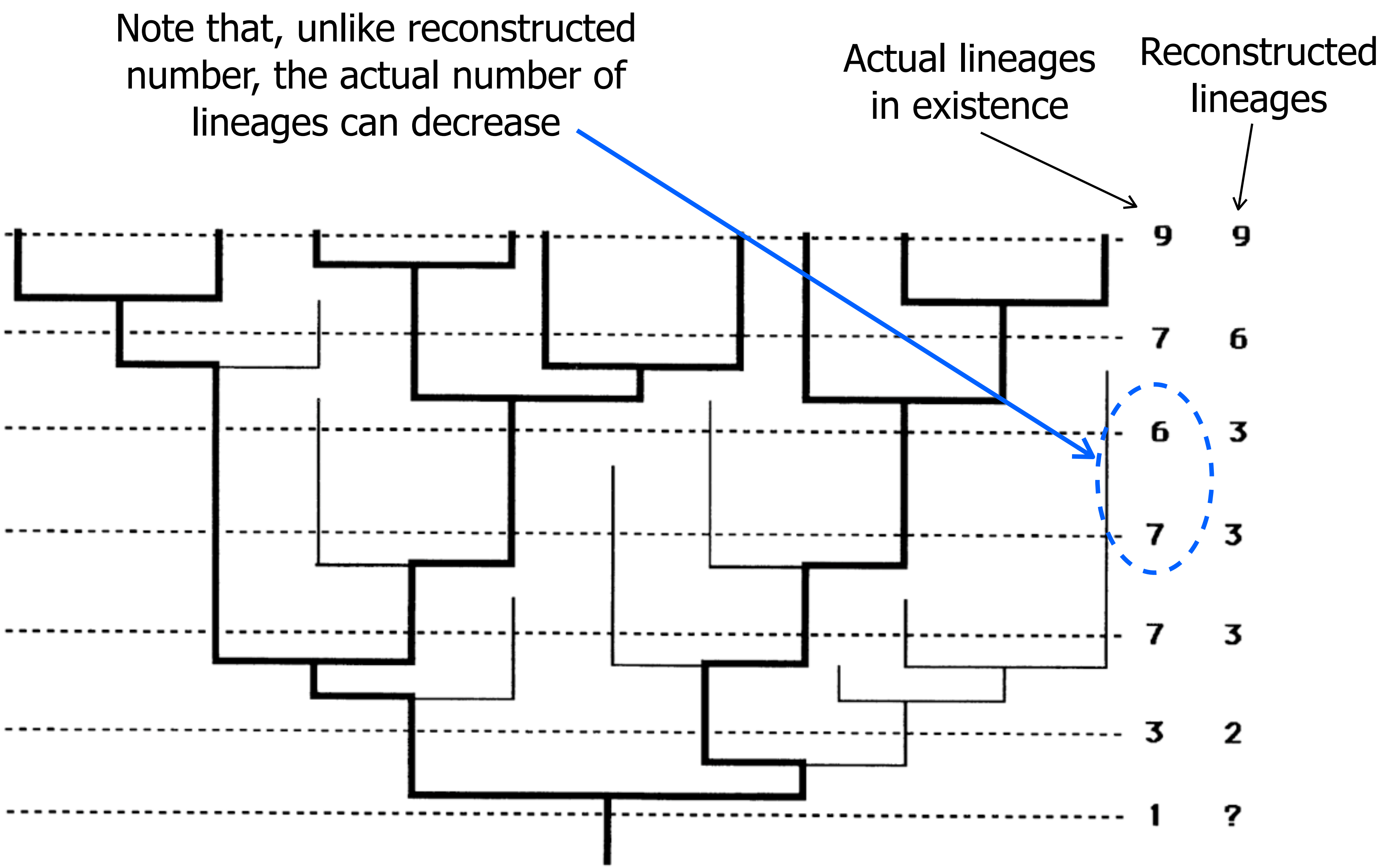
Diversification and Turnover

diversification rate = speciation rate − extinction rate

$$= \lambda - \mu$$

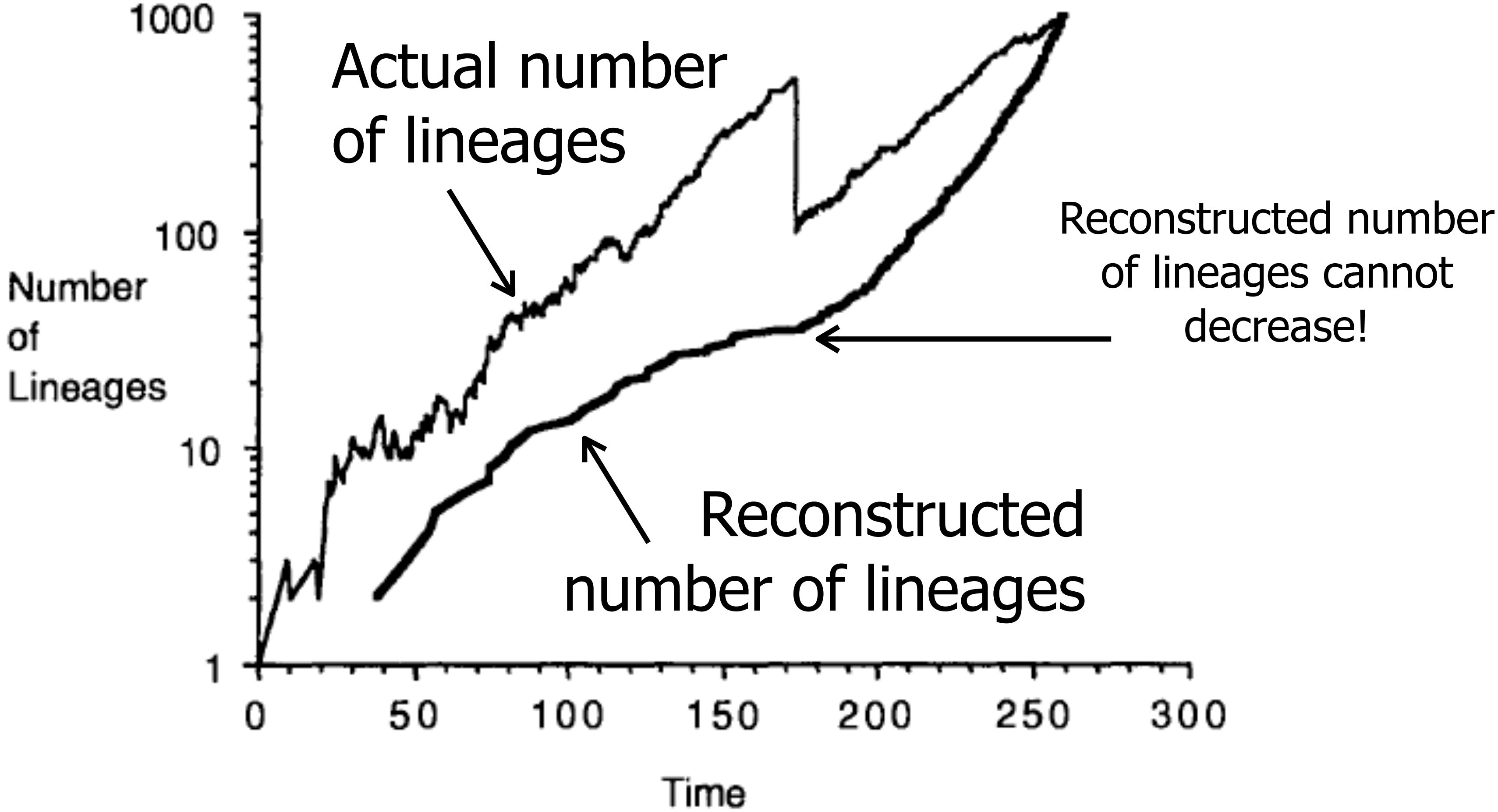
$$\text{turnover} = \frac{\text{extinction rate}}{\text{speciation rate}} = \mu/\lambda$$

Lineages-through-time (LTT) plot



Harvey et al. (1994)

Can extinction events be detected using phylogenies of extant taxa?



Harvey et al. (1994)

The pull of the present

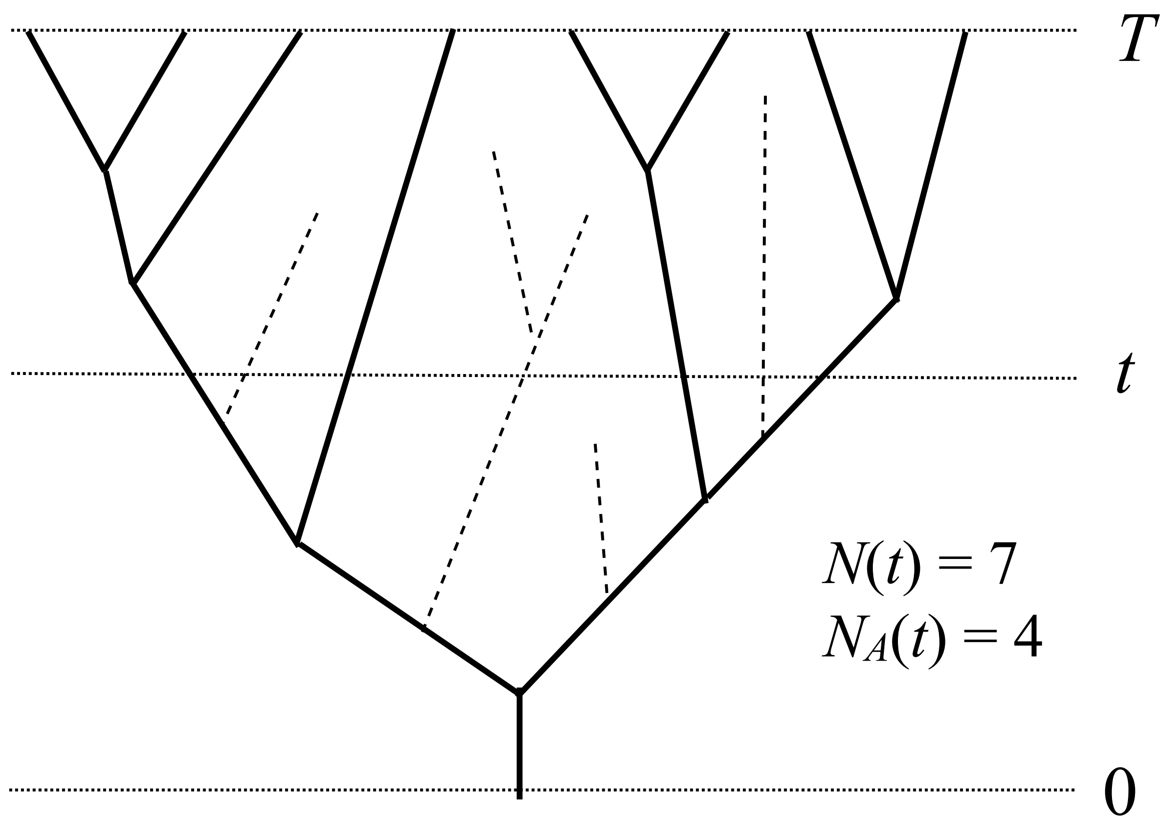
Ancestral vs. total lineages

$$E[N(T)] = N_A(t) \times E[N(T-t)]$$

E[total number] = (no. ancestors at time t) × E[(no. descendants/ancestor)]

N(t) gives the number of lineages existing at time t (given that you start with 1 lineage). Some of these will have gone extinct by time T.

$N_A(t)$ is the number of lineages that persist to the present (T). It is thus interesting to plot N(t) against $N_A(t)$...



Box 3 from: Ricklefs (2007)

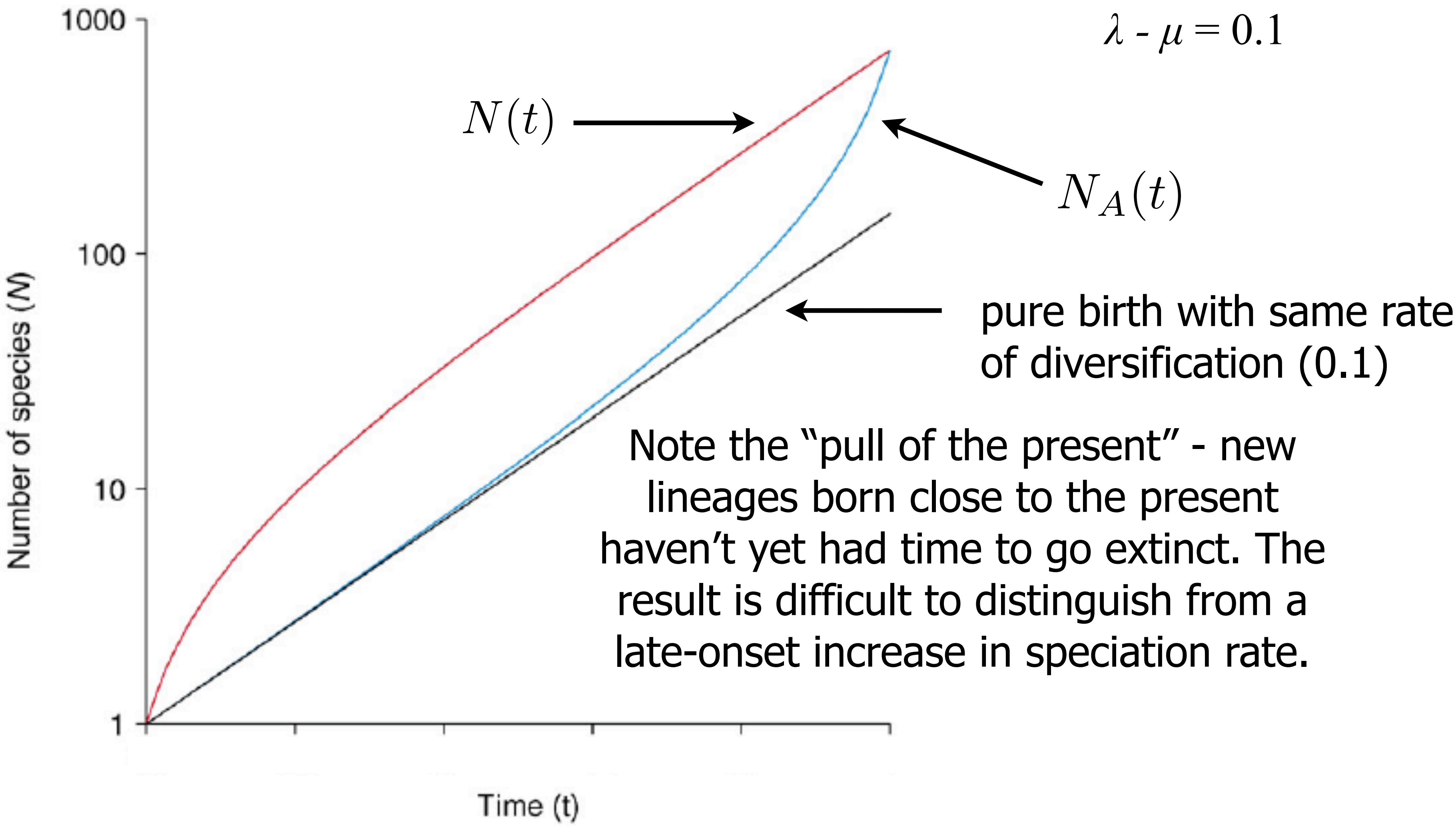
The pull of the present

Assumes constant birth (λ) and death (μ) rates.

$\lambda = 0.5$

$\mu = 0.4$ (80% of λ)

$\lambda - \mu = 0.1$



Note the "pull of the present" - new lineages born close to the present haven't yet had time to go extinct. The result is difficult to distinguish from a late-onset increase in speciation rate.

Box 3 from: Ricklefs (2007)

Pybus & Harvey's gamma

Testing for diversification trends

Pybus and Harvey (2000) devised a test for whether diversification is consistent with a pure-birth (Yule) model. Under constant birth and no extinction, the following statistic is expected to be ~ N(0, 1):

$$\gamma = \frac{\left(\frac{1}{n-2}\sum_{i=2}^{n-1}\sum_{k=2}^{i} k t_k\right) - \frac{T}{2}}{T\sqrt{\frac{1}{12(n-2)}}}$$

Under a pure-birth process (birth rate b), t_k is expected to equal 1/(kb); make this substitution and you can prove that gamma is zero under a pure-birth model.

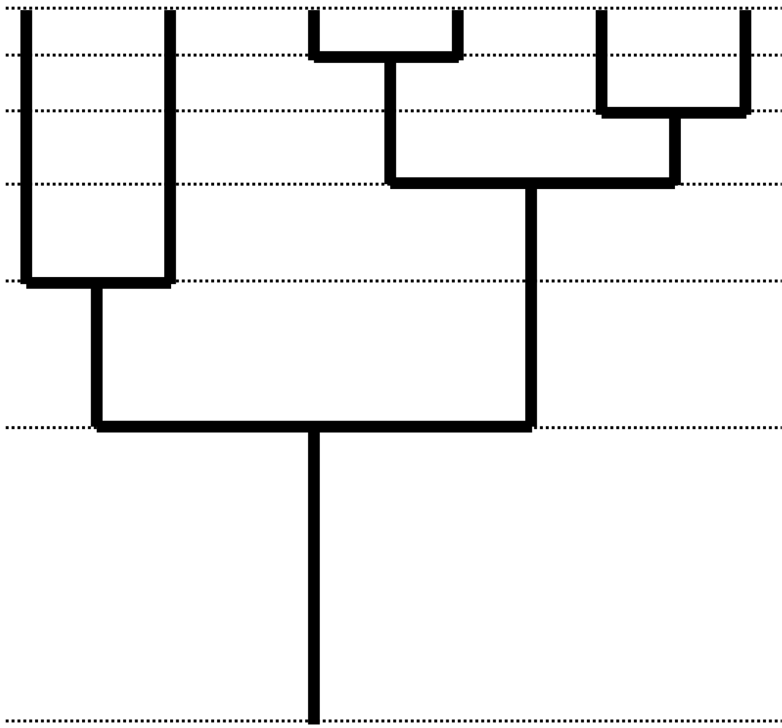
where $$T = \sum_{k=2}^{n} k t_k$$ (tree length)

and t_k is the length of time k lineages were in existence

Pybus and Harvey (2000)

Yule vs. extinction

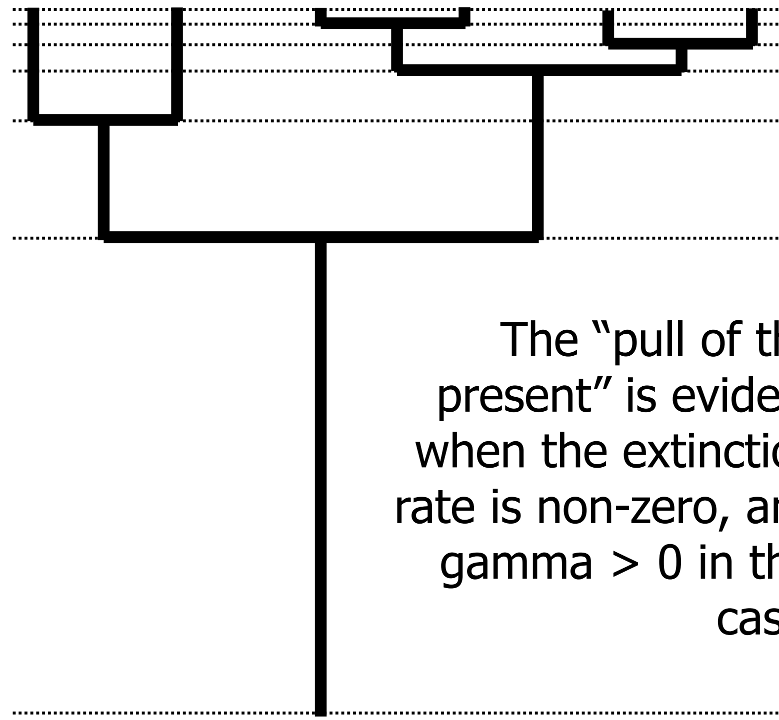
Constant speciation rate, no extinction



$$\gamma = 0.00$$

Zero is the expected lower bound for gamma if speciation and extinction rates are both constant

Constant speciation and extinction rates



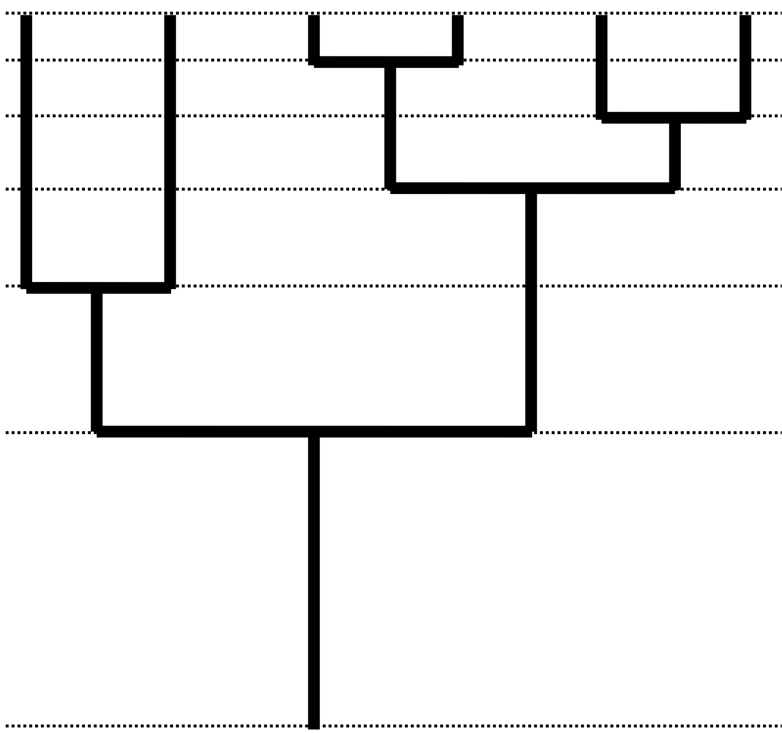
The “pull of the present” is evident when the extinction rate is non-zero, and gamma > 0 in this case.

$$\gamma = 0.88$$

Pybus and Harvey (2000)

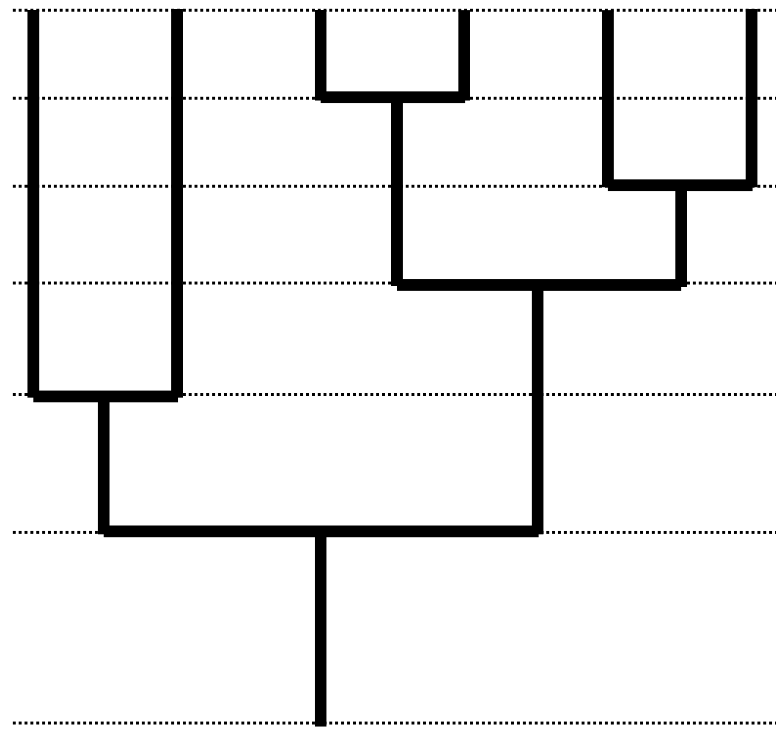
Yule vs. declining speciation rate

Constant speciation rate, no extinction



$$\gamma = 0.00$$

Speciation rate declines as clade ages



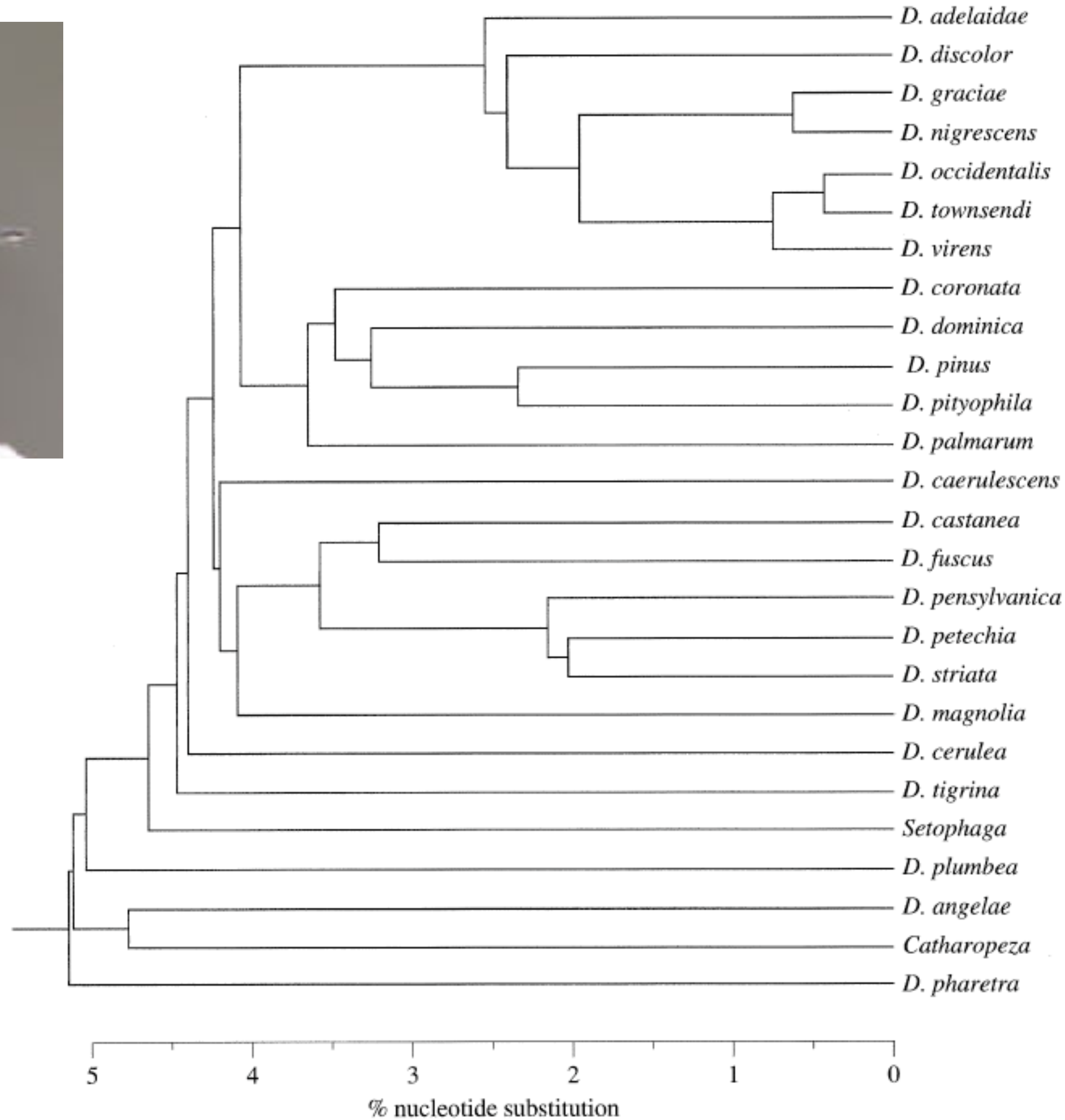
$$\gamma = -0.46$$

Negative values of gamma indicate a declining diversification rate through time

Gamma and adaptive radiations

Blackburnian warbler (*Dendroica fusca*)
http://en.wikipedia.org/wiki/Dendroica

Pybus and Harvey (2000) computed gamma to be -4.171 (P = 0.0001) for this phylogeny of *Dendroica* warblers. Adaptive radiations such as this involve initially high speciation rates that decline once available niches are filled.

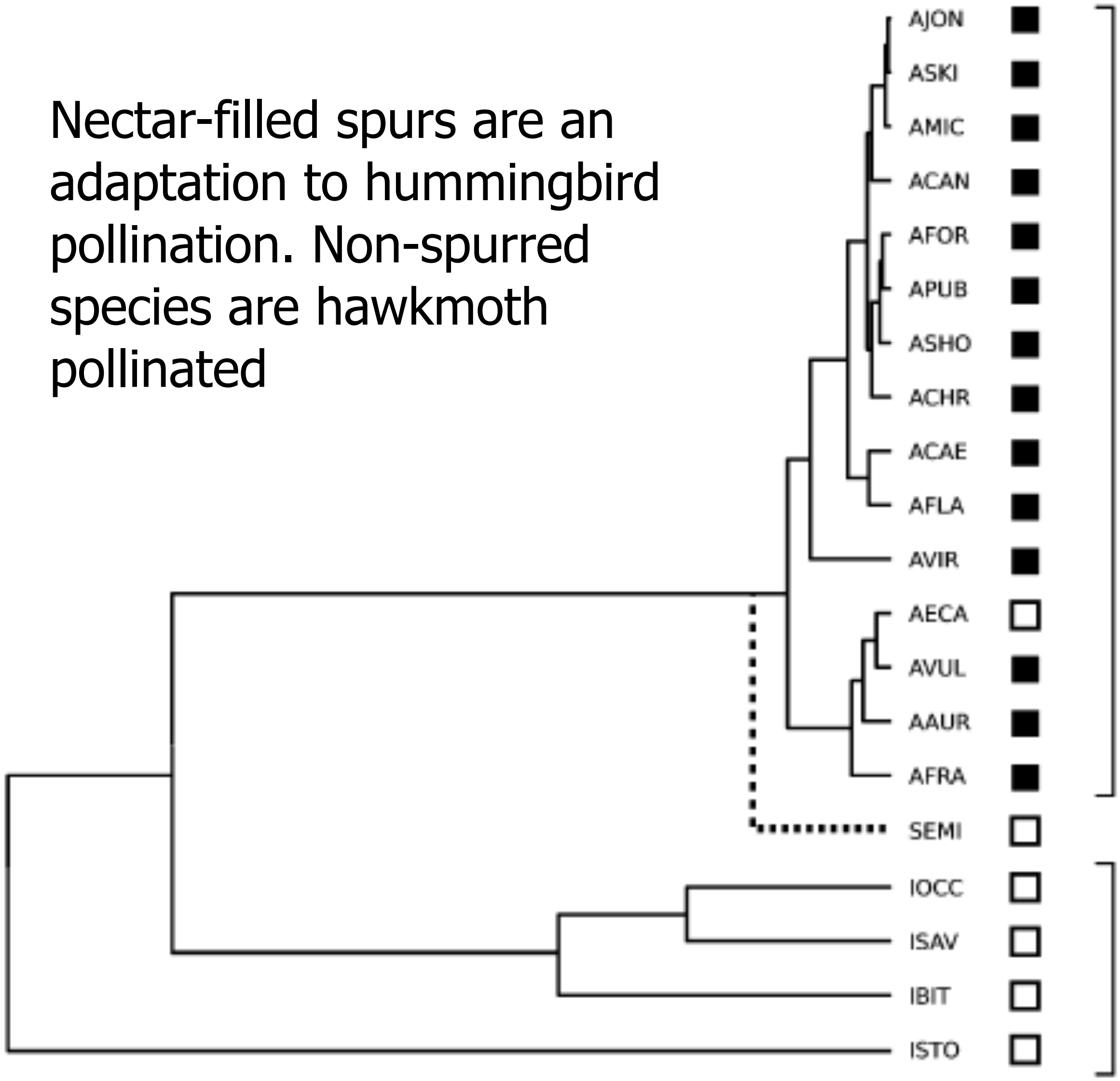


Lovette and Bermingham (1999)

State-dependent Diversification

Are columbine spurs a key adaptation?

Nectar-filled spurs are an adaptation to hummingbird pollination. Non-spurred species are hawkmoth pollinated



A. ecalcarata

Semiaquilegia image from http://www.flemings.com.au/australiangarden/plants.htm
Isopyrum thalictroides from http://www.botgarden.uni-tuebingen.de/tiki-index.php?page=Isopyrum
Aquilegia ecalcarata http://www.botanic.jp/plants-ha/fuodam.htm

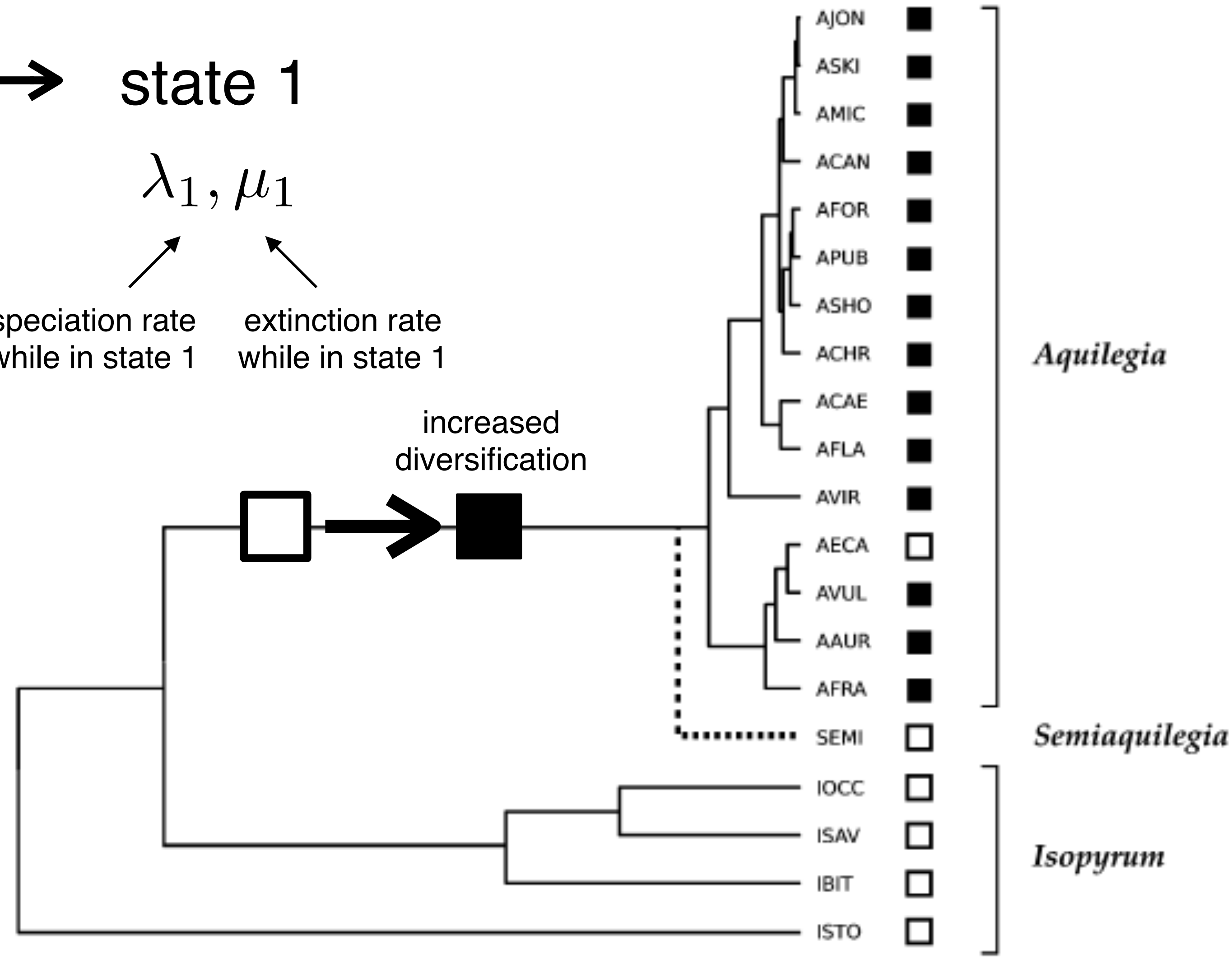
Fig. 4 from: Ree (2005)

Binary State Speciation and Extinction (BiSSE)

state 0 ⟷ state 1

λ_0, μ_0 — speciation rate while in state 0; extinction rate while in state 0

λ_1, μ_1 — speciation rate while in state 1; extinction rate while in state 1

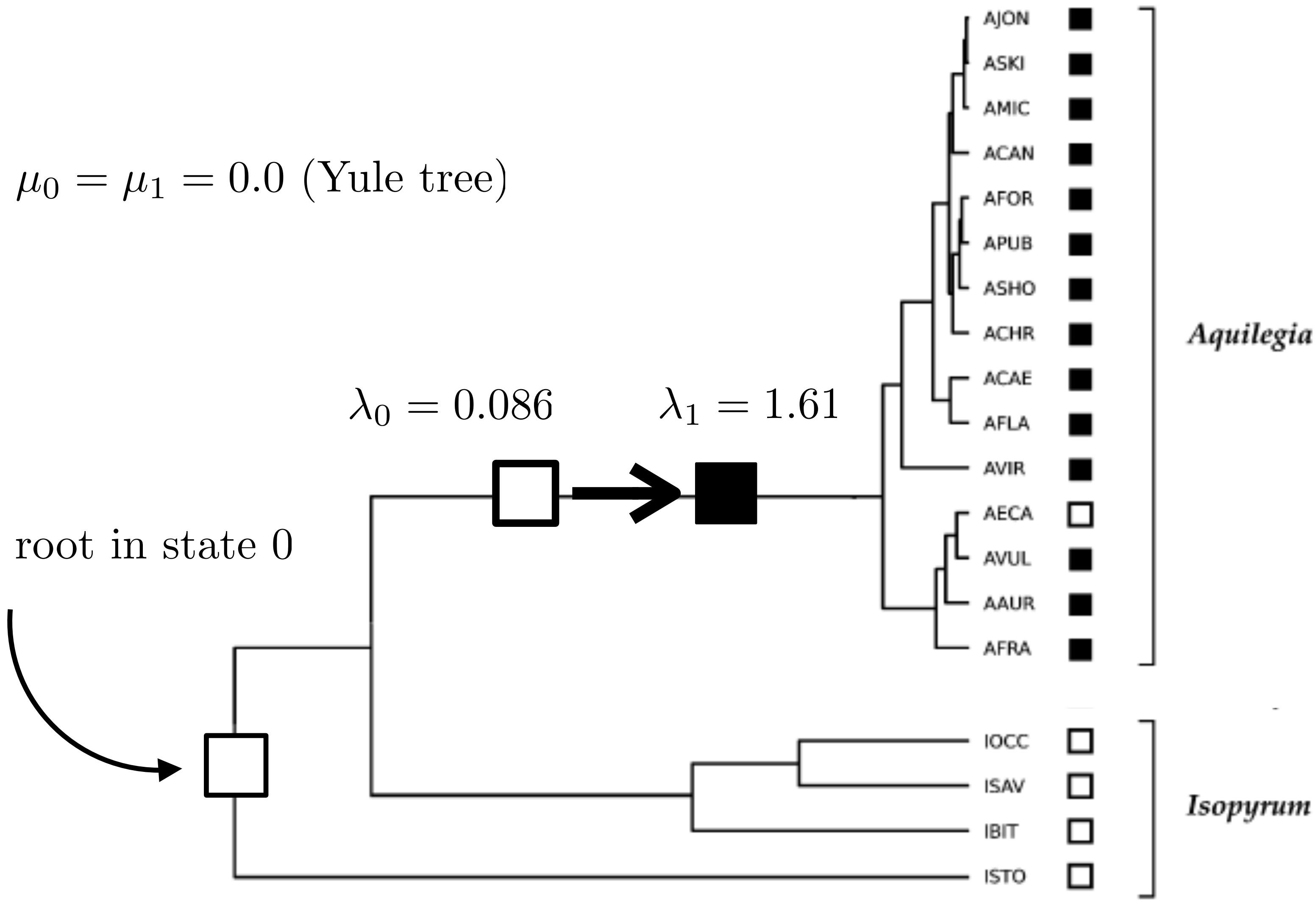


Maddison et al. (2007)

BiSSE analysis using diversitree

Assumed $\mu_0 = \mu_1 = 0.0$ (Yule tree)

Assumed root in state 0



diversitree: FitzJohn (2012)

*SSE models

Binary **S**tate **S**peciation and **E**xtinction (BiSSE)

Multi**S**tate **S**peciation and **E**xtinction (MuSSE)

Maddison et al. (2007)

FitzJohn (2012)

Geographic **S**tate **S**peciation and **E**xtinction (GeoSSE)

Goldberg et al. (2011)

Quantitative **S**tate **S**peciation and **E**xtinction (QuaSSE)

FitzJohn (2010)

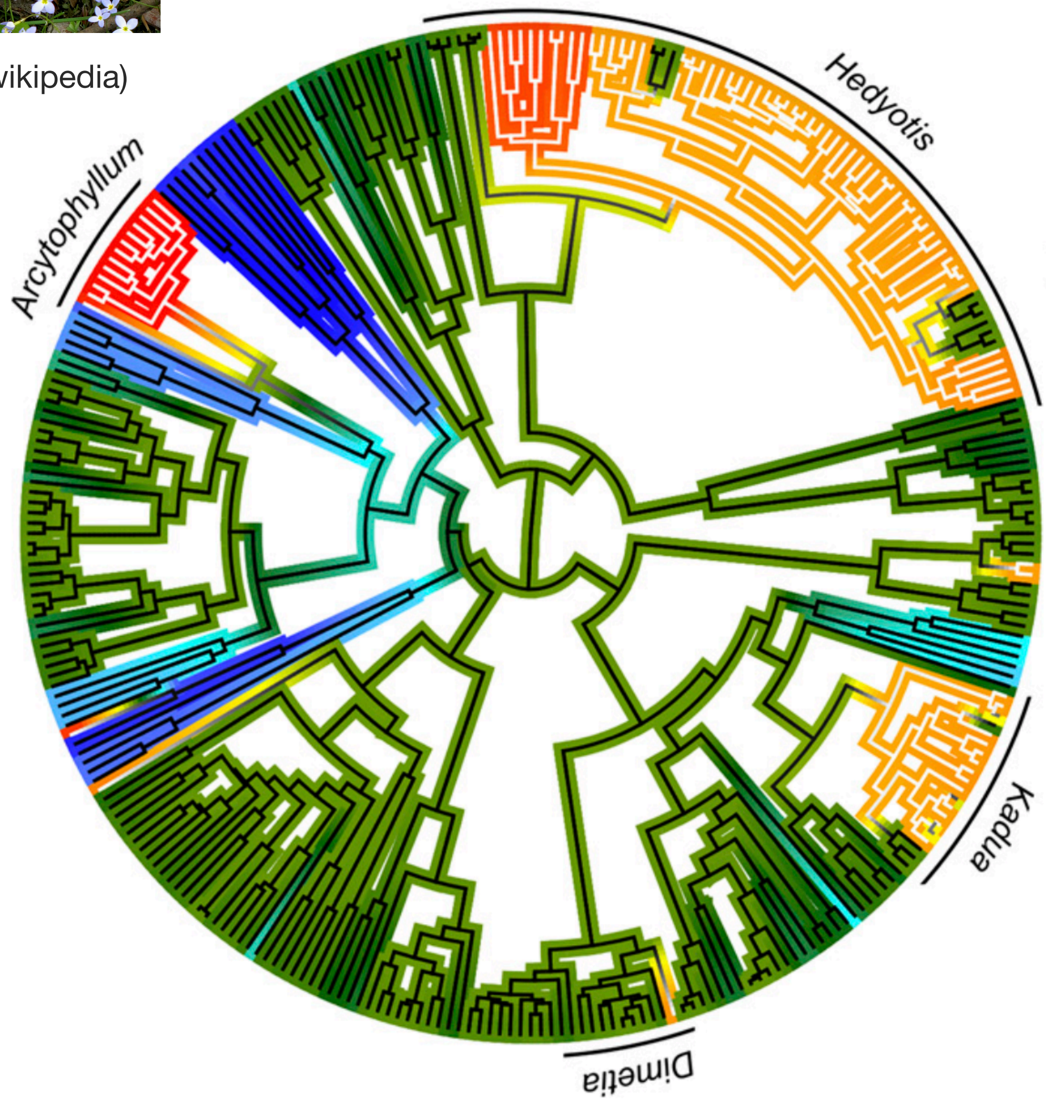
Hidden **S**tate **S**peciation and **E**xtinction (HiSSE)

Beaulieu and O'Meara (2016)

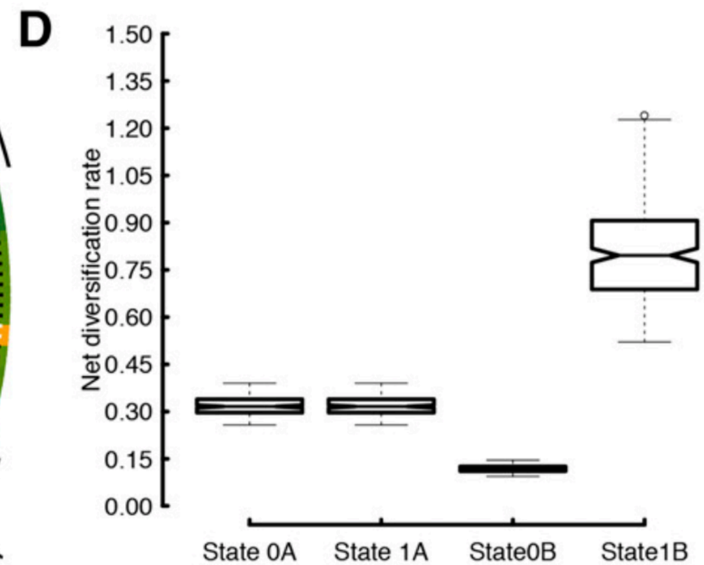
bluets (wikipedia)

Hidden **S**tate **S**peciation and **E**xtinction (HiSSE)

Beaulieu and O'Meara (2016)



white lineages: tropical upland (1)
black lineages: other (0)



other = temperate upland, lowland, or mixed habitat for widespread species

Fig. 3 from Neupane et al. (2017)

BAMM

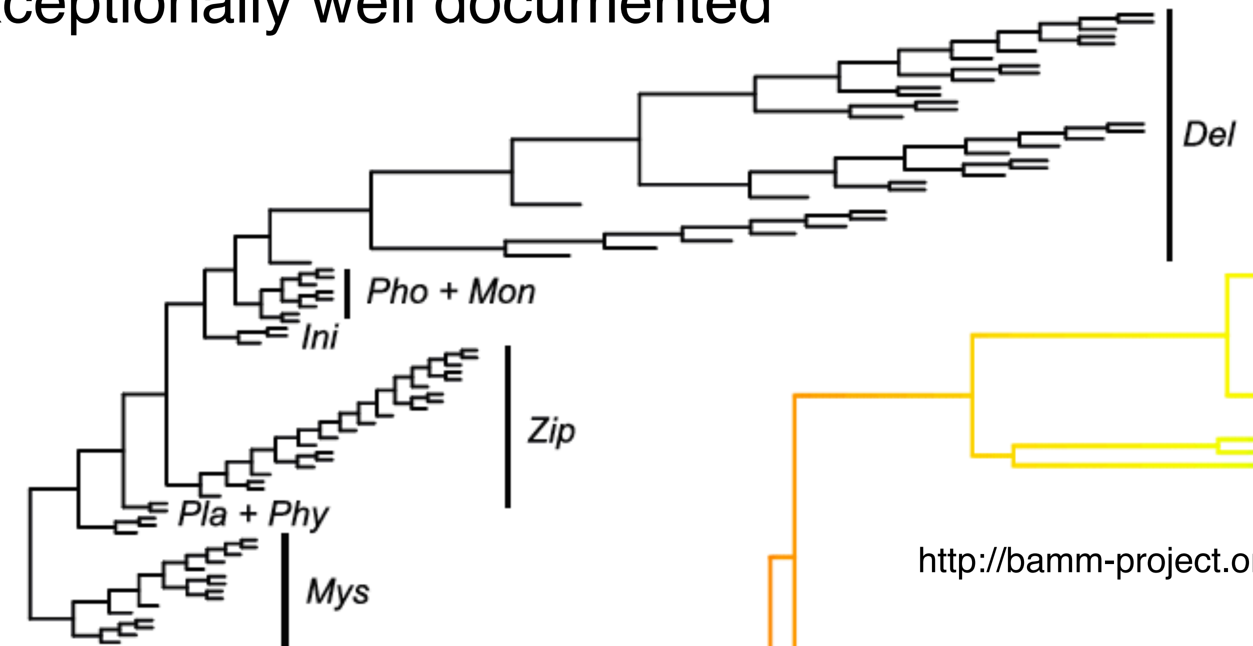
(Bayesian Analysis of Macroevolutionary Mixtures)

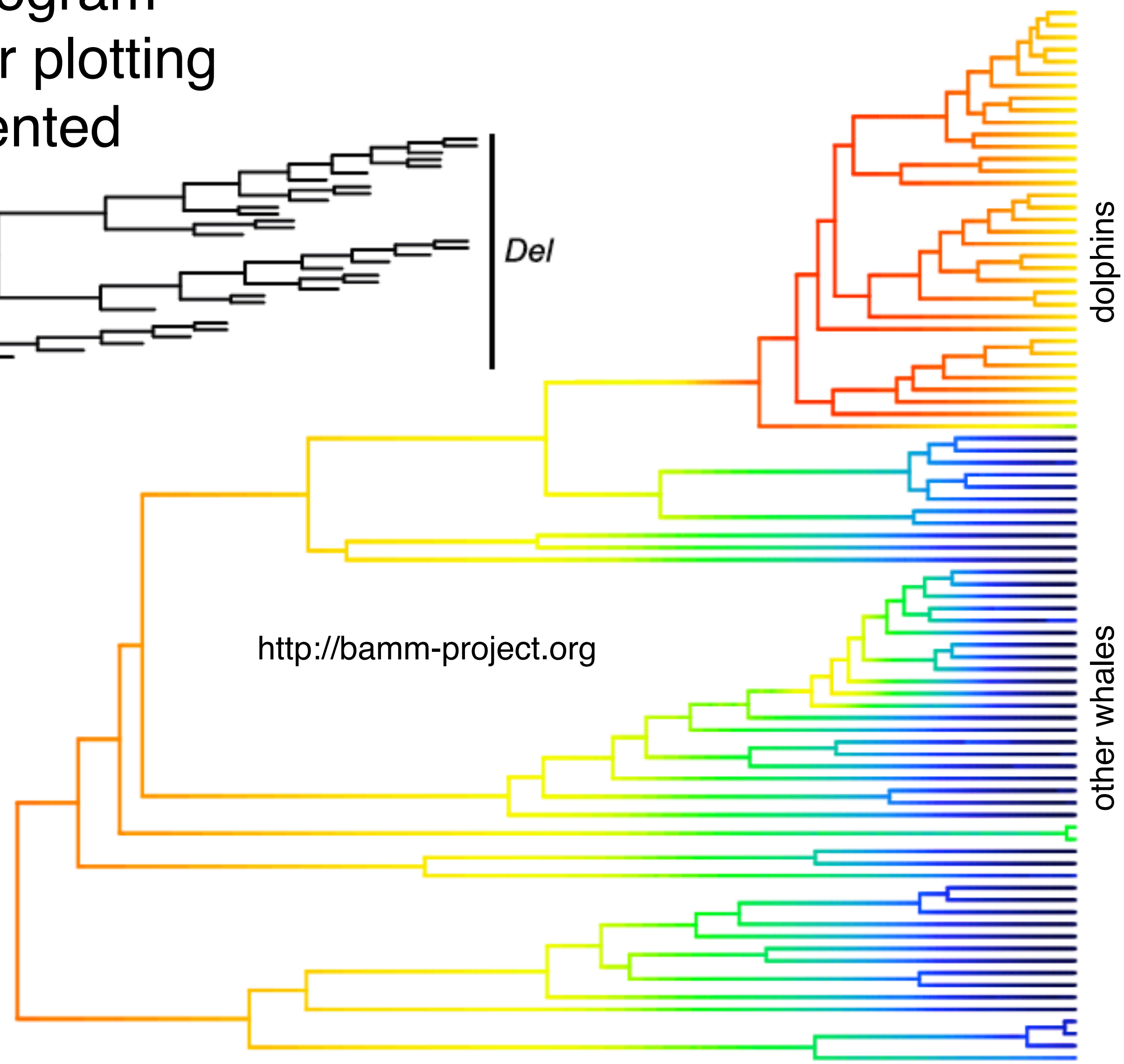
Rabosky et al. (2013)
Rabosky (2014)
Rabosky et al. (2014)
Shi and Rabosky (2015)

Moore et al. (2016): critique of BAMM
Rabosky et al. (2017): convincing response

Bayesian Analysis of Macroevolutionary Mixtures (BAMM)

rjMCMC command line program
BAMMtools **R package** for plotting
Exceptionally well documented





http://bamm-project.org

Fig. 9a in Rabosky (2014)

BAMM model

μ_0

constant extinction rate

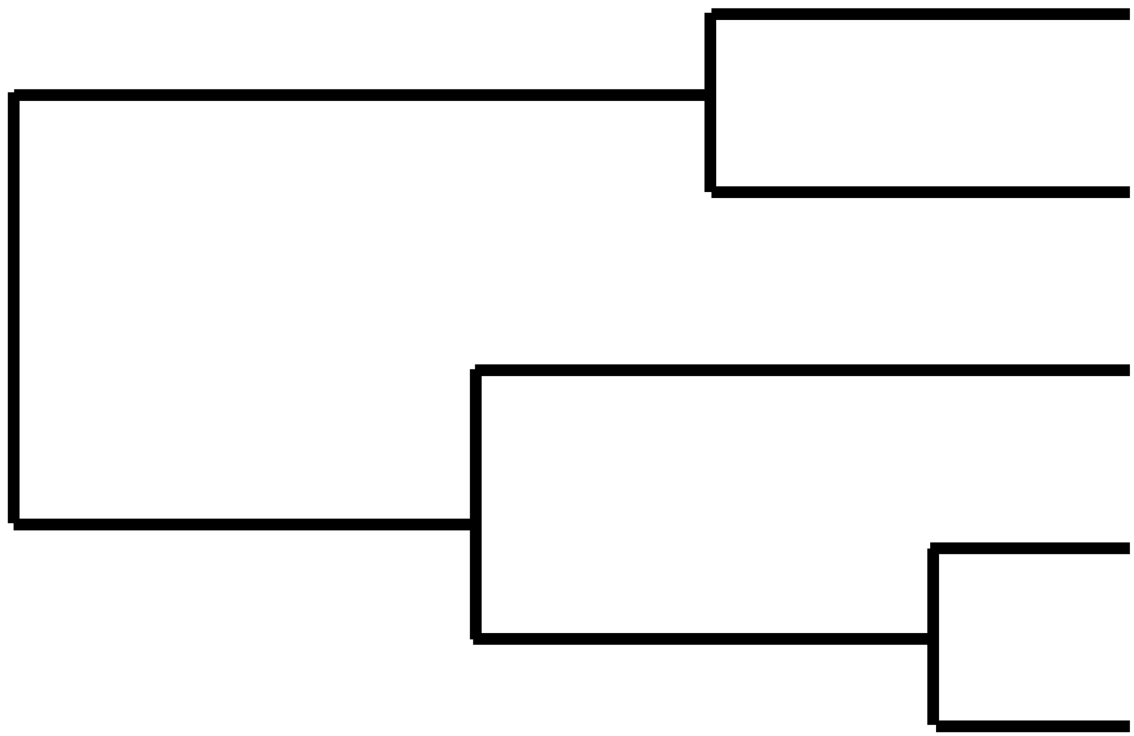
(at start of MCMC)
0 rate changes

Λ

Poisson mean number of rate-change events

$\lambda_{0,0}$

speciation rate at root



t_0 increasing →

$$\lambda(t_0) = \lambda_{0,0} e^{z_0 t_0}$$

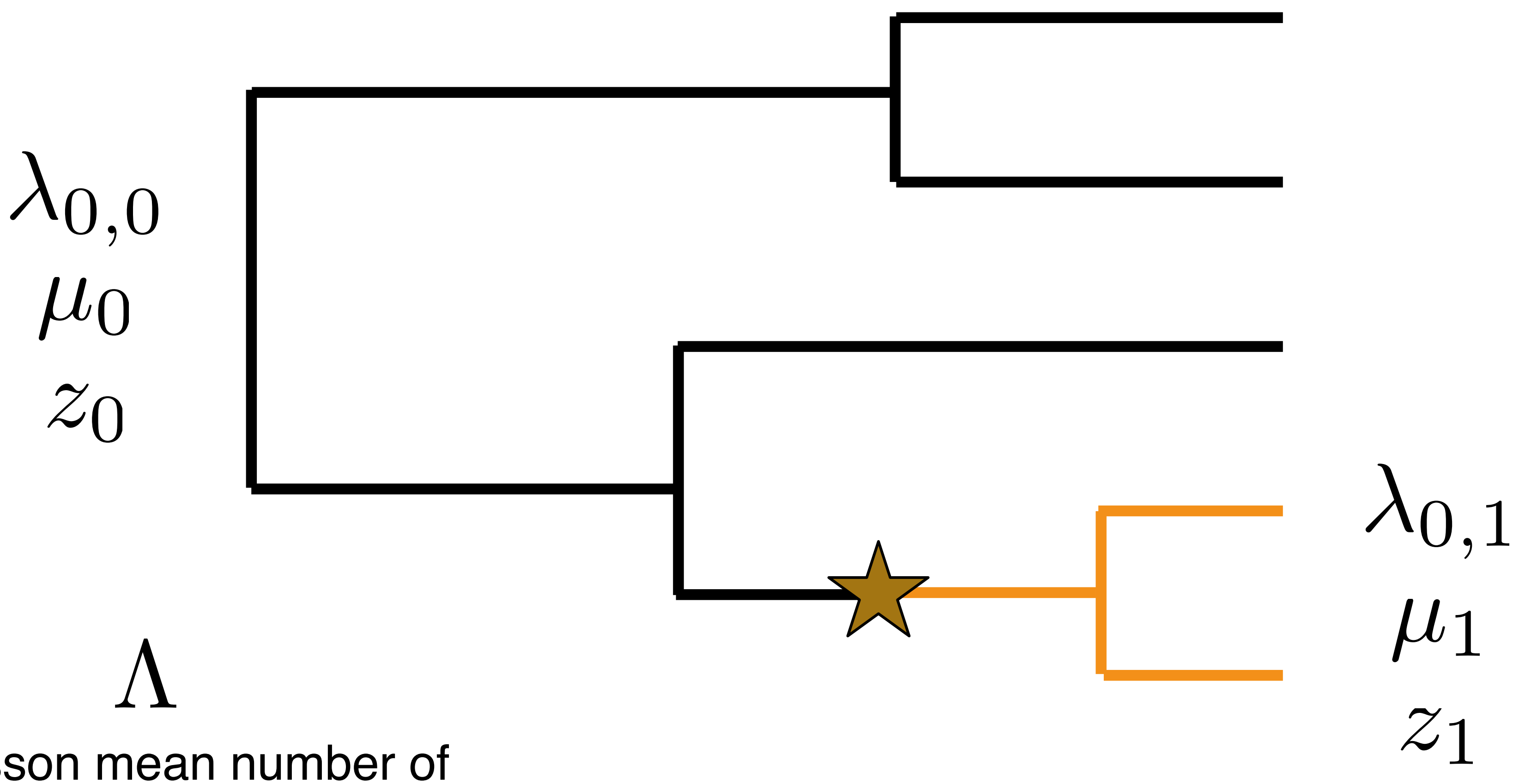
z_0

z_0 positive: speciation rate increases over time

z_0 negative: speciation rate decreases over time

BAMM model

1 rate change

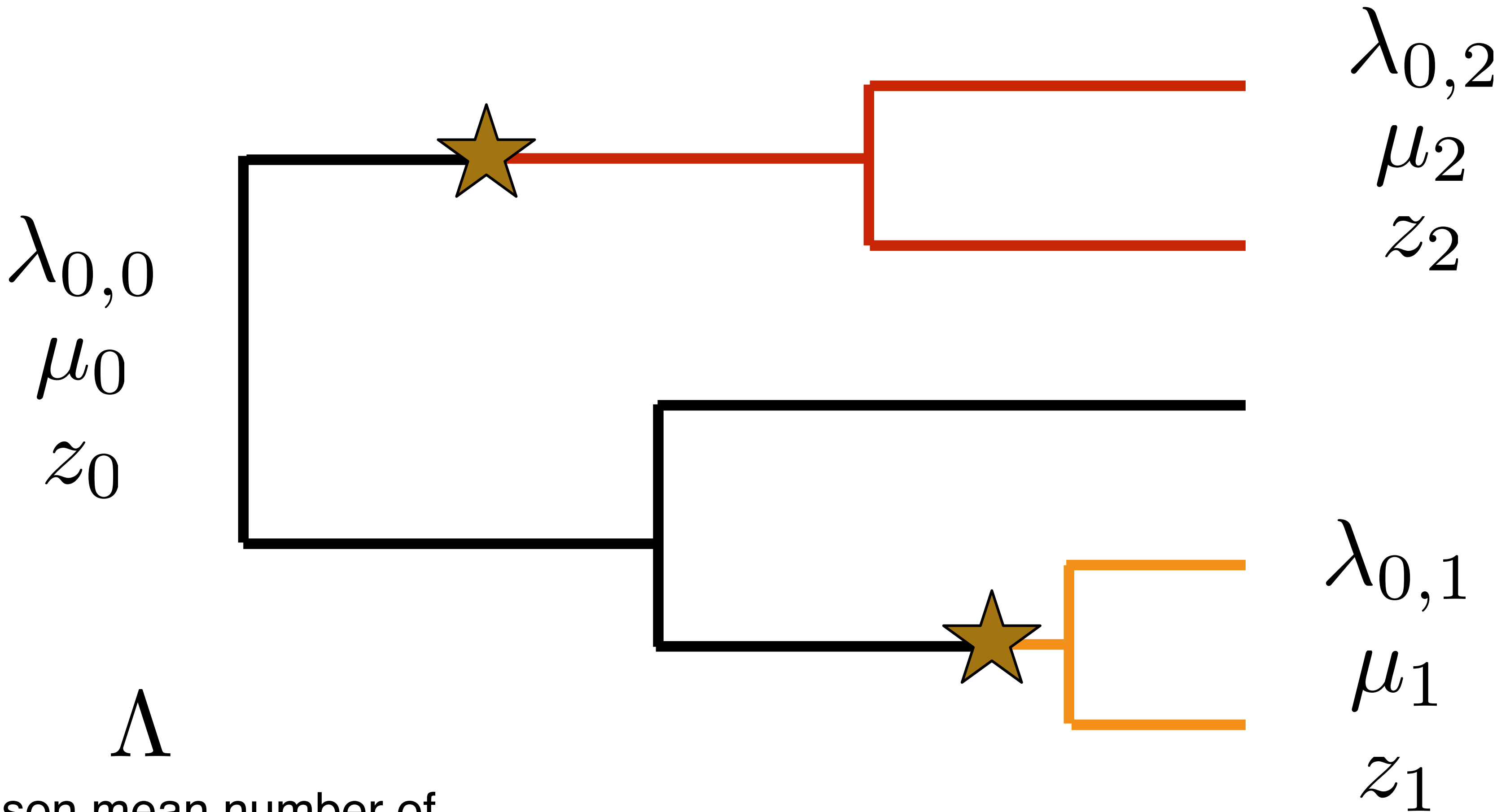


Λ

Poisson mean number of rate-change events

BAMM model

2 rate changes

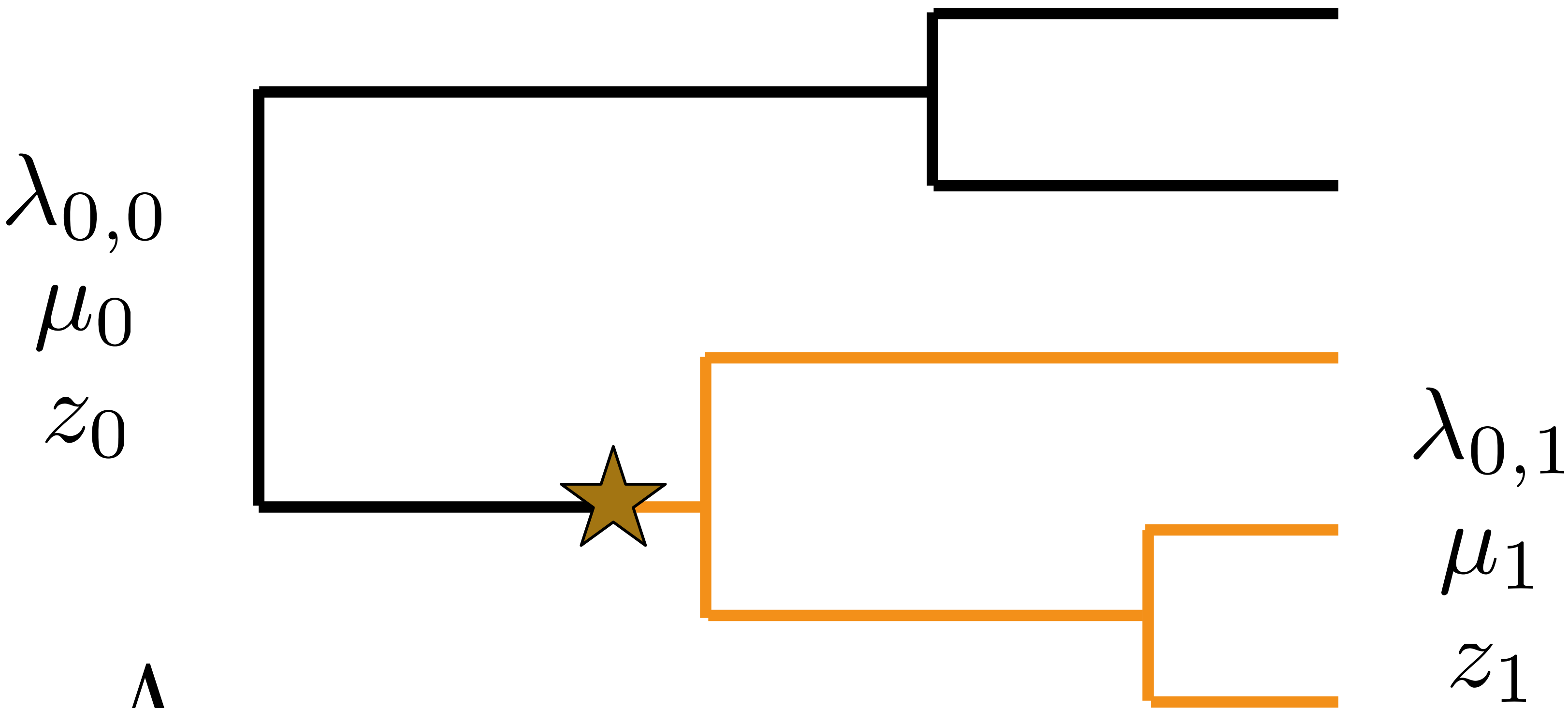


Λ

Poisson mean number of rate-change events

BAMM model

back to 1 rate change

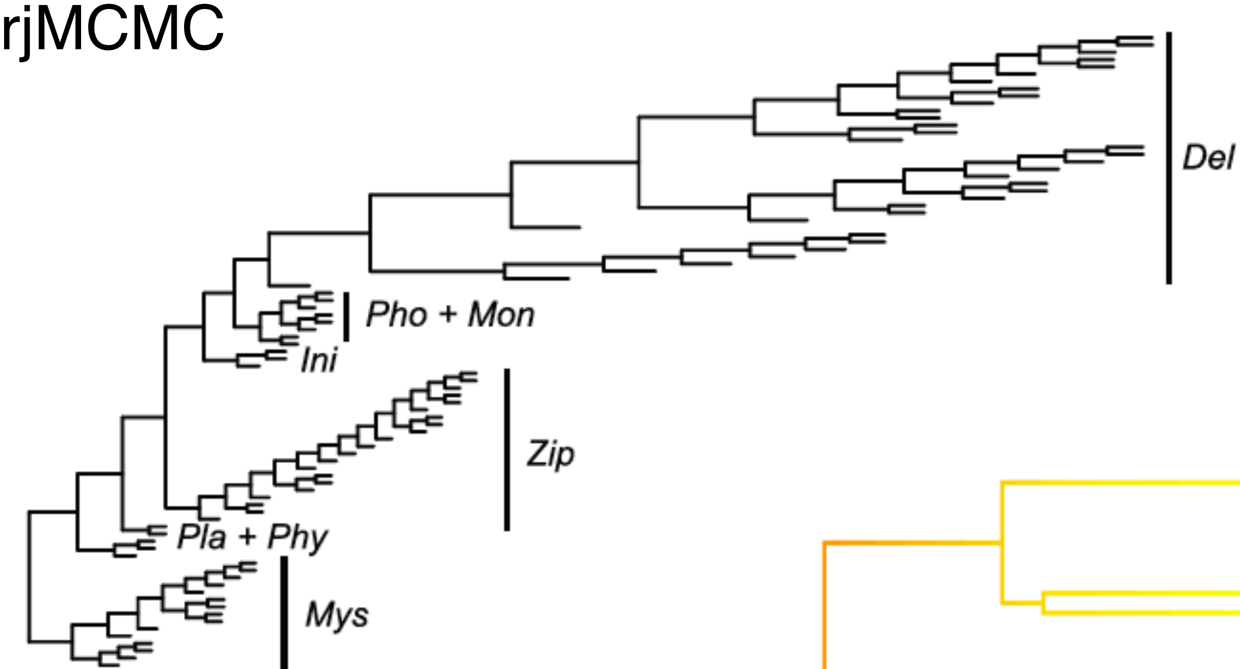


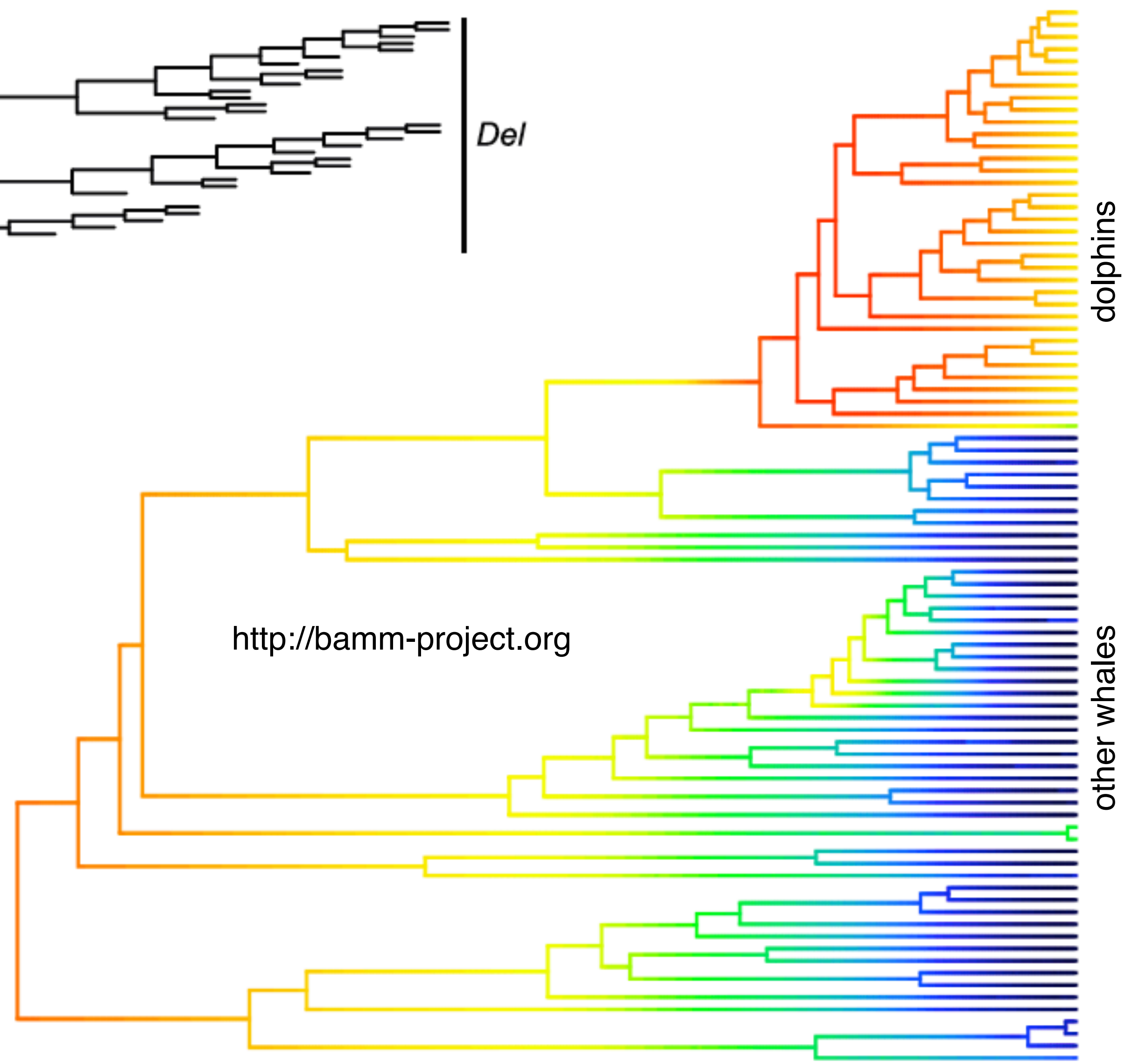
Λ

Poisson mean number of rate-change events

Bayesian Analysis of Macroevolutionary Mixtures (BAMM)

rjMCMC





http://bamm-project.org

Fig. 9a in Rabosky (2014)