Outline

- Pure-birth model: lineage through time plots, $\gamma$ statistic and lineage diversification index
- Constant birth-death model: estimating speciation and extinction rates from molecular phylogenies
- Complex models: clade-dependent, time-dependent (incl. diversity-dependent) & trait-dependent models
- State dependent diversification
State-dependent diversification
Models of lineage diversification

- Yule or pure birth (pb)
- Constant birth-death (bd)
- Clade dependent
- Time dependent (more complex, non-constant)
- State dependent (trait dependent)
State-dependent diversification

• Trait evolution and its effects on diversification

• de Saporta and Darwin: the evolution of insect pollination may have resulted in the angiosperm radiation

State-dependent diversification

- Do speciation and extinction rates depend on the state of a particular character?

Pyron & Burbrink (2014) - TREE
State-dependent diversification

Character-independent model vs. Character-dependent model

<table>
<thead>
<tr>
<th>Character State</th>
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<tbody>
<tr>
<td>0</td>
<td>0</td>
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<tr>
<td>1</td>
<td>1</td>
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</table>

Diversification rate

\begin{array}{cc}
\lambda & \mu \\
\hline
\text{Character State} & \text{Character State} \\
0 & 0 \\
1 & 1 \\
\end{array}
State-dependent diversification

- Do speciation and extinction rates depend on the state of a particular character?

- Need to decouple the confounding effect of clade age & clade richness

State-dependent diversification

- Do speciation and extinction rates depend on the state of a particular character?
- Need to decouple the confounding effect of clade age & clade richness
- The old way of addressing this question: sister-clade comparisons
- Sister clades are the same age!

The old way: sister-clade comparisons

Has herbivory promoted diversification in insects?

Futuyma (2013)
Has herbivory promoted diversification in insects?

Why are sister-clade comparisons limited?
Why are sister-clade comparisons limited?

- Discard useful information from other branches in the tree (limited power)
Why are sister-clade comparisons limited?
Why are sister-clade comparisons limited?

- Discard useful information from other branches in the tree (limited power)
- Cannot distinguish differential speciation from differential extinction

Why are sister-clade comparisons limited?

- “Confounding asymmetries in evolutionary diversification and character change”

- Do not account for a possible bias in transition rates
  - For instance, higher transition rates of trait B into trait A (relative to A into B) may result in more species with trait A, without varying diversification rates.

BiSSE: binary state speciation and extinction

- Originally a likelihood method, now extended in a MCMC framework (diversitree)

- The most general BiSSE model has six parameters:

  - $\lambda_0$: speciation rates in 0 (e.g., herbivores)
  - $\lambda_1$: speciation rates in 1 (e.g., carnivores)
  - $\mu_0$: extinction rates in 0
  - $\mu_1$: extinction rates in 1
  - $q_{01}$: transition rates from 0 to 1
  - $q_{10}$: transition rates from 1 to 0

BiSSE: binary state speciation and extinction

A. Scenarios for observed lineages
- i. no speciation
- ii. speciation left branch, subsequent extinction
- iii. speciation right branch, subsequent extinction

B. Scenarios for unobserved lineages
- i. no rate shift, no speciation, extinction
- ii. no rate shift, no speciation, subsequent extinction
- iii. no rate shift, speciation, subsequent extinctions

Lineage with state 0 yields a clade
Lineage with state 0 goes extinct

BiSSE: accounts for confounding asymmetries

O’Meara & Beaulieu (2017) - Am. J. Bot
O’Meara & Beaulieu (2017) – Am. J. Bot

80% species in state 1
20% species in state 0

All transitions into state 1

Div. rate 1 / Div. rate 0 = 1x (equal)

Div. rate 1 / Div. rate 0 = 1.4x

Equal transition rate

Div. rate 1 / Div. rate 0 = 2x

All transitions into state 0

q10 / q01 = 0.3x

q10 / q01 = 1x (equal)

q10 / q01: 10x
BiSSE: accounts for confounding asymmetries

- In Solenaceae, species with self-incompatibility have a much higher diversification rate than those with self-compatibility (self-fertilization)

- In fact, the diversification rate of self-compatible lineages is negative

- Despite this, 57% of the species self-compatible

Goldberg et al. (2010) - Science
BiSSE: accounts for confounding asymmetries

- Why would evolution result in a high frequency of a trait that tends to cause the extinction of groups possessing it?

- Asymmetric transition rates maintains self-incompatibility in Solenaceae through a breakdown of incompatibility mechanisms
BiSSE: accounts for confounding asymmetries

Net diversification rate is higher in self-incompatible than in self compatible lineages

But transition rates are asymmetric. Higher frequency of SI-to-SC than the reverse.

Goldberg et al. (2010) - Science
80% species in state 1
20% species in state 0

All transitions into state 1

Div. rate 1 / Div. rate 0 = 1x (equal)

q10 / q01 = 0.1x

Div. rate 1 / Div. rate 0 = 1.4x

Equal transition rate

q10 / q01 = 1x (equal)

Div. rate 1 / Div. rate 0 = 2x

q10 / q01: 10x

All transitions into state 0
Fish species richness in marine and freshwater habitats

Marine fishes
- 15,300-15,500 species

Freshwater fishes
- 15,100-15,300 species

50% ~ 50%
Fish species richness in marine and freshwater habitats

Marine fishes

- 15,300-15,500 species

Freshwater fishes

- 15,100-15,300 species

50% ~ 50%

But do similar levels of species richness translate into similar diversification dynamics?
“Net diversification rates are similar in predominantly freshwater and saltwater clades”
BiSSE: do diversification rates vary as a function of habitat in fishes?

Net diversification rates (speciation - extinction)

BiSSE: are transition rates in fishes symmetric or asymmetric?

- Marine families that have colonized freshwater habitats

- Freshwater families that have diversified in the sea
BiSSE: are transition rates in fishes symmetric or asymmetric?

Transition rates

Caveats: are rates within each state homogeneous?

Freshwater “Living fossils” (<100 spp)

Freshwater radiation (Otophyssi; > 10k spp.)
It allows for explicit tests of biological hypotheses related to speciation, extinction, and transition rates.

Are alternative biological models supported?

For instance, a model in which speciation and extinction are fixed as equal across habitats ($\lambda M = \lambda F$; $\mu M = \mu F$) while transition rates are free to vary ($q MF \neq q FM$) is strongly rejected ($\Delta AIC = 22–58$)

Extensions of BiSSE: the SSE family

- **BiSSE**: binary state SE (Maddison et al, 2007)
  - 2 states, 6 parameters

- **MuSSE**: multi-state SE (FitzJohn et al., 2009)
  - $(2^N - 2) + 2N$ parameters

- **GeoSSE**: geographic state SE (Goldberg et al., 2011)
  - 3 states (areas), seven parameters

- **QuaSSE**: quantitative state SE (FitzJohn, 2010)
  - Multiple parameters

- **HiSSE**: hidden state SE (Beaulieu & O’Meara, 2016)
  - Multiple parameters

- **FiSSE**: fast, intuitive SSE (Rabosky & Goldberg, 2017)
  - Nonparametric
MuSSE: multi-state speciation and extinction

- An extension of BiSSE for characters with multiple states
- It has \((2^N - 2) + 2N\) parameters. For 3 states the maximum number of parameters is 12

MuSSE: net diversification rates across trophic states in terapontid fishes

Net diversification rates (speciation - extinction)

Carnivores (>90% animal prey)
Omnivores (10%-90% animal prey)
Herbivores (<10% animal prey)

GeoSSE: geographic state speciation and extinction

• An extension of BiSSE for geographic areas
• 3 states: area A, area B, and intermediate area AB
• The most general GeoSSE model has seven parameters:

\[ \lambda_A: \text{speciation rates in A} \]
\[ \lambda_B: \text{speciation rates in B} \]
\[ \lambda_{AB}: \text{speciation rates in AB} \]
\[ \mu_A: \text{extinction rates in 0} \]
\[ \mu_B: \text{extinction rates in 1} \]
\[ q_{AB}: \text{transition rates from A to B} \]
\[ q_{BA}: \text{transition rates from B to A} \]
GeoSSE: geographic state speciation and extinction

- Ideal for biogeography: it does not allow instantaneous transitions from area A to B

GeoSSE: rates in tropical vs. temperate squamate reptiles

QuaSSE: quantitative state speciation and extinction

- An extension of BiSSE for continuous traits
- Is smaller body size associated with increased rate of diversification?
- Replaces Brownian motion with a diffusion process as the null model for continuous traits
- Diffusion is a model proposed by A. Einstein under which particles move randomly until they are evenly spread
- QuaSSE has multiple parameters

QuaSSE: quantitative state speciation and extinction

- Alternative QuaSSE models

QuaSSE: do speciation rates vary as a hump-shaped function of dispersal?

Hand-wing index, a surrogate for aspect ratio, in turn a surrogate for dispersal ability

- Aerodynamics of avian flight: wings with high aspect ratio are the key to efficient long-distance flight

Hand-wing index superimposed onto the phylogeny - 290 species in the family Furnariidae

QuaSSE analysis: hump-shaped model not supported

- Lineages with higher dispersal ability experienced lower speciation rates

QuaSSE: net diversification rates in relation to proportion of animal prey

Caveats of SSE methods

- Power to detect differential rates across states (type 2 error)
The power of BiSSE

Speciation

Differences in rates

Transitions

Differences in rates

Extinction

Differences in rates

Davis et al. (2013) - BMC Evol. Biol.
SSE methods: caveats

- Power to detect differential rates across states (type 2 error) - may need large trees
The power of BiSSE

Notes on the Statistical Power of the Binary State Speciation and Extinction (BiSSE) Model

Alexander Gamisch
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ABSTRACT: The Binary State Speciation and Extinction (BiSSE) method is one of the most popular tools for investigating the rates of diversification and character evolution. Yet, based on previous simulation studies, it is commonly held that the BiSSE method requires phylogenetic trees of fairly large sample sizes (>300 taxa) in order to distinguish between the different models of speciation, extinction, or transition rate asymmetry. Here, the power of the BiSSE method is reevaluated by simulating trees of both small and large sample sizes (30, 60, 90, and 300 taxa) under various asymmetry models and root state assumptions. Results show that the power of the BiSSE method can be much higher, also in trees of small sample size, for detecting differences in speciation rate asymmetry than anticipated earlier. This, however, is not a consequence of any conceptual or mathematical flaw in the method per se but rather of assumptions about the character state at the root of the simulated trees and thus the underlying macroevolutionary model, which led to biased results and conclusions in earlier power assessments. As such, these earlier simulation studies used to determine the power of BiSSE were not incorrect but biased, leading to an overestimation of type-II statistical error for detecting differences in speciation rate but not for extinction and transition rates.

KEYWORDS: BiSSE, simulation, low sample size, type-II statistical error, key innovation model
SSE methods: even more worrisome!

- Power to detect differential rates across states (type 2 error) - may need large trees

- Model inadequacy & Type I (?) error:
  
  Unexamined characters (Rabosky & Goldberg, 2015)

  Phylogenetic pseudo-replication (Maddison & FitzJohn, 2015)
SSE methods: even more worrisome!

Simulated characters under trait independent diversification always reject the supposed null model!!!

SSE methods: even more worrisome!

Effect of taxon name length on speciation rate

Why is this happening?

• Underlying trees show diversification rate heterogeneity

• Null model (trait independent diversification on a constant rate tree) does not explain data well

• BiSSE alternative model (traits explain heterogeneity) is a much better explanation for data set
What does it mean?

• This is not Type I error. When model correct, BiSSE shown to have acceptable Type I rates

• The alternative models are *inadequate*

• Rejecting null does not mean alternative is true!

SSE methods: even more worrisome!

- Power to detect differential rates across states (type 2 error) - may need large trees

- Model inadequacy & type 1 error:

  Unexamined characters (Rabosky & Goldberg, 2015)

  Phylogenetic pseudo-replication (Maddison & FitzJohn, 2015)
SSE methods: phylogenetic pseudo-replication

• One of the most severe criticisms of SSE

• When trait that has evolved only once or just a few times, an observed effect on rates could be spurious

SSE methods: phylogenetic pseudoreplication
Solutions

- Apply SSE on traits that have evolved multiple times (true phylogenetic replicates)

- Simulations of traits on underlying tree

- Better null models (HiSSE)

- Apply non-parametric SSE tests (FiSSE)

Solutions: simulations

Methods in Ecology and Evolution
Methods in Ecology and Evolution 2016, 7, 806–810
doi: 10.1111/2041-210X.12531

APPLICATION
PHYLOMETRICS: an R package for detecting macroevolutionary patterns, using phylogenetic metrics and backward tree simulation

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Character-dependent model vs. Character-dependent hidden state

HiSSE: hidden state speciation and extinction

- HiSSE (hidden state SSE)
- HiSSE allows for null models where diversification rate changes on tree independent of character
- Hidden state also reveals how much your trait model explains relative to all of the trait-related heterogeneity present on the tree

<table>
<thead>
<tr>
<th>Character State</th>
<th>Diversification rate</th>
<th>λ</th>
<th>μ</th>
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HiSSE: hidden state speciation and extinction
HiSSE: hidden state speciation and extinction (achene vs. non-achene fruits in campanululids)

Caveats: are rates homogeneous within each state?

Try HiSSE!

- Freshwater “Living fossils” (<100 spp)
- Freshwater radiation (Otophyii; > 10k spp.)
FiSSE: A simple nonparametric test for the effects of a binary character on lineage diversification rates

Daniel L. Rabosky, Emma E. Goldberg

First published: 4 April 2017  Full publication history
DOI: 10.1111/evo.13227  View/save citation
Cited by (CrossRef): 0 articles  Check for updates  Citation tools
FiSSE: fast, intuitive SSE

- Nonparametric test
- FiSSE computes a test statistic that compares the distributions of branch lengths for lineages with and without the trait of interest
FiSSE: fast, intuitive SSE

- FiSSE test statistic:
  - Estimate speciation rate for each tip (Equal Splits or ES of Jetz et al., 2012)
  - The metric does not explicitly account for extinction (or net div.) and is simply a measure of the splitting rate for surviving lineages
  - Compute the mean tip speciation with each state
  - The difference in these values is the test statistic
FiSSE: fast, intuitive SSE

- The FiSSE statistic is compared to a null distribution generated by simulating character histories on the observed tree
- No likelihood estimation - very fast!
- Low false-positive rates relative to BiSSE

Rabosky & Goldberg (2017) - Evolution
FiSSE: fast, intuitive SSE

- Low false-positive rates relative to BiSSE

Rabosky & Goldberg (2017) - Evolution
The future of SSE

Past, future, and present of state-dependent models of diversification

Brian C. O’Meara and Jeremy M. Beaulieu

O’Meara & Beaulieu (2017) - Am. J. Bot
The future of SSE

• “It seems to us that the initial wave of interest and use of SSE models is quickly being replaced with widespread skepticism”

• “However, we feel the pendulum has unnecessarily swung too far in this direction”

• “We urge practitioners to use prudent caution, but do not abandon all hope”