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Mesophotic ecosystems: Distribution, impacts and conservation in the South Atlantic

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Abstract

Aim: This study reviews recent research on the South Atlantic Mesophotic ecosystems (MEs) and the pressures threatening them, and offers suggestions for their management and conservation.

Location: The South Atlantic Ocean.

Methods: A comprehensive compilation of the scientific literature was performed to examine the distribution, human impacts and conservation status of the South Atlantic MEs.

Results: Our review indicated that the South Atlantic Ocean (SAO) is one of the major MEs areas in the world's oceans. The South Atlantic MEs are composed of a mosaic of distinct seascapes, mainly rhodolith beds, mesophotic reefs (i.e., rocky and biogenic) and marine animal forests (e.g., sponge aggregations, octocoral and black coral forests) that occur along the East South American and West African coasts, seamounts and oceanic islands. Throughout the SAO, the distinct seascapes of MEs are usually formed on the middle and outer continental shelves, shelf-edge, seamounts, submarine canyons, incised valleys and paleochannels, reef structures and insular shelves. We highlighted sea temperature anomalies, ocean acidification, extreme floods and droughts, fisheries, invasive species, marine debris, mining, and oil and gas exploitation as major threats to these ecosystems.

Main conclusions: Given the threats to the South Atlantic MEs, growing human pressures may degrade these ecosystems in the next years and undermine their unique biodiversity as well as their potential to provide connectivity between regions and depths. Our review revealed the existence of some extensive and unprotected formations, which urgently demand in-depth investigations and conservation action.

KEYWORDS

climate change, coral reef, deep-sea refugia, marine biogeography, marine conservation, rhodolith bed

1 | INTRODUCTION

Developments in the marine sciences, especially in terms of methodology and equipment, have allowed the exploration of progressively deeper oceanic zones, providing a more detailed picture of the hidden biodiversity in mesophotic ecosystems (MEs; Loya, Eyal, Treibitz, Lesser, & Appeldoorn, 2016). These ecosystems are characterized by the presence of light-dependent corals and associated species (e.g.,

algae, sponges and fishes), constituting complex communities at mesophotic depths (i.e., between 30 and 150 m; Hinderstein et al., 2010). Studies on MEs have revealed that these deep-water habitats, when compared to their shallow-water counterparts, usually display several characteristics in terms of health status (Tornabene, van Tassell, Robertson, & Baldwin, 2016), coral coverage (Hoeksema, Bongaerts, & Baldwin, 2017) and fish endemism (Lindfield, Harvey, Halford, & McIlwain, 2016). Often, for example, there seems to be a turnover of species and a reduction in biodiversity with depth, but some taxa seem to peak at the mesophotic zone (Semmler, Hoot, & Reaka, 2017). On account of these characteristics, most researchers agree that MEs could act as marine biodiversity reservoirs, and thus should be more thoroughly studied (Kahng, Copus, & Wagner, 2017; Loya et al., 2016).

The good health status of MEs is often linked to their depth and distance from the coast, which seem to reduce the impact of direct anthropogenic pressures (Glynn, 1996; Kahng et al., 2017). However, a growing body of evidence suggests that even isolated formations may have been affected by pollution, sedimentation, oil spills, bottom-contact fishing and bio-invasion (Andradi-Brown et al., 2017; Baker, Puglise, & Harris, 2016; Rocha et al., 2018). Moreover, Rocha et al. (2018) show that mesophotic reefs are ecologically distinct, threatened and in as much need of protection as shallow reefs. Therefore, there is scientific interest in understanding if and how MEs may act as refuge areas and ecological corridors, where marine species would be kept away from local and global stressors, such as thermal anomalies and pollution, which have been affecting shallow-water ecosystems (Turner, Babcock, & Kendrick, 2017).

MEs (mainly the upper zone, 30–60 m depth) are frequently regarded as extensions of shallow-water reefs since both ecosystems share some species (Kahng et al., 2017). This suggests that mesophotic assemblages may act as deep-sea ecological corridors providing large-scale connectivity (i.e., stepping stones) between species (Rocha, 2003) and that they might be able to reseed or replenish populations from shallow endangered habitats. The latter possibility is referred to as the deep-sea refugia hypothesis (Bongaerts, Ridgway, Sampayo, & Hoegh Guldberg, 2010; Bongaerts et al., 2017; Glynn, 1996; Riegl & Piller, 2003; Smith et al., 2016), and it highlights the potential importance of these habitats for the future of marine conservation and management.

Despite their potential ecological importance, basic knowledge about many aspects of MEs, such as their unique biodiversity (Pinheiro et al., 2017; Rocha et al., 2018), susceptibility to human impacts and conservation status (Turner et al., 2017), is still limited. Most studies have been conducted in the Red Sea (Shoham & Benayahu, 2017), the Caribbean Sea and the Indo-Pacific region (Hinderstein et al., 2010; Loya et al., 2016). Thus, large parts of the ocean have not yet been studied. Even in frequently surveyed areas, the limited number of studies makes it difficult to create hypotheses to test the structure and functioning of MEs (Kahng et al., 2017). For example, although the deep-sea refugia hypothesis has been supported by statistical models and studies on genetic and community composition (Holstein, Paris, Vaz, & Smith, 2016), there is evidence of physiological and reproductive modifications in deep-water populations that could prevent a recolonization of shallow habitats (Shlesinger, Grinblat, Rapuano, Amit, & Loya, 2018; Smith et al., 2016). Additionally, Semmler et al. (2017) observed different refugium potential between upper (where ~30%–45% of total species were shared with shallow habitats) and mid-lower (~15%–25%) mesophotic ecosystems. Therefore, new studies are needed to assess the limitations and applicability of this and other ecological hypotheses (i.e., beta diversity, turnover and endemism) about MEs (Bongaerts et al., 2017; Rocha et al., 2018). Moreover, particular attention should be given to regions where these ecosystems are poorly studied (Turner et al., 2017), as in the case of the South Atlantic Ocean (SAO).

In the present paper, a comprehensive compilation of the scientific literature (Supporting Information Appendix S1) was carried out to examine the distribution, human impacts and conservation status of the South Atlantic MEs. For this review, we have considered benthic communities located at mesophotic depths on the South Atlantic Ocean (SAO), between ~0.00°S and 23.00°S (Figure 1). This area contains many different seascapes, including rhodolith beds, rocky reefs, biogenic reefs, sponge bottoms, and octocoral or black coral forests, to which we have attributed the general term "mesophotic ecosystems." The present study reviews recent advances in knowledge about the geographical distribution of MEs in the SAO basin and discusses major anthropogenic pressures on them to provide useful and synthetic information for science, management and conservation. Finally, we suggest some urgent conservation measures to protect the tropical biodiversity and ecosystem services of South Atlantic MEs in consideration of their role in a changing ocean.

2 | SOUTH ATLANTIC MESOPHOTIC ECOSYSTEMS

The SAO shelters distinctive mesophotic ecosystems. This ocean basin does share some species with neighbouring areas, such as the Caribbean Sea, but this flux seems to be limited by biogeographical barriers, isolation by distance and differences in speciation and extinction rates (Leão et al., 2016; Pinheiro et al., 2018; Soares, Lotufo, et al., 2017). For example, whereas the Caribbean sustains dozens of scleractinian coral species, in the SW Atlantic there are only 23 of them, many of which are endemic (Leão et al., 2016), and so far, only 15 coral species have been recorded on the West African coast (Laborel, 1974; Moses, Helmle, Swart, Dodge, & Merino, 2003). Additionally, on both east and west sides of the SAO, the construction of biogenic reefs is at its most discontinuous (Hopley, 2011). Accordingly, the contribution of scleractinian corals to MEs seems lower in the SAO compared to the Caribbean Sea and Indo-Pacific. On the other hand, sponge bottoms, rhodolith beds and other hard-bottom environments, such as rocky and biogenic reefs (built mainly by coralline algae, scleractinian corals and bryozoans), which are structurally similar to coral-dominated ecosystems, are common in this ocean basin.

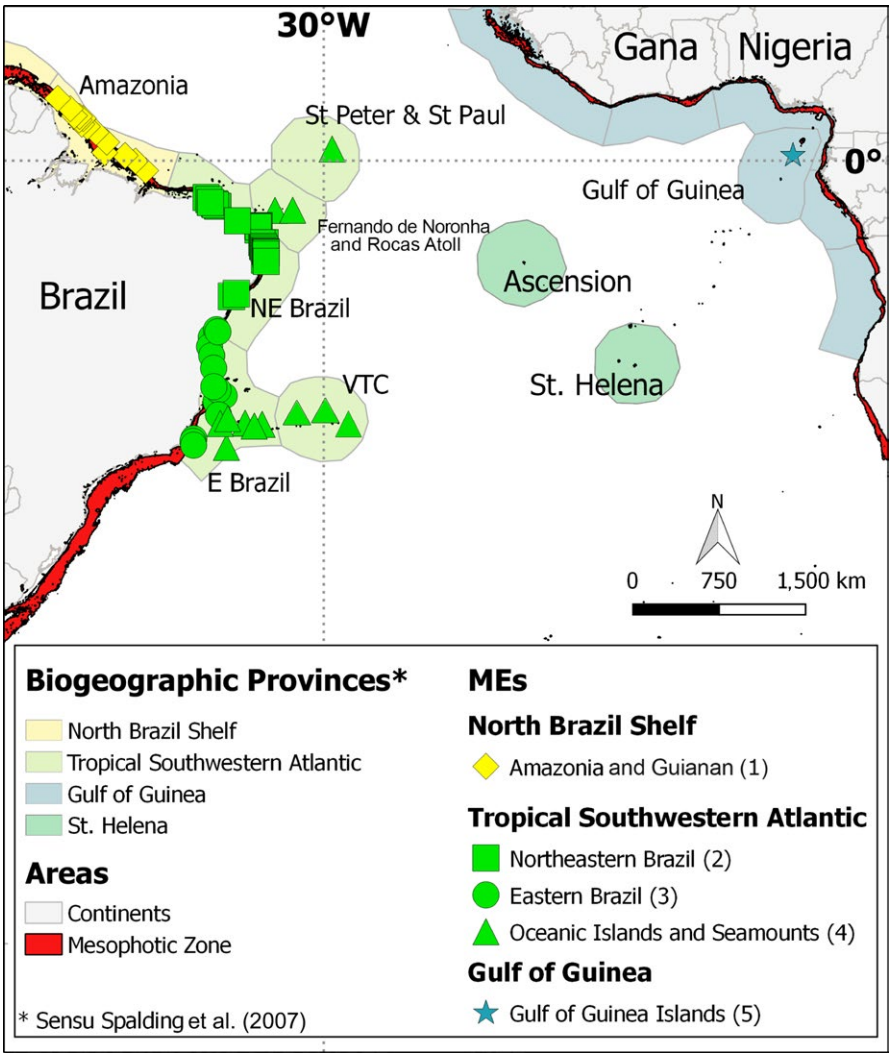

FIGURE 1 Distribution of currently known mesophotic ecosystems, within biogeographical provinces and ecoregions (*sensu* Spalding et al., 2007), in the South Atlantic Ocean. The names on the map show relevant ecoregions. Legends: NE Brazil (Northeastern Brazil), E Brazil (Eastern Brazil) and VTC (Vitória-Trindade Chain) [Colour figure can be viewed at wileyonlinelibrary.com]

Many of these benthic ecosystems show three-dimensional complexity and sustain high marine biodiversity while providing important ecosystem services and performing functions, such as carbon sinks, nursery grounds and refuge areas. Rossi (2013), expanding the concept of reef, designated the assemblages dominated by sponges, cnidarians (hydrocorals, black corals, octocorals, scleractinian corals), bryozoans and ascidians, organisms which are considered to be "ecosystem engineers" based on their ability to modify sea-floor habitats, as marine animal forests. These benthic species are primarily responsible for the structure of animal-dominated ecosystems, especially in the lower mesophotic zone, where there is less light and sessile suspension feeders are abundant.

In this regard, sponge bottoms (also known as sponge aggregations) are among the most important animal forests worldwide, occurring mainly under suboptimal conditions for coral growth, such as turbid waters with sediment resuspension (Maldonado et al., 2017; Soares, Lotufo, et al., 2017). Among the SAO mesophotic ecosystems, there are many of these aggregations, which are composed of massive demosponges in the forms of balls, tubes, fans, vases or branches, such as *Agelas*, *Aplysina*, *Xestospongia*, *Callyspongia*, *Clathria*, *Monanchora*, *Oceanapia*, and *Geodia* (Moura et al., 2016; Soares, Lotufo, et al., 2017). Additionally, extensive coverage of sponges can be found atop submerged rocky outcrops (Soares, Rossi, Martins, & Carneiro, 2017).

Besides the animal-dominated ecosystems, rhodolith beds, while apparently absent from the African coast (Amado-Filho, Bahia, Pereira-Filho, & Longo, 2017), are a ubiquitous feature along the Southwestern Atlantic Ocean (Horta et al., 2016). Where they occur, these extensive algal build-ups constitute an important component of the MEs, with the coalescence of rhodoliths having been hypothesized as a possible mechanism for the formation of carbonate reefs (Amado-Filho et al., 2016). In fact, many Brazilian biogenic reefs are primarily formed by the growth of calcareous red algae, bryozoans, milleporids and scleractinian corals (Bastos et al., 2018; Leão et al., 2016).

Throughout the SAO, the distinct seascapes of MEs (rocky and biogenic reefs, sponge bottoms, rhodolith beds, octocoral and black coral forests) are usually formed on the middle and outer continental shelves, shelf-edge, seamounts, submarine canyons, incised valleys and paleochannels, reef structures (such as reef walls and reef banks) and insular shelves. Within these geomorphological settings, MEs often seem to be associated with drowned reefs or beachrock

lines, which were apparently formed in past periods of marine regression, especially during the Last Glacial Maximum, when the sea level was approximately 130 m below the present, essentially exposing the entire continental shelf (Clapperton, 1993). As the ocean began to rise again, these now drowned reefs could not cope with the ascending sea level (Camargo, Araujo, Ferreira, & Maida, 2015; Silva, Gomes, & Vital, 2018); however, they developed into topographic structures that offered suitable habitats for the establishment of ecosystem engineers (e.g., algae, sponges and cnidarians) in the mesophotic zone.

Finally, we have noticed the occurrence, on both sides of the SAO, of reefs at even greater depths (>150 m depth), reaching below the mesophotic zone. These deeper formations have also received little scientific attention (Soares, Lotufo, et al., 2017) and are probably distinct and ecologically apart from the shallow and mesophotic ecosystems (Hovland, 2008), being formed by ecosystem engineers, such as corals *Lophelia pertusa*, *Madrepora oculata* and *Solenosmilia variabilis* (Cordeiro, Kitahara, & Amaral, 2012; Kitahara, 2007). It is outside the scope of this study to discuss these deeper marine animal forests; however, a review of their distribution and conservation status is urgently needed, since they are also vulnerable to human pressures, such as those caused by the fishing industry (Kitahara, 2009; Soares, Lotufo, et al., 2017).

3 | RECENT ADVANCES IN KNOWLEDGE ABOUT THE SOUTH ATLANTIC MEs

The South Atlantic MEs are distributed in distinct marine ecoregions along the continental shelves of South America and Africa and on seamounts and oceanic islands (Figure 1). They are found at the Amazon River mouth, Northeastern Brazil, Abrolhos Bank, Eastern Brazil, Gulf of Guinea, seamounts (such as the Vitória-Trindade Chain), oceanic islands (Trindade and Martin Vaz, Saint Helena and Ascension islands, Fernando de Noronha Archipelago, Saint Peter and Saint Paul Archipelago) and on the only atoll in the South Atlantic (Rocas Atoll; Supporting Information Appendix S2), and they comprise four main biogeographical provinces (*sensu* Spalding et al., 2007), namely the North Brazil Shelf, Tropical Southwestern Atlantic, Saint Helena and Ascension islands and the Gulf of Guinea (Figure 1).

3.1 | The North Brazil Shelf

The North Brazil Shelf (*sensu* Spalding et al., 2007) is a poorly understood biogeographical province in terms of MEs. The first evidence for the occurrence of an extensive mesophotic ecosystem in this province was provided by Collette and Rutzler (1977), who reported the existence, next to the mouth of the Amazon River, of diverse fish assemblages associated with sponge aggregations that possibly acted as a deep-water ecological corridor between the Caribbean and Brazil (Rocha, 2003).

Thirty-eight coral species (octocorals, scleractinians, hydrocorals and black corals) were later reported in this area (Cordeiro, Neves, Rosa-Filho, & Pérez, 2015), along with a complex mosaic of carbonate structures and rhodolith beds (Moura et al., 2016). Moura et al. (2016), considering the geographical distribution, divided the Amazonian ME into three sectors, based on the degree of exposure to the Amazon River, namely northern (under permanent estuarine plume influence), central (seasonal plume influence) and southern (intermittent riverine influence), the latter constituting the boundary with the Tropical Southwestern Atlantic Province. Francini-Filho et al. (2018) suggested that these MEs comprise a significant diversity of environments, including rhodolith beds, sponge grounds and reef structures, such as biogenic walls and platforms.

These Amazonian MEs (the Great Amazon Reef *sensu* Francini-Filho et al., 2018) are distributed across a large area (56,000 km^2) of the North Brazil Shelf, between the shelf-edge and the upper slope (70–220 m depth; Francini-Filho et al., 2018). Despite the variability of seascapes, this ecosystem has a clear bathymetric gradient: Rhodolith beds and algal frameworks dominate the shallowest sector (70–180 m), but in the deepest sector (180–220 m), marine animal forests (composed of black corals, barrel sponges and octocorals) and associated fishes (e.g., butterflyfish) are more common. Moreover, Vale et al. (2018) characterized the structure and composition of rhodoliths between water depths of 23 and 120 m. Important mesophotic ecosystem engineers, such as bryozoans, coralline algae and encrusting foraminifera built these rhodolith beds while under the influence of the Amazon river.

Overall, the reef biota (algae, sponges, cnidarians and fishes) recorded in the Great Amazon Reef inhabit a wide range of depths (Moura et al., 2016). Red algae were the predominant benthic plant group, with 25 species. The sponge assemblage comprised 61 species and was dominated by massive forms (Francini-Filho et al., 2018; Moura et al., 2016). Two black coral species, *Antipathes furcata* and *Tanacetipathes tanacetum*, typical of mesophotic reefs, were detected in the deeper zones. The most common scleractinian corals included small-sized colonies, massive species and branching forms, such as *Meandrina braziliensis*, *Montastraea cavernosa*, *Madracis decactis*, *Agaricia* spp., *Scolymia wellsii*, *Millepora* cf. *alcicornis* and *Favia gravida*. Overall, scleractinians comprised only 12 species, with Octocorallia being the most diverse cnidarian group with 26 species. Octocoral animal forests (*sensu* Rossi, 2013) provide a unique seascape and probably form a "canopy" in this mesophotic zone. Finally, Moura et al. (2016) recorded 73 reef fish species in this ME on the North Brazil Shelf, most of which were carnivores (86%). Also, aggregations of threatened and commercially important fishes, such as *Lutjanus purpureus* and *Hyporthodus niveatus*, have been detected using video-surveys of the region (Francini-Filho et al., 2018). Considering the importance of these MEs, Francini-Filho et al. (2018) suggested that this ecosystem should be urgently included in a network of marine protected areas (MPAs).

3.2 | Tropical Southwestern Atlantic Province

3.2.1 | The Northeastern Brazil ecoregion

In Northeastern Brazil, the outer continental shelves are relatively shallower (60–80 m deep) than elsewhere along the South American coast and are covered by warm and oligotrophic waters (Silva et al., 2018). Additionally, there are quite a few records of deep beachrock lines in this area, which are commonly seen as relics of ancient shorelines (Camargo et al., 2015). These oceanographic and geological characteristics provide a suitable habitat for the occurrence of MEs, mainly sponge bottoms, rhodolith beds, and rocky and biogenic reefs associated with the continental shelf (Camargo et al., 2015; Eduardo et al., 2018; Olavo, Costa, Martins, & Ferreira, 2011; Silva et al., 2018; Soares, Davis, Paiva, & Carneiro, 2018). However, there currently seem to be many large gaps in the occurrence of MEs along the continental margin of Northeastern Brazil, which we attribute to the lack of benthic habitat mapping in this area. The currently available data, for example, came mostly from the upper mesophotic zone (30–70 m; Camargo et al., 2015; Eduardo et al., 2018; Feitoza, Rosa, & Rocha, 2005; Morais & Santos, 2018; Rocha, Rosa, & Feitoza, 2000). We hypothesized that the Amazonian ME is not restricted to the North Brazil Shelf. This ecosystem is probably semicontinuous on the Northeastern Brazil ecoregion (especially on the equatorial margin) due to occurrence of similar seascapes and biodiversity, the absence of biogeographical barriers and the connectivity provided by the North Brazil current. Therefore, we hypothesized the existence of a large tropical mesophotic ecosystem in this ecoregion, especially on the outer shelf, shelf-edge and in incised valleys.

This ecoregion (*sensu* Spalding, Ravilious, & Green, 2001) comprises the tropical coast of Northeastern Brazil (Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe and Alagoas states) and may be divided into two distinct sectors based on the orientation of the continental margin: I) the equatorial sector (comprising Ceará and Rio Grande do Norte states), and II) the eastern sector (encompassing Paraíba, Pernambuco, Sergipe and Alagoas Brazilian states).

The occurrence of MEs in the Brazilian equatorial margin, in an area not under Amazon River influence, has been recently described (Almeida, Vital, & Gomes, 2015; Silva et al., 2018; Soares, Davis, Paiva, et al., 2018). Freitas and Lotufo (2015) described reef fishes in a mesophotic reef (36 m), and Soares, Davis, Paiva, et al. (2018) described reef fishes and scleractinian corals at depths of 37 m. Both articles reported the presence of a mosaic of benthic habitats, composed of carbonate sediment deposits and reef outcrops located in incised shelf valleys off the Ceará state coast. Two resilient scleractinian coral species were mainly found on these reef outcrops, namely *Siderastrea stellata* and *Montastraea cavernosa*. Silva et al. (2018) provided important geological information on shelf-edge reefs located in the Açu incised valley off the Rio Grande do Norte equatorial coast. The described mesophotic reefs occurred in a depth range of 30–55 m and were covered by red algae, scleractinian corals (e.g., *Montastraea cavernosa*) and sponges. In addition, Soares, Lotufo, et al. (2017) indicated that ascidians are an important component of the reefs in the northeastern Brazil. Two species (*Stomozoa gigantea* and *Eudistoma saldanhai*) stand out in the seascape because of their size and abundance.

The coral and fish compositions in the Northeastern equatorial Brazil MEs between 35 and 37 m depths were similar to that reported for nearby shallow reefs (Freitas and Lotufo, 2015; Soares, Davis, Paiva, et al., 2018). This finding suggests possible limited vertical connectivity between the shallow and upper mesophotic zones (Morais & Santos, 2018) in these reef formations. Additionally, these equatorial MEs are positioned approximately halfway between the Eastern Atlantic and the Amazonian reefs, and they could offer a more extensive east–west connection than the one provided by the existing shallow-water coral-poor formations. However, the absence of genetic studies in this region prevents precise conclusions about these hypotheses.

The eastern sector of the Northeastern Brazil ecoregion also sustains several MEs. Sponge bottoms in mesophotic depths off the states of Rio Grande do Norte, Paraíba, Pernambuco and Alagoas represent an important habitat for species, including endemic sponge-dwelling fishes. Moreover, although not necessarily in direct association with the sponges, angelfish, surgeonfish, butterflyfish, parrotfish and triggerfish were found inhabiting these formations (Rocha et al., 2000). Feitoza et al. (2005) analysed reef fish off this coast in the upper mesophotic depths (35–70 m depth). A total of 158 fish species belonging to 49 families was recorded, and the most abundant families, in order of importance, were Carangidae, Gobiidae, Lutjanidae, Labridae, Serranidae, Haemulidae and Scaridae. These fishes occurred in shelf-edge reefs composed of sandstone outcrops dominated by algae and massive sponges that were also characterized by the occurrence of living corals (such as *Montastraea cavernosa*, *Porites branneri*, *Siderastrea stellata*, *Meandrina braziliensis*). The main finding was that these MEs might indeed function as a corridor for fish populations between Brazil and the Caribbean because of the presence of several species previously considered to have disjunct or anti-equatorial distributions (Feitoza et al., 2005). Moreover, Eduardo et al. (2018) described elevated fish diversity in specific seascapes along the outer shelf, but particularly in the upper mesophotic zone (40–60 m). This region, characterized by macroalgae, sponge bottoms and coralline algae formations, concentrates fishing resources and benthic biodiversity.

Morais and Santos (2018) described coral communities along a bathymetric gradient (3–61 m) in reefs off the Paraíba state coast. The authors reported that coral assemblages presented twice as more gamma diversity in shallow than in MEs (13 vs. seven species), and only three out of 17 species occurred along the entire gradient. On the other hand, the alpha diversity was similar between shallow and deep reefs. The authors concluded a limited potential of MEs to serve as refuges, probably only for the two dominant coral species (*Siderastrea stellata* and *Montastreaea cavernosa*). The mesophotic reefs off Northeastern Brazil also sustain endemic species. On the Pernambuco state coast, Pereira, Santos, Lippi, and Silva (2016) studied patterns of parrotfish (endemic *Scarus zelindae*) ontogenetic foraging activity and feeding selectivity in mesophotic reefs (30–35 m depth) due to the presence of different fish life-phases. The

preservation of topographic features off Pernambuco state coast, such as wave-cut erosion steps, shelf valleys and canyons results in greater biodiversity and therefore a greater potential for MEs (30–50 m depth), especially on drowned reefs and beachrock lines (Camargo et al., 2015).

3.2.2 | The Eastern Brazil ecoregion

One of the most extensive reef complexes in the SAO is located on the Abrolhos Bank, in the Eastern Brazil ecoregion (*sensu* Spalding et al., 2007). The occurrence of reefs and rhodolith beds has been reported at depths from 30 to 93 m (Bastos et al., 2013; Moura et al., 2013) and 40 to 200 m (Olavo et al., 2011). Geomorphologically, these reefs are described as banks, paleochannels and submerged pinnacles as well as coalescent structures with sinkhole-like depressions (cup-shaped), which are known as "buracas." These sinkhole-like features are novel and unusual (Bastos et al., 2013) and may enhance biomass and productivity. These MEs are often described as drowned reefs, with walls dominated by encrusting coralline algae and low coral coverage. In the mesophotic reef pinnacles, *M. cavernosa* is the dominant species, and there are also rare occurrences of several species from different genera, such as *Siderastrea*, *Agaricia*, *Porites*, *Madracis*, *Favia* and *Scolymia*, as well as the black corals *Cirripathes* and *Antipathes* (Moura et al., 2013).

Shelf-edge reefs (40–200 m) have been recorded across the Eastern Brazil, from Salvador city, across the Abrolhos Bank to the southernmost region (Espírito Santo and Rio de Janeiro coast). In this region, fish species from the families Serranidae, Lutjanidae, Malacanthidae, Muraenidae, Sparidae, Balistidae, Carangidae, Haemulidae, Scorpaenidae and Priacanthidae were observed to be associated with marine hard-bottom environments at mesophotic depths (Olavo et al., 2011).

The Abrolhos Bank encompasses the largest known continuous rhodolith bed worldwide, which occupies an area of approximately 20,900 km^2. Rhodolith-forming calcareous red algae are ubiquitous along the eastern South American coast, but, like biogenic reefs, they seem to thrive around the Abrolhos bank, apparently becoming the foremost hard-bottom feature in the mesophotic zone of the eastern Brazil ecoregion (Amado-Filho et al., 2017; Horta et al., 2016). Among the rhodoliths, some reef-building coral species could be found (such as *Mussismilia hispida*, *M. cavernosa* and *Siderastrea* spp.), but they usually achieved low coverage (Amado-Filho, Moura, et al., 2012). Simon et al. (2016) reported 74 fish species, including new species and new records for the SAO. The authors also found threatened species in these MEs, highlighting the importance of these habitats for conservation action. Moreover, due to its sheer size, this rhodolith bank may produce significant amounts of $CaCO_3$, suggesting that this area is an important area for calcium carbonate deposition in the oceans (Amado-Filho et al., 2017).

Concerning conservation of this large and rich coral complex, Francini-Filho and Moura (2008), found that only 2% of the Abrolhos Bank was designated as a "no-take" area and that implementation was inadequate even for this small fraction. As a result, the fragile ecosystems in the region are significantly threatened by human activities. For the MEs that are not yet legally protected, particularly those that have been adequately described (such as the deeper reefs and rhodolith beds in Eastern Brazil), it is recommended that they should be given protection as soon as possible by establishing new conservation areas or expanding existing ones. For example, on the Abrolhos Bank, the marine protected areas (MPAs) do not cover important and geomorphologically diverse mesophotic habitats (Moura et al., 2013).

3.2.3 | Oceanic islands and seamounts

Several islands and seamounts occur off the continental shelf and constitute important biodiversity hotspots within the Tropical SW Atlantic. They include the archipelagos of Fernando de Noronha and Saint Peter and Saint Paul (SPSPA), the Rocas Atoll and the Vitória-Trindade Seamount Chain (VTC). These formations vary in size (the largest is Fernando de Noronha) and distance from the mainland (the most remote is SPSPA, located on the Mid-Atlantic Ridge). These islands and seamounts may provide insights into the evolutionary history, ecology of marine taxa, and seascape-wide connectivity (Pinheiro et al., 2017). For example, Peluso et al. (2018) detected migration and connectivity of the reef-building coral *M. hispida* between the Eastern Brazil and oceanic islands. The MEs may provide a more continuous area of suitable habitat for this coral, favouring the maintenance of gene flow between the Trindade Island, Rocas Atoll and Fernando de Noronha Archipelago through the oceanic currents (Peluso et al., 2018).

The VTC extends approximately 1,200 km offshore from the Brazilian continental shelf, from the Vitória seamount to the isolated oceanic islands of Trindade and Martin Vaz. The VTC consists of 11 seamounts with summits reaching euphotic and mesophotic zones (~10–110 m depth) (Pereira-Filho et al., 2011). MEs found on the VTC are a mosaic of habitats dominated by macroalgae, including crustose coralline algae (CCA) at approximately 40 m deep, and fleshy species on the rhodolith beds below 50 m deep (Meirelles et al., 2015). The scleractinian corals *Siderastrea* spp., *M. cavernosa* and *M. hispida*, along with sponges, comprise the main benthic suspension feeders in these MEs (Pinheiro et al., 2017). With a total of 211 species recorded on the seamounts (Pinheiro et al., 2015), the structural reefs shelter richer and more abundant fauna than the surrounding flatbeds. The fish fauna has a composition partly similar to that of coastal reefs, but also shares certain characteristics, such as the abundance of planktivores, with Fernando de Noronha and Rocas Atoll (Pinheiro, Ferreira, Joyeux, Santos, & Horta, 2011).

The insular complex formed by the Rocas Atoll and Fernando de Noronha Archipelago represents a significant portion of the island surface in the SAO. The productive oceanic waters here are important for the reproduction and feeding of many taxa (UNESCO, 2017), and they were designated a Natural World Heritage Site in 2001. They are also protected by MPAs (Biological Reserve in Rocas Atoll, and Marine National Park and Environmental Protected Area in

Fernando de Noronha Archipelago). It is noteworthy that the Rocas, located at the top of a chain of seamounts, which are 267 km off the coast of Brazil and at 4,000 m depth, is the sole atoll in the South Atlantic (Leão et al., 2016). This atoll is approximately 150 km west of the Fernando de Noronha Archipelago, with which it shares some endemic species (Soares, Lotufo, et al., 2017). MEs in the Rocas Atoll (Amado-Filho et al., 2016) and Fernando de Noronha Archipelago have been recently described (Amado-Filho, Pereira-Filho, et al., 2012; Pereira-Filho et al., 2015; Santos et al., 2016). In these studies, rhodolith beds were reported as the principal seascape. These rhodoliths appeared both as free and coalesced forms and produced patch reefs on both islands (Amado-Filho et al., 2016; Pereira-Filho et al., 2015).

The most remote MEs in this area are located in the Saint Peter and Saint Paul Archipelago, on the mid-Atlantic ridge. Spalding et al. (2007) defined this archipelago as a distinct marine ecoregion due to its distance from the coast and its unique biodiversity (Supporting Information Appendix S2). In this area, some shifts in the benthic and reef fish assemblages between shallow and mesophotic depths have been reported (Amaral et al., 2000; Magalhães et al., 2015; Rosa et al., 2016; Soares, Lotufo, et al., 2017). At least one bryozoan, *Margaretta buski*, is considered to be an ecosystem engineers species and is abundant at depths of 10–45 m depth. This bryozoan forms erect colonies, providing an animal forest for the associated species (such as crustaceans and echinoderms). Rosa et al. (2016) observed that scleractinian corals and macroalgae (turf and fleshy) were more abundant between 30 and 40 m depths. As the depth increased, they were progressively replaced by more animal-dominated assemblages (such as sponges, bryozoans and black corals). These authors also found that some reef fishes were clearly associated with the black coral forests (*Tanacetipathes* spp.), indicating that these animal forests play a key nursery function in the lower depth limit of these MEs.

3.3 | Saint Helena and Ascension islands

The Saint Helena and Ascension islands (Central Atlantic) constitute one of the least studied biogeographical provinces in the SAO. Ascension Island (7°57′S 14°22′W) is one of the most remote volcanic islands in the South Atlantic and is located ~1,200 km from St Helena (the nearest island) and ~2,300 km from Recife (Brazilian coastline). Seamounts, canyons and insular shelves are common features around the Ascension and Saint Helena islands, which provide habitat for the occurrence of MEs without the presence of coral reefs (Irving, 2013). For example, the shallowest part of the Grattan seamount near Ascension Island is 72 m deep, with the occurrence of algae (dominated by coralline algae), marine animal forests (sponge bottoms, scleractinian corals and octocoral animal forests) and associated reef fishes. Rocky formations around Ascension Island consist of bedrock reefs, vertical cliffs and steep boulder slopes, as well as a variety of caves, canyons and lava tubes providing significant geodiversity for the little-studied MEs (Irving, 1989, 2013; Wirtz et al., 2017).

Irving (1989) described benthic communities of Ascension Island and reported the occurrence of the corals *Astrangia solitaria*, *Madracis decactis* and *Siderastrea radians* (Irving, 2013). In addition, Zibrowius, Wirtz, Nunes, Hoeksema, & Benzoni (2017) detected the presence of the coral *Cladocora debilis* in the lower mesophotic zone (72 m depth). Moreover, fishes from shallow and mesophotic depths (0–60 m) were also associated with the slopes of these seamounts and insular shelves (Wirtz et al., 2017).

MEs in these remote seamounts and oceanic islands may act as centres of endemism and "stepping stones," providing opportunities for certain species to expand their ranges between the Eastern and Western Atlantic (Irving, 1989, 2013; Wirtz et al., 2017). Indeed, seamounts in this ocean basin (especially near Saint Helena Island) are the least known habitats for the occurrence of MEs due to the lack of research conducted away from the coast in Brazil and Africa. Overall, there is little information (i.e., mapping and quantitative studies) about the MEs around these remote South Atlantic islands, which clearly suggests the need for more studies.

3.4 | The Gulf of Guinea Province

This region comprises the marine ecoregion of the Gulf of Guinea islands on the west coast of Africa (Spalding et al., 2007). The MEs in the Eastern Atlantic Ocean are composed of rocky reefs with biogenic patches that support shore fishes (Morais & Maia, 2017; Wirtz et al., 2007). This area has very distinct oceanographic features that prevent the development of extensive coral reefs, such as large inputs of freshwater from the mainland and cold water from oceanic currents. As a result, corals are often limited by temperature to the first 20 m (Spalding et al., 2001). Wirtz et al. (2007) report fishes mainly in shallow waters (0–30 m) and in mesophotic depths (between 32 and 45 m depth) around São Tomé and Príncipe islands.

Considering that shallow-water scleractinian corals in this province are usually restricted to warm waters, the presence of MEs in cool waters (São Tomé island), recently described by Morais and Maia (2017), is surprising. Although the warm shallow-water formations (<30 m) were dominated by coralline algae, with few species of scleractinian corals (*M. cavernosa* and *Siderastrea* sp.), which are also common in the South America (Leão et al., 2016) and other African islands (Laborel, 1974), the upper mesophotic zone (35–50 m) showed a benthic composition that changed due to the thermocline. At this depth, the seascape became dominated by a marine animal forest of black corals (mainly *Antipathes gracilis* and *Tanacetipathes spinescens*) and associated reef fishes, such as *Paranthias furcifer*, *Clepticus africanus*, and *Lutjanus fulgens* (Morais & Maia, 2017). In this case, it would be possible to test whether temperature-driven differences in the assemblages would prevent the areas acting as effective deep-sea refugia. Moreover, the shallow and mesophotic biodiversity of this African archipelago is of scientific interest due to the occurrence of easterly flowing Equatorial currents that link the western and the eastern Atlantic at this tropical latitude (Laborel, 1974; Wirtz et al., 2007).

4 | HUMAN PRESSURES ON THE SOUTH ATLANTIC MES

MEs are commonly viewed as being less affected by disturbance than shallow-water ecosystems (Kahng et al., 2017). Local and regional human impacts (e.g., overfishing, sedimentation, dredging and pollution) and natural disturbances (e.g., storms, extreme heat waves, hurricanes, severe floods and droughts) tend to decrease with increasing depths and distance from the coast (Baker et al., 2016; Loya et al., 2016). However, MEs may also be less resilient than shallow reefs (Pyle et al., 2016), and assessments of their health status and possible threats are surely needed to ensure their conservation. MEs are gradually becoming part of the international list of vulnerable marine ecosystems (VMEs; Aguilar, Perry, & López, 2017), and in the South Atlantic Ocean, protective measures need to be developed to ensure their conservation.

The South Atlantic MEs are receiving pressure from fishing, carbonate deposit surveys, submarine cables, biotechnological product development, mining, oil and gas exploration, dispersion of invasive species and marine debris (Supporting Information Appendix S2). These increasing pressures have been observed along the tropical and subtropical coasts of both South America and Africa (all four biogeographical provinces considered in the present review) and thus are threatening the MEs in these areas, including reef species (Supporting Information Appendix S2).

At regional levels, these anthropogenic pressures can be managed (e.g., fisheries regulations, marine spatial planning and marine protected areas) within the regions covered in the present review. On the other hand, global stressors, such as "global warming and sea-surface temperature anomalies (SST) anomalies, acidification, and extreme floods and droughts, are unmanageable at local and regional scales. However, they should still be included in global conservation strategies (e.g., reduction in carbon emissions).

4.1 | Local and regional stressors

Fishing is one of the main anthropogenic pressures on MEs, and all biogeographical provinces included in this study sustain important fishing grounds (Supporting Information Appendix S2). Artisanal and commercial boats operate mainly with lines, traps and bottom trawling. The MEs, characterized by high population densities and species richness, concentrate fishing grounds and sustain an important multispecific reef fishery (Eduardo et al., 2018; Pinheiro et al., 2015; Rosa et al., 2016). These activities affect even the remote Saint Peter and Saint Paul Archipelago where overfishing may have caused local extinction of the shark species *Carcharhinus galapagensis* (Luiz & Edwards, 2011). Significant fisheries for the Southern red snapper, *Lutjanus purpureus* (2,900 metric tons/year), and spiny lobsters, *Palinurus* spp. (1,360 metric tons/year), were recorded for the MEs along the Amazon coast. Reef fisheries have been carried out by small- to medium-sized boats (8 to 20 m lengths) operating with traps (for lobsters) and hand lines or long lines (for reef fishes) on the outer shelf (Moura et al., 2016). The lack of monitoring of fishing activity in the South Atlantic MEs (Magalhães et al., 2015; Morais & Maia, 2017; Moura et al., 2016; Soares, Lotufo, et al., 2017) means that it is now urgent to quantify fishing impacts to test the refugia hypothesis (Lindfield et al., 2016). In addition, it is important to monitor the effects of fishing and other human pressures on the shallow and mesophotic reef fishes. Pinheiro et al. (2018) provided a recent database on reef fishes (0–150 m depth), which detected 733 fish species, of which 405 were Southwestern Atlantic (SWA) resident reef fishes or strictly reef species, 111 were endemic to the SWA and 78 were considered to be threatened with extinction.

Bottom trawling, bottom-set long lines, bottom-set gillnets and abandoned fishing gear are particularly important threats to mesophotic ecosystems (Soares, Lotufo, et al., 2017), and they have also been reported in the South Atlantic MEs (Supporting Information Appendix S2). Ecosystem engineers (e.g., sponges and black corals) in mesophotic depths have low growth and recovery rates, which suggest the vulnerability of these taxa to fishing activities. Bottom trawling is a fishing activity that has been impacting shallow marine ecosystems along the Brazilian coast and has extended into offshore areas in the last decades. Indeed, bottom trawling has a negative impact on MEs worldwide (Baker et al., 2016; Cánovas-Molina et al., 2016). Another regional pressure that occurs in MEs on the South Atlantic is the presence of marine debris (e.g., macroplastics, microplastics, pellets and abandoned fishing gear; Supporting Information Appendix S2). The marine debris in the mesophotic zone can introduce invasive species as well as threaten the life of marine organisms by entrapment, ingestion of solid wastes or contamination by microplastics. Moreover, plastic debris stresses reef-building species through anoxia, light deprivation and toxin release, increasing the risk associated with pathogens (Lamb et al., 2018).

On the Brazilian and West African coasts, mining activities that target oil, gas, metals and carbonates have been receiving strong public support and private investments, especially in deeper waters. In the VTC, mining activities are expected to increase in the next decades by targeting metals on slopes and carbonates on seamount summits (Pinheiro et al., 2015). These mining activities could threaten local MEs. Recent discoveries of oil and gas fields near mesophotic ecosystems may also increase the pressure on MEs. International companies have acquired exploratory drilling blocks that will soon be producing oil, if approved by the national agencies, near the extensive MEs off the North and Northeastern coast of Brazil, increasing the risk of bio-invasion and oil spills in a little-studied ecosystem. It is therefore crucial to carefully evaluate the exploitation of these marine resources and assess possible environmental risks associated with mining activities, considering their direct and indirect impacts on MEs (Creed et al., 2017; Silva, Etnoyer, & MacDonald, 2016). It is also important to note that these activities are already subject to environmental licensing in Brazil (Santos et al., 2016; Soares, Lotufo, et al., 2017) and therefore require a detailed description of the MEs and the effects of the proposed activities.

Finally, biological invasions usually have negative consequences on MEs (Andradi-Brown et al., 2017) by affecting ecosystem goods

and services and leading to financial losses and biodiversity changes (Baker et al., 2016). Recent investigations have identified the introduction and proliferation of alien species worldwide (e.g., *Carijoa* sp., *Avrainvillea* sp., *Pterois* spp.), which may alter the mesophotic community structure at the expense of native biodiversity (Baker et al., 2016). Brazilian and African coasts have experienced significant transoceanic ship traffic since the 16th century, but the consequences of this maritime transport on bio-invasions have only recently received academic and governmental attention (Castro, Fileman, & Hall-Spencer, 2017). Indeed, recent studies have reported the presence of invasive species in the South Atlantic MEs (Supporting Information Appendix S2), for example, ophiuroids (*Ophiothela mirabilis*) on the Amazon shelf (Moura et al., 2016).

Other potential alien invaders are lionfish (*Pterois volitans*) and orange cup corals (*Tubastraea coccinea* and *T. tagusensis*), which have been associated with impacts on marine ecosystems in the Western Atlantic (Andradi-Brown et al., 2017; Creed et al., 2017). Lionfish has been reported in shallow waters on the east South American coast (Ferreira et al., 2015) but have also been observed at mesophotic depths in the Caribbean Sea (Baker et al., 2016). Orange cup corals were the first invasive scleractinian species introduced into the SAO, with known occurrences near the Northeastern Brazil MEs (Soares, Davis, & Carneiro, 2018) and the Abrolhos Bank (Costa et al., 2014). Considering the threats imposed by invasive species to biodiversity, it is essential that international and national environmental agencies operating in the SAO adopt guidelines to restrain invasive species expansion.

4.2 | Global stressors

Regarding global environmental stressors, little is known about their effects on MEs, mainly due to the lack of long-term monitoring. For example, ocean acidification, which is expected to accelerate in the 21st century (Hoegh-Guldberg et al., 2017), compromises carbonate production by reef-building species (e.g., calcareous algae and corals) and is the least studied global change stressor in the SAO (Kerr et al., 2016). Nevertheless, coralline algae are among the most important framework builders in the South Atlantic MEs. Thus, ocean acidification is a real threat to these MEs, which may experience a considerable shift in their structure and function in the near future (Amado-Filho, Moura, et al., 2012; Horta et al., 2016).

Coral-bleaching events, mainly in shallow-water reefs, are related to both local and global stressors, such as anomalies in SST, including several weeks of above-average temperatures and positive hotspot values (Leão et al., 2016; Soares, Lotufo, et al., 2017). Despite increasing rates of bleaching and coral diseases in the shallow-water reefs of the SAO, mass mortality of reef-building species has not yet been detected in coastal reefs. This may be due to the higher resilience of corals in the SAO, which are often adapted to suboptimal conditions (Leão et al., 2016). Thus, we hypothesize that the presence of resilient reef-building corals (e.g., *Siderastrea* spp., *M. cavernosa* and *Mussismillia* spp.) in the mesophotic zone and the abundance of non-coral organisms (e.g., sponges and calcareous algae) may provide the South Atlantic MEs with some degree of resilience to thermal stresses. The susceptibility to temperature anomalies must take into consideration not only the low-bleaching threshold of South Atlantic MEs but also the exposure to elevated temperatures. Greater depths may also buffer these deeper ecosystems from some pressures (e.g., irradiance and local impacts). For example, at Trindade Island within the VTC, tissue necrosis and bleaching affected >90% of the coral colonies in shallow waters, whereas >90% of the coral colonies in MEs were healthy (Meirelles et al., 2015). However, this resilience may be compromised in the face of the increased frequency and duration of thermal stress predicted as a result of climate change and other stressors (eutrophication, acidification and sea-level rise; Hoegh-Guldberg et al., 2017).

A commonly overlooked global driver of pressures on MEs is the occurrence of extreme events, such as droughts and floods. Lack of information on the impact of such events is partly due to the distance between MEs and the coastline, which diminishes the influence of estuarine plumes, freshwater inputs and precipitation regimes. However, MEs in North Brazil are seasonally under the influence of large rivers and are directly influenced by the input of fine sediments, nutrients and turbid water. The Amazon coast has already been affected by droughts and floods due to climatic anomalies (Marengo & Espinoza, 2016). Moura et al. (2016) have indicated that such extreme events are on the rise under climate change scenarios and will probably influence the functioning of MEs off the Amazon River.

5 | FUTURE DIRECTIONS: RESEARCH AND MANAGEMENT

The present review integrates studies on the geographical distribution, human impact and conservation status of the MEs in the SAO and aims to be a first step in the elaboration of a more detailed scenario regarding these deep-water habitats within the tropical zone of this ocean basin. It was outside the scope of our review to integrate information on subtropical, temperate and polar ecosystems in the mesophotic zone of the SAO. Nevertheless, integrative studies on these southern environments are much needed, due to their ecological importance. For example, it is known that the distribution of rhodoliths and rocky reefs in Brazil extends beyond the tropical zone, crossing through the subtropical zone to the temperate coast of Santa Catarina state (Horta et al., 2016).

Future research should focus on four main topics: (a) baseline assessment (biodiversity, ecology, physiology, geodiversity and chemical and physical oceanography), (b) evaluation of the ME goods and services, (c) impacts and (d) conservation strategies. Work on the first and second topics is essential to provide the basis on which the other two topics can be studied and to investigate the potential role of MEs as refuges in a changing ocean.

In terms of biodiversity, it is necessary to conduct studies (i.e., beta diversity, nestedness and turnover) comparing shallow (<30 m), upper (30–60 m) and lower (>60 m) mesophotic zones to verify the

similarity of their assemblages using meta-analysis and large-scale studies with a standardized methodology. Studies in the Caribbean Sea and Indo-Pacific Ocean have shown that shallow and upper mesophotic zones are frequently similar (Kahng et al., 2017; Slattery, Lesser, Brazeau, Stokes, & Leichter, 2011). However, the lower community is a distinct assemblage with a high degree of endemism (Kahng, Copus, & Wagner, 2014). Semmler et al. (2017), studying a dataset of over 9,000 species found throughout the Gulf of Mexico, observed that the taxonomic overlap between shallow and progressively deeper zones declined steadily with depth. The authors concluded that the mesophotic zone is home to three ecological communities: the upper, which is confluent with shallow reefs; a distinct mesophotic assemblage spanning 60–120 m; and a third that extends onto the outer continental shelf, with limited potential to serve as a refuge.

Another important aspect is the limited connectivity between the shallow and mesophotic ecosystems, observed only in a small number of species in the Caribbean Sea and the South Atlantic (Bongaerts et al., 2017; Morais & Santos, 2018). Within each zone, it is necessary to verify the patterns of bathymetric distribution and genetic connectivity of marine populations, particularly considering the peculiarities of large rhodolith beds, sponge bottoms, black coral forests, octocoral animal forests and reefs in turbid waters of the SAO. Finally, horizontal connectivity (i.e., between MEs) remains poorly understood worldwide (Kahng et al., 2014) and it should also be assessed in the SAO, especially in relation to previous hypotheses of large-scale connectivity between Brazilian and Caribbean species (Francini-Filho et al., 2018; Rocha, 2003; Rocha et al., 2000).

It is necessary to understand the cumulative impact of human stressors that affect ecosystem goods and services provided by the MEs in order to discuss the challenges faced and the role of science in improving South Atlantic Ocean governance in this twilight zone (Baker et al., 2016). The mapping and assessment of these goods and services would be a highly valuable source of information and would contribute to an understanding of their current and potential benefits to society.

The present review has compiled information (Supporting Information Appendix S2) on anthropogenic pressures on MEs. The quantitative impacts of these pressures are still poorly understood worldwide (Turner et al., 2017), and this is another limitation of this review. A better comprehension requires consideration of scales at which these pressures are acting, an assessment of the degree of change in key mesophotic ecological indicators, and an analysis of the resilience of these ecosystems. It also should be considered that the way these pressures act is cumulative and synergistic (Mumby, & Anthony, 2015). Thus, appropriate metrics and indicators should be used (Cánovas-Molina et al., 2016).

The current scarcity of information on the structure and functioning of the SAO MEs should not limit conservation action and the management of these ecosystems. The "precautionary principle," known in maritime and environmental laws (Santos et al., 2016), should be adopted in this case and consider the recent and future human pressures. Therefore, considering the economic activities with environmental impacts on MEs (Supporting Information Appendix S2), we suggest five main management and conservation actions: (a) adoption of ocean zoning (Yates, Schoeman, & Klein, 2015) and large marine spatial planning (Dunstan et al., 2016); (b) creation and expansion of marine protected areas (MPAs) using systematic conservation planning; (c) rigorous fishing regulations and environmental licensing for human activities, based on sound scientific knowledge; (d) reduction in carbon emissions to the atmosphere, considering the vulnerability of MEs to ocean acidification and SST anomalies; and (e) extending environmental monitoring programs to include the South Atlantic MEs.

The major challenges in the conservation of MEs in the SAO are related to surveillance in offshore areas (especially in seamounts), the financial cost of environmental monitoring and the lack of detailed seabed mapping to identify required management actions. The latter should be the subject of scientific research efforts to obtain detailed information on the distribution of MEs. Regarding environmental monitoring and surveillance, the use of technologies should be encouraged, such as the use of remote sensing by satellites, the Internet of the oceans and the use of automatic identification systems for surveillance of fishing activities and shipping lines in MEs. Kroodsma et al. (2018), who detected the global footprint of industrial fisheries and its results, found a lack of data from the fisheries in the Southwestern Atlantic, which harbours unique MEs.

The management plans of the MPAs that cover mesophotic habitats in the SAO generally do not directly contemplate actions to conserve these ecosystems. Therefore, these documents need to be updated to include specific actions for deeper ecosystems, such as no-take zones, environmental monitoring and surveillance. Moreover, Soares and Lucas (2018) discussed aspects of the recent and large MPAs in Vitória-Trindade Chain and St. Paul and St. Peter Archipelago, as well as the need for a participatory management plan. The authors also noted that most of the area (~87%) covered by these specific MPAs was under a regime of sustainable use, which permitted a range of human activities, including fishing and mining. Giglio et al. (2018) and Magris and Pressey (2018) revealed the absence of large no-take zones in vulnerable habitats (including MEs), uninformed opportunism by the Brazilian government in the creation of these MPAs, and poor adherence to best practices in MPA planning (e.g., lack of connectivity between habitats).

The increase in MPAs in the world's oceans as well as their management should aim the protection of multiple components of mesophotic biodiversity (taxonomic, phylogenetic and functional), and the ecosystem goods and services. However, a clear spatial mismatch between the existing degree of protection and all conservation priorities worldwide has been detected (Lindegren, Holt, Mackenzie, & Rahbeck, 2018). The MEs provide an opportunity to avoid past mistakes in the design of MPAs planning and to provide effective action to protect these vulnerable habitats (e.g., no-take zones). Specific studies for the creation and expansion of MPAs should provide information about

their size, spacing, connectivity, management and shape in order to achieve ecological effectiveness for conservation action.

6 | CONCLUSIONS

In this study, we reviewed recent research on South Atlantic MEs and the pressures threatening these ecosystems. We also provided options for their conservation. Conservation policies have generally focused on mesophotic biogenic reefs. However, our review indicated that there is a need for a change of approach to conservation and that measures should be taken to protect the distinct seascapes identified in the mesophotic zone (e.g., sponge aggregations, biogenic and rocky reefs, octocoral forests, black coral forests and rhodolith beds).

Recent descriptions of MEs in the South Atlantic demonstrate how little we know about this ocean and how much of its biodiversity may still be hidden. A solid scientific knowledge base for the South Atlantic MEs is essential to build a clear unifying picture to share with stakeholders and to gain public support for MEs conservation.

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DATA ACCESSIBILITY

All bathymetric and environmental GIS layers, and results generated for this study are available as raster grids from the Pangaea database.

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REFERENCES

Aguilar, R., Perry, A. L., & López, J. (2017). Conservation and management of vulnerable marine benthic ecosystems. In S. Rossi (Ed.), *Marine animal forests: The ecology of benthic biodiversity hotspots of the world*. Major Reference Book (pp. 1–43). New York, NY: Springer.

Almeida, N. M., Vital, H., & Gomes, M. P. (2015). Morphology of submarine canyons along the continental margin of the Potiguar Basin, NE Brazil. *Marine and Petroleum Geology*, *68*, 307–324. https://doi.org/10.1016/j.marpetgeo.2015.08.035

Amado-Filho, G. M., Bahia, R. G., Pereira-Filho, G. H., & Longo, L. L. (2017). South Atlantic rhodolith beds: Latitudinal distribution, species composition, structure and ecosystem functions, threats and conservation status. In R. Riosmena-Rodríguez, W. Nelson, & J. Aguirre (Eds.), *Rhodolith/Maërl Beds: A global perspective*. Coastal research library. (vol. 15, pp. 299–317). New York, NY: Springer. https://doi.org/10.1007/978-3-319-29315-8

Amado-Filho, G. M., Moura, R. L., Bastos, A. C., Francini-Filho, R. B., Pereira Filho, G. H., Bahia, R. G., … Motta, F. S. (2016). Mesophotic ecosystems of the unique South Atlantic atoll are composed by rhodolith beds and scattered consolidated reefs. *Marine Biodiversity*, *46*(4), 933–936. https://doi.org/10.1007/s12526-015-0441-6

Amado-Filho, G. M., Moura, R. L., Bastos, A. C., Salgado, L. T., Sumida, P. Y., Guth, A. Z., … Thompson, F. L. (2012). Rhodolith beds are major $CaCO_3$ bio-factories in the tropical south West Atlantic. *PLoS ONE*, *7*(4), e35171. https://doi.org/10.1371/journal.pone.0035171

Amado-Filho, G. M., Pereira-Filho, G. H., Bahia, R. G., Abrantes, D. P., Veras, P. C., & Matheus, Z. (2012). Occurrence and distribution of rhodolith beds on the Fernando de Noronha Archipelago of Brazil. *Aquatic Botany*, *101*, 41–45. https://doi.org/10.1016/j.aquabot.2012.03.016

Amaral, F. M. D., Hudson, M. M., Silveira, F. L., Migotto, A. E., Pinto, S. M., & Longo, L. L. (2000). Cnidarians from St. Peter and St. Paul Archipelago, Northeast Brazil. Proc. 9th Intern Coral. Reef. Symp., *1*, 567–572.

Andradi-Brown, D. A., Vermeij, M. J. A., Slattery, M., Lesser, M., Bejarano, I., Appeldoorn, R., … Exton, D. A. (2017). Large scale invasion of Western Atlantic mesophotic reefs by invasive lionfish potentially undermine culling-based management. *Biological Invasions*, *19*(3), 939–954. https://doi.org/10.1007/s10530-016-1358-0

Baker, E., Puglise, K., & Harris, P.T.(2016). *Mesophotic coral ecosystems: a lifeboat for coral reefs?* The United Nations Environment Programme (UNEP) and GRID-Arendal, Nairobi and Arendal. 98p. Retrieved from http://www.unep.org/ourplanet/may-2016/unep-publications/mesophotic-coral-ecosystems

Bastos, A. C., Moura, R. L., Amado-Filho, G. M., D'Agostini, D. P., Secchin, N. A., Francini-Filho, R. B., … Thompson, F. L. (2013). Buracas: Novel and unusual sinkhole-like features in the Abrolhos Bank. *Continental Shelf Research*, *70*, 118–125. https://doi.org/10.1016/j.csr.2013.04.035

Bastos, A. C., Moura, R. L., Moraes, F. C., Vieira, L. S., Braga, J. C., Ramalho, L. V., … Webster, J. M. (2018). Bryozoans are major modern builders of South Atlantic oddly shaped reefs. *Scientific Reports*, *8*, 9638. https://doi.org/10.1038/s41598-018-27961-6

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh Guldberg, O. (2010). Assessing the "deep reef refugia" hypothesis: Focus on Caribbean reefs. *Coral Reefs*, *29*, 309–327. https://doi.org/10.1007/s00338-009-0581-x

Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S. R., & Hoegh-Guldberg, O. (2017). Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Science Advances*, *3*(2), e1602373. https://doi.org/10.1126/sciadv.1602373

Camargo, J. M. R., Araujo, T. C. M., Ferreira, B. P., & Maida, M. (2015). Topographic features related to recent sea level history in a sediment-starved tropical shelf: Linking the past, present and future. *Regional Studies in Marine Science*, *2*, 203–211. https://doi.org/10.1016/j.rsma.2015.10.009

Cánovas-Molina, A., Montefalcone, M., Bavestrello, G., Cau, A., Bianchi, C. K., Morri, C., … Bo, M. (2016). A new ecological index for the status of mesophotic assemblages in the mediterranean based on ROV fotography and video footage. *Continental Shelf research*, *121*, 13–20. https://doi.org/10.1016/j.csr.2016.01.008

Castro, M. C. T., Fileman, T. W., & Hall-Spencer, J. M. (2017). Invasive species in the Northeastern and Southwestern Atlantic Ocean: A review. *Marine Pollution Bulletin*, *116*, 41–47. https://doi.org/10.1016/j.marpolbul.2016.12.048

Clapperton, C. M. (1993). Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *101*(3), 189–208. https://doi.org/10.1016/0031-0182(93)90012-8

Collette, B. B., & Rutzler, K. (1977). Reef fishes over sponge bottoms off the mouth of the Amazon river. Proceedings of the 3rd International Coral Reef Symposium, Miami, Florida.

Cordeiro, R. T., Kitahara, M. V., & Amaral, F. M. D. (2012). New records and range extensions of azooxanthellate scleractinians (Cnidaria: Anthozoa) from Brazil. *Marine Biodiversity Records*, *5*, 1–6.

Cordeiro, R. T. S., Neves, B. M., Rosa-Filho, J. S., & Pérez, C. D. (2015). Mesophotic coral ecosystems occur offshore and north of the Amazon River. *Bulletin of Marine Science*, *91*, 491–510. https://doi.org/10.5343/bms.2015.1025

Costa, T. J. F., Pinheiro, H. T., Teixeira, J. B., Mazzei, E. F., Bueno, L., Hora, M. S. C., … Rocha, L. A. (2014). Expansion of an invasive coral species over Abrolhos Bank, Southwestern Atlantic. *Marine Pollution Bulletin*, *85*(1), 252–253. https://doi.org/10.1016/j.marpolbul.2014.06.002

Creed, J. C., Fenner, D., Sammarco, P., Cairns, S., Capel, K., Junqueira, A. O. R., … Oigman-Pszczol, S. (2017). The invasion of the azooxanthellate coral Tubastraea (Scleractinia: Dendrophyllidae) throughout the world: History, pathways and vectors. *Biological Invasions*, *19*(1), 283–305. https://doi.org/10.1007/s10530-016-1279-y

Dunstan, P. K., Bax, N. J., Dambacher, J. M., Hayes, K. R., Hedge, P. T., Smith, D. C., … Smith, A. D. M. (2016). Using ecologically and biologically significant marine areas (EBSAs) to implement marine spatial planning. *Ocean and Coastal Management*, *121*, 116–127. https://doi.org/10.1016/j.ocecoaman.2015.11.021

Eduardo, L. N., Frédou, T., Lira, A. S., Ferreira, B. P., Bertrand, A., Ménard, F., … Frédou, F. L. (2018). Identifying key habitat and spatial patterns of fish biodiversity in the tropical Brazilian continental shelf. *Continental Shelf Research*, *166*, 108–118. https://doi.org/10.1016/j.csr.2018.07.002

Feitoza, B. M., Rosa, R. S., & Rocha, L. A. (2005). Ecology and zoogeography of Deep-Reef Fishes in northeastern Brazil. *Bulletin of Marine Science*, *76*, 725–742.

Ferreira, C. E. L., Luiz, O. J., Floeter, S. R., Lucena, M. B., Barbosa, M. C., Rocha, C. R., … Rocha, L. A. (2015). First record of invasive Lionfish (*Pterois volitans*) for the Brazilian coast. *PLoS ONE*, *10*(4), e0123002. https://doi.org/10.1371/journal.pone.0123002

Francini-Filho, R., Asp, N. E., Siegle, E., Hocevar, J., Lowyck, K., D'Avila, N., … Thompson, F. L. (2018). Perspectives on the Great Amazon Reef: Extension, biodiversity, and threats. *Frontiers in Marine Science*, *5*, 142. https://doi.org/10.3389/fmars.2018.00142

Francini-Filho, R., & Moura, R. L. (2008). Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *18*(7), 1166–1179. https://doi.org/10.1002/aqc.966

Freitas, J. E. P., & Lotufo, T. M. C. (2015). Reef fish assemblage and zoogeographic affinities of a scarcely known region of the western equatorial Atlantic. *Journal of Marine Biological Association of the United Kingdom*, *95*(3), 623–633. https://doi.org/10.1017/S0025315414001404

Giglio, V. J., Pinheiro, H. T., Bender, M. G., Bonaldo, R. M., Costa-Lotufo, L. V., Ferreira, C. E. L., … Francini-Filho, R. B. (2018). Large and marine protected areas are flawed and raise concerns: Comments on Soares and Lucas (2018). *Marine Policy*, *96*, 13–17. https://doi.org/10.1016/j.marpol.2018.07.017

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses, and implications. *Global Change Biology*, *2*, 495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

Hinderstein, L. M., Marr, J. C. A., Martinez, F. A., Dowgiallo, M. J., Puglise, K. A., Pyle, R. L., … Appeldoorn, R. (2010). Theme section on 'mesophotic coral ecosystems': Characterization, ecology and management'. *Coral Reefs*, *29*, 247–251. https://doi.org/10.1007/s00338-010-0614-5

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., … Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90. https://doi.org/10.1038/nature22901

Hoeksema, B. W., Bongaerts, P., & Baldwin, C. C. (2017). High coral cover at lower mesophotic depths: A dense Agaricia community at the leeward side of Curaçao, Dutch Caribbean. *Marine Biodiversity*, *47*, 67–70. https://doi.org/10.1007/s12526-015-0431-8

Holstein, D. M., Paris, C. B., Vaz, A. C., & Smith, T. B. (2016). Modeling vertical connectivity and mesophotic refugia. *Coral Reefs*, *35*(1), 23–37. https://doi.org/10.1007/s00338-015-1339-2

Hopley, D. (2011). *Encyclopedia of modern Coral Reefs: Structure, form and process*. Encyclopedia of Earth Sciences Series. New York, NY: Springer. https://doi.org/10.1007/978-90-481-2639-2

Horta, P. A., Riul, P., Amado-Filho, G. M., Gurgel, C. F. D., Berchez, F., Nunes, J. M. C., … Figueiredo, M. (2016). Rhodoliths in Brazil: Current knowledge and potential impacts of climate change. *Brazilian Journal of Oceanography*, *64*(2), 117–136. https://doi.org/10.1590/S1679-875920160870064sp2

Hovland, M. (2008). *Deep-water coral reefs: Unique biodiversity hot-spots*, 1st ed. (pp. 278). Amsterdam, the Netherlands: Springer.

Irving, R. A. (1989). A preliminary investigation of the sublittoral habitats and communities of Ascension Island, South Atlantic. *Progress in Underwater Science*, *13*, 65–78.

Irving, R. A. (2013). Ascension Island's hermatypic but non-reef building corals. In C. R. C. Sheppard (Ed.), *Coral reefs of the United Kingdom overseas territories*, *coral reefs of the world 4* (pp. 213–221). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/978-94-007-5965-7

Kahng, S. E., Copus, J. M., & Wagner, D. (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, *7*, 72–81. https://doi.org/10.1016/j.cosust.2013.11.019

Kahng, S., Copus, J. M., & Wagner, D. (2017). Mesophotic coral ecosystems. In S. Rossi (Ed.), *Marine animal forests* (pp. 185–206). New York, NY: Springer International Publishing. https://doi.org/10.1007/978-3-319-21012-4

Kerr, R., Cunha, L. C., Kikuchi, R. K. P., Horta, P., Ito, R. G., Muller, M. N., … Copertino, M. S. (2016). The Western South Atlantic Ocean in a High-CO2 World: Current measurement capabilities and perspectives. *Environmental Management*, *57*, 740–752. https://doi.org/10.1007/s00267-015-0630-x

Kitahara, M. V. (2007). Species richness and distribution of azooxanthellate Scleractinia in Brazil. *Bulletin of Marine Science*, *81*(497–518), 2007.

Kitahara, M. V. (2009). The deep-sea demersal fisheries and the azooxanthellate corals from southern Brazil. *Biota Neotropica*, *9*, 1–10.

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., … Worm, B. (2018). Tracking the global footprint of fisheries. *Science*, *359*, 904–908. https://doi.org/10.1126/science.aao5646

Laborel, J. (1974). West African reef corals, an hypothesis on their origin. Proceedings of the Second International Coral Reef Symposium, Brisbane, Australia, *1*, 425–443.

Lamb, J. B., Willis, B. L., Fiorenza, E. A., Couch, C. S., Howard, R., Rader, D. N., … Harvell, C. D. (2018). Plastic waste associated with disease on coral reefs. *Science*, *359*(6374), 460–462. https://doi.org/10.1126/science.aar3320

Leão, Z. M. A. N., Kikuchi, R. K. P., Ferreira, B. P., Neves, E. G., Sovieroski, H. H., Oliveira, M. D., … Johnsson, R. (2016). Brazilian coral reefs in a period of global change: A synthesis. *Brazilian Journal of Oceanography*, *64*, 97–116. https://doi.org/10.1590/S1679-875920160916064sp2

Lindegren, M., Holt, B. G., Mackenzie, B. R., & Rahbeck, C. (2018). A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Scientific Reports*, *8*, 4099. https://doi.org/10.1038/s41598-018-22419-1

Lindfield, S. J., Harvey, E. S., Halford, A. R., & McIlwain, J. L. (2016). Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs*, *35*, 125–137. https://doi.org/10.1007/s00338-015-1386-8

Loya, Y., Eyal, G., Treibitz, T., Lesser, M. P., & Appeldoorn, R. (2016). Theme section on mesophotic coral ecosystems: Advances in knowledge and future perspectives. *Coral Reefs*, *35*, 1–9. https://doi.org/10.1007/s00338-016-1410-7

Luiz, O., & Edwards, A. L. (2011). Extinction of a shark population in the Archipelago of Saint's rocks (equatorial Atlantic) inferred from the historical record. *Biological Conservation*, *144*, 2873–2881. https://doi.org/10.1016/j.biocon.2011.08.004

Magalhães, G. M., Amado-Filho, G. M., Rosa, M. R., Moura, R. L., Brasileiro, P., Moraes, F. C., … Pereira-Filho, G. H. (2015). Changes in benthic communities along a 0-60 m depth gradient in the remote St. Peter and St. Paul Archipelago (Mid-Atlantic Ridge, Brazil). *Bulletin of Marine Science*, *91*, 377–396. https://doi.org/10.5343/bms.2014.1044

Magris, R. A., & Pressey, R. L. (2018). Marine protected areas: Just for show? *Science*, *360*(6390), 723–724. https://doi.org/10.1126/science.aat6215

Maldonado, M., Aguilar, R., Bannister, R. J., Bell, J. J., Conway, K. W., Dayton, P. K., … Young, C. M. (2017). Sponge grounds as Key Marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. In S. Rossi (Ed.), *Marine animal forests: the ecology of benthic biodiversity hotspots of the world* (pp. 145–183). Basel, Switzerland: Springer. https://doi.org/10.1007/978-3-319-21012-4

Marengo, J. A., & Espinoza, J. C. (2016). Extreme seasonal droughts and floods in Amazonia: Causes, trends and impacts. *International Journal of Climatology*, *36*(3), 1033–1050. https://doi.org/10.1002/joc.4420

Meirelles, P. M., Amado-Filho, G. M., Pereira-Filho, G. H., Pinheiro, H. T., de Moura, R. L., & Joyeux, J. C. (2015). Baseline assessment of mesophotic reefs of the Vitória-Trindade Seamount Chain based on water quality, microbial diversity, benthic cover and fish biomass data. *PLoS ONE*, *10*, e0130084. https://doi.org/10.1371/journal.pone.0130084

Morais, R. A., & Maia, H. A. (2017). Lush underwater forests in mesophotic reefs of the Gulf of Guinea. *Coral Reefs*, *36*(1), 95. https://doi.org//10.1007/s00338-016-1523-z

Morais, J., & Santos, B. A. (2018). Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. *Ecosphere*, *9*(7), e02281. https://doi.org/10.1002/ecs2.2281

Moses, C. S., Helmle, K. P., Swart, P. K., Dodge, R. E., & Merino, S. (2003). Pavements of *Siderastrea radians* on Cape Verde reefs. *Coral Reefs*, *22*, 506. https://doi.org/10.1007/s00338-003-0346-x

Moura, R. L., Amado-Filho, G. M., Moraes, F. C., Brasileiro, P. S., Salomon, P. S., Mahiques, M. M., … Yager, P. L. (2016). An extensive reef system at the Amazon River mouth. *Science Advances*, *2*, e1501252. https://doi.org/10.1126/sciadv.1501252

Moura, R. L., Secchin, N. A., Amado-Filho, G. M., Francini Filho, R. B., Freitas, M. O., Minte-Vera, C. V., … Bastos, A. C. (2013). Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Continental Shelf Research*, *70*, 109–117. https://doi.org/10.1016/j.csr.2013.04.036

Mumby, P. J., & Anthony, K. R. N. (2015). Resilience metrics to inform ecosystem management under global change with application to coral reefs. *Methods in Ecology and Evolution*, *6*, 1088–1096. https://doi.org/10.1111/2041-210X.12380

Olavo, G., Costa, P. A. S., Martins, A. S., & Ferreira, B. P. (2011). Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *21*(2), 199–209. https://doi.org/10.1002/aqc.1174

Peluso, L., Tascheri, V., Nunes, F. L. D., Castro, C. B., Pires, D. O., & Zilberberg, C. (2018). Contemporary and historical oceanographic processes explain genetic connectivity in a Southwestern Atlantic coral. *Scientific Reports*, *8*, 2684. https://doi.org/10.1038/s41598-018-21010-y

Pereira, P. H. C., Santos, M., Lippi, D. L., & Silva, P. (2016). Ontogenetic foraging activity and feeding selectivity of the Brazilian endemic parrotfish *Scarus zelindae*. *PeerJ*, *4*, e2536. https://doi.org/10.7717/peerj.2536

Pereira-Filho, G. H., Amado-Filho, G. M., Guimarães, S. M. P. B., Moura, R. L., Sumida, P. Y. G., Abrantes, D. P., … Francini-Filho, R. B. (2011). Reef fish and benthic assemblages of the Trindade and Martin Vaz Island Group, southwestern Atlantic. *Brazilian Journal of Oceanography*, *59*(3), 201–212. https://doi.org/10.1590/S1679-87592011000300001

Pereira-Filho, G. H., Francini-Filho, R. B., Pierozzi-Jr, I., Pinheiro, H. T., Bastos, A. C., Moura, R. L., … Amado-Filho, G. M. (2015). Sponges and fish facilitate succession from rhodolith beds to reefs. *Bulletin of Marine Science*, *91*, 45–46. https://doi.org/10.5343/bms.2014.1067

Pinheiro, H. T., Bernardi, G., Simon, T., Joyeux, J. C., Macieira, R. M., Gasparini, J. L., … Rocha, L. A. (2017). Island biogeography of marine organisms. *Nature*, *549*, 82–85. https://doi.org/10.1038/nature23680

Pinheiro, H. T., Ferreira, C. E. L., Joyeux, J. C., Santos, R. G., & Horta, P. A. (2011). Reef fish structure and distribution in a south-western Atlantic Ocean tropical island. *Journal of Fish Biology*, *79*, 1984–2006. https://doi.org/10.1111/j.1095-8649.2011.03138.x

Pinheiro, H. T., Mazzei, E., Moura, R. L., Amado-Filho, G. M., Carvalho-Filho, A., Braga, A. C., … Joyeux, J. C. (2015). Fish biodiversity of the Vitória-Trindade Seamount Chain, Southwestern Atlantic: An updated database. *PLoS ONE*, *10*, e0118180. https://doi.org/10.1371/journal.pone.0118180

Pinheiro, H. T., Rocha, L. A., Macieira, R. M., Carvalho-Filho, A., Anderson, A. B., Bender, M. G., … Floeter, S. R. (2018). South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. *Diversity and Distributions*, *24*(7), 951–965. https://doi.org/10.1111/ddi.12729

Pyle, R. L., Boland, R., Bolick, H., Bowen, B. W., Bradley, C. J., Kane, C., … Spalding, H. L. (2016). A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian Archipelago. *PeerJ*, *4*, e2475. https://doi.org/10.7717/peerj.2475

Riegl, B., & Piller, W. E. (2003). Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences*, *92*, 520–531. https://doi.org/10.1007/s00531-003-0328-9

Rocha, L. A. (2003). Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, *30*(8), 1161–1171. https://doi.org/10.1046/j.1365-2699.2003.00900.x

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018). Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*, *361*(6399), 281–284. https://doi.org/10.1126/science.aaq1614

Rocha, L. A., Rosa, I. L., & Feitoza, B. (2000). Sponge-dwelling fishes of Northeastern Brazil. *Environmental Biology of Fishes*, *59*(4), 453–458. https://doi.org/10.1023/A:1026584708092

Rosa, M. R., Alves, A. C., Medeiros, D. V., Coni, E. O. C., Ferreira, C. M., Ferreira, B. P., … Francini-Filho, R. B. (2016). Mesophotic reef fish assemblages of the remote St. Peter and St. Paul's Archipelago, Mid-Atlantic Ridge, Brazil. *Coral Reefs*, *35*(1), 113–123. https://doi.org/10.1007/s00338-015-1368-x

Rossi, S. (2013). The destruction of the "animal forests" in the oceans: Towards an over-simplification of the benthic ecosystems. *Ocean and Coastal Management*, *84*, 77–85. https://doi.org/10.1016/j.ocecoaman.2013.07.004

Santos, C. S. M., Lino, J. B., Veras, P. C., Amado-Filho, G. M., Francini-Filho, R. B., Motta, F. S., … Pereira-Filho, G. H. (2016). Environmental licensing on rhodolith beds: Insights from a worm. *Natureza & Conservação*, *14*(2), 137–141. https://doi.org/10.1016/j.ncon.2016.06.002

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2017). Are mesophotic coral ecosytems distinct communities and can they serve as refugia for shallow reefs? *Coral Reefs*, *36*(2), 433–444. https://doi.org/10.1007/s00338-016-1530-0

Shlesinger, T., Grinblat, M., Rapuano, H., Amit, T., & Loya, Y. (2018). Can mesophotic reefs replenish shallow reefs? Reduced coral

reproductive performance casts a doubt. *Ecology*, *99*(2), 421–437. https://doi.org/10.1002/ecy.2098

Shoham, E., & Benayahu, Y. (2017). Higher species richness of octocorals in the upper mesophotic zone in Eilat (Gulf of Aqaba) compared to shallower reef zones. *Coral Reefs*, *36*(1), 71–81. https://doi.org/10.1007/s00338-016-1528-7

Silva, M., Etnoyer, P. J., & MacDonald, I. R. (2016). Coral injuries observed at Mesophotic reefs after the Deepwater Horizon oil discharge. *Deep Sea Research Part II: Topical Studies in Oceanography*, *129*, 96–107. https://doi.org/10.1016/j.dsr.2.2015.05.013

Silva, L. L. N., Gomes, M. P., & Vital, H. (2018). The Açu reef morphology, distribution, and inter reef sedimentation on the outer shelf of the NE Brazil equatorial margin. *Continental Shelf Research*, *160*, 10–22. https://doi.org/10.1016/j.csr.2018.03.011

Simon, T., Pinheiro, H. T., Moura, R. L., Carvalho-Filho, A., Rocha, L. A., Martins, A. S., … Joyeux, J. C. (2016). Mesophotic fishes of the Abrolhos Shelf, the largest reef ecosystem in the South Atlantic. *Journal of Fish Biology*, *89*(1), 990–1001. https://doi.org/10.1111/jfb.12967

Slattery, M., Lesser, M. P., Brazeau, D., Stokes, M. D., & Leichter, J. J. (2011). Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, *408*(1–2), 32–41. https://doi.org/10.1016/j.jembe.2011.07.024

Smith, T. B., Gyory, J., Brandt, M. E., Miller, W. J., Jossart, J., & Nemeth, R. S. (2016). Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Global Change Biology*, *22*(8), 2756–2765. https://doi.org/10.1111/gcb.13175

Soares, M. O., Davis, M., & Carneiro, P. B. M. (2018). Northward range expansion of the invasive coral (*Tubastraea tagusensis*) in the southwestern Atlantic. *Marine Biodiversity*, *48*(3), 1651–1654. https://doi.org/10.1007/s12526-016-0623-x

Soares, M. O., Davis, M., Paiva, C. C., & Carneiro, P. B. M. (2018). Mesophotic ecosystems: Coral and fish assemblages in a tropical marginal reef (northeastern Brazil). *Marine Biodiversity*, *48*(3), 1631–1636. https://doi.org/10.1007/s12526-016-0615-x

Soares, M. O., Lotufo, T. M. C., Vieira, L. M., Salani, S., Hajdu, E., Matthews-Cascon, H., … Kikuchi, R. K. P. (2017). Brazilian marine animal forests: A New world to discover in the Southwestern Atlantic. In S. Rossi (Ed.), *Marine animal forests: The ecology of benthic biodiversity hotspots of the world*. Major Reference Book (pp. 73–110). New York, NY: Springer.

Soares, M. O., & Lucas, C. C. (2018). Towards large and remote protected areas in the South Atlantic Ocean: St. Peter and St. Paul′s Archipelago and the Vitória-Trindade Seamount Chain. *Marine Policy*, *93*, 101–103. https://doi.org/10.1016/j.marpol.2018.04.004

Soares, M. O., Rossi, S., Martins, F. A. S., & Carneiro, P. B. M. (2017). The forgotten reefs: Benthic assemblage coverage on a sandstone reef (Tropical South-western Atlantic). *Journal of the Marine Biological Association of the UK*, *97*, 1585–1592. https://doi.org/10.1017/S0025315416000965

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., … Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, *57*, 573–583. https://doi.org/10.1641/B570707

Spalding, M. D., Ravilious, C., & Green, E. P. (2001). *World atlas of coral reefs*. Berkeley, CA: University of California Press.

Tornabene, L., van Tassell, J. L., Robertson, D. R., & Baldwin, C. C. (2016). Repeated invasions into the twilight zone: Evolutionary origins of a novel assemblage of fishes from deep Caribbean reefs. *Molecular Ecology*, *25*, 3662–3682. https://doi.org/10.1111/mec.13704

Turner, J. A., Babcock, R. C., & Kendrick, G. A. (2017). Deep thinking: A systematic review of mesophotic coral ecosystems. *ICES Journal of Marine Sciences*, *74*(9), 2309–2320. https://doi.org/10.1093/icesjms/fsx085

UNESCO (2017). *Brazilian Atlantic Islands: Fernando de Noronha and Atol das Rocas reserve*. Retrieved from http://whc.unesco.org/en/list/1000

Vale, N. F., Amado-Filho, G. M., Braga, J. C., Brasileiro, P. S., Karez, C. S., Moraes, F. C., … Moura, R. L. (2018). Structure and composition of rhodoliths from the Amazon River mouth, Brazil. *Journal of South American Earth Sciences*, *84*, 149–159. https://doi.org/10.1016/j.jsames.2018.03.014

Wirtz, P., Bingeman, J., Bingeman, J., Fricke, R., Hook, T. J., & Young, J. (2017). The fishes of Ascension Island, central Atlantic Ocean – New records and an annotated check-list. *Journal of the Marine Biological Association of the United Kingdom*, *97*, 783–798. https://doi.org/10.1017/S0025315414001301

Wirtz, P., Ferreira, C. E. L., Floeter, S. R., Fricke, R., Gasparini, J. L., Iwamoto, T., … Schliewen, U. K. (2007). Coastal fishes of São Tomé and Príncipe islands, Gulf of Guinea (Eastern Atlantic Ocean) – An update. *Zootaxa*, *1523*, 1–48.

Yates, K. L., Schoeman, D. S., & Klein, C. J. (2015). Ocean zoning for conservation, fisheries and marine renewable energy: Assessing trade-offs and co-location opportunities. *Journal of Environmental Management*, *152*(1), 201–209. https://doi.org/10.1016/j.jenvman.2015.01.045

Zibrowius, H., Wirtz, P., Nunes, F. L. D., Hoeksema, B. W., & Benzoni, F. (2017). Shallow-water scleractinian corals of Ascension Island, Central South Atlantic. *Journal of Marine Biological Association of United Kingdom*, *97*(4), 713–725. https://doi.org/10.1017/S0025315414001465

BIOSKETCH

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SUPPORTING INFORMATION

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

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