MODELING THE DYNAMICS OF DIVERSIFICATION

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Archaeology as an evolutionary science

“The goal of this session to discuss the practical application of computational methods for identifying drift, selection, innovation, transmission bias, extinction, and many other evolutionary processes in the archaeological record”
Archaeology as an evolutionary science

Evolutionary thinking in archaeology has often balanced precariously between micro and macro scales of analysis.

Micro-evolutionary questions
  - Drift, selection, mutation, transmission bias

Macro-evolutionary questions
  - Origination, extinction, diversification

Archaeological data is often most informative at the macro-evolutionary scales.
Archaeology as an evolutionary science

Our ability to evaluate macro-evolutionary questions depends on our ability to track changes in diversity

Diversity as the “consequence of evolution”

**Richness**

How many types of things?

\[ N \]

**Evenness**

How many of each type of thing?

\[ \sum p_i^2 - \sum p_i \ln p_i \]

Figures adapted from Stirling (2007)  
Hegmon et al. 2016
Diversity in the archaeological record

- Diversity indices do not consider that the diversity in one time step is a product of the diversity in the previous time step.

- Diversity indices are summary statistics and mask that diversity is a product of both origination and extinction.

- Measuring diversity does not always capture the patterns and processes of diversification.
Modeling diversification

A stratigraphic approach

‣ Does not require a phylogeny
‣ Uses richness (counts) and occurrence data (first, last)

Raup et al. 1973
Lyman and O’Brien 2000; 2009
Modeling diversification

A stratigraphic approach was integrated into a model-based Bayesian framework by Silvestro et al. (2014)

- Joint estimation of origination and extinction rates through continuous time
- Birth-death model
- Incorporates uncertainty about occurrence data
Modeling diversification

PyRate

- Available at github.com/dsilvestro (Daniele Silvestro)

Six tutorials available
- Generating input files
- Estimating origination and extinction rates
- Plotting and summarizing output

- Birth-Death models with time-continuous correlates
- Other Birth-Death models (trait dependent, age dependent, chronospecies)
- Dispersal Extinction Sampling

Draft tutorial for cultural data under development at github.com/erikgjes (PyRate for Cultural Evolution)
Diversification of Pottery Wares

Southwest Social Networks Database

- 4.3 million ceramic artifacts from 700 sites
- 635 types
- 78 wares
- Age ranges for each type and ware

<table>
<thead>
<tr>
<th>Region</th>
<th>Ware</th>
<th>First_Year (BP)</th>
<th>Last_Year (BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cent_Highlands</td>
<td>Grasshopper Ware</td>
<td>620</td>
<td>575</td>
</tr>
<tr>
<td>Chihuahua</td>
<td>Aztec Black Ware</td>
<td>750</td>
<td>500</td>
</tr>
<tr>
<td>Chuska / Chaco</td>
<td>Cloverdale Brown Ware</td>
<td>900</td>
<td>800</td>
</tr>
<tr>
<td>Hopi</td>
<td>Kinishba Ware</td>
<td>700</td>
<td>650</td>
</tr>
<tr>
<td>Phoenix Basin</td>
<td>Almeda Brown Ware</td>
<td>1250</td>
<td>550</td>
</tr>
<tr>
<td>Puerco West</td>
<td>San Carlos Brown Ware</td>
<td>750</td>
<td>550</td>
</tr>
</tbody>
</table>
Diversification of Pottery Wares

python PyRate.py -d sw_pottery.txt -A 4

Additional graphics done in R
### Diversification of Pottery Wares

#### American SW

<table>
<thead>
<tr>
<th>Model</th>
<th>Origination</th>
<th>Extinction</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-rate</td>
<td>0.4285</td>
<td>0.0841</td>
<td></td>
</tr>
<tr>
<td>2-rate</td>
<td>0.3875</td>
<td>0.4141</td>
<td></td>
</tr>
<tr>
<td>3-rate</td>
<td>0.1323</td>
<td>0.3263</td>
<td></td>
</tr>
<tr>
<td>4-rate</td>
<td>0.0288</td>
<td>0.1118</td>
<td></td>
</tr>
</tbody>
</table>

#### Extinction Shift Point 1

<table>
<thead>
<tr>
<th>Time (BP)</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>700-600</td>
<td>0.9991</td>
</tr>
<tr>
<td>900-800</td>
<td>0.0009</td>
</tr>
</tbody>
</table>

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**Python Command**

```python
python PyRate.py --d sw_pottery.txt --A 4
```
Diversification of Pottery Wares

American SW

What is the added value?

Decline in ware diversity

- Stable origination with dramatic rise in extinction

What underlying processes does this suggest?

- Rapid environmental change
- Increased competition
- Coextinction

Stable origination

Decreasing origination

Increasing extinction

Increasing extinction

Stable extinction
Archaeology as an evolutionary science

Conclusions

The scale of archaeology data makes it difficult to infer micro-evolutionary processes.

Potential for modeling “macro-evolutionary” patterns that can help narrow the range of evolutionary processes:

- Rates of diversification within traditions across time
- Interaction between origination and extinction rates

PyRate and other emerging model-based methods in paleobiology may offer significant benefits.
Special thanks to:

Michael Alfaro  Jonathan Chang  Christopher Kelty  Daniele Silvestro

META KNOWLEDGE NETWORK  John Templeton Foundation

References listed here available on request: eg540@cam.ac.uk or @gjesfjeld
BAYESIAN ESTIMATION OF RATES

Posterior Probability

\[ P(s, e, q, \lambda, \mu | D, N_{OBS}) \propto P(D | s, e, q) P(s, e | \lambda, \mu) P(\lambda, \mu | N_{OBS}) p(q) \]

1. Times of origination and extinction (s, e)
2. Preservation rate (q)
3. Rates of origination and extinction (\lambda, \mu)

Likelihood

Probability of occurrences and waiting times conditional on at least one occurrence

Prior Probability

Probability of the reconstructed origination / extinction times given the origination/extinction rates

Hyperprior

Probability of the reconstructed origination / extinction rates as a result of the number of observed at present

Prior Probability

Probability of preservation rate given an arbitrary prior distribution (gamma)

Silvestro et al. 2014 (Sys Bio)
BDMCMC ANALYTICAL PROCESS

1. Initialize the model (starts with constant rates)

2. Calculate death rates for each component of the model based on a constant birth rate
   a. Each component is a point in parameter space based on origination and extinction rates

3. Calculate the total death rates assigned to each component

4. Simulate next model jump based on the continuous time Markov birth-death process
   a. Jump will either be a new “birth” or a “death”

5. Rescale all model components and continue until time is reached