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FEATURE

Ancient Forests and Peripatetic Primates: Alan de Queiroz's *The Monkey's Voyage*

Nicholas J Matzke

Biogeography is the study of the geographic distribution of species in space and time. Historical biogeography focuses on estimating the evolutionary events that led to observed geographic ranges. The subject *seems* simple enough—the raw data are basically nothing more than records of where and when identified species have been found. On a local scale, and from a straightforward functionalist perspective, biogeography usually "makes sense." Trees with large, soft leaves like bigleaf maples are found in wet areas; oaks with waxy leaves are found in drier areas; noble firs with their slender cone form are found at high elevations with heavy winter snowpacks. These sorts of biogeographical changes can be observed on a day's hike up a mountain ridge in Oregon.

Form fits function, and function plus environment predicts biogeography. This fits commonsense notions of "design," and, if one's view is restricted to a small region, the creationist design argument makes a certain amount of sense.

However, the design perspective breaks down as soon as biogeography is examined at larger scales. First, almost all species have restricted ranges, rather than appearing in any habitat where they would thrive. One example of thousands is the cactus group: cacti species are found in deserts and some other environments throughout North and South America, but they are totally absent from the deserts of Africa and Asia. In many cases, we can be sure that the environments are appropriate, because when humans introduce an exotic species to a new area, it spreads like wildfire. The North American prickly pear cactus, for instance, is a major invasive weed in game parks and rangelands in sub-Saharan Africa.

Second, species are often more closely related (evolutionarily speaking; or taxonomically related, in a pre-Darwinian framework) to species in nearby regions with different habitats, than they are to species in far-away regions with identical habitats. California has different species of poppies that live in the coast, desert, or mountains. In African deserts, aloes often occupy the ecological role that cacti would occupy in the New World, but aloes are more closely related to lilies than to cacti.

These sorts of observations are extremely puzzling from the creationist perspective. During the *Beagle* voyage, the young Darwin, not yet a convinced evolutionist, contemplated the peculiar biota of Australia (for example, most mammals there are marsupials, whereas placental mammals dominate elsewhere), writing in 1836, "An unbeliever in everything beyond his own reason might exclaim, 'Surely two distinct Creators must have been at work'" (quoted in Armstrong 2002). Biogeographical data thus revealed some of the first cracks in the creationist paradigm, starting Darwin on the path towards the conclusion that these general biogeographical patterns are better explained as the natural byproduct of species being produced by descent from other species.

It is not hard to find biogeographical hints from the scientists on the trail of evolution. In the second edition of his *Journal of Researches* (popularly known as *The Voyage of the Beagle*), Darwin writes on the Galápagos: "Most of the organic productions are aboriginal creations, found nowhere else; there is even a difference between the inhabitants of the different islands; yet all show a marked relationship with those of America [...] Hence, both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this earth" (Darwin 1845:377–378)

Wallace, writing from Sarawak, Borneo, in the midst of his exploration of Indonesia, proposed a biogeographical law which is just a hairsbreadth from evolution: "Every species has come into existence coincident both in space and time with a pre-existing closely allied species." Wallace (1855) was cited prominently by Darwin in the *Origin*, and Darwin concludes his chapters on biogeography with "On my theory these several relations throughout time and space are intelligible; for ... the more nearly any two forms are related in blood, the nearer they will generally stand to each other in time and space" (Darwin 1859:410).

The observations of Wallace and Darwin are known to every historical biogeographer, almost by heart, and they still hold up well today. For example, a massive metaanalysis of the biogeography of amphibians, birds, and mammals largely confirmed Wallace's zoogeographic regions (Wallace 1876) and demonstrated a strong correlation between geographic distance between regions and the phylogenetic distance between regional faunas (Holt and others 2013). They are, however, general rules of thumb rather than universal statements. As with every scientific discovery, the answer to one question leads to many new questions, and this is decidedly true in biogeography. The discovery of descent with modification explained the most general and obvious biogeographical patterns described above—the "first order" patterns in biogeography. However, common descent also made a certain biogeographical phenomenon puzzling.

The puzzling phenomenon goes by the technical term "range disjunction." Range disjunctions are cases where the geographical range of a group of closely related species, such as those within a single genus, is split into two or more distant regions, with the species being absent in between. In some cases, it's relatively easy to grasp how this pattern could emerge. Birds with long-distance migrations, for example, or other organisms that have a large dispersal range might come to populate a new area some distance away from the parent population without populating the area in between.

But in other cases, the pattern is much harder to explain. How could species within a single genus come to be on both sides of an ocean, for example? The problem becomes compounded when many groups seem to share the same disjunction. Famous cases include the temperate hardwood forests of eastern North America and eastern China, and the southern beech forests of New Zealand, Tasmania, and the high elevations of eastern Australia, and southern South America. In these cases, you can stand in such a forest and almost think you are in the same forest as on the other side of the Earth. Eastern Asian forests, for example, have maples, beeches, hazelnuts, hickories, oaks, chestnuts, and many of the other tree types familiar to residents of the Eastern United States, though the exact species differ.

Such disjunctions were as obvious in the nineteenth century as they are now, and the major explanations in play today can be traced back to Darwin and his contemporaries. Darwin's position was "dispersalist": he argued that even apparently poor dispersers could sometimes make long journeys by hitching rides on birds, floating vegetation mats, or even icebergs. However, Darwin's close friend and colleague, the botanist Joseph Hooker, was particularly impressed by the commonalities he observed in disjunct floras separated by oceans. His preferred explanation was that disjunct ranges were once connected, and that the contiguous range was broken up by environmental or geological change in intervening regions. In some cases, environmental change is an eminently plausible explanation. For example, the disjunction of Northern Hemisphere temperate forests is basically explained by the fact that during most of the Cenozoic the climate was warmer than it is now. Temperate forests could live in what is now the tundra of Alaska and Siberia, so the forests formed a continuous band from North America to Asia. As the climate cooled, the temperate forests were forced south and became disjunct.

Accounting for the Southern Hemisphere's temperate forests is not so simple, however, for there is no mostly land route from Australia to South America. Geologists of the nineteenth century were ignorant of plate tectonics, but they had abundant evidence that land sometimes rose or sunk with respect to sea level. Hooker and colleagues used this idea to postulate "land bridges" connecting continents across oceans to explain disjunct distributions. This idea is not without validity—one good extant example is the Panamanian Isthmus, the narrow strip of land that connects North and South America. But the invention of land bridges became a minor cottage industry, sometimes postulated based on nothing more than biogeography in the absence of any support from geology or the terrain of the ocean floor. Darwin, rather famously, got frustrated with the looseness of it all, telling Hooker in a letter from 1856 that land bridges were being invented "as easily as a cook [makes] pancakes" (Darwin 1887:74).

The easy invocation of land bridges was always pretty woolly but the concept was transformed by Alfred Wegener's (1920) continental drift theory. He replaced many of the postulated land bridges with hypotheses about shifting landmasses. The dispersal-versus-land bridge debate was thought to be resolved with the acceptance of plate tectonics in the 1950s and 1960s. The southern continents were indeed connected, when they were part of the supercontinent Gondwanaland. The idea that disjunctions in geographic range could be explained by the formation of barriers (due to separation of the continents, environmental change, or other causes) came to be called "vicariance."

The plate tectonics revolution in geology coincided with the cladistics revolution in taxonomy. In traditional taxonomy, classification of species into higher taxa had been based on rather subjective concepts of overall similarity, perception of morphological gaps between groups, hypotheses about complex concepts like "adaptive zones," and selection of organismal characters that the systematist considered "significant." Hypotheses about the evolutionary history of species also sometimes played a role, but often not a primary role, and in any event there was little clarity about how phylogenetic hypotheses should be tested, or how, if at all, they should be related to Linnaean taxonomy. Cladistics changed all this by making the estimation of the phylogenetic relationships the primary question, and by proposing a replicable method for doing so: essentially, use as many independent homologous characters as possible, weight them equally, and take the tree that explains these character data with as few transformations as possible as the best hypothesis. These basic principles became widely accepted.

These twin revolutions of plate tectonics and cladistics had a profound influence on the dispersal-vicariance debate in biogeography. The "old guard" in historical biogeography had accepted the geological conventional wisdom on the fixity of the continents, had been similarly skeptical of most land bridge proposals, and had thus of necessity been dispersalists. This logic was, at least apparently, overthrown if the continents were not fixed. Younger biogeographers also attacked dispersalism on the grounds that it could not explain congruent biogeographical disjunctions between unrelated groups, arguing that such patterns were better explained by vicariance, when geological or other processes formed a barrier in the middle of an originally contiguous ecosystem. A final argument reinforced the others in asserting that the rare, long-distance dispersal events, favored in so many cases by the dispersalists, are wildly unlikely. Sure, coincidences of weather and luck and millions of years could be dreamed up to get monkeys rafting across the Atlantic (for instance), but this was little better than invocation of miracles to explain distributions. Vicariance biogeographers claimed that any observations could be explained by such creative speculations. Long-distance dispersal was unfalsifiable and therefore, apparently, vicariance should be the preferred explanation of disjunct distributions.

The advocates of vicariance biogeography were aggressive and prolific, and furthermore, they had quantitative methods—cladistics applied to biogeography—when little else in the way of quantitative methods was available. As a result, it is fair to say that vicariance biogeography became the new conventional wisdom in the 1980s and 1990s, at least as judged by what books one would find on the historical biogeography shelf in a university library, and what was taught in textbooks and courses about historical biogeography.

Here we reach the entry point for Alan de Queiroz. De Queiroz got his PhD in evolutionary biology during the heyday of vicariance biogeography, but in 2005 he wrote an influential review article for *Trends in Ecology and Evolution*, "The resurrection of oceanic dispersal in historical biogeography," which detailed many published cases where it appeared that clades were too young for their distributions to be explained by the breakup of continents. Basically, the big breakups of continental plates occurred mostly before the Cenozoic, but dating studies indicate that most of the divergence times recorded in the phylogenies of living genera and families occurred within the Cenozoic. These findings have become even more common since 2005, such that studies disconfirming (transoceanic) vicariance hypotheses are now the norm, and studies confirming them (which exist; see for example Wood and others 2013) appear to be the rare exceptions.

In *The Monkey's Voyage*, de Queiroz argues that long-distance dispersal is a crucial process in biogeography, and that vicariance biogeography, "while taking advantage of cladistics and incorporating continental drift, also made a turn down an intellectual cul-de-sac" (2014:76). I agree that it is well past time for the field of biogeography to abandon the use of vicariance as the default explanation, as well as the methods that rely on this assumption. However, much as the baby Hercules strangled attacking snakes in the crib, vicariance biogeography was born in battle against traditional systematics and dispersalist biogeography, and it is not going down without a fight (for example, Grehan and Schwartz 2009; Heads 2012).

The Monkey's Voyage is a fascinating tour of the science behind the dispersal/vicariance debate, and an even more fascinating tour of the scientists involved in the debate, particularly when it explores why vicariance biogeography proponents seem so resistant to letting it go. De Queiroz makes the most of an almost unique combination of interests and abilities. He is a trained, published researcher in phylogenetics and historical biogeography. This means he is familiar with the modern methods of phylogenetics and divergence-time estimation. However, unlike most of us phylogeneticists, who would soon bury the reader in the details of the subject when attempting a popular account, de Queiroz has a knack for boiling the subject down to essentials, and thus gives the best introduction to these complex methods that I have seen written for the general public.

Phylogenies, ubiquitous in modern evolutionary biology, are often missing in most science journalism and popular science books on evolution. This is not the case in de Queiroz's book. He shows the reader some of the trees and dates, the bread and butter of the modern research. Furthermore, de Queiroz reviews in a quite nuanced way the common difficulties with molecular clock dating studies, which are well known in the field, and successfully balances this with a careful explication of why the admitted difficulties are not enough to overturn the common conclusions of dating studies: that many groups are much too young to be explained by ancient vicariance events, particularly those attributed to the breakup of the continents. Solely on this basis, *The Monkey's Voyage* can be recommended strongly for students with scientific aptitude who are thinking of careers in evolutionary biology but want to get a sense of how the field works on the inside.

Another advantage de Queiroz has is a deep grasp of the history of historical biogeography. I studied this topic for my PhD, and I still learned a great deal about the key people and how they thought about the issues—Croizat, Hennig, Brundin, Briggs, Nelson, Platnick, Cracraft, Donoghue, Heads, and so on. Partly this comes from de Queiroz having read the key papers, and partly from having done interviews in person or by e-mail with the researchers themselves, most of whom are still alive (and, usually, still kicking!).

De Queiroz's advocacy of the dispersalist position, and his frustration with the vicariance biogeography holdouts, is forthrightly presented—a major asset of the book. The topic might seem like just another obscure, dry bit of academic minutia if presented in a neutral, nonpartisan fashion, but de Queiroz is a partisan in the fight, as well as a scientist, historian, and journalist. The science is punctuated with colorful assessments of the scientists and their psychology. For example, de Queiroz says that early vicariance biogeography resembled "an unruly cult, an intellectual gang, complete with passwords ('synapomorphy,' 'area cladogram,' 'component analysis'), a deity (Hennig), and gang leaders (Nelson chief among them)" (2014:71). Speaking of the modern vicariance biogeographer extraordinaire Michael Heads, de Queiroz calls him a "panbiogeographic fundamentalist" (2014: 89), although I'm not sure fundamentalists of the more traditional sort would have him.

De Queiroz takes up the suggestion by Nelson and Platnick in *Systematics and Biogeography* (1981) that, if, hypothetically, the branching order of the great ape phylogenetic tree matched the breakup order of the continents, then we should consider the possibility that *Homo sapiens* extended back into the age of dinosaurs, all other evidence (fossils, DNA, species lifetimes, and so on) be damned. De Queiroz rightly finds this astonishing, and, for lack of any better explanation, suggests at first that the writers "were on some kind of 'vicariance high' and had a temporary loss of perspective" (2014:90). He missed the obvious wisecrack—"Worst. High. Ever." But de Queiroz did e-mail Nelson and ask directly if he was really serious. Nelson answered with one word: "Yep." Whether with the terseness of Nelson or the laid-back casualness of Michael Donoghue, the quotes from the key participants scattered throughout the book bring the debate to life.

In addition to the phylogenetics and history, de Queiroz makes his case for dispersalism in another way. The end of each chapter contains a short anecdote documenting a case where long-distance dispersal was actually observed by modern eyewitnesses. Cases include elephants swimming to distant islands, African locusts showing up in the Caribbean, and vegetation rafts, complete with living animals, being found far out at sea. These kinds of observations hark back to Darwin, and they serve to emphasize one of Darwin's main points—naive intuitions about long-distance dispersal events being improbable might be accurate from the point of view of a single human observer in a particular place, but on a roiling globe covered in reproducing organisms, the improbable is happening all the time, and over geological time, some of these events will result in successful colonization.

In the penultimate chapter of *The Monkey's Voyage*, "The structure of biogeographical revolutions," de Queiroz asks whether or not the burgeoning popularity of vicariance biogeography represents a paradigm shift. He concludes that it doesn't, as dispersalism always retained adherents. De Queiroz suggests that historical biogeography is really still in Kuhn's "pre-paradigm" state, as fundamental debates are still going on about what the most important biogeographical processes are, and what methods should be used to infer biogeographical history. He suggests that the addition of divergence-time estimation to historical biogeography constitutes an important step towards a biogeographical paradigm.

In the final chapter, de Queiroz gives a stirring, imaginative vision of what biology and evolutionary history look like when interpreted through a lens emphasizing long-distance dispersal. His vision deliberately provides an alternative to the imaginative vision that undergirds vicariance biogeography— namely, that by looking at the pattern of continental breakups, we have the key to understanding biogeography. The vicariance view is still ubiquitous in the displays and exhibits of zoos and museums, and is particularly popular in countries like New Zealand that relish their Gondwanaland heritage, where park signs invite visitors to consider that they are standing in ancient forests much like those that existed when dinosaurs walked the Earth. If the pendulum is shifting back towards dispersal, as seems clear, then de Queiroz's imaginative work is sorely needed, although I think it will be quite some time before the park signs start telling stories of transoceanic voyagers.

De Queiroz's work is a masterpiece of science writing, a rare case where a book serves both the public and the technical community simultaneously. My criticisms are relatively minor. I think de Queiroz's focus on Kuhnian analysis, paradigms, and imaginative stories, is, rather like disco and vicariance biogeography—a little bit too 1970s. Modern evolutionary biology is driven more by advances in methods and data than by explanatory paradigms and their shifts. Beyond the really big paradigms—common ancestry, natural selection explaining adaptation, and so on—much of the rest is a matter of details and percentages. Does morphology change during or between speciation events? What traits influence speciation and extinction rates? These sorts of questions do not appear to have simple, universal answers to discover. Instead, we want to *estimate* these parameters from the data, and measure how these parameters change from clade to clade and region to region. The classic "dispersal or vicariance" debate should be addressed the same way; I have taken a first stab at this in my own research, and de Queiroz might be pleased to learn that I found that long-distance dispersal is usually a crucial explanatory variable (Matzke 2014).

However, no matter how much technical methods advance, there will always be a need for synthetic works that review important issues in science for nonspecialist readers both inside and outside the professional science community. De Queiroz succeeds spectacularly, and I expect his book will serve as a key introduction for the next generation of biogeography students and biogeography fans.

References

Armstrong P. 2002. Antlions: A link between Charles Darwin and an early Suffolk naturalist. *Transactions of the Suffolk Natural History Society* 38:81–86. Available from: http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=A339&viewtype=text.

Darwin CR. 1845. *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of HMS* Beagle *Round the World, under the Command of Capt Fitz Roy, RN,* 2nd edition. London: John Murray.

Darwin CR. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Darwin F, editor. 1887. *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter*, vol 2. London: John Murray.

de Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution* 20(2):68–73.

de Queiroz A. 2014. *The Monkey's Voyage: How Improbable Journeys Shaped the History of Life*. New York: Basic Books.

Grehan JR, Schwartz JH. 2009. Evolution of the second orangutan: Phylogeny and biogeography of hominid origins. *Journal of Biogeography* 36:1823–1844.

Head M. 2012. *Molecular Panbiogeography of the Tropics*. Berkeley (CA): University of California Press.

Holt BG, Lessard J-P, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre P-H, Graham CH, Graves GR, Jønsson KA, and others. 2013. An update of Wallace's zoogeographic regions of the world. *Science* 339(6115):74–78.

Matzke NJ. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63(6):951–970.

Nelson G, Platnick NI. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. New York: Columbia University Press.

Wallace AR. 1855. On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology* 16:(September):184–196.

Wallace AR. 1876. *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface.* London: Macmillan.

Wegener A. 1920. *Die Entstehung der Kontinente und Ozeane*. Braunschweig, Germany: Friedrich Vieweg & Sohn.

Wood HM, Matzke NJ, Gillespie RG, Griswold CE. 2013. Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the Palpimanoidea spiders. *Systematic Biology* 62(2):264–284.

About the author

Nicholas J Matzke is a Postdoctoral Fellow in Mathematical Biology at the National Institute for Mathematical and Biological Synthesis (NIMBioS). He worked at NCSE from 2004 to 2007, assisting the legal team for the plaintiffs throughout the *Kitzmiller v Dover* case.

Author's address

Nicholas J Matzke
National Institute for Mathematical and Biological Synthesis
Claxton Bldg #110B
1122 Volunteer Blvd, Suite 106
University of Tennessee
Knoxville TN 37996-3410
matzke@nimbios.org