# SSE Type Model Annotated Bibliography

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## History of Ideas

Brief synopsis of seminal papers that aim to understand the processes that produces the patterns of biodiversity.

**Darwin, C. (1859). *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. London: J. Murray.**
Introduce us to Evolution.

**Mitter , C. , B. Farrell , and B. Wiegmann . 1988 . The phylogenetic study of adaptive zones—Has phytophagy promoted insect diversification? American Naturalist 132 : 107 – 128.**
Introduces Sister Clade Comparison. This paper introduce a formal statistical method of testing for character state and diversification. By the **Sister Clade comparison approach**. The idea behind this approach is identify a pair of sister clades that different in your trait of interest (in this case they tested shifts between herbivory and carnivory in beetles). Each sister clade represents a single data point using a linear regression we can test if character state can predict species richness. In order for this method to identify a statistically significant result at least six sister clades must be analyzed. Using this method and 13 pair of sister clades they showed that 11 of these pairs, herbivorous clades of beetles were more specious than their carnivorous sister clades.

**Pagel , M. 1994 . Detecting correlated evolution on phylogenies—A general-method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London, B, Biological Sciences 255 : 37 – 45.**
This is a seminal paper describes the use of continuous-time Markov model correlated evolution of discrete traits across a phylogeny. While this paper has formed the foundation of contemporary comparative methods, it highlights an approach that implicitly assumes that traits evolution occurs independently of speciation

**Maddison , W. P. 2006 . Confounding asymmetries in evolutionary diversification and character change. Evolution 60 : 1743 – 1746 .**
Identifies a problem between distinguishing changes in speciation/extinction rates and changes in transition rate in asymmetrical trees. This paper identifies a major issue in the literature up until that point. Asymmetrical trees. describes the the principle goal which SSE models address. Specifically, approaches which consider phylogenetic inference independently of trait evolution, when character states may influence speciation rate or extinction rates, thus phylogeny. This assumption that phylogeny and character state evolution is only true for neutral character states.

**Maddison , W. P. , P. E. Midford , and S. P. Otto . 2007 . Estimating a binary character's effect on speciation and extinction. Systematic Biology 56 : 701 – 710 .**
Introduce the first SSE type model BiSSE. This paper is a solution to the problems that Madison 2006 bring up. In order to discriminate between asymmetrical trait transition rates and asymmetrical speciation/extinction rates the authors jointly estimate these parameters for binary

character states in their new program called BiSSE. In addition to this implementation they also use a novel application of ordinary differential equation to determine the likelihood function of a tree given a

**Goldberg , E. E. , and B. Igic . 2012 . Tempo and mode in plant breeding system evolution. Evolution 66 : 3701 – 3709 .**
Introduces trait transition during cladogenetic events with ClaSSE. The original BiSSE paper only took into account anagenetic trait transitions (along the branch) this paper makes an important improvement by adding cladogenetic character changes with ClaSSE. With this method new question can be asked, Do changes in trait cause cladogenesis? They apply their finding to the shifts between self-incompatibility and self- compatibility in the Solanaceae, the nightshade family (tomatoes and stuff).

**Maddison, Wayne P., and Richard G. FitzJohn. "The unsolved challenge to phylogenetic correlation tests for categorical characters."** ***Systematic biology*** **64.1 (2014): 127-136.**
Highlights the problem of psuedoreplication in BiSSE. While the Species Clade Comparison Method, was inadequate because it could not discriminate between two different biological process shifts in transition rate and shifts in speciation/ extinction rates. The method did make an attempt to account for replication by taking multiple pairs of sister clades in order to obtain statistical support. In contrast this is not a requirement for BiSSE and therefore it may fail where there is investigation of traits where there was a single transition on the tree. Therefore it may be important

Figure 4 from this paper is fun

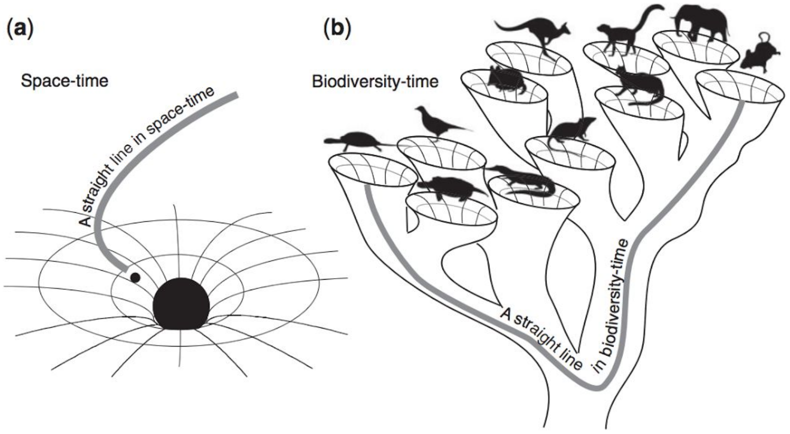

FIGURE 4. A relativistic perspective on motion in space-time (a), compared with a phylogenetic perspective on comparisons among lineages (b). Our intuition of a straight-line motion or comparison is incorrect in both cases. We are tempted to compare extant species directly, seeing differences in the thin horizontal slice of time we experience, but in fact a straight-line comparison in biodiversity-time is vertical, following changes along the lineages joining the species. Based on a similar figure in Maddison and Pérez (2001). Silhouettes of animals from http://phylopic.org; last accessed December 1, 2014. ©Michael Keesey under a Creative Commons 3.0 Unported or Share-alike Unported license, except the felid, which is in the public domain.

**Rabosky, Daniel L., and Emma E. Goldberg. "Model inadequacy and mistaken inferences of trait-dependent speciation." Systematic Biology 64.2 (2015): 340-355.**
This paper identify high rates of false positives using the BiSSE model. They identified these thru a series of BiSSE modeling using real and simulated data. They first tested whether rates of speciation diversification body size (binary: small/ Large) in extant whales using BiSSE. They found that there was a significant correlation between small body size and speciation. To test if

the tree topology had an influences on this correlation, they simulated 100 neutral binary characters using BiSSE on 1) the whale phylogeny and 2) a phylogeny with the same number of tips (87) generated from a pure-birth process. They find that with the 1) Whale phylogeny there was a significant association between greater than 77% of the neutral simulated trait and speciation, despite no such association actually existing (Fig 2 top row). This held true with varying shifts of transition between traits (q). This association was not found in 2) the phylogeny generated from pure birth (Fig 2 bottom row).
They conclude that this problem is due to replication that methods such as

**Beaulieu, Jeremy M., and Brian C. O'Meara. "Detecting hidden diversification shifts in models of trait-dependent speciation and extinction."** ***Systematic biology*** **65.4 (2016): 583-601.**
Introduce HiSSE a method to reduce the amount of false positives addressed by Rabosky and GoldBerg 2015.

## Derivatives of SSE Models

BiSSE sparked a revolution that continued to expand on the the basic principle of jointly estimating speciation/extinction with traits transitions to other biologically relevant questions. Continuous traits, multistate traits, chromosomes etc...

**FitzJohn , R. G. 2010 . Quantitative traits and diversification. Systematic Biology 59 : 619 – 633 .**
Applies BiSSE for quantitative traits. While BiSSE showed to be interesting model, a drawback is that it models discrete binary states (either blue or yellow) while many of the character states we are interested in are quantitative (continuous). This paper address this problem by introducing **QuaSSE** a derivative of BiSSE that allows for quantitative traits. Assumes that each tip has a mean continuous value representative of that group. Continuous character evolution are modeled with a diffusion process.

**Goldberg , E. E. , L. T. Lancaster , and R. H. Ree . 2011 . Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. Systematic Biology 60 : 451 – 465 .**
Applies BiSSE for Geographic traits. An expansion of the BiSSE type model to biogeography with **GeoSSE**. Instead of trait, the character state are occupancy of biogeographical regions. Accounts for range expansion through dispersal events or range contraction by extripation.

**FitzJohn , R. G. 2012a . Diversitree: Comparative phylogenetic analyses of diversification in R. Methods in Ecology and Evolution 3 : 1084 – 1092 .**
Makes SSE type models accessible in R and introduces multistate SSE model. This paper made the BiSSE models accessible to research by implementing many of the SSE type model published to that point into a R package Diversitree - a favorite coding language of many biologist. Additionally this paper also generalized the BiSSE model by expanding it from two character states of multistate with **MuSSE** (MUltistateSSE).

**Fryman, W., and HÖhna. S,. 2017 Cladogenetic and Anagenetic Models of Chromosome Number Evolution: A Bayesian Model Averaging Approach. Systematics Biology**
Introduce SSE type models for changes in Chromosome number at both anagenetic and cladogenetics events. In the latest and greatest expansion of SSE type models, Berkeley's very

own Will Fryman and collaborators establishes ChromoSSE. This models the influences of chromosome number changes like polyploidy (increase in number) or disploidy (decrease in number) as they are correlation with cladogenic and anagenetic events. This model is powerful because it can address the degree to which changes in chromosome number is correlated with speciation or extinction of lineages a long standing question.