Diversification and Turnover

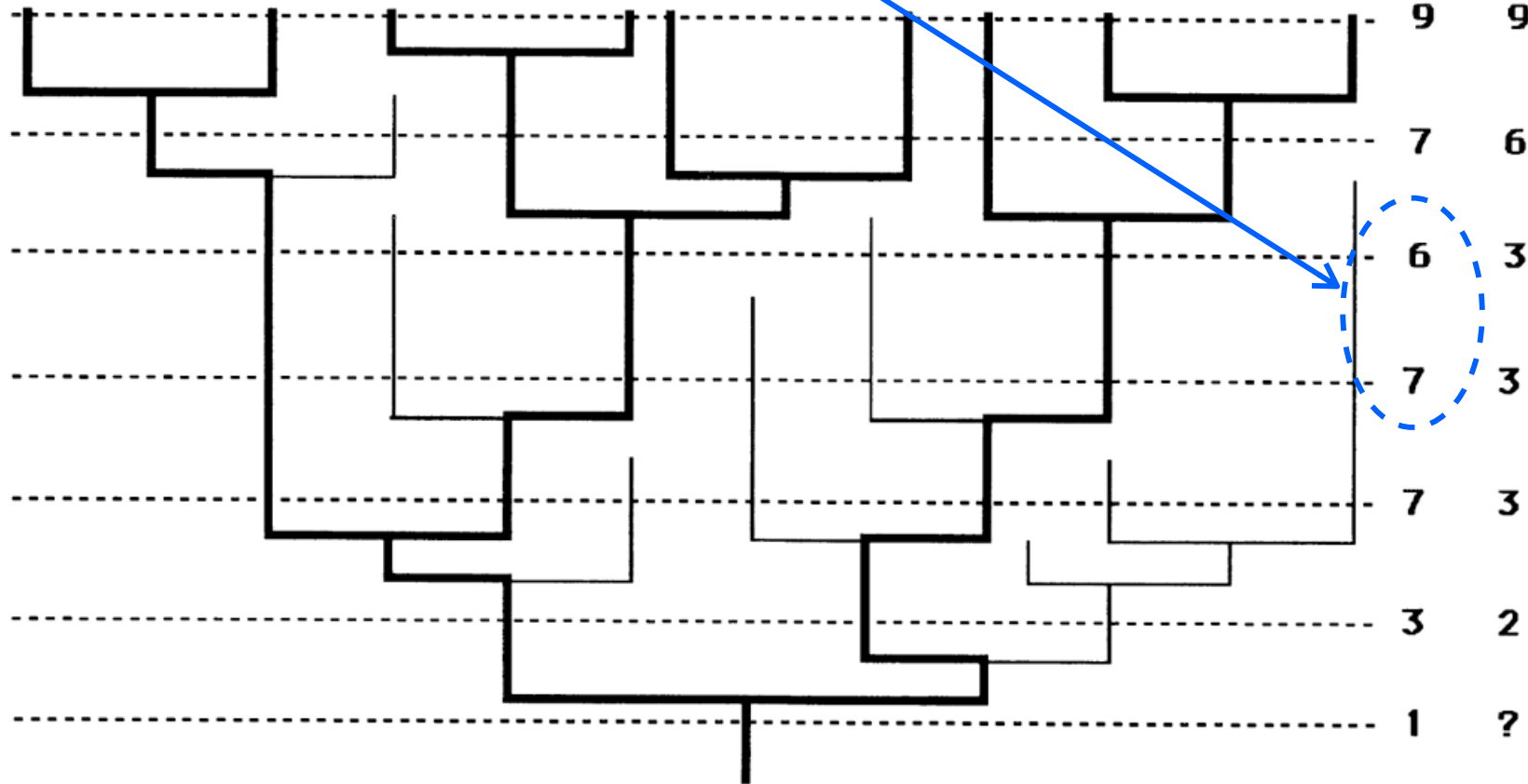diversification rate = speciation rate — extinction rate

$$= \lambda - \mu$$

turnover = $\dfrac{\text{extinction rate}}{\text{speciation rate}}$ = μ/λ

Lineages-through-time (LTT) plot


Note that, unlike reconstructed number, the actual number of lineages can decrease

Actual lineages in existence

Reconstructed lineages

	Actual	Reconstructed
	9	9
	7	6
	6	3
	7	3
	7	3
	3	2
	1	?

Harvey et al. (1994)

Can extinction events be detected using phylogenies of extant taxa?

Actual number of lineages

Reconstructed number of lineages cannot decrease!

Reconstructed number of lineages

Harvey et al. (1994)
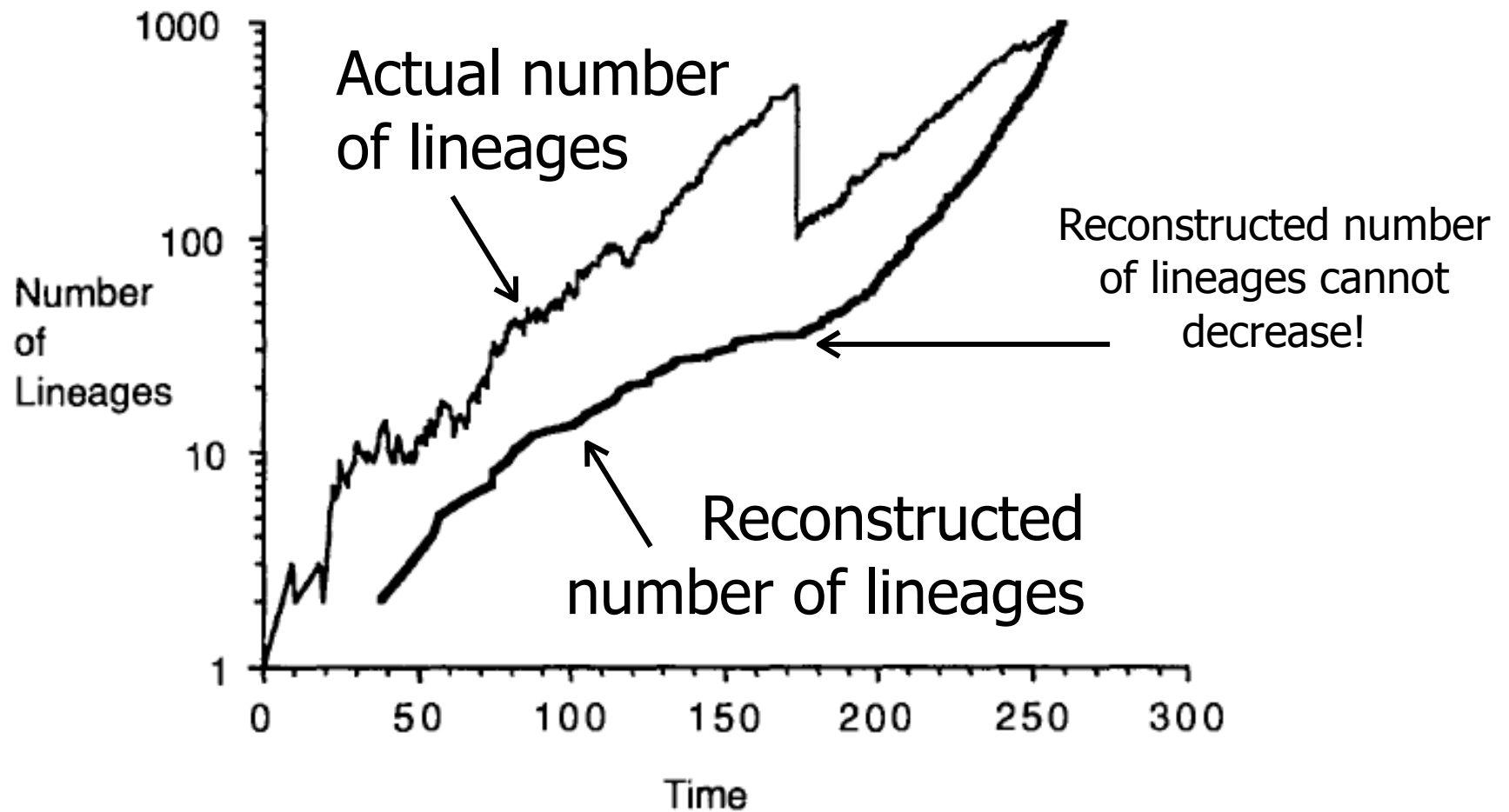
The pull of the present

# 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 $N_A(t)$...
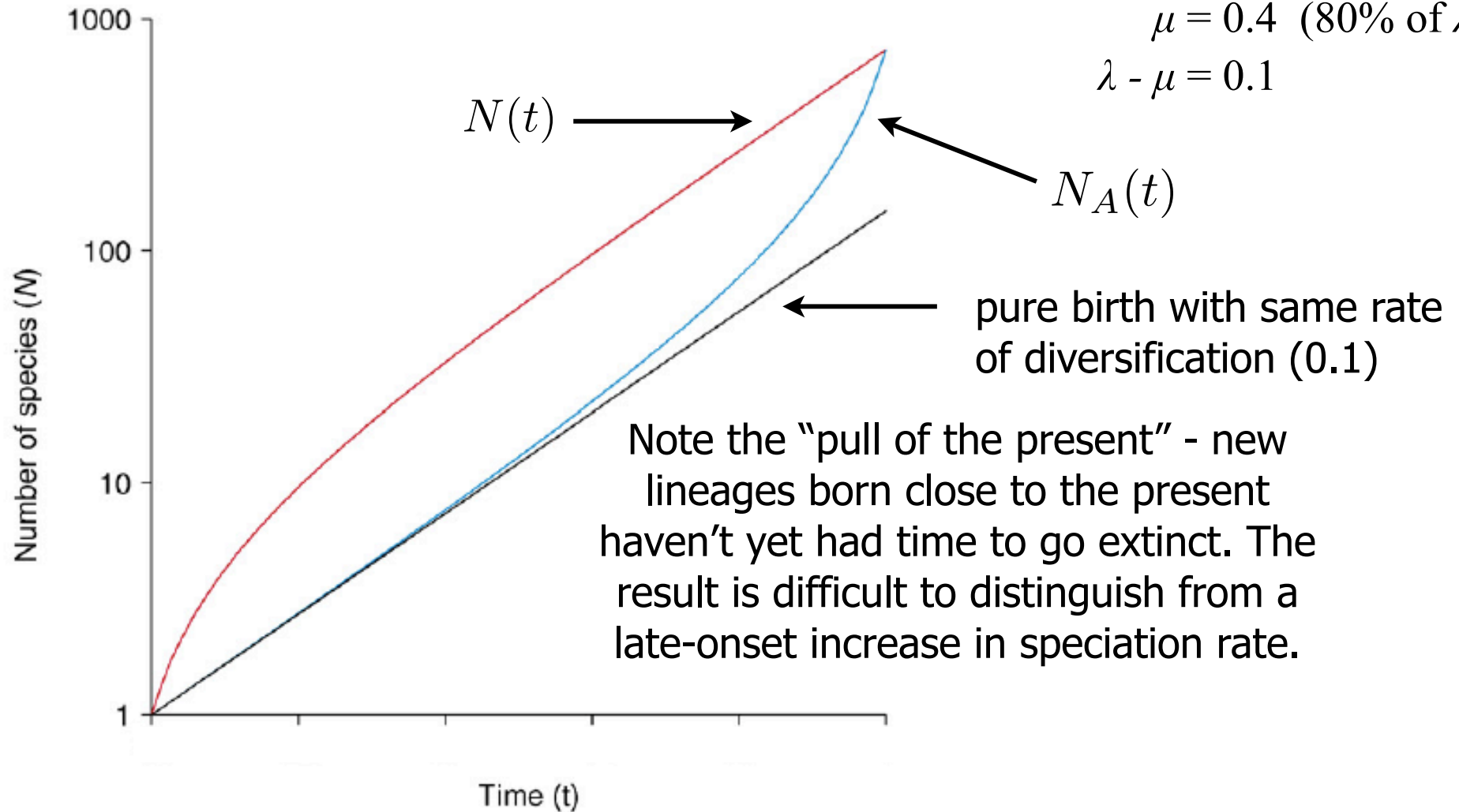
T

t

$N(t) = 7$
$N_A(t) = 4$

0

Box 3 from: Ricklefs (2007)
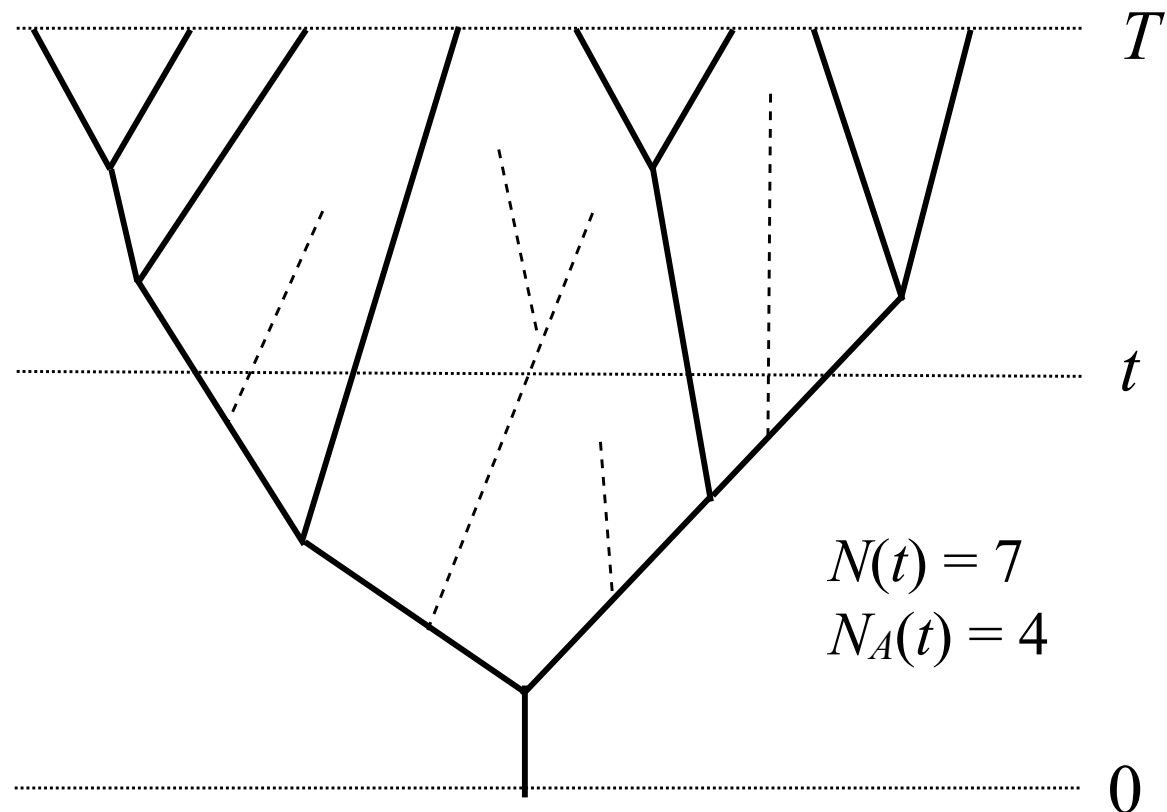
The pull of the present

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

$$\lambda = 0.5$$
$$\mu = 0.4 \ \ (80\% \text{ of } \lambda)$$
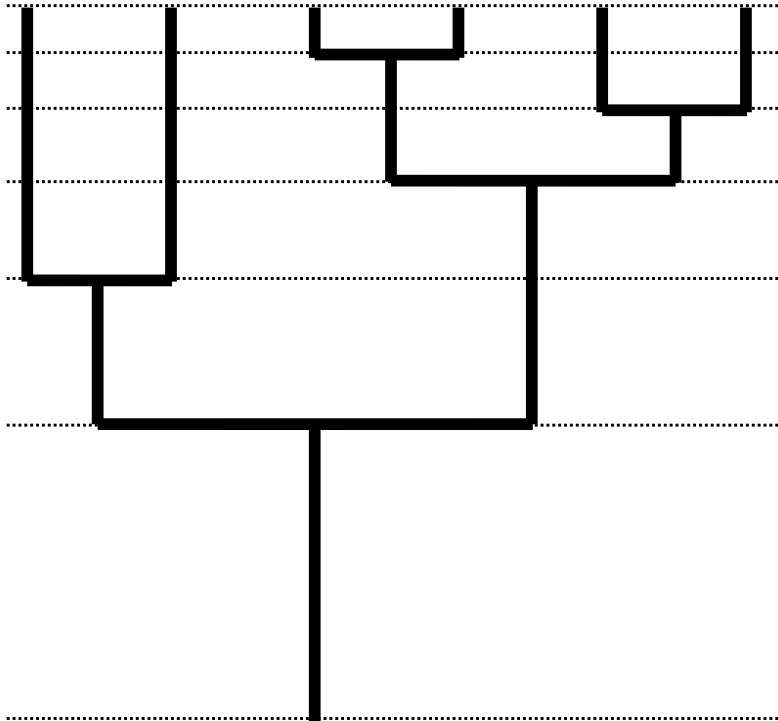$$\lambda - \mu = 0.1$$

$N(t) \longrightarrow$

$N_A(t)$

pure birth with same rate
of diversification (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

Yule vs. extinction

Constant speciation
rate, no extinction

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.
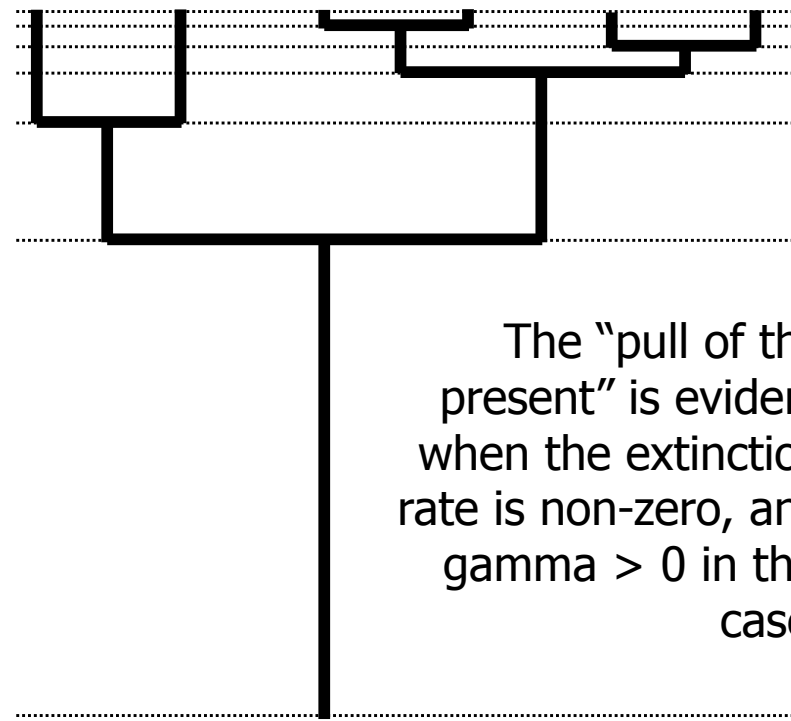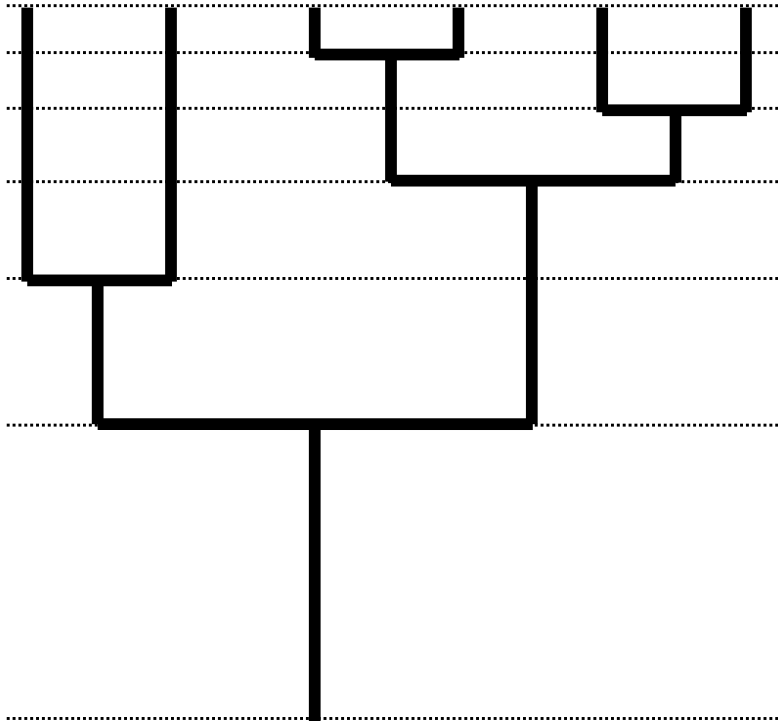
$$\gamma = 0.00$$

Zero is the expected lower bound for gamma if speciation and extinction rates are both constant
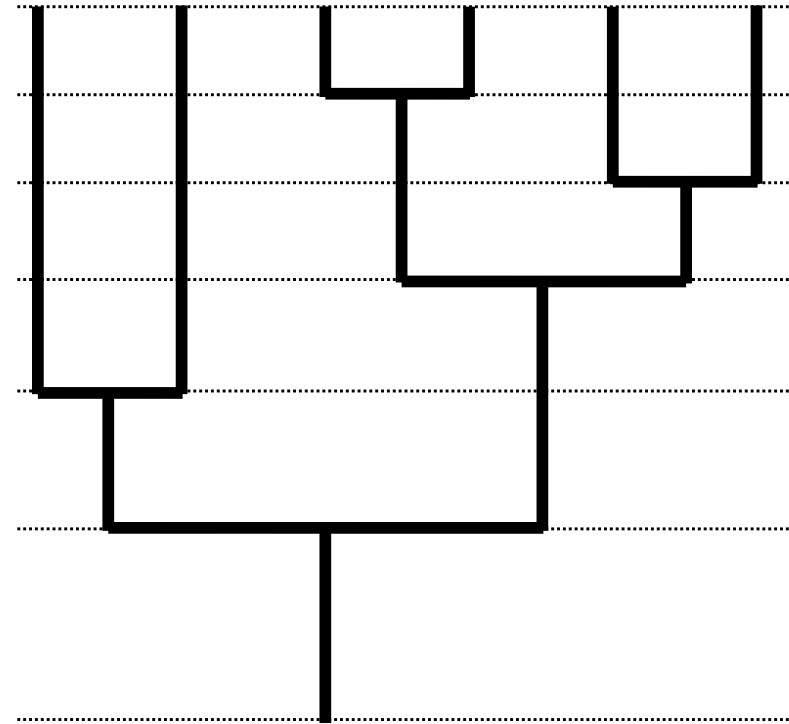
$$\gamma = 0.88$$

Pybus and Harvey (2000)

Yule vs. declining speciation rate

Constant speciation
rate, no extinction

Speciation rate declines as
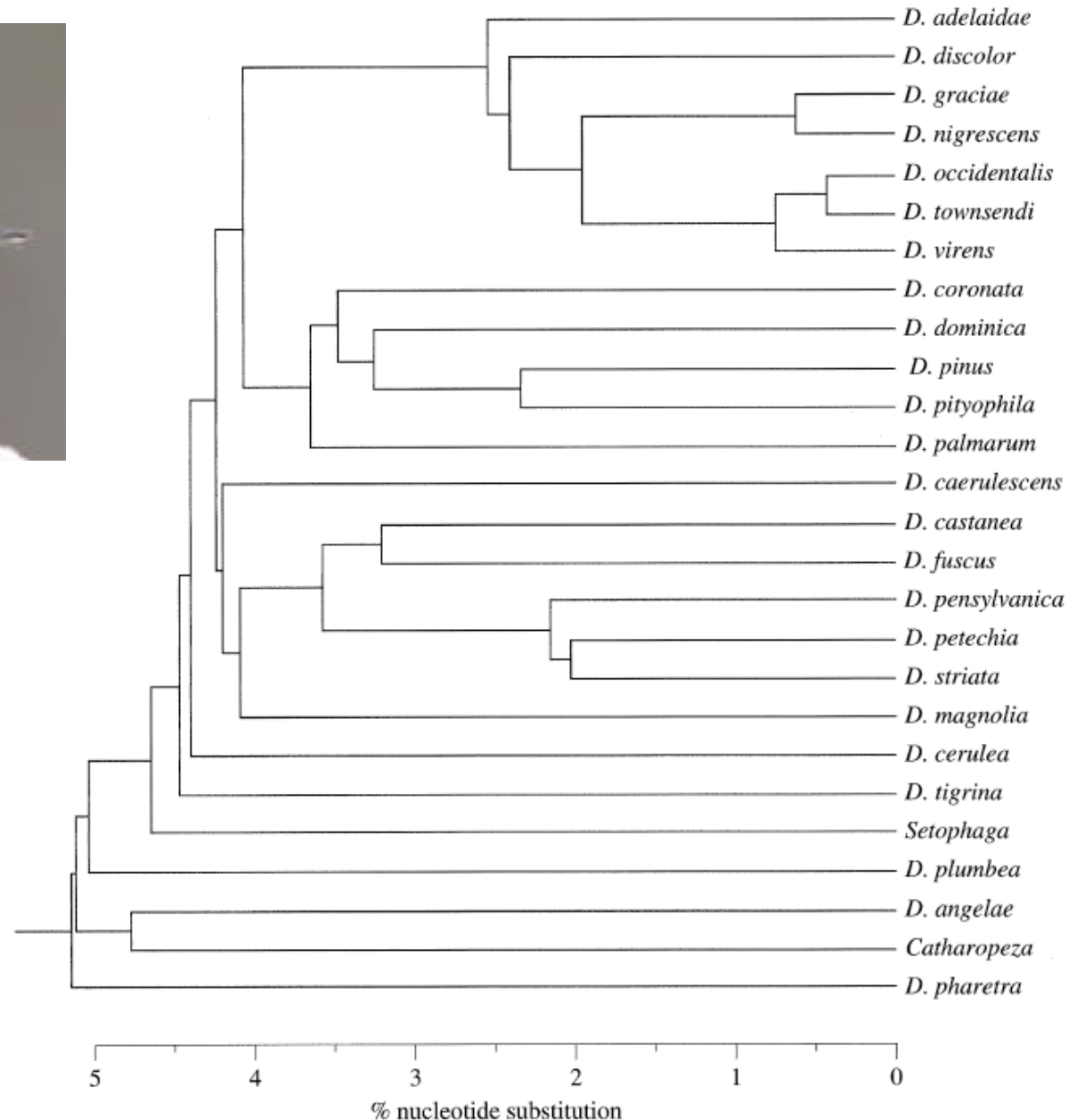clade ages

$$\gamma = 0.00$$

$$\gamma = -0.46$$

Negative values of gamma
indicate a declining
diversification rate through time

Gamma and adaptive radiations

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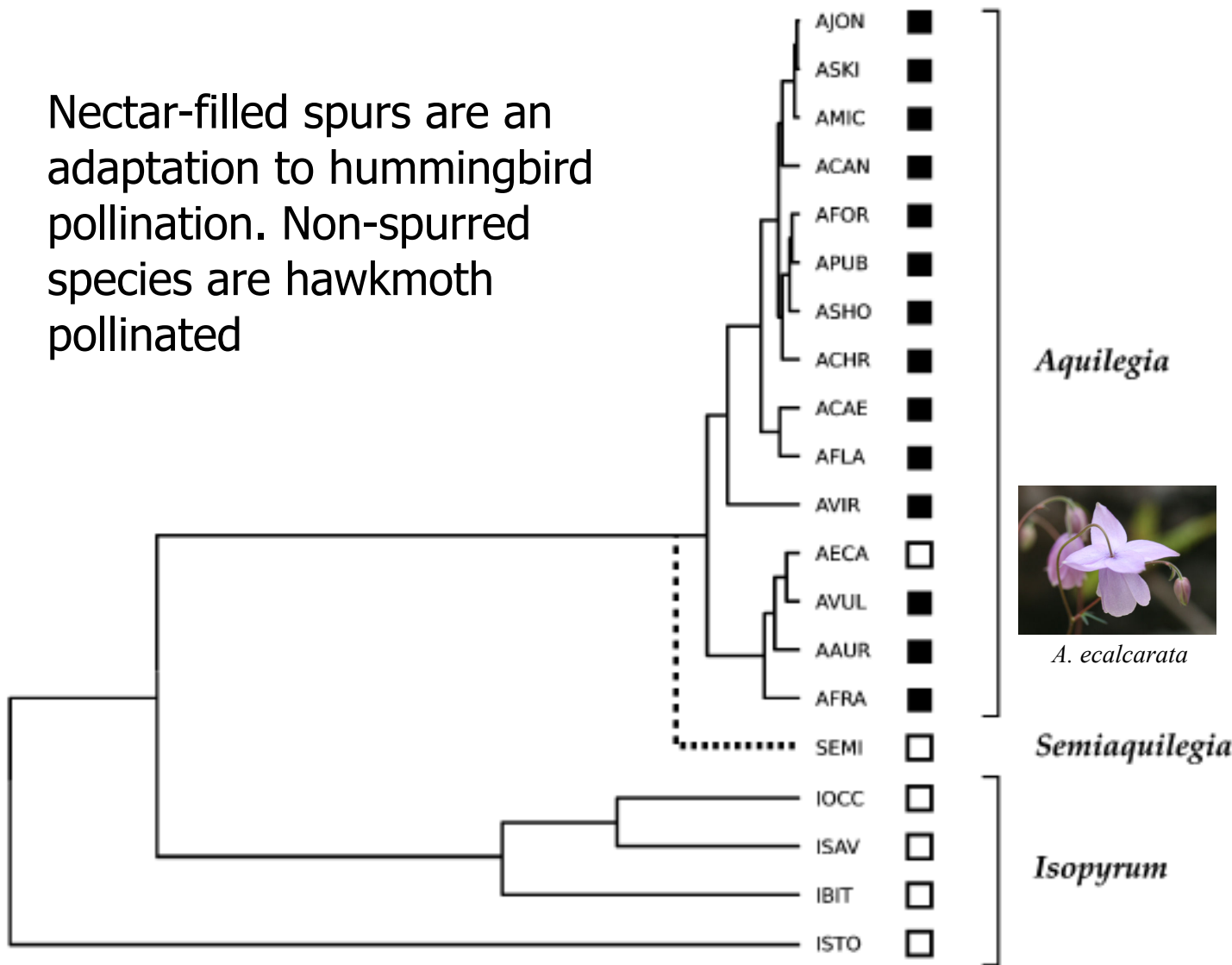http://en.wikipedia.org/wiki/Dendroica

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.

D. adelaidae
D. discolor
D. graciae
D. nigrescens
D. occidentalis
D. townsendi
D. virens
D. coronata
D. dominica
D. pinus
D. pityophila
D. palmarum
D. caerulescens
D. castanea
D. fuscus
D. pensylvanica
D. petechia
D. striata
D. magnolia
D. cerulea
D. tigrina
Setophaga
D. plumbea
D. angelae
Catharopeza
D. pharetra

5   4   3   2   1   0
% nucleotide substitution

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

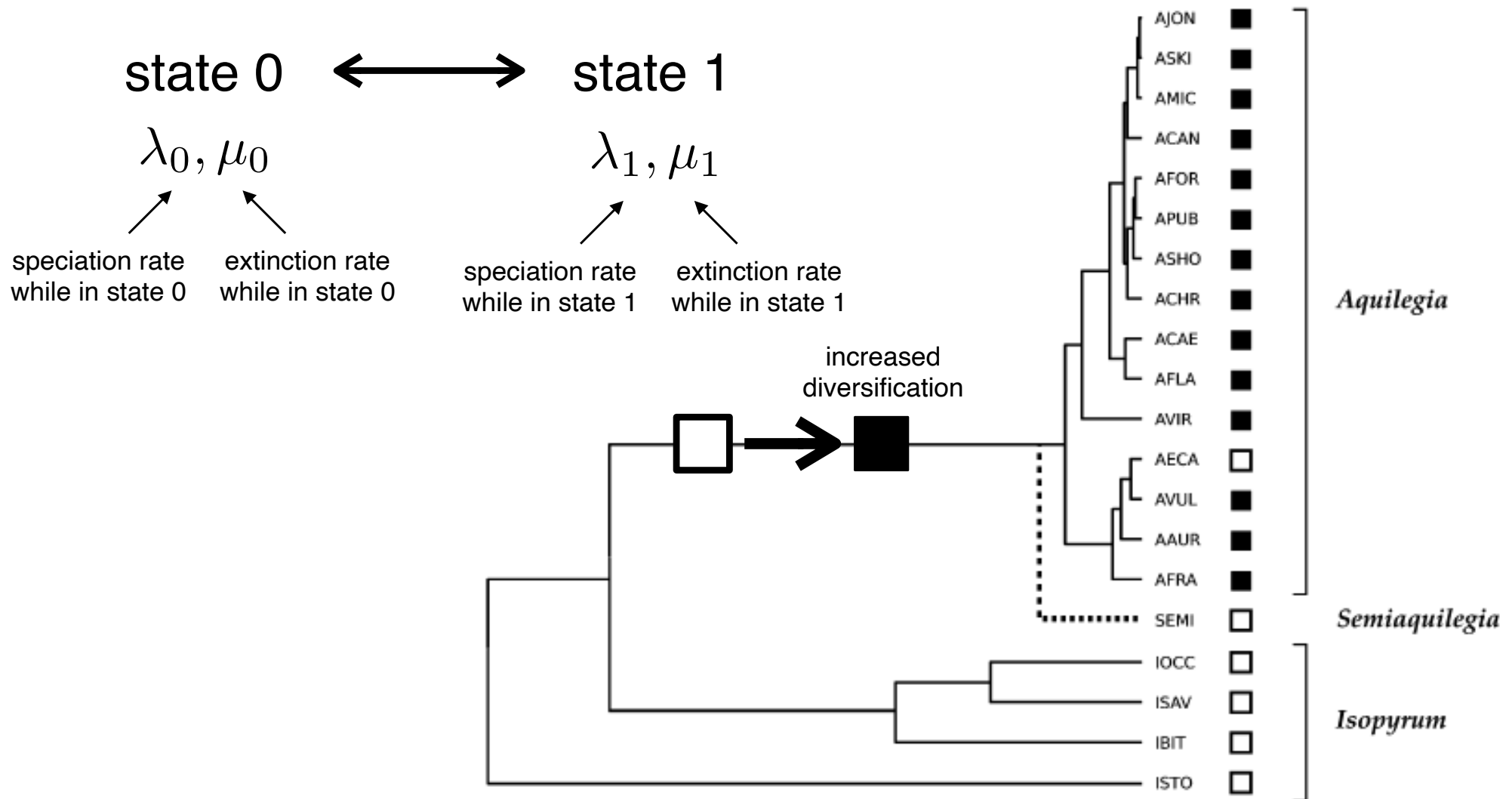*Semiaquilegia* image from http://www.flemings.com.au/australiangarden/plants.htm
Isopyrum thalictroides from http://www.botgarden.uni-tuebingen.de/tiki-index.php?page=Isopyrum
Aquilegia ecalcarata http://www.botanic.jp/plants-ha/fuodam.htm

Fig. 4 from: Ree (2005)

Binary State Speciation and Extinction (BiSSE)

state 0 $\longleftrightarrow$ state 1

λ_0, μ_0 $\qquad$ λ_1, μ_1

speciation rate while in state 0 $\qquad$ extinction rate while in state 0

speciation rate while in state 1 $\qquad$ extinction rate while in state 1

increased diversification

AJON
ASKI
AMIC
ACAN
AFOR
APUB
ASHO
ACHR
ACAE
AFLA
AVIR
AECA
AVUL
AAUR
AFRA

Aquilegia

SEMI — *Semiaquilegia*

IOCC
ISAV
IBIT
ISTO

Isopyrum

Maddison et al. (2007)

BiSSE analysis using diversitree

□
state 0 ⟷ ■ state 1

λ_0, μ_0 λ_1, μ_1

speciation rate
while in state 0   extinction rate
while in state 0   speciation rate
while in state 1   extinction rate
while in state 1

$\lambda_0 = 0.000$

$\lambda_1 = 2.503$

$\mu_0 = 0.633$

$\mu_1 = 2.515$

$q_{01} = 0.000$

$q_{10} = 0.183$
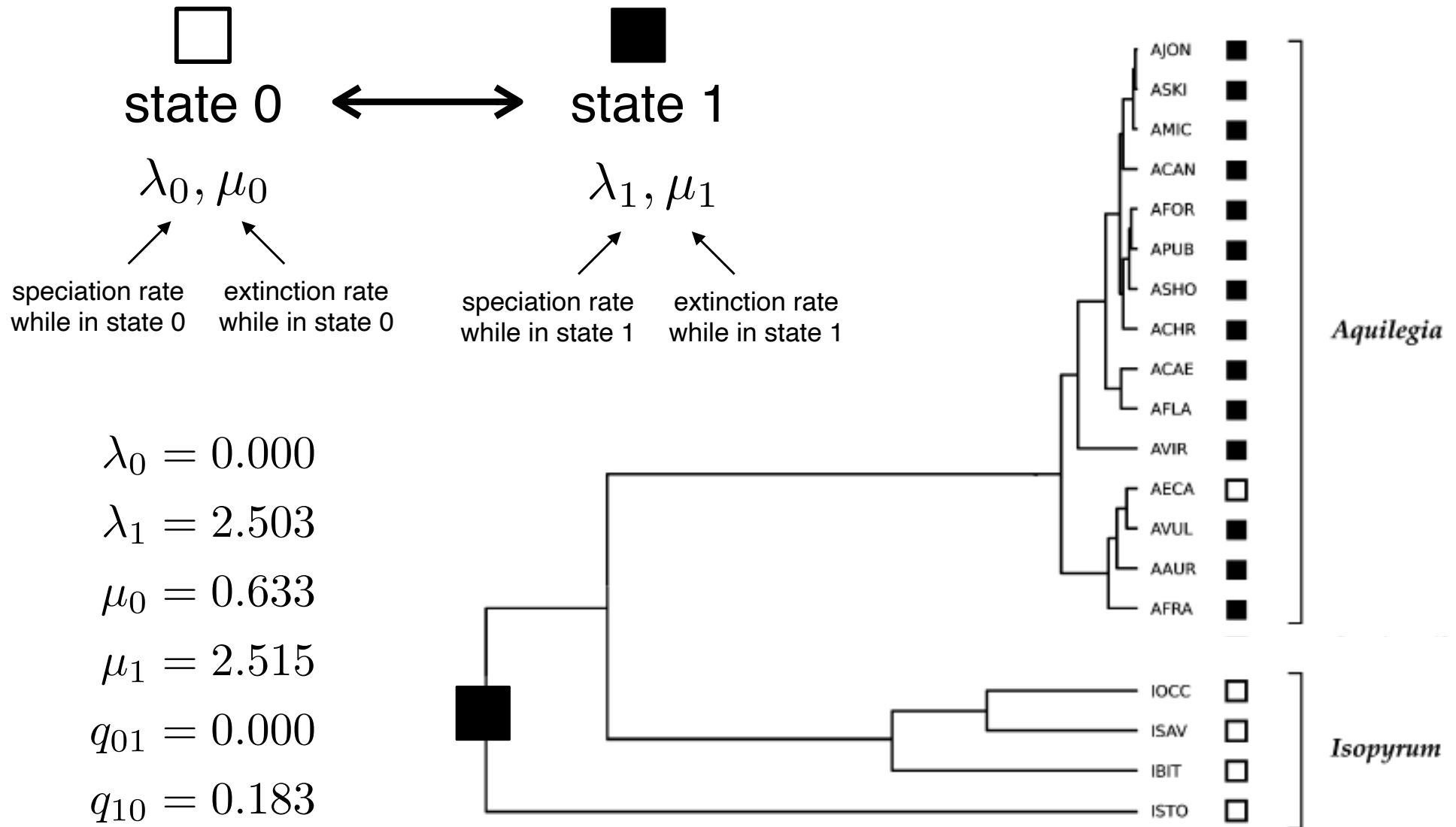
FitzJohn (2012)

*SSE models

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

Maddison et al. (2007)

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

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)

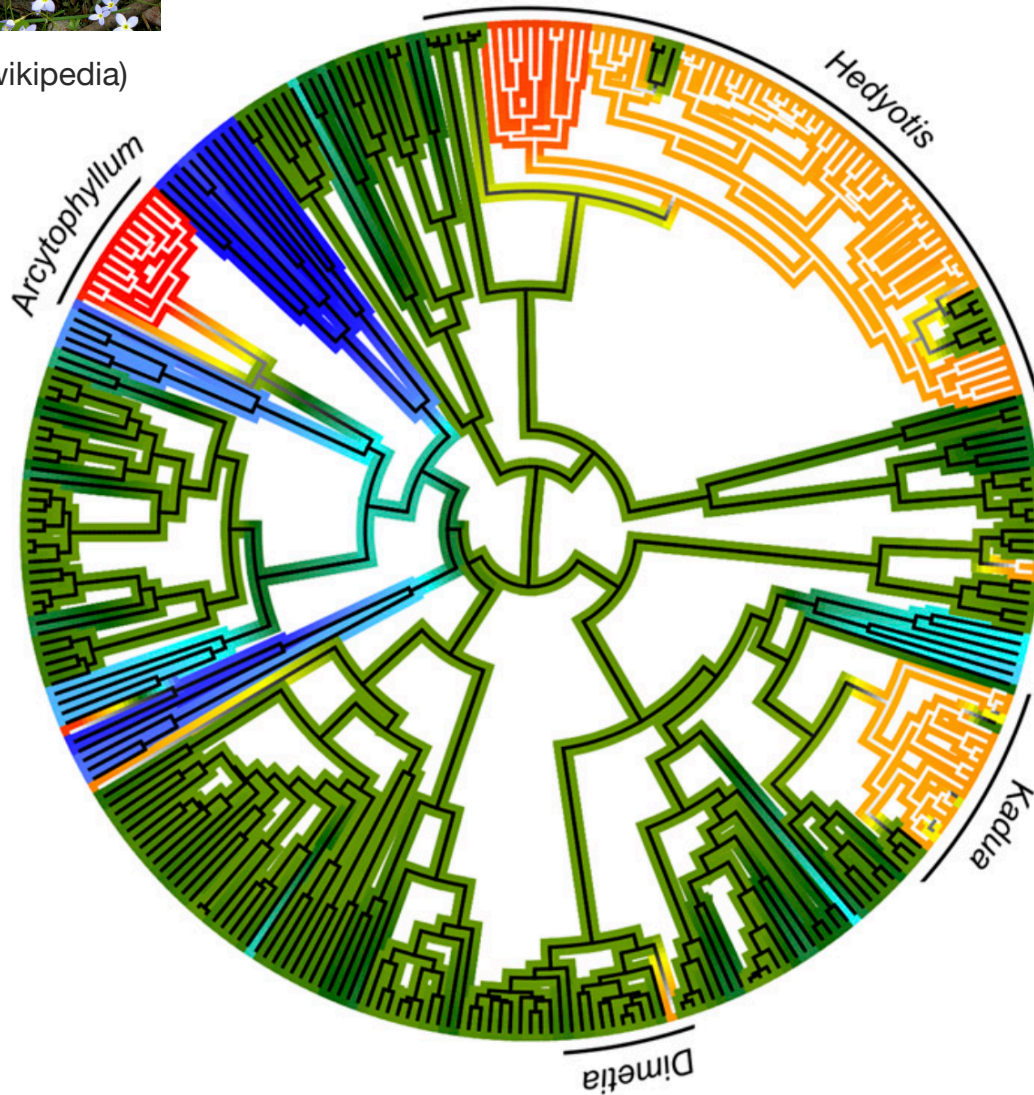**Hi**dden **S**tate **S**peciation and **E**xtinction (HiSSE)
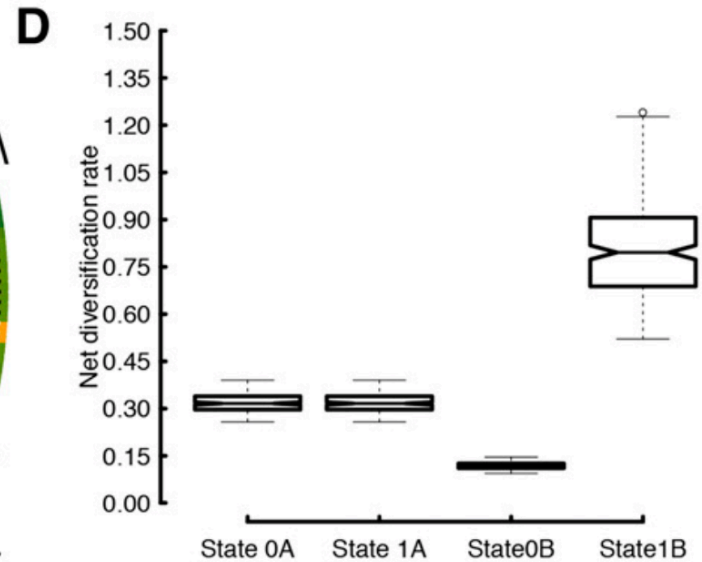
Beaulieu and O'Meara (2016)

Hidden State Speciation and Extinction (HiSSE)

Beaulieu and O'Meara (2016)

bluets (wikipedia)

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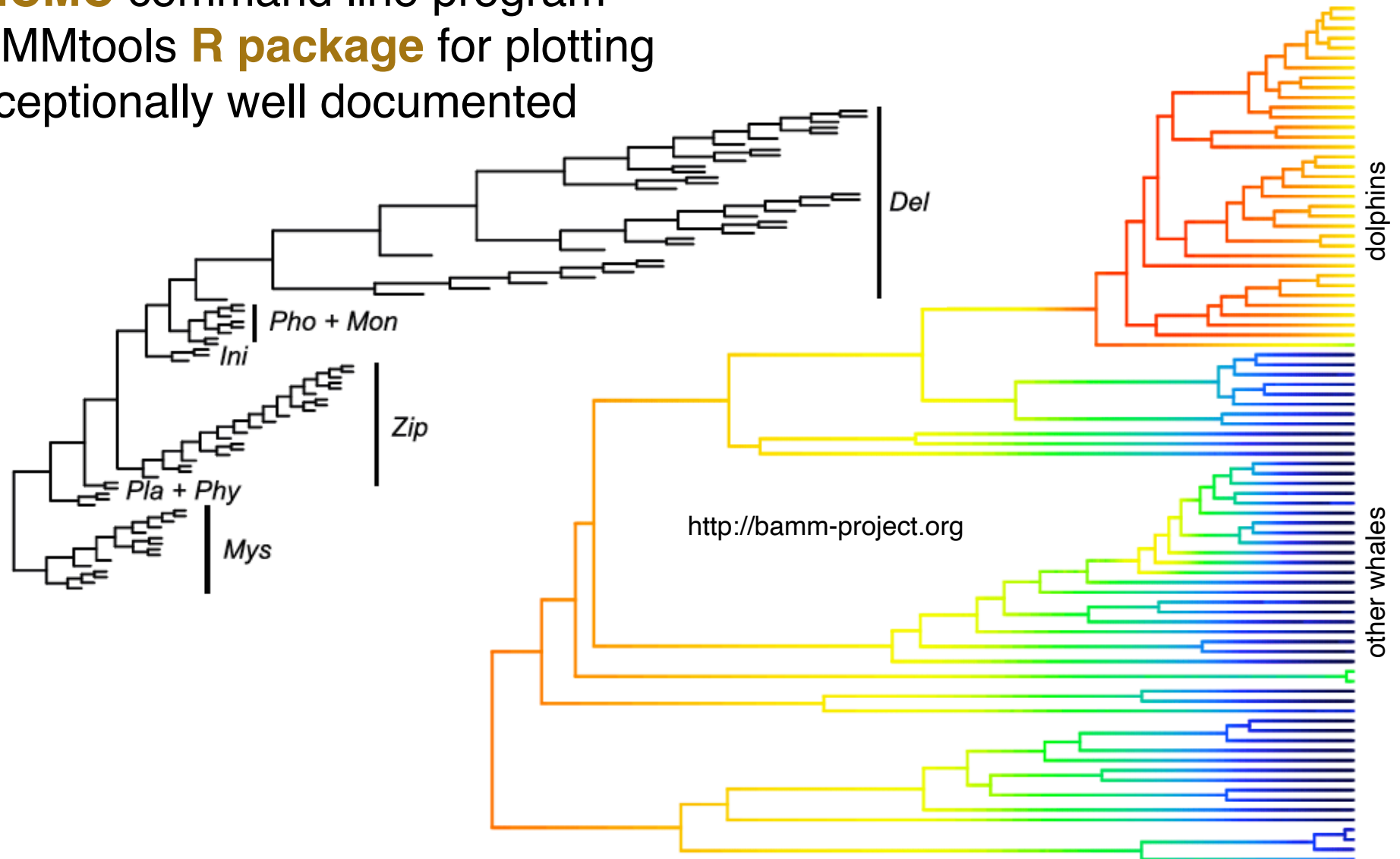Rabosky (2014)
Rabosky et al. (2014)
Shi and Rabosky (2015)

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
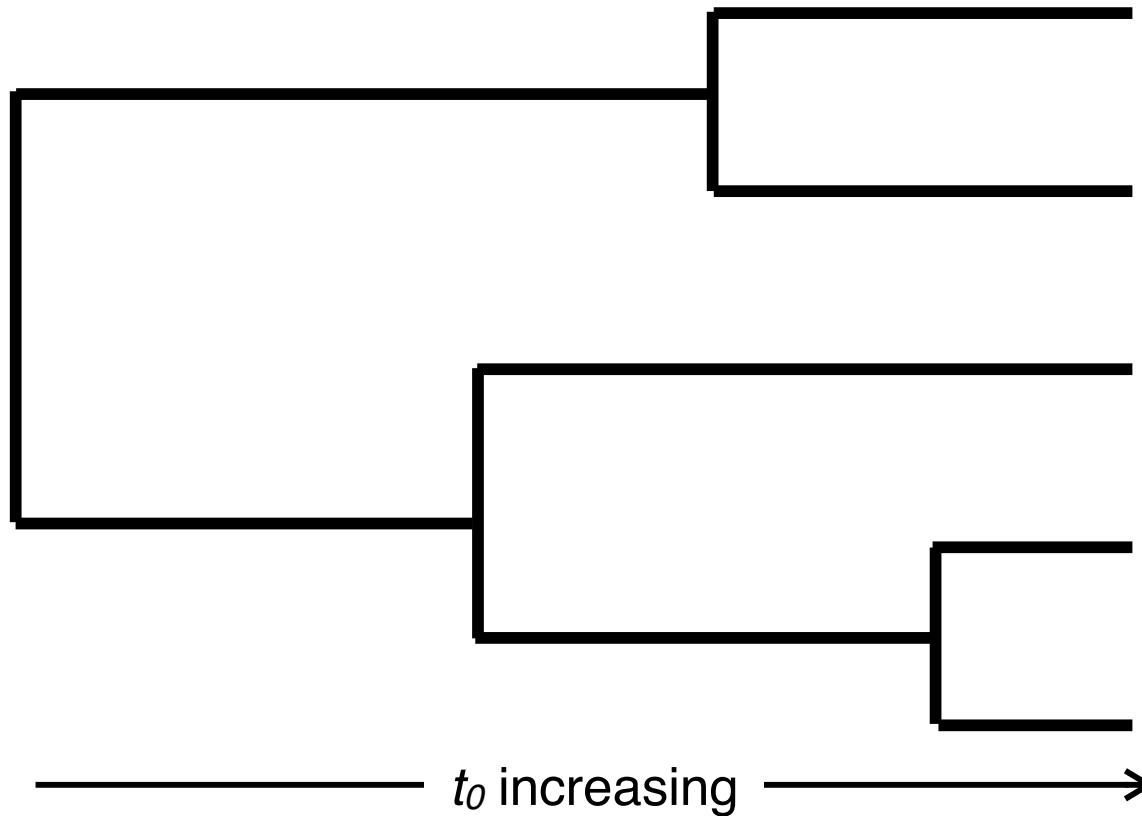Exceptionally well documented

http://bamm-project.org

Del

Pho + Mon

Ini

Zip

Pla + Phy

Mys

dolphins

other whales

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

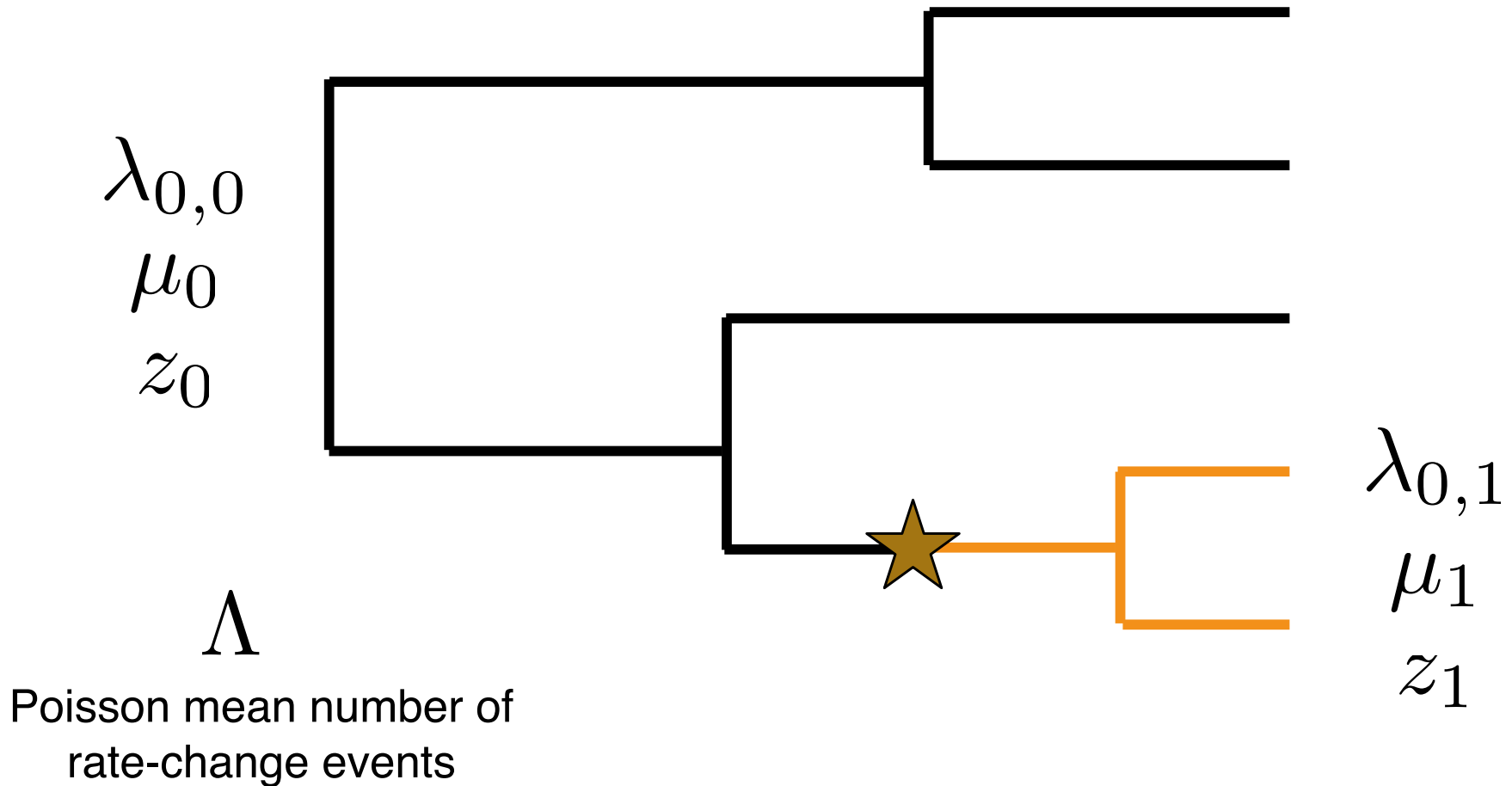$\longrightarrow$ t_0 increasing $\longrightarrow$

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

z_0

z_0 positive: speciation rate increases over time
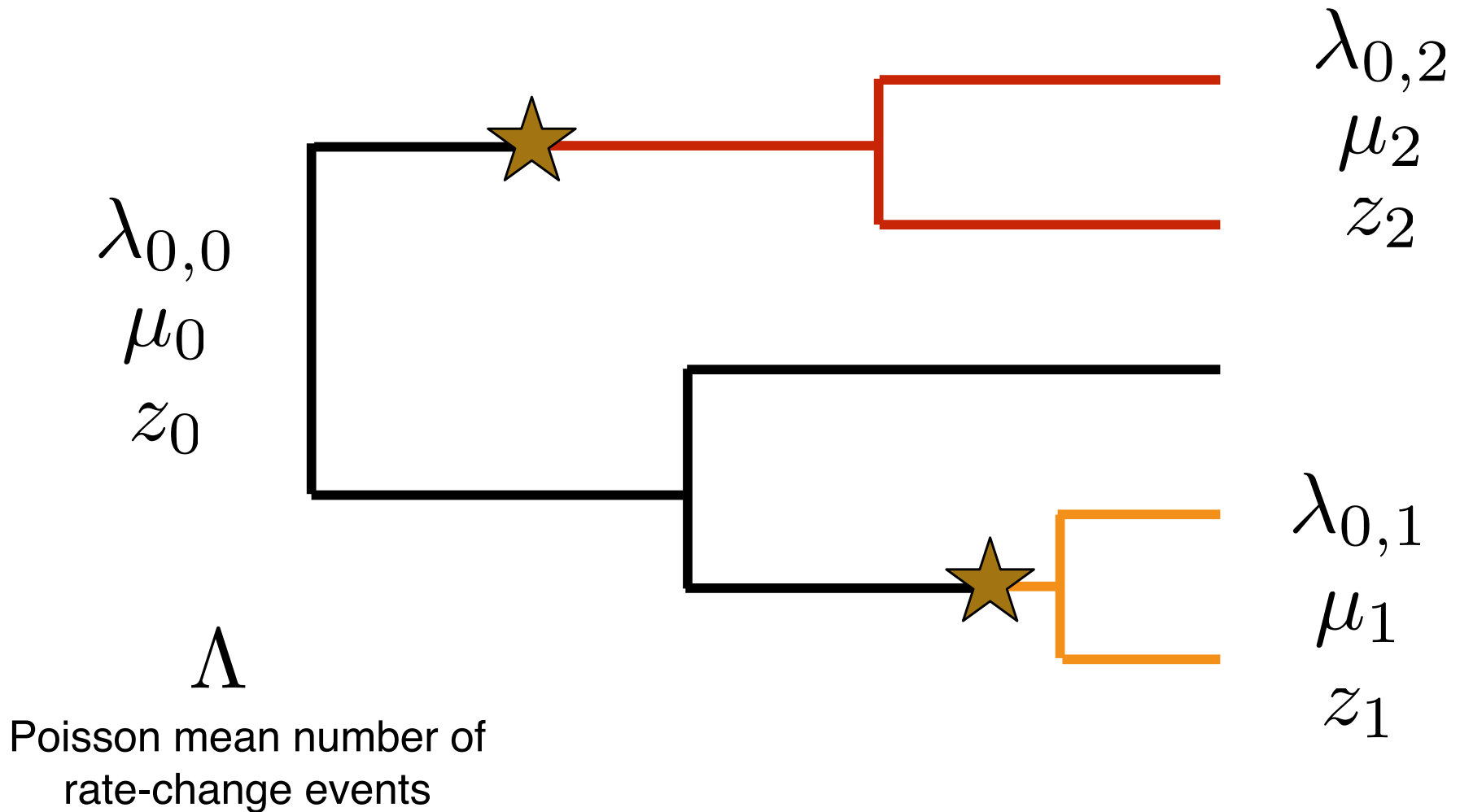z_0 negative: speciation rate decreases over time

BAMM model

1 rate change

$\lambda_{0,0}$
μ_0
z_0

$\lambda_{0,1}$
μ_1
z_1

Λ

Poisson mean number of
rate-change events

BAMM model

2 rate changes

$$\lambda_{0,2}$$
$$\mu_2$$
$$z_2$$

$$\lambda_{0,0}$$
$$\mu_0$$
$$z_0$$

$$\Lambda$$
Poisson mean number of
rate-change events

$$\lambda_{0,1}$$
$$\mu_1$$
$$z_1$$

BAMM model

back to 1 rate change

$$\lambda_{0,0}$$
$$\mu_0$$
$$z_0$$

$$\lambda_{0,1}$$
$$\mu_1$$
$$z_1$$

$$\Lambda$$

Poisson mean number of
rate-change events

Bayesian Analysis of Macroevolutionary Mixtures (BAMM)

rjMCMC

http://bamm-project.org

Fig. 9a in Rabosky (2014)