

The timing of speciation events in a phylogenetic tree provides insight into key evolutionary processes like speciation and extinction. Was there a mass extinction (and when)? Are rates of speciation correlated with a particular biological trait (a key innovation) or geographic area (a cradle of diversity)? Does the rate of speciation in a clade depend on the number of species? Such questions concern a process called lineage diversification. To determine if nectar spurs increase rates of speciation, an evolutionary biologist asks if the observed phylogeny can be explained by a null model, or if the null can be rejected in favor of an alternative that allows speciation rates to be higher in lineages that have nectar spurs. The results of such a comparison are only as good as the null model; if it is overly simplistic, it will always be rejected, even if the alternative models are incorrect or nonsensical.

In studies of lineage diversification, the null model is a fully-sampled, constant-rate, birth-death process. That is, the null model describes a process where there is a single rate of speciation and a single rate of extinction for all species throughout the history of the studied clade, and assumes that every extant descendant of the ancestral species is sampled in the phylogeny. Biologically, there are reasons to be suspicious that this model does not adequately describe diversification. For example, mass extinction events and diversity-dependence cause temporal heterogeneity in speciation and extinction. Key innovations can cause variation among species in rates of diversification. Indeed, it has been shown that diversification both varies through time (Morlon et al. 2010) and across the lineages in a phylogeny (Heard and Cox 2006). Further, most phylogenies do not include every descendant of the ancestral species, and the choice of species included in the phylogeny can bias inferences of diversification (Höhna 2014). It is no surprise that Rabosky and Goldberg (2015) demonstrated that the constant-rate birth-death process is a completely inadequate null model. Using simulation, they show that arbitrary biological traits frequently, and falsely, appear correlated with rates of diversification. The trait-dependent model is not correct (the trait has no effect on diversification), but it allows diversification rates to vary, while the null model does not. Clearly, new null models of lineage diversification must be developed.

Models account for diversification-rate variation in one of two ways: either a whole tree obeys a single, time-dependent process (a whole-tree approach), or individual lineages have unique, usually constant, rates of diversification (a lineage-specific approach). Given the apparent prevalence of among-lineage rate variation, a whole-tree approach would be inadequate for a null model of lineage diversification. The most promising direction for developing new null models is to account for incomplete sampling of species and among-lineage rate variation. A good place to start developing such models is to examine relaxed clock models for nucleotide sequence evolution. These models are based on the idea that molecular evolution occurs at a consistent rate, but they allow for that rate to vary across the lineages in a phylogeny. A probability distribution is chosen that describes how rates of substitution vary within a phylogeny, that is, it describes how to relax the evolutionary clock. These relaxed-clock models are flexible largely due to the ability to choose from a wide range of probability distributions, allowing rates to cluster tightly or to be highly variable. But there is also flexibility stemming from the ability to choose whether variation is uncorrelated among all lineages, or autocorrelated such that the descendants of a lineage have substitution rates that are more like that of their ancestor. Similarly, I seek to allow the rate of lineage diversification to vary among lineages. I

