Digest: Trait-dependent diversification and its alternatives*

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Species selection—variation in diversification rates associated with variation in species traits—was once a fringe idea, at least among population biologists. But following the development of a novel suite of phylogenetic comparative methods (e.g., BiSSE; Maddison et al. 2007), comparative biologists went looking for evidence of species selection and found it, seemingly everywhere. However, recent studies have shown that state-dependent speciation and extinction models (SSE) were prone to detecting associations between diversification rates with phenotypic traits under a variety of situations where the diversification rates were simulated completely independently of the traits (Maddison and FitzJohn 2015; Rabosky and Goldberg 2015). These findings led to a crisis in the field; it was unclear which previous discoveries were actually discoveries, and which were false positives. In this issue, Rabosky and Goldberg (2017) develop an approach, which they call FiSSE that is less likely to find spurious associations between binary traits and diversification rates.

Unlike its SSE predecessors, FiSSE is a semi-parametric and likelihood-free method. FiSSE computes a statistic from the branch lengths and values of the binary trait at the tips of a given phylogeny (Fig. 1); this test-statistic is then compared to expectations if diversification rates and the binary state were completely uncorrelated. A benefit of this approach is that it avoids the computationally demanding likelihood calculations that underlie previous SSE methods (Fig. 1). But most impor-

tantly, FiSSE has lower false-positive rates compared to other SSE models.

An outstanding challenge, which the authors fully acknowledge, is that the "proper" null hypothesis is difficult to define. As pointed out by Beaulieu and O'Meara (2016), the conventional null hypothesis of the SSE models implies both no association between binary states and diversification rates and constant diversification rates across the phylogeny. It is not logically necessary to assume both of these things. For instance, one could set up the null hypothesis such that diversification rate variation across the tree is driven by another partially observed trait that may be correlated or uncorrelated with the binary trait being considered (Beaulieu and O'Meara 2016). Fortunately, FiSSE had lower false-positive rates than other SSE methods under a variety of null hypotheses, making this approach more robust under complicated diversification scenarios.

FiSSE will help researchers assess the true prevalence of trait-dependent diversification. With meaningful test statistics, which would ideally be tied to both speciation and extinction rates, semi-parametric, and/or likelihood-free methods could be extended beyond binary traits. However, FiSSE should generally be used alongside the model-based SSE approaches, and not as a replacement. There is key, and generally untapped, information in the actual parameter estimates. For example, the comparison of rates can allow us to understand the maintenance of traits that are deleterious at the population level or to disentangle true species selection from species drift (Chevin 2016). By pairing parameter estimation with rigorous hypothesis testing, we will be able to gain a more comprehensive understanding as to why lineage and trait diversity are so unevenly distributed across the tree of life.

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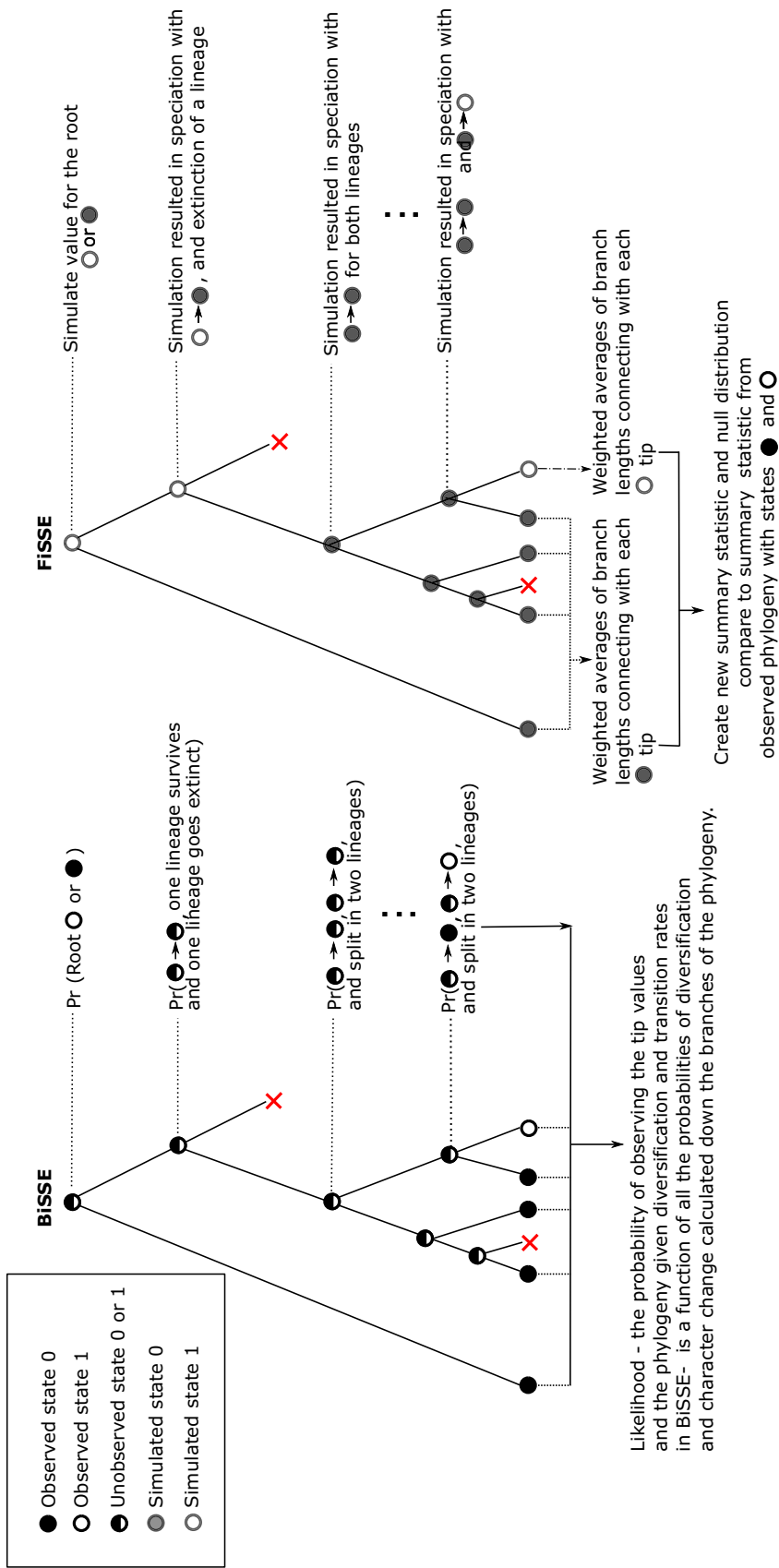
Figure 1. Left: An example of BiSSE calculations (Maddison et al. 2007). Transition probabilities must be calculated along every branch. These calculations are numerically expensive because neither the states at internal nodes nor extinct lineages can be observed, meaning that all plausible changes have to be accounted for in the likelihood calculations. Right: The simulation procedure used to generate the null distribution of the summary statistic for FiSSE.

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