

Biogeography Off the Tracks

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We write to convey our concerns that some mainstream evolutionary journals continue to publish articles that, in our view, present misleading accounts of biological evolution. Specifically, we argue that “panbiogeographic” studies of spatiotemporal biological history (e.g., [Craw 1988](#); [Heads 2010a, 2010b, 2011, 2012a, 2012b](#)) are detrimental to the progress of biogeography as a discipline. The panbiogeographic approach usually ignores long-distance dispersal and considers alternative hypotheses only within the narrow confines of assumed ancient vicariance. Although previous commentators have already penned epitaphs for the panbiogeographic paradigm (e.g., [Cox 1998](#); [McDowall 2004](#); [McGlone 2005](#); [Briggs 2007](#)), some editorial and review processes continue to allow this misleading approach to be promulgated as a useful scientific method. Despite the approach being termed “moribund” ([Briggs 2007](#)), recent years have seen an apparent upswing in the number of panbiogeographic studies published (e.g., [Kutschker and Morrone 2012](#); [Mercado-Salas et al. 2012](#); [Silva et al. 2012](#)).

Panbiogeography represents a worldview of biology seemingly fixated on ancient earth history and evaluates alternative biological hypotheses only within the limited confines of assumed ancient vicariance. The lack of scope for considering alternative hypotheses makes panbiogeography of dubious utility, especially relative to the far more developed biogeographic methods that are increasingly available (see [Crisp et al. 2011](#)). As presented in recent studies, the panbiogeographic approach involves little more than mapping species distributions and drawing lines (tracks) connecting them. As early as 1989, when the approach was being developed by New York and New Zealand systematists ([Briggs 2007](#)), there were calls for panbiogeography to become more quantitative ([Craw 1989](#); [Page 1989](#)), but the approach has remained broadly qualitative and lacking in reproducibility ([Cox 1998](#)) (although we note a recent attempt by [Echeverría-Londoño and Miranda-Esquivel 2011](#) to systematize the approach).

The methods of panbiogeography and their shortcomings are best illustrated with an example, for which we use ratite birds (Fig. 1). Using a map of current distributions, the following features are drawn: “tracks,” which connect all distribution features to form a minimal spanning tree; “nodes,” which are intersection points of tracks; “main massings,” which identify more diverse regions of the distribution; and “baselines,” which represent major landscape features traversed by tracks. First, as a general criticism, the meaning of a track is ill defined. Specifically, [Craw et al. \(1999\)](#) (p. 20) state that tracks “... give shape or expression to the space and time that necessarily intervenes between disjunct localities,” a hazy description underpinning a mysterious approach. If tracks are meant to indicate paths of dispersal or vicariant events, there is also no apparent reason why they should take the minimal distance (although indeed they are rarely depicted as great circle distances). Second, it is not always clear how the tracks are arrived at. Although they purport to be minimal spanning acyclic graphs, the specific tracks drawn are sometimes not the shortest available, but are seemingly swayed by locations of main massings within distributions. For example, it is not clear why Australasian ratites are linked by a track through an Indian Ocean baseline, rather than by a track from China to Papua New Guinea to create a shorter network (Fig. 1a). Third, the main massings are said to represent: “the greatest concentration of biological diversity ...,” including taxonomic, genetic, phenotypic, or behavioral characteristics ([Craw et al. 1999](#); p. 21), but it is unclear how this diversity is objectively quantified. Fourth, track analysis and ancient vicariant scenarios are often discordant with respect to phylogenetic reconstructions (e.g., track analysis suggests a closer relationship of moa and kiwi [Fig. 1a], yet moa is more closely related to rhea [Fig. 1b]). Fifth, as with many methods, accumulating fossil data (e.g., new Montana record; Fig. 1a) and consideration of extinction events (which will be common over geological timeframes; [van](#)

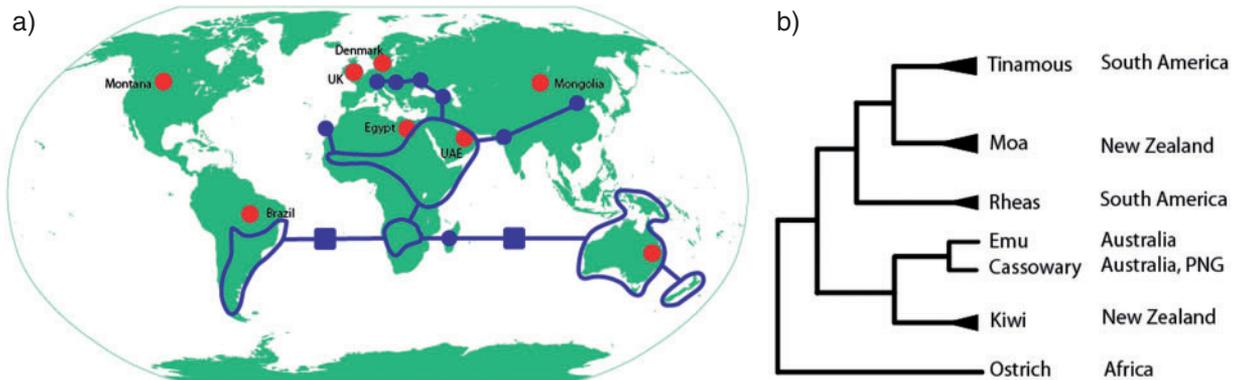


FIGURE 1. Panbiogeographic studies routinely assume that ancient tectonic processes explain modern biological distributions. a) Blue lines show a panbiogeographic analysis of ratite birds (flightless members of superorder Palaeognathae; redrawn from [Craw et al. 1999](#)), with “tracks” (straight lines connecting distributional records) supposedly representing ancient tectonically mediated fragmentations of an ancestral taxon, blue squares representing “baselines,” and blue circles representing fossil localities included by [Craw et al. \(1999\)](#). In contrast, recent palaeognath fossil discoveries (red circles) indicate a broader biogeographic history, indicating the past presence of this group from many additional regions of the globe ([Houde and Olson 1981](#); [Houde 1986](#); [Houde and Haubold 1987](#); [Leonard et al. 2005](#); [Bibi et al. 2006](#)). b) A well-resolved total evidence molecular phylogeny of Palaeognathae ([Smith et al. 2012](#)) reveals evolutionary relationships incompatible with [Craw et al.’s \(1999\)](#) panbiogeographic tracks (e.g., the nonsister relationship of kiwi and moa).

[Valen 1973](#)) have the potential to change the network substantially.

Earth and life, so the story goes, evolve together ([Croizat 1964](#)), so the possibility of long-distance biological dispersal and establishment is typically discounted or discarded at the outset of the panbiogeographic exercise. [Croizat et al. \(1974\)](#), for instance, explicitly reject “dispersal of species, as a conceptual model of general applicability in historical biogeography.” Although the assumptions of panbiogeography often allow for some “normal” local dispersal ([Craw et al. 1999](#); [Crisci 2001](#); [Grehan and Schwartz 2009](#)), we have yet to see an empirical panbiogeographic study that argues for anything other than the primacy of some ancient vicariant process to explain distributional data. Unfortunately, this a priori rejection of long-distance dispersal as an explanation for multitaxon biogeographic pattern ignores abundant evidence supporting this important process (e.g., [Muñoz et al. 2004](#); [Renner 2004](#); [de Queiroz 2005](#); [Lomolino et al. 2005](#); [Warren et al. 2009](#); [Ali and Huber 2010](#); [Gillespie et al. 2012](#); [Samonds et al. 2012](#)). Indeed, recent analyses suggest that such dispersal may well be a common and repeated process, mediated by predictable phenomena such as ocean currents, storms, and prevailing winds ([Gillespie et al. 2012](#)).

We suggest that, for any rigorous scientific approach, the proof of the pudding is in the eating: that is, that results should wherever possible be validated by independent data. In contrast, panbiogeographers have proposed scenarios that seemingly dismiss all other data regarding the history of life on earth. For example, [Grehan and Schwartz \(2009\)](#) reject the wealth of molecular evidence supporting a human–chimpanzee clade, instead proposing a human–orangutan sister relationship that better satisfies assumptions of vicariance. Furthermore, [Heads \(2010a\)](#)

invokes an early Jurassic origin for primates, around 100 million years before this clade is generally accepted to have evolved (as based on congruent fossil and molecular data; [Goswami and Upchurch 2010](#)). A similarly discordant age is implied by [Heads \(2011\)](#) for the Asteraceae (see [Swenson et al. 2012](#)). Additionally, panbiogeographers routinely scorn the role of long-distance dispersal in assembling oceanic island biotas ([Heads 2010b, 2011, 2012a](#)), instead invoking continental land bridges and island arcs of little or no geological credibility (see critique by [O’Grady et al. 2012](#)). Such extraordinary claims surely demand extraordinary evidence, but these ideas seem to be derived simply by assuming vicariance and ignoring dispersal. When panbiogeographic hypotheses of ancient vicariance conflict with data from geology, palaeontology, and molecular genetics (as they almost inevitably do), panbiogeographers tend to dismiss these other information sources as unreliable. In our view, this attitude is akin to a young-earth creationist insisting that the world was created in 4004 BC, regardless of what geological dating, biogeography, genetics, or palaeontology might independently indicate. We note that a near-exclusive focus on vicariance and dismissal of evidence supporting alternative explanations are not unique to proponents of panbiogeography: such views are also shared by several cladistic biogeographers ([Ebach and Tangney 2007](#)).

Application of the panbiogeographic approach to the Chatham Islands biota led to claims that ancient tectonic evolutionary processes stretching back over 100 Ma explained its apparently composite nature with respect to the distribution of relatives on different parts of the New Zealand mainland ([Craw 1988](#)). Subsequent geological and palaeontological analyses, however, clearly show that the islands themselves were completely submerged until less than 10 Ma

(Campbell 2008; Heenan et al. 2010). Corroborating these geological findings, molecular data from numerous species independently indicate that biotic relationships between the Chathams and mainland New Zealand are far too young for the panbiogeographic conclusions to be considered plausible (Paterson et al. 2006; Goldberg et al. 2008; Wallis and Trewick 2009; Heenan et al. 2010; Goldberg and Trewick 2011). For example, the oldest estimated divergence of contemporary Chathams and mainland sister taxa known to date is 14 Ma for the Chatham Island forget-me-not (*Myositidium hortensium*), whereas most other Chathams–mainland species divergences appear <3 Ma (Heenan et al. 2010). Overall, multiple independent lines of evidence clearly indicate that the modern Chathams biota was established by transoceanic dispersal, and not by ancient vicariance.

Practitioners of the panbiogeographic approach routinely deny the utility of molecular-clock dating, presumably because molecular date estimates are usually much younger than those expected under vicariance (e.g., Wallis and Trewick 2009). Molecular clocks (Zuckerandl and Pauling 1962; Sarich and Wilson 1967) and their imperfections (Langley and Fitch 1974; Donoghue and Smith 2003) have been known for many years and are mainstream to our understanding of evolution (Penny et al. 1982; Graur and Li 2000; Nei and Kumar 2000). Rather than throwing the baby out with the bathwater, molecular evolutionists test each particular data set for clock-like substitution accumulation and strive to apply the most appropriate models (Felsenstein 2004). Numerous molecular phylogenetic studies have demonstrated a correlation, albeit imperfect, between geological time and molecular evolutionary change (Knowlton et al. 1993; Fleischer et al. 1998; Bromham and Penny 2003; Burridge et al. 2008; Ho et al. 2011). At the same time, molecular genetic dating methods are continually being improved and refined, allowing for several calibration points, and including confidence intervals on calibrations (e.g., Near et al. 2005; Meredith et al. 2011; Heath 2012). In this way, new methods are providing increasingly detailed tests of evolutionary hypotheses, relationships, and timeframes.

We have no doubt that vicariance is an important driver of evolution in some regions and systems and that geological processes often play a major role in structuring biodiversity (Avice 2000; Wallis and Trewick 2009). However, there is also clear evidence that many spatial biodiversity patterns are underpinned by climatic, ecological, and density-dependent factors (Avice 2000; Lomolino et al. 2005; Waters et al. 2013). Unfortunately, panbiogeographers appear arbitrarily to favor ancient geological events over the many more recently superimposed geological, climatic, and ecological events, processes that often continue to the present. Although the geological record retains little or no preserved evidence of topographic features in 200-million-year-old orogens, there remains abundant visible evidence of topographic barriers in young mountain belts. Regardless, panbiogeographers

apparently ignore the latter events, along with numerous intervening geological processes. For example, young (<5 Ma) geologically and glacially mediated vicariance events have induced diversification in numerous New Zealand taxa (Trewick and Wallis 2001; Waters et al. 2001; Wallis and Trewick 2009; McCulloch et al. 2010), and rates of genetic divergence have been quantified in internally consistent analyses that are also consistent with fossil evidence (Burridge et al. 2008, 2012). By contrast, panbiogeographic studies routinely attribute such biological radiations to ancient (>20 Ma) geological processes (e.g., Heads and Craw 2004; Heads 1998; Heads 2012b, Figs. 5 and 6), but without the quantitative evidence needed to discount younger processes.

In summary, we contend that—as it stands—panbiogeography is not a useful approach for evolutionary biology. Although there should be no need to defend mainstream evolutionary biology against a simple approach for plotting species distributions, we are concerned that evolutionary journals, perhaps in the interest of apparent fair play, might inadvertently offer tacit support for an approach that is biased and misleading. Over the past 2 years, at least 24 articles published in 21 different journals (including *Journal of Biogeography*, *Systematic Entomology*, and *PLoS One*) have implemented panbiogeographic approaches to the study of species distributions. (A search of Web of Knowledge on 10 December 2012 using the search-string “panbio*” in the subject field for the time period 2011–2012 returned a list of 61 items, from which we removed items off the topic, book reviews, books, and book chapters.) We note, too, that our concerns do not only represent arguments among evolutionary theorists but also they have practical implications. Panbiogeographers are, for example, arguing for conservation decisions to be made using their approach (Grehan 1988; Arzamendia and Giraudo 2012; Maltchik et al. 2012). Conservation science should, of course, be informed by total evidence, rather than by biased approaches that reject dispersal a priori. Although panbiogeography might well have seemed an attractive notion several decades ago (Croizat 1964; Craw 1988), continued (postmodern) acceptance of this paradigm simply ignores the subsequent decades of scientific progress in evolutionary theory, molecular genetics, computational biology, and geology.

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