# Phylogenetic comparative methods: Continuous characters

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# Outline

1. Lecture on models of continuous evolution
2. Tutorial on fitting a model; lambda
3. Tiny lecture on ancestral states
4. Tutorial on estimating ancestral states
5. Tiny lecture on Phylogenetic Generalized Least Squares
6. Tutorial on correlated evolution

# Continuous characters in linguistics and anthropology

In biology, it is easy: body mass, brain size, metabolic rate, etc.

In linguistics, many well-studied comparative traits are discrete. However, consider:
- phonemic inventory size (number of vowels, consonants, tones, contrasts, etc.)
- lexicon size (number of numeral classifiers, genders, body part terms, color inventories, kinship terms, other specific semantic classes)
- morphology (number of cases, verbal and nominal affixes, length of maximally inflected verb or noun (in morphemes), amount of compounding)
- syntax (percentage of SOV word order in corpus, amount of inflection when not obligatory)
- psycholinguistics (age of acquisition of particular lexical items, reading speed)
- evolutionary anthropology (brain size, position of larynx)

Anthropology:
- subsistence (amount of time spent farming, herding, hunting, fishing, gathering)
- material culture (size of floor area in housing, amount of dowry)
- anthropometric characters (height, weaning age, age at circumcision, amount of formal schooling, age at first birth, length of post-partum sex taboo)

# Components of a phylogenetic comparative analysis

- **data**: trees + trait data on tips

- **model**: description of evolutionary change

- **inference method**: Maximum Parsimony, Maximum Likelihood, Bayesian

- **parameter estimates**: node values, rates, etc.

# Models of continuous character evolution

"I simply want to correct for phylogenetic relatedness, just tell me what to do"

phylogenetic regression (R: pgls() in caper)

phylogenetic ANOVA (R: aov.phylo() in geiger)

phylogenetic principal component analysis
(R: phyl.pca() in phytools)

phylogenetic t-test (R: phyl.pairedttest() in phytools)

# Models of continuous character evolution

- Brownian motion
- Ornstein Uhlenbeck / stabilizing selection
- Spectational model of evolution / punctuated equilibrium
- Adaptive radiation / ecological niche-filling model

See Nunn (2011: 101-104) for an introduction and relevant references

# Models of continuous character evolution

- Which evolutionary model is preferred?

- Are there differences across groups of taxa in which model is preferred?

- Do both directions of change happen at equal rates?

- Are there temporal evolutionary trends?

- Is evolutionary change bounded or unbounded?
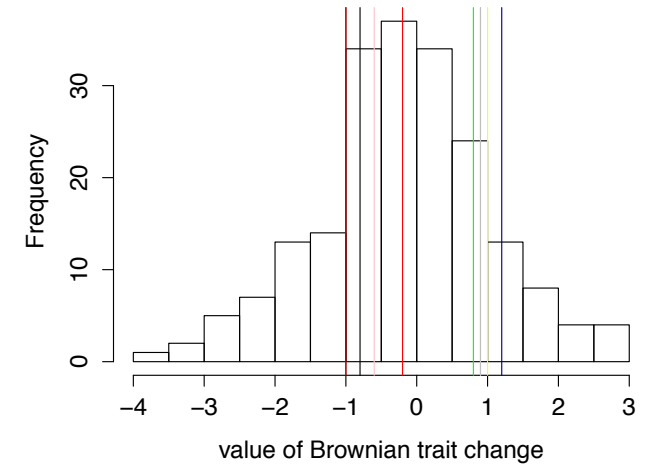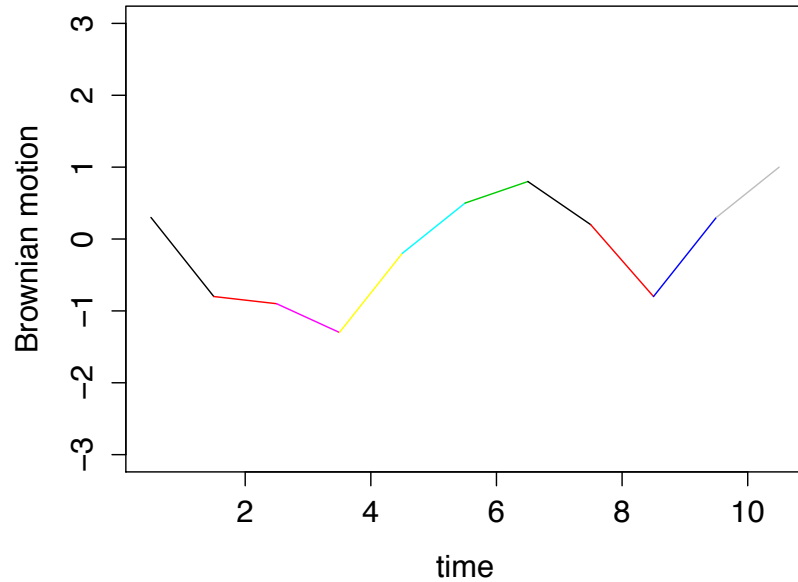
# Brownian motion

- can be considered a 'neutral' model of evolution
- a trait changes value at each of a huge number of very tiny time steps:
1. Each change is independent of previous change on that branch and on other branches;
2. Each change is randomly drawn from a normal distribution.
- For a collection of Brownian trait changes:
1. the mean change is zero
2. the variance of changes is constant
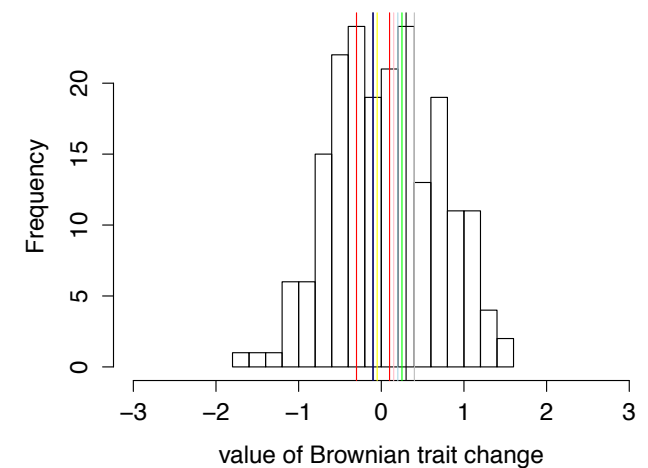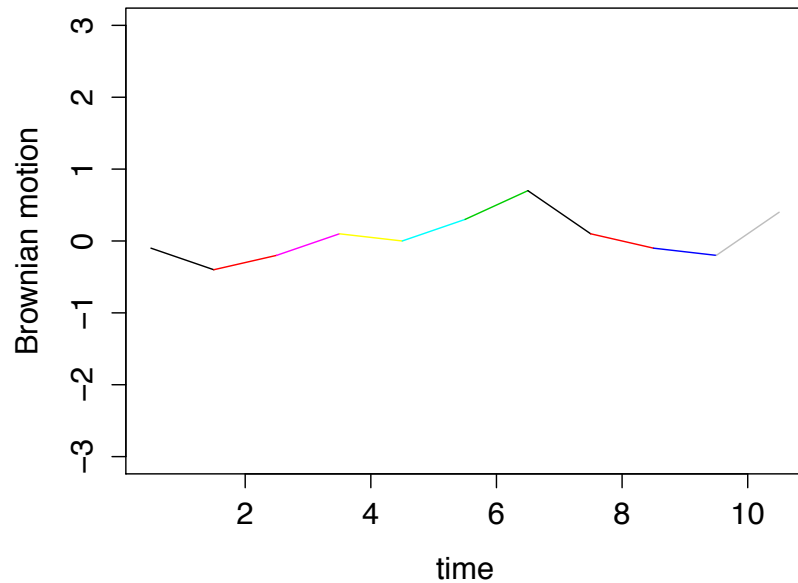3. the expected variance of trait change is proportional to branch length

# Brownian motion

A single trait on a a single branch through trait space over time
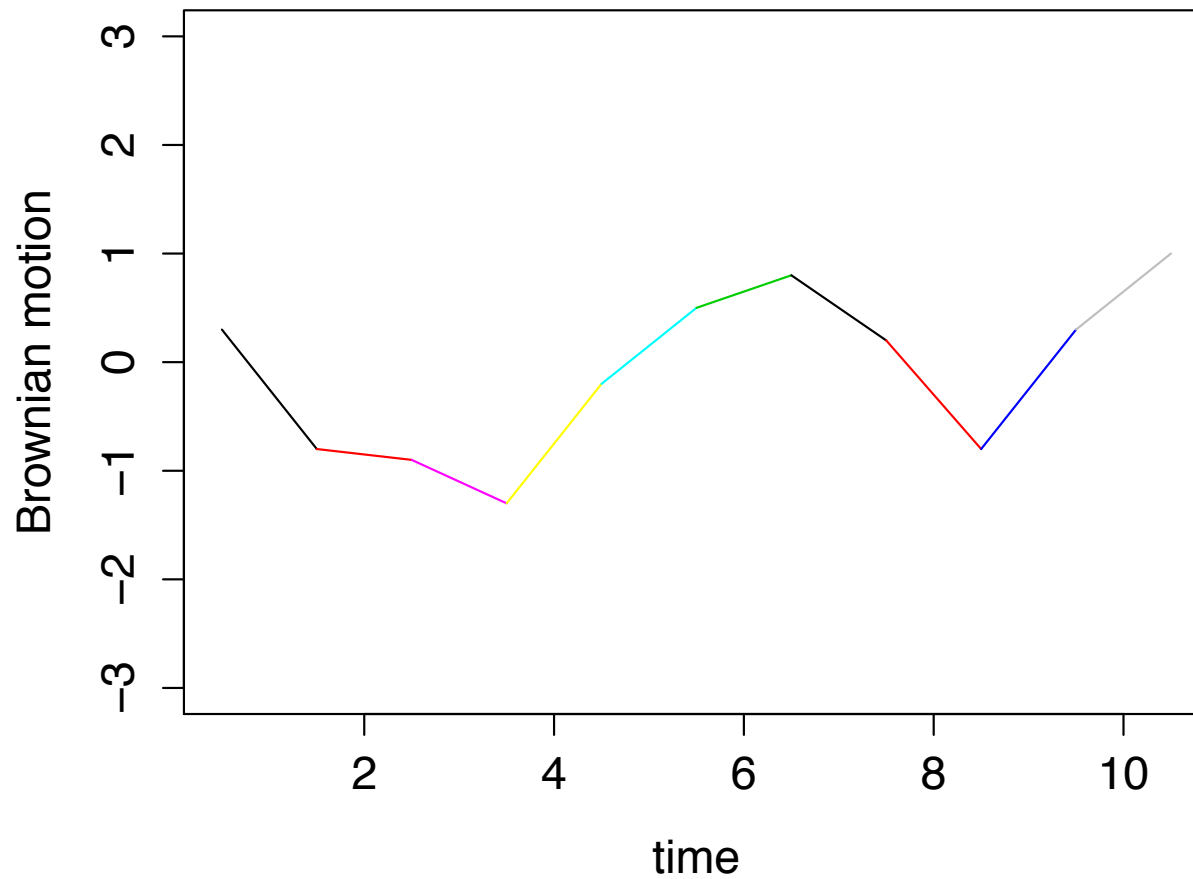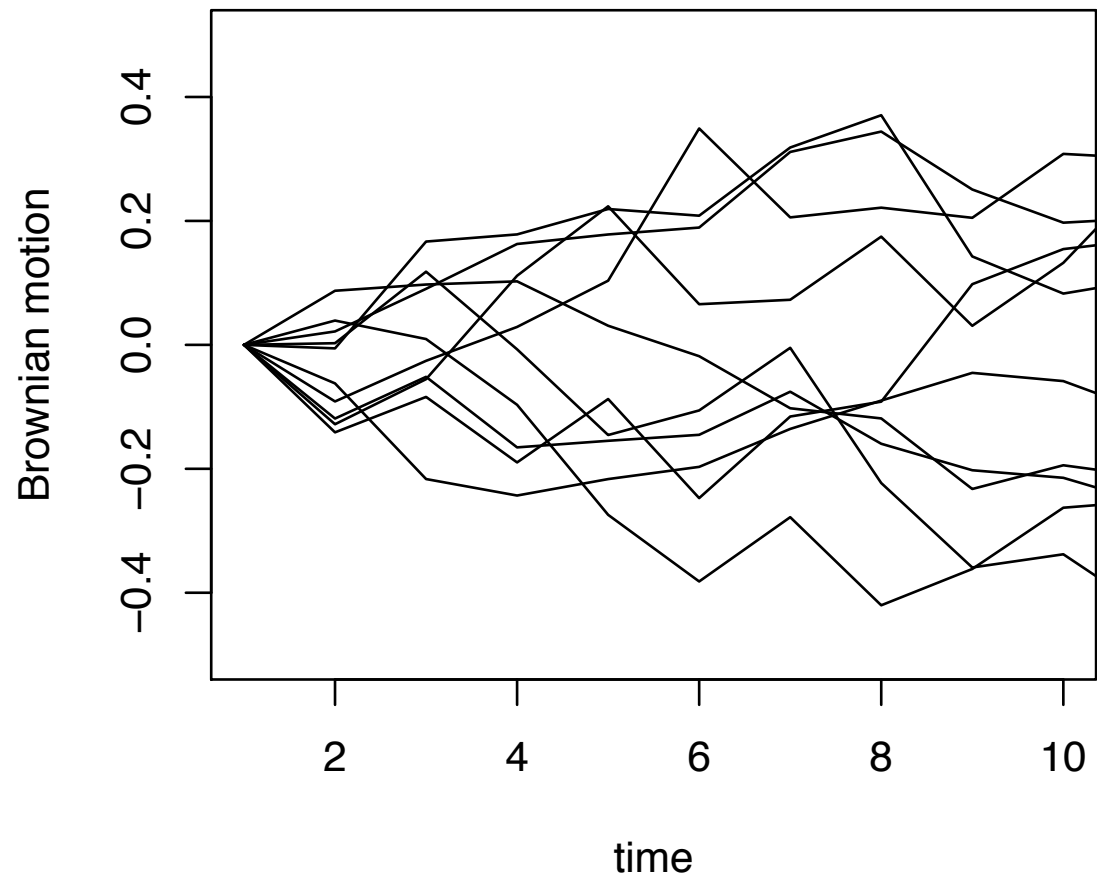
# Brownian motion



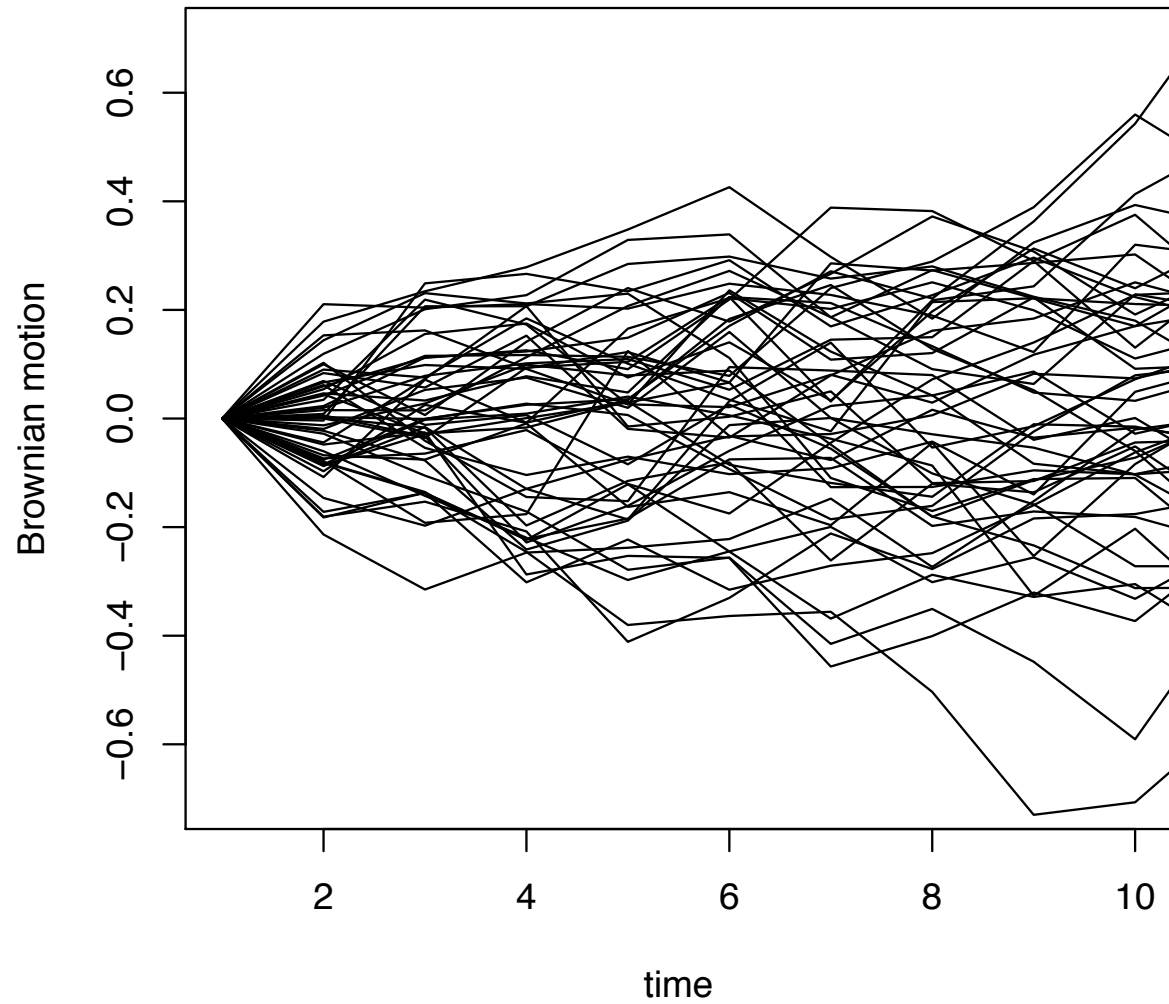higher variance = higher rate of trait change $\sigma^2$

lower variance = lower rate of trait change $\sigma^2$
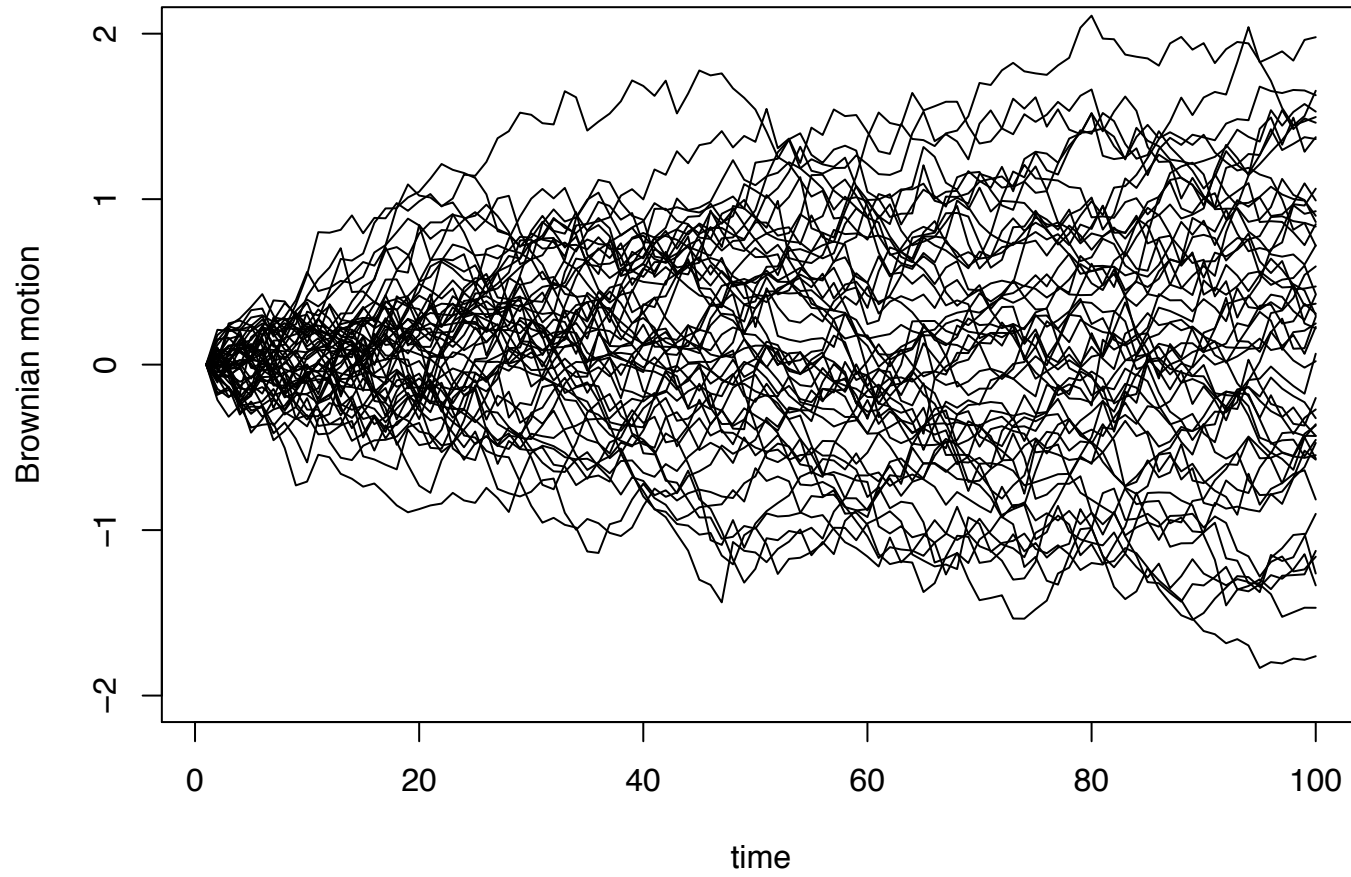
Brownian motion

Brownian motion

# Brownian motion



rate σ²
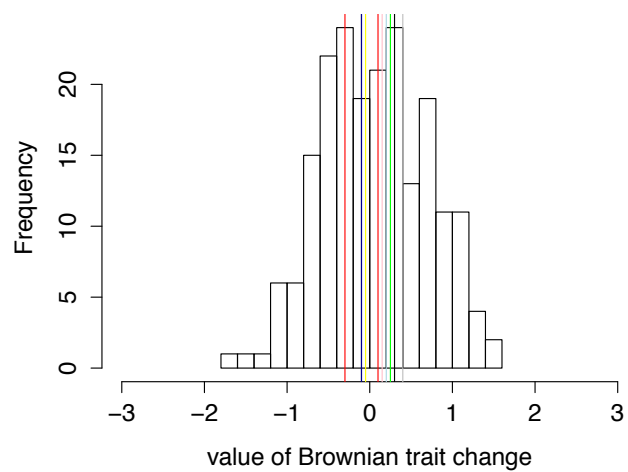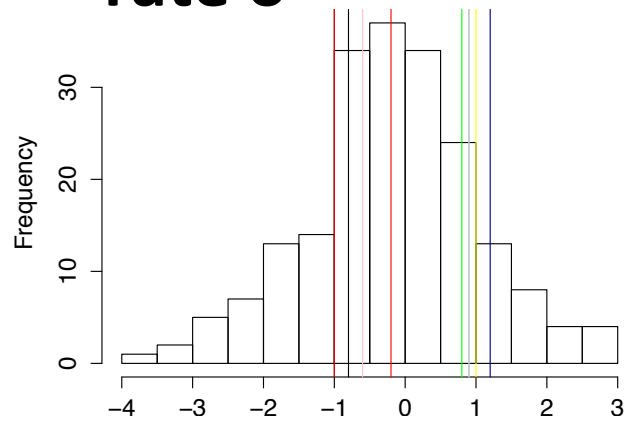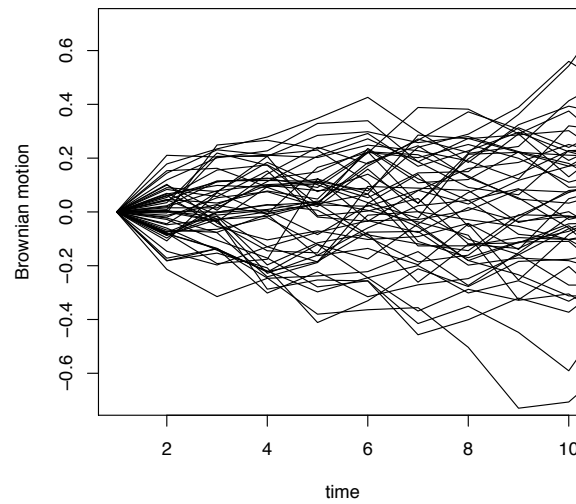
phylogenetic structure
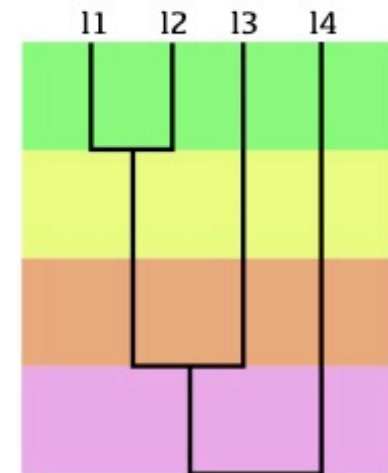
time

# Phylogenetic variance-covariance matrix

|    | l1 | l2 | l3 | l4 |
|----|----|----|----|----|
| **l1** | 1+2+1 | | | |
| **l2** | 2+1 | 1+2+1 | | |
| **l3** | 1 | 1 | 3+1 | |
| **l4** | 0 | 0 | 0 | 4 |
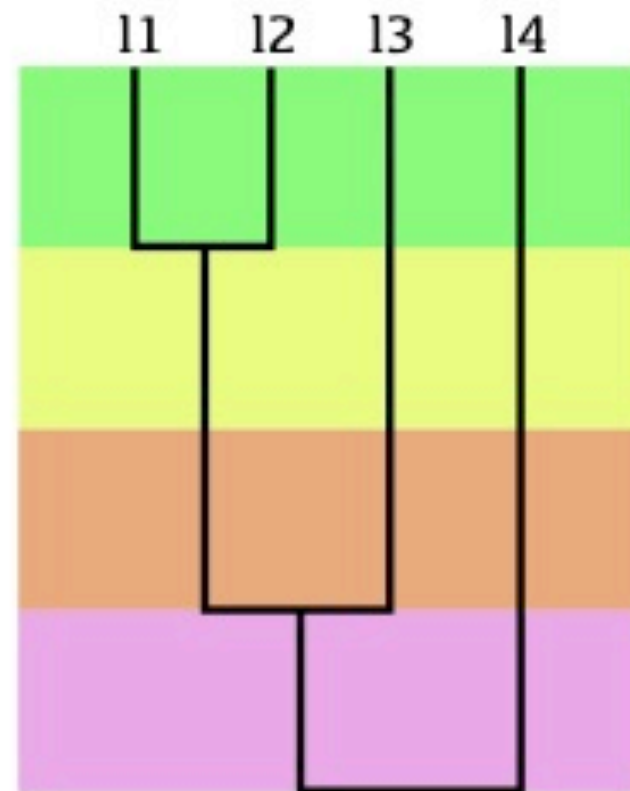
# Brownian motion

### rate σ²
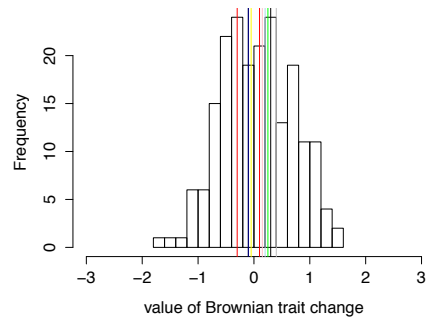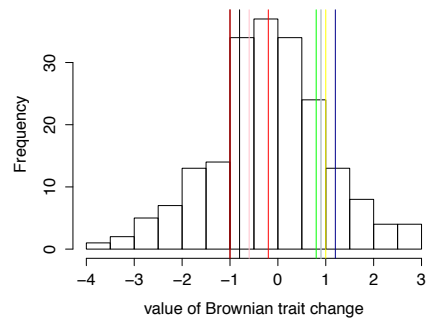


### time
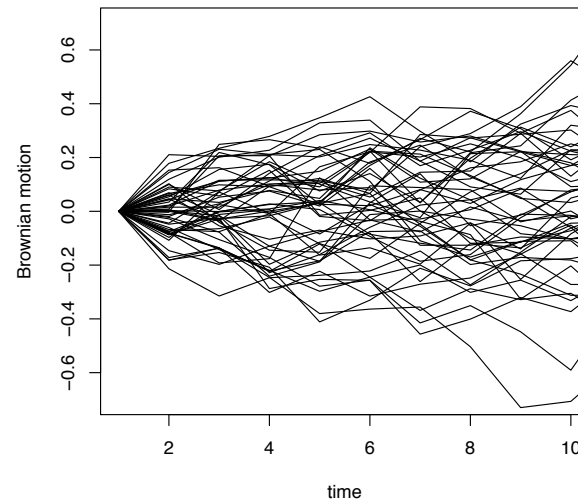


### phylogenetic structure
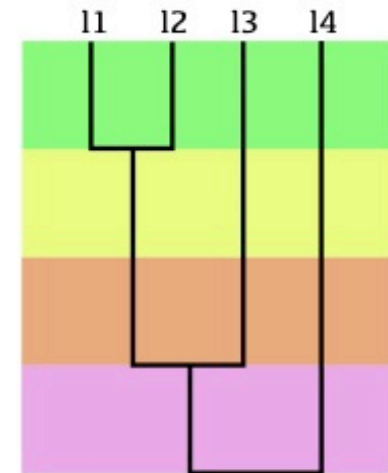


|     | l1 | l2 | l3 | l4 |
| --- | --- | --- | --- | --- |
| l1  | 1+2+1 |     |     |     |
| l2  | 2+1 | 1+2+1 |     |     |
| l3  | 1   | 1   | 3+1 |     |
| l4  | 0   | 0   | 0   | 4   |

(A)
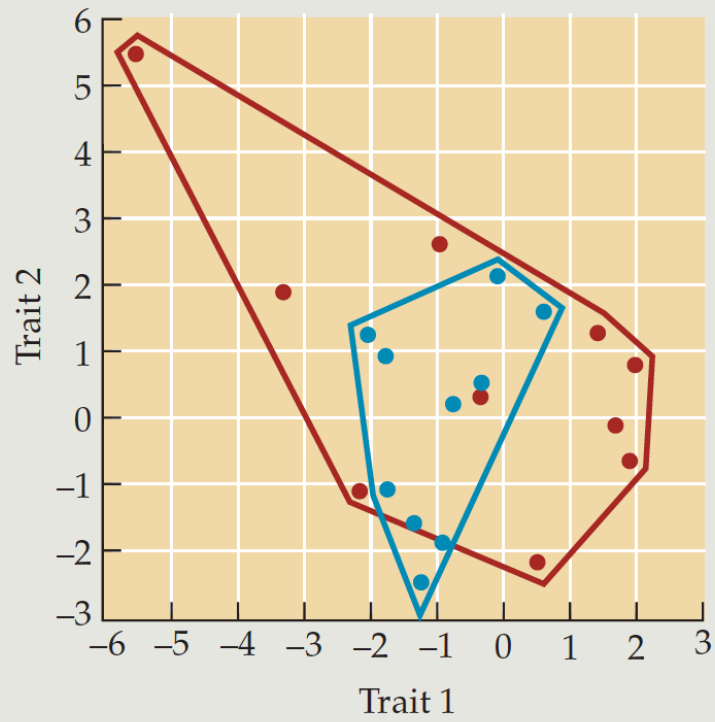
(B)

Losos and Mahler (2010)
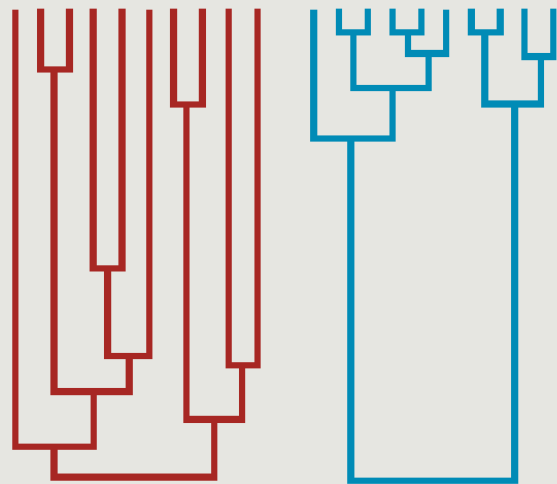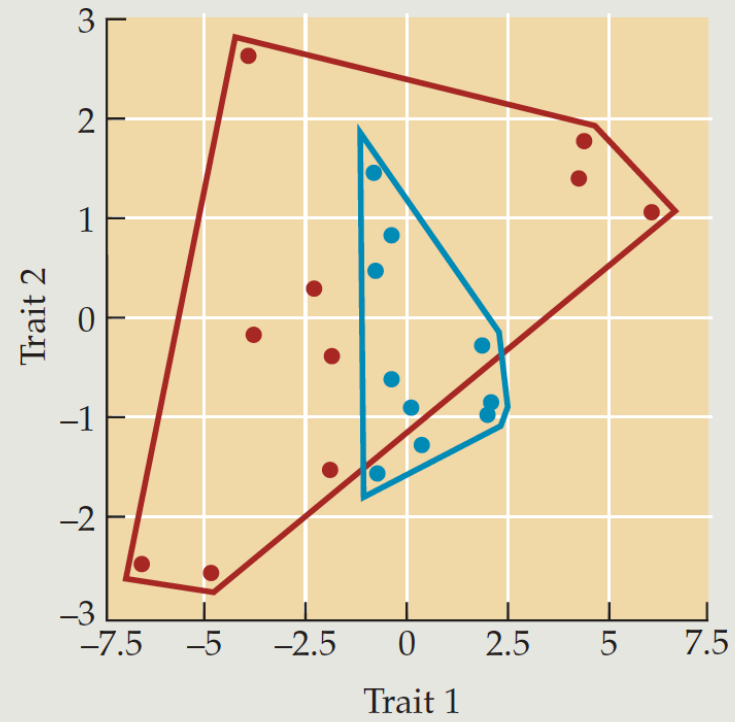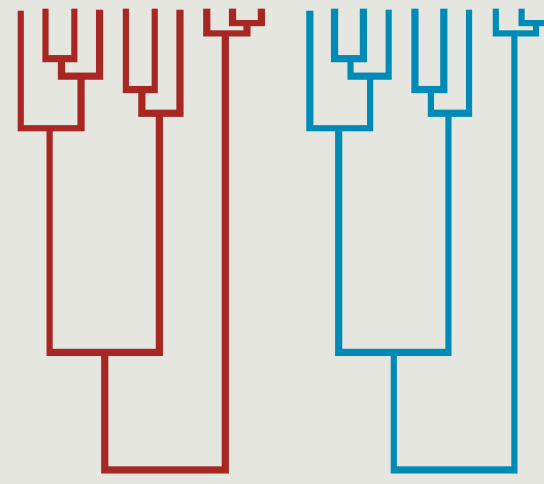
# Models of continuous character evolution

- Brownian motion
- Ornstein Uhlenbeck / stabilizing selection
- Spectational model of evolution / punctuated equilibrium
- Adaptive radiation / ecological niche-filling model

See Nunn (2011: 101-104) for an introduction and relevant references

# Models of continuous character evolution

Nunn (2011: 103ff): the <span style="color:magenta">Ornstein Uhlenbeck</span> / <span style="color:magenta">stabilizing selection</span> model captures the force of selection on adaptive traits. In this model, the trait wanders around an optimum following Brownian motion. The model adds a parameter that tends to pull back the trait towards the optimum. The larger the restraining factor, the more reduced the expected variance of trait values.

Butler and King (2004)

# Models of continuous character evolution

Pagel (1999): κ (kappa) is a power function that raises the length of each of the branch segments on the tree to the power κ. As it approaches 0, all branch segments have a length = 1, this is evidence for punctuational evolution.

κ is used to analyze spectational evolution or punctuated equilibrium: "changes is assumed to occur rapidly at, or shortly after, speciation, and stasis follows until the next speciation event." Mooers (1999: 250). See also Nunn (2011: 119ff).

# Models of continuous character evolution

Pagel (1999): δ (delta) is a power function that raises the length of the total path (root to tip) to the power δ. A value < 1 transforms branch lengths to be increasingly shorter towards the tips, suggesting that trait change occurs rapidly early in the tree and then slows down over time. Value > 1 describe an increasing rate of character evolution through time.

δ is used to analyze a model of adaptive radiation or ecological niche-filling, when early change is important and the rate of evolution slows down over time. Also known as early burst model. Changes in rate are captured by the initial rate of evolution and an additional slowdown parameter. See Nunn (2011: 121ff) for a discussion of approaches other than δ.

# Models of continuous character evolution

Pagel (1999): λ (lambda) is a multiplication of only the internal branches by a constant λ, with a value = 0 resulting in no internal branches and thus a star phylogeny, a value = 1 suggesting the data evolves as Brownian motion predicts on the tree, and a value > 1 suggesting more covariance than predicted under Brownian motion.

λ is used to investigate phylogenetic signal, an assessment of whether closely related species, languages, or cultures resemble each others. It should always be investigated for any comparative analysis! See Nunn (2011: 110) for discussion of more methods.
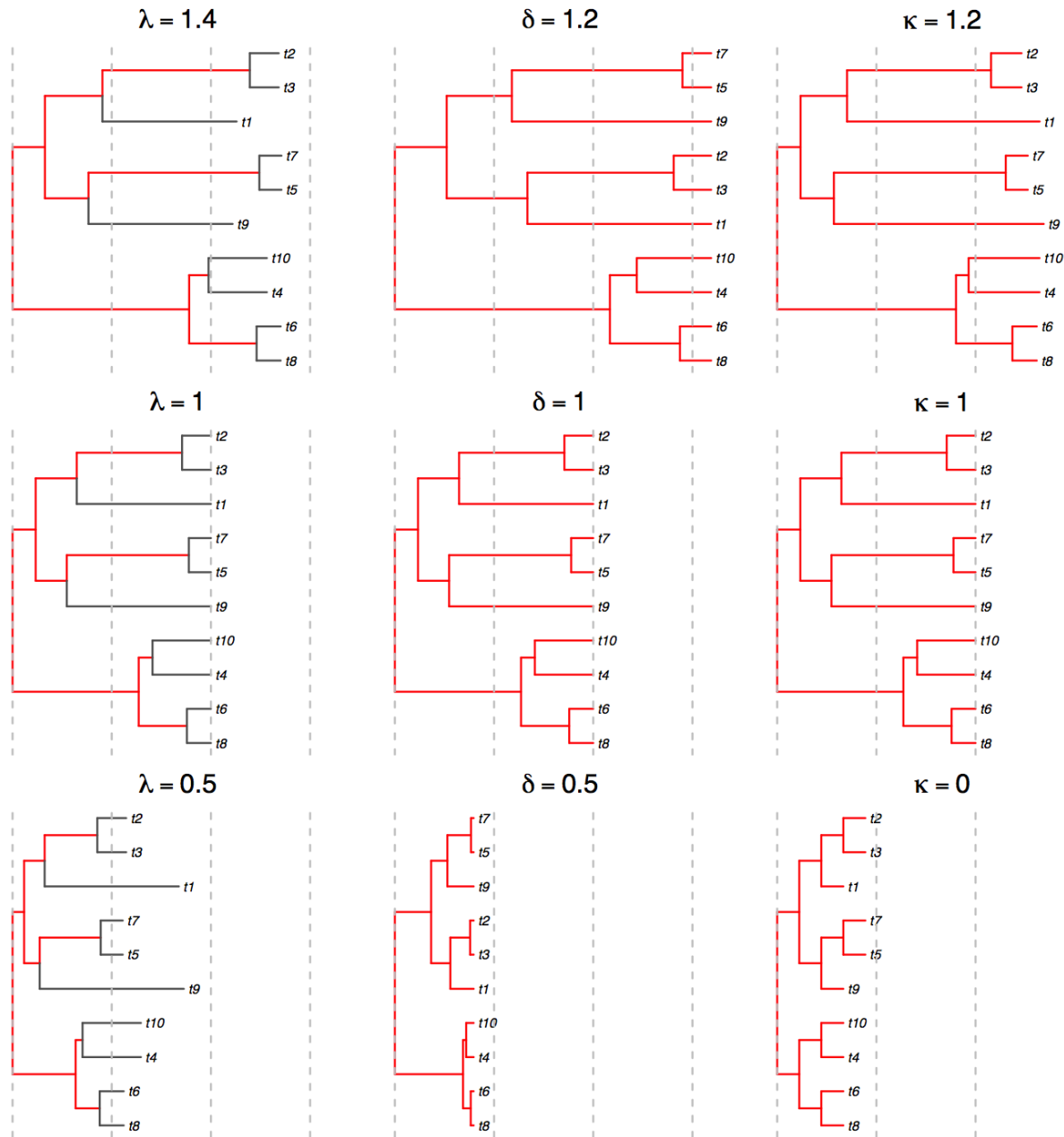
**Figure 3:** Examples of $\lambda$, $\delta$ and $\kappa$ branch length transformations. The branches affected by a given transformation are shown in red.

# Relevance of models

- Bentz et al. (2015): $\lambda$ between .46 and 1 for lexical diversity measured in several parallel texts;

- Currie (2013): investigates the fit of $\lambda$ and $\kappa$ in a study of demographic factors of societal violence;

- Kamilar & Cooper (2013): review phylogenetic signal in 31 variables for primates;

- Verkerk (2013): finds high $\lambda$ values for a variety of lexical/typological scores related to motion

# Models of continuous character evolution in R

package ape can generate several phylogenetic error structures, i.e. variance-covariance matrices based on different evolutionary models:

corBlomberg() – fits Early-burst model AKA ACDC (accelerated/ decelerated) model according to Blomberg et al. (2003)

corBrownian() – Brownian model

corGrafen() – adjusted branch lengths according to Grafen (1989)

corMartins() – covariance structure according to Martins and Hansen (1997)

corPagel() – fits $\lambda$ (lambda)

These are then added to gls() (Generalized Least Squares) in package nlme. More on GLS later.

# Models of continuous character evolution in R

package mvMORPH and geiger in R implement continuous character evolution.

fitContinuous() in geiger can deal with:

- Brownian motion
- Ornstein Uhlenbeck / stabilizing selection
- Early-burst model / ACDC
- lambda
- kappa
- delta
- and more…

# Resources: online

- Bodega Applied Phylogenetics Workshop: http://treethinkers.org/tutorials/
- Anthrotree: http://www.anthrotree.info
- Liam Revell's graduate level course "Methods in Phylogenetic and Macroevolutionary Analysis", http://www.phytools.org/mpma/
- r-sig-phylo: http://www.mail-archive.com/r-sig-phylo@r-project.org/
- BayesTraits manuals: http://www.evolution.reading.ac.uk/SoftwareMain.html

# Resources: (hand)books

- Lemey, Philippe, Salemi, Marco, & Vandamme, Anne-Mieke (Eds.). (2009) The phylogenetic handbook: A practical approach to phylogenetic analysis and hypothesis testing. Cambridge: Cambridge University Press.
- Nunn, Charles L. 2011. *The comparative approach in evolutionary anthropology and biology*. Chicago: University of Chicago Press.
- Mace, R., Holden, C.J. and Shennan, S. (Eds.) (2005) *The evolution of cultural diversity: a phylogenetic approach*. London: UCL Press.
- Whiten, Andrew, Hinde, Robert A., Stringer, Christopher B., and Laland, Kevin N. (2011). *Culture evolves*. Oxford: Oxford University Press.
- Zsolt Garamszegi, Lásló (Ed.). (2014). *Modern phylogenetic comparative methods and their application in evolutionary biology: Concepts and practice*. Heidelberg: Springer.

# Tutorial 1

## Phylogenetic signal; fitting lambda

https://github.com/shh-dlce/qmss-2017/tree/master/continuous_character_evolution

Ancestral state estimation

# Ancestral states

To be able to estimate what languages/cultures were like in the past is one of the main aims of phylogenetic comparative studies.

We can do this under Brownian motion, so: we aim to find the set of ancestral states that maximize the probability of our data and tree – aside from the rate parameter and the state of the root of the tree, we infer the behavior of each of the internal nodes of the tree.

Schluter et al. (1997)
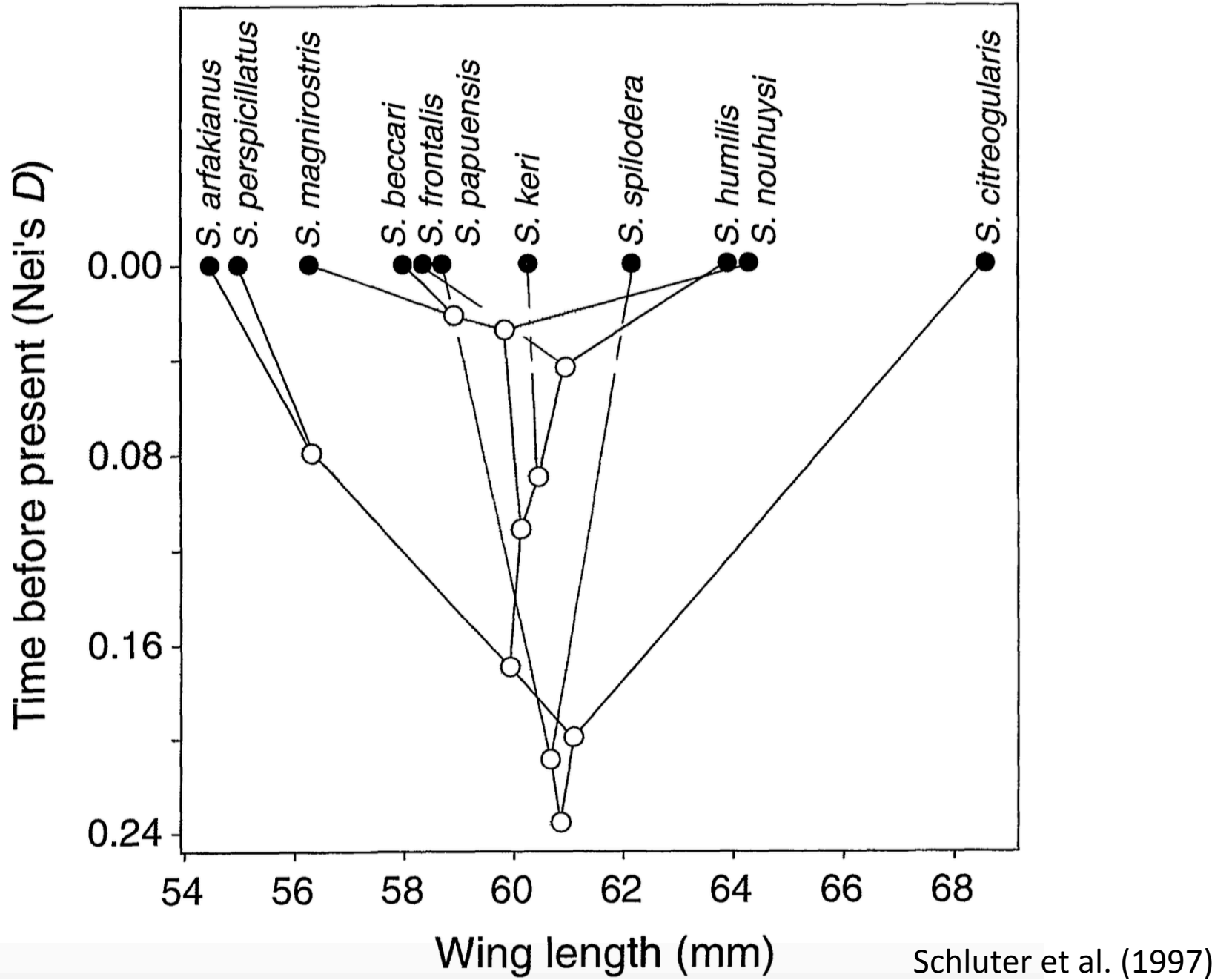
# Some info on trends

- FitzJohn, R.G. 2010. Quantitative traits and diversification. *Syst. Biol.* **59:** 619–633.

- Hunt, G. 2006. Fitting and comparing models of phyletic etic evolution: random walks and beyond. *Paleobiology* **32:** 578-601.

- Hunt, G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proc. Natl. Acad. Sci. USA* **104:** 18404–18408.

- Pennell, M.W. & L.J. Harmon. 2013. An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. *Ann. N.Y. Acad. Sci*. **1289**: 90-105.

- Slater, G.J., L.J. Harmon & M.E. Alfaro. 2012. Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* **66:** 3931–3944.

# Ancestral states

There are a number of different approaches to fit a Brownian model for continuous ancestral state estimation, the most common of which are implemented in R's ape, function ace():

Maximum Likelihood (Schluter et al. 1997)

Least Squares (Felsenstein 1985)

Generalized Least Squares (Martins and Hansen 1997)

If you want to infer ancestral states with Bayesian methods, use Continuous in BayesTraits (Pagel and Meade n.d.)

# Tutorial 2

Ancestral state estimation

Correlated evolution

*Table 11.1*   *Demographic correlates of sex ratio at birth, using CONTINUOUS.*

| Variables correlated | LR | p | $\lambda$ | r(given $\lambda$) | |
|---|---|---|---|---|---|
| SRB × SRC | 24.21 | 0.000 | 0.69 | 0.70 | *** |
| SRB × SRA | 0.45 | 0.341 | 0.59 | 0.11 | |
| SRB × lnTFR | 3.33 | 0.010 | 0.73 | −0.30 | ** |
| SRB × lnIMR | 1.99 | 0.045 | 0.79 | −0.23 | * |
| LnTFR × lnIMR | 20.42 | 0.000 | 0.70 | 0.66 | *** |
| SRB × lnMMR | 2.60 | 0.023 | 0.70 | −0.26 | * |

*Key: SRB = sex ratio at birth, SRC = sex ratio in children between 0–14, SRA = sex ratio in adults between 15–65, lnTFR = natural log of the Total Fertility Rate, lnIMR = natural log of the mortality rate of those under one year of age, lnMMR = natural log of the maternal mortality ratio (mothers death at or around childbirth per 100,000 births). LR = likelihood ratio, $\lambda$ is a scaling parameter, r(given $\lambda$) is the correlation coefficient when the scaling parameter is applied (see CONTINUOUS manual: www.ams.rdg.ac.uk/zoology/pagel).*

Mace & Jordan (2005)

# Ordinary Least Squares

$$y = X\beta + \varepsilon$$

vector of
response values

matrix with
predictor values

vector of
regression
coefficients

matrix with errors
(residuals)
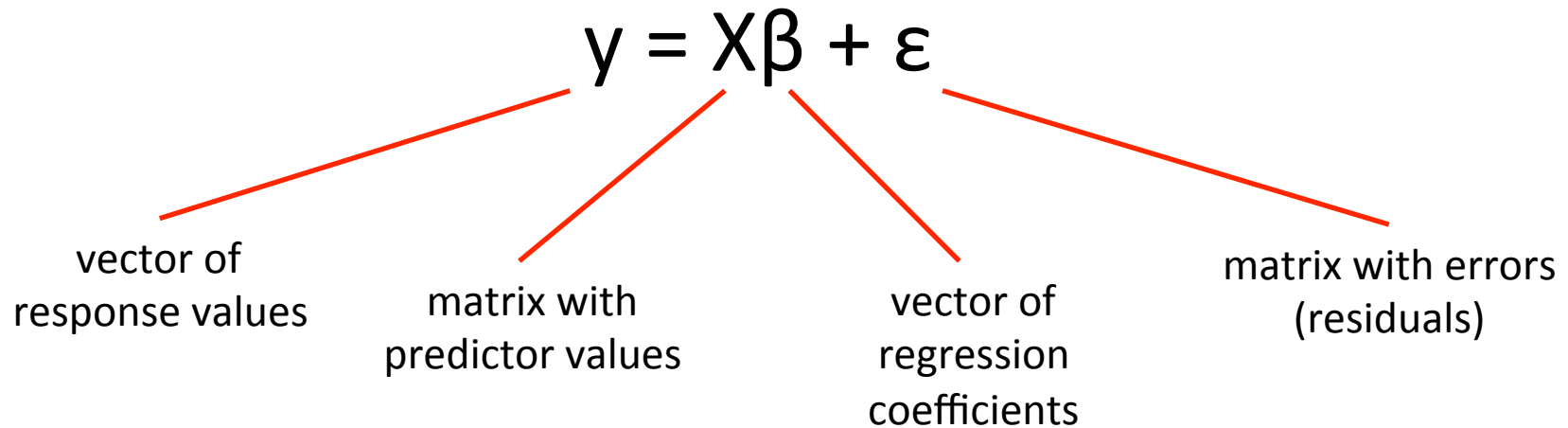
Assumption of OLS: Errors must be
independent and identically distributed

|     | I1  | I2  | I3  | I4  |
| --- | --- | --- | --- | --- |
| I1  | 1   |     |     |     |
| I2  | 0   | 1   |     |     |
| I3  | 0   | 0   | 1   |     |
| I4  | 0   | 0   | 0   | 1   |

# (Phylogenetic) Generalized Least Squares

$$y = X\beta + \varepsilon$$

vector of
response values

matrix with
predictor values

vector of
regression
coefficients

error term incorporates
VCV matrix



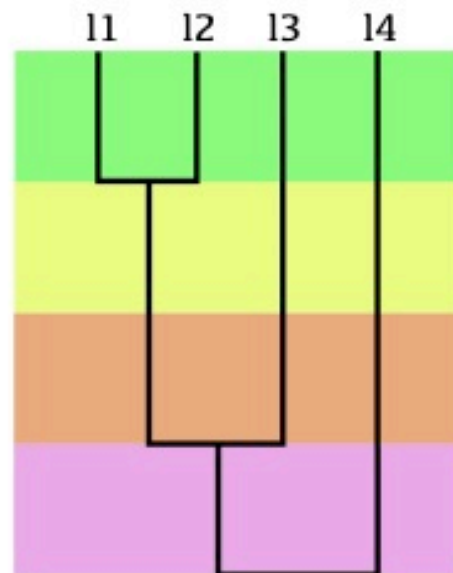|    | l1       | l2       | l3    | l4 |
|----|----------|----------|-------|----|
| l1 | 1+2+1    |          |       |    |
| l2 | 2+1      | 1+2+1    |       |    |
| l3 | 1        | 1        | 3+1   |    |
| l4 | 0        | 0        | 0     | 4  |

# (Phylogenetic) Generalized Least Squares

$$y = X\beta + \varepsilon$$

vector of
response values

matrix with
predictor values

vector of
regression
coefficients

error term incorporates
VCV matrix

|        | l1        | l2        | l3    | l4  |
|--------|-----------|-----------|-------|-----|
| l1     | 1+2+1     |           |       |     |
| l2     | 2+1       | 1+2+1     |       |     |
| l3     | 1         | 1         | 3+1   |     |
| l4     | 0         | 0         | 0     | 4   |
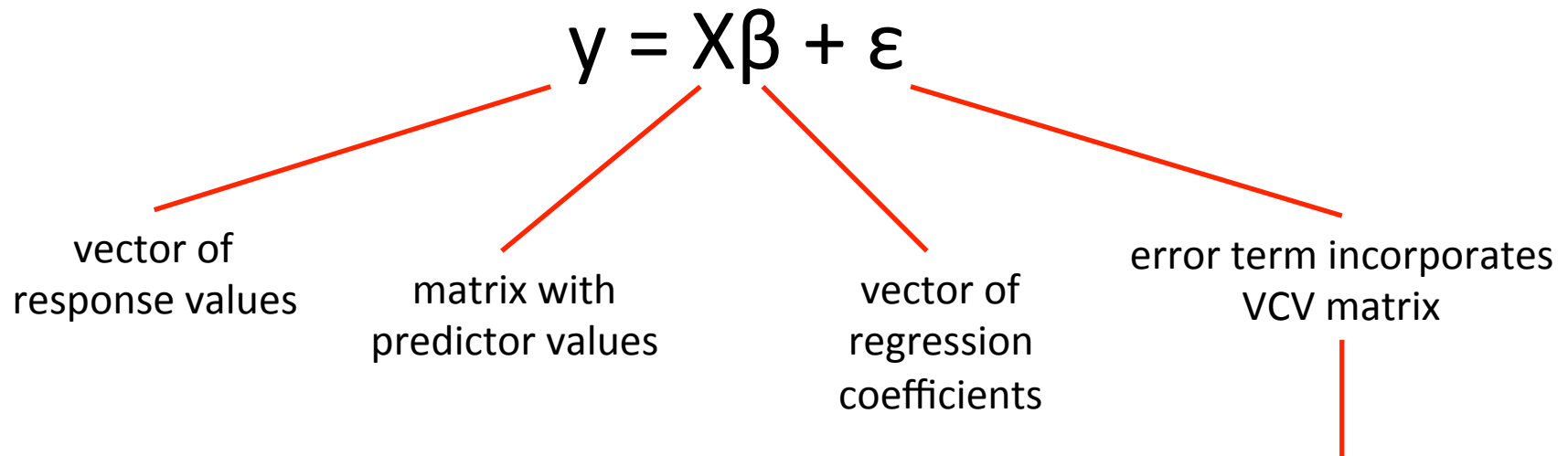
!!! Evolutionary models other
than Brownian motion
can be substituted here !!!
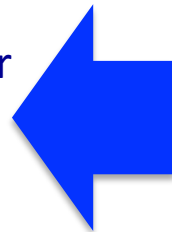
# Mixed Models...?

This has been a single level model; what about multi level models as presented by Heidi?

R has a package MCMCglmm (MCMC Generalised Linear Mixed Models) that can deal with that – introduction by Cara tomorrow.

# (Phylogenetic) Generalized Least Squares

In R: pgls() in package caper; there is also a package pGLS that I am not familiar with but seems promising

# Tutorial 3

Correlated evolution with PGLS

# References

- Bentz, Christian, Verkerk, Annemarie, Kiela, Douwe, Hill, Felix, & Buttery, Paula. 2015. Adaptive communication: Languages with more non-native speakers tend to have fewer word forms. *PLoS ONE,* 10(6). e0128254.
- Blomberg, Simon P., Jr., Theodore Garland, & Ives, Anthony R. 2003. Testing for phylogenetic signal in comprative data: Behavioral traits are more labile. *Evolution,* 57(4). 717-745.
- Butler, Marguerite A., & King, Aaron A. 2004. Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist,* 164(6). 683-695.
- Currie, Thomas E. 2013. Cultural evolution branches out: The phylogenetic approach in cross-cultural research. *Cross-Cultural Research*. 1069397112471803.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, 125, 1–15.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society London B,* 326. 119-157.
- Kamilar, Jason M., & Cooper, Natalie. 2013. Phylogenetic signal in primate behaviour, ecology, and life history. *Philosophical transactions of the Royal Society B Biological Sciences,* 368(1618).
- Losos, Jonathan B., & Mahler, D. Luke. 2010. Adaptive radiation: The interaction of ecological opportunity, adaptation, and speciation. In Bell, M. A., Futuyma, D. J., Eanes, W. F. & Levinton, J. S. (Eds.), *Evolution since Darwin: The first 150 years* 381-420. Sunderland, MA: Sinauer Associates.
- Mace, Ruth, & Jordan, Fiona. 2005. The evolution of human sex ratio at birth: A bio-cultural analysis. In Mace, R., Holden, C. J. & Shennan, S. (Eds.), *The evolution of cultural diversity: a phylogenetic approach* 207-216. London: UCL Press.
- Martins, Emilia P., & Hansen, Thomas F. 1997. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist,* 149(4). 646-667.
- Mooers, Arne Ø., Vamosi, Steven M., & Schluter, Dolph. 1999. Using phylogenies to test macroevolutionary hypotheses of trait evolution in cranes (Gruinae). *The American Naturalist,* 154(2). 249-259.
- Moran, Steven & McCloy, Daniel & Wright, Richard (eds.) 2014. PHOIBLE Online. Leipzig: Max Planck Institute for Evolutionary Anthropology. (Available online at http://phoible.org, Accessed in March 2016.)
- Nunn, Charles L. 2011. *The comparative approach in evolutionary anthropology and biology*. Chicago: University of Chicago Press.
- Orme, David. (2011). *The caper package: Comparative analysis of phylogenetics and evolution in R*.
- Pagel, Mark. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.
- Pagel, Mark, & Meade, Andrew. n.d. *[Draft] Manual BayesTraits*. Reading: University of Reading.
- Schluter, D., Price, T., Mooers, A. O. and Ludwig, D. (1997) Likelihood of ancestor states in adaptive radiation. *Evolution*, 51, 1699–1711.
- Symonds, Matthew R. E., & Blomberg, Simon P. 2014. A primer on phylogenetic generalised least squares. In Zsolt Garamszegi, L. (ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology: Concepts and practice*. Heidelberg: Springer.
- Verkerk, Annemarie. 2013. Scramble, scurry and dash: The correlation between motion event encoding and manner verb lexicon size in Indo-European. *Language Dynamics and Change,* 3(2). 169-217. Special issue, "Phylogeny and beyond: Quantitative diachronic approaches to language diversity", edited by Michael Dunn.
- Verkerk, Annemarie. 2014. Diachronic change in Indo-European motion event encoding. *Journal of Historical Linguistics,* 4(1). 40-83.

# Credits

- Luke Mahler's continuous presentation
- Nunn (2011)
- Fiona Jordan ☺