Review

Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands

Sérgio P. Ávila[a,b,c,*], Ricardo Cordeiro[a,b,c], Patrícia Madeira[a,b,c], Luís Silva[a,b], António Medeiros[b], Ana C. Rebelo[a,b,c], Carlos Melo[a,c,i], Ana I. Neto[b,d], Ricardo Haroun[e], António Monteiro[f], Kenneth Rijsdijk[g], Markes E. Johnson[h]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores, Azores, Portugal
[b] Departamento de Biologia, Faculdade de Ciências e Tecnologia, Universidade dos Açores, 9501–801 Ponta Delgada, Açores, Portugal
[c] MPB–Marine PalaeoBiogeography Working Group of the University of the Azores, Rua da Mãe de Deus, 9501–801 Ponta Delgada, Açores, Portugal
[d] Grupo de Investigação em Ecologia Aquática de Sistemas Insulares do Grupo de Biodiversidade dos Açores, cE3c - Centro de Ecologia, Evolução e Alterações Ambientais, Universidade dos Açores, Departamento de Biologia, 9501-801 Ponta Delgada, São Miguel, Açores, Portugal
[e] Biodiversity and Conservation Research Group, IU-ECOAQUA, Scientific & Technological Marine Park, Universidad de Las Palmas de Gran Canaria, 35214 Telde, Spain
[f] Rua Carlos Calisto 3-4 E, 1400-043 Lisboa, Portugal
[g] Theoretical and Computation Ecology, Institute for Biodiversity and Ecosystem Dynamics & Institute for Interdisciplinary Studies, University of Amsterdam, Sciencepark 904, 1098 XH Amsterdam, The Netherlands
[h] Department of Geosciences, Williams College, Williamstown, MA 01267, USA
[i] Departamento de Geologia, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

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ABSTRACT

Past climate changes provide important clues for advancement of studies on current global change biology. We have tested large-scale biogeographic patterns through four marine groups from twelve Atlantic Ocean archipelagos and searched for patterns between species richness/endemism and littoral area, age, isolation, latitude and mean annual sea-surface temperatures. Species richness is strongly correlated with littoral area. Two reinforcing effects take place during glacial episodes: i) species richness is expected to decrease (in comparison with interglacial periods) due to the local disappearance of sandy/muddy-associated species; ii) because littoral area is minimal during glacial episodes, area per se induces a decrease on species richness (by extirpation/extinction of marine species) as well as affecting speciation rates. Maximum speciation rates are expected to occur during the interglacial periods, whereas immigration rates are expected to be higher at the LGM. Finally, sea-level changes are a paramount factor influencing marine biodiversity of animals and plants living on oceanic islands.

1. Introduction

Oceanic island biotas have been at the core of fundamental evolutionary and biogeographic theories since the contributions by Darwin (1859) and Wallace (1880). While the relationship between species richness and area are known from the first half of the nineteen century as revealing power law relationships, it took more than a century to develop a theory that explained why species richness is related to area in an insular setting (Rosenzweig, 1998). The dynamic equilibrium theory by MacArthur and Wilson (1967) postulated that island area and distance of islands (isolation) to the continents influenced immigration and extinction rates. Therefore, area and isolation also were proposed by the latter authors as the most important variables to explain the biodiversity of islands, with larger and less isolated islands having more species than those smaller and more isolated. Insular biotas are the direct result of chance events of long-range dispersal and successful colonization, followed by in situ speciation events producing neo-endemic species. In this respect, isolation also is believed to play an important role on the biodiversity profile of oceanic islands. Less isolated islands should have higher chances of being reached and colonized than more isolated ones. More recently, the amount of terrestrial endemisms was related to island age, such that older ages reflect more time for the arrival of migrants, with a higher rate of in situ speciation events on intermediate-age (in fact comparatively youthful) islands (Whittaker and Fernández–Palacios, 2007). In this case, endemism is promoted by the rapid and intense ecological, climatological and evolutionary

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changes that result from a very dynamic environment caused by historical and contemporary volcanic and erosional processes typical of oceanic islands (Ramalho et al., 2013).

Island biogeography and the impacts of global change (both current and past) on insular habitats are two of the most promising research areas in present-day studies. This is because islands lack hinterland effects and are therefore less complex for multi-causal analyses into species richness and evolutionary patterns as compared with continental settings (Warren et al., 2015). However, most of the published literature concerns biogeographical patterns and processes, as well as global change-associated impacts on species from the terrestrial realm, despite recent calls for expansion of theories to integrate marine systems (e.g. Dawson, 2015). The former topic is the focus of some papers (Ávila, 2006, 2013; Hachich et al., 2015). Whereas the species–area relationship (SAR) is well–established for terrestrial species (see Triantis et al., 2012) for an extensive review), it still remains to be properly assessed for the marine realm. Triantis et al. (2012) tested the goodness of fit of 20 functions for insular specific SARs using 465 data sets and found that, for terrestrial species, island species area curves were best fitted by the power model and other simple functions (Kobayashi, exponential and linear functions). The few exceptions that assess SARs for marine species are early contributions by Dexter (1972) and Abele (1974), who showed a positive correlation between marine species number and habitat diversity. Simberloff (1974) and Sepkoski (1976) also used SARs to explain mass–extinctions and diversity trends over deep-time, assessing SARs of littoral marine invertebrates over the Phanerozoic (515 Myr until present). Further biogeographic studies are few and we summarise here the most important. Tuya and Haroun (2009) analysing the macroalgal composition of the Macaronesian Region (Azores, Madeira, Selvagens and Canary Islands) concluded that the proximity to nearby continental shores (i.e., isolation) controls the richness patterns found across those archipelagos. Using a limited amount of data, Hart and Pearson (2011) found that species richness of reef-dwelling and benthic fishes on seamounts and banks of the Hawaiian-Emperor seamount chain was a humped function of seamount age. Hachich et al. (2015) studied large-scale island biogeographical patterns for marine littoral organisms (but see criticisms by Ávila et al., 2016b), including the marine species–age relationships for which a linear relationship between reef fishes diversity and island age was reported. Hachich et al. (2015) also concluded that the biogeographical patterns from the marine realm are highly taxon-dependent. Pinheiro et al. (2017) studied the evolutionary history of reef fishes that are endemic to a volcanic ridge of seamounts and islands and found that most endemics speciated during Pleistocene sea-level changes. They also concluded that immigration rate is negatively correlated with marine speciation rate.

Whittaker et al. (2008, 2010) postulated a General Dynamic Model (hereafter GDM) to explain the biogeography of terrestrial insular species on oceanic islands. The GDM places the equilibrium theory of MacArthur and Wilson (1967) in a geological and evolutionary context, thereby providing "a general explanation of biodiversity patterns through describing the relationships between fundamental biogeographical processes - speciation, immigration, extinction - through time and in relation to island ontogeny" (Whittaker et al., 2008: 997). The GDM takes into account that volcanic islands are dynamic on geological time scales. Due to the isolation of oceanic island systems, this model relates that evolutionary processes show a strong signal in biogeographical patterns at the group level (i.e. they are 'Darwinian' islands). Speciation, extinction (and in sum diversification) rates and migration rates are influenced by the ontogeny of the islands, whereby the life cycle of volcanic islands over millions of years, includes the volcanic emergence stage, the post-volcanic erosion stage, as well as the final subsidence stage. These stages influence endemic species richness patterns which are postulated to follow a parabolic species richness dependency with volcanic island age.

The geological history and evolution of Atlantic volcanic oceanic

islands is complex, with many islands from different archipelagos exhibiting opposing trends during different stages of their ontogenic life cycles. For example, a subsidence trend, usually occurring during the early volcanic stages of an island's history, might be reversed during later stages, on response to an uplift trend that may last for several million years (Ramalho et al., 2013). Superimposed on these vertical movements of an island's edifice, sea-level fluctuations further complicate such matters (Muhs et al., 2014, Fernández-Palacios et al., 2016). Some islands (e.g., Santa Maria in the Azores) have even more complex histories, with the submergence of the first island due to subsidence and erosion, followed by a reversal of subsidence with an uplift trend and new volcanism promoting the island's re-emergence (Ávila et al., 2012a; Ramalho et al., 2017). Other islands may become united during sea-level lowstands, thus forming a single island. Such was the case of the "Laurinsula" palaeo-island (Azores archipelago), that incorporated modern Pico and Faial islands (Rijsdijk et al., 2014). Thus, in order to test large-scale biogeographic patterns such as the marine species–age relationships, a robust knowledge of the island's geological evolution and state-of-the-art age-datings are crucial.

In this study, we propose to test whether or not marine large-scale biogeographic patterns around oceanic islands behave in a similar manner as terrestrial patterns. For this purpose, we used different marine organisms inhabiting the shallow waters of oceanic islands from twelve Atlantic islands/archipelagos, and searched for patterns between species richness/endemism and a number of abiotic variables [such as island littoral area, age of the oldest island of the archipelago, isolation, average latitude of the island/archipelago, and mean annual sea surface temperatures (SST)] by means of several models (null, linear, logarithmic, power, logistic and the GDM). For the main characteristics of these different models, consult Hachich et al. (2015). Finally, we also discuss the impact of global-changes caused by glacial and interglacial episodes on the shallow marine fauna and flora living around volcanic oceanic islands.

2. Materials and methods

2.1. The archipelagos

Twelve islands/archipelagos in the Atlantic Ocean were selected, ranging in latitude from 38˚N to 20˚S. They include the Azores, Bermuda, Madeira, Selvagens, Canaries, Cabo Verde, São Tomé and Príncipe, Saint Peter and Saint Paul Rocks, Fernando de Noronha, Ascension Island, Saint Helena Island and Trindade (Fig. 1). Based on the high number of archipelagic endemics in each archipelago (e.g., the marine gastropods of Cabo Verde) we consider each of the analysed islands/archipelagos as a different biogeographical unit (see below).

2.2. Abiotic variables

The concept of "littoral area" depends on the marine organism in question. For marine species that live in close association with macro-algae (= seaweeds) and with a strong bathymetrical zonation, as is the case for molluscs (e.g., Ávila, 2003), the littoral area of volcanic oceanic islands is here defined as the shelf surface located between the present mean sea level (MSL) and the 50-m isobath. This 50-m spread in bathymetric range encompasses the intertidal down to the infralittoral biological zones. At a depth of 50 m, a more-or-less gradual change occurs in the composition of invertebrate species associated with a significant decrease of algal richness and domination by a few algal species below such a depth (Tittley et al., 2014). Thus, we determined the sizes (in km^2) of littoral surface areas (0–50 m depth) and used this value for gastropods, echinoderms and macroalgae. Reef fishes and some echinoderms have a wider bathymetrical range. Therefore, for these two marine groups we defined and calculated littoral area as the shelf area located between the intertidal zone and the 200-m isobaths.

Island/archipelagic littoral areas were calculated from Shuttle