Independent Contrasts

- Any question that involves comparisons among multiple species should be done in a phylogenetic context.

- For most traits, expectation is that phenotypic differences will correlate with phylogenetic differences.

“Nothing in biology makes sense except in the light of evolution”
T. Dobzhansky, 1973

Independent Contrasts

- Evolution of the rete mirabile associated with swimbladder. Occurred 4 times independently, sample size is thus 4.

- In this other example, a trait changed once. Sample size is 1 regardless of how many species sampled.

Independent Contrasts

- Two habitats: desert and grassland

- Within each habitat you sample 5 species, measure a response variable related to precipitation (nephron length).

- Hypothesis: nephron length evolves in response to selection pressures in desert environments.

Hypothesis assumes statistical independence for each species. For each species, desert conditions selected for longer nephrons independently (and vice versa).

We know species inherit traits from common ancestors (phylogenetic constraints).

Assuming we know the “true” phylogenetic history of your 10 species, how do we test for or correct for this?
Independent Contrasts

- 10 species, all derived from one common ancestor. No phylogenetic information.

- Phylogeny known. Is trait of interest evolved independently?

Packages

- Analyses of Phylogenetics and Evolution
  - Reading/writing phylogenetic trees
  - Manipulating phylogenetic
  - Reading/writing DNA sequences
  - Computing distances from DNA sequences
  - Phylogenetic comparative methods
  - Estimation of ancestral characters
  - Analysis of diversification
  - http://ape.mpl.ird.fr/

- Geiger
- Picante
- Ade4
- phytools
Independent Contrasts

- Function `pic` (ape package)
  - `pic(x, phylo)`
    - `x` is the trait of interest
    - `phylo` is a phylogeny
    - The names in `x` must match the names in the phylogeny
    - Output is a series of independent contrasts of `x` as outlined in Felsenstein (1985).

```r
> tree.primates
Phylogenetic tree with 5 tips and 4 internal nodes.

Tip labels:

Rooted; includes branch lengths.
- weight
Homo Pongo Macaca Ateles Galago
4.094345 3.610918 2.370244 2.028148 -1.469676
> pic(weight, tree.primates)

6         7         8         9
3.3583164 1.1929305 1.5847389 0.7459435
```

```r
> cor.test(pic.X, pic.Y)
Pearson's product-moment correlation

data:  pic.weight and pic.longevity

r = 0.8296107, df = 4, p-value = 0.08224
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
0.1964310 0.9884173
sample estimates:
cor 0.8296107
```

```r
> cor.test(weight, longevity)
Pearson's product-moment correlation

data:  weight and longevity

r = -0.5179156, df = 3, p-value = 0.4821
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
-0.9874751 0.8823934
sample estimates:
cor -0.5179156
```

Fig. 1. A rooted tree for the five species of primates based on data from Gingerich (1984). The measurements body weights and longevity are taken from Eisenberg (1981).
Phylogenetic Signal
- Given a phylogenetic tree (topology and branch lengths), do closely related species tend to be more similar?
- If so, variance in independent contrasts will be low
- Permuting the tips of the trees and recalculating variance provides a test of significance:
  \[ K = \frac{\text{observed variance}}{\text{expected variance}} \]
  - \( K < 1 \) – no phylogenetic signal
  - \( K > 1 \) – close relatives more similar than expected at random

Phylogenetic signal
- Function `phylosignal` (picante package)
  - `phylosignal(x, phylo, reps, checkdata=TRUE)`
    - `X` is the trait of interest
    - `Phyl` is a phylogeny
    - `Reps` = number of permutations
    - `Checkdata=TRUE` will check that the phylogeny names match the trait names, otherwise the function assumes the order is the same
    - Returns measure of \( K \) (Bloomberg et al. 2003), observed variation in PIC, randomized variation in PIC and probability.

Mapping traits onto a phylogeny
- Function `contMap` (phytools package) will color a phylogeny by a continuous trait.
- Note that these are the raw values:
  ```
  > weights
  [1] 4.094345  3.610918  2.370244  2.028148 -1.469676
  ```
- `contMap(tree.primates, weight)`
Phylogenetic Signal

- Pagels $\lambda$
  - Scale the internal branches of the tree
  - $\lambda = 0$, "star tree" and no signal
  - $\lambda = 1$, full branch lengths best fit

Infering the historical patterns of biological evolution

Models of Evolution

- Phylogenetic signal indicates closely related species will be more similar than expected at random.

  - How do traits change?

  Brownian motion: traits change randomly.

  Differences among species should be tightly correlated with phylogenetic distance (time since divergence)
Models of Evolution

- Ornstein-Uhlenbeck model is Brownian motion with an attraction or tendency to return to the mean.

- In evolutionary terms, this would represent random variation around but not away from an optima.

- Parameter $\alpha$ represents the strength of attraction.
  - $\alpha = 0$ is Brownian

![Graph of Ornstein-Uhlenbeck model](image)

Function `fitContinuous` will evaluate multiple models of evolution for a trait or series of traits (model=\"lambda\" etc.)

- Default is Brownian Motion (leave out model=)
- \"lambda\" – Pagel’s lambda
- \"ou\” – Ornstein-Uhlenbeck
- \"white\” – white noise (all species from random normal distribution with no phylogenetic signal)
- Others…see help file

- Similar model comparison logic we used for AIC model selection can be used to evaluate these models – which is the best predictor of the observed data?

Assignment

- Reading


For longevity
Brownian, lambda, ou, white noise delta AIC:
[1]  2.162422  2.000013  1.999927  0.000000

For weight
Brownian, lambda, ou, white noise delta AIC:
[1]  0.00000  2.00000  2.00000  2.49594

What is the conclusion?
Is this consistent with the other analyses?
Assignment

- Starter script and phylogenetic tree:
  - Loads tree based on mtDNA data (652 bp COI) for 63 species

- Trait data: egg diameter for 63 species

- Is there a phylogenetic signal? Which model is the best fit?

- Does egg size differ among habitats?