

# Branch Lengths and Diversification

Lecture 3  
March 24, 2009

## Outline

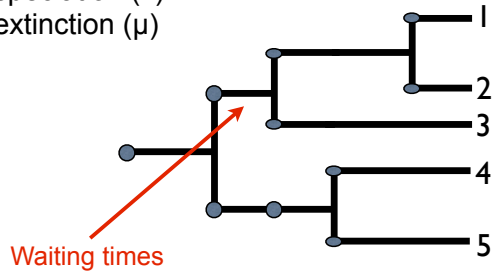
- How do lineages accumulate under the birth-death model?
- Estimating speciation and extinction rates from trees
- Testing hypotheses about diversification

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- How do lineages accumulate under the birth-death model?
- Estimating speciation and extinction rates from trees
- Testing hypotheses about diversification

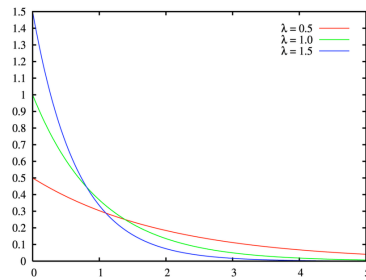
## Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



## Waiting times

- Under a birth-death model, the time intervals between successive events are always drawn from exponential distributions



$$f(x; \lambda) = \begin{cases} \lambda e^{-\lambda x} & , x \geq 0, \\ 0 & , x < 0. \end{cases}$$

Expected species diversity under a birth-death model:

$$E[N_t] = N_o e^{(b-d)t}$$

$N_t$  = species diversity after time  $t$

$N_o$  = starting species diversity

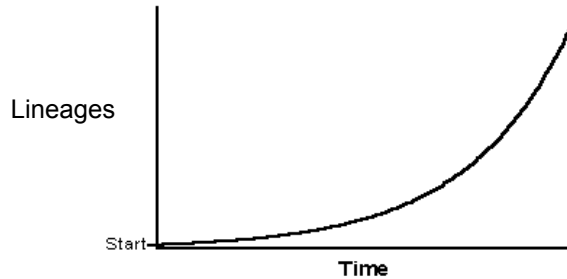
$b$  = birth rate

$d$  = death rate

$t$  = time

## Species Accumulation

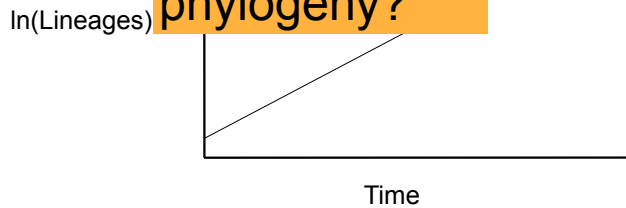
- Expected number of species increases exponentially with  $\lambda - \mu$



## Diversification Model

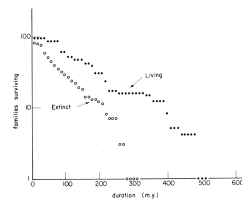
- Expected number of species increases exponentially with  $\lambda - \mu$

What if we just have the phylogeny?

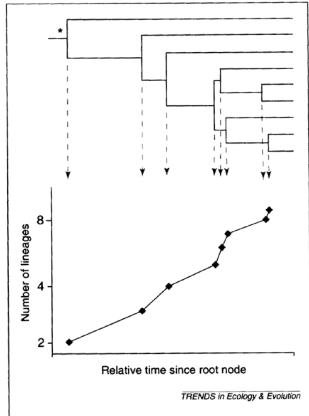


## Lineage-through-time plots

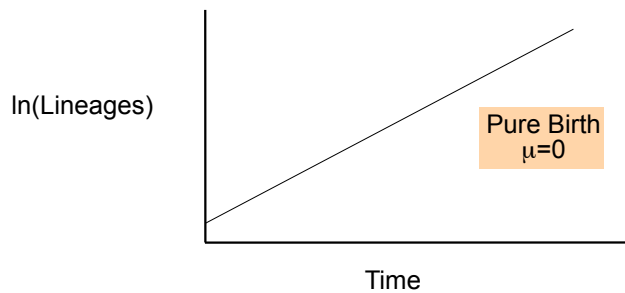
- Plot cumulative number of lineages through time
- Compare to expectations under null model
- Related to Van Valen's taxonomic survivorship curves



## Lineage-through-time

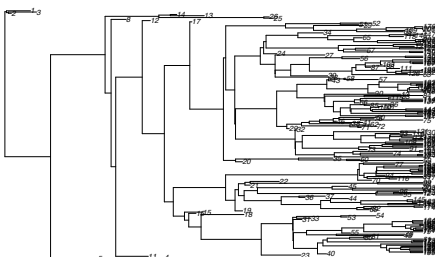


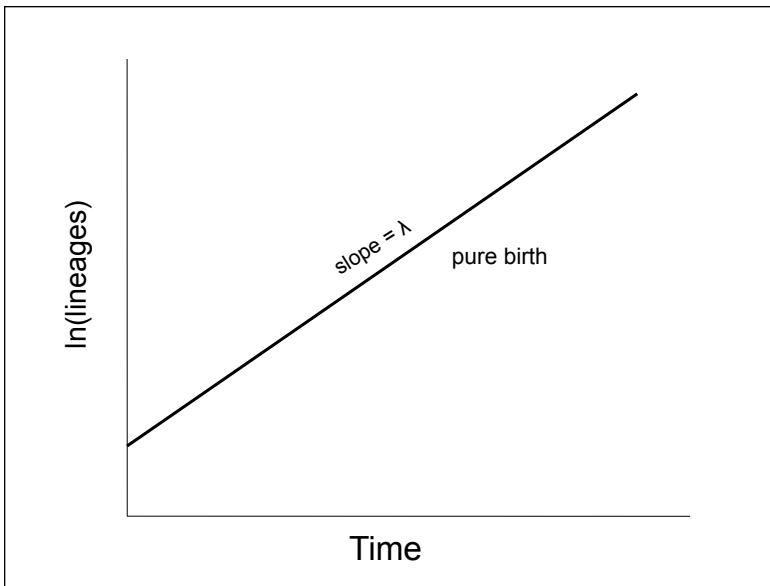
## LTT Plot



## Extinction

- Can leave an imprint on present-day phylogenies
- Older lineages are more likely to have gone extinct than younger ones





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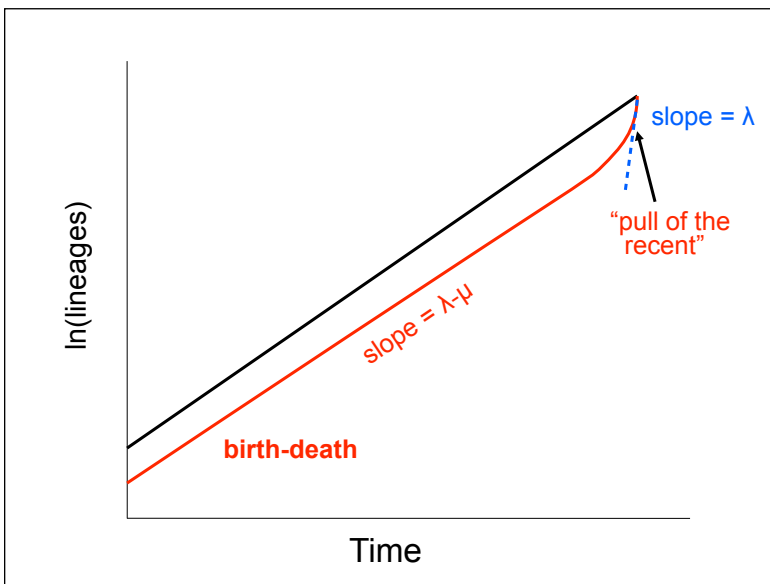
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## Outline

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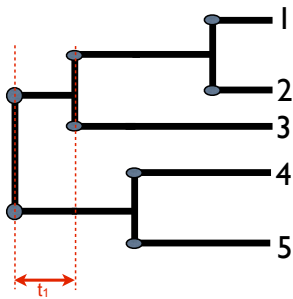
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## Pure Birth

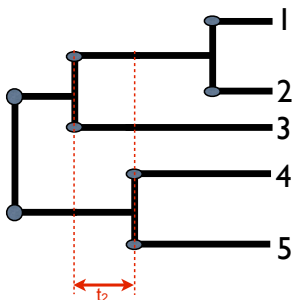
- Can use maximum likelihood to estimate parameters
- $L = \Pr[\text{tree} \mid \lambda]$



$t_1$  = First waiting time

Drawn from exponential distribution with parameter  $2\lambda$

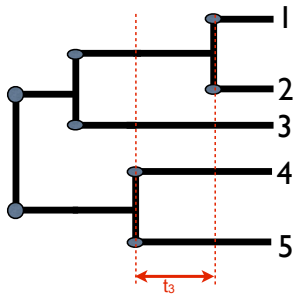
$$\Pr[t_1 = x] = 2\lambda e^{-2\lambda x}$$



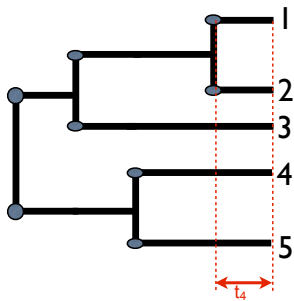
$t_2$  = Second waiting time

Drawn from exponential distribution with parameter  $3\lambda$

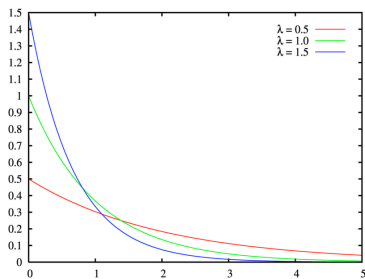
$$\Pr[t_2 = x] = 3\lambda e^{-3\lambda x}$$



$t_3$  = Third waiting time  
 Drawn from exponential  
 distribution with parameter  $4\lambda$   
 $\Pr[t_3 = x] = 4\lambda e^{-4\lambda x}$



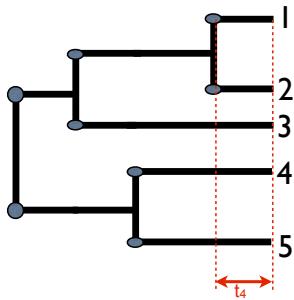
$t_4$  = Fourth waiting time (but no speciation!)  
 What is the probability of NO  
 speciation event in time  $t_4$ ?  
 Consider exponential distribution  
 with parameter  $5\lambda$



$$F(x; \lambda) = \begin{cases} 1 - e^{-\lambda x} & , x \geq 0, \\ 0 & , x < 0. \end{cases}$$

Cumulative distribution function

$$\begin{aligned} \Pr[\text{no event} \mid t=x] &= \\ 1 - \text{CDF} &= \\ 1 - (1 - e^{-\lambda x}) &= \\ e^{-\lambda x} \end{aligned}$$



$t_4$  = Fourth waiting time (but no speciation!)

What is the probability of NO speciation event in time  $t_4$ ?

Consider exponential distribution with parameter  $5\lambda$

$$\Pr[t_4 = x] = e^{-5\lambda x}$$

$$\Pr[t_1 = x] = 2\lambda e^{-2\lambda x}$$

$$\Pr[t_2 = x] = 3\lambda e^{-3\lambda x}$$

$$\Pr[t_3 = x] = 4\lambda e^{-4\lambda x}$$

$$\Pr[t_4 = x] = e^{-5\lambda x}$$

$$\text{likelihood} = P[\text{tree} \mid \lambda] = 2\lambda e^{-2\lambda t_1} 3\lambda e^{-3\lambda t_2} 4\lambda e^{-4\lambda t_3} e^{-5\lambda t_4}$$

In general,

$$\text{likelihood} = P[\text{tree} \mid \lambda] = e^{-n\lambda x_n} \prod_{i=2}^{n-1} i\lambda e^{-i\lambda x_i} = (n-1)! \lambda^{n-2} e^{-\lambda s}$$

$$s = \sum_{i=2}^{n-1} ix_i$$

## Likelihood for a tree under a Pure-birth model

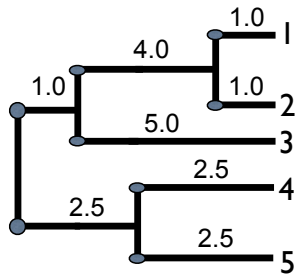
$$L = P[\text{tree} \mid \lambda] = (n-1)! \lambda^{n-2} e^{-\lambda s}$$

$n$  = number of taxa

$\lambda$  = speciation rate

$s$  = sum of all branch lengths in the tree





$$L = \Pr[\text{tree} \mid \lambda] = (n-1)! \lambda^{n-2} e^{-\lambda s}$$

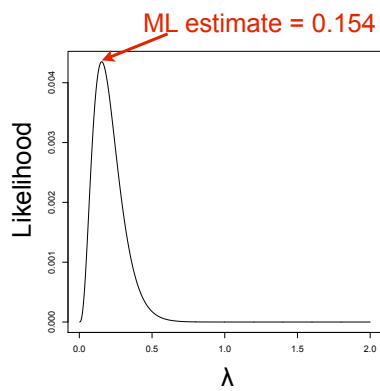
$$n = 5$$

$$s = 19.5$$

For  $\lambda = 1$ ,

$$L = (5-1)! 1^3 e^{-19.5}$$

$$L = 8.16 \times 10^{-8}$$

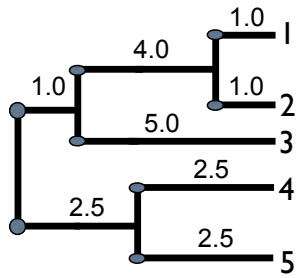


## Analytic solution

$$\hat{\lambda} = \frac{n-2}{s}$$

$$SE_{\hat{\lambda}} = \frac{\hat{\lambda}^2}{n-2}$$

Maximum likelihood  
estimate of  $\lambda$  under  
PB model



$$\hat{\lambda} = \frac{n-2}{s} = 0.154$$

$$0.154 \pm 0.0079$$

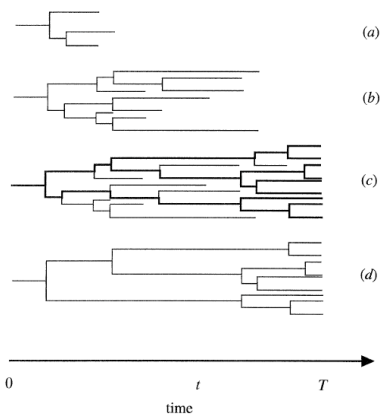
$$SE_{\hat{\lambda}} = \frac{\hat{\lambda}^2}{n-2} = 0.0079$$

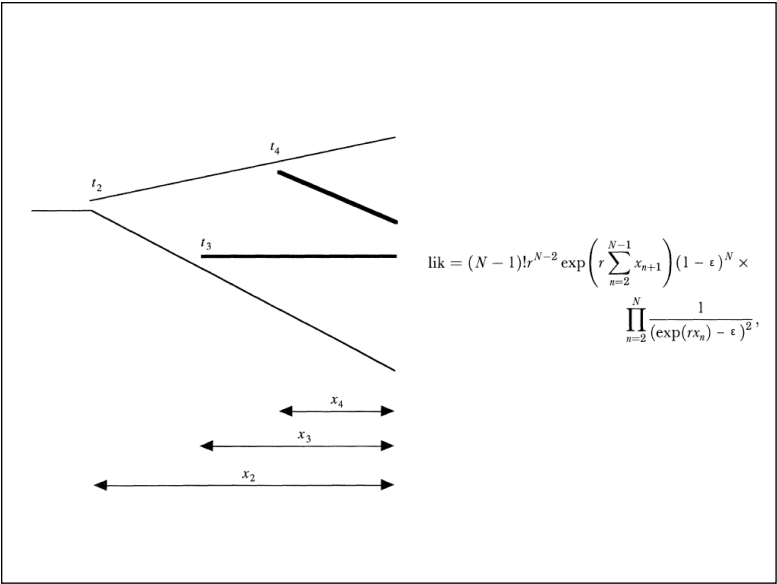
## Birth-death models

- Can use maximum likelihood to estimate parameters of a birth-death process
- $L = \text{Pr}[\text{tree} \mid \lambda, \mu]$
- Can be difficult to estimate  $\lambda$  and  $\mu$
- Easier to estimate composite parameters

$$r = \lambda - \mu$$

$$\varepsilon = \mu/\lambda$$





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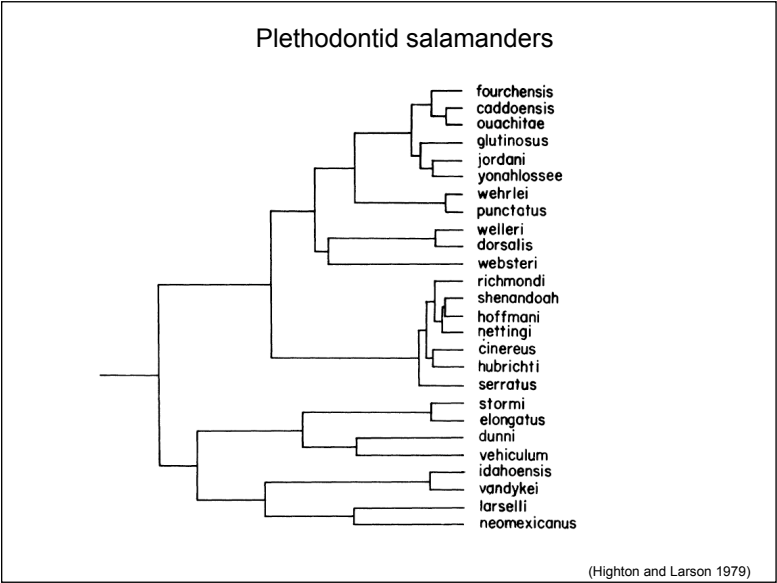
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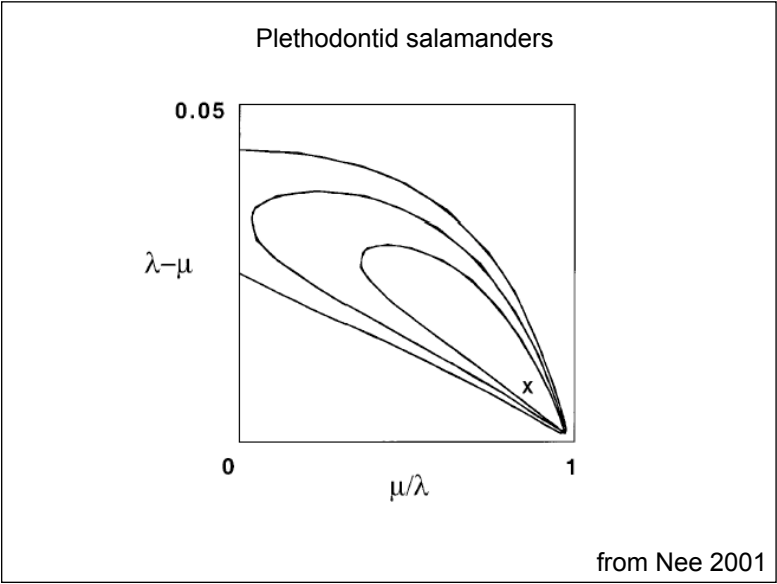
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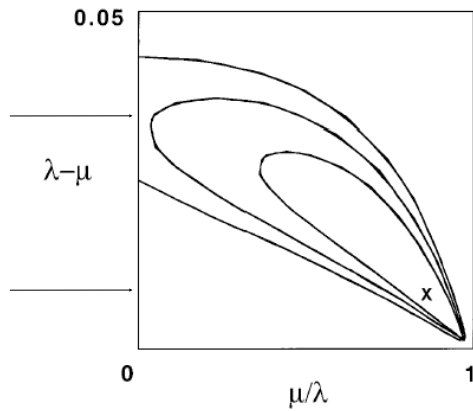
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### Plethodontid salamanders



from Nee 2001

### PB vs. BD

- Two simple ways to test for extinction in a tree
- Likelihood Ratio Test

$$\Delta = 2(\ln L_2 - \ln L_1)$$

Under model 1,  $\Delta$  should follow a  $\chi^2$  distribution with df equal to the difference in parameters

### PB vs. BD

- Two simple ways to test for extinction in a tree
- Akaike Information Criterion (AIC)

$$AIC = 2k - 2 \ln L \quad AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

Choose the model with the lowest AIC score

Can also gauge support by the difference in AIC scores

$\Delta_{AIC}$	Interpretation
0-3	no support
3-7	weak
7-10	intermediate
>10	strong