

Marine island biogeography. Response to comment on 'Island biogeography: patterns of marine shallow-water organisms'

ABSTRACT

In this response we have incorporated data on gastropod and seaweed biodiversity referred to by Ávila *et al.* (2016, *Journal of Biogeography*, doi:10.1111/jbi.12816) to allow an updated analysis on marine shallow-water biogeography patterns. When compared to the biogeography patterns reported in Hachich *et al.* (2015, *Journal of Biogeography*, **42**, 1871–1882), we find (1) no differences in the patterns originally reported for reef fish or seaweeds, (2) minor differences in gastropod species–area and species–age patterns and (3) a significant difference for the gastropod species–isolation pattern. In our original work, we reported that there was limited evidence that gastropod species richness was influenced by island isolation; however, our new analysis reveals a power-model relationship between these variables. Thus, we are now able to conclude that gastropod species diversity, whose dispersal capacity is intermediate between seaweeds (lowest) and reef fish (highest), is also influenced by island isolation.

Keywords gastropod, island biogeography, marine biodiversity, reef fish, seaweed, species–age, species–isolation

INTRODUCTION

Our work on marine island biogeography revealed large-scale patterns in the Atlantic Ocean for reef fish, gastropod and seaweed species richness, as well as reef fish endemism (Hachich *et al.*, 2015). We focused our analysis on species patterns related to island area, age and isolation. In addition to a strong endemism–isolation pattern for reef fish, we showed that the island features that influenced species richness were (1) age for reef fish, (2) area and age for gastropods and (3) all three island features (area, age and isolation) for seaweeds.

In a recent comment on our paper, Ávila *et al.* (2016) pointed out some possible weaknesses in our data, especially regarding (1) glaciation events and

endemism in islands, (2) gastropod and seaweed richness, (3) age of some islands and (4) the isobaths used to calculate shallow-shelf surface area for the islands. Here, we address each of these concerns, incorporating some of the data and suggestions and, where appropriate, providing additional arguments for the original patterns we reported in Hachich *et al.* (2015).

GLACIATION EVENTS AND ENDEMISM IN ISLANDS

Glacial events and corresponding temperature drops are traditionally regarded as a primary influence on biodiversity in the Northern Hemisphere (Briggs, 1966). Nonetheless, the work by Ávila *et al.* (2008) showed no evidence that Azorean endemic molluscs became extinct as a result of these drops in water temperature during the Pleistocene. However, there is compelling evidence that glacial cooling events in this region may have had significant impacts on reef fish biodiversity.

During glacial periods, sea surface temperatures reached 8–14 °C in Bermuda, Azores and Canaries (Briggs, 1966; Keffer *et al.*, 1988; Smith-Vaniz *et al.*, 1999; Paul & Schäfer-Neth, 2003). These temperatures are known to strongly impact reef fish assemblages (Beitinger & Fitzpatrick, 1979; Bohnsack, 1983; Smith-Vaniz *et al.*, 1999; Hsieh *et al.*, 2008). We have therefore removed these islands from the endemism analysis, as they might have been affected by events other than the island parameters (i.e. area, age and isolation).

We do think that it is important to develop a more explicit test of Briggs' (1966) hypothesis that glaciations caused local extinctions of reef fish (and other groups) in these islands, as Ávila *et al.* (2008) verified for gastropods. Such a test would require much better knowledge of reef fish fossils and of the interplay between past climate and extinction dynamics in reef fish (Weigelt *et al.*, 2016), which are much less explored than molluscs (Madeira *et al.*, 2007).

REVISED RESULTS ON MARINE ISLAND BIOGEOGRAPHY

We are grateful to Ávila *et al.* (2016) for providing new updated data on gastropod and seaweed richness and island age. We used this updated species richness data to re-analyse marine shallow-water biogeography patterns, using both the original

(Hachich *et al.*, 2015) and updated (Ávila *et al.*, 2016) island ages. The conclusions for species–age patterns were the same using either island age data. Here, we will present results using the ages originally compiled by Hachich *et al.* (2015) as these were obtained from reliable scientific papers, published in peer-reviewed journals specialized on geophysics or geochemistry. We agree that a shallower, for example, 50 m, depth would be more appropriate to estimate habitat area, but were unable to obtain the necessary data from satellite or nautical sources. However, as we used the same isobaths (200 m) in all islands and given that these are primarily oceanic with steep slopes (Gillespie & Clague, 2009), we expect the 200 m shelf surfaces to be highly correlated with the shallow-shelf surfaces available for the three shallow-water marine groups.

With respect to Hachich *et al.* (2015), we found no differences in the patterns observed for reef fish or seaweed species richness with area, age and isolation (Figure 1). There were, however, minor differences in the gastropod species–area and species–age patterns (Figure 1). Although island area and age still explain variation in gastropod richness, the linear relationship was as appropriate as the power model in explaining the gastropod species–area pattern ($\Delta\text{AICc} = 0.62$). For the gastropod species–age relationship, the logistic pattern also appeared as an appropriate model explaining gastropod richness when compared to the linear, logarithmic and power models ($\Delta\text{AICcs} = 1.13, 0.17$ and 0.14 respectively).

The main difference between our original results and the ones obtained with the updated data concerned the gastropod species–isolation pattern. Our original analysis showed no evidence of island isolation influencing gastropod richness, but the new analyses revealed that a power-model provides a better fit to the data than the null model ($\Delta\text{AICc} = 4.31$, Figure 1). Thus, gastropods, whose dispersal capacity is intermediate between seaweeds and reef fish (Kinlan & Gaines, 2003), are, like seaweeds, influenced by island isolation.

CONCLUSIONS AND THE CHALLENGE OF ANALYSING LARGE-SCALE PATTERNS OF BIODIVERSITY

Macroecological studies focus on large-scale biodiversity patterns and entail



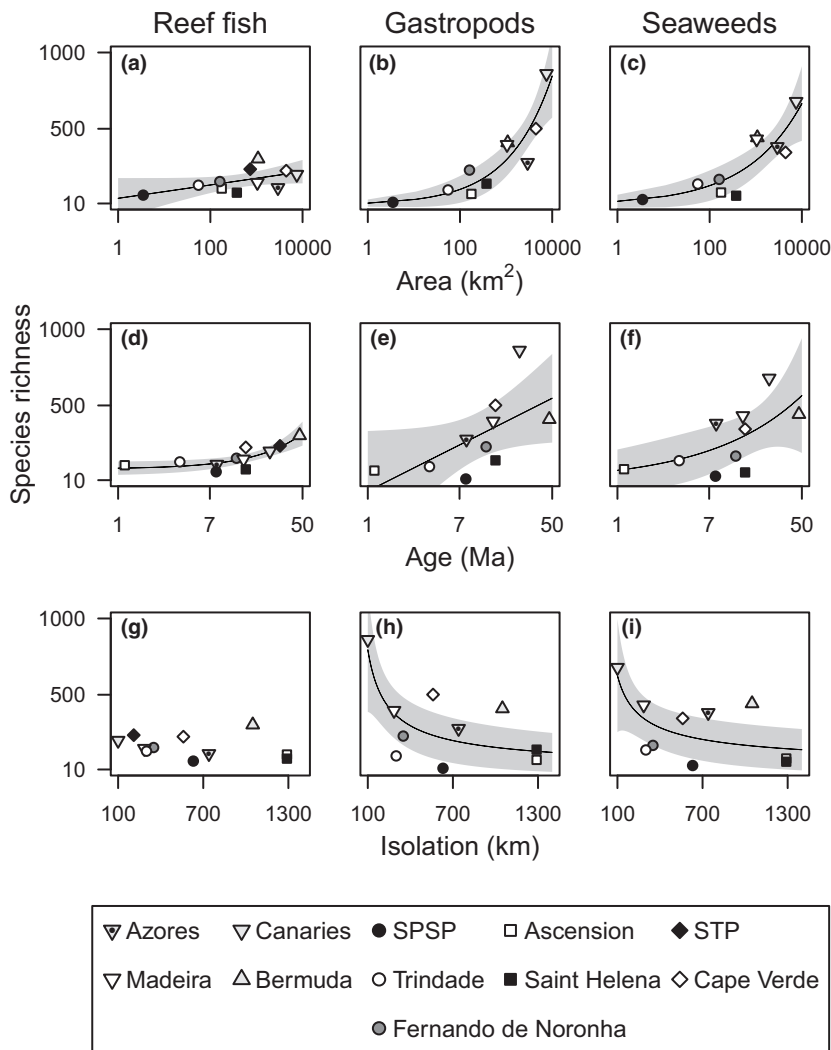


Figure 1 Model averaging curves of the best models (when several models fitted the data equally well: a, b, e and f) and single best models (c, d, g–i) for the effects of area, age or isolation of the Atlantic oceanic islands on the species richness of three taxa. The only result that differs from those reported in Hachich *et al.* (2015) is the additional presence of a relationship between gastropods and island isolation. The predictor–response relationships with alternative models that improved on the null model are shown in b–f, h–i. The shaded areas represent confidence intervals of the models with the lowest corrected Akaike's information criterion values. SPSP, Saint Peter and Saint Paul's Archipelago; STP, São Tomé and Príncipe Islands.

collecting substantial amounts of both biotic and abiotic data at multiple locations. Such task is ultimately constrained by the availability of well-organized databases and collaborations between macroecologists and other specialists. In our recent attempt to characterize marine shallow-water biogeography patterns in the Atlantic (Hachich *et al.*, 2015) we employed, and benefited from, both strategies. Nonetheless, despite our efforts, some studies went unnoticed, so not all our checklists were comprehensive. Ávila *et al.* (2016) presented additional data found in books,

conference abstracts, as well as in personal communication and a scientific paper unavailable to Hachich *et al.* (2015). This goes to show (1) how scientific knowledge is scattered in the literature and (2) the pressing need to standardize biodiversity information repositories with sound data, which are ultimately needed to enhance the understanding of biodiversity patterns (Hortal *et al.*, 2015).

It bears restating that both this and our previous work on marine island biogeography (Hachich *et al.*, 2015) aimed to explore large-scale biogeography patterns

associated with marine shallow-water groups. Compared with terrestrial ecosystems, marine island biogeography studies are rare. New species and new occurrences of known species will be continuously added and future studies based on more accurate data, for instance for islands in the Mid-Atlantic Ridge (Ascension and Saint Helena), can either refute or concur with the patterns here presented. Nonetheless, the reanalysis based on more complete data suggested by Ávila *et al.* (2016) supported all the patterns detected by Hachich *et al.* (2015), except for the previously undemonstrated gastropod species-isolation relationship. This suggests a robustness of those patterns.

ACKNOWLEDGEMENTS

The authors thank an anonymous referee for comments on a previous version of this manuscript. We are also grateful for the financial support provided by FAPESP, CAPES, CNPq, Rede Clima, INCT Climate Change, UK Natural Environment Research Council and Oxford University.

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Editor: Dr Kostas Triantis

doi:10.1111/jbi.12863