Hypothesis testing in biogeography

Michael D. Crisp[1], Steven A. Trewick[2] and Lyn G. Cook[3]

[1] Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia
[2] Institute of Natural Resources, Massey University, Palmerston North, New Zealand
[3] The University of Queensland, School of Biological Sciences, Brisbane, Qld 4072, Australia

Often, biogeography is applied only as a narrative addition to phylogenetic studies and lacks scientific rigour. However, if research questions are framed as hypothe-

Box 1. The pattern-first and hypothesis-testing approaches can lead to different conclusions

A common question in biogeography asks 'what is the geographical origin of taxon A?' Recent examples include Nilsson *et al.* [65] in respect of marsupials and Brown *et al.* [48] in respect of *Rhododendron* sect. *Vireya*. Here, we illustrate two different approaches to formulating and testing biogeographical hypotheses, using the Southern Hemisphere Callitroid clade of the cypress family (Cupressaceae) as a hypothetical example. Each approach results in a different interpretation of the biogeographical history.

The first is a 'pattern before process' approach (Figure Ia), in which the distributions of extant taxa are mapped at the tips of a phylogeny and ancestral areas are reconstructed at internal nodes using any of several methods [14]. Here, both parsimony (mapped in Figure Ia) and maximum likelihood infer that the common ancestor of the Callitroid clade probably originated in Australia and that its descendants subsequently dispersed to New Zealand (green), New Caledonia (red, twice), Patagonia (purple, three times) and South Africa (yellow).

ancestral areas are reconstructed at internal nodes of the phylogeny; for example, using ancestral area reconstruction (AAR) methods (reviewed in [14,15]), which are sometimes combined with relaxed molecular-clock dating of nodes (

no (or minimal) gene flow, the separated (allopatric) populations evolve independently and, ultimately, speciate.

Tests of vicariance

If the pattern and timing of the origin of potential vicariance events are known from geological data, vicariance hypotheses are testable because they make several predictions (Table S1 in Supplementary Material Online). The advent of molecular dating has led to the ability to test the timing of divergences and thus test hypotheses of vicariance (Box 2). Surprisingly, most transoceanic plant disjunctions [8] and many of those in animal taxa [26,32,33] have been determined to be asynchronous or too young to be fully explained by the break up of Gondwana. This applies even in the case of iconic taxa, such as *N* [34] and kauri pines (*A*) [35] in New Zealand, ostriches in Africa [36] and primates and rodents in South America [37].

Importantly, divergences can be too old to have been caused by a particular geological event [26,31]: the prediction of timing requires a two-tailed test (Box 2). By this criterion, many of the cases of species-poor lineages that are presented as evidence of long-term occupancy resulting from vicariance, for example, tuatara in New Zealand and *A* in New Caledonia, fail the test of a vicariance explanation [26].

Box 2. Tests of vicariance are two-tailed

Divergence times in molecular phylogenies can be used to test hypotheses of vicariance [27]. Vicariance hypotheses predict that the divergence time between taxa on either side of a barrier should coincide with the timing of the origin of that barrier. The test is two tailed. Vicariance is rejected if the divergence between the taxa is too young (post-dates the origin of the barrier) or too old (pre-dates origin of barrier) and, thus, the barrier could not have caused the divergence (Figure I

Another important prediction from a hypothesis of vicariance is that multiple lineages will probably be affected by the origin of the putative barrier [7,29]. Thus, a further prediction is that there should be divergences in multiple taxa either side of that barrier dating to that time [7,38,39]. For example, alternative vicariance hypotheses have been proposed for the middle of the Baja Peninsula, California, putatively owing to either climate change during the Pleistocene or marine incursion during the late Miocene–early Pliocene [38]. These were tested for coincident divergence times across the barrier in multiple animal and plant taxa, with some support found for vicariance at the earlier time in nine taxa [40].

Are hypotheses of dispersal testable?

Commonly, dispersal is inferred as the default explanation of a biogeographical disjunction following rejection of a vicariance hypothesis, for example by molecular dating. Therefore, it is important that LDDE hypotheses should be testable using independent evidence. Despite claims that hypotheses of dispersal are not testable [13], careful framing of hypotheses enables some to be tested. As illustrated by the following examples, ecology has an increasing role in testing dispersal hypotheses in historical biogeography.

Example 1. Model-fitting approaches can be used to test dispersal-based hypotheses. For example, Sanmartín . [20] used parsimony-based tree fitting to test the prediction [19,41,42] that atmospheric and oceanic West Wind Drift should cause an easterly bias in plant dispersals in the Southern Hemisphere. Inferred LDDE events in 23 phylogenies were significantly asymmetrical in the predicted direction, rejecting the null hypothesis of equal rates of inferred dispersal in both directions, as determined from randomizations.

Example 2. Stepping-stone dispersal routes have often been inferred to explain what, for some, might be seemingly impossible LDDE events across extreme barriers. This approach has been especially adopted for terrestrial taxa that are disjunct across oceans, such as between Australia, New Zealand and New Caledonia [43,44], Antarctica and Africa via the Kerguelen Plateau [36] and between Africa and Madagascar [32]. However, stepping-stone routes might be even more problematic than a single jump across a wider gap, because a stepping-stone hypothesis assumes that an intermediate, reproducing population was large enough and existed long enough to produce a ‘propagule (or migrant) pressure’ [30] sufficient to colonize the next landmass along the chain. For example, it has been suggested that a single extreme LDDE event could be more probable than multiple shorter LDDE (stepping-stone model) events. Long-distance seed ‘dispersal kernels’ (i.e. probability distributions of LDDE) appear to be ‘fat tailed’ [45,46]; that is, extreme LDDE is not much less probable than LDDE over much shorter distances. This is partly because of stochasticity and partly because of infrequent atypical processes (e.g. cyclones and tsunamis) [45]. Given that probabilities multiply in a chain of independent events, a single, long LDDE is likely to be more probable than are multiple, shorter steps. Using the hypothetical dispersal kernel of Nathan ([45]: Figure 2, corrected version, published 17 October 2006), the probability of a single seed arrival over 500 km is $P = 10^{-16}$ and that of a single tend to invite speculation about their origins and biogeography. Examples include *G*[illegible] in China, tuatara and *A*[illegible] in New Zealand, and the endemic shrub *A*[illegible] in New Caledonia. However, extant taxa indicate persistence in time only, not in space (Box 3, Figure Id), and

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