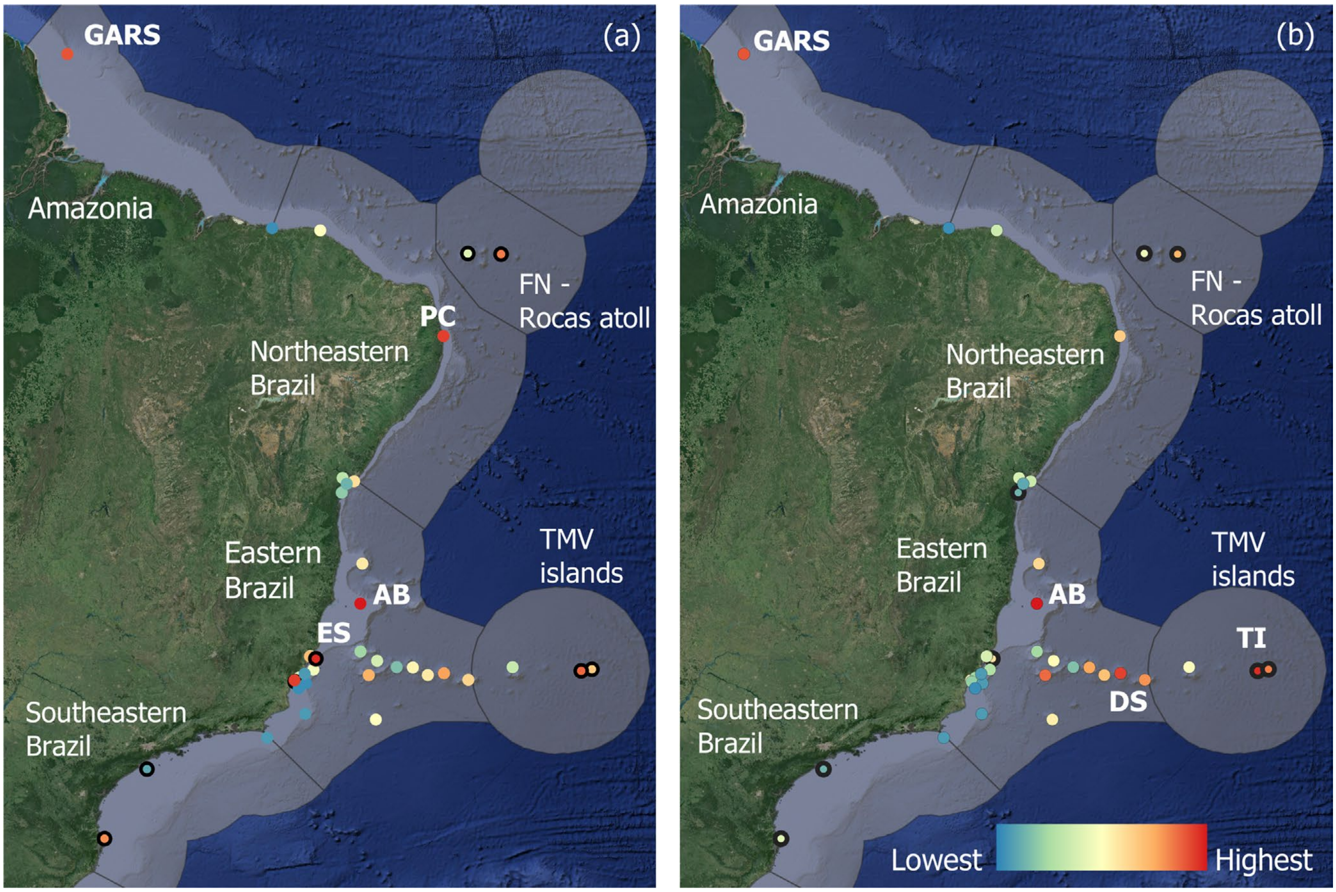

FIGURE 4 | Comparison of site-specific species richness associated with rhodolith beds. (a) Total species richness in different rhodolith beds and (b) site ranking according to our summation approach, (see Table S2 and Figure S2 for the individual ranks). Gradient of colours indicates the overall ranking for species richness (a) and considering all categories (b). The highest-ranking sites are highlighted by uppercase letters (GARS—Great Amazon Reef System, PC—Paraiba coast, AB—Abrolhos bank, ES—Espirito Santo coast, TI—Trindade Island, DS—Davis seamount). Dots with a black outline highlight the sites within MPAs.

multiple-use MPAs (Figure 5b). The RBs under this multiple-use regime of protection can be subjected to relatively high human disturbances, such as extractive uses of biodiversity, unless they occur within more restricted zones within the MPAs. Bathymetrically, 57% of RBs located within MPAs are shallow (< 30 m depth) and 43% are mesophotic. Also, nearly all RBs covered by no-take MPAs were classified as shallow (~93%), while RBs covered by multiple-use MPAs include a similar number of shallow and mesophotic beds, except for a predominance of multiple-use MPAs for the Southeastern region (Figure 5b).

Our results highlight a clear spatial overlap between anthropogenic threats (bottom trawling, land-based pollution, oil and gas exploration, seabed mining) and RB distribution (Figures 6 and 7). Bottom trawling revealed the largest superimposition (almost 52%) with RBs, especially in the Southeastern, Eastern, Northeastern and Amazonia ecoregions, but not with RBs located in the Fernando de Noronha and Rocas Atoll insular shelves (Figure 6a and Figure S3). Similarly, land-based pollution is recorded along almost the entire Brazilian coast and hence, RBs located at the coastal shelves, but not those at oceanic islands, are exposed to this threat (Figure 6b and Figure S3). However, the overlap with the pollution threat was 12% lower than the overlap for bottom trawling.

Although there is currently little spatial overlap between RBs and oil and gas fields and seabed mining (0.6% and 0.1%, respectively), they are often located in close vicinity from each other (Figure 7a,c and Figure S3). Moreover, activities associated with oil and gas exploration and seabed mining are predicted to increase onshore and offshore on the Brazilian EEZ, with spatial overlap of 0.7% and 3.5%, respectively (Figure 7b,d and Figure S3).

Lastly, we ascertained the potential cumulative threats to RBs by examining the overlap of more than one threat to the areas containing RBs (Figure 8). While there were reasonable cumulative threats in the Amazonia, Northeastern and Eastern ecoregions, RBs in the Southeastern coast were mostly affected by more than a single threat.

4 | Discussion

Our unprecedented large-scale quantitative analysis of biodiversity associated with RBs, an extensive benthic habitat in Brazil, highlights their role as hotspots and key habitats for a number of species that are endemic, threatened and of commercial importance and hence, corroborates their importance as a natural heritage (*sensu* UNESCO Institute for Statistics 2009).

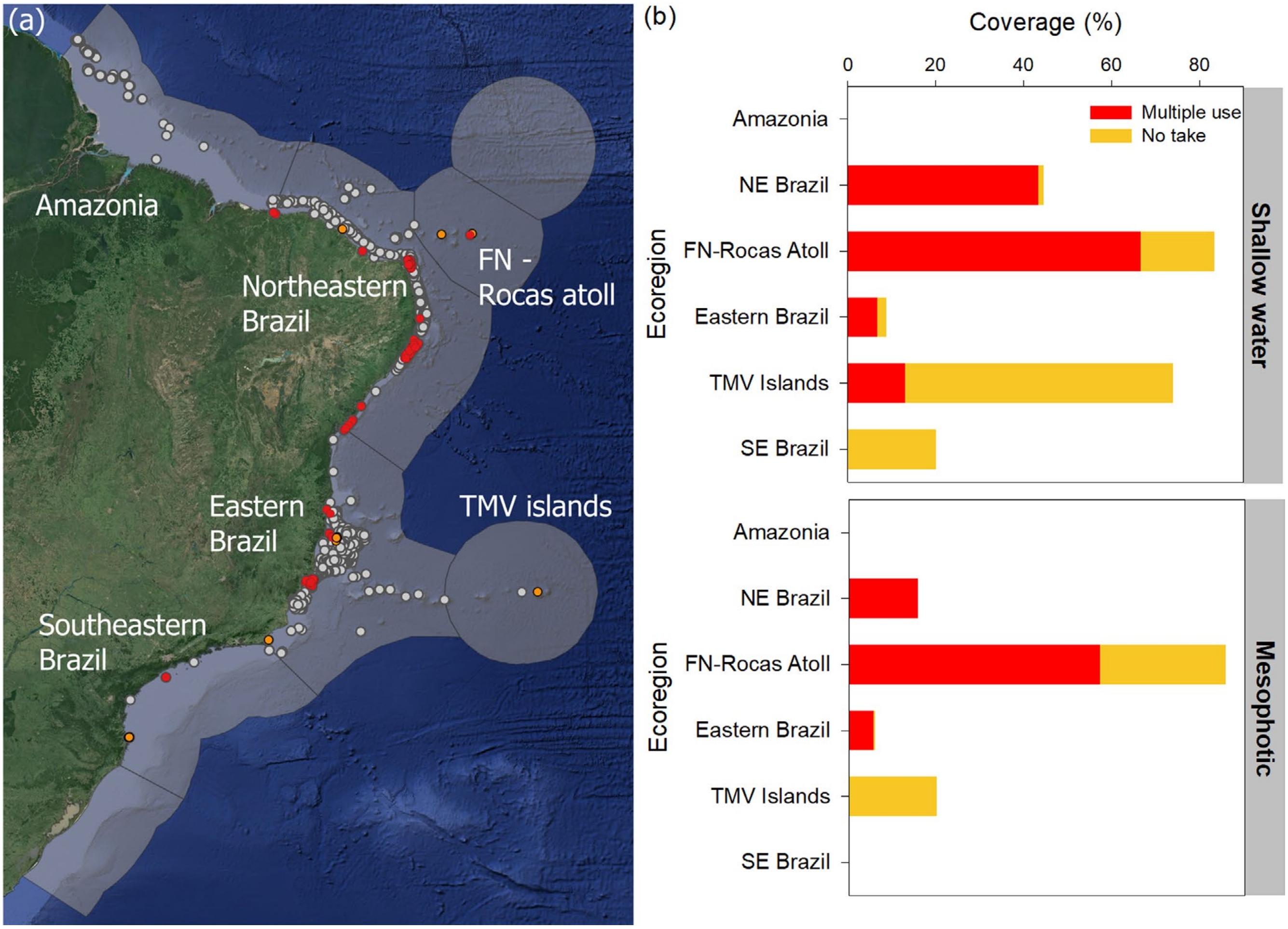

FIGURE 5 | Distribution of Brazilian rhodolith beds and their presence in marine protected areas (MPAs). (a) Rhodolith bed distribution along the Brazilian coast, based on published records (orange circles—RBs within no—take MPAs, red circles—RBs within multiple—use MPAs, grey circles—RBs not included in MPAs) and (b) the proportion (%) of shallow and mesophotic rhodolith beds covered by MPAs in the different marine ecoregions within Brazil.

This is particularly important considering the illustrated lack of conservation efforts to adequately protect these habitats. In this context, our analysis might contribute to the implementation of improved spatial management tools focused on RBs, by identifying specific biodiversity hotspots and areas potentially heavily impacted, representing an important first step towards the incorporation of those habitats as priorities for conservation in Brazil.

4.1 | Rhodolith Beds—Hotspots for Biodiversity

Our study shows that RBs are important biodiversity hotspots in the SW Atlantic and comparison with available information, regarding species richness for the Brazilian continental/insular shelves (Miloslavich et al. 2011), indicates that RBs harbour 12% of the recorded richness. For example, for macroalgae and fishes, the most studied groups, these numbers correspond to 39% and 19% of the total number of species known for Brazil, respectively (Miloslavich et al. 2011). This is consistent with other regions, for example, New Zealand and the NE Atlantic, where the recorded number of macroalgal species associated with RBs corresponded to ~30% of the local flora (Nelson et al. 2014; Peña et al. 2014). However, our study also strongly suggests that the current species records for RBs are plausibly underestimated (see rarefaction curves). This is unsurprising, considering the extensive areas and bathymetric range covered by RBs, but also due to the fact that available biodiversity studies often only focus on specific taxa, instead of a multi-taxa inventory.

Our study further confirms that RBs are important hotspots for threatened and vulnerable species, as recently highlighted by Tuya et al. (2023), harbouring 22% of the marine invertebrate and fish species included in the national Brazilian red list (ICMBio 2022). Moreover, Brazilian RBs harbour numerous endemic species, ~70% of those being fishes. Our results indicate that 18% of the 174 endemic fish species known for Brazil (Pinheiro et al. 2018) are associated with RBs. The highest numbers of endemic species were recorded for the geographically isolated RBs of the TMV Islands and the seamounts of the Vitoria-Trindade chain in Eastern Brazil. This was expected considering that isolated oceanic islands and seamounts in the Atlantic are characterised by poor connectivity and high endemism (Pinheiro et al. 2018). Furthermore, our data demonstrate the potential importance of RBs for

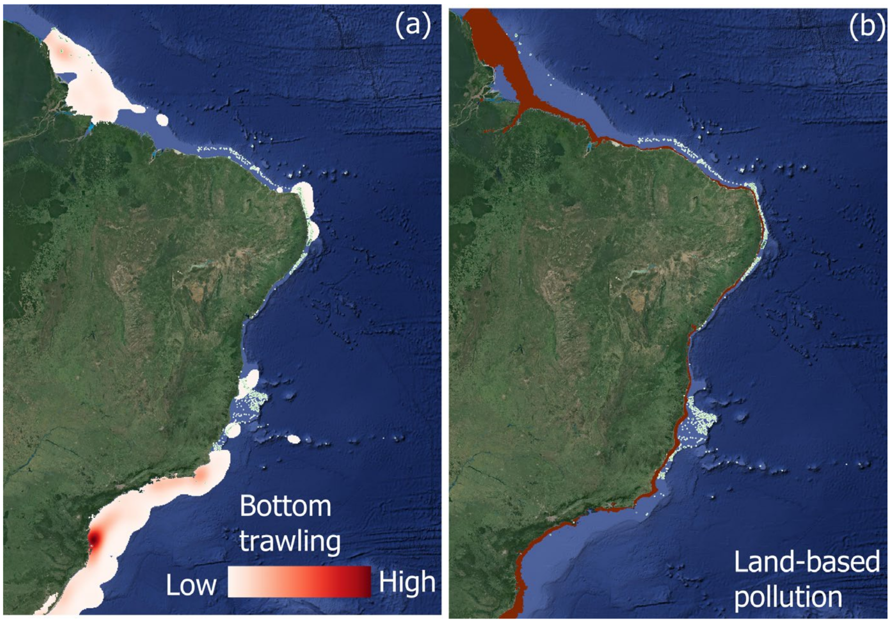

FIGURE 6 | Exposure of Brazilian marine regions to anthropogenic activities, such as (a) fishing intensity due to bottom trawling and (b) land-based pollution, highlighting the overlap with known rhodolith beds (shades of green).

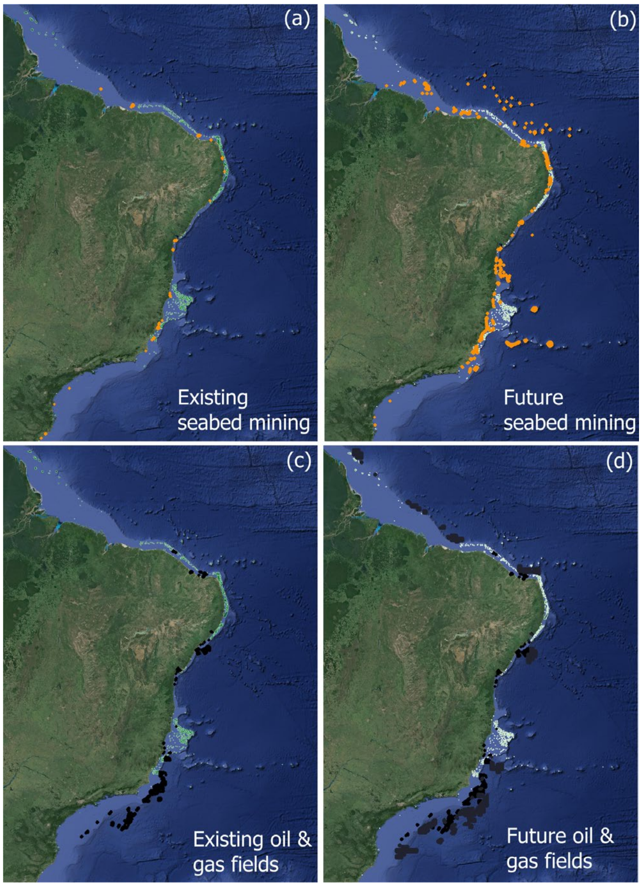

FIGURE 7 | Exposure of Brazilian marine regions to current (left) and future (right) anthropogenic activities, such as (a, b) seabed mining and (c, d) oil and gas fields, highlighting the overlap and close proximity of threats to rhodolith beds (shades of green).

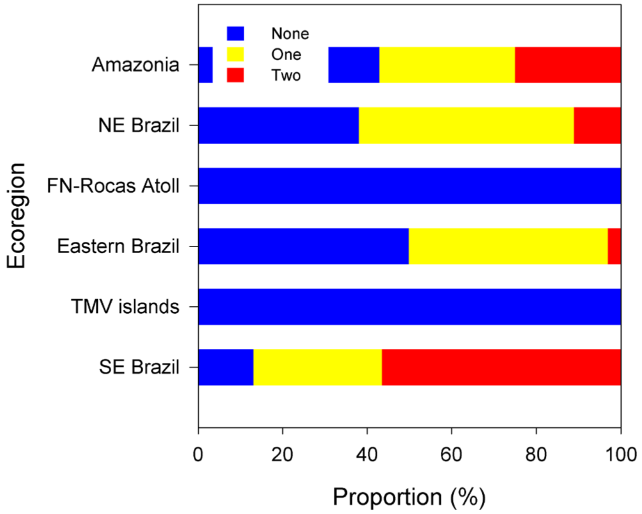

FIGURE 8 | Individual and combined threats to rhodolith beds for each marine ecoregion in Brazil.

fisheries, as the records show that 15% of the fish species associated with RBs are of commercial importance (Quimbayo et al. 2021). The high fish biodiversity in RBs is unsurprising, as along the Brazilian coast, these habitats can often be found physically interconnected with coral and rocky reefs (Figure S4a,b). In this regard, previous studies highlighted not only the relevance of RBs as nursery and foraging grounds for many juvenile and adult fish species, respectively, but also their importance for increasing the total abundance and provide corridors for the migration of reef fishes towards possible spawning grounds (Costa et al. 2020; Moura et al. 2021; Anderson et al. 2023). The common physical interconnection of RBs with coral and rocky reefs, which represent the three major marine hard-bottom habitats in Brazil, and the high proportion of shared species indicates that ecological connectivity exists between these habitats (Pinheiro et al. 2015; Reis-Filho et al. 2019; Moura et al. 2021). This is evidenced by studies on fish diversity at the Abrolhos Bank and the Vitoria-Trindade chain, showing that a significant number of fish species in the RBs (> 60%) are shared with adjacent coral reefs (Figure S4c; Pinheiro et al. 2015; Moura et al. 2021). In addition, another study provided evidence of the connectivity of RBs with seagrass habitats, showing that the two habitats shared 57% of fish larval species (Costa et al. 2020). At a larger scale, a recent analysis of the biogeographical patterns of fish species associated with RBs indicated that they might function as stepping stones that connect fish populations from the Brazilian tropical and subtropical regions (Anderson et al. 2023). Furthermore, the Brazilian Province and the Caribbean have historical connection via mesophotic habitats across the Amazon shelf through large and complex biogenic reefs, sponge bottoms and extensive RBs, which together comprise the Great Amazon Reef System (GARS) (Francini-Filho et al. 2018; Banha et al. 2022). Such a connecting corridor shapes the evolution and history of several taxa in the Western Atlantic (Araujo et al. 2022).

4.2 | Current Protection and Threats

In the past decades, Brazil has made important progress in the establishment of MPA networks to conserve different habitats, such as coral reefs, mangroves and oceanic islands. RBs, as well as mesophotic reefs, in contrast, have mostly been neglected, even though they cover extensive seafloor areas of Brazilian seas and support high biodiversity (Almada and Bernardino 2017). RBs are especially abundant in the Amazonia, Northeastern and Eastern marine ecoregions (Figure 5a), which together are assumed to represent ~95% of the total RB area in Brazil (Santos et al. 2023). Still, modelling predictions suggest that they might be also more prevalent in the Southeastern ecoregion than previously anticipated (i.e., along the São Paulo and Paraná coast; Carvalho et al. 2020). Despite their widespread distribution and their ecological and socio-economic value (Amado-Filho et al. 2017), the conservation efforts to protect RBs are lagging behind the initiatives for other habitats and are poorly implemented.

Our country-level assessment of the protection status of RBs, as well as their spatial overlap with major anthropogenic pressures highlights the current lack and urgent need for conservation planning efforts tailored specifically for RBs. Only one of the biodiversity hotspots identified here (Trindade Island) is currently protected by a no-take MPA (Figure 4b; see Giglio et al. 2018), and only a small fraction of shallow-water and mesophotic RBs are within any type of MPAs (about 15.2% and 12.7%, respectively). The MPA coverage is reduced to 3.4% and 0.4% for shallow-water and mesophotic RBs, respectively, when only no-take MPAs are considered. Moreover, there is a clear bathymetric bias in the protection of RBs, with most RBs covered by no-take MPAs occurring in depths < 30 m (~93%). This consideration is especially relevant in view of the recent findings indicating an increase in RB beta-diversity with depth. This suggests that deeper RBs may act as long-term depth refugia (Voerman et al. 2022), while RBs in shallow, euphotic zones usually support a higher abundance of organisms and species richness (Veras et al. 2020; Voerman et al. 2022). In this context, large protection gaps exist in the Amazonia and Eastern ecoregions (for both shallow and mesophotic RBs) and in the Southeastern ecoregion (for mesophotic RBs). Specifically, the Amazonia ecoregion harbours one of the most important mesophotic reef ecosystems of the South Atlantic (GARS; Soares, Tavares, and Carneiro 2019), which also includes large extents of RBs (Moura et al. 2016; Francini-Filho et al. 2018; Araújo et al. 2021) that are not protected by any MPA. Increasing efforts over the last years have been made to delimit the occurrence and map the extension of RBs and other habitats in the GARS region (e.g., Moura et al. 2016; Francini-Filho et al. 2018; Vale et al. 2018). The available information indicates that benthic megahabitats in the GARS, which include RBs, cover an area of > 22,000 km^2 (Araújo et al. 2021), while suitable habitat model-based estimations suggest an even larger area in this region (~63,000 km^2; Carvalho et al. 2020; Santos et al. 2023).

In Brazil, increasing the conservation efforts for RBs is a pressing issue, as they are exposed to multiple and escalating human threats (Table 1). Bottom trawling activities and land-sea pollution have been identified here as the potential threats with the largest spatial overlap with RBs. Live rhodoliths are composed of slow-growing fragile organisms that are easily damaged by trawling nets, and the algal breakage and removal (as by-catch) leads to decreased habitat complexity (Hall-Spencer and Moore 2000; Kamenos, Moore, and Hall-Spencer 2003; Bernard et al. 2019). Bottom trawling may also impact RBs through sediment resuspension and deposition over rhodoliths, leading to their death (Paiva et al. 2023b). Furthermore, the presence of RBs in areas experiencing increasing coastal urbanisation and pollution (e.g., untreated sewage and agricultural run-off leading to eutrophication) represents yet another threat to RBs, which has been shown to negatively affect rhodolith physiological performance (Schubert et al. 2019; Koerich et al. 2021).

Other anthropogenic activities, such as seabed mining and oil and gas exploitation have been identified as potential threats to coastal benthic habitats, including RBs (Table 1; Araújo et al. 2021; Santos et al. 2023). These activities cause massive sediment dislodgement that can expand over considerable distances, which in conjunction with the discharges of drill cuttings from onshore oil and gas exploration activities, can cause a significant increase in sediment deposition over rhodoliths, as well as the release of pollutants that leads to the burial and subsequent death of rhodoliths (Table 1). Furthermore, the Brazilian coastline is highly vulnerable to accidental oil spills (within estuaries and offshore) associated to these activities, which can cause significant impacts on coastal ecosystems and marine biodiversity (Magris and Giarrizzo 2020; Zacharias et al. 2024). Unfortunately, evidence for the impacts of oil spills on Brazilian RBs are very limited, but studies on the impact of the 2010 BP Deepwater Horizon oil spill in the Gulf of Mexico indicate a significant decrease in the biodiversity associated with RBs (Fredericq et al. 2014). This potential threat due to activities related to oil and gas exploitation is especially imminent

TABLE 1 | Overview of major threats to Brazilian rhodolith beds associated with anthropogenic activities, based on available evidence.

Threat	Pathways of impact	References
Oil and gas exploitation and associated pollution	• Burial of rhodoliths due to sediment dislodgement • Lethal and sublethal effects due to pollution from oil slicks and drill cuttings	Nilssen et al. (2015), Reynier et al. (2015) and Cordes et al. (2016)
Seabed mining	• Removal of rhodoliths and other habitat-forming organisms • Burial of rhodoliths due to sediment dislodgement	Villas-Boas et al. (2014), Figueiredo et al. (2015), Osterloff et al. (2016) and Paiva et al. (2023a)
Run-offs and discharges from coastal urbanisation and agriculture	• Burial of rhodoliths due to sediment dislodgement • Decreased rhodolith physiological performance and productivity due to eutrophication	Schubert et al. (2019) and Koerich et al. (2021)
Destructive fishing activities	• Habitat destruction • Burial of rhodoliths due to sediment dislodgement	Paiva et al. (2023b) and Costa, Schwarz, and Perez (2024)
Accidental spills from land based mining (e.g., the Fundão dam collapse)	• Burial of rhodoliths due to sediment dislodgement	Francini-Filho et al. (2019), Magris et al. (2019) and Holz et al. (2020)
Accidental oil spills	• Reduced associated biodiversity	Fredericq et al. (2014)

in the GARS region, as some proposed blocks spatially overlap with RBs, leading to legal disputes between oil companies and the Brazilian Environmental Agency (IBAMA) over the licensing of those exploitations (Araújo et al. 2021; Banha et al. 2022; Rodrigues 2023). The GARS region is also an important fishing ground (Moura et al. 2016; Araújo et al. 2021; Eggertsen et al. 2024). Thus, in view of the increasing pressure from fisheries and the oil and gas industry to exploit the Amazonian shelf, actions to identify and protect priority areas for the establishment of MPAs using an ecosystem-based approach are urgently needed to safeguard the biodiversity and ecosystem services provided by RBs and other habitats in the region (Francini-Filho et al. 2018; Banha et al. 2022).

5 | Conclusions and Future Perspectives for Effective Conservation of RB

Our study provides the first insights into how biodiversity inventories could be used to identify potential priority areas for RB conservation and represents an important step towards the development of an ecosystem-based network of MPAs. Such a conservation planning approach should be based on the principles of complementarity and demographic/genetic connectivity with other major coastal (e.g., mangroves) and benthic marine habitats (e.g., coral and rocky reefs, seagrass meadows), as these megahabitats may work as a functional and interconnect seascape mosaic for several species (e.g., ontogenetic fish migrations; Moura et al. 2011; Reis-Filho et al. 2019; Costa et al. 2020). However, it is important to note that our 'multi-criteria' hotspot delimitation approach is limited by major knowledge gaps regarding several geographical areas and taxa, and future studies focused on RB biodiversity and ecological functioning are warranted. Moreover, regarding potential threats, we used only a subset of threats deemed important for impacting RBs, while others, such as global warming, ocean acidification, non-indigenous species and plastic pollution could not be included due to the unavailability of spatially explicit data and a lack of understanding about the mechanisms associated with some of these impacts. In addition, the relationship between the presence of human activities and the actual condition of RBs (and other marine ecosystems) is also driven by several other aspects, such as the effects of interactions between multiple stressors (Tekin et al. 2020), the temporal variation in the intensity of impacts (Volery et al. 2023), and the nonlinear relationships between ecosystem condition and the intensity of both individual stressors and multiple stressors (Korpinen and Andersen 2016). A detailed understanding of the associated vulnerabilities is important to enable cutting-edge risk assessments and conservation planning strategies. Incorporating this new knowledge (when such information becomes available) may yield a more accurate and comprehensive assessment of priority sites for protecting RBs.

The nuances in prescriptive actions that we have discussed here reiterate the importance of spatially explicit prioritisation assessments, incorporating both detailed information on biodiversity patterns and threats (Magris et al. 2021). This is particularly relevant in the context of resolving the inherent trade-off in choosing sites for protection that are of high conservation value and relatively secure (avoiding regions subjected to increasing threats) or those that are vulnerable (prioritising areas facing increasing threats). In this time of increasing competition between developing industries, fisheries and other sea uses, and the scenario of accelerated ocean warming, acidification and sea level rise, the importance of our analyses lies in the ability to identify biodiversity hotspots that are lacking protection, facing high vulnerability to additive and synergistic impacts (e.g., RBs along the Southeastern ecoregion) and are projected to face increased vulnerability in the future (Villa, Cimatti, and Di Marco 2024). Hence, it is imperative that the fine-scale maps of RBs, the biodiversity supported by these habitats and the potential interaction between stressors are considered in Brazil's marine spatial planning actions. If Brazil manages to diversify and rapidly expand MPAs and ecosystem-based marine spatial planning to effectively protect RBs, it will not only contribute to achieve the target of protecting 30% of the planet by 2030 but also take the lead in the conservation of the largest known extension of RBs worldwide.

Author Contributions

N.S., R.A.M. and P.A.H. conceived the idea. N.S. and R.A.M. conducted the literature review and data collection. N.S. and R.A.M. performed the data analysis. N.S. and R.A.M. wrote the paper with inputs from all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors declare that all data supporting the findings of this study are available within the paper and its Supporting Information files.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.