e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG41470

PERSPECTIVE

Archipelagos and meta-archipelagos

Robert J. Whittaker[1,2,*], José María Fernández-Palacios[3], Thomas J. Matthews[4,5], François Rigal[5,6] and Kostas A. Triantis[7]

1 School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK.

2 Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark.

3 Island Ecology and Biogeography Research Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna, Tenerife, Canary Islands, Spain.

4 School of Geography, Earth and Environmental Sciences, and Birmingham Institute of Forest Research, University of Birmingham, Birmingham B15 2TT, UK.

5 Centre for Ecology, Evolution and Environmental Changes (CE3C)–Azorean Biodiversity Group and Universidade dos Açores–Depto. de Ciências Agrárias e Engenharia do Ambiente, PT-9700-042, Angra do Heroísmo, Açores, Portugal.

6 CNRS - Université de Pau et des Pays de l'Adour – E2S UPPA, Institut des Sciences Analytiques et de Physico-Chimie pour l'Environnementet les Materiaux, MIRA, UMR5254, 64000, PAU, France

7 Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens GR-15784, Greece.

*Corresponding author. Email: robert.whittaker@ouce.ox.ac.uk

Abstract. The term meta-archipelago has been in use in cultural studies for some time, to refer to certain complex island areas in which the boundaries between conventionally recognised archipelagos are indistinct, although the concept also carries additional connotations. Use of the term in biogeography appears more recent and without effort to prescribe its meaning. We outline, from a biogeographical perspective, distinctions between meta-archipelagos and archipelagos and those islands not occurring within either collective grouping, highlighting that network analysis tools provide metrics for formal analytical purposes.

Keywords: Biogeographical regions, island biogeography, meta-archipelago, modularity, network analysis

> *"…the Antilles are an island bridge connecting, in "another way," North to South America. This geographical accident gives the entire area, including its continental foci, the character of an archipelago, that is, a discontinuous conjunction…* [which] *can be seen as an island that "repeats" itself….Which one, then would be the repeating island, Jamaica, Aruba, Puerto Rico, Miami, Haiti, Recife? Certainly none of the ones that we know. That original, that island at the center, is as impossible to reach as the hypothetical Antilli*[a] *that reappeared time and again, always fleetingly, in the cosmographers' charts. This is again because the Caribbean is a meta-archipelago…"* Benítez Rojo and Maraniss (1985, p. 431–432)

The etymology of the word archipelago points to a derivation linked to the Italian *arcipelago* as a name for the Aegean (principal sea) (Fig. 1). The wider meaning developed presumably since the Aegean Sea is replete with large numbers of islands. We use the term today for chains, clusters, or collections of islands. Yet in complex island regions such as the Caribbean or South-East Asia (Sunda Islands, New Guinea, Philippines) and parts of the South Pacific/Polynesia, it is often debatable where one archipelago ends and another begins (Benítez Rojo and Maraniss 1985, above). This matters in island biogeography as many of our analyses are based on data sets structured into archipelagos (e.g., Bunnefeld and Phillimore 2012). The rationale for this is that islands configured in isolated geographical groups exchange information (i.e., there are movements and exchanges of pollen, spores, propagules, individuals, semi-nomadic flocks, and perhaps even nutrients and energy) and they do so to a significantly greater degree than they do with any other more distant land-masses.

In analytical terms, some might argue the islands within such archipelagos to be spatially auto-correlated and thus non-independent data points. But this depends on the questions being asked. In practice, for some purposes island biologists are engaged in studying process and pattern at the intra-island level, while for other purposes it is the inter-island patterns within the archipelago (such as the species–area relationship) that are the focus of interest and analysis (e.g., Whittaker et al. 2017, Price et al. 2018). Moreover, to establish the generality of our models and hypotheses, we often wish to

Figure 1. A map of the Aegean, by Nicolaum Visscher (1649–1702), published around 1681, illustrating a complex island region in which it is challenging to decide on archipelago or meta-archipelago membership from a biological perspective. Sourced from Wikimedia Commons, wherein it is stated that this is an image from the digital and/or physical collections of the Koninklijke Bibliotheek, the Dutch National Library.

extend our analyses to encompass islands belonging to many sets of archipelagos (e.g., Bunnefeld and Phillimore 2012, Norder et al. 2018). This generates a further challenge, which is to determine the degree to which nearby archipelagos are truly independent 'replicates' as opposed to being interconnected by similar levels of information exchange as the islands within our archipelagos. As, increasingly, evidence of movement behaviours and of past propagule exchange and colonization events encoded in phylogenetic data demonstrates that even quite distant archipelagos can and do exchange 'information' (e.g., Gillespie et al. 2008, Hembry and Balukjian 2016), it is not always straightforward to determine 'natural units' for specific biogeographical analyses. Answering such a question becomes a matter of quantification and determining thresholds that might permit objective determination of where the boundaries between archipelagos can be drawn (see Box 1).

Box 1. Distinguishing the meta-archipelago from the archipelago: a biogeographical definition

A meta-archipelago is a group of archipelagos that have and continue to exhibit a meaningful level of information exchange (e.g., propagules, colonization events) and within which such exchanges occur substantially more often than with other areas but significantly less often than is the case within a single archipelago. In cases of large, persistent and well isolated systems, the meta-archipelago may be equivalent to a biogeographical sub-region or perhaps to a biogeographical network, but the concept may also be applied to groups of entities within smaller, impermanent and less isolated systems, such as constellations of habitat islands.

Biogeographers have of course been working on these questions since the foundations of the discipline (Box 2). At the coarsest of scales it is what biogeographical regionalization schemes are all about (Wallace 1880, Holt et al. 2013). In practice, the placing of distant oceanic islands into regionalization schemes has proven problematic because such islands often exhibit multiple source regions (Jønsson and Holt 2015). However, efforts have been made to draw lines sub-dividing ocean basins. Examples include the subdivision of the South East Asian / Sunda shelf island region by Wallace's Line, Weber's Line and etc., based on zoogeographical data (Whittaker and Fernández-Palacios 2007) or of the Indian Ocean region based on phytogeographical data (e.g., Renvoize 1979).

Box 2. Extract from the preface of *The Malay Archipelago*, by Alfred Russel Wallace (1869, Vol. I)

The question of how to treat complex archipelagic regions has been of interest since the foundations of the discipline of biogeography. In an attempt to identify distinct units within the broad Malay archipelago, Wallace stated:

"…I divide the Archipelago into five groups of islands, as follows: I. The Indo-Malay Islands: comprising the Malay Peninsula and Singapore, Borneo, Java, and Sumatra, II. The Timor Group: comprising the islands of Timor, Flores, Sumbawa, and Lombock, with several smaller ones, III. Celebes: comprising also the Sula Islands and Bouton, IV. The Moluccan Group: comprising Bouru, Ceram, Batchian, Gilolo, and Morty; with the smaller islands of Ternate, Tidore, Makian, Kaióa, Amboyna, Banda, Goram, and Matabello, V. The Papuan Group: comprising the great island of New Guinea, with the Aru Islands, Mysol, Salwatty, Waigiou, and several others. The Ke Islands are described with this group on account of their ethnology, though zoologically and geographically they belong to the Moluccas…"

Later, he referred to the "Philippine Archipelago" as part of the Malay Archipelago: an archipelago within an archipelago.

More recently, efforts have been made to apply sophisticated modern methods of network analysis to Wallacea (the island region between South-East Asian and Australasian continental shelfs) and to the Caribbean that do more than simply identify the boundaries between different sub-regions (i.e., groups of islands), also called modules in network theory. These analyses determine the degree of compositional connectedness based on species distributions and identify the degree of local vs regional topological linkage using null models to assess the significance of the linkages. In two papers, Carstensen et al. (2012) and Dalsgaard et al. (2014) develop this approach to identify four biogeographical roles for islands in the network: (i) network hubs are islands possessing both many local species and many shared across the region; (ii) module hubs have many local species but few of regional distribution; (iii) connectors possess a few local species but many shared across the region; and finally (iv) peripheral islands have few local species and few shared regionally. Their analyses identified four modules within Wallacea and six within the West Indies, assigning islands within these modules to the four categories just listed. In general, remote large islands tend to possess high richness of endemics and therefore feature local linkage, whereas stronger regional topological linkages, reflecting richness of non-endemics, is characteristic of typically smaller islands distant from mainland sources but situated near the boundaries between modules. These analyses thus help determine, within complex island regions, how best to delimit archipelago membership and inter-connectedness from a biogeographical perspective.

In slightly simpler circumstances than Wallacea, the Caribbean, or the Indian Ocean, the North Atlantic archipelagos west of Northern Africa and Iberia have been grouped phytogeographically into the Macaronesian region (Fig. 2; Vanderpoorten et al. 2007, Whittaker and Fernández-Palacios 2007, Torre et al. 2018), a label that has recently been used for a new line of gin distilled in the Canaries. Rather fine it is too: evidently benefitting from the indigenous botanical ingredients. But, for analytical purposes, should we lump the islands at the level of the Macaronesian region, or by archipelago (Canaries, Azores, etc), or even, for the Azores, for example, sub-divide the archipelago into three sub-groups? Perhaps the answer depends on the question being asked? We should also note that the boundaries and even the validity of Macaronesia itself has also been the subject of controversy, with evidence to suggest that the Cape Verde islands, far to the south (Fig. 2), may not properly belong in a grouping with the other archipelagos (Azores, Madeira, Savage

[Salvage] Islands, Canaries) and that the degree of Macaronesian distinctiveness depends on the choice of taxa (cf. García-Talavera 1999, Fernández-Palacios and Dias 2001, Vanderpoorten et al. 2007).

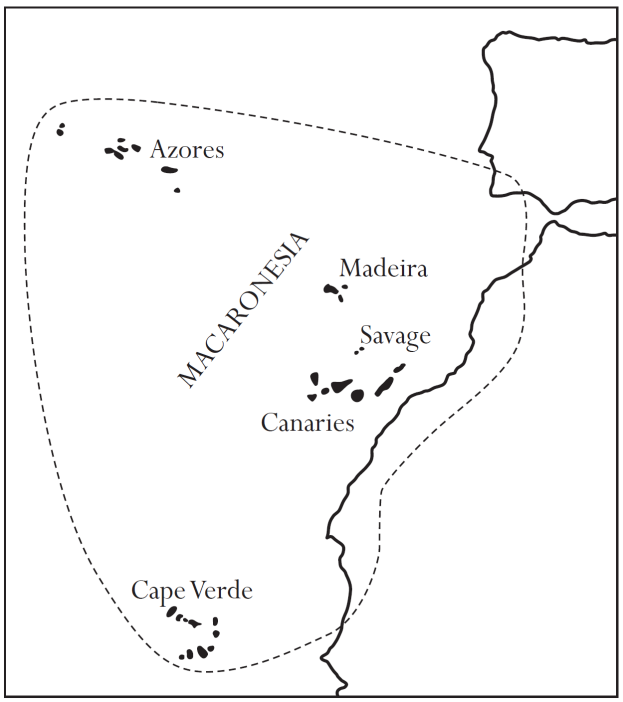

Figure 2. Macaronesia is a recognized but controversial biogeographical (in origin phytogeographical) region consisting of the archipelagos shown, together with a narrow coastal strip of north-west Africa and with affinities to the tip of the Iberian peninsula (after García-Talavera 1999).

To accommodate the notion of different degrees of connectivity between and among groups of islands, we suggest adoption of the term meta-archipelago (Box 1). This term does not yet appear to be in common usage in island biogeography, although some very brief mentions have occurred (e.g., see Kueffer et al. 2016, Triantis et al. 2016; the latter defining meta-archipelagos simply as archipelagos of archipelagos). However, the term has appeared in cultural studies, in which it appears to trace back to the work of the Cuban writer Antonio Benítez-Rojo (see Benítez-Rojo and Maraniss (1985) or Benítez-Rojo's (1992) *The repeating island: the Caribbean and post-modern perspective*). In his work the meta-archipelago is described as a chaos "having neither a boundary nor a center" and within which culturally, each island is a "copy of a different one, founding and refounding ethnological materials like a cloud will do with its vapor." Well, we get the drift and the concept proposed captures much of what we are after, particularly in the idea of replication of units which actually embrace difference as well as degrees of connectivity, and the notion of the importance of connection not only amongst islands but between the meta-archipelago and other areas. Yet, for biogeographical purposes we need a rather different formulation.

We propose that the term archipelago be used for a group of islands, typically closely spaced, which have historically exchanged biological information and which have continued to do so, with significantly higher frequency than they do with any other land masses. Mostly, islands within archipelagos have similar origins and geo-environmental dynamics, and share a common source pool(s). By contrast, the meta-archipelago should be used for a collection of nearby archipelagos whereby the information exchange is at a lower level (see Fig. 3), yet has been and remains sufficient to denote the membership of the islands as having shared legacies distinguishing them from other collections of islands and/or mainlands. The archipelagos within a meta-archipelago are likely to embrace more varied origins, geo-dynamics and source pool biases. These usages are thus akin, in terms of compositional pattern, to the notions of modules and networks (sensu Newman 2006, Carstensen et al. 2012, Poisot 2013, Thébault 2013, Dalsgaard et al. 2014) but have perhaps broader intuitive appeal, extendable across historical and contemporary pattern and process, from oceanic island systems (in which many species are generated through in situ diversification) to networks of habitat islands (Box 1).

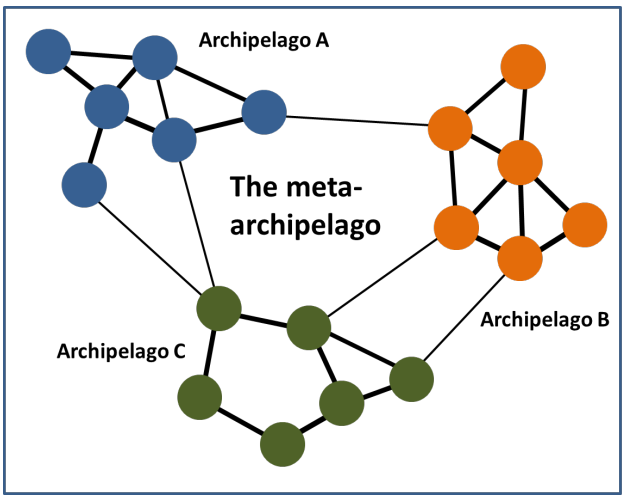

Figure 3. The meta-archipelago: in this hypothetical case, a constellation of three archipelagos that have and continue to exhibit a meaningful level of information exchange (e.g., propagules) signified by the lines of varying thickness joining the islands; exchanges among constituent archipelagos should occur significantly less often than the level of exchange typical within an archipelago, but significantly more than with other areas. Inspired by a sketch in Poisot (2013).

In a previous essay, Triantis et al. (2016) introduced the idea of the meta-archipelago level without, however, elaborating on it. In illustration, they mentioned *Tarphius* beetles, a genus with representatives in both Old and New Worlds and which are monophyletic at the level of Macaronesia (Amorim et al. 2012). They occur on three of the Macaronesian archipelagos (Madeira, Azores and Canaries), and are also monophyletic for the

Azores as a whole, although on an island level within the Azores this is not the case and instead multiple colonization events have been invoked. Such data provide clear indication of more frequent exchange amongst islands within an archipelago than between archipelagos, while justifying the treatment of the meta-archipelago as being distinct from the mainland source regions. Other plant and animal lineages have also radiated repeatedly in multiple archipelagos within Macaronesia, while typically generating single island endemic species on particular islands (Price et al. 2018). Similar patterns are found in other complex island regions (e.g., French Polynesia: Gillespie et al. 2008).

It seems likely that the appropriate scales of separation of membership and the particular data and metrics best suited to identify groups of islands as belonging to either archipelagos or meta-archipelagoes will depend on the particular biogeographical purposes. Depending on the data that are fed into such analyses and the methods of analysis selected, it may be possible to develop these approaches to emphasize either contemporary patterns of movement and exchange, or to emphasize past process regimes, reflecting deeper time evolutionary linkages or, for example, the regimes of currents, climate and sea-level conditions of the Pleistocene glacial episodes (Norder et al. 2018). For at least some of these purposes, the analytical tools are already well developed (e.g., Dalsgaard et al. 2014, Torre et al. 2018, Triantis et al. 2018).

In some geographical circumstances (e.g., islands within long, thin lakes), islands may actually be exchanging biological information with the mainland more frequently than with each other. In such circumstances, the groups of islands concerned may be useful for many island biogeographical purposes, but arguably do not warrant the label of archipelago by the above definition. Paradoxically, by this approach might the islands of the Aegean Sea be deemed merely an island group or region, rather than one archipelago, or meta-archipelago? Here the evidence for five out of the nine taxa considered in Triantis et al. (2018, p. 287), is that, for example, Crete and the surrounding islets are quite distinct from the rest of the Aegean islands, and thus Crete and its islets can be seen as an archipelago within an Aegean meta-archipelago.

Were it the case that all taxa have similar scales of interaction with fragmented land- and seascapes, then it might be realistic to think of prescribing a single framework of islands, archipelagos and meta-archipelagos. But as previous regionalization and filter effect analyses have shown, and as recent modularity analyses of Macaronesia also show (Torre et al. 2018), this is not the case. Hence, the distributions and exchanges of more vagile taxa frequently span multiple archipelagos, whilst the least vagile taxa exhibit largely within-archipelago or within-island scales of distribution and exchange. Even within a single taxon (e.g., bryophytes, seed plants, beetles, birds, land mammals, etc), there is always a significant span of movement or dispersal attainment. In using the terms island, archipelago and meta-archipelago, therefore, there is a further question of how broadly applicable across different taxa the labelling needs to be for it to be useful? Methods and approaches applied for biogeographical regionalization and/or network analyses that use distributional (sometimes with phylogenetic) data from multiple taxa might be of use in resolving this question (e.g., Holt et al. 2013, Ficetola et al. 2017).

Do we need a new term? The proliferation of terms is not always helpful to a discipline, although arguably the greater problem is the inconsistent use of the terms we have. In this instance, we suggest that the term meta-archipelago has appeal and may prove useful. In particular, it may encourage ecological island biogeographers to conceptualize the islands they study as belonging not simply to one group, framed in relation to a particular, distant mainland, but to consider and to analyse how the biota of each island may be part of a loose, but structured network of concentric layers of relatedness and exchange. The layers of archipelago and meta-archipelago provide the two closest layers of the networks that exist around many islands, while the failure to identify such patterns of linkage would identify an island as either a truly isolated island, an island that sits in the pocket of a dominant mainland, or one that belongs to a continuum or patchwork of more or less connected habitat patches. Ecologists and biogeographers are familiar with the terms meta-population and meta-community, which denote the subdivision of populations and communities into areas that are insufficiently connected to form a single entity but yet are not entirely independent of one another (e.g., Leibold and Chase 2017). The term meta-archipelago in its essence, simply extends this concept into island biogeographical pattern and process, embracing both ecological-island-biogeography and 'evolutionary/historical-island biogeography', hopefully encouraging a free flow of discussion bridging these traditions.

References

Amorim, I.R., Emerson, B.C., Borges, P.A.V. & Wayne, R.K. (2012) Phylogeography and molecular phylogeny of Macaronesian island *Tarphius* (Coleoptera: Zopheridae): why are there so few species in the Azores? Journal of Biogeography, 39, 1583–1595.

Benítez-Rojo, A. (1992) The repeating island: The Caribbean and the postmodern perspective. Duke University Press, Durham, N.C. [or see 1989 version in Spanish]

Benítez-Rojo, A. & Maraniss, J. (1985) The repeating island. New England Review and Bread Loaf Quarterly, 7, 430–452.

Bunnefeld N. & Phillimore A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect

design of nature's experiments. Ecography, 35, 15–22.

Carstensen, D.W., Dalsgaard, B., Svenning, J-C., Rahbek, C., Fjeldså, J., Sutherland, W.J. & Olesen, J.M. (2012) Biogeographical modules and island roles: a comparison of Wallacea and the West Indies. Journal of Biogeography, 39, 739–749.

Dalsgaard, B., Carstensen, D.W., Fjeldså, J., Maruyami, P.K., Rahbek, C., Sandel, B., Sonne, J., Svenning, J-C., Wang, Z. & Sutherland, W.J. (2014) Determinants of bird species richness, endemism, and island network roles in Wallacea and the West Indies: is geography sufficient or does current and historical climate matter? Ecology and Evolution, 20, 4019–4031.

Fernández-Palacios, J.M. & Dias, E. (2001) Marco biogeográfico Macaronésico. In Naturaleza de las Islas Canarias. Ecología y conservación (eds. J.M. Fernández-Palacios & J.L. Martín-Esquivel) pp. 45–52. Editorial Turquesa, Santa Cruz de Tenerife.

Ficetola, G.F., Mazel, F. & Thuiller, W. (2017) Global determinants of zoogeographical boundaries. Nature Ecology & Evolution, 1, 0089.

García-Talavera, F. (1999) La Macaronesia. Consideraciones geológicas, biogeográficas y paleoecológicas. In Ecología y Cultura en Canarias (eds. J.M. Fernández-Palacios, J.J. Bacallado, & J.A. Belmonte) pp. 39–63. Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Gillespie, R.G., Claridge, E.M. & Goodacre, S.L. (2008) Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagos. Philosophical Transactions of the Royal Society B: Biological Sciences, 363, 3335–3346.

Hembry. D.H. & Balukjian, B. (2016) Molecular phylogeography of the Society Islands (Tahiti; South Pacific) reveals departures from hotspot archipelago models. Journal of Biogeography, 43, 1372–1387.

Holt, B.G., Lessard, J.P., Borregaard, M.K., et al. (2013) An update of Wallace's zoogeographic regions of the world. Science, 339, 74–78.

Jønsson, K.A. & Holt, B.G. (2015) Islands contribute disproportionately high amounts of evolutionary diversity in passerine birds. Nature Communications, 6, 8538.

Kueffer, C., Drake, D. & Fernández-Palacios, J.M. (2016) Island biology, Oxford Bibliographies, OUP, Oxford. doi:10.1093/OBO/9780199830060-0149.

Leibold, M.A. & Chase, J.M. (2017) Metacommunity ecology. Princeton University Press, Princeton.

Newman, M.E.J. (2006) Modularity and community structure in networks. Proceedings of the National Academy of Sciences USA 103, 8577–8582.

Norder, S.J., Proios, K.V., Whittaker, R.J., et al. (2018) Beyond the Last Glacial Maximum: Island endemism is best explained by long-lasting archipelago configurations. Global Ecology and Biogeography, doi:10.1111/geb.12835.

Poisot, T. (2013). An *a posteriori* measure of network modularity. *F1000Research*, 2, doi: 10.12688/f1000research.2-130.v3.

Price, J.P., Otto, R., Menezes de Sequeira, M., Kueffer, C., Schaefer, H., Caujapé-Castells, J. & Fernández-Palacios, J.M. (2018) Colonization and diversification shape species–area relationships in three Macaronesian archipelagos. Journal of Biogeography, 45, 2027–2039.

Renvoize, S.A. (1979) The origins of Indian Ocean island floras. In Plants and islands (ed. D. Bramwell), pp. 107–129. Academic Press, London.

Thébault, E. (2013) Identifying compartments in presence-absence matrices and bipartite networks: insights into modularity measures. Journal of Biogeography, 40, 759–768.

Torre, G., Fernández-Lugo, S., Guarino, R. & Fernández-Palacios, J.M. (2018) Network analysis by simulated annealing of taxa and islands of Macaronesia (North Atlantic Ocean). Ecography, doi.org/10.1111/ecog.03909.

Triantis, K.A., Whittaker, R.J., Fernández-Palacios, J.M. & Geist, D.J. (2016) Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces. Frontiers of Biogeography, 8.2, e29605.

Triantis, K.A., Kougioumoutzis, K., Legakis, A., et al. (2018) The zoogeographic regions of the Aegean Sea: A multi-taxon approach. In Biogeography and biodiversity of the Aegean. In honour of Prof. Moysis Mylonas (eds S. Sfenthourakis, P. Pafilis, A. Parmakelis & K. A. Triantis), pp. 279–290. Broken Hill Publishers Ltd.

Vanderpoorten, A., Rumsey, F.J. & Carine, M.A. (2007) Does Macaronesia exist? Conflicting

signal in the bryophyte and pteridophyte floras. American Journal of Botany, 94, 625– 639.

Wallace, A.R. (1869) The Malay Archipelago. Macmillan, London.

Wallace, A.R. (1880) Island Life. Macmillan, London.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: taking the long view of nature's laboratories. Science, 357, eaam8326.

Submitted: 29 October 2018
First decision: 20 November 2018
Accepted: 30 November 2018

Edited by Michael N Dawson

