

**Evaluating the Fossil Record with Model Phylogenies**  
Cladistic relationships can be determined without ideas about stratigraphic completeness; implied gaps might be useful for evaluating stratigraphy.

Sum of range extensions / ghosts = stratigraphic debt *sensu* Fisher (1992).

Many metrics attempting to quantify sampling make naïve assumptions about the minimum possible gaps!

### Tree-based evaluations of the fossil record

- Phylogeny can be estimated independently of stratigraphic distributions
  - Necessarily implies gaps in the record
- Two basic types of metrics:
  - Consistency: measures general agreement between predicted and observed orders of appearance;
  - Gap: measure the sum of gaps implied by a phylogeny.

### Tree-based Assessments of Sampling: Stratigraphic Consistency Index

- Consistent node: one in which the sister taxon appears prior to the node;
- $SCI = \text{Consistent nodes} / \text{All nodes}$

### Relative Completeness Index

- $RCI = 1 - (\sum \text{Gaps} / \sum \text{Ranges})$

### Gap Excess Ratio

- $GER = (M-g)/(M-m)$  where:
  - M = maximum possible gaps (=  $\sum$  first appearances);
  - g = implied gaps;
  - m = minimum possible gaps.

### Manhattan Stratigraphic Metric

- $MSM = m/g$  where:
  - g = implied gaps;
  - m = minimum possible gaps.

- Based on consistency index.

### Relationships between Sampling & Tree-Based Sampling Metrics

- RCI & SCI reflect sampling; GER & (especially) MSM do not.

### Properties of the Components to Metrics: Gaps

- Sum of gaps increases exponentially as sampling gets worse.
- Sum of minimum gaps also increases exponentially as sampling gets worse.
- Sum of maximum gaps also increases exponentially as sampling gets worse.
- Sum of ranges decreases exponentially, but with minimum determined by the number of taxa.

Problem: People often forget that we do not always have gaps!

If taxa have good fossil records, then many trees will have minimum possible gaps of 0.

### Ignoring Ancestors greatly exaggerates implied Range Extensions

Based on 1000 simulations of 36 sampled OTU's at each  $R$  with  $\mu = 0.4$  per unit.

The expectations for wide range of preservation rates become indistinguishable.

Distortion is huge at sampling levels thought to be typical for marine invertebrates and even some land vertebrates.

This is not the case if one accommodates ancestors.

### Relationships between Sampling & Tree-Based Sampling Metrics

- Failing to account for ancestors makes things worse...

### Using stratigraphic data to assess phylogenies

- Stratocladistics: minimize stratigraphic gaps and homoplasies.
- Confidence Interval Sieving: rejects trees with gaps exceeding 95% confidence intervals (a la Strauss & Sadler 1989).
- Stratolikelihood: determines the probability of stratigraphic distributions given tree and sampling rates.

### Stratocladistics

- First and last stratigraphic occurrences of each taxon noted.
- A gap through an interval treated as evidence against a phylogeny equal to that of an extra morphological change.
- “Stratigraphic debt” reduced by ancestor-descendant relationships as well as by altering cladistic topology.
- Generates phylogeny, not just a cladogram.
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- Sampled ranges of 6 taxa.
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- 6 taxa coded for 7 characters (each row a character).
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- Parsimony tree for 6 taxa given matrix.
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- Phylogeny matching parsimony tree; 8 steps, but gaps (= 3 units of strat. debt) or 11 “steps” overall.
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- Phylogeny matching parsimony tree; B set as ancestor to C because it has no apomorphies.
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- D not considered ancestral because it has an apomorphy; however, that causes 2 gaps.
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- Making D ancestral increases steps to 9 but reduces strat. debt to 1, giving a total score of 10.
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- Making E ancestral saves 1 step and induces 1 gap.
- No total savings, but making E ancestral reduces unsampled ancestors (another parsimony criterion).

### Assumptions of Stratocladistics

- Probability of a character changing comparable to probability of a unit of stratigraphic debt.
  - $(\ln P[\text{gap}] + \ln P[\text{stasis}]) \leq \ln P[\text{change}]$
- Probability of all gaps has the same meaning throughout the tree.

### Confidence Interval Sieving

- Probability of gaps assessed based on confidence intervals;
  - Number of sampling opportunities over gap considered.
    - If there are no opportunities, then there really is no gap.
  - Probability of missing a taxon  $n$  times assessed given the number of finds and the number of possible finds within its range;
  - Separate “time scales” used for different geographic / environmental units.
- If significant gaps exists between a “younger” sister taxon and an “older” species, then apomorphies will be reversed;
  - This lengthens the tree and makes it possible for another tree to be shorter;
  - The most poorly sampled member of a clade used to formulate CI for that clade;
- If significant gaps exist between sister clades, then the tree is simply rejected.
- Shortest tree with no significant gaps is taken.
- Case simplest for bifurcations...
- ... but not much different for polytomy.
- Example of how stratigraphy rejects one phylogeny in favor of another.
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### Confidence Interval Sieving Assumptions

- Strength of characters uniting a clade ignored;
  - Gap supported by slowly evolving characters treated no different than a gap supported by highly homoplastic ones;
  - Degree of significance no considered.
- Method simply rejects hypotheses; it does not show how well they

predict data.

### “Horizon Scales” for Different sampling realms

- “Height” measures number of sampling opportunities; the “duration” of a time interval can be very different in different sampling realms.

### Stratolikelihood

- Exact probability of gaps calculated given sampling opportunities.
- Likelihoods of gaps based on sampling rates within lineages;
  - Because sampling rate is unknown, the rate and gap can be maximized;
  - Shifts in sampling rates within lineages or within clades taken into account.
- $L[\tau \mid \text{stratigraphy}] \times L[\tau \mid \text{morphology}] = L[\tau \mid \text{data}]$

### Sampling Rates ( $\theta$ ) of Stratolikelihood

- Given that a taxon is found  $n=7$  times in  $R=11$  horizons, the most likely sampling rate is *not*  $7/11$ , but instead is  $5/9$ .....

### Sampling Rates ( $\theta$ ) of Stratolikelihood (assessment from simulations)

- ... as  $n/R$  chronically overestimates  $R$ . This is because we do not know the true duration over which we made those  $n$  finds.

Use sampling rate ( $\theta$ ) maximizing the probability of a  
sampling gap AND of the observed finds

- i.e., use  $n / D$  (where  $D$  is the number of finds over the hypothesized duration).

### Finding Variable $\theta$ in Stratolikelihood

- Within lineages, one can test whether  $\theta$  differs significantly early or late in a stratigraphic range.

### Stratolikelihood

- Like stratocladistics, tree evaluated “equally” by both morphologic and stratigraphic data.
- Like confidence interval sieving, importance of gap depends on the density of sampling and in which sampling realm the gaps should exist.
- Unlike either, it allows different characters to present different levels of evidence against phylogeny.