

Modeling adaptive evolution

AC/DC model

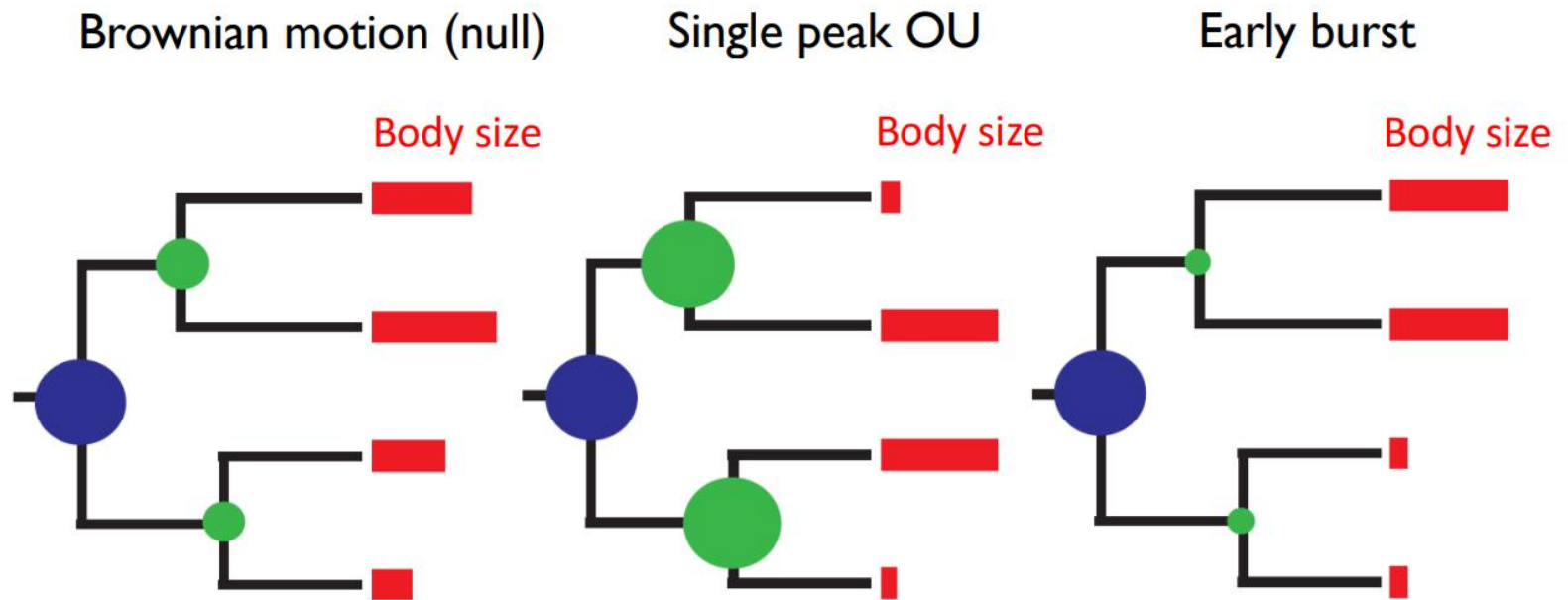
BM, but with a declining rate parameter:

$$\sigma^2(t) = \sigma_0^2 e^{bt}$$

If b is negative, declining rates (i.e. Early burst)

If b is positive, increasing rates (late bursts, not identifiable from OU in ultrametric trees)

Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck



Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck

EARLY BURSTS OF BODY SIZE AND SHAPE EVOLUTION ARE RARE IN COMPARATIVE DATA

Luke J. Harmon,^{1,2,3} Jonathan B. Losos,⁴ T. Jonathan Davies,⁵ Rosemary G. Gillespie,⁶ John L. Gittleman,⁷ W. Bryan Jennings,⁸ Kenneth H. Kozak,⁹ Mark A. McPeck,¹⁰ Franck Moreno-Roark,¹¹ Thomas J. Near,¹² Andy Purvis,¹³ Robert E. Ricklefs,¹⁴ Dolph Schluter,² James A. Schulte II,¹¹ Ole Seehausen,^{15,16} Brian L. Sidlauskas,^{17,18} Omar Torres-Carvajal,¹⁹ Jason T. Weir,² and Arne Ø. Mooers²⁰

¹*Department of Biological Sciences, University of Idaho, Moscow, Idaho 83844*

²*Biodiversity Centre, University of British Columbia, Vancouver, BC V6T1Z4, Canada*

³*E-mail: lukeh@uidaho.edu*

Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck

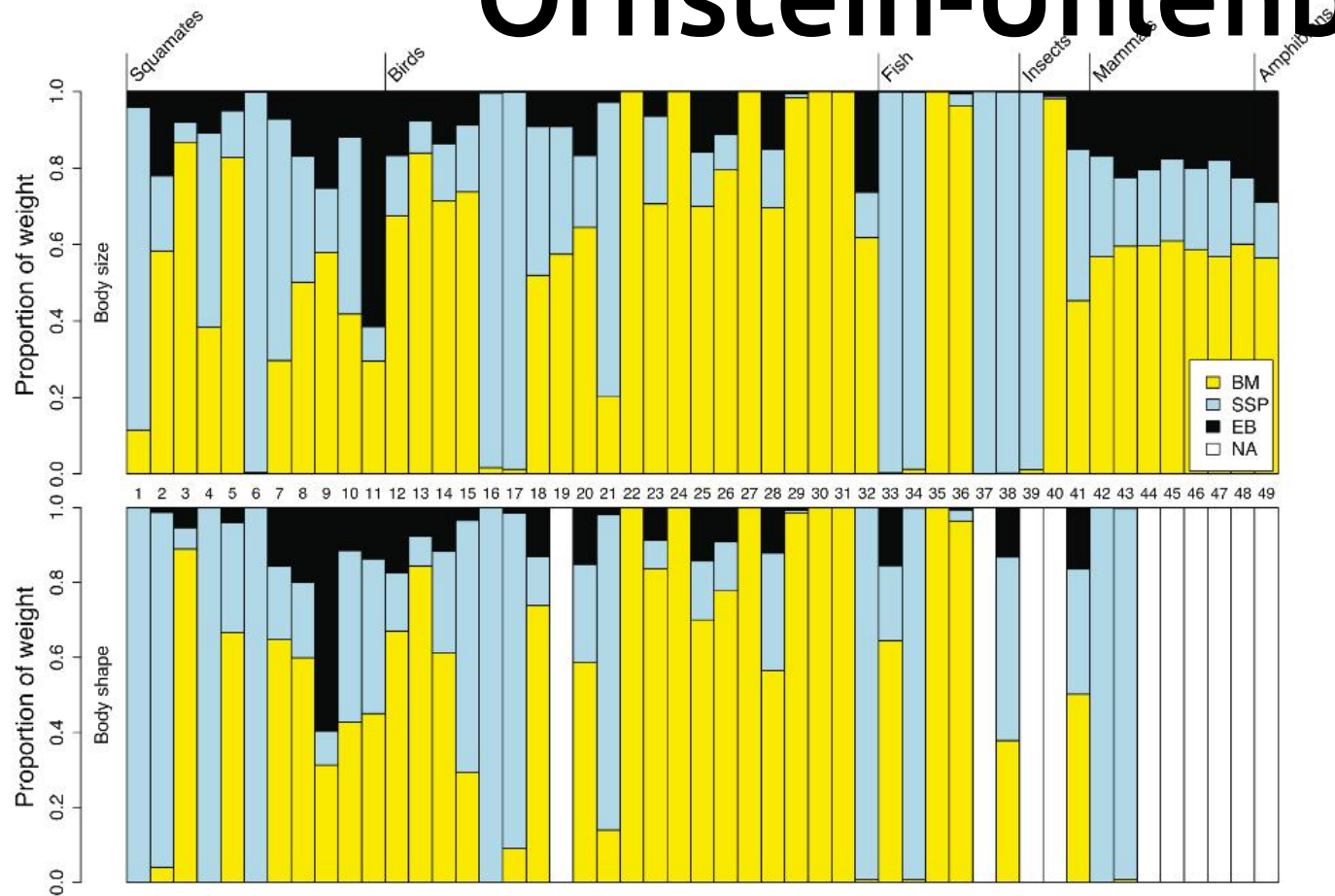


Figure 2. Akaike weights for three models of phenotypic evolution (BM, Brownian motion; SSP, single stationary peak; EB, early burst; NA, not applicable because shape data were unavailable) for all phylogenetic trees in the dataset. Numbers correspond to the datasets as listed in Table 1. Relative area of the bar filled with any color is proportional to the Akaike weight for that model given the data.

Model Adequacy and the Macroevolution of Angiosperm Functional Traits

Matthew W. Pennell,^{1,*} Richard G. FitzJohn,² William K. Cornwell,³ and Luke J. Harmon¹

1. Department of Biological Sciences and Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho 83844;

2. Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia; 3. School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

Submitted April 7, 2014; Accepted March 31, 2015; Electronically published June 12, 2015

Online enhancement: supplemental PDF.

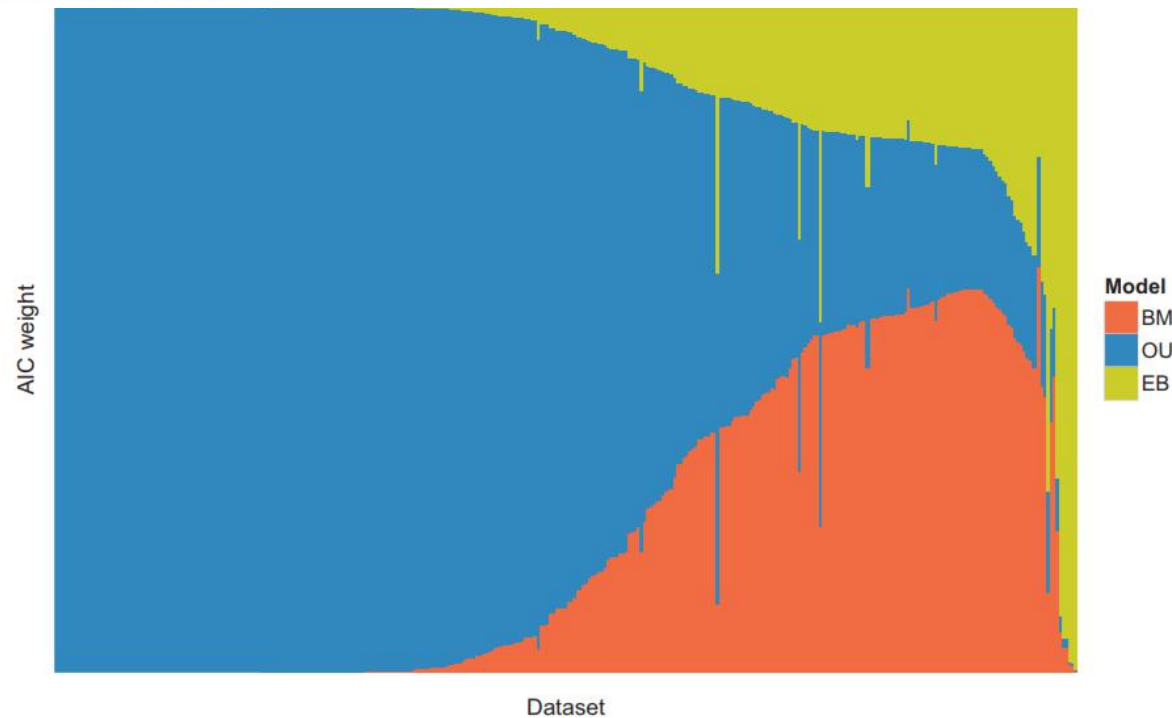


Figure 3: The relative support, as measured by Akaike information criterion (AIC) weight, for the three models used in our study (Brownian motion [BM], Ornstein-Uhlenbeck [OU], and early burst [EB]) across all 337 data sets. An OU model is highly supported for a majority of the data sets.

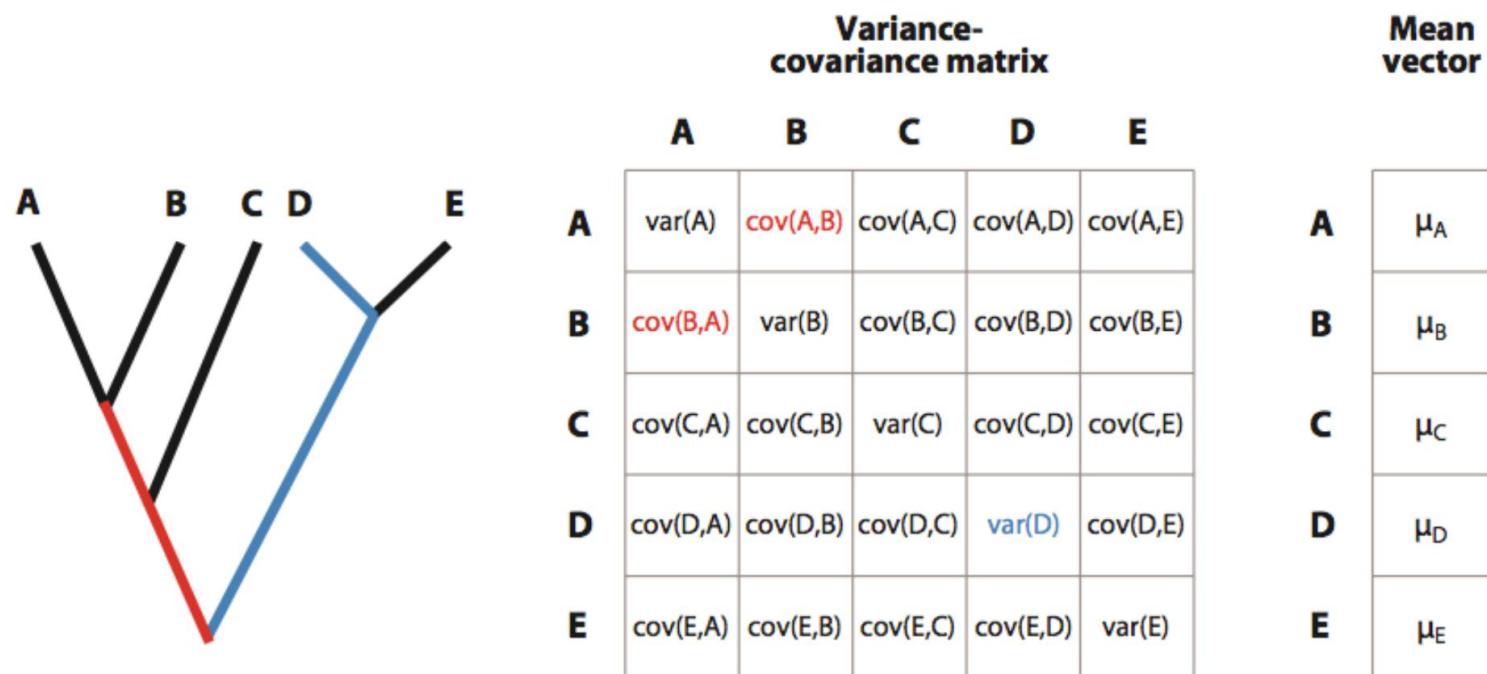


Figure 4

Multivariate normal distribution. The figure shows a tree, the tree's variance-covariance matrix, and the vector of means (which, under Brownian motion, would equal the root state). Highlighted are the branches leading to covariance between taxa A and B (*red*) and the branches leading to variance in D (*blue*).

Why we must account for “measurement” error

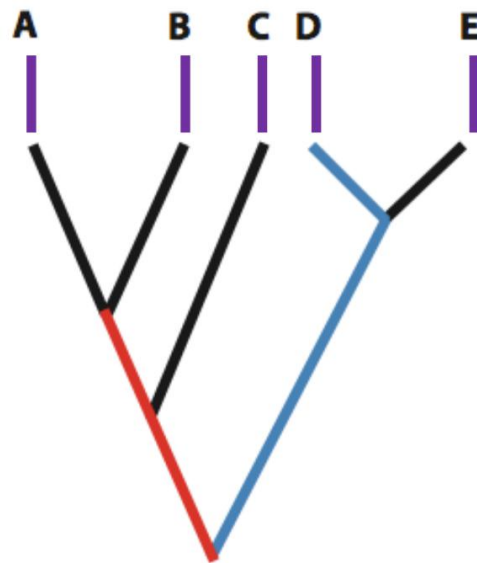


Figure 4

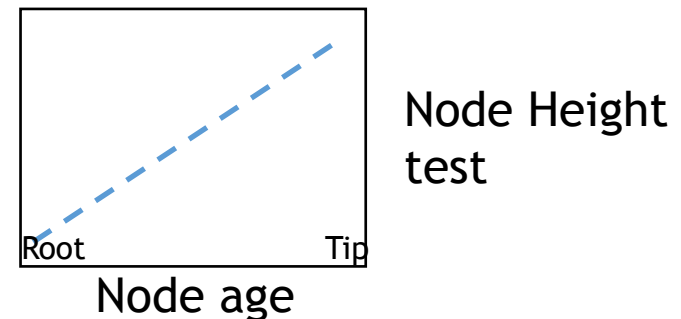
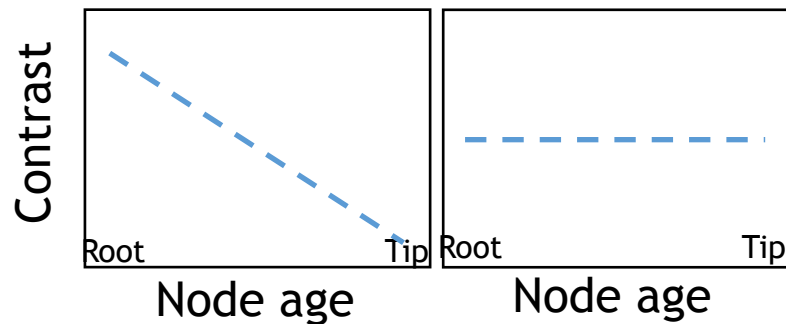
Variance-covariance matrix						Mean vector	
	A	B	C	D	E		
A	var(A) + error	cov(A,B)	cov(A,C)	cov(A,D)	cov(A,E)	A	μ_A
B	cov(B,A)	var(B) + error	cov(B,C)	cov(B,D)	cov(B,E)	B	μ_B
C	cov(C,A)	cov(C,B)	var(C) + error	cov(C,D)	cov(C,E)	C	μ_C
D	cov(D,A)	cov(D,B)	cov(D,C)	var(D) + error	cov(D,E)	D	μ_D
E	cov(E,A)	cov(E,B)	cov(E,C)	cov(E,D)	var(E) + error	E	μ_E

EB

BM

OU

WN



Measurement error +
“Biological error”



PGLS + OU : Not a full OU model

Statistically, much like PGLS + Lambda

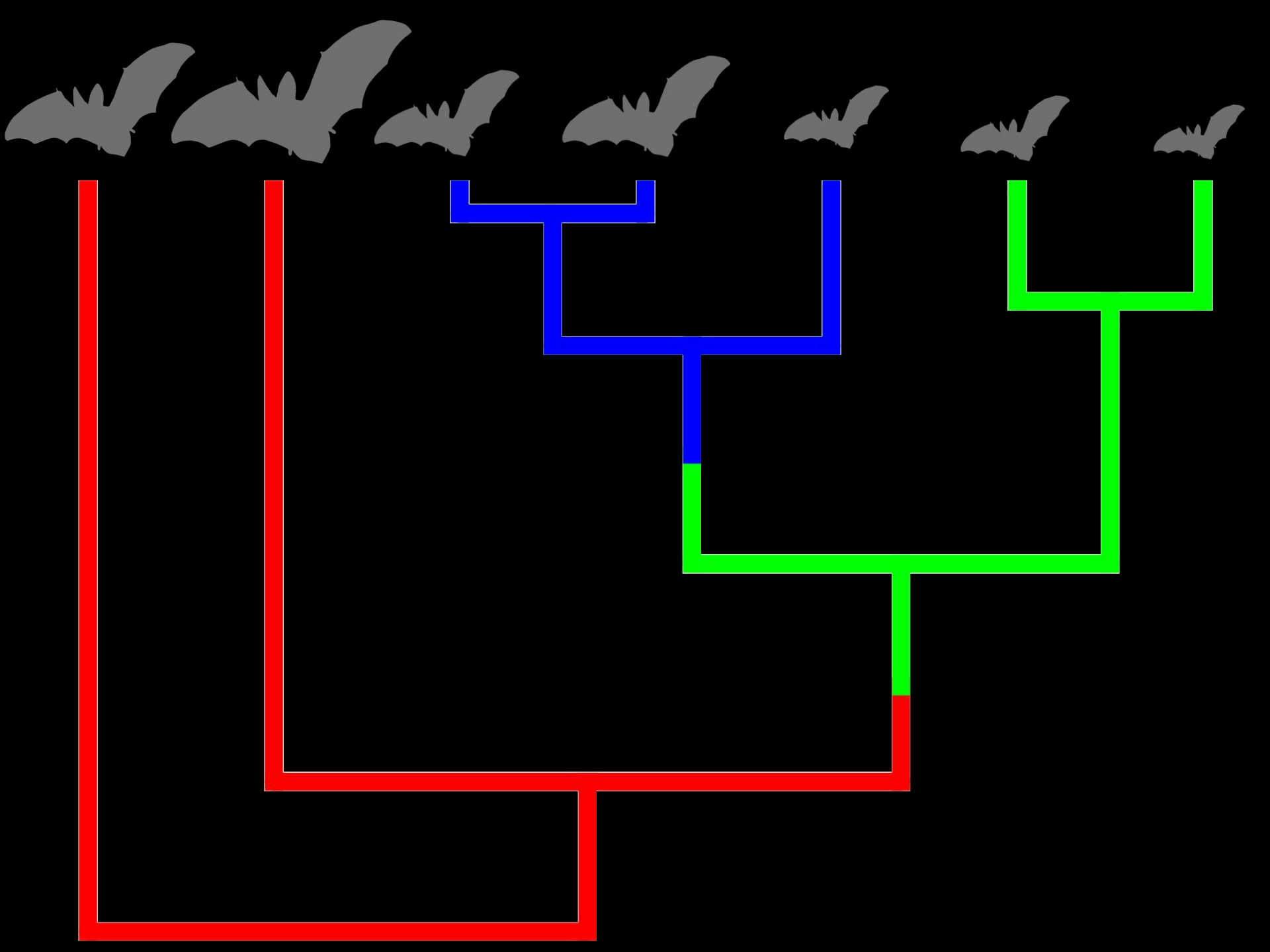
Appropriate only for “Allometric-type” relationships between predictor and response

OU model in variance, but not in mean
(instantaneous adaptation)

Phylogenetic half-life with no predictors =
measure of phylogenetic signal

..... with predictors =
measure of REMAINING
phylogenetic signal in residuals

Modeling adaptive shifts



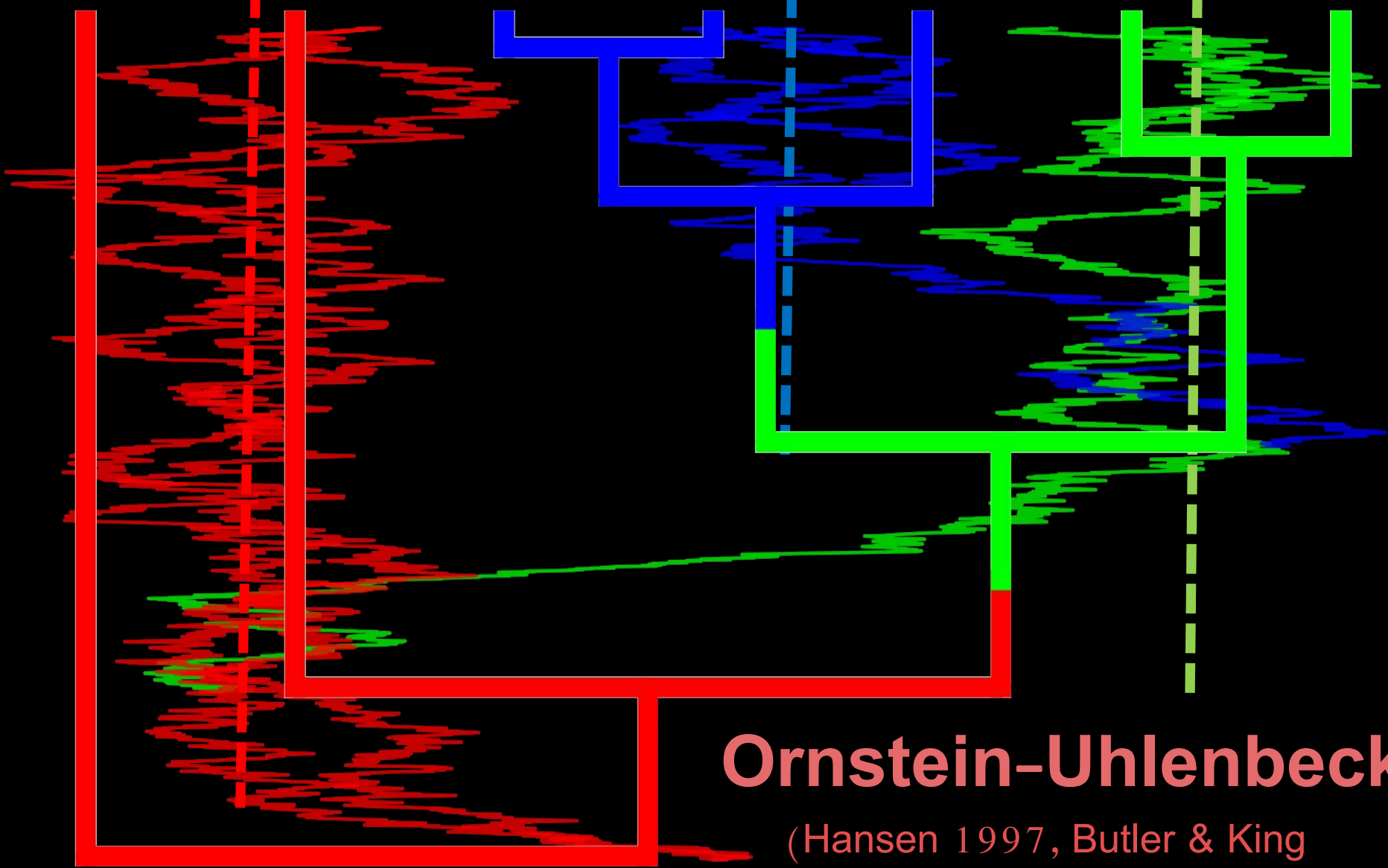
θ_1

θ_2

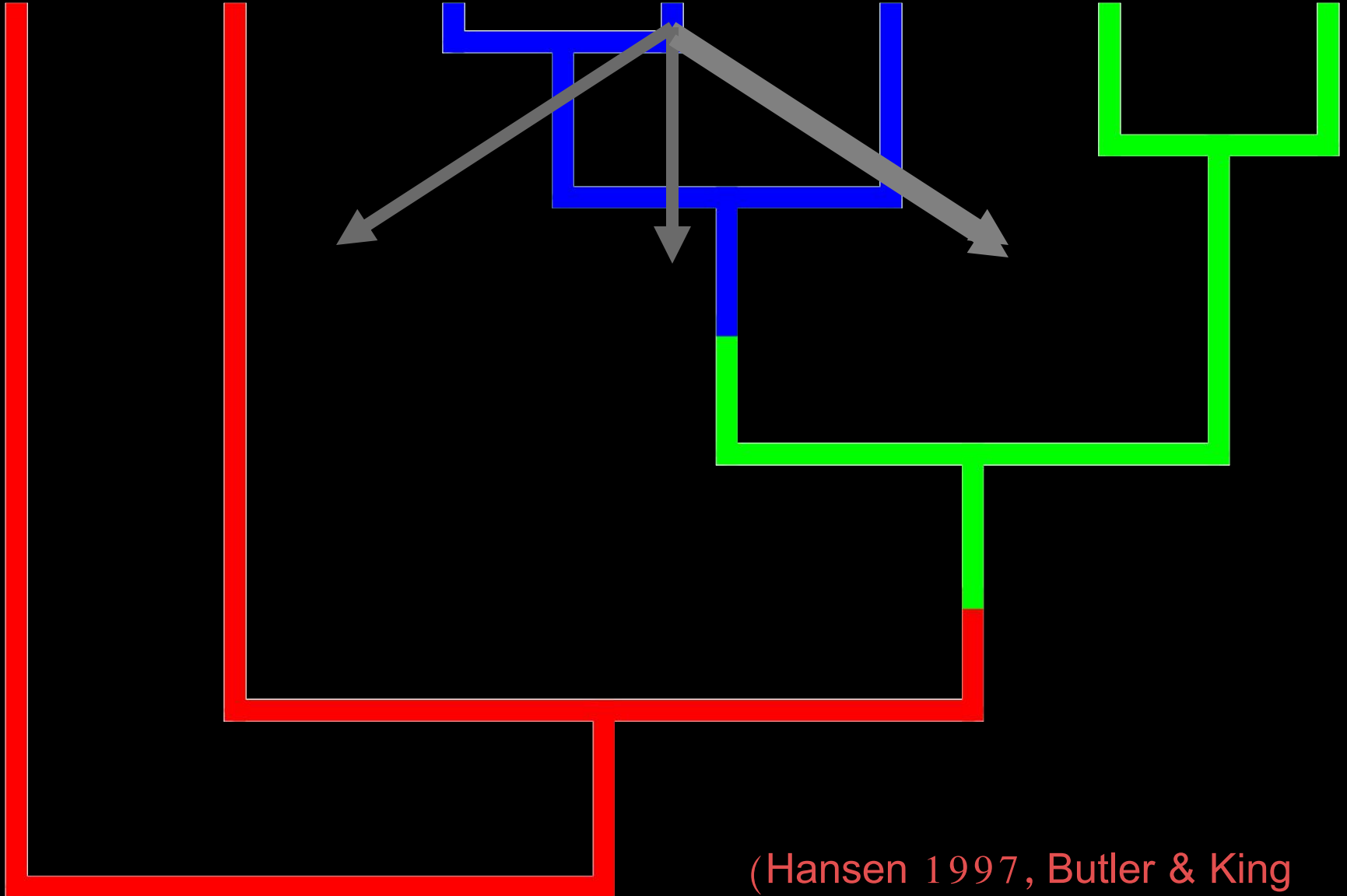
θ_3

Ornstein-Uhlenbeck

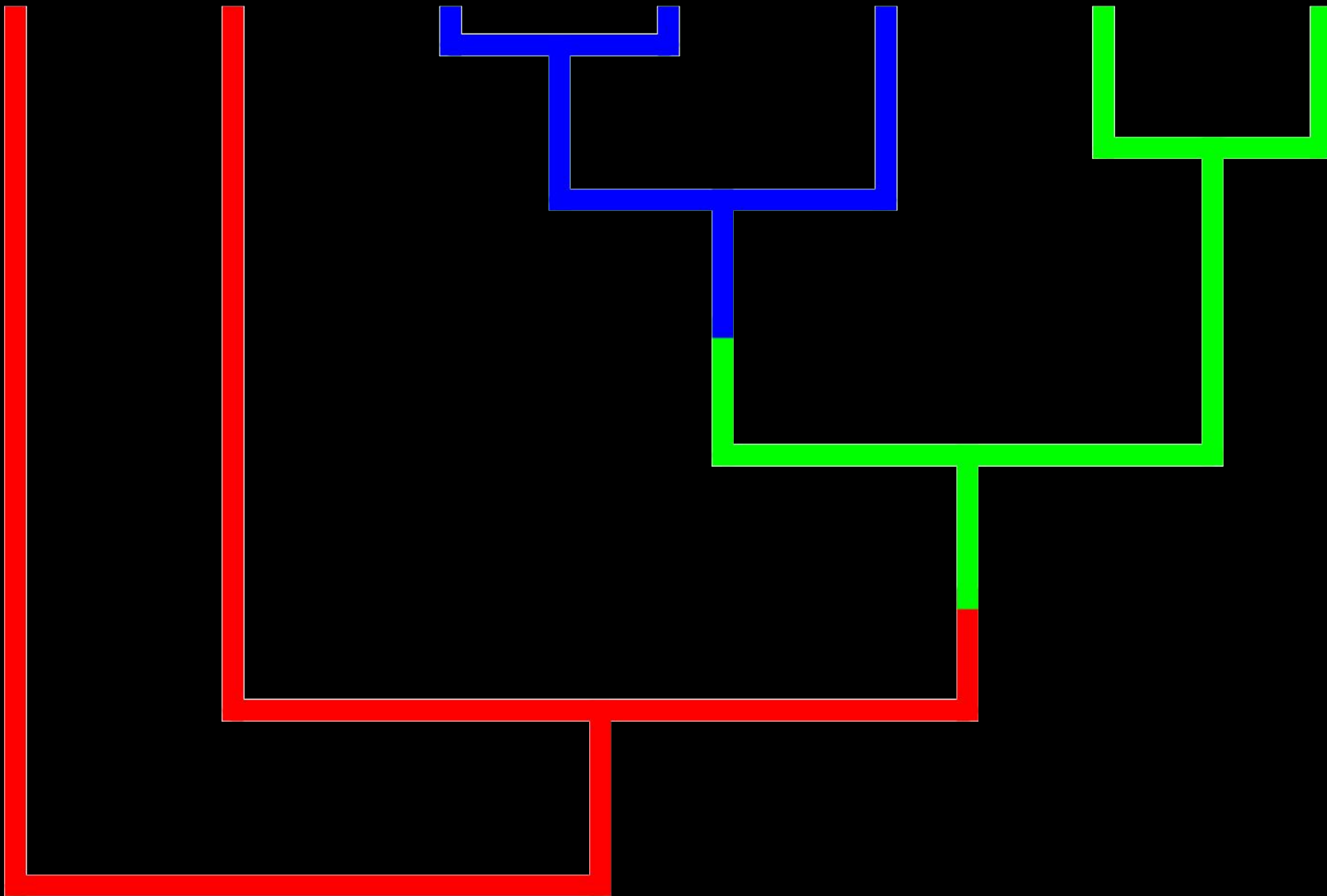
(Hansen 1997, Butler & King
2004)

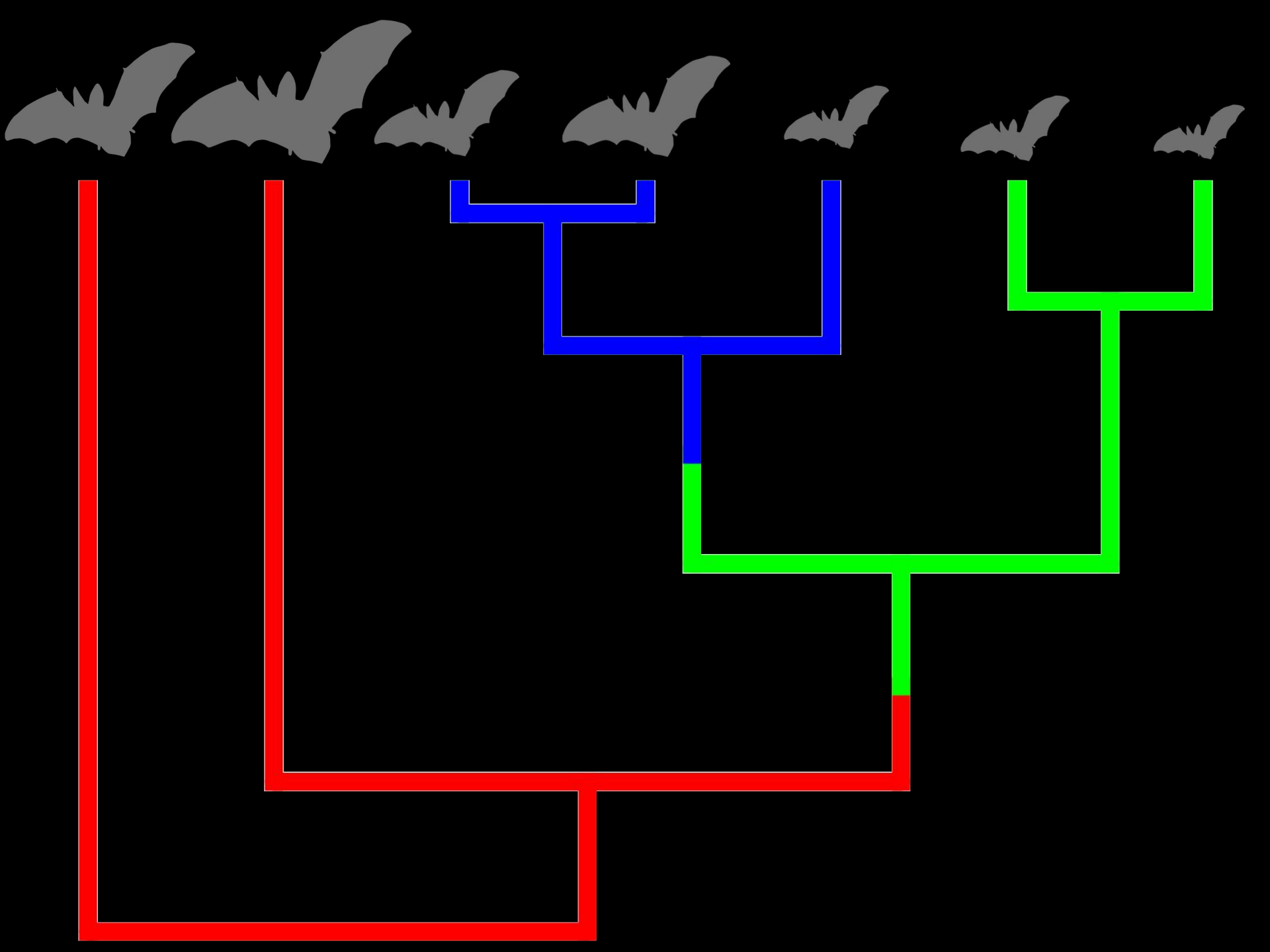


Compare models (Best Model)



(Hansen 1997, Butler & King
2004)





Like phylogenetic models, lots of PCMs devoted to *heterogeneity in the tempo & mode of evolution*

Continuous traits:

BM (bayestraits, Auteur, BAMM, OUwie)

OU (bayou, l1ou, PhylogeneticEM)

Discrete traits

Hidden State Models (corHMM)

Diversification Models (BAMM, HiSSE, FiSSE)

You can change any parameter of the model (or the model itself) at the shift

Brownian Motion - σ^2

Brownian Motion w/trend - σ^2, μ

OU - θ, σ^2, α

EB - σ^2, b

Example questions:

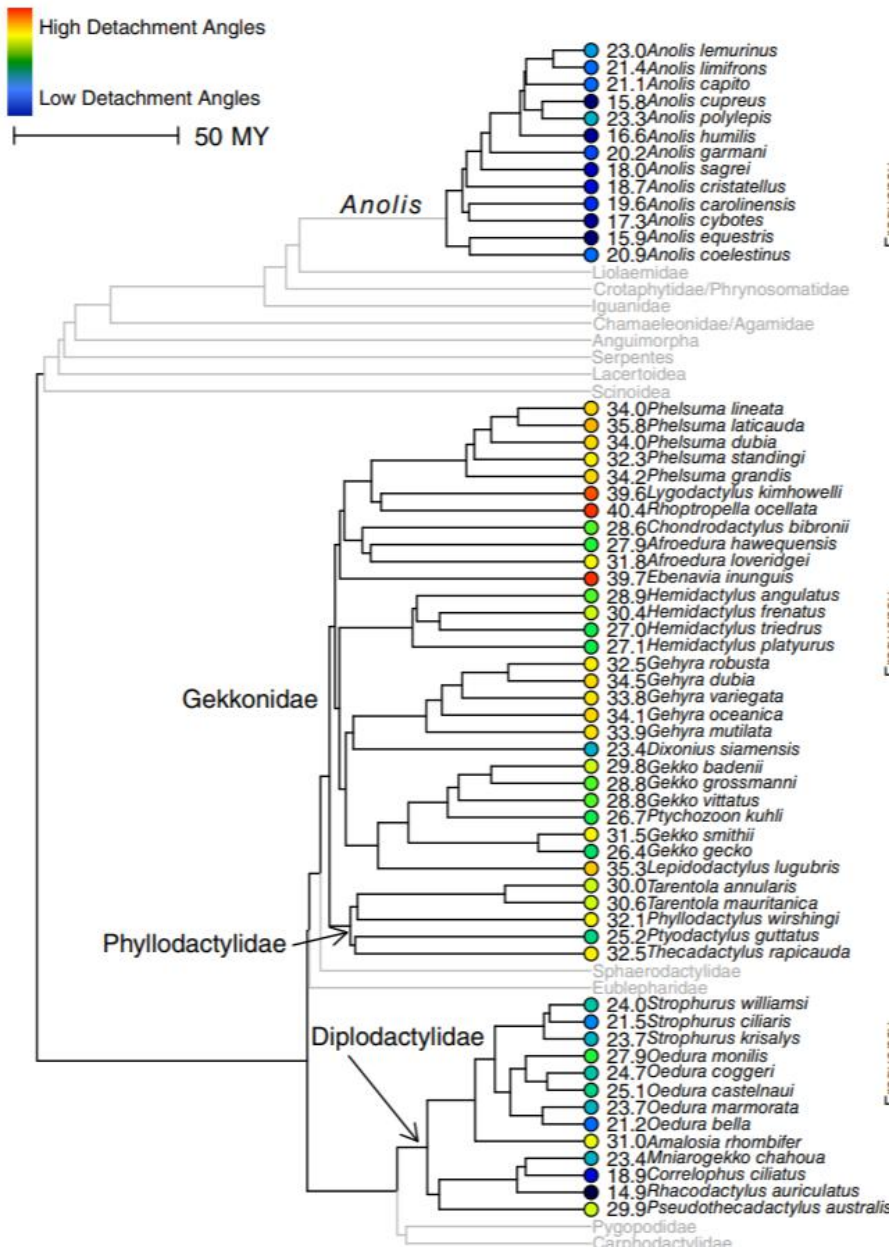
Does the rate of evolution change with habitat?

Does niche space expand on islands?

Do ectotherms have more constrained trait evolution than endotherms?

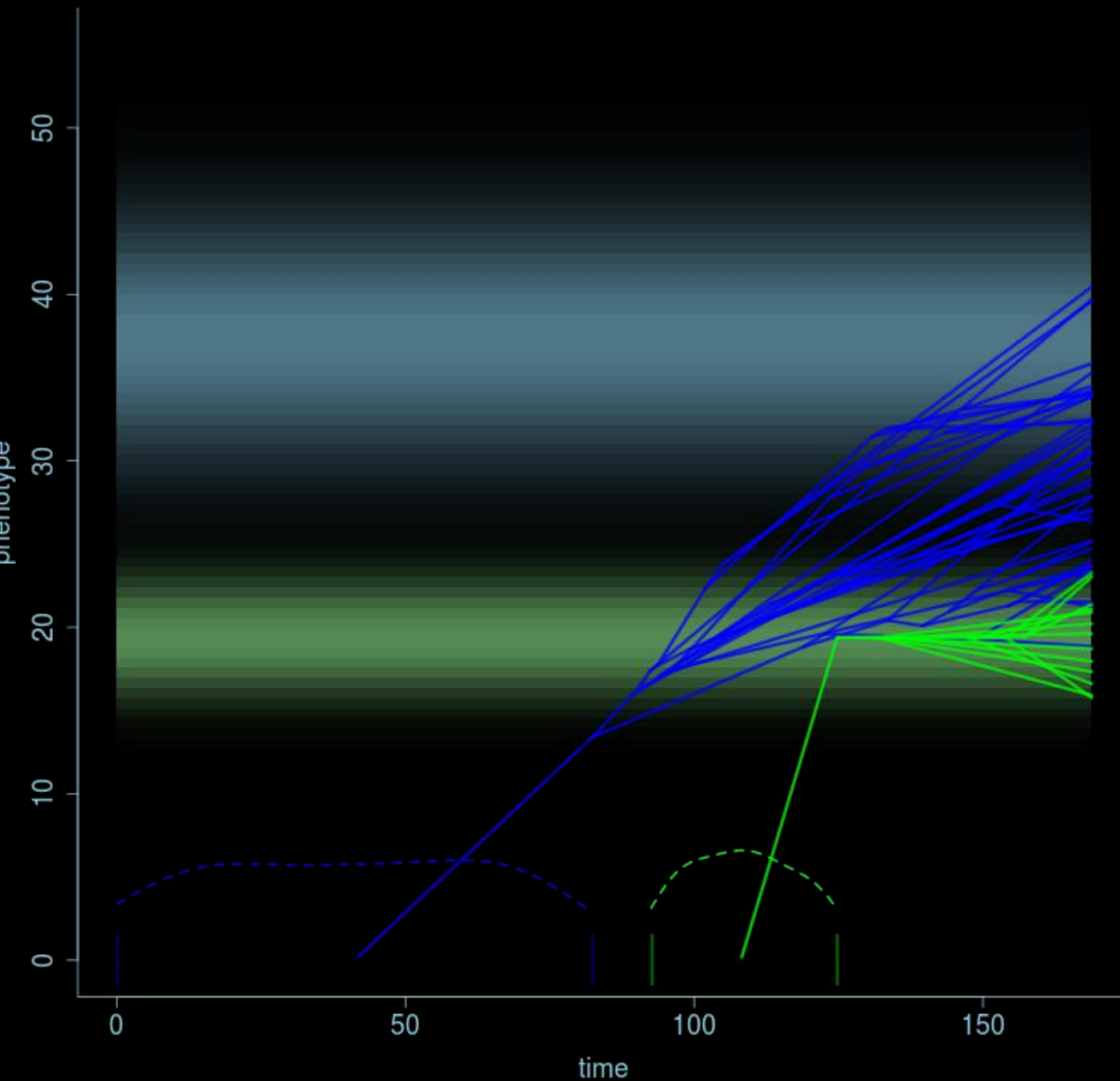
Is gene expression more constant early or late in cancer progression?

Are Anolis lizard ecomorphs convergent?



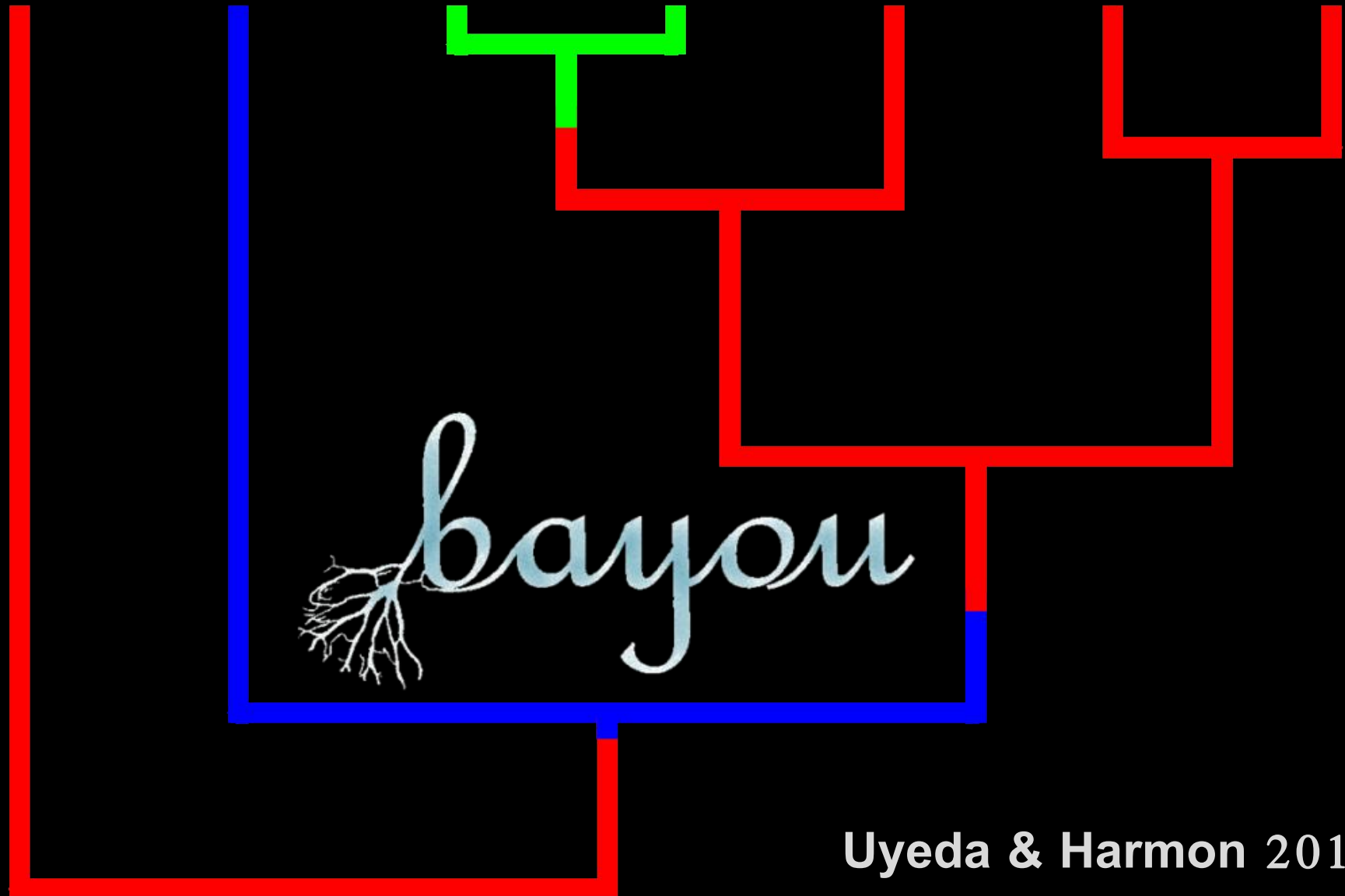
Do convergent pad-bearing lizards have similar evolutionary dynamics in functional performance?

Travis Hagey



Hagey et al. 2017,
Evolution

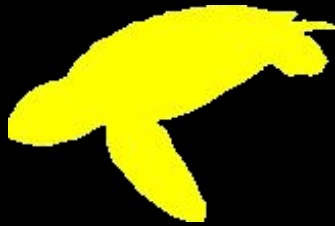
Geckos:
OU/BM w trend
Unconstrained
Anoles:
Strongly OU
Very constrained



Uyeda & Harmon 2014

Turtles and Tortoises

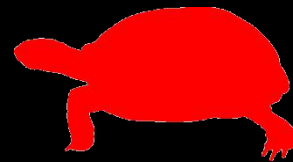
(Jaffe et al. 2011)



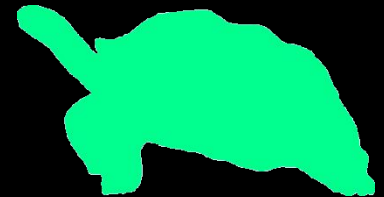
Marine



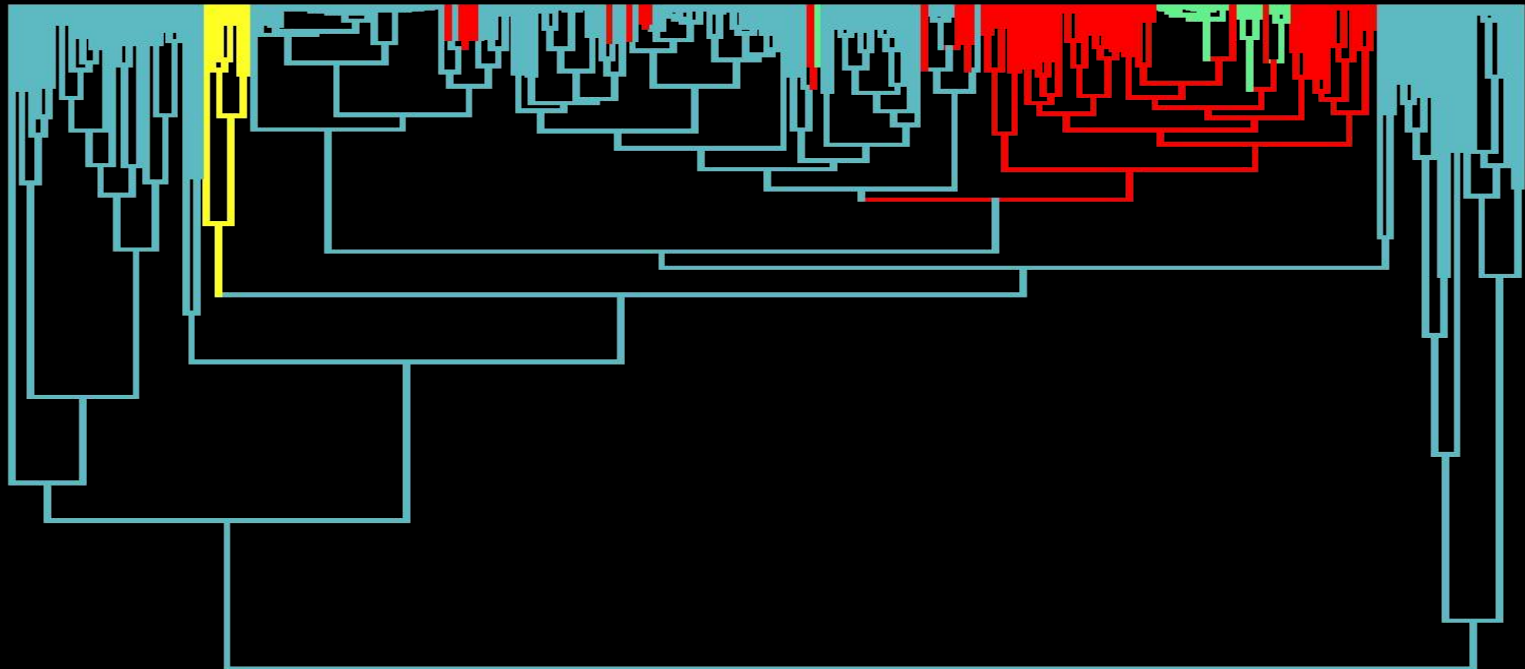
Freshwater



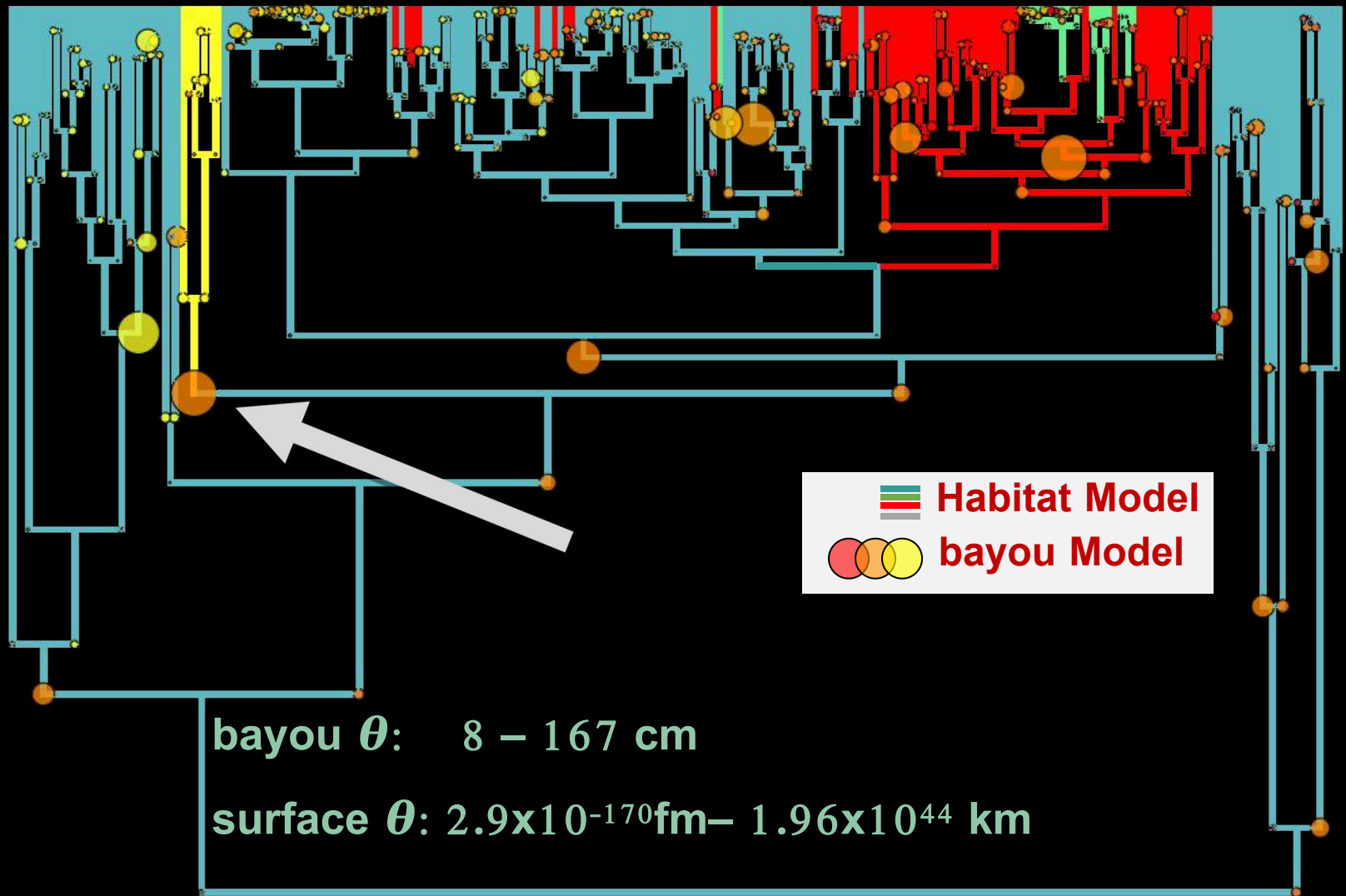
Terrestrial

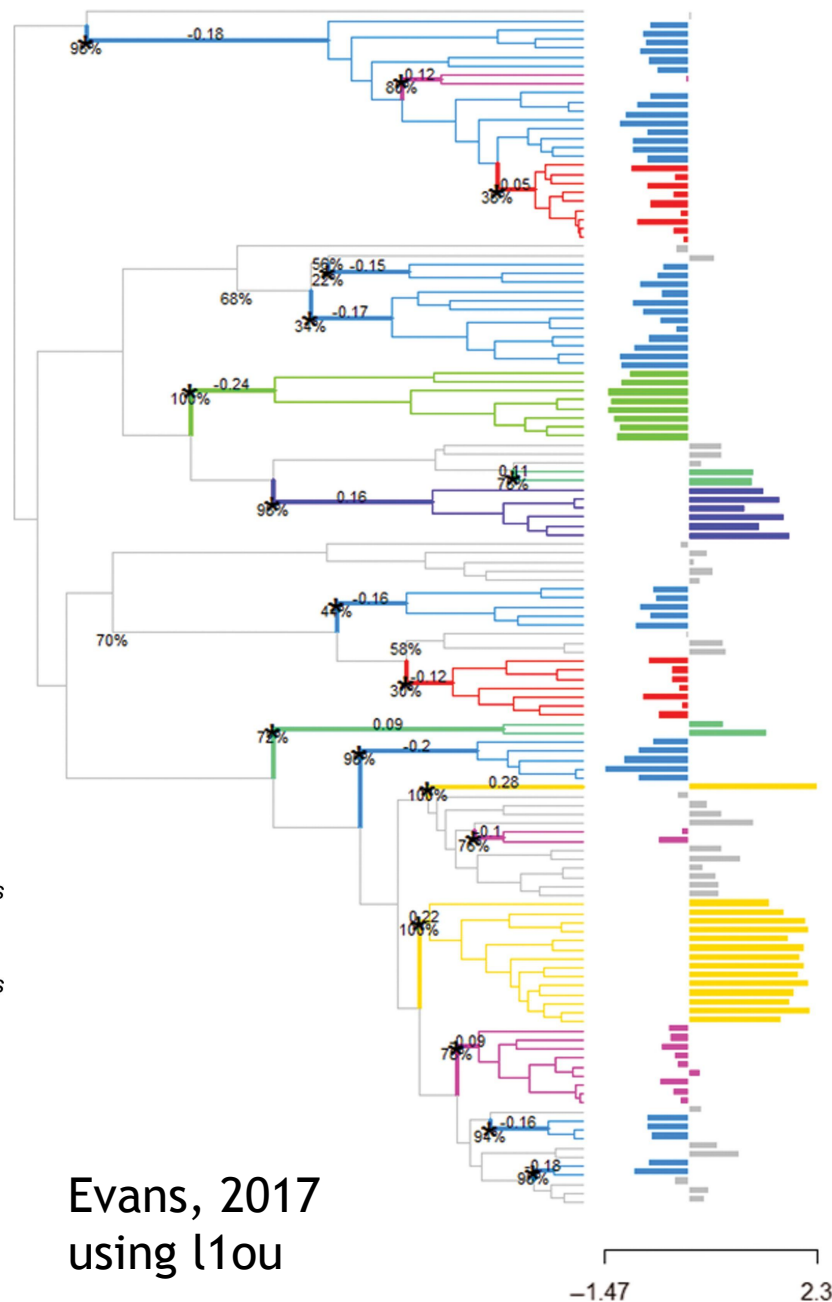
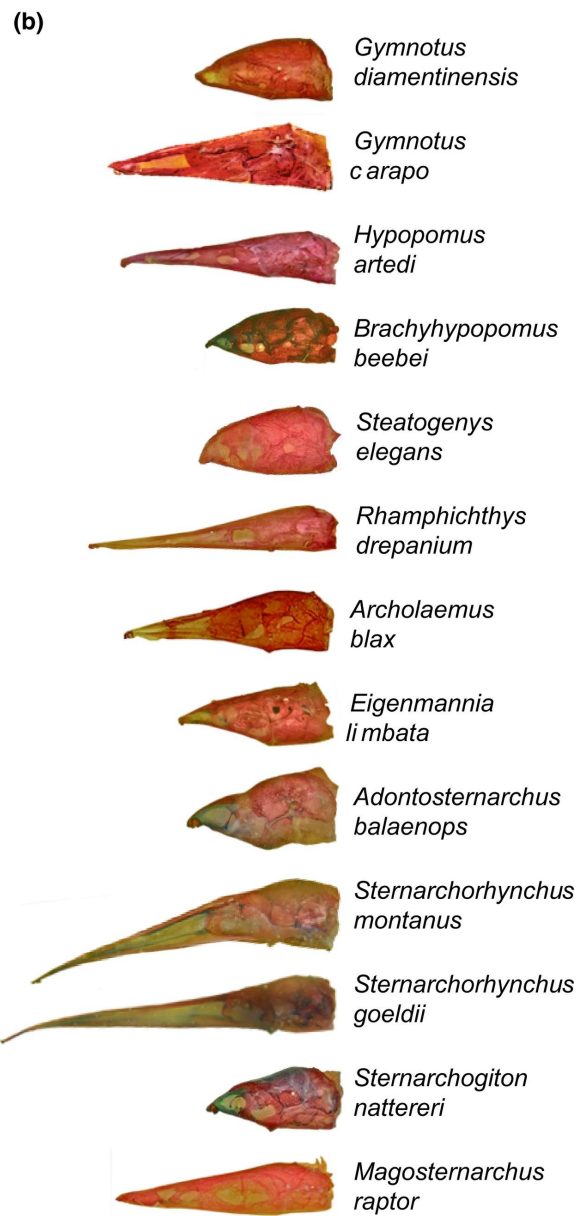
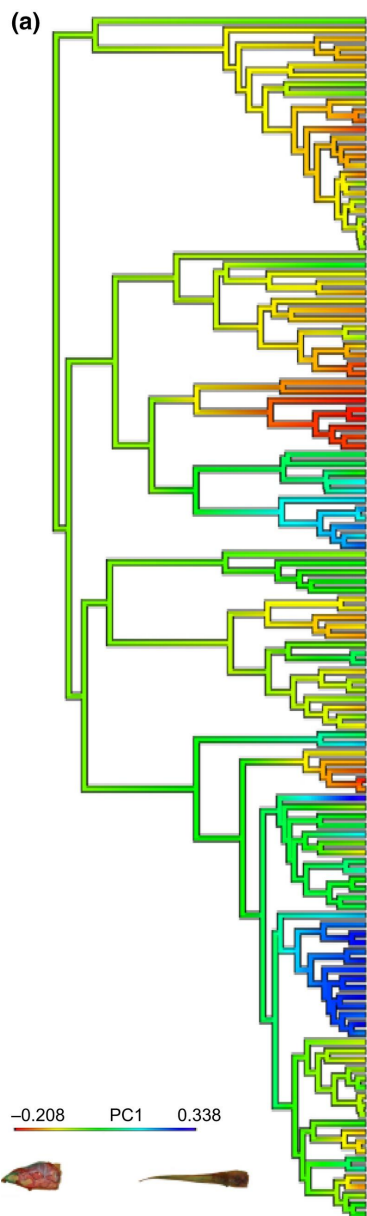


Island



bayou (Uyeda and Harmon, 2014)

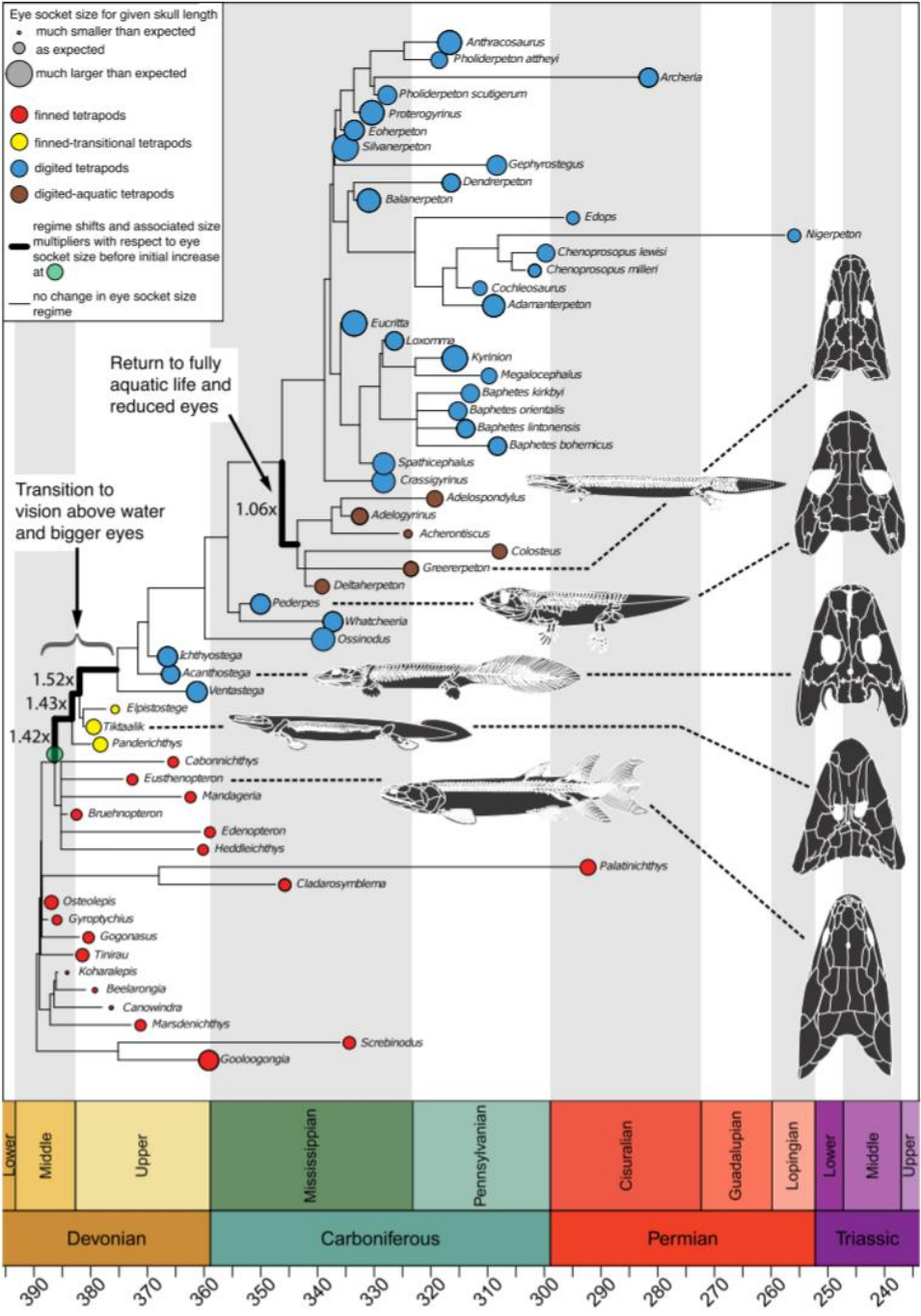
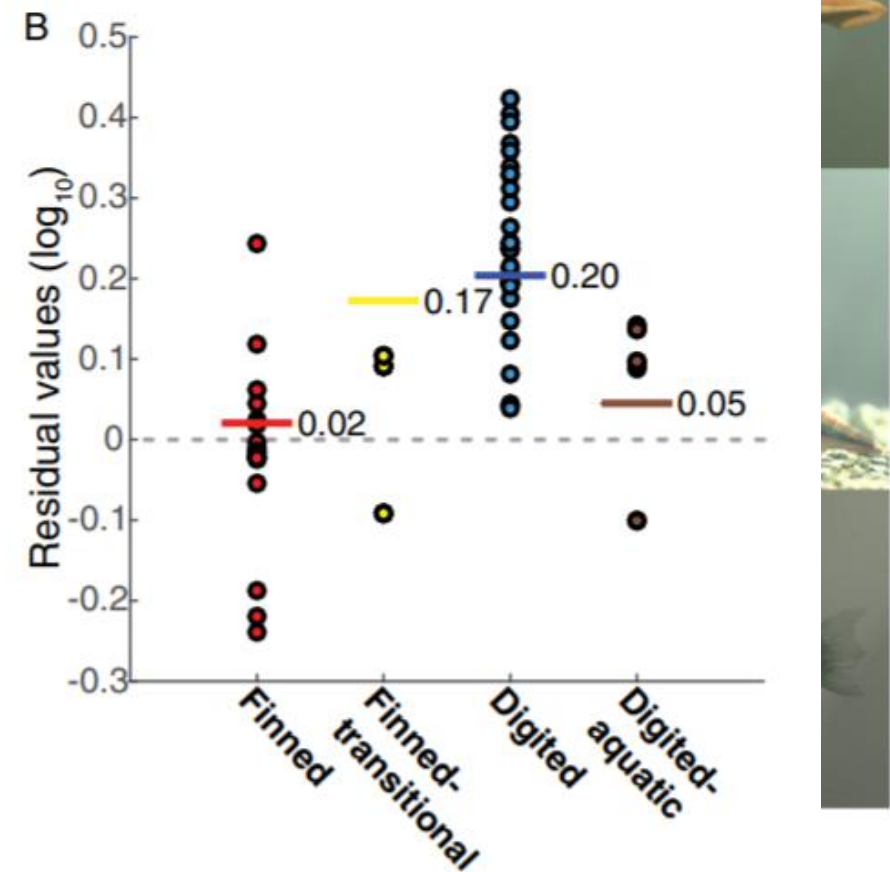




Shifts in Fossil Data: Unique Opportunities



halflife =
5.79 my



Hunt, Bell & Travis 2007

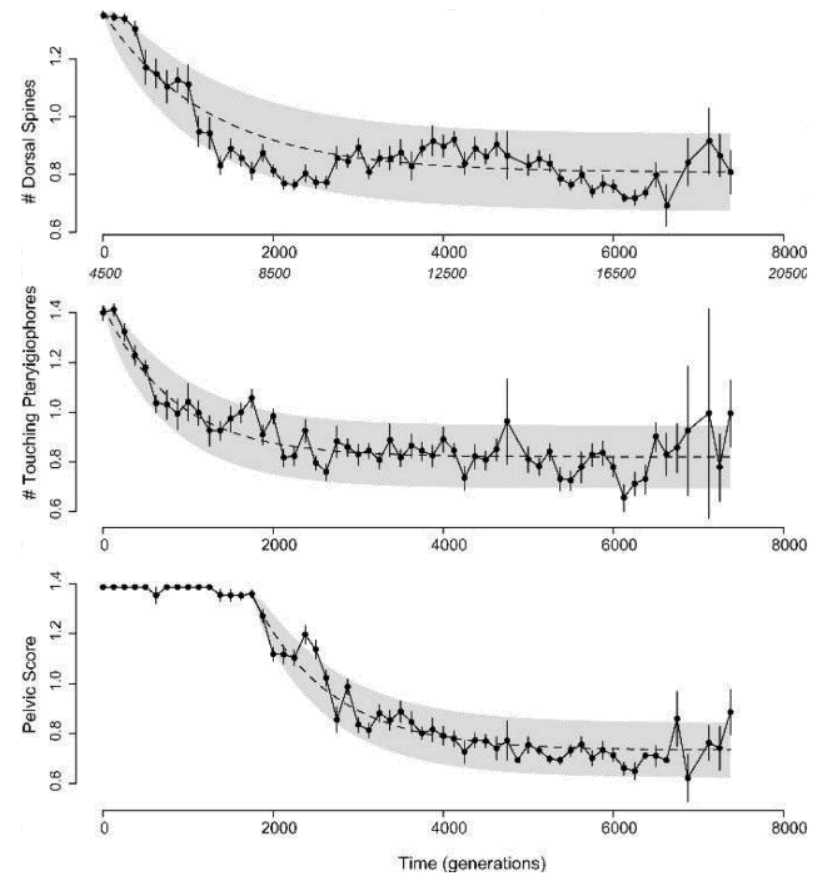
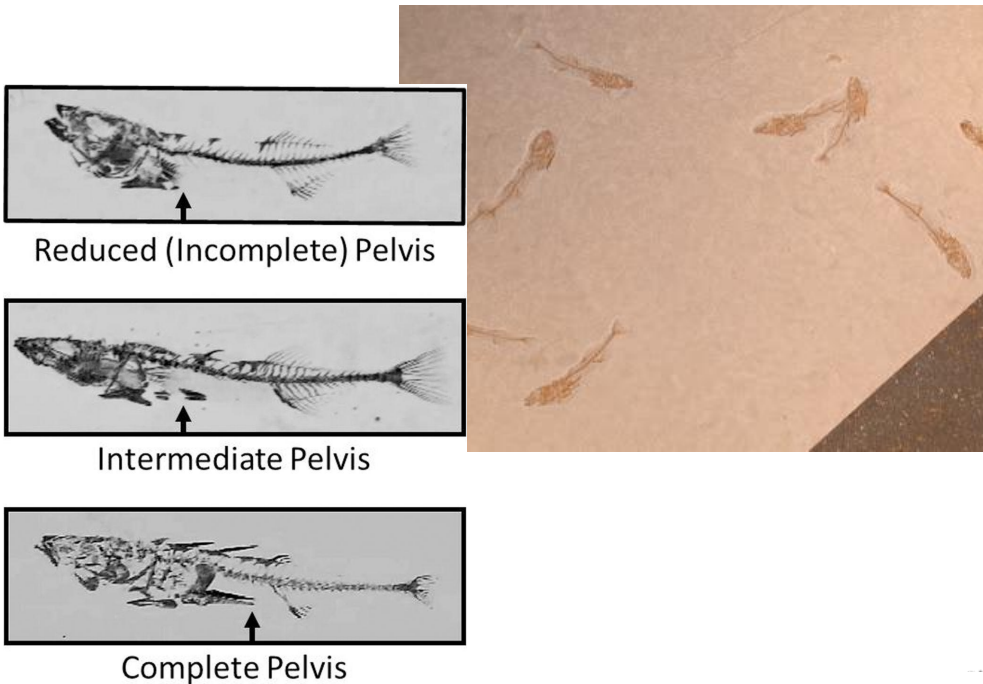


Table 3. Estimates and ranges for population genetic and selective parameters, derived from the maximum-likelihood parameter estimates for the adaptive model. Displacement is the phenotypic distance between the starting morphology and the optimal morphology, in standard deviation units (computed from the phenotypic variance pooled across samples, σ^2_p). Calculations of the effective population size (N_e) and strength of stabilizing selection (ω^2) require knowledge of trait heritabilities, which were assumed to range between 0.1 and 0.7. The ranges reported for N_e and ω^2 reflect calculation using these two different end-member heritability values. Finally, $t_{1/2}$ is the expected time it takes the population to traverse half the distance to the phenotypic optimum, in generations. For details on the calculation of these quantities, see the Appendix.

Trait	Displacement	σ^2_p	N_e	ω^2	$t_{1/2}$
No. of dorsal spines	-2.80	0.041	575–4023	5.0–35.2	853
Pterygiophores	-2.13	0.081	851–5957	6.7–47.3	580
Pelvic score	-2.57	0.059	889–6222	5.3–37.5	635

Strength of OU models: It looks like evolution! Parameters (could potentially) have biological meaning!

Weaknesses: Statistical “bad dog”. Without constraints, can behave poorly.

**But what if the optimum doesn't
have discrete shifts?**

What if it moves continuously?

SLOUCH (Hansen, Pienaar & Orzack 2008)

ORIGINAL ARTICLE

doi:10.1111/j.1558-5646.2008.00412.x

A COMPARATIVE METHOD FOR STUDYING ADAPTATION TO A RANDOMLY EVOLVING ENVIRONMENT

Thomas F. Hansen,^{1,2,3} Jason Pienaar,^{2,4} and Steven Hecht Orzack⁵

¹*Center for Evolutionary and Ecological Synthesis, Department of Biology, University of Oslo, PB 1066, Blindern, 0316 Oslo, Norway*

²*Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306*

³*E-mail: thomas.hansen@bio.uio.no*

⁵*Fresh Pond Research Institute, Cambridge, Massachusetts 02140*

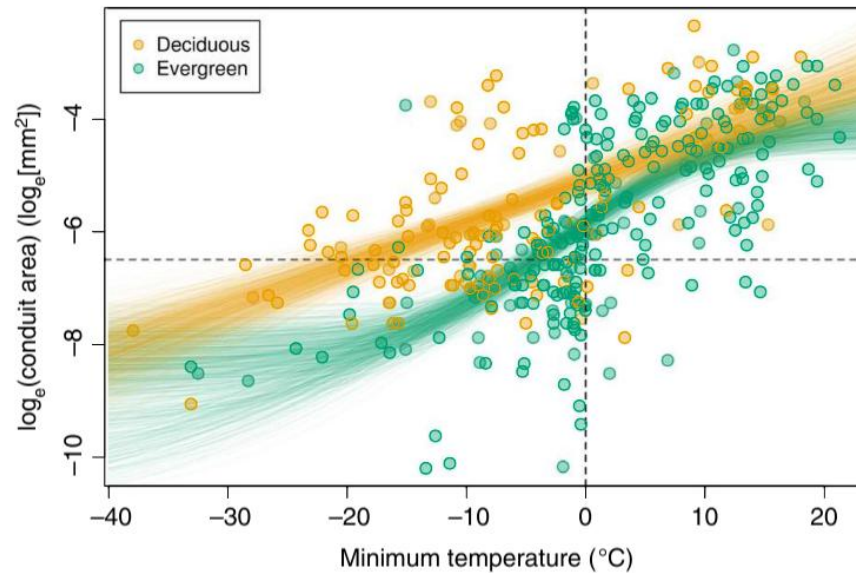
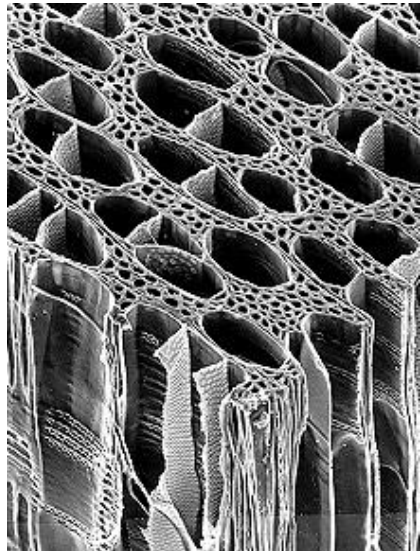
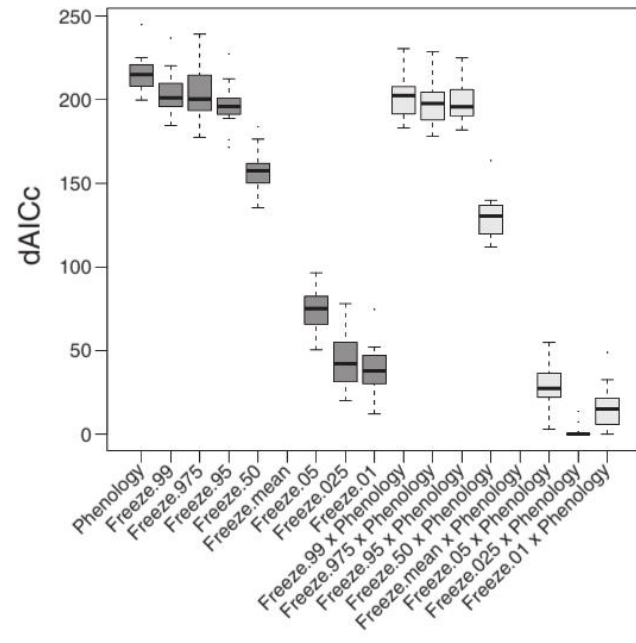
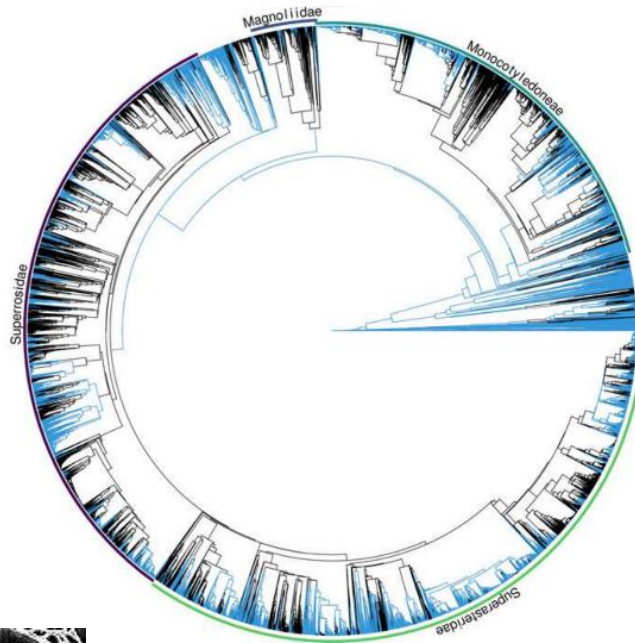


Fig. 6 Bayesian posteriors of estimates of best-fitting functional relationships between macroevolutionary adaptive optima for natural log of conduit area and minimum temperature at the 2.5th percentile of geographic distribution. Functions are fit separately for deciduous (gold) and evergreen (green) species. Best-fitting models for deciduous species are linear, whereas evergreen species follow a sigmoid relationship with the center around freezing (vertical dashed line). The horizontal black dashed line is at 0.0015 mm² (i.e. the 0.044 mm diameter threshold above which freezing induced embolisms are believed to become frequent at modest tensions; Davis *et al.*, 1999).

Method	Shift mapping	α & σ	Multivariate?	Optimum change	Inference approach	Predictors?	Convergent regimes?
OUCH (Butler & King 2004)	User hypotheses	Global	Yes	Discrete	Maximum Likelihood	Discrete regimes	Yes
Ouwie (Bealieu et al. 2012)	User hypotheses/ simmap	Regime-specific	No	Discrete	Maximum Likelihood	Discrete regimes	Yes
mvMORPH (Clavel 2015)	User hypotheses/ simmap	Global	Yes	Discrete	Maximum Likelihood	Discrete regimes	Yes
SLOUCH (Hansen et al. 2008)	None	Global	No	Brownian Motion	Maximum Likelihood	Continuously-evolving predictors	N/A
mvSLOUCH (Bartoszek et al. 2012)	None	Global	Yes	Brownian Motion/O U	Maximum Likelihood	Continuously co-evolving	N/A
SURFACE (Ingram & Mahler 2013)	Data driven (Stepwise AIC)	Global	Pseudo	Discrete	Maximum Likelihood	No	Yes
l1ou (Khabbazian et al. 2016)	Data driven (Lasso)	Global	No	Discrete	Maximum Likelihood	No	Yes
PhylogeneticEM (Bastide et al. 2018)	Data driven (Expectation maximization)	Global	Yes	Discrete	Maximum Likelihood	No	Yes
Bayou (Uyeda & Harmon 2014)	Data driven (RJMCMC)	Global	No	Discrete +	Bayesian	Regression framework	Not with RJMCMC

Overwhelmed? Take-home:

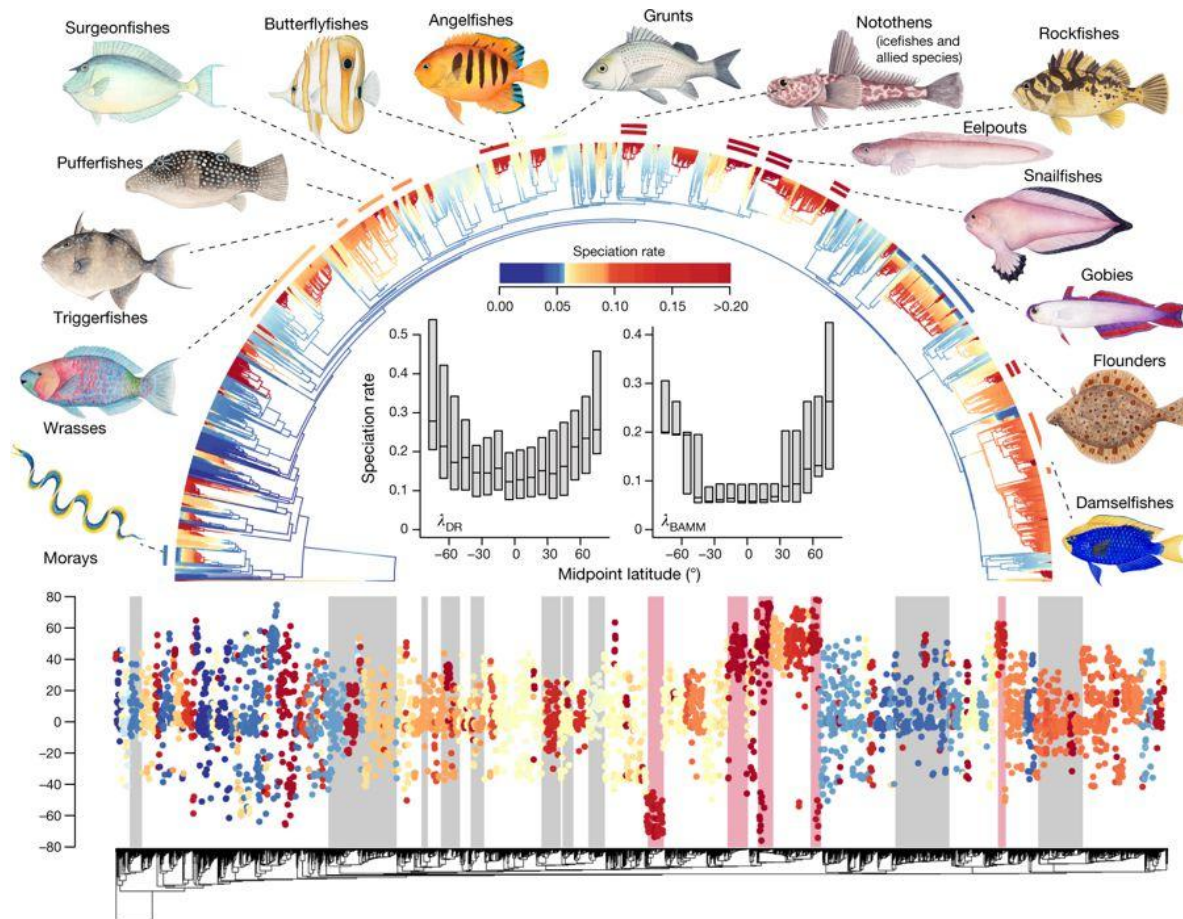
Lots of variations on a basic model (OU)

Models where everything vary -> Probably too complicated to fit to real data!

How you can simplify the model with what you KNOW.

Choose software that tests YOUR hypothesis and lets you incorporate YOUR knowledge

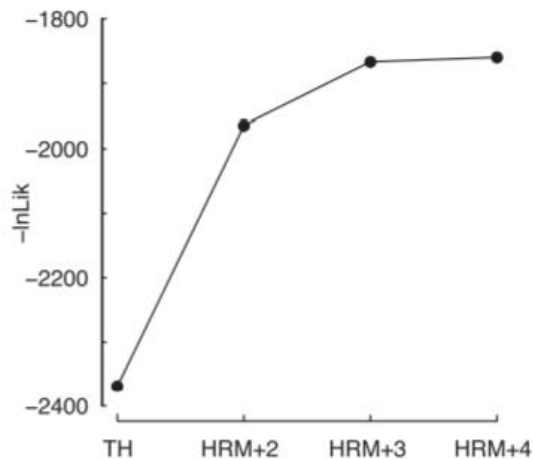
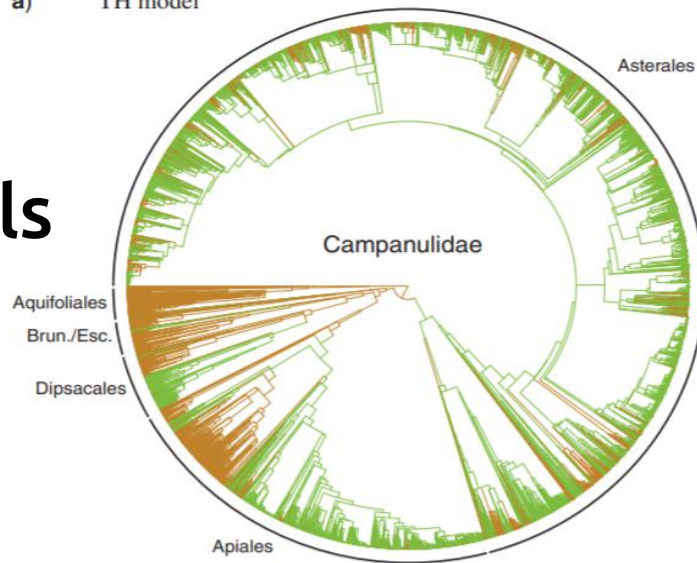
Similar models for Diversification: BAMM (Rabosky 2014)



Rabosky et al. 2018, Nature

Shifts in Discrete Character Data: Hidden State Models

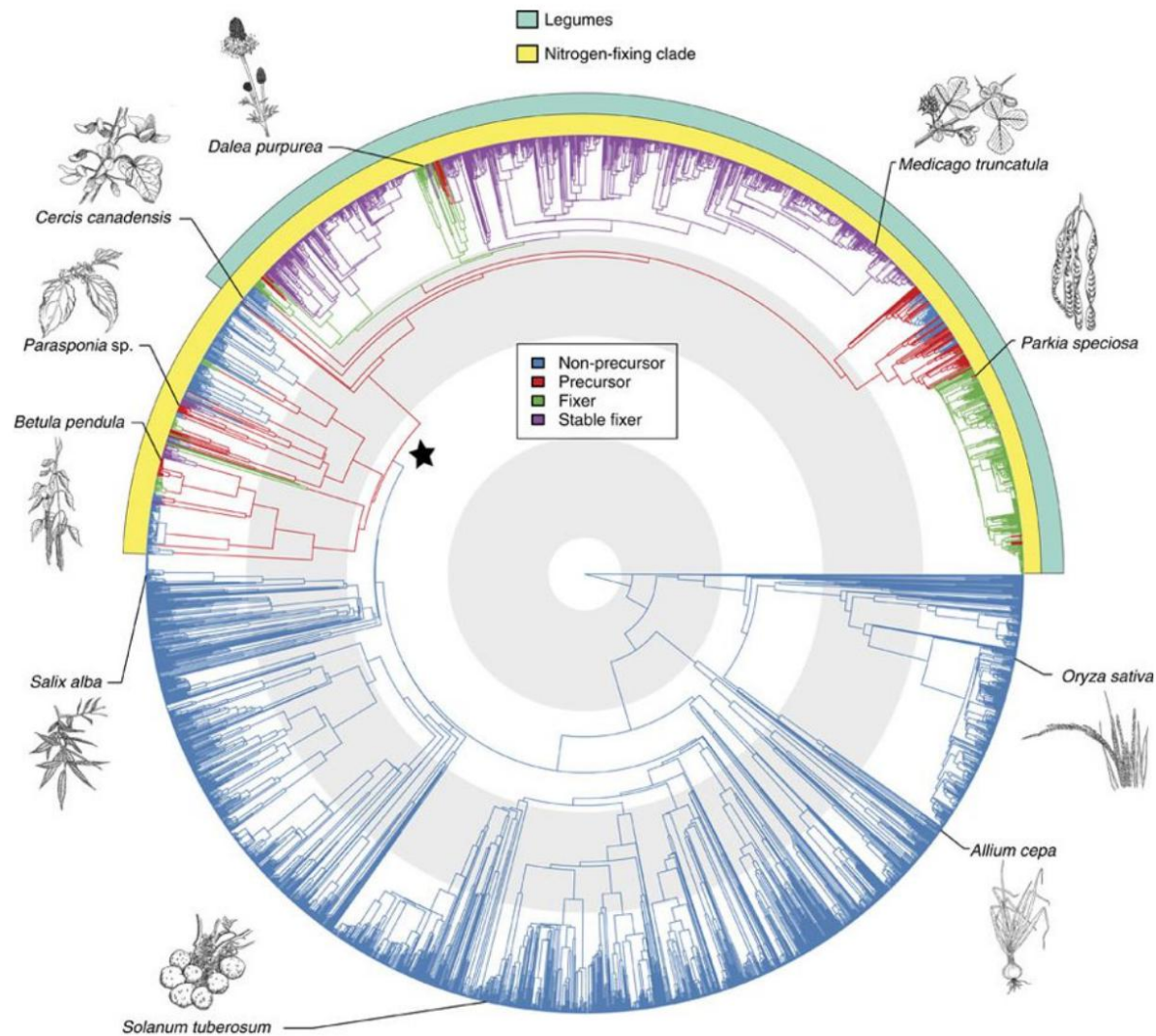
a) TH model



Identifying Hidden Rate Changes in the Evolution of a Binary Morphological Character:
The Evolution of Plant Habit in Campanulid Angiosperms

JEREMY M. BEAULIEU^{1,*}, BRIAN C. O'MEARA², AND MICHAEL J. DONOGHUE¹

`install.packages("corHMM")`



A single evolutionary innovation drives the deep evolution of symbiotic N₂-fixation in angiosperms

Gijsbert D.A. Werner¹, William K. Cornwell^{1,†}, Janet I. Sprent², Jens Kattge^{3,4} & E. Toby Kiers¹

A word about Ancestral State Reconstruction...