

PHYLOGENETIC INFERENCE USING FOSSIL AND MOLECULAR DATA IN REVBayes

Tracy Heath, April Wright, Walker Pett

@trayc7 | @WrightingApril | @WalkerPett

Ecology, Evolution, & Organismal Biology
Iowa State University

<http://phyloworks.org>

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ACKNOWLEDGEMENTS

Collaborators: Tanja Stadler, Alexandra Gavryushkina, Chi Zhang, Michael Landis, Mark Holder, Rachel Warnock, Alexei Drummond, Daniel Ksepka, Rob Meredith, & Sebastian Höhna

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and the LSU SSB Meeting
Organizers!

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- NSF DEB-1256993 & DEB-1556615



OUTLINE

- Brief intro to RevBayes
- Overview of divergence time estimation and models used in this tutorial
 - Clock models
 - Tree models with fossil samples
 - Morphology models
- Q & A
- RevBayes Tutorial — Estimating the Phylogeny and Divergence Times of Fossil and Extant Bears

CHALLENGES OF STATISTICAL PROGRAMMING

Prior options in MrBayes v3.2

Parameter	Options	Current Setting
Tratiopr	Beta/Fixed	Beta(1.0,1.0)
Revmatpr	Dirichlet/Fixed	Dirichlet(1.0,1.0,1.0,1.0,1.0,1.0)
Aamodelpr	Fixed/Mixed	Fixed(Poisson)
Aarevmatpr	Dirichlet/Fixed	Dirichlet(1.0,1.0,...)
Omegapr	Dirichlet/Fixed	Dirichlet(1.0,1.0)
Ny98omega1pr	Beta/Fixed	Beta(1.0,1.0)
Ny98omega3pr	Uniform/Exponential/Fixed	Exponential(1.0)
M3omegapr	Exponential/Fixed	Exponential
Codoncatfreqs	Dirichlet/Fixed	Dirichlet(1.0,1.0,1.0)
Statefreqpr	Dirichlet/Fixed	Dirichlet(1.0,1.0,1.0,1.0)
Shapepr	Uniform/Exponential/Fixed	Exponential(2.0)
Ratecorrpr	Uniform/Fixed	Uniform(-1.0,1.0)
Pinvarpr	Uniform/Fixed	Uniform(0.0,1.0)
Covswitchpr	Uniform/Exponential/Fixed	Uniform(0.0,100.0)
Symdirihyperpr	Uniform/Exponential/Fixed	Fixed(Infinity)
Topologypr	Uniform/Constraints/Fixed	Uniform
Brlenspr	Unconstrained/Clock/Fixed	Unconstrained:Exp(10.0)
Treeagepr	Gamma/Uniform/Fixed/ Truncatednormal/Lognormal/ Offsetlognormal/Offsetgamma/ Offsetexponential	Gamma(1.00,1.00)

CHALLENGES OF STATISTICAL PROGRAMMING

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Treeagepr	Gamma/Uniform/Fixed/ Truncatednormal/Lognormal/ Offsetlognormal/Offsetgamma/ Offsetexponential	Gamma(1.00,1.00)

MODULAR BAYESIAN PHYLOGENETIC SOFTWARE

Several software packages in phylogenetics are moving toward a more modular framework

- reuse code
- easier to extend existing models and implement new models through a rich, language-based interface
- provides a unified framework for analyses under complex models

RevBayes

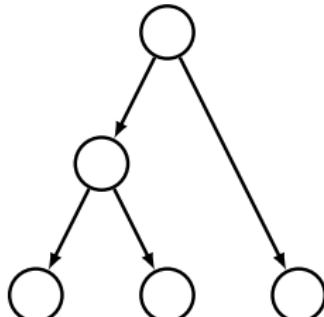
Bali-Phy

BEAST2

RevBayes

Höhna et al. 2016. **RevBayes:**
Bayesian phylogenetic inference using
graphical models and an interactive
model-specification language.
Systematic Biology.
(doi: 10.1093/sysbio/syw021)

<http://revbayes.com>



Development team members at SSB 2017

Höhna

Landis

Heath

Pett

Freyman

Wright

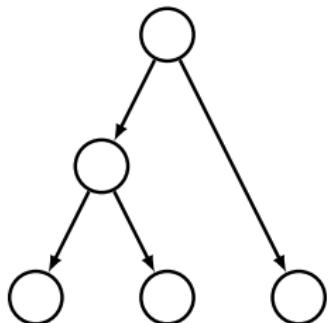
J. Brown

Coghill

GRAPHICAL MODELS IN RevBAYES

Graphical models provide tools for visually & computationally representing complex, parameter-rich probabilistic models

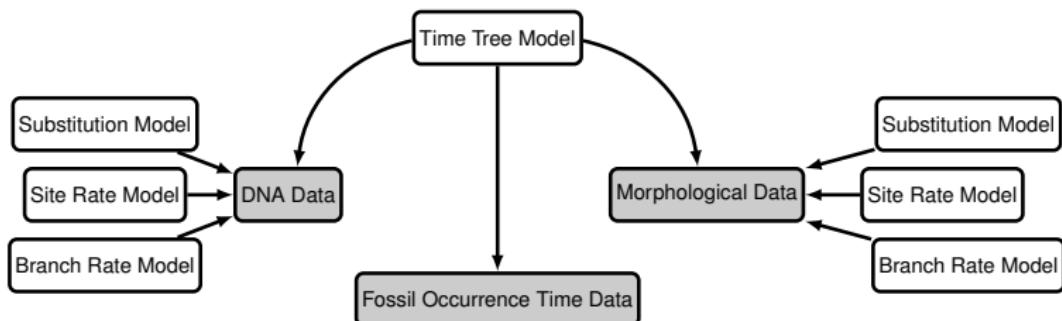
We can depict the conditional dependence structure of various parameters and other random variables



Höhna, Heath, Boussau, Landis, Ronquist, Huelsenbeck. 2014.
Probabilistic Graphical Model Representation in Phylogenetics.
Systematic Biology. (doi: 10.1093/sysbio/syu039)

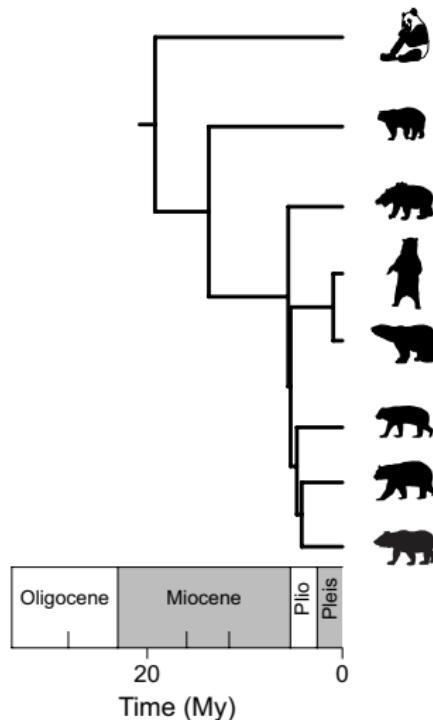
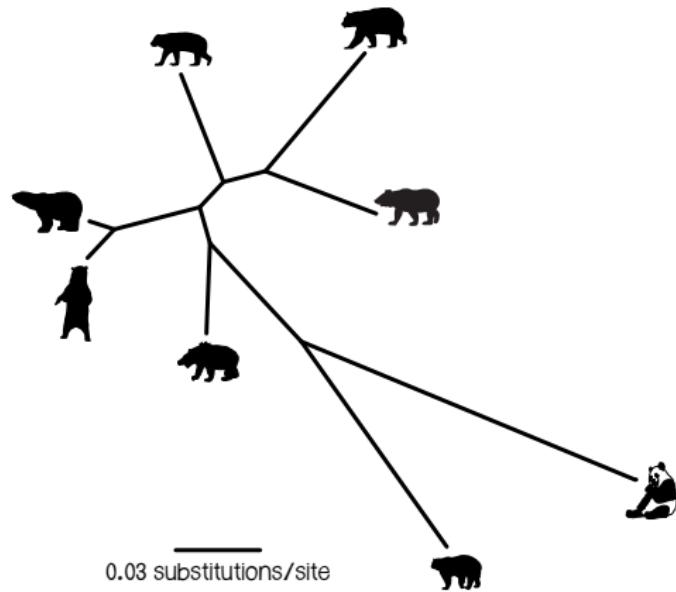
GRAPHICAL MODELS IN RevBAYES

The graphical model framework provides the flexibility and toolkit to create complex, hierarchical Bayesian models for integrative statistical analyses.



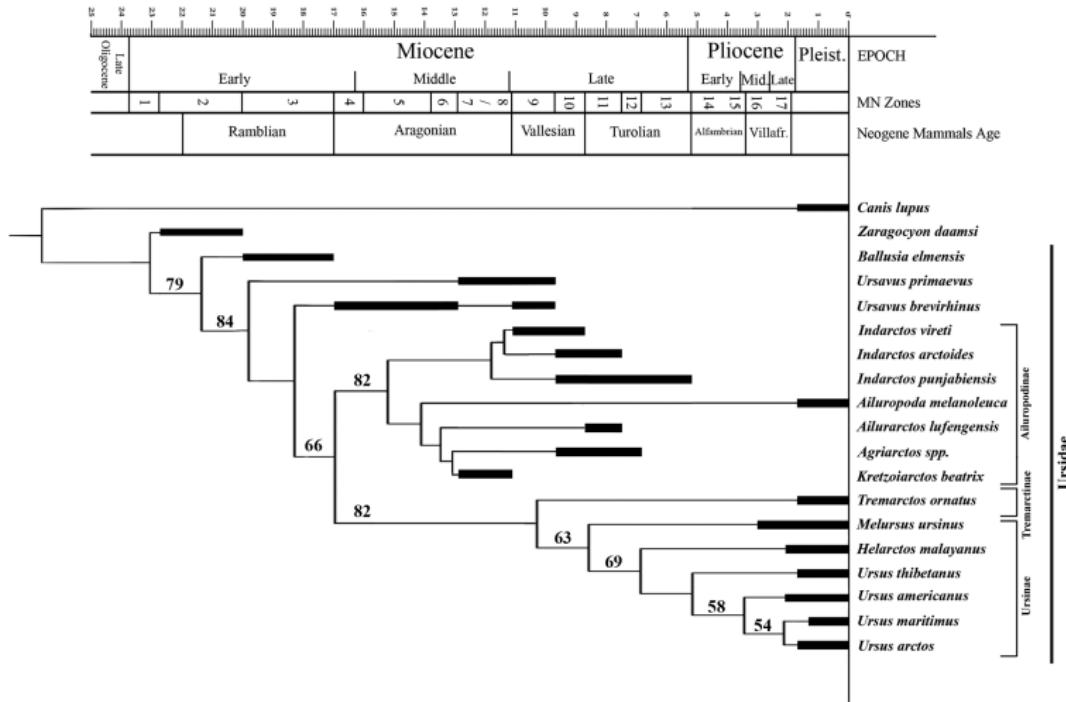
A TIME-SCALE FOR EVOLUTION

Phylogenies with branch lengths proportional to time provide more information about evolutionary history than unrooted trees with branch lengths in units of substitutions/site.



A TIME-SCALE FOR EVOLUTION

If fossil taxa are available, then these data can be incorporated into macroevolutionary studies



PALEONTOLOGY & NEONTOLOGY



Biology and Philosophy **19:** 687–720, 2004.

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The role of fossils in phylogeny reconstruction: Why is it so difficult to integrate paleobiological and neontological evolutionary biology?

TODD GRANTHAM

Department of Philosophy, College of Charleston, Charleston, SC 29424, USA
(e-mail: granthamt@cofc.edu)

PALEONTOLOGY & NEONTOLOGY

"Except during the interlude of the [Modern] Synthesis, there has been limited communication historically among the disciplines of evolutionary biology, particularly between students of evolutionary history (paleontologists and systematists) and those of molecular, population, and organismal biology. There has been increasing realization that barriers between these subfields must be overcome if a complete theory of evolution and systematics is to be forged.".

Reaka-Kudla & Colwell. "Toward the next century and beyond: The unity of evolutionary biology and its importance". In Dudley (ed.), *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic & Evolutionary Biology*, Discorides Press, Portland, OR, p. 16. (1994)

COMBINING FOSSIL & EXTANT DATA

Statistical methods provide a way to integrate paleontological & neontological data

Syst. Biol. 50(6):913–925, 2001

A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data

PAUL O. LEWIS

Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269-3043, USA;
E-mail: paul.lewis@uconn.edu

Syst. Biol. 61(6):973–999, 2012

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DOI:10.1093/sysbio/sys058

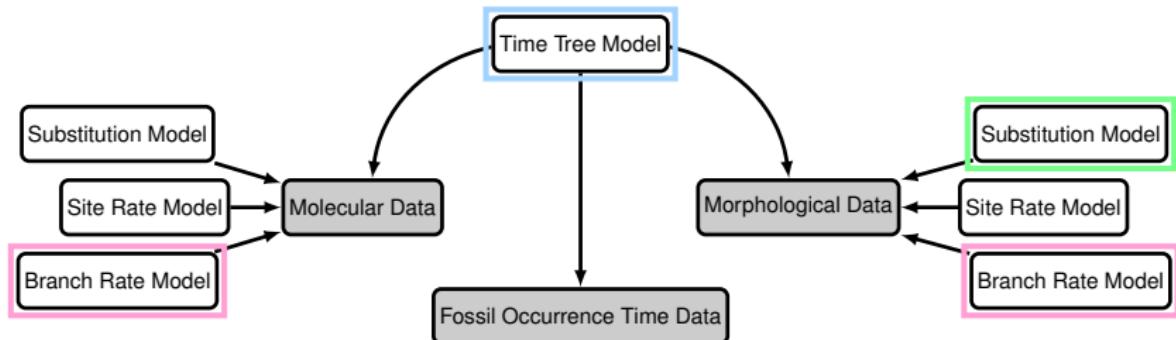
Advance Access publication on June 20, 2012

A Total-Evidence Approach to Dating with Fossils, Applied to the Early Radiation of the Hymenoptera

FREDRIK RONQUIST^{1,*}, SERAINA KLOPFSTEIN¹, LARS VILHELMSEN², SUSANNE SCHULMEISTER³, DEBRA L. MURRAY⁴, AND ALEXANDR P. RASNITSYN⁵

MODEL FRAMEWORK

Combine models for sequence evolution, morphological change, & fossil recovery to jointly estimate the tree topology, divergence times, & lineage diversification rates

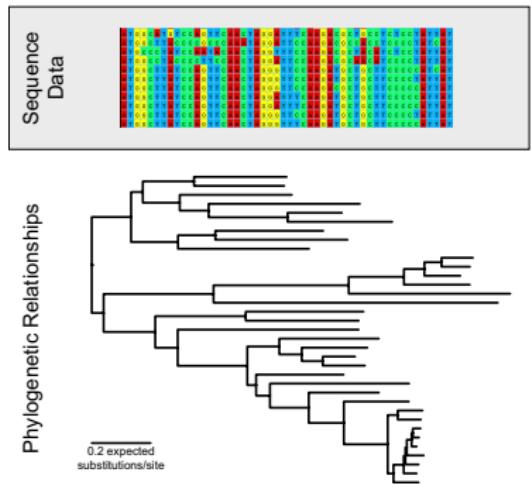


ESTIMATING RATE & TIME

Sequence data provide information about **branch lengths**

In units of **the expected # of substitutions per site**

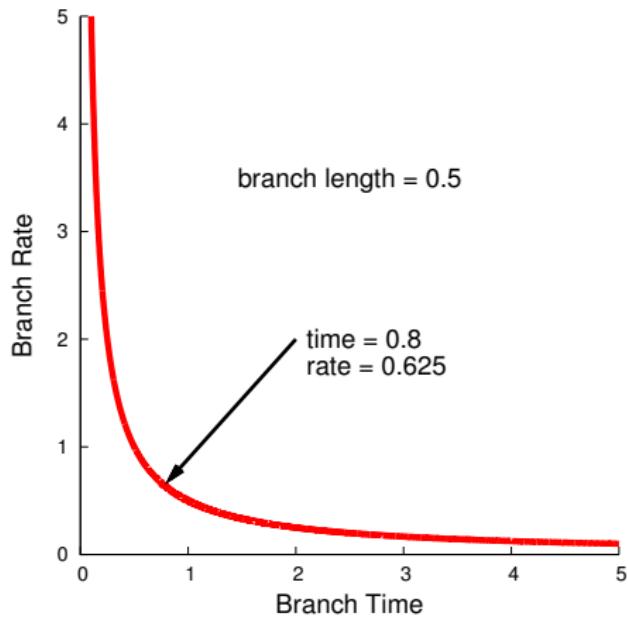
$$\text{branch length} = \text{rate} \times \text{time}$$



ESTIMATING RATE & TIME

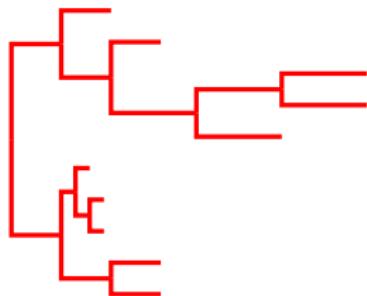
The sequence data provide information about branch length

for any possible rate, there's a time that fits the branch length perfectly

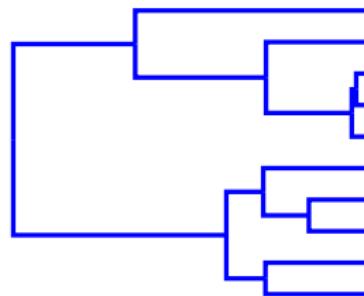


Methods for dating species divergences estimate the **substitution rate** and **time** separately

BAYESIAN DIVERGENCE TIME ESTIMATION



length = rate



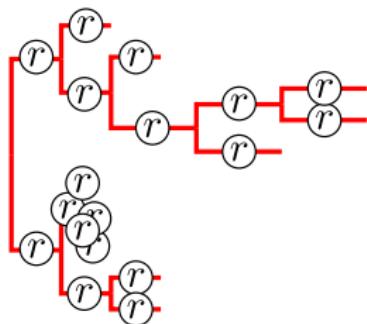
length = time

$$\mathcal{R} = (r_1, r_2, r_3, \dots, r_{2N-2})$$

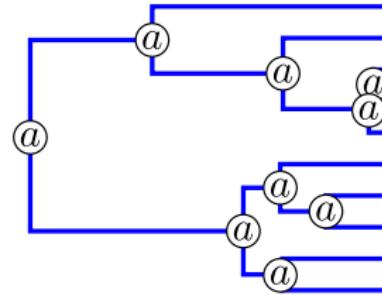
$$\mathcal{A} = (a_1, a_2, a_3, \dots, a_{N-1})$$

N = number of tips

BAYESIAN DIVERGENCE TIME ESTIMATION



length = rate



length = time

$$\mathcal{R} = (r_1, r_2, r_3, \dots, r_{2N-2})$$

$$\mathcal{A} = (a_1, a_2, a_3, \dots, a_{N-1})$$

$$N = \text{number of tips}$$

BAYESIAN DIVERGENCE TIME ESTIMATION

Posterior probability

$$f(\mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s, \mathcal{T} | D)$$

\mathcal{R} Vector of rates on branches

\mathcal{A} Vector of internal node ages

$\theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s$ Model parameters

D Molecular or morphology data

\mathcal{T} Tree topology

BAYESIAN DIVERGENCE TIME ESTIMATION

$$f(\mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s \mid D) =$$

$$\frac{f(D \mid \mathcal{R}, \mathcal{A}, \theta_s) \ f(\mathcal{R} \mid \theta_{\mathcal{R}}) \ f(\mathcal{A} \mid \theta_{\mathcal{A}}) \ f(\theta_s)}{f(D)}$$

$f(D \mid \mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s)$	Likelihood
$f(\mathcal{R} \mid \theta_{\mathcal{R}})$	Prior on rates
$f(\mathcal{A} \mid \theta_{\mathcal{A}})$	Prior on node ages
$f(\theta_s)$	Prior on substitution parameters
$f(D)$	Marginal probability of the data

MODELING RATE VARIATION

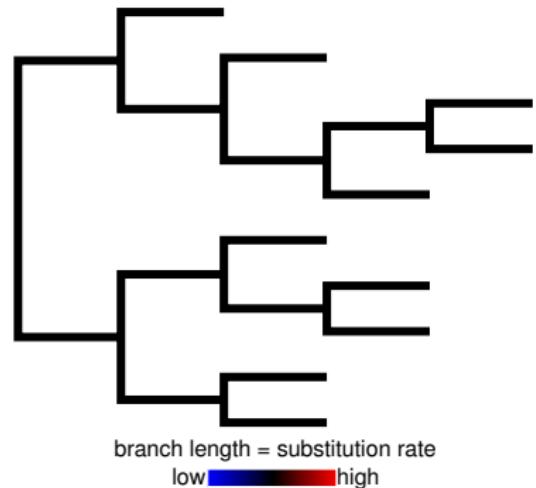
Some models describing lineage-specific substitution rate variation:

- **Global clock** (Zuckerkandl & Pauling, 1962)
- **Local clocks** (Hasegawa, Kishino & Yano 1989; Kishino & Hasegawa 1990; Yoder & Yang 2000; Yang & Yoder 2003, Drummond and Suchard 2010)
- **Punctuated rate change model** (Huelsenbeck, Larget and Swofford 2000)
- **Log-normally distributed autocorrelated rates** (Thorne, Kishino & Painter 1998; Kishino, Thorne & Bruno 2001; Thorne & Kishino 2002)
- **Uncorrelated/independent rates models** (Drummond et al. 2006; Rannala & Yang 2007; Lepage et al. 2007)
- **Mixture models on branch rates** (Heath, Holder, Huelsenbeck 2012)

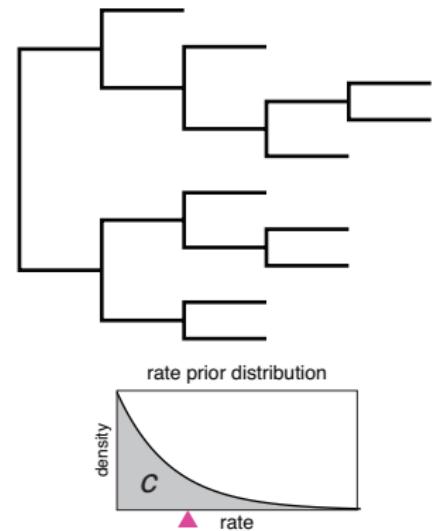
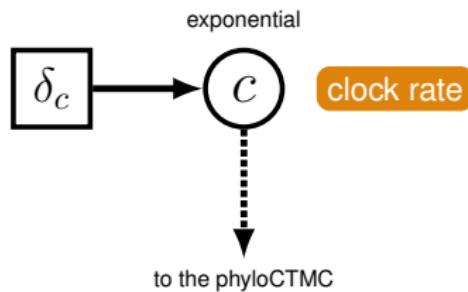
GLOBAL CLOCK

The substitution rate is constant over time

All lineages share the same rate

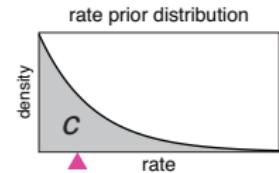
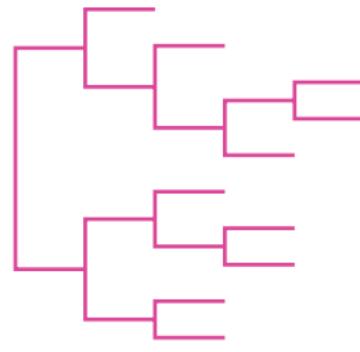


GLOBAL CLOCK



GLOBAL CLOCK

The sampled rate is applied to every branch in the tree



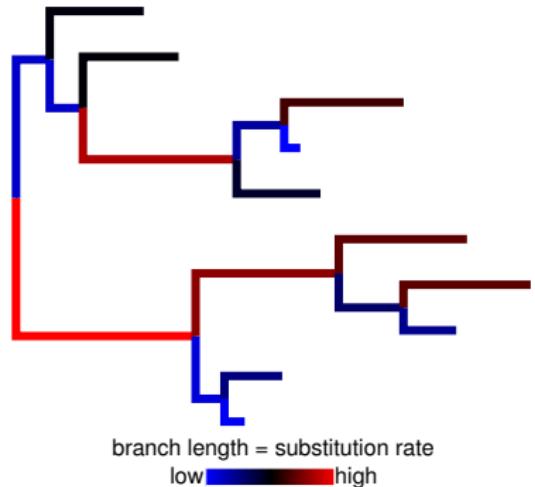
RELAXED-CLOCK MODELS

To accommodate variation in substitution rates
'relaxed-clock' models estimate lineage-specific substitution rates

- Local clocks
- Punctuated rate change model
- Log-normally distributed autocorrelated rates
- Uncorrelated/independent rates models
- Mixture models on branch rates

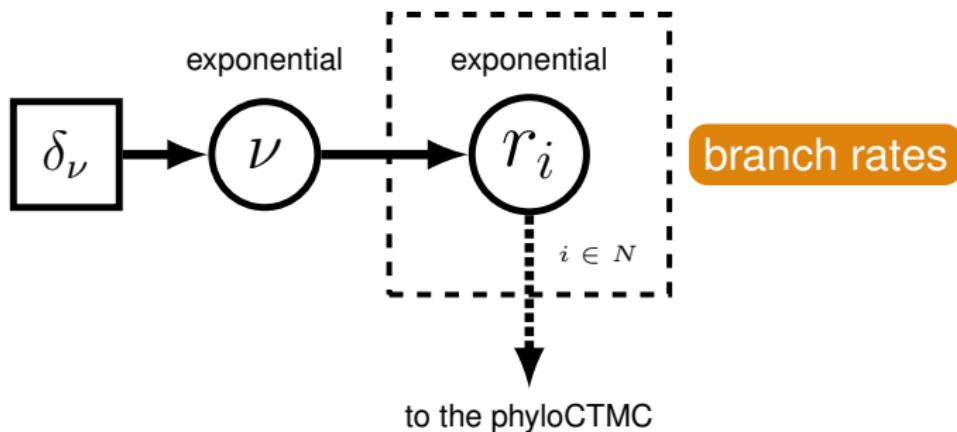
INDEPENDENT/UNCORRELATED RATES

Lineage-specific rates are uncorrelated when the rate assigned to each branch is independently drawn from an underlying distribution

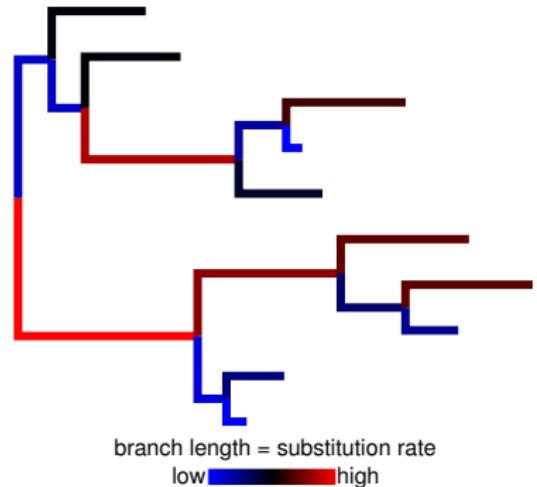
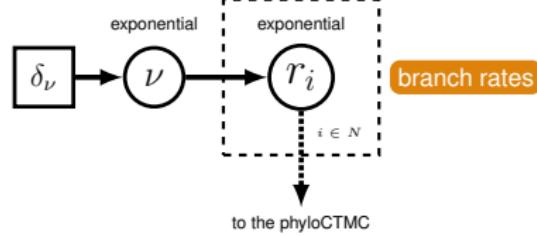


INDEPENDENT/UNCORRELATED RATES

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INDEPENDENT/UNCORRELATED RATES



MODELING RATE VARIATION

These are only a subset of the available models for branch-rate variation

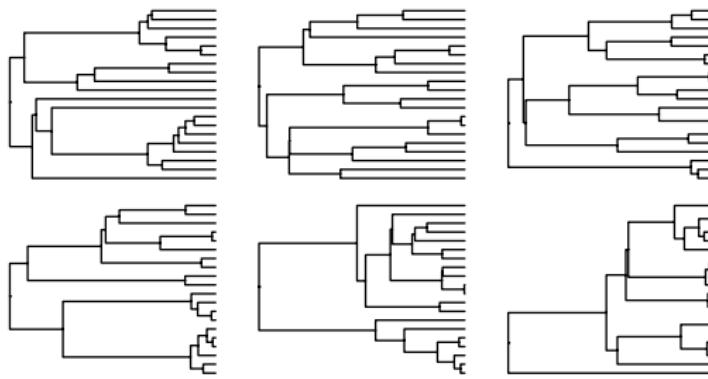
- Global clock
- Local clocks
- Punctuated rate change model
- Log-normally distributed autocorrelated rates
- Uncorrelated/independent rates models
- Dirichlet process prior

Considering model selection, uncertainty, & plausibility is **very** important for Bayesian divergence time analysis



PRIORS ON THE TREE AND NODE AGES

Relaxed clock Bayesian analyses require a prior distribution on time trees



Different node-age priors make different assumptions about the timing of divergence events

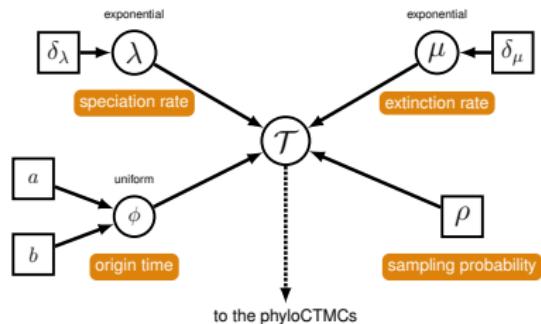
STOCHASTIC BRANCHING PROCESSES

Node-age priors based on stochastic models of lineage diversification

Birth-death-sampling

process: at any point in time a lineage can speciate at rate λ or go extinct with a rate of μ

Conditions on a probability of sampling a tip, ρ and the origin time of the process, ϕ

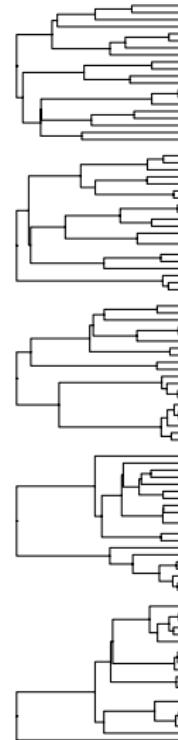


STOCHASTIC BRANCHING PROCESSES

Different values of λ and μ lead to different trees

Bayesian inference under these models can be very sensitive to the values of these parameters

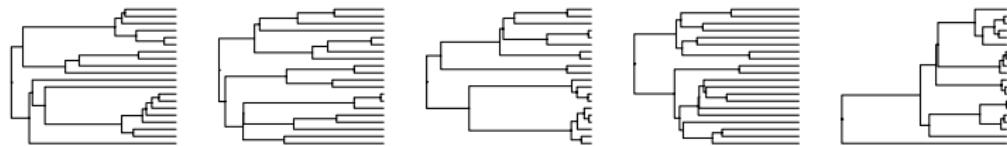
Using hyperpriors on λ and μ accounts for uncertainty in these hyperparameters



PRIORS ON NODE TIMES

Sequence data are only informative on *relative* rates & times

Node-time priors cannot give precise estimates of *absolute* node ages



We need additional data (like fossils) to provide absolute time scale

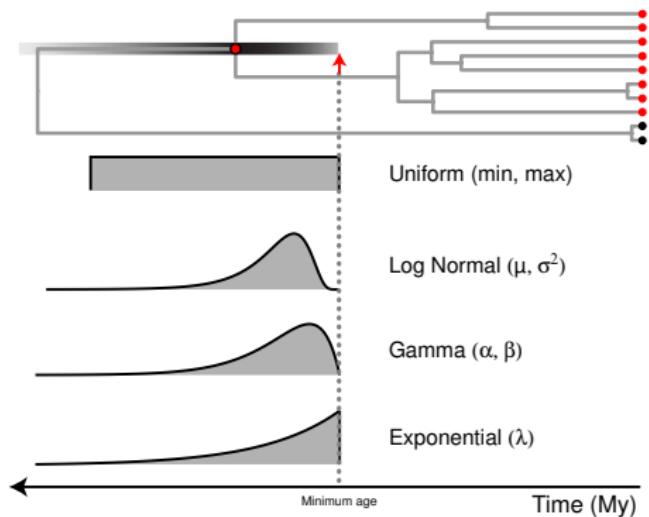


PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

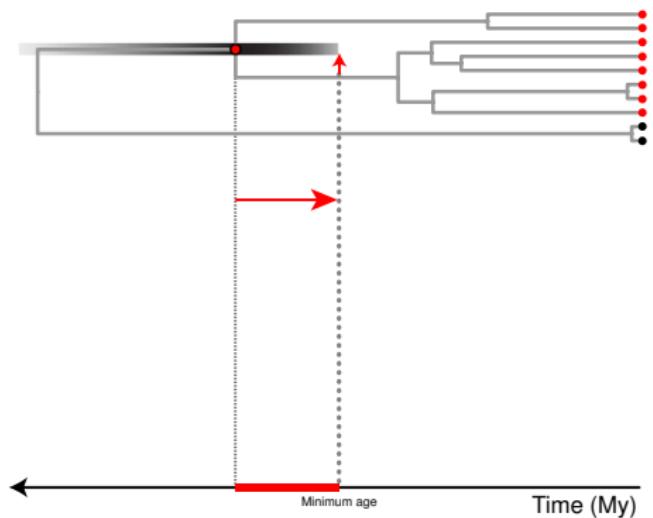
Parametric distributions are typically off-set by the age of the oldest fossil assigned to a clade

These prior densities do not (necessarily) require specification of maximum bounds



PRIOR DENSITIES ON CALIBRATED NODES

Describe the waiting time
between the divergence
event and the age of the
oldest fossil

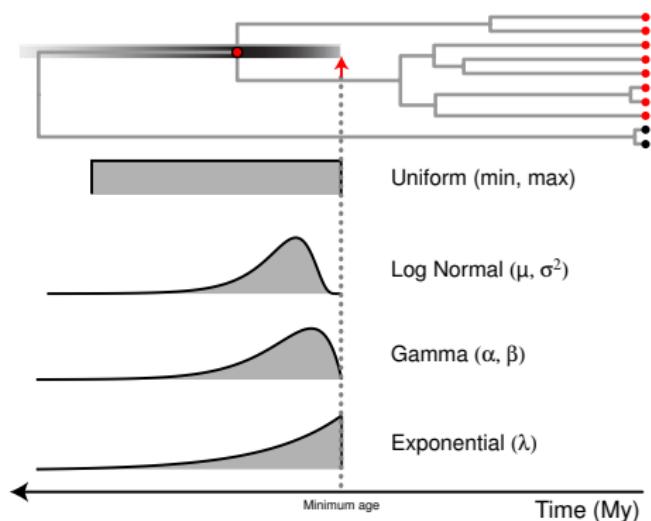


PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

Estimates of absolute node ages are driven primarily by the calibration density

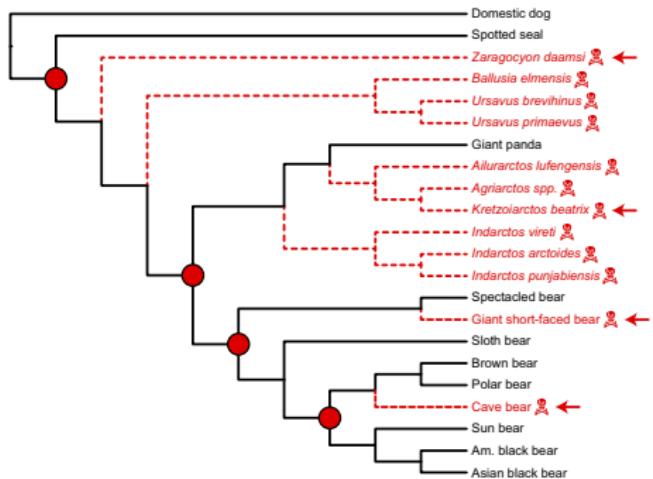
Specifying appropriate densities is a challenge for most molecular biologists



IMPROVING FOSSIL CALIBRATION

We would prefer to eliminate the need for *ad hoc* calibration prior densities

Calibration densities do not account for diversification of fossils

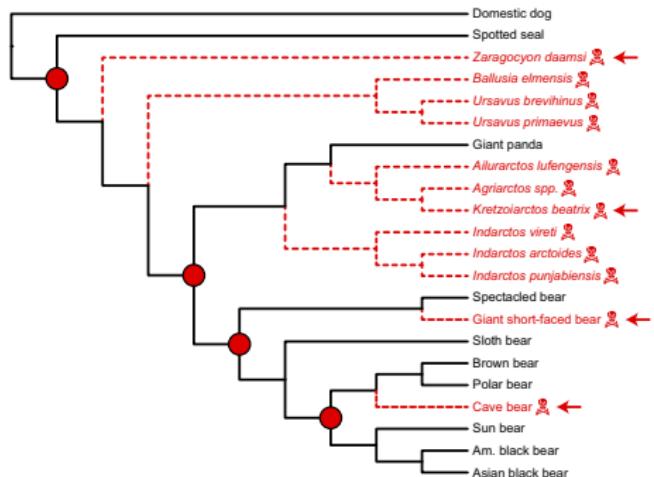


IMPROVING FOSSIL CALIBRATION

We want to use all of the available fossils

Example: Bears

12 fossils are reduced to 4 calibration ages with calibration density methods

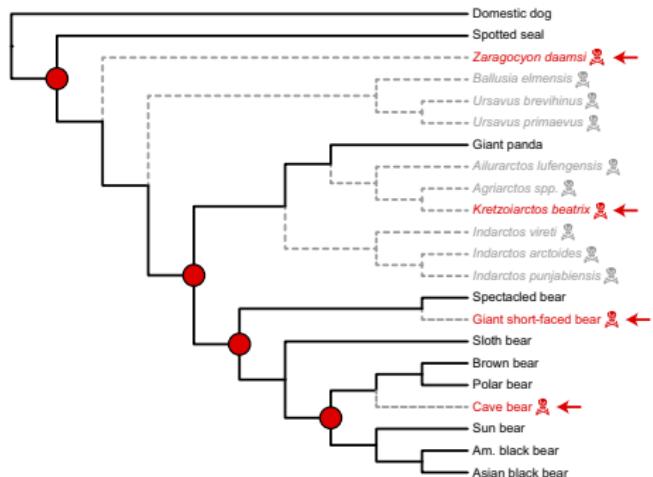


IMPROVING FOSSIL CALIBRATION

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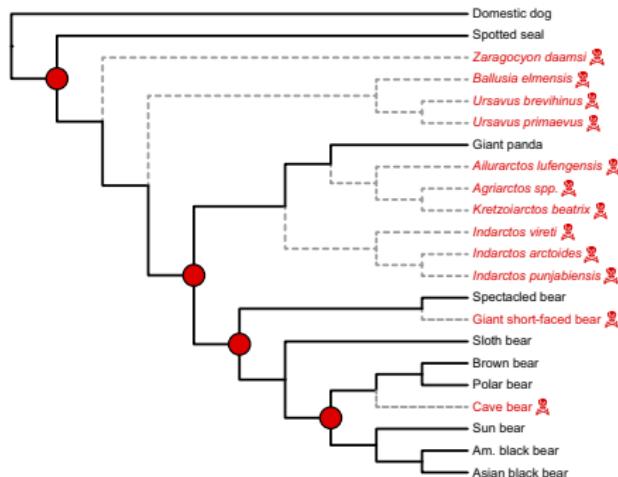
Example: Bears

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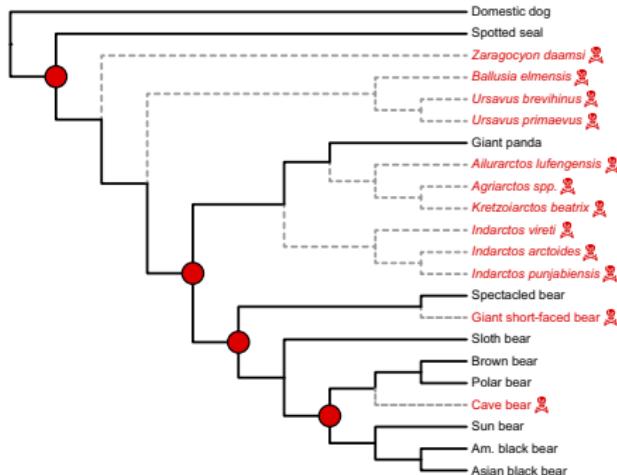
IMPROVING FOSSIL CALIBRATION

Because fossils are part of the diversification process, we can combine fossil calibration with birth-death models



IMPROVING FOSSIL CALIBRATION

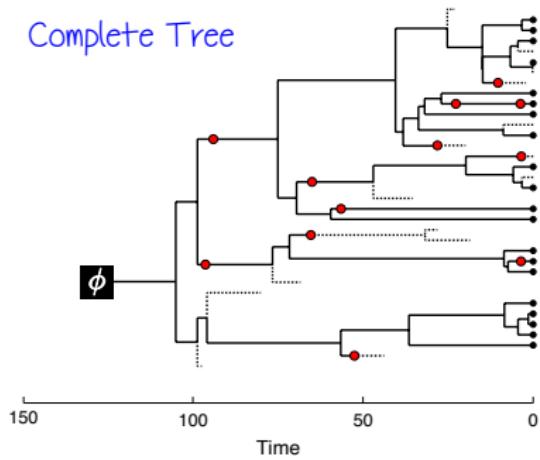
This relies on a branching model that accounts for **speciation, extinction, and rates of fossilization, preservation, and recovery**



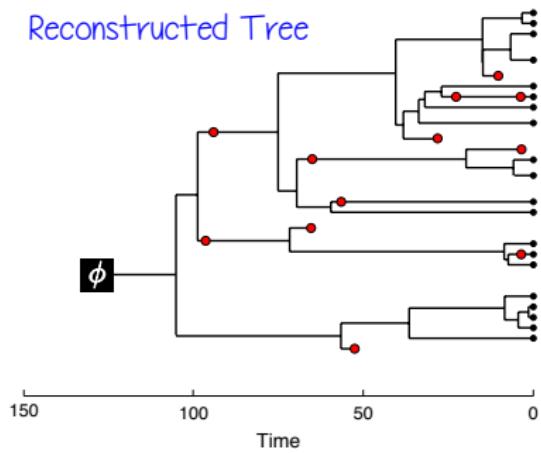
MODELING THE TREE & OCCURRENCE TIMES

Stadler (2010) introduced a generating model for a serially sampled time tree — this is the *fossilized birth-death process*.

Complete Tree

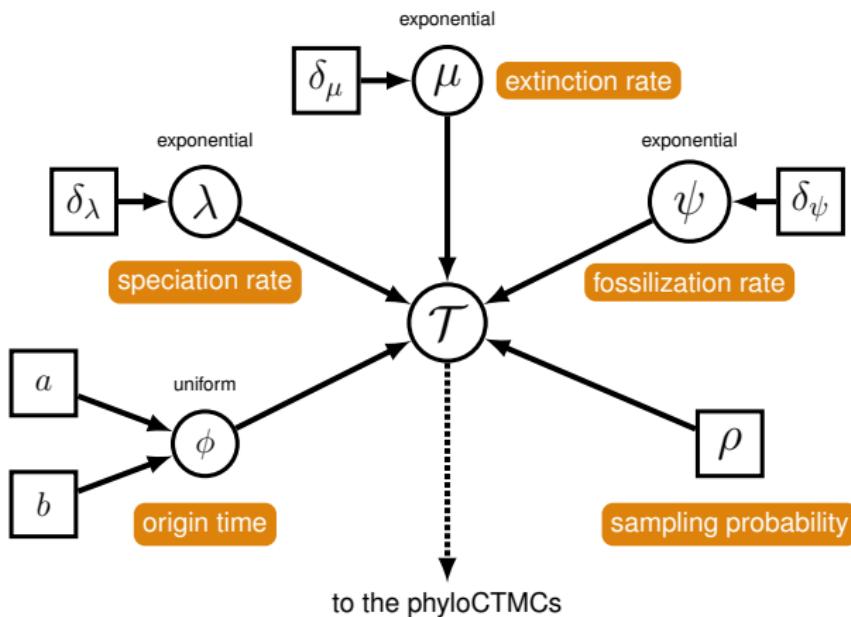


Reconstructed Tree



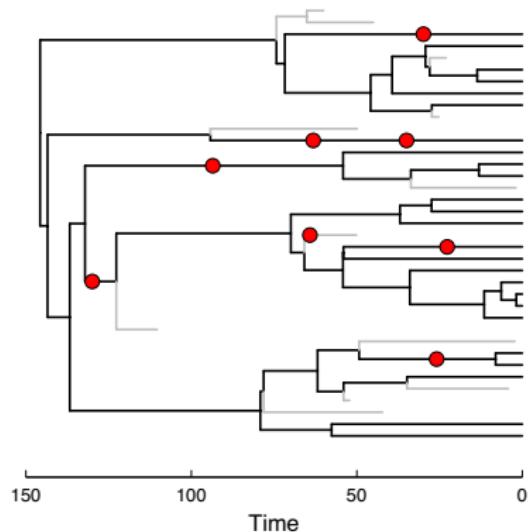
PARAMETERS OF THE FBD

This graph shows the conditional dependence structure of the FBD model, which is a generating process for a sampled, dated time tree and fossil occurrences



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Recovered fossil specimens provide historical observations of the diversification process that generated the tree of extant species



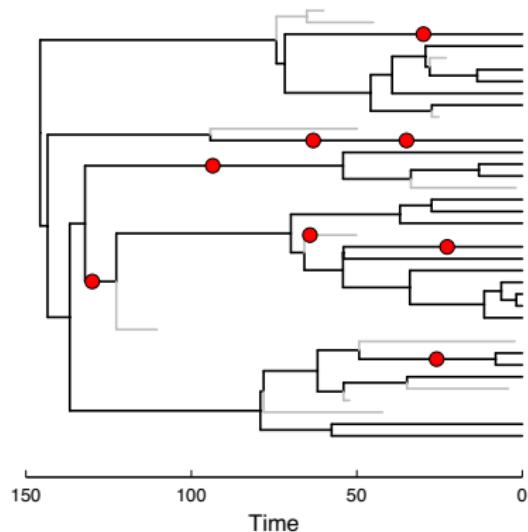
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The probability of the tree and fossil observations under a birth-death model with rate parameters:

λ = speciation

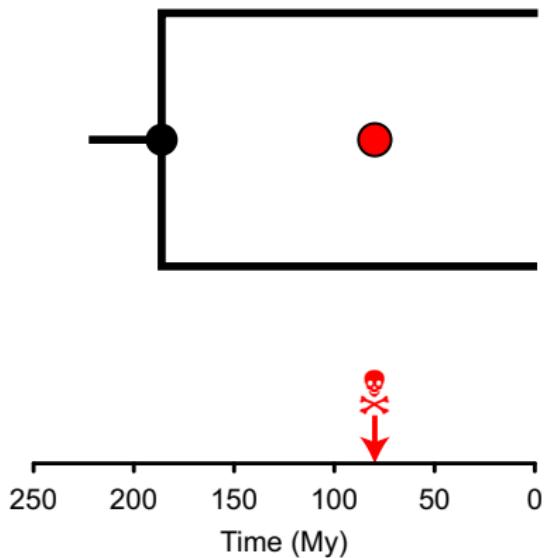
μ = extinction

ψ = fossilization/recovery



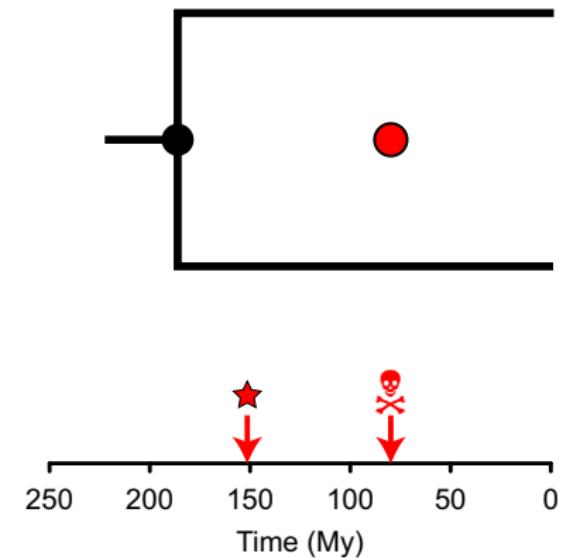
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The occurrence time of the fossil  indicates an observation of the birth-death process before the present



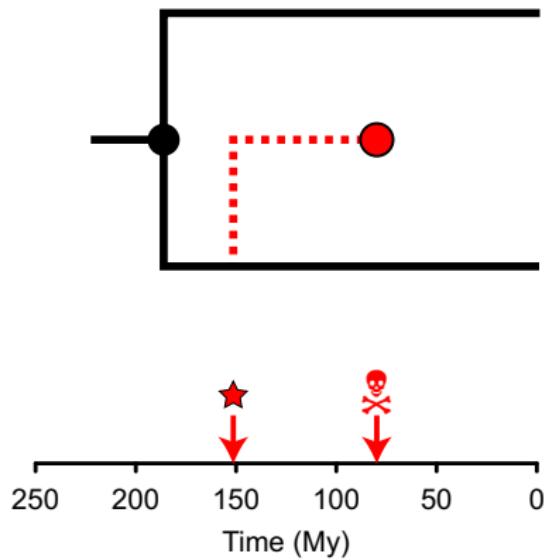
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The fossil must attach to the tree at some time and to some branch: ★



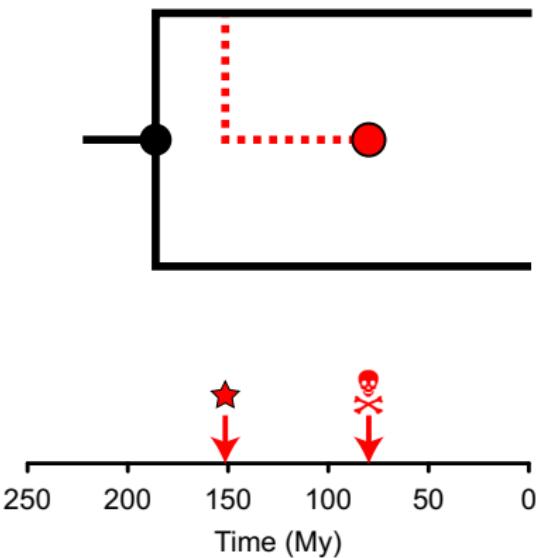
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

If it is the descendant of an unobserved lineage, then there is a speciation event at time \star



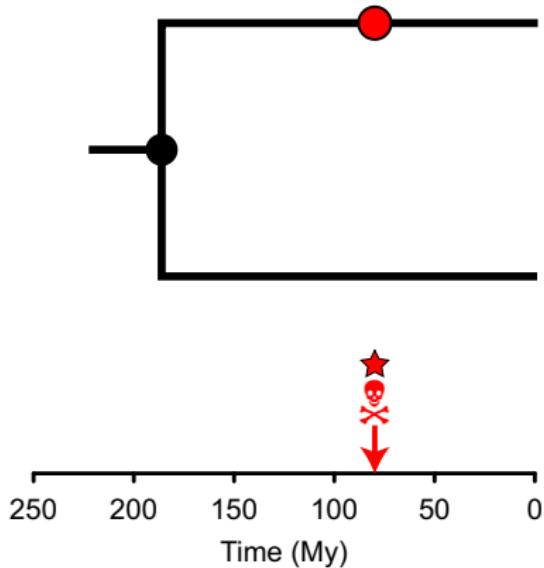
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

MCMC is used to propose new topological placements for the fossil



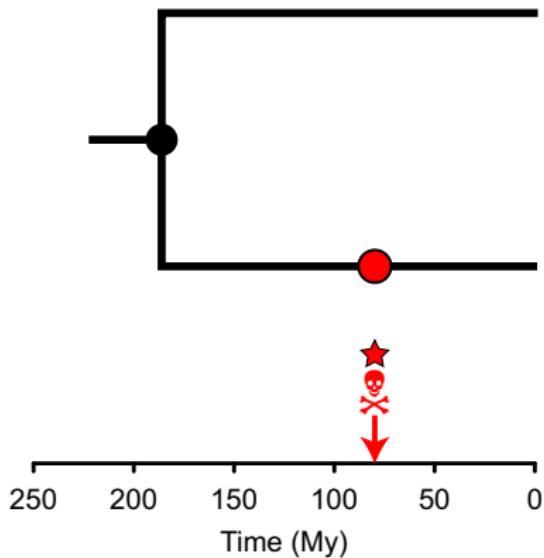
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Using rjMCMC, we can propose $\star = \text{💀}$, which means that the fossil is a "sampled ancestor"



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

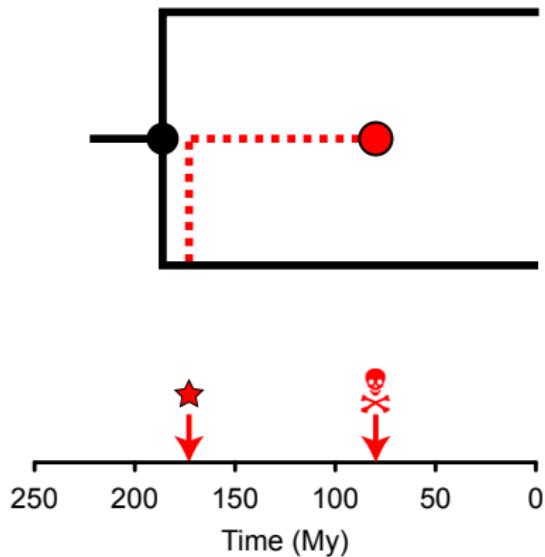
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THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

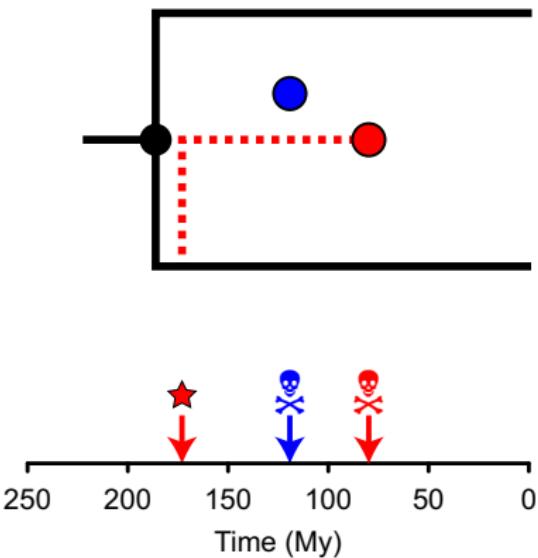
The probability of any realization of the diversification process is conditional on:

λ , μ , and ψ



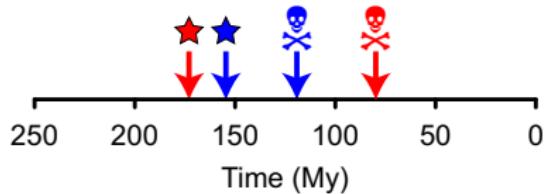
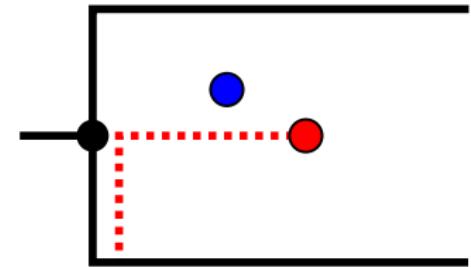
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Under the **FBD**, multiple fossils are considered, even if they are descended from the same MRCA node in the extant tree



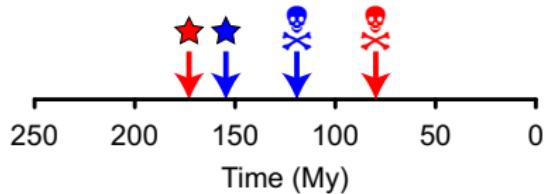
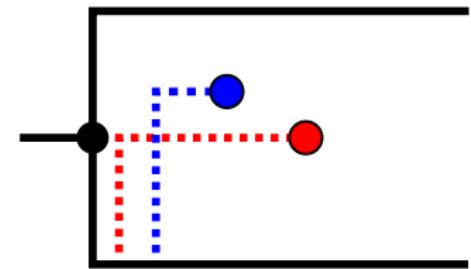
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Given  and , the new fossil can attach to the tree via speciation along either branch in the extant tree at time 



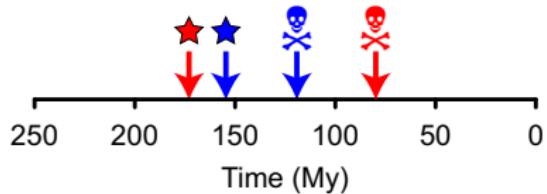
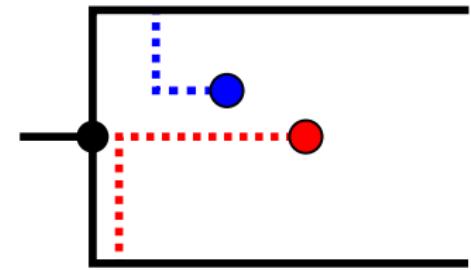
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Given  and , the new fossil can attach to the tree via speciation along either branch in the extant tree at time 



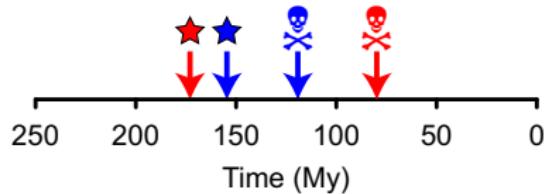
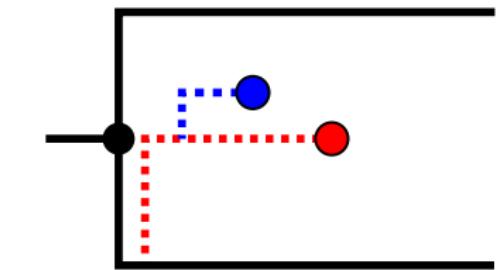
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Given  and , the new fossil can attach to the tree via speciation along either branch in the extant tree at time 



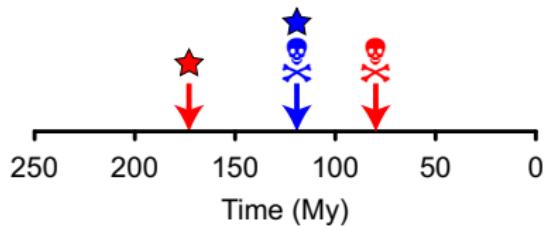
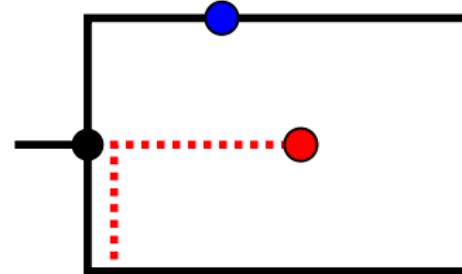
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Or the unobserved branch leading to the other fossil



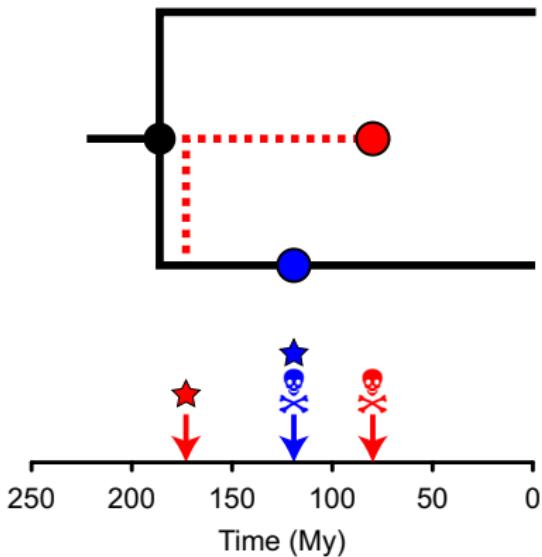
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

If $\star = \text{💀}$, then the new fossil lies directly on a branch in the extant tree



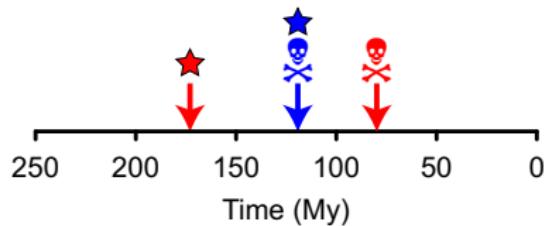
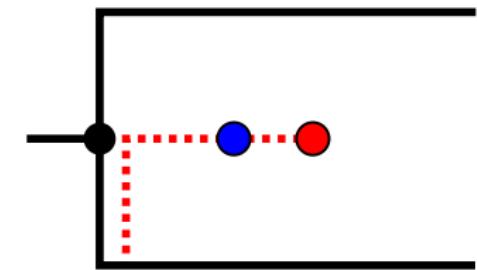
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

If $\star = \text{💀}$, then the new fossil lies directly on a branch in the extant tree



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

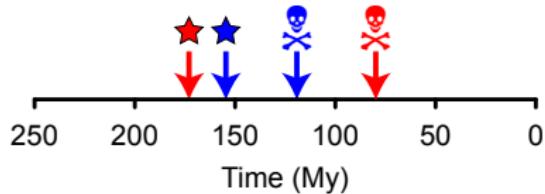
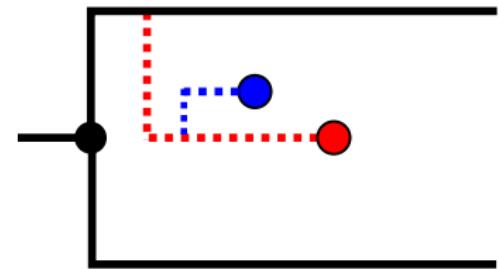
Or it is an ancestor of the other sampled fossil



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The probability of this realization of the diversification process is conditional on:

λ , μ , and ψ



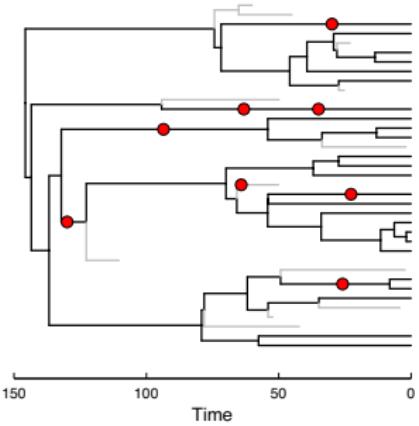
SAMPLED ANCESTORS

Sampled lineages with sampled descendants

Paleobiology, 22(2), 1996, pp. 141–151

On the probability of ancestors in the fossil record

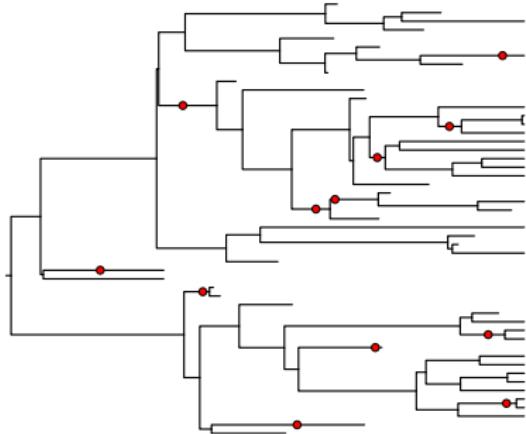
Mike Foote



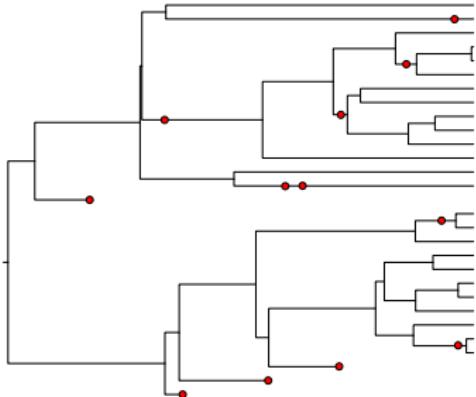
There is a non-zero probability of sampling ancestor-descendant relationships from the fossil record

SAMPLED ANCESTORS

Complete FBD Tree



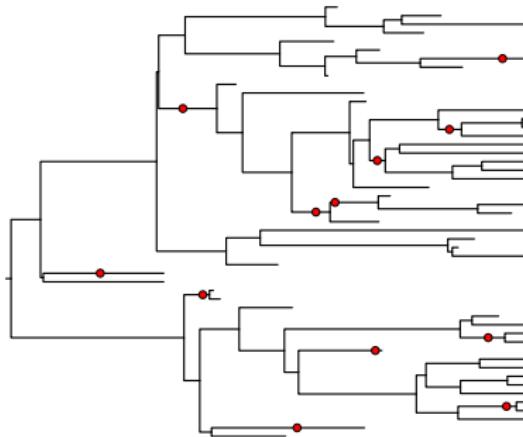
Reconstructed FBD Tree



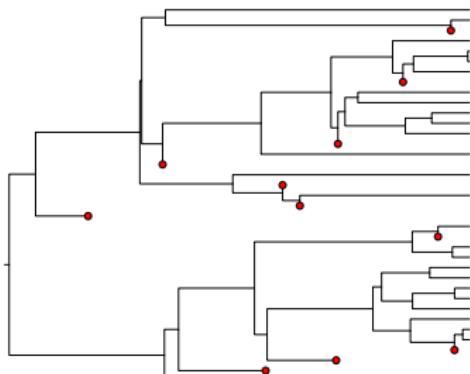
Because fossils & living taxa are assumed to come from a single diversification process, there is a non-zero probability of sampled ancestors

SAMPLED ANCESTORS

Complete FBD Tree



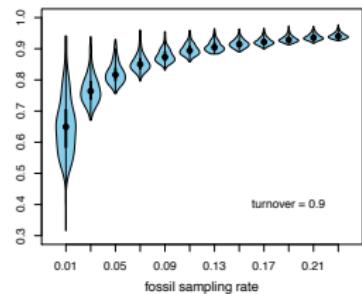
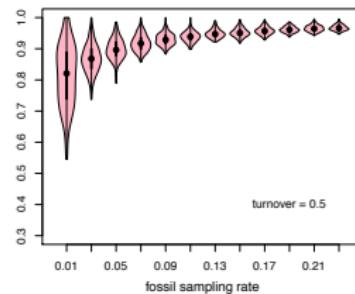
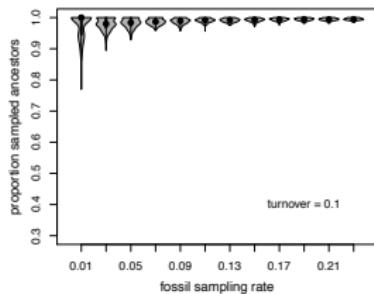
No Sampled Ancestor Tree



If all fossils are forced to be on separate lineages, this induces additional speciation events and will, in turn, influence rate & node-age estimates.

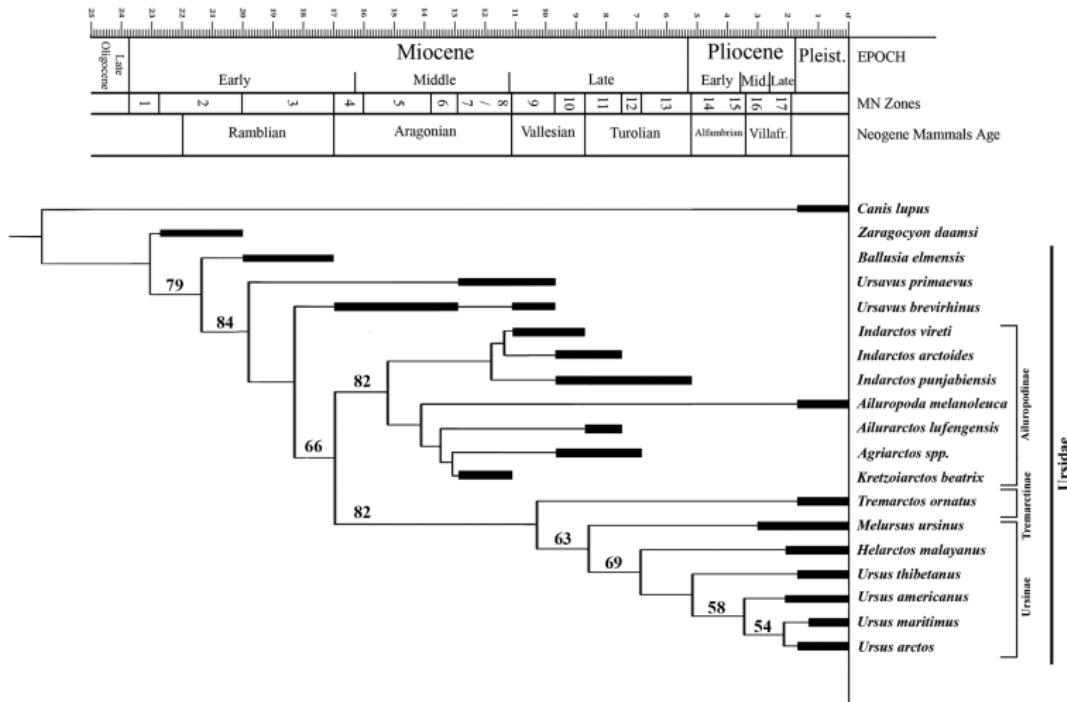
SAMPLED ANCESTORS

The proportion of sampled ancestors depends on the turnover rate, probability of sampling an extant tip, and rate of sampling fossils back in time



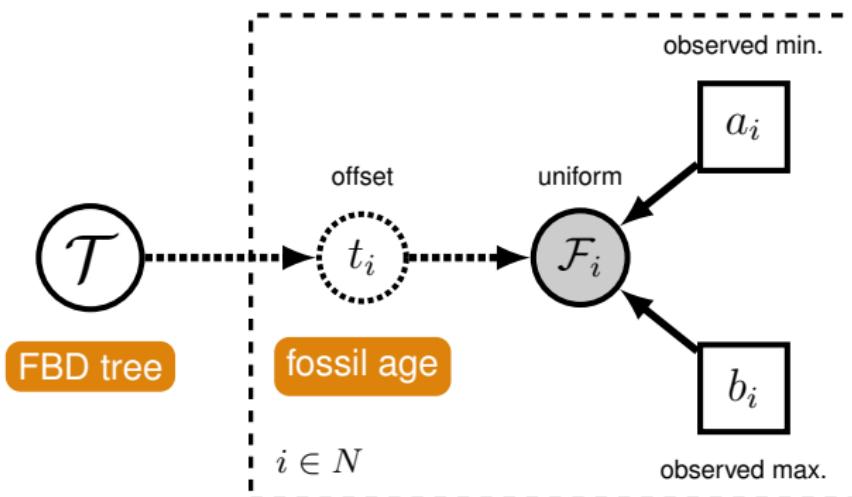
Fossil Range Data

Fossil occurrence data are uncertain and are often given as stratigraphic ranges



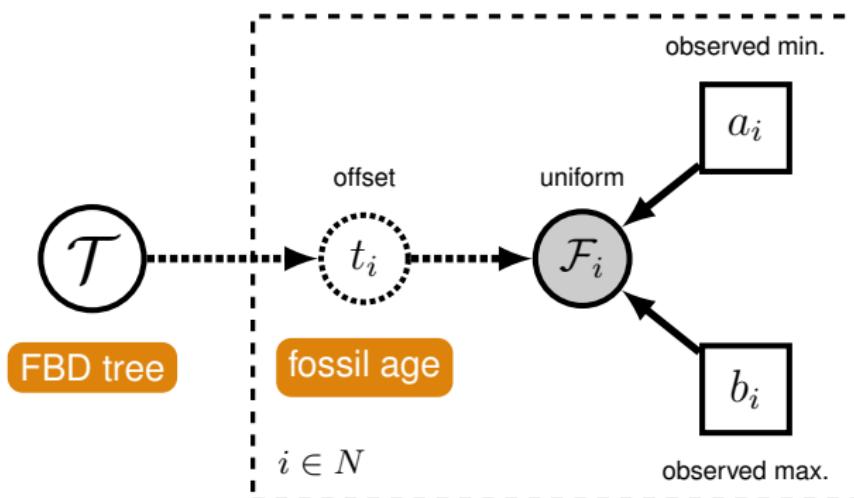
Fossil Range Data

We can account for this by assuming each fossil can occur with uniform probability anywhere within its observed stratigraphic range while conditioning on the FBD tree

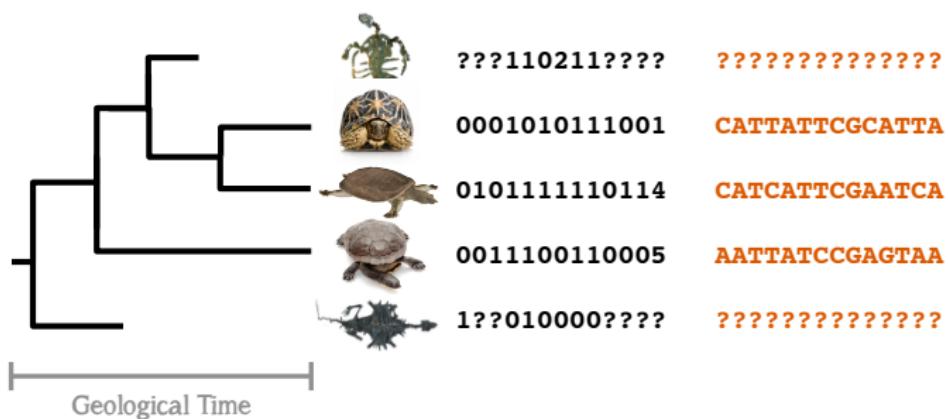
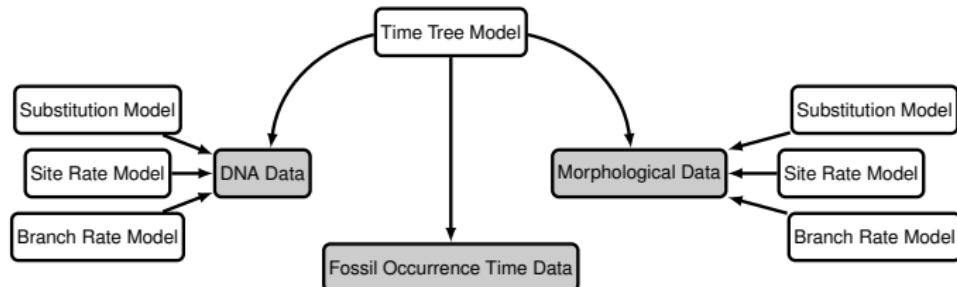


Fossil Range Data

This treats the calibration density as an additional prior distribution on the tree, we treat it as the *likelihood* of our fossil data given the tree parameter.

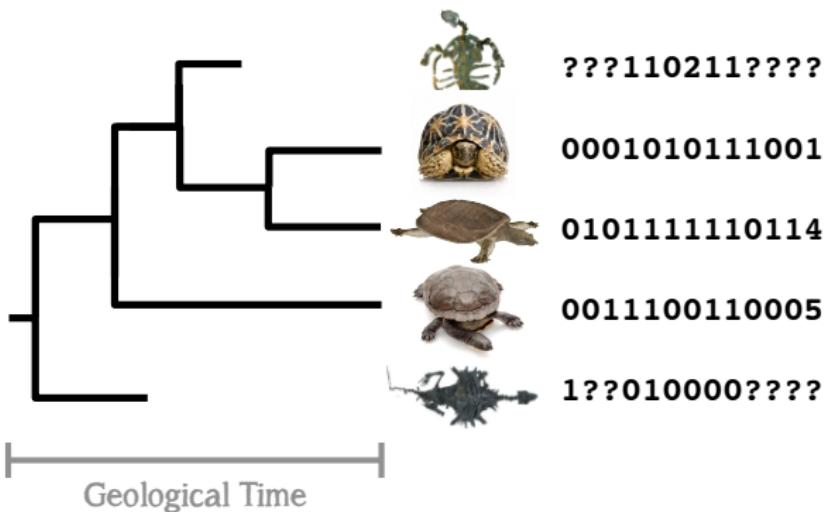


COMBINING FOSSIL & EXTANT DATA



(turtle tree image by M. Landis)

MODELING MORPHOLOGICAL CHARACTER CHANGE



Syst. Biol. 50(6):913–925, 2001

A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data

PAUL O. LEWIS

Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269-3043, USA;
E-mail: paul.lewis@uconn.edu

(turtle tree image by M. Landis)

MODELING MORPHOLOGICAL CHARACTER CHANGE

The Lewis Mk model

Assumes a character can take
 k states

T1 0

T2 0

T3 1

T4 2

T5 2

T6 1

T7 1

$$Q = \alpha \begin{bmatrix} 1 - k & 1 & \dots & 1 \\ \vdots & 1 - k & \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 & \dots & 1 - k \end{bmatrix}$$

MODELING MORPHOLOGICAL CHARACTER CHANGE

The Lewis Mk model

In the tutorial, all characters are binary, where $k = 2$

$$Q = \alpha \begin{bmatrix} 1 - k & 1 \\ 1 & 1 - k \end{bmatrix}$$

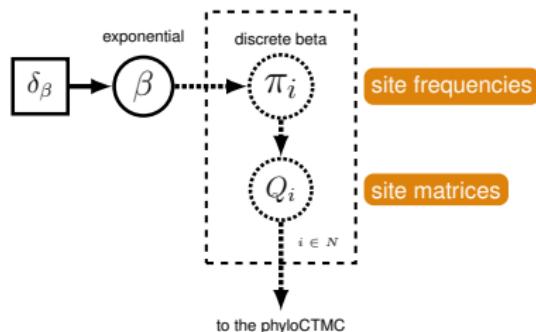
T1	0
T2	1
T3	1
T4	1
T5	1
T6	0
T7	1

MODELING MORPHOLOGICAL CHARACTER CHANGE

The Lewis Mk model with asymmetric transition rates

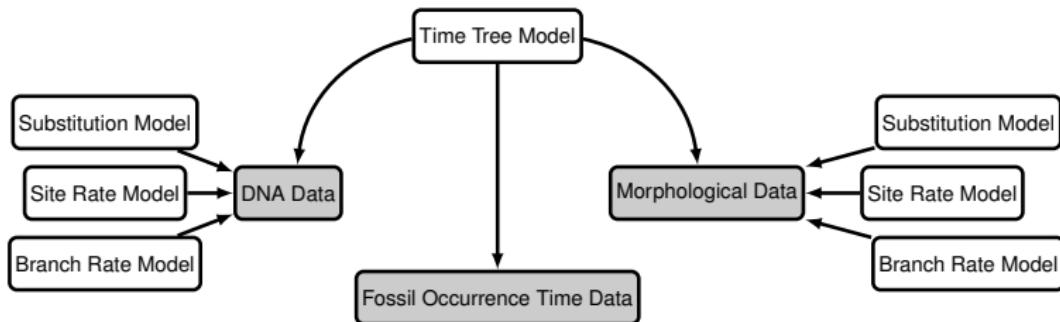
In this tutorial we allow the transition rates between states to be asymmetric by drawing the state frequencies from a beta distribution

And each character in the matrix can have a different transition rate matrix, by discretizing the beta prior and analytically marginalizing over rate categories



"TOTAL-EVIDENCE" ANALYSIS

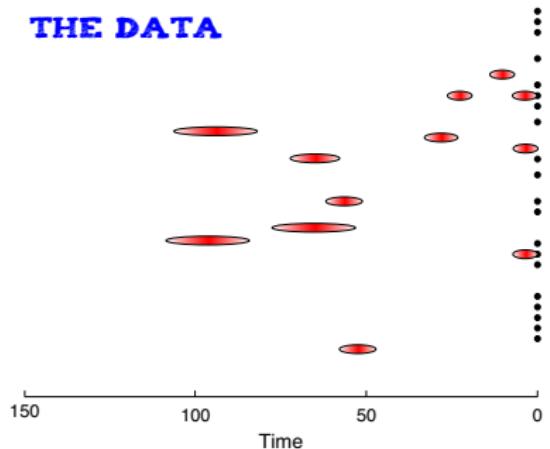
Integrating models of molecular and morphological evolution with improved tree priors enables joint inference of the tree topology (extant & extinct) and divergence times



"TOTAL-EVIDENCE" ANALYSIS

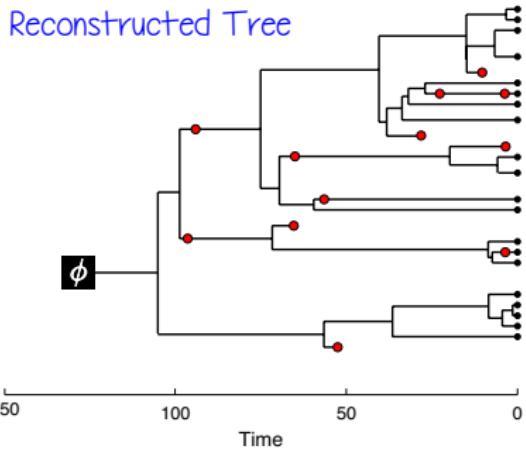
Allows us to estimate the reconstructed tree of our sampled fossils and extant taxa along with the diversification dynamics and rates of molecular and morphological evolution

THE DATA



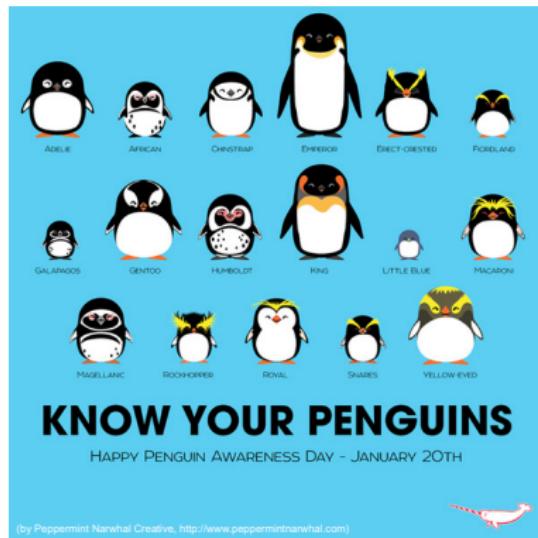
“TOTAL-EVIDENCE” ANALYSIS

Allows us to estimate the reconstructed tree of our sampled fossils and extant taxa along with the diversification dynamics and rates of molecular and morphological evolution

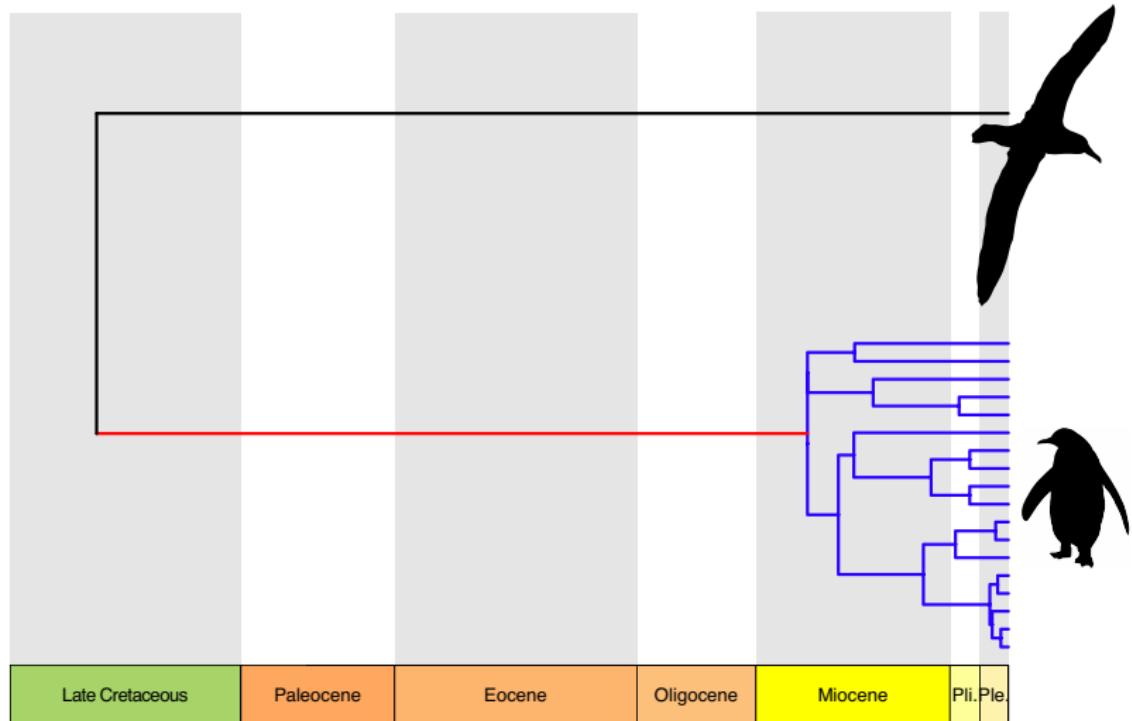


PENGUIN DIVERSITY IN DEEP TIME

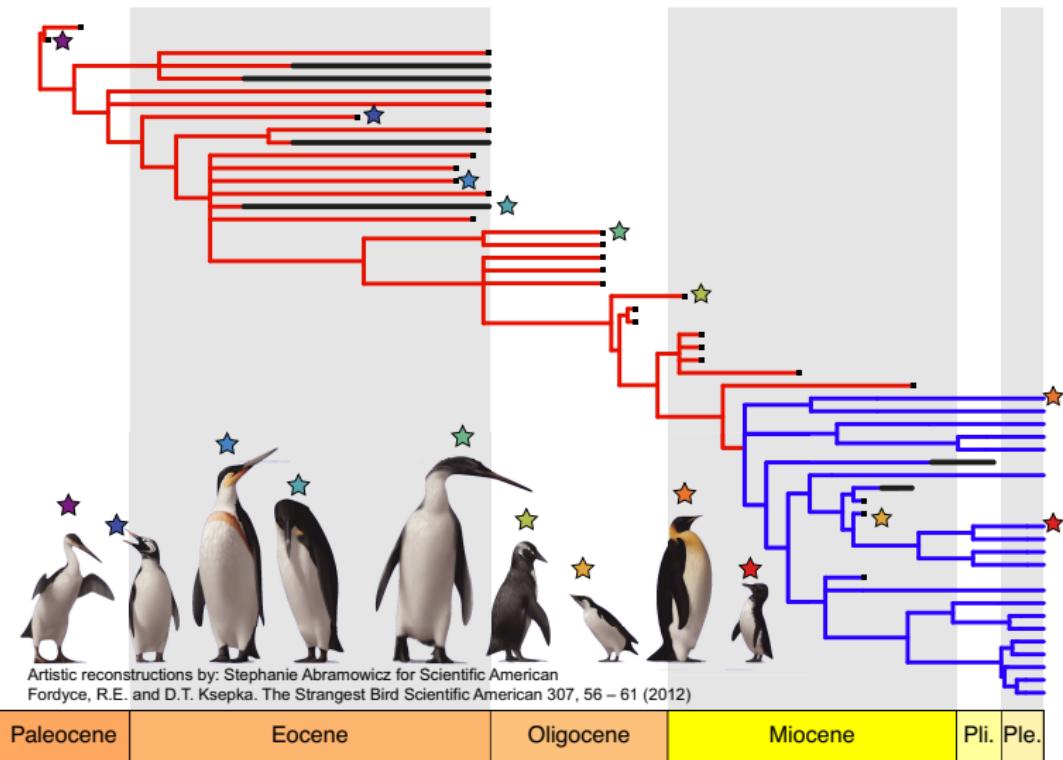
How does our understanding of penguin evolution improve when we consider both extant and fossil taxa?



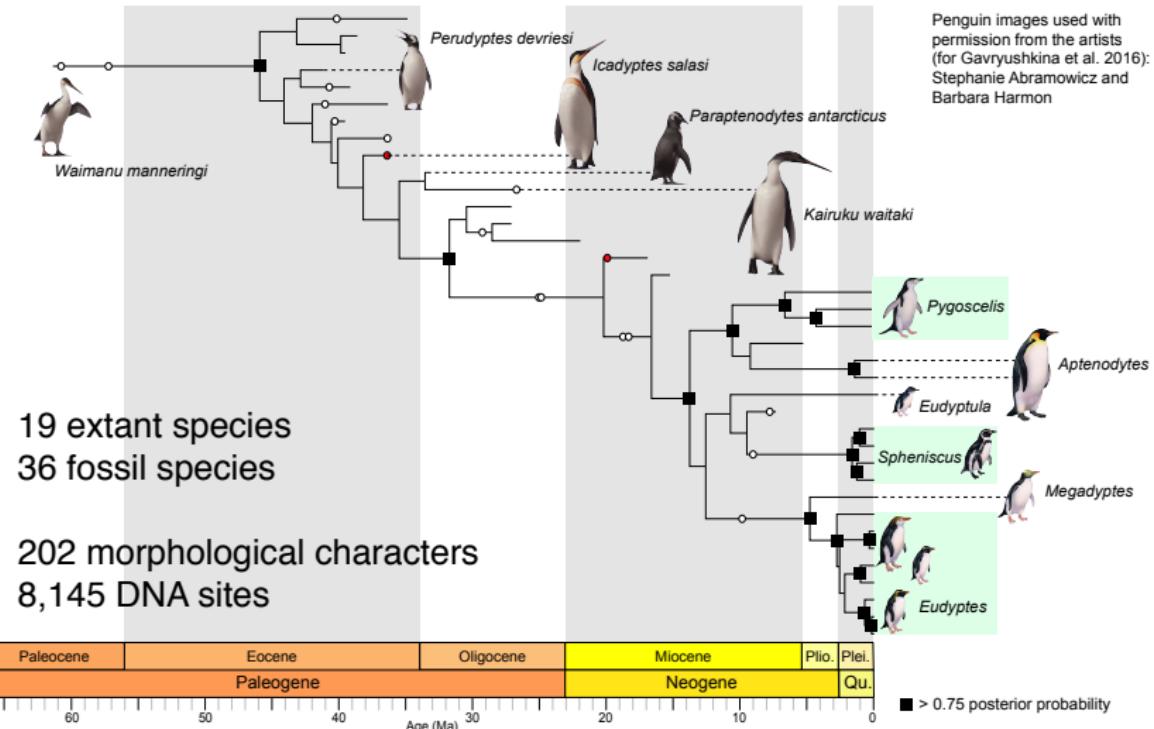
PENGUIN DIVERSITY



PENGUIN DIVERSITY IN DEEP TIME



PENGUIN DIVERSITY IN DEEP TIME



PENGUIN DIVERSITY IN DEEP TIME

