

South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean

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Abstract

Aim: To present an updated database of fish species recorded on south-western Atlantic reef environments and to explore the ecological drivers of the structure, the latitudinal gradient of biodiversity and the centre of endemism in this peripheral province.

Location: South-western Atlantic (SWA): Brazilian and Argentinian Provinces.

Methods: A database composed of 733 fish species along 23 locations in the SWA (00°55' N to 43°00' S) was compiled based on primary data, literature and museum

records. Cluster and beta diversity analyses were carried out to evaluate faunal overlaps among locations and subprovinces. “Target-area-distance effect” and “stepping stones dispersal” hypotheses for assemblage composition were tested through Mantel tests. Relationships between the distribution patterns and ecological traits of reef fish species were investigated through generalized linear mixed-effect models.

Results: Out of the 733 fish species, 405 are SWA resident reef fishes, of which 111 (27%) are endemics and 78 are threatened with extinction. Cluster analysis detected six subprovinces in the SWA structured following the target-area-distance model, and with no evidence for a latitudinal gradient in diversity. The greatest overall richness and endemic species richness were found in the east-south-eastern region. Depth range, habitat use and body size were the main drivers of SWA reef fish assemblage structure.

Main conclusions: The Brazilian and Argentinian coasts constitute different provinces structured by oceanographic barriers and environmental filters. Similarities among oceanic islands indicate connectivity driven by stochastic and ecological factors. Species richness and endemism indicate that peripheral provinces may also bear centres of origin and biodiversity, patterns driven by parapatric/ecological speciation and the overlap between tropical and subtropical reef fish species. Ecological drivers of reef fish distribution, such as habitat specialization and body size, support hypotheses of speciation in the periphery. New approaches for spatial planning, marine protected areas and off-reserve marine management are essential for the conservation and sustainability of SWA reef fishes.

KEYWORDS

biogeography, conservation, endemism, evolution, periphery, threatened species

1 | INTRODUCTION

Understanding biodiversity and endemism patterns is a central goal in ecology and biogeography, with important implications that range from evolutionary studies to applied conservation (Cowman, 2014; Pinheiro et al., 2017). The assessment of biogeographic patterns depends on sound taxonomic and faunistic databases, yet the south-western Atlantic (SWA) reef-associated fish fauna represented a major gap in the global database until the late 1990's (Floeter & Gasparini, 2000; Floeter et al., 2008; Rocha, 2003). The first efforts to describe and catalogue reef fishes in the SWA date back to the mid-17th century, with the publication of *Historia Naturalis Brasiliae* in 1648, by Willem Piso and George Marcgrave (the latter is the sole author of the natural history chapters). A century and a half later, Marcus Bloch formally described the first Brazilian endemic reef fish, *Labrus brasiliensis* Bloch 1791 (valid as *Halichoeres brasiliensis*), based on Marcgrave's illustrations. Other iconic reef fishes, such as the goliath grouper, *Serranus itajara* Lichtenstein 1822 (now valid as *Epinephelus itajara*), were subsequently described based on the same source.

Descriptions of reef fishes increased in the early 19th Century (Figure 1a), with remarkable contributions by Cuvier and

Valenciennes (1828–1840), who studied specimens confiscated by Napoleon's troops in Portuguese museums (Moura & Lindeman, 2007; Vanzolini, 1996). In the mid-19th century, American and European expeditions to the SWA enabled the discovery and study of more endemic reef fishes, which were described by naturalists such as Louis Agassiz, Charles Hartt and Franz Steindachner (von Spix & Agassiz, 1831; Hartt, 1870; Steindachner, 1878; Figure 1a,b). From the late 19th century onwards, contributions were mostly made by North American naturalists, and the first Brazilian ichthyologists (Figure 1b). However, it was only by the end of the 20th century that Brazilian-led reef ichthyology significantly advanced. The increase in number of local researchers (Figure 1a,b) and the use of SCUBA resulted in a steep increment of descriptions of new species (starting with Moura, 1995), as well as a flourishing expansion of studies focusing on a wide range of themes such as faunistic surveys, natural history, behavioural ecology, ecology and molecular genetics (Figure 1c).

The Brazilian Biogeographic Province, as first proposed by Briggs (1974), has been largely supported for reef fishes and corals with the recent consolidation of species distribution databases for the SWA (Floeter & Gasparini, 2000; Floeter et al., 2001, 2008; Leão, Kikuchi, & Testa, 2003; Rocha, 2003). The Brazilian Province extends from

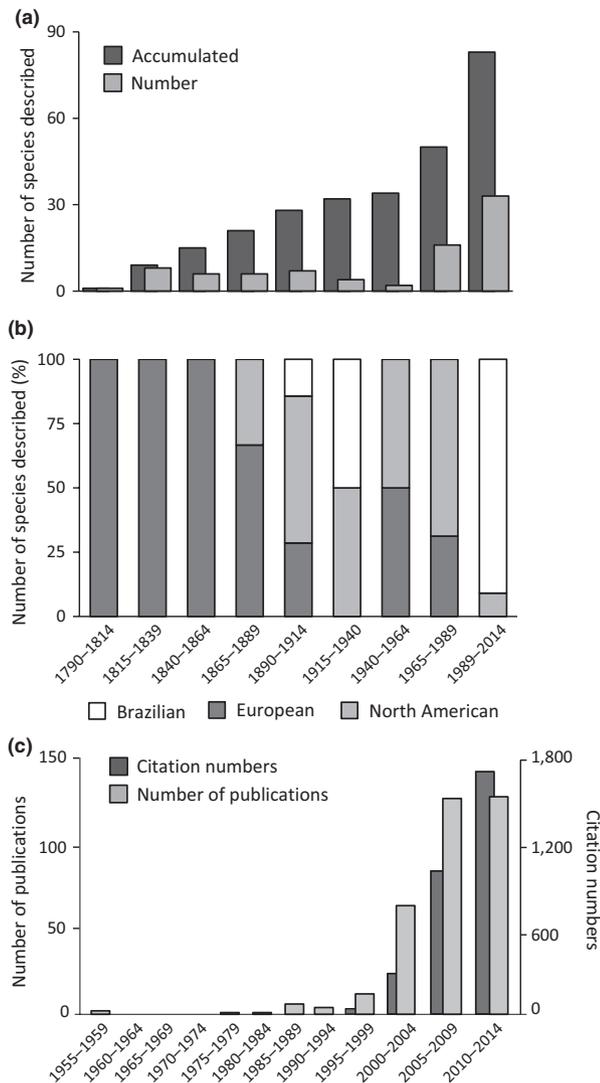


FIGURE 1 (a) Number of Brazilian endemic reef fishes described through the years 1790–2014, (b) the nationality of species' description authors and (c) the number of publications and citations related to the keywords "Brazilian reef fish" until December 2014

the Amazon River mouth (on the equator) to the state of Santa Catarina (29°S), includes oceanic islands as peripheral outposts and is closely related to the Caribbean Province (Floeter et al., 2008; Kulbicki et al., 2013; Reis et al., 2016). Phylogenetic and phylogeographic studies are also increasingly elucidating the origin of the Atlantic and Brazilian reef fish faunas (Cowman & Bellwood, 2013; Floeter et al., 2008; Pinheiro et al., 2017; Robertson, Karg, Moura, Victor, & Bernardi, 2006; Rocha, Robertson, Roman, & Bowen, 2005; Rocha, Rocha, Robertson, & Bowen, 2008). Their origin and evolution are related to the opening and development of the Atlantic Ocean, followed by the closure of the Tethys Sea, the latter constituting a biodiversity "palaeo-hotspot" that connected widespread lineages worldwide until the Oligocene (Cowman & Bellwood, 2013). The isolation of the Atlantic Ocean was followed by high diversification rates (Cowman & Bellwood, 2013). However, increased distance from the Malay Archipelago (the global marine hotspot:

Cowman, 2014; Pellissier et al., 2014), as well as high extinction and faunal turnover rates due to severe environmental changes (caused by the rise of the Isthmus of Panama and glacial periods), kept the Atlantic biodiversity lower than that of the Indo-Pacific (Budd, 2000; Cowman & Bellwood, 2013).

Within the Atlantic, the tropical SWA is partially isolated by three soft barriers: the Amazon Plume to the north, which divides the Brazilian and Caribbean Provinces, the Mid-Atlantic Barrier to the east, which isolates the SWA from the Mid-Atlantic Islands and Africa, and cold waters from upwelling events and the Falklands (Malvinas) current, which blocks the spread of tropical species south of Brazil (Anderson et al., 2015; Luiz et al., 2012; Moura et al., 2016). Such barriers, associated with contrasting selective pressures, have driven the speciation of SWA reef fishes through allopatric and parapatric processes (Joyeux, Floeter, Ferreira, & Gasparini, 2001; Robertson et al., 2006; Rocha, 2003; Rocha, Robertson, Roman et al., 2005). Most Brazilian endemic reef fishes are closely related to Caribbean congeners, but immigration from the eastern Atlantic and the Indian Ocean, as well as speciation at Brazilian oceanic islands, have been important for diversification (Floeter et al., 2008; Pinheiro et al., 2017). Furthermore, the SWA exports biodiversity to the Mid-Atlantic Islands and eastern Atlantic, as well as genetic diversity and taxa to the Caribbean (Beldade et al., 2009; Floeter et al., 2008; Freitas et al., 2014; Rocha et al., 2008) through a biodiversity feedback mechanism (Bowen, Rocha, Toonen, & Karl, 2013).

Despite a substantial increase in knowledge about Atlantic reef fish biogeography and evolution (Floeter et al., 2008), several areas in the SWA remained unknown and poorly studied until recently (Anderson et al., 2015; Freitas & Lotufo, 2014; Pinheiro, Joyeux, & Moura, 2014; Pinheiro, Mazzei et al., 2015). Therefore, several questions on the biogeography and evolutionary processes that shaped the reef fish fauna in the SWA are still unresolved. For instance, the effect of latitudinal gradients, which is mostly negatively correlated to species richness in terrestrial systems (Willig, Kaufmann, & Stevens, 2003), has an important role on the trophic structure of reef fish communities of the SWA (Ferreira, Floeter, Gasparini, Ferreira, & Joyeux, 2004; Floeter, Ferreira, Dominici-Arosemena, & Zalmon, 2004). However, little is known about the effects of latitude on the SWA reef fish diversity *per se*. Moreover, fish characteristics such as large body size, non-reef habitat use and ability to raft with flotsam allow species to cross the main barriers that isolate the SWA (Luiz et al., 2012), but the ecological characteristics that drive composition and endemism along the SWA are still little explored (Bender et al., 2013). The Caribbean is the centre of marine biodiversity in the Atlantic, but the mechanisms through which this centre influences species composition along the SWA are still unknown. Reef fish assemblages along the SWA might be structured by a propagule rain model, where localities closer to the Caribbean and with longer coastlines would have more chances to recruit larvae, and consequently share more species (Fattorini, 2010). On the other hand, assemblages may be organized by a stepping-stone process, where localities that are closer to each other share more species and have similar species composition (Fattorini, 2010).

To better understand the processes shaping patterns of reef fish biodiversity, endemism and distribution in this province, an extensive database of SWA reef fishes was compiled, updating previous databases and improving the resolution on species richness and distribution in the region. The main goal of this study was to address the following questions: (1) What are the main ecological drivers structuring the composition of reef fish assemblages and geographic distribution of species in the SWA? (2) Is there a latitudinal gradient in reef fish biodiversity? and (3) is there a centre of endemism along peripheral provinces?

2 | METHODS

2.1 | Database

The reef fish database was updated from Floeter et al. (2008) and Halpern and Floeter (2008). All fish species (elasmobranchs included) recorded over reef environments (i.e., consolidated bottoms, including rhodolith beds, coral, coralline algae and rocky reefs) up to 150 m depth and their vicinity (i.e., pelagic and demersal interfaces), which may use reefs for shelter, feeding and/or spawning, were considered. Scientific literature was reviewed extensively (over 100 journal articles and books cited in Table S1), museum records were checked (Table S1), and authors' personal observations were added. Main additions to Floeter et al. (2008) include data from north Brazil (states of Pará and Maranhão), seamounts of the Vitória-Trindade Chain (Pinheiro, Mazzei et al., 2015), the improvement of the resolution for the north-eastern Brazilian coast (organized by States) and the Argentinian Province (Argentina and Uruguay), as well as recent records from mesophotic ecosystems and distributional range extensions made by the authors. The checklist is available online (<https://swatlanticreeffishes.wordpress.com>) and will be periodically updated by the authors to account for new species descriptions, new records, systematic reviews and nomenclature changes.

Classification above genus level follows Nelson (2006), with exception of Epinephelidae and Labridae, for which the classification of Craig, Mitcheson, and Heemstra (2011) and Westneat and Alfaro (2005) was used, respectively. Genus and species nomenclature follow Eschmeyer and Fong (2015). Species, listed in alphabetical order, were classified as residents (primarily associated with hard substrata), demersal over unconsolidated bottoms (benthic-occasional) or pelagic (pelagic-occasional). Traits of each species (spawning mode, trophic guilds, depth range, body size, geographic distribution, conservation status and rafting use—i.e., ability to use flotsam for migration) were compiled from the literature (Randall, 1967; Carvalho-Filho, 1999; Humann & DeLoach, 2002; Ferreira et al., 2004; Machado, Drummond, & Paglia, 2008; Luiz et al., 2012; IUCN, 2013; Froese & Pauly, 2014; MMA, 2014) and complemented by authors' observations (Table S1). The habitats in which each fish species was found (biogenic or rocky reefs, rhodolith beds, tide pools, sea grass beds, soft bottoms, estuaries/mangroves and/or water column) were assigned for each occurrence, and species were classified as habitat specialists (occurring in one or two habitats),

intermediate generalists (three to four habitats) and generalists (five to seven habitats). An annotated checklist of the Brazilian endemic fish species is also provided, with images, comments on selected biological features and distributional aspects.

2.2 | Statistical analysis

A cluster analysis (complete linkage method) encompassing the 23 studied sites (countries, Brazilian states and/or oceanic localities; Table S1) was carried out using a binary distance similarity matrix derived from the presence-absence data of all resident species ($n = 405$). A cophenetic correlation analysis for the cluster was performed to calculate the degree of reliability of the clustered branches (Sneath & Sokal, 1973). A similarity profile analysis (SIMPROF) was also performed to determine the number of significant clusters produced. Analyses were made using the package "pvclust" and "clustsig" in R version 3.1.2 (R Core Development Team 2014; available at <http://www.R-project.org>).

A matrix of beta diversity among studied sites was built using the Jaccard dissimilarity index and used to test whether the composition of each site fits one of the following hypotheses: (1) the "target-area-distance" (propagule rain) hypothesis, in which species would disperse from the Caribbean ("putative main source") and sites with similar coastline extension and distance from the source (Caribbean) would have a similar chance to share the same pool of colonists (low beta diversity; Figure 2a); or (2) the "stepping stones dispersal" hypothesis, in which beta diversity results from faunal exchange between sites, with a positive correlation between beta diversity and inter-site isolation (geographic distance among sites; Figure 2b; Fattorini, 2010). For testing the "target-area-distance effect" hypothesis, the distance from the Caribbean and the coastline extension were standardized to Z-scores [$Z = (\text{raw score} - \text{mean})/SD$], and an inter-site distance matrix, considered as the independent variable to this test, was computed using Euclidean distance over Z-scores (Fattorini, 2010). For testing the "stepping stones dispersal" hypothesis, the independent variable was the inter-site (site, island or state) overwater geographic distances. Both hypotheses predict positive correlation between dependent and independent variables. Correlations between matrices (beta diversity and independent variables) were evaluated with Mantel and partial Mantel tests (Fattorini, 2010), performed with the package *VEGAN* in R. Partial Mantel test differs from Mantel test by allowing a comparison between two matrices while removing the influence of a third one. Thus, we performed the partial Mantel test twice, first controlling for the influence of inter-site isolation (stepping stones dispersal) and later controlling for the influence of the coastline extension and distance from the source (target-area-distance effect). To decrease chances of type II errors, we did not apply Bonferroni corrections and focused on p -values and consistency of results (Fattorini, 2010).

Multiple-site dissimilarity measures of the nestedness and turnover components of the Jaccard dissimilarity index were carried out between neighbouring sites within the SWA using the method described by Baselga and Orme (2012). Pairwise dissimilarity measures

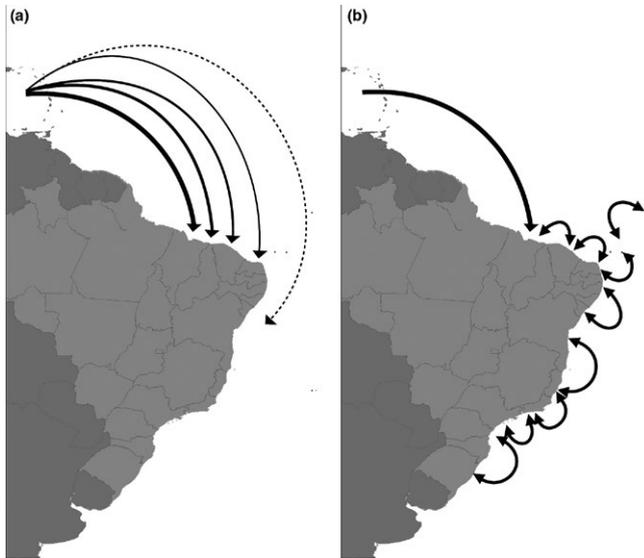


FIGURE 2 Models of assemblage structure in the south-western Atlantic: (a) target-area-distance, or propagule rain, hypothesis, in which sites with similar coastline extension and distance from the Caribbean would have a similar pool of colonists and low beta diversity. (b) “Stepping stones dispersal” hypothesis, where a positive correlation between beta diversity and geographic distance is expected

of the same components were conducted to test differences between provinces (Baselga & Orme, 2012). Both analyses were made using the package `BETAPART` in R.

Relationships between ecological traits (independent variables) and species distributions (the presence–absence data, dependent variable; Table S1) were investigated with generalized linear mixed-effect models (GLMMs). GLMMs can handle binomial distributions such as the presence–absence data (Bolker, 2008) and have already been used to assess drivers of reef fish species distribution over marine barriers and association with flotsam (Luiz et al., 2012, 2013). A suite of species-level traits (habitat association, body size, maximum depth, trophic guild, spawning type and rafting ability) was used as independent variables. These traits were chosen because they can potentially influence species dispersal and geographic range size (Luiz et al., 2012, 2013). Models were fitted using a logit link function, which is an appropriate transformation to the binomial distribution of the dependent variable (the presence–absence data). All independent variables were included in the models and further removed in a stepwise backward procedure that entailed sequential removal of fixed-effect terms that did not contribute significantly for model improvement (p -value $>.05$; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Only one variable was removed at a time; when two or more variables were non-significant, we removed the one which removal resulted in the lowest Akaike information criteria (AIC) and rerun the model until only significant variables remained. Taxon (genus nested within family) was included as a random variable to account for the non-independence of species owing to shared ancestry (Luiz et al., 2012, 2013). This nested random variation is represented as taxon-level differences in families and genera around

the overall “fixed” effects, attributable to other variables, which can then be generalized to the entire fauna (Pinheiro & Bates, 2000). GLMMs investigated seven distributional patterns, with “1” or “0” values assigned to each species depending on whether it fits to that respective distribution pattern or not, respectively. Analyses were conducted using the “lmer” function in package “lme4” of R.

3 | RESULTS

3.1 | Reef fishes of south-western Atlantic reef environments

The updated database includes 733 species from 129 families and 371 genera recorded on reef environments in the SWA (Table S1), 405 of which are considered as reef residents or strictly reef species (Table S1). Demersal species primarily associated with unconsolidated bottoms and pelagic species that are frequent in reef habitats sum 179 and 149, respectively (Table S1). Regarding taxonomy, 54.2% of the recorded species are Perciformes, followed by Anguilliformes (7.3%), Tetraodontiformes (5.5%), Scorpaeniformes (3.8%) and Pleuronectiformes (3.4%). The richest family is Carangidae (35 species), followed by Gobiidae (31), Epinephelidae (25), Serranidae (25), Scorpaenidae (23), Labridae (21), Haemulidae (19), Muraenidae (19) and Ophichthidae (19). The most species-rich genera are *Scorpaena* (14 species), *Carcharhinus* (11), *Haemulon* (10), *Lutjanus* (9), *Serranus* (9), *Gymnothorax* (8), *Halichoeres* (8) and *Anchoa* (8).

Concerning the geographic distribution of resident reef fishes (405 species), 111 species (27%) are endemic to the SWA (including oceanic islands), mostly from the Brazilian Province (102 species). Most species are widely distributed in the western Atlantic (186 species, 46%). Transatlantic and interoceanic species account for 20 and 6% of the fish fauna, respectively (Figure S1). Nine species have invaded the SWA recently, via natural and/or anthropogenic processes (Table S1). Historical records of *Scarus guacamaia*, considered currently extinct in the SWA (Ferreira, Gasparini, Carvalho-Filho, & Floeter, 2005), likely constituted vagrant specimens from the Caribbean.

The SWA reef fish fauna contains predominantly mobile invertebrate feeders (46%) and macrocarnivores (27%; Figure S1). Species composition is evenly distributed in size classes (Figure S1). Most taxa are sedentary or have roving mobility and display pelagic and demersal spawning strategies (Figure S1). Most species are intermediate generalists (48%) recorded in two to five habitats, and most (61%) occur in depths >50 m (Figure S1).

3.2 | Endemic species

In addition to 111 reef resident SWA endemics (27% of residents), another 49 endemic species are benthic-occasional and 14 are pelagic-occasional species, totalling 174 SWA endemic reef fishes (24% of the total species), distributed in 45 families (Table S1; Annotated Checklist S2). When all endemics are considered, Gobiidae and Labridae are the most species-rich families, with 15 species each,

followed by Labrisomidae (10), Serranidae (10), Pomacentridae (8) and Blenniidae (8). Invertebrate feeders comprise 60% of the SWA endemic species, followed by planktivores (14%), herbivores (12%) and macrocarnivores (12%). In terms of habitat association, 48% of the endemic species are considered specialists (one or two different habitats), 43% are intermediate generalists (three or four habitat types), and the remaining 9% are generalists (five or more habitats; Table S1). Most endemics are small (0–10 cm, 42%) or medium-sized (10–25 cm, 28%) fishes, have sedentary (55%) and roving (39%) mobility, with demersal (41%) and pelagic (40%) spawning strategies, and reach mid (25–50 m, 21%) and deep (>50 m, 47%) ranges (Table S1). None of the Brazilian endemics display rafting dispersal abilities.

3.3 | Endangered species

A total of 186 fish species (26% of the total number) from the database were evaluated globally according to IUCN criteria, with 45 (24% of the evaluated species) included in one of the three following threat categories: Critically Endangered (four species), Endangered (8) or Vulnerable (33). Regional-level evaluations using IUCN criteria (MMA, 2014) and covering 627 reef-associated species (348 resident) resulted in 66 species recognized as threatened in Brazil. When combining both assessments, 78 species are considered to be under some level of extinction risk, 39 of which are reef residents, 27 pelagic-occasional and 12 benthic-occasional (Table S1). The family with the greatest number of threatened species is Epinephelidae (eight species), followed by Carcharhinidae and Labridae (seven species each), Mobulidae (5), Pomacentridae and Sphyrnidae (four each) and Lamnidae, Lutjanidae, Rhinobatidae and Syngnathidae (three each). Eighteen Brazilian endemics (11 families) are considered threatened (Annotated Checklist S2). Families with the greatest number of threatened endemics are Labridae (6) and Pomacentridae (3). Forty-five species (58%) are fisheries targets (Table S1), whereas the remaining ones are primarily threatened by other stressors (e.g., loss of habitat and sensibility to anthropogenic actions associated with restricted geographic distribution).

3.4 | South-western Atlantic reef fish zoogeography

The cluster and SIMPROF analyses with the presence and absence data of the 405 SWA resident reef fish species revealed 10 significant clusters of sites, which match six major geographic groups with high cophenetic correlation values (Figure 3), named here as subprovinces (SP): SP 1) St. Peter and St. Paul's Rocks; SP 2) Fernando de Noronha Archipelago and Rocas Atoll; SP 3) seamounts of the Vitória-Trindade Chain plus the Trindade–Martin Vaz insular complex (VTC); SP 4) north and north-east Brazil; SP 5) east and south-east Brazil; and SP 6) Uruguay and Argentina (Argentinian Province). The greatest species richness is found in the east–south–east (SP 5), with 326 species, followed by north–north–east (SP 4, 259 species) and VTC (SP 3, 186 species; Figure 4). While the north–north–east subprovince (SP 4) shares most of its reef fish fauna (95%) with

the east–south–east subprovince (SP 5), 27% of species recorded in SP 5 do not occur in SP 4 (Figure 4). Both SP 4 and SP 5 share about 50% of their species with the oceanic sites of Fernando de Noronha Archipelago and Rocas Atoll (SP 2) and VTC (SP 3), respectively. Although farther away, the north–north–east subprovince (SP 4) shares more species with VTC (SP 3) than with the Fernando de Noronha Archipelago and Rocas Atoll (SP 2). The oceanic subprovinces SP 2 and SP 3 share 101 species, more than 55% of the fauna present in each of those subprovinces. Towards the south, the east–south–east subprovince (SP 5) shares only 36 species (11% of its fauna) with the Argentinian Province (SP 6; Figure 4).

From the 111 SWA resident endemic reef fishes, 36 are restricted to oceanic islands (SPs 1, 2, 3) and PML, 40 are restricted to the continental shelf and slope (SP 4 and 5), 28 occur in both Brazilian continental and oceanic subprovinces, and seven reach the Argentinian Province (SP 6). The east–south–east (SP 5) shelters the highest number of SWA endemic species (71), 26 of which are not recorded in the north–north–east (SP 4) and 16 are exclusive to this subprovince (Figure 4). The north–north–east subprovince (SP 4) harbours 48 SWA endemics but displays one of the lowest local endemism among all subprovinces (two species). St. Peter and St. Paul's Rocks (SP 1) has the highest local endemism level (9%) in the SWA, followed by the VTC subprovince (SP 3; 6%; Figure 4).

The reef fish fauna of the Argentinian Province (SP 6) is the most dissimilar among the SWA subprovinces (Figure 5). Forty-two of the 59 families recorded in the Brazilian subprovinces are not found in subprovince SP 6 (Figure 5). Two families, Nototheniidae and Sebastidae, are restricted to SP 6, and Clinidae is more diverse in the Argentinian Province than in any Brazilian subprovince (Figure 5). Labridae, Gobiidae and Epinephelidae are generally highly diverse in the Brazilian subprovinces (Figure 5). Exceptions for Labridae and Epinephelidae are the northern St. Peter and St. Paul's Rocks (SP1) and Fernando de Noronha Archipelago plus Rocas Atoll (SP 2), where these two families are proportionally less diverse than in other subprovinces. Gobiidae is more species rich in continental subprovinces (SPs 4 and 5) than in oceanic ones (SPs 1, 2 and 3). Haemulidae and Labrisomidae are less species rich in the VTC (SP 3) than in the other subprovinces, the former being absent from St. Peter and St. Paul's Rocks (SP 1). Syngnathidae is more species rich in the east–south–east subprovince (SP 5) than in any other subprovince. Diodontidae and Synodontidae are less species rich, and Sparidae, Chlopsidae and Callionymidae are absent in the northern oceanic subprovinces (SPs 1 and 2). Grammatidae, Microdesmidae, Ogocephalidae and Ophidiidae are absent in oceanic islands (SPs 1, 2 and 3), and Dactyloscopidae, Antennariidae, Fistulariidae and Ehippididae are absent in the VTC (SP 3). Clinidae is absent in the northern SPs 1, 2 and 4. Bythitidae is restricted to the east–south–east subprovince (SP 5), and Carapidae is found only in the eastern Brazil (SPs 3 and 5).

3.5 | Community structure drivers

Reef fish assemblage composition along the Brazilian coast can be explained by both the stepping stones (Mantel test, $r = .6345$,

$p = .001$) and target-area-distance ($r = .9892$, $p = .001$) models. Fattorini (2010) attributed similar results in his study on insular beta diversity patterns to an intercorrelation between explanatory matrices, possibly due to the strong effect of the variable “distance” on beta diversity in both models. However, when using partial Mantel test and controlling for the influence of inter-site isolation, the Brazilian reef fish fauna was still associated with the target-area-distance model (partial Mantel test, $r = .982$, $p = .001$), whereas the stepping stones model was not significant after controlling for the influence of the coastline extension and distance from the source ($r < .001$, $p = .777$).

Along the continental shelf, beta diversity is higher on the latitudinal edges of the Brazilian Province, between Uruguay and the State of Santa Catarina (southern Brazil), and between the states of Maranhão and Ceará (north-eastern Brazil; Figure S2). Oceanic islands, in turn, also showed relatively high values of beta diversity, between islands and other subprovinces (Figure S2). When comparing beta diversity between subprovinces, the highest value was found between the east-south-east (SP 5) and the Argentinian Province (SP 6), resulting from a strong nestedness (Figure 6). Beta diversity between oceanic subprovinces and the continental shelf was much higher than that between the north–north-east and east-south-east subprovinces (Figure 6). Beta diversity was strongly influenced by nestedness, except for Fernando de Noronha Archipelago and Rocas

Atoll (SP 2) versus the north–north-east subprovince (SP 4), for which turnover was more important (Figure 6).

Habitat use, body size, depth range and diet were among the main drivers of the composition of reef fish assemblages in the Brazilian Province (Table 1). Brazilian endemics are habitat specialists and intermediate generalists (associated with one to four habitats), small-sized (negatively correlated to large, medium and medium–small size categories) and shallow-water dwellers (negatively correlated with wide depth range). Brazilian endemics are also negatively correlated with the carnivore and mobile invertebrate feeding modes. On the other hand, widely distributed species that occur in all Brazilian subprovinces inhabit a wider depth range and are mostly generalists (found in five or more habitats; Table 1).

The south-east subprovince (SP 5) harbours 87 species that do not occur in the north–north-east subprovince (SP 4), including a higher number of endemics. In the south-east subprovince, there is an important contribution of habitat specialists (more dependent on reef framework), omnivorous diets and several spawning strategies (Table 1). However, species recorded further south, reaching the Argentinian Province (SP 6), are negatively related to habitat specialization (Table 1).

Species restricted to the continental shelf are positively correlated with brackish habitats and with the mobile invertebrate feeder feeding mode and are mostly small-sized and shallow-water

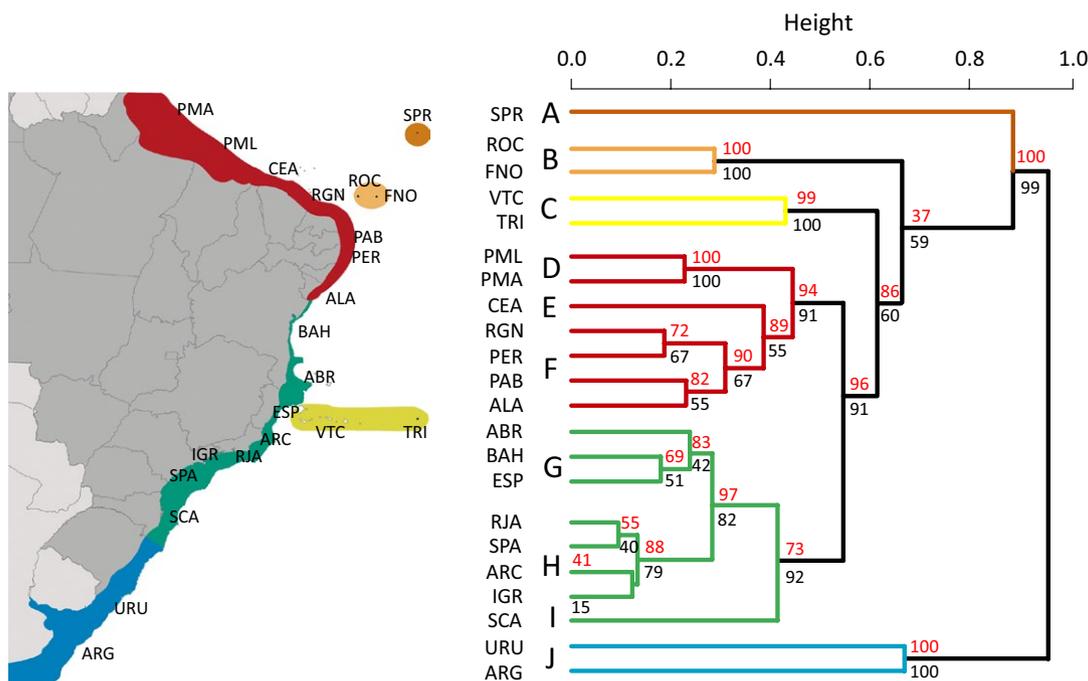


FIGURE 3 South-western Atlantic subprovinces defined by cluster analysis (complete linkage method and binary distance) of reef fish species. Values of cophenetic correlation analyses, Approximately Unbiased (red) and Bootstrap probability (black), are shown. Letters, A through J, indicate significant clusters pointed by SIMPROF analysis. 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 (not including Abrolhos); ESP: state of Espírito Santo (not including Abrolhos); RJA: state of Rio de Janeiro (not including ARC and IGR); ARC: region of Arraial do Cabo; IGR: Ilha Grande Bay; SPA: state of São Paulo; SCA: state of Santa Catarina; URU: Uruguay; ARG: Argentina. [Colour figure can be viewed at wileyonlinelibrary.com]

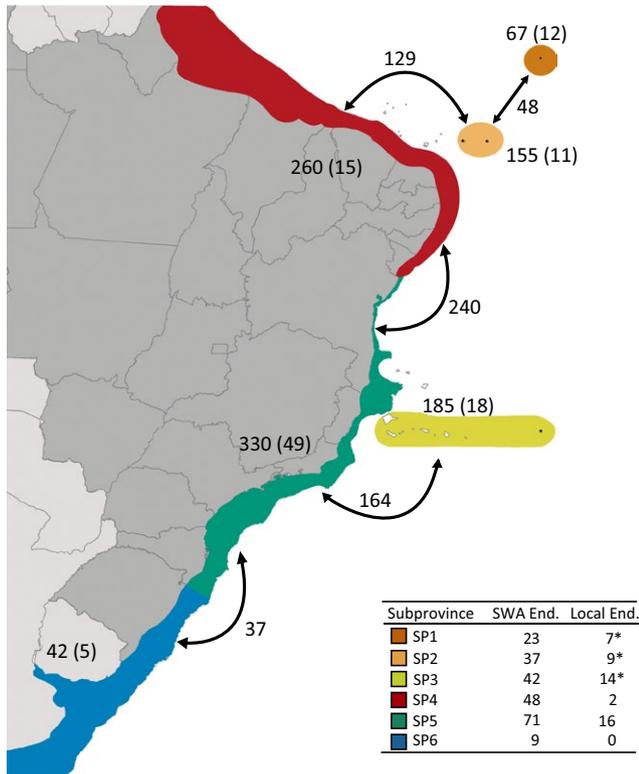


FIGURE 4 Richness, number of exclusive species (in parentheses) and number of shared species (in the arrows) among subprovinces in Brazil, south-western Atlantic. *Odd shared species: SP 1 and SP 2 share additional six exclusive endemic species; SP 2 and SP 3 share one additional exclusive endemic species. [Colour figure can be viewed at wileyonlinelibrary.com]

dwellers (negatively related to large sizes and great depths; Table 1). Species recorded in oceanic islands are positively related to rafting use, great depth ranges and large body sizes (Table 1). Reef fish species that occur in oceanic islands are generalists in terms of habitat use and negatively related to specialist, intermediate generalist and brackish habitat use (Table 1).

4 | DISCUSSION

The mechanisms of biodiversity formation and distribution in peripheral provinces have remained unclear, and allopatry still stands as the most important hypothesized driver of speciation in such regions (Briggs, 2006). Here, we explored zoogeographic and ecological patterns of reef fishes along the Brazilian Province to better understand the underlying processes shaping biodiversity in peripheral provinces. The Brazilian Province encompasses the continental shelf and upper slope between the Amazon River mouth and the state of Santa Catarina, including several oceanic islands, and is distinct from the Argentinian Province in the south-western Atlantic (Briggs & Bowen, 2012; Floeter et al., 2008). This peripheral province was originally proposed by Briggs (1974) and was supported by several subsequent studies on Atlantic reef fish biogeography and evolution (Floeter & Gasparini, 2000; Floeter et al., 2008; Joyeux et al., 2001;

Pinheiro et al., 2017; Robertson et al., 2006; Rocha, 2003), including the updated database presented herein. However, composition, richness and endemism patterns within the region remained poorly understood, as revealed by continuous descriptions of new species, new records and range extensions (see Moura, Gasparini, & Sazima, 1999), as well as due to different criteria used to define “reef fishes”. The database presented herein contains a total of 733 species recorded from SWA reefs and adjacent environments and increases reef fish richness in the region from 438 to 450 species (22% endemics) following criteria from Moura and Sazima (2000), from 353 to 400 species (24% endemics) following Rocha (2003) and from 471 to 508 species (22% endemics) following Floeter et al. (2008).

The number of Brazilian endemic reef fishes and levels of endemism have been updated for the same reasons mentioned above: new taxonomic and/or distributional discoveries and different “reef fish” definitions. Currently, considering all resident endemic reef fishes, endemism in the Brazilian Province is responsible for 94% of the endemism level of the entire SWA. However, records of vagrants Brazilian endemics outside Brazil—15 species in the Caribbean, Mid-Atlantic Ridge and/or eastern Atlantic, and seven in the Argentinian Province (Galván, Venerus, & Irigoyen, 2009; Freitas et al., 2014; present paper), may decrease the number of Brazilian endemics (see Rocha, 2003) to 89 species (from 26% to 22%). Moreover, the number and level of endemism in the continental shelf are greater than previously suspected (Floeter et al., 2008; Rocha, 2003), reaching 17%. Brazilian endemics exclusive to the oceanic islands contribute to an additional 9%, which is a considerable level compared to the number of endemics in other islands of the Atlantic Ocean (Hachich et al., 2015) and also taking into account the relatively small reef area of Brazilian islands (220 km²; <0.001% of the Brazilian continental shelf).

Recent biogeographic studies have shown that the Brazilian coastal reef fish fauna may form two different clusters [north-east and south-east, in Floeter et al. (2008); Espírito Santo State grouping with the north-east coast, in Kulbicki et al. (2013) and Barroso, Lotufo, and Matthews-Cascon (2016)] or five ecoregions (Spalding et al., 2007). However, our results revealed a robust clustering of east Brazil with south-eastern Brazil, contrasting with previous analyses that highlighted differences between biogenic (coralline algae or coral) reefs and rocky reefs that characterize those regions (Floeter et al., 2001, 2008). Despite habitat peculiarities, two factors may determine the novel pattern uncovered herein: the relatively high species richness found in the east, followed by south-east areas, and vicariant barriers. In fact, the highest richness of resident reef fish species is found in the states of Bahia and Espírito Santo (eastern coast). Barroso et al. (2016) also found the highest richness for prosobranch gastropods in Bahia. Such richness can be attributed either to the long coastline of Bahia (the longest among Brazilian states) and its habitat diversity or by the transition region in Espírito Santo state, which shelters biogenic reefs to the north and rocky reefs under upwelling influence to the south (Floeter et al., 2007; Pinheiro, Madureira, Joyeux, & Martins, 2015; Mazzei et al., 2017). Finally, the Abrolhos Shelf, the largest reef system in the south Atlantic, spans

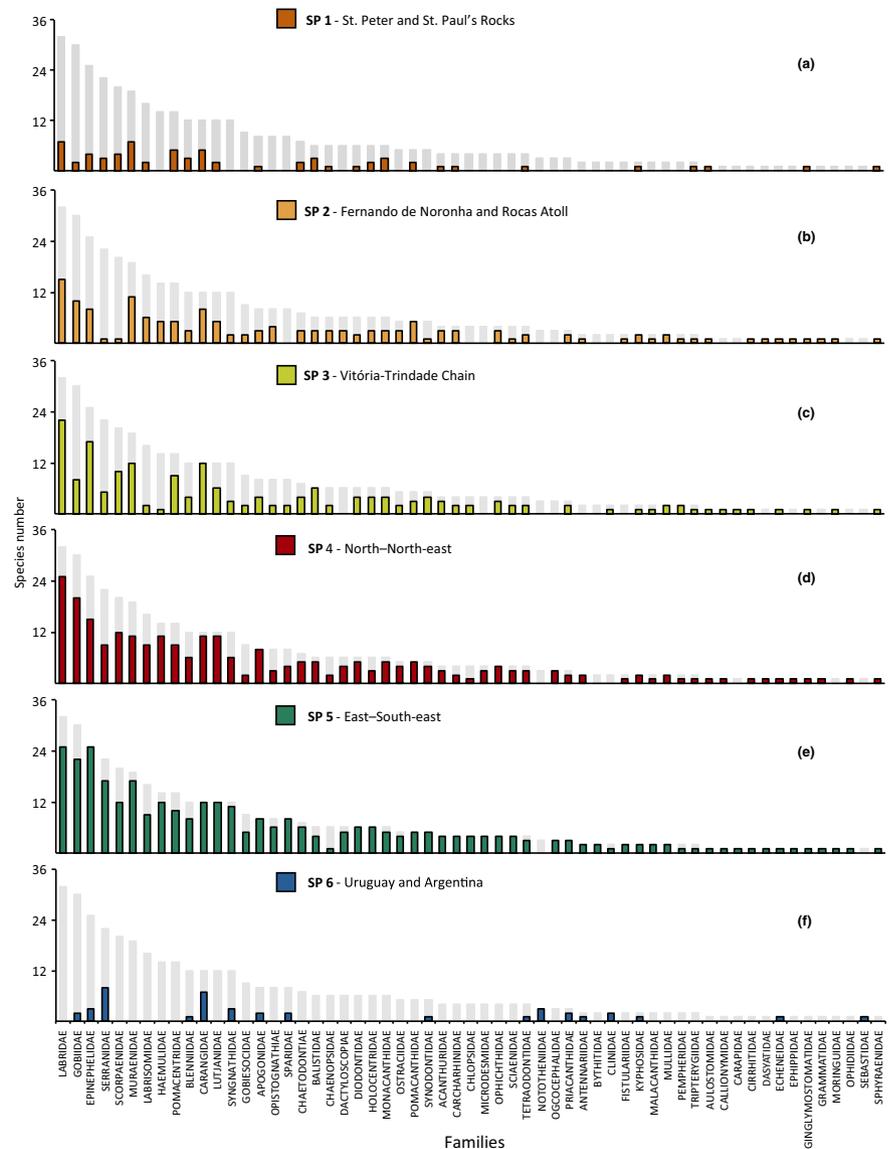


FIGURE 5 Reef fish family richness in communities across the south-western Atlantic zoogeographical subprovinces. Shades indicate the total number of species per family found in the south-western Atlantic. [Colour figure can be viewed at wileyonlinelibrary.com]

both the Bahia and Espírito Santo States (Mazzei et al., 2017; Moura et al., 2013). Despite lacking well-developed coralline reefs, the south-eastern states within the Brazilian Province (Rio de Janeiro, São Paulo, Paraná and Santa Catarina) have wide continental shelves and numerous coastal islands with rocky reefs. Therefore, species richness patterns may be driving the compositional boundary between the east-south-east and the north-east coast.

Additionally, the South Equatorial Current bifurcates between 10 and 14°S (Rodrigues et al., 2007), creating the south-flowing Brazil Current, and the North Brazil Current flowing north-west. The splitting of the Brazil Current from the South Equatorial Current, in conjunction with the São Francisco River mouth (one of the largest river basins in South America), can contribute to this subprovincial boundary, constraining northwards faunal movements. These barriers, together with ecological drivers such as colder waters in the south, are known to influence the genetic structure of populations and species in these regions (Cunha et al., 2014; Santos, Schneider, & Sampaio, 2003), and they may contribute to dissimilarities (turnover and nestedness) in species composition between the subprovinces.

Southwards, part of the south-eastern coast has been characterized as warm temperate waters (Spalding et al., 2007). More recently, Briggs and Bowen (2012), following Floeter et al. (2008), considered the Argentinian Province to extend into the western Atlantic warm region. However, the present study shows that, due to strong nestedness, the Argentinian Province has few similarities with tropical Brazil, supporting only about 10% of the SWA reef fish richness, as well as presenting a unique fauna. Thus, regarding tropical reef fishes, we propose an alteration of the recently defined categories (not the areas), switching the “warm temperate Argentinian Province” to “cold temperate South America region” (Briggs & Bowen, 2012).

The Brazilian oceanic islands are impoverished outposts of the Brazilian Province (Floeter & Gasparini, 2000; Floeter et al., 2008) and contribute with 9% of Brazilian reef fish endemics. However, despite their isolation, the islands are connected among themselves, with the coast, and with different provinces. The remote insular group of Trindade and Martin Vaz, for instance, is connected to the continental shelf by a series of seamounts (VTC), with endemics being closely related to coastal species (Pinheiro, Mazzei

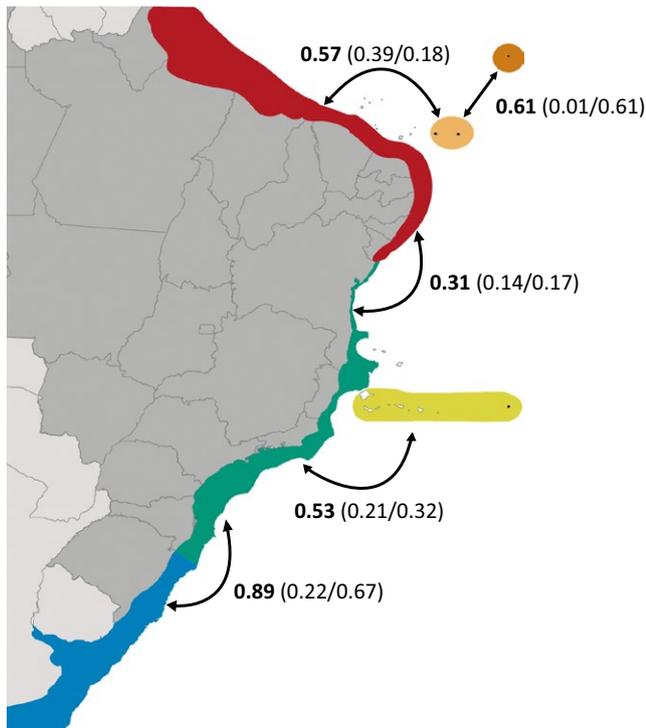


FIGURE 6 Jaccard beta diversity decoupled in its respective turnover and nestedness components among south-western Atlantic subprovinces. [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2015, 2017). The small and remote St. Peter and St. Paul's Rocks share endemics with Fernando de Noronha, Rocas Atoll and Manoel Luiz Reefs, in the Brazilian Province, and with Ascension and St. Helena oceanic islands, in the Mid-Atlantic Ridge. Even Fernando de Noronha and Trindade, 1,850 km apart, share one endemic, still undescribed, species (*Opistognathus* sp.). Such unexpected distribution patterns suggest an oceanic "pathway" connecting species among oceanic islands. This "pathway" would be driven by stochastic and ecological factors, as there are no oceanic currents directly connecting those islands. However, there is remarkable habitat similarity (e.g., temperature, productivity and water transparency) among Brazilian oceanic islands and the Caribbean. Therefore, these islands might promote the settlement, maintenance and connectivity of species and populations that are unable to get established in the continental shelf. Thus, several species might have the ability to disperse, but the environment is a key factor for their persistence in the islands. Ecological similarity has been considered as a cause of speciation in oceanic islands and seamounts (Pinheiro, Mazzei et al., 2015; Rocha, Robertson, Roman et al., 2005), but little attention has been given to its effect on species distribution (Bender et al., 2013). Brazilian oceanic islands may indeed work as stepping stones, bridging species between different provinces, as some of them shelter Caribbean species (Rocha, 2003; Rocha, Robertson, Roman et al., 2005), or may work as landing spots for Indian Ocean species (Bowen, Muss, Rocha, & Grant, 2006; Rocha, Robertson, Rocha et al., 2005). An opposite pathway may also occur, as Brazilian and Caribbean species have been

found in east Atlantic oceanic islands (Freitas et al., 2014; Pinheiro, Camilato, Gasparini, & Joyeux, 2009).

Ecological factors are also important evolutionary drivers in continental shelf assemblages. The Greater Caribbean is recognized as the centre of Atlantic marine biodiversity (Briggs & Bowen, 2012; Floeter et al., 2008) and is considered a centre of both origin and accumulation of species (Bowen et al., 2013; Rocha et al., 2008). As reef fish composition in the Brazilian coast fits a propagule rain model, it is presumed that sites closer to the Caribbean Province would have higher richness. However, this was not observed in our analyses. The latitudinal peak of species richness in the Brazilian Province is located in the east-south-east subprovince (12–25°S; Figure 4), a transitional zone between tropical and subtropical waters. This latitudinal band also shelters the highest number of endemic species in the SWA, and many other species do not reach the north-north-east subprovince. Therefore, we propose that the Brazilian Province hosts an additional and relevant secondary Atlantic centre of biodiversity.

In this scenario, ecological factors such as habitat, temperature and productivity (in addition to the intermittent vicariant barrier of the Amazon River; see Rocha, 2003 and Moura et al., 2016) may contribute as speciation drivers in the east-south-east of the Brazilian Province. Ecological/parapatric speciation would explain the adaptation and divergence from Caribbean lineages in Brazil. Sea-level fluctuations and climate changes in the Pleistocene implied a more subtropical, rather than tropical, climate condition along most of the SWA during that period. During glacial maxima, while the tropical marine fauna in Brazilian waters was constrained by the Amazon River discharge, the subtropical and Argentinian fauna may have just switched or expanded their ranges northwards. Extinctions occurred widely in the Caribbean since the Pliocene (Budd, 2000; Bellwood & Wainwright, 2002; Briggs, 2003), but were probably more pervasive in the tropical Brazilian coast (Cowman, 2014; Pinheiro et al., 2017). Unlike the south-eastern Brazilian continental shelf, the north-eastern coastal shelf is narrow and shallow, presenting a steeper slope and a significantly smaller coastal area during sea-level lowstands. That situation probably resulted in higher extinction rates of coastal/reef-associated species in that region, a condition that is still reflected in the lower species richness of the north-eastern coast when compared to the east-south-east subprovince. In addition, oceanic hotspots, such as the VTC seamounts, seem to have a singular role in the maintenance of relict tropical lineages in eastern Brazil, maintaining coral and reef fish lineages through the Pleistocene climate anomalies (Leão et al., 2003; Pinheiro, Mazzei et al., 2015; Pinheiro et al., 2017; Rocha, Pinheiro, & Gasparini, 2010). Thus, the high richness and endemism of the subtropical Brazilian water can be explained by its potential to (1) originate species due to ecological factors, (2) accumulate species evolved by vicariance, due to the Amazon River or the Brazil Current, as well as relict species isolated in Pleistocene refuges (seamounts and oceanic islands), and to (3) being an area with considerable overlap of tropical and subtropical/temperate species.

Disentangling ecology, biogeography and evolution have been important to understand the origin and structure of

TABLE 1 Significant variables of the generalized linear mixed-effect models of various traits on distribution patterns of reef fishes in the south-western Atlantic

Distribution pattern	Variable	Estimate	SE	Z-value	p Value
Along the entire coast	Depth: Great	1.2776	0.4728	2.702	.0068
	Habitat: Generalist	-1.2092	0.3746	-3.228	.0012
	Habitat: Specialist	-3.2255	0.432	-7.467	<.0001
Coastal exclusives	Brackish water	1.82955	0.54658	3.347	.0008
	Diet: Mob. Inv. Feeder	1.47964	0.65749	2.25	.0244
	Depth: Great	-1.65641	0.56992	-2.906	.0036
	Size: Large	-2.43477	1.04489	-2.33	.0197
Island inhabitants	Size: Large	2.2814	0.7437	3.068	.0021
	Depth: Great	2.623	0.9917	2.645	.0081
	Rafting	1.3426	0.6374	2.106	.0351
	Brackish water	-1.2125	0.5326	-2.277	.0228
	Habitat: Generalist	-1.2961	0.4876	-2.658	.0078
	Habitat: Specialist	-3.1714	0.7218	-4.394	<.0001
East-south-east inhabitants	Diet: Omnivore	3.0669	1.399	2.192	.0283
	Habitat: Specialist	1.9486	0.4495	4.335	<.0001
	Spawning: Live bearing	4.6287	1.5577	2.971	.0029
	Spawning: Pelagic	3.6294	1.4725	2.465	.0137
	Spawning: Brooder	3.3733	1.656	2.037	.0416
SWA Endemic	Habitat: Specialist	2.3392	0.6488	3.606	.0003
	Habitat: Generalist	1.582	0.5863	2.698	.0069
	Size: Medium-small	-1.0479	0.4427	-2.367	.0179
	Size: Medium	-1.6702	0.6435	-2.595	.0094
	Size: Large	-4.3069	1.2295	-3.503	.0004
	Depth: Very Great	-2.6323	0.8362	-3.148	.0016
	Diet: Macrocarivore	-2.7901	0.945	-2.953	.0031
	Diet: Mob. Inv. Feeder	-1.7343	0.7123	-2.435	.0148
Argentinian Province	Habitat: Specialist	-2.9533	1.5574	-1.896	.0579

zoogeographical provinces (e.g., Bowen et al., 2013; Cowman & Bellwood, 2013). Depth range, habitat use, body size and diet are here proposed as being among the main drivers of community structure in the SWA. Body size and multihabitat use were recently recognized as major ecological predictors of western Atlantic species that are able to cross the Amazon barrier (Luiz et al., 2012). The same traits are also noted here as important drivers for the speciation of Brazilian endemics, but with an opposite pattern—Brazilian endemics are smaller and use shallower waters (traits that constrain the crossing; see Moura et al., 2016). Important ecological traits such as rafting ability, body size and multihabitat use, in turn, are more common in species that inhabit both oceanic islands and those that cross the Mid-Atlantic Barrier (Luiz et al., 2012), supporting the idea that oceanic islands function as stepping stones between provinces. The ecological drivers identified in our study also support the centre of origin hypothesis, as habitat specialization is a factor that promotes diversification (Bowen et al., 2013). In addition, distributional patterns of several subtropical species (and also of Brazilian

endemics) also support the ecological speciation hypothesis, as areas in the south-eastern and north-eastern coast are connected through deep and cold shelf-edge reef corridors (Feitoza, Rosa, & Rocha, 2005). Thus, peripheral provinces also harbour centres of biodiversity supported by the overlap of tropical and subtropical species, and species diversification driven by ecological factors in addition to vicariance.

4.1 | Conservation issues

The relatively high number of endemic species concentrated in small and highly impacted areas makes the Brazilian Province a priority area for conservation efforts of coralline reefs in the Atlantic (Moura, 2000). Reef fisheries management and monitoring are almost non-existent, and only 2% of the Brazilian Exclusive Economic Zone (EEZ) is set aside as marine protected areas (MPAs), with only 0.8% of the coastal zone within no-take areas (Di Dario et al., 2015; Vila-Nova, Ferreira, Barbosa, & Floeter, 2014). In addition, the few MPAs are ill-designed (Moura

et al., 2013) and are not evenly distributed along the coast, with many hotspots (of richness, endemism, threatened and targeted species) remaining unmanaged and unprotected (Vila-Nova et al., 2014; Vilar, Joyeux, Loyola, & Spach, 2015). Although there is a commitment to increase MPAs to 10% of the EEZ by 2020 (CBD, 2010), the actual perspective is of accelerated urban and industrial development in coastal regions. Such pervasive trend is largely catalysed with government incentives, which are followed by social conflicts and environmental degradation (Pinheiro, Di Dario et al., 2015). While MPA declarations have been halted and the few existing MPAs have been poorly implemented, licences for new ports and mining are regularly issued, including extreme measures such as MPA decommissioning. The high levels of fishing effort have also led to the overexploitation of Brazilian reefs (Araújo & Martins, 2009; Di Dario et al., 2015; Pinheiro, Joyeux, & Martins, 2010). Fishing ban or fishing restriction proposals for all endangered fishes in Brazil (MMA, 2014) have been recently rejected, although more than 60% of the red-listed marine species are primarily threatened by overfishing. The remaining 40% are primarily threatened by habitat degradation and other non-fisheries related impacts (Pinheiro, Di Dario et al., 2015). Federal funding has been widely available for fisheries development, but there is a huge mismatch between subsidies and fisheries management and comanagement initiatives, especially when reef fisheries are taken into account (e.g., small-scale fleets, traditional and impoverished fishers).

Brazilian reefs are far from pristine, and in many areas they are collapsed, with important ecological functions (e.g., herbivory) already compromised. On the other hand, some no-take MPAs within fisheries management zones showed recovery potential (Francini-Filho & Moura, 2008a), as did strict no-entry marine reserves (Anderson et al., 2014). Although the establishment of MPAs alone does not ensure the recovery of reef communities (Cox, Valdivia, McField, Castillo, & Bruno, 2017), in Brazil, even paper parks and poorly enforced MPAs have more abundant fish fauna than open areas (Floeter, Halpern, & Ferreira, 2006; Francini-Filho & Moura, 2008b; Morais, Ferreira, & Floeter, 2017). At the global scale, protection from fishing has the potential to recover fish biomass within a few decades, and fishery restrictions can maintain fish biomass above half of the "pristine" state on reef environments (MacNeil et al., 2015). Reversion of this biogeographic-scale tragedy on SWA needs coordinated efforts between agencies (Agriculture, Mines and Energy and Environment ministries) and Federal Governments (Brazil, Uruguay and Argentina) to foster cooperation among researchers, fishers and other relevant stakeholders (tourists and coastal communities). Key features of MPAs, such as no-take zones, staff and enforcement, are fundamental to their success (Edgar et al., 2014; Gill et al., 2017). However, new approaches are essential not only for spatial planning and MPA declaration and implementation, but also to promote ecosystem-based management, a much-needed step even in the improbable scenario of CDB targets' meeting by Brazil in terms of MPA declarations.

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This manuscript is dedicated *in memoriam* to our dear friend and coauthor, Thiony Simon (1985–2016), who passed away during the preparation process of this article. He is sorely missed and those of us who were fortunate enough to know him will always remember his happiness, excitement, scientific rigour, dedication and generosity. HTP thanks CNPq for the PhD scholarship (GDE 202475/2011-5). CELF thanks CNPq and FAPERJ grants. JCJ thanks CNPq grants (470725/2009-5, 557043/2009-3 and 405426/2012-7). SRF thanks CNPq grants (563276/2010-0 and 305358/2015-4). MB thanks CNPq (503384/2014-3). IS thanks the CNPq and FAPESP for past grants. RMM thanks CAPES for PNPd grant. RBFF thanks the CNPq for grants. RLM thanks CNPq, FAPERJ, FAPES, CAPES/IODP and ANP/Brasol for continued funding.

DATA ACCESSIBILITY

The database, annotated checklist and the literature used in this research are available at <https://swatlanticreeffishes.wordpress.com>. This database will be periodically updated so as to account for new species descriptions, new records, systematic reviews and nomenclatural changes. Additionally, updates will include new information and images for data-deficient species and will welcome citizen science contributions.

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BIOSKETCH

Hudson T. Pinheiro studies the biodiversity, biogeography, ecology and evolution of reef fishes in the Atlantic and Indo-Pacific. He is currently interested in mesophotic reef fish communities and fishes from isolated seamounts and oceanic islands. Hudson also uses his data and knowledge to engage in conservation initiatives.

Author contributions: All authors contributed equally to conceiving and designing the manuscript, compiling information for the database and annotated checklist, analysing the data and writing the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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