

## A biogeographic approach to the insular marine ‘prosobranch’ gastropods from the southwestern Atlantic Ocean

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### ABSTRACT

The MacArthur & Wilson theory of island biogeography predicts that the balance between immigration and extinction rates results from the size and degree of isolation of the island. Here, we test this assumption using data from the marine gastropods of Brazilian oceanic islands. Species lists were compiled for Rocas Atoll, the Fernando de Noronha Archipelago, the São Pedro and São Paulo Archipelago and Trindade Island. These were compared with the predictions of the theory based on the shallow platform area and distance from the mainland (Model 1) and the nearest reef habitat (Model 2). Results corroborated at least in part the assumptions proposed by MacArthur & Wilson. São Pedro and São Paulo and Fernando de Noronha fitted the equilibrium model of extinction and immigration rates, while Trindade and Rocas Atoll stood out as an exception to Model 1 and to Models 1 and 2, respectively. The relevance of the age of the island and presence of seamount chains is discussed to explain this discrepancy.

### INTRODUCTION

MacArthur & Wilson’s seminal paper (1963) and book (1967) presenting the theory of island biogeography are considered milestones in the development of the foundations of biogeography. Their theory of island biogeography is based on the balance between extinction and immigration rates which, in turn, are determined by the island size and distance from the mainland. It is proposed that, in islands and other isolated systems, species diversity tends to increase proportionally to the area and decrease with isolation. According to MacArthur & Wilson (1963, 1967), a high degree of isolation should lead to a lower immigration rate, while smaller areas impose restrictions that increase the extinction rate of species.

Studies of insular biota are particularly relevant because the interplay among distribution, speciation and adaptation are easier to detect and understand. Islands are simpler than continents, more clearly delimited and more isolated. By their variation in shape, size, degree of isolation and resident populations, islands provide the necessary replications to test evolutionary hypotheses (MacArthur & Wilson, 1967). Most studies that have tested the assumptions of island biogeography theory were conducted using data from terrestrial biomes (Gilpin & Diamond, 1976; Diamond & May, 1977; see Losos & Ricklefs, 2010, for

review). Only a few studies have used marine organisms as models to test this theory (e.g. Shimizu & Rodrigues, 1988; Floeter & Gasparini, 2000; Floeter *et al.*, 2008; Sandin, Vermeij & Hurlbert, 2008; Hobbs *et al.*, 2012; Hachich *et al.*, 2015). Gastropods are mostly easily identified and have a relatively stable taxonomy. Therefore, we used shallow-water marine ‘prosobranch’ gastropods from oceanic islands in the South Atlantic Ocean as a model system to test the equilibrium model proposed by MacArthur & Wilson (1963, 1967).

There are only a few insular formations in the South Atlantic Ocean, with most islands situated on the African and Brazilian shelves (Soares, 1968). In this study, we considered four sets of oceanic islands: (1) the São Pedro and São Paulo Archipelago (SPSPA), (2) Rocas Atoll, (3) the Fernando de Noronha Archipelago and (4) Trindade Island.

In previous work, Leal (1991, 2000) and Leal & Bouchet (1991) conducted studies with marine ‘prosobranchs’ from Fernando de Noronha, Rocas Atoll and the Vitória–Trindade chain (which includes Trindade). Leal (1991) discussed the species composition and geographical distributions of taxa, performing similarity analyses and correlating the larval development mode with geographical distribution. Leal & Bouchet (1991) related the dispersion mode to the distribution of gastropods along the Vitória–Trindade chain and tested how species

richness varied along this chain. [Leal \(2000\)](#) also studied the relationship between endemism rates in insular environments and the developmental mode of the species. None of these studies, on the other hand, assessed the gastropod assemblage from the SPSPA.

[Hachich \*et al.\* \(2015\)](#) used shallow-water marine groups (gastropods, reef fish and macroalgae) to examine how the species-area, species-isolation and species–age relationships vary among marine taxa and if the patterns differ from those found in terrestrial habitats. Although that study used a larger dataset (all gastropods from 11 oceanic islands in the Atlantic Ocean) to address the question, the authors based their list on a single source ([Gomes \*et al.\*, 2006](#)) to compile gastropod data from the SPSPA, Fernando de Noronha and Trindade, and did not include the endemic gastropods of these islands.

We present here an analysis restricted to the Brazilian oceanic islands based on a carefully reviewed list of records to assess the classical island biogeography theory and discuss the effect of features such as seamounts on the insular marine fauna.

## MATERIAL AND METHODS

### Study sites

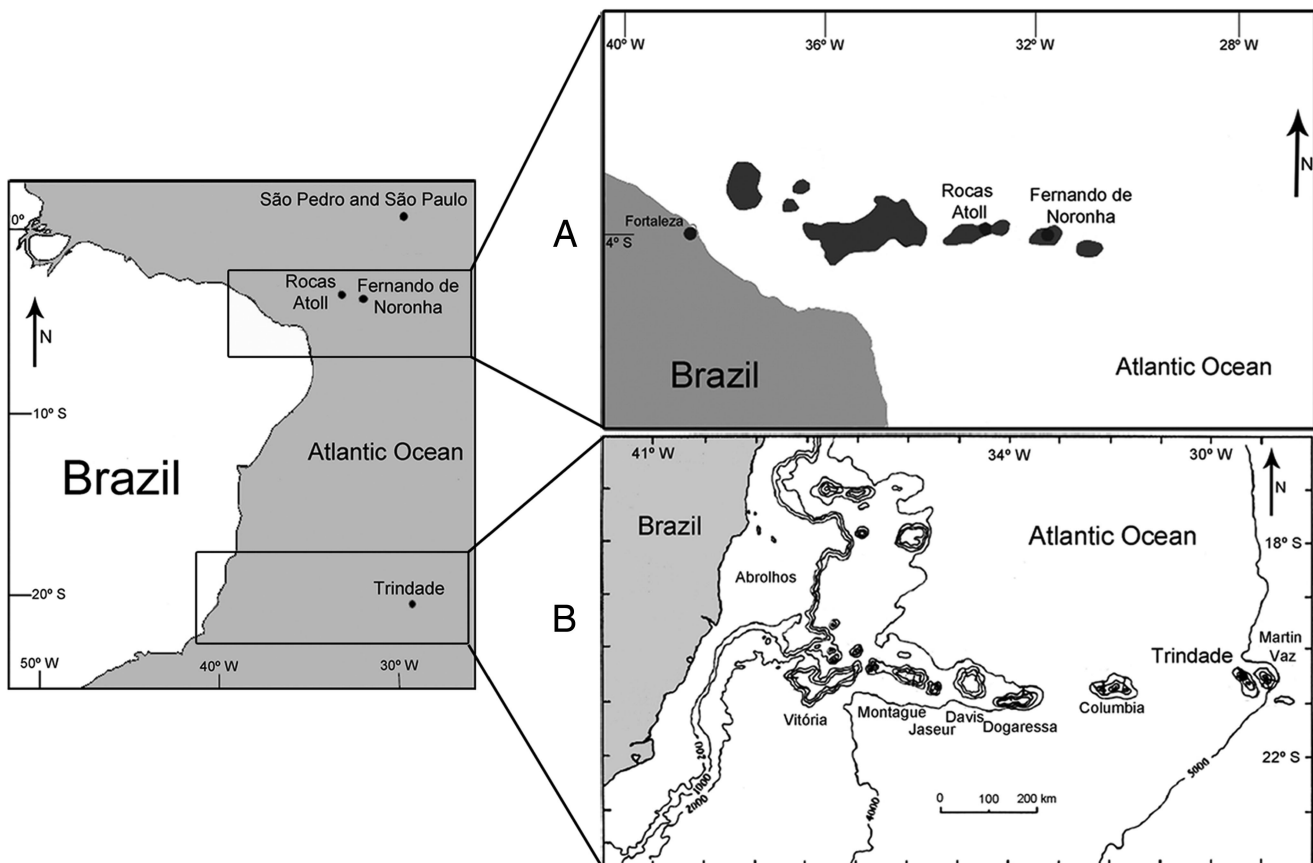
The SPSPA (a.k.a. St. Paul's Rocks), Rocas Atoll, Fernando de Noronha and Trindade are located in the western portion of the South Atlantic and are, respectively, 1,010, 267, 350 and 1,140 km distant from the Brazilian coast (Fig. 1; Table 1). Rocas Atoll, Fernando de Noronha and Trindade are the result of different volcanic events ([Castro & Antonello, 2006](#)), while

SPSPA are not typically volcanic in nature ([Campos \*et al.\*, 2010](#)).

The SPSPA (0°56'N 29°22'W) is a set of 15 islets, located over the Mid-Atlantic Ridge ([Vaske Júnior \*et al.\*, 2010](#)). The islets are rocky outcrops, devoid of beaches or any significant sediment deposition, and the rocky shores are irregular and steep. This same aspect is present underwater, with abrupt topography marked by almost vertical walls around the archipelago.

Fernando de Noronha (3°51'S 32°25'W) and Rocas Atoll (3°51'S 33°49'W) are part of a seamount chain (covered with biogenic carbonates when shallower than 100 m) extending in an east-west orientation and reaching close to the coast of Ceará state, northeastern Brazil ([Morais, 1969](#); [Almeida, 2006](#)) (Fig. 1A). Fernando de Noronha is surrounded by rocky coasts, coral reefs and small beaches with biogenic sediments and volcanic pebbles ([Castro & Antonello, 2006](#)). In contrast, Rocas is the only atoll in the South Atlantic, located 124 km west of Fernando de Noronha, with different geohabitats: reef crest, fore-reef, reef flat, sandy islands, sand depositions and a lagoon ([Kikuchi & Leão, 1997](#)).

Trindade Island (20°30'S 29°20'W) is part of the Vitória–Trindade seamount chain (20–21°S; Fig. 1B). This chain is aligned in an east-west direction, formed by seamounts reaching shallow depths (10–110 m) and rising to the surface at the Trindade and Martin Vaz islands in the western portion ([Gasparini, 2004](#)). Trindade Island is composed of highly alkaline volcanic rocks, narrow beaches, dunes and small fluvial deposits, and is surrounded by coralline reefs in the littoral zone ([Castro & Antonello, 2006](#)).



**Figure 1.** Location of the studied oceanic islands (São Pedro and São Paulo Archipelago, Rocas Atoll, Fernando de Noronha Archipelago and Trindade Island). **A.** Seamount chain with Fernando de Noronha and Rocas Atoll (modified from [Almeida, 2006](#)). **B.** Vitória–Trindade chain, which comprises seamounts (Vitória, Montague, Jaseur, Davis, Dogaressa and Columbia), Trindade Island and Martin Vaz Island (modified from [Leal & Bouchet, 1991](#)).

**Table 1.** Characteristics of the oceanic islands of the South Atlantic Ocean: São Pedro and São Paulo Archipelago (SPSPA), Fernando de Noronha Archipelago, Rocas Atoll and Trindade Island.

Island	Age (Ma)	Shallow platform area (to 200 m depth) (km <sup>2</sup> )	Distance from continent (km)	Isolation from nearest reef (km)	Number of endemic species
SPSPA	8–9 <sup>(1)</sup>	3.5 <sup>(4)</sup>	1,010 <sup>(5)</sup>	630 <sup>(4)</sup> /Fernando de Noronha	5
Fernando de Noronha	8–12 <sup>(2)</sup>	160.5 <sup>(4)</sup>	350 <sup>(5)</sup>	124 <sup>(6)</sup> /Rocas Atoll	2
Rocas Atoll	>8–12 <sup>(2)</sup>	239.5	267 <sup>(6)</sup>	124 <sup>(6)</sup> /Fernando de Noronha	3
Trindade	3.7 <sup>(3)</sup>	55.1 <sup>(4)</sup>	1,140 <sup>(7)</sup>	300 <sup>(8)</sup> /Columbia seamount	11

<sup>(1)</sup>Hekinian *et al.* (2000), <sup>(2)</sup>Lopes & Ulbrich (2015), <sup>(3)</sup>Ferrari & Riccomini (1999), <sup>(4)</sup>Hachich *et al.* (2015), <sup>(5)</sup>Floeter & Gasparini (2000), <sup>(6)</sup>Kikuchi & Leão (1997), <sup>(7)</sup>Castro (2009), <sup>(8)</sup>Leal & Bouchet (1991).

### Data collection

This study was based on marine ‘prosobranch’ species inhabiting waters down to 200 m deep. The term ‘prosobranch’ is used here to designate all non-Heterobranchia gastropods, i.e. Patellogastropoda, Neritimorpha, Cocculinoidea, Vetigastropoda and Caenogastropoda. Most of the families of Conoidea (*sensu* Bouchet *et al.*, 2011) were also excluded due to difficulties of species-level taxonomy, but Conidae and Terebridae were included. Pelagic species of marine gastropods were also removed from the dataset since our focus was on the benthic forms.

The fauna from each insular area were determined using secondary data and visits to Brazilian scientific collections (Prof. Henry Ramos Matthews Malacological Collection, CMPHRM series A and B, Universidade Federal do Ceará; Paulo Young Invertebrates Collection, Universidade Federal da Paraíba; Malacological Collection of Museu Nacional do Rio de Janeiro, MNRJ; Malacological Collection of Museu de Zoologia da Universidade de São Paulo, MZUSP) (see Supplementary Material for complete dataset).

The areas of SPSPA, Fernando de Noronha and Trindade (sea-bottom area down to 200 m depth) were obtained from Hachich *et al.* (2015). Using the same methodology as these authors (SRTM30\_PLUS bathymetry, Shuttle Radar Topography Mission, available at [http://topex.ucsd.edu/WWW\\_html/srtm30\\_plus.html](http://topex.ucsd.edu/WWW_html/srtm30_plus.html)), we calculated the area of Rocas Atoll. Data on island geological ages, nearest distances from each island to the continent and isolation (distance from each island to the nearest reef habitat) were compiled from the literature (Table 1).

### Data analysis

The compiled data for each island (species richness, distance from continent, isolation and size) were compared with the equilibrium model proposed by MacArthur & Wilson (1967: 22, fig. 8) regarding extinction and immigration rates. In this analysis, the sizes of the shallow platforms (down to 200 m depth) around each island and their nearest distances to the continent (Model 1) and to the nearest reef habitat (Model 2) were considered (Table 1).

## RESULTS

A total of 17 species (11 families; 5 endemic species—29.41%) were recorded for the SPSPA, 130 species for Fernando de Noronha (51 families, 2 endemic species—1.53%), 90 for Rocas Atoll (42 families, 3 endemic species—3.33%) and 109 for Trindade Island (45 families, 11 endemic species—10.1%) (Table 2).

The SPSPA shares eight species with each other insular area (Rocas Atoll, Fernando de Noronha and Trindade). Of the 130 species recorded at Fernando de Noronha, 69 are present in

**Table 2.** Endemic prosobranch gastropods from insular areas of the South Atlantic Ocean: São Pedro and São Paulo Archipelago (SPSPA), Fernando de Noronha Archipelago, Rocas Atoll and Trindade Island.

Island	Endemic species
SPSPA	<i>Sinezona insularis</i> Simone, 2009; <i>Fissurella mesoatlantica</i> Simone, 2008; <i>Synaptocochlea belmonti</i> Simone, 2009; <i>Thylaeodus equatorialis</i> Spotorno & Simone, 2013; <i>Zafrona macronata</i> Simone, 2009
Fernando de Noronha	<i>Fissurella emmanuelae</i> Métivier, 1970; <i>Granulina</i> sp. 2
Rocas Atoll	<i>Barleeia</i> sp. 2, <i>Anachis</i> sp. 4; <i>Olivella</i> sp. 2
Trindade	<i>Diodora</i> sp. 5; <i>Lottia marcusi</i> (Righi, 1966); <i>Solariella</i> sp. 1; <i>Arene boucheti</i> Leal, 1991; <i>Arene</i> sp. 1; <i>Melanella</i> sp. 2; <i>Anachis</i> sp. 3; <i>Nassarius</i> sp. 3; <i>Granulina</i> sp. 1; <i>Vexillum</i> sp. 7; <i>Conus jorioi</i> (Petuch, 2013)

Rocas Atoll and 54 are also found in Trindade. Rocas Atoll shares 39 species with Trindade (Supplementary Material).

Most species present in the four insular areas are restricted to the Western Atlantic, but there are a few ampho-Atlantic and cosmopolitan species (Fig. 2). The ampho-Atlantic component was more prominent in the SPSPA, but cosmopolitan species were not recorded.

Figure 3 was based on MacArthur & Wilson’s (1967) graphic model, using our data. It shows that the islands only partially agree with the patterns predicted by the theory of island biogeography, as discussed in detail below.

## DISCUSSION

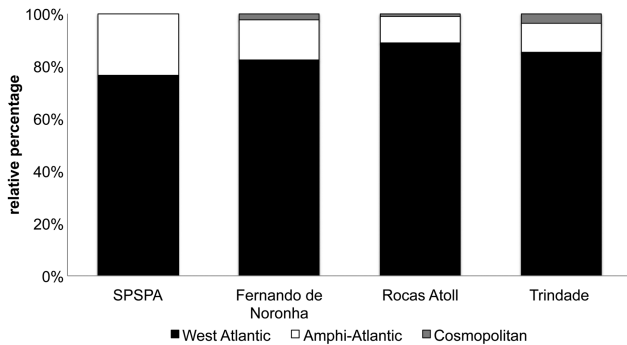
Our results corroborate at least in part the assumptions proposed by MacArthur & Wilson (1963, 1967). Considering SPSPA and Fernando de Noronha, the data are in accordance with the equilibrium model of extinction and immigration rates (Models 1 and 2). The SPSPA is smaller (3.5 km<sup>2</sup>), further from the nearest reef (630 km from Fernando de Noronha) and further from the continent (1,010 km) and thus has fewer species (17). Fernando de Noronha, on the other hand, is larger (160.5 km<sup>2</sup>), located 350 km off the Brazilian coast and is closer to Rocas Atoll (124 km) and 130 species are recorded.

Rocas Atoll was an exception to the equilibrium model (Models 1 and 2): since it was the largest island (239.5 km<sup>2</sup>), nearest to the mainland (267 km) and close to Fernando de Noronha (124 km), it should have more species than other islands. However, only 90 species were recorded at Rocas, i.e. 19 and 40 fewer species than Trindade and Fernando de Noronha, respectively (Fig. 3).

Trindade Island was also an exception to Model 1 (which considers the closest distance to the mainland): since it was the third largest island (55.1 km<sup>2</sup>) and furthest from the continent (1,160 km), it should have fewer species than the SPSPA. However, Trindade has 109 recorded species, which is 92 more species than the SPSPA. On the other hand, Trindade is in accordance with equilibrium Model 2 (which considers the distance to the nearest reef habitat, Columbia seamount 300 km away; Fig. 3).

Two hypotheses may be raised to explain why Rocas did not fit the models: (1) there were uneven sampling efforts among the areas or (2) the age of the island influences species richness.

Most surveys at Rocas Atoll were restricted to the inner part of the atoll ring, except for some dredging conducted during an

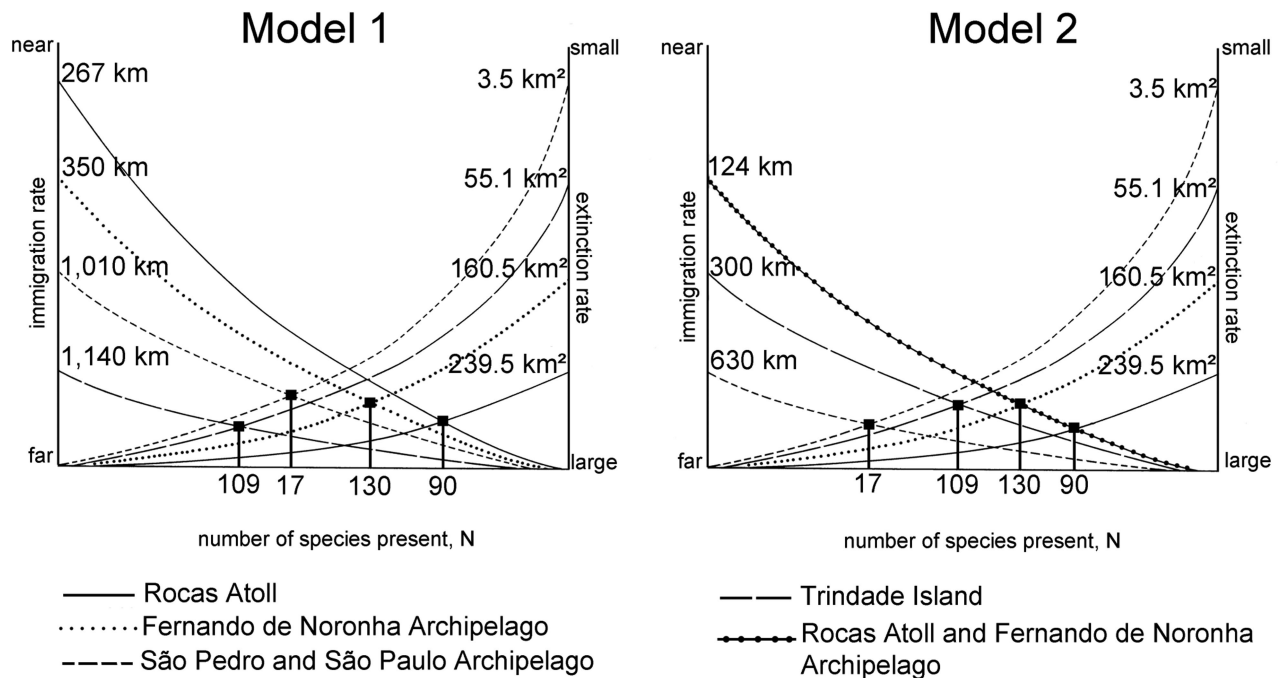


**Figure 2.** Relative percentages of marine 'prosobranch' gastropods of the studied oceanic islands (São Pedro and São Paulo Archipelago—SPSPA, Fernando de Noronha Archipelago, Rocas Atoll and Trindade Island) of the South Atlantic Ocean, by longitudinal distribution.

expedition by the RV *Almirante Saldanha* in 1967 (Kempf & Matthews, 1968; Matthews & Kempf, 1970). Leal (1991) also pointed out that sampling was deficient in the subtidal areas of Rocas Atoll. Therefore, this difference in the number of species among Rocas, Fernando de Noronha and Trindade may result from their respective sampling efforts, especially in the subtidal zone.

The second hypothesis refers to the effect of the island age on species richness. Whittaker, Triantis & Ladle (2008) proposed a general dynamic model (GDM), in which biological processes (migration, speciation and extinction) were combined with the life cycle of oceanic islands to provide a framework for explaining patterns of biodiversity, endemism and diversification on oceanic archipelagos. Borregaard, Matthews & Whittaker (2015) performed a simulation of this model, adding two geological scenarios (arc islands and continental fragment islands), thus demonstrating the significance of the GDM. Applying the classifications of Whittaker *et al.* (2008) to the ontogeny of the islands, Rocas Atoll could be classified as in 'old age', although this is more evident from its stage of development than its chronological age (>8–12 Ma). According to this classification, an island in 'old age' is near the end of the geological progression of islands, having a smaller area, lower altitudinal range, less topographic complexity and consequently lower habitat diversity. Rocas did not fit the GDM perfectly, since it was the largest in area (239.5 km<sup>2</sup>) in this study. The effect of this large area of shallow reef platform must also be taken into consideration.

As proposed by MacArthur & Wilson (1967), a larger area is expected to decrease the species extinction rate. Although these authors acknowledged that larger islands provide larger targets for propagule colonization than smaller ones, their conclusion was that such an effect on immigration rates would be negligible when compared with the effect of size effect on extinction.



**Figure 3.** Equilibrium models of marine 'prosobranch' gastropods of the studied South Atlantic oceanic islands (São Pedro and São Paulo Archipelago, Fernando de Noronha Archipelago, Rocas Atoll and Trindade Island) with varying distances from the Brazilian continent (Model 1), varying distances from the nearest reef habitat (Model 2) and varying size (shallow platform area down to 200 m; Models 1 and 2). The x-axis indicates the species richness of each island. The y-axis indicates the relative extinction (right side) and immigration (left side) rates. The numbers on the curves are the distance from continent or nearest reef (left) and size of the island (right). An increase in distance (near to far) lowers the immigration curve, while an increase in island shallow-platform area (small to large) lowers the extinction curve (modified from MacArthur & Wilson, 1967).

Hobbs *et al.* (2012) strengthened this argument, pointing out that the extent and variety of habitats may also influence extinction and immigration rates and so are critical to determining if arriving individuals are able to colonize the island and maintain viable populations. In other words, larger areas provide a more diverse habitat setting, which in turn may host a larger number of species. On the other hand, the other factors mentioned (less topographic complexity and lower habitat diversity) should decrease the species richness in Rocas. Further studies, including collections in subtidal areas, should help to clarify these patterns.

According to the classification of Whittaker *et al.* (2008), Trindade could be considered an 'immature' island (3.7 Ma). In 'immature' islands, speciation and cladogenesis rates reach their peaks, but the number of species continues to increase due to the presence of still-unoccupied niches (Whittaker *et al.*, 2008). The exception to Model 1 and the agreement with Model 2 shown by Trindade reinforce the important role of seamounts as an immigration corridor or an extension of area. The seamount chain may explain at least in part the lower level of endemism (10.1%) when compared with the endemism of the SPSPA (29.41%) and the higher number of species in the island (109). MacArthur & Wilson (1967) also discussed the role of islands as stepping-stones that enhance dispersal potential. They suggested that even small islands may increase biotic exchange considerably, but only if, initially, they are capable of supporting species populations. In fact, Trindade was the third largest (55.1 km<sup>2</sup>) and second richest island.

Simon, Macieira & Joyeux (2013), using data from shorefishes, examined the role of the Vitória–Trindade seamount chain and claimed that the 'stepping-stone' effect was in fact very limited, at least for cryptobenthic fish with low dispersal capabilities. Their argument was based on the similar endemism levels of Trindade (9.6%) and the SPSPA (9.3%); this is in contrast with the gastropod data compiled here, in which the SPSPA's endemism (29.41%) is three times higher than Trindade's (10.1%). This disparity reinforces the assertion of Floeter *et al.* (2008) that dispersal potential and, consequently, speciation rates vary among taxa, resulting from ecological and life history traits. The Vitória–Trindade seamount chain might have served as stepping-stones between Trindade and the mainland at a different time-scale, during the glacial periods (Simon *et al.*, 2013). Studies evaluating the connectivity of marine gastropod populations may help to uncover the actual role of the seamounts for these animals.

The connection with the continent through the seamount chain could also be a key factor for the low level of endemism (1.53%) and high species richness in Fernando de Noronha, as well as the low level of endemism (3.33%) in Rocas Atoll. These aspects are also reinforced by the relatively shorter distance from both areas to the mainland ( $\leq 350$  km), which increases the immigration rate, as proposed by island biogeography theory. Furthermore, as Rocas and Fernando de Noronha aged, the species present there were colonizing other islands, losing their endemic status.

The effect of a seamount chain (as both migration route and area extension) is also observed in Fernando de Noronha, the richest island in this study. This hypothesis is also supported by data from the SPSPA. The SPSPA is not part of a seamount chain and is as isolated as Trindade. The isolation effect is noticeable in the higher level of endemism in the SPSPA (30%) when compared with all other Brazilian oceanic islands. This isolation limits the flow of larvae from the continent (reducing the immigration rate) and also promotes speciation. These data highlight the relevance of the seamounts in the colonization of the other insular areas. The SPSPA is not only isolated, but it also has the smallest platform area (3.5 km<sup>2</sup>) in the study, leading to higher extinction rates and a limited availability of suitable substrates for larval recruitment. The SPSPA is,

therefore, in accordance with MacArthur and Wilson's predictions. High endemism and low species richness were also observed for reef fish in the SPSPA (Floeter *et al.*, 2008).

The lower number of endemic species detected in Fernando de Noronha and Rocas Atoll are in agreement with previous observations of lower levels of marine endemic species even on isolated islands, suggesting that dispersal is frequent enough to prevent the divergence between populations from the islands and source areas (Vermeij, 2004). There is no doubt that larvae are the main natural dispersal mechanism in marine gastropods. However, inferences about dispersal ability and geographic distributions must be made through combined analysis of larval type (planktotrophic or nonplanktotrophic) and the ecological requirements of both larvae and juveniles. Furthermore, the role of ocean currents in the transportation of larvae should be considered, because they can enhance the chances for immigration and successful colonization. These factors make it more challenging to assess reproductive isolation and speciation in marine than in terrestrial ecosystems.

The work of Hachich *et al.* (2015) revealed that gastropod richness was influenced by island area and age, while reef-fish endemism was influenced solely by island isolation. The present study corroborates in part this assertion, with Rocas as an exception to the equilibrium model of extinction and immigration rates. However, we emphasize the importance of seamounts, which seem to influence both species richness and endemism. Trindade Island highlights once again the importance of the seamounts to colonization processes in insular areas. A similar pattern was observed for reef fishes in the eastern Indian Ocean, except for species abundance data, which differ from those typically found in terrestrial ecosystems (Hobbs *et al.*, 2012). Hachich *et al.* (2015) likewise showed that some island biogeographical patterns differ between terrestrial marine and ecosystems. These authors emphasized that, within marine shallow-water environments, biogeographical patterns are highly taxon-dependent. Further studies dealing with different scales of time and space will certainly improve the understanding of the patterns and processes involved in the current distribution of marine benthic animals. A good understanding of the effects of seamounts on the insular fauna is also essential to the development of sound strategies aimed at the conservation of these unique marine ecosystems.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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