Comparative methods wrap-up and “key innovations”

The study of character evolution

• Many methods allow one to study the evolution of single traits or pairs of potentially correlated traits, given a phylogeny
• What do we do about phylogenetic uncertainty?

One approach

• Repeat the analysis over a number of plausible trees and see if the results are robust to phylogenetic uncertainty

A better approach

• Treat the phylogeny as a nuisance parameter
• E.g., estimate the posterior probability of two traits being correlated, given the trait data, some sequence data for the same species, a model for the evolution (both traits and sequences), and priors on all the parameters

Stochastic mapping


• Use a posterior distribution of trees
• Simulate evolution up each tree (only keeping simulations that arrive at the observed data)
• Look at the simulations to see if they show evidence of directionality, correlated evolution, etc.
• Implemented in SimMap (brahms.ucsd.edu/simmap.html)

Obtain a distribution of histories
Testing Causal Hypotheses

- Taking account of phylogeny we can establish the extent of correlations between traits.
- What about causal statements?
  - This trait evolved because it improved performance of this biological role (a hypothesis of adaptation).
- Can be assessed if one has a clear causal model.

Are opposable thumbs in humans adaptations for tool use?

- Opposable thumb improves performance of this biological role.
- Making better tools improves fitness.
- Opposable thumbs evolved after tool use.

Are flexible shoulders in humans adaptations for throwing?

- Flexible shoulder improves performance of this biological role.
- Throwing projectiles better improves fitness.
- Flexible shoulder evolved before tool use.

The concept of key innovation

- Originally referred to traits that permitted invasion of a new “adaptive zone” (Simpson).
- Nowadays, associated with changes in diversification rate.
- Adaptations are to natural selection what key innovations are to lineage (“species”) selection.

How do we show that a trait is a key innovation?

- Correlation: the trait evolves on a branch to which we map a jump in the rate of diversification.
- Causation: the trait is repeatedly associated with accelerated diversification and/or we have a model that predicts a causal effect.
Detecting changes in the rate of species accumulation

- Under a constant rate of speciation (with no extinction), which of the following trees is more likely?

They are equally likely!

Explanation

What is the probability that the next speciation event will be on the ‘A’ side? 50%

A B

The counterintuitive result

- All basal splits equally likely: e.g., for 100 taxa, a 1:99 basal split is as likely as a 50:50 split
- If we have a prior hypothesis: need a 95:5 imbalance or more to statistically support the hypothesis

Becomes stronger when there is a repeated pattern

- If the delay until the second speciation ($t$) is long, then acceleration in the ingroup is implied (Sanderson and Donoghue 1994; Science)

Taking account of time helps

- If the delay until the second speciation ($t$) is long, then acceleration in the ingroup is implied (Sanderson and Donoghue 1994; Science)

<table>
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<th>Taxon with motor types</th>
<th>Species</th>
<th>Motor type</th>
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<td>Nigella, Actaea, Cimicifuga</td>
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<td>Gymnura, Buixia, Noroniana and Saussurea</td>
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<td>0.598</td>
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</table>
Application to *Aquilegia*

How can one study changes in diversification rate?

- Look for a repeated pattern that trait x correlates with clades that are bigger than their non-x sister groups
- Provides evidence that the character is a **key innovation**