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Since the contributions of Charles Darwin and Alfred Russel Wallace, oceanic archipelagos have played a central role in the development of biogeography. However, despite the critical influence of oceanic islands on ecological and evolutionary theory, our focus has remained limited to either the island-level of specific archipelagos or single archipelagos. Recently, it was proposed that oceanic archipelagos qualify as biotic provinces, with diversity primarily reflecting a balance between speciation and extinction, with colonization having a minor role. Here we focus on major attributes of the archipelagic geological dynamics that can affect diversity at both the island and the archipelagic level. We also re-affirm that oceanic archipelagos are appropriate spatiotemporal units to frame analyses in order to understand large scale patterns of biodiversity.

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perspective

Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces

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Abstract. Since the contributions of Charles Darwin and Alfred Russel Wallace, oceanic archipelagos have played a central role in the development of biogeography. However, despite the critical influence of oceanic islands on ecological and evolutionary theory, our focus has remained limited to either the island-level of specific archipelagos or single archipelagos. Recently, it was proposed that oceanic archipelagos qualify as biotic provinces, with diversity primarily reflecting a balance between speciation and extinction, with colonization having a minor role. Here we focus on major attributes of the archipelagic geological dynamics that can affect diversity at both the island and the archipelagic level. We also reaffirm that oceanic archipelagos are appropriate spatiotemporal units to frame analyses in order to understand large scale patterns of biodiversity.

Keywords. Diversity, island biogeography, hotspot, mantle, macroecology, macroevolution, meta-archipelagos, subsidence, island evolution, volcanic islands

Introduction

Oceanic islands have been the archetypes of biogeographical and evolutionary studies since the contributions of Charles Darwin and Alfred Russel Wallace in the 19th Century. One of the key features of remote island biotas and environments is their comparative simplicity. Oceanic islands are well-defined geographically, and they present a great array of configurations, sizes, degrees of isolation, ages and climatic and biogeographical contexts (Whittaker and Fernández-Palacios 2007, Fernández-Palacios and Whittaker 2010, Heaney et al. 2013, Weigelt et al. 2013, Geist et al. 2014, Borregaard et al. 2016, Fernández-Palacios et al. 2016). Oceanic islands are geologically young and there is scarcely any oceanic crust older than about 200 million years (Nunn 2009).

Oceanic archipelagos have at least three principal geological origins, each of which results in different biogeographical patterns. Most are volcanic, and one set results from the passage of tectonic plates over regions of melting in the mantle; these are referred to as hotspot islands. Volcanic arcs arise from the subduction of plates into the mantle, and most of the earth's island arcs surround the northern and western Pacific. In the Atlantic Ocean, the Lesser Antilles and South Sandwich Islands are examples of volcanic arcs. Finally, along tectonically active margins, crustal blocks become elevated due to faulting. In addition to these three broad classes, there are other modes of origin followed by particular oceanic archipelagos, sometimes involving combinations of processes (e.g., Azores, Iceland; see e.g., Jones

and MacLennan 2005, Nunn 2009).

Among oceanic islands, those formed over upwelling plumes in the Earth's mantle (i.e. hotspots), such as the islands of Hawaii, Galápagos, Canary, Society, Austral, Madeira, Mascarenes and Guinean Gulf, hold an exceptional place in biogeography, evolution, and ecology. These islands are formed by volcanic activity of relatively limited duration, followed by subsidence and erosion, which results in their eventual demise. In tropical waters, they persist as low-lying atolls, sustained by coral growth (Whittaker and Fernández-Palacios 2007, Nunn 2009). A hotspot island exhibits a life-cycle, which can be described by six major stages (Fernández-Palacios and Whittaker 2010, Fernández-Palacios et al. 2011, Borregaard et al. 2016): 1 – submarine construction; 2 – emergence and subaerial construction; 3 – erosion and tectonic subsidence; 4 – reduction to a low-lying plain (or, in the case of environments conducive to coral reefs, atoll formation); 5 – terminal disappearance via subsidence; and 6 – guyot formation (a flat-summit seamount). The temporal extent of this life cycle depends on the generating mechanisms of each archipelago. For example Hawaiian volcanoes require at least 0.6 million years to grow from the ocean floor to their full size, whereas those of the Galápagos may require just 10% of this timespan (Moore and Clague 1992, Geist et al. 2014).

The geologic evolution of hotspot islands inspired the development of the general dynamic model of oceanic island biogeography (hereafter GDM) (Whittaker et al. 2008, 2010), which broke from a long tradition in island biogeographical modeling (e.g., MacArthur and Wilson 1963) by explicitly incorporating the physical 'life cycle' dynamics of the islands alongside the biological dynamics of immigration, extinction, and most importantly speciation. Despite the long and important influence of hotspot islands on ecological and evolutionary theories, in some respects our focus has remained limited to either the island-level of specific archipelagos or single archipelagos; the analysis of biogeographical dynamics viewed through the comparative study of multiple archipelagos have been limited (but see: Hall and

Holloway 1998, Adler and Dudley 1994, Keast and Miller 1996, Ricklefs and Bermingham 2007, Price and Wagner 2011, Bunnefeld and Phillimore 2012, Heads 2012, Cabral et al. 2014, Triantis et al. 2015, 2016).

Central to the present article is the notion that oceanic archipelagos qualify as biotic provinces (e.g., Triantis et al. 2015). In biotic provinces, diversity mainly reflects a balance between speciation and extinction. Thus, they are areas wherein most species are endemic (Rosenzweig 1995), although whether this implies 60, 80 or even 90% endemism is an open question (Triantis et al. 2008). However, in broad terms, for many taxa and considering the most isolated oceanic archipelagos, it is often the case that the majority of species have arisen by speciation within the archipelago and comprise a mix of single-island and multi-island endemics, consistent with the notion of Darwinian islands and the archipelago constituting a biotic province. Considering that we lack a general consensus about the causes of large-scale patterns of geographic variation in the number of species (Ricklefs 2004), oceanic archipelagos present important natural laboratories for synthetic analysis and modeling in macroecology, biogeography and macroevolution. An illustration of this potential is provided by Triantis et al. (2015), who undertook analyses at the archipelagic level, of species richness of birds, spiders, land snails and plants from 14 major oceanic archipelagos (see also Triantis et al. 2016). They demonstrated an intriguing parallel scaling of species richness with archipelago area regardless of the variation in the ecological requirements, dispersal abilities and typical population sizes of the four taxa considered (see Figure 1).

Here we emphasize that oceanic archipelagos are appropriate spatiotemporal units to frame analyses in order to understand large scale patterns of biodiversity, and we focus on major attributes of the archipelagic geological dynamics.

Geological history of islands and archipelagos

The critical parameter for establishing the time-scales of biological evolution on oceanic islands is the age of emergence of an island. Oceanic islands

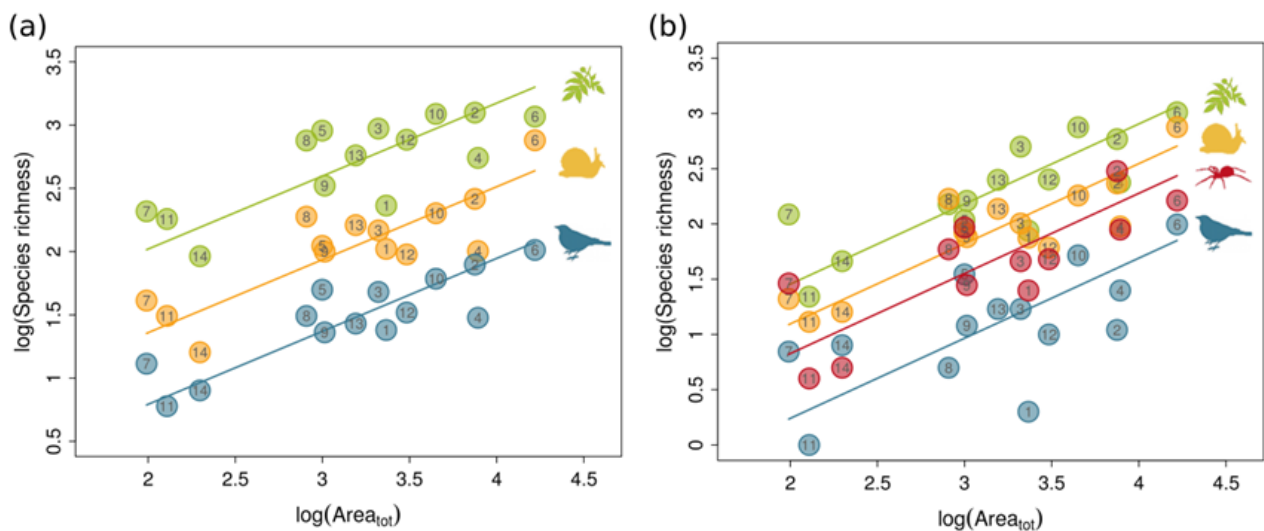


Figure 1. Individual relationships between archipelagic total area and taxon richness. (a) Indigenous and (b) archipelagic endemic species for land birds, vascular plants, land snails and spiders. Each number represents an oceanic archipelago. Archipelagos are: (1) Azores, (2) Canary, (3) Comoros, (4) Galápagos, (5) Gulf of Guinea, (6) Hawaii, (7) Juan Fernández, (8) Madeira, (9) Marquesas, (10) Mascarene, (11) Northern Marianas, (12) Samoa, (13) Society, and (14) Tristan da Cunha. The slope (z) of the relationship is indistinguishable across taxa for indigenous and archipelagic endemics and the values are 0.57 and 0.72 respectively (from Triantis et al. 2015).

start as submarine volcanoes, and only serve as a potential target for terrestrial plant and animal colonization when emergent. Unfortunately, tightly constraining the age of emergence of most islands is nearly impossible, because the rocks that provide evidence of the emergence are almost always buried by thick sequences of younger lavas. Moreover, studies from Hawaii (Garcia et al. 2007) and Galápagos (Geist et al. 2014) show that as lavas are added to the top of a volcano and as it moves away from the hotspot, the volcano typically subsides due to isostasy. Thus, the rocks that indicate emergence of an island may currently be over 1 km below sea level. Deep drilling (Garcia et al. 2007) provides the best evidence for the date of emergence of a single location, but in general the recent growth rate of a volcano must be extrapolated back in time to estimate the age of emergence of an island. Complicating matters further, maximum age estimates may also significantly over-estimate the time for evolutionary processes due to reiterative episodes of destruction and renewal of construction.

Furthermore, in many, perhaps most archipelagos, the current geography of the archipelago may be misleading of the configuration(s) relevant to understanding the evolutionary assemblage processes. The most important recent processes

that change the geography of an archipelago are volcanism (which mostly grows the islands), episodes of displacement and collapse (causing sudden loss of terrain), and Pleistocene sea level changes due to (largely) Northern hemisphere glaciation and deglaciation. The latter process has caused global sea level to rise and fall over a range of about 150 m during the last 2.6 million years (with low points around 135 m lower than at present), causing islands to shrink, grow, interconnect, and become isolated multiple times (Lambeck et al. 2014). In general, sea level rise since the low stand of the last glacial maximum (c. 20,000 years ago) has affected oceanic archipelagos by decreasing island size and elevation, dividing formerly continuous units to form additional islands and drowning low lying islands within or nearby the archipelago. At high latitudes, loading by growing glaciers depresses the islands and interglacial removal of the ice causes rebound and island growth. For example, Iceland uplifted as much as 170 m following the most recent deglaciation (Le Breton et al. 2010). These geologic processes of island growth and subsidence have reiteratively mixed and isolated populations, creating a mechanism for vicariant speciation and for hybridization of closely related forms (e.g., see discussion in Fernández-Palacios et al. 2011, 2016, Ali

and Aitchison 2014, Geist et al. 2014).

Over time scales of 10^5 to 10^7 years, sub-aerial and marine erosion and subsidence of islands take on key roles in shaping changes in island and archipelago configuration. Erosion regimes are largely climatically determined and thus vary between archipelagos. Subsidence is common to almost all mid-oceanic archipelagos. It occurs due to several processes. Subsidence due to loading by glaciers and lavas occurs on a very short time frame. The most important process is thermal contraction: when an island is over the hotspot, the lithosphere expands, lifting islands (and all of the surrounding terrains) as much as hundreds of meters. Then, as the island is carried by plate tectonics away from the hotspot, the lithosphere cools and thermally contracts, leading to sinking of the island, shrinking of its area (thereby affecting the species richness of the island), and its eventual drowning after several million years. A third process that accelerates island subsidence is lower crustal flow, a recently discovered process in Iceland (Jones and MacLennan 2005) and Galápagos (Orellana-Roviroso and Richards 2016). At high temperature, the oceanic lower crust is ductile, and within archipelagos the crust is especially thick. The thick crust drives flow outward, widening the archipelago and causing the central axis to subside. In the Galápagos, for example, the central platform may have subsided 210 m over about 3 million years (Orellana-Roviroso and Richards 2016). Rates of subsidence are thus archipelago-dependent (e.g., Ali and Aitchison 2014). If, for example, the Canarian island chain had experienced a subsidence history similar to that of the Hawaiian chain, then just two islands out of the existing seven, La Palma and El Hierro, would still be above sea level (Carracedo and Pérez-Torrado 2013).

Long-lived (>10 million years) islands, such as those of the Canary and Cape Verde archipelagos can undergo hundreds of meters of uplift, hence expanding the area of the islands. The mechanisms of uplift of hotspot islands are not well understood (Ramalho et al. 2013). Uplift and subsidence of volcanic arc islands are even more complicated, owing to tectonic factors that com-

plete or complement the magmatic growth and thermal history of islands.

Geological age of islands and archipelagos

Following from the above, when conducting analyses considering multiple oceanic islands from various archipelagos (e.g., Cameron et al. 2013, Triantis et al. 2015, 2016), data on the age of each island should be considered with caution, as islands of similar age may be at very different ontogenetic stage. Hence, analysis should take account of the context of the archipelago they belong to. For example Fogo in the Cape Verde (476 km^2) is older than 3 million years (Ma) and is a volcanically active island, whereas Bora Bora, an island of similar age in the Society Islands (c. 3.4 Ma, 30 km^2), is a highly eroded, inactive shield volcano.

The life span of archipelagos typically exceeds the life span of individual islands and so most archipelagos are older than the oldest extant island. For example, the maximum geological age for the Madeiran volcanic province is estimated as 68 Ma, whereas the oldest current island in the archipelago, Porto Santo, originated 14 Ma. For the Canarian archipelago, with a similar maximum geological age, Fuerteventura is only 20 Myr old. Similarly, the Hawaiian-Emperor island chain has a geological history dating back to 83 Ma (Meiji Seamount) but the oldest of the large extant islands, Niihau, is dated to just 5.1 Ma and Kauai 4.7 Ma (e.g., Price and Clague 2002). It is not known, however, whether there were emergent islands for the entire time span of 83 Ma to the present. In the case of the Azores, on the other hand, the oldest island appears to set the time frame of the existence of the archipelago. Continued advances in the understanding of those seamounts yet to emerge and those now drowned will help us understand better the long-term dynamics of oceanic archipelagos (e.g., Etnoyer et al. 2010, Fernández-Palacios et al. 2011).

In general, the maximum age of the existing islands of an archipelago may be used as a conservative reference point for the time over which biological processes have established modern diversity patterns (e.g., Price and Clague 2002, Amorim et al. 2012). However, there can be a number

of lineages that have histories in the archipelago that extend beyond the maximum age of the current islands. For example Givnish et al. (2009) based on a molecular phylogeny of the Hawaiian lobeliads, one of the largest monophyletic plant radiations across archipelagos (126 species belonging to six genera), estimated the colonization event to the archipelago to have happened approximately 13 million years ago (more than twice the age of the current oldest large island). In cases of ancient continental fragment islands such as New Caledonia, the Seychelles, and New Zealand, distinguishing the availability of land over great lengths of time, and generating agreed ages of lineages has provided considerable disagreement and debate (e.g., Heads 2008, 2012, Giribet and Boyer 2010). Establishing the timing of the founding events at the archipelagic level for oceanic island lineages, which requires reliable independent calibration points (to constrain molecular clocks) and tight geological dating, thus remains an important challenge for oceanic island biogeography.

The rule of two — or the missing step scenario

Within volcanic archipelagos comprising islands of multiple geologic stages, for the younger, growing islands, the nearby older islands are generally the dominant sources of colonizers. This pattern of the sequential immigration of lineages from older to younger islands generates distributional patterns within clades termed the 'island progression rule' (reviewed in Funk and Wagner 1995, Whittaker and Fernández-Palacios 2007). This progressive island-hopping has two major prerequisites: the simultaneous existence of at least two islands in an island chain and the existence of suitable habitat for the dispersing species. The first prerequisite is straightforward; if there are not at least two islands co-existing in an archipelago, the pre-existing biota of an archipelago might go extinct before the new island emerges. In the case of the Hawaiian chain there was a period between at least 33 and 29 Ma in which no islands existed, and distant colonization was thus crucial in populating the younger portion of the Hawaiian chain, which began to emerge between about 29 and 23

Ma. The final submergence of the summit of Koko Seamount by about 33 Ma confirms that biota on older Hawaiian–Emperor Islands could not have migrated from island to island along the entire chain to eventually colonize the present Hawaiian Islands (Clague et al. 2010); indeed, the subsequent history of terrain availability means that there are few lineages with Hawaiian origins older than c. 10 Ma (reviewed in Whittaker and Fernández-Palacios 2007). Similarly, the Azorean archipelago dates back to around 6–7 Ma, but for almost 3–4 million years, only one island, Santa Maria, was in existence. It not only provided a small platform for life for most of this time, but it is also possible that lineages which did colonize early in the lifespan of the archipelago have failed to find suitable habitat in enough places to ensure their persistence to the present day (e.g., Triantis et al. 2012, Parmakelis et al. 2015).

Crucially, even when more than a single island is present in an archipelago at a certain time period, suitable habitats have to be present on the young islands emerging for habitat specialists from older islands to be able to colonize. On oceanic islands habitat variety is closely related to island elevational range; thus if for a certain period the only islands available are low-lying islands, then lineages specialized to high elevation habitats will perish (e.g., Price and Clague 2002).

The area – number of islands trade-off

Most, if not all, aerially extensive oceanic islands consist of more than a single volcanic edifice. Hawaii island (10,432 km²), also known as the Big Island, consists of five volcanoes, Isabela (4,640 km²) in the Galápagos of six, and Reunion (2512 km²) in the Mascarene archipelago of two. If within a window of geological time, the number of volcanoes that rise above the sea level and can thus form islands is limited, then the merging of volcanoes will lead to a reduction of the number of islands within the archipelago at the respective time window. Analysing the species richness of land birds, plants, spiders and snails from 14 oceanic archipelagos of the globe, Triantis et al. (2015) found a consistent negative effect of the number of islands constituting each archipelago

on the species diversity of indigenous and endemic of all taxa, reflecting the acceleration of the gain in species richness with larger island size inherent to dominant patterns of species-area relationships (Triantis et al. 2012). While higher levels of archipelagic fragmentation may allow more species to exist within the same total area and increase diversification, these results provide support to the notion that fragmentation, at this scale, reduces the area of the component islands so as to reduce the number of species that can maintain viable populations, increasing extinction rates (see Cabral et al. 2014 for an opposite finding). Alternatively, high archipelagic fragmentation can lead to island areas insufficient for, or at least limiting intra-island speciation (e.g., Kisel et al. 2011). Further to the archipelagic fragmentation *per se*, the geographical structure of islands within an archipelago through time in combination with the dispersal ability of a clade can be important factors controlling the number of islands that can be colonized and influencing the history of colonization (e.g., Kisel et al. 2011, see also Fernández-Palacios et al. 2016).

Overall, these trade-offs between the island areas and the number of islands in an archipelago may be expected to have a direct effect expressed in the overall environmental and topographic complexity of the archipelago, posing a macroecological and evolutionary SLOSS (single large or several small) question (cf. Santos et al. 2010 and also see review of SLOSS debate in Whittaker and Fernández-Palacios 2007).

Meta-archipelagos: archipelagos of archipelagos

Many oceanic archipelagos are parts of larger regions, such as Macaronesia and Polynesia. Macaronesia is a collection of five archipelagos in the North Atlantic Ocean off the coast of the continents of Europe and Africa, i.e. Azores, Madeira, Selvagens (Savage Islands), Canaries and Cape Verde (Figure 2). At evolutionary scales these meta-archipelagos provide stepping-stones involving multiple and variable numbers of islands and archipelagos through time for dispersing lineages, providing both greater antiquity and greater connectivity during sea-level low stands of the Pleis-

tocene (Fernández-Palacios et al. 2011, 2016). Evidence exists for single founding events for some taxa at the meta-archipelagic level. In the case of the beetle genus *Tarphius*, it seems that a single colonization event to the Macaronesian islands took place about 21 Ma (Amorim et al. 2012). A high number of genera of animals and plants of Macaronesia are endemic at the meta-archipelagic level and many of them have repeatedly radiated in the different archipelagos of the region, after a single colonization event (see Fernández-Palacios 2010). Thus, understanding diversity dynamics at the island or even the archipelagic level, necessitates understanding of the dynamics at the meta-archipelagic, regional level (e.g., Figure 2).

Epilogue

A range of increasingly well-specified Earth System processes operates over comparatively compressed geological time scales in the context of oceanic archipelagos, rendering them the most geodynamically active biotic provinces on Earth. Models of biodiversity and speciation must take this dynamism into account. Knowledge, for example, of continuous increase of the total archipelagic area of an archipelago within the recent geological time could explain observed high diversification rates that might not be readily explicable from a consideration of islands individually, or from viewing them as static entities. Not only do oceanic islands provide generally useful sites for the study of ecological and evolutionary processes, but in their evolutionary dynamics they can be characterized as biotic provinces, for some lineages at the individual island level, and for most, if not all, at the archipelago level: hence providing a suite of nested 'natural laboratories' with considerable further potential for biogeographical research. The number of oceanic archipelagos for which satisfactorily complete knowledge of the flora and fauna is available is limited, posing a limit to sample size, but analyses at the archipelagic level can offer:

- a) More accurate species lists and species presences/absences, more readily available, compared to single islands. Species may be

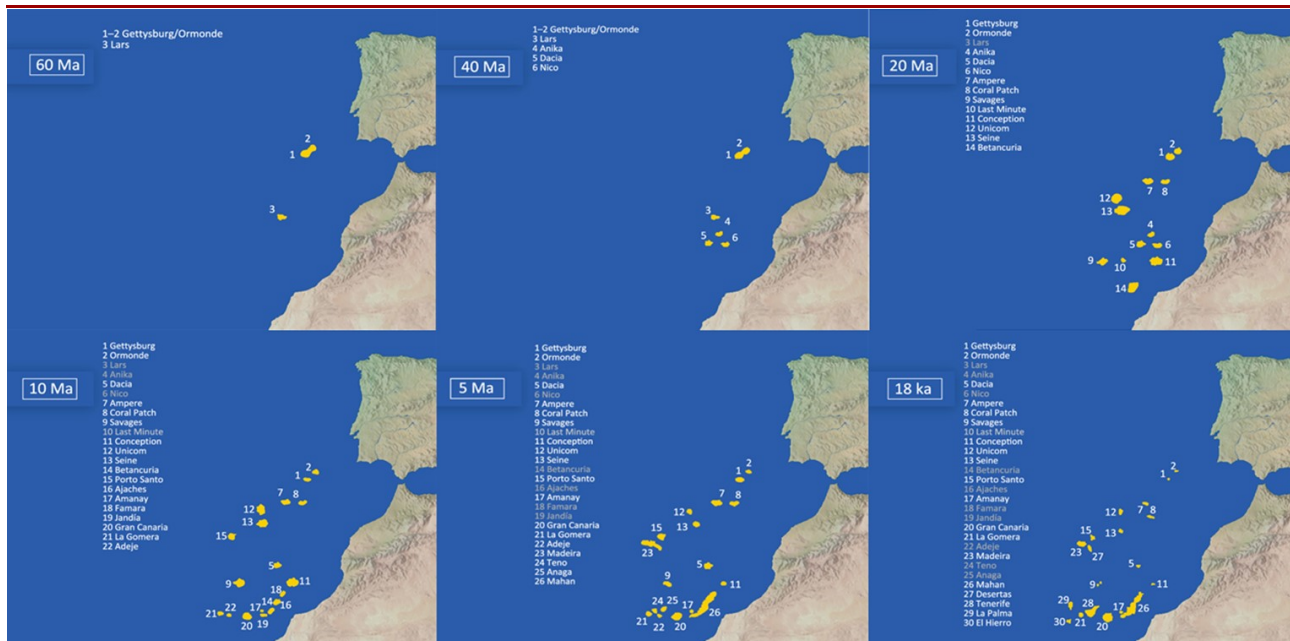


Figure 2. Tentative reconstruction of Palaeo-Macaronesia: (a) 60 Ma, (b) 40 Ma, (c) 30 Ma, (d) 20 Ma, (e) 10 Ma, (f) 5 Ma, and (g) 18 ka; names of the emerged islands at the designated date are given in bold. The positions and configurations of the continents are shown for the present day throughout for ease of reference (from Fernández-Palacios et al. 2011).

dynamically colonizing and going extinct from islands within an archipelago, but the species presence, i.e. the metapopulation at the archipelago level, is conserved.

- b) The presence of species now extinct from an island is difficult to verify for most taxa, even for those that a sufficient fossil record exists (e.g., Steadman, 2006), when at the archipelagic level is more evident.
- c) Phylogenetic data of certain lineages are easier to obtain and to interpret at the archipelagic level than for single islands (e.g., Valente et al. 2015) and indeed most phylogenetic analyses concern themselves with whole clades across an archipelago rather than within a single island (e.g., Givnish et al. 2009). Estimations of colonization and speciation events, times of arrival or speciation of taxa are expected to be better resolved compared to single islands. Thus, questions such as why some lineages undergo evolutionary radiation and others do not can be addressed more effectively (e.g., Ricklefs and Bermingham 2007).

In conclusion, we reaffirm the claim that oceanic archipelagos, as distinct and distinctive spatio-temporal units, provide unique opportunities for macroecology and macroevolution studies

(see Triantis et al. 2015). Exploiting these opportunities to the full will benefit from improved understanding of geological and environmental dynamics alongside and integrated with improved field ecological survey data, systematic review, biological records and phylogenetic data on the one hand, supported by modelling work on the other (e.g., Valente et al. 2015, Borregaard et al. 2016).

Acknowledgements

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