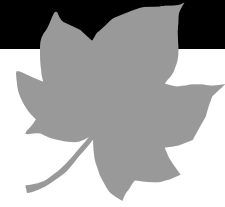


COMMENTARY



## Is biogeography emerging from its identity crisis?

Biogeography has had an unusually protracted identity crisis (e.g. Brown & Lomolino, 2000; Donoghue & Moore, 2003), although the discipline took on a relatively 'modern' look well over a century ago – the thoroughly 'modern' observations of Alfred Russel Wallace have been discussed elsewhere (Funk, 2004), and Joseph Dalton Hooker's views about floristic histories across lands of the southern hemisphere lacked only the foundation of plate tectonics to be completely modern. From these promising beginnings in the nineteenth century, one might have thought that biogeographers would by now have developed fully integrative approaches to determining the roles of earth history and ecology in the geography of diversification. Unfortunately, this has not yet happened.

Rather, by the latter part of the twentieth century, biogeographers had turned de Candolle's original delineation between 'ecological vs. historical' biogeography into largely separate research perspectives, motivated by two independent revolutions in biogeography. MacArthur and Wilson's island biogeographic model lured ecologists with its clearly stated and testable predictions based on a dynamic interaction between colonization and extinction rates, while soon after the geologists resurrected Wegener's theory of continental drift with a modern model of plate tectonics, historical biogeography was transformed by Nelson, Platnick and Rosen's synthesis of Hennig's phylogenetics and Croizat's panbiogeography into cladistic (originally called vicariance) biogeography. Cladistic biogeography was elegant in its simplicity. Historical biogeography now had one fundamental goal – to reconstruct the sequence of events on a dynamic earth that would have passively isolated co-distributed groups of ancestral species, resulting in subsequent allopatric speciation and biotic diversification.

Interestingly, the late twentieth century rift between ecological and historical biogeographers appears to have been motivated more by methodological limitations than a conceptual myopia. As summarized by Funk

(2004), Gareth Nelson never believed that all patterns were the result of vicariance, only that vicariance was the clearest mechanism for producing general, testable, patterns – dispersal became noise and individual taxon histories became uninteresting. Nor did MacArthur and Wilson dismiss *in situ* speciation on islands. Where speciation likely took on more importance in remote island archipelagoes, they suggested that intra-archipelago species exchange could be modelled as a dynamic equilibrium (Whittaker, 2000). In retrospect, much time, sometimes contentious, was spent arguing over the 'reality' of these models that were never intended to capture the entirety of biogeographic patterns and processes in a system.

As influential as dynamic equilibrium and vicariance have been, there are strong indications that biogeographers are becoming increasingly dissatisfied with the questions and methods utilized within these paradigms, as indicated from an historical biogeographic perspective by Ebach & Humphries's (2003) statement that 'the aims of biogeography...still remain ambiguous'. Should historical biogeography be restricted to discovering a general pattern of vicariant history, or should incongruence also be addressed analytically in order to discover the full range of vicariant and dispersal events that underlay speciation and diversification (cf. chapters by Brooks and by Humphries & Ebach in Lomolino & Heaney, 2004)? Perhaps this state of unrest is unsurprising in that, three decades after cladistic biogeography was introduced as the revolutionary synthesis of Croizat's panbiogeography with Hennig's phylogenetics, Donoghue & Moore (2003) suggest that cladistic biogeography has failed to become a truly productive research programme because its scope has been fatally over-simplified by being restricted to assessing the topological congruence of phylogenetic trees as depicted by general area cladograms. The logic of cladistic biogeography is simple: two taxonomic groups, X and Y are co-distributed across geographic areas A, B, and C. Each group has three species (X1, X2, X3, and Y1, Y2, Y3),

and a phylogenetic analysis shows that X1 and X2 are sister species relative to X3; likewise, Y1 and Y2 are sister species relative to Y3. Now, if X1 and Y1 are distributed in area A, X2 and Y2 in area B, X3 and Y3 in area C, then a general area cladogram can be constructed stating that biotas in areas A and B were more recently split apart through a vicariant event than an earlier event that split C from an ancestral A + B. The problem is that it might be the case that the biogeographic events leading to speciation in groups X and Y actually occurred during entirely different timeframes, turning the biogeographic 'congruence' between X and Y into an example of 'pseudocongruence'.

Recent advances on several fronts may be setting the stage for a rejuvenated historical biogeography. If one can estimate divergence times using molecular phylogenetic data, pseudocongruence might be addressed by introducing an explicit temporal component into an analysis of area relationships. An increasing number of molecular-based phylogenies are demonstrating a surprising level of temporal complexity in the historical assembly of biotas. For example, the analysis of area-relationships among four major Laurasian areas using evergreen plant phylogenies (Donoghue & Moore, 2003) postulates two temporally stratified episodes of North Atlantic and three of Beringian dispersal and vicariance during the Tertiary.

Biogeographers are also discovering a substantial level of spatial complexity. Areas of endemism often share historical affinities with more than one other area leading to reticulate, rather than simple bifurcating area cladograms. The key advance for deciphering highly reticulate area relationships is the approach called primary and secondary Brooks Parsimony Analysis (BPA; chapter by Brooks in Lomolino & Heaney, 2004). This method is designed to reveal unique events such as post-speciation dispersal and peripheral isolates speciation that depart from a general divergence backbone on an area cladogram. These kinds of events could be at least as important as vicariance in the overall history of geographic speciation

and diversification. This emerging new form of Hennig's original phylogenetic biogeography is already showing the promise of becoming a rigorous analytical tool for addressing a temporally and spatially enormous range of biogeographic phenomena, from the deep history of Paleozoic palaeobiogeography (chapter by Lieberman in Lomolino & Heaney, 2004) to the latest Cenozoic realm of phylogeography (chapter by Riddle and Hafner in Lomolino & Heaney, 2004). Soon, an algorithmic implementation of the otherwise rather cumbersome primary and secondary BPA will be available: phylogenetic analysis for comparing trees (PACT, D.R. Brooks, pers. comm.).

Ecological biogeographers have also recently called for new paradigms, observing that 'a dynamic equilibrium between contemporary rates of immigration and extinction, is clearly contradicted by phylogenetic and fossil evidence of a long, pervasive legacy of history on the diversity and composition of most insular lineages' (Brown & Lomolino, 2000). Stated differently, a dynamic equilibrium is only one of several states, including the extremes of stable equilibrium to dynamic non-equilibrium, in which island systems can and do exist (Whittaker, 2000).

Changing paradigms and the advent of new models in biogeography have always tracked closely and depended on prevailing ideas in geology and palaeoclimatology – e.g. the long delay between Wegener's original model of continental drift and the modern model of plate tectonics certainly goes a long way towards explaining the arrested development of historical biogeography. A study reported in this issue (Heaney *et al.*, 2005) demonstrates the irreplaceable value of good geological information for interpreting biogeographic patterns. Using protein electrophoresis data from six species of fruit bats and a rodent, this study suggests that intraspecific population structure within all seven species retains a strong, shared signal of land and habitat configurations in the Philippine archipelago during the late Pleistocene, when most of the current islands were connected into four much larger islands during periods of lowered sea levels. Furthermore, it appears that the degree to which population structure was influenced by open water stretches between Pleistocene islands depends on the ecological traits of the species – those that are specialized to living in closed forests exhibit more structure than those that readily travel across open and disturbed habitats. The signal

derived from the protein data is perhaps not as clear as one might get from analysis of rapidly evolving partitions of mitochondrial and/or nuclear DNA, but certainly this study establishes a good reason to test these results with other types of data.

What makes this study of even greater interest to biogeographers is how it fits into the longer temporal framework of biotic diversification in the Philippine archipelago. All of the islands in their study are true oceanic islands that have never had connections to Southeast Asia, and so any non-volant species now found on them must have arrived by dispersal over water. However, dispersal has not been frequent, as shown by recent molecular studies of rodents (e.g. citations in Heaney *et al.*, 2005). Each of the greater Pleistocene islands has its own monophyletic groups of species derived from a common ancestor sometime during the Pliocene, and with diversification continuing throughout the Pleistocene in concert with cycles of isolation and coalescence of islands within each of the larger Pleistocene islands. Clearly, biotic diversification in this archipelago retains an imprint of geological events as well as Pleistocene climatic cycles, and provides a nice example of relatively recent events developing a broadly similar pattern layered on an older biogeographic structure. These are exactly the sorts of repeated cycles that worry those who believe pseudocongruence might be much more common than is accounted for in modern cladistic biogeography (Donoghue & Moore, 2003).

Increasingly, for biogeographers who have been raised on the more synthetic disciplines of macroecology and phylogeography, on the breadth of questions tractable with molecular data, and on the analytical power of phylogenetics, population genetics, and sophisticated ecological modelling, the dichotomy between an ecological vs. historical biogeography simply does not track the many patterns and processes considered relevant and worthy of our attention. Perhaps an expanding knowledge of the geological and climatic dynamics of earth history, the development of a new generation of analytical methods sophisticated enough to decipher temporal and spatial complexity, and the accessibility of high quality molecular data are now giving us a chance to unify the field of biogeography in ways that would not have been anticipated until now. Ultimately, even more integration of ecological and historical components promise to produce innovative perspectives on topics such as: the historical assembly of ecological communities (Webb *et al.*, 2002); the ecology of generalized

divergence among co-distributed taxa (Donoghue & Moore, 2003); and the ecological response of whole biotas following erosion of barriers between areas of endemism (chapter by Riddle and Hafner in Lomolino & Heaney, 2004). The current revolution should bring an end to the protracted identity crisis by replacing the ecological and historical biogeographies of the twentieth century with an integrated biogeography for the twenty-first century.

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