



The geographical distribution of life and the problem of regionalization: 100 years after Alfred Russel Wallace

This editorial marks the collation of a set of papers published in the *Journal of Biogeography* between 1983 and 2013 into a virtual issue highlighting the enduring legacy of Alfred Russel Wallace (1823–1913) within biogeography. Widely regarded as one of the founding fathers of biogeography, Wallace died in Dorset, England, on 7 November 1913, in a house he designed and built himself (Beccaloni, 2011). By the time of his death Wallace had a global reputation that went far beyond his fame as the co-discoverer of evolution by natural selection (<http://people.wku.edu/charles.smith/index1.htm>). His popularity during his lifetime derived from a vast breadth of interests, including his core scientific work in evolutionary biology, biogeography and glaciology, but also the more eccentric and difficult to appreciate interests in astrobiology, spiritualism and land reform (Smith, 2011). He was a prolific writer, and several of his fundamental contributions to biogeography were also accessible to an educated public, resulting in books such as *The Malay Archipelago* (Wallace, 1869), *The Geographical Distribution of Animals* (Wallace, 1876) and *Island Life* (Wallace, 1880) becoming popular and broadly read. Revolutionary technical scientific papers included the ‘Sarawak’ paper on speciation (Wallace, 1855) and the ‘Ternate’ paper on natural selection (Wallace, 1858). A vast array of additional insights into Wallace’s thinking is to be found scattered within his many letters, essays and book reviews spanning from 1843 until his death (see <http://people.wku.edu/charles.smith/index1.htm>).

Some commentators feel that history has not been particularly kind to Wallace’s legacy – relegating him to the role of Darwin’s less inspired co-founder of the theory of natural selection (Gould, 2002) – perhaps a consequence of his turn towards

teleological thinking and more metaphysical interests in his later years (Birx, 1998). Nevertheless, over the past decade or so, many scholars have attempted to resurrect Wallace’s reputation as a leading Victorian scientist (Shermer, 2002; Smith, 2005; Smith & Beccaloni, 2011). The centenary of his passing has been marked by a number of commentaries (e.g. Heaney, 2013; Knapp, 2013) and by the publication of two new analyses of global zoogeographical regions that have explicitly paid tribute to Wallace’s legacy as the creator of the first widely adopted map of global regions (Holt *et al.*, 2013; Rueda *et al.*, 2013).

Rather than attempting a comprehensive overview of Wallace as a scientist and activist, here we highlight his enduring contribution to the modern science of biogeography. We do so by introducing a virtual issue of the *Journal of Biogeography* in which we have gathered a series of key contributions published between 1983 and 2013 on a matter to which he devoted much attention – the problem of regionalization. These papers illustrate the enduring debt we still owe to the foundational work of Wallace and his contemporaries. With the extraordinary growth of scientific data and publications in recent decades, much of this legacy of knowledge and ideas is no longer routinely attributed back to 19th century (or even earlier) foundations. However, it can often be salutary to spend time browsing the back catalogue to rediscover not only the forgotten gems and insights (e.g. Hooker, 1867; Brown *et al.*, 2004) but also the many blind alleys.

Wallace was both a highly original thinker and a great synthesizer and promoter of scientific understanding through books such as *The Malay Archipelago* (1869), *The Geographical Distribution of Animals* (1876) and *Island Life* (1880). To complete the set of papers highlighting his legacy we therefore include a few papers that are not primarily focused on the problem of regionalization. Reading sections of Wallace’s books can lead to a rather surprising realization that many of his insights have a

distinctly modern ring to them (see summary in Box 2.1 in Lomolino *et al.*, 2010). Yet, he has been criticized retrospectively by several more recent biogeographers, notably Leon Croizat and the late 20th century vicariance biogeographers, as having been nothing more than a non-relevant old-school dispersalist (Michaux, 2011). In this context it is important to note that Wallace had no access to many of the foundational concepts (e.g. plate tectonics, Hennigian phylogenetics, phylogeography) or analytical tools (e.g. molecular systematics, stable isotopes, satellite imaging, geographical information systems, advanced statistics or mechanistic modelling) that we depend on today. It is thus intriguing to ask not only how relevant does his work remain to framing modern biogeographical scholarship, but also to what extent did his biogeographical syntheses and ideas withstand the test of time?

Wallace was not the inventor of the idea of zoogeographical regions, nor was he the first to publish a global map of the regions. Rather, he built upon a pioneering scheme by Phillip Lutely Sclater (1858), who subdivided the world into six regions based upon the distribution of birds. Wallace, however, played a key role in developing the analysis of regions, promoting their use as an organizing principle of zoogeographical analysis (Wallace, 1876). He defended Sclater’s initial efforts (Wallace, 1894) while popularizing the regions, not least through using them as an organizing framework in his books (e.g. Wallace, 1880). In his 1894 article *What are zoological regions?* Wallace wrote:

Zoological regions are those primary divisions of the earth’s surface of approximately continental extent, which are characterised by distinct assemblages of animal types. Though strictly natural... they have no absolute character as equal independent existences, since they may have been different in past ages, but are more or less conventional, being established solely for the purpose of facilitating the study of the existing geographical

distribution of animals in its bearing on the theory of evolution. There is thus, in my opinion, no question of who is *right* and who is *wrong* in the naming and grouping of these regions, or of determining what are the *true* primary regions. All proposed regions are, from some points of view, natural, but the whole question of their grouping and nomenclature is one of convenience and of utility in relation to the object aimed at.

Wallace (1894) was adamant in this paper that biogeographical regions provided a crucial framework for zoogeography and that it was unhelpful to be promoting multiple regionalization schemes for different major taxa or subordinate taxa. He did not welcome the notion of separate schemes for reptiles, butterflies, beetles, or for tribes or families being developed as competing schemes. Instead he wrote: '[I]aws of distribution can only be arrived at by comparative study of the different groups of animals, and for this study we require a common system of regions and a common nomenclature'. He then expanded on this by commenting that the purpose of the unified system of regions was to provide a single framework encapsulating the *law* of distribution so that, by working out the 'details in the different groups', we might identify the 'certain difficulties or anomalies' that require special explanation. He was also clear that regions could best be determined by analyses commencing with the distribution of terrestrial mammals '... supplemented in doubtful cases by that of the other vertebrates' (Wallace, 1876, p. 58). In short, he saw Sclater's scheme of six regions, and his refinement of it, as the expression of the general rules, the major natural subdivisions of the world the explanation for which '... can only be because during the more recent geological periods they have formed single more or less continuous areas, while separated either by geographical, climatal or biological barriers from the adjacent areas'. One can only imagine how this line of thinking would have been influenced had Wallace's view been informed by the modern plate tectonics model of Earth history. Wallace was aware of and discussed those parts of the world where the zoogeographical regions did not neatly fit the current distribution of continental boundaries and where transitional faunas could be discerned, but he felt it was premature to attempt definite naming of subdivisions on the basis of knowledge then available.

As regards the essential ingredients of a successful scheme of regionalization, Wallace (1894) argued that it boiled down to three elements:

- (1) They should be founded upon, and approximate to, the great primary geographical divisions of the earth, which there is reason to believe have been permanent during considerable geological periods.
- (2) They should be rich and varied in *all* the main types of animal life.
- (3) They should possess great individuality; whether exhibited by the *possession* of numerous peculiar species, genera, or families, or by the entire *absence* of genera or families which are abundant and widespread in some of the adjacent regions.

He closed the article as follows:

It is because I think that the future progress of a branch of biological study in which I take great interest will depend on our arriving at some uniformity of view as to this question of zoological regions, that I have devoted so much space to this discussion.

Determining, refining and applying zoogeographical regions have been enduring themes of the biogeographical research agenda since these words were written. Within conservation practice, for example, zoogeographical regionalization schemes (generally closely similar to the Sclater–Wallace system), have been integral to the development of global and continental-scale systems for strategic conservation planning purposes in both terrestrial and marine realms (see discussions in Ladle & Whittaker, 2011; Briggs & Bowen, 2012). The regions thus hold continuing relevance to pure and applied biogeography. To highlight recent developments in the study of biogeographical regions, we turn now to our featured articles.

Our first featured paper is by Charles H. Smith (1983a), who undertook an analysis based on the distribution of 115 families of mammals across the 24 subregions of Wallace's (1876) system. Smith undertook a pioneering analysis designed to assess the efficiency of this system and whether it provided a logical set of relationships among the subregions, i.e. how well they nest within the higher level regions. He constructed a similarities matrix of the subregions and applied an ordination technique, non-metric multidimensional scaling, in combination with classification techniques, to determine an optimal set of regions and subregions. This analysis pro-

duced a novel set of four regions, subdivided into a set of 10 subregions, which displayed significant differences from Wallace's original system. Smith (1983b) wrote an innovative companion paper which set out to assess the proposition that evolution might be regarded as a stochastic spatial process with inter-regional affinities explicable through chance interactions between the subregions and a deterministic distance-decay effect on the diffusion of evolutionary innovations. This approach was in some ways rather ahead of its time, as the computer power and computerized distributional datasets required to develop this line of thinking further were lacking in the early 1980s and this, combined perhaps with a somewhat impenetrable writing style, may explain the lack of attention that has been paid to Smith's efforts and especially to the 1983b paper.

By way of contrast with the computational/analytical approach taken by Smith (1983a,b), our next featured article by Barry Cox (2001), published 18 years later, took the form of an expert synthesis in which the author reviews both existing zoogeographical (essentially updating Wallace's map) and phytogeographical regionalizations (updating the scheme proposed by A. L. Takhatajan, 1986), focusing especially on the comparison of the two. The six zoogeographical regions identified by Cox at the outset as the 'currently recognized set' comprise the Neotropical (South and Central America), the Nearctic (North America), the Palearctic (Eurasia and the northern portion of Africa and Arabia), the African (Africa and Arabia south of the Sahara), the Oriental (Southeast Asia) and Australian. Cox (2001) proposed two main modifications to these regions: first, redrawing the boundary between the Palearctic and the African region more or less along the boundaries of the African continent (contrary to Wallace); and second, withdrawing the scope of the regions back to the edges of continental plates, or to the low point of Pleistocene sea-level minima. Cox's solution to the long debate about the placing of Wallace's Line, which bisects Bali and Lombok, was to remove the oceanic islands between 'mainland' Southeast Asia and the Sahul landmass of the Pleistocene from the area encompassed by the adjacent regions, and to follow an earlier proposal to name this transitional area 'Wallacea'. Cox's major modification to the earlier phytogeographical schemes was to drop the tiny but notable Cape Region of southern Africa from the top

level of the classification, giving the following set: Holarctic, African, Indo-Pacific, South American and Australian regions (note that Cox follows prior practice in using the term kingdom instead of regions for the top level for plants). The relegation of the Cape to a second tier level in the regionalization could conceivably have implications for the treatment of this area in global conservation prioritization schemes, but judging from the frequency of use of 'Cape Floristic Region' in the scientific literature, this proposal has been widely ignored. Cox's restriction of the zoogeographical, mostly mammal-based, regionalization to the continents contrasts with his inclusion of oceanic regions in the phytogeographical regionalization. Of course, as Cox recognizes, many oceanic islands display the influence of multiple colonization sources and are thus less easily assigned to a particular region than are continental areas (Whittaker & Fernández-Palacios, 2007). For recent advances in network analysis of island regions in relation to biogeographical dynamics, linking pattern to process, see Carstensen & Olesen (2009) and Carstensen *et al.* (2012). And, for recent advances in the use of phylogenetic data to refine the positioning of Wallace's Line, see Esselstyn *et al.* (2010).

Cox's (2001) update has been well cited, but so too has a response by Morrone (2002), who in a very short critique proposed an alternative regionalization scheme. Morrone's analysis was rooted in a personal interpretation of cladistic and panbiogeographical studies published by other authors. He claimed that these analyses supported a fairly radical redrawing of the boundaries of the major regions, fusing zoogeographical and phytogeographical evidence together to form a single biogeographical scheme. Morrone's scheme differs from others in seeking evolutionary connections produced through the vicariant history generated by the Earth's tectonic history. This leads, for example, to his splitting Wallace's original Neotropical region into an Andean region with affinities to western Gondwanan terranes, and a Neotropical region with affinities to eastern Gondwanan terranes. The contrast between these two reviews reveals something of the gulf in philosophy, theory and method that still persists between different schools of thought within biogeography.

There is clearly still a place for expert reviews and syntheses in the field of bio-

geographical regionalizations, as illustrated by the latest recasting of marine biogeographical regions by Briggs & Bowen (2012). However, as Cox (2010) has commented, more recent analytical, computationally intensive regionalization schemes provide a more satisfactory basis for advancing towards an agreed set of global maps as they generate a quantitative basis for drawing the boundaries and for determining at what level of the hierarchy of regions the distinctions occur: a concern that motivated Smith's (1983a,b) analyses and to which Wallace himself devoted considerable attention (Wallace, 1876). Alternative maps produced within and across such analyses also generate insight into which assumptions, steps or parameters exhibit sensitivity in terms of outcomes (below).

The next papers we feature are examples of such schemes, being motivated by the development of both improved availability of systematic distributional data for many higher taxa and by ongoing developments in analytical techniques and data handling capacity. Procheş (2005) illustrates the application of cluster analysis to the regionalization of bats, a group that might be thought unlikely to follow the boundaries between regions as closely as less mobile forms of mammals. In practice, the cluster analysis identified 10 groups showing similarities with elements of both previous zoogeographical and phytogeographical mapping exercises. Procheş also usefully reviews previous regionalizations and, rather than promoting his scheme as replacing previous schemes, he follows Wallace in explaining how the differences between taxa or even ecological classifications of species may be used to 'partial out the role of dispersal abilities, body size, evolutionary age, etc., in determining global distribution patterns' (Procheş, 2005, p. 607).

There have been three new attempts in the last three years to generate global regionalization schemes, two published in the *Journal of Biogeography*, and featured here. The first paper, by Kreft & Jetz (2010), illustrates something of a step-change in both data resolution and analytical power. Their analysis, based on a global database of *species* distributions of mammals, employs a combination of ordination (using non-metric multidimensional scaling) and cluster analysis, with the latter providing a means to generate a hierarchical representation of groups and their degree of relationship to one another. They

also illustrate how switching the temporal/evolutionary 'depth' of the analysis from families, to genera, to species, can generate subtle but significant differences in the outcomes of analyses, as can distinguishing volant from non-volant species – very much as envisaged by previous papers reviewed herein (e.g. Wallace, 1894; Procheş, 2005). In a recent paper published in *Science*, Holt *et al.* (2013) take this approach a step further in their analysis of amphibians, birds and mammals (both separately and in combination). Again, they use cluster analyses and species-level distributional data (for 21,037 species), but complement this approach with algorithms that take into account the phylogenetic relationships between species. This, they claim, is consistent with Wallace's intent that the regions of the world express ancestral relationships among species, although in practice their means of attaining this is rather different from the approaches open to Wallace (1894), when he wrote that the '... intelligent study of the distribution of animals... derives its chief interest and importance from its relation to the theory of organic evolution... [and] must therefore include the comparative distribution of the various classes, orders, and minor groups'.

The latest contribution to the problem of global regionalization is by Rueda *et al.* (2013). They employ an innovative approach to classification, termed affinity propagation, based on range map data for birds, mammals and amphibians, but excluding bats and migratory birds. They argue that according to Wallace's criteria for zoogeographical regions, the appropriate taxonomic resolution to use is the genus rather than species or families. Accordingly they focused mostly on genus-level analyses but compared these results with those for species and family levels. They find the greatest similarity to Wallace's original scheme in their genus-level analyses. Although they found eight regions for mammals and birds as opposed to the six of Wallace and the six they found for amphibians, the additional boundaries coincided fairly closely to sub-regions in Wallace's scheme. The adherence to a particular taxonomic level is entirely sensible within contemporary quantitative analyses of this sort, but it is worth noting that in *The Geographical Distribution of Animals* Wallace (1876, e.g. pp. 53–54) indicated that the unique (or largely unique) possession of particular families and genera and the absence of

families and genera were the key characteristics of the primary zoological regions, implying that he did not envisage only using a single taxonomic level (whether families, genera or species) to determine regions.

These recent papers illustrate how changing the quality and resolution and taxonomic coverage of data, and the power, sophistication and character of the analytical tools, can generate suites of alternative regionalization schemes, with differences of detail too numerous to describe here. The differences, which include (1) areas of a transitional nature, subject to past episodes of faunal exchange, and (2) variation in the level at which region/subregion boundaries occur, are important, and may be crucially important within a conservation biogeographical perspective (Jepson & Whittaker, 2002; Ladle & Whittaker, 2011; Briggs & Bowen, 2012). Comparison of these studies illustrates that the problem of biogeographical regionalization really doesn't have a single objective solution and that it may be appropriate to choose different schemes for different purposes, or at least to conduct sensitivity analyses to determine the impact of the choices taken. However, perhaps the most striking feature of these schemes is the degree of similarity between them and the various 'expert' precursor schemes, including Wallace's (1876) original. This is striking given that the 19th century schemes were necessarily conducted with much more limited and patchy data and without the sophisticated statistical and modelling tools of the modern era. It will be fascinating to see which of these recent schemes (terrestrial: Kreft & Jetz, 2010; Holt *et al.*, 2013; Rueda *et al.*, 2013; marine: Briggs & Bowen, 2012) gain greatest traction with the passage of time or whether they will be superseded as new forms of analysis continue to be developed (Mouillot *et al.*, 2013).

In closing our discussion of regionalization we feel it important to note that there are other ways to subdivide the planet that could be regarded as biogeographical and yet are radically different from the compositionalist regionalizations discussed thus far. One such system is the ecological subdivision of the world into biomes or major ecosystem types. Indeed, for many purposes in ecology, land management and conservation, such functional classifications may be of greater utility, or alternatively may constitute required input data alongside the com-

positionalist regions, as is the case within the WWF ecoregions scheme (see review in Ladle & Whittaker, 2011). In illustration of the methodological and theoretical parallels and distinctions between compositionalist and functionalist regionalization schemes, we have included a paper by Mackey *et al.* (2008). Although taking a different path to the other papers highlighted, this analysis can also be regarded as ultimately following on from the work initiated in the 19th century by Sclater, Wallace and their contemporaries.

We have focused on the problem of regionalization because first, as Wallace argued, this is a fundamental step in understanding the 'laws of distribution' and in mapping biodiversity at a continental, ocean basin or global scale, and second, because the *Journal of Biogeography* has carried some of the key papers on this theme over the last three decades. Of course, Wallace's influence is far more pervasive within biogeography. Lomolino *et al.* (2010, Box 2.1) list as many as 17 biogeographical principles advocated by Wallace that retain contemporary relevance. These include: (1) the classification of islands into continental shelf, continental fragments and oceanic, which remains a key start point of many contemporary island biogeographical analyses (e.g. Triantis *et al.*, 2012); (2) recognition that long-distance dispersal is not only possible, but probable as a means of colonizing remote islands (Swenson *et al.*, in press); while (3) the distributions of species lacking long-distance dispersal powers provides good evidence of past land connections [a line of thinking that led to credibility problems for biogeography in the early 20th century as geologically unsupportable land bridges across ocean basins were imagined (Hallam, 1967), but which was used more productively by Alfred Wegener as he developed his revolutionary theory of continental drift (Wegener, 1915), and which was later to become a major feature of the late 20th century vicariance biogeography revolution (Nelson & Platnick, 1981)]; (4) that distance of itself does not determine the degree of affinity between the biotas or pairs of regions; and (5) statements of the relative roles of climate and history in controlling patterns of diversity.

While Wallace's Line (Esselstyn *et al.*, 2010) is the demarcation most closely associated with Wallace himself – and its discovery played a key role in shaping his own understanding – Wallace also had important formative experiences working

in the Amazon. It was for this region that he put forward the riverine barrier hypothesis, which postulated that differences between closely related forms on opposing sides of river barriers could be attributed to the role of the river in isolating the populations on either side (Wallace, 1852). Whereas other theories of Amazonian diversity, especially the Pleistocene refuge model, took centre stage in the final decades of the 20th century, some recent phylogeographical analyses – such as the paper featured in the virtual issue by Fernandes *et al.* (2012) – have found renewed support for the role of riverine barriers, largely as Wallace envisaged.

As mentioned above, Wallace's work was by no means restricted to the problem of understanding the 'laws of distribution' for the biological world. But the weight of his contribution to this problem was and remains highly significant, and is recognized as such among biogeographers. It was in tribute to this aspect of his legacy that the term Wallacean shortfall was coined to refer to the problem of incomplete data on distributions of species (e.g. Lomolino *et al.*, 2010; Ladle & Whittaker, 2011). Moreover, while we now have much better resolution on species distributions than we did in the 19th century, it remains the case that our analyses can be sensitive to, or undermined by, the still partial and incomplete nature of our data on distributions. The final paper featured in this virtual issue, by Yang *et al.* (2013), neatly dissects the impact of such inventory shortfalls on our understanding of patterns and causal processes of species diversity, illustrated with data for vascular plants from China. Their paper, while alluding only tangentially to Wallace, is included in this set because it highlights how much work remains to be done in the continuing effort to refine our knowledge of the patterns of distribution from which we can, in Wallace's footsteps, hope to infer much of interest about the functioning of the natural world.

EXPLANATORY NOTE

The virtual issue is currently available as an easily linkable set of papers via the Wiley Online Library system. It features a subset of the papers cited in this article that were published in the *Journal of Biogeography*. Those published prior to 1996 are available only by subscription via the JSTOR journal archive.

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