

## update

## The (often ignored) role of vicariance in evolutionary diversification on oceanic islands

Elucidating the evolutionary history of diversifying lineages in space and time remains a major challenge in biology. The value of islands and island-like systems for studying this question has been long recognized by professional and amateur biologists alike. First, many islands are young and thus have relatively low species diversity; this natural simplicity makes them easier to study. Second, most islands are geographically isolated, which means that insular lineages are often on an evolutionary track independent of external influences from other areas. Finally, if part of an archipelago, islands can be viewed as replicates or snapshots in time of a natural experiment occurring at a spatial scale and a temporal scale of which experimental biologists could only dream. The considerable scientific attention devoted to island biotas has resulted in an increasingly complete picture of the geographical distribution of insular species. In addition, with the more recent advances in genetics and phylogenetics, it is now possible to infer the evolutionary processes responsible for generating these observed biogeographical patterns. Indeed, by combining information about the current geographical location of populations or species with a description of their genetic or phylogenetic relationship, it becomes possible to reconstruct the evolutionary history of diversifying lineages in their specific geographical contexts, a key step in evaluating the relative importance of determinism and contingency in evolutionary diversification (Losos and Ricklefs 2009).

However, despite the relative simplicity of island systems, the study of their diversifying lineages poses its own set of challenges. First, although island biogeographical studies often assume that islands are fixed in time and space, they are rather dynamic entities that might change in size, location, elevation, etc. over time. Oceanic islands in particular go through a series of predictable “life” stages that are likely to influence their carrying capacity via changes in island area, topography, etc. (Whittaker et al. 2008). Furthermore,

over time, geological forces combined with sea-level changes might create or eliminate land connections between islands, which could facilitate or hinder the dispersal and colonization of the geographical areas involved. Second, island biotas often are at greater risk of extinction. This greater risk stems from a combination of factors. Importantly, island species have limited ranges and associated smaller population sizes, and they also are more susceptible to changes in their environment caused by introduced species or habitat destruction by human activities. Extinction events are difficult to detect and, if ignored, might lead researchers to draw erroneous conclusions from the observed patterns of biodiversity. Finally, not necessarily specific to island systems, the evolutionary history of any diversifying lineage might be blurred by human-mediated dispersal. This effect is exacerbated on islands where dispersal can be quite limited between islands, and where humans might artificially increase the rates and/or modify the trajectories of organisms’ natural dispersal.

These three sources of variation— island dynamics, extinction, and introduction—most often are ignored, or in the best-case scenario simply assumed to add noise to the diversification patterns observed. However, in a recent study of giant Galápagos tortoises, Poulakakis et al. (2012) tackled these three challenges by incorporating information about the dynamic geography of Galápagos, genetic data from extinct species, and information regarding human-based dispersal of individuals in this group of species – highlighting their influence on the diversification patterns observed and reaching a better understanding of the diversification process in this lineage. In their study, Poulakakis and colleagues integrated DNA data from all known extinct and extant species, past information about inter-island dispersal of giant tortoises by humans, and newly available data on the dynamics of the islands themselves. Overall this results in an updated and more comprehensive picture of the diversification patterns

in giant Galápagos tortoises, and, more importantly, exemplifies the importance of considering all available sources of information when inferring processes of diversification from the combined patterns of species relatedness and geographical distributions.

Arguably the most significant contribution of the study by Poulakakis et al. (2012) is their successful attempt at considering the consequences of the geological dynamics of the Galápagos islands for the biological diversification of giant tortoises. Grant and Grant (1996) had previously proposed a palaeogeographic scenario to help elucidate the speciation process in Darwin's finches. However, their scenario was based on plate movement alone. Poulakakis et al. (2012) combined information about plate movement, rate of subsidence of islands, and sea level changes to infer how the Galápagos' geographical setting might have changed since the formation of the oldest currently emerged island of San Cristobal. In their resulting simple 3-time-step scenario, some of the current islands were previously connected into a single land mass at some point in the past, allowing for the on-land dispersal of tortoises. Populations then might have become isolated via vicariance events, when the central land mass was subsequently subdivided into islands because of subsidence and sea-level changes. Two of the 12 between-island colonization events inferred from the reconstructed phylogeny of the group and the current biogeographical distribution of the species are attributed to such vicariance events. While the contribution of vicariance in the evolutionary history of the giant tortoises does not necessitate a complete paradigm shift on the importance of dispersal versus vicariance in diversification on oceanic islands (Cowie and Holland 2006), it does highlight the potentially important contribution of vicariance events in the diversification of insular lineages.

It is likely that such vicariance events, resulting from the dynamics of islands, have a greater impact on lineages that have poor dispersal ability, since the formation or elimination of water barriers between island land masses probably have less influence on the colonization patterns of active or good dispersers such as birds, certain insects and plants. In their study, Poulakakis et al. (2012) assumed that a split in the phylogeny involving two species presently occurring on different islands that are inferred to have been connected at the time of the split is necessarily the result of a vicariance event, rather than dispersal. This assumption seems reasonable for organisms that are flightless, but might not be so for organisms that can disperse in the air. Furthermore, in addition to dispersal ability, other biological attributes of lineages might influence the importance that vicariance events have on their evolutionary history. For example, organisms with tight ecological interactions (e.g. insects that specialize on a single host plant species) may be more likely to occur on multiple islands because of vicariance than because of dispersal.

In the dispersal versus vicariance debate that has been a focus in the field of biogeography since the 1970s, vicariance mechanisms have often been considered as sources of testable hypotheses as well as generators of predictable patterns. Dispersal has most often been pushed into the background on the premise that its main contribution was to add noise to predictable patterns of vicariance biogeography. However, for island biogeographers, the importance of these two processes in determining the geographic distributions of species is reversed. Dispersal is considered a fundamental process leading to predictable patterns in island biogeography, whereas vicariance events more often than not are ignored (Cowie and Holland 2006). With their latest study of giant Galápagos tortoises, Poulakakis et al.

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(2012) highlight the importance of considering both processes in the interpretation of biogeographical patterns of insular biotas. Furthermore, by proposing a simple yet plausible palaeogeographic scenario of island formation, they bring both processes into the realm of hypothesis-driven research. The palaeogeographic scenario of Galápagos islands proposed by Poulakakis et al. (2012) is simple yet revealing. As geological information about island formation accumulates and palaeogeographic scenarios are refined and become more detailed and accurate, it will be possible to improve proposed palaeogeographic scenarios and gain a better grasp of the role of geographical context in the progression of adaptive radiations on islands.

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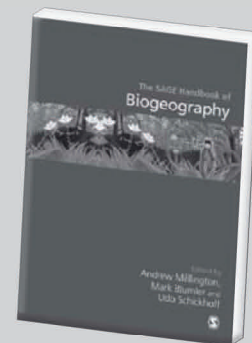
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