Island Biogeography of Marine Shallow-Water Organisms

Nayara Fernanda Hachich, Instituto VerdeCoral Pró-Ciência, Ribeirão Preto, Brazil
Débora Silva Ferrari, Universidade Federal de Santa Catarina, Florianópolis, Brazil
Juan Pablo Quimbayo, Universidade de São Paulo, São Sebastião, Brazil
Hudson Tercio Pinheiro, California Academy of Sciences, San Francisco, CA, United States
Sergio Ricardo Floeter, Universidade Federal de Santa Catarina, Florianópolis, Brazil

Abstract

Marine shallow-water habitats include reefs, sand beaches, kelp forests, estuaries, and others, which have a high biological and economic importance. The study of island biogeography has uncovered the processes shaping species distribution patterns and have recently expanded to encompass the marine realm. In this article we provide an overview about marine shallow-water island biogeography. We explore the taxonomic and functional marine island biogeography, considering islands area, isolation, and geological age, as well as scale and taxon-dependency. We then discuss endemism patterns and speciation in remote marine systems and conclude with a discussion about methods of studying island biogeography in such habitats.

Introduction

Marine shallow-water habitats are normally considered as those within the neritic zone (littoral and sublittoral), typically extending to the edge of the shelf. In continental shelves this can reach as down as 200 m depth, although the shelf-break in islands generally occurs on shallower depths (Lalli and Parsons, 1997). These shallow-water habitats include reefs (rocky, biogenic or artificial), sand beaches, kelp forests, and estuaries (including marshals and mangroves; Fig. 1). The latter, although brackish, is closely associated with the sea and can be considered the most productive of the marine systems (Hemingson and Bellwood, 2018).

These marine shallow-water habitats have high biological and economic importance. For instance, marine shallow-water habitats are occupied or visited by 34 of the 35 extant animal phyla, and half of them are exclusively marine (Carr et al., 2003). Notwithstanding, they provide services as coastline protection, food production, nitrogen fixation, carbon dioxide sink, within others (Moberg and Folke, 1999; Holmlund and Hammer, 1999). But, besides its importance, the comprehension of most of these systems remains poor when compared to terrestrial and freshwater systems (Field et al., 2008).

Island biogeography, as a science that studies biodiversity distribution through the globe, has advanced our knowledge about the processes shaping species distribution patterns, and how physical and biological aspects of islands and species interfere on such patterns. The theories of island biogeography were initially built upon terrestrial island systems and have been extended to marine systems more recently (Hachich et al., 2015; Pinheiro et al., 2017; Ávila et al., 2019).

In this article we explore marine island biogeography through the perspective of shallow-water organisms. Our overall goal was to provide an overview of processes and patterns related to marine shallow-water island biogeography, considering taxonomic and functional biodiversity, as well as scale and taxon-dependency. We start by briefly presenting the most prominent island biogeography theories. This sets a theoretical background for the discussion of differences between terrestrial and marine island biogeography. We then present the state of art for taxonomic marine island biogeography, considering species-area, species-isolation and species-age patterns, as well as the applicability of more complex models on explaining marine shallow-water species richness distribution. The next section includes the discussion about marine island biogeography related to the functional component of diversity. We then proceed giving more emphasis to speciation and endemism patterns in marine systems, and finish with a brief discussion about methods of studying island biogeography in such habitats. Although reefs are by

Illustrated by Julia Locatelli
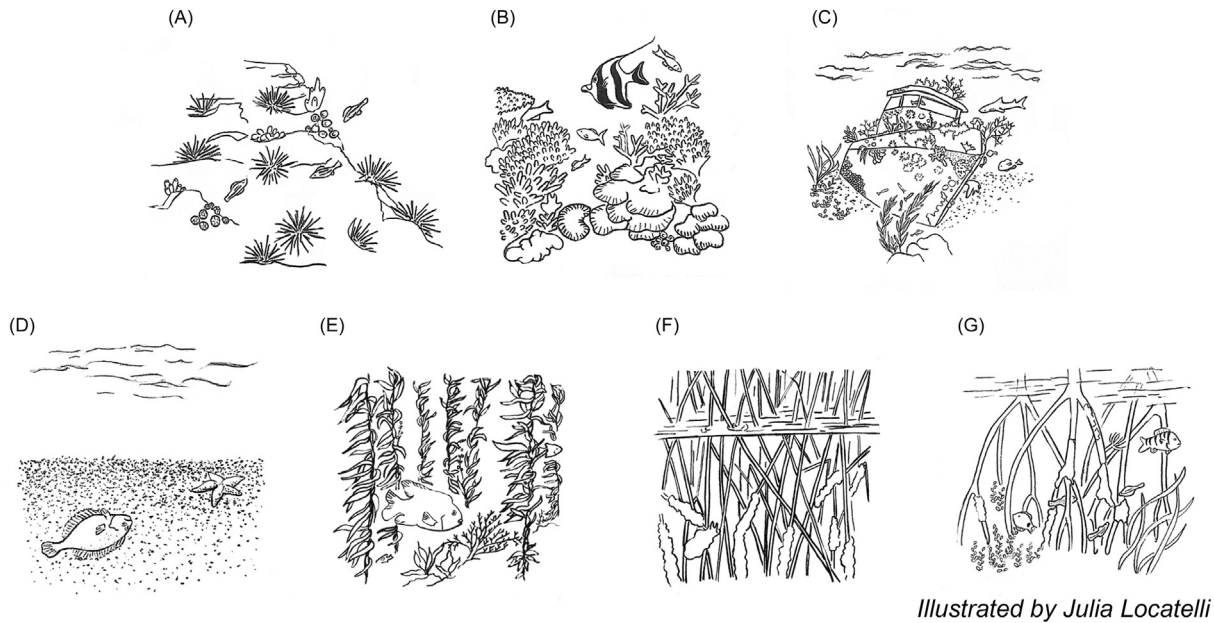
Fig. 1 Marine shallow-water habitats: (A) rocky reef, (B) coral reef (biogenic), (C) artificial reef, (D) sand beach, (E) kelp forest, (F) marsh, (G) mangrove. Illustrated by Julia Locatelli.

far the most well studied marine shallow-water habitats, as are reef fish, gastropod and seaweed the most well studied marine shallow-water groups, examples on other shallow-water habitats and taxa were brought to light whenever as possible.

Classical Theories of Island Biogeography: Predicted Patterns

The Theory of Island Biogeography (IBT) predicts a variation of species richness with island area and isolation (MacArthur and Wilson, 1967). According to the IBT, the species–area relationship (SAR) is due to larger habitat heterogeneity, that results on lower extinction rates and therefore, higher species richness maintenance. At the same time, such richness is expected to decrease as a function of island isolation, due to reduced immigration rates.

Further studies of island biogeography also pointed for an increase in species richness with island geological age due to longer times for species accumulation either by arrival of new immigrants or arise of a new species by speciation (Rosenzweig, 1995). The General Dynamic Theory of Oceanic Island Biogeography (GDM; Whittaker et al., 2008) also included island age as an important factor for predicting islands species richness, combined with island area. The explanation for the GDM also relies into the interaction between immigration, speciation and extinction rates. According to the GDM, species richness would increase linearly with island area, but would vary as a unimodal function of island age, due to the variation of habitat heterogeneity in the life cycle of an oceanic island. Such islands, which are mainly volcanic, tend to increase in area and height in their youth, due initially to volcanic activity and latter to erosion (that also increases habitat heterogeneity). An advanced stage of erosion leads to loss of habitats—increasing extinction rates—and, in older stages, the disappearance of the island, turning into an atoll or seamount, sinking into the sea.

Besides the influence of island area, age and isolation in species richness, it is also expected for those environmental variables to affect the level of endemism in islands. In the terrestrial realm, bigger islands are expected to show increased numbers of endemics, given the possibility of diversification driven by sympatric and ecological speciation—a process known as adaptive radiation. Older islands are also expected to show increased levels of endemism, due to longer times for cladogenesis. Notwithstanding, isolated islands shall exhibit increased percentage of endemic species as well, due to reduced gene flow.

The processes that influence biodiversity distributions on terrestrial and marine realms—i.e. immigration, speciation and extinction—although the same, interact differently and vary differently with such island physical features (area, isolation and age), leading to differences on island biogeography patterns.

Island Biogeography Patterns and Process of Marine Shallow-Water Organisms

Understanding island biogeography patterns for marine shallow-water organisms is key for the conservation of marine systems. For example, the richness patterns of reef fishes, corals, marine snails and lobsters are concordant across the globe and such richness is mainly concentrated in islands, with a predominance of their centers of endemism in the most isolated ones (Roberts et al., 2002; Tittensor et al., 2010; Fig. 2).
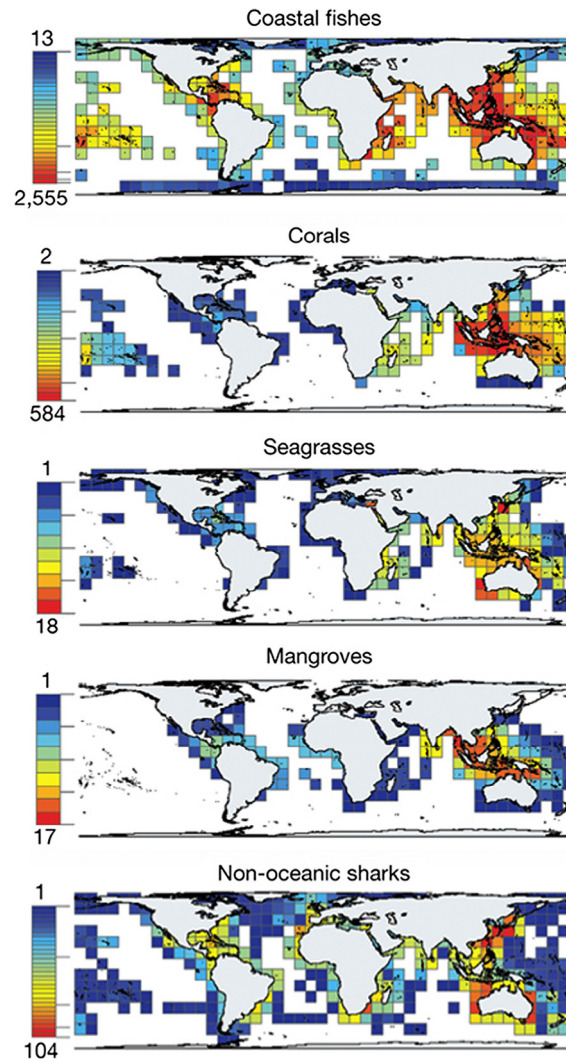
Fig. 2 Distribution of different marine shallow-water taxa across the globe. For seagrasses and mangroves only plant species were considered. Figure from Tittensor, D. P., Mora, C., Jetz, W., et al. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1103.

Yet, although the term biodiversity was originally related to the number of biological species units solely (Wilson and Peter, 1988), on a broader concept, biodiversity could embrace any variety of life. Moreover, the study of the diversity of species ecological traits and evolutionary history contributes to elucidate the processes shaping the distribution of the marine shallow-water biota in islands (Cavender-Bares et al., 2009). For this reason, we discuss herein the island biogeography patterns relying not only on taxonomic metrics of biodiversity but also on a functional approach.

Taxonomic Approach

The taxonomic approach for community ecology is based on the species as the lower measurable unit of biodiversity. The most classical island biogeography theories, briefly presented above, were developed upon this concept.

Species–area relationship

With regards to the most accepted biogeography pattern—the species–area relationship (SAR)—an increase of species richness with area is observed as a multiscale general pattern in both terrestrial and marine systems. For shallow-water marine organisms, the SAR was already detected with multiple taxa, on multiple geographical regions and over multiple spatial scales. This fact strengths the statement as the SAR being "one of community ecology's few genuine laws" (Schoener, 1976). Although few variations were shown, the power-model seems to be the best to explain SAR in both marine and terrestrial systems (Hachich et al., 2015; Triantis et al., 2012).

On a global scale, evidences of SAR were observed for reef fish (Parravicini et al., 2013; Pérez-Ruzafa et al., 2005), molluscs and echinoderms (Pérez-Ruzafa et al., 2005). On an oceanic scale, an increase of species richness with area was evident in the Atlantic Ocean for reef fishes, gastropods, seaweeds (Fig. 3; Hachich et al., 2015, 2016) and echinoderms (Ávila et al., 2018), and for reef fishes and corals in the Indo-Pacific Ocean (Bellwood and Hughes, 2001).

At the scale of a biogeographic region, the SAR was evident for reef fishes in the Caribbean (Sandin et al., 2008), and for sponges in the Eastern Atlantic (Xavier and Van Soest, 2012). The variation in seaweeds species richness between islands in the same archipelago, in the Lusitanian Macaronesia region, that comprises Azores, Madeira, the Salvage and Canary Islands, also varied in function of islands area (Tuya and Haroun, 2009), and the patterns found were consistent when considering red, green and brown algae separately or the three groups together. At smaller scales, the SAR was also evident in marine systems; the richness of decapod crustaceans associated with coral in the Gulf of Panama increases in function of coral heads sizes (Abele and Patton, 1976), and the richness of sessile and mobile marine invertebrates increased with boulders sizes in New South Whale (McGuinness, 1984).

The main explanation for SAR is equivalent for terrestrial and marine systems: bigger islands are expected to hold greater habitat variability and maintain larger populations, experiencing lower extinction rates and sustaining higher species richness. The target effect explanation, in which larger islands are more prone to be reached by chance by a propagule, has also been evoked for marine island biogeography (Velasquez et al., 2018), although its effect can be only marginal (Ávila et al., 2018). However, the hypothesis of higher speciation rates on larger islands, seems not to be so important for marine organisms. Their larger dispersal capacity hamper intra-island allopatric speciation, so in situ cladogenesis is low. A study of endemic reef fish in the seamounts and islands
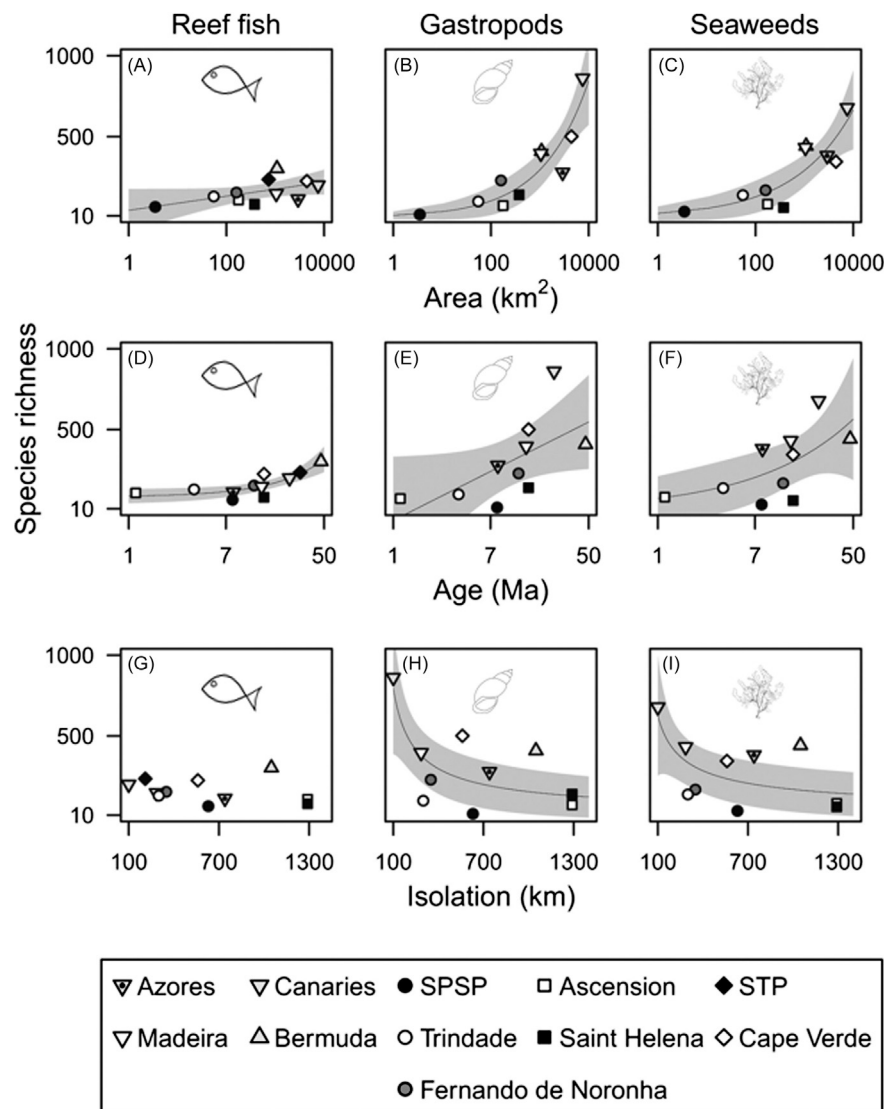
Fig. 3 Variation of marine shallow-water species richness with islands area (A–C), age (D–F) and isolation (G–I) for 11 oceanic islands in the Atlantic Ocean. Figure from Hachich N. F., Bonsall M. B., Arraut E. M., et al. (2016). Marine island biogeography. Response to comment on 'island biogeography: Patterns of marine shallow-water organisms. *Journal of Biogeography* **43**, 2517–2519.

of the Vitória-Trindade Chain (VTC), South-western Atlantic, showed evidences that speciation rates increased with the accumulation of species with low dispersal capacity, that suffered differentiation after immigration (Pinheiro et al., 2017). Speciation of marine shallow-water organisms in islands will be deeper discussed below.

Species–isolation relationship

The distribution of either marine or terrestrial organisms are influenced by geographical barriers, whose permeability is felt distinctively between the two realms. The seas represent a semipermeable matrix for the immigration of species to islands and the dispersion of organisms from one island to the other. For marine organisms such matrix is much easier to transpose than for terrestrial ones, mainly due to their resistance to water and salt. A study showed that terrestrial plants, which dispersal is within the widest from terrestrial groups, disperse one to two orders of magnitude less than sedentary marine species (Kinlan and Gaines, 2003).

Most marine shallow-water organisms, although sedentary when adults, have a planktotrophic larvae or other planktonic propagule stage on its life cycle. This capacity to live or even feed or photosynthesize while floating in the water surface favors dispersal though ocean currents (Thorson, 1949). Those marine organisms without a planktonic stage can have their dispersal facilitated through rafting. This is especially important for small-sized organisms that have the ability of attaching to migratory animals (e.g. birds or sea turtles) or drifting substrates (e.g. trunks or seaweeds). Rafting was shown to be an important mean of dispersal to marine shallow-water organisms through biogeographic barriers (Luiz et al., 2011). An overview on this subject pointed out for 946 species of marine invertebrates with clues of rafting (Table 1; Thiel and Gutow, 2005). The colonization of the reef fish *Chromis limbata* in the southern brazilian coast was probably a consequence of rafting of specimens from the Macaronesian region through the Atlantic Ocean—although other hypotheses are also discussed (Anderson et al., 2017), and the dispersal of the seastar *Patiriella exigua* is also suggested to occur via rafting on macroalgae (Waters and Roy, 2004).

Such wide dispersal capacity has implications to marine island biogeography. The IBT postulates that species richness is expected to decrease in function of island isolation due to reduced immigration rates. Although small coastal islands present higher diversity of reef fish species than larger oceanic islands (Pinheiro et al., 2015), for marine shallow-water groups, the species–isolation relationship seems to be not universal, but highly scale- and taxon-dependent (Fig. 3G–I). For example, in oceanic islands of the Atlantic Ocean the species-isolation pattern was detected for gastropods and seaweeds, but not for reef fishes (Fig. 3; Hachich et al., 2016) and echinoderms (Ávila et al., 2018). However, even for gastropods and seaweeds, the role of isolation on bounding species richness in the Atlantic islands seems to be secondary, as island area was by far the best model on explaining such richness variation (Hachich et al., 2015, 2016). On the other hand, at a smaller spatial scale, across the Lusitanian Macaronesia, seaweeds species richness decreases with distance from mainland when considering green, red or brown algae together or separately (Tuya and Haroun, 2009). Such variations in the influence of island isolation within marine shallow-water groups are also due to variations in species dispersal capacity. It was shown that while seaweeds dispersal ranges from few meters to 5 km, reef fish dispersal ranges from few to several hundreds of kilometers, and, finally, the dispersal of marine invertebrates varies from tens of meters to hundreds of kilometers (Fig. 4; Kinlan and Gaines, 2003).

Studies on large spatial-scale showed contrasting conclusions about the influence of isolation on reef fish species richness (Mora et al., 2003; Parravicini et al., 2013; Jacquet et al., 2017). The differences between these studies were their study area and the isolation metric used. Mora et al. (2003) included only the Indo-Pacific and showed a strong influence of the distance from the Coral Triangle (biodiversity center) on species richness. The two other studies spanned worldwide. Parravicini et al. (2013) found an extremely weak influence of isolation on reef fish species richness and used two measures of connectivity: (i) the relative proximity of each site to patches of reef fish habitat, using a nearest neighbor approach, and (ii) the distance of the site from the mid-domain, relative to the domain size. Finally, although Jacquet et al. (2017) showed a significant decrease of reef fishes with isolation ($p < 0.05$), they also showed that their isolation measure (based on nearest neighbor approach) was negatively correlated with reef area.

Those results highlight an important issue when investigating the influence of isolation on biodiversity, that is the measure of isolation used. Not only the distance to species sources and present ocean currents can influence connectivity between marine

Table 1   Number of species with evidence of rafting dispersal per marine invertebrate taxon.

Taxon	Number of spp.
Porifera	3
Cnidaria	131
Annelida	81
Mollusca	186
Arthropoda	398
Echinodermata	40
Ectoprocta	96
Chordata	11
Total	946

Data from Thiel, M., and Gutow, L. (2005). The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review* **43**, 279–418.
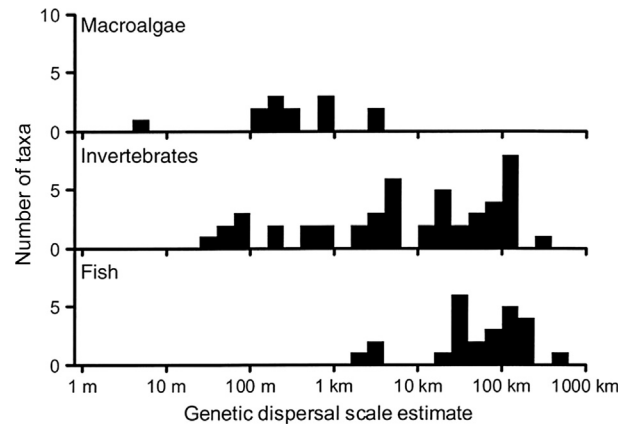
Fig. 4   Mean genetic dispersal distance estimates for marine benthic macroalgae (513 spp.), sessile and sedentary invertebrates (548 spp.) and demersal fish (525 spp.). Reproduced from Kinlan, B. P. and Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* **84**, 2007–2020.

habitats. Past ocean currents, presence of stepping-stones (islands and seamounts), sea level variation and distance to Quaternary coral reef refugia are other variables to be considered when studying marine shallow-water distributional patterns (Pellissier et al., 2014; Brown and Lomolino, 2006). The high species richness found in Trindade Island, for instance, is related to the presence of a seamount chain between the island and the continental coast, which was exposed during the low sea-level periods of the Pleistocene (Pinheiro et al., 2017; check the methodological caveat section for more examples).

Species–age relationship

The age of an island has also been shown to influence marine shallow-water species richness (although studies on marine species–age relationship are scarce). In a large-scale analysis of oceanic islands in the Atlantic, the species richness of seaweeds, gastropods and reef fishes were strongly correlated with islands geological age (**Fig. 3**). Moreover, when islands area, age and isolation were considered, age showed to be the best predictor of reef fish richness—although it was the worst predictor for seaweeds, reinforcing the taxon-dependency in marine shallow-water island biogeography patterns (Hachich et al., 2015). Still, the richness of epibiont species on pumice rafts also showed an influence of pumices age—measured as numbers of days since eruption (Velasquez et al., 2018).

The explanations for the marine shallow-water species-age patterns are equivalent for those of terrestrial biota, such as longer time for species accumulation by immigration and speciation (Hachich et al., 2015; Whittaker and Fernandez-Palacios, 2007). Moreover, the increase of island area through time (Whittaker et al., 2008; Ávila et al., 2019) can also intensify the relationship between islands age and species richness and will lie upon the life cycle of an oceanic island.

Multivariables models for species richness

The present geographical distribution of biodiversity in islands is expected to be a result of ecological, evolutionary and historical forces acting in different timescales. The GDM, explained above, is an attempt to incorporate to the IBT those processes operating in large timescales, and therefore, includes on a single model, island area and age as species richness predictors (Whittaker et al., 2008).

Although tests of this model proved it to be adequate for the terrestrial biota, it seems not to be satisfactory on explaining marine shallow-water biodiversity. For example, the GDM did not explain the richness variation of reef fish, gastropod, seaweed and echinoderm species in the Atlantic better than when considering only area or age as predictors variables alone (Hachich et al., 2015; Ávila et al., 2018).

To discuss the applicability of GDM to the marine realm with assertion, additional tests would be needed, including other taxa, biogeographic regions or spatial scales. Anyway, due to differences on the impact of island ontogeny on terrestrial and marine habitats, adaptations for the GDM model to embrace marine organisms are indeed necessary and are already being suggested. The main adaptation regards the influence of time in marine habitat area. As cited before, the GDM assumes that the erosion of islands enhances habitats heterogeneity on an initial stage, but drastically reduces it on advanced stages of erosion (Whittaker et al., 2008). However, longer times of erosion are needed for islands to reach a stage in which marine habitat heterogeneity starts to decrease, and so the species richness (**Fig. 5**). In fact, the seamount stage, achieved when islands are extremely old, is the one with greater marine area availability—but not necessarily the higher marine shallow-water species richness (Hachich et al., 2015; Pinheiro et al., 2017; Ávila et al., 2019).

The Vitória-Trindade Chain Model (VTCM; Pinheiro et al., 2017) and the Sea-Level Sensitive dynamic model (SLS; Ávila et al., 2019) are both models that comprise the effect of island ontogeny into marine systems processes, and show differences of predicted immigration, extinction and speciation rates if compared to the GDM. Those, in turn, result in differences on the estimated species richness and the system carrying capacity (**Fig. 5**). Notwithstanding, the SLS also comprises a more complex relationship of marine
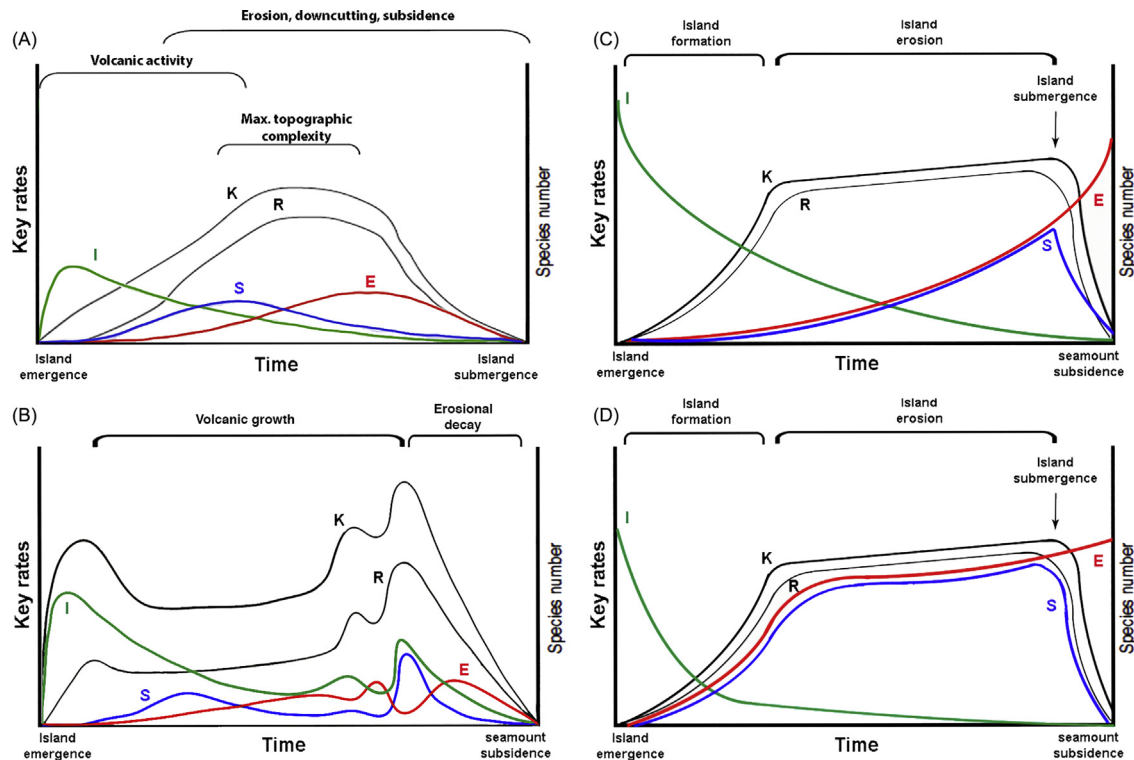
Fig. 5 Graphical representation of Immigration (I, green lines), Extinction (E, red lines) and Speciation (S, blue lines) rates of (A) the General Dynamic Model (GDM) of oceanic island biogeography; (B) the Sea-Level Sensitive (SLS) model of marine island biogeography; and (C, D) the Vitória-Trindade Chain general dynamic model (VTCM) of oceanic island biogeography for marine species, in which (C) immigration, extinction and speciation rates are only related with time (evolutionary history of the island—geological timescale) or (D) immigration, extinction and speciation rates are occurring in an ecological scale, strongly related to richness. For all models, K (*black bold line*) is the potential carrying capacity measured in species number, and R (*black line*) is the realized species richness. Adapted from Whittaker R. J., Triantis K. A., and Ladle R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**, 977–994; Pinheiro, H. T., Bernardi, G., Simon, T., et al. (2017). Island biogeography of marine organisms. *Nature* **82**, 82–86. and Ávila, S. P., Melo, C., Berning, B., et al. (2019). Towards a 'sea-level sensitive' dynamic model: Impact of island ontogeny and glacio-eustasy on global patterns of marine island biogeography. *Biological Reviews of the Cambridge Philosophical Society* **94**, 1116–1142.

habitat heterogeneity and time, due to sea-level changes during glacial periods (Fig. 5; Ávila et al., 2019). Although neither the VTCM nor the SLS make predictions on how species richness must vary with islands features (such as area, age or isolation), they give important insights for the discussion of immigration, extinction and speciation rates of marine biota in islands (Fig. 5).

Functional Approach on Island Biogeography

The studies on biodiversity distribution patterns through time and space have originally considered only species richness as a measure of biodiversity (Gotelli and Colwell, 2001). The theories of island biogeography, for example, deal mainly with species counts. However, the foreseen equilibrium between immigration, extinction and (for some models) speciation rates, although predicts a stable species richness to be hold by an island, also predicts a constant species turnover (MacArthur and Wilson, 1967; Whittaker et al., 2008). Little is known whether other biodiversity components than species richness would also remain constant or would vary through this turnover.

On relying on species richness solely, these theories consider species as being equivalent, disregarding their intrinsic features. Species phenotypic traits have been related to potential ecological functions played in the ecosystems (Mouchet et al., 2010). Such traits can be classified by morphological, behavioral and trophic characteristics (Mouillot et al., 2014). Through the combination of them—for example, body size, diet, and grouping behavior—it is possible to classify species on functional groups and, therefore, infer the community's functional richness.

Island systems show singular environmental features that could lead to nonrandom processes over its biota composition. Mechanisms like environmental filtering and competitive exclusion can favor functional traits by selective extinction (Si et al., 2017) or immigration (on the perspective of regional processes). The selective extinction or immigration caused by environmental filters would result on a higher functional similarity, that is, a functional clustering, while the selective extinction caused by competitive exclusion would result on lower functional similarity, that is, a functional overdispersion (Cavender-Bares et al., 2009; Si et al., 2017; Fig. 6).
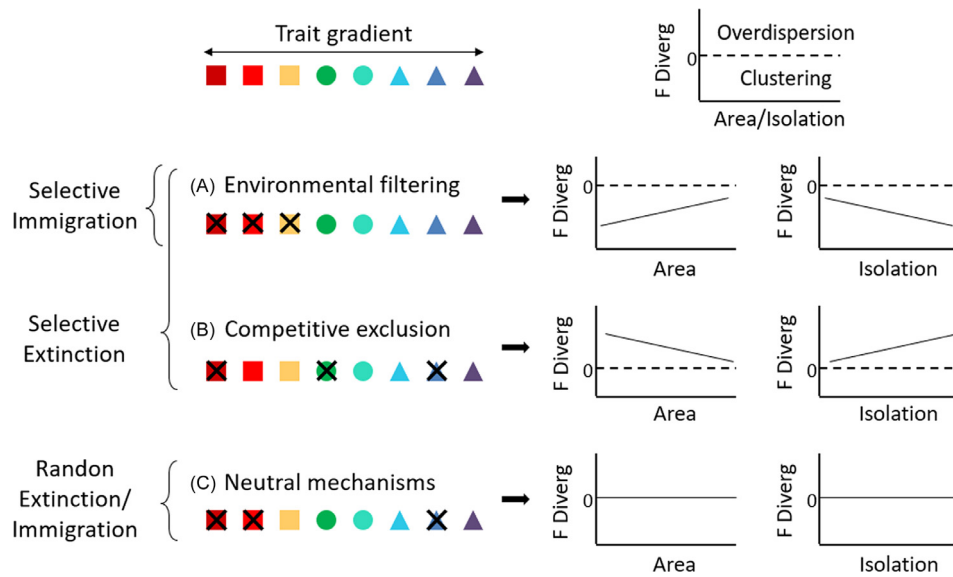
Fig. 6 Expected functional island biogeography patterns. The color and shape of symbols express the similarity in functional traits, where shape represents a categorical trait value and color a continuous trait value. F Diverg is a hypothetical measure of functional divergence between species. (A) Regional environmental conditions would cause a selective immigration, preventing the arrival of species with (or without) certain functional traits. Similarly, local environmental conditions would cause a selective extinction, eliminating species whose traits are unfavorable to these conditions. These selective immigration or extinction as result of environmental filtering would cause a clustering on the functional space and is expected to be more intense on smaller and more isolated islands, intensifying the clustering pattern with reducing area and increasing isolation. (B) Local competitive exclusion would cause a selective extinction, eliminating ecologically similar species and causing a functional overdispersion. This overdispersion intensity would decrease with islands area and increase with island isolation, due to the reduced habitat heterogeneity and rescue effect, respectively. (C) On the prevalence of neutral processes, there would be no selective immigration or extinction, so these processes would be random, and no patterns of varying functional overdispersion or clustering with islands area or isolation would be observed. Adapted from Si, X., Cadotte, M. W., Zeng, D., et al. (2017). Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology* **86**, 532–542.

On the assumption of an increasing habitat complexity with area, the effects of environmental filtering or competitive exclusion are expected to be more prominent on smaller islands. Given that, on the presence of local environmental filters, smaller islands would show even more functional clustering than bigger islands. In the same way, on the advent of competitive exclusion, the functional overdispersion will be stronger on smaller than on bigger islands (**Fig. 6**).

The IBT also predicts isolated islands to have lower immigration rates and, consequently, show reduced species richness (MacArthur and Wilson, 1967). Again, no assertations were made whether these immigration events are random regarding species functional traits (Whittaker et al., 2014). The challenges to achieve a remote island are tougher, as there is more chance for facing physical and environmental barriers in the way. Therefore, affected by regional environmental filtering, isolated islands would show even higher functional clustering than more connected ones (**Fig. 6**). Moreover, on the assumption of a reduced rescue effect on more isolated islands, the outcomes of competitive exclusion would be more intense, as the species are not receiving inputs of individuals from source communities, that could soften the extinction rates. Therefore, the functional overdispersion would increase with island isolation (Si et al., 2017; **Fig. 6**).

Finally, regarding island age, Borregaard et al. (2017) included a functional approach to the original General Dynamic Model of Oceanic Island Biogeography (GDM), but, again, focusing on terrestrial systems. According to them, young islands, on an initial stage of colonization, would hold a reduced pool of functional traits. These traits variability would increase with speciation events while the island is increasing in habitat heterogeneity. However, on its most advanced stage, habitat loss caused by excessive erosion would imply into lower niche availability, causing selective extinction of species with specialized traits and, also, intensifying extinction rates of those with similar traits—as a result of stronger competition between ecologically similar species (Borregaard et al., 2017).

Functional island biogeography for marine shallow-water species

To our knowledge, there are no studies relating marine shallow-water functional richness to islands features, although a few studies relates single marine shallow-water biota traits to islands area and isolation. Jacquet et al. (2017) proposed two process-based models including the functional component of biodiversity into the IBT. The Allometric Theory of Island Biogeography (ATIB) treats mainly of the variation on species body-size with island area and isolation, while the Allometric and Trophic Theory of Island Biogeography (ATTIB) emphasizes the importance of species trophic level together with body size (Jacquet et al., 2017).

On what concerns selective immigration, it is known that species dispersal ability influences their immigration capacity, so that weak dispersers would be almost absent in remote islands. In marine systems, functional traits like pelagic larval duration (PLD),

species body size, grouping behavior and nocturnal activity have been related to dispersal capacity (Reaka, 1980; Shanks et al., 2003; Mora et al., 2003; Luiz et al., 2013; Stier et al., 2014). For instance, larger coral-dwelling mantis shrimp species show a wider longitudinal spam (Reaka, 1980). Likewise, a study on reef fish distributions through 134 tropical reefs across the globe showed an increase of species mean body size with isolation (Fig. 7B; Jacquet et al., 2017). Reef fish body size was also showed to be a predictor of their capacity to cross both the Mid-Atlantic and the Amazon-Orinoco Plume barriers in the Atlantic Ocean, mainly due to the faster growth rate of large species, which reduces the risk of predation while dispersing (Luiz et al., 2011). Still, reef fish species recorded in oceanic islands of the southwestern Atlantic are positively related to rafting use, great depth ranges and large body sizes, while their endemism is mainly related to small body sizes (Pinheiro et al., 2018). Exceptions for that would be for cases
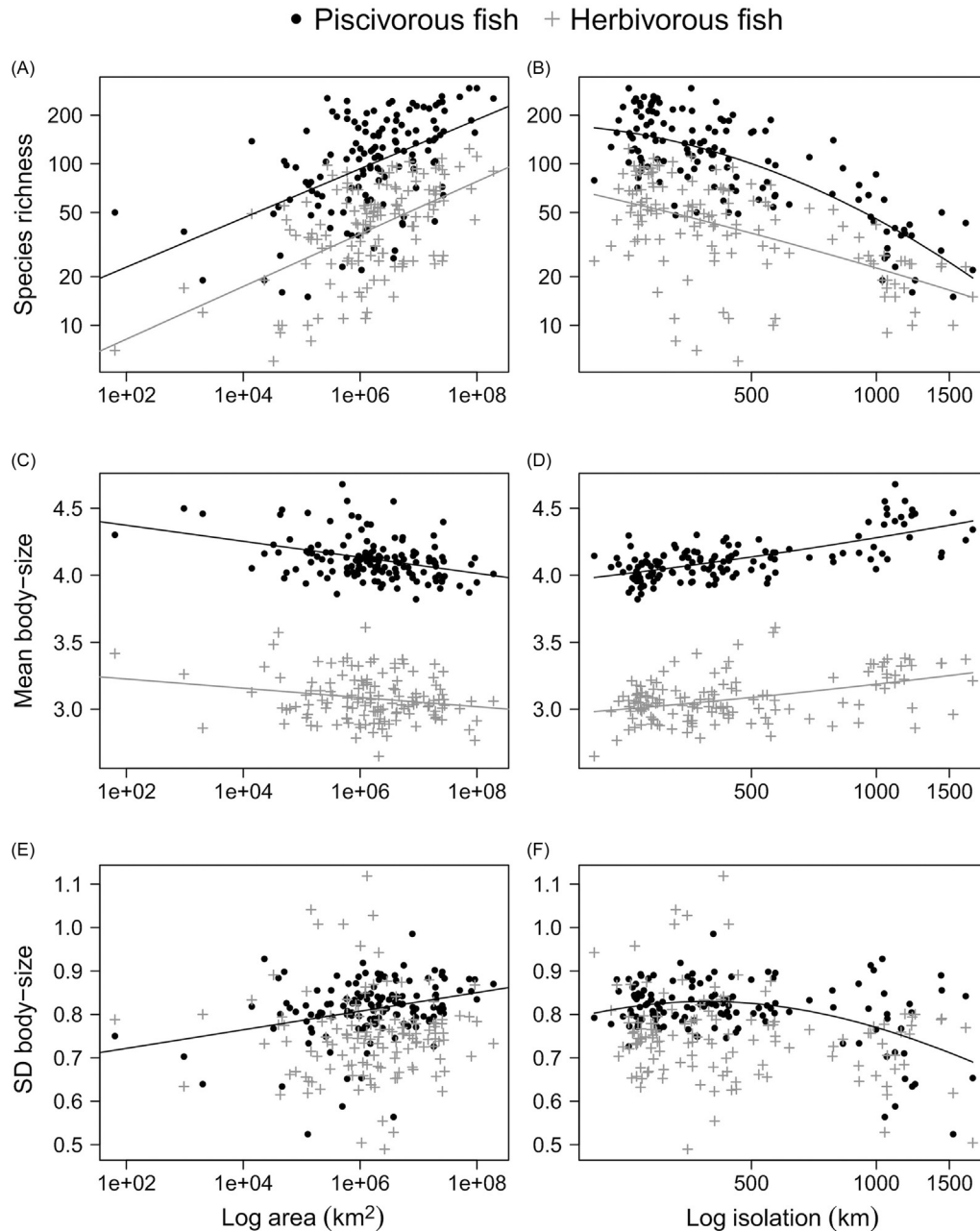
Fig. 7 Relationship between body sizes and reef area and isolation for piscivorous (*black circles*) and herbivorous (*gray crosses*) reef fish on 134 tropical reefs across the world. The lines illustrate significant ($p < 0.05$) relationships between the variables. Piscivorous and herbivorous mean body size (A) decreased with area and (B) increased with isolation. (C) The standard deviation (SD) of body size increased with area only when piscivorous fish were considered, showing that larger areas hold a greater variability of piscivorous fish body size. Figure from Jacquet, C., Mouillot, D., Kulbicki, M. and Gravel, D. (2017). Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters* **20**, 135–146.

such as the VTC, in which an evolutionary path toward reduced reef fish dispersal capacity was followed through an anagenesis speciation process (Pinheiro et al., 2017), as a relationship between species evolutionary age and dispersion capacity was evident.

On what concerns selective extinction, species with generalist diets are expected to be less vulnerable to extinction than others with restricted diets, especially on smaller islands, in which resources are more limited. Although Jacquet et al. (2017) found no differences between piscivorous and herbivorous fish species-area and species-isolation patterns on islands (Fig. 7A–D), they verified a higher prevalence of extreme reef fish body sizes on larger areas only when piscivorous fish were considered (Fig. 7E). That is, while larger islands show variable sizes of piscivorous species, the smaller islands show a prevalence of fish species with intermediate mean body sizes. The explanation for this pattern relies on the relationship between the species body size, trophic group and extinction and immigration rates of this taxon. Reef fish intermediate-sized species are less susceptible to extinction than those with extreme body sizes, due either to their more generalist diet, when compared to smaller species, or to the maintenance of higher population densities, when compared to larger species (Jacquet et al., 2017). Therefore, the piscivorous fish, on being more specialist and therefore even more susceptible to extinction (if compared to herbivorous species), presented a pattern of increasing size standard deviation with island area (Fig. 7E).

Therefore, when comparing the ATIB and ATTIB, the latter, by also including the species trophic level as an important functional trait, was shown to be a better model than the ATIB (that included only species body size) on explaining reef fish distributions across the globe (Jacquet et al., 2017). However, although either the ATIB and ATTIB give important insights to functional island biogeography, generalizations to other marine shallow-water groups must bear in mind taxa specificity on the relationship between body size, trophic level and extinction and colonization rates (Jacquet et al., 2017).

On what concerns island age, although no tests on the GDM functional approach were done to marine biota yet, we would expect that adaptations equivalent to those proposed for taxonomic marine shallow-water GDM would be necessary, due to the increased marine shallow-water habitat area of islands on advanced erosion phases.

Speciation and Endemism Patterns in Marine Shallow-Water Habitats

Speciation is an evolutionary process that consists in the formation of one or more descendent species from an ancestral one (Mayr, 1947). Despite the advances in the knowledge about the origins of the terrestrial biodiversity, the understanding of how new species arise in marine habitats is still poorly known (Bowen et al., 2013). Major differences are related to the few opportunities for geographical isolation in a circumglobal aquatic medium, where few obvious physical barriers are present and for which most organisms have a pelagic larvae stage with a high dispersal potential. Anyway, an average of 42% of "endemicity" can be seem within each marine realm—benthic molluscs and arthropods contribute the most for this endemicity—so that major biogeographic barriers constrain species distribution worldwide (Costello et al., 2017). But, in general, many marine populations are genetically connected among different ocean basins, as it is the case for many pelagic and bathypelagic fish species (Gaither et al., 2016), the brown algae *Dictyota ciliolate* and *D. crenulata*, among other species that display a circumtropical distribution (Tronholm et al., 2012). Therefore, the combination of few physical barriers and high dispersal capacity reduces opportunities for allopatric speciation—classical model where populations become isolated due to the rise of physical barriers and end up in different evolutionary paths (Rocha et al., 2005). However, since many marine habitats (e.g. reefs, estuaries, kelp forests, sand beaches) shelter high biodiversity levels—some of them comparable to the highly diverse rainforests—the generalization that speciation must be rare in taxa with high dispersal capacity is inaccurate (Rocha et al., 2005; Pinheiro et al., 2017; Delrieu-Trottin et al., 2019).

Speciation in marine systems has been explored in biodiversity hotspots—e.g., Coral Triangle in the Indo-Pacific and the Caribbean—where richness levels are explained by three main hypotheses (Bowen et al., 2013). The first considers biodiversity hotspots as "Centers of origin," where intensive competition among species would promote the emergence of new species (Briggs, 2003). According to this hypothesis, species originated in the biodiversity center could colonize marginal provinces and evolve in different species (Bowen et al., 2013). The second hypothesis, known as "Center of accumulation," suggests that new species arise in peripheral areas, such as oceanic islands and archipelagos, and then colonize and accumulate in biodiversity hotspots, with the aid of prevailing currents (Kool et al., 2011). Some cases involve a biodiversity feedback process, where species migrate from biodiversity hotspots, evolve in a different species in the periphery, and finally colonize back the original province (Bowen et al., 2013). For instance, the Ember parrotfish (*Scarus rubroviolaceus*) and the Yellow tang (*Zebrasoma flavescens*) occur in the Indo-Pacific region, however population genetic data indicates that their ancestral lineage had first colonized and evolved in Hawaii, spreading back to the central Pacific later (Eble et al., 2011; Fitzpatrick et al., 2011). Finally, the "Center of overlap" hypothesis suggests that the high species richness observed in biodiversity hotspots is the result of different communities overlap, which were previously divided by historical events, such as changes in the sea level (Gaither and Rocha, 2013; Pinheiro et al., 2017) and movements of tectonic plates (Leprieur et al., 2016). In the Atlantic Ocean and in the Coral Triangle, low sea-levels intensified biogeographic barriers for marine organisms due to land exposing, reducing gene flow and driving allopatric speciation (Rocha et al., 2005; Floeter et al., 2008; Gaither and Rocha, 2013). In higher sea level stands, species expanded their distribution and overlapped in the biodiversity hotspot. However, sea-level oscillations played different roles on driving speciation, depending on the availability of shallow habitats. In the VTC, southwestern Atlantic, for example, low-stand sea levels, instead to promoting vicariance, allowed dispersal from mainland to the arising seamounts (Pinheiro et al., 2017), similarly to the effect of low sea levels in improving terrestrial connectivity. In summary, the Center of origin hypothesis involves speciation without complete geographic isolation—i.e., parapatric and sympatric speciation—while the Center of accumulation and the Center of Overlap hypotheses include some level of vicariance and isolation—i.e., allopatric or peripatric speciation. These hypotheses put oceanic islands in

opposing roles in what concerns marine shallow water biodiversity, since for the Center of origin model, islands are evolutionary dead ends for some species, whereas in the Center of accumulation and Center of overlap, islands are cradles of biodiversity (Bowen et al., 2013).

On contrasting terrestrial and marine realms, endemism is much more common on land than in the sea, again, due to the high dispersal capacity of marine organisms, allowing a greater connectivity between populations and, therefore, reducing extinction and speciation rates (Pinheiro et al., 2017; Ávila et al., 2019). For example, endemism levels for reef fish in the Atlantic Ocean, even considering its most isolated oceanic islands (Ascension and Saint Helena), varied from 0% to 13.2% (Hachich et al., 2015; Floeter et al., 2008). Conversely, in the Atlantic islands, the endemism of terrestrial plants—group within the ones with higher dispersal ability in land—ranged from 7.2% to 40% (Whittaker et al., 2008; Emerson and Oromí, 2005).

Another interesting contrast between the terrestrial and marine biotas is that isolated archipelagos are functionally "islands" for most marine species. Speciation within islands in a given archipelago is commonplace for terrestrial species, while in the sea it can be very uncommon. For example, while the speciation of tortoises and finches in the different islands of the Galapagos is well known (Román-Palacios and Wiens, 2018), endemic reef fishes there are spread over the entire archipelago (Bernardi et al., 2014). Despite the relatively lower rate of endemic shallow-water species in the ocean, there are 18 marine centers of endemism, which together, embrace >50% of the world's restricted-range species of fishes, corals, snails and lobsters (Fig. 8). Such centers are mainly composed by groups of islands that, although distributed across all the oceans, prevail in the Indo-Pacific region (Roberts et al., 2002).

Endemicity relies into specific spatial and temporal boundaries. Geographic or ecological characteristics allow the delimitation of an area that encompass the distribution of an endemic species, while the evolutionary history of a species allows its classification as a new or an old endemic (Anderson, 1994). Neoendemic species would occupy a restricted area due to their recent origin, while paleoendemics would be the remnants of a more widespread ancestral species (Tedesco et al., 2012). In practical terms, paleoendemic species could be distinguished from neoendemics as the formers display deep divergence times from their sister species together with signals of distribution contraction (Cowman et al., 2017). Oceanic islands appear to harbor a combination of paleo and neoendemic species (Fig. 9; Cowman et al., 2017; Pinheiro et al., 2017; Delrieu-Trottin et al., 2019). The marine gastropod genus *Conus*, for instance, suffered an explosive radiation in Cape Verde during the last few million years, resulting in >40 neoendemic species in the archipelago (Duda and Rolán, 2005; note that this within-archipelago speciation is an exception for marine organisms). On the other hand, the Trindade parrotfish *Sparisoma rocha* and the wrasse *Halichoeres rubrovirens* had their ancestral lineages extinct from the continental coast, only remaining in the VTC, that serves as a museum for these old lineages (Pinheiro et al., 2017). However, most endemic fishes of the VTC are indeed neoendemics (Fig. 9), with limited dispersal potential, which colonized the most distant islands when the sea-level was lower than today, exposing seamounts that acted as stepping stones. The sea-level rise created a vicariant barrier and contributed to speciation (Pinheiro et al., 2017). Therefore, the speciation scenario in the VTC follows the premises of the IBT, where good dispersers colonize distant islands first, and weak dispersers later. These good dispersers evolve by parapatric and ecological speciation, while the weak dispersers, if do not get extinct, evolve by allopatric or peripatric speciation. In the most extreme example of island isolation, the Easter Island shows one of the highest endemism levels of marine species in the world, with nearly 22% for reef fishes (Randall and Cea, 2011). The evolutionary history of Easter Island endemics also shows a majority of neoendemics with restrict geographic range, together with a few wide distributed older endemics (Delrieu-Trottin et al., 2019).

Our knowledge about the drivers of marine endemism patterns is still in its infancy, and few information is available regarding the variation of marine shallow-water endemism with islands area, age and isolation. The GDM foresees for the proportion of endemism the same trend behavior as for the variation on species richness with area and age. That is, endemism would increase linearly with area and as a unimodal function of age (Whittaker et al., 2008). Although this has been observed for terrestrial organisms (Whittaker et al., 2008; Cameron et al., 2012; Triantis et al., 2015), the GDM is not a good model for marine gastropod and reef fish endemism in the Atlantic (Hachich et al., 2015; Ávila et al., 2018). In fact, among the two groups, only gastropod shows an increase of endemism with area (Fig. 10B). Moreover, it seems to be no relation at all between reef fish and gastropod endemism with island age (Fig. 10A; Hachich et al., 2015, Ávila et al., 2018). Finally, only reef fish endemism varied with island isolation (positive relationship; Fig. 10C). Despite its high dispersal ability, reef fishes exhibit a high auto-recruitment, especially for endemic species (Robertson, 2001), which can also influence endemism spatial patterns.
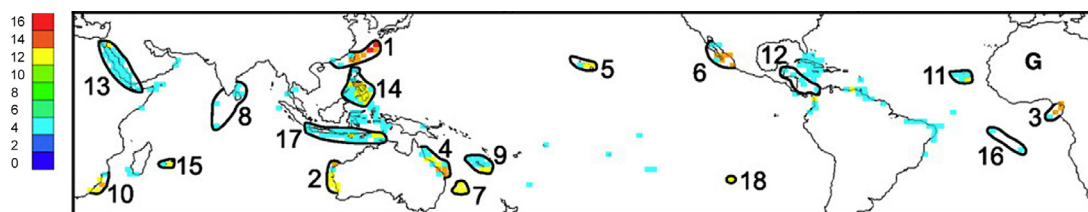
Fig. 8 The 18 multitaxa centers of marine endemism, considering fishes, corals, snails and lobsters. Figure from Roberts, C. M., McClean, C. J., Veron, J. E. N., et al. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**, 1280–1284.
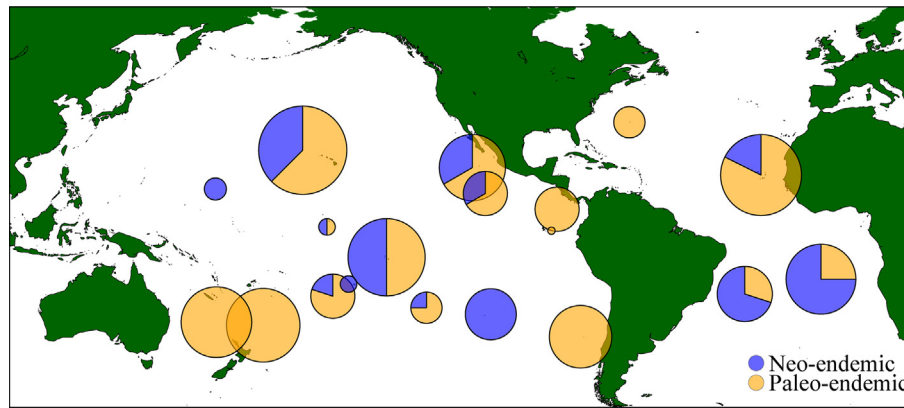
Fig. 9 Proportion of reef fish endemic species found in different oceanic islands across the marine biogeography regions. Size of circles indicates the proportion of the assemblage made up by endemic species. Colors show the different types of endemism observed in oceanic islands: neo-endemics (blue, ≤ 2.6 Ma), paleo-endemics (orange, >2.6 Ma). Data was extracted from Cowman P. F., Parravicini V., Kulbicki M., and Floeter S. R. (2017). The biogeography of tropical reef fishes: Endemism and provinciality through time. *Biological Reviews* **92**, 2112–2130; Pinheiro, H. T., Bernardi, G., Simon, T., et al. (2017). Island biogeography of marine organisms. *Nature* **82**, 82–86, and Delrieu-Trottin, E., Brosseau-Acquaviva, L., Mona, S., et al. (2019). Understanding the origin of the most isolated endemic reef fish fauna of the Indo-Pacific: Coral reef fishes of Rapa Nui. *Journal of Biogeography.* doi:10.1111/jbi.13531.
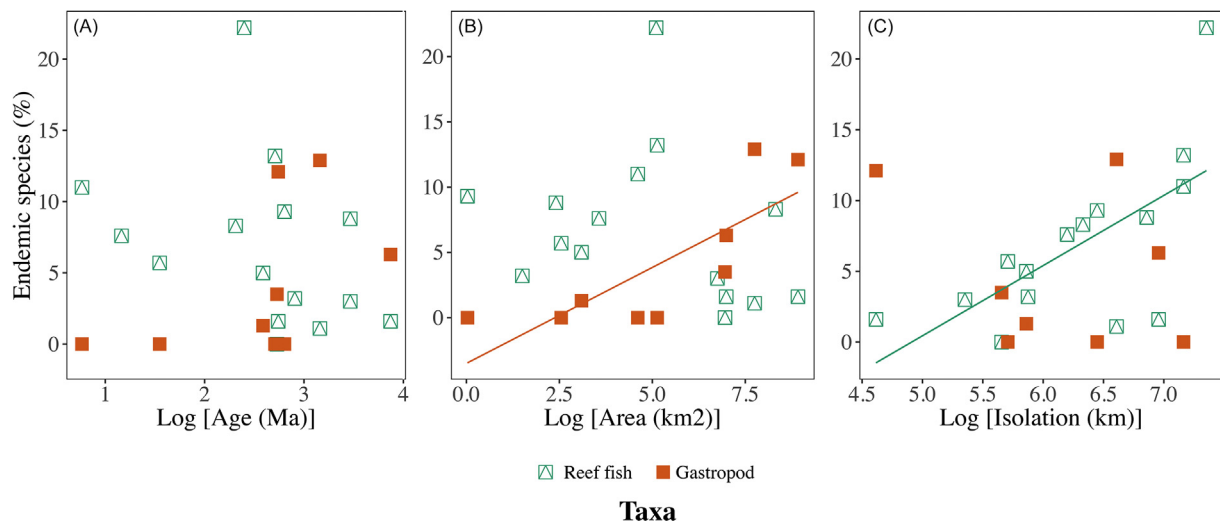
Fig. 10 Variation of marine shallow-water endemism with islands (A) age, (B) area and (C) isolation for reef fish and marine gastropod. Reef fish data are from 15 islands in the Atlantic and Tropical Eastern Pacific plus Easter Island (compiled from Robertson, 2001, Floeter et al., 2008, and Hachich et al., 2015). Gastropod data are from eight island in the Atlantic Ocean (obtained from Ávila et al., 2018). Only significant ($p < 0.05$) regressions lines were presented.

Methodological Caveats for Marine Shallow-Water Island Biogeography

The study of marine habitats, for those that are used to study the terrestrial biota, would be, in some ways, equivalent as looking to the world on an upside-down vision. Thus, adaptations to conventional research methods developed based on terrestrial studies are needed. Regarding island biogeography, except for the VTCM (Pinheiro et al., 2017), SLS (Ávila et al., 2019) and the ATIB and ATTIB (Jacquet et al., 2017), that were specially (and recently) designed for the marine biota, other theories and amends were conceived based on the terrestrial realm. Therefore, attention is required when bringing island biogeography to the marine sphere, either related to the measures of islands features—such as area, age and isolation—or to the limits to line off marine communities.

A first point of concern is related to island definition. For marine shallow-water organisms, depending on the scale of analysis, even a shipwreck or a small group of rocks can be treated as an island. On the other hand, for large spatial scale analysis, given the higher dispersal capacity of most of these organisms, a whole archipelago could be treated as a single island—in the sense that its component islands and islets show great within-island biota affinities. For sure such island definition must bear in mind taxon features specificity and the component of biodiversity being analyzed, as little is known about the distribution of functional groups within-islands in archipelagos.

When accounting for island area, although some authors have considered the emerged island area or coastal perimeter as a proxy for the real habitat area available for marine shallow water organisms (e.g. Tuya and Haroun, 2009), islands shallow shelf area would be, by far, a better unit of measure. The slope of an island aid on determining the availability of shallow shelf habitats, so that steeper surfaces imply in smaller areas. The terrain steep above and below water are not necessarily equivalent, especially for old islands on a high degree of erosion, which display a higher shallow water area compared to emerged area (Ávila et al., 2019). The shallow shelf surface of marine systems can be obtained by bathymetry from nautical charts or satellite data.

Another concern related to island area is that glacial periods were shown to have impacted the slope of islands terrain and their habitat variability directly, by selectively wiping out substrates such as beach sand (Ávila et al., 2019). And because islands shelf-break are generally shallower than continental ones, sea-level reduction would have hugely impacted their total available shallow area during glacial periods. Given that, also the past shallow shelf surface availability could have influenced the actual islands biodiversity, particularly when considering their functional diversity.

Another important discussion is about down to which depth to consider as shallow. Traditionally, shallow-water habitats are those down to depths of 200 m, just before the continental slope (Lalli and Parsons, 1997). However, authors have defined different depths for shallow-water organisms, even when the same taxon is being considered. For instance, although sponge richness increases with depth (Alcolado, 1994), depths limits from 10 to 30 m have been applied for sponge shallow-water studies (Longakit et al., 2007; Lim et al., 2012; Hadi et al., 2018; Ávila et al., 2011). On a quick literature overview, maximum depths delimitations for shallow-water organisms varied from 6 to 200 m deep (Sangil et al., 2018; Ávila et al., 2011; Edgar et al., 2004, Villaça and Pitombo, 1997, Flórez et al., 2018, Floeter et al., 2008), and a few papers did not even use a depth limitation. Whether this definition should rely on an arbitrary depth limit or be related to each taxon ecology, a standardization for the phrase, or at least a better definition in each paper—based on scientific arguments—would allow better grounded syntheses and multiple studies comparisons. For instance, there are evidences of a high malacofauna turnover about the 50 m isobath (Ávila et al., 2019) and the 30 m depth isobath was showed to be a transitional zone between reef fish shallow and deep species composition (Brokovich et al., 2008).

Measuring island isolation as a geographical parameter, is not that challenging, although measuring the real isolation between communities can be tricky, especially when considering marine organisms. Originally, the IBT has been measuring island isolation as the distance from mainland or even the distance to the nearest larger suitable habitat. These isolation measures rely on the source-sink dynamic model (Pulliam, 1988), in which larger areas, with high quality habitats, serve as source of species to smaller areas (impoverish habitats), such as islands. The distance from a hotspot can also be used as a measure of isolation, based on the "Center of origin" hypothesis on marine shallow-water biodiversity. However, especially when considering the "Center of accumulation" or "Center of overlap" hypotheses, in which islands are cradles of biodiversity, more complex measures of isolation, that consider the mosaic of suitable habitats in which the island is located, needs to be applied.

Finally, islands age measures are tricky to determine, mainly because islands can span long periods of formation—eastern Azores islands, for example, show rock fragments dated between 0.95 and 8.12 millions of year from the present (Abdel-Monem et al., 1975). The oldest age in which an island has reached a certain shallow water depth (again, depending on shallow-water definition) would be a reasonable estimate of the availability for colonization. Technology has advanced toward facilitating access to many of these data, so that IBT studies is expected to improve in accuracy and quality.

References

Abdel-Monem, A.A., Fernandez, L.A., Boone, G.M., 1975. K-Ar ages from the eastern Azores group (Santa Maria, Miguel and the Formigas Islands). Lithos 8, 247–254.

Abele, L.G., Patton, W.K., 1976. The size of coral heads and the community biology of associated decapod crustaceans. Journal of Biogeography 3, 35–47.

Alcolado, P.M., 1994. General trends in coral reef sponge communities of Cuba. In: Van Soest, R.W., Van Kempen, T.M., Braekman, J.C. (Eds.), Sponges in time and space. Balkema, Rotterdam.

Anderson, S., 1994. Area and endemism. The Quarterly Review of Biology 69, 451–471.

Anderson, A.B., Salas, E., Rocha, L., Floeter, S.R., 2017. The recent colonization of South Brazil by the Azores chromis *Chromis limbata*. Journal of Fish Biology 91, 558–573.

Ávila, E., Carballo, J.L., Vega, C., et al., 2011. Deposition of shallow water sponges in response to seasonal changes. Journal of Sea Research 66, 172–180.

Ávila, S.P., Cordeiro, R., Madeira, P., et al., 2018. Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands. Marine Pollution Bulletin 126, 101–112.

Ávila, S.P., Melo, C., Berning, B., et al., 2019. Towards a 'Sea-Level Sensitive' dynamic model: Impact of island ontogeny and glacio-eustasy on global patterns of marine island biogeography. Biological Reviews of the Cambridge Philosophical Society 94, 1116–1142.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292, 1532–1535.

Bernardi, G., Ramon, M., Alva-Campbell, Y., McCosker, J.E., Bucciarelli, G., Garske, L.E., Crane, N.L., 2014. Darwin's fishes: Phylogeography of Galápagos Islands reef fishes. Bulletin of Marine Science 90, 533–549.

Borregaard, M.K., Amorim, I.R., Borges, P.A., et al., 2017. Oceanic island biogeography through the lens of the general dynamic model: Assessment and prospect. Biological Reviews 92, 830–853.

Bowen, B.W., Rocha, L.A., Toonen, R.J., Karl, S.A., 2013. The origins of tropical marine biodiversity. Trends in Ecology and Evolution 28, 359–366.

Briggs, J.C., 2003. Marine centres of origin as evolutionary engines. Journal of Biogeography 30, 1–18.

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M., Kark, S., 2008. Descending to the twilight-zone: Changes in coral reef fish assemblages along a depth gradient down to 65 m. Marine Ecology Progress Series 371, 253–262.

Brown, J.H., Lomolino, M.V., 2006. Biogeografia. Funpec, Ribeirão Preto.

Cameron, R.A.D., Triantis, K.A., Parent, C.E., et al., 2012. Snails on oceanic islands: Testing the general dynamic model of oceanic island biogeography using linear mixed effect models. Journal of Biogeography 40, 117–130.

Carr, M.H., Neigel, J.E., Estes, J.A., et al., 2003. Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. Ecological Applications 13, 90–107.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12, 693–715.

Costello, M.J., Tsai, P., Wong, P.S., Cheung, A.K.L., Basher, Z., Chaudhary, C., 2017. Marine biogeographic realms and species endemicity. Nature Communications 8, 1057.

Cowman, P.F., Parravicini, V., Kulbicki, M., Floeter, S.R., 2017. The biogeography of tropical reef fishes: Endemism and provinciality through time. Biological Reviews 92, 2112–2130.

Delrieu-Trottin, E., Brosseau-Acquaviva, L., Mona, S., et al., 2019. Understanding the origin of the most isolated endemic reef fish fauna of the Indo-Pacific: Coral reef fishes of Rapa Nui. Journal of Biogeography 46, 723–733. https://doi.org/10.1111/jbi.13531.

Duda, T.F., Rolán, E., 2005. Explosive radiation of Cape Verde Conus, a marine species flock. Molecular Ecology 14, 267–272.

Eble, J.A., Toonen, R.J., Sorenson, L., Basch, L.W., Papastamatiou, Y.P., Bowen, B.W., 2011. Escaping paradise: Larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang (*Zebrasoma flavescens*). Marine Ecology Progress Series 428, 245–258.

Edgar, G.J., Banks, S., Fariña, J.M., Calvopiña, M., Martínez, C., 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. Journal of Biogeography 31, 1107–1124.

Emerson, B.C., Oromí, P., 2005. Diversification of the forest beetle genus *Tarphius* on the Canary Island, and the evolutionary origins of island endemics. Evolution 59, 586–598.

Field, R., Hawkins, B.A., Cornell, H.V., et al., 2008. Spatial species-richness gradients across scales: A meta-analysis. Journal of Biogeography 36, 132–147.

Fitzpatrick, J.M., Carlon, D.B., Lippe, C., Robertson, D.R., 2011. The West Pacific diversity hotspot as a source or sink for new species? Population genetic insights from the Indo-Pacific parrotfish *Scarus rubroviolaceus*. Molecular Ecology 20, 219–234.

Floeter, S.R., Rocha, L.A., Robertson, D.R., et al., 2008. Atlantic reef fish biogeography and evolution. Journal of Biogeography 35, 22–47.

Flórez, P., Zapata-Ramírez, P., Klaus, J.S., 2018. Early Miocene shallow-water corals from La Guajira, Colombia: Part I, Acroporidae–Montastraeidae. Journal of Paleontology 93, 1–24.

Gaither, M.R., Rocha, L.A., 2013. Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: Evidence for the centre of overlap hypothesis. Journal of Biogeography 40, 1638–1648.

Gaither, M.R., Bowen, B.W., Rocha, L.A., Briggs, J.C., 2016. Fishes that rule the world: Circumtropical distributions revisited. Fish and Fisheries 17, 664–679.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Hachich, N.F., Bonsall, M.B., Arraut, E.M., et al., 2015. Island biogeography: Patterns of marine shallow-water organisms in the Atlantic Ocean. Journal of Biogeography 45, 1871–1882.

Hachich, N.F., Bonsall, M.B., Arraut, E.M., et al., 2016. Marine island biogeography. Response to comment on 'Island biogeography: Patterns of marine shallow-water organisms. Journal of Biogeography 43, 2517–2519.

Hadi, T.A., Hafizt, M., Hadiyanto, H., Budiyanto, A., Siringoringo, R.M., 2018. Shallow water sponges along the south coast of Java, Indonesia. Biodiversitas, Journal of Biological Diversity 19, 485–493.

Hemingson, C.R., Bellwood, D.R., 2018. Biogeographic patterns in major marine realms: Function not taxonomy unites fish assemblages in reef, seagrass and mangrove systems. Ecography 41, 174–182.

Holmlund, C.M., Hammer, M., 1999. Ecosystem services generated by fish populations. Ecological Economics 29, 253–268.

Jacquet, C., Mouillot, D., Kulbicki, M., Gravel, D., 2017. Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. Ecology Letters 20, 135–146.

Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology 84, 2007–2020.

Kool, J.T., Paris, C.B., Barber, P.H., Cowen, R.K., 2011. Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. Global Ecology and Biogeography 20, 695–706.

Lalli, C.M., Parsons, T.R., 1997. Biological oceanography: An introduction. Elsevier, London.

Leprieur, F., Descombes, P., Gaboriau, T., Cowman, P.F., Parravicini, V., 2016. Plate tectonics drive tropical reef biodiversity dynamics. Nature Communications 1–31.

Lim, S.C., de Voogd, N.J., Tan, K.S., 2012. Biodiversity of shallow-water sponges (Porifera) in Singapore and description of a new species of *Forcepia* (Poecilosclerida: Coelosphaeridae). Contributions to Zoology 81, 55–71.

Longakit, M.B., Sotto, F., Kelly, M., 2007. The shallow water marine sponges (Porifera) of Cebu, Philippines. Science Diliman 17, 52–74.

Luiz, O.J., Madin, J.S., Robertson, D.R., et al., 2011. Ecological traits influencing range expansion across large oceanic dispersal barriers: Insights from tropical Atlantic reef fishes. Proceedings of the Royal Society 279, 1033–1040.

Luiz, O.J., Allen, A.P., Robertson, D.R., et al., 2013. Adult and larval traits as determinants of geographic range size among tropical reef fishes. Proceedings of the National Academy of Sciences 110, 16498–16502.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton.

Mayr, E., 1947. Ecological factors in speciation. Evolution 1, 263–288.

McGuinness, K.A., 1984. Species-area relations of communities on intertidal boulders: Testing the null hypothesis. Journal of Biogeography (5), 439–456.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29, 215–233.

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P., Ludsin, S.A., 2003. Patterns and processes in reef fish diversity. Nature 421, 933–936.

Mouchet, M.A., Villéger, S., Mason, N.W., Mouillot, D., 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24, 867–876.

Mouillot, D., Villéger, S., Parravicini, V., et al., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proceedings of the National Academy of Sciences 111, 13757–13762.

Parravicini, V., Kulbicki, M., Bellwood, D.R., et al., 2013. Global patterns and predictors of tropical reef fish species richness. Ecography 36, 1254–1262.

Pellissier, L., Leprieur, F., Parravicini, V., et al., 2014. Quaternary coral reef refugia preserved fish diversity. Science 344, 1016–1019.

Pérez-Ruzafa, A., Marcos, C., Bacallado, J.J., 2005. Biodiversidad marina en archipiélagos e islas: patrones de riqueza específica y afinidades faunísticas. Vieraea 33, 455–475.

Pinheiro, H.T., Madureira, J.M.C., Joyeux, J.-C., Martins, A.S., 2015. Fish diversity of a southwestern Atlantic coastal island: Aspects of distribution and conservation in a marine zoogeographical boundary. Check List 11, 1615.

Pinheiro, H.T., Bernardi, G., Simon, T., et al., 2017. Island biogeography of marine organisms. Nature 82, 82–86.

Pinheiro, H.T., Rocha, L.A., Macieira, R.M., et al., 2018. Southwestern Atlantic reef fishes: Zoogeographic patterns and ecological drivers reveal a secondary biodiversity center in the Atlantic Ocean. Diversity and Distributions 24, 951–965.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. The American Naturalist 132, 652–661.

Randall, J.E., Cea, A., 2011. Shore fishes of Easter Island. University of Hawai'i Press.

Reaka, M.L., 1980. Geographic range, life history patterns, and body size in a guild of coral-dwelling mantis shrimps. Evolution 34, 1019–1030.

Roberts, C.M., McClean, C.J., Veron, J.E.N., et al., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280–1284.

Robertson, D.R., 2001. Population maintenance among tropical reef fishes: Inferences from small-island endemics. Proceedings of the National Academy of Sciences 98, 5667–5670.

Rocha, L.A., Robertson, D.R., Roman, J., Bowen, B.W., 2005. Ecological speciation in tropical reef fishes. Proceedings of the Royal Society B: Biological Sciences 272, 573–579.

Román-Palacios, C., Wiens, J.J., 2018. The Tortoise and the Finch: Testing for island effects on diversification using two iconic Galápagos radiations. Journal of Biogeography 45, 1701–1712.

Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Sandin, S.A., Vermeij, M.J.A., Hurlbert, A.H., 2008. Island biogeography of Caribbean coral reef fish. Global Ecology and Biogeography 17, 770–777.

Sangil, C., Martins, G.M., Hernández, J.C., et al., 2018. Shallow subtidal macroalgae in the North-eastern Atlantic archipelagos (Macaronesian region): Aspatial approach to community structure. European Journal of Phycology 53, 83–98.

Schoener, T.W., 1976. The species-area relation within archipelagos: Models and evidence from island land birds. In: Proceedings of the 16th international ornithological congress. Australian Academy of Sciences, Canberra, pp. 629–642.

Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13, 159–169.

Si, X., Cadotte, M.W., Zeng, D., et al., 2017. Functional and phylogenetic structure of island bird communities. Journal of Animal Ecology 86, 532–542.

Stier, A.C., Hein, A.M., Parravicini, V., Kulbicki, M., 2014. Larval dispersal drives trophic structure across Pacific coral reefs. Nature Communications 5, 5575.

Tedesco, P.A., Leprieur, F., Hugueny, B., Brosse, S., Dürr, H.H., Beauchard, O., Busson, F., Oberdorff, T., 2012. Patterns and processes of global riverine fish endemism. Global Ecology and Biogeography 21, 977–987.

Thiel, M., Gutow, L., 2005. The ecology of rafting in the marine environment. II. The rafting organisms and community. Oceanography and Marine Biology: An Annual Review 43, 279–418.

Thorson, G., 1949. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25, 1–45.

Tittensor, D.P., Mora, C., Jetz, W., et al., 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466, 1098–1103.

Triantis, K.A., Guilhaumon, F., Whittaker, R.J., 2012. The island species–area relationship: Biology and statistics. Journal of Biogeography 39, 215–231.

Triantis, K.A., Economo, E.P., Guilhaumon, F., Ricklefs, R.E., 2015. Diversity regulation at macro-scales: Species richness on oceanic archipelagos. Global Ecology and Biogeography 24, 594–605.

Tronholm, A., Leliaert, F., Sanson, M., et al., 2012. Contrasting geographical distributions as a result of thermal tolerance and long-distance dispersal in two allegedly widespread tropical brown algae. PLoS One 7, e30813.

Tuya, F., Haroun, R.J., 2009. Phytogeography of Lusitanian Macaronesia: Biogeographic affinities in species richness and assemblage composition. European Journal of Phycology 44, 405–413.

Velasquez, E., Bryan, S.E., Ekins, M., et al., 2018. Age and area predict patterns of species richness in pumice rafts contingent on oceanic climatic zone encountered. Ecology and Evolution 8, 5034–5046.

Villaça, R., Pitombo, F.B., 1997. Benthic communities of shallow-water reefs of Abrolhos, Brazil. Revista Brasileira de Oceanografia 45, 35–43.

Waters, J.M., Roy, M.S., 2004. Phylogeography of a high-dispersal New Zealand Sea-star: Does upwelling block gene-flow? Molecular Ecology 13, 2797–2806.

Whittaker, R.J., Fernandez-Palacios, J.M., 2007. Island biogeography: Ecology, evolution, and conservation. Oxford University Press, Oxford.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. Journal of Biogeography 35, 977–994.

Whittaker, R.J., Rigal, F., Borges, P.A.V., et al., 2014. Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. PNAS 111, 13709–13714.

Wilson, E.D., Peter, F.M., 1988. Biodiversity. National Academy Press, Washington.

Xavier, J.R., Van Soest, R.W.M.V., 2012. Diversity patterns and zoogeography of the Northeast Atlantic and Mediterranean shallow-water sponge fauna. Hydrobiologia 687, 107–125.