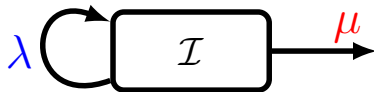# THE BIRTH-DEATH PROCESS

Considers the birth and death of individuals (e.g., species, infected hosts, B cells, languages, etc.)

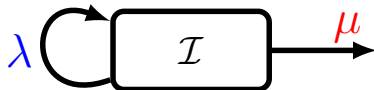The process gives rise to the phylogenetic tree

*Phylodynamic* methods seek to understand the parameters of the process that generated the tree

# The Birth-Death Process

New individuals $\mathcal{I}$ enter at rate $\lambda$

And individuals leave at rate $\mu$
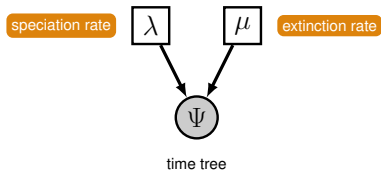
# THE BIRTH-DEATH PROCESS

New **Species** (lineages) arise at rate $\lambda$

And **Species** go extinct at rate $\mu$

# THE BIRTH-DEATH PROCESS

The tree topology and branching times are conditionally dependent on the rates of speciation ($\lambda$) and extinction ($\mu$)
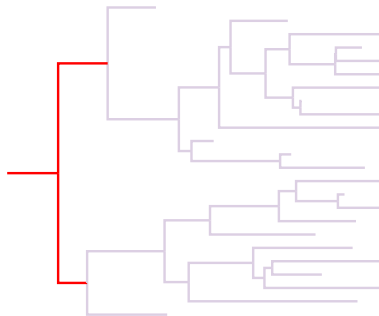
# THE BIRTH-DEATH PROCESS

When considering a single lineage:

—

# THE BIRTH-DEATH PROCESS

When considering a single lineage:

$\lambda \Delta t =$ The probability of —
speciating in a very small
time step $\Delta t$

# THE BIRTH-DEATH PROCESS
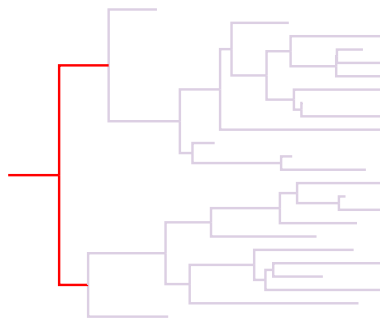
When considering a single lineage:

$\mu \Delta t =$ The probability of —
going extinct in a very
small time step $\Delta t$

# THE BIRTH-DEATH PROCESS

When considering a single lineage:

The waiting time to a speciation event is exponentially distributed with rate parameter $\lambda$

When considering a single lineage:

The waiting time to an extinction event is exponentially distributed with rate parameter $\mu$

# THE BIRTH-DEATH PROCESS

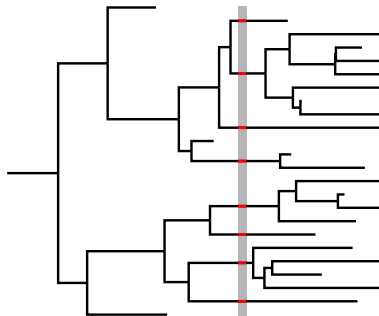When considering a <span style="color:red">single lineage</span>:

The waiting time the **first** event (speciation or extinction) event is exponentially distributed with rate parameter $\lambda + \mu$

___

# THE BIRTH-DEATH PROCESS

When considering *N* lineages existing at an instant in time:

The waiting time the **next** event (speciation or extinction) event is exponentially distributed with rate parameter $N(\lambda + \mu)$

# THE BIRTH-DEATH PROCESS

When considering *N lineages* existing at an instant in time:

Simulation under the
constant-rate process is
straightforward and simply
requires drawing waiting
times from an exponential
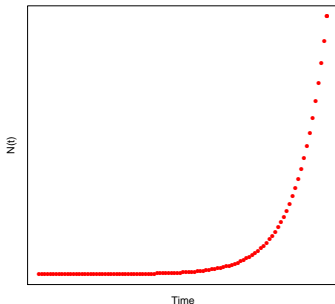distribution (and
bookkeeping)
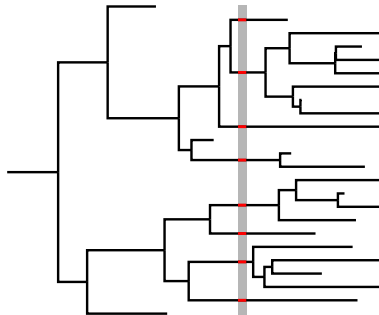
# Lineage Accumulation Through Time

Under the pure-birth model (Yule model where $\mu = 0$)

The number of species grows exponentially over time
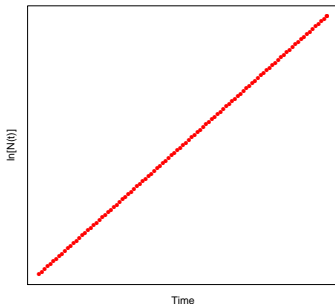
$$N(t) = N(0)e^{\lambda t}$$

# LINEAGE ACCUMULATION THROUGH TIME

Under the pure-birth model (Yule model where $\mu = 0$)
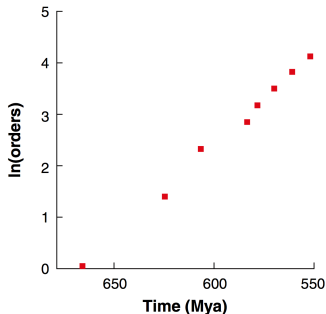
The ln(# of lineages) over time is linear

$$N(t) = N(0)e^{\lambda t}$$

# LINEAGE ACCUMULATION THROUGH TIME

Under the pure-birth model (Yule model where $\mu = 0$)

The cumulative increase in the number of metazoan orders over the Vendian and Lower Cambrian (Data from Sepkoski 1978)
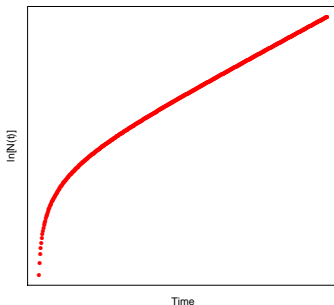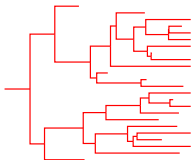
# Lineage Accumulation Through Time

When considering at the complete phylogeny

The **total** number of species over time is a function of both $\lambda$ and $\mu$

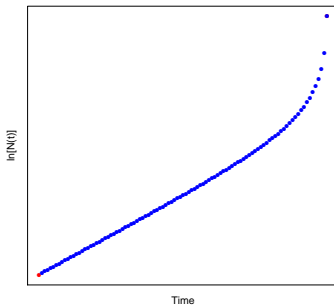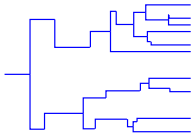$$N(t) = \frac{\lambda e^{(\lambda - \mu)t} - \mu}{\lambda - \mu}$$

# LINEAGE ACCUMULATION THROUGH TIME

When considering at the reconstructed phylogeny

The **apparent** number of species over time is a function of $\lambda$, $\mu$, and the age of the tree $\mathcal{T}$

$$N(t) = \frac{\lambda e^{(\lambda-\mu)\mathcal{T}} - \mu}{\lambda e^{(\lambda-\mu)(\mathcal{T}-t)} - \mu}$$
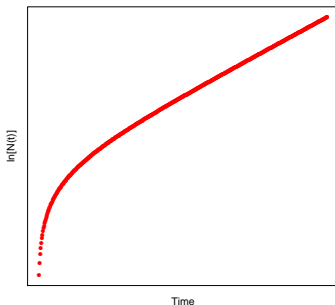
# Lineage Accumulation Through Time

When considering at the complete phylogeny

The beginning part of the trajectory appears as though there is accelerated speciation early on

This is because we only consider initial lineages that survived to the present — "the push of the past"
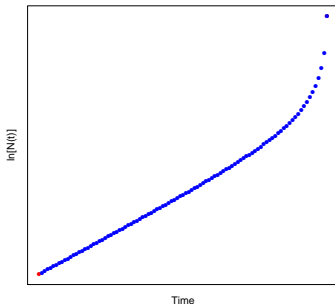
# Lineage Accumulation Through Time

When considering at the reconstructed phylogeny

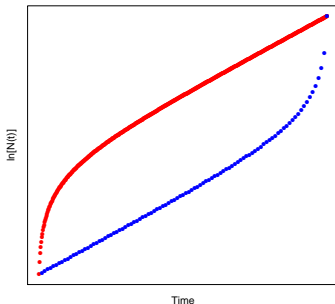It appears that there is an increase in the rate of speciation toward the present day

This is because lineages that arose more recently have had less time to go extinct — "the pull of the present"

# LINEAGE ACCUMULATION THROUGH TIME

Lineage-through-time plots can be used to estimate $\lambda$ and $\mu$

The slopes of the lines at various stages provide an estimate of these parameters
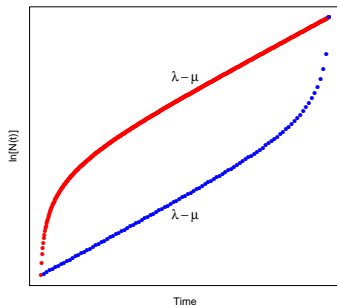
# Lineage Accumulation Through Time

Lineage-through-time plots can be used to estimate $\lambda$ and $\mu$

Most of the time lineages increase at a rate equal to $\lambda - \mu$
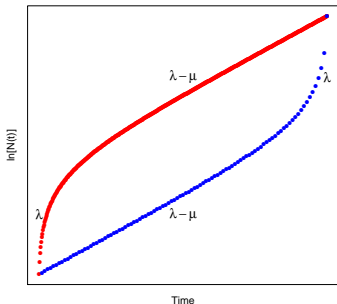
The slope of the line is the estimate of the net diversification rate

# Lineage Accumulation Through Time

Lineage-through-time plots can be used to estimate $\lambda$ and $\mu$

The slope of the line in the "pull to the present" or "push of the past" is approximately equal to the speciation rate and provides an estimate of $\lambda$

# LINEAGE ACCUMULATION THROUGH TIME

Lineage-through-time plots can be used to estimate $\lambda$ and $\mu$

This requires us to assume that $\lambda$ and $\mu$ are constant, because these patterns can also be explained by an acceleration in diversification
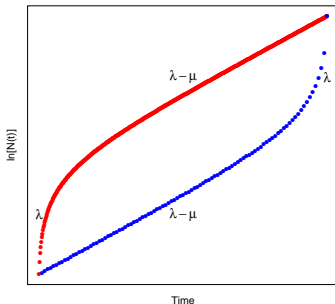
# Diversification

We are more interested in cases when rates vary:

- What are the rates of speciation and extinction (or diversification) for my favorite clade?

- Has the rate of diversification changed over time or across the tree?

- If there were shifts in diversification rate, on what branches or at what time point did they occur?

- Are the rate changes correlated with the evolution of a morphological character, biogeographical event, or ecological change?

# Next Week: Jetz et al. (2012)

The global diversity of birds in space and time

LTT plots for visualizing and estimating species diversification rates