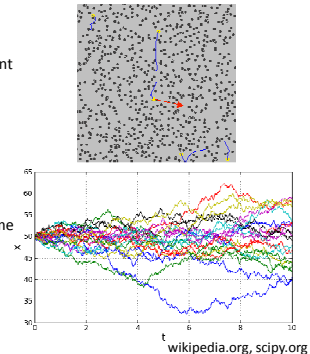


Topic 11: Models of Trait Evolution

- Revisiting the Brownian Motion model
- Building on BM with tree transformations
 - Pagel's Lambda, Kappa, & Delta
- More complex models of trait evolution
 - Early burst model
 - Ornstein-Uhlenbeck model
- Multivariate modeling and statistics

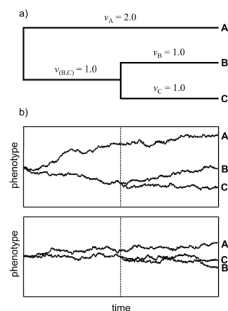
Revisiting the Brownian Motion Model

- Brownian motion
 - Describes random movement of particles in a gas/liquid
 - Undirected random walk
 - Mean of zero
 - Variance proportional to time



Revisiting the Brownian Motion Model

- BM on a phylogeny
 - Time is represented by branch lengths
 - Trait variance is proportional to time/branch lengths
 - Trait diverges from a value at each node following BM
 - After a node, two lineages evolve independently

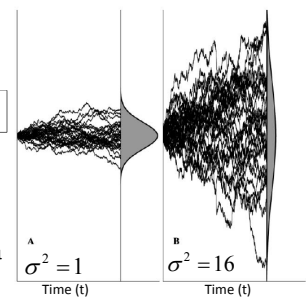


Revell et al. 2008

Brownian Motion Model

- The BM model

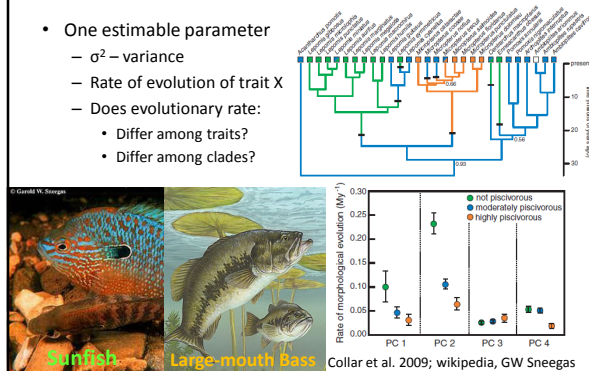
$$dX(t) = \sigma dB(t)$$
 - Change in trait X by time t
 - SD
 - Random Noise by time t
 - $X(0) = 0$
 - X_t is continuous
 - $X_t - X_s \sim N(0, t-s)$, where $N(\mu, \sigma^2)$ is a normal distribution with mean μ and variance σ^2



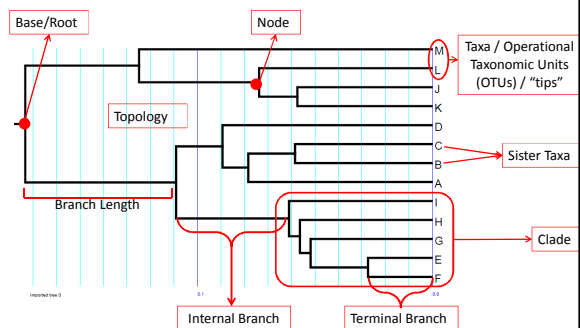
Butler & King 2004

Brownian Motion Model

- One estimable parameter
 - σ^2 – variance
 - Rate of evolution of trait X
 - Does evolutionary rate:
 - Differ among traits?
 - Differ among clades?



Phylogeny Terminology



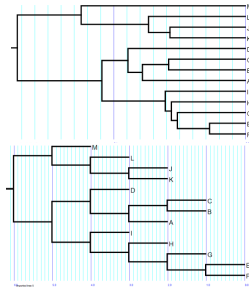
Building on Brownian Motion

- Does evolution follow BM?

- Evolution is not just a random walk
- Different types of selection
- Directional evolution
- Correlated trait evolution
- Character displacement

- Can transform branch lengths and keep BM

- The longer a branch, the more phenotypic evolution is possible
- Branches no longer represent time



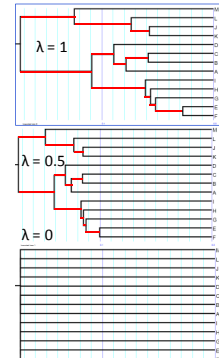
- Same taxa, same topology
- Different amount of evolution on the branches

Pagel 1997, 1999

Building on Brownian Motion

- Lambda (λ)

- Internal branches multiplied by λ
- Terminal branches untransformed
- λ ranges from 0 to 1
- $\lambda = 1$
 - Brownian Motion
 - Branch lengths unchanged
- $0 < \lambda < 1$
 - Decreasing Impact of phylogeny
 - More independent trait evolution
- $\lambda = 0$
 - Completely independent evolution
 - Not phylogenetic signal
- λ is a measure of phylogenetic signal

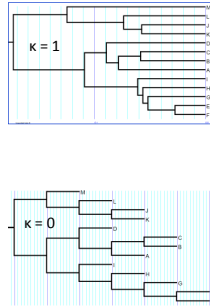


Pagel 1997, 1999

Building on Brownian Motion

- Kappa (κ)

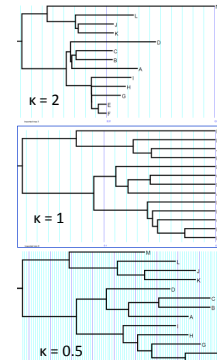
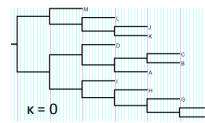
- Raises all branch lengths to the power of κ
- κ ranges zero and up
- Used to test whether evolution of a trait is gradual or punctuational
- $\kappa = 1$: Gradualism, Brownian Motion
- $\kappa = 0$
 - All branch lengths are 1
 - Mimics Punctual Equilibrium (Gould & Eldredge)
 - Trait evolution happens at speciation
 - Stasis between speciation events



Pagel 1997, 1999

Building on Brownian Motion

- $\kappa > 1$: Disproportionate evolution occurs on longer branches
- $\kappa = 1$: Gradualism, BM
- $0 < \kappa < 1$: More stasis on longer branches
- $\kappa = 0$: Punctuational evolution

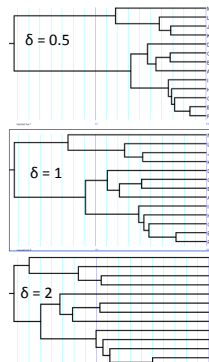


Pagel 1997, 1999

Building on Brownian Motion

- Delta (δ)

- Raises all node depths to the power of δ
- δ must be positive
- Tests whether trait evolution follows a pattern of adaptive radiation or species specialization
- $0 < \delta < 1$
 - Most trait evolution at base of tree
 - Adaptive radiation
- $\delta = 1$: Brownian Motion
- $\delta > 1$
 - Most trait evolution near tips
 - Species specialization



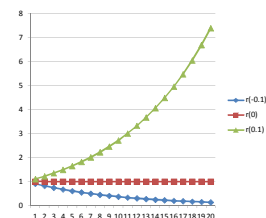
Pagel 1997, 1999

Building on Brownian Motion

- More Complex models

- Early Burst of Evolution

- Sigma changes with time
- What is sigma?
 - If $r < 0$, sigma decreases exponentially through time
 - This is Early Burst
 - If $r > 0$, sigma increases exponentially through time
 - This may not make biological sense
- If $r = 0$, BM model
- Another way of modeling adaptive radiation



$$dX(t) = \sigma(t)dB(t)$$

$$\sigma(t) = \sigma_0 e^{rt}$$

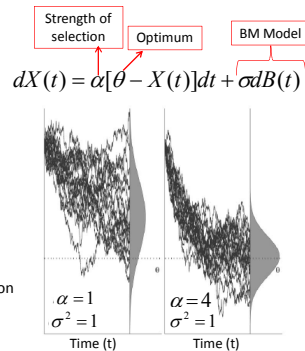
Harmon et al. 2010

Building on Brownian Motion

• More Complex Models

– Ornstein-Uhlenbeck

- Used to model stabilizing selection for a trait value
- Trait value optimum: θ
- Strength of stabilizing selection: α
- BM, but being pulled towards an optimal value
- If α is small (<0.01) & θ is outside tip value range, models directional evolution



Butler & King 2004

Building on Brownian Motion

• A comparison of models

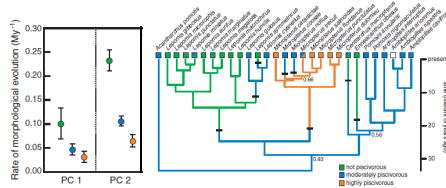
- 1 parameter isn't available for manipulation

Model	K	Parameters	What we can measure
BM	2	σ^2	Rate of evolution
BM + λ	3	σ^2, λ	Rate of evolution, phylogenetic signal
BM + κ	3	σ^2, κ	Rate of evol, gradual vs. punctuational evol
BM + δ	3	σ^2, δ	Rate of evol, early vs. late evolution
EB	3	σ^2, r	Initial rate of evol, slowing vs. speeding up
OU	4	σ^2, α, θ	Rate of evol, strength of stabilizing selection, trait optimum

Even More Complex Models

• Brownian Motion model with multiple rates

- Different evolutionary rate for a trait for different clades
- Differs from just estimating rate for each of several clades
- Allows test of whether a multi-rate model fits the data better than a single rate model
- 1 extra parameter per rate fitted

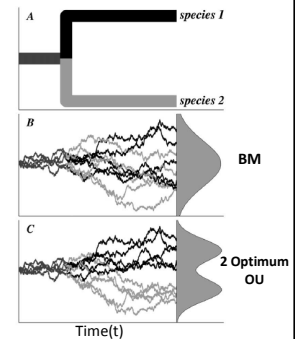


Collar et al. 2009

Even More Complex Models

• OU with multiple optima

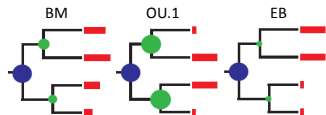
- Different θ for different clades or groups of species
 - Different ecomorphs
 - Different sizes
 - Different habitats...
- Are different groups evolving to different optimal trait values?
- 1 extra parameter per optimum



Butler & King 2004

Comparing Models

• How would we choose one model over another?



• How has body size evolved in different clades?

Clade	n	BM	OU.1	EB
Birds	236	0.01	0.01	0.98
Squamates	554	0.32	0.57	0.12
Mammals	325	0.45	0.38	0.16
Carnivores	192	0.25	0.66	0.09
Primates	133	0.59	0.21	0.21

Harmon et al. 2010

Statistical analyses that take phylogeny into account

Analysis	Function	Package	Authors
Calculate PICs	pic()	ape	Paradis et al.
Model Fitting	fitContinuous()	geiger	Harmon et al.
Evolutionary VCV matrix	ic.sigma() evol.vcv()	geiger phytools	Harmon et al. Revell
Phylogenetic ANOVA	phy.anova() phyANOVA()	geiger phytools	Harmon et al. Revell
Phylogenetic MANOVA	phy.manova()	geiger	Harmon et al.
OU model fitting	hansen()	OUCH	King & Butler
BM model fitting	brown()	OUCH	King & Butler
Multirate BM fitting	brownie.lite()	phytools	Revell
Phylo. Canonical Correlation Analysis	phyl.cca()	phytools	Revell
Phylo. Paired t-test	phyl.pairedttest()	phytools	Revell
Phylo. pairwise t-tests	tTests()	phytools	Revell
Phylo. PCA	phyl.pca()	phytools	Revell
Phylo. RMA regression	phyl.RMA()	phytools	Revell

Many more model-based analyses are available...