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SANTA CRUZ

**FISHES OF THE VITÓRIA-TRINDADE CHAIN  
BIODIVERSITY, BIOGEOGRAPHY AND EVOLUTION**

A dissertation submitted in partial satisfaction  
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

**Hudson T. Pinheiro**

September 2016

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## **Abstract**

**Hudson T. Pinheiro**

### **Fishes of the Vitória-Trindade Chain: Biodiversity, biogeography and evolution**

Studies on the ecology and biogeography of seamounts and oceanic islands have advanced substantially in the last 60 years. However, few seamounts have been scientifically characterized, with basic aspects of their biodiversity still unknown and many hypotheses not empirically tested. Consequently, the role of seamounts in the evolution for marine species is still unclear. In the south Atlantic, the Vitória-Trindade Chain (VTC) extends ca. 1,200 km offshore the Brazilian coast. For a long time, most of the biological information available was limited to the emergent islands, where a high richness and endemism is found. The seamount chain, situated between the islands and the mainland, is thought to contribute importantly to the regional biodiversity, and has been suggested as stepping-stones, repositories and museums for coral reef species. The goal of this dissertation is to characterize the biogeographic patterns of reef fishes that inhabit the VTC and test hypotheses to explain those patterns. The results reveal large mesophotic reefs sheltering a very high biodiversity, where new records, depth range extensions and new species were reported. The regional biogeography is very complex; species richness does not decrease with distance from the mainland and it is related instead to seamount and island environmental characteristics and ecological traits of the species. Speciation is not only resulted from the islands isolation, as many endemics are widely distributed along the seamounts, and selection and adaptation are stronger drivers of genomic differentiation than is

isolation. In conclusion, oceanic islands would unlikely exhibit the biogeographic patterns we observe today in the absence of seamounts as intermittent stepping-stones, reservoirs of coral reef biodiversity.

## Dedication

I would like to dedicate this dissertation to my dear spouse Flavia Carnelli Frizzera Pinheiro, for all the support and happiness she offers to my life. I also would like to dedicate this dissertation to my dear friend Thiony Simon (*in memoriam*), for the unforgettable learning, adventures and friendship we had together.

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## GENERAL INTRODUCTION

### *Studies in the Vitória-Trindade Chain*

Although studies of the Caribbean reef fish fauna began in the 1950s (Hixon 2011), the ichthyofauna of the southwestern Atlantic (SWA) reefs remained largely unknown until the beginning of the 1990s. The first efforts to describe and catalogue SWA reef fishes date back to the mid 17<sup>th</sup> century, increasing in the 18<sup>th</sup> and 19<sup>th</sup> centuries by efforts of European and American naturalists. However, it was just at the end of the 20<sup>th</sup> Century that locally-led reef fish studies significantly advanced, with the growing number of Brazilian researchers and the use of SCUBA gear resulting in a steep increase in species descriptions and research.

Studies of reef fishes of the southwestern Atlantic oceanic islands followed a similar pattern. The first ichthyological surveys at Trindade Island date back to early 1900's, when Murray (1902) reported eight species collected by the Discovery expedition. Few years later, in 1913, R.C. Murphy, during the expedition of the American Museum of Natural History, collected 16 species (Nichols and Murphy, 1914). From this collection, Nichols and Murphy described *Anisotremus sarugo* and *Balistes vetula trinitatis*, both currently invalid. The first significant expedition organized by Brazilian researchers was in 1916, led by B. Lobo and P.P. Peixoto Velho, from the Museu Nacional do Rio de Janeiro (Miranda-Ribeiro, 1919). From this collection, a total of 37 species were catalogued and analyzed by A. de Miranda Ribeiro (1919), who also described three other species: *Muraena trinitatis*, *Kyphosus palpebrosus* and *Ophioblennius trinitatis* – only the last is valid, but it is not an

endemic. Later, in May 1950, a new expedition led by W. Besnard, from the Instituto Paulista de Oceanografia, sampled 32 species in the island (Carvalho, 1950). At this point, the four expeditions summed a total of 66 species for Trindade Island.

Almost half a century later, the naturalist J.L. Gasparini joined the Brazilian Navy crew to six expeditions to Trindade, from 1995 to 2000. At this time, the Brazilian Navy was already maintaining a military station on the island and conducting periodic visits, which had a significant contribution to the characterization of the island biodiversity. Bringing SCUBA equipment for the first time to the island and spending 86 days of field work, Gasparini surveyed the ichthyofauna from tide pools to reefs down to 35m depth, preparing the first comprehensive checklist for the shore fishes of Trindade Island (Gasparini & Floeter, 2001). A total of 97 species was recorded, of which six species and one sub-species are endemics. It was also the first time that the species richness, composition, and origin of endemic fishes were hypothesized to be influenced by the Vitória-Trindade Seamount Chain (VTC). The summits of the seamounts come close to the surface and may contribute to current and past population connectivity, as many of them became exposed during the last glacial maximum.

A few years later, a new generation of ichthyologists had several opportunities to visit the island, thanks to a partnership between the Projeto TAMAR/ICMBio (Governmental project for coastal conservation and marine turtles protection) and the Brazilian Navy. During a short period of five years (2007-2012), these surveys increased greatly our understanding of the VTC biodiversity and ecology, including

information from the remote Martin Vaz Archipelago. Today, a partnership between the Brazilian Navy and the Brazilian Ministry of Science, Technology and Innovation maintains a Research Station at the Island, boosting the science by diversifying the research and scientists that visit the place.

Nevertheless, among these new ichthyologists, spending 133 days on the Trindade Island and three days around Martin Vaz, and performing over 100 dives (2007 and 2009), I had the opportunity to find 32 new records of fishes and discover another four endemic species, including a parrotfish and a wrasse from mesophotic depths (Pinheiro et al., 2009). I also described events of mass mortality of fishes (Pinheiro et al., 2010a), patterns of community structure in shallow and mesophotic reefs (up to 46 m) (Pinheiro et al., 2011) and impacts of commercial and recreational fisheries (Pinheiro et al., 2010b and Pinheiro & Joyeux, 2015, respectively) around the island. Another important recent contributor was T. Simon, who visited Trindade eight times in the last few years. His extensive biodiversity work reported another 11 new records for Trindade Island, including two new species and a sub-species (Simon et al., 2013). T. Simon updated the number of species in Trindade to 154 species, prepared the first comprehensive checklist for Martin Vaz Archipelago, with 67 species (Simon et al., 2013), and also produced substantial ecological contributions and evolutionary insights (in Macieira et al., 2015). An expedition of the Jardim Botânico do Rio de Janeiro conducted in March 2009 also yielded important contribution, providing the first quantitative assessment of Martin Vaz reef fishes,

and exploring shallow and mesophotic reefs of the insular complex (Pereira-Filho et al., 2011).

The VTC is composed of volcanic mounts distributed in an E-W alignment, from 200 to 1,200 km off the Brazilian coast, where Trindade and Martin Vaz are the farthest locations and the only islands of the chain. The remainder of the VTC is composed of 17 seamounts with heights up to 2,500 m above the sea bed (Motoki et al. 2012), where at least ten seamounts have summits with depths varying from 50 to 120 m below water surface. The oldest mounts are those nearer to the Brazilian continental shelf (Motoki et al. 2012), while the islands of Trindade and Martin Vaz emerged more recently, between 3 and 0.5 Mya (Almeida 2006). Columbia is the seamount closest to the islands (250 km west of Trindade), and is also the youngest seamount, with nearly 10 My (Fodor and Hanan 2000).

Only two ichthyological surveys had been previously conducted on the VTC seamounts: a Brazilian-French expedition in 1987 (Seret & Andreata, 1992; Andreata & Seret, 1995), with use of bottom trawling and dredging, and the 1990's Program of Evaluation of the Sustainable Potential of Living Resources in the Brazilian Exclusive Economic Zone (REVIZEE), with use of midwater trawls (Braga et al, 2007; 2014), surface and bottom longlines (Martins et al., 2005; 2007). Despite constraints of the limited sampling methods, results from these studies allowed an initial biogeographical analysis in which the VTC was indicated as a Brazilian zoogeographical transitional zone (Martins et al., 2007).

This dissertation aims to present an updated and comprehensive database of the fish biodiversity of the Vitória-Trindade Chain, exploring aspects of its fish biogeography and evolutionary history. The longitudinal arrangement of the VTC, with seamounts summits at mesophotic depths, provides an appropriate context to investigate the role of seamounts as functional islands, including their influence on species richness and endemism levels. These assessments were based, in addition to the previously mentioned expeditions to the islands, on three recent expeditions to the VTC seamounts. Remotely operated underwater vehicles and mixed-gas technical diving with standard open circuit and rebreather apparatus were used to collect fish information and samples. An extensive compilation of unpublished information from scientific fishing, museum vouchers and literature records was also conducted and presented here. The dissertation is thus organized in three sections: Biodiversity, Biogeography and Evolution. This dissertation also calls attention to the conservation of these unique ecosystems, and comments on human impacts that are already reaching these seamounts.

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## RESEARCH ARTICLE

## Fish Biodiversity of the Vitória-Trindade Seamount Chain, Southwestern Atlantic: An Updated Database

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### Abstract

Despite a strong increase in research on seamounts and oceanic islands ecology and biogeography, many basic aspects of their biodiversity are still unknown. In the southwestern Atlantic, the Vitória-Trindade Seamount Chain (VTC) extends ca. 1,200 km offshore the Brazilian continental shelf, from the Vitória seamount to the oceanic islands of Trindade and Martin Vaz. For a long time, most of the biological information available regarded its islands. Our study presents and analyzes an extensive database on the VTC fish biodiversity, built on data compiled from literature and recent scientific expeditions that assessed both shallow to mesophotic environments. A total of 273 species were recorded, 211 of which occur on seamounts and 173 at the islands. New records for seamounts or islands include 191 reef fish species and 64 depth range extensions. The structure of fish assemblages was similar between islands and seamounts, not differing in species geographic distribution, trophic composition, or spawning strategies. Main differences were related to endemism, higher at the islands, and to the number of endangered species, higher at the seamounts. Since unregulated fishing activities are common in the region, and mining activities are

405360/2012-6 to GAF) and Paleocceanographic reconstruction of the Vitoria-Trindade Chain based in calcareous algae records (grant 405419/2012-0 to AB). HTP (Ciência sem Fronteiras; GDE 202475/2011-5) and TS are recipients of doctoral fellowships from CNPq and CAPES (<http://capes.gov.br>), respectively, and EFM of a MSc fellowship from CAPES. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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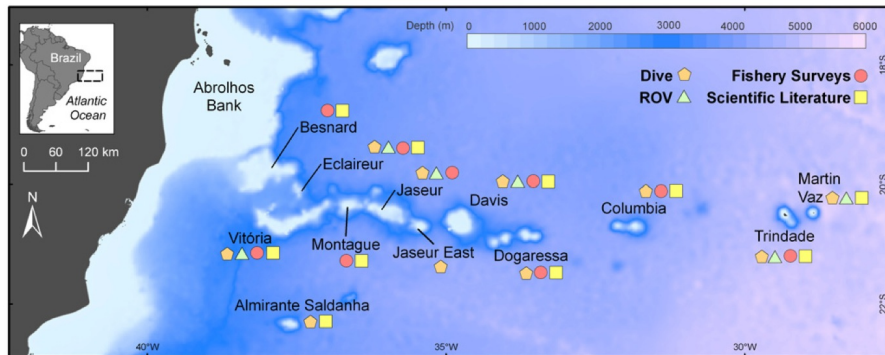
expected to drastically increase in the near future (carbonates on seamount summits and metals on slopes), this unique biodiversity needs urgent attention and management.

## Introduction

Despite the general perception that seamounts are small isolated spots scattered in remote areas, this habitat is one of the most extensive of all oceanic environments [1]. There are hundreds of thousands of seamounts [2] comprising an estimated area of approximately 28.8 million km<sup>2</sup> [1]. The largest contiguous area of seamounts is found in the central portion of the Pacific Plate, where most studies have been conducted [3]. The number of ichthyological surveys on seamounts has increased, and recent data from fishing [4–6] and SCUBA sampling [7–9] have been incorporated into an extensive database for seamount fishes [10–12]. This database has provided the opportunity to study several aspects of seamount fish biodiversity and ecology [10,13], as well as connectivity, biogeography and speciation [11,14–16]. However, biological surveys of seamounts remain sparse [1], mainly due heavy logistics and costs, and consequently extensive marine areas still remain poorly known [17].

Data on south Atlantic seamounts is best described as patchy and of variable quality [18]. For a long time, most of the biological information available on the Vitória-Trindade Seamount Chain (VTC) (19°–21°S, 28°–38°W, Fig. 1) solely referred to the islands. Ichthyological surveys at Trindade Island date back to the early 1900's [19–21]. Present knowledge depicts a rich reef fish fauna [22–26] connected to the continental coast through a stepping-stone process across the VTC seamounts [22,23,27]. However, the high number of endemic species at the islands indicates that genetic connectivity between the continent and islands is limited, although it could have been more effective during low sea levels [25,26,28]. Only two ichthyological surveys had been previously conducted on the VTC seamounts: a Brazilian-French expedition in 1987 [29,30], with use of bottom trawling and dredging, and the 1990's Program of Evaluation of the Sustainable Potential of Living Resources in the Brazilian Exclusive Economic Zone (REVIZEE), with use of midwater trawls [31,32], surface and bottom longlines [33,34]. Despite constrained by the limited sampling methods, results from these studies allowed an initial biogeographical analysis in which the VTC was indicated as a Brazilian zoogeographical transitional zone [34].

The VTC is composed of volcanic mounts disposed in an E-W alignment, from 200 to 1,200 km off the Brazilian coast. Trindade and Martin Vaz Archipelago, the farthest locations from the continental shelf, are the only islands of the chain, and, therefore, the sole areas able to support species restricted to very shallow habitats. The remainder of the VTC is composed of 17 seamounts with height up to 2,500 m above the sea bed [35], where at least ten seamounts have summits with depths varying from 50 to 120 m below water surface. The VTC lays over the South American Plate, between 19° and 21°S, along a fracture zone disposed transversely to the Mid-Atlantic Ridge. The chain was formed by the activity of the Trindade hotspot mantle plume [35–37], with the plate moving westward at a rate of 23.1 km My<sup>-1</sup> [36], but the development of its central segment may have been synchronous, involving an event associated with the lateral spreading of the plume over weaker mantle zones [38]. Despite this controversy, it is widely accepted that the VTC emerged during the Cenozoic, starting in the Tertiary (60–40 Mya) [39]. The oldest mounts are those nearer to the Brazilian continental shelf [40], while the islands emerged more recently, between 3 and 0.5 Mya [36]. Columbia is the seamount closest to the islands (250 km west of Trindade, Fig. 1) and is also the youngest seamount, with nearly 10 My [37].



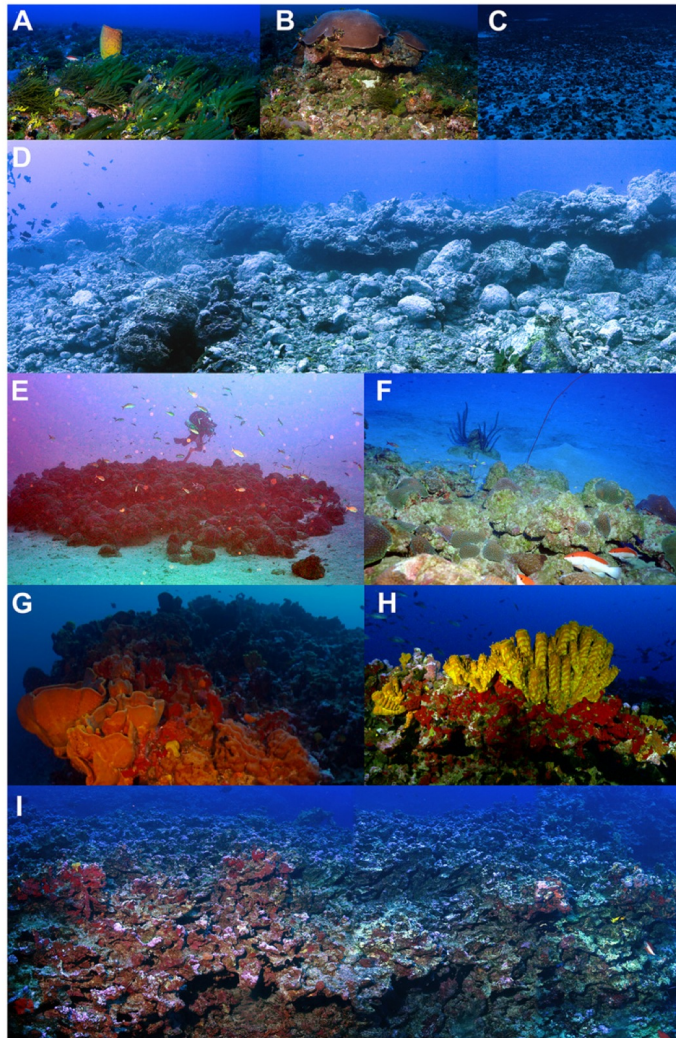
**Fig 1. Vitória-Trindade Chain, Southwestern Atlantic.** Sites surveyed in this study are named. Bathymetric data from Smith and Sandwell [105].

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Oceanic circulation in the western part of the VTC is dominated by the Brazil Current, which flows south from about 13° to 38° S [41]. This superficial current mostly follows the continental shelf edge and may form a barrier to larval movements and faunal migration from the adjacent coastline [42]. On the other hand, eddies, Taylor cones, dynamical uplifts and amplification of tidal movements are common oceanographic features associated with seamounts [43–45] and can contribute to water mass and biological connectivity. Upwelling events driven by topographical complexity and oceanographic features are also frequent and promote nutrient enrichment of the oligotrophic oceanic surface waters of the VTC region [45–47].

Rhodolith beds are the main benthic habitat found at mesophotic depths (30–120m) of the VTC, with the calcareous algae nodules associated with many invertebrate species and frequently covered by macroalgae (Fig. 2; [48,49]). Calcareous algae that compose the rhodoliths are major benthic primary producers delivering substantial amounts of dissolved carbon in the oligotrophic waters of the VTC region [49]. Coralline and rocky reefs are common in the shallow zones of the islands (Fig. 2), but sparse and patchy biogenic reef structures are also found at mesophotic depths on seamount summits, with some high-relief structures reaching depths as shallow as 17 m and sheltering rich shallow water reef fish communities [50]. These biogenic reefs are predominantly built and covered with encrusting coralline algae, besides important contributions from sponges and corals (Fig. 2). Thirteen hermatypic coral species are known to occur in the VTC mesophotic zone [51].

Although sheltering a high diversity of habitats and species, the fragility of seamount ecosystems is widely recognized [33,52,53]. Worldwide, they have been targeted by intense fishing activities [54,55], leading to over-exploitation and habitat damage [11,34,56]. The VTC is targeted by Brazilian and foreign fishing vessels using surface and bottom longlines, hand lines and trawling [57]. Trawling by foreign vessels has been allowed in the continental slope and at seamounts off the N-NE Brazilian Economic Exclusive Zone (EEZ) [58]. On these habitats, overexploitation is generally followed by drastic reduction (boom-and-burst cycle, [52]) or even extinctions [59]. This occurs because seamounts and oceanic islands have similar features, such as low carrying capacity due to isolation and limited population size. Processes such as larval input from continental shelves or other oceanic sources are generally unable to sustain high fishing levels in these relatively small and isolated systems.



**Fig 2. Diversity of habitats on the VTC.** (A) rhodolith beds, extensively found on seamount summits and island' shelves, (B) rocky reefs from Trindade and Martin Vaz islands, (C) patch reefs from Trindade Island, (D) Coralline reef structures covered of sponges at Davis Seamount; (E) High relief and complex reef structures that reaches depths of 17 m at Davis Seamount. Photos by R.M. Macleira, R. Francini-Filho, R.L. Moura, H.T. Pinheiro, PANGEA expedition.

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In order to better understand the biodiversity and distribution of species in the VTC, this paper presents and analyzes an extensive database about the composition of the fish assemblages associated to the VTC seamounts and islands (Fig. 1), highlighting the main biogeographical and macroecological implications from this new and updated database [17]. This assessment provides a comprehensive coverage of the VTC ichthyofauna built on the use of remotely operated underwater vehicles and mixed-gas technical diving with standard open circuit and rebreather apparatus, as well as from a compilation of unpublished information from scientific fishing, museum vouchers and literature records. This database includes new records and depth range extensions, and provides insights upon the structure of assemblages. The present paper also calls attention to the conservation of these unique ecosystems, and comments on human impacts that are already reaching these seamounts.

## Results

### Scientific Diving Contribution

The scientific diving expeditions yielded 128 fish species on the seamounts, 119 of them (93%) being new records, and 113 species at the two islands (12 new records) (see [S1 Annotated Checklist](#)). Known depth range was extended for 49 species, six to shallower and 43 to deeper waters (see [S1 Annotated Checklist](#)). Two new species belonging to the genera *Opistognathus* and *Lythrypnus* were found at seamounts and Trindade Island. Five species previously considered endemic to Trindade and Martin Vaz islands were recorded on seamounts [*Elacatinus pridisi*, *Halichoeres rubrovirens*, *Hypoleurochilus brasil*, *Lythrypnus* sp.2 (as in [60]) and *Sparisoma rocha*]. However, the islands still shelter endemic fishes that were not found on the seamounts (*Acyrtus* sp., *Entomacrodus* sp., *Malacoctenus brunoi*, *Scartella poiti*, and *Tomicodon* sp.).

### REVIZEE and Fishery Surveys Contribution

The REVIZEE Program and our fishery surveys yielded 102 species over the VTC seamounts and 46 in the islands. These captures added 72 new records for the seamounts and 11 new records for the islands (see [S1 Annotated Checklist](#)). Known depth range was extended for 15 species, nine to shallower and six to deeper waters (see [S1 Annotated Checklist](#)).

### VTC Fish Diversity

A total of 273 fish species (26 elasmobranchs and 247 bony fishes) were recorded on the VTC (see [S1 Annotated Checklist](#)). The fish fauna of the VTC is composed of 21 orders and 82 families, with dominance of Perciformes (39 families, 145 species), followed by Anguilliformes (6 families, 23 species) and Tetraodontiformes (6 families, 22 species). Labridae was the most speciose family (22 species), followed by Epinephelidae (17), Carangidae (16), Myctophidae (14), Muraenidae (12), Carcharhinidae (11), Scorpaenidae (9), Gobiidae (8) and Pomacentridae (8). The most speciose genus was *Carcharhinus*, with 9 species, followed by *Diaphus* (8), *Gymnothorax* (7), *Sparisoma* (6), *Halichoeres* and *Scorpaena* (5), and *Chromis*, *Mycteroperca* and *Thunnus* (4). One hundred and eighty-nine species are primarily associated with reef environments, whereas 87 species have pelagic or bathydemersal habits. Most species have a wide geographic distribution; 58% are western or amphi-Atlantic and 22% are circumglobal. Twenty-two species occur only in the Brazilian Province (*sensu* [61]) (8% of the total or 14% of the reef fish fauna) and 11 species are endemic to the VTC: *Acyrtus* sp., *Elacatinus pridisi*, *Entomacrodus* sp., *Halichoeres rubrovirens*, *Hypoleurochilus brasil*, *Lythrypnus* sp. 1, *Lythrypnus* sp. 2, *Malacoctenus brunoi*, *Scartella poiti*, *Sparisoma rocha* and *Tomicodon* sp.

Macro-carnivores composed the richest trophic guild (117 species), followed by macro-invertivores (58), planktivores (47) and roving herbivores (14). Most of the species are pelagic spawners (192) and the remainder lay demersal eggs (27) or are viviparous (28). Twenty-four species are considered endangered: 20 of them are listed in the IUCN Red List as critically endangered (CR;  $n = 2$ ), endangered (ED;  $n = 2$ ) or vulnerable (VU;  $n = 16$ ). Eight species are listed as endangered in the Brazilian Red List [62]. Additional 13 species are considered near threatened (IUCN Red List) and nine are over-exploited (Brazilian Red List; see [S1 Annotated Checklist](#)). Habitats with the highest number of species were reefs, with 160 species, followed by rhodolith beds (130 species), water column (100) and sandy bottoms (28). The water column had the highest number of exclusive species (70 species only occur in this habitat), followed by reefs (59), rhodolith beds (20) and sand (7).

### Comparison between seamounts and islands

Two hundred and eleven fish species (67 families) were recorded on the seamounts and 171 (63 families) at the islands. One hundred and ten species (40%) were widely distributed across the VTC on both seamounts and islands, whereas 101 (37%) occurred exclusively on seamounts and 61 were exclusive to the islands (23%). Only six species were recorded at all sampled sites: *Balistes vetula*, *Cephalopholis fulva*, *Coryphopterus thryx*, *Holocentrus adscensionis*, *Malacanthus plumieri* and *Stegastes pictus*. Trindade Island features the richest fauna, followed by Vitória and Davis seamounts (Table 1).

Fish assemblages did not differ significantly between seamounts and islands in regards to geographic distribution of the species (Chi-squared test;  $p = 0.568$ ), trophic habit (Chi-squared test;  $p = 0.257$ ) or spawning mode (Chi-squared test;  $p = 0.536$ ) (Fig. 3). However, the islands shelter almost twice the number of endemic species than the seamounts, whereas seamounts showed a higher number of endangered species (Fig. 3).

Reef habitats showed higher species richness than other habitats, sheltering 70% of all species at islands and 58% at seamounts. The number of exclusive species found in each habitat differed significantly between islands and seamounts (Chi-squared test;  $p = 0.003$ ). At seamounts, exclusive species for the water column were three times more numerous than that of rhodolith beds, while at islands reefs held six times more exclusive species than rhodolith beds (Fig. 3).

### Discussion

Seamounts of the VTC have a relatively high fish diversity that is, overall, similar or higher than those at several oceanic islands in the Atlantic Ocean [63,64] or in other biogeographical provinces such as Caribbean Sea [9,65,66], Tropical Eastern Pacific [67], Southwestern Indian Ocean [68] and the northwestern Hawaiian seamount chain [69]. The recent increase in the number and scope of scientific diving expeditions, which take advantage of breathing-gas mixes and rebreathers, is improving the biodiversity assessment of mesophotic reefs at remote oceanic spots and is leading to many important discoveries. So far, scientific diving on the VTC seamounts increased the list of known fish species by 80% (an increase of 85% when considering fishery data) and extended the known depth range for 64 species. Additionally, almost all species recorded on the VTC seamounts have not been listed in worldwide reviews of seamount fish fauna [70] and the present database increases by more than 25% the number of fish species known to inhabit seamounts [71].

The endemism level of reef fishes at the VTC (7% for the entire chain and 9.6% for the islands only) is high compared to other Atlantic oceanic localities [63]. VTC endemics are also important for southwestern Atlantic, since they represent about 11% of the total number of endemic reef fishes found in the Brazilian Province. Thus, the VTC can be considered a

Table 1. Number of species recorded in each sampling site of the Vitória-Trindade Chain, southwestern Atlantic.

	Vitória	Al Saldanha	Besnard	Montague	Jaseur	Jaseur East	Eclaireur	Davis	Dogaressa	Columbia	Trindade	Martin Vaz
Total number	108	28	44	45	48	71	38	103	70	43	173	73
Reef fishes	94	22	24	19	47	65	35	88	68	42	137	67
ACANTHURIDAE	3	0	0	0	3	3	2	3	1	0	2	2
BALISTIDAE	3	3	3	1	4	3	2	3	4	3	4	3
CHAETODONTIDAE	4	1	0	0	1	2	0	3	3	0	3	2
EPINEPHELIDAE	6	2	4	1	7	7	5	7	7	7	11	6
HAEMULIDAE	0	0	0	0	0	0	0	0	0	0	1	0
LABRIDAE	11	6	0	0	6	5	4	14	7	3	16	10
LUTJANIDAE	2	0	3	0	3	1	2	4	1	2	3	0
POMACANTHIDAE	3	1	0	1	2	3	3	3	2	1	2	2
POMACENTRIDAE	5	1	0	0	2	6	3	6	2	2	7	6
SERRANIDAE	4	0	0	0	3	1	1	1	2	0	2	1

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biodiversity hotspot where the number of known endemic species is still increasing with additional collections and taxonomic studies (Fig. 4) [23,26].

Increase in maximum depth and presence of fishes previously considered as Trindade endemics on several seamounts raise some interesting evolutionary hypothesis about adaptation and speciation processes for reef fishes in this region. Populations of typically shallow-water herbivores (e.g., *Acanthurus bahianus* and *Stegastes fuscus*) and invertivores fish (e.g., *Hali-choeres poeyi* and *H. penrosei*) which were unexpectedly found on mesophotic seamount's summits (55–70 m deep) can be evolving in isolation since the last oceanic transgression 20 Ky

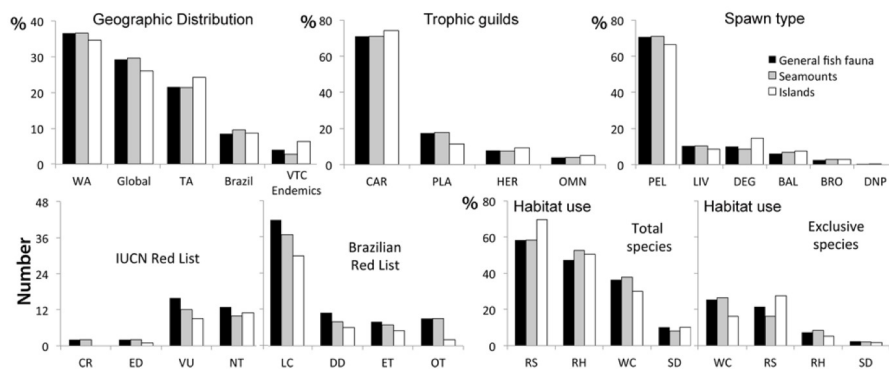
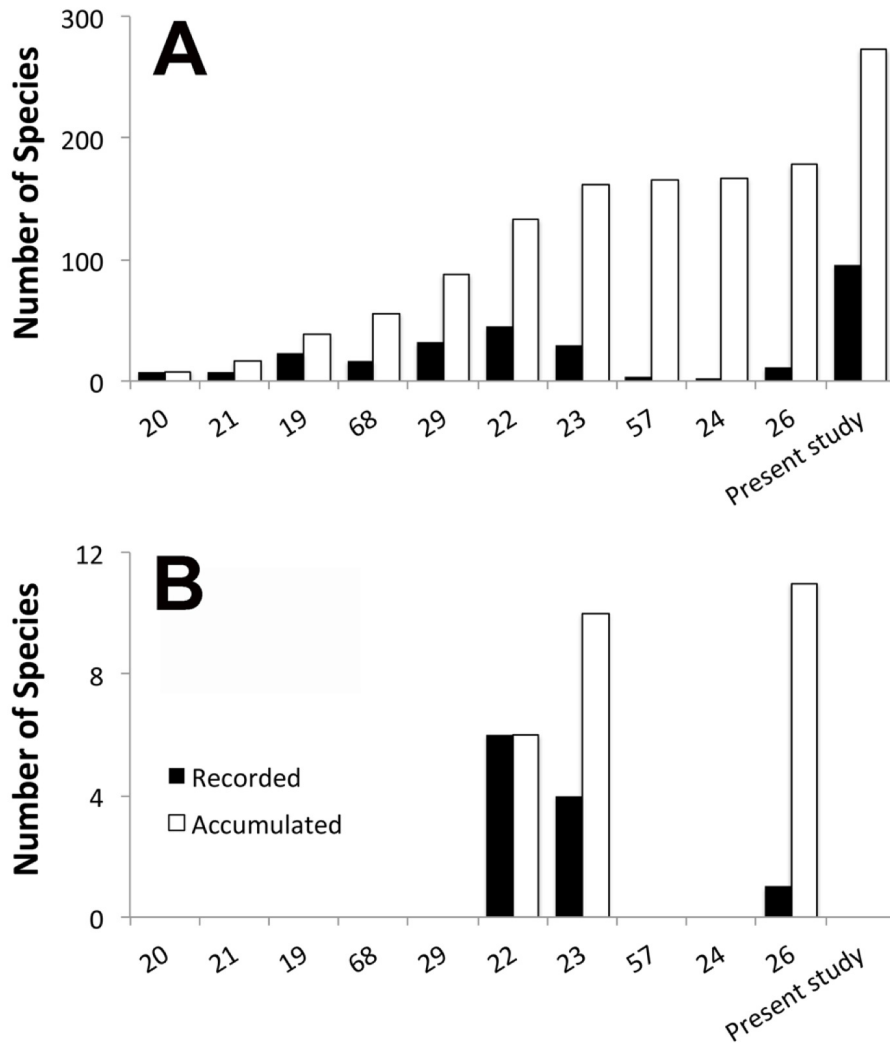


Fig 3. Summary of the fish assemblage characteristics found along the VTC. Geographic distribution (WA = Western Atlantic; TA = Trans Atlantic). Trophic guilds (CAR = carnivores; PLA = planktivores; HER = herbivores; OMN = omnivores). Spawn type (PEL = Pelagic eggs; LIV = Live birth; DEG = Demersal egg; BAL = Balistid-type demersal eggs; BRO = Brooded egg; DNP = Demersal eggs no pelagic phase). Endangered status following IUCN (CR = Critically Endangered; ED = Endangered; VU = Vulnerable; NT = Near threatened; LC = Least concern; DD = Data deficient) or Brazilian Red List (ET = Threatened of extinction; OT = Over-exploited). Habitat use (total species = proportion between the number of species that use one habitat on the total number of species found in this habitat); exclusive species = proportion between the number of species that use exclusively one habitat on the total number of species found in this habitat) (RS = reefs; RH = rhodolith beds; WC = water column; SD = sand).

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**Fig 4. Number of species presented per published manuscripts about Vitória-Trindade Chain ichthyofauna. A) General fish species. B) Endemic fish species.**

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B.P. or suffering strong selection towards life in deeper habitats. Moreover, before the present study, endemism at Trindade and Martin Vaz islands was considered to be a result of allopatry between insular and continental populations [22]. As the islands are positioned at the extreme of the ridge and hold the only strictly-shallow habitats of the chain (tidepools, sandy beaches and rocky shores), a considerable portion of their species, especially the strictly-shallow water dwellers (e.g., Blenniidae, Gobiiesocidae and Labrisomidae) could actually have colonized these islands via stepping stones in regressive periods of low sea level [22,25,26,28].

The presence of endemic species over the VTC seamounts also calls attention for a strong ecological barrier between the continental shelf and the westernmost oceanic mounts, a barrier that can bolster ecological and/or parapatric speciation [72]. Environmental differences among continental shelf, seamounts and islands may be strong drivers for natural selection and speciation and, in addition, the Brazil Current (BC), which flows south along the outer shelf and slope, may also intensify this ecological barrier, mainly constraining larval flow between continental coast and seamounts. Most of species hindered by such constraint are dependent on specific shallow-water habitats (e.g. tidepools, seagrass beds, mangroves) or on demersal connectivity such as cross-shelf gradients [73]. For instance, several fish groups, such as haemulids, gobiids, and lutjanids, do not readily cross this environmental barrier. On the other hand, despite differences in habitat diversity and fish composition between seamounts and islands (only 40% of compositional overlap), their similarities in assemblage structure (regarding geographic distribution of species, trophic habit and spawning mode) suggest similar equilibrium mechanisms for community organization and maintenance.

Genetic analyses supported the remarkable singularity of the VTC environments, showing that some of those VTC endemics, such as *H. rubrovirens* and *S. rocha*, are relict [74,75], or paleo-endemic species [76]. This suggests that old evolutionary lineages may have been preserved on the VTC seamounts and islands while continental lineages evolved in different species or became extinct. A recent study shows that such refugia contributed to current patterns of biodiversity distribution in the Indo-Pacific region [77]. Brazilian seamounts are hypothesized as refuges for scleractinian corals during the last ice ages, with further re-colonization of the continental shelf during the last transgression [78,79]. Conversely, the paleoendemic reef fishes seem to have remained isolated on the VTC. Such relict lineages deserve special attention for conservation efforts since they carry important and unique genetic and evolutionary information [80].

Despite the ubiquity of large carnivorous fishes such as groupers, jacks and barracudas on the VTC seamounts (authors' personal observations), indications of overfishing are very evident, especially at the Trindade and Martin Vaz islands [25,57]. Unmanaged fishing activities done by domestic and foreign fishing vessels have been regularly recorded at VTC [57] albeit the vulnerability of oceanic islands and seamounts to fishing activities is well known [56,59]. On seamounts, little regeneration is observed even after trawling over deep-coral ecosystems has been discontinued, and full habitat regeneration is estimated to require centuries [81]. Apparently, highly destructive trawling activities have not yet occurred in the VTC like those conducted at seamounts off N-NE Brazil [58], but VTC seamount chain is presently lacking legal protection.

Carbonate's extraction is an emergent and highly destructive activity threatening the VTC seamounts, and has been already conducted at Davis Seamount between 2009 and 2011 [82]. This industry aims at extracting the slow-growing rhodoliths to produce fertilizers for sugar cane and other agricultural commodities upon which Brazil's economy is dependent [82]. This activity thus directly threatens almost half of the species listed in the present study. Besides mining of carbonates, other possible threats to VTC biodiversity are the extraction of iron-manganese [83] and cobalt-rich crusts in deeper areas of the slope and seabed [84]. These mining activities tend to destroy the sea bed and its associated biodiversity [85], representing major threats to the VTC, similarly to the situation in some areas of the Pacific [86–88].

While hindering seabed mining based on National-level permits, the fact that some VTC seamounts are still Areas Beyond National Jurisdiction (ABNJ) challenges the management of fisheries and other natural resources. However, UN General Assembly call upon states and Regional Fisheries Management Organizations (RFMOs) to protect Vulnerable Marine Ecosystems (VMEs) in ABNJ—including seamounts—from destructive fishing practices. The area of the VTC outside the Brazilian EEZ is presently within the area requested by Brazil for continental shelf extension. If accepted by the Commission on the Limits of the Continental Shelf (CLCS) of the United Nation Convention of the Law of the Sea (UNCLOS), Brazil would not only have the full right to exploit living and non-living (mineral) resources, but also the duty of protecting its unique biodiversity. The establishment of Marine Protected Areas is a recommended measure for the region, following the example of many countries that have already set aside seamounts within their EEZs for protection (such as Australia, New Zealand and UK—Chagos Archipelago [54,89,90]). Additionally, programs and actions for monitoring, evaluating and managing fishery resources in the VTC region are urgently needed [91]. One option is the application of the Brazilian National Satellite Tracking Project (PREPS), which monitors fishing boats over 15 m of length. This program should be expanded to include the smaller 10 m-vessels that operate in critical areas such as the VTC and elsewhere in Brazil [57].

The VTC is possibly among the most endangered and important oceanic regions of the world (based in criteria detailed in [92,93]), and is an important ecological corridor and an evolutionary hotspot that has a vital role in the maintenance of the biodiversity of the remote Trindade and Martin Vaz islands. However, if not managed effectively, it is possible that several peculiarities of this diverse and extraordinary oceanic system will soon be permanently lost. Immediate action at the VTC must be included in the priority agenda for environmental conservation in Brazil, the country that owns and claims additional rights and duties over the unique Vitória-Trindade Seamount Chain.

## Methods

### Fish database

Primary data was acquired during three scientific diving expeditions to the VTC seamounts and islands, in 2009 (12–26 March) and 2011 (3–26 February and 1–18 April). These expeditions covered the photic and upper mesophotic zones (0–120 m depth) of the two islands and eight seamounts: Almirante Saldanha, Vitória, Eclairer, Jaseur, “Jaseur East” (Columbia Bank in [35]), Davis, Dogaressa and Columbia (Fig. 1). Sampling included visual, video and photo records, as well as collection of voucher specimens by divers (hand nets and spear-guns in April 2011) using technical open-circuit SCUBA or closed-circuit rebreathers (Megalodon) with mixed-gases (TRIMIX and EAN). Fish collection at all localities along the VTC seamounts and islands and collection of the protected species *Elacatinus figaro* at the same sites were authorized by the Brazilian Environmental Agency [Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 12786–1 and 20880–2)]. Ten hours of video from two remotely operated underwater vehicles (ROVs) (Seabotix LBV 150S2 and Video Ray SCOUT) were used for habitat descriptions and provided extra faunal records.

Primary data from fishery surveys (surface longline, bottom longline, midwater trawling and angling activities; see [31–34,91,94]) were incorporated in the database. Fishery sampling was performed over eight volcanic mounts (Vitória, Eclairer, Besnard, Montague, Jaseur, Davis, Dogaressa, Columbia and Trindade) during scientific cruises of the REVIZEE Program and to a much lesser extent TAMAR/ICMBio monitoring assessments. REVIZEE stands for Program for the evaluation of the sustainable potential of living resources of the exclusive economic zone, a government-supported program conducted between 1994 and 2006. Only

**Table 2. Summary of sampling effort, data sources and sampling site characteristics of the Vitória-Trindade Seamount Chain, southwestern Atlantic.**

Site	Summit area (km <sup>2</sup> )	Substrate type	Sampling techniques	Dive depth range (m)	Number of dives	Primary data type	References
Vitória	1184	RH/RS/PR/SD	DIV/ROV/ ZEE/CF	35–120	38	VO/PHO/VID/VIS/OB/ZEE	Primary data; [94]
Almirante Saldanha	37	RH/RH/SD	DIV	66	3	PHO/VID/VIS/	Primary data; [94]
Besnard	1978	Unknown	ZEE	-	-	ZEE	Primary data; [33,94]
Montague	124	Unknown	ZEE/CF	-	-	ZEE/OB	Primary data; [29,94]
Jaseur	89	RH/RS/SD	DIV/ROV/ ZEE	62	5	PHO/VID/VIS/ ZEE/OB	Primary data
Jaseur East	99	RH/RS/SD	DIV	62	20	VO/PHO/VID/VIS/	Primary data
Eclaireur	6,4	RH/SD	DIV/ROV	71	6	PHO/VID/VIR	Primary data; [33]
Davis	1002	RH/RS/SD	DIV/ROV/ ZEE	17–57	46	VO/PHO/VID/VIR/ UVC/ZEE	Primary data; [33]
Dogaressa	80,5	RH/SD	DIV/ZEE	65	14	VO/PHO/VID/VIR/ ZEE	Primary data; [29]
Columbia	36,5	RH//PR/SD	DIV/ZEE	84	3	PHO/VID/VIR/ZEE	Primary data; [29,33]
Trindade	85	RH/RR/PR/SD	DIV/ROV/ ZEE	0–85	200	VO/PHO/VID/VIR/ UVC/ZEE	Primary data; [19–24,26,28,57,104]
Martin Vaz	24	RR/SD	DIV/ROV	0–30	20	VO/PHO/VID/VIR/ UVC	Primary data; [23,24,26,57]

Type of substrate: RS—Reef structure (carbonatic); RR—Rocky reef; PR—patch reef; RH—Rhodolith bed; SD—Sand and unconsolidated substrate. Sampling techniques: DIV—Diving; ROV—Remote operated vehicle; CF—Commercial fishing; ZEE—REVIZEE scientific fishing. Primary data type: VO—Voucher specimen; PHO—photo record; VID—video record; VIS—*in situ* visual record; UVC—underwater visual census; ZEE—REVIZEE project record; OB—onboard observer record during commercial fishing.

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records in waters shallower than 120 m were used here. Information about sampling effort and general characteristics of the sites surveyed are provided in Table 2.

Publications on the fish fauna of the seamounts are limited to the results of the 1987 Brazilian-French expedition MD55 Brazil [29,30] and REVIZEE reports [31–34,91,94]. For the islands, all earlier published material was recently reviewed by [26]. This later study includes a checklist of Martin Vaz, cited as “H.T. Pinheiro pers. comm.” that originated from a three-day, 15 diving hours expedition in February 2007. New records for species not covered in [26] were obtained by ACF (pers. comm.) and the above-mentioned recent scientific expeditions.

A species list, with comments on selected biological features was built using all available records. Information was broken down by seamount/island and was given in order of record reliability: deposited vouchers, literature, photo/video records, unpublished records (REVIZEE and fishery surveys) and visual records (S1 Annotated Checklist). The VTC fish database is also available at <https://marinebiodiversity.lncc.br> (access number knb.9.2), a public and easily accessible online database for marine biodiversity.

Traits of each species (spawning mode, trophic guilds, depth range, geographic distribution and conservation status) were compiled from the literature [62,95–102] and were complemented by the authors’ observations. The habitats in which species were found (reefs, rhodolith beds, water column or sand) were assigned for each recorded occurrence. A short video entitled “Fishes of the Vitória-Trindade Chain”, showing the various habitats of VTC seamounts, is available at <http://youtu.be/ZsV3AkDvvvE> (a trailer of the movie is also available as S1 Movie). Differences between assemblages composition at seamounts and islands were tested

by Chi-squared tests in respect to species traits [103]. Summit area, displayed in Table 2, was calculated in the program ArcGis based on the 150 m isobaths from nautical charts (Diretoria de Hidrografia e Navegação—DHN: 20 and 21).

### Ethics Statement

The collection of fishes during the April 2011 expedition is in accordance with the ethical principles for animal experimentation and approved by the Ethics Committee for the Use of Animals of the Universidade Federal do Espírito Santo (CEUA-UFES 017–2009). There were no collections in the March 2009 and February 2011 expeditions. Fish collection at all localities along the VTC seamounts and islands and collection of the protected species *Elacatinus figaro* at the same sites were authorized by the Brazilian Environmental Agency, Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 12786–1 and 20880–2 to JJC).

### Supporting Information

#### **S1 Annotated Checklist. Annotated checklist of the fishes from the Vitória-Trindade Chain, southwestern Atlantic.**

(PDF)

#### **S1 Movie. Trailer of the movie “Fishes of the Vitória-Trindade Seamount Chain”.**

(MP4)

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### Author Contributions

Conceived and designed the experiments: JLG JJC RMM EM RLM HTP TS. Performed the experiments: GAF PASC BPF RBFF JJC RMM ASM EM RLM GO CRP HTP TS LBX ACF. Analyzed the data: GAF ACB PASC BPF CELF SRF RBFF ASM GO LAR IS LBX ACF. Wrote the paper: JLG JJC RMM EM RLM CRP HTP JBT TS.

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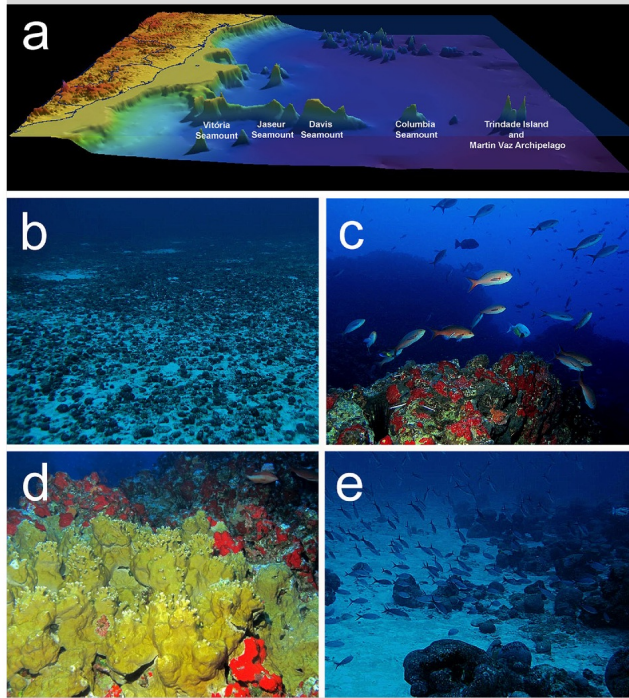
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# Reef sites

## Reef oases in a seamount chain in the southwestern Atlantic



**Fig. 1** Reef habitats of the Vitória-Trindade Chain (a), off central Brazil: (b) rhodolith beds (60 m depth); (c) and (d) coralline algae reefs of Vitória Seamount, with details of the reef crests (35 m) and (e) reef-sand interface (55 m). Map: J. B. Teixeira. Photos: H. T. Pinheiro

The Vitória-Trindade Chain (VTC) is a line of seamounts extending 1,200 km eastwards from the central Brazilian coast (20°S) to the Trindade and Martin Vaz islands (Fig. 1a). These seamounts present mesophotic summits (60–55 m depths) that are predominantly flat and covered by soft sediments and rhodolith beds (Pereira-Filho et al. 2011; Fig. 1b). High-relief biogenic reefs (Fig. 1c) were only recently found in the VTC, during two expeditions in 2011. These singular structures are mostly built by crustose coralline algae and sparse corals and hydrocorals (Fig. 1d), reaching up to 35–17 m (Vitória and Davis seamounts) and 62–84 m depths (Jaseur and Columbia seamounts). Structural reefs shelter a richer and more abundant fauna than the surrounding flat beds, including large, endangered, and commercially important reef fishes (Fig. 1e). Although being small and sparse, reef patches represent a critical habitat in the VTC, functioning as connectivity stepping-stones for several reef organisms that reach and maintain permanent populations in the isolated islands (Floeter and Gasparini 2000). As fishing effort is largely unregulated and mining of carbonates is already taking place at the VTC, the region urgently needs increased scientific and conservation efforts.

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**Ecological drivers enlighten the role of seamounts as functional islands for reef fishes****ABSTRACT**

**Aim** To identify the drivers of reef fish distribution and assemblage structure along a volcanic ridge composed by seamounts and oceanic islands.

**Location** The seamounts and oceanic islands of the Vitória-Trindade Chain, southern Atlantic, and the central coast of Brazil.

**Methods** The distribution and ecological traits of 247 species was compiled for mainland, seamounts and islands. Cluster analysis was used to assess the faunal similarity among mainland regions, seamounts and islands sites. Correlations between matrices of beta diversity and independent variables, built to test “target-area-distance”, “stepping stones assembly” and “age” hypotheses, were evaluated with Mantel tests. Ecological drivers of species dispersal from mainland, habitat characteristics and different faunistic distribution patterns over the volcanic ridge were explored through generalized linear models.

**Results** Similarity analysis clustered seamounts and islands according to species richness, habitat diversity and distance from the coast. Richness did not decrease with distance from mainland. Similarity among volcanic buildings increases with distance from mainland. A stepping-stones process thus appears to assemble the VTC reef fish composition. Multihabitat use and maximum depth were the main species traits

accounting for the distribution range. Others traits, such as body size, spawning type, mobility and rafting hability, were important in characterizing different distribution patterns.

**Main conclusions** Assembly rules on seamounts and islands seem to be led by habitat suitability to recruitment and population establishment, followed by connectivity and geographical isolation, that are determinant factors for persistence across the region. Habitat characteristics and ecological traits of species are the main drivers for assemblage composition and biogeography, and consequently the stepping stones assembly. The contemporary reef fish biogeography gives insights about the changes of dispersal along the VTC with sea-level oscillations. This work provides evidence of the role of seamounts as functional islands for reef fishes that cannot colonize oceanic islands directly from mainland.

**Keywords** biogeography, dispersal, oceanic islands, southwestern Atlantic, stepping-stones, Vitória-Trindade Chain.

## INTRODUCTION

Numbering more than 40 thousands, seamounts cover approximately 10 million km<sup>2</sup> of the oceans (Etnoyer *et al.*, 2010), and although considered one of Earth's most representative biomes, they are poorly described and understood, remaining among the least known ecosystems on earth (Clark *et al.*, 2010, 2012; Etnoyer *et al.*, 2010; Kim & Wessel, 2011). Globally, less than 600 seamounts have been biologically surveyed (Etnoyer *et al.*, 2010; Kvile *et al.*, 2014), few belonging to seamount chains (Rowden *et al.*, 2010), and generalizations about their biodiversity and ecology are still incipient (Pinheiro *et al.*, 2015a). However, efforts to study this system are growing (Kvile *et al.*, 2014), and extensive databases have been organized and analyzed in order to better understand the processes and mechanisms that drive seamounts communities (Clark *et al.*, 2012).

Seamounts, in most cases, are emergent or old islands (Stuessy *et al.*, 2012), and the mechanisms that regulate their ecology match with those observed for islands in many aspects, including the balance of species richness by immigration and extinction (Losos & Ricklefs, 2009), ecosystem area (Heaney, 2007; Losos & Ricklefs, 2009), geological history (e.g. erosion, bioconstruction, vicariance events) and oceanography (Hobbs *et al.*, 2012; Keith *et al.*, 2013). Over the vast deep ocean, seamounts are often subject to upwellings and higher primary production (Worm *et al.*, 2003; Genin, 2004; Samadi *et al.*, 2007), and may be considered as islands for reef-associated species for providing patches of suitable habitat (Stocks & Hart, 2007; Wessel, 2007; Hart & Pearson, 2011; Pinheiro *et al.*, 2014).

Seamount endemism levels can be higher than on nearby continental shelves (Schlacher *et al.*, 2010; Pante *et al.*, 2015), but in some cases smaller than in oceanic islands (Pinheiro *et al.*, 2015a). However, evolutionary mechanisms and processes that shape seamount endemism and assemblages dynamics remain poorly understood, challenged by observation and theoretical approaches (Gaines *et al.*, 2007; O'Hara *et al.*, 2010; Rowden *et al.*, 2010; Clark *et al.*, 2012). A common assumption is that seamount chains work as stepping-stones for reef-associated species, attenuating the ecological (richness and community assembly) and evolutionary consequences of isolation by the presence of intermediate sub-populations (Hubbs, 1959).

In the southwestern Atlantic, the seamounts of the Vitória-Trindade Chain (VTC) have been assigned as stepping-stones for propagules, boosting a high diversity of species in the distant Trindade-Martin Vaz insular complex (TMVIC) (Floeter & Gasparini, 2000; Joyeux *et al.*, 2001; Coimbra & Carreño, 2012; Pinheiro *et al.*, 2015a). However, the endemism level of reef fishes at TMVIC is considered high (9.6%) (Simon *et al.*, 2013a; Pinheiro *et al.*, 2016), comparable to other remote oceanic islands in the Atlantic such as St. Paul's Rocks and Cape Verde Islands (Floeter *et al.*, 2008). This high endemism have been usually hypothesized to be driven by vicariance events and decrease in connectivity during high-stand sea levels (Gasparini & Floeter, 2001; Simon *et al.*, 2013a; Macieira *et al.*, 2015). However, more recently, ecological factors have also been suggested to promote speciation in this seamount chain (Pinheiro *et al.*, 2015a).

The longitudinal arrangement of the VTC, with seamount summits at mesophotic depths, provides an appropriate context to investigate the role of seamounts as functional islands (FIs; islands in function if not in nature), including their influence on species richness and endemism levels in the TMVIC (Leal & Bouchet, 1991; Gasparini & Floeter, 2001; O'Hara *et al.*, 2010; Pinheiro *et al.*, 2015a). Initial studies on the effect of geographic isolation on gastropods, algae and other invertebrates highlight the continental shelf as an important source of propagules for VTC populations, suggesting the role of the seamounts as stepping-stones (Leal & Bouchet, 1991; O'Hara *et al.*, 2010). Reef-associated organisms, in general, disperse primarily during their larval stage (Victor, 1991; Leibold *et al.*, 2004; Kritzer & Sale, 2006), and although Stocco & Joyeux (2015) showed that reef fish larvae are abundant along the VTC, ecological and biogeographical factors that drive species composition along the chain are still unknown (Pinheiro *et al.*, 2015a).

This study aims to identify which factors drive the biogeography of reef fishes along the VTC. Patterns of richness and species distribution were explored in order to determine (1) the relationship between reef fish assemblage composition, distance from continental shelf, degree of isolation, habitat diversity, summit area and age (geological history) of seamounts and islands; and (2) what species traits, as indicative of environmental tolerance, dispersal ability and evolutionary history, drive such patterns of distribution along the chain.

## **METHODS**

### **Study area**

The present study was carried out in the central coast of Brazil, southwestern Atlantic, in a region that comprises the VTC and the mainland, restricted in this study from the north of Abrolhos Bank to the south of the continental shelf of the state of Espírito Santo (Fig. 1). The VTC is composed of several non-emerging seamounts (Motoki *et al.*, 2012) and the islands group TMVIC. Hereafter, islands and major seamounts are synonyms of Functional Islands (FIs) (Fig. 1).

The VTC was formed by the activity of a stationary hotspot (Jason Morgan, 1983; Gibson *et al.*, 1995, 1997; Ferrari & Riccomini, 1999), as the oceanic crust moved westward at a rate of 23.1 km/My (Almeida, 2006). The VTC emerged during the Cenozoic, a process initiated in the Tertiary (60 - 40 Mya) (Crough *et al.*, 1980; Fainstein & Summerhayes, 1982). This volcanic formation was partially connected to the mainland and the first seamounts are hypothesized to be fragments of adjacent continental shelf (Motoki *et al.*, 2012). The oldest volcanic edifices are those near the continental shelf (Siebel *et al.*, 2000; Motoki *et al.*, 2012) and the more recent magmatic activity occurred at the TMVIC around 5,000 years ago (Almeida, 2006). Seamounts are isolated from the continental shelf and from each other by deep water (1,000–4,500 m) and moderate distances (50–250 km), forming a 1,000 km west-east chain that culminates in the TMVIC (Fig. 1).

The VTC and its adjacent continental margin encompasses the highest reef-associated biodiversity in the south Atlantic (Leão *et al.*, 2003; Dutra *et al.*, 2005; Lavrado & Ignacio, 2006). This region corresponds to an ecological and biogeographic transitional zone between tropical and subtropical marine biota

(Floeter & Soares-Gomes, 1999; Lavrado & Ignacio, 2006; Spalding *et al.*, 2007; Fortes & Abasalao, 2011; Marins *et al.*, 2012; Pinheiro *et al.*, 2015b), characterized by the occurrence of range boundaries of multiple species (Andreatta & Séret, 1995; Absalão *et al.*, 2006; Paiva, 2006; Serejo *et al.*, 2006).

Superficial circulation in the VTC region is dominated by coastal waters with riverine inputs over the continental shelf and by the Brazil Current (BC) off the shelf brake (Silveira *et al.*, 2000). When flowing through the VTC, the BC follows three different paths, either simultaneously or not (Evans & Signorini, 1985; Pimentel, 2012). The strongest branches flow between the Abrolhos Bank and Besnard seamount and between Besnard and Vitória seamounts, while the third path flows more offshore, between Vitória and Jaseur seamounts (Appendix S1 in Supporting Information). After crossing the VTC, the BC tends to reorganize itself as a jet, flowing south along the shelf break (Appendix S1). The topographical complexity of the VTC region under the BC influence induces upwelling driven by eddies (Schmid *et al.*, 1995; Gaeta *et al.*, 1999) and possibly processes such as Ekman pumping (Calado *et al.*, 2010) and tidal currents (Pereira *et al.*, 2005). These oceanographic features promote a shallow water nutrient enrichment through the rise of the colder South Atlantic Central Water (SACW), located below the mixed layer (Gaeta *et al.*, 1999; Carlos *et al.*, 2007).

The portion of the mainland adjacent to the VTC is highly complex and encompasses mangroves, estuaries, deep *Laminaria abyssalis* beds, the largest continuous rhodolith beds of the world, coralline and rocky reefs, and coastal islands

(Floeter *et al.*, 2001; Leão *et al.*, 2003; Amado-Filho *et al.*, 2007; Marins *et al.*, 2012). Rhodolith beds are found mainly at mesophotic depths (40-120 m) and are remarkable for being the predominant benthic habitat along the outer continental shelf and on the VTC seamounts' shallower summits (50-120 m) and islands. There are indications that these beds are seasonally covered by macro algal canopies (Pereira-Filho *et al.*, 2011; Amado-Filho *et al.*, 2012; Dias & Villaça, 2012), mainly on those westernmost seamounts (e.g. Vitória, Eclairer and Almirante Saldanha) (Lavrado & Ignacio, 2006; O'Hara *et al.*, 2010).

### **Fish database**

A reef fish presence/absence database based on previously published records was built with only species belonging to the 40 fish families typically associated with reefs (Thresher, 1991; Floeter & Gasparini, 2000). From the VTC, data include photic and mesophotic zones (0-120 m) of ten FIs, including Trindade and Martin Vaz islands and seamounts Vitória, Eclairer, Jaseur, Jaseur East [listed as Columbia Bank in Motoki *et al.* (2012)], Davis, Dogaressa, Columbia and Almirante Saldanha (Pinheiro *et al.*, 2015a; Fig. 1). Fish dataset from mainland encompasses the Abrolhos Bank (Moura & Francini-Filho, 2005; Simon *et al.*, *in press*) and the narrow continental shelf of the state of Espírito Santo, south of the Doce River mouth (Floeter *et al.*, 2007; Simon *et al.*, 2013b; Pinheiro *et al.*, 2015b; J.L. Gasparini, Reef fishes of Guarapari database).

Species were characterized by a set of eight aspects related to fish biology and ecological traits, focusing on components that can determine dispersal ability. These

traits were collected from scientific literature (Böhlke & Chaplin, 1993; Carvalho-Filho, 1999; Luiz *et al.*, 2012, 2013; Froese & Pauly, 2015) and complemented by the authors' observations (Appendix S2 in Supporting Information).

Spawning type was categorized in six types: balistid, demersal (*i.e.*, substrate-spawning), restricted demersal (*i.e.*, no pelagic phase), live-bearer (*i.e.*, no larval phase), brooder (*i.e.*, oral or pouch incubator) and pelagic. Body size (maximum total length) was organized in four categories: large ( $\geq 60.1$  cm), medium (20.1–60 cm), small (10.1–20 cm) and very small ( $\leq 10$  cm). Depth range was characterized, based on published and observed maximum living depth, in five categories: shallow (0–30 m), upper mesophotic (30–70 m), intermediate mesophotic (70–110 m), lower mesophotic (110–150 m) and deep ( $>150$  m). Mobility was coded using three categories: sedentary (including small territorial species), roving (species that can make small-scale movements within and between adjacent reefs) and highly mobile (species that can make large scale movements and are able to cross large extensions of deep water). Geographical distribution was coded into five categories: Brazilian endemic, VTC endemic (seamounts and islands), global distribution (widespread across both tropical or temperate waters), Trans-Atlantic (found on both sides of the Atlantic) and Western-Atlantic. Multihabitat-use details whether species inhabit multiple habitats or not. Habitats were classified as reef-complex structures (carbonate or rocky), patch reefs, rhodolith beds, rhodolith beds with sparse structures, sand-mud unconsolidated bottoms and water column. Brackish-water usage (yes or no) indicates whether species require coastal or estuarine habitats to

complete their life cycle. The ability to rafting with floating objects (yes or no) as an mechanism of dispersal for reef-associated species (Luiz *et al.*, 2012, 2013).

## **Data analysis**

### *Spatial structure of assemblages*

In order to summarize the relationship of assemblage composition among sites, a cluster analysis was run over a Jaccard similarity matrix derived from presence/absence data and using the UPGMA grouping method (Clarke & Warwick, 2001). In order to minimize the effects of each FI characteristic (i.e. distance from continental shelf, habitat diversity, summit depth and area; Table 1) and to facilitate biogeographical inferences based on assemblages composition, the analysis of similarity was also run for sites classified into five groups: continental shelf (Mainland), three groups of seamounts with increasing distance from mainland (SG I: Vitória, Eclairer and Almirante Saldanha; SG II: Jaseur, Jaseur-East and Davis; and SG III: Dogaressa and Columbia) and islands (TMVIC).

### *How islands characteristics affect biogeographical patterns?*

To further examine the relationships among FIs characteristics (*i.e.*, geographical and geological attributes; Table 1) and reef fishes biogeographical patterns, assemblage dissimilarity (beta diversity) analysis was used to test the three following hypotheses. 1) The “target-area-distance effect” hypothesis, where fish propagules flow from a mainland source and FIs’ area and distance from the source determine their ability to receive species. This model expects a positive correlation between inter-FIs beta

diversity and a dissimilarity matrix computed using FIs size (area) and distances from mainland. 2) In the “stepping stones assembly” hypothesis, beta diversity results from the amount of faunal exchange between FIs, and the expectation is to detect a positive correlation between beta diversity and inter-FI isolation (geographic distances). 3) The “island age” hypothesis posits that beta diversity is related to site age as a result of the balance between colonization and extinction of species and thus expects a lower variation (*i.e.*, higher similarity) in species composition among sites of similar age (see Fattorini, 2010). Almirante Saldanha seamount was excluded from these analyses due to its latitudinal distance (~180 km) from remaining of the VTC volcanic ridge.

Age estimates were compiled from (Ferrari & Riccomini, 1999) and distances between sites were measured as the shorter linear geographic distance between 120 m isobaths. Summit areas were calculated as the area comprised within the 120 m isobath. Because distance (km) and area (km<sup>2</sup>) are expressed in different units, they were standardized to Z-scores ( $Z = (\text{raw score} - \text{mean}) / \text{standard deviation}$ ) and inter-FI distance matrix was computed using Euclidean distance over Z-scores (Dapporto & Cini, 2007). Beta diversity was computed as the difference (turnover) between species composition among sites (Koleff *et al.*, 2003). In order to generate beta diversity matrices, we utilized Jaccard (J) and Kulczynski 2 (K) coefficients (Fattorini, 2010; Villéger & Brosse, 2012). Correlations between matrices (beta diversity and independent variables) were evaluated with a Mantel test run in the software PAST 2.17 (Hammer *et al.*, 2001).

### *Ecological drivers of dispersal and distribution*

Species with high-dispersal ability (i.e. large size, high mobility, rafter behavior and pelagic spawning) are predicted to be more widespread distributed (Cowie & Holland, 2006). In the other hand, species with low-dispersal ability (i.e. small size, sedentary habits, non-rafter and demersal spawning) are predicted to have more difficulty to cross marine barriers. The relative influence of different species traits over the species geographical ranges was explored through two distinct analyses with generalized linear models (GLMs). Such models are adequate methods for analyzing binary or multinomial data (McCulloch, 2000; Venables & Ripley, 2002) and have already been used to assess drivers of reef fish distribution and range size (Luiz *et al.*, 2012, 2013; Keith *et al.*, 2013).

First, relationships between dispersal ability (*a priori* defined) and farthest population from continental shelf were investigated. The dependent variable "maximum distance from continental shelf" has a multinomial distribution corresponding to the lowest distance between continental shelf and the most distant population, i.e. Mainland: 0 km, SG I: 76 km, SG II: 272 km, SG III: 500 km and TMVIC: 915 km. Due to the presence of only one species reaching only SG I, this category was not included in the analysis. Species traits are independent variables. Data were examined using a cumulative probit link function, an appropriate transformation to the multinomial distribution of the dependent variable. All independent variables were included in the models and were removed in a backward procedure in which the least significant ( $p > 0.05$ ) trait was removed before re-

running the model until all remaining variables were significant. The independent variable "family" was left in all models, independently of its significance, to account for phylogenetic redundancy in traits among species.

GLMs analyses were also utilized to investigate how species traits are expressed within the various patterns of regional distribution (Appendix S3 in Supporting Information). Five regional distribution patterns on the VTC were tested: 1) species restricted to the continental shelf (mainland); 2) species found on the continental shelf and seamounts, but absent from the islands (coastal and seamounts distribution); 3) species found on the continental shelf and islands, but absent from seamounts (disjunct distribution); 4) species found on seamounts and islands, but absent from the continental shelf (FIs-restricted distribution); and 5) species found on the continental shelf, seamounts and islands (widespread distribution). Species restricted to the islands or to the seamounts were not analyzed due to the small number of representatives ( $n = 7$  in each case) (Appendix S3). Each distribution pattern was tested separately. The independent categorical variable "family" was included in all models. Data were examined using a probit link function. Pairwise post-hoc Bonferroni tests with sequential adjustment using estimated marginal means were done on significant variables in order to detect differences among categories. In all GLMs, only main effects were tested, with significance level  $\alpha = 0.05$ . All GLM models were run in the software SPSS 16.

## **RESULTS**

### **Spatial patterns of biodiversity**

A total of 247 species belonging to the 40 fish families typically associated with reefs is present on mainland, seamounts and/or islands of the VTC (Appendix 3). Sixty-nine reef fishes (27 families, 28% of total species) are widely distributed across the entire studied region. Twenty-seven species (19 families, 11%) have a disjunct (~1,000 km) regional distribution, encompassing the TMVIC and the mainland, but not the seamounts. Another twenty-seven species (11 families, 11%) occur exclusively in the FIs and are not recorded in the mainland. Within this group, seven are restricted to seamounts (5 families, 3%), seven others are restricted to islands (5 families, 3%) and 13 occur at both seamounts and islands (7 families, 5%). One hundred thirty-two reef fish species (32 families, 53%) were absent from the TMVIC and were solely recorded on the continental shelf and/or seamounts (Appendix S3). Eighty-eight species (27 families, 35%) are restricted to the Espírito Santo shelf and the Abrolhos Bank. Eighteen reef fishes found across the studied region are endemics from the Brazilian Province (approx. 7% of total species). Twelve species are endemics exclusively found in the FIs (approx. 7% for the VTC and 9.6% for TMVIC species), with endemics richness decreasing from the islands towards mainland (Fig. 2).

### **Spatial structure of assemblages**

The similarity analysis clustered sites into two major groups, each one composed by two sub-groups (Fig. 3A). The first group is composed of the two mainland sites (Abrolhos and Espírito Santo) and five volcanic buildings: the island complex TMVIC and the three seamounts having the greatest habitat diversity (Vitória, Davis

and Jaseur-East) (Fig. 3A). The second group of sites is composed by the two easternmost, smallest and deepest seamounts (Dogaressa and Columbia) and three seamounts relatively closer to mainland (Almirante Saldanha, Eclairer and Jaseur) (Fig. 3A). The similarity analysis among groups of sites (concatenated datasets as a function of distance from mainland) showed that the continental shelf (mainland) is more similar and shares a higher number of species with the TMVIC than with closer seamounts (Fig. 3B). On the other hand, there is a higher similarity between TMVIC and seamounts assemblages than with mainland, a similarity that decreased with increasing distance from the islands complex (Fig. 3B).

### **The role of seamounts as functional islands**

Highest assemblage dissimilarity (beta-diversity) was found on the edges of the VTC, both between mainland and seamounts and between seamounts and islands (Appendix 4 in Supporting Information). Geographic distance between sites doesn't explain beta-diversity values, since highest turnover were found between Trindade and Columbia (largest inter-FI distance) and between mainland and Vitória seamount (the smallest distance, Appendix 4). Smoothing obtained among groups of sites suggests that dissimilarity is particularly high between the continental shelf and the closest seamounts (Appendix 4).

Both the high similarity among mainland, islands and specific seamounts, and the highest beta-diversity found between mainland and closest seamounts were indicative that assemblages structure was led by the ability of FIs in capture propagules through a "mainland-island" process (propagule rain). However, Mantel test (Table 2)

suggested that the structuring processes for assemblages composition appears mainly guided by inter-FI isolation, in accordance to the “stepping-stones assembly” hypothesis. Effects of distance from a putative mainland source, even accounting for summit area extension (“target-area-distance” hypothesis) or geological age (“age” hypothesis), were not significant (Table 2).

### **Ecological drivers of dispersal and distribution**

Four species traits did not influence the range size of regional distribution between mainland and FIs: body size, brackishwater-use, spawning type and adulthood mobility. These variables were dropped from the analysis (Table 3a), with multihabitat use and maximum depth being the only significant variables (Table 3b). A higher proportion of shallow water species was detected on the continental shelf and TMVIC (~915 km away) and of deeper water species over the seamounts (Fig. 4a), while generalists dominated on FIs (seamounts and islands) and specialists were more frequent on mainland (Fig. 4b).

The relationship between species traits and the five regional distribution patterns is presented in Table 4. When compared, species restricted to the continental shelf were more sedentary (57% vs. 29% for all other species), dwellers of shallower waters (47% vs. 8%), smaller-bodied (48% vs. 16%), and more rarely use floating objects as raft (7% vs. 14%) than species not presenting this distribution pattern (Fig. 5). Fishes following a disjunct distribution pattern, i.e. that are present on the continental shelf and at islands, include a higher proportions of pelagic spawners (73% vs. 61%) and of rovers (69% vs. 57%), higher use of floating objects (16% vs.

9%) and are medium-bodied (62% vs. 40%) (Fig. 5). Species widely over the continental shelf, the seamounts and the islands include a higher proportion of habitat generalists (67% vs. 40%) and of mesophotic dwellers (78% vs. 48%) and no species inhabits shallow waters (0% vs. 30%) (Fig. 5).

## **DISCUSSION**

Worldwide, the relationship among mainland, seamounts and oceanic islands assemblages composition is still unclear (Schlacher *et al.*, 2010). From this perspective, this work filled some scientific knowledge gaps on seamounts biogeography, showing evidences of ecological drivers of fish composition, richness and similarity among these ecosystems. The results, based on the entire VTC, did not support the hypothesis that richness decreases with distance from mainland. Even when we clustered FIs, in order to combine a variety of habitat per unit, distance from mainland did not provide a major influence on seamount assemblage similarities. Thus, ecological characteristics of the habitats seem to have a major influence on the VTC assemblages, contrasting with others that pointed distance from continental shelf as being the most important factor of fauna composition and richness (Leal & Bouchet, 1991; Paiva, 2006; O'Hara *et al.*, 2010).

Assemblage turnover analysis showed highest dissimilarity between mainland and seamounts, and between seamounts and islands, showing that these different ecosystems harbor distinct reef fish compositions. On the other hand, clustered FIs analyses showed that assemblage similarity decrease from the islands towards mainland. These results allow us to conclude that, although strong differences among

ecosystems exists, both mainland and major seamounts are more closely related to the islands than to each other, and that similarity between volcanic buildings increases with distance from mainland. In fact, previous results highlighted the high similarity between the community structure of seamount and islands, suggesting homologous eco-evolutionary drivers for the FIs reef fish assemblages (Pinheiro *et al.*, 2015a). Thus, similarity and assemblages turnover analyses indicate that the islands also contribute to the diversity of the seamounts, in a feedback mechanism similar to those found in marine biodiversity centers (Bowen *et al.*, 2013).

Since composition and similarity among sites seem to be driven by FI habitat characteristics, the viability of FIs in capturing mainland propagules was expected to rule the assemblage dynamics. However, inter-FIs isolation was the most important environmental predictor for assemblage composition across the VTC, with no key effect for mainland-distance or FI area. This evidences that seamount summits act as *stepping-stones* for assembling reef fish communities, an important driver of biogeography and assemblage structure patterns on FI chains, corroborating with previous hypotheses on biodiversity and evolution on the VTC (Gasparini & Floeter, 2001; Joyeux *et al.*, 2001; Simon *et al.*, 2013a; Macieira *et al.*, 2015; Pinheiro *et al.*, 2015a). This does not mean that all species hop over each and every one seamount to the islands, but so that adjacent sites contribute most to the similarity of each other than distant ones.

In addition to the FIs characteristics, ecological traits of species influence assemblage composition and biogeography, and consequently the stepping stones

assembly. Traits such as depth range and multi-habitat use are ecological determinants for the species distributional patterns across the entire region. Analysis of the ecological traits of the species also reveals that great dissimilarities between mainland and seamounts are due to characteristics that restrict dispersal, such as low mobility and small size, or limit recruitment, through ecological habitat requirements (*i.e.*, shallow water and nursery habitat dependency). For instance, despite having high dispersal abilities and/or wide distributions along the continental shelf and in other remote locales of the south Atlantic, several species (e.g. belonging to Gobiidae, Labrisomidae, Blenniidae, Acanthuridae, Haemulidae, Labridae, Lutjanidae and Sparidae) show limited patterns of distribution on the VTC (Pinheiro *et al.*, 2015a). Moreover, the high diversity of reef species found in the larval pool (with some adults restricted to mainland see Stocco & Joyeux, 2015), and the widespread distribution of endemics (some good dispersers such as *Halichoeres* and *Sparisoma* species) along the VTC indicate that dispersal ability, although important, may not constitute the main driver for species distribution, either towards islands or towards mainland. Thus, assembly rules on seamounts and islands seem to be led by habitat suitability to recruitment and population establishment, followed by connectivity and geographical isolation that are determinant factors for persistence across the region.

Contemporary reef fish biogeography, ecological traits of species and of ecosystems provided important clues and explanations on the biodiversity assembly, connectivity and maintenance on seamounts and oceanic islands. The presence of many endemic species exclusive to TMVIC and disjunct populations indicate that

connectivity along the VTC changed with sea-level oscillations (Gasparini & Floeter, 2001; Simon *et al.*, 2013a; Macieira *et al.*, 2015; Pinheiro *et al.*, 2015a). During low-stand sea levels [i.e. 90% of the Pleistocene, Lambeck *et al.* (2002)], many seamounts were exposed and shallow water habitats available, increasing connectivity for shallow-water dependent, sedentary and/or weak dispersers species through the chain. Sea-level transgressions would work as a vicariant barrier, where species unable to persist over mesophotic seamount's summits would become extinct. On the other hand, adaptation to live in deeper environments may explain the record of many depth range extensions on the mesophotic reefs of the VTC (Pinheiro *et al.*, 2015a), also evidenced for coral species (Vermeij & Bak, 2002; Diekmann *et al.*, 2003; Polato *et al.*, 2010). High-stand periods would also have driven speciation for sedentary species, tide-pool permanent residents and shallow-waters dwellers on the islands reefs (Simon *et al.*, 2013a; Macieira *et al.*, 2015; Pinheiro *et al.*, 2015a). Thus, historical sea-level changes have a direct influence on contemporary FIs assemblage structure and biogeography, with seamounts contributing to species formation and also acting as refugium hotspots (Pinheiro *et al.*, 2015a).

Despite being considered an area of extreme biological relevance (MMA, 2002), the VTC remains poorly known and has not been included in most of recent global biogeographic and macro-ecological analyses (Floeter *et al.*, 2008; Kulbicki *et al.*, 2013; Parravicini *et al.*, 2013). The high biodiversity of species and habitats and the strategic central geographical position make Davis Seamount an important ecosystem for the connectivity and FIs populations' maintenance along the VTC. This seamount

is considered a priority area for conservation initiatives (Meirelles *et al.*, 2015), such as the creation of marine protected areas (Simon, 2015). The VTC ridge, a true laboratory of evolution and connectivity, is already at risk due to inadequate use of its natural resources and habitats (see Pinheiro *et al.*, 2010; Vasconcelos, 2012), needing urgent and effective conservation strategies. The lack of commitment by the Brazilian government leaves relevant ecosystem services, such as eco-evolutionary dynamics, carbon sequestration and fishing resources under severe risk.

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## FIGURES

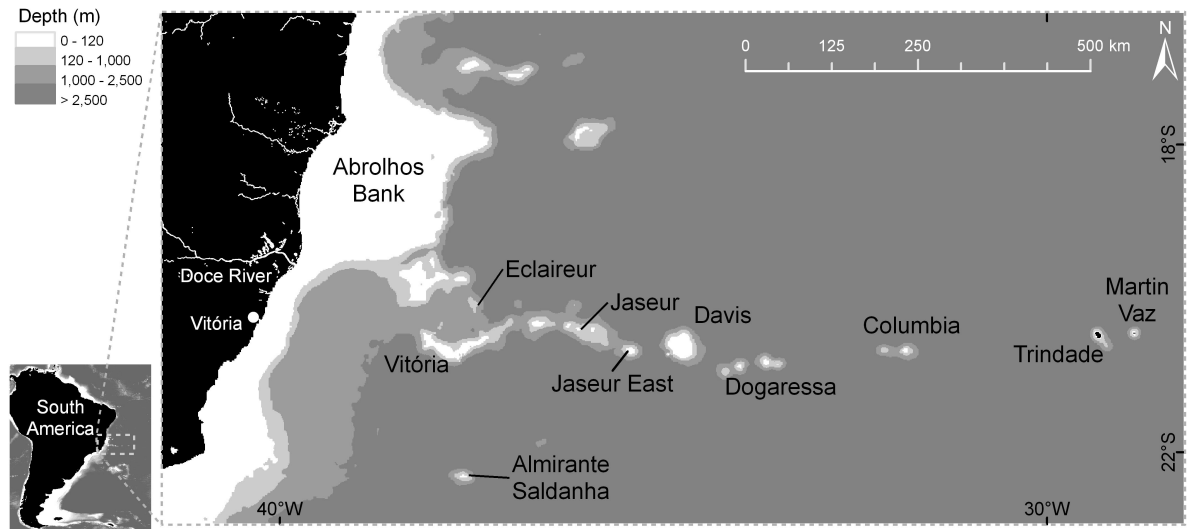


Figure 1 The studied area, showing mainland continental shelf (state of Espírito Santo-ES and Abrolhos Bank) and the Vitoria-Trindade Chain. The ten sampled seamounts and islands of the VTC are shown. Shades of white to grey indicate depth as estimated from satellite altimetry with bathymetric data from Smith & Sandwell (1997).

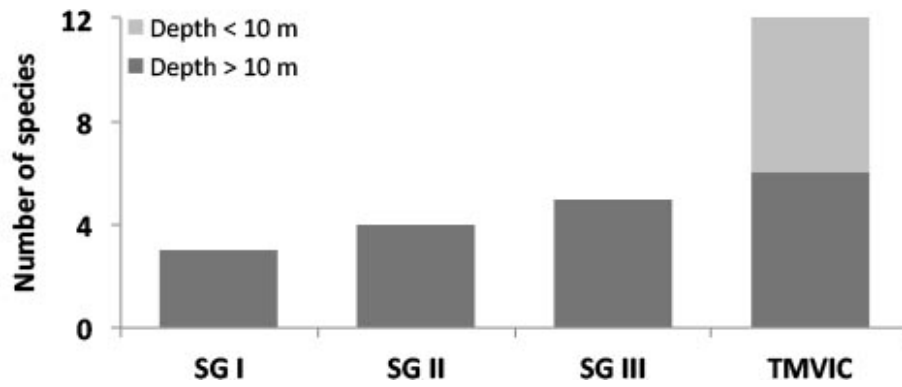


Figure 2 Number of endemic species along the VTC regional compartments. Species were segregated by habitat depth with the light-gray representing species restricted to very shallow waters (< 10m). By definition, there is no VTC endemic on Mainland.

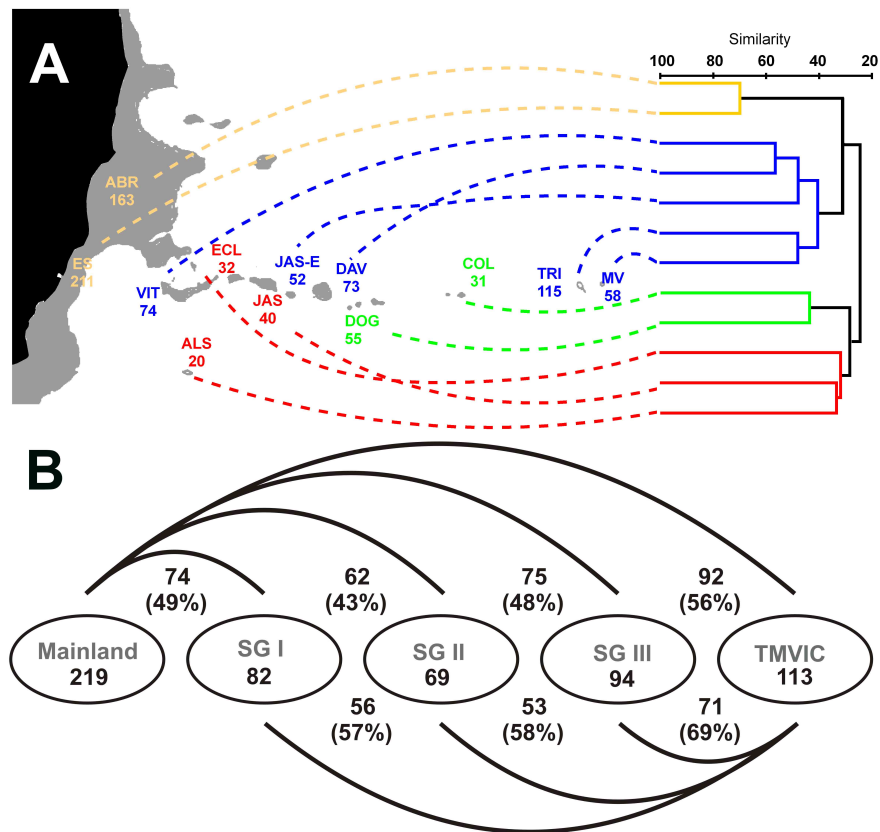


Figure 3 A) Cluster analysis of the reef fish assemblages in the VTC region. The number of species per site is given followed by the number of habitat types between parentheses. Four sub-groups of sites are highlighted: mainland (yellow), the two islands and the three larger and shallow seamounts (blue), three seamounts relatively close to mainland and the two easternmost and deepest seamounts (green). B) Similarity within the VTC regional compartments (groups of sites). Number inside the ellipse refers to reef fish richness. Values outside ellipses refer to the number and proportion of species shared between geographic areas. Proportion is based in the pool of species of the two regional compartments analyzed.

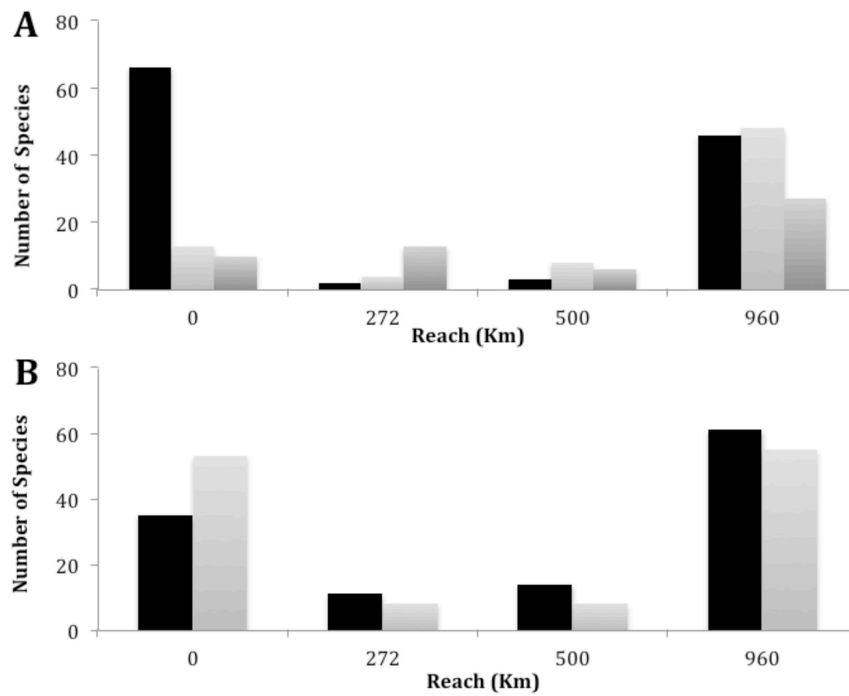


Figure 4 Total number of species per distributional (how far offshore species reach along the VTC) regional compartments. In the X-axis, 0 means group of species restricted to mainland, while, on the other side, 960 means group of species that reach TMVIC. (A) Depth and (B) Multihabitat, the only significant variables in GLM model predicting significant influences of species traits on range size (distance from mainland). Depth (A): black bars show shallow-water (< 30m) plus shallow mesophotic species (30-70m), pale gray bars intermediate and deep mesophotic (respectively, 70 – 110 m and 110 – 150 m), dark gray bars means deep (>150 m); Multihabitat (B): black bars means YES, while gray NO.

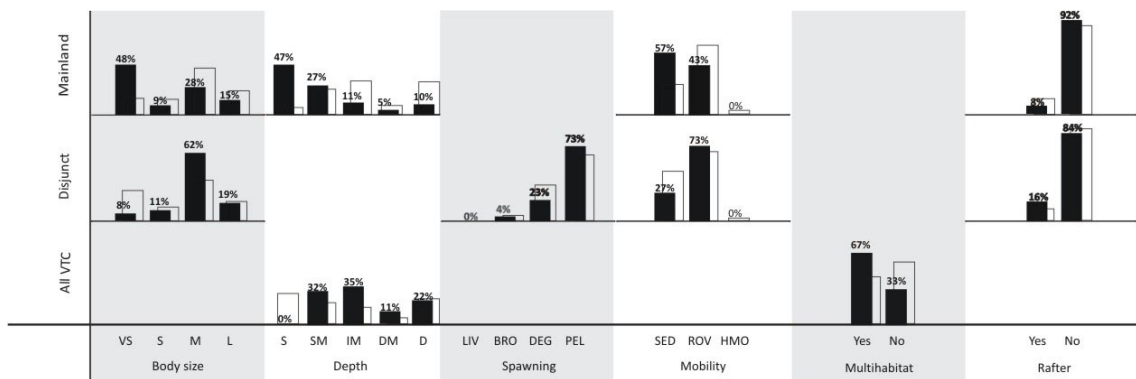


Figure 5 Significant species traits in GLM models and regional patterns of distribution on the VTC Region. Black bars are percentage of species from that determined pattern of distribution. Open bars are percentage of the pool of all species not belonging that particular pattern of distribution. Patterns of distribution are: Mainland, species restricted to the continental margin and absent from FIs; Disjunct, species restricted to mainland and islands; all VTC, species present on mainland, seamounts and islands). Body size: VS, very small; S, small; M, medium; L, large. Depth: S, shallow; SM, shallow mesophotic; IM, intermediate mesophotic; DM, deep mesophotic; D, deep. Spawning: LIV, live bearer; BRO, brooder; DEG, demersal eggs; PEL, pelagic eggs. Mobility: SED, sedentary/territorial; ROV, roving; HMO, highly mobile/migratory. Multihabitat: Yes, habitat generalists; No, habitat specialists. Rafter: Yes, rafting ability; No, no rafting ability.

## Tables

**Table 1** Summary of data sources and characteristics of sampling site. **Distance:** distance from the nearest continental shelf. **Substrate type:** RS– Reef structure (carbonate); RR- Rocky reef; PR- patch reef; RH- Rhodolith bed; \*RH- Rhodolith bed with sparse structures; SD- Sand and unconsolidated substrate.

<b>Site</b>	<b>Summit area (km<sup>2</sup>)</b>	<b>Distance (km)</b>	<b>Substrate type</b>	<b>Shallowest Depth studied (m)</b>
<b>Vitoria</b>	1184	170	RH/*RH/R S/PR/SD	35-120
<b>Almirante Saldanha</b>	37	235	RH/*RH/S D	66
<b>Jaseur</b>	89	272	RH/RS/SD	62
<b>Jaseur East</b>	99	316	RH/*RH/R S/SD	62
<b>Eclaireur</b>	6,4	107	RH/SD	71
<b>Davis</b>	1002	386	RH/*RH/R S/SD	17-57
<b>Dogaressa</b>	80,5	500	RH/*RH/S D	65
<b>Columbia</b>	36,5	670	RH/*RH/P R/SD	84
<b>Trindade</b>	85	915	RH/*RH/R R/PR/SD	0-85
<b>Martin Vaz</b>	24	960	RR/SD	0-30

**Table 2** Summary of results for the Mantel tests between assemblages dissimilarity matrices and FIs characteristics (distance from mainland + area, inter-geographic distance, and age). Test result values (R) and associated probabilities (p) are given for both distances, Jaccard and Kulczynski. Significant ( $p < 0.05$ ) results are in bold.

Coefficient	Target-area-distance (FIs ability to capture propagules)		Stepping-stones dispersal (Inter-FIs distances)		Age	
	R	p	R	p	R	p
<b>Jaccard</b>	- 0.188	0.806	0.319	<b>0.047</b>	0.326	0.559
<b>Kulczynski</b>	- 0.151	0.719	0.2641	0.0941	0.285	0.065

**Table 3** Summary of generalized linear model statistics for the effects of species traits over the distribution of reef fishes along VTC. (a) Initial model with all explicative variables included, and (b) final predictive model after sequentially removing the least significant variables. Significant p-value are in bold ( $p < 0.05$ ). Akaike information criteria (AIC) provides a measure of the relative quality of model through an estimate of information loss; the best model has smallest AIC.

<b>a) Initial model (n= 247)</b>					<b>b) Final model after backward removal of non-significant variables (n=247)</b>				
<b>Variable</b>	<b>df</b>	<b>Chi-square statistics</b>	<b>Sig.</b>	<b>AIC</b>	<b>Variable</b>	<b>df</b>	<b>Chi-square statistics</b>	<b>Sig</b>	<b>AIC</b>
Full model	52	155,0	<0,001	546,7	Full model	44	136,4	<0,001	549,3
Family	36	42,6	0,211		Family	39	37,0	0,560	
Depth range	4	16,2	0,003		Depth range	4	17,4	0,002	
body size	3	7,1	0,069		Multihabitat	1	5,9	0,015	
Brackish use	1	3,2	0,074						
Multihabitat	1	4,7	0,029						
Spawning type	n.a.	n.a.	n.a.						
Mobility	2	3,8	0,150						
Rafting ability	2	6,7	0,035						

**Table 4** Summary of generalized linear models for the effects of species traits on the distribution patterns of the reef fish fauna of the study region. Significant ( $P < 0.05$ ) relationships are in bold. NA = not evaluated due to numerical limitations. Note that models for Mainland-Seamounts and Seamounts-Islands are not significant despite having a number of significant variables.

REGIONAL DISTRIBUTION PATTERN (Species number)		MAINLAND (88)	MAINLAND-SEAMOUNTS (37)	MAINLAND-ISLANDS (DISJUNCT) (27)	MAINLAND-SEAMOUNTS-ISLANDS (69)	SEAMOUNTS-ISLANDS (13)
<b>Full model</b>	Chi-square	<b>154.921</b>	76.669	81.146	114.611	57.969
	df	<b>55</b>	55	55	55	55
	Sig	<b>&lt;0.001</b>	0.280	<b>0.012</b>	<b>&lt; 0.001</b>	0.366
<b>Intercept</b>	Chi-square	1,904	<b>5.451</b>	n.a.	n.a.	n.a.
	df	1	<b>1</b>	n.a.	n.a.	n.a.
	Sig	0,168	<b>0.020</b>	n.a.	n.a.	n.a.
<b>Body size</b>	Chi-square	<b>11,935</b>	<b>55.148</b>	<b>7.269</b>	7.670	<b>71.376</b>
	df	<b>3</b>	<b>3</b>	<b>2</b>	3	<b>3</b>
	Sig	<b>0.008</b>	<b>&lt;0.001</b>	<b>0.026</b>	0.053	<b>&lt;0.001</b>
<b>Maximum depth range</b>	Chi-square	<b>17,251</b>	<b>57.312</b>	7.409	<b>49.559</b>	<b>2325.859</b>
	df	<b>4</b>	<b>4</b>	4	<b>4</b>	<b>4</b>
	Sig	<b>0.002</b>	<b>&lt;0.001</b>	0.116	<b>&lt; 0.001</b>	<b>&lt;0.001</b>
<b>Multihabitat use</b>	Chi-square	0.016	0.201	1.676	5.552	0.197
	df	1	1	1	1	1
	Sig	0.899	0.654	0.195	<b>0.018</b>	0,658
<b>Mobility</b>	Chi-square	<b>70.646</b>	3.042	31.654	1.073	4,349
	df	<b>2</b>	2	2	2	2
	Sig	<b>&lt; 0.001</b>	0.218	<b>&lt; 0.001</b>	0.585	0,114
<b>Brackish use</b>	Chi-square	1.273	1.190	1.168	0.080	<b>101,819</b>
	df	1	1	1	1	<b>1</b>
	Sig.	0.259	0.275	0.280	0.777	<b>&lt;0,001</b>
<b>Spawning type</b>	Chi-square	6.943	6.488	<b>58.405</b>	4.230	<b>48,560</b>
	df	3	3	<b>3</b>	3	<b>3</b>
	Sig	0.074	0,090	<b>&lt; 0.001</b>	0.238	<b>&lt;0,001</b>

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<b>Rafting ability</b>	Chi-square	<b>8.557</b>	2.432	440.223	0.769	n.a.
	df	<b>2</b>	2	2	2	
	Sig.	<b>0.014</b>	0.296	<b>&lt; 0.001</b>	0.681	
<b>Family</b>	Chi-square	186.503	<b>616.553</b>	n.a.	n.a.	n.a.
	df	5	<b>5</b>			
	Sig.	<b>&lt; 0.001</b>	<b>&lt;0.001</b>			

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**Seamounts as natural laboratories for reef fish evolutionary studies: the Vitória-Trindade Chain****Abstract**

Evolutionary processes in oceanic islands have been well studied, however, the role of seamounts in marine species evolution is still unclear. Here we use data from recent biodiversity surveys in previously unexplored southwestern Atlantic seamounts of the Vitória-Trindade Chain (VTC) to develop and explore hypotheses about connectivity and evolution in oceanic islands and seamounts. Contemporary colonization is subject to a gradient from strong and regular to weak and rare, depending on species distribution, species ecological traits, regional ocean currents and stochastic events. Moreover, dispersal and colonization are also related to sea-level fluctuations, which change the amount of suitable habitat for reef-associated species. Isolated populations on seamounts are likely to be under natural selection to live in deeper reefs and self-recruitment. In addition to vicariance, adaptation and ecological speciation could also have driven endemism in the deep habitats of the seamounts and islands. Paleo-endemic species are evidence of the importance of seamount habitats to the maintenance of relict fauna. Genetic drift and extinction can influence some seamounts populations and impacts caused by fishing activities, mining and climate change can accelerate extinction.

**Keywords:** adaptation; evolution; extinction; genetic drift; oceanic island; speciation.

## **Introduction**

Oceanic islands were important models for developing initial ideas about evolution and the origin of species (Wallace 1855; Darwin and Wallace 1858). Today they are still considered essential natural laboratories for ecological and evolutionary studies (Grant and Grant 2002; Whittaker et al. 2008; Kuriyama et al. 2011, MacArthur and Wilson 1967). Isolation and the contrasting environment of different islands causes colonizers to evolve independently from mainland populations (Wallace 1855; Darwin 1859) and to show at local scales evolutionary processes that usually occur among biogeographic provinces (*e.g.*, in Darwin 1859). Thus, at evolutionary time scales, these isolated ecosystems are able to generate high endemism, contributing to the overall diversification and increase of biodiversity (Bowen et al. 2013).

Speciation on islands is among the last steps of a continuous evolutionary pathway (Losos and Ricklefs 2009; Sobel et al. 2010). Species must first colonize the isolated site and be able to maintain a viable population. The more isolated the island is, the lesser the rate of colonization and gene flow between populations (MacArthur and Wilson 1967; Johnson et al. 2000). Founder effects (colonization by a small fraction of a larger population) and strong genetic drift may also represent a challenge to population maintenance in isolated islands (Planes and Lecaillon 1998). Moreover, ecological differences between mainland and oceanic habitats, or among islands, might result in strong selective pressure (Rocha et al. 2005; Rogers et al. 2012; Gaither et al. 2015). Thus, new populations are subject to the balance between genetic drift and natural selection (Sobel et al. 2010).

While oceanic islands have been used as models of allopatric speciation, as illustrated above, the role of seamounts as functional islands for species evolutionary processes, especially as stepping stones, is still understudied (Hart and Pearson 2011). Indeed, there is a dire need of adequate data, with only 0.4 – 4% of the global seamounts that have been directly sampled thus far (Kvile et al. 2014). In general, hypotheses explaining fish endemism on islands are linked to isolation, high levels of self-recruitment and local larval retention (Bernardi et al. 2014). This work presents new hypotheses about evolutionary processes and speciation models for reef fishes in oceanic islands and seamounts. We use the Vitória-Trindade Chain (VTC), southwestern Atlantic, as a case study for highlight the potential influence of seamounts on evolutionary processes in the marine realm.

### **The Vitoria-Trindade chain**

The Vitória-Trindade Chain is a volcanic ridge that extends for 1,000 km into the tropical southwestern Atlantic, starting 200 km off the central coast of Brazil (Figure 1). The first hypothesis for its formation is that it was generated by the Trindade hotspot, where the oldest activity occurred 85 Ma in the continent, and later in the continental shelf, forming the Abrolhos Archipelago (40 – 50 Ma - Fodor and Hanan 2000; Almeida 2006). The South American plate would have changed its movement direction about 40 Ma, and since then took an east to west direction (Almeida 2006), shaping the present configuration of the chain. More recent analyses presented evidence that the older seamounts, Vitória and Besnard, which are closer to the

coastline, are in fact fragments disconnected from the continental crust (Motoki et al. 2012). The emerged sites today, Trindade Island (about 3 Ma) and Martin Vaz Archipelago (0.5 – 1 Ma), are the most recent and farthest ones (Almeida 2006; Figure 1). The youngest seamount is Columbia (10 Ma; Fodor and Hanan 2000), whose summit reaches 84 m depth and is about 190 km from Dogaressa Seamount and 260 km from Trindade (Figure 1).

Most of the seamounts are guyots, with flat summits probably shaped by erosion resulting from aerial exposure (*e.g.*, wind and rain) during sea-level low-stands, and by ocean hydrodynamics (*e.g.*, currents and wave) (Schmieder 1991). Although these summits are extensively covered by rhodolith beds (Pereira-Filho et al. 2011a), large coralline reefs are present at Vitória and Davis seamounts (Pinheiro et al. 2014). These biogenic structures rise from the bank summits (about 50 – 60 m deep) to about 17 m depth. In addition, coralline patch reefs were also found at depths of 55 and 84 m, in the Jaseur and Columbia seamounts, respectively. These reefs support a richer and more abundant reef fish fauna compared to the rhodolith beds (Pinheiro et al. 2015), and may function as stepping stones connecting shallow reefs in the islands to those in the adjacent coastline (Floeter and Gasparini 2000; Floeter et al. 2008; Macieira et al. 2015).

### **The fish fauna**

A recent inventory of the VTC fish fauna (Pinheiro et al. 2015) records 273 species in the area, 211 of which are found in the seamounts and 173 in the islands, 110

common to both seamounts and Trindade-Martin Vaz insular complex. Twelve species are considered endemics, six of which are present in the summits of the seamounts and in the insular complex, and six are restrict to the insular complex. The fish fauna on seamounts and island reefs does not seem to differ in species geographic distribution, trophic composition, or spawning strategies, but does differ for endemism, higher in the islands, and number of endangered species, higher at the seamounts (Pinheiro et al. 2015).

Large reefs and shallow habitats were recently described for seamounts such as Davis, Vitória and Jaseur East (Pinheiro et al. 2014). Mazzei et al. (submitted) show that the ichthyofauna found over these bigger seamounts is more similar to that from the islands and mainland than from those smaller seamounts with deeper summits and where just rhodolith bed habitats were sampled (*e.g.*, Columbia, Dogaressa). Thus, Davis Seamount possibly represents the final stepping-stone for connectivity of shallow water reef species between the continental shelf and Trindade-Martin Vaz insular complex (Meirelles et al. 2015).

### **Colonization Processes**

The distribution patterns of the reef fish species along the VTC (Figure 2) raises questions about the processes for island and seamount colonization. These can be contemporary (*i.e.*, during the present interglacial) or past (*i.e.*, during past glacial periods). Contemporary colonization events may occur as gradients from strong and regular, driven by a high larval flow and movement of individuals, to weak and rare,

driven by stochastic natural events, occasional larval flow or movement of individuals (Figure 3). The gradient of dispersal is strongly influenced by life-history traits of species such as pelagic larval duration, adult-size, latitudinal and depth-range, ability to raft with floating materials, adult habitat usage, schooling behavior and diel activity (Luiz et al. 2012, 2013; Mazzei et al. submitted). Moreover, colonization is also influenced by the sea level, which changes habitat availability, and consequently can change population size and isolation. Figure 3 summarizes a hypothetical framework of the intertwined relationships between distribution patterns, species dispersal potential (influenced by life history traits), colonization frequency, habitat use and consequent gene flow.

Species widely distributed along the VTC (94 species; Figure 2A) likely have a higher colonization frequency and gene flow through the continental shelf to the islands (Figure 3). A generalist habitat usage is characteristic of this group of species (Mazzei et al. submitted; Figure 3). Colonization of seamounts and islands, through larval exchange is probably ongoing (Stocco and Joyeux 2015). However, some widely distributed species have ecological traits that can constrain their potential of dispersal, such as small size, sedentary mobility and demersal spawning (14 species, 15%; Figure 3). In addition to the reduced potential of dispersal, these species seem to have a higher ability to self-recruit in the seamounts and islands (Parker and Tunnicliffe 1994), and their dispersal between each spot can occur, or has occurred, via stepping stones in a lower colonization frequency. These species are also prone to

isolation by distance, a common evolutionary process in natural populations (Alberto et al. 2010; Polato et al. 2010; Baums et al. 2012).

Shallow water species could have had higher colonization frequency and strength in the past, during low sea-level stands, when the seamounts became islands (Figure 4B), offering shallow water habitats (*e.g.*, intertidal, surf zone). Thus, the distance between these habitats was reduced and, consequently, the populations of shallow water species were more connected (Macieira et al. 2015). On the other hand, deeper habitats (mesophotic, 30 – 100m depth) may follow an opposite pattern, contracting during low sea-level stands (Figure 4A). Thus, mesophotic species should show weaker colonization in the glacial periods (Figure 3) but a higher connectivity today.

Some common coastal species were recorded on reef habitats of the seamounts, but not at the islands (55 species; Figure 2B). Moreover, 142 coastal species were not recorded in the oceanic sites (Figure 2D). Many species have the ability to disperse (Stocco and Joyeux 2015) and possibly recruited there from the continental shelf, but the lower habitat availability and population size found in seamounts may reduce their potential of dispersal and colonization strength along the chain (Figure 3). The great distance between Dogaressa seamount and Trindade Island (~450 km) can also represent a filter for some species to reach the islands. Only a small and deep seamount (Columbia, 36 km<sup>2</sup>, top at ~85 m) connects these two sites.

Additionally, new records of reef fishes for oceanic islands (Pineiro et al. 2009, 2011b; Pereira-Filho et al. 2011b; Batista et al. 2012; Simon et al. 2013a) can also represent isolated contemporary colonization events (especially for non cryptic and rare species), and not necessarily established populations (Pineiro et al. 2009). So, seamounts may be contributing to island immigration, since most of these “new colonizers” were also recorded in the seamounts (Pineiro et al. 2015). Compared to the islands, populations at the seamounts, even maladapted, have a higher chance to be maintained due the proximity to mainland, increasing immigration and gene flow rates, a phenomenon known as rescue effect (Lester et al. 2007).

Some species exhibit a disjunct distribution (41 species, Figure 2C, with populations ~1,200 km from the mainland (or 800 km from the continental shelf). Two main hypotheses can explain these distributions. One is related to vicariant events in long time-scales, such as sea level change. During periods of low sea-level stands, when seamounts were exposed (Figure 4), these species could colonize islands and spread along the VTC. Sea level rise acted as a vicariant event, eliminating shallow water habitats and isolating continental and island populations - mostly for shallow water species (Macieira et al. 2015). A second hypothesis of colonization is related to dispersal by stochastic events, when rare meteoceanographic phenomena contribute to the colonization of these isolated sites (Luiz et al. 2012; Mazzei et al. submitted). For example, strong storms or exceptional vortices could drive floating debris and with it coastal species, contributing to spread species to a broader area (Johnston and Purkis 2015). These stochastic events might not be rare, since other

extreme cases of apparently natural long distance dispersal have been reported for Brazilian waters (e.g., *Acanthurus moronviae*, Luiz et al. 2004; *Chromis limbata*, Leite et al. 2009; *Sphoeroides spengleri*, Pinheiro et al. 2009). Luiz et al. (2012) showed that some ecological traits of reef fish species, such as rafting ability, size and habitat usage contribute to species crossing biogeographical barriers and maintenance of populations even in a contemporary time scale.

## **Evolutionary Processes**

### ***Selection and local adaptation***

In the Vitória-Trindade Chain, more than 50 coastal shallow water species were found in mesophotic areas of seamounts and had their depth range extended (Pinheiro et al. 2015). In an evolutionary time-scale, adaptation to a deep environment can be driven by natural selection, where individuals able to settle and survive at high depths can be selected, a phenomena known as “matching habitat choice” (Edelaar et al. 2008). In addition to local adaptation, the matching habitat choice also promotes the evolution of niche width, adaptive peak shifts and speciation in the presence of gene flow (Edelaar et al. 2008). The VTC can impose strong selection to reef fishes since seamounts display wide variation of summit depths and area. On one extreme, pelagic spawning species with long pelagic larval duration (PLD) and widely distributed along the chain can show high gene flow and consequent weak selection – high gene flow between populations exposed to different environments can constrain natural selection (García-Ramos and Kirkpatrick 1997; Lenormand 2002; Garant et al. 2007).

On the other hand, 27 species present populations distributed on few seamounts and islands (less than 40% from those studied), and show low mobility, demersal spawning and/or short PLD, which can translate into lower gene flow among populations, and stronger selection. Some of these species may be isolated and under selection since the last transgression (~19,000 years ago). Two examples of selection and adaptation to the deeper reefs in seamounts may involve the herbivores *Acanthurus bahianus* Castelnau 1855 and *Stegastes fuscus* (Cuvier 1830). Both species are very abundant along the Brazilian coast and in the VTC seamounts and islands. However, they show a depth distribution difference among these environments (Figure 5). *Acanthurus bahianus* reaches a maximum size of 35 cm, displays a roving behavior, has pelagic spawning, a PLD of about 52 days (Rocha et al. 2002) and is found over the extensive rhodolith bed habitats as well as in the reefs of the seamounts. This species occurs in five VTC seamounts and has ecological traits that result in high gene flow through the chain. On the other hand, *S. fuscus* is a small fish (max.15 cm), with sedentary behavior, demersal spawning, and short PLD (average of the genus is 27.1 days; Luiz et al. 2013), and has its distribution restricted to the few shallow reefs in the seamounts (large populations were only seen in the shallow reefs of Davis Seamount). The ecological traits of this species intertwined with the seamount isolation suggest lower gene flow through the chain. In fact, the *S. fuscus* population of Trindade Island already shows genetic isolation and morphological divergence, and is considered a subspecies (*Stegastes fuscus trinidadensis*, Gasparini and Floeter 2001). The isolation and great habitat difference

of the seamount environment expose the *S. fuscus* population to a different adaptive seascape.

### ***Speciation***

Allopatry has been pointed out as the main evolutionary process acting over the VTC ichthyofauna (Gasparini and Floeter 2001; Macieira et al. 2015). This process of speciation occurs when gene flow between geographically isolated populations is negligible. Five endemic to the islands species are suggested to have undergone allopatric speciation by vicariance – after the sea level rise isolated continental and island populations (Gasparini and Floeter 2001): *Malaccoctenus brunoi* Guimarães, Nunan and Gasparini 2010, *Scartella poiti* Rangel, Gasparini and Guimarães 2004 and the undescribed *Acyrtus* sp., *Entomacrodus* sp. and *Tomicodon* sp. (Figure 6). These species are small and have limited dispersal ability, which are characteristics consistent with a scenario of negligible gene flow between island and coastal populations. Gasparini and Floeter (2001) stated that most of these species have great morphological similarity with their mainland sister species, suggesting a recent divergence.

Populations in the seamounts and islands are smaller than in the continental margin, due to limited habitat availability, and therefore subject to faster evolutionary change (Sobel et al. 2010). In addition, small sized species with faster life cycles and shorter generation time might also be evolving faster due to differences in metabolic and mutation rates (Martin and Palumbi 1993; Gillooly et al. 2005). Nevertheless,

despite small genetic and morphologic differences, these species could be evolving over a larger time-scale, perhaps even since the Pliocene when Trindade Island was formed (3 Ma). In this scenario, morphological similarities between sister species can reflect intermittent hybridization during periods of low sea-level stands, when shallow water habitat is available through the entire VTC. In fact, the frequent change in environment makes the adaptive zones bounce forth and back, leaving evolution seems slow in a long time interval (Grant and Grant 2002; Carlson and Quinn 2007; Johnson 2011).

Although many endemics are restricted to the islands shallow waters, others are widely spread along deep-water environments of the entire VTC and are not found on the adjacent Brazilian continental shelf. A possible evolutionary history for *Lythrypnus* species 2 (see Maxfield et al., 2012) and *Elacatinus pridisi* Guimarães, Gasparini and Rocha 2004 is ecological speciation. The sister species to those two VTC endemics, *Lythrypnus* sp. 1 (Maxfield et al. 2012) and *Elacatinus figaro* Sazima, Moura and Rosa 1997 respectively, occur only in continental waters (between 3-35 m) and don't occur in the VTC (Figure 7). The coastal species are widely distributed in the continental margin and the VTC species are widespread in the VTC, what indicates that they are good dispersers.

Ecological speciation occurs when different populations experience environmental contrast, which causes divergent selective pressure and adaption, ultimately resulting in reproductive isolation (Rundle and Nosil 2005; Schluter 2009; Thibert-Plante and Hendry 2011). Common drivers of pre-zygotic reproductive

barriers, and consequent ecological speciation, are habitat preference, selection against migrants and mate choice (Nosil et al. 2005; Rundle and Nosil 2005; Schemske 2010). In reef fishes, a common example is divergence in color, which directly relates to adaptation to different environments and mate choice (Puebla et al. 2007). Rocha et al. (2005) found evidence for habitat preference driving divergence in western Atlantic fish populations. Seamount environments on VTC strongly differ from the nearby mainland mainly due their higher water transparency, higher temperature, and greater depths. All endemic species mentioned above have sister species found in the southwestern Atlantic continental shelf and their evolutionary history can be traced to isolation, ecological speciation or both.

However, two other species do not have clear sister species in the Brazilian Province (Figure 8). These species are considered relicts from past communities, examples of paleo-endemism (Brandley et al. 2010). The wrasse *Halichoeres rubrovirens* Rocha, Pinheiro and Gasparini 2010 has its closer related species found in the Pacific Ocean [*Halichoeres notospilus* (Günther, 1864); Rocha et al. 2010], and *Sparisoma rocha* Pinheiro, Gasparini and Sazima 2010 has no clear sister species in the Atlantic (Pinheiro et al. 2010; G. Bernardi, unpublished data). Sea level fluctuations during the Plio-Pleistocene decreased the area of shallow water habitat drastically (more than 90%, see figure 4 and Ludt and Rocha 2015), possibly resulting in loss of species. In the Caribbean, at least two genera of reef fishes went extinct between the Eocene and Miocene, but a major period of faunal turnover occurred in the Plio-Pleistocene (Bellwood and Wainwright 2002). In the Brazilian

province, on the other hand, VTC seamounts became a refuge for coral reef fauna, preserving these relict lineages, probably due to environmental stability. A similar case is seen in corals: the Brazilian endemic species *Mussismilia* spp. and *Favia leptophylla* Verrill 1868 are considered relict from the Tethys Sea (Miocene), and survived in the seamounts during ice ages (Leão et al. 2003), recolonizing the coastal zones in the last 7,000 years (Andrade et al. 2003). Therefore, VTC islands and seamounts seem to be acting as a stable ecosystem for some ancient genetic lineages.

### **Eco-evolutionary Dynamics**

The evolution of the oceanic islands and seamounts brings great environmental and ecological changes (Whittaker et al. 2008), what influence species evolutionary feedbacks. Understanding the dynamic feedback that arises due to bi-directional interactions of ecological and evolutionary processes is the main goal of eco-evolutionary studies (Palkovacs and Hendry 2010). Evolutionary processes can influence multiple levels of the ecology of the ecosystems, such as population growth, survival or reproduction rates of species, community structure, and nutrient cycling (Palkovacs and Hendry 2010). In this context, VTC seamounts and islands appear as a useful scenario to study eco-evolutionary dynamics in reef fishes in nature, since they have populations that evolved in different levels of isolation and environmental pressure (*e.g.*, depth, habitat availability). For instance, herbivores have a high importance in reef environments by shaping benthic communities (Bellwood and Choat 1990; Francini-Filho et al. 2008), and their evolution and adaptation to live in

the mesophotic reefs of the VTC can strongly influence the ecosystem. In this scenario, comparisons between size of herbivore populations and benthic communities in different depths of the continental margin, seamounts and islands would clarify the ecological consequences of their evolution. At the community level, the integration of evolution, dispersal and community structure can be evaluated into an “evolving meta-community” framework (Urban and Skelly 2006). Effects of environmental changes on phenotypic traits can be influencing the community structure of mainland, seamounts and islands. On the other hand, similar habitats at different isolation levels are subject to distinct evolutionary processes. For instance, while effects of selection and adaptation can be influencing communities in contemporary time-scales (Palkovacs and Hendry 2010), the formation of VTC endemic species can be shaping ecological processes in a longer time-scale.

### **Extinction**

Oceanic islands usually have a relatively short life-cycle (Whittaker et al. 2008), commonly submerging completely after about six million years due subsidence and erosion (Stuessy et al. 2012). Both speciation and richness peak during the maximum topographic complexity of the island (Whittaker et al. 2008). Thus, the VTC islands could be considered mature, where the maximum of richness and speciation was already attained, and the actual number of species found is a balance of immigration and extinction (Whittaker et al. 2008). The seamounts can be considered old islands

already submerged, where extinction is a strong process, and the distance from the mainland can be crucial for the maintenance of local populations.

Causes of natural extinctions remain largely unknown and their role as a selective agent and potentially creative force has not been resolved (Losos and Ricklefs 2009). The VTC looks like an ideal area to study extinction processes. In the past, extinction was probably an important process in seamounts, extirpating shallow water populations due to the rise of sea water level and erosion of summits. This process is supposed to play a major role in allopatric speciation and disjunct distributions. However, some species may currently be undergoing severe bottlenecks on seamounts. For example, *Hypleurochilus brasil* Pinheiro, Gasparini and Rangel 2013 shows a shallow genetic divergence to its sister species *H. fissicornis* (Quoy and Gaimard 1824). This species is abundant at the islands (Pinheiro et al. 2013b), but despite strong search efforts, only one individual was observed and caught on the seamounts (Davis) (Pinheiro et al. 2015). The shallow genetic difference suggests recent speciation, probably driven by vicariance. It is possible that the populations found on the seamount were extirpated by the sea level transgression, being isolated and under bottlenecks effects, below the minimum viable size, at Davis Seamount. Therefore, seamounts can have an important role in the theory of oceanic island biogeography, influencing speciation rates on islands independently of their age or maturation.

Two other possible examples of contemporary extinction process are related to the high variation of population size and colonization effects. Oceanic islands and

isolated reefs experience strong variations on their community (Mellin et al. 2010), and some populations can decrease under a viable number, becoming extinct in unfavorable conditions (Melbourne and Hastings 2008). Other possibility involves dispersal, when few individuals colonize seamounts or islands but are not able to maintain their populations. Many records for Trindade Island constitute rare sightings and may be examples of failed colonization. Three reef species, *Acanthurus chirurgus* (Bloch, 1787), *Bothus ocellatus* (Agassiz, 1831) and *Pythonichthys sanguineus* Poey 1868 were collected in the beginning of the 20th century (Murray 1902; Miranda Ribeiro 1919) and despite a significant increase of scientific effort in the past six years, these species have not been sighted again. Others species such as *Eucinostomus argenteus* Baird and Girard 1855, sampled in the 50's (Carvalho 1950), and *Gymnothorax polygonius* Poey 1875, *Lutjanus vivanus* (Cuvier 1828), *Moringua edwardsi* (Jordan and Bollman 1889) and *Myrophis* sp., in the 90's (Andreatta and Séret 1995; Gasparini and Floeter 2001), have not been recorded again recently. Although it is not possible to exclude the possibility of misidentifications in some cases, these species are probably punctuated records of non-viable populations present in the past and now naturally extinct on Trindade reefs.

### **Human Influence**

Local and global impacts are potentially threatening VTC fishes and habitats. In a local scale, fishing activities and mining of rhodolith beds have threatened the seamounts summits and/or oceanic islands (Martins et al. 2005; Martins et al. 2007;

Pinheiro et al. 2010b; Vasconcelos 2012). Climate change, in a larger scale, can impact coralline habitats (Ragazzola et al. 2012) and contribute to changes in the distribution of species. Fishing, which target many apex predators, has the potential to extirpate those species from isolated islands and seamounts (Koslow 2000; Luiz and Edwards 2011). Direct effects of habitat loss include massive extinction of the seamount populations and an impoverishment of all the VTC fauna.

### **Conclusions**

The variety of life history traits in reef fishes and species distribution patterns combined with a known geological history of the seamounts and islands make them a great system for studying evolutionary processes. Colonization, gene flow, adaptation, speciation, and extinction can be studied independently as well as intertwined, and in contemporary or longer time scales. Colonization processes and gene flow are linked to distribution patterns and dispersal potential or habitat usage. These processes are likely to occur both in contemporary time scales as well as in the past, with different colonization frequency and strength depending of sea-level and habitat availability.

Environmental changes and the geographic isolation of seamounts and islands are agents of change, bringing phenotypic plasticity and/or adaptive divergence to species. Allopatric speciation is suggested for those endemics that live in the isolated islands and have their sister species living only in the continental coast. These species depend on shallow habitat absent from the seamounts, and speciation was likely

driven by vicariant events (sea level change) or founder effects (dispersal). Ecological speciation occurred between species with adjacent distributions and is probably driven by habitat differences between the coast and seamounts. The entire seamount chain acts as a refuge for ancient lineages, and paleo-endemism is common.

In the VTC, endemic species are found in all seamounts and islands, however, their richness is higher in the islands and decreases towards the mainland. This pattern is probably related to the diversity of habitats and isolation of the islands, and higher colonization and gene flow rates in the seamounts closer to the mainland. As the islands and the seamounts seem to have already reached their maturation ages (Whittaker et al. 2008; Stuessy et al. 2012) and are undergoing an advanced erosion process (in geologic time scales), extinctions are expected. However, they have been intensified by human impacts such as fishing, mining and ocean acidification. The increase of research activity, as well as conservation and management initiatives, are extremely important for the understanding and maintenance of endemic species and evolutionary processes of these unique natural laboratories.

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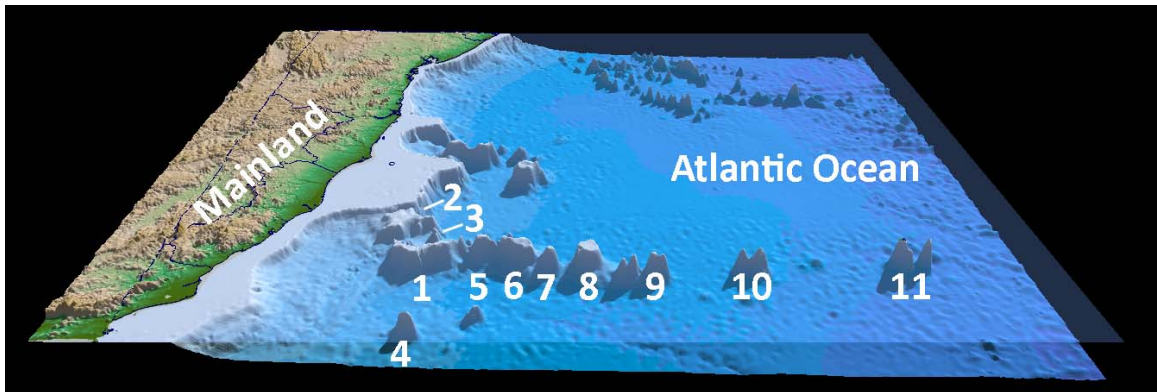


Figure 1 – The Vitoria-Trindade Chain, Central Coast of Brazil, Southwestern Atlantic. Seamounts and islands as follows: 1) Vitória; 2) Besnard; 3) Eclairer; 4) Almirante Saldanha; 5) Montague; 6) Jaseur; 7) Jaseur East; 8) Davis; 9) Dogaressa; 10) Columbia. 11) Trindade Island and Martin Vaz Archipelago.

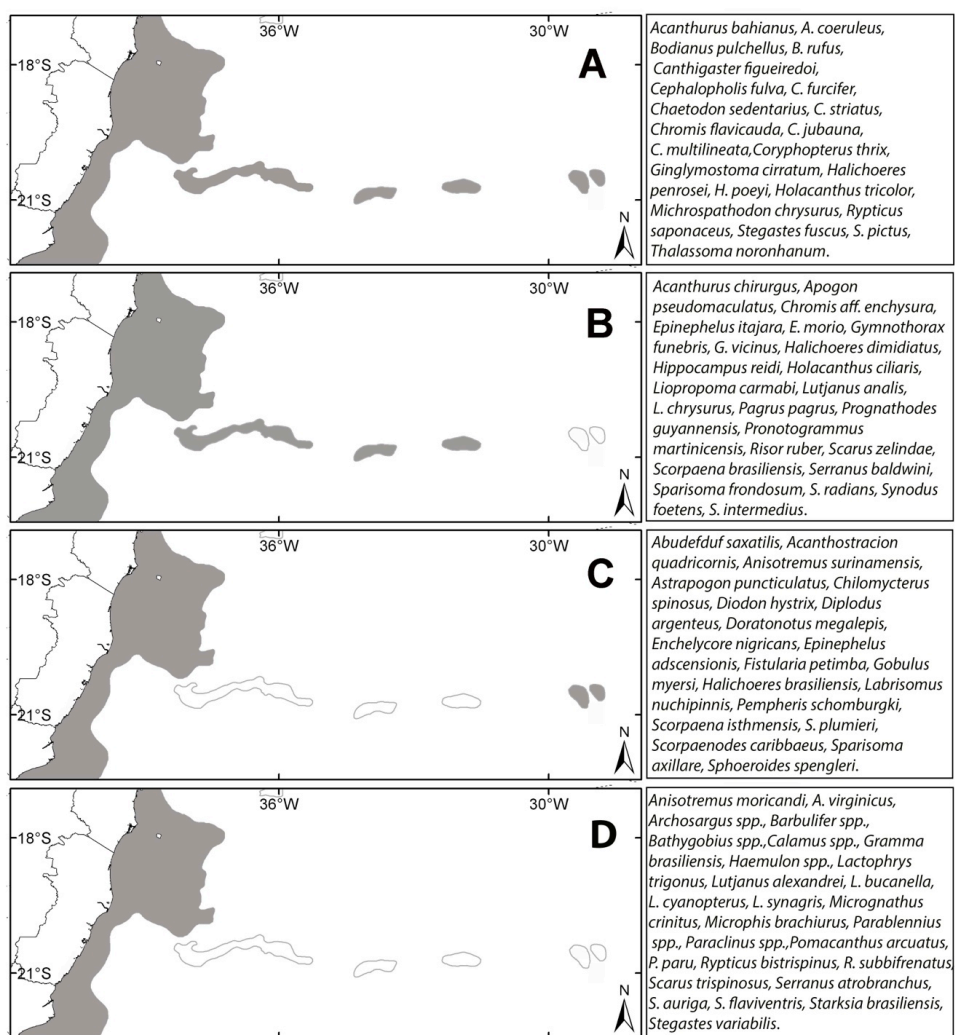


Figure 2 – General patterns of distribution of reef fishes along the Vitória-Trindade Chain, off Brazil. The boxes in the right represent examples of species included in the respective pattern of distribution. A) Species widely distributed, present on the continental margin, seamounts and islands; B) Species distributed on the continental margin and seamounts; C) Species with disjunct distribution, present on the continental margin and the islands but absent from seamounts; D) Species restricted to the continental margin.

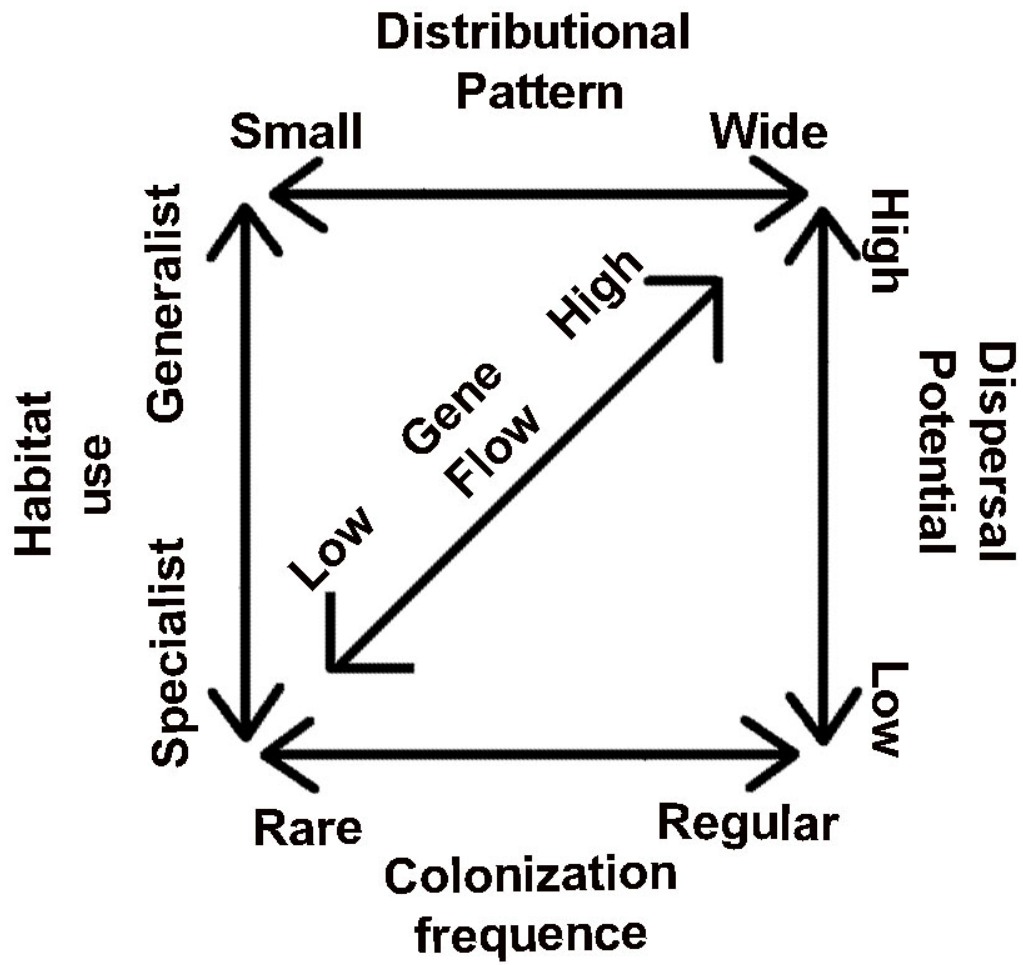


Figure 3 – Hypothetical framework of the relationships between distribution patterns, species dispersal potential, colonization frequency, habitat use and consequent gene flow along Vitória-Trindade Chain, Southwestern Atlantic.

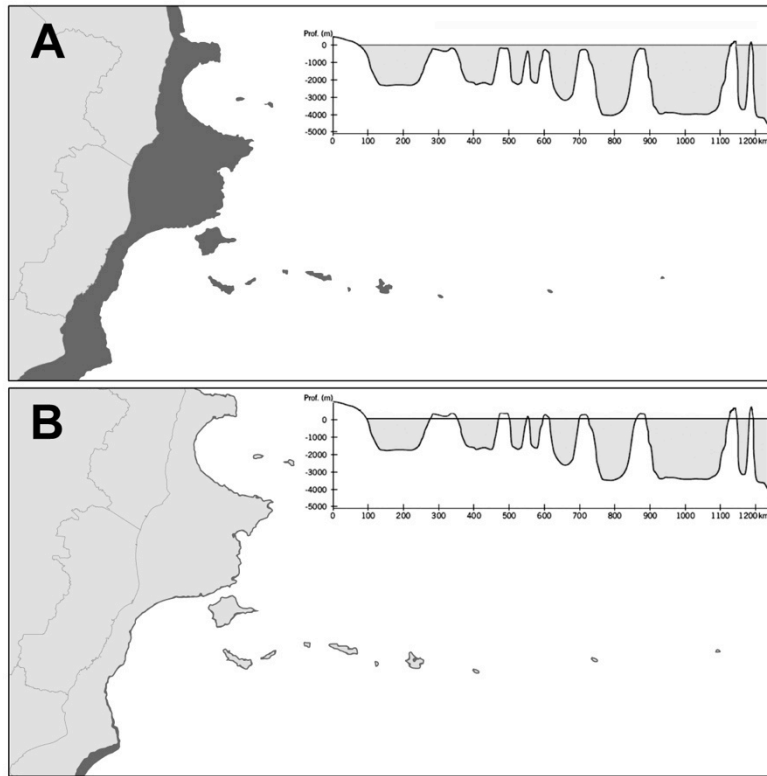


Figure 4 – Central coast of Brazil showing the amount of shallow area available (0 to 100 meters deep – dark gray) in the present (A) and during the last Pleistocene transgression period (B, sea level 100 m below the actual). Note increase of shallow habitats in the VTC during transgression periods, but decrease of mesophotic habitats.

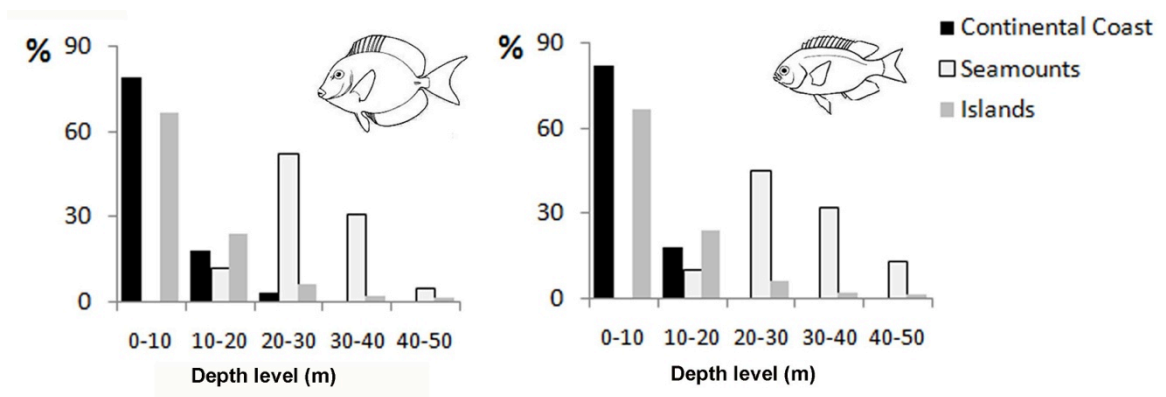


Figure 5 – Depth distribution of *Acanthurus bahianus* and *Stegastes fuscus* over mainland, seamount and island reefs. Abundance data from the mainland was obtained from Pinheiro et al. (2013b) and Simon et al. (2013a), islands from Pinheiro et al. (2011) and seamounts from video footage recorded in recent expeditions (Pinheiro et al., 2015; authors' unpublished database).

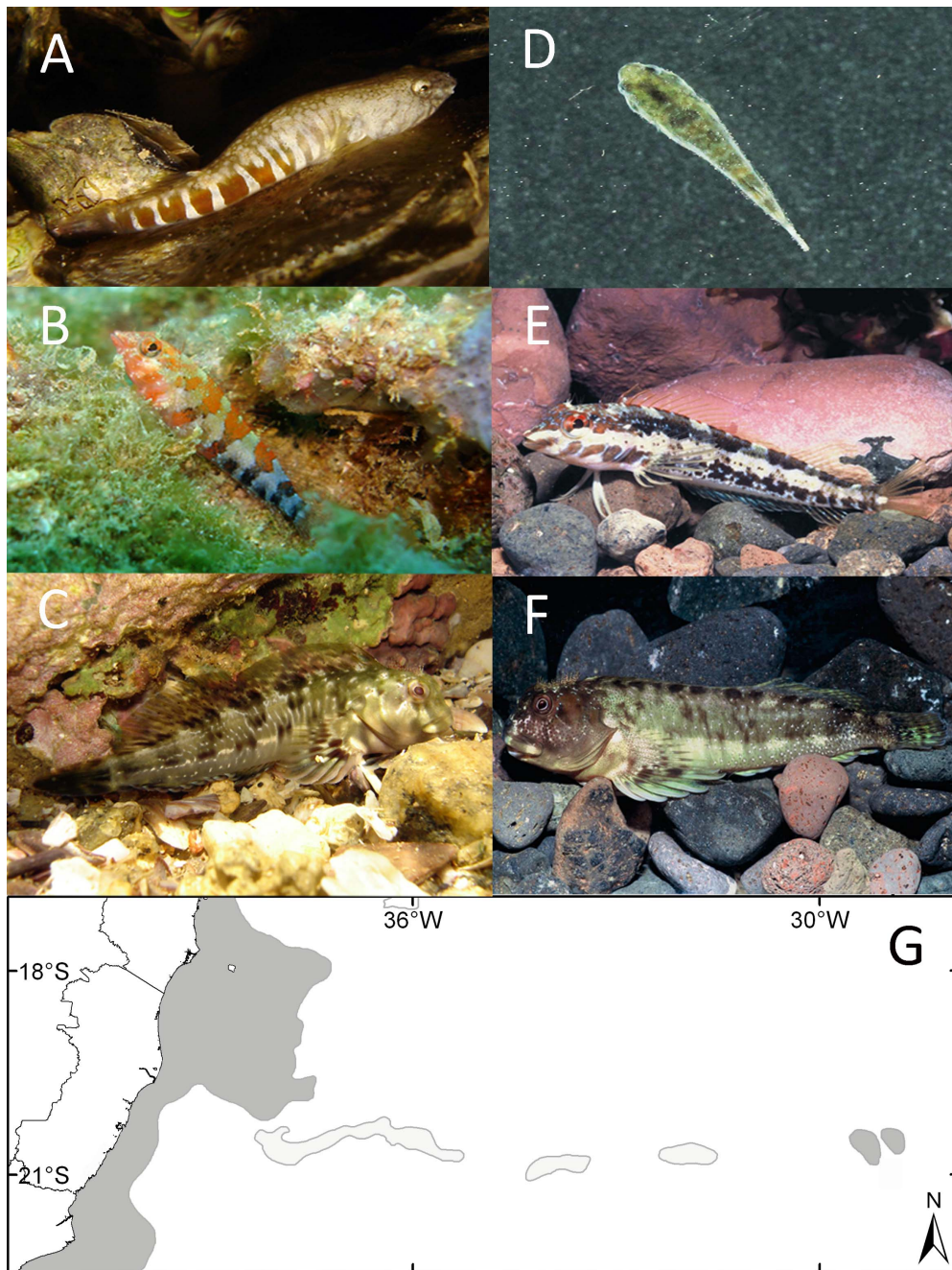


Figure 6 – Coastal species and their respective VTC endemic sister species. A) *Tomicodon australis*, B) *Malacoctenus* aff. *triangulatus*, C) *Scartella cristata*, D) *Tomicodon* sp., E) *Malacoctenus brunoi*, F) *Scartella poiti*, G) Allopatric distributions.

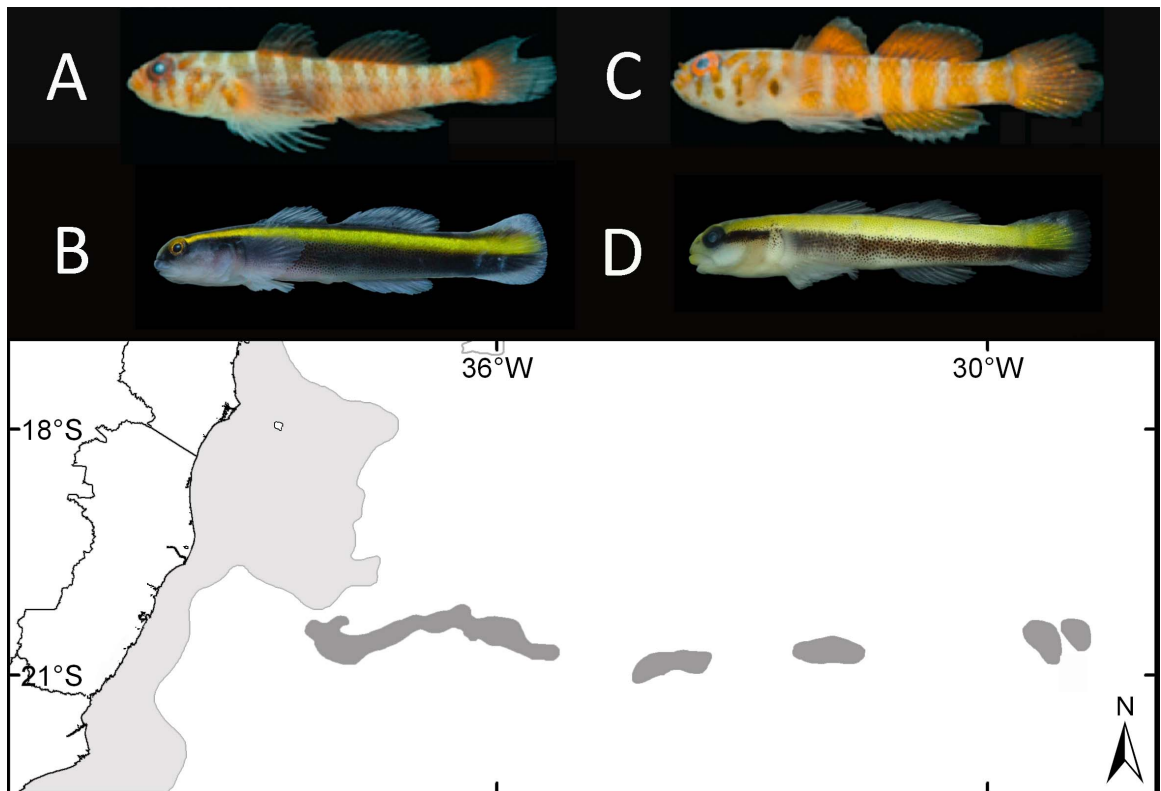


Figure 7 – Coastal species, A) *Lythrypnus* sp. 1, and B) *Elacatinus figaro*, and their respective VTC endemic sister species, C) *Lythrypnus* sp. 2 and D) *Elacatinus pridisi*.  
 E) Parapatric distributions: coastal species in light gray, insular species in dark gray.

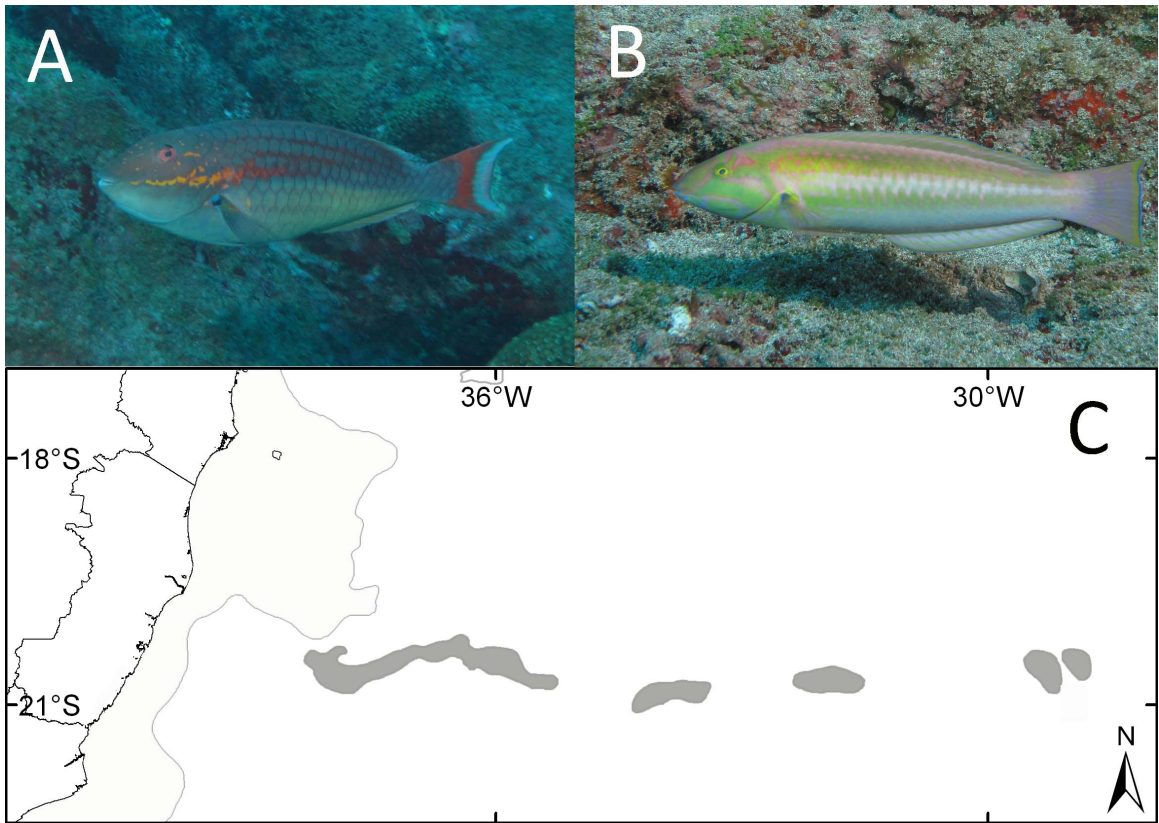


Figure 8 –VTC paleo-endemics. A) *Sparisoma rocha*, B) *Halichoeres rubrovirens*. C)

Distribution of paleo-endemic species.

**Sea-level shifts drive island and seamount reef fish endemism in the South Atlantic**

Studies on the biogeography and evolution of oceanic islands have advanced towards a dynamic perspective<sup>1</sup>, where terrestrial endemism results from the island geographic and geologic history<sup>2</sup> intertwined with sea-level changes<sup>3</sup>. However, the little scientific attention received by marine organisms makes island and seamount evolutionary processes less clear<sup>4</sup>. In this paper we analyze the evolutionary history of endemic reef fishes of a volcanic ridge of seamounts and islands in the South Atlantic to understand their relation to island evolution and sea level changes. We find that most endemic species have evolved recently (in the Pleistocene), during a period of intense sea level change and intermittent connectivity caused by repeated exposure and drowning of seamounts. Three older endemics preceded the Pleistocene and are considered relicts. Two species evolved when only seamounts were present, and finally one species' appearance coincides with an island formation. Contrary to previous findings on terrestrial biodiversity<sup>3</sup>, our data suggest that seamounts play a critical role in marine evolution at oceanic islands mainly by providing stepping stones for island colonization.

Oceanic islands have been considered great laboratories for evolutionary biologists as their isolation, overall low diversity and high richness in endemic species decrease confounding effects, making the interpretation of evolutionary patterns easier<sup>5</sup>. A general dynamic model, where rates of immigration–speciation–extinction are influenced by changes in island characteristics over millions of years<sup>2</sup>, has improved the classical knowledge on terrestrial island biogeography<sup>6</sup>. The shift of island conditions during Pleistocene glacial cycles seems to drive the number and proportion of endemic species in oceanic islands, whereas present island characteristics are more relevant for current richness<sup>3</sup>.

Despite equivalencies in isolation and area<sup>7</sup>, research on the evolution and biogeography of marine organisms has not advanced as much as those on terrestrial systems<sup>4</sup>. Studies on seamounts are still incipient and little is known about their influence on island biodiversity and endemism. Patterns observed for terrestrial organisms may not apply for marine ones, since sea level regression decreases available area<sup>8</sup> instead of increasing it<sup>3</sup>. However, small, shallow water sedentary species, that display limited dispersal, may expand their distributions using exposed seamounts as stepping stones<sup>9</sup>, enhancing island biodiversity and possibilities for speciation.

Here we evaluate the distribution, connectivity and age of reef fishes endemic to seamounts and oceanic islands of the Vitória-Trindade Chain (VTC), in the South

Atlantic. Our goals were to determine whether the evolutionary history of the endemic species is related to island geological history or sea-level changes, and whether our data support temporal patterns of species origin consistent with cradle or museum models<sup>10</sup>. The VTC presents a remarkable opportunity for the study of speciation of marine species in oceanic island and seamounts because of its geography and geological history. The origin of its volcanic buildings spans a 40 million years process, it is relatively isolated from other seamounts and islands, and sea-level low stands increase the number of islands from two to 11, decreasing present shallow water habitat isolation from 1200 km to an average of 200 km (Figure 1).

Genetic divergence between VTC endemics and mainland sister species and clades ranged from 0.5 to 12 % in mitochondrial genes, with seven species that appeared during the Pleistocene (~0.5 – 1.5 Mya) and three older species from the Pliocene and late Miocene (~2.7 – 7.2 Mya) (Figure 2). Although waves of divergence have been reported from other oceanic islands<sup>11</sup>, reasons for those events are not well understood and have mostly been related to favorable conditions for colonization and establishment. Population analyses for neo-endemics show strong isolation, and signs of founder effect and bottlenecks. Overall,  $F_{st}$ s are high and haplotype and nucleotide diversity are low in islands and seamount populations compared to mainland sister species (Table 1). Although significant  $F_{st}$  values were found between islands and seamounts, the presence of large populations on seamounts seems to contribute to a

higher genetic diversity in islands, as shown by *Elacatinus pridisi* (Table 1). Lower  $F_{st}$  was observed between seamount and coastal sister clades than between seamount and island endemic populations (Table 1), a fact probably associated with higher rates of migration from the much larger mainland population.

Our data support that most endemics were formed during a geological period of intense sea level fluctuations, not following a constant speciation rate as suggested by dynamic models of oceanic island biogeography<sup>4</sup>. Sea level fluctuations are also indicated as a strong driver of speciation in the coral triangle<sup>12</sup>, but acting in a different perspective. While low sea-level stands promoted vicariant barriers and diversification in the coral triangle, in the South Atlantic it seems to have opened gateways to oceanic islands, where subsequent speciation happened with strong signs of incomplete lineage sorting (Figure 3a–c). Recent speciation in oceanic islands has been related to strong selection<sup>13</sup>, which may also represent an ongoing driver of differentiation in seamounts as well<sup>14</sup>. However, we show that the presence of seamounts between islands and mainland plays a cryptic role for speciation. The open ocean is a strong ecological barrier for many small shallow water species<sup>15</sup>, and these traits are shared by all neo-endemics. During low sea-level stands, shallow water habitat became available on the top of the seamounts, and dispersal of these species was facilitated, likely causing intermittent vicariant events. Signs of alternated isolation and connectivity are clearly observed in *Elacatinus pridisi* and *E. figaro* (Figure 3a), and a scenario of secondary colonization followed by convergent

evolution or introgression was found in *Hypleurochilus brasil* in the Davis Seamount (Figure 3b).

A completely different scenario is shown by the older paleo-endemic species, which lack sister species in the Brazilian Province, indicating a relict status. The origin of *Pempheris gasparinii* may be related to the origin of Trindade Island in the late Pliocene, but the others were formed earlier in the Pliocene and Miocene, when only seamounts were present (Figure 2). These species are likely survivors of extinction events along the Western Atlantic, mainly in the Brazilian Province, during the climatic changes of the Pleistocene. In fact, during low sea-level stands (glaciations) the Western Atlantic suffered a reduction of over 90% of reef habitat<sup>8</sup>, where alterations of temperature and oceanographic currents resulted in biodiversity losses and turnover<sup>16</sup>. Our results, thus, evidence an important role for seamounts in the formation and maintenance of biodiversity in oceanic islands along geological times.

In conclusion, Pleistocene sea-level fluctuations could not have led to the biogeographic patterns we observe today in the absence of seamounts as intermittent stepping-stones or gateways. The sea-level influence differs on the formation of terrestrial and marine island endemics, and also on the origin of species on oceanic islands and biodiversity hotspots. We strongly suggest that general dynamic models of oceanic island biogeography for marine biodiversity heretofore need to incorporate processes of sea-level shifts and post island submergence.

## **METHODS**

**Vitória-Trindade Chain (VTC).** The VTC is a volcanic ridge that extends for 1,000 km into the tropical southwestern Atlantic (Figure 1). Present day emerged sites, Trindade and Martin-Vaz Insular Complex (TMVIC), are the most recent (about 0.5 – 3 My old) and farthest of the volcanic buildings<sup>17</sup>. At least ten seamounts have summits with depths varying from 50 to 120 m below water surface<sup>18</sup>, with the nearest to mainland being the oldest (~200 km and ~40 My old), and the farthest from mainland (~900 km), the youngest (~10 My old). All the volcanic building are in advanced level of erosion<sup>18</sup>. Most of the shallow seamounts are guyots, with flat summits covered by rhodolith beds<sup>19</sup>, where large coralline reefs are also present<sup>20</sup>. More detailed information about the VTC natural and geologic history is available elsewhere<sup>14</sup>.

**Fish sampling.** VTC fishes were acquired during a scientific diving expedition in 2011 (1–18 April), where upper mesophotic zones (0–85 m depth) of five seamounts were visited: Vitória, Eclairer, Jaseur East, Davis, Dogaressa and Columbia<sup>14</sup>. The collection of specimens was made by divers (hand nets and spear) using technical open-circuit SCUBA or closed-circuit rebreathers with mixed-gases (TRIMIX and EAN). Tissues from TMVIC and mainland sister species (from Espírito Santo and Bahia states, Brazil) came from several expeditions led by the Ichthyological Collection of the Espírito Santo Federal University (CIUFES). All tissues were

preserved in 96 % alcohol, deposited at the CIUFES and their collections were authorized by the Brazilian Environmental Agency [Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 12786–1 and 20880–2)].

**Phylogenetic Analyses.** Mitochondrial cytochrome c oxidase subunit I (COI) and cytochrome b (CytB) DNA were analyzed for all endemic and mainland sister species (exceptions for CytB are *Pempheris* spp., *Scartella* spp. and *Sparisoma rocha*). DNA extraction and PCR amplification of the COI were performed following Weigt et al.<sup>21</sup> and CytB following Rocha et al.<sup>22</sup>. Neither *Sparisoma rocha* nor *Halichoeres rubrovirens* have known sister species in the Atlantic and their sequences were added to previously constructed phylogenies of their genera<sup>22,23</sup>. Sequences were aligned using Geneious 8.1.5 (Biomatters) and unique sequences deposited into GenBank. Phylogenetic relationships were assessed by neighbor-joining (NJ) methods implemented by the Software package PAUP (Phylogenetic Analyses Using Parsimony, version 4.0<sup>24</sup>). Rates of divergence per million of years, for both COI (1.5 % per My) and CytB (1.3 % per My), were calculated as an average of the divergence of sister clades assumed to have been initiated at the final closure of the Isthmus of Panama (*i.e.* 3 Mya)<sup>25</sup>.

Phylogeographic analyses, based in concatenated COI and CytB mtDNA, were performed for three species complex (*Elacatinus* spp., *Hyleurochilus* spp. and *Malacoctenus* spp.), where endemics have three distinct distributional patterns.

*Elacatinus pridisi* is very abundant in the island complex and all seamounts, *Hycleurochilus brasil* is very abundant in the island complex and a single individual was observed and sampled from Davis Seamount (about 600 km far from mainland and the island complex) and *Malaccoctenus brunoi* is exclusive from the island complex. All mainland sister species (*Elacatinus figaro*, *Hycleurochilus fissicornis* and *Malaccoctenus* aff. *triangulatus*) are very abundant and widespread along the Brazilian Province. Population structure and gene flow were assessed in the program Arlequin version 3.5.1.2. Genealogical relationships among haplotypes were estimated for three species complex with a median-joining haplotype network algorithm using NETWORK v.4.6.1.1 ([http://www.fluxus-engineering.com/network\\_terms.htm](http://www.fluxus-engineering.com/network_terms.htm)).

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Our dear friend Thiony Simon (1985 - 2016; *in memoriam*) passed away during the preparation process of this paper. He is sorely missed and those of us who were fortunate enough to know him will always remember his happiness, excitement, scientific rigor, dedication, and generosity. We are grateful to our colleagues that contributed to the studies on the VTC: Amado-Filho G.M., Carvalho-Filho A., Braga A.C., Costa P.A.S., Ferreira B.P., Ferreira C.E.L., Floeter S.R., Francini-Filho R.B.,

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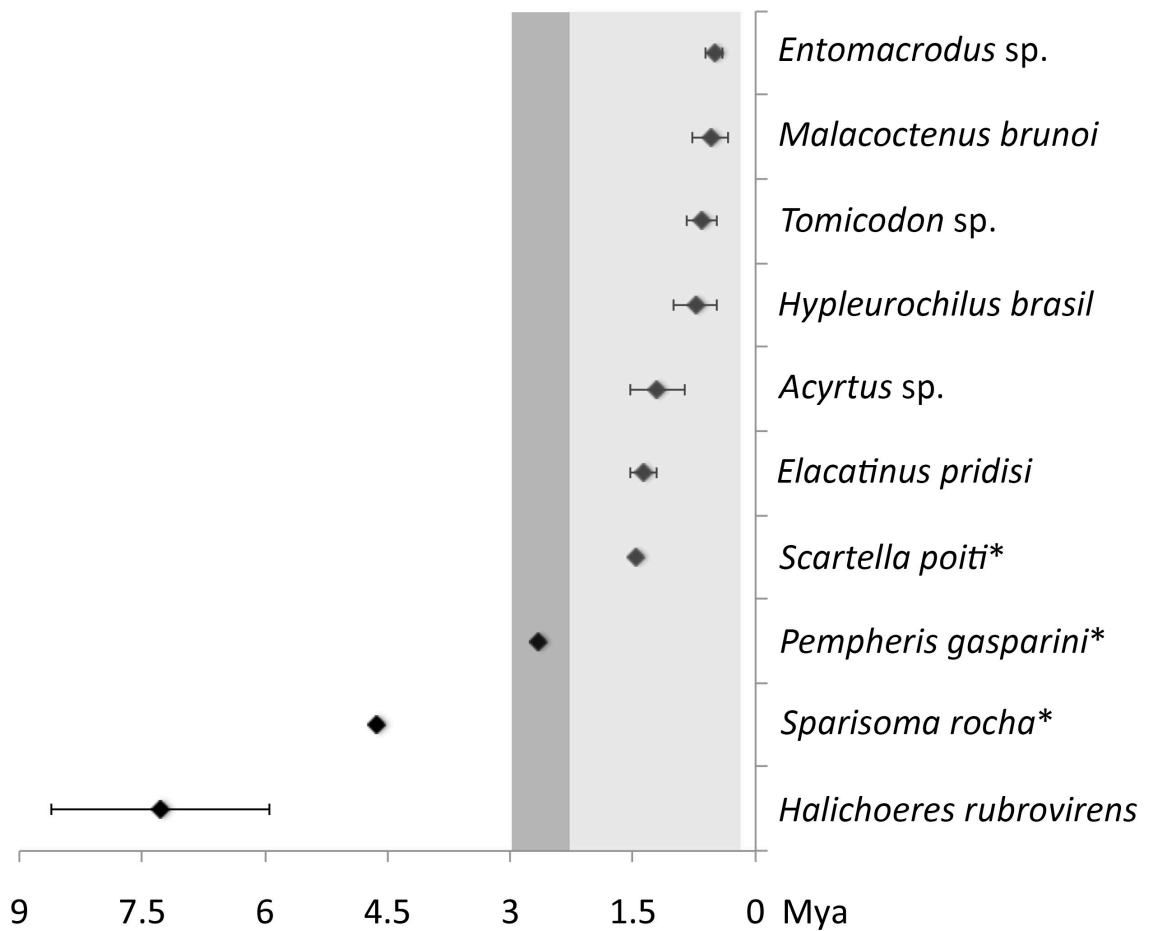
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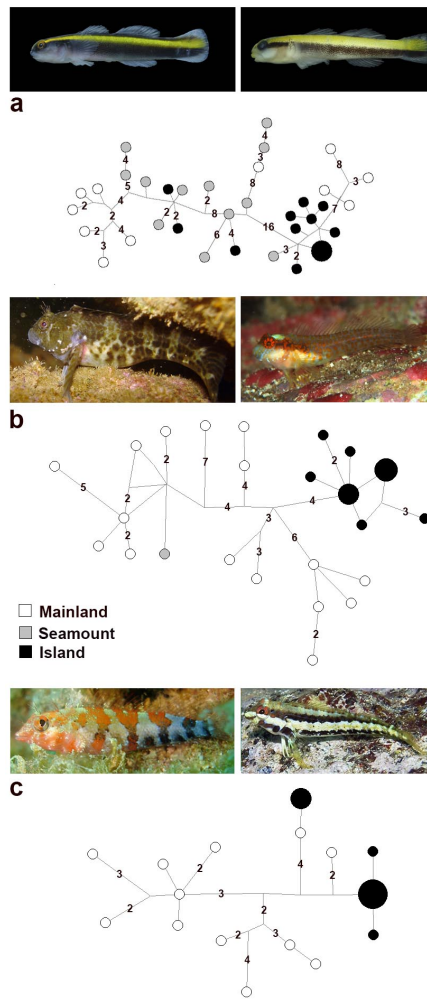
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**Figure 1 | Vitória-Trindade Chain in the Southwestern Atlantic.** A) Current sea-level scenario, where only the Trindade-Martin Vaz Insular Complex, at the eastern end of the volcanic ridge, has exposed landmass and shallow reefs. B) Low-stand sea-level scenario, where nine seamounts and the insular complex are exposed, decreasing distance between insular shallow waters from 1200 to ~200 km. Green color indicates mainland while red means bathymetric range of 0-100 m.



**Figure 2 | Origin of endemic reef fishes from the Vitória-Trindade Chain, Southwestern Atlantic.** Age ranges are based in COI and CytB MtDNA and phylogenetic analyses assessed by neighbor-joining (NJ) methods using PAUP (see Methods). \* only COI PCRs were amplified. Dark gray shade indicates Trindade Island origin while the light gray Pleistocene sea level changes periods.



**Figure 3 | Median-joining network for endemic reef fishes and respective mainland sister taxa.** a) *Elacatinus figaro* (mainland species, left) and *E. pridisi* (VTC endemic, right), a taxa extensively found along the chain. b) *Hypleurochilus fissicornis* (mainland species, left) and *H. brasil* (VTC endemic, right), found mainly in the insular complex but Davis Seamount. c) *Malacoctenus aff. triangulatus* (mainland species, left) and *M. brunoi* (VTC endemic, right), exclusive from the insular complex. Each circle represents a unique mitochondrial haplotype (concatenated COI and CytB), with the size being proportional to the total frequency. Numbers of mutations (> 1) are presented. Photos by R. M. Macieira, J.-C. Joyeux and T. Simon.

**Table 1 | Summary statistics for endemics of the Vitória-Trindade Chain and mainland sister species based in MtDNA concatenated datasets.**

	Population	N	Number of Haplotypes	Haplotype diversity	Nucleotide diversity	Tajima's D	Fu's statistics	F	Fst *
<i>Elacatinus</i> spp.	Mainland	11	11	1	0.01473	-0.26276	-2.462		Mainland x Seamount: 0.24845
	Seamount	12	12	1	0.01205	-0.58006	-3.536		Seamount x Island: 0.40398
	Island	14	11	0.934	0.0079	-0.66639	-1.467		Island x Mainland: 0.4189
	All	37	34	0.991	0.01543	-0.20529	-13.972		
<i>Hypleurochilus</i> spp.	Mainland	16	16	1	0.01007	-0.5039	-7.201		Island x Mainland: 0.44561
	Seamount	12	12	0.824	0.00148	-1.40872	-2.422		
	Island	14	7	0.966	0.0087	-1.06892	-8.065		
	All	31	24						
<i>Malaccoctenus</i> spp.	Mainland	12	12	1	0.00628	-0.92177	-5.769		Island x Mainland: 0.32326
	Seamount	14	4	0.626	0.00259	0.72217	2.717		
	Island	14	4	0.895	0.00534	-0.91313	-3.421		
	All	26	16						

n= number of individuals;

\* all Fst values are significant (P<0.001)

**Reef fish selection and adaptation on seamounts**

In 60 years of advances in seamounts studies, the amount and quality of ecological data are still incipient<sup>1</sup>, but already indicate the uniqueness and fragility of these ecosystems<sup>2-4</sup>. The high biodiversity and endemism level found in some seamounts stimulated assumptions on the role of these environments for oceanic dispersion and origin-maintenance of species<sup>2,5,6</sup>. However, we still barely know about the evolutionary history and processes of their biodiversity<sup>1,7</sup>. Here we show for the first time the genomic signatures of reef fish populations from seamounts, mainland and oceanic islands, disentangling the effects of isolation, selection, adaptation and beginning of speciation in these oceanic environments. Primarily we discovered that many reef fishes inhabiting the seamounts are living down below its previous known depth range from mainland and oceanic islands. Further, through genomic analyses, we found that all populations are connected, but significantly structured between oceanic sites and mainland. Seamount and island populations seems to have the same origin, however, the islands, although twice more distant, have a higher connectivity with mainland. We found a high number of loci under selection, and unexpectedly, these loci show the seamount population evolving further away from the mainland than the island one is. Our results demonstrate that selection is a stronger driver of genomic divergence than the seamount isolation.

**Moreover, as opposed to a recent colonization process and founder effects, adaptation from sea-level transgressions can play a major role for speciation on seamounts.**

Seamounts are one of the largest marine biomes of the world<sup>1</sup>. These environments are often considered islands, sheltering a high level of endemism<sup>4</sup>, and working as stepping stones to reach further oceanic islands and seamounts<sup>5</sup>. However, only 0.4–4% of the world's large seamounts have been scientifically sampled<sup>1</sup>, and consequently, almost nothing is known about colonization and evolution of seamount biodiversity<sup>7,8</sup>. Important evolutionary processes such as speciation is mainly inferred from geographic isolation<sup>1,2,5</sup>. Alternative hypotheses address the role of seamounts for maintenance of endemic species. In one of the first studies on seamount biodiversity, Hubbs<sup>5</sup> expresses that some species may have become adapted to increasing depths as the seamounts have subsided or become flooded. In another hand, differences in the variability of environmental conditions along geological times may have preserved species in some seamounts and oceanic islands while extirpated elsewhere<sup>2,9</sup>.

In the South Atlantic, the Vitória-Trindade Seamount Chain (VTC; Figure 1) has been suggested as stepping stones, repositories and museums for coral reef biodiversity<sup>9–13</sup>. The stepping stone hypothesis is referred to explain the high diversity and new records of fishes found on the islands reefs at the end of the chain<sup>10,14</sup>, and

also to justify past colonization and speciation of small and sedentary island endemic fishes<sup>11</sup>. The repository (or Pleistocene refuge) hypothesis is related to the Brazilian endemic corals of the *Mussismilia* genus. The existence of these relict corals is related to their maintenance on seamounts when adverse environment regimes of Ice Ages crushed mainland populations<sup>13</sup>. Nonetheless, only the museum hypothesis have been empirically corroborated, where recent genetic studies have described the importance of Trindade Island for the conservation of relict endemic lineages<sup>12,15</sup>.

In order to understand the role of the seamounts for the biogeography and evolutionary history of the VTC reef fishes, we first conducted a scientific diving expedition visiting five seamount summits<sup>9</sup>. A remarkable result was the presence of massive coralline reefs and a high diversity of shallow water species at mesophotic depths<sup>16</sup>. Our findings extended the previous geographic distribution and depth range of several species (including endemics), suggesting possible roles of seamounts to phenotypic plasticity, adaptive divergence and speciation<sup>9</sup>.

Within this scenario, we further choose the Brazilian damsel *Stegastes fuscus* (Cuvier, 1830) as model to understand for the first time the genomic signatures of isolation and adaptation for living on seamounts. The Brazilian damsel is a well known shallow-water species very abundant in sheltered reefs along the entire Brazilian Province<sup>17</sup>, where it is found in an average depth of 3.5 m (Figure 1b). As very territorial, solitary, small-sized and demersal spawning, the species is supposed to

have restricted dispersal capabilities<sup>18,19</sup>. Moreover, pursuing morphometric and color differences, Trindade Island population was described as an endemic species (*Stegastes trindadensis* Gasparini, Moura and Sazima 1999), but it is today considered a subspecies – due preliminary shallow genetic divergence<sup>10</sup>. While the species inhabit an average depth of 10 m at Trindade (Figure 1b), we found a large population living at 44 m at Davis Seamount (Figure 1b), situated ~550 km between Trindade Island and mainland (Figure 1a). We sampled populations from four different sites on the Brazilian Province, Davis Seamount and Trindade Island, and used next-generation sequencing (ddRAD-Seq) to answer the following questions: How connected are mainland, seamount and island populations? Have the seamount and island populations the same origin? What is the most important evolutionary driver on seamounts and islands, selection or isolation?

Our genomic analyses selecting 11,382 polymorphic loci indicate that *Stegastes fuscus* populations are structured in two main groups (Figure 2a). Although all populations are well connected, as indicated by overall low  $F_{st}$  values, significant pairwise  $F_{st}$  values point out genetic differentiation between Davis Seamount and Trindade Island, and between them and mainland (Figure 2a). The two isolated volcanic spots seem to have the same origin, exchange 23.7 migrants per generation ( $N_m$ ), and exchange an average of 10 individuals each with the mainland. The mainland sites are highly connected, showing a very low average of  $F_{st}$  among sites (Figure 2a), relative to ~500 migrants ( $N_m$ ) between sites. Principal component

analysis shows that the island, seamount and mainland individuals clustered in three different groups (Figure 2a). Mainland and the oceanic sites are separated in the 1<sup>st</sup> component, and widespread and separated, respectively, in the 2<sup>nd</sup> component (Figure 2a).

Genetic divergence (Fst) within the genome shows most loci presenting low Fst, with just 3% (359 loci) of outliers exhibiting high levels of divergence. An unexpected great number of outliers (78 loci - 21%) are protein coding, an observation that would be expected under a scenario of evolution driven by selection<sup>20</sup>. Population analysis based on these 359 outliers points out a stronger structure between mainland and oceanic sites, where 10 fold higher Fsts indicate that less than one migrant per generation time is shared (Figure 2b). These loci are present in only 0.6% of the total number of migrants originally found among mainland sites, and, despite low values, all Fsts are also significant. Seamounts and islands also show a stronger isolation (Figure 2b). However, although Davis is situated half way between Trindade and mainland, its population is less connected to mainland than that of the island (Figure 2b), and PCA highlights its genomic distancing in the 1<sup>st</sup> component (Figure 2b). This result indicates that the genomic effect of selection towards adaptation to live in the deep seamount summits is a stronger evolutionary component than the geographic isolation.

Moreover, we found a higher genetic diversity in the seamount (17.6 % of polymorphic loci) and island (also 17.6 %) than in the mainland populations (15.5 %). This result does not suggest recent colonization, since neither founder effect nor bottlenecks evidence was found. On the other hand, this result is consistent with the repository (Pleistocene refuge) hypothesis, where relict populations were maintained on seamounts and oceanic islands during Ice Ages, displaying current connectivity and broad distribution. Under this scenario, the seamount drowning, after the last glacial period, seems to have driven an adaptive peak shift triggering disruptive selection in the seamount population. This adaptive divergence scenario is consistent with the beginning of a speciation with gene flow process<sup>21,22</sup>.

Summarizing, even under gene flow, seamount and island populations are different from mainland and between themselves. Although *Stegastes* larvae are distributed along the entire seamount chain<sup>23</sup>, the highest genetic connectivity is found between the oceanic sites, followed by between island and mainland. The seamount seems to be recruiting only part of the available pool of larvae, selecting those individuals able to settle and survive at depth, a filtering mechanism known as “matching habitat choice<sup>24</sup>”. However, the high genetic diversity and genomic divergence of the seamounts and islands indicate that their populations are not only a result from recent mainland immigration, and that adaptation from sea-level transgressions constitute a stronger driver of phenotypic and genotypic diversification. Our results show for the first time that the selective pressure of seamounts environments on the evolution of

marine species can be stronger than the geographic isolation, promoting phenotypic plasticity and adaptive divergence, and sparkling speciation even in the presence of gene flow.

## **METHODS**

**Vitória-Trindade Chain (VTC) and Fish sampling.** The VTC is situated in the tropical southwestern Atlantic, extending for 1,000 km perpendicularly to the South America coastline (Figure 1a). In the present day, Trindade and Martin-Vaz Insular Complex, found at the end of the chain, constitute the only emerged sites. We visited five seamounts of the chain, where summit depths varied from 50 to 85 m. We found large populations of the Brazilian damsel *S. fuscus* only in the Davis Seamount, situated ~550 km far from mainland and Trindade Island – although one vagrant individual was recorded at 55 m on Jaseur-East Seamount<sup>9</sup>, ~450 km from mainland. The collection of specimens was made by divers (hand nets and spear) using technical open-circuit SCUBA or closed-circuit rebreathers with mixed-gases (TRIMIX and EAN). Tissues from Trindade Island and mainland populations (states of Santa Catarina, Espírito Santo, Bahia and Pernambuco) came from several expeditions led by the authors. All tissues were preserved in 96 % alcohol, and their collections were authorized by the Brazilian Environmental Agency [Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO 12786–1 and 20880–2)].

**Genomic Analyses.** Double-digested Rad-Seq libraries were prepared following Gaither et al.<sup>20</sup> and sequenced at the Genomics Sequencing Laboratory, UC Berkeley, on an Illumina HiSeq 4000 (100 bp single end reads). Sequencing runs resulted in 254 million reads passing initial quality control at the sequencing facility. Nine individuals with <40 thousand reads were discarded, leaving 68 individuals across six populations (Santa Catarina, N = 12; Espírito Santo, N = 11; Bahia, N = 12; Pernambuco, N = 10; Davis Seamount, N = 11; Trindade Island, N = 12). Loci were assembled using the STACKS `denovo_map.pl` pipeline. Loci assemblage followed Gaither et al.<sup>20</sup> and resulted in 696,194 stacks. A data set with 11,832 loci was filtered using the ‘populations’ component in STACKS, where only those loci with  $\geq 8X$  coverage (‘m’ command) and aligned in  $\geq 75\%$  of individuals (‘r’ command) of at least four populations (‘p’ command). GENEPOP 4.2 and STRUCTURE 2.3.4 input files, with the ‘write\_single\_snp’ option, were also produced using the ‘populations’ component in STACKS and used for population level analyses. We determined as outlier loci those presenting  $F_{st}$  values higher than the sum of two standard deviation and the average of all  $F_{st}$  values across all populations. These loci were uploaded in genbank, where 21% were identified as protein coding. Thus, these outliers were treated as under selection.

We used ARLEQUIN for  $F_{st}$  comparisons and analysis of molecular variance (AMOVA) among populations (99,999 permutations), and STRUCTURE for genetic partitioning, performing 10 runs of 100,000 replicates burn-in and 1,000,000

replicates for each of  $K = 1-8$ . The most likely number of genetic clusters ( $K$ ) was obtained using STRUCTURE HARVESTER 0.6.94. We then analyzed the STRUCTURE results using CLUMPP 1.1.2 and generated the final output using the software DistructLinux1.1. We also conducted principal component analyses (PCA), constructed from a matrix of covariances between allele frequencies among individuals using Genodive. We plotted the 1st and 2nd component in the x and y axes with the help of custom scripts in R.

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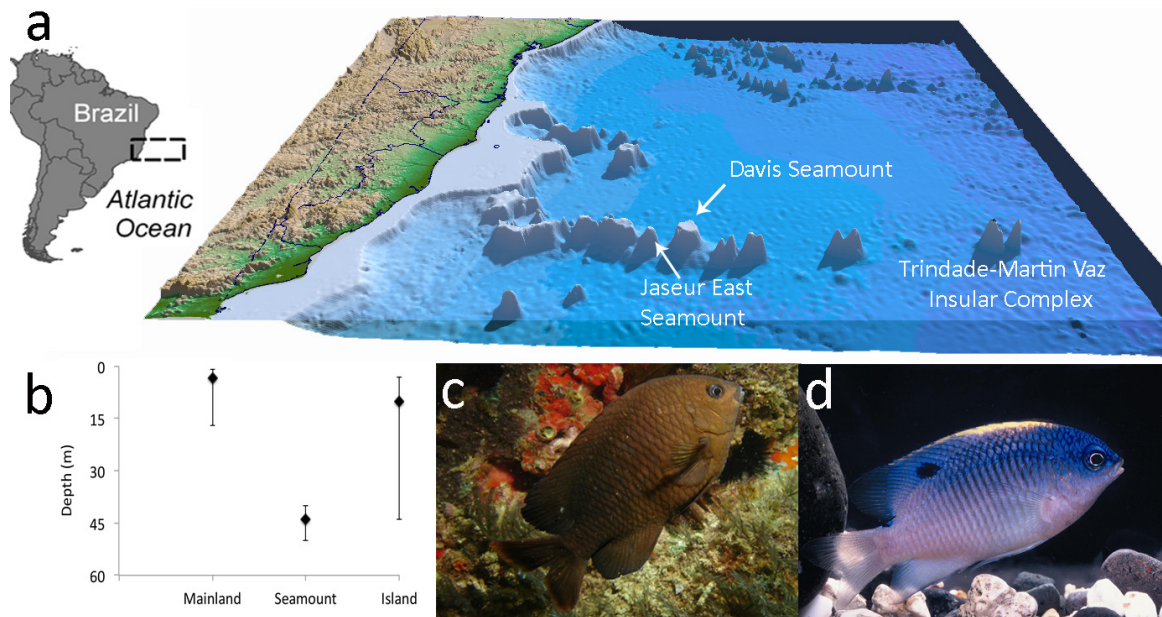
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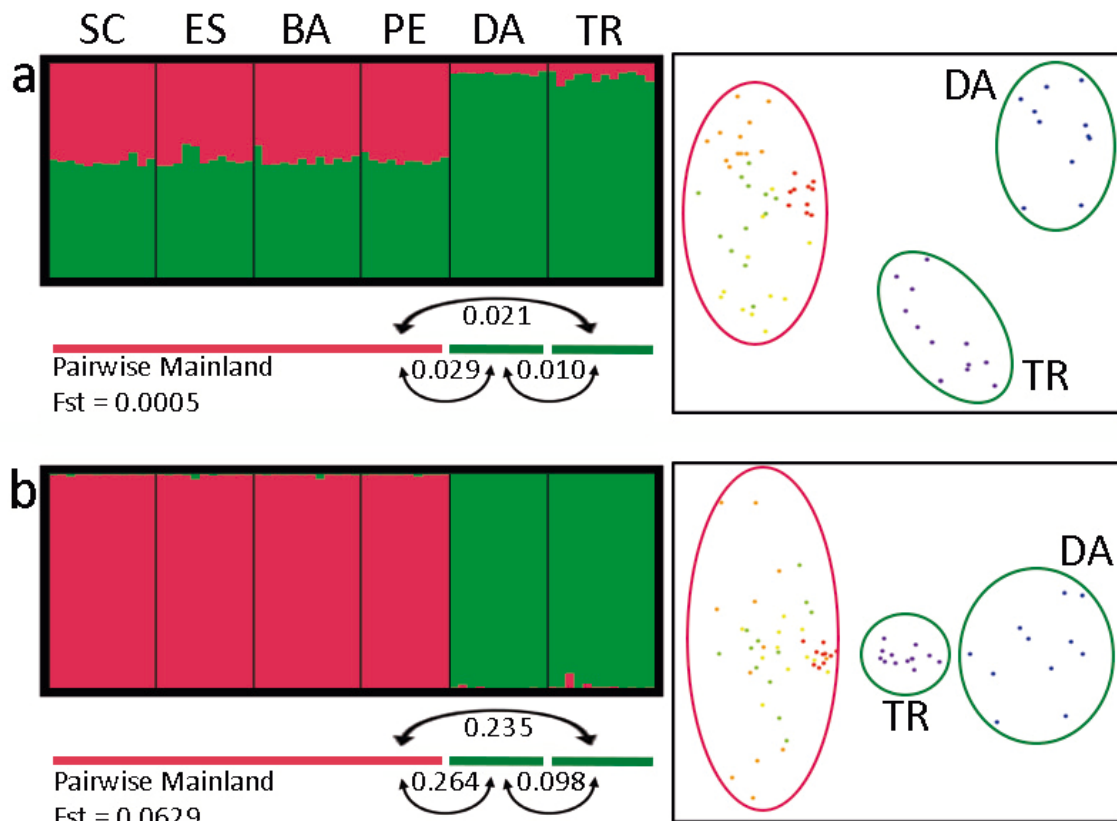
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**Figure 1 | Vitória-Trindade Seamount Chain and the Brazilian damsel *Stegastes fuscus*.** **a**, map of the study area showing the South America mainland, Jaseur East and Davis Seamounts, and the Trindade-Martin Vaz Insular Complex. **b**, Average depth (dot) and depth range (bars) of *S. fuscus* in the mainland<sup>25,26</sup>, seamount<sup>9</sup> and island<sup>27</sup>. **c**, *Stegastes fuscus fuscus*, from mainland (photo by Jean-Christophe Joyeux taken in Guarapari, Espírito Santo state, Brazil). **d**, *Stegastes fuscus trinidadensis*, from Trindade Island (photo by João Luiz Gasparini).



**Figure 2 | Genomic Analyses comparing *Stegastes fuscus* populations from the mainland, seamount and islands. a**, structure plots, Fst and principal component analyses, using all 11382 polymorphic loci, among mainland (SC, ES, BA and PE as a group), Davis Seamount (DA) and Trindade Island (TR). Pairwise Mainland Fst corresponds to the mean of all mainland sites pairwise Fst comparisons. **b**, structure plots, Fst and principal component analyses, using the 359 outliers loci assumed under selection. Abbreviations of mainland sites: Santa Catarina (SC), Espírito Santo (ES), Bahia (BA) and Pernambuco (PE) states.

## **GENERAL CONCLUSION**

Knowledge of the VTC reef fishes has advanced substantially in the last years, from studies restricted to the islands to a comprehensive biodiversity assessment of the seamount chain, biogeographic studies, and an initial understanding of its evolutionary history. As result, a total of 273 fish species are recorded, 211 of which occur on seamounts and 173 at the islands. New records for seamounts or islands include 191 reef fish species and 64 depth range extensions. The structure of fish assemblages is similar between islands and seamounts, not differing in species geographic distribution, trophic composition, or spawning strategies. Main differences are related to endemism, higher at the islands, and to the number of endangered species, higher at the seamounts. Assembly rules on seamounts and islands seem to be led by habitat suitability to recruitment and population establishment, followed by connectivity and geographical isolation, that are determinant factors for persistence across the region. Habitat characteristics and ecological traits of species are the main drivers for assemblage composition and biogeography, and consequently assembly that is concordant with a “stepping stone” biogeographic model. Contemporary colonization of seamounts and islands is subject to a gradient from strong and regular to weak and rare, depending on species distribution, species ecological traits, regional ocean currents and stochastic events. Moreover, dispersal and colonization are also related to sea-level fluctuations, which change the amount of suitable habitat for reef-associated species. Most of the

endemic species have evolved recently in the Pleistocene, during a period of intense sea level change and intermittent connectivity caused by repeated exposure and drowning of seamounts. In addition to vicariance, adaptation and ecological speciation could also have driven endemism in the deep habitats of the seamounts and islands. Paleo-endemic species are evidence of the importance of seamount habitats to the maintenance of relict fauna. Isolated populations on seamounts are likely to be under natural selection to live in deeper reefs and self-recruit. Results of this work demonstrate that selection is a stronger driver of genomic divergence than the geographic isolation. Moreover, as opposed to a recent colonization process and founder effects, adaptation from sea-level transgressions can play a major role for speciation on seamounts. Since unregulated fishing activities are common in the region, and mining activities are expected to drastically increase in the near future (carbonates on seamount summits and metals on slopes), this unique biodiversity needs urgent attention and management.