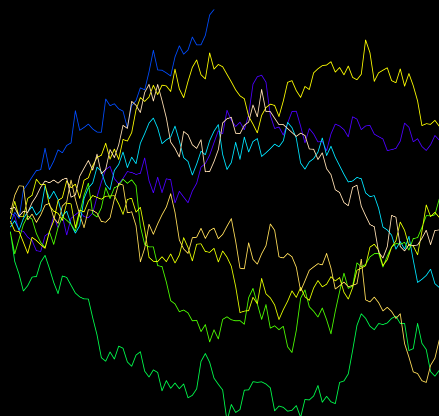
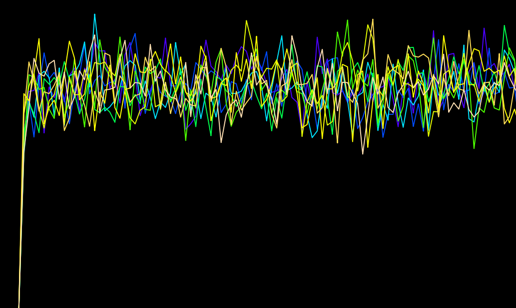
Trait Evolution





SSB Workshop 26th June 2015

Samantha Price

Outline

- **Section 1:** Discrete traits
- **Section 2:** Basic models of continuous trait evolution (Brownian motion & OU)
- **Section 3:** Combining discrete and continuous traits

1: Modeling discrete traits with continuous time Markov models

- Q matrix

	0	**1**
0	-0.5	0.5
1	0.5	-0.5

Equal Rates

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0	-1	1
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All Rates Different

1: Modeling discrete traits with continuous time Markov models

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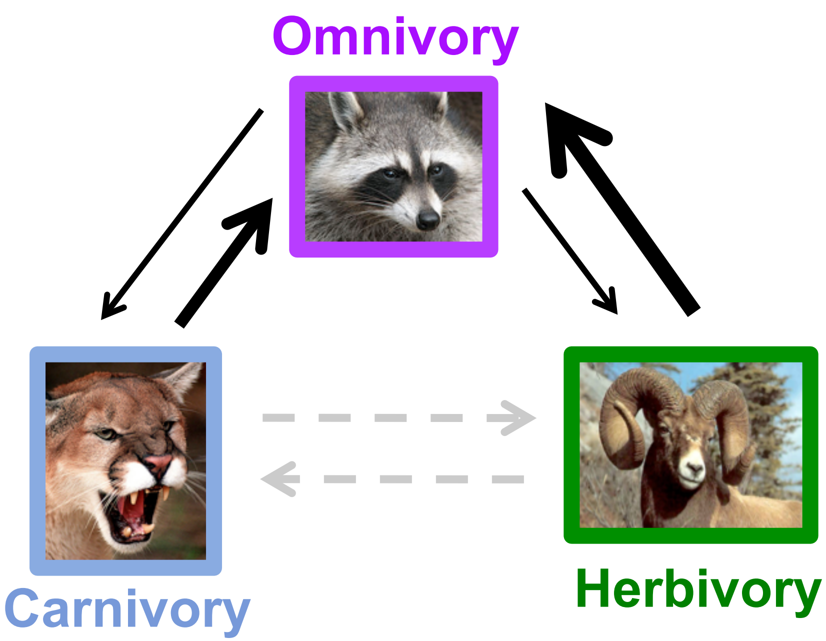
All Rates Different

Over time: $P_{(t)} = e^{-Qt}$

1: Examples

- Are the transition rates between states equal or is it easier to change between some states than others?



- Mammalian omnivory as a transitionary state and evolutionary sink.

Price et al. 2012 PNAS

1: Examples

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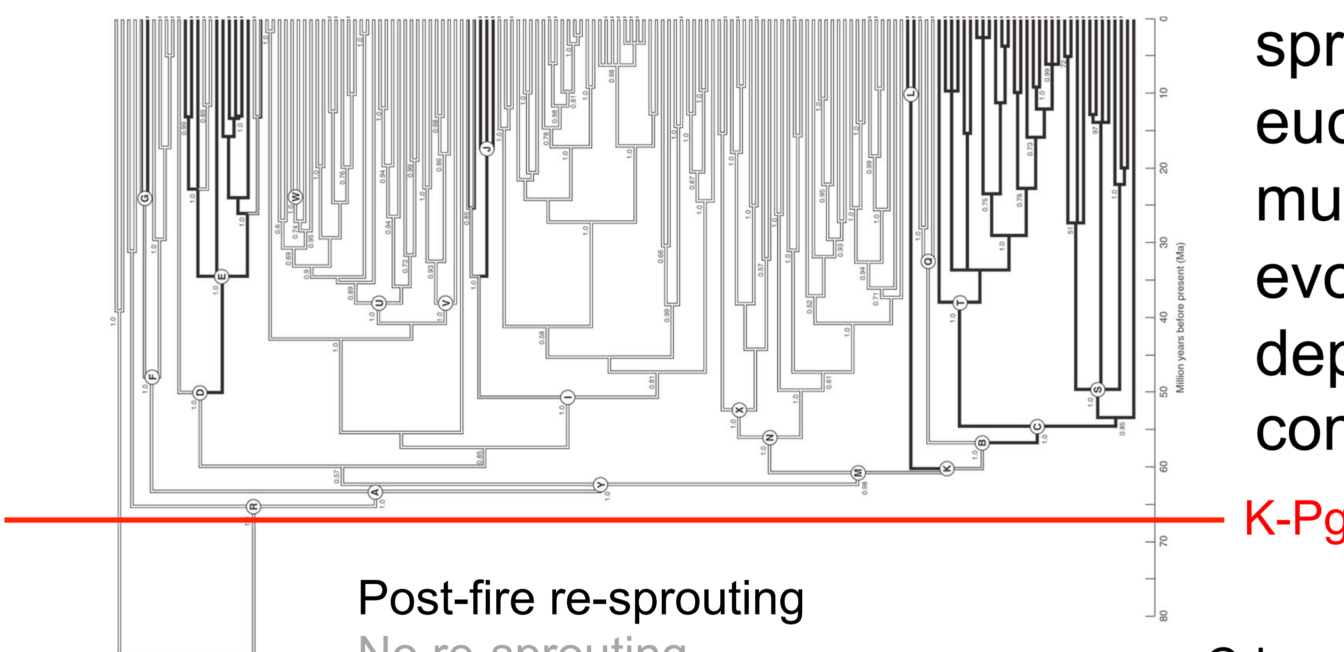
- What is the history of the character on the phylogeny?



- Timing of post-fire re-sprouting in eucalypts suggests much earlier evolution of fire-dependent communities

Crisp et al. 2011 Nature Comm.

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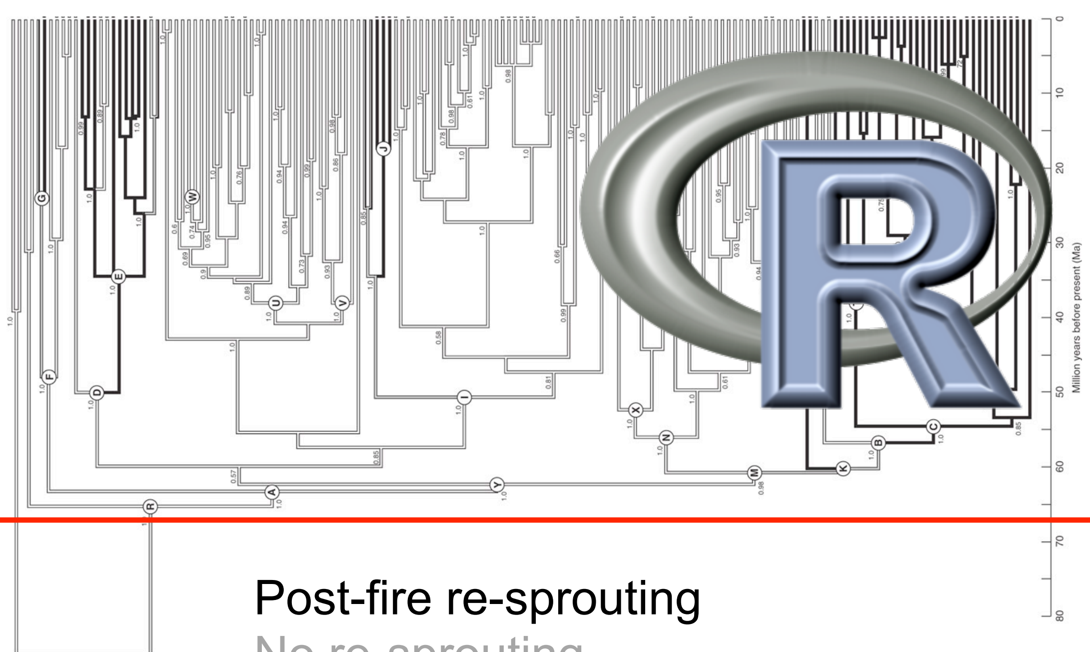

K-Pg

Post-fire re-sprouting
No re-sprouting

- Timing of post-fire re-sprouting in eucalypts suggests much earlier evolution of fire-dependent communities

Crisp et al. 2011 Nature Comm.

1: Caution & Caveats

- Potential importance of the root state and not being at equilibrium state frequencies.

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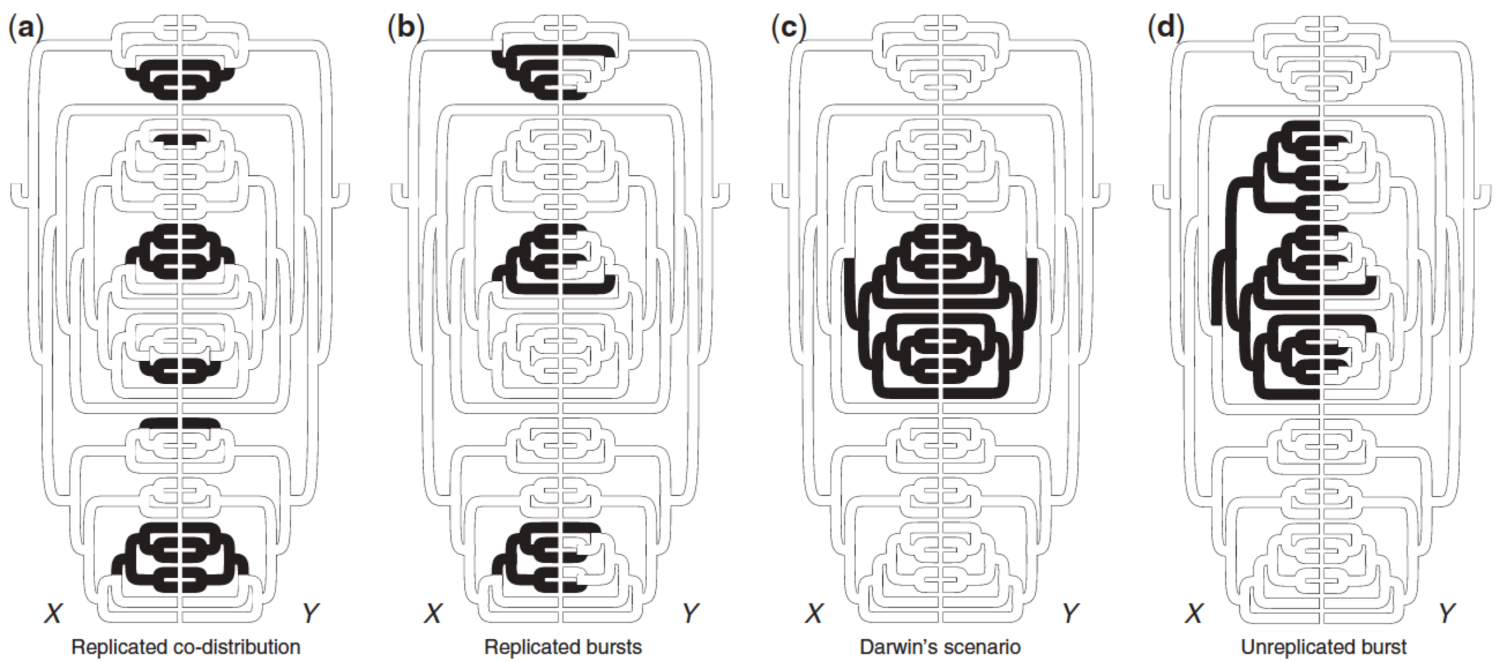
- Potential importance of the root state and not being at equilibrium state frequencies.
- Difficult to correlate discrete traits (Maddison & Fitzjohn 2015; Rabosky & Goldberg 2015).



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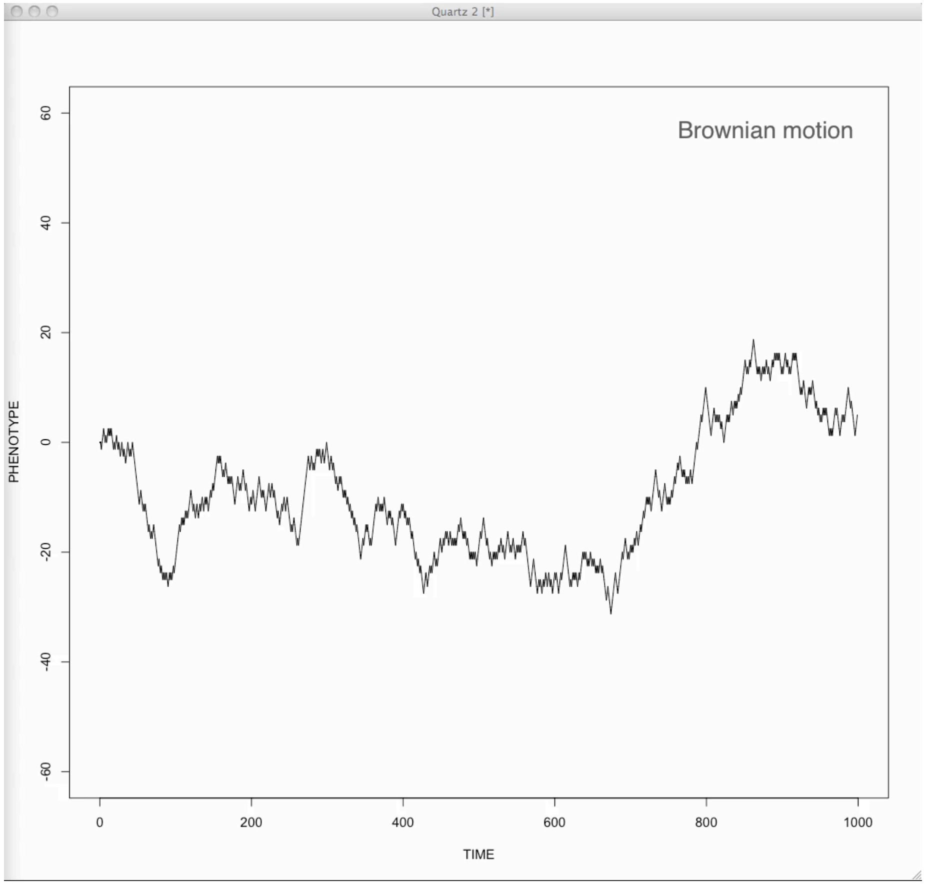
2: Brownian motion

At a point in time:

- A character can increase, decrease or stay the same
- Direction and magnitude of change is independent of current or past character states
  - Probability of change is drawn from a normal distribution with a mean of 0
- Constant rate

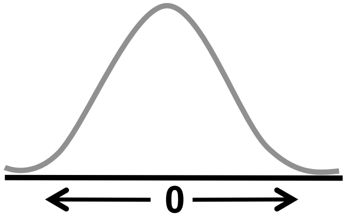


2: Brownian motion

$$dX_{(t)} = \sigma \, dB_{(t)}$$

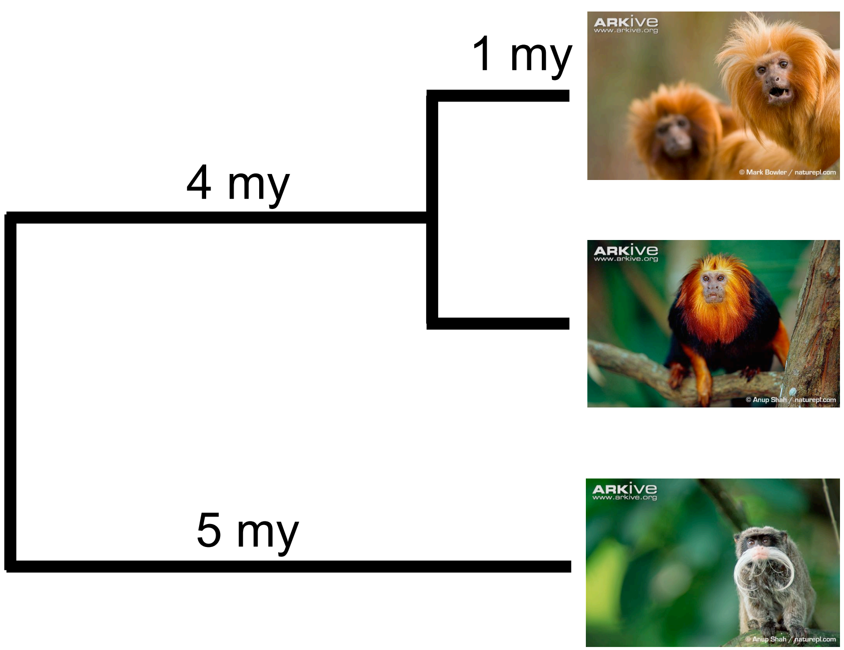
Rate

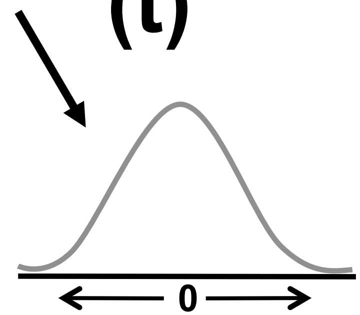
Trait change as described by normal distribution mean = 0



2: Brownian motion on a phylogeny

$$dX_{(t)} = \sigma \, dB_{(t)}$$





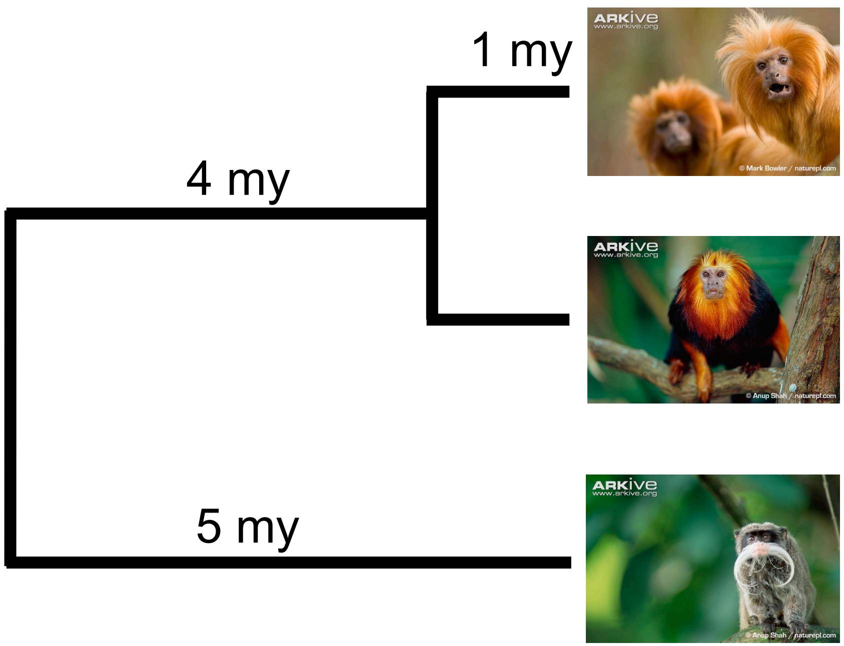
$$SD = \sqrt{\sigma^2 * time}$$

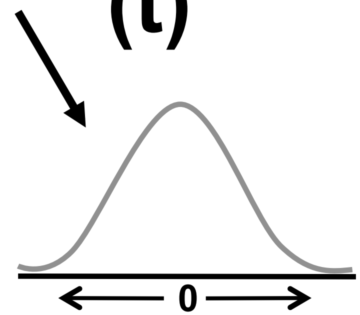
* Disclaimer these ages are entirely made up and do not reflect reality

2: Brownian motion on a phylogeny

Variance proportional to time and rate

$$dX_{(t)} = \sigma \, dB_{(t)}$$





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2: Ornstein-Uhlenbeck

Strength of selection
is proportional to distance of
current trait value from optimum

$$dX_{(t)} = \alpha\overbrace{[\theta - X_{(t)}]}dt + \underbrace{\sigma dB_{(t)}}$$

Primary optimum

Pull towards optimum
(Strength of selection)

Brownian motion
(Brownian motion rate σ^2)

2: Ornstein-Uhlenbeck = Brownian motion when α is 0

$$dX_{(t)} = 0[\theta - X_{(t)}]dt + \underbrace{\sigma dB_{(t)}}_{\textbf{Brownian motion}}$$

2: Ornstein-Uhlenbeck = Brownian motion when α is 0

Variance determined by time, σ and α

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \underbrace{\sigma dB_{(t)}}_{\textbf{Brownian motion}}$$

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

Are σ and α identifiable? As a decrease in rate (σ^2) and an increase in α both reduce variance of the trait at the tips of the tree.

- Yes (theoretically) an increase in α will erode the phylogenetic pattern of the trait but a decrease in σ^2 will not.
- However there will be cases where various estimates σ of and α are equally likely.

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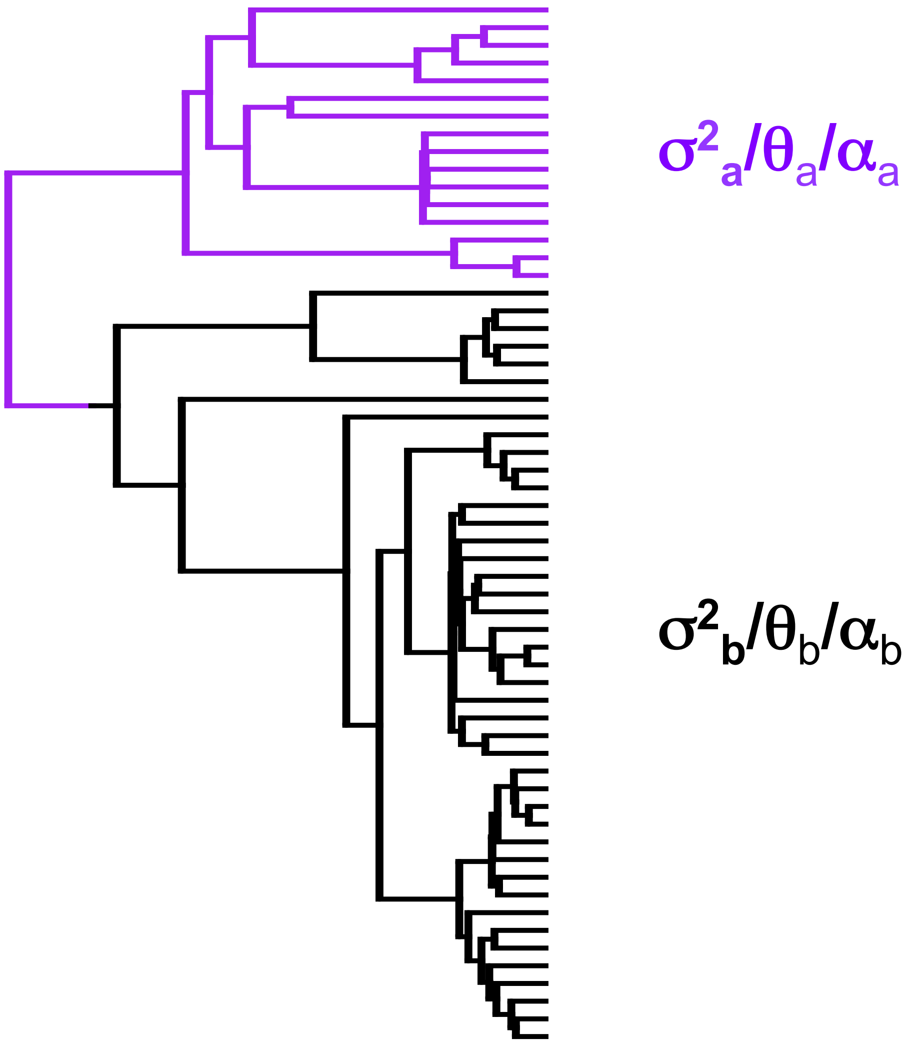
3: Different θ, α and/or σ on different branches



Hypothesis testing

OUCH
OUWIE
Geomorph
MotMot
Phytools
mvMORPH
SLOUCH
mvSLOUCH

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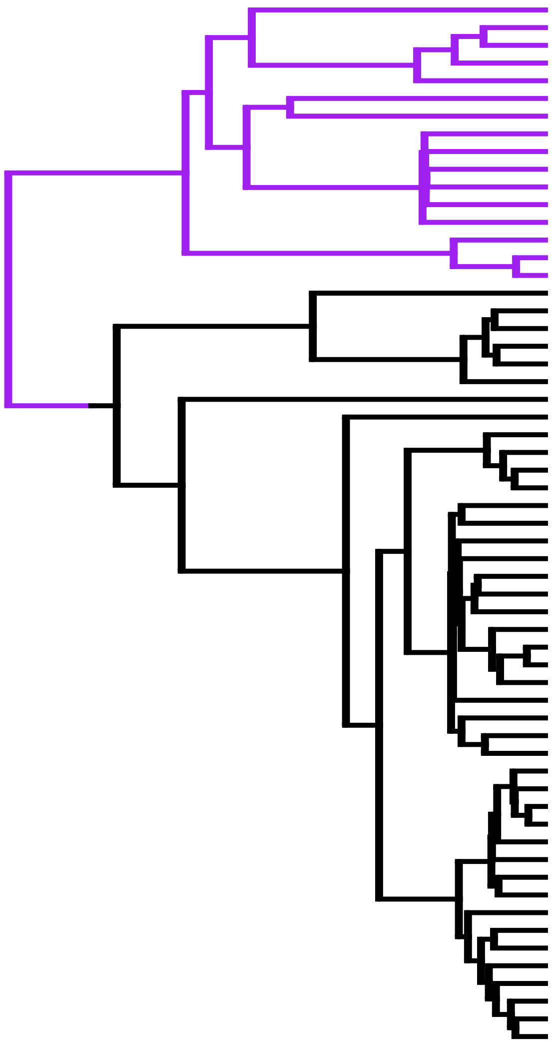


$\sigma^2_a/\theta_a/\alpha_a$

$\sigma^2_b/\theta_b/\alpha_b$

<u>Hypothesis testing</u>

OUCH
OUWIE
Geomorph
MotMot
Phytools
mvMORPH
SLOUCH
mvSLOUCH

<u>Identification of shifts with no *a priori* hypothesis</u>

MotMot
bayOU
phytools
SURFACE (convergence)
BAMM (not in R)

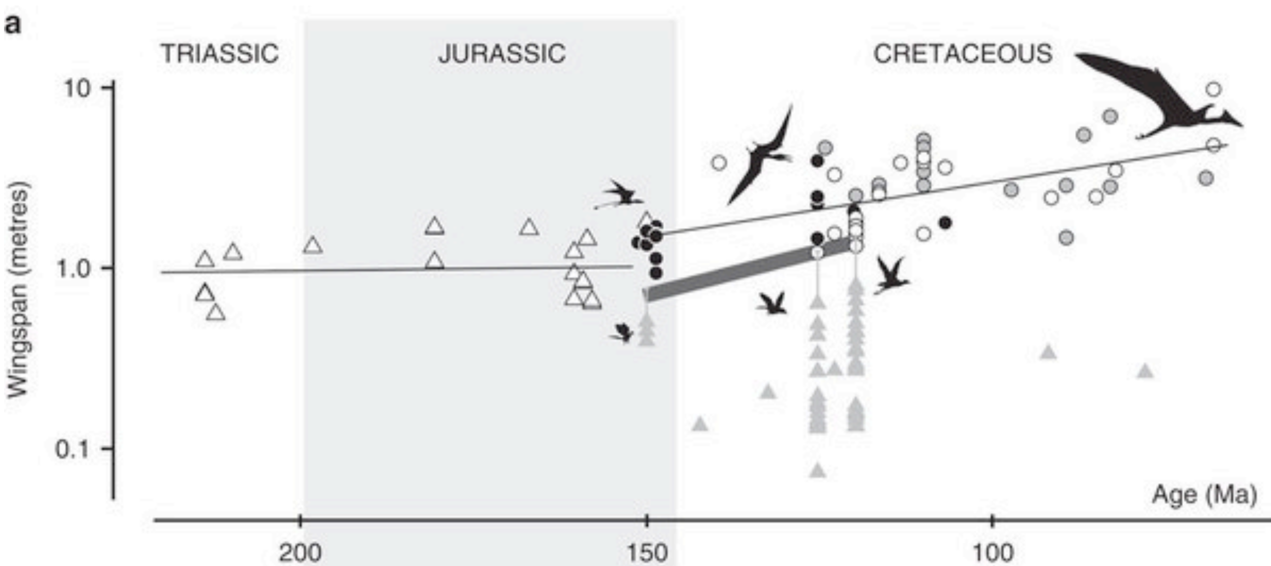
3: Examples

- Does the loss of heterostyly constrain floral morphology in primroses?

de Vos et al. 2014 Evolution 68 (4)

3: Examples

- Do did the evolution of birds drive larger body size in pterosaurs?



Benson et al. 2014 Nature

3: Different θ, α and/or σ on different branches

Model	θ	σ	α
BM1	-	Universal	-
OU1	Universal	Universal	Universal
BMS	-	Variable	-
OUM	Variable	Universal	Universal
OUMA	Variable	Universal	Variable
OUMV	Variable	Variable	Universal
OUMVA	Variable	Variable	Variable

doi:10.1111/j.1558-5646.2012.01619.x

MODELING STABILIZING SELECTION: EXPANDING THE ORNSTEIN–UHLENBECK MODEL OF ADAPTIVE EVOLUTION

Jeremy M. Beaulieu,[1,2] Dwueng-Chwuan Jhwueng,[3,4] Carl Boettiger,[5] and Brian C. O'Meara[6]

OUwie

3: Caution/Caveat

- BM/OU models influenced by
  - Tree shape
  - Measurement error
  - Number of regimes/parameters estimated vs number taxa
  - Evenness of species number in each regime.

Remember: simulation!

MACROEVOLUTIONARY EXPERIMENTAL DESIGN

Either pick your questions appropriate to your clade (i.e. that you have the power to answer) or pick your clade to answer your question of interest.

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Either pick your questions appropriate to your clade (i.e. that you have the power to answer) or pick your clade to answer your question of interest.

- **Simulation is your friend**, with small datasets you can demonstrate what you have the power to detect.