

Chapter 3

Origins, Biogeography and Macroecology of the Southwestern Atlantic Reef Biodiversity



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Abstract The origin of most reef biodiversity of the southwestern Atlantic Ocean dates back to the Eocene, when the center of diversity of modern reef organisms was in the Tethys Sea, a vast extent of tropical shallow marine habitats situated between the Atlantic and Indian oceans. Following the closure of the Tethys Sea, the Atlantic reef biodiversity became increasingly isolated from the world's centers of biodiversity (*i.e.* tropical Indo-Pacific). Moderate rates of origination and extinction shaped endemic lineages and a lower diversity of species compared with the Indo-Pacific. Within the Atlantic, the Brazilian Province is characterized by high endemism and by the presence of a secondary center of biodiversity, driven by a combination of isolation, distinct ecological conditions, and the overlap of tropical and subtropical species. Many evolutionary processes shape the current distribution of species along the coast and in offshore areas such as seamounts and oceanic islands. The taxonomic and functional structure of reef fishes and benthic organisms in the Brazilian Province are related to both historical events and environmental factors, and changes considerably along its latitudinal extent. Today, increased and disordered human development, associated with inadequate conservation measures, is quickly

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threatening millions of years of eco-evolutionary processes responsible for the origin of this unique biodiversity.

Keywords Brazilian Province · Reef fish · Corals · Conservation · Distribution · Evolution

3.1 Introduction

The biodiversity associated with reef environments has a long and turbulent evolutionary history marked by shifts in global geological and climatic events. In our current geological time, shallow coral reefs exhibit the highest levels of species diversity among all marine ecosystems (Roberts et al. 2002; Tittensor et al. 2010), and biodiversity in marginal and mesophotic reefs is mostly derived from shallow coral ecosystems (Bellwood and Wainwright 2002; Tornabene et al. 2016). Most modern reef fish families originated during the Eocene, 56 to 33.9 million years ago (mya) (Bellwood et al. 2017). During that time, the center of marine diversity was the Tethys Sea, a shallow water marine seaway connecting the Atlantic and Indian oceans, where Europe and the Mediterranean Sea are today (Bellwood and Wainwright 2002; Stanley 2003; Floeter et al. 2008). However, analyses comparing the fossil record and extant species reveal many differences between the composition of the Eocene fauna and modern fish and coral assemblages (Bellwood et al. 2017). Many lineages that were widespread in the past went extinct, while others diversified and evolved into Atlantic and Indo-Pacific endemics (Stanley 2003; Siqueira et al. 2019).

The Oligocene (33.9 to 23 mya) and Miocene (23 to 5.3 mya) were marked by the origin and initial diversification of reef fish genera and coral groups that dominate modern reef assemblages (Stanley 2003; Bellwood et al. 2017). During this period, Africa collided with Eurasia, and the Tethys Sea closed. The center of diversity thus migrated from the Tethys to the Indo-west Pacific Region, where it is located today, further from the Atlantic Ocean (Renema et al. 2008; Leprieur et al. 2016), with secondary coral diversity centers found in the Red Sea and in Northern Madagascar (Veron et al. 2015). During that time, innovations in feeding strategies and changes in the trophic structure of fish communities prompted more complex fish–reef interactions, and adaptations to new habitats had a pivotal role in shaping fish diversity (Bellwood et al. 2017; Siqueira et al. 2020).

During the past five million years, diversification rates, strongly influenced by sea-level driven vicariant events, peaked both for fishes and corals, resulting in phylogenetic signatures as evident as strong variation in fish colors (Bellwood et al. 2017; Pinheiro et al. 2017; Hemingson et al. 2018), and as cryptic as molecular differences in morphologically identical coral species (Nunes et al. 2008, 2011). Today, reefs are marked by an astonishing diversity of conspicuous fish and coral families, many of which have global distributions, such as Labridae, Pomacentridae, and Chaetodontidae for fish, and Faviidae, Poritidae, and Caryophyllidae for

corals. These numerous reef organisms generate and occupy many niches, delivering a great diversity of ecosystem functions and services that directly and indirectly benefit humankind (Bellwood et al. 2017).

3.2 Historical Biogeography of the Reef Biodiversity in the Atlantic Ocean

Scleractinian corals started flourishing and building reef-like structures in the Eocene, after surviving through the K/T mass extinction (66 mya), likely using several refugia, and a Paleocene characterized by low coral diversity, paucity of tropical reefs and little carbonate accretion (Stanley 2003). Some modern reef fish lineages also originated in the Eocene Tethys, including ancestors of Labridae and damselfishes (Cowman and Bellwood 2013). These lineages showed little diversification along the Oligocene, and with the Atlantic becoming isolated by the movements of tectonic plates and the migration of the center of diversity towards the Indo-Pacific, few lineages were added by migration (Cowman and Bellwood 2013). During that time, the tropical Eastern Pacific was connected with the Atlantic in the Caribbean region, but reduced exchange of lineages between these provinces is reported (Cowman and Bellwood 2013; Cowman et al. 2017).

In the Miocene, a high diversification of modern lineages was observed worldwide, including a higher exchange of fish lineages between the Atlantic and tropical Eastern Pacific (TEP). The Miocene was characterized by the uplift of the Isthmus of Suez, which created a hard-biogeographic barrier separating tropical faunas of the Red Sea and Mediterranean. During this time, the Atlantic reef fish fauna experienced a strong reduction in diversity and turnover of its functional richness compared to the ancestral Tethyan trait space (Siqueira et al. 2019). Some lineages that adapted and diversified in the Atlantic and TEP include the genera *Anisotremus*, *Haemulon*, *Halichoeres*, and *Holacanthus*, many of them diverging between the Atlantic and TEP lineages after the closure of the Isthmus of Panama (Bernardi et al. 2008; Floeter et al. 2008; Rocha et al. 2008). The biogeographic barriers from the Miocene are linked to the origin of the coral genus *Mussismilia*, which was previously widely distributed in the Atlantic and is now a relict paleo-endemic, restricted to the Brazilian coast (Nunes et al. 2008). After the closure of the Tethys Sea, lineages that invaded the Atlantic in the Miocene came from the Indian Ocean, crossing through the southern African coast, and from the TEP, (Cowman and Bellwood 2013).

Overall species richness, nonetheless, has remained lower in the Atlantic and TEP compared to the Indo-Pacific, especially due to reduced immigration potential and high faunal turnover led by increased rates of lineage extinction (Budd 2000). Relict reef fishes and higher genetic diversity of endemic corals found in oceanic islands, identified as sources to coastal populations, are evidence of lineage extinctions along the continental margin of the Southwestern Atlantic (Pinheiro et al.

2017; Peluso et al. 2018). The closure of the Isthmus of Panama during the Pliocene completely isolated the Atlantic from the tropical Eastern Pacific, promoting vicariant events that split lineages of many families, such as Chaetodontidae, Gobiesocidae, Haemulidae, Labridae, Lutjanidae, Pomacanthidae, Pomacentridae, among others (Lessios 2008). Still in the Pliocene, and during the Pleistocene, rare events of migration from the Indian Ocean via southern Africa were capable of colonizing Atlantic provinces. These events are constrained due to the increasing strength of the biogeographic barrier formed by the cold-water upwelling off southwestern Africa (Rocha et al. 2005a). These colonization events occurred with contributions of the Agulhas Leakage, where Agulhas Rings containing warm Indian Ocean waters enter the Atlantic and join the South Atlantic Gyre. This process is suggested to have contributed to the colonization of the Eastern Atlantic by lineages of *Chromis* and *Lethrinus* (Floeter et al. 2008), and possibly also *Prionurus* and *Plectorhinchus*. *Centropyge* and *Gnatholepis* lineages found in the Western Atlantic and Mid-Atlantic Ridge, seem to have invaded the Atlantic even more recently (Rocha et al. 2005a; Bowen et al. 2006). Maps presenting the main routes of colonization over time and possible evolutionary scenarios are provided in Fig. 3.1.

3.3 Biogeographic Barriers and the Origin of Southwestern Atlantic Endemics

The modern lineages that evolved in the Atlantic diversified between and within biogeographical provinces. Allopatric speciation, one of the most common drivers of evolution in the terrestrial realm, is also driving diversification between biogeographic provinces in the Atlantic. A classic example is provided by the Amazon River discharge of freshwater and sediments, the greatest in the world, which has its origin around 10 mya, corresponding with the uplift of the Andes. The Amazon River discharge is considered a soft barrier, stronger during Ice Ages when the sea level is lower and the extensive continental shelf exposed, leaving little habitat available for migration between provinces (Rocha 2003; Nunes et al. 2011; Araujo et al. 2022) (Fig. 3.2). During high sea-level times, like today, an extensive mesophotic reef is present under the plume of the Amazon River, which can serve as a corridor for reef species able to live in these deeper habitats and conditions (Rocha et al. 2002; Rocha 2003; Nunes et al. 2009; Moura et al. 2016; Francini-Filho et al. 2018) (Fig. 3.2). Consequently, many species have crossed this barrier in both directions. However, speciation occurs mainly in small fishes and those that live in shallow waters (Floeter and Gasparini 2001; Rocha et al. 2002; Araujo et al. 2022; Pinheiro et al. 2018), as they cannot migrate under the Amazon plume and their colonization depends on stochastic events. Some examples of Brazilian fishes that share Caribbean sister species or clades include the genus *Acanthurus*, *Acyrtus*, *Bathygobius*, *Elacatinus*, *Gramma*, *Halichoeres*, *Malacoctenus*, *Opistognathus*, *Scarus*, *Sparisoma*, *Thalassoma*, among many others, in addition to corals within

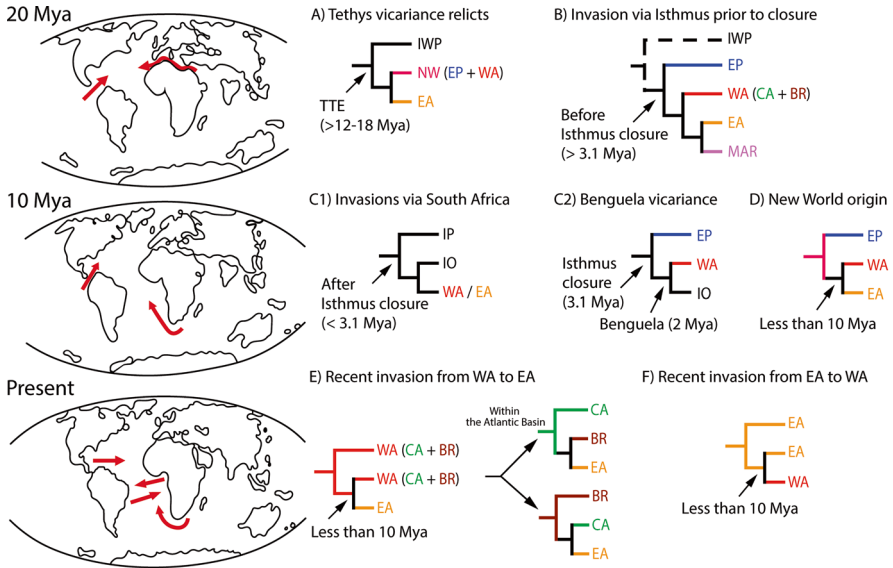


Fig. 3.1 Main routes (red arrows) of colonization over time (20 Million years ago—Mya, 10 Mya, and present) and possible evolutionary scenarios for Atlantic reef fish species. (A) Tethys vicariance relicts, (B) Invasion via Isthmus prior to closure, (C1) Invasions via South Africa, (C2) Benguela vicariance, (D) New World origin, (E) Recent invasion from Western Atlantic (WA) to Eastern Atlantic (EA), (F) Recent invasion from EA to WA. Different colours represent geographical marine areas: black: IWP Indo-West Pacific, IP Indo-Pacific, IO Indian Ocean, magenta: NW New World, blue: EP Eastern Pacific, red: WA Western Atlantic, orange: EA Eastern Atlantic, green: CA Caribbean, brown: BR Brazil, pink: MAR Middle Atlantic Ridge. (Maps adapted from Prof. Larry Braile (available at <http://web.ics.purdue.edu/~braile>). Evolutionary scenarios adapted from Floeter et al. (2008))

the genus *Favia* (*Favia gravida* in Brazil and *Favia fragum* in the Caribbean; see Nunes et al. 2008) (Fig. 3.3).

Species with great dispersal capacity are able to cross the Atlantic and have the chance to colonize new provinces (Nunes et al. 2008, 2009, 2011). Some ecological characteristics are good predictors of species that maintain their distribution in both Eastern and Western Atlantic, such as large body size and the ability to raft with flotsam for fish (Luiz et al. 2012), and the reproductive system in corals (*i.e.* brooders or spawners; Nunes et al. 2011). Other species cross barriers only very rarely, and the lack of connection causes them to evolve in different lineages. For instance, Brazilian species that share closely-related species with the Eastern Atlantic include *Clepticus brasiliensis* (Beldade et al. 2009), *Scartella* aff. *cristata* (Araújo et al. 2020) and *Stegastes fuscus* (Tang et al. 2021) (Fig. 3.4). Others, however, arrived in Brazilian waters more recently, being able to establish populations, as *Chromis limbata* (Anderson et al. 2017, 2020), or stay rare as vagrants, such as *Acanthurus monroviae* (Luiz et al. 2010) and *Heniochus acuminatus* (Luiz et al. 2014).

Species diversification (cladogenesis) within the southwestern Atlantic has been suggested to occur by a variety of speciation processes. The Brazilian Province

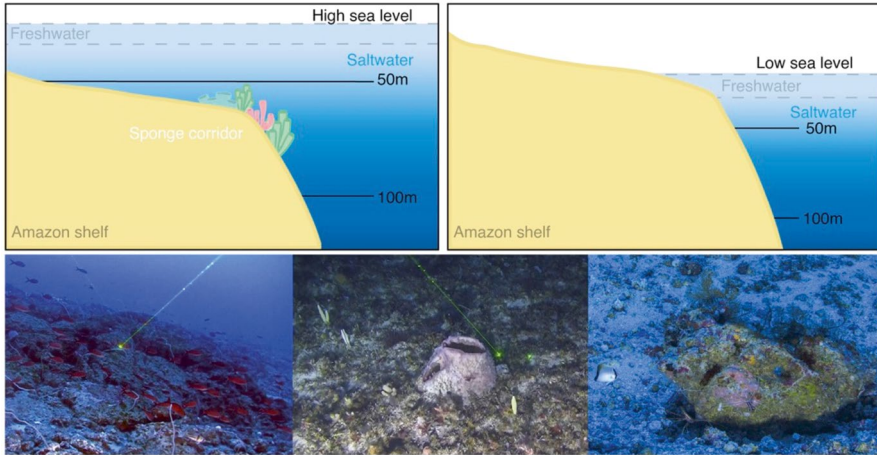


Fig. 3.2 The effect of sea-level fluctuations on the soft biogeographic barrier of the Amazon River discharge. During high sea-level periods (above-left), as today, a mesophotic ecosystem, known as Great Amazon Reefs (photos below), is extensive over the continental shelf, acting as a corridor for reef fish species and other marine organisms. However, this ecosystem is constrained in the sheer slopes and walls during periods of low-stand sea-levels (above-right), which decreases its corridor effect. (Schematic figure adapted from Rocha (2003). Photos by R.B. Francini-Filho)

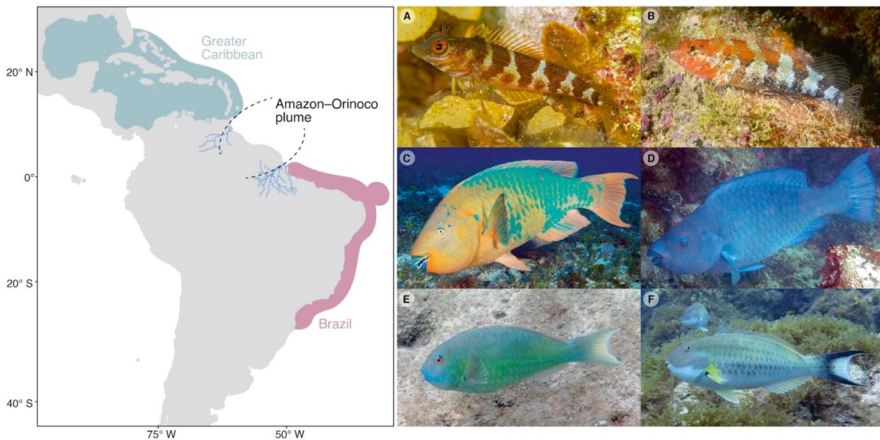


Fig. 3.3 Amazon-Orinoco biogeographical barrier between the Greater Caribbean and the Brazilian Province. In the right, examples of sister fish species found in Brazilian reefs (right bar) and Caribbean (left bar): (a) *Malacoctenus triangulatus*, (b) *Malacoctenus zaluari*, (c) *Scarus guacamaia*, (d) *Scarus trispinosus*, (e) *Sparisoma rubripinne*, and (f) *Sparisoma axillare*. (Photos by (a) F. Krasovec, (b) J.P. Krajewski, (c) J. Lyle, (d) C. Sampaio, (e) and (f) by S.R. Floeter)

harbors a center of diversity in its eastern coast, presenting a high number of endemic species that is not shared with the north-northeastern region (Pinheiro et al. 2018). The eastern coast presents a zoogeographical boundary between tropical and subtropical ecosystems (Pinheiro et al. 2015), and parapatric speciation has been suggested to explain the evolution of endemic species predominantly found in

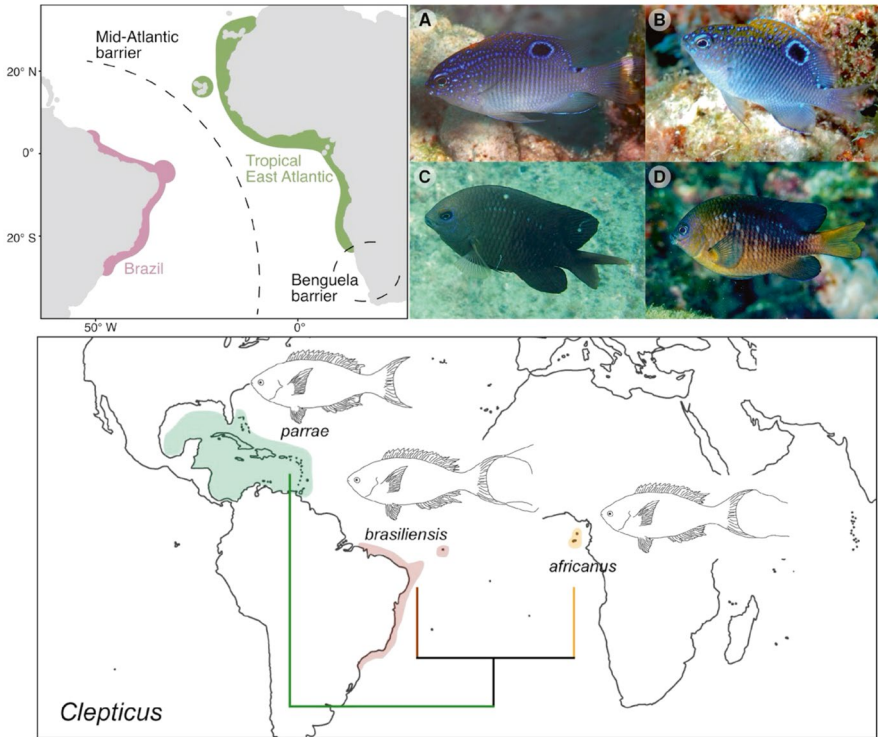


Fig. 3.4 Biogeographical barrier between Brazil and the Tropical Eastern Atlantic. A closely-related damselfish species found in Brazilian and Eastern Atlantic reefs: (a) *Stegastes fuscus* juvenile, (b) *Stegastes imbricatus* juvenile, (c) *Stegastes fuscus* adult, and (d) *Stegastes imbricatus* adult. Below, the phylogeny of the *Clepticus* genus, showing closely-related species occurring in the Caribbean region (*C. parrae*), Brazilian Coast (*C. brasiliensis*) and Sao Tome and Principe Island—Tropical East Atlantic (*C. africanus*). (Photos by (a) O.J. Luiz, (c) S.R. Floeter, (b) and (d) L.A. Rocha)

subtropical waters, potentially involving reef species within the genera *Gobiosoma*, *Opistognathus*, *Paraclinus*, *Serranus*, *Sparisoma* (Fig. 3.5), and the soft-bottom *Macrodon* (Santos et al. 2006; Pinheiro et al. 2018). However, vicariance is also important. The large São Francisco River discharge, associated with the split of the Brazil Current from the South Equatorial Current, is also suggested to influence reef fish biogeography and the genetic structure of marine populations in Brazil (Cunha et al. 2014; Pinheiro et al. 2018). Hydrocorals within the genus *Millepora* are an interesting example comprising four species in the Western Atlantic: *M. alcicornis*, broadly distributed in the tropical Atlantic, the Brazilian endemics *M. brasiliensis* and *M. nitida*, which occur north and south of the São Francisco river, respectively, and *M. laborelli* restricted to a small area in northern Brazil (Souza et al. 2017) (Figs. 3.5 and 3.6); these patterns highlight the importance of diversification within the Southwestern Atlantic.

Antitropical species, such as *Mycteroperca microlepis*, *Chromis flavicauda* and *Halichoeres sazimai*, probably presented a wider distribution during Ice Ages,

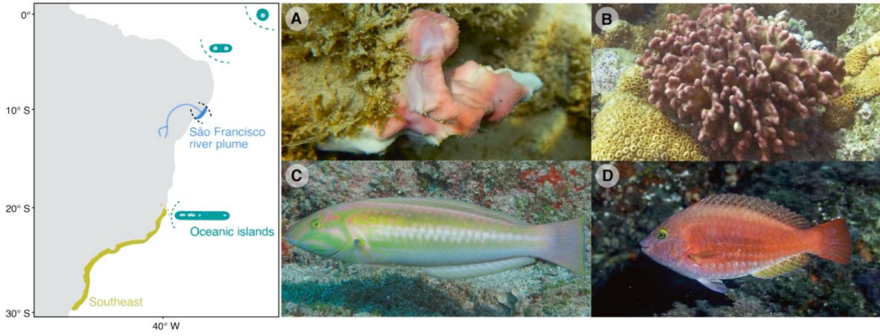


Fig. 3.5 Diversification within the Southwestern Atlantic. São Francisco River as a vicariant barrier, as for the hydrocoral species: (a) *Millepora braziliensis* (occurring in the north) and (b) *Millepora nitida* (occurring in the south); Speciation in peripheral oceanic islands: (c) *Halichoeres rubrovirens*; and allopatric speciation with possible extinction in the hump of Brazil: (d) *Sparisoma tuiupiranga*. (Photos by (a) E.A. Vieira, (b) R.B. Francini-Filho, (c) H.T. Pinheiro, and (d) J.P. Krajewski)

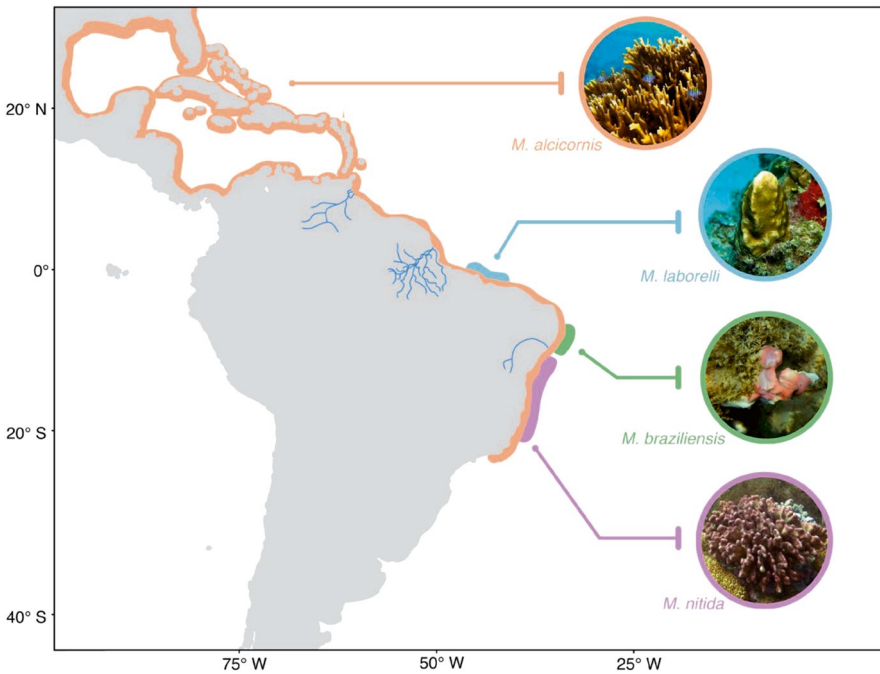


Fig. 3.6 Diversification and distribution of *Millepora* species in the Western Atlantic. *Millepora alcornis* is widely distributed in the tropical Atlantic. The endemic *M. laborelli* is restricted to a small area in northern Brazil, and *M. braziliensis* and *M. nitida* which occur in the north and the south of the São Francisco River, respectively. (Photos by J. Bleuel, N. Roos, E.A. Vieira, and R.B. Francini-Filho)

evolving in isolation with the expansion of warm coastal waters during interglacial times. Moreover, vicariance is directly related to allopatric speciation in the Vitória-Trindade Chain (VTC) (Pinheiro et al. 2017). During the Pleistocene, lowstand sea-levels exposed deep seamounts, allowing weakly dispersing fishes to colonize remote islands via a stepping stones process. Sea level rise isolated these species, driving speciation (Pinheiro et al. 2017). Interestingly, low sea-level during the Last Glacial Maximum (~30,000–19,000 years ago) exposed most of the continental shelf, constraining coral populations to a much narrower area (e.g. for *Mussismilia braziliensis*; see Menezes et al. 2020) and seamounts (e.g. *Mussismilia hispida* see Peluso et al. 2018). During that time, oceanic locations like seamounts may have acted as refugia for coral populations, subsequently colonizing coastal areas as sea-level rose to current levels (Peluso et al. 2018).

Oceanic islands shelter 32% of the Brazilian endemic reef fishes, and the Saint Peter and Saint Paul's Archipelago (SPSPA), situated 1100 km off the northeastern Brazilian coast, presents the greatest relative endemism level of the province (Pinheiro et al. 2018). With one of the lowest biodiversity levels of shorefishes (86 species), SPSPA endemism reaches 9.3% (8 species), however, considering additional endemic species shared with other oceanic islands, its endemic fauna increases to 20.9% (Pinheiro et al. 2020). This high level of endemism is suggested to be related to the process of peripatric speciation, in which speciation of an isolated peripheral population occurs.

Ecological speciation may occur in any geographical context, driven by adaptations to different habitats, food, mating options, and among other biological factors. In Atlantic coral reefs, this process has been suggested to drive speciation in *Haemulon*, *Halichoeres*, *Hypoplectrus* and *Grama* species (Bowen et al. 2013), most related to sexual and habitat selection. In Brazil, ecological speciation is suggested to drive the boundaries between *Halichoeres radiatus* and *Halichoeres brasiliensis*, found respectively in insular and mainland tropical waters of northeastern Brazil (Rocha et al. 2005b).

3.4 Composition and Distribution of Fishes and Corals

The Southwestern Atlantic shelters over 730 fish species associated with reef environments, of which 405 species are considered reef residents or strictly reef species (Pinheiro et al. 2018). Overall, when all species associated with reef environments are considered, Carangidae is the richest family recorded, with 35 species, followed by Gobiidae (31 species), Epinephelidae (25), Serranidae (25), Scorpaenidae (23), Labridae (21), Haemulidae (19), Muraenidae (19), and Ophichthidae (19). According to Morais et al. (2017), the families with highest biomass in the Brazilian Province are Haemulidae, Balistidae, Kyphosidae, Epinephelidae, Acanthuridae, Labridae, Holocentridae, Pomacentridae, Lutjanidae, Pomacanthidae, and Carangidae. Regarding the most species-rich genera, among all associated with reef environments, *Scorpaena* (14 species), *Carcharhinus* (11), *Haemulon* (10), *Lutjanus*

(9), *Serranus* (9), *Gymnothorax* (8), *Halichoeres* (8) and *Anchoa* (8) are the most important in the SWA (Pinheiro et al. 2018).

In terms of trophic structure of SWA reefs, mobile invertebrate feeders are the most important guild in richness (46%) (Pinheiro et al. 2018) and biomass (lower-level carnivores: 44%) (Morais et al. 2017). Macrocarnivores, although being the second richest trophic guild in the SWA with 27% of the reef fish fauna (Pinheiro et al. 2018), constituted only a small fraction of the standing biomass of most localities in the Brazilian Province (Morais et al. 2017). Species richness is evenly distributed through size classes (Pinheiro et al. 2018), however, most of the biomass is represented by fishes between 10 and 30 cm (Morais et al. 2017).

Concerning the geographic distribution of reef fishes occurring in the SWA, most species are widely distributed in the western Atlantic (46%), transatlantic and inter-oceanic species account for 20 and 6%, respectively, and SWA endemics constitute 27% of the resident reef fish fauna (Pinheiro et al. 2018) (Fig. 3.7). Another 49 endemic species are benthic-occasional and 14 are pelagic-occasional species, totaling 174 SWA endemic fishes (24% of the total species) associated with reef environments. Endemics are distributed in 45 families, in which Gobiidae and Labridae are the most species-rich families (15 species each), followed by Labrisomidae (10), Serranidae (10), Pomacentridae (8) and Blenniidae (8). Most endemics are small (0–10 cm, 42%) or medium-sized (10–25 cm, 28%) fishes, have sedentary (55%) and roving (39%) mobility, and none display rafting dispersal abilities (Pinheiro et al. 2018) (Fig. 3.7).

Coral fauna in the SWA is considered impoverished but highly endemic (~31%; Leão et al. 2016). The SWA coral biodiversity comprises 8 families of zooxanthellate scleractinian corals (Agariciidae, Astrocoeniidae, Faviidae, Meandrinidae, Montastraeidae, Pocilloporidae, Poritidae and Siderastreaeidae), 11 genera (*Agaricia*, *Stephanocoenia*, *Favia*, *Mussismilia*, *Scolymia*, *Meandrina*, *Montastraea*, *Madracis*, *Porites* and *Siderastrea*) and 16 species of which 5 are endemic (*Favia leptophylla*, *Mussismilia braziliensis*, *M. harttii*, *M. hispida* and *Siderastrea stellata*; despite recent debate on the endemic status of the last one, see Garcia et al. 2017). In addition to scleractinian corals, SWA shallow reefs are also home to four species of hydrocorals (family Milleporidae), three of which are endemic (*Millepora braziliensis*, *M. nitida* and *M. laborelli*) (Fig. 3.6). This high endemism is related to large-scale barriers, such as the Amazon River discharge and the large distance that separates the eastern and western Atlantic, but also to meso-scale barriers, such as the São Francisco River (Nunes et al. 2008, 2009, 2011; Souza et al. 2017).

Within the SWA, a recent biogeographic analysis based on reef fish showed six sub-provinces (Fig. 8; Pinheiro et al. 2018): (1) St. Peter and St. Paul's Archipelago; (2) Fernando de Noronha Archipelago and Rocas Atoll; (3) Vitória-Trindade Chain (seamounts and islands) (VTC); (4) north and northeast Brazil; (5) east and southeast Brazil; and (6) Uruguay and Argentina (Argentinian Province). The greatest species richness is found in the east–southeastern Brazil (326 species), followed by north–northeastern Brazilian coast (259 species) and VTC (186 species) (Fig. 3.8). While the north–northeast subprovince shares most of its reef fish fauna (95%) with the east–southeast subprovince, over a quarter of the species found in the latter do

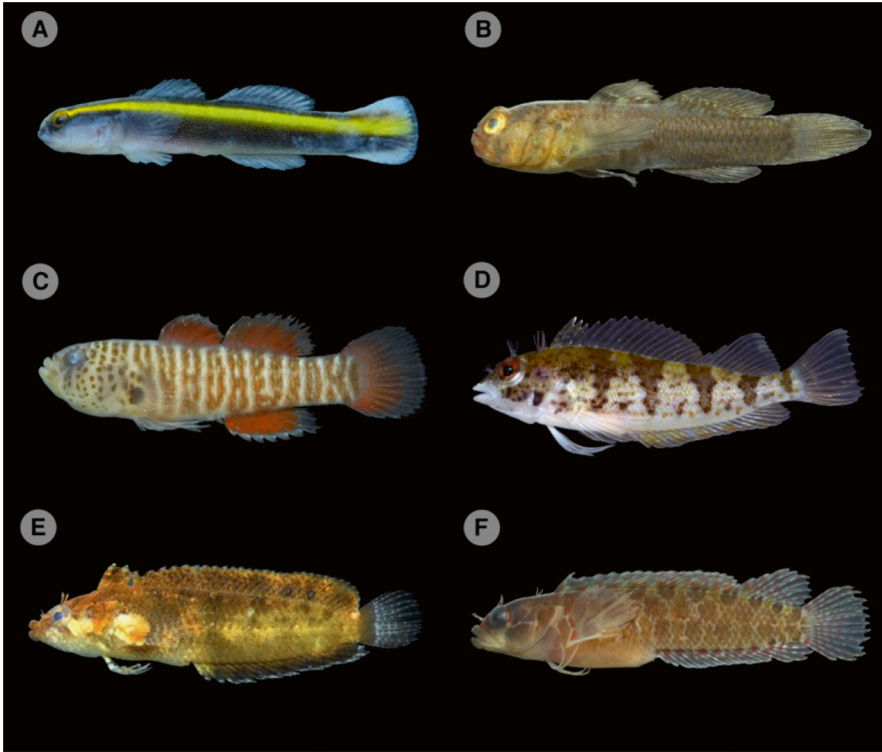


Fig. 3.7 Most of the endemic species in the Brazilian Province have small body size and sedentary mobility: (a) *Elacatinus figaro*, (b) *Gobiosoma alfie*, (c) *Lythrypnus brasiliensis*, (d) *Malacoctenus zaluari*, (f) *Paraclinus arcanus*, and (e) *Starksia brasiliensis*. (Photos by R.M. Macieira)

not occur in the former. Both sub-provinces in the mainland Brazilian coast share about 50% of their species with their adjacent oceanic islands.

When it comes to corals, there are two main diversity centers based on species composition: (1) eastern Brazil, encompassing the Arolhos Bank and the states of Bahia and Espírito Santo; and (2) Northeastern Brazil, encompassing coastal areas between the states of Rio Grande do Norte and Alagoas, in addition to the oceanic islands of Fernando de Noronha and Rocas Atoll. Southern subtropical areas, like the state of São Paulo, and the remote locations, like St. Peter and St. Paul's Archipelago, have the lowest coral richness, and share widely distributed species such as *Madracis decactis*.

The Brazilian oceanic islands harbour 36 resident endemic reef fishes, while 40 are restricted to the continental shelf and slope, 28 occur in both Brazilian continental and oceanic subprovinces, and seven reach the Argentinian Province. The east-southeastern coast shelters the highest number of SWA endemic reef fish species (71 species), 26 of which are not recorded in the north-northeast coast, and 16 are exclusive to this subprovince. The north-northeastern coast shelters 48 SWA

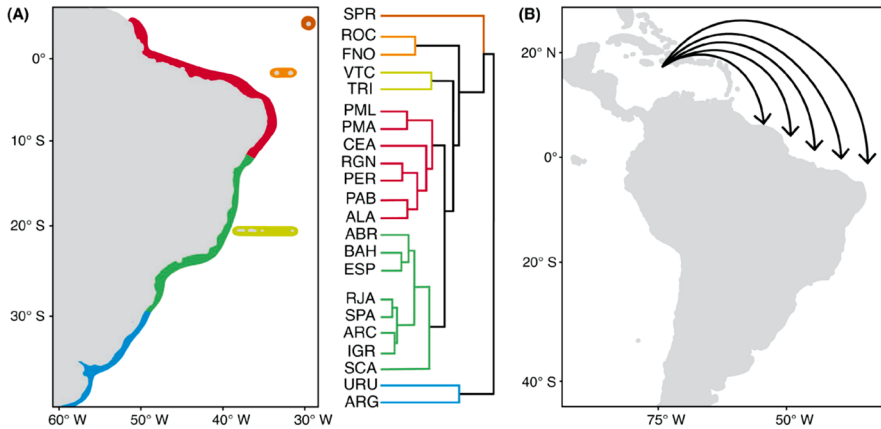


Fig. 3.8 (a) Southwestern Atlantic sub-provinces of reef fish species. For more details about the cluster and methods implemented, see Pinheiro et al. (2018). SPR St. Peter and St. Paul's Rocks, ROC Rocas Atoll, FNO Fernando de Noronha Archipelago, VTC Vitória-Trindade Chain, TRI Trindade-Martin Vaz insular complex, PML Parcel de Manuel Luís, PMA states of Pará and Maranhão, CEA state of Ceará, RGN state of Rio Grande do Norte, PER state of Pernambuco, PAB state of Paraíba, ALA state of Alagoas, ABR Abrolhos shelf, BAH state of Bahia, ESP state of Espírito Santo, RJA state of Rio de Janeiro, SPA state of São Paulo, ARC region of Arraial do Cabo, IGR Ilha Grande Bay, SCA state of Santa Catarina, URU Uruguay, ARG Argentina. (b) The reef fish composition in the Southwestern Atlantic is partially shaped by the target-area-distance model, also known as the propagule rain hypothesis, in which regions with similar coastline extensions and distance from the Caribbean (the biodiversity hotspot in the Atlantic) would have similar pool of colonist species, presenting low beta diversity. (Maps and cluster adapted from Pinheiro et al. (2018))

endemics, however, it displays one of the lowest local endemism among all SWA subprovinces (two species). St. Peter and St. Paul's Rocks has the highest local percent endemism level (9.3%, or 20.9% including oceanic island endemics; Pinheiro et al. 2020) in the SWA, followed by the VTC subprovince (6%) (Pinheiro et al. 2018). Differently from fishes, there are no coral species endemic to the oceanic islands. An interesting endemism case is that of the hydrocoral *Millepora laborelli* restricted to Parcel Manoel Luis and adjacent areas in the state of Maranhão, Northern Brazil (Souza et al. 2017).

3.5 Macroecological Patterns of Reef Fish Biodiversity

The taxonomic and functional structure of Atlantic fish assemblages are shaped both by historical events and environmental factors (Bender et al. 2013b). The proportion of species richness in fish families reveals a strong imprint of historical events that delineated reef fish biogeography. Nevertheless, proportions of species in different body-size classes and trophic groups respond to isolation from the center of biodiversity, and reef complexity. The number of species and relative

abundance of fishes relying on relatively low-quality food (algae, detritus and sessile invertebrates) increase towards the tropics (Floeter et al. 2004). This pattern is likely related to algal productivity and rate of detritus decomposition. Moreover, these feeding strategies are a relatively recent evolutionary phenomenon, and a higher diversification of these groups in diversity hotspots helps explain their predominance in the tropics (Siqueira et al. 2020). Biogenic Caribbean reefs are also composed mainly by small species, a pattern driven largely by environmental factors, such as temperature and habitat complexity (Bender et al. 2013b). Peripheral provinces, which include Brazil, are dominated by larger species with diverse diets, which is related to dispersal abilities that allows them to migrate out of regional diversity hotspots.

Therefore, the Southwestern Atlantic is part of a biogeographic continuum that extends along the whole Western Atlantic. The biodiversity of the Brazilian Province is associated with the target-area-distance model, which is related to the propagule rain hypothesis (Pinheiro et al. 2018) (Fig. 3.8b). According to this hypothesis, the Caribbean as the center of diversity in the Atlantic, is the putative main source of propagules, and SWA regions with similar coastline extension and distance from the source (Caribbean) would have a similar chance to share the same pool of colonists, presenting low beta diversity. Indeed, many species widespread in the Caribbean occur in the north-northeastern Brazilian coast or in the northern oceanic islands, such as *Chromis scottii*, *Haemulon chrysargyreum*, *Haemulon melanurum*, *Haemulon vittata*, *Halichoeres radiatus* and *Lachnolaimus maximus* (Pinheiro et al. 2018). Conversely, the southeastern Brazilian coast presents many endemic fishes only shared among subtropical reefs, what increases dissimilarity from northeastern Brazil and the Caribbean, and decreases beta diversity among neighboring regions. The region where tropical and subtropical faunas overlap (~18–22 degrees latitude) hosts the highest richness of reef fishes and benthic organisms along the Brazilian coast (Aued et al. 2018; Pinheiro et al. 2018). Such a pattern does not conform with the classic latitudinal gradient of biodiversity.

This biogeographic gradient along the latitudinal extent also changes the trophic structure of fish assemblages (Fig. 3.9). While roving herbivores, such as parrotfishes (Scarinae) and surgeonfishes (Acanthuridae), are more abundant at low latitudes, browsing herbivores of the family Kyphosidae increase in relative importance with latitude (Ferreira et al. 2004). Omnivores, piscivores, and carnivores are more important in subtropical reefs (Fig. 3.9), while planktivores are more abundant in oceanic islands (Ferreira et al. 2004). However, snappers (Lutjanidae) present higher abundance and biomass in tropical waters (Ferreira et al. 2004; Morais et al. 2017). Such trophic structure is reflected in the intensity and composition of fish feeding pressure on the benthos, which is higher and dominated by roving herbivores (mostly Acanthurids) within the tropical region (from Parcel Manuel Luiz at 0° to Rio de Janeiro at 23°S). In comparison, subtropical reefs (e.g. Santa Catarina at 27°S) present about half the feeding pressure of tropical reefs, mostly dominated by omnivorous and invertivorous fishes (families Sparidae and Haemulidae, respectively; Longo et al. 2019). Algal turfs and macroalgae (including crustose coralines) are the dominant components of reef benthic communities throughout the

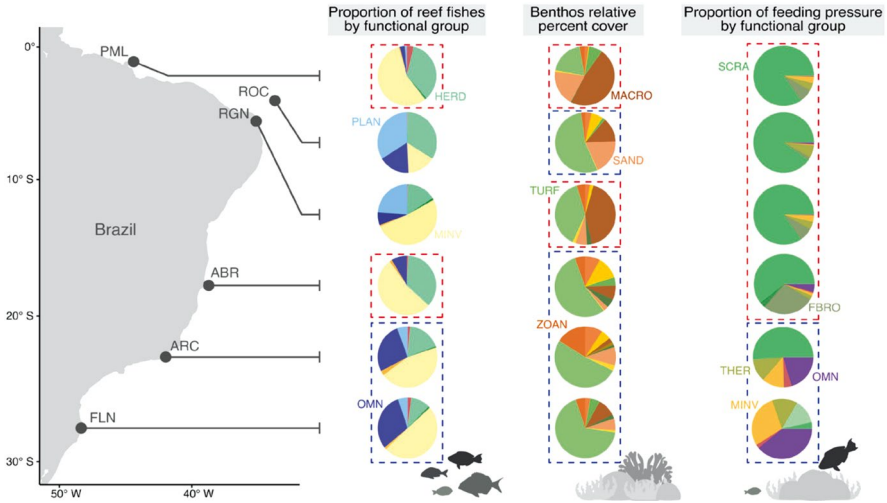


Fig. 3.9 Macroecological patterns of the Southwestern Atlantic reef biodiversity, considering the abundance-based proportion of reef fish functional groups, the relative percent cover of benthos, and the feeding pressure of reef fish functional groups on the benthos. Dashed lines indicate groups revealed by cluster analysis. Main reef fish trophic groups and categories of benthos cover are indicated—for more details please see Morais et al. (2017), Aued et al. (2018), and Longo et al. (2019), from which pie charts were adapted, respectively. Fish functional groups abbreviation: HERD herbivore detritivore, PLAN planktivore, OMN omnivore, SCRA scraper, FBRO fine browser, THER territorial herbivores, MIN mobile invertebrate feeder. Benthos cover abbreviation: MACRO macroalgae, SAND sand, TURF turf algae, ZOAN zoanthid. Abbreviation of the common sites between the three studies: PML Parcel de Manuel Luís, ROC Rocas Atoll, RGN Rio Grande do Norte, ABR Abrolhos shelf, ARC region of Arraial do Cabo, FLN Florianópolis

Brazilian province, but in the tropics, sponges can be abundant in deeper and corals and zoanths in shallower reefs, while in the tropical-subtropical transition zones seaweeds, sponges, and corals share the benthic cover with gorgonids and octo-corals (Aued et al. 2018; Roos et al. 2019).

Brazilian oceanic islands harbor the highest reef fish biomass of the province, followed by other remote and protected sites (Morais et al. 2017). In the oceanic islands, the great biomass is in part explained by the abundance of the black triggerfish *Melichthys niger* particularly in Trindade Island (Pinheiro et al. 2011) and St. Paul's Archipelago (Luiz et al. 2015). At the only atoll in South Atlantic, Rocas Atoll, reef fish biomass is dominated by large predators such as sharks (*Negaprion brevirostris*), snappers (*Lutjanus jocu*), and herbivorous fishes (*Acanthurus* spp.; Longo et al. 2015). Fish feeding pressure at these oceanic islands are mostly related to herbivory by Acanthuridae (Longo et al. 2015) or even by the omnivorous *M. niger* acting as a functional herbivore (Mendes et al. 2019) (Fig. 3.9).

Some ecological traits are associated with endemism and distributional patterns in Brazil (Pinheiro et al. 2018). Most of the Brazilian endemics have small sizes, occur only in shallow waters and are habitat specialists, occurring in few habitats. Conversely, species that occur across all Brazilian regions are mostly habitat

generalists and present a wider depth range. Species restricted to the continental shelf have small sizes, most occur only in shallow waters and are dependent on brackish habitats. Species recorded in oceanic islands show better dispersal potential, as they are positively related to rafting use and large body sizes, but also are habitat generalists and are distributed along great depth ranges, characteristics that influence establishment (Pinheiro et al. 2018; Mazzei et al. 2021).

3.6 Final Remarks: Conservation of Brazilian Reef Biodiversity

Distributed along the tropical and subtropical coasts of a developing nation, Brazilian reefs are threatened by unsustainable human population growth near shore, which leads to increased pollution, habitat degradation, and overfishing (Floeter et al. 2006; Leão et al. 2010; Pinheiro et al. 2019) (Fig. 3.10). Human population density is a predictor of fish biomass and functional dispersion in coastal and oceanic reefs, with high biomass identified for remote locations (*e.g.*, Parcel do Manuel Luís, Maranhão State, reefs distant from the coast at Rio Grande do Norte state, and oceanic islands), or no-entry marine protected areas, such as Alcatrazes (São Paulo State). The impacts imposed by humans to reefs and associated habitats (Vila-Nova et al. 2011) prevent marine populations from recovering from frequent and intense disturbances. As a result, 12.4% ($n = 78$) of the fish species in Brazil are threatened with extinction (Bender et al. 2013a; Pinheiro et al. 2018; Ceretta et al. 2020). Among the threatened fishes, 23% ($n = 18$) are endemic to Brazilian reefs.

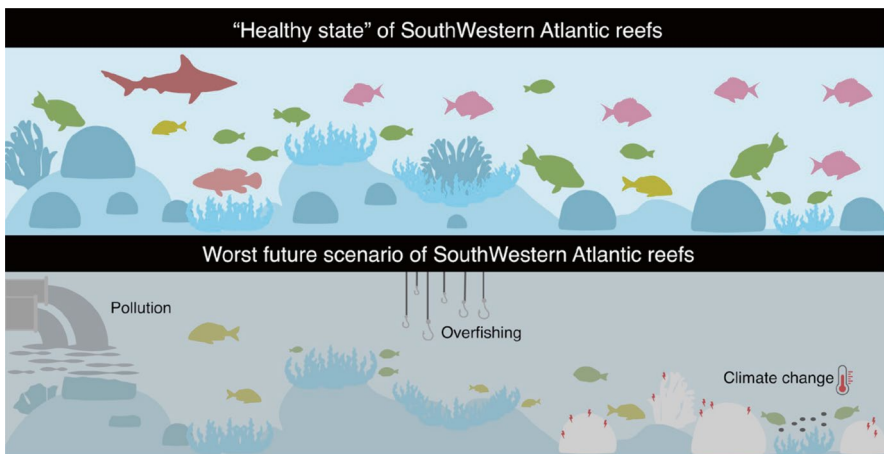


Fig. 3.10 Scenarios of the Brazilian reef biodiversity. Above, a “healthy state” of Brazilian reefs, which presents high endemism level, high abundance of large bodied species, mesopredators, and herbivores. However, currently, Brazilian reefs are threatened by pollution, overfishing and climate change (below), which cause habitat degradation and general biodiversity loss

Different biological and ecological attributes contribute to the extinction vulnerability of species. For Brazilian reef fishes, traits such as large body size, macrocarnivorous diet and high mobility are good predictors of vulnerability to extinction (Bender et al. 2013a; Ceretta et al. 2020). Some species characteristics also interact with specific threats, enhancing their vulnerability. For instance, small-bodied species with complex reproductive strategies are targeted by the ornamental trade (Bender et al. 2013a), and the interaction of both—trait and threat—works as a double jeopardy (Hawkins et al. 2000). Traits of the coral fauna are highly conserved and present limited redundancy, particularly in areas of lower richness such as the Brazilian coast, enhancing their vulnerability to anthropogenic stressors (McWilliam et al. 2018). This is particularly true for functions such as carbonate accretion and structural complexity that can scale-up and affect the entire reef ecosystem.

Along the Brazilian coast, São Paulo and Espírito Santo states present the highest proportion of threatened reef fish species (Ceretta et al. 2020). Moreover, an astonishing marine biodiversity is found in the region that lies between Espírito Santo and Bahia. The coast of Espírito Santo can be considered a hotspot for endemic, threatened and targeted reef fish species (Vila-Nova et al. 2014). However, Vila-Nova et al. (2014) have also shown that this region is the least protected along the Brazilian coast. Unfortunately, the current network of Brazilian Marine Protected Areas does not protect hotspots of reef fish biodiversity (Vila-Nova et al. 2014). More recently, Magris et al. (2021) have combined the distribution of human-derived impacts, habitat types and threatened species, including reef habitats and species, into a large-scale spatial prioritization activity. This study identified coastal areas as high priorities for marine conservation in Brazil, and pointed to industrial fisheries, land-based activities, and climate change as the greatest threats to biodiversity.

Despite the great concentration of human threats and impacts on coastal reefs, the unique biodiversity of Brazilian oceanic islands must also be considered in conservation planning and efforts. These isolated sites have remarkable endemism levels (Pinheiro et al. 2018, 2020), which reach the highest proportion in St. Peter and St. Paul's Rocks (9%). In addition to such endemism, these islands have a greater contribution of large-bodied and macrocarnivore species to the composition of fish assemblages (Bender et al. 2013b), and concentrate higher fish biomass relative to the coast (Morais et al. 2017). Therefore, islands are havens of biodiversity in the Anthropocene ocean, which makes them a fisheries target. Recent efforts by the Brazilian Environmental Agency (Ministério do Meio Ambiente) have focused on protecting islands (Giglio et al. 2018), and have helped the country to achieve Aichi's Biodiversity Targets by protecting vast areas of open-ocean. Nevertheless, the islands still need targeted conservation efforts.

Despite being protected on paper, the Brazilian oceanic islands have been impacted by several types of fishing, from spearfishing on Trindade island (Pinheiro and Joyeux 2015; Guabiroba et al. 2020), to the industrial fishing vessels in the remote St. Paul's Rocks (Luiz and Edwards 2011; Giglio et al. 2018). Fishing efforts in these isolated islands have overexploited and threatened local populations of

predators (Pinheiro et al. 2010; Luiz and Edwards 2011), which may cause disruptive ecological cascades and change insular community patterns (Guabiroba et al. 2020), influencing biogeographic inferences.

In addition to local stressors, global climate change can impose significant changes to Brazilian reef biodiversity. Although subject to 50–60% less thermal-stressed events in comparison to the Indo-Pacific and the Caribbean (Mies et al. 2020), coral bleaching and mortality affect the Brazilian reefs (Duarte et al. 2020), and ocean warming should also cause strong ecological changes along the Brazilian coast. Feeding pressure, for instance, can be severely reduced in tropical areas because predicted temperatures are likely to exceed the thermal limit of herbivorous fishes, and these species are likely to shift their distribution southwards (Inagaki et al. 2020), influencing community structure patterns. Similarly, the territorial behavior of the Brazilian endemic and ubiquitous damselfish *Stegastes fuscus* will likely be severely impaired by increasing temperatures (Silva-Pinto et al. 2020). This species has a critical role in shaping benthic communities (Ferreira et al. 1998) and structuring agonistic interactions (Fontoura et al. 2020), and the disruption of these processes can affect reef functioning. Therefore, climate change impacts on Brazilian reefs can go beyond coral bleaching, and although less evident than species extinction, still threaten low-redundant functions and impose severe changes to the reefs and the benefits they currently provide.

In conclusion, Brazilian reefs present a biodiversity that varies along the coastline and among oceanic and remote localities. Species distributions are driven by both ecological and evolutionary processes, shaping singular subprovinces, endemism hotspots and distinct macroecological patterns. However, the increased and disordered human development along the coast, associated with critical gaps in conservation and the global effects of climate change, is increasingly threatening these unique eco-evolutionary processes responsible for the origins of the biodiversity of the Brazilian Province.

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