Are we truly estimating the mode of speciation with state-dependent diversification methods?

Jenna McCullough1,\* and Rosana Zenil-Ferguson1

1Biology Department, University of Kentucky, Lexington, KY 40506

\*Corresponding author: [jmmccullough@uky.edu](mailto:jmmccullough@uky.edu)

Abstract

Understanding how and why species diversify is an overarching goal of evolutionary biology. It is well established that traits, phenotypic or geographic, can impact the tempo and mode of speciation (citations). State-dependent speciation and extinction (SSE) models are an important and widely-used tool to test hypotheses of lineage and trait diversification (citations). BiSSE [(binary state-dependent speciation and extinction; Maddison et al. 2007)](https://paperpile.com/c/myIbrC/qHZR/?prefix=binary%20state-dependent%20speciation%20and%20extinction%3B) was the first model to jointly infer speciation, extinction, and transition rates between character states of a trait and has since been extended to encompass different types of data, such as as a single continuous trait [(QuaSSE; FitzJohn 2010)](https://paperpile.com/c/myIbrC/31wl/?prefix=QuaSSE%3B) and multiple traits [(MuSSE; FitzJohn 2012)](https://paperpile.com/c/myIbrC/K3Vy/?prefix=MuSSE%3B). Because these models explicitly allow for trait change to occur along a branch without a speciation event (i.e., anagenetic trait evolution) rather than at the time of speciation (i.e., cladogenetic trait evolution), comparisons of state-dependent diversification are really comparing differences in tempo between character states rather than the mode in which speciation occurs.

Differences in diversification between two character states may answer hypotheses about the tempo of evolution, but how traits change during a speciation event answers questions regarding its mode. Cladogenetic evolution is best illustrated by the model of allopatric evolution [(Mayr 1942)](https://paperpile.com/c/myIbrC/R4KX), in which a population is split due to the formation of a geographic barrier that contributes to lineage divergence in allopatry. Body size evolution of *Anolis* lizards, color patterning of *Heliconius* butterflies, and beak shape of Galapagós ground finches are classic examples of trait change occurring during—not between—speciation events. Models that incorporate cladogenetic evolution include those focused on geography [(GeoSSE; Goldberg et al. 2011)](https://paperpile.com/c/myIbrC/zSR3/?prefix=GeoSSE%3B), binary traits [(ClaSSE; Goldberg and Igić 2012; BiSSE-ness; Magnuson-Ford and Otto 2012)](https://paperpile.com/c/myIbrC/FQvg+Qa06/?prefix=ClaSSE%3B,BiSSE-ness%3B), and chromosome number [(ChromoSSE; Freyman and Höhna 2018)](https://paperpile.com/c/myIbrC/OFAa/?prefix=ChromoSSE%3B). Models that allow for cladogenetic trait evolution both model anagenetic transitions between character states (defined in the Q matrix, Fig. 1A) and cladogenetic events that allow one or both of the descendant daughter lineages to have a character state change (defined in the cladogenetic matrix, Figure 1C–D).

To answer whether a trait has an effect on diversification, it is imperative to reject the null hypothesis that it does not. If it does have an effect, a particular character state will have a result of higher net diversification, supporting a hypothesis of state-dependent diversification. If all rates are equal between states, that means that the trait in question has no effect on diversification and supports the null hypothesis. Described as “one rate to rule them all” by Caetano et al. [(2018)](https://paperpile.com/c/myIbrC/hxz5/?noauthor=1), this null hypothesis is inherent to all models discussed thus far.

But evolution varies so widely across time and space; numerous studies have shown that the “one rate to rule them all” hypothesis is often outperformed by one that incorporates even a small amount of complexity [(Rabosky and Goldberg 2015; O'Meara and Beaulieu 2016; Rabosky and Goldberg 2017; Alves et al. 2017)](https://paperpile.com/c/myIbrC/K67u+atvJ+dwgw+3PIH). By manually adding heterogeneity to our empirical data (i.e., applying a “hidden state”)

With the introduction of hidden state models [(HiSSE; Beaulieu and O'Meara 2016)](https://paperpile.com/c/myIbrC/gJjt/?prefix=HiSSE%3B), we had ability to test whether the trait of interest (observed state) or a “hidden state” influences diversification, thereby allowing for a more robust null model in which to test for state-dependent speciation. The application of hidden state models has been widespread to binary (HiSSE; [(Miller et al. 2018)](https://paperpile.com/c/myIbrC/0BNT)), continuous (QuaHiSSE), multi-state (MuHiSSE; [(Bouchenak-Khelladi and Linder 2017; Padilla-Morales et al. 2022)](https://paperpile.com/c/myIbrC/1wYy+rg0J)), chromosomal (ChromoHiSSE; [(Tribble et al. 2025)](https://paperpile.com/c/myIbrC/PCrU)), and geographic (GeoHiSSE; [(Caetano et al. 2018; McCullough et al. 2022)](https://paperpile.com/c/myIbrC/hxz5+ZsJe)) traits.