Faial in the Azores (CC BY 2.0)
PHOTO CREDIT: David Stanley (https://www.flickr.com/photos/davidstanleytravel/)

THE DIVERSIFICATION AND EVOLUTION OF MARINE INVERTEBRATES IN OCEANIC ISLANDS

by PEDRO VIEIRA and FILIPE COSTA

University of Minho, Braga, Portugal

Unravelling long-established divergence patterns and remarkable geographic segregation that has endured over millions of years in marine invertebrates.

Oceanic islands constitute prime evolutionary grounds for terrestrial organisms, promoting extensive isolation and harboring exceptional levels of diversity and endemism. Marine organisms, on the contrary, are not expected to experience evolutionary forces with the same intensity and, therefore, their diversification and evolution in oceanic landscapes has been somewhat disregarded. Shore-dwelling marine benthic invertebrates are unique relative to both terrestrial organisms and other marine taxa. Most shore species have planktonic larvae that facilitate dispersal over open water. However, some small invertebrates, such as free-living peracarids (Peracarida: Crustacea), are more prone to isolation due to life histories characterized by direct development and putatively reduced vagility.

As a result of a DNA barcode-based screening of the diversity of littoral peracarids along Macaronesia and nearby continental shores, we have found an exceptional amount of cryptic diversity, together with a very structured geographic assortment within multiple morphospecies. We investigated, with particular detail, two common and distinct peracarid taxa present in the Macaronesian archipelagos of Azores, Madeira, and Canaries, namely 3 morphospecies of the isopod genus Dynamene[1] and 7 morphospecies of the amphipod family Hyalidae[2]. We unraveled an additional 34 suspected new species (75% endemic of Macaronesia) with no apparent discriminative morphological features, including the noteworthy cases of the isopod *Dynamene edwardsi* and the amphipod *Apohyale stebbingi* comprising 9 and 13 putative species, respectively.

Adding to this surprising cryptic diversity, lineages within each morphospecies were also frequently exclusive to one island (50%), despite the general geographic proximity of the islands within each archipelago (e.g., from as little as 50 km between Porto

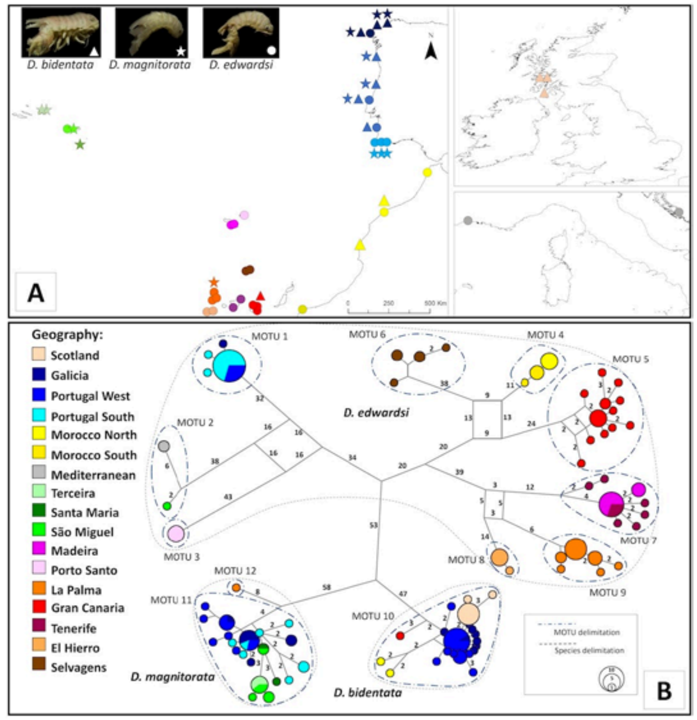
Santo and Madeira). Globally, the genetic divergences among lineages within a morphospecies were also comparatively high (e.g., *D. edwardsi* up to 22% and *A. stebbingi* up to 21%), indicating a very deep evolutionary history in the region which pre-dates the Pleistocene glacial cycles (*D. edwardsi* lineages probably started diverging between 20 and 30 MYA).

There were several noteworthy findings in these studies. First, the unexpectedly high amount of diversity and endemism in these Macaronesian marine invertebrates, even within the same archipelago. Although peracarids can be assumed to have comparatively low vagility, since they lack a planktonic larval stage, there is extensive evidence for their dispersal capability and population connectivity. Namely, both our and other authors' studies report peracarid morphospecies displaying little genetic structure over wide geographic ranges, for example, along the European continental Atlantic coasts.

Second, we were surprised to find marked geographic segregation among the newly found species. They were frequently restricted to a single island where they constituted the only representative of the cryptic complex. To a certain extent, the geographical segregation of these peracarids more closely resemble what would be expected for terrestrial organisms than marine invertebrates.

Finally, the combined evidence on diversity, geographic segregation, and divergence times, unraveled long-established divergence patterns and a remarkable geographic segregation that endured over millions of years till present. Therefore, the current distribution patterns of many of these peracarids cannot be elucidated through common accounts of marine invertebrates in the north-eastern Atlantic, namely processes involving dispersal, geographic proximity or Pleistocene glacial cycles. We propose alternative mechanisms for the speciation of these invertebrates in Macaronesia, such as those involving priority effects and pre-emptive exclusion, which have been seldom evoked to explain the deep segregation in the open ocean.

In the near future, we intend to investigate the genetic variability of taxa with planktonic larvae from these oceanic islands to verify if the long-term segregation patterns are exclusive of peracarid crustaceans or, instead, are more widespread patterns in marine invertebrates in Macaronesia.



A. Sampling locations for each Dynamene species. B. Reduced median network of COI data from the genus Dynamene. Size of the circles are proportional to the number of similar haplotypes. Number of mutations separating each haplotype and inferred ancestors (median vectors) are displayed in black. Links displaying a single mutation do not display the number.

IMAGE CREDIT: Pedro Vieira

References:

1. Vieira PE, Desiderato A, Holdich DM, Soares P, Creer S, Carvalho GR, Costa FO, Queiroga H (2019) Deep segregation in the open ocean: Macaronesia as an evolutionary hotspot for low dispersal marine invertebrates. *Molecular Ecology*. https://doi.org/10.1111/mec.15052

2. Desiderato A, Costa FO, Serejo CS, Abbiati M, Queiroga H, Vieira PE (2019) Macaronesian islands as promoters of diversification in amphipods: The remarkable case of the family Hyalidae (Crustacea, Amphipoda). *Zoologica Scripta*. https://doi.org/10.1111/zsc.12339

Online:

https://ibol.org/barcodebulletin/research/the-diversification-and-evolution-of-marine-invertebrates-in-oceanic-islands/