Testing for Rapid Radiation Over Clade History Using the Gamma Statistic

Did a clade ‘adaptively radiate’?
Expect initial diversification to be fast
Pybus and Harvey (2001)* proposed a test for rate shift across the tree

The gamma statistic

- A tree branching under a constant-rates model should have a balance of node depths around the midpoint of the tree.

- $\gamma$ describes this distance.
Early branching

- rapid, early diversification will create an imbalance of young nodes
- this will be reflected by a $-\gamma$
- evidence for adaptive radiation

$\gamma < 0$
Late branching

- recent accelerated net diversification will concentrate nodes towards the tips
- could be due to increase in birth rate or decrease in death rate

\[ \gamma > 0 \]
If gamma is less than 2 std. deviations from mean ($\gamma \leq -1.645$), reject constant rate of diversification.

Keypoint: Negative $\gamma$-statistic consistent with early elevation of diversification rate (this is the CR test).

Midpoint of BLs
What about incomplete sampling?

- with random sampling of four taxa, what nodes would be expected to miss?
- how would this affect gamma?
MCCR: The constant rates test for incompletely sampled trees*

- Complete sampling: $\gamma \leq -1.645$
- Incomplete sampling means that old nodes more likely to be recovered, biasing CR test
- Solution: MCCR test*
  - Simulate tree with $n$ taxa
  - Randomly prune missing taxa
  - Calculate the $\gamma$-statistic on pruned tree
  - Repeat
  - Calculate corrected $p$-value

* Pybus and Harvey (2000)
Example of Gamma Statistic: Diversification of Homalopsid Snakes

- 34 species distributed across S.E. Asia
- Aquatic to semi-aquatic

Alfaro et al. 2007
A timetree for homalopsid diversification

- Bayesian timetree using BEAST
- 4 genes (12S, 16S, cytB, C-Mos)
- 9 of 10 genera, 20 of 34 species
- MCCCR test suggests rapid initial diversification (P < 0.001)
Log-Lineages Through Time

Time From Basal Divergence

Log Lineages
Models of diversification: Constant-rate models

- Pure birth (PB)
- Death = 0
Models of diversification: Constant-rate models

- Birth-Death (BD)
- Birth & Death constant
**Rate-variable models: Density-dependent**

- Density-dependent: Exponential

\[ R(t) = R_0 \cdot (N(t))^{-x} \]
Rate-variable models: Density-dependent

- Density-dependent: Logistic
- \( R(t) = R_0 \times (1 - N(t)/K) \)
Models of diversification: Variable-rate models

- Yule-2-Rate (Y2R)
- Death = 0
Models of diversification: Variable-rate models

- Rate-variable BD (RVBD)
- Death/Birth is constant
## Model scores

<table>
<thead>
<tr>
<th>Model</th>
<th>LH</th>
<th>dAIC</th>
<th>Rate 1</th>
<th>Rate 2</th>
<th>Shift Time</th>
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<tbody>
<tr>
<td>PB</td>
<td>75.73</td>
<td>12.07</td>
<td>0.153</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>BD</td>
<td>75.73</td>
<td>14.07</td>
<td>0.153</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>DDL</td>
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<td>7.4</td>
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<td>NA</td>
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<td>0.352</td>
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<tr>
<td>Y2R</td>
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<td>0</td>
<td>0.177</td>
<td>0.036</td>
<td>1.127</td>
</tr>
<tr>
<td>RVBD</td>
<td>83.77</td>
<td>2.0</td>
<td>0.177</td>
<td>0.036</td>
<td>1.127</td>
</tr>
</tbody>
</table>

density-dependent models rejected for rockfish
HOW CAN WE TEST FOR UNEQUAL RATES OF DIVERSIFICATION?

- Construct a timetree
- Calculate rates
- Test for significant differences using comparative methods
**Step 1: molecular phylogeny**

- Molecular sequence data from three loci Rag1, 12S, 16S (Holcroft, 2005, plus additional data)

- Sampled 86 ingroup taxa including members of all extant families

- Bayesian analysis using MrBayes, $1 \times 10^7$ generations, multiple independent runs
**Step 4: Compare Diversification Rates**

1. Estimate mean diversification rate of tetraodontiformes ($\lambda_G$)
   
   \[
   \lambda_G = \frac{\ln(n) - \ln(2)}{t}
   \]
   
   \[= \frac{\ln(350) - \ln(2)}{70\text{MY}} \]
   
   \[= 0.07 \text{ species/MY} \]

2. Test whether family species richness

   key point: species richness exceptionally high in reef groups

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<table>
<thead>
<tr>
<th>Taxon</th>
<th>Age (MY)</th>
<th>Extant #</th>
<th>Faster?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balistidae</td>
<td>22.9</td>
<td>43</td>
<td>**</td>
</tr>
<tr>
<td>Diodontidae</td>
<td>10.9</td>
<td>22</td>
<td>**</td>
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<tr>
<td>Monacanthidae</td>
<td>24.6</td>
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</tr>
<tr>
<td>Ostraciidae</td>
<td>20.8</td>
<td>23</td>
<td>*</td>
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<tr>
<td>Tetraodontidae</td>
<td>38.3</td>
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<tr>
<td>Aracanidae</td>
<td>6.7</td>
<td>13</td>
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<tr>
<td>Molidae</td>
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</tbody>
</table>

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*Magallon and Sanderson, 2001*
A Timetree for Jawed Vertebrates

- ~60,000 species total
- Molecular Phylogeny
  - RAG-1 genbank data
  - 221 tip species
- Relaxed molecular clock
- 42 fossil calibrations
- Major gnathostome lineages represented
\( \lambda_G = \frac{\ln(n) - \ln(2)}{t} \)

\( n = 57,859 \) species

\( t = 549 \) mya

\( \lambda_G = \frac{\ln(57859) - \ln(2)}{549} \)

\( \lambda_G = 0.019 \)
\[ \lambda = 0.019 \]
Thanks!!!

- we will send course materials out--make sure you gave us your email
- please send comments and feedback with ‘FEEDBACK’ in the header to michaelalfaro@ucla.edu
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