

Archipelagos and meta-archipelagos

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1Perspective

2Archipelagos and meta-archipelagos

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23Abstract

24The term meta-archipelago has been in use in cultural studies for some time, to refer

25to certain complex island areas in which the boundaries between conventionally

26recognised archipelagos are indistinct, although the concept also carries additional

27connotations. Use of the term in biogeography appears more recent and without effort

28to prescribe its meaning. We outline, from a biogeographical perspective, distinctions

29between meta-archipelagos and archipelagos and those islands not occurring within

30either collective grouping, highlighting that network analysis tools provide metrics for

31formal analytical purposes.

32Keywords: Biogeographical regions, island biogeography, meta-archipelago,

33modularity, network analysis

34Text

35 “...the Antilles are an island bridge connecting, in “another way,” North to South America.

36 This geographical accident gives the entire area, including its continental foci, the character of

37 an archipelago, that is, a discontinuous conjunction... [which] can be seen as an island that

38 “repeats” itself...Which one, then would be the repeating island, Jamaica, Aruba, Puerto
39 Rico, Miami, Haiti, Recife? Certainly none of the ones that we know. That original, that island
40 at the center, is as impossible to reach as the hypothetical Antilli[a] that reappeared time and
41 again, always fleetingly, in the cosmographers’ charts. This is again because the Caribbean is
42 a meta-archipelago...” Benítez Rojo and Maraniss (1985, p. 431–432)

43

44The etymology of the word archipelago points to a derivation linked to the Italian *arcipelago*
45as a name for the Aegean (principal sea) (Fig. 1). The wider meaning developed presumably
46since the Aegean Sea is replete with large numbers of islands. We use the term today for
47chains, clusters, or collections of islands. Yet in complex island regions such as the Caribbean
48or South-East Asia (Sunda Islands, New Guinea, Philippines) and parts of the South
49Pacific/Polynesia, it is often debatable where one archipelago ends and another begins
50(Benítez Rojo and Maraniss 1985, above). This matters in island biogeography as many of
51our analyses are based on data sets structured into archipelagos (e.g., Bunnefeld and
52Phillimore 2012). The rationale for this is that islands configured in isolated geographical
53groups exchange information (i.e., there are movements and exchanges of pollen, spores,
54propagules, individuals, semi-nomadic flocks, and perhaps even nutrients and energy) and
55they do so to a significantly greater degree than they do with any other more distant land-
56masses.

57 In analytical terms, some might argue the islands within such archipelagos to be
58spatially auto-correlated and thus non-independent data points. But this depends on the
59questions being asked. In practice, for some purposes island biologists are engaged in
60studying process and pattern at the intra-island level, while for other purposes it is the inter-
61island patterns within the archipelago (such as the species–area relationship) that are the
62focus of interest and analysis (e.g., Whittaker et al. 2017, Price et al. 2018). Moreover, to
63establish the generality of our models and hypotheses, we often wish to extend our analyses
64to encompass islands belonging to many sets of archipelagos (e.g., Bunnefeld and Phillimore
652012, Norder et al. 2018). This generates a further challenge, which is to determine the
66degree to which nearby archipelagos are truly independent ‘replicates’ as opposed to being
67interconnected by similar levels of information exchange as the islands within our
68archipelagos. As, increasingly, evidence of movement behaviours and of past propagule
69exchange and colonization events encoded in phylogenetic data demonstrates that even quite
70distant archipelagos can and do exchange ‘information’ (e.g., Gillespie et al. 2008, Hembry
71and Balukjian 2016), it is not always straightforward to determine ‘natural units’ for specific
72biogeographical analyses. Answering such a question becomes a matter of quantification and
73determining thresholds that might permit objective determination of where the boundaries
74between 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 than 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.



76

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

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

91

92 **Box 2. Extract from the preface of *The Malay Archipelago*, by Alfred Russel Wallace**
 93 **(1869, Vol. I).**

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

97 “...I divide the Archipelago into five groups of islands, as follows: I. The Indo-Malay Islands: comprising the
 98 Malay Peninsula and Singapore, Borneo, Java, and Sumatra, II. The Timor Group: comprising the islands of
 99 Timor, Flores, Sumbawa, and Lombok, with several smaller ones, III. Celebes: comprising also the Sula
 100 Islands and Bouton, IV. The Moluccan Group: comprising Bouru, Ceram, Batchian, Gilolo, and Morty; with the
 101 smaller islands of Ternate, Tidore, Makian, Kaióá, Amboyna, Banda, Goram, and Matabello, V. The Papual
 102 Group: comprising the great island of New Guinea, with the Aru Islands, Mysol, Salwatty, Waigiou, and several

103others. The Ke Islands are described with this group on account of their ethnology, though zoologically and
104geographically they belong to the Moluccas...”

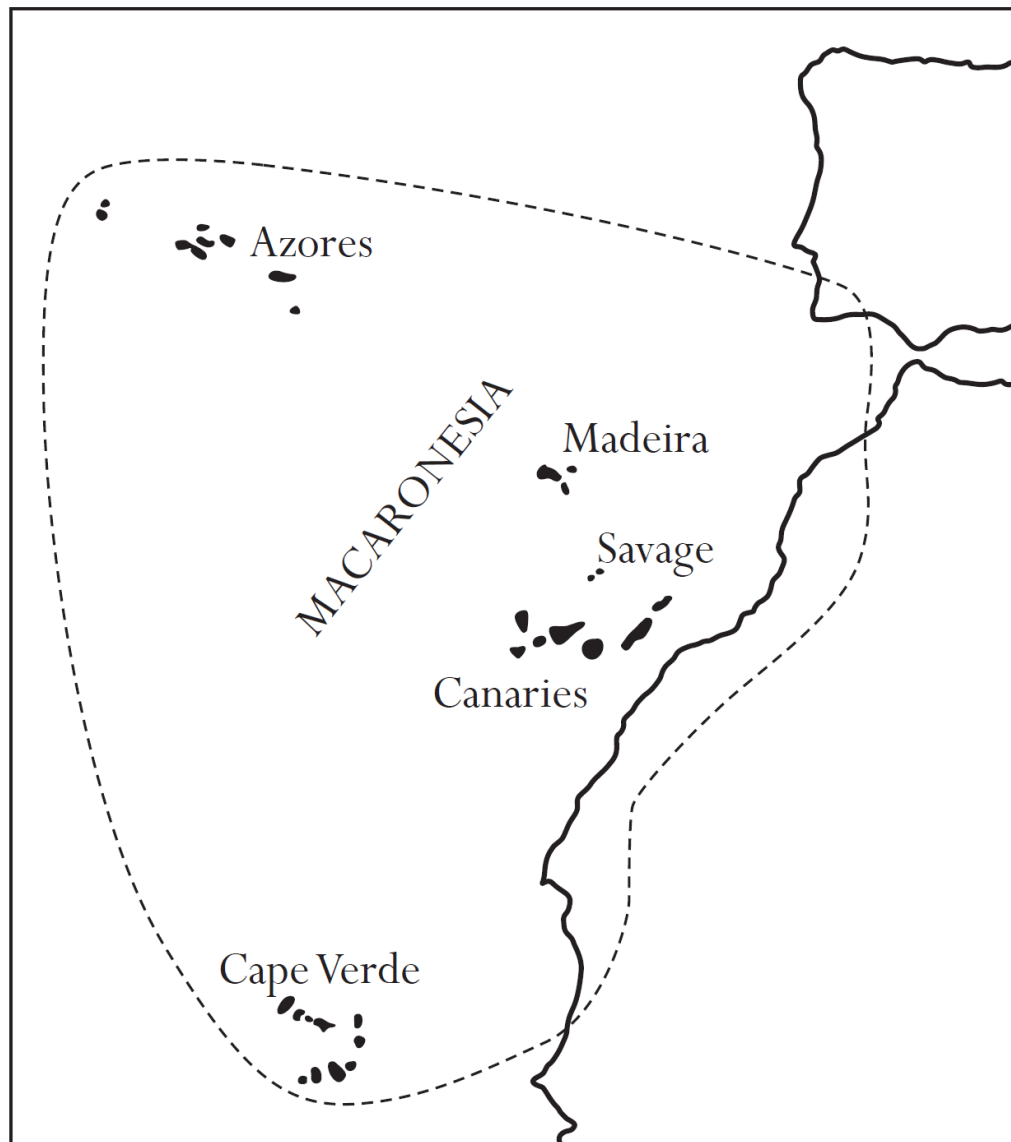
105Later, he referred to the “Philippine Archipelago” as part of the Malay Archipelago: an
106archipelago within an archipelago.

107

108 More recently, efforts have been made to apply sophisticated modern methods of network
109analysis to Wallacea (the island region between South-East Asian and Australasian
110continental shelves) and to the Caribbean that do more than simply identify the boundaries
111between different sub-regions (i.e., groups of islands), also called modules in network theory.
112These analyses determine the degree of compositional connectedness based on species
113distributions and identify the degree of local vs regional topological linkage using null
114models to assess the significance of the linkages. In two papers, Carstensen et al. (2012) and
115Dalsgaard et al. (2014) develop this approach to identify four biogeographical roles for
116islands in the network: (i) network hubs are islands possessing both many local species and
117many shared across the region; (ii) module hubs have many local species but few of regional
118distribution; (iii) connectors possess a few local species but many shared across the region;
119and finally (iv) peripheral islands have few local species and few shared regionally. Their
120analyses identified four modules within Wallacea and six within the West Indies, assigning
121islands within these modules to the four categories just listed. In general, remote large islands
122tend to possess high richness of endemics and therefore feature local linkage, whereas
123stronger regional topological linkages, reflecting richness of non-endemics, is characteristic
124of typically smaller islands distant from mainland sources but situated near the boundaries
125between modules. These analyses thus help determine, within complex island regions, how
126best to delimit archipelago membership and inter-connectedness from a biogeographical
127perspective.

128 In slightly simpler circumstances than Wallacea, the Caribbean, or the Indian Ocean, the
129North Atlantic archipelagos west of Northern Africa and Iberia have been grouped
130phytogeographically into the Macaronesian region (Fig. 2; Vanderpoorten et al. 2007,
131Whittaker and Fernández-Palacios 2007, Torre et al. 2018), a label that has recently been used
132for a new line of gin distilled in the Canaries. Rather fine it is too: evidently benefitting from
133the indigenous botanical ingredients. But, for analytical purposes, should we lump the islands
134at the level of the Macaronesian region, or by archipelago (Canaries, Azores, etc), or even, for
135the Azores, for example, sub-divide the archipelago into three sub-groups? Perhaps the
136answer depends on the question being asked? We should also note that the boundaries and
137even the validity of Macaronesia itself has also been the subject of controversy, with evidence
138to suggest that the Cape Verde islands, far to the south (Fig. 2), may not properly belong in a
139grouping with the other archipelagos (Azores, Madeira, Savage [Salvage] Islands, Canaries)
140and that the degree of Macaronesian distinctiveness depends on the choice of taxa (cf.
141García-Talavera 1999, Fernández-Palacios and Dias 2001, Vanderpoorten et al. 2007).

142



143
144

145**Figure 2.** Macaronesia is a recognized but controversial biogeographical (in origin
146phytogeographical) region consisting of the archipelagos shown, together with a narrow
147coastal strip of north-west Africa and with affinities to the tip of the Iberian peninsula (after
148García-Talavera 1999).

149

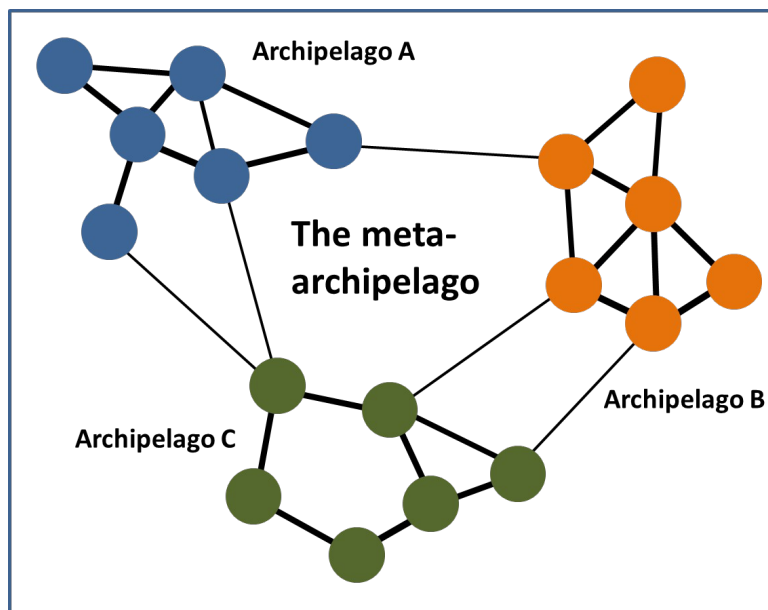
150 To accommodate the notion of different degrees of connectivity between and among
151groups of islands, we suggest adoption of the term meta-archipelago (Box 1). This term does
152not yet appear to be in common usage in island biogeography, although some very brief
153mentions have occurred (e.g., see Kueffer et al. 2016, Triantis et al. 2016; the latter defining
154meta-archipelagos as the archipelagos of archipelagos). However, the term has appeared in
155cultural studies, in which it appears to trace back to the work of the Cuban writer Antonio
156Benítez-Rojo (see Benítez-Rojo and Maraniss (1985) or Benítez-Rojo’s (1992) *The repeating*
157*island: the Caribbean and post-modern perspective*). In his work the meta-archipelago is
158described as a chaos “having neither a boundary nor a center” and within which culturally,
159each island is a “copy of a different one, founding and refounding ethnological materials like
160a cloud will do with its vapor.” Well, we get the drift and the concept proposed captures much
161of what we are after, particularly in the idea of replication of units which actually embrace

162 difference as well as degrees of connectivity, and the notion of the importance of connection
163 not only amongst islands but between the meta-archipelago and other areas. Yet, for
164 biogeographical purposes we need a rather different formulation.

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

180

181



182

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

189

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

195although on an island level within the Azores this is not the case and instead multiple
196colonization events have been invoked. Such data provide clear indication of more frequent
197exchange amongst islands within an archipelago than between archipelagos, while justifying
198the treatment of the meta-archipelago as being distinct from the mainland source regions.
199Other plant and animal lineages have also radiated repeatedly in multiple archipelagos within
200Macaronesia, while typically generating single island endemic species on particular islands
201(Price et al. 2018). Similar patterns are found in other complex island regions (e.g., French
202Polynesia: Gillespie et al. 2008).

203 It seems likely that the appropriate scales of separation of membership and the particular
204data and metrics best suited to identify groups of islands as belonging to either archipelagos
205or meta-archipelagoes will depend on the particular biogeographical purposes. Depending on
206the data that are fed into such analyses and the methods of analysis selected, it may be
207possible to develop these approaches to emphasize either contemporary patterns of movement
208and exchange, or to emphasize past process regimes, reflecting deeper time evolutionary
209linkages or, for example, the regimes of currents, climate and sea-level conditions of the
210Pleistocene glacial episodes (Norder et al. 2018). For at least some of these purposes, the
211analytical tools are already well developed (e.g., Dalsgaard et al. 2014, Torre et al. 2018,
212Triantis et al. 2018).

213 In some geographical circumstances (e.g., islands within long, thin lakes), islands may
214actually be exchanging biological information with the mainland more frequently than with
215each other. In such circumstances, the groups of islands concerned may be useful for many
216island biogeographical purposes, but arguably do not warrant the label of archipelago by the
217above definition. Paradoxically, by this approach might the islands of the Aegean Sea be
218deemed merely an island group or region, rather than one archipelago, or meta-archipelago?
219Here the evidence for five out of the nine taxa considered in Triantis et al. (2018, p. 287), is
220that, for example, Crete and the surrounding islets are quite distinct from the rest of the
221Aegean islands, and thus Crete and its islets can be seen as an archipelago within an Aegean
222meta-archipelago.

223 Were it the case that all taxa have similar scales of interaction with fragmented land- and
224seascapes, then it might be realistic to think of prescribing a single framework of islands,
225archipelagos and meta-archipelagos. But as previous regionalization and filter effect analyses
226have shown, and as recent modularity analyses of Macaronesia also show (Torre et al. 2018),
227this is not the case. Hence, the distributions and exchanges of more vagile taxa frequently
228span multiple archipelagos, whilst the least vagile taxa exhibit largely within-archipelago or
229within-island scales of distribution and exchange. Even within a single taxon (e.g.,
230bryophytes, seed plants, beetles, birds, land mammals, etc), there is always a significant span
231of movement or dispersal attainment. In using the terms island, archipelago and meta-
232archipelago, therefore, there is a further question of how broadly applicable across different
233taxa the labelling needs to be for it to be useful? Methods and approaches applied for
234biogeographical regionalization and/or network analyses that use distributional (sometimes
235with phylogenetic) data from multiple taxa might be of use in resolving this question (e.g.,
236Holt et al. 2013, Ficetola et al. 2017).

237

238 Do we need a new term? The proliferation of terms is not always helpful to a discipline,
239although arguably the greater problem is the inconsistent use of the terms we have. In this
240instance, we suggest that the term meta-archipelago has appeal and may prove useful. In
241particular, it may encourage ecological island biogeographers to conceptualize the islands
242they study as belonging not simply to one group, framed in relation to a particular, distant
243mainland, but to consider and to analyse how the biota of each island may be part of a loose,

244but structured network of concentric layers of relatedness and exchange. The layers of
245archipelago and meta-archipelago provide the two closest layers of the networks that exist
246around many islands, while the failure to identify such patterns of linkage would identify an
247island as either a truly isolated island, an island that sits in the pocket of a dominant
248mainland, or one that belongs to a continuum or patchwork of more or less connected habitat
249patches. Ecologists and biogeographers are familiar with the terms meta-population and
250meta-community, which denote the subdivision of populations and communities into areas
251that are insufficiently connected to form a single entity but yet are not entirely independent of
252one another (e.g., Leibold and Chase 2017). The term meta-archipelago in its essence, simply
253extends this concept into island biogeographical pattern and process, embracing both
254ecological-island-biogeography and ‘evolutionary/historical-island biogeography’, hopefully
255encouraging a free flow of discussion bridging these traditions.

256

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