

Island biogeography: patterns of marine shallow-water organisms in the Atlantic Ocean

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ABSTRACT

Aim The aim of this study was to understand whether the large-scale biogeographical patterns of the species–area, species–island age and species–isolation relationships associated with marine shallow-water groups in the Atlantic Ocean vary among marine taxa and differ from the biogeographical patterns observed in terrestrial habitats.

Location Atlantic Ocean.

Methods Reef fish, gastropod and seaweed species richness as well as reef fish endemic species data were obtained for 11 Atlantic oceanic islands. Using a multimodel inference approach based on linear and nonlinear regressions, we tested hypotheses regarding the variation in species richness and endemism as a function of island area, age and isolation. Best models were selected using ratios between Akaike weights corrected for small sample size (AIC_c). Results were compared between the three shallow-water species groups and contrasted against previous studies of marine and terrestrial systems.

Results Island area was the best single predictor of gastropod and seaweed richness, although it was not an improvement compared to the null model for reef fish. Island age explained richness in all taxa and was the best single predictor of reef fish richness. Isolation was a good predictor of seaweed richness but not of fish and gastropod richness, possibly because of their overall higher dispersal capacity. Reef fish endemism was influenced solely by island isolation.

Main conclusions This work reveals large-scale island biogeographical patterns for marine shallow-water organisms in the Atlantic Ocean. Our results suggest that reduced gene flow is a potentially important mechanism for the maintenance of reef fish endemism in oceanic islands. The role of island age regarding the species richness of all taxa emphasizes the importance of habitat history for the geographical distribution of marine shallow-water biodiversity. Finally, we show that some island biogeographical patterns differ not only between marine and terrestrial ecosystems but also, importantly, within marine shallow-water environments, where the biogeographical patterns are highly taxon-dependent.

Keywords

Area, Atlantic Ocean, endemism, gastropod, island age, island biogeography, isolation, reef fish, seaweed, species richness.

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INTRODUCTION

The theory of island biogeography developed by MacArthur & Wilson (1967) postulates that larger islands should maintain larger populations and offer more habitat heterogeneity,

therefore experiencing lower extinction rates and maintaining higher richness. At the same time, according to this theory, isolated islands should receive fewer immigrants and consequently maintain lower species richness (MacArthur & Wilson, 1967) and, as a result of decreased gene flow, are

expected to have more endemic species (Whittaker & Fernández-Palacios, 2007). Furthermore, older islands are expected to show increased richness and endemism because there is more time for migrant arrival and speciation (Whittaker & Fernández-Palacios, 2007; but cf. Whittaker *et al.*, 2008).

Although island biogeographical patterns have been well documented and accepted, to date research has focused largely on terrestrial organisms and habitats. It is already known that multiple factors may act at different scales and affect species richness and endemism on islands (Levin, 1992; Crawley & Harral, 2001; Whittaker *et al.*, 2001; Sax & Gaines, 2008; Triantis *et al.*, 2012). The factors that potentially influence species distribution can be quite different between terrestrial and marine systems (Carr *et al.*, 2003). For example, the majority of marine species have complex life cycles and disperse mainly via propagules, for which dispersal is probably facilitated by fluid dynamic processes (Strathmann, 1990; Kinlan & Gaines, 2003). Therefore the distribution of marine species may be strongly influenced by ocean currents.

The few studies on marine island biogeography have presented evidence of the species–area and species–isolation patterns commonly observed in studies on terrestrial organisms (Mora *et al.*, 2003; Sandin *et al.*, 2008; Tuya & Haroun, 2009; Parravicini *et al.*, 2013). However, to our knowledge, the relationship between species richness and island geological age (the species–age pattern) has not been investigated in marine systems. Furthermore, mechanisms can contribute differentially to island biogeographical processes, leading to taxon-specific patterns (Whittaker & Fernández-Palacios, 2007), hence the need to study multiple taxa in marine systems.

In this study we investigated whether large-scale biogeographical patterns of marine shallow-water groups in the Atlantic Ocean differ from those of terrestrial habitats or among marine taxa. We examined the relationships between species richness or endemism and island area, age or isolation. Our cross-taxon analyses encompassed shallow-water reef fishes, gastropods and seaweeds.

MATERIALS AND METHODS

Study region

Our study comprised 11 oceanic islands or archipelagos in the Atlantic Ocean. Oceanic islands, by definition, are those that have arisen from the ocean floor and have never been connected to continental landmasses (Thornton, 2007). The advantage of studying island biogeographical patterns based on oceanic islands/archipelagos is that, unlike continental islands, they are less influenced by variation in connectivity to species source pools outside the archipelago caused by sea-level changes. Moreover, oceanic islands normally have steeper platforms that result in less variation in continuous habitat area during glacial periods. Islands within oceanic

archipelagos in the Atlantic show strong connectivity between their reef communities, although these archipelagos are highly isolated from other reef habitats. This results in a peculiar endemism in each archipelago and in a strong affinity of the reef biota between an archipelago's islands, so that each archipelago can be viewed as a biogeographical unit (Ávila, 2000; Floeter *et al.*, 2008; Tuya & Haroun, 2009). Therefore, when focusing on marine shallow-water systems at an ocean-wide biogeographical scale, each of the Atlantic archipelagos can be treated as an island in studies of reef biota island biogeography. Given this, we refer to an archipelago in this paper as an island, because it is being treated as a biogeographical unit.

Our study spanned almost all tropical and subtropical oceanic islands within the Atlantic Ocean. The islands/archipelagos included were: Saint Helena Island, Ascension Island, São Tomé and Príncipe Islands, Cape Verde Archipelago, the Canaries, Archipelago of Azores, Archipelago of Madeira, Bermuda Island, Trindade Island, Saint Peter and Saint Paul's Archipelago and Fernando de Noronha Island (Fig. 1). These sites belong to five biogeographical provinces, according to their biotic affinities (Floeter *et al.*, 2008): south-western Atlantic, north-western Atlantic, tropical-eastern Atlantic, north-eastern Atlantic and Mid-Atlantic Ridge (Fig. 1).

Among the 11 Atlantic oceanic islands studied, three (Bermuda, Azores and Canaries) are believed to have been affected by Pleistocene glaciations (Briggs, 1966; Crowley, 1981). The drop in water temperature is thought to have affected extinction rates in these islands' local shallow-water biota, and although the elapsed time (12,000 years) may have been sufficient for species richness to recover through immigration, it is not considered long enough to have allowed significant evolutionary change (Briggs, 1966). Therefore, these islands are expected to show reduced levels of endemism (Briggs, 1966).

Biotic data

The marine shallow-water groups chosen for the study were reef fishes, gastropods and seaweeds. The term reef fishes encompasses fishes of shallow marine waters that are consistently associated with hard substrates or occupy adjacent sand substrates, excluding the Chondrichthyes (Floeter *et al.*, 2008). Reef fish richness and endemism data were compiled for the 11 islands and represented an updated version of the database used by Floeter *et al.* (2008). The updates were taken from published papers, personal communication with reef fish experts and/or information from recent expeditions run by Dr S.R. Floeter's research group (Table 1).

Data on gastropod richness were obtained for nine of the 11 islands (excluding the Canaries and São Tomé and Príncipe). These data were compiled from published papers and unpublished data offered by mollusc experts (Table 1). When we compiled the whole species list, and not just the number of species, we initially included all gastropod names, from

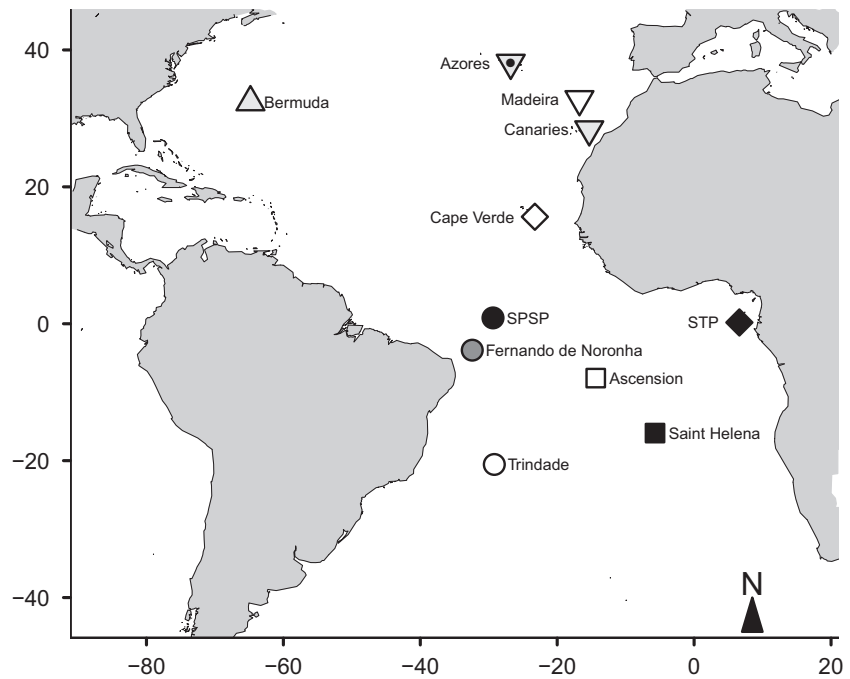


Figure 1 The islands included in the study to test island biogeographical patterns of marine shallow-water groups in the Atlantic Ocean. The biogeographical regions (after Floeter *et al.*, 2008) accounted for were the south-western (circles), north-western (triangle), tropical-eastern (diamonds), north-eastern (inverted triangles) and Mid-Atlantic Ridge (squares). Light-grey coloured islands suffered significant extinctions because of glaciation in the Pleistocene (Briggs, 1966) and were excluded from endemism analyses. SPSP, Saint Peter and Saint Paul's Archipelago; STP, São Tomé and Príncipe Islands.

which synonymies were eliminated following Rosenberg (2009), and species that do not live in shallow marine waters were excluded.

All macroalgae belonging to Rhodophyta, Chlorophyta and Phaeophyta were grouped as seaweeds. Richness data were obtained for 10 of the 11 islands (excluding São Tomé and Príncipe), based on published papers and unpublished data from algae experts (Table 1).

Abiotic data

We defined island area as the shallow shelf surface of the islands, measured as the sea-bottom area down to 200 m depth. Island areas were obtained from SRTM30_PLUS bathymetry (Shuttle Radar Topography Mission, available at http://topex.ucsd.edu/WWW_html/srtm30_plus.html). Data on island geological age, considered to be the probable time since the island first reached the water surface, were compiled from the literature (Table 2). Isolation was measured as the orthodromic (great-circle) distance from each island to the nearest reef habitat outside the same archipelago. The abiotic data and data sources for island age and nearest reef habitat are shown in Table 2.

Hypotheses and models

In the absence of ecological constraints, the increase of habitat heterogeneity with area or niche partitioning with age may allow species richness and endemism to increase linearly with island area or age (Cornell, 2013). On the other hand, if ecological constraints reduce the pace of increase of habitat availability or niche partitioning, the increase of species richness or endemism should slow down on larger or older islands (Cornell, 2013), in the form of a power or logarithmic

function with area or age. However, even with ecological constraints, there is no asymptotic limit to species richness and endemism because speciation events and niche subdivision can always add or accommodate new species (Cornell, 2013).

Isolation restricts immigration rates and gene flow and is predicted to cause a constant decrease in species richness and increase in endemism (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007). However, if the distribution of species dispersal capacity is skewed to the right, i.e. if the majority of species have low dispersal capacity and only a few are capable of long-distance dispersal, the decrease in the number of colonizers or the increase in the number of endemics can be expected to slow down on very isolated islands. In such cases, the relationships will follow a power or logarithmic function. Alternatively, the variation in richness or endemism with area, age or isolation can be negligible on very small, young and highly connected islands (MacArthur & Wilson, 1967), which should therefore exhibit a logistic function of area, age or isolation.

Alternatively, species richness can be expected to vary as a unimodal function of island age combined with a positive linear function of area. Such a species–age humped pattern would reflect the degeneration of very ancient islands (e.g. deep seamounts in marine shallow-water habitats; Hart & Pearson, 2010) which would lose both area and complexity of suitable habitats. This hypothesis is based on Whittaker's general dynamic model of oceanic island biogeography (GDM; Whittaker *et al.*, 2008).

Analyses

We used different mathematical models to test the null hypotheses of richness or endemism being independent of area, age or isolation. The alternative hypotheses presented

Table 1 Biotic data (reef fish richness and endemism, and gastropod and seaweed richness) for 11 islands/archipelagos in the Atlantic Ocean for the study of large-scale marine island biogeography, and the sources for the data. See text for the concept of island as employed here.

Island	Reef fish richness	Endemic reef fishes (<i>n</i>)	Endemic reef fishes (%)	Additional fish data sources*	Gastropod richness	Source of gastropod data	Seaweed richness	Source of seaweed data
Ascension	108	11	10.2	Wirtz <i>et al.</i> (2014)	73	Rosewater (1975), Padula <i>et al.</i> (2014)	82	Tsiamis <i>et al.</i> (2014)
Azores	113	NA	NA	Afonso <i>et al.</i> (2013)	216	Ávila (2000)	382	Tuya & Haroun (2009)
Bermuda	303	NA	NA	Smith-Vaniz & Collete (2013)	409	Rosenberg (2009)	442	C. Schneider, Trinity College, Hartford, CT (pers. comm.)
Cape Verde	225	19	8.4	Wirtz <i>et al.</i> (2013)	501	E. Rolán, Museo de Historia Natural, Santiago de Compostela, Spain (pers. comm.)	317	C. Schneider (pers. comm.)
Canaries	200	NA	NA	A. Brito, Universidad de La Laguna, La Laguna, Spain (pers. comm.)	NA	NA	678	Tuya & Haroun (2009)
Fernando de Noronha	154	7	4.5	S.R. Floeter, Universidade Federal de Santa Catarina, Florianópolis, Brazil (pers. comm.)	229	Gomes <i>et al.</i> (2006)	168	Villaça <i>et al.</i> (2006)
Madeira	147	0	0	Wirtz <i>et al.</i> (2008)	175	Ávila (2000)	369	Tuya & Haroun (2009)
São Tomé and Príncipe Islands	235	7	3.0	Wirtz <i>et al.</i> (2007)	NA	NA	NA	NA
Saint Helena	81	10	12.3	P. Wirtz, Universidade do Algarve, Faro, Portugal (pers. comm.)	140	Rosewater (1975), Rosenberg (2009)	61	Tittley & Neto (1995)
Saint Peter and Saint Paul's Archipelago	65	5	7.7	S.R. Floeter (pers. comm.)	18	Gomes <i>et al.</i> (2006)	36	Villaça <i>et al.</i> (2006)
Trindade	130	12	9.2	Simon <i>et al.</i> (2013)	99	Gomes <i>et al.</i> (2006)	138	Villaça <i>et al.</i> (2006)

NA, not available.

*The fish data came from the database used by Floeter *et al.* (2008), updated based on the sources listed and recent expeditions by the Floeter research group.

Table 2 Abiotic data (island area, age and isolation), the source of island age, and nearest reef habitat used to measure island isolation in the analyses of island biogeographical patterns of marine shallow-water groups in the Atlantic Ocean.

Island	Area (km ²)	Age (Ma)	Source of age data	Isolation (km)	Nearest reef
Ascension	176.6	1.15	Nielson & Sibbett (1996)	1290	Saint Helena
Azores	2927.9	8.12	Abdel-Monem <i>et al.</i> (1975), Feraud <i>et al.</i> (1980), Calvert <i>et al.</i> (2006), de Lima <i>et al.</i> (2011)	740	Madeira
Bermuda	1082.7	47	Vogt & Jung (2007)	1049	Continent
Cape Verde	4430	15	Holm <i>et al.</i> (2008)	560	Continent
Canaries	7515.7	25	Geldmacher <i>et al.</i> (2005)	100	Continent
Fernando de Noronha	160.5	12.3	Castro (2009)	350	Continent
Madeira	1048	14.3	Geldmacher <i>et al.</i> (2000)	285	Selvage Islands
São Tomé and Príncipe Islands	732.5	31	Dunlop & Fitton (1979), Lee <i>et al.</i> (1994)	210	Fernando Pó (=Bioko)
Saint Helena	375.6	15	Edwards (1990)	1290	Ascension
Saint Peter and Saint Paul's Archipelago	3.5	9	Hekinian <i>et al.</i> (2000)	630	Fernando de Noronha
Trindade	55.1	3.7	Ferrari & Riccomini (1999)	300	Vitória–Trindade Chain seamounts

above for the relationship between each predictor and each shallow-water marine group species richness and fish endemism were tested based on linear, logarithmic, power and logistic models using univariate linear and nonlinear regressions. The models and functions applied to test the hypotheses are shown in Table 3.

Endemism was only analysed for fishes, excluding those islands that are likely to have suffered higher extinction rates during the last glaciation, i.e. Bermuda, Azores and the Canaries (Briggs, 1966). Except for the GDM, which combines area and age in a single model, for each marine group we tested each model separately for each predictor variable (area, age and isolation). Best-fitting models were selected using ratios between Akaike information criterion weights (w_i) corrected for small sample size (AIC_c ; Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004). When this ratio was less than two, we considered both models described the data equally well, in which case we used γ -model averaging to infer a consensus response curve (Burnham & Anderson, 2002). We also selected the overall best predictors of richness and endemism using the same procedure as above (based on AIC_c values) but comparing all models for all predictors. However, in the latter analysis, we only calculated w_i between models that showed AIC_c values that exceeded the smallest AIC_c of each response variable by less than two units. We used the percentage of the sum of squares explained by the model (SS_{exp}) to evaluate the goodness-of-fit of the tested models. The fact that there are so few oceanic islands in the Atlantic Ocean imposes restrictions on the statistical inferences we could make. This is a real-world small data set, which should not be conflated with inadequately small sample sizes or experimental designs. Every analysis adjusts for sample size and therefore requires a stronger relation-

ship to indicate a non-null effect with smaller sample sizes. Whether test power adequately adjusts for sample size, in different procedures, is open to debate (Hoenig & Heisey, 2001).








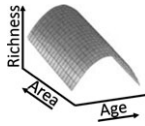
Although we used the power model nonlinear equation on the species–area model selection, we also fitted its log–log form so that the coefficient values would be comparable with studies in the literature. When the log–log power models significantly explained richness data ($P < 0.05$), we used t -tests to evaluate whether z -values were within the range (0.2–0.4) expected according to previous studies (MacArthur & Wilson, 1967). To explore patterns of endemism we analysed the variation in number and proportion of endemic fish species.

To corroborate the results of the predictors of each group's richness and fish endemism, we also fitted multiple regression models, based on power relationships between the response and predictor variables (see Appendix S1 in Supporting Information). Correlations among predictor variables were not significant (Appendix S1). All analyses were run in R (R Core Team, 2013).

RESULTS

Gastropod and seaweed species richness were positively correlated with island area (Table 4, Fig. 2). For reef fish richness, however, none of the tested models was an improvement compared with the null model: the logarithmic, power and null models had similar explanatory power (Table 4). The gastropod and seaweed species–area relationships (SAR) were best described by the power model (Table 4). The log–log form of the SAR was significant for all three taxa (Table 5). Although gastropod and seaweed z -values were within the expected range, the z -value for reef fishes was much lower (Table 5).

Table 3 The models of the variation in species richness or endemism (y) as a function of island area, age or isolation (x) that were compared by model selection in order to reveal island biogeographical patterns for marine shallow-water groups in the Atlantic Ocean.

Model	Function	Relationship	Graph
Null	$y = a$	Species–area, species–age, species–isolation, endemism–area, endemism–age, endemism–isolation	
Linear	$y = a + b.x$	Species–area, species–age, endemism–area, endemism–age, endemism–isolation	
		Species–isolation	
Logarithmic or power	$y = a + b.\log(x)$ or $y = a.x^b$	Species–area, species–age, endemism–area, endemism–age, endemism–isolation	
		Species–isolation	
Logistic	$y = a / \{1 + e^{[(x_{mid}-x)/b]}\}$	Species–area, species–age, endemism–area, endemism–age, endemism–isolation	
		Species–isolation	
General dynamic model (GDM)	$y = a + b.\log(\text{area}) + c.\text{age} + d.\text{age}^2$	Species richness with area and age	

a , b , c and d , constant variables; e , Euler’s number; x_{mid} , inflection point of the logistic curve.

Island age was positively correlated with species richness for all taxa. However, there were noteworthy differences among taxa. Reef fish richness was best explained by the linear model, while the linear, logarithmic and power models fit the seaweed and gastropod species–age relationships equally well (Table 4). Isolation was negatively correlated only with seaweed richness (Fig. 2, Table 4), whereas reef fish and gastropod richness were unaffected by isolation. The proportion of endemic fish species did increase with isolation (Fig. 2, Table 4). Other variables did not explain endemism in reef fishes (Table 4).

In general, the single best predictors were age for reef fish richness, area for gastropod and seaweed richness, and isolation for reef fish endemism (Table 4). Although Whitaker’s *et al.*’s (2008) GDM explained a large part of reef fish species richness, it was not the best model for any of these marine shallow-water groups (Table 4). Interestingly, the power model with richness increasing with both area and age combined was an improvement compared with the GDM model (which predicted that richness would

increase linearly with area together with a unimodal variation with island age). This indicated the prevalence of a monotonic relationship between richness and age over the unimodal relationship. The multiple regressions corroborated the results of the simple regressions concerning the predictors of richness for each taxon and of fish endemism (Appendix S1).

DISCUSSION

We have explored the biogeographical patterns of oceanic islands in the Atlantic. We focused on patterns of species richness and endemism varying with island area, age and isolation as key determinants for the distribution of these marine shallow-water groups.

Patterns of endemism

Reef fishes showed low endemism values (0–12.3%) compared with endemism values associated with previous studies

Table 4 Results of model selection between null, linear, logarithmic, power and logistic models testing the relationships between reef fishes, gastropods or seaweeds species richness or fish endemism and island area, age or isolation, in order to establish island biogeographical patterns for marine shallow-water groups in the Atlantic ocean. Best models for each predictor (area, age and isolation) are in bold letters, overall best models are highlighted in grey.

Area	Model	Fish richness			Gastropod richness			Seaweed richness			Endemic fishes (%)			Endemic fishes (π)		
		AIC _c	w _i	% SSexp	AIC _c	w _i	% SSexp	AIC _c	w _i	% SSexp	AIC _c	w _i	% SSexp	AIC _c	w _i	% SSexp
Area	Null	128.98	0.18	–	120.13	0.03	–	138.39	0.00	–	48.82	0.65	–	53.84	0.41	–
	Linear	130.62	0.08	12.1	115.97	0.24	57.0	130.15	0.18	68.2	52.55	0.10	0.1	54.00	0.38	36.1
	Logarithmic	127.67	0.35	32.8	116.02	0.24	56.8	131.36	0.10	64.1	52.09	0.13	5.6	56.73	0.10	10.1
	Power	127.98	0.30	28.9	114.53	0.49	63.2	127.43	0.70	75.9	52.11	0.12	5.0	56.53	0.11	14.9
	Logistic	130.60	0.08	39.4	NC	NC	NC	135.27	0.01	64.1	NC	NC	NC	NC	NC	NC
Age	Null	128.98	0.00	–	120.13	0.13	–	138.39	0.12	–	48.82	0.43	–	53.84	0.65	–
	Linear	118.12	0.72	71.8	118.87	0.24	40.6	137.01	0.23	36.8	50.35	0.20	24.0	57.37	0.11	2.5
	Logarithmic	125.43	0.02	45.1	118.84	0.24	40.8	137.00	0.23	36.9	50.44	0.19	23.2	57.26	0.12	3.9
	Power	121.42	0.14	67.5	118.12	0.35	44.3	136.31	0.33	40.1	50.60	0.18	20.4	57.25	0.12	4.1
	Logistic	121.78	0.12	72.7	122.03	0.05	52.2	138.96	0.09	53.9	NC	NC	NC	NC	NC	NC
Isolation	Null	128.98	0.51	–	120.13	0.65	–	138.39	0.16	–	48.82	0.05	–	53.84	0.59	–
	Linear	131.42	0.15	5.5	123.53	0.12	0.3	139.31	0.10	20.5	45.65	0.25	57.8	56.94	0.13	7.7
	Logarithmic	131.25	0.17	6.9	123.55	0.12	0.1	137.57	0.24	33.2	44.74	0.39	62.3	56.63	0.15	11.2
	Power	131.22	0.17	7.3	123.56	0.12	0.0	136.18	0.49	45.7	45.22	0.31	58.7	56.71	0.14	9.4
	Logistic	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
GDM		123.62	–	79.8	123.61	–	73.5	138.69	–	73.28	65.23	–	24.57	70.16	–	33.14

AIC_c, Akaike information criterion values for each model corrected for small sample sizes; w_i, AIC_c weights; % SSexp, percentage of the sum of squares explained by the model; NC, no convergence.

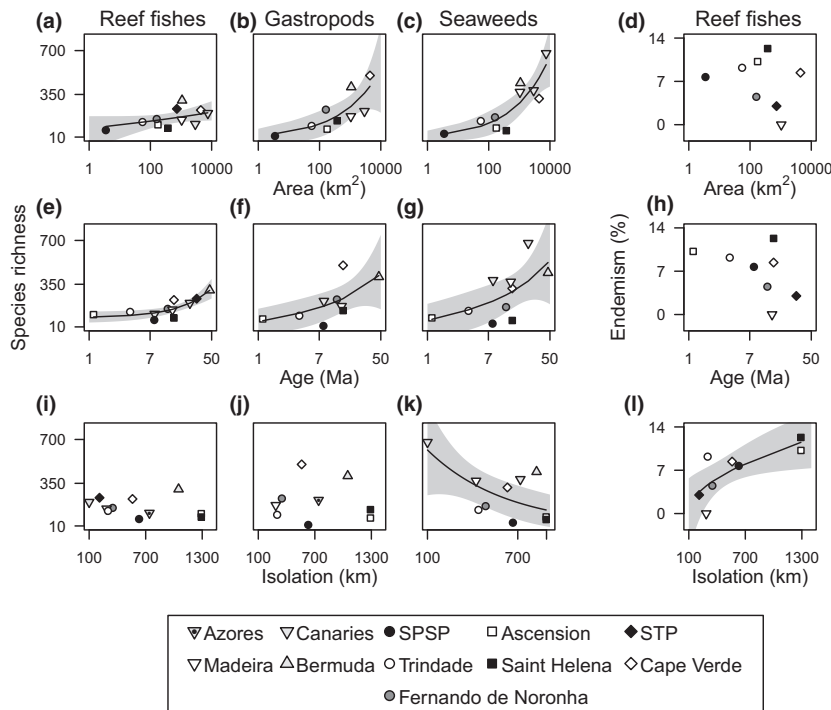


Figure 2 Model averaging curves of the best models (when several models fitted the data equally well: a, f, g and l) and single best models (b–e and h–k) for the effects of area, age or isolation of the Atlantic oceanic islands on the species richness of three taxa and on endemic fishes. The predictor–response relationships that had alternative models that were an improvement on the null model are shown in b, c, e–g, k and l. Note that the area and age axes are log-transformed, and that the shapes of the curves cannot be compared directly with the graphs of Table 3. The shaded areas represent the confidence intervals of the models with the lowest corrected Akaike information criterion values. SPSP, Saint Peter and Saint Paul’s Archipelago; STP, São Tomé and Príncipe Islands.

Table 5 Power model species–area relationship for reef fishes, gastropods and seaweeds in the Atlantic Ocean calculated based on the log–log model.

Group	C	z	r ² -adj	P	t (0)	t (0.2)	t (0.4)
Reef fish	61.58	0.14	0.36	< 0.05	8.62	−3.67	−15.95
Gastropod	14.33	0.40	0.77	< 0.005	15.97	8.08	0.20
Seaweed	21.42	0.36	0.70	< 0.005	14.87	6.57	−1.74

C, intercept; z, exponent; r²-adj, adjusted coefficient of determination; P, coefficient of significance; t, t-values of t-tests of the z-values against 0, 0.2 and 0.4. Significant values (P < 0.05) of t are in bold letters.

of island terrestrial biota (7.2–99%) (Bieler & Slapcinsky, 2000; Emerson & Oromi, 2005; Whittaker *et al.*, 2008; Lienhard & Ashmole, 2011). This may be attributed mainly to the peculiarities of the marine system. Oceanic islands are embedded in a matrix of water masses, which are more permeable to the majority of reef organisms than to terrestrial organisms (Vermeij, 2004).

The larger percentage of endemic fishes on more isolated islands presumably reflects reduced gene flow in more isolated populations (Floeter & Gasparini, 2000; Whittaker & Fernández-Palacios, 2007). In contrast with findings from terrestrial studies (Storch *et al.*, 2012), there was no evidence that island area or age contributed to the proportion of endemic reef fishes in each island.

The mechanisms that promote speciation in marine and terrestrial habitats are considered to be distinct (Bowen *et al.*, 2013), especially for reef fishes, which are able to disperse further than gastropods and seaweeds (Kinlan &

Gaines, 2003; Robertson *et al.*, 2004; Luiz *et al.*, 2012; Bowen *et al.*, 2013). Because of this high dispersal capacity, not even the larger islands impose isolation on reef fish communities, so they may not be subject to within-island allopatric speciation. In addition, there is strong evidence for sympatric ecological speciation in marine environments (Bowen *et al.*, 2013). Moreover, in groups with high dispersal capacity, such as reef fishes, the current distribution of an endemic species is not necessarily related to their location of origin (Bellwood & Meyer, 2009). In many cases, reef fish endemics have long evolutionary lineages (Bernardi *et al.*, 2004; Bellwood & Meyer, 2009) and it has also been established that some endemic reef fishes once had a wider distribution that has since contracted, turning them into palaeoendemic species (Bellwood & Meyer, 2009; Rocha *et al.*, 2010). In conclusion, the evolutionary processes related to the emergence of new reef fish species are complex and our study indicates that they do not seem to be related to area or age.

While many studies have sought to explain reef fish endemism on islands, their findings often conflict (Hughes *et al.*, 2002; Mora *et al.*, 2003; DeMartini & Friedlander, 2004; Bellwood & Meyer, 2009; Rocha *et al.*, 2010; Hobbs *et al.*, 2012; Bowen *et al.*, 2013). Our work, limited to the quantitative distributional patterns of present-day endemism in the Atlantic, provides evidence of the role of isolation in driving reef fish endemism, despite the great dispersal capacity of these organisms. However, further studies on reef fish speciation are required to elucidate the additional mechanisms that generate or maintain endemic marine shallow-water species on islands.

Patterns of species richness

Gastropod and seaweed richness increased with island area, with a prevalence of the power model for describing these SARs. This supports findings from previous studies (Triantis *et al.*, 2012). The increase of species richness with island area has been attributed to reduced extinction rates, greater niche variability and a higher chance of migrants reaching larger islands (MacArthur & Wilson, 1967). Niche subdivision and speciation events enable a continuous increase of richness with island area, so that there is no intrinsic limit to species richness with increasing area (Cornell, 2013). However, the prevalence of convex-shaped models indicates that niche availability does not increase linearly with area.

The variation in seaweed richness with area seems to be highly scale dependent (Tuya & Haroun, 2009). Previous work found no seaweed SAR between archipelagos of the Macaronesian region; however, this pattern was derived from a study on a much more refined scale, between islands within each Macaronesian archipelago (Tuya & Haroun, 2009). Our study has extended our understanding of seaweed biogeographical patterns to a broader scale, comprising the whole Atlantic, and revealed that, at this large scale, seaweed richness is highly dependent on island area.

Although the power model significantly explained the relationship between island area and reef fish richness (Table 5), it did not improve on the null model (AIC_c values were similar for both models; Table 4). Given this, we cannot ascertain whether island area influenced reef fish richness in the Atlantic. However, previous studies on wider (world-wide; Parravicini *et al.*, 2013) and smaller (Caribbean; Sandin *et al.*, 2008) scales have shown the important role of island area in limiting reef fish richness. Because we did establish a trend of increasing reef fish richness with area (Fig. 2), we therefore presume that reef fish richness is influenced by island area. However, this relationship is attenuated by other important island features, such as geological age, which can determine habitat complexity as a result of geological and geomorphological dynamics, especially those involved in the long-term erosion of islands (Whittaker *et al.*, 2008). The *z*-value of the log–log power-law SAR was lower for the group with the highest dispersal capacity (Table 5). This is in agreement with higher *z*-values reflecting greater effective isolation (Triantis *et al.*, 2012).

Species richness increased with island age in all taxa. The importance of island age in explaining species richness is probably because of (1) historical–evolutionary processes, such as the accumulation of colonizers and speciation events, but also (2) ecological mechanisms associated with higher habitat complexity in older islands. Older islands accumulate species over longer periods (Whittaker & Fernández-Palacios, 2007) and the erosion of rocks and growth of calcareous algae and coral colonies through time increases substrate surface complexity and habitat heterogeneity (Hart & Pearson, 2010). Nonetheless, the increase of richness with island age

should slow down on older islands because of ecological constraints that reduce colonization and speciation (Whittaker *et al.*, 2008; Cornell, 2013). The convex-shaped curves describing the species–age relationship for gastropods and seaweeds agree with the latter pattern, which in fact represents the first phase of GDM (Whittaker *et al.*, 2008). However, our results indicate that reef fish diversity is not limited by such constraints because of the prevalence of a linear species–age relationship for this group.

Our finding that island age was the chief determinant of reef fish richness, together with the fact that age also explained gastropod and seaweed richness, underlines the importance of incorporating an evolutionary dimension into the theory of island biogeography (Whittaker *et al.*, 2008). However, within the scope of this study, the relationship between species richness and island age does not seem to be unimodal, as proposed by the GDM (Whittaker *et al.*, 2008). Our result does not refute the GDM, but to test it adequately a contingent of senescent islands would need to be included.

The decrease of seaweed richness with isolation in the Atlantic, as detected in this study, has been found previously at a smaller scale (Tuya & Haroun, 2009) and is probably because of the relatively lower dispersal capacity of seaweeds (Kinlan & Gaines, 2003; Kinlan *et al.*, 2005). Although isolation explained seaweed richness, it was a poor predictor of fish and gastropod species richness. This indicates that the isolation of oceanic islands in the Atlantic is not important per se to limit the richness of groups with higher dispersal capacities (Scheltema, 1972; Kinlan & Gaines, 2003; Luiz *et al.*, 2012). Moreover, taxon-specific traits, such as dispersal capacity, make biogeographical patterns highly taxon-dependent.

CONCLUSIONS

Our work has revealed large-scale island biogeographical patterns for marine shallow-water organisms in the Atlantic. Reef fish endemism is influenced solely by island isolation, which suggests that reduced gene flow is an important mechanism for the origination and maintenance of reef fish endemism in islands. For all taxa, species richness was influenced by island age, highlighting the importance of incorporating an evolutionary dimension into studies of island biogeography. Although the richness of all three taxa (reef fishes, gastropods and seaweeds) was influenced by island age, there were noteworthy differences in biogeographical patterns between taxa. Reef fish richness was highly and solely influenced by island age, whereas gastropod richness was influenced by island area and age, and seaweed richness by all three island features considered (area, age and isolation). We have therefore shown not only that some island biogeographical patterns differ between marine and terrestrial ecosystems but also, importantly, that within marine shallow-water environments biogeographical patterns are highly taxon-dependent. This contributes to

our understanding of the structure, function and conservation of marine ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Correlations and multiple regressions analyses.

BIOSKETCH

Nayara Hachich's current research is on marine shallow-water community structure. The present study was begun during her undergraduate course in biology at Universidade Federal de Santa Catarina, Brazil, and extended during an internship at the Mathematical Ecology Research Group, University of Oxford, Oxford, as part of her MSc dissertation presented to the graduate program in ecology at Universidade Estadual de Campinas (Unicamp), Brazil.

Author contributions: S.R.F., M.B.B. and N.F.H. conceived the main ideas; N.F.H. and S.R.F. compiled the data; all the authors contributed substantially with ideas, analyses and writing.

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