



Digest: Hypothesis testing in biogeography using phylogenetic trees*

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How can we test whether biogeographic dispersal rates coincide with geologic events? Hua and Bromham developed a model-based approach to generate a null distribution of colonization times under constant dispersal rates, overcoming a problem related to the geometry of phylogenetic trees.

Take any place on Earth. How did the flora and fauna of that place get there? The answer is a combination of dispersal from other places and in situ speciation (Wiens and Donoghue 2004). Knowing when a region's fauna was assembled can help us understand what geologic events may have played a role in their arrival. For example, we may wish to know whether the closure of the Tethys Ocean of Europe induced a mass migration of coral reef fishes to the present-day Coral Triangle hotspot (Renema et al. 2008). One approach is to perform an ancestral reconstruction of geographic ranges on a time-calibrated molecular phylogeny of fishes, and then count the number of transitions from the Atlantic to the Indo-Pacific that occurred during the purported window of the Tethys closure.

An outstanding problem with this approach concerns the geometry of phylogenetic trees. As there are more branches near the tips of the trees, we expect more colonization events to be reconstructed toward the present by chance. How can we distinguish this pattern from a biologically meaningful result? In this issue, Hua and Bromham (2020) developed a general and flexible solution to this problem. This approach uses a biogeographic model (such as GeoSSE; Goldberg et al. 2011) to generate a null distribution of colonization times expected if colonization rates were constant over time. The observed distribution can then be statistically compared to this null distribution. This is analogous to detecting departures from a constant-rate birth–death model, as

if speciation peaked in the past. Hua and Bromham (2020) apply this approach to show that dispersal of squamates to Madagascar was most frequent during the Early Cenozoic, coincident with the formation of an oceanic current away from Africa.

This technique is well suited to questions about the origins of a single assemblage (such as Indo-Pacific fishes or Malagasy squamates). Their approach can be used with the GeoSSE model (Goldberg et al. 2011), so it can accommodate the effect of diversification-rate differences among regions on the inferred ancestral states (Maddison et al. 2007). Alternatively, it can be used with the DAISE model (Valente et al. 2015), so it can account for density dependence in diversification rate and dispersal rate. Importantly, their approach will work well for assemblages where the constituent species are distantly related, as is often the case. If one tallies all the bird species in their city, they will find representatives from different families. A well-sampled phylogeny spanning all bird families is within reach (Jetz et al. 2012) and may be needed to detect branches representing new dispersal events from the regional species pool.

It is up to the investigator to discern if this approach is suitable for their clade or biogeographic question. For example, if all the members of a region are descended from a single colonization event, then there will only be one observation of colonization to compare against the null distribution. A phylogenetic hypothesis for both the members of the assemblage and regional species pool is needed, which may be unavailable for some clades. Finally, it may be tricky to compare results for multiple regions. For example, do colonizations of the Indo-Pacific tend to be older than those to the East Pacific? The solution to test this hypothesis could be to add a third geographic state to the GeoSSE model.

*This article corresponds to Hua, X., and L. Bromham. 2020. Modelling colonization rates over time: Generating null models and testing model adequacy in phylogenetic analyses of species assemblages. *Evolution*. <https://doi.org/10.1111/evo.14086>.

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