IX. Hierarchical Birth-Death Models, 2

1 Incorporating genus-level origination rate

1.1 $p$ in models is the rate of species origination within a paraclade. (This helps make sense of why estimates of $p$ can be less than estimates of $q$ even though diversity is not waning.)

1.2 We can add an additional parameter $g$, the rate of genus origination per lineage-million-years. Each genus is monotypic at its origin. Thus, the total rate of production of new species is $S = p + g$. 

![Diagram of paraclades and lineages]

**Figure 1.** Structure of the probabilistic branching model (cf. Raup 1985). For each lineage at any time $t$ there is a probability that: (1) the lineage will branch within the existing paraclade ($\lambda$) such as at time 1; (2) the lineage will branch to form a new paraclade ($\gamma$) such as at time 3; (3) the lineage will terminate ($\mu$) such as at time 5; or (4) the lineage may merely persist unchanged. Note that this model can track diversity of lineages and paraclades simultaneously.
1.3 Computational details (Patzkowsky 1995)

Appendix 1: Analytic Solution for the Diversification of Paraclades with the Hierarchical Branching Model

Important variables and equations:

\[ \lambda = \text{speciation events within a paraclade per lineage million years (Lma)} \]
\[ r = \text{years (Lma)} \]
\[ \mu = \text{species extinction events per Lma} \]
\[ \gamma = \text{speciation events that found new paraclades per Lma} \]
\[ t = \text{time in millions of years from some arbitrary starting point} \]
\[ G_t = \text{number of paraclades at time } t \]

The expected number of species at some time \( t \) is:
\[ S_t = S_0 e^{rt} \quad (A1) \]

where \( r = \lambda + \gamma - \mu \).

The number of paraclades originating at time \( t \) is:
\[ G_{t, \text{orig}} = S_{t-1} \gamma \quad (A2) \]

The probability of extinction of a paraclade at or before time \( t \) is:

if \( \lambda = \mu \) (Bailey 1964: eq. 8.46; Raup 1985: eq. A11):
\[ p_{0,t} = (\lambda \cdot t) / (1 + \lambda \cdot t) \quad (A3) \]

if \( \lambda \neq \mu \) (Bailey 1964: eq. 8.46; Raup 1985: eq. A13):
\[ p_{0,t} = \frac{\mu (e^{\lambda \cdot t} - 1)}{(\lambda e^{\lambda \cdot t} - \mu)} \quad (A4) \]

The probability of survival of a paraclade until time \( t \) is (Raup 1985):
\[ p_{st} = 1 - p_{0,t} \quad (A5) \]

where \( p_{0,t} \) is equation A3 or A4.
The number of paraclades at any time \( t \) is a function of the number of paraclades at time \( t - 1 \) that survive to time \( t \) and the number of species at time \( t - 1 \) that give rise to new paraclades at time \( t \). Keeping track of the probability of survival for each paraclade involves determining the contribution of the origination cohort at time \( t \) to diversity at some time \( t + i \). That is, of the paraclades that originated at time \( t \), how many survived to time \( t + 1 \), how many survived to time \( t + 2 \), and so on. Below is the equation used to determine paraclade diversity. First, the equations are written out for time \( t = 0 \) to \( t = 4 \) followed by the more general equation for any time \( t \).

\[
G_0 = G_0
\]

\[
G_1 = G_0 p_{s,1} + G_{1,\text{org}}
\]

\[
G_2 = G_0 p_{s,2} + G_{1,\text{org}} p_{s,1} + G_{2,\text{org}}
\]

\[
G_3 = G_0 p_{s,3} + G_{1,\text{org}} p_{s,2} + G_{2,\text{org}} p_{s,1} + G_{3,\text{org}}
\]

\[
G_4 = G_0 p_{s,4} + G_{1,\text{org}} p_{s,3} + G_{2,\text{org}} p_{s,2} + G_{3,\text{org}} p_{s,1} + G_{4,\text{org}}
\]

\[
G_t = \sum_{i=0}^{t-1} G_{i,\text{org}} p_{s,t-i} + G_{t,\text{org}} \quad (A6)
\]

Equation A6 is a difference equation for paraclade diversity for the time-homogeneous branching model (fig. 2). It gives the statistical expectation of the model including the possibility of extinction of the "superclade" before time \( t \).
1.4 Principal results

1.4.1 Exponential growth in number of genera (after initial stabilization)

- Note that number of species also follows exponential growth with rate \( r = p + g - q \).
- Expected genus trajectory independent of initial species:genus ratio.
- Even though probability of extinction and of spawning new genus is age-dependent for each genus, the net origination and extinction rates of genera (in aggregate) reach constant values.
- This is seen in stochastic simulations as well as in model calculations.
1.4.2 Stabilization of species:genus ratio

- Independent of initial species:genus ratio.

**Figure 4.** Analytic solutions for the species/genus ratios given the origination and extinction probabilities and initial diversity conditions for the two cases in figure 3. Note that for both cases the species/genus ratio initially changes rapidly, but stabilizes by about 15 to 20 million model years; this coincides with the beginning of exponential growth in genera shown in figure 3.
Appendix 2: Demonstration that the Paraclade Size Frequency Distribution Stabilizes with the Hierarchical Branching Model

The probability that a paraclade, beginning with one lineage, will have exactly \( n \) species at time \( t \) is given by the equation (Bailey 1964: eq. 8.46; Raup 1985: eq. A17):

\[
p_{n,t} = (p_{n,t})(1 - \beta)^{\beta_{n-1}} \tag{A7}
\]

where \( p_{n,t} \) is equation A5 in Appendix 1, and

\[
\beta = (p_{o,t})\lambda/\mu \tag{A8}
\]

where \( p_{o,t} \) is equation A4 in Appendix 1.

When equation A7 is solved for all "reasonable values" of \( n \), a paraclade size frequency distribution is produced for a single paraclade that survives until time \( t \) (Raup 1985). If this distribution is multiplied by all paraclades arising at the same time, a size frequency distribution for a cohort of paraclades at time \( t \) is generated. Summing this distribution for all cohorts arising up to \( t - 1 \) will produce the paraclade size frequency distribution for all paraclades surviving to time \( t \). This distribution is given by the following general summation:

\[
\sum_{j=1}^{t-1} (p_{n,j})(G_{\text{orig}})(p_{n,t-1}) \tag{A9}
\]

where \( G_{\text{orig}} \) is equation A2 in Appendix 1.

The size frequency distribution converted to percent for the diversifying superclade in case 2 of figure 3 is shown for six time intervals in table 4. Only data for \( n = 1 \) to 10 species are shown.

Note that the size frequency distribution stabilizes by about 20 m.y., the same time that exponential growth begins in figure 3. Yule (1924) showed the same phenomenon for a slightly different evolutionary model that incorporated probabilities of creating new species and new genera, but ignored species extinction. The data shown here are only for the number of species 1 to 10, and the percents given total to values much less than 100, indicating that there are many genera with species numbers greater than 10. This is a result of the asymptotic properties of equation A7, and hence, Raup’s caution that this equation be solved only for all reasonable values of \( n \).
1.5 Estimating parameters

1.5.1 Patzkowsky’s approach is to estimate $p$ and $q$ by survivorship analysis of genera...

1.5.2 ...then to estimate $g$ by finding value that yields best fit to apparent exponential phase of diversification.

This is done by numerical optimization.

![Graph showing diversity over time](image)

**Figure 5.** Global post-Cambrian diversity curve for bivalve genera plotted on semilogarithmic coordinates. Bivalves appear to have undergone sustained exponential growth at least since the Carboniferous. Note the periods of apparently high rates of origination of genera in the Ordovician and following most of the mass extinctions, indicated by arrows.
1.5.3 Note that long-term genus diversity trajectories of most groups are not exponential (in violation of model).

Thus it would be difficult to fit parameters to *entire* diversity history.
1.6 Applications

1.6.1 Macroevolutionary lags

- Use simulation to determine range of diversity trajectories expected under homogeneous model.

- Test whether observed trajectory is significantly delayed.
1.6.2 Accelerations in diversification following extinction events.

- Use simulation to determine range of diversity trajectories expected under homogeneous model.

- Test whether observed rebound is more rapid than expected.

- Are results affected by not conditioning on survival to the Recent?

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**Figure 10**: Model and empirical rebounds for the periods following the Late Permian (A) and end-Cretaceous (B) mass extinctions. The median and high and low values for 100 Monte Carlo simulations are shown as solid black lines and indicate the complete range of values produced (95% confidence interval). The empirical rebounds are shown as solid black lines with triangles and indicate the complete range of values produced (95% confidence interval). Note that for both cases, the empirical rebound falls outside of the highest values produced by the model rebound.
1.6.3 Proportion of speciation events that give rise to new genera.

- Under homogeneous model this should be constant.

- Empirically the ratio of \( g/S \) is sometimes higher during early phases of diversification ("adaptive radiations").

## Table 2.

<table>
<thead>
<tr>
<th>Articulate brachiopods</th>
<th>( \lambda^* )</th>
<th>( \mu^* )</th>
<th>( \gamma )</th>
<th>( \gamma/S )</th>
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</thead>
<tbody>
<tr>
<td>Cambro-Ordovician radiation</td>
<td>0.04</td>
<td>0.09</td>
<td>0.11</td>
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<tr>
<td>Carboniferous background</td>
<td>0.07</td>
<td>0.08</td>
<td>0.02</td>
<td>0.22</td>
</tr>
<tr>
<td>Bivalves</td>
<td>( \lambda^* )</td>
<td>( \mu^* )</td>
<td>( \gamma )</td>
<td>( \gamma/S )</td>
</tr>
<tr>
<td>Silurian rebound</td>
<td>0.10</td>
<td>0.11</td>
<td>0.07</td>
<td>0.41</td>
</tr>
<tr>
<td>Silurian background</td>
<td>0.10</td>
<td>0.11</td>
<td>0.01</td>
<td>0.09</td>
</tr>
<tr>
<td>Carboniferous rebound</td>
<td>0.01</td>
<td>0.02</td>
<td>0.03</td>
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<td>0.04</td>
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<td>Triassic rebound</td>
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<td>0.08</td>
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</tr>
<tr>
<td>Triassic background</td>
<td>0.05</td>
<td>0.06</td>
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<tr>
<td>Tertiary rebound</td>
<td>0.00</td>
<td>0.05</td>
<td>0.12</td>
<td>1.00</td>
</tr>
<tr>
<td>Tertiary background</td>
<td>0.10</td>
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<td>0.02</td>
<td>0.17</td>
</tr>
<tr>
<td>Carboniferous-Cenozoic expansion</td>
<td>0.07</td>
<td>0.09</td>
<td>0.03</td>
<td>0.30</td>
</tr>
<tr>
<td>Chelostome bryozoans</td>
<td>( \lambda^* )</td>
<td>( \mu^* )</td>
<td>( \gamma )</td>
<td>( \gamma/S )</td>
</tr>
<tr>
<td>Cretaceous radiation</td>
<td>0.08</td>
<td>0.11</td>
<td>0.22</td>
<td>0.73</td>
</tr>
<tr>
<td>Cretaceous background</td>
<td>0.12</td>
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<td>Mammals</td>
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<td>( \gamma )</td>
<td>( \gamma/S )</td>
</tr>
<tr>
<td>Paleocene radiation</td>
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<td>0.05</td>
<td>0.15</td>
<td>0.94</td>
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<tr>
<td>Paleocene background</td>
<td>0.00</td>
<td>0.05</td>
<td>0.06</td>
<td>1.00</td>
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</table>

*All estimates of \( \lambda \) and \( \mu \) based on dynamic survivorship analysis of genera with stage or substage resolution except for mammals which are based on families with stage resolution. Time scale is from Harland et al. (1990) with a revised Cambrian time scale based on Bowring et al. (1993) and Jansa et al. (1994). Stratigraphic range data for articulate brachiopod, bivalve, and chelostome bryozoan genera provided by J. J. Sepkoski, Jr. Stratigraphic range data for mammal families from Stucky and McKenna (1993). Brachiopods: Ordovician radiation rates based on 209 genera originating in the early to middle Ordovician (Tremadoc-Llandeilo). Background rates based on 275 genera originating in the Carboniferous (Tournaisian-Moscovian). Bivalves: Silurian, Carboniferous, Triassic, and Tertiary rates based on genera originating during radiation and background times. Silurian rebound (Llandovery-Pridoli, 43 genera); background (Gedinnian-Prasinian, 34 genera). Carboniferous rebound (Tournaisian-Serpkovan, 42 genera); background (Bushkovan-Sakmarian, 42 genera). Triassic rebound (Induan-Carnian, 87 genera); background (Norian-Pliensbachian, 80 genera). Tertiary rebound (Danian-lower Eocene, 120 genera); background (middle and upper Eocene and Oligocene, 79 genera). Carboniferous-Cenozoic expansion rates based on 913 genera originating in Mesozoic and Cenozoic. Chelostomes: Cretaceous radiation rates based on 53 genera originating in middle Albian through Coniacian. Background rates based on 49 genera originating in middle Eocene through Miocene. Mammals: Tertiary radiation rates based on 67 families originating in the Danian and Thanetian. Background rates based on 139 families originating in Eocene through Miocene.
• Use bootstrap resampling of genus ranges, each time followed by estimation of 
\((p, q, g)\), to determine overall sampling distribution of \(g/S\). Find that some observed 
values fall in extreme tail.

| Table 3. Results of a randomization test that compared 
| \(\gamma\) as a proportion of total speciation rate (\(S\)) during evo-
| lutionary radiations to \(\gamma\) as a proportion of \(S\) during 
| background times (see text). Significance levels \((p)\) re-
| present the proportion of comparisons in which \(\gamma/S\) was 
| larger for the radiation. For each taxonomic group, the 
| bootstrapped data for the radiation or rebound period 
| were compared to the bootstrapped data for the appro-
| priate background period (table 2). For bivalves, two 
| comparisons were made for each of the four rebound 
| intervals, one comparison was made to the appropriate 
| background period and one was made to the Carbonif-
| erous–Cenozoic background rates. 

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</tr>
</tbody>
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* Significant at 95% level.
** Significant at 99% level.
*** The result for the Paleocene radiation of mammals does not imply 
that \(\gamma\) for the radiation is significantly less than \(\gamma\) for the background period. 
The calculated \(p\)-values are for a one-tailed hypothesis and represent the 
proportion of comparisons where \(\gamma\) for the radiation exceeded \(\gamma\) for the 
background period.
2 Assessing alternative survivorship models with higher taxa

Ongoing work by Carl Simpson

2.1 Three models

\( p \) and \( q \) denote species-level rates; \( Q \) denotes genus-level extinction rate.

2.1.1 Genus is focal level of extinction:

\[
P_{s,t} = e^{-Qt}
\]

Model has one relevant parameter.

2.1.2 Genus extinction results purely from upward causation of events at species level:

\[
P_{s,t} = \frac{1}{1 + pt}
\]

\[
= 1 - \frac{q[e^{(p-q)t} - 1]}{pe^{(p-q)t} - q}
\]

if \( p = q \)

\[
if \quad p \neq q
\]

Model has two relevant parameters.

2.1.3 Genus extinction results from both upward causation and genus-level process:

\[
P_{s,t} = \left[\frac{1}{1 + pt}\right] \cdot e^{-Qt}
\]

\[
= \left[1 - \frac{q[e^{(p-q)t} - 1]}{pe^{(p-q)t} - q}\right] \cdot e^{-Qt}
\]

if \( p = q \)

\[
if \quad p \neq q
\]

Model has three relevant parameters.
2.2 Statistical question: how to assess relative fit?

2.2.1 More complex model must have higher support.

2.2.2 Use $\text{AIC}$ to compare the models of different complexity.

2.2.3 Note that at high species-level turnover rates, survivorship of genera that results from upward causation can roughly mimic exponential model, especially if you do not sample the right tail.

![Figure 3](image.png)

**Figure 3.** A: Cohort survivorship plotted logarithmically as a function of time after origin. Rectangles represent Cambrian cohorts and diamonds represent Ordovician cohorts. The two curves represent the best fit to the data, the lower curve for the Cambrian and the upper curve for the Ordovician. B: Measures of longevity tabulated from stratigraphic range data. Best-fit curves as in A are included for comparison. X’s represent the generic half-life, 75-percent-life and 90-percent-life based on the first convention for the placing of origins and extinctions. Triangles represent the generic half-life, 75-percent-life and 90-percent-life based on the second convention. (See the text for a discussion of conventions.) Circles represent generic half-life, 75-percent-life and 90-percent-life based on Equations (4) and (5). Note that the tabulated half-lives for the Cambrian and Ordovician nearly coincide, in contrast to the half-lives calculated from Equation (4).

2.3 Biological question: what is (or could be) the nature of genus-level process?