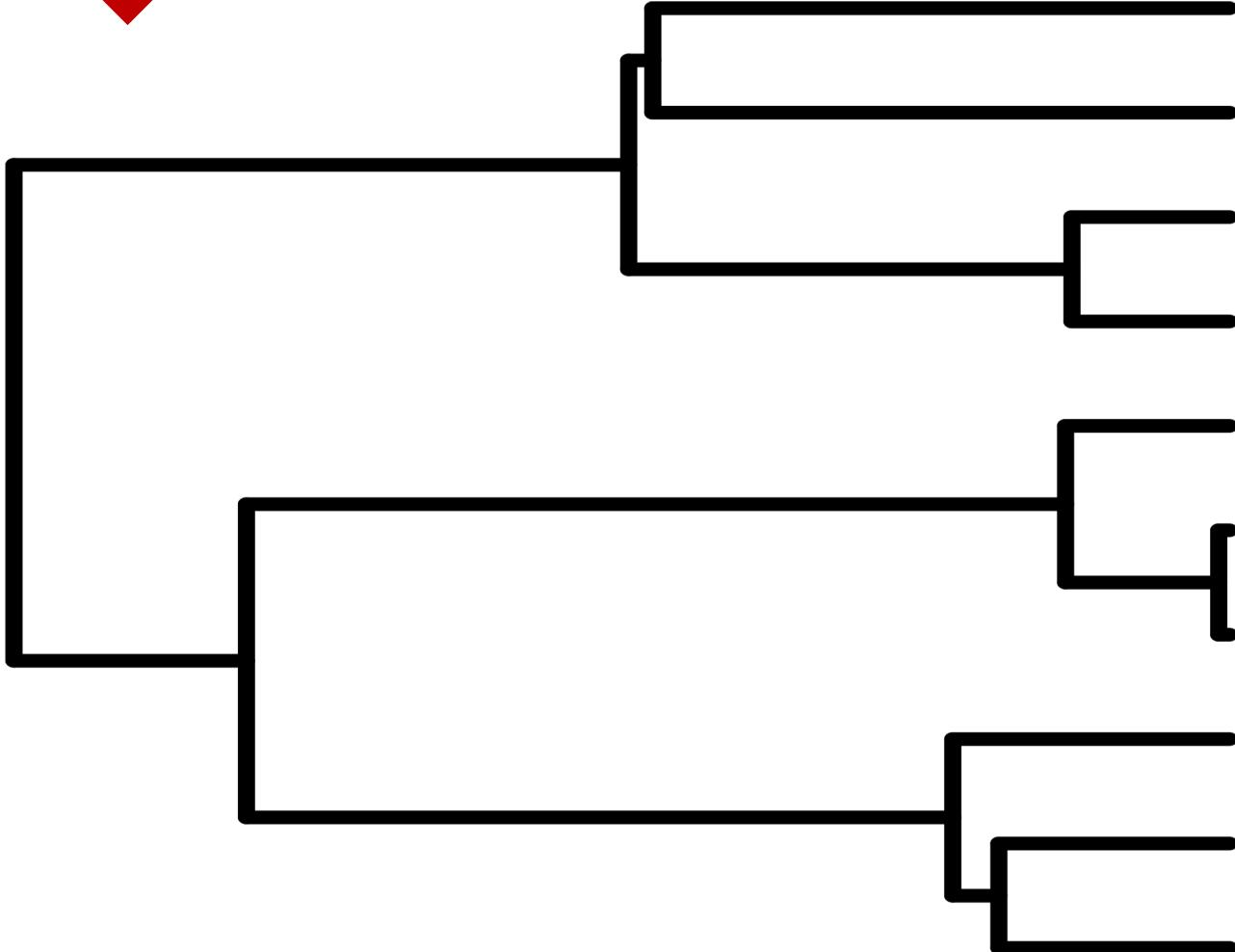


$$\lambda = x$$



Yule

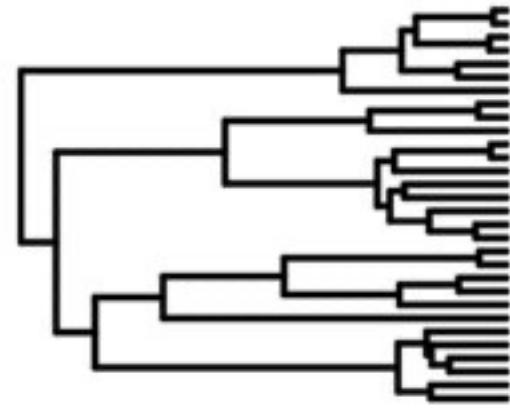
$$\lambda = x$$

BD

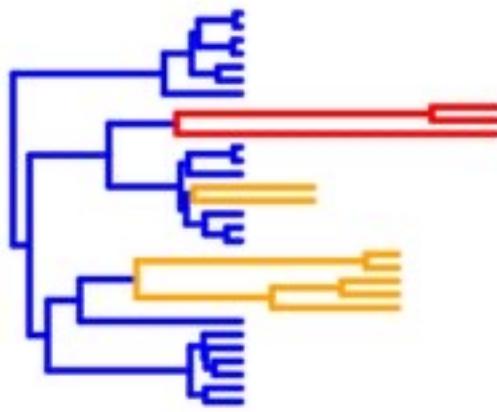
$$\lambda = x$$

$$\mu = y$$

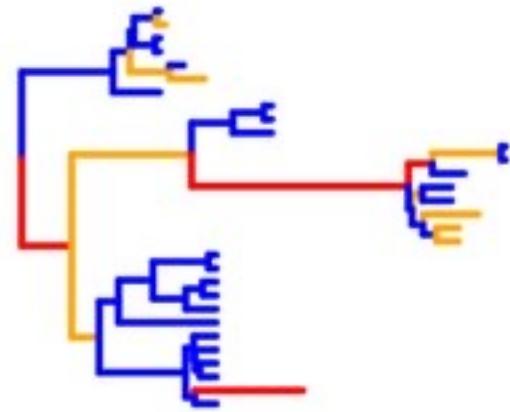
**(a) Strict clock**



**(b) Local clocks**

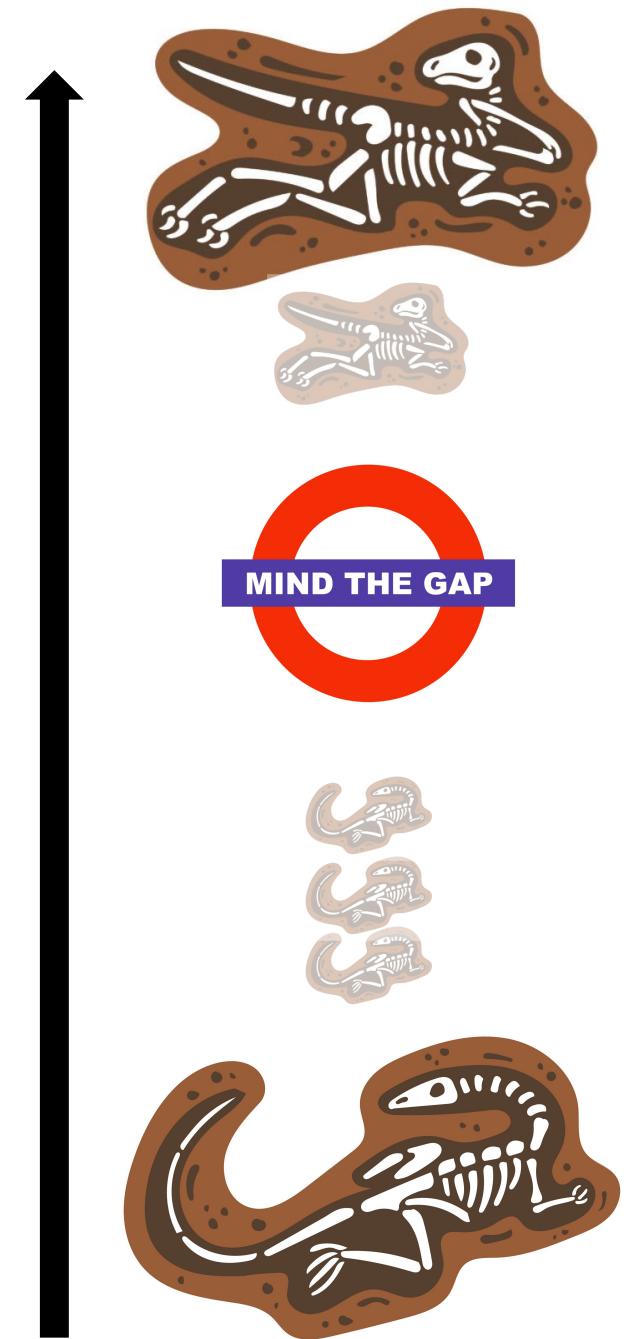


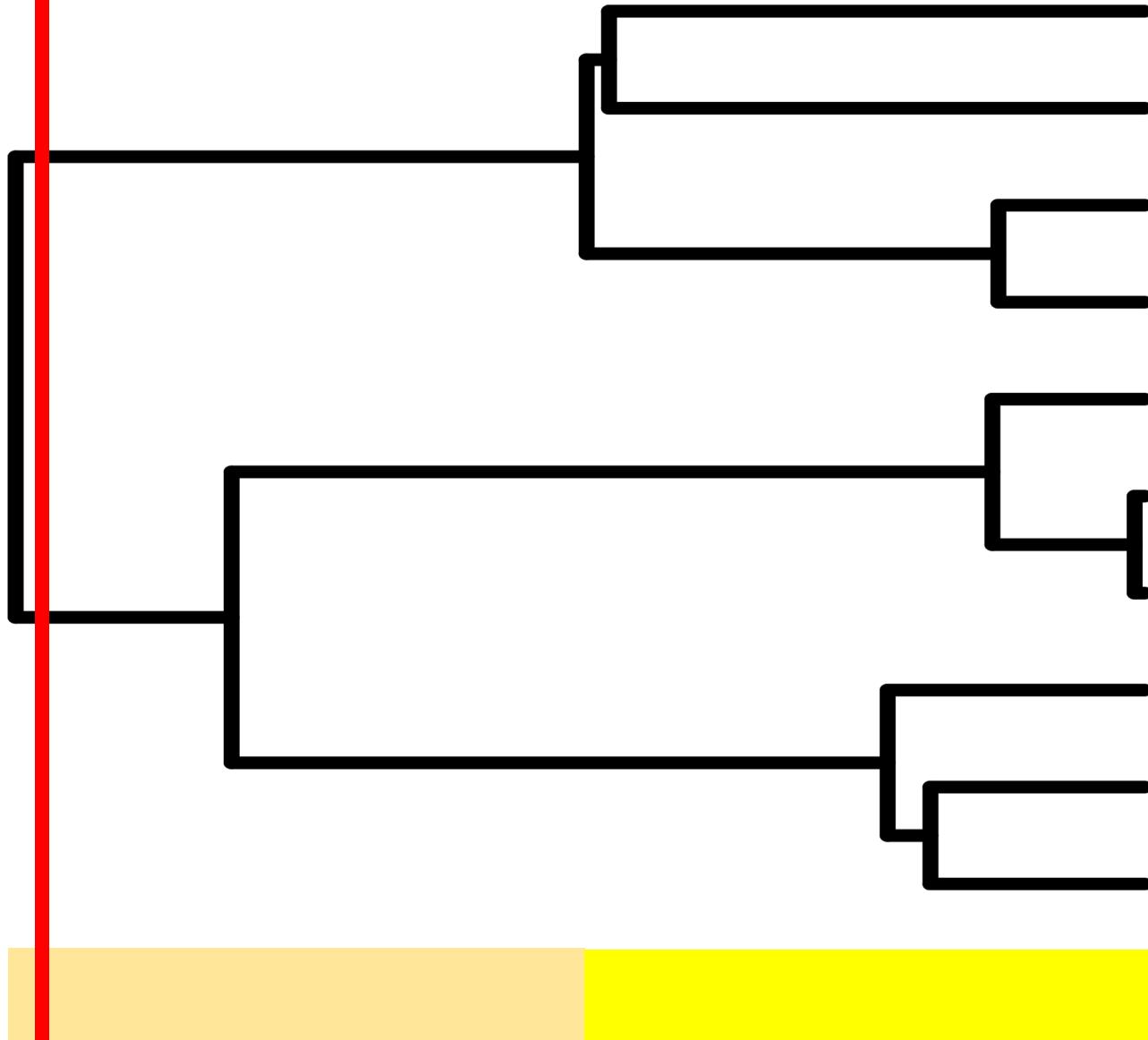
**(c) Discrete multi-rate clock**



Probability density

Evolutionary rate



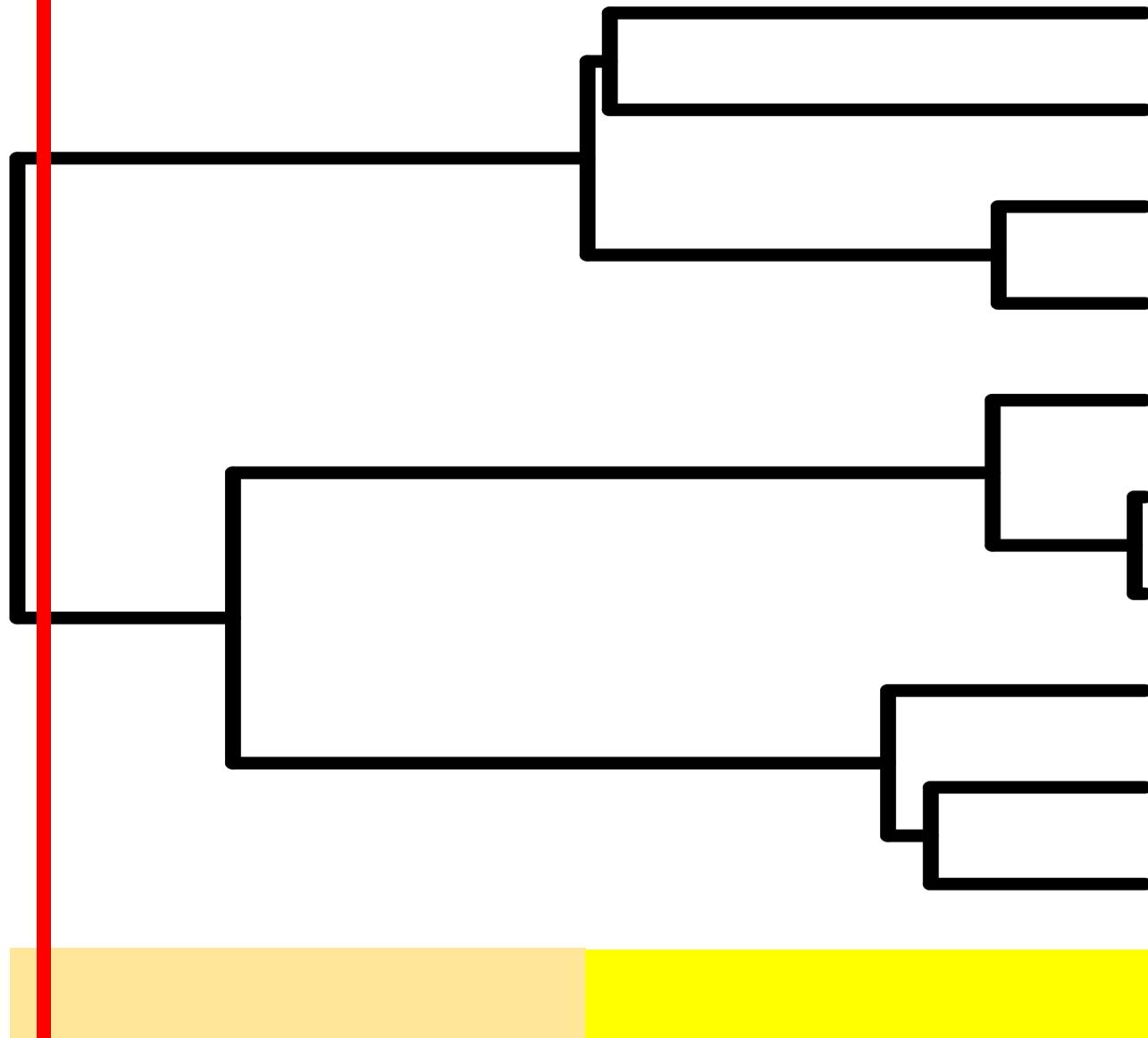


Se han propuesto varios métodos para estimar cambios en las tasas de diversificación.

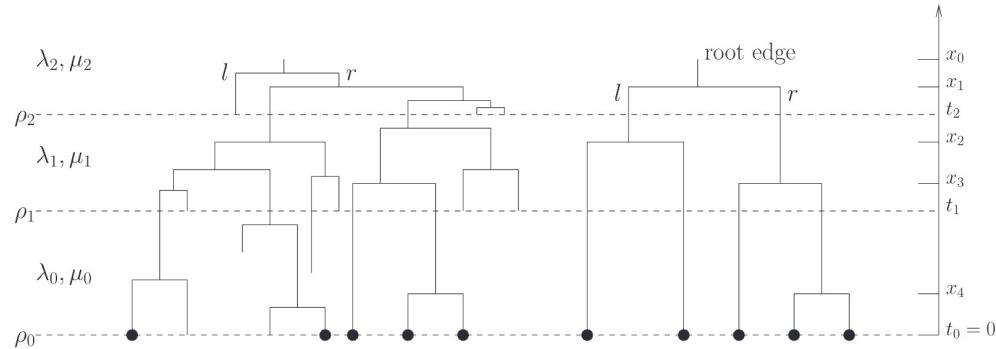
- Birth-Death-Shift model.  
Stadler, 2011; PNAS
- Episodic Birth-Death model.  
Höhna 2015; J. Theor Biol.  
Magee and Höhna 2021;  
bioRxiv.:426715
- BAMM; Bayesian Analysis of Macroevolutionary Mixtures  
Rabosky et al. 2013; Nat Comm

- Birth-Death-Shift model.

Stadler, 2011; PNAS



## (TreePar R package)



**Fig. 5.** Tree notation. (Left) An example of a tree that evolved under the birth-death shift process. The sampled species are denoted with a solid circle.  
(Right) The corresponding sampled tree with root edge. The labels  $l$  and  $r$  are suppressed on most branches for clarity.

**bd.shifts.optim(x, c(sampling, shifts), grid, start, end,**

**yule = FALSE, ME = FALSE, survival = 1)**

**bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)**

## (TreePar R package)

Longitud de las ramas



```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

## (TreePar R package)

Porcentaje de efectividad del muestreo,  
número de veces que ha cambiado la tasa de diversificación



```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

```
bd.shifts.optim(x, c(0.84,1), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

## (TreePar R package)

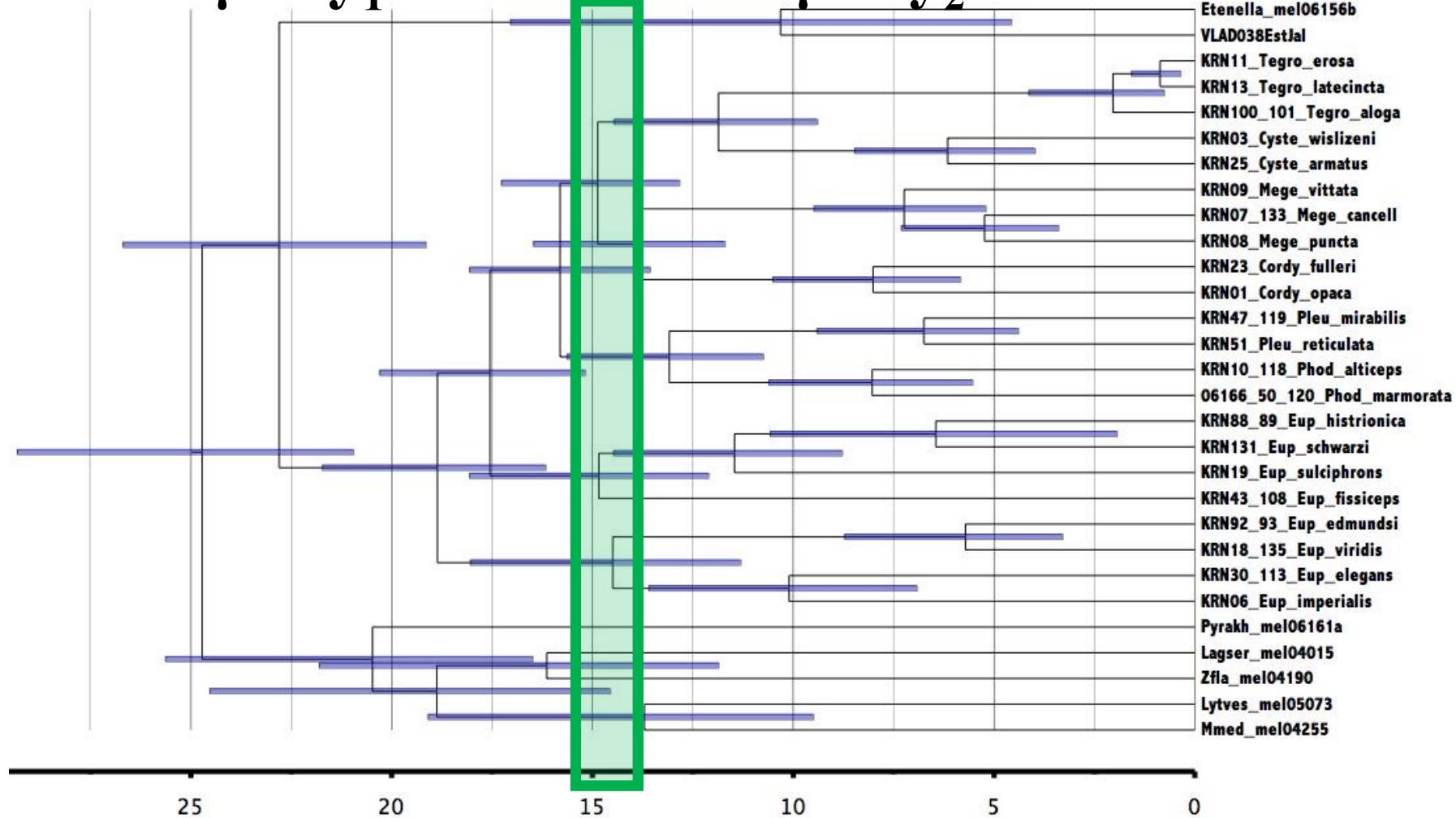
“ventana” de actualización



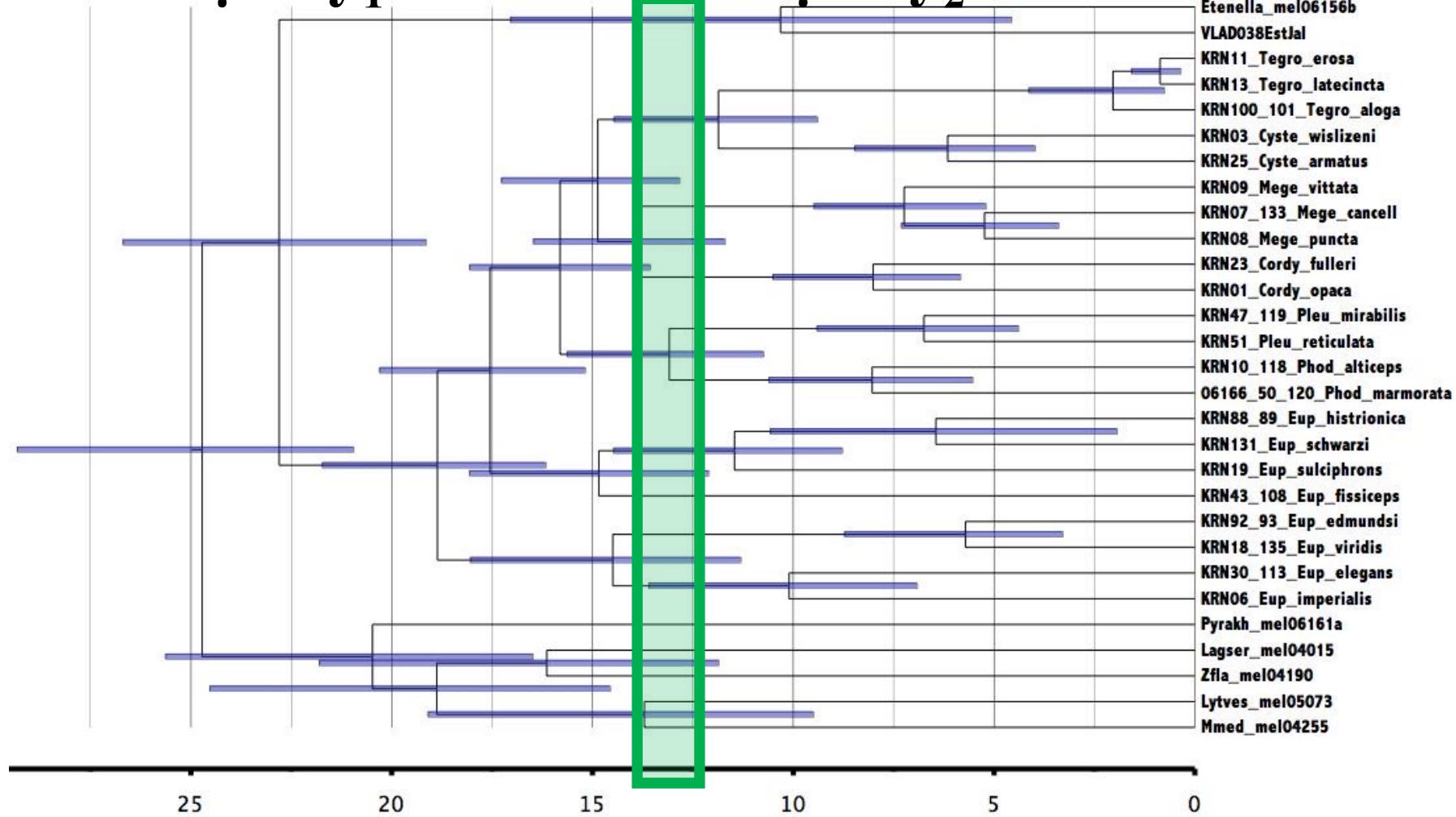
```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

```
bd.shifts.optim(x, c(0.84, 1), 0.2, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

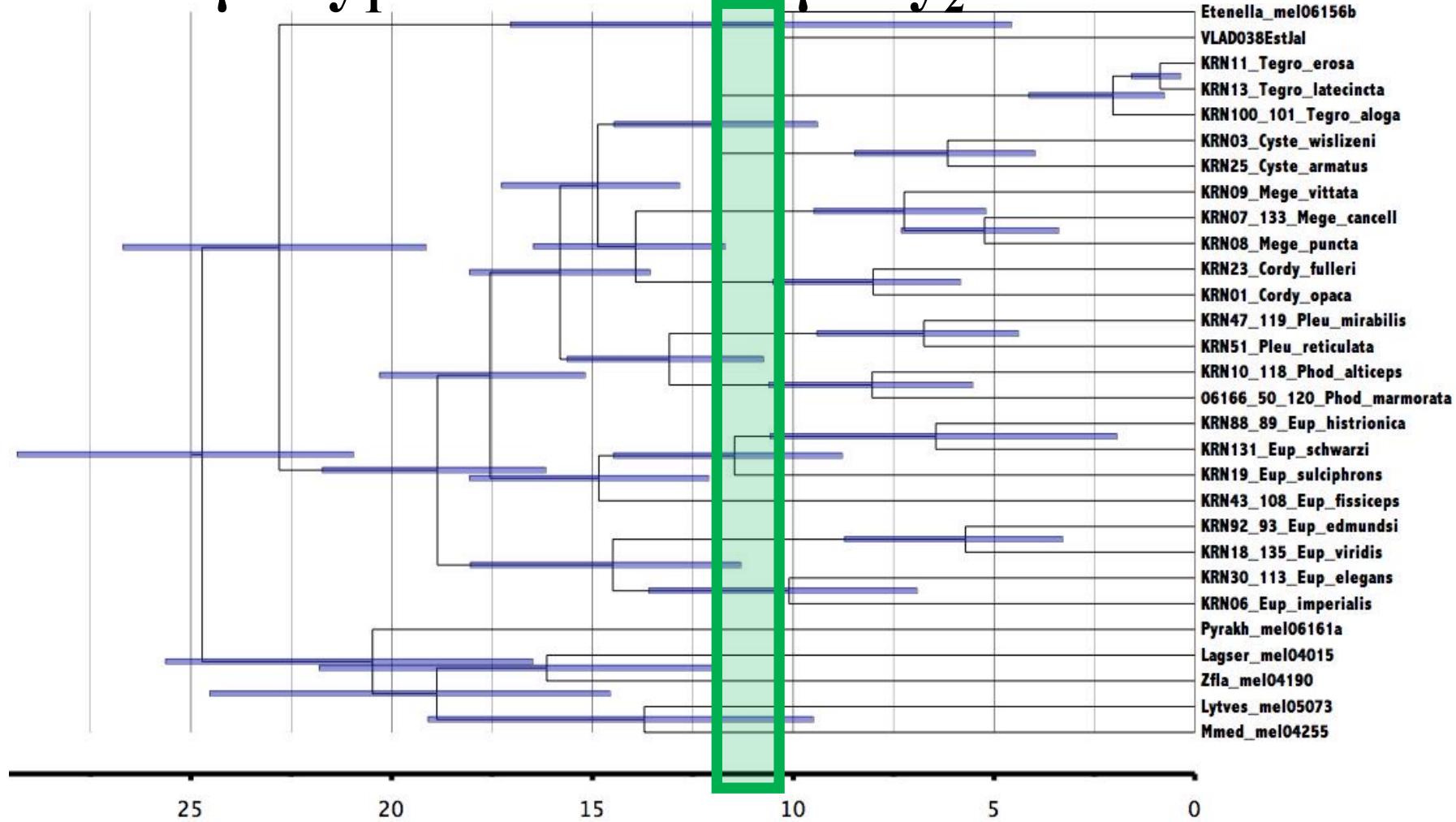
$$\begin{array}{c} \lambda = x_1 \\ \mu = y_1 \end{array} > / < / = \begin{array}{c} \lambda = x_2 \\ \mu = y_2 \end{array}$$



$$\begin{array}{c} \lambda = x_1 \\ \mu = y_1 \end{array} > / < / = \begin{array}{c} \lambda = x_2 \\ \mu = y_2 \end{array}$$



$$\begin{array}{c} \lambda = x_1 \\ \mu = y_1 \end{array} > / < / = \begin{array}{c} \lambda = x_2 \\ \mu = y_2 \end{array}$$



## (TreePar R package)

$t_0$   
↓  
**bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)**

**bd.shifts.optim(x, c(0.84, 1), 0.2, 0.5522438, end,  
yule = FALSE, ME = FALSE, survival = 1)**

## (TreePar R package)

Último evento de especiación



**bd.shifts.optim(x, c(sampling, shifts), grid, start, end,**

**yule = FALSE, ME = FALSE, survival = 1)**

bd.shifts.optim(x, c(0.84, 1), 0.2, 0.5522438, **19.9102699**,  
yule = FALSE, ME = FALSE, survival = 1)

## (TreePar R package)

```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```



$\mu = 0$

$\mu \neq 0$

```
bd.shifts.optim(x, c(0.84, 1), 0.2, 0.5522438, 19.9102699,  
yule = FALSE, ME = FALSE, survival = 1)
```

## (TreePar R package)

```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```



**Considera Eventos de  
Extinción Masiva (MEE)  
en la filogenia**

```
bd.shifts.optim(x, c(0.84, 1), 0.2, 0.5522438, 19.9102699,  
yule = FALSE, ME = FALSE, survival = 1)
```

## (TreePar R package)

```
bd.shifts.optim(x, c(sampling, shifts), grid, start, end,  
yule = FALSE, ME = FALSE, survival = 1)
```

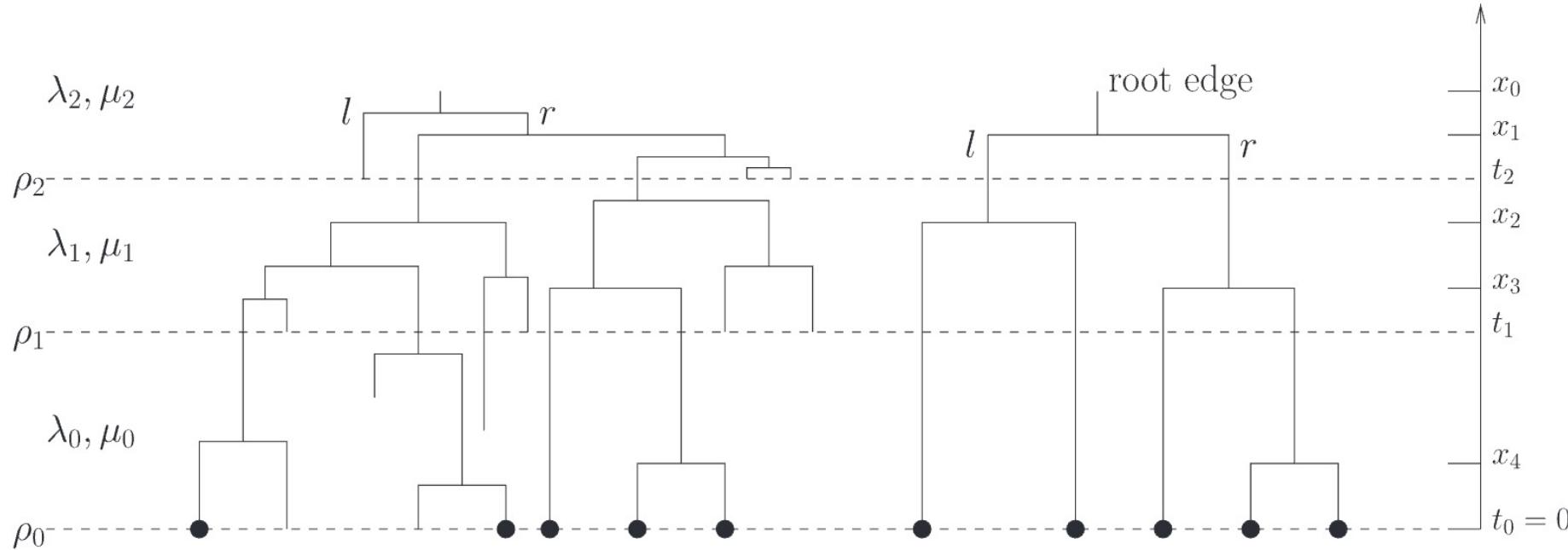


Usa N para condicionar el valor de  
likelihood

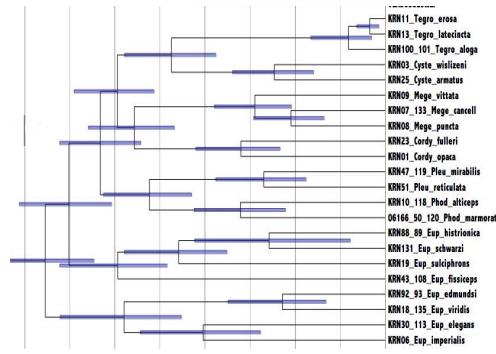
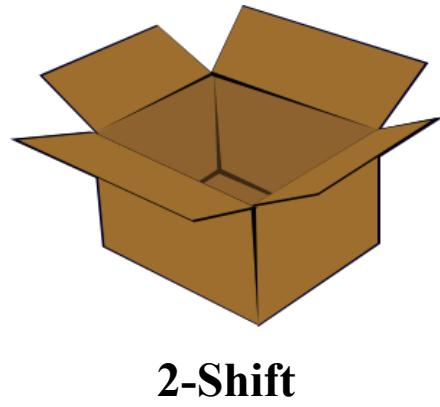
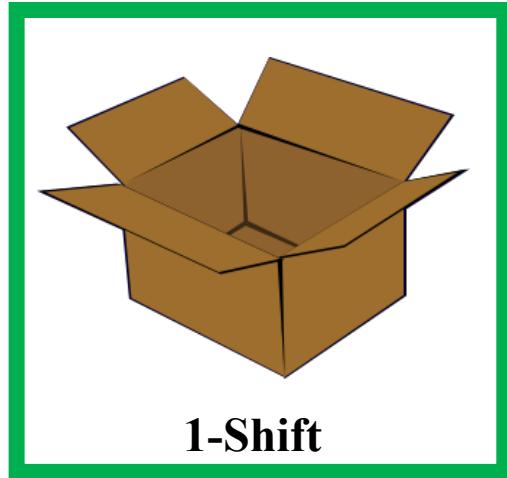
```
bd.shifts.optim(x, c(0.84, 1), 0.2, 0.5522438, 19.9102699,  
yule = FALSE, ME = FALSE, survival = 1)
```

- Birth-Death-Shift model.

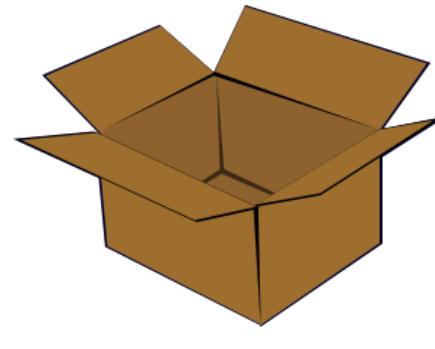
Stadler, 2011; PNAS



**Fig. 5.** Tree notation. (Left) An example of a tree that evolved under the birth-death shift process. The sampled species are denoted with a solid circle. (Right) The corresponding sampled tree with root edge. The labels *l* and *r* are suppressed on most branches for clarity.

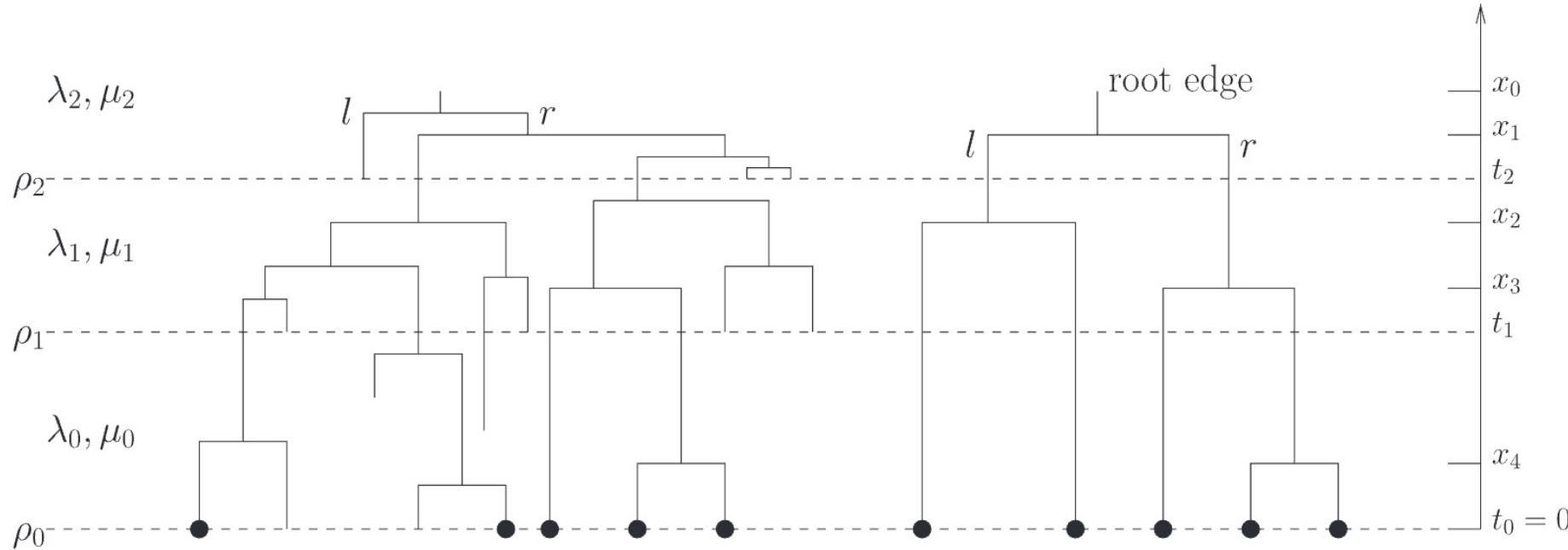


## Likelihood ratio test



- Birth-Death-Shift model.

Stadler, 2011; PNAS



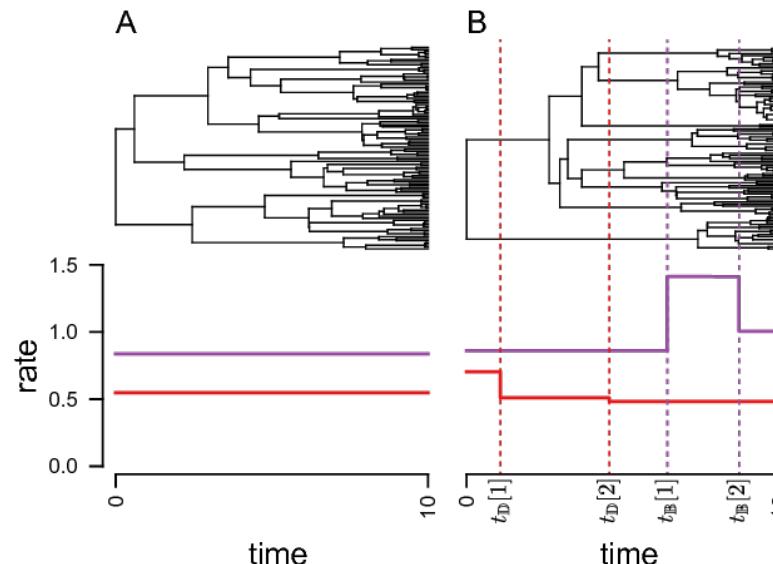
**Fig. 5.** Tree notation. (Left) An example of a tree that evolved under the birth-death shift process. The sampled species are denoted with a solid circle. (Right) The corresponding sampled tree with root edge. The labels *l* and *r* are suppressed on most branches for clarity.

# Modelos episódicos de nacimiento-muerte

## Episodic Birth-Death models

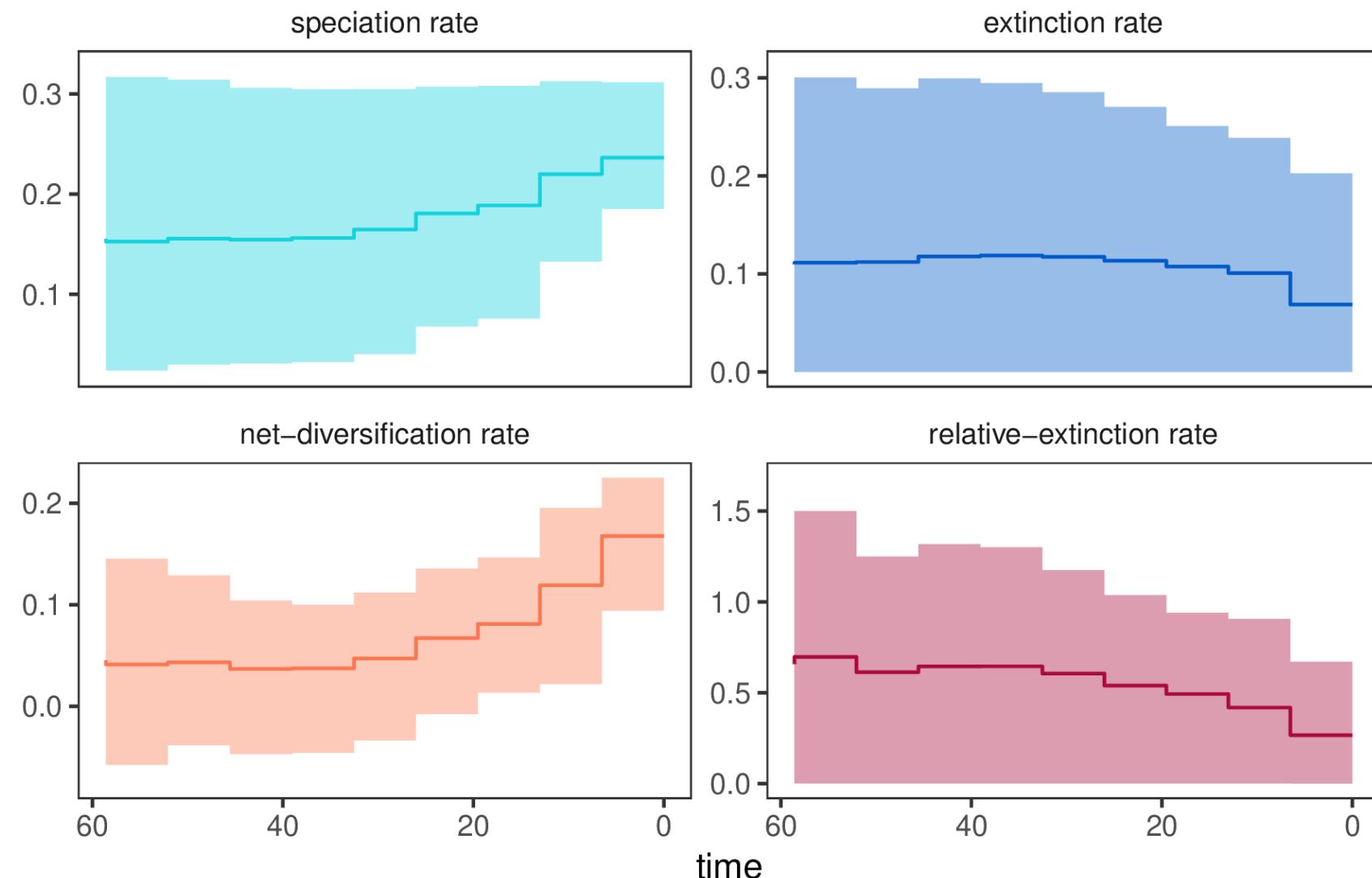
Höhna 2015; J. Theor Biol. Magee and Höhna 2021;  
bioRxiv.:426715

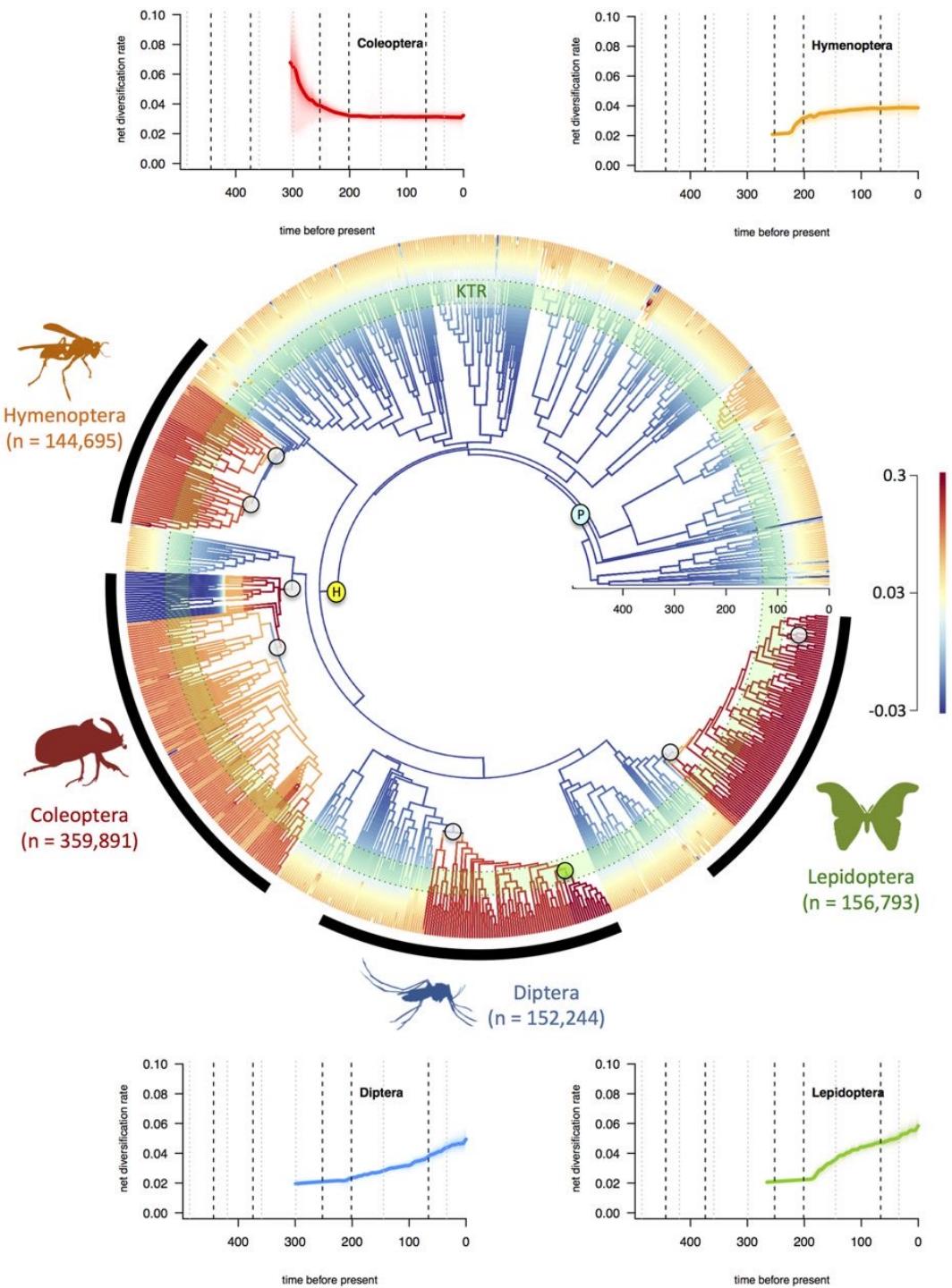
— speciation rate  
- - - speciation-rate shift  
— extinction rate  
- - - extinction-rate shift



Distribución  
Horseshoe Markov

- Auto correlación de las tasas





Condamine et al., 2016

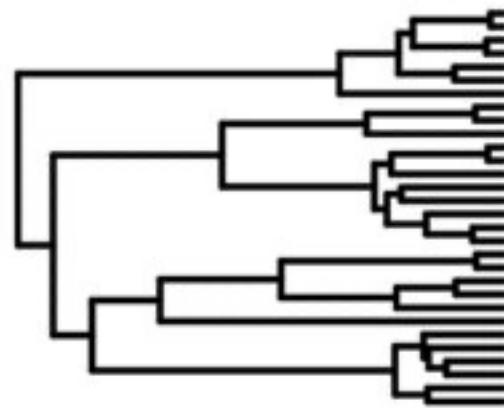
¿La especiación en coleópteros es mucho más alta que en el resto de los insectos ?

$$\lambda_{\text{(Insectos)}} < \lambda_{\text{(Coleoptera)}}$$

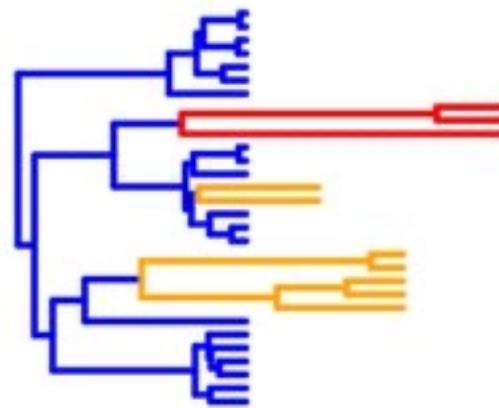
¿El resto de los insectos se extingue más que los coleópteros?

$$\mu_{\text{(Insectos)}} > \mu_{\text{(Coleoptera)}}$$

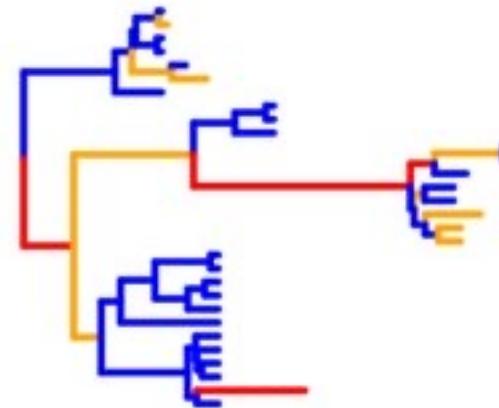
**(a) Strict clock**



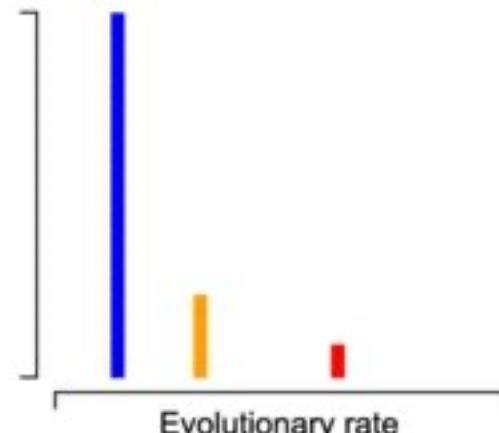
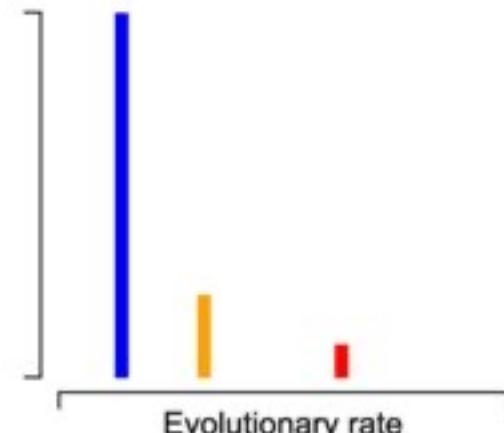
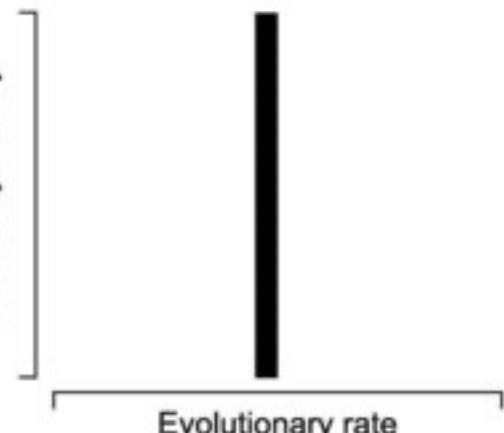
**(b) Local clocks**



**(c) Discrete multi-rate clock**



Probability density



# Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates

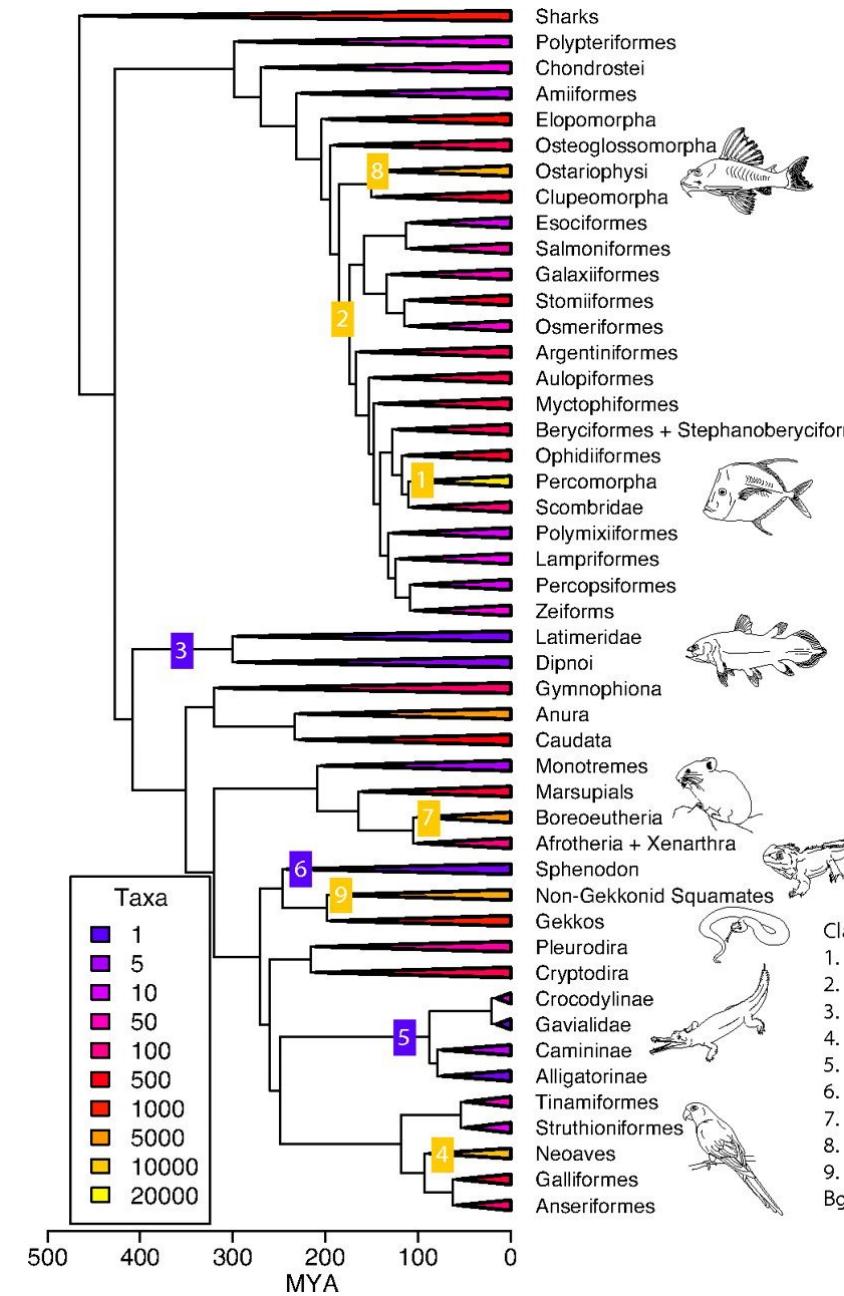
Michael E. Alfaro<sup>a,1</sup>, Francesco Santini<sup>a</sup>, Chad Brock<sup>b</sup>, Hugo Alamillo<sup>b</sup>, Alex Dornburg<sup>c</sup>, Daniel L. Rabosky<sup>d,e</sup>, Giorgio Carnevale<sup>f</sup>, and Luke J. Harmon<sup>g</sup>

<sup>a</sup>Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095; <sup>b</sup>School of Biological Sciences, Washington State University, Pullman, WA 99164; <sup>c</sup>Department of Ecology and Evolutionary Biology and <sup>d</sup>Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850; <sup>f</sup>Dipartimento di Scienze della Terra and Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, 56100 Italy; <sup>g</sup>Department of Biology, University of Idaho, Moscow, ID 83843; and <sup>e</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520

Edited by David M. Hillis, University of Texas, Austin, TX, and approved June 12, 2009 (received for review November 2, 2008)

## MEDUSA r Package Modeling Evolutionary Diversification Using Stepwise Akaike Information Criterion

Asume filogenia completa



ARTICLE

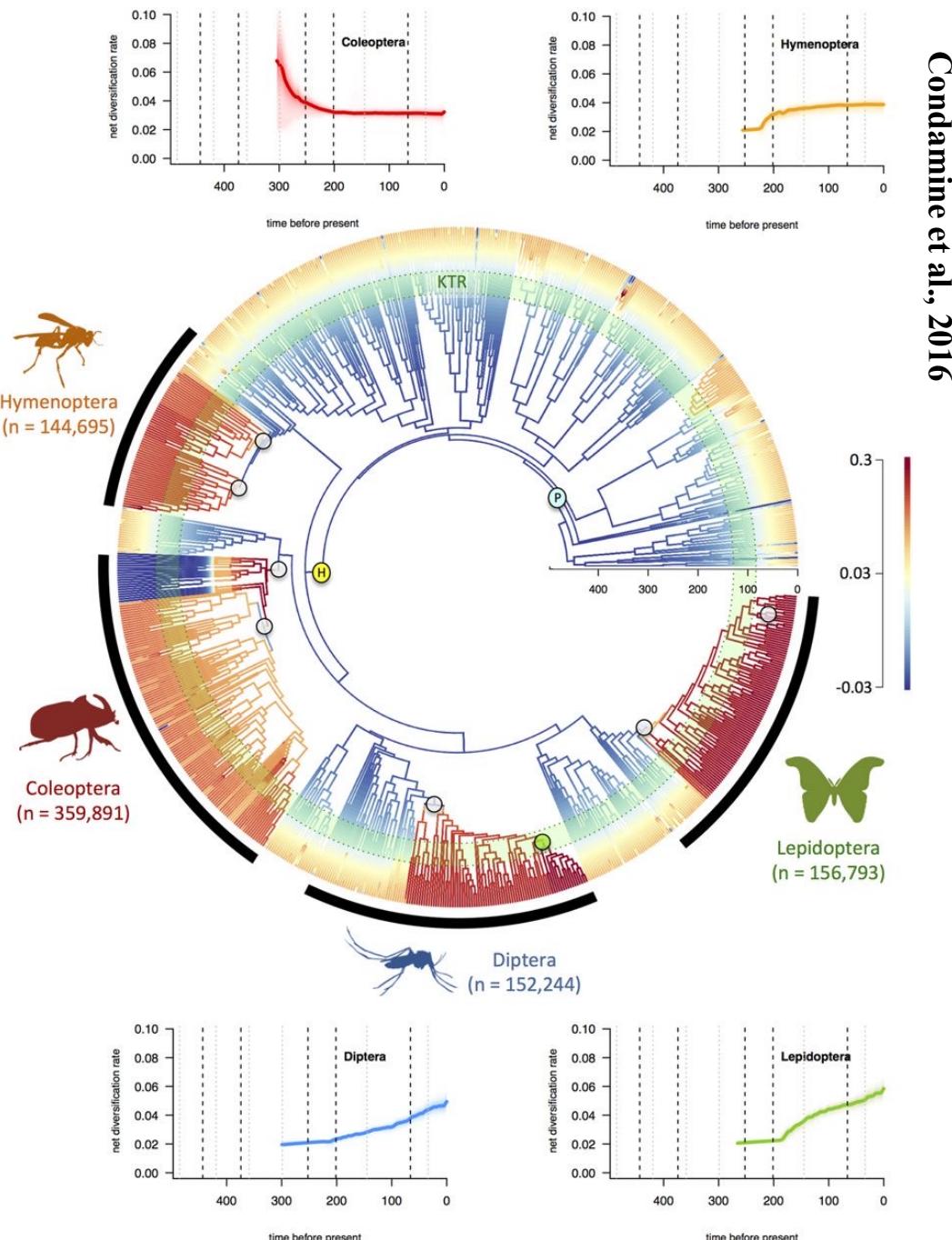
Received 13 Sep 2012 | Accepted 29 Apr 2013 | Published 6 Jun 2013

DOI: 10.1038/ncomms2958

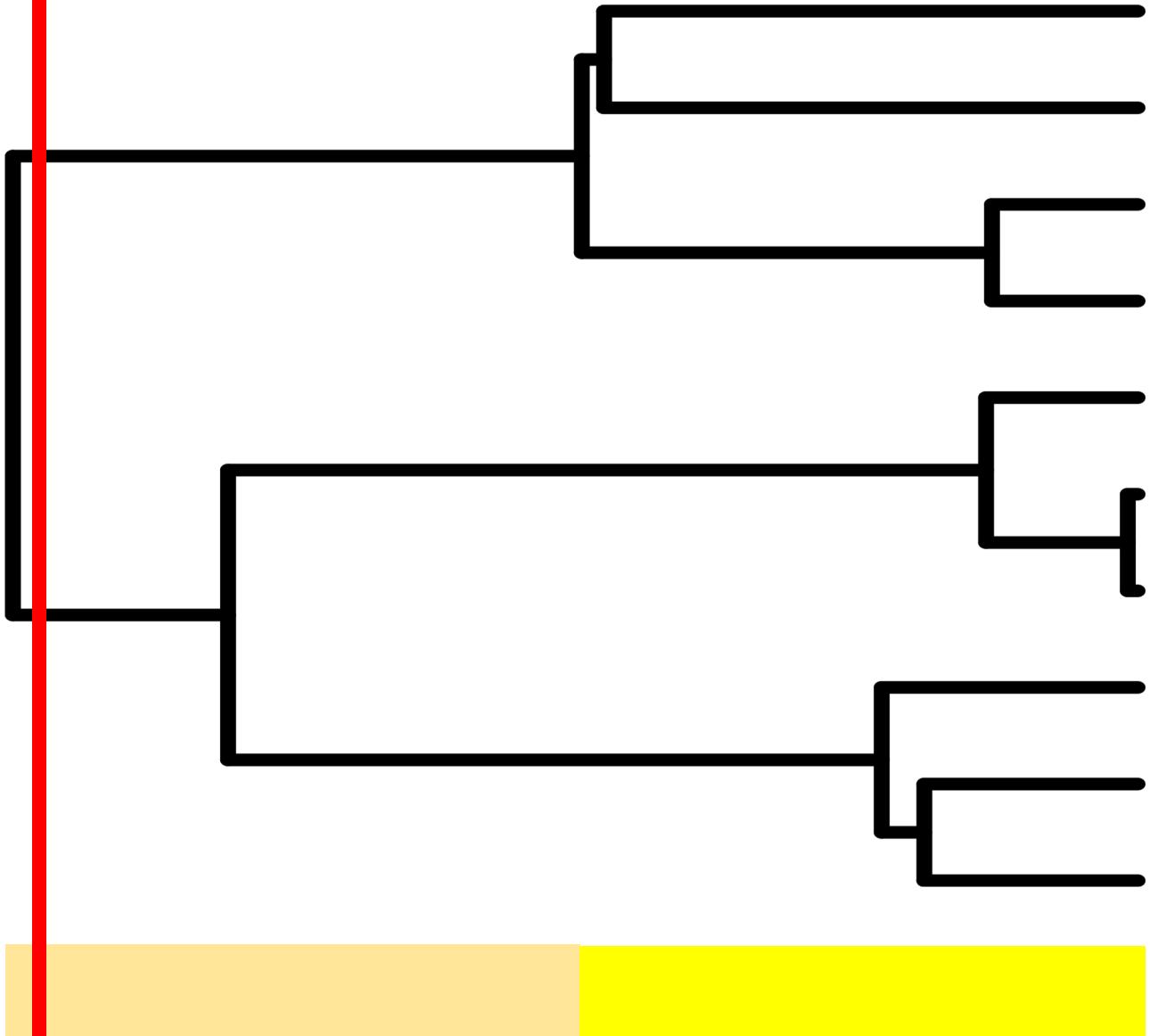
# Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation

Daniel L. Rabosky<sup>1,2</sup>, Francesco Santini<sup>3</sup>, Jonathan Eastman<sup>4</sup>, Stephen A. Smith<sup>2</sup>, Brian Sidlauskas<sup>5</sup>, Jonathan Chang<sup>6</sup> & Michael E. Alfaro<sup>6</sup>

## BAMM Bayesian analysis of macroevolutionary mixtures

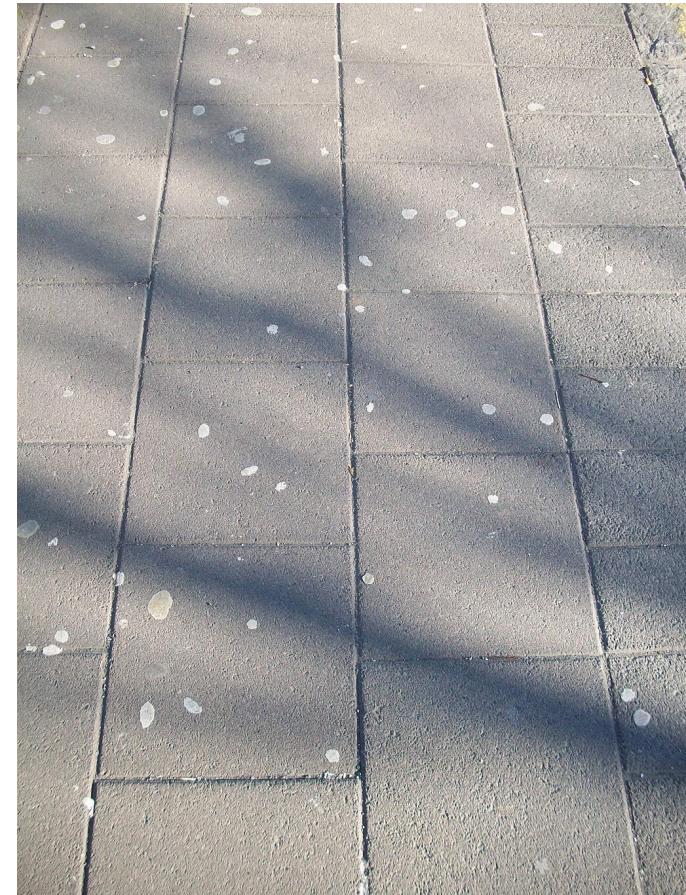


- BAMM.



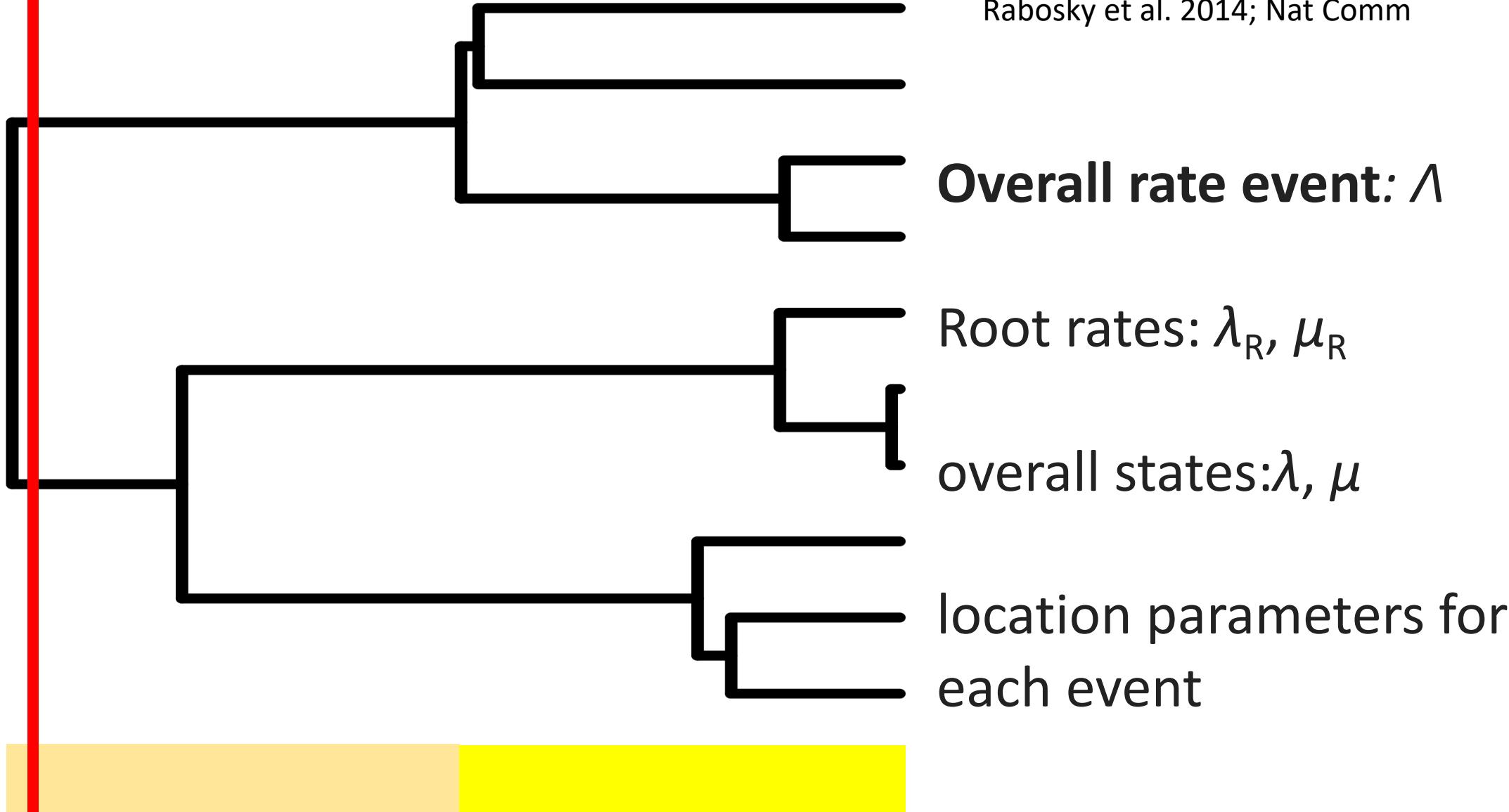
Rabosky et al. 2014; Nat Comm

Poisson process



- BAMM.

Rabosky et al. 2014; Nat Comm



Galería de BAMM en  
<http://bamm-project.org/bammgraph.html>



# Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures

Brian R. Moore<sup>a,1</sup>, Sebastian Höhna<sup>b,c</sup>, Michael R. May<sup>a</sup>, Bruce Rannala<sup>a</sup>, and John P. Huelsenbeck<sup>b</sup>

<sup>a</sup>Department of Evolution and Ecology, University of California, Davis, CA 95616; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; and <sup>c</sup>Department of Statistics, University of California, Berkeley, CA 94720

Edited by Michael J. Donoghue, Yale University, New Haven, CT, and approved June 27, 2016 (received for review September 21, 2015)



# Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures

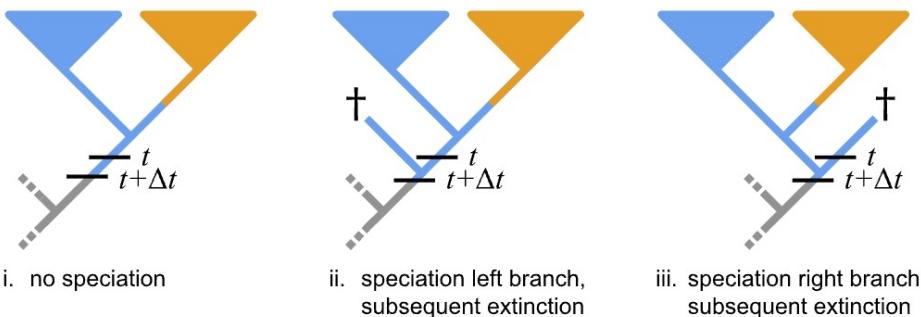
Brian R. Moore<sup>a,1</sup>, Sebastian Höhna<sup>b,c</sup>, Michael R. May<sup>a</sup>, Bruce Rannala<sup>a</sup>, and John P. Huelsenbeck<sup>b</sup>

<sup>a</sup>Department of Evolution and Ecology, University of California, Davis, CA 95616; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; and <sup>c</sup>Department of Statistics, University of California, Berkeley, CA 94720

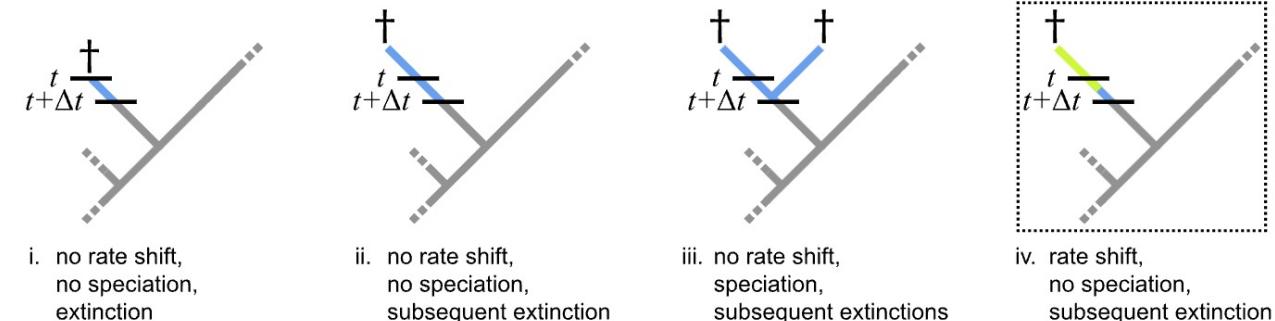
Edited by Michael J. Donoghue, Yale University, New Haven, CT, and approved June 27, 2016 (received for review September 21, 2015)



## A Scenarios for observed lineages



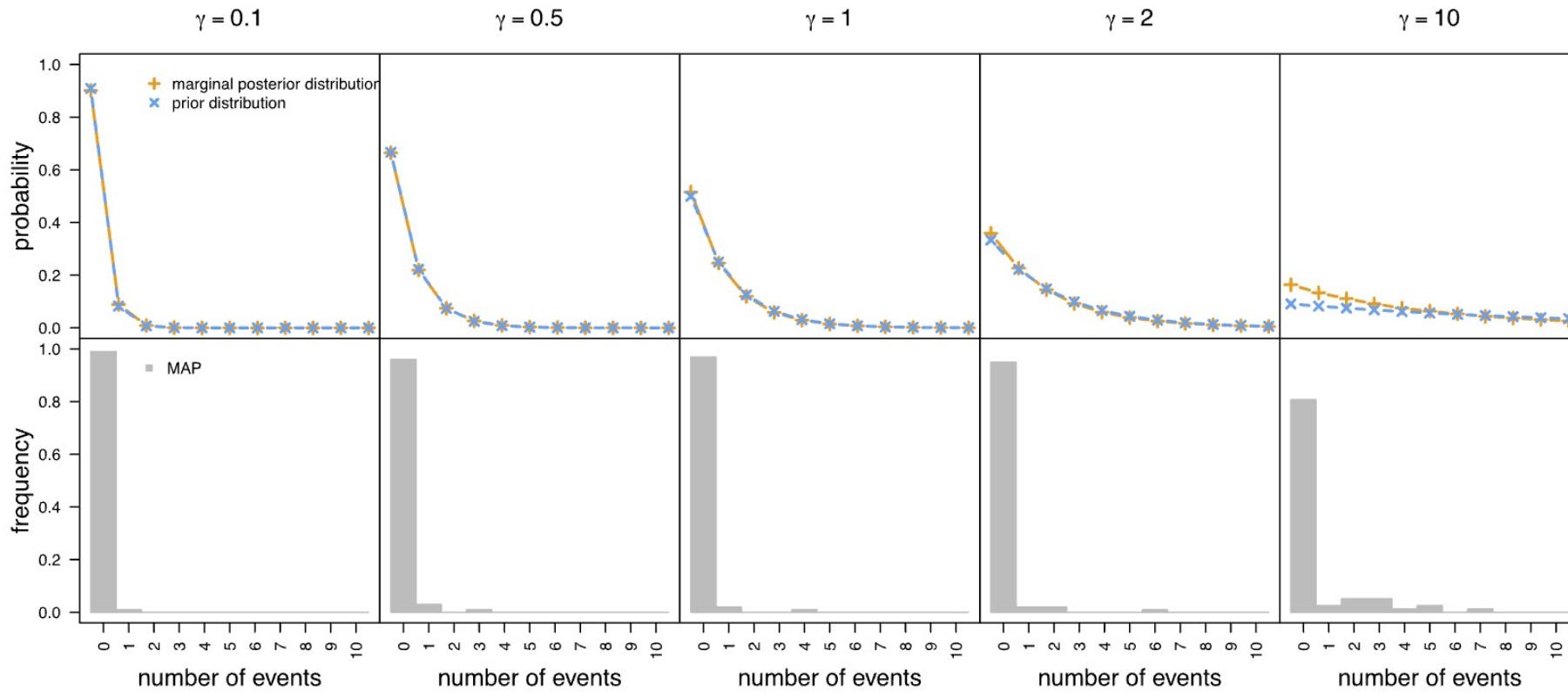
## B Scenarios for unobserved lineages



**Fig. 1.** Approximation of the likelihood under the BAMM model ignores diversification-rate shifts on extinct lineages. In lieu of an analytical solution for the likelihood function, the probability of observing the data under the BAMM model is approximated by an algorithm that traverses the tree from the tips to the root in small time steps,  $\Delta t$ . At each step, two terms are computed: (A) the probability of realizing the observed lineage,  $N$ , over time  $t$ , given that it is in process  $i$ —denoted  $D_{N,i}(t)$ —which simply sums over all of the possible scenarios that could occur in the instant  $\Delta t$ , and; (B) the probability of unobserved (extinct or unsampled) lineages,  $E_i(t)$ , which is computed similarly. The last scenario—iv, where diversification-rate shifts occur on an extinct lineage—is not included in the likelihood computation, causing BAMM to incorrectly estimate the extinction probabilities (cf. Fig. 2).

See control file en:

<http://bamm-project.org/quickstart.html#control-file>



**Fig. 4.** The posterior number of diversification-rate shifts inferred by BAMM is extremely sensitive to the assumed prior. We simulated 100 constant-rate trees and analyzed each using BAMM under a variety of priors for the expected number of diversification-rate shifts,  $\gamma$  (columns). (*Upper*) For each value of the  $\gamma$  prior, we combined the MCMC samples from analyses of the 100 trees and plotted the marginal posterior probability density of the number of rate shifts estimated by BAMM (dashed orange lines) and the corresponding prior density (dashed blue lines). For all values of the  $\gamma$  prior, the estimated posterior is virtually indistinguishable from the assumed prior, and the mode of the prior densities is zero (i.e., zero diversification-rate shifts). (*Lower*) We then summarized the results of our simulation following Rabosky (5). For each value of the  $\gamma$  prior, we recorded the mode of the posterior density (MAP) for each of the 100 trees and then summarized these 100 MAP values as a histogram. For all values of the  $\gamma$  prior, the most frequent MAP has a value of zero (simply because the mode of the geometric prior is always zero, and the estimated posterior density closely mirrors the assumed prior). Rabosky (5) misinterpreted the consistency of these MAP histograms for all values of the  $\gamma$  prior as evidence that BAMM is insensitive to the assumed prior. This erroneous conclusion is based on an erroneous summary of the results: simple visual inspection confirms that the (assumed) prior and (inferred) posterior distributions for the number of diversification-rate shifts are virtually identical (i.e., demonstrating the extreme prior sensitivity of inferences using BAMM).



## Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures

Brian R. Moore<sup>a,1</sup>, Sebastian Höhna<sup>b,c</sup>, Michael R. May<sup>b</sup>, Bruce Rannala<sup>a</sup>, and John P. Huelsenbeck<sup>b</sup>

<sup>a</sup>Department of Evolution and Ecology, University of California, Davis, CA 95616; <sup>b</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720; and <sup>c</sup>Department of Statistics, University of California, Berkeley, CA 94720

Edited by Michael J. Donoghue, Yale University, New Haven, CT, and approved June 27, 2016 (received for review September 21, 2015)



New Results

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## A Bayesian Approach for Estimating Branch-Specific Speciation and Extinction Rates

Sebastian Höhna, William A. Freyman, Zachary Nolen, John P. Huelsenbeck, Michael R. May, Brian R. Moore

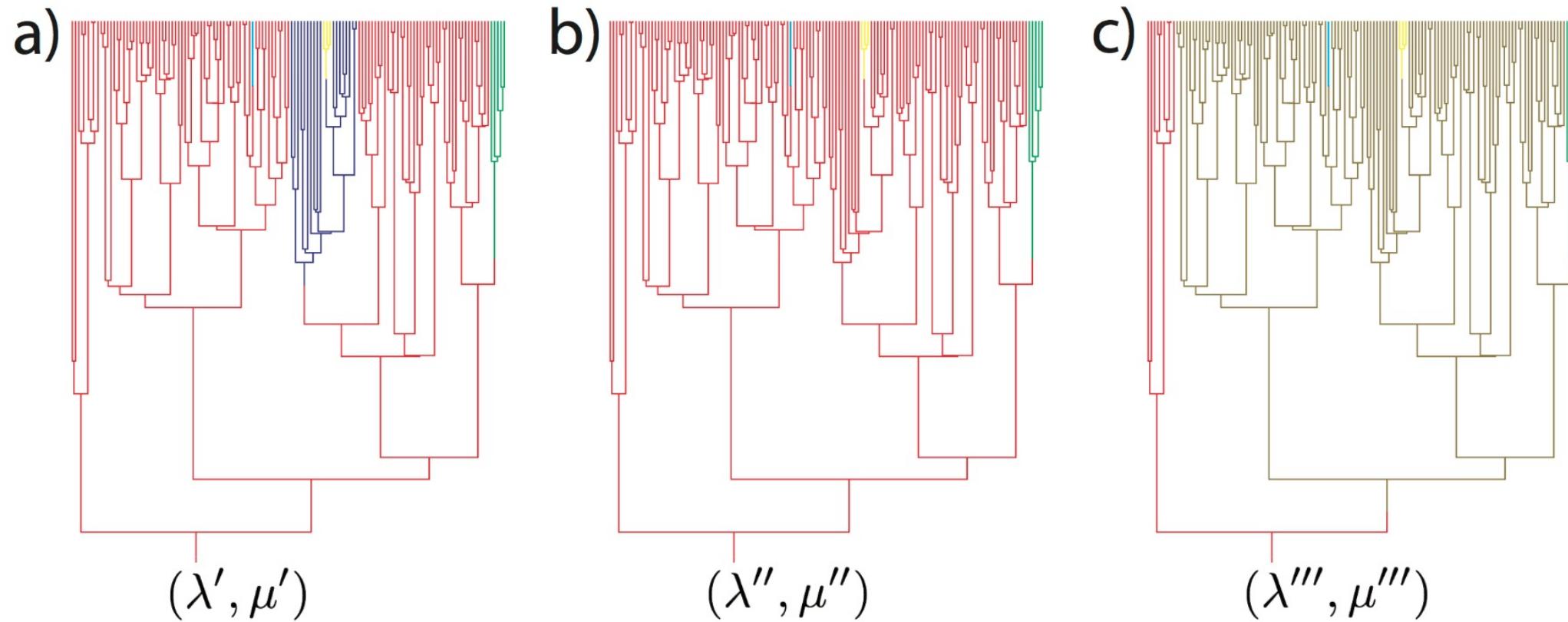
**doi:** <https://doi.org/10.1101/555805>

This article is a preprint and has not been certified by peer review [what does this mean?].

Posted February 20, 2019.

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# RevBayes



**Figure 2.** Samples of an MCMC analysis under a *Birth-Death-Shift* model. The colors represent different classes of rates for the speciation and extinction rates ( $\lambda$  and  $\mu$ , respectively). Note that the speciation and extinction rates at the root of the tree differ for the different MCMC samples:  $(\lambda', \mu')$ ,  $(\lambda'', \mu'')$ , and  $(\lambda''', \mu''')$ .