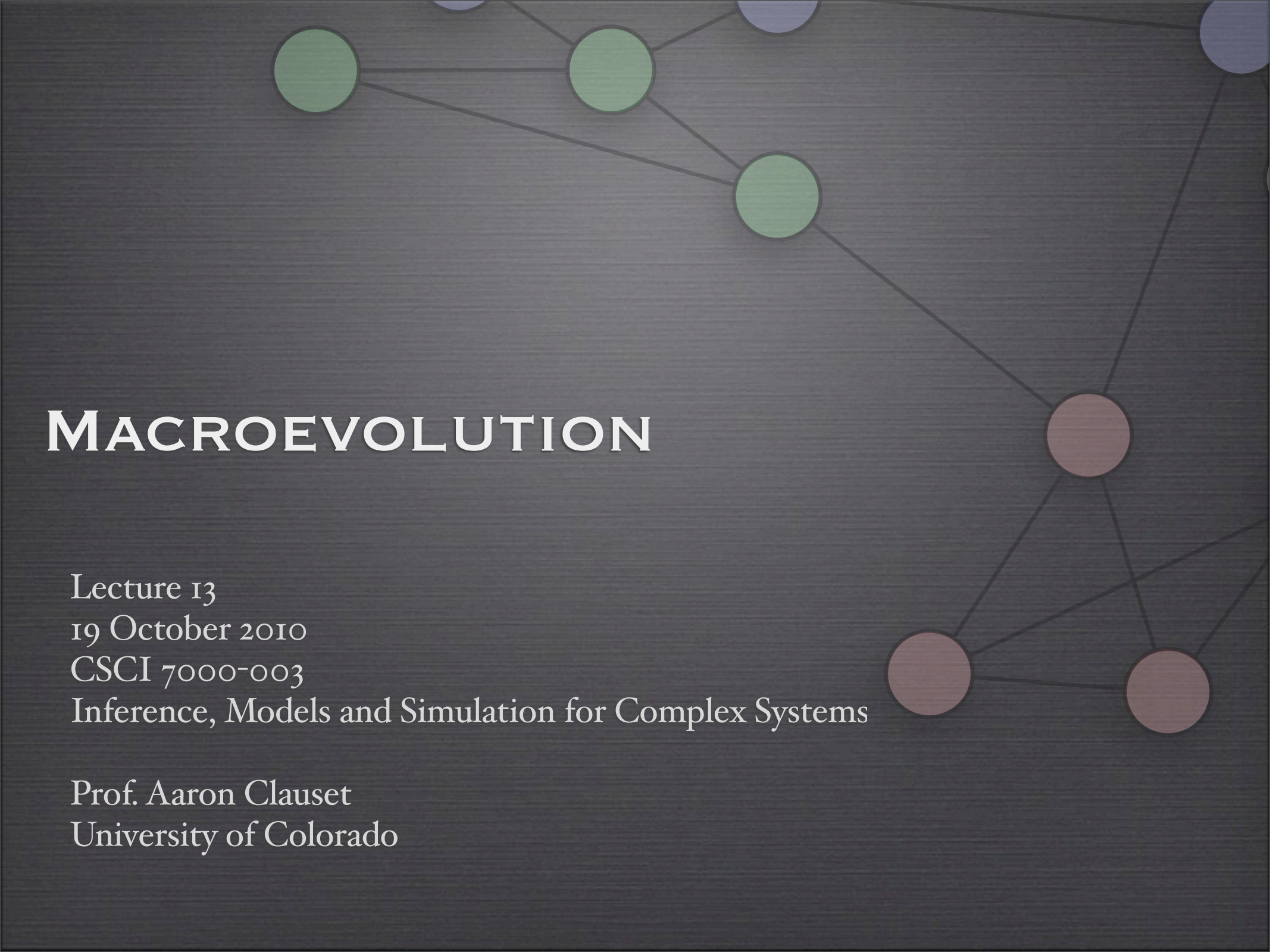
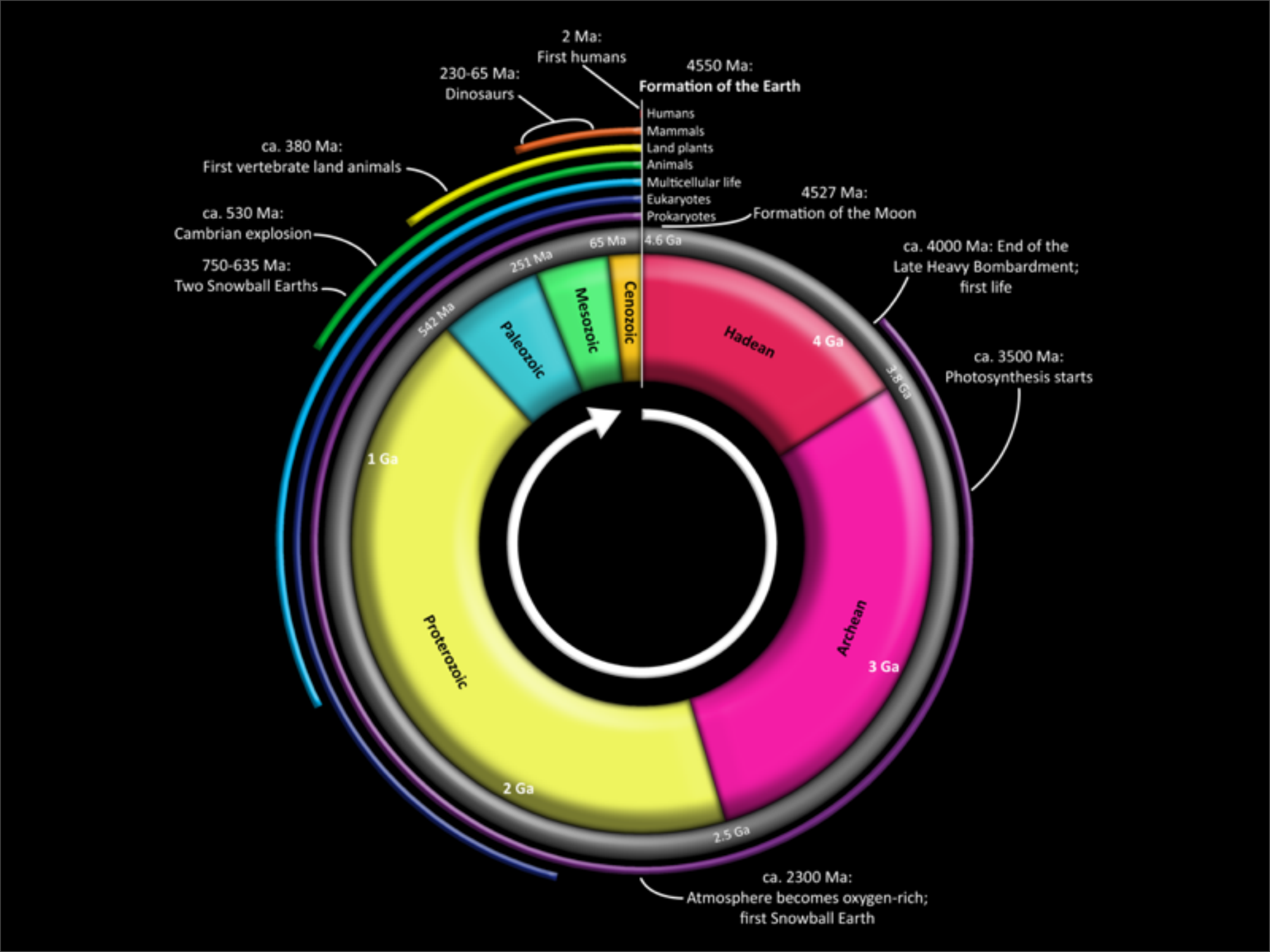
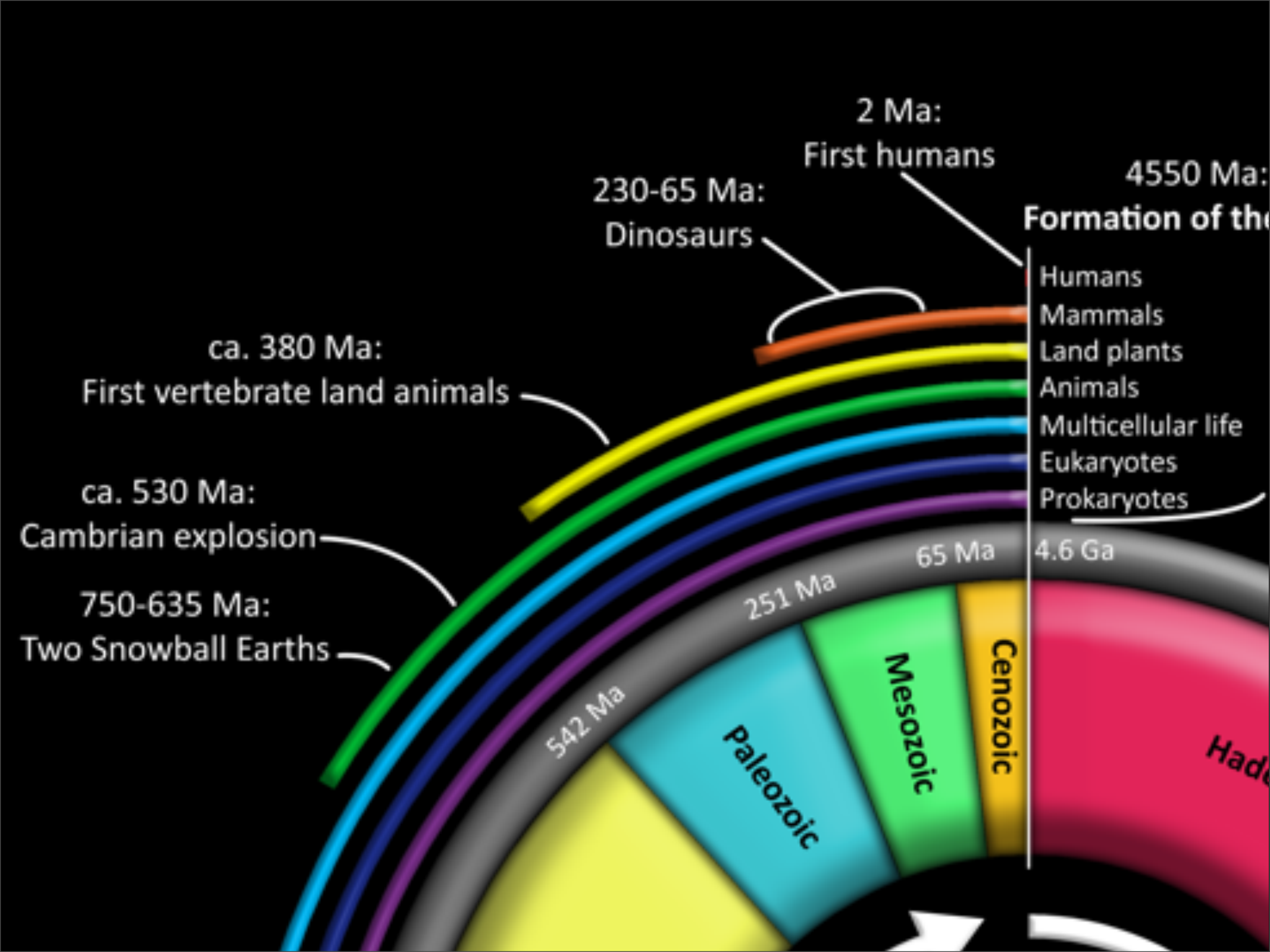


# Macroevolution

Lecture 13
19 October 2010
CSCI 7000-003
Inference, Models and Simulation for Complex Systems

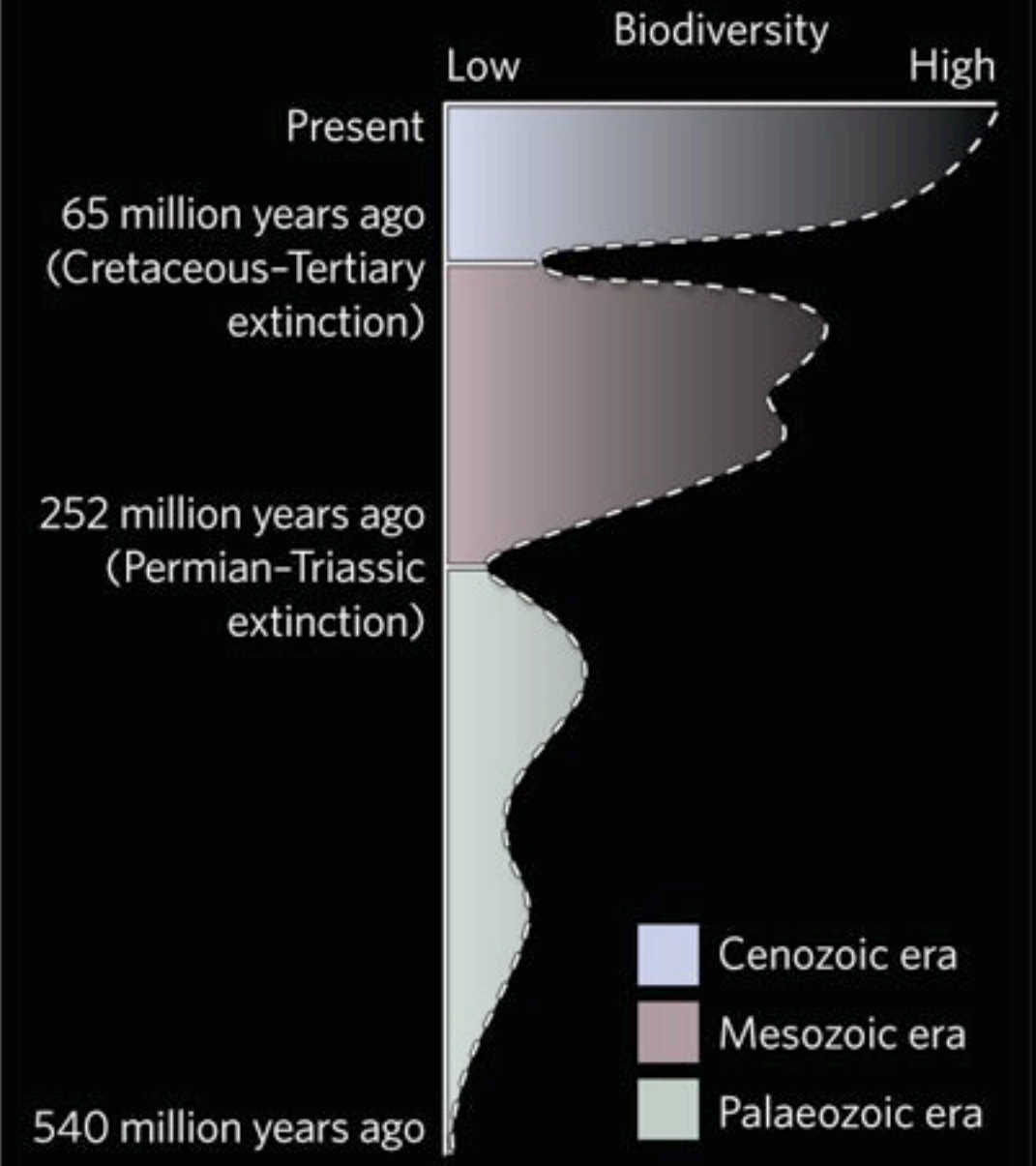
Prof. Aaron Clauset
University of Colorado


2 Ma:
First humans
230-65 Ma:
Dinosaurs
4550 Ma:
Formation of the Earth
Humans
Mammals
Land plants
Animals
Multicellular life
Eukaryotes
Prokaryotes
ca. 380 Ma:
First vertebrate land animals
ca. 530 Ma:
Cambrian explosion
750-635 Ma:
Two Snowball Earths
4527 Ma:
Formation of the Moon
65 Ma
4.6 Ga
251 Ma
542 Ma
Cenozoic
Mesozoic
Paleozoic
Hadean
4 Ga
1 Ga
Proterozoic
2 Ga
Archean
3 Ga
2.5 Ga
3.8 Ga
ca. 4000 Ma: End of the
Late Heavy Bombardment;
first life
ca. 3500 Ma:
Photosynthesis starts
ca. 2300 Ma:
Atmosphere becomes oxygen-rich;
first Snowball Earth


2 Ma:
First humans
230-65 Ma:
Dinosaurs
4550 Ma:
Formation of th
ca. 380 Ma:
First vertebrate land animals
ca. 530 Ma:
Cambrian explosion
750-635 Ma:
Two Snowball Earths
Humans
Mammals
Land plants
Animals
Multicellular life
Eukaryotes
Prokaryotes
65 Ma
4.6 Ga
251 Ma
542 Ma
Cenozoic
Mesozoic
Paleozoic
Hade

# AN 1860 RECONSTRUCTION OF THE FOSSIL RECORD

The first of many, hotly-debated, estimates of Phanerozoic biodiversity.




**Kingdom: Animalia**
**Phylum: Chordata**
**Subphylum: Vertebrata**
**Class: Mammalia**
**Order: Proboscidea**
**Family: Elephantidae**

*Elephas maximus*

*Loxodonta africana*

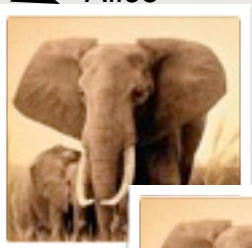
## Macroevolution

*species level and above*

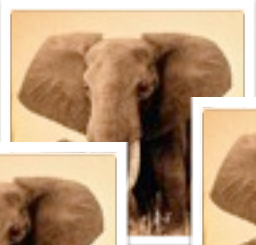
## Microevolution

*below species level*

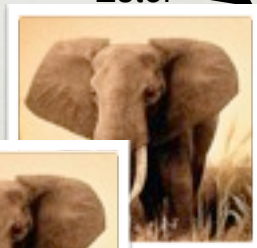
Alice



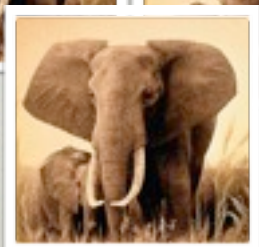
Carol

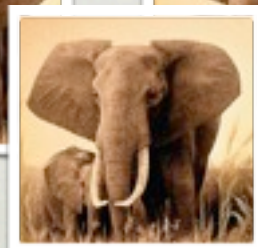


Ester



Bob



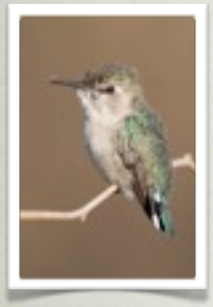


Dan

# Macroevolutionary Questions

- body size (or mass)
- metabolism
- diversity [number of species, morphology, taxonomy, behavior]
- complexity [prokaryote ⟶ eukaryote ⟶ multi-cellularity ⟶ sociality]
- carrying capacities
- mass extinctions & recoveries
- adaptive radiations

# Species Size Diversity



2g

40g

75,000g

165, 000g

2g

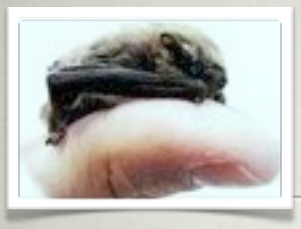
288g

250,000g

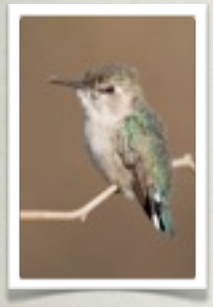
5,500,000g

images from Wikipedia

# Species Size Diversity



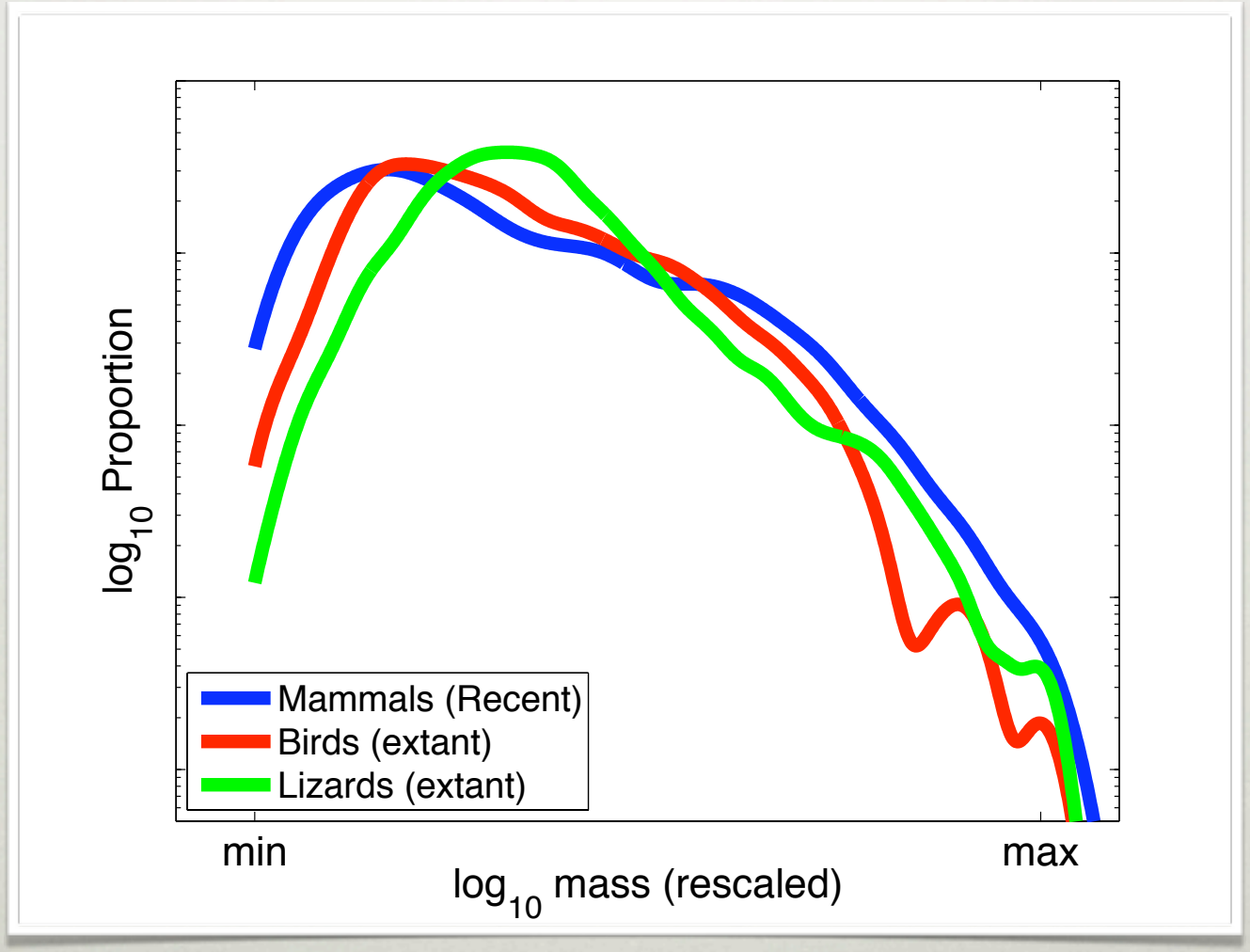
2g



2g

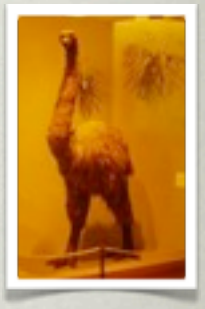
40g

288g




75,000g

165,000g



250,000g

5,500,000g

data from Smith *et al.* (2003), Dunning Jr. (2007), Meiri (2008)

# Past Work

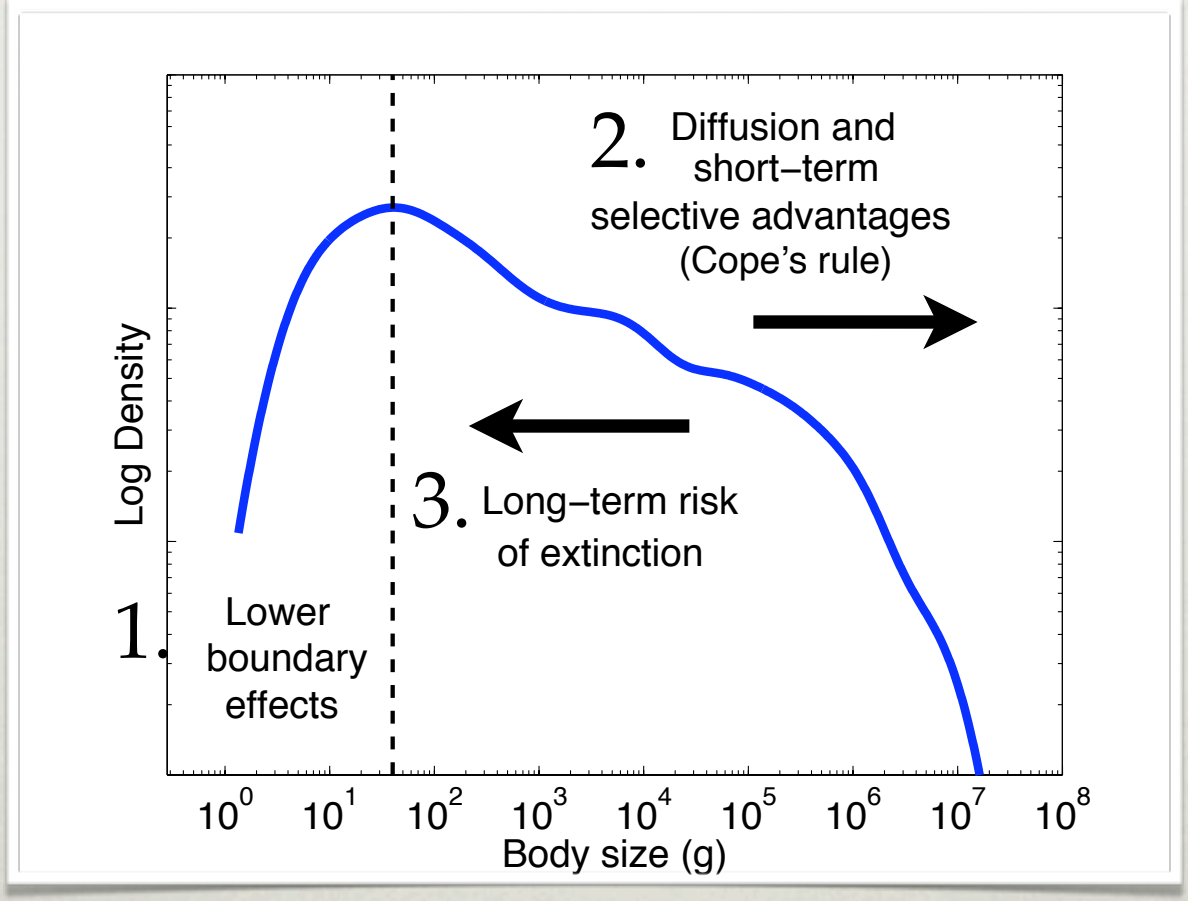
- focus on right-skew and mode's location
- mainly terrestrial mammals (best data)

1. energetic optima + competition
   - Lomolino (1985)
   - Sebens (1987)
   - Brown, Marquet, Taper (1993, 1996)

2. minimum size + cladogenetic diffusion (+ Cope's rule)
   - Stanley (1973)
   - McShea (1994)

# Macroevolutionary Model

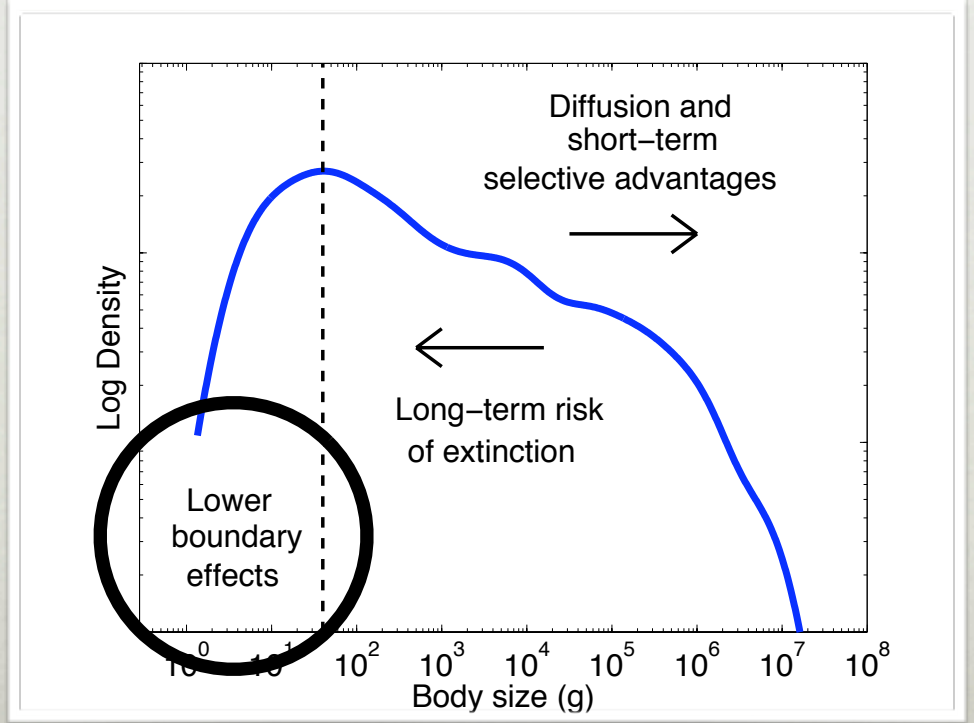
three mechanisms




Clauset, Erwin, *Science* **321**, 399-401 (2008)

# Macroevolutionary Model

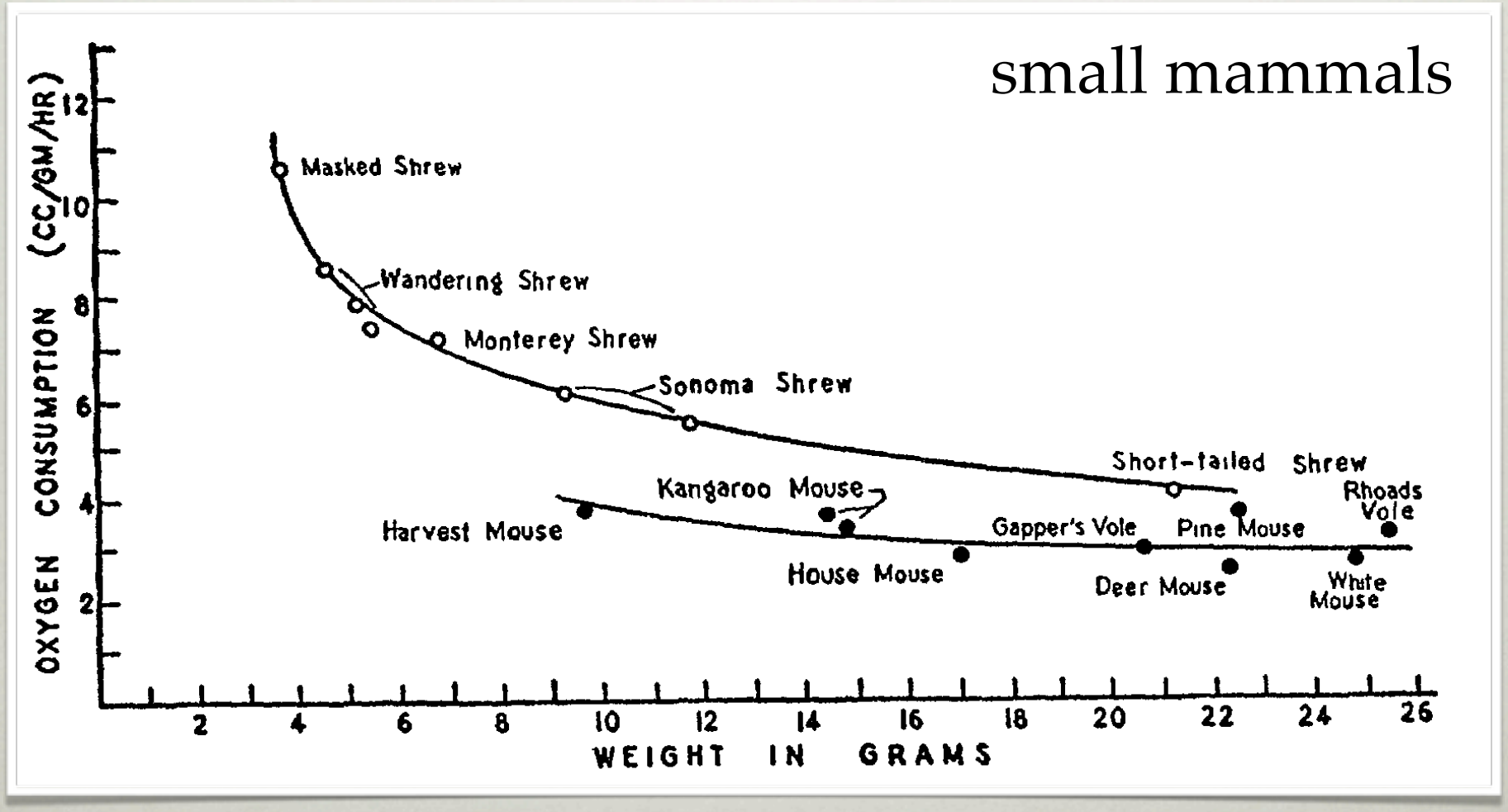
1. hard lower boundary = **physiology, metabolism**
2. biased diffusion = **short-term advantages**
3. size-dependent extinction rates = **long-term risks**




data from Smith *et al.* (2003)

# Hard Lower Limit

**metabolic constraints** $x_{\min} \approx 2\text{g}$

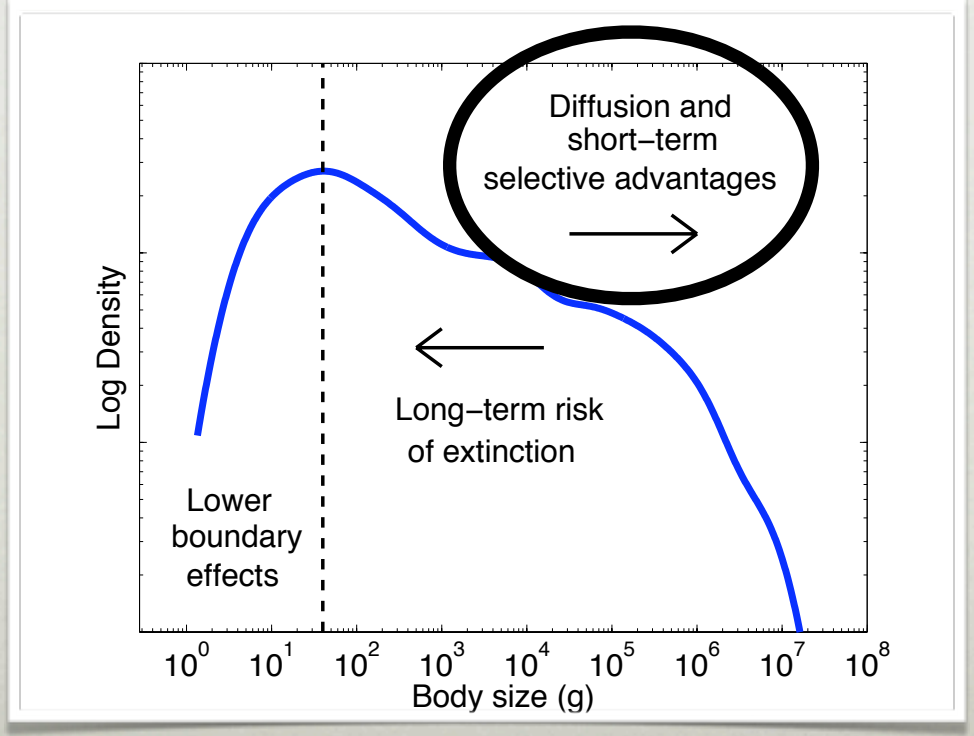



Note: West et al. (2002) predict 1g for lower limit of mammals

from Pearson (1948)

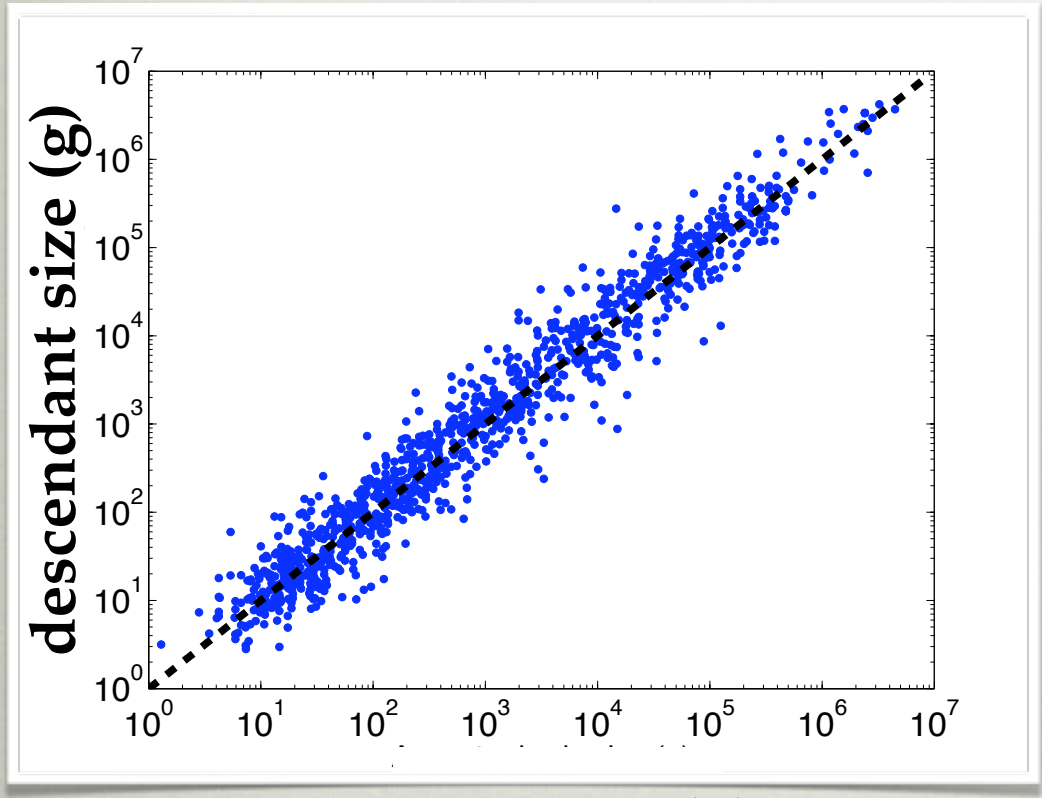
# Macroevolutionary Model

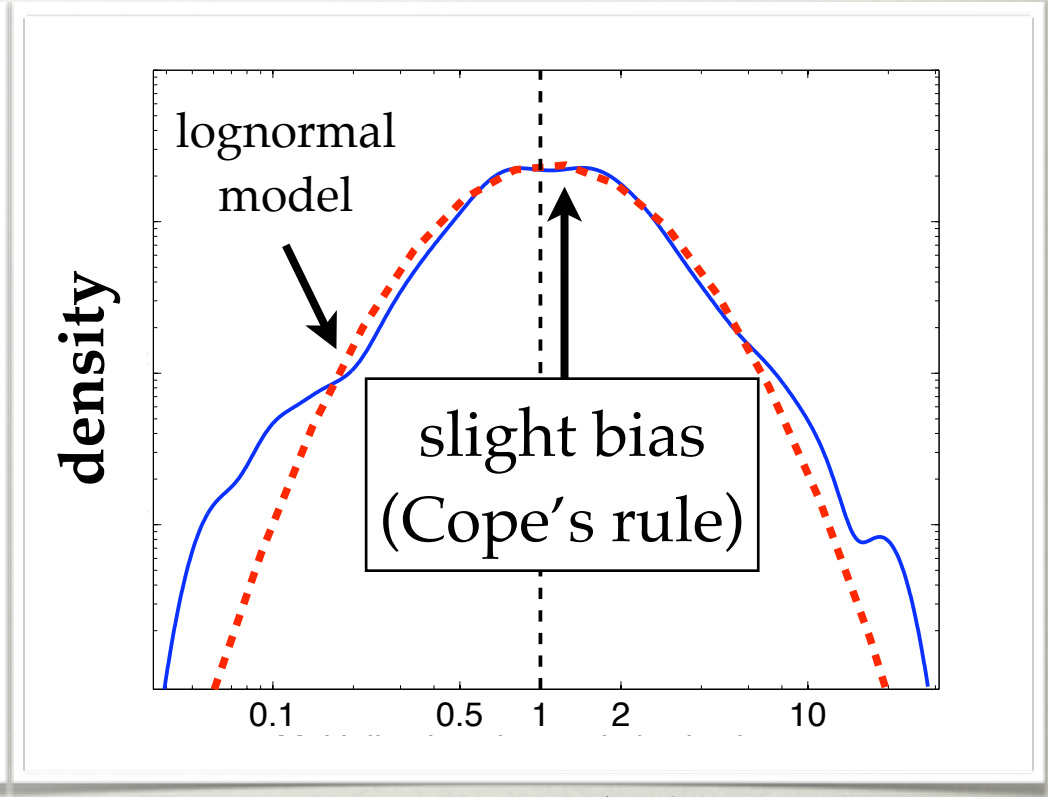
1. hard lower boundary = **physiology, metabolism**
2. biased diffusion = **short-term advantages**
3. size-dependent extinction rates = **long-term risks**



# Biased Diffusion

**ancestor-descendant data** [North Am. mammals]

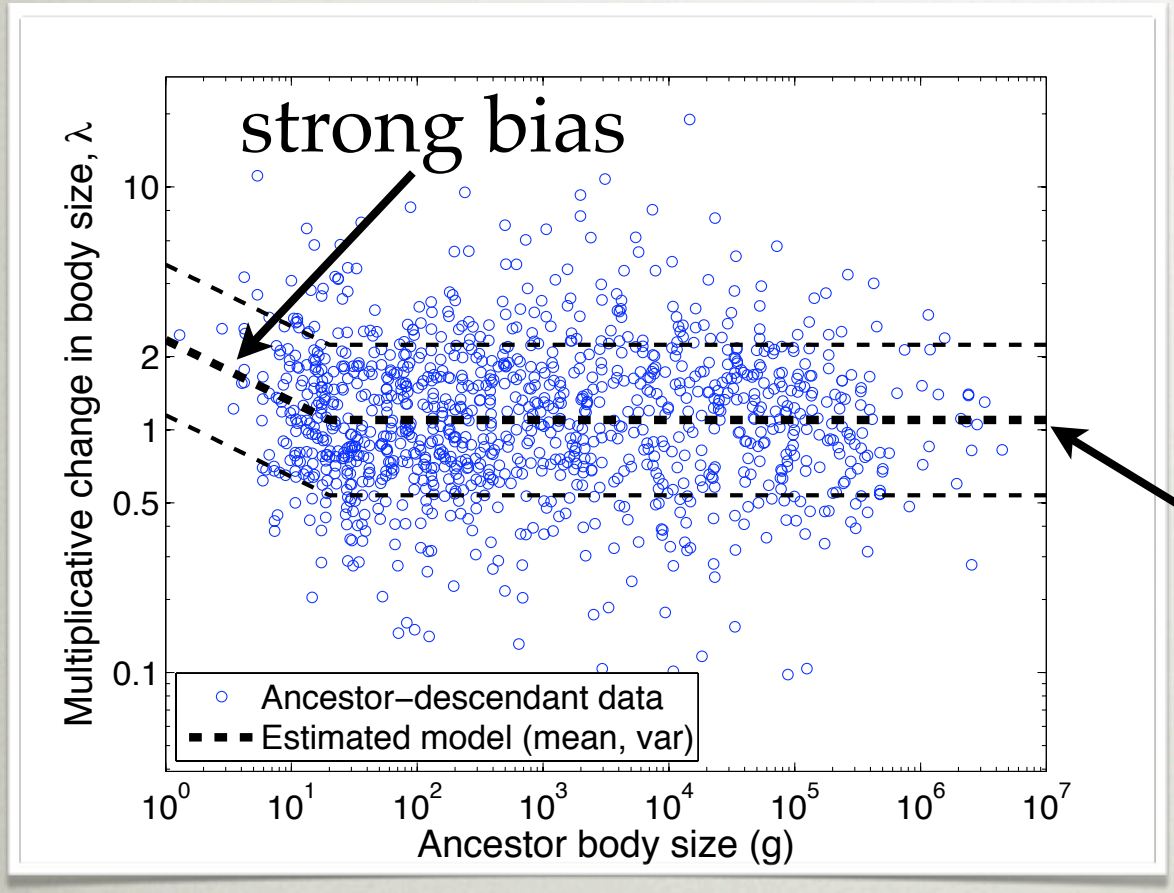



data from Alroy (2000)

# Cope's Rule

**ancestor-descendant data** [North Am. mammals]




$$F(\lambda) = \mathcal{N}(\mu(x_A), \sigma)$$

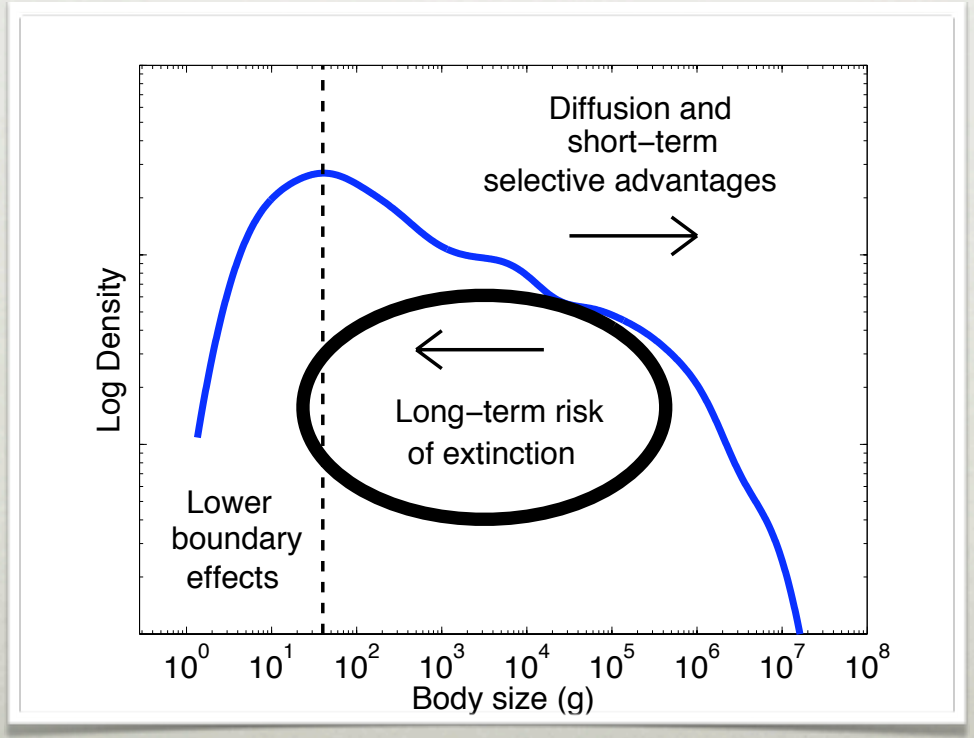
$\mu(x)$ is piece-wise log-linear

slight bias (4.1%)

data from Alroy (2000)

# Macroevolutionary Model

1. hard lower boundary = **physiology, metabolism**
2. biased diffusion = **short-term advantages**
3. size-dependent extinction rates = **long-term risks**



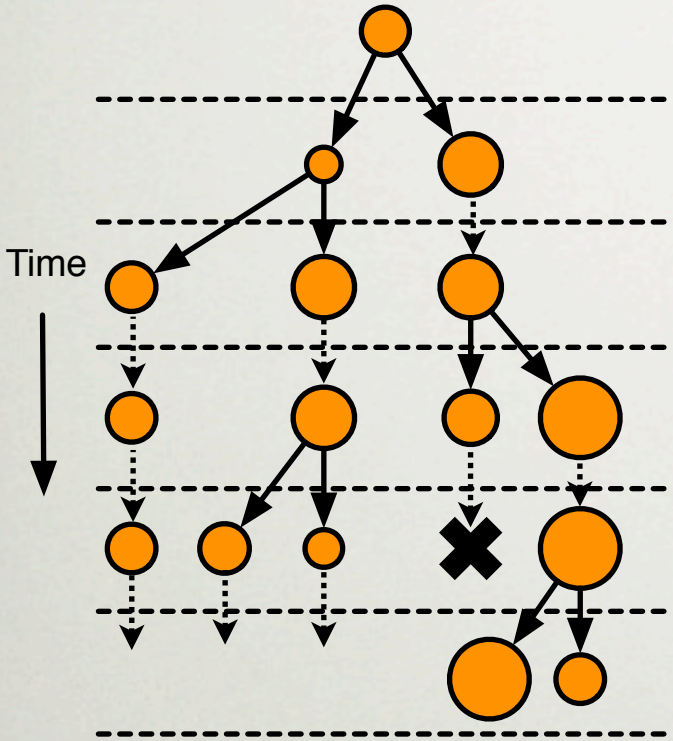
# Extinction / Speciation

1. extinction rates difficult to estimate from data
2. simple parametric model
   - rate depends on size $\mathrm{d}p_{\mathrm{extinct}}/\mathrm{d}x > 0$

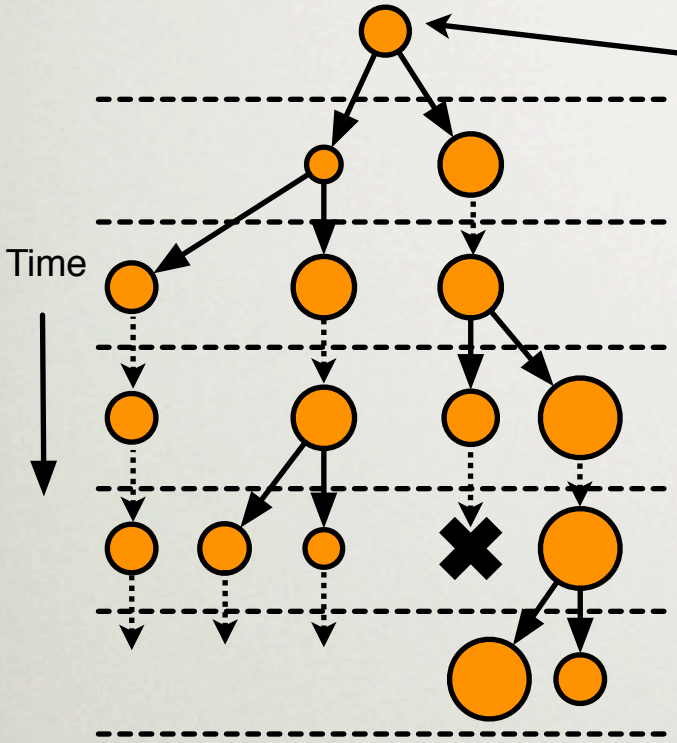
     [Van Valen (1973), Van Valkenburgh et al. (2004), Liow et al. (2008), Alroy (unpublished)]
   - speciation rate independent of size*
   - fitted to data

*only ratio of extinction-to-speciation rate matters

# Cladogenesis

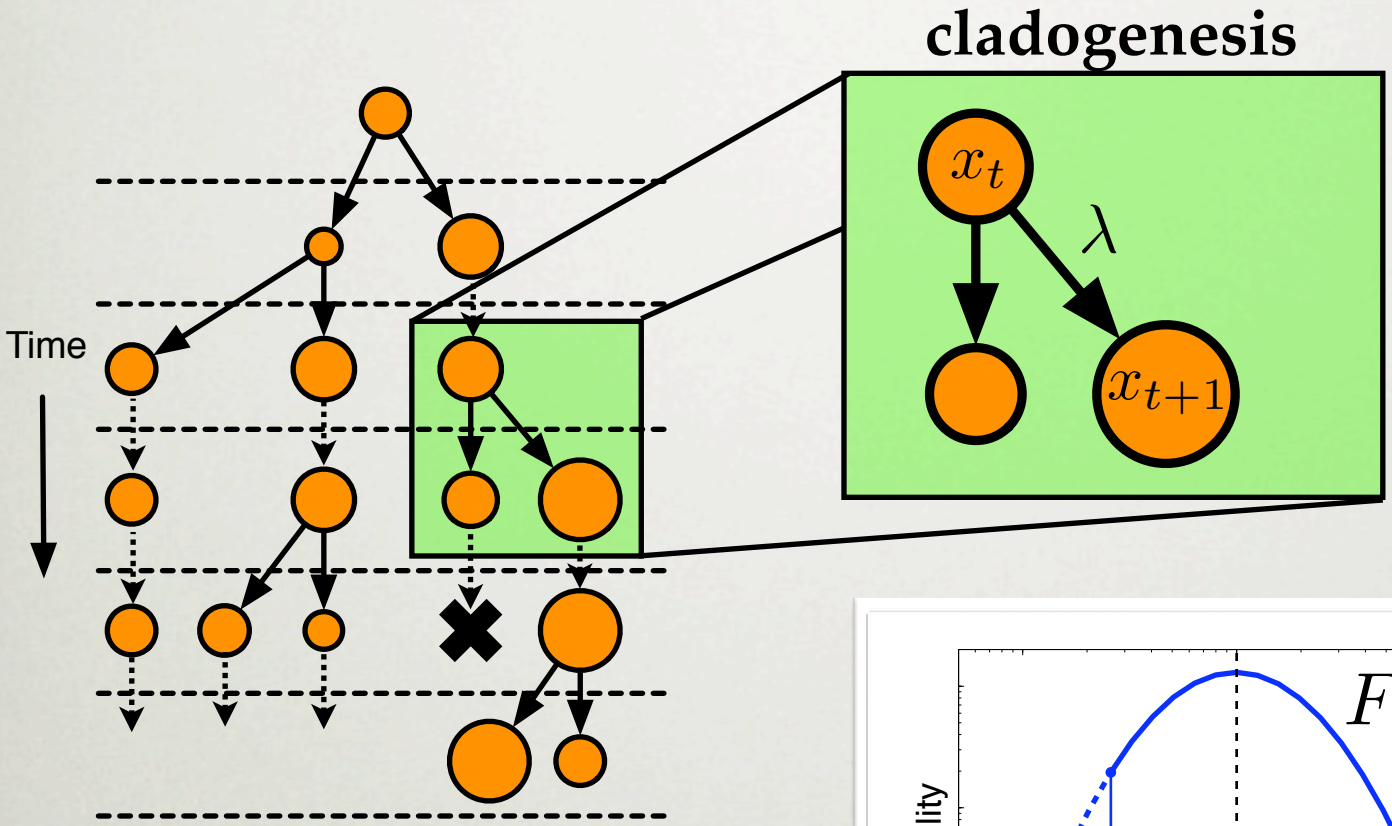


# Cladogenesis

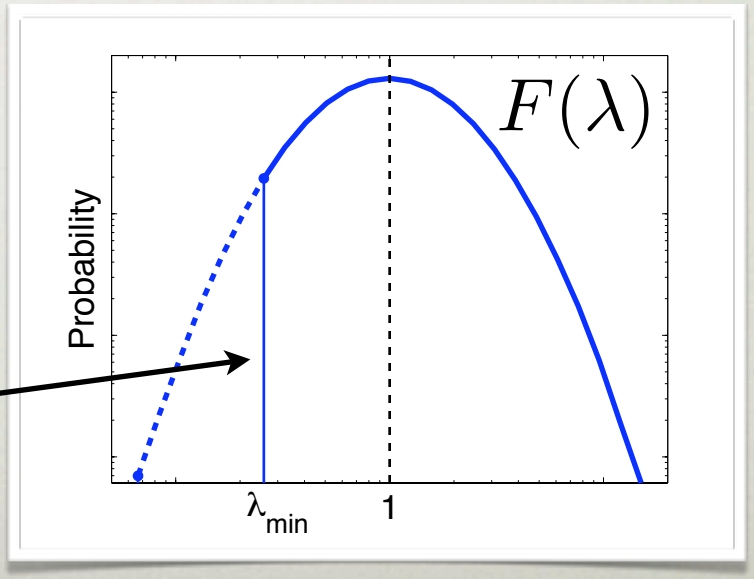



**founder species**

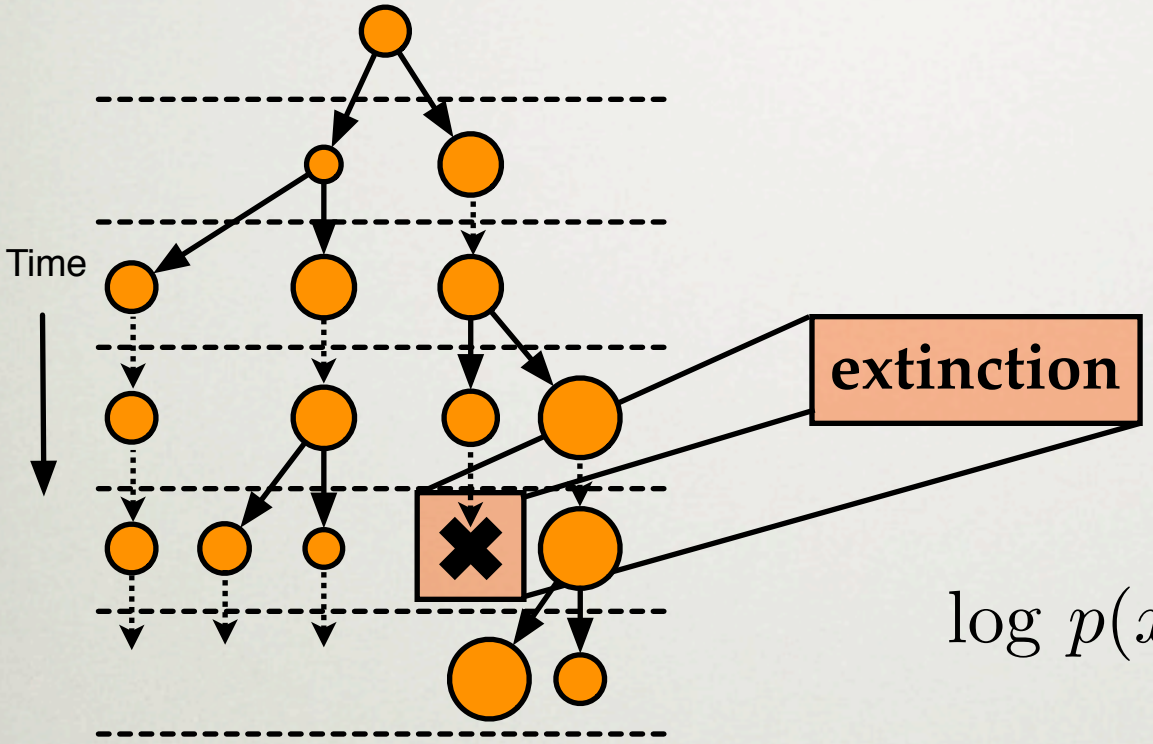
# Cladogenesis




lower limit



# Cladogenesis



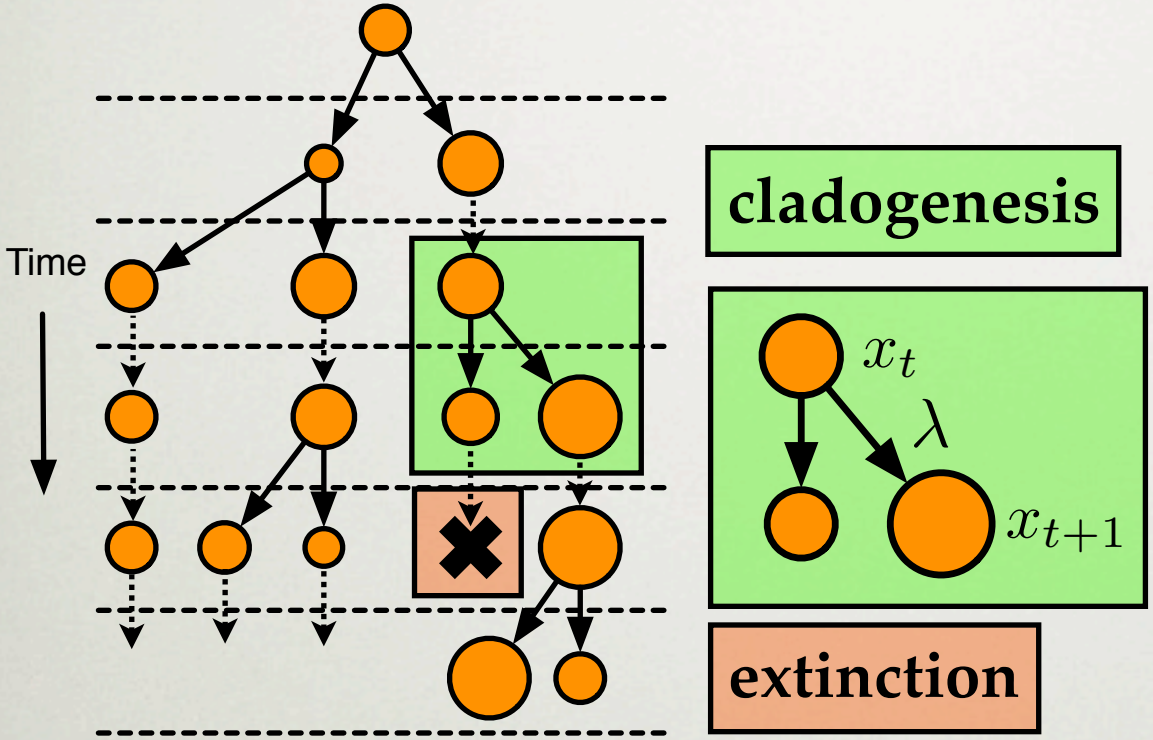

independent events
prob. depends on size

$$\log\, p(x) = \rho \log\, x + \log\, \beta$$

size dependence

basal rate

# Cladogenesis




**model features**

- size-dependent fluctuations
- Cope's rule
- size-dependent extinction rate
- lower limit $x_{\min}$

# Comments

**Ecology-free model**

- no inter-specific interaction (competition, predation, etc.)
- no population dynamics
- no environment
- no mass extinctions
- no anagenetic variation in body size

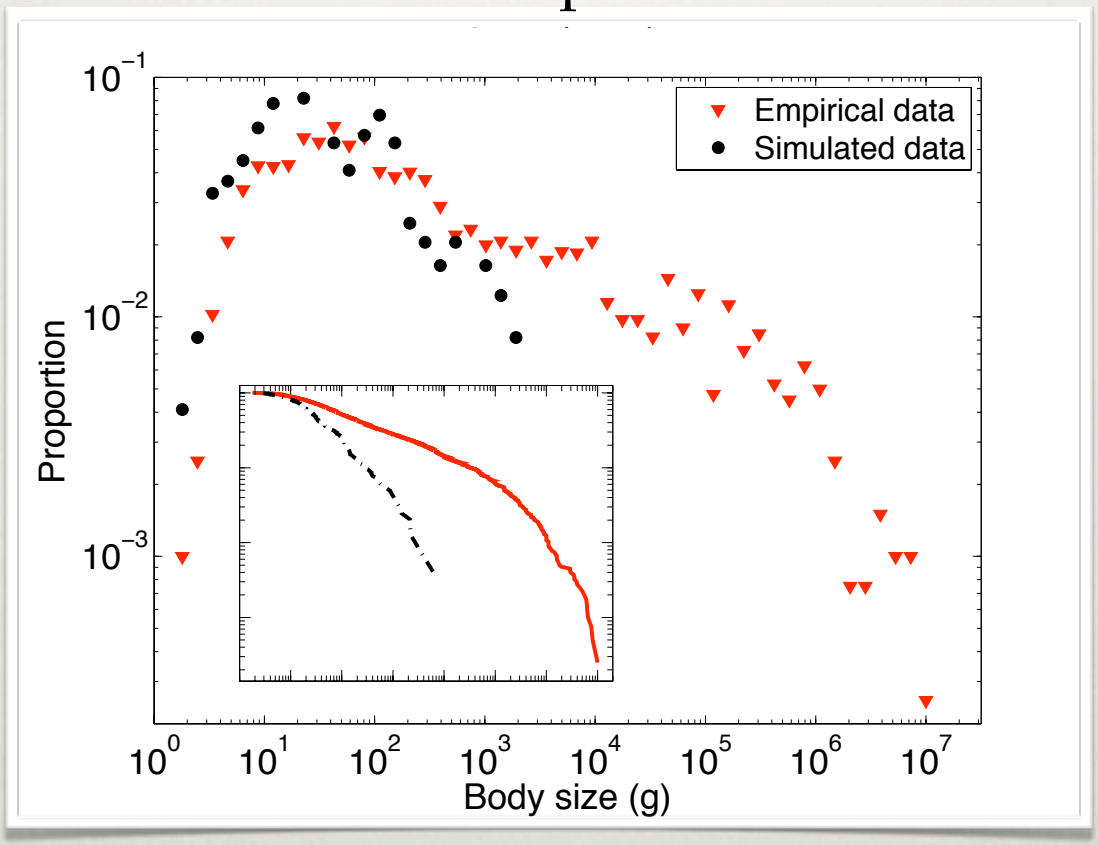
# Parameters

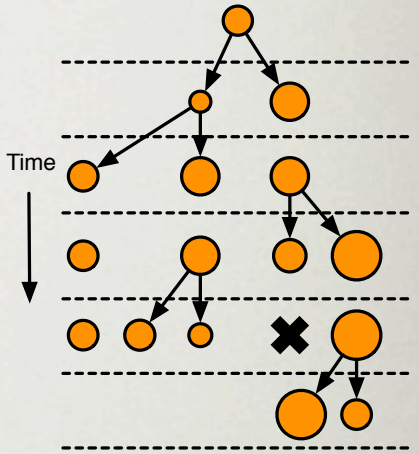
| | | | |
|---|---|---|---|
| initialization | founder body size | $x_0$ | 40g |
| length of sim. | mean species lifetime | $\nu$ | 1.60(1) My |
| | years in equilibrium | $\tau$ | 60 My |
| boundary | lower bound | $x_{\min}$ | 1.8g |
| diffusion | $\log \lambda$-intercept | $c_1$ | 0.33 |
| | $\log x$-intercept | $c_2$ | 1.30 |
| | systematic bias | $\delta$ | 0.04 |
| | variance | $\sigma$ | 0.63 |
| extinction | species at equilibrium | $n$ | 5000 |
| | baseline extinction rate | $\beta$ | $1/n$ |
| | rate of extinction increase | $\rho$ | 0.025 |

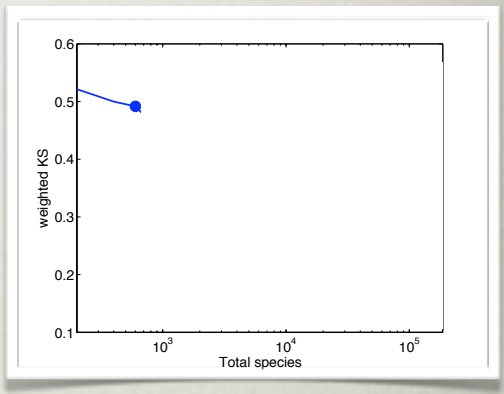
# Simulation

- ▼ empirical
- ● simulated

500 species



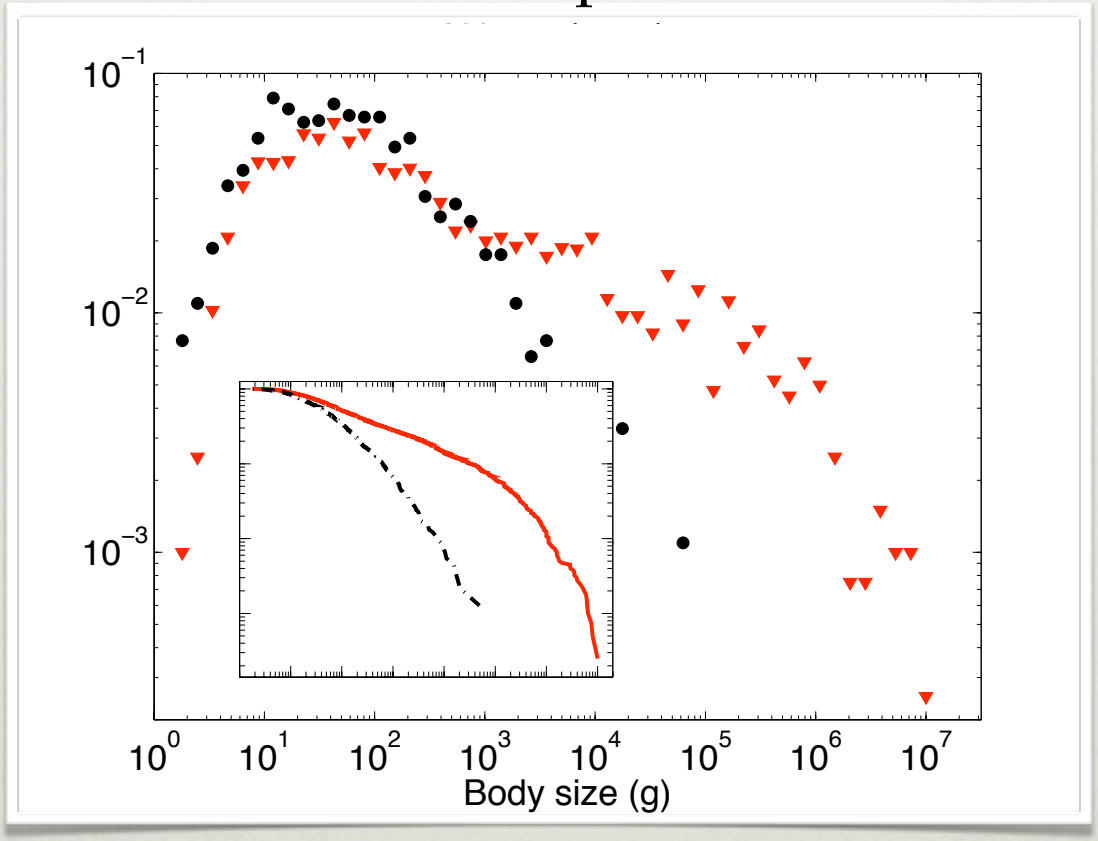



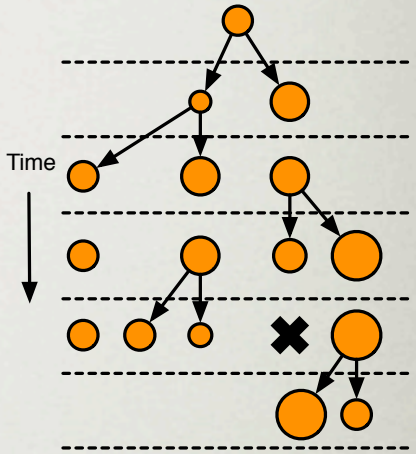



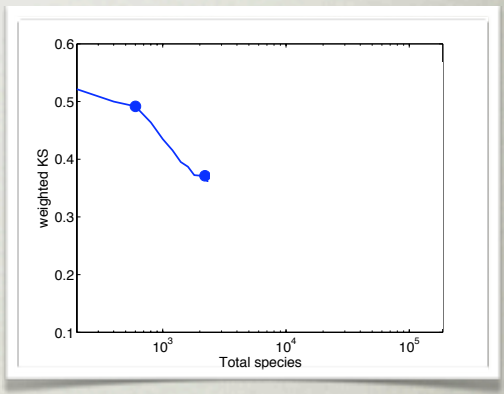
# Simulation

- empirical
- simulated

2000 species



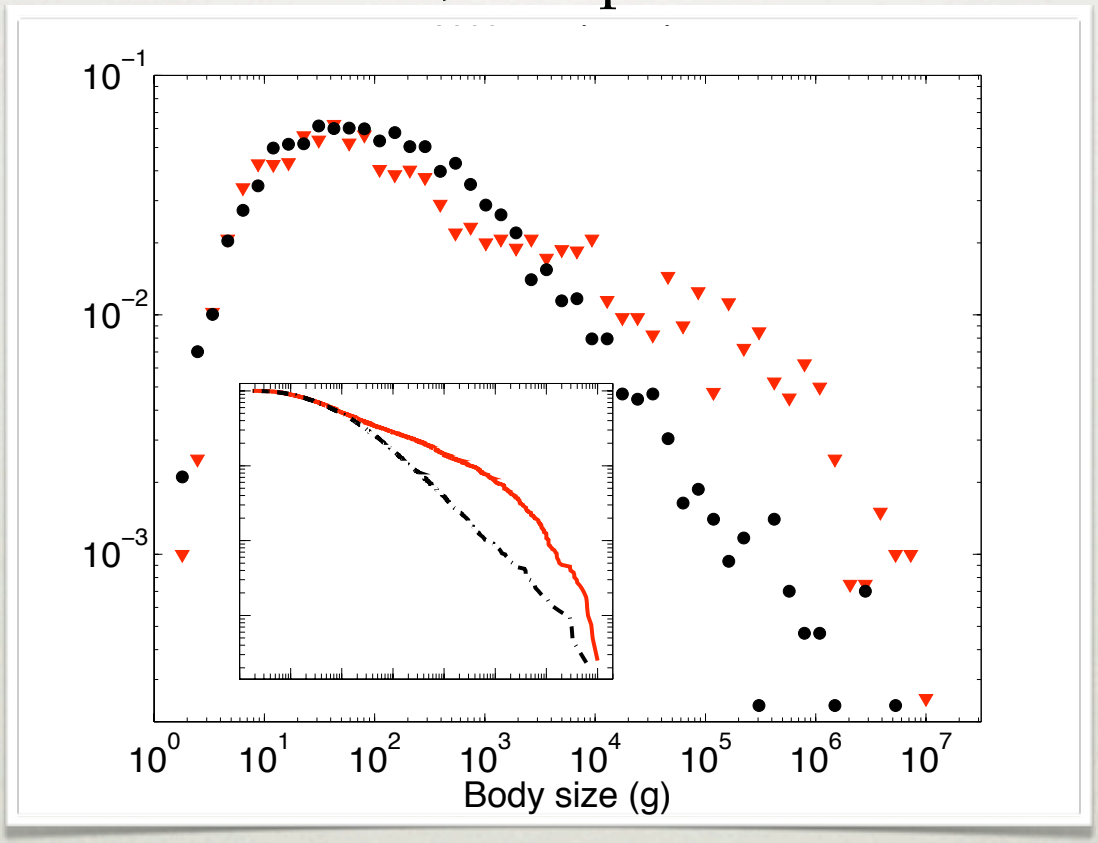



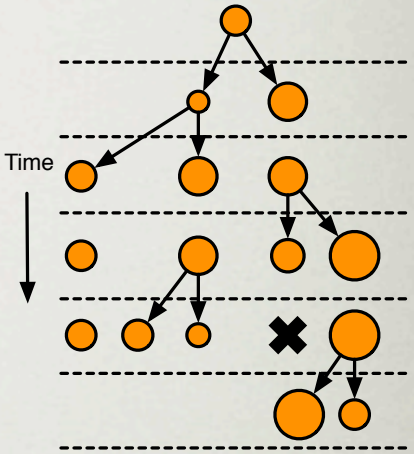



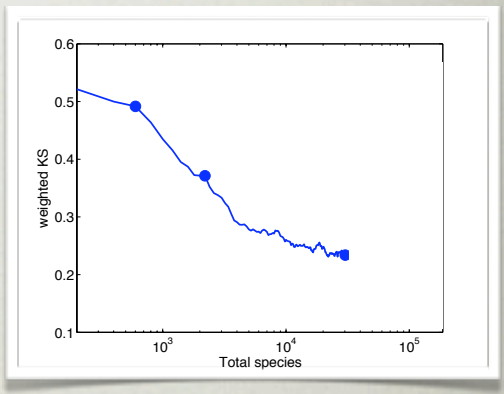
# Simulation

- empirical
- simulated

30,000 species



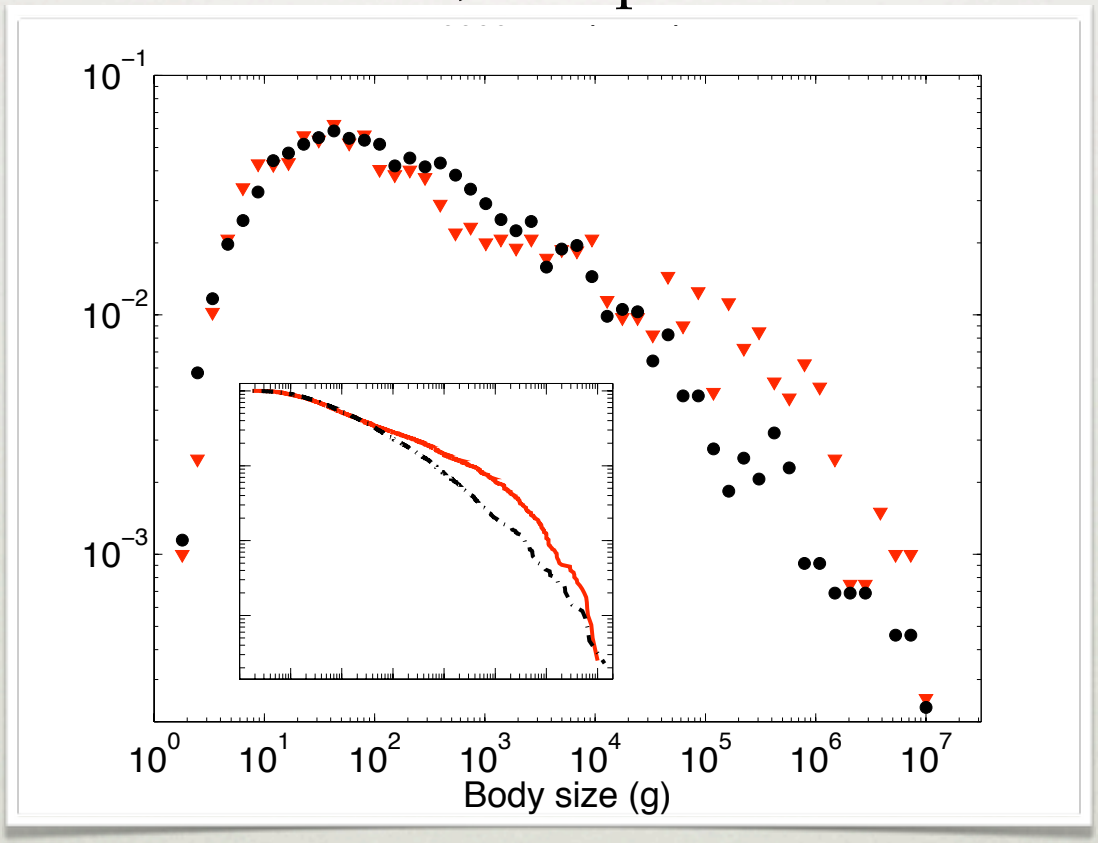



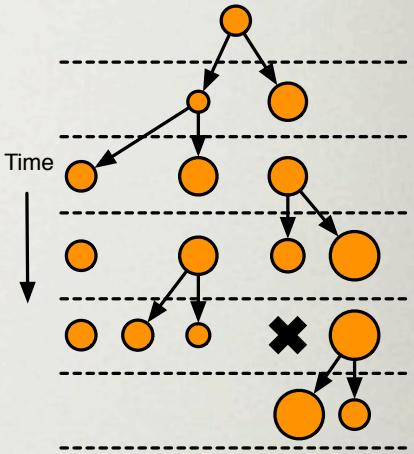



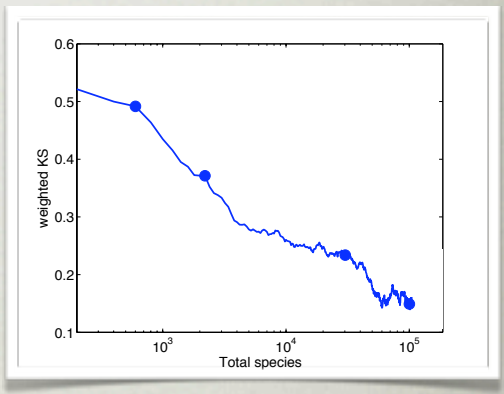
# Simulation

- ▼ empirical
- ● simulated

100,000 species



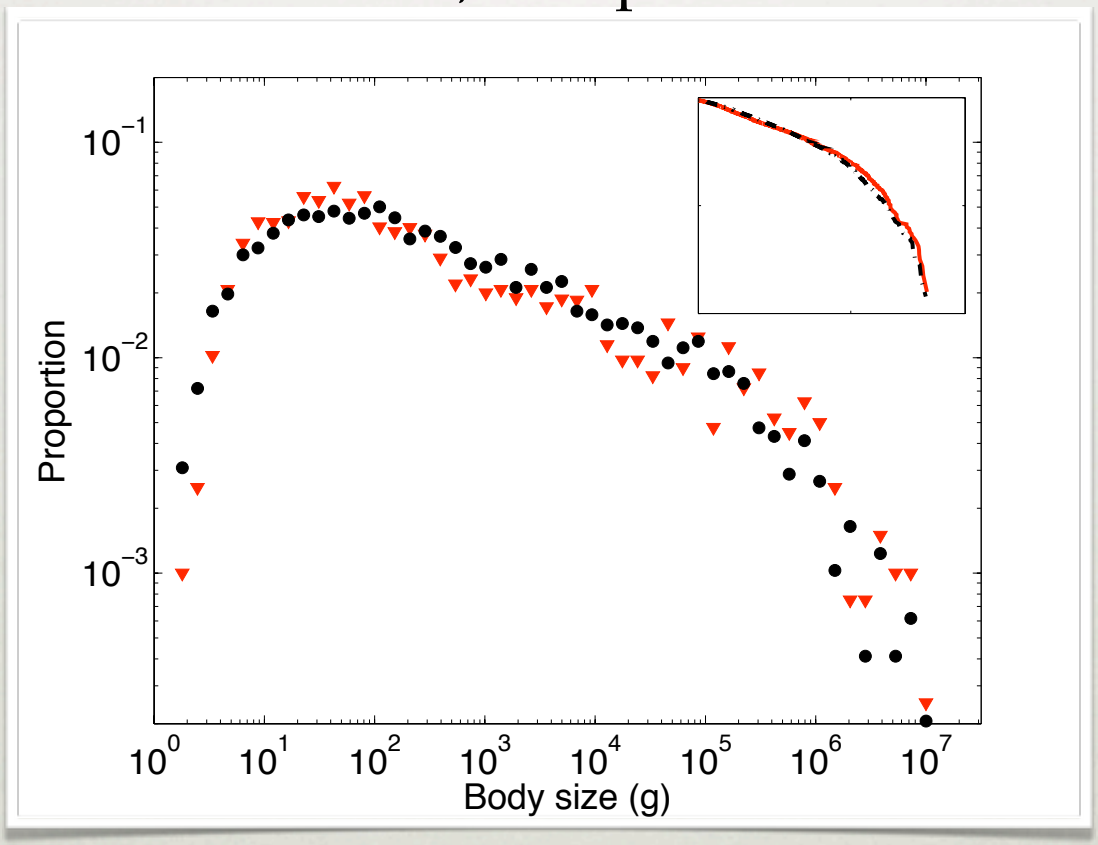



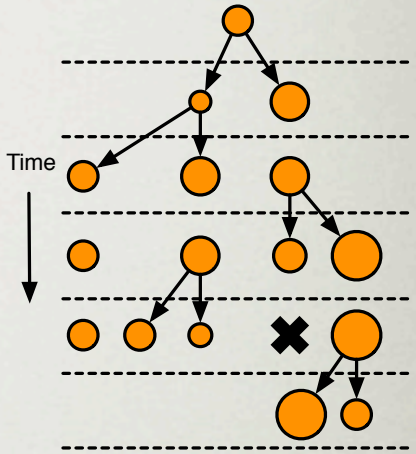



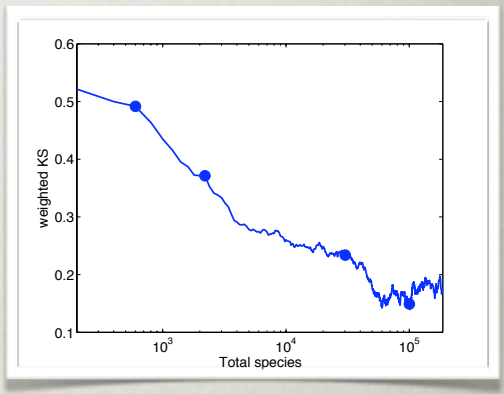
# Simulation

- ▼ empirical
- ● simulated

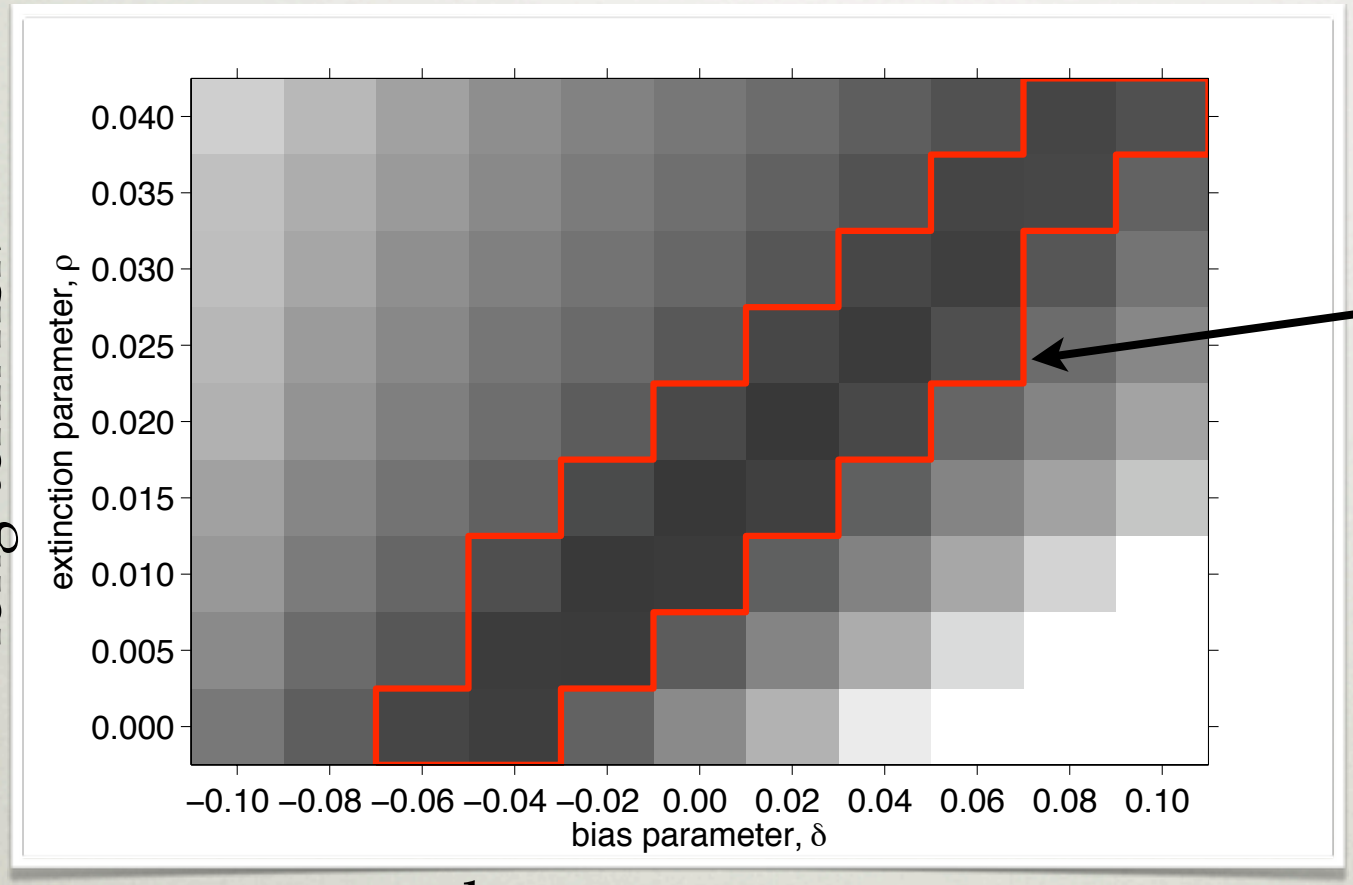
60 million years
180,000 species



# Short-term Gain vs. Long-term Risk

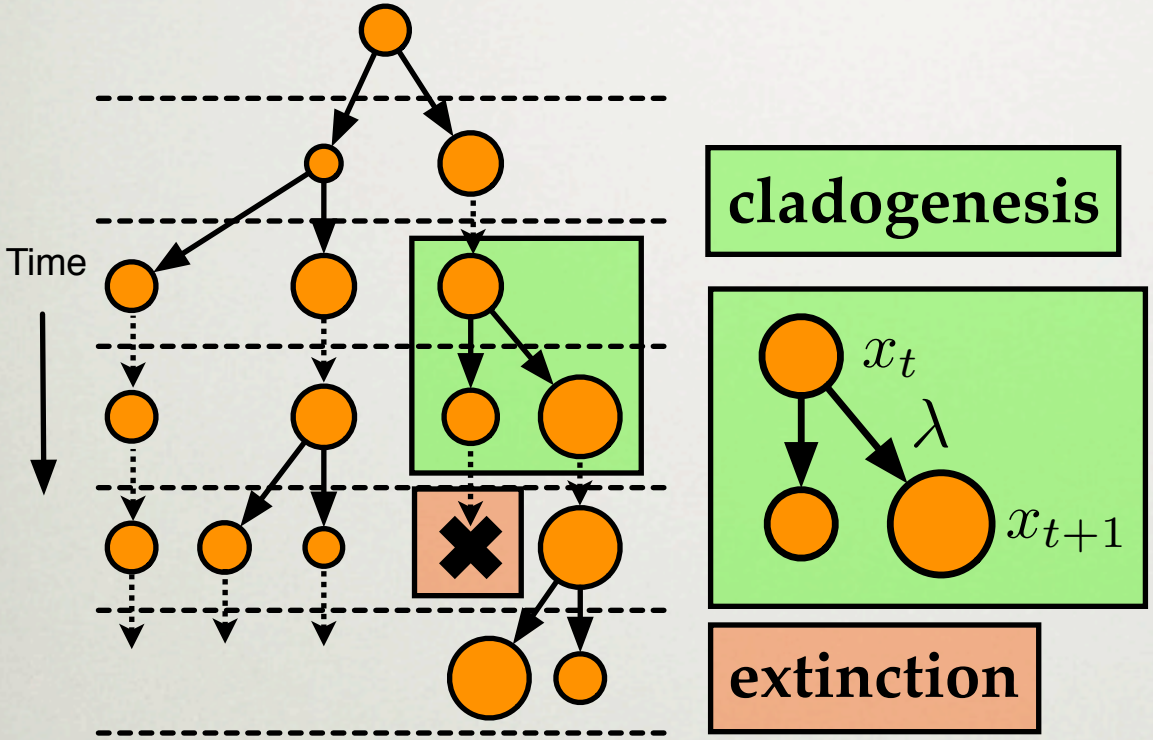



long-term risk

region of best fit

short-term gain

# Cladogenetic Model



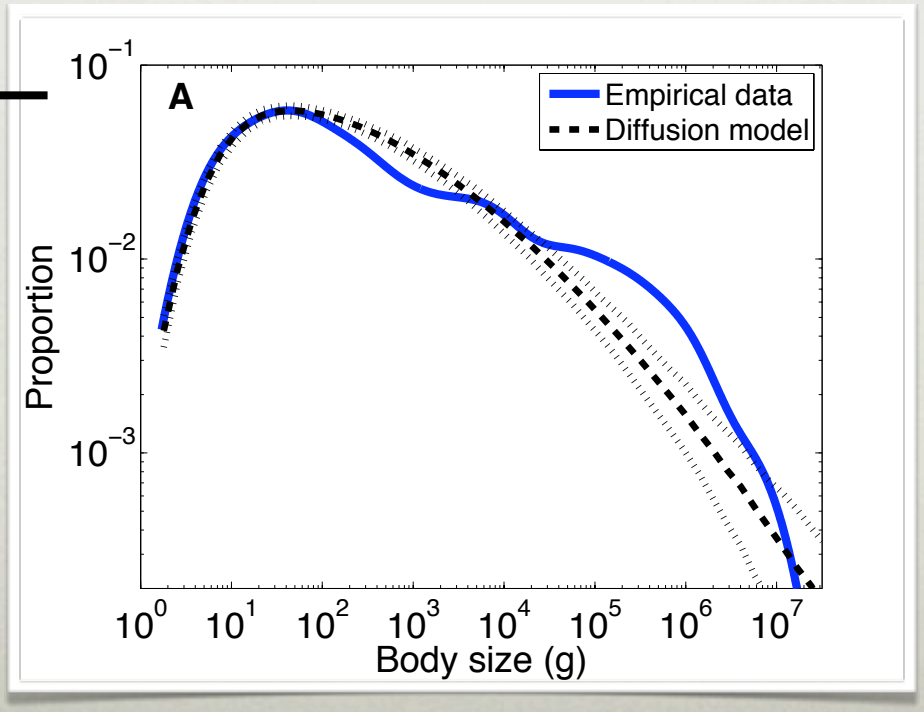

**model features**

- size-dependent fluctuations
- Cope's rule
- size-dependent extinction rate
- lower limit $x_{\min}$

**are all these features necessary?**

# Model Comparison

| model features | | | ⟨wKS⟩ | support |
|---|---|---|---|---|
| Cope's rule | size-dependent extinction | lower limit $x_{\min}$ | | |
| ■ | ■ | ■ | 0.181 | good |
| | ■ | ■ | 2.97 | poor |
| ■ | | | 11.72 | none |
| | ■ | | 10.37 | none |



# Analytic Version

**reaction-diffusion-convection equation:**

$$\frac{\partial c}{\partial t} + \underbrace{v\frac{\partial c}{\partial x}} = \underbrace{D\frac{\partial^2 c}{\partial x^2}} + \underbrace{(k - A - Bx)c}$$

**drift term (Cope's rule)** — **diffusion term** — **speciation and extinction**

**3 parameters:** $\beta = B/D$

$\mu = v/D$

$x_{\min}$

} **estimated from fossil data**

# Analytic Version

**Reaction-diffusion-convection equation*:**

$$\frac{\partial c}{\partial t} + v\frac{\partial c}{\partial x} = D\frac{\partial^2 c}{\partial x^2} + (k - A - Bx)c$$

**Solving yields size distribution:**

$$c(x,t) = \sum_n \mathcal{C}_n(x_0)\mathcal{C}_n(x)\mathrm{e}^{-\gamma_n t}$$

where

$$\mathcal{C}_n(x) \propto \mathrm{e}^{\mu x/2}\mathrm{Ai}\Big[z_n + (B/D)^{1/3}(x - x_{\min})\Big]$$

$$z_n = z_0 - \frac{\gamma_n}{D(B/D)^{2/3}}$$

* no “small-size bias” here

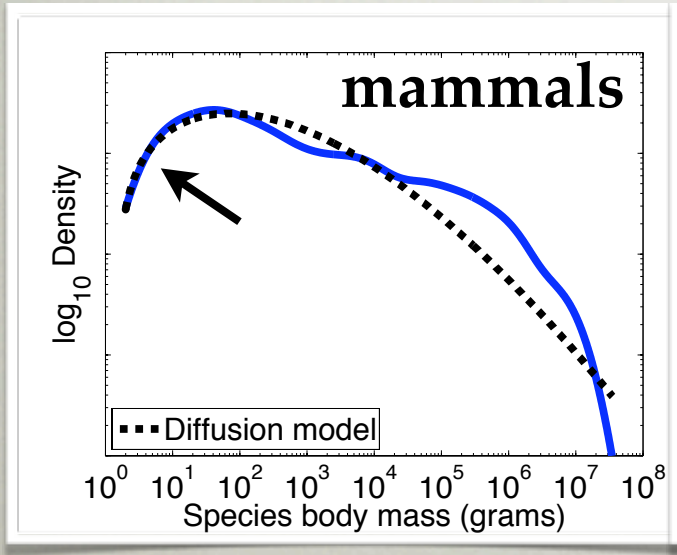
# Analytic Version

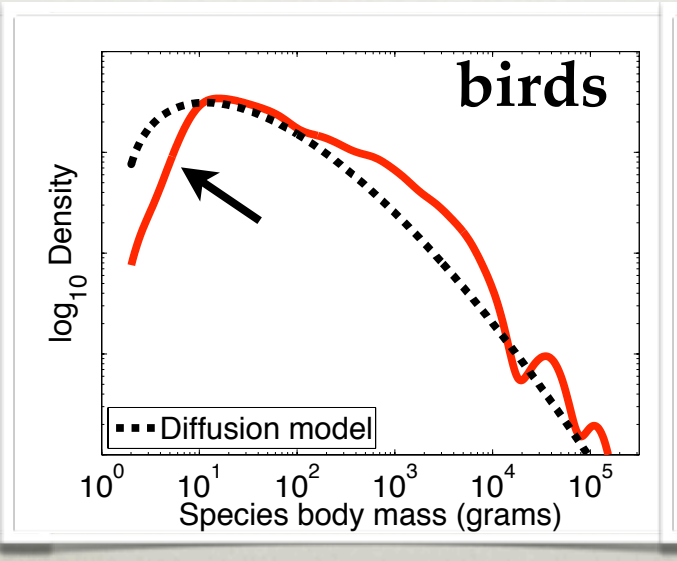
**Reaction-diffusion-convection equation*:**

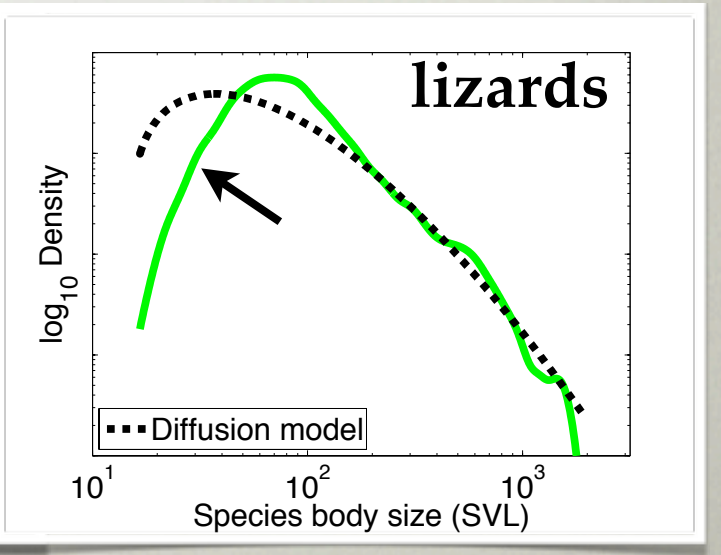
$$\frac{\partial c}{\partial t} + v\frac{\partial c}{\partial x} = D\frac{\partial^2 c}{\partial x^2} + (k - A - Bx)c$$

**Solving yields size distribution:**

$$\mathcal{C}_n(x) \propto e^{\mu x/2}\,\mathrm{Ai}\left[z_n + \beta^{1/3}(x - x_{\min})\right]$$



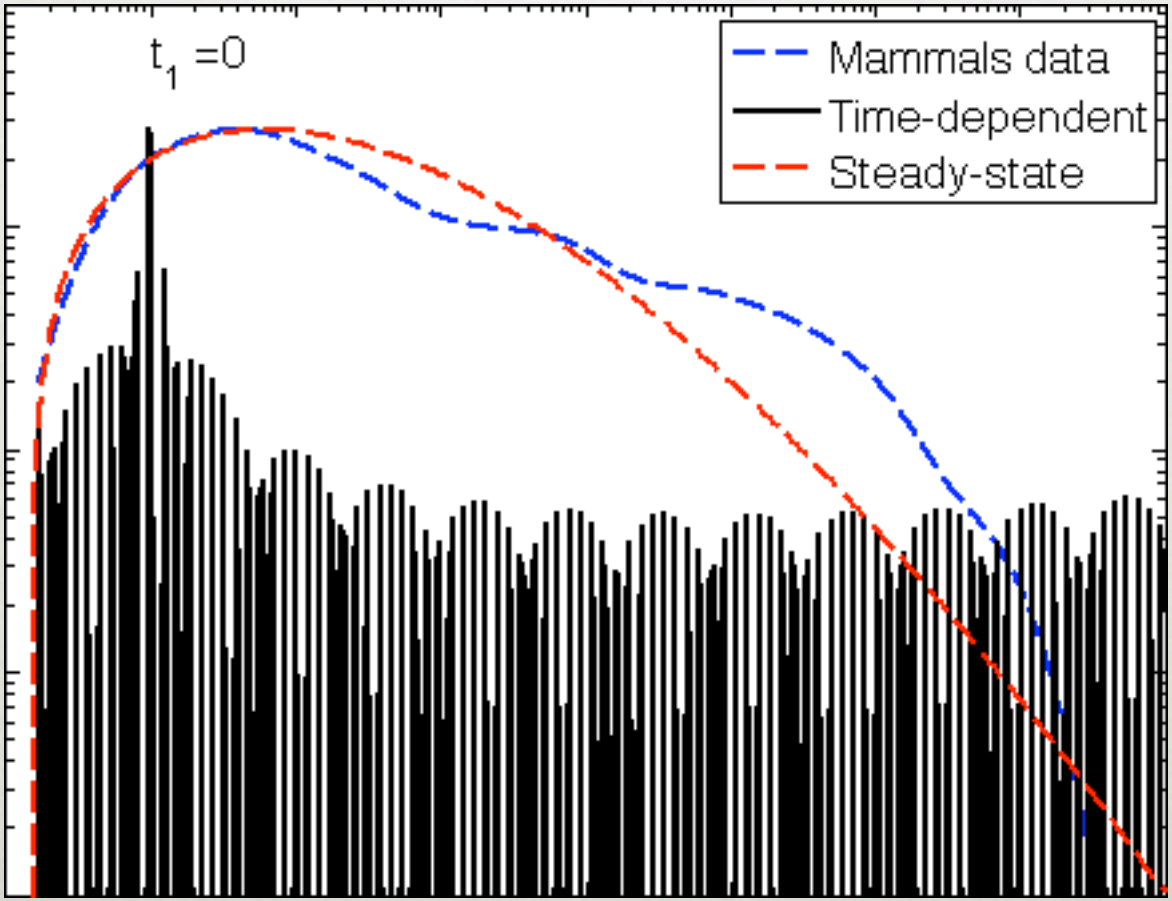

* no "small-size bias" here

# Size Diversification

simulate model dynamics

# Size Diversification

simulate model dynamics



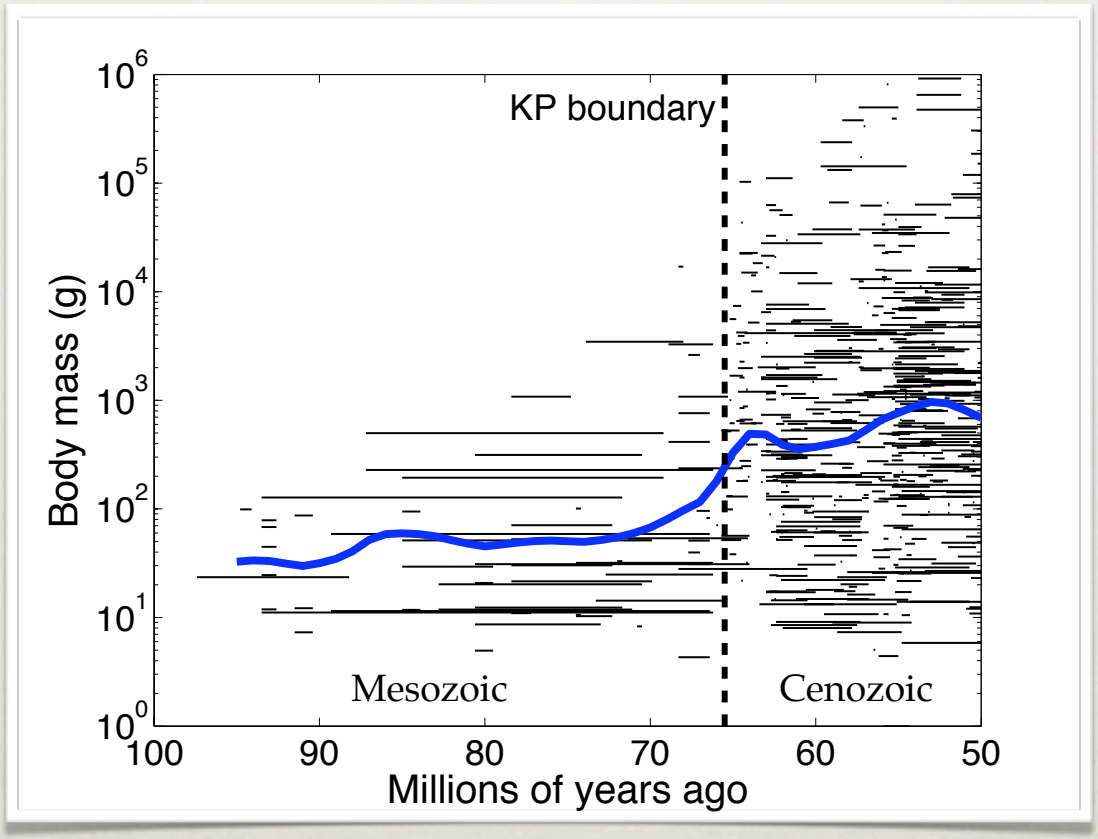

initially, 100,000 modes in eigen summation

# Size Diversification

but, do dynamics agree with fossil data?

# Size Diversification

but, do dynamics agree with fossil data?

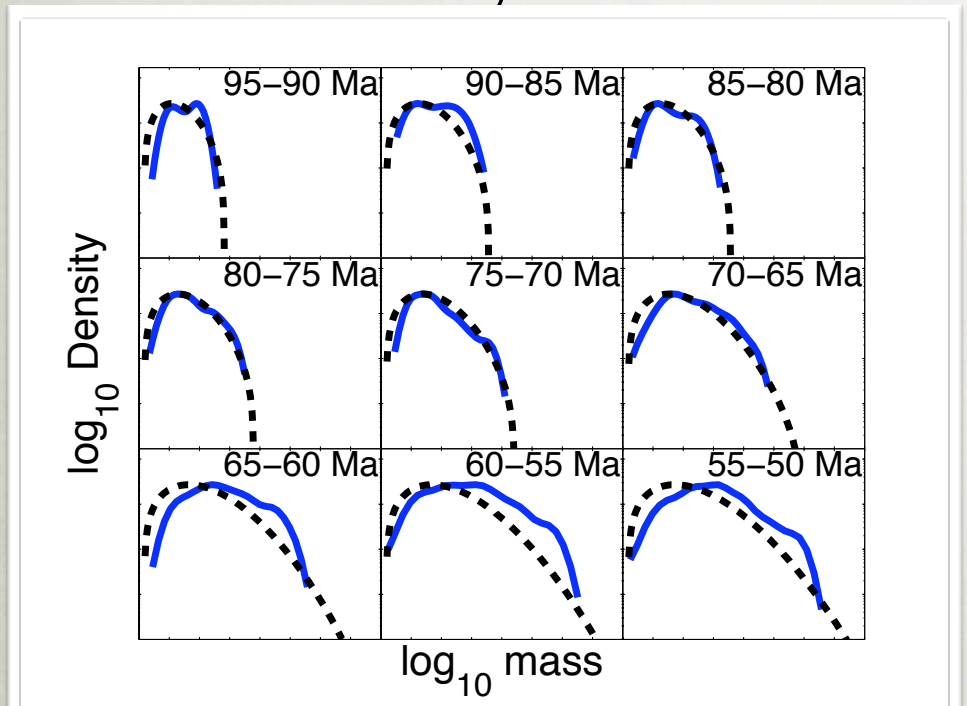



[North Am. terrestrial mammals]

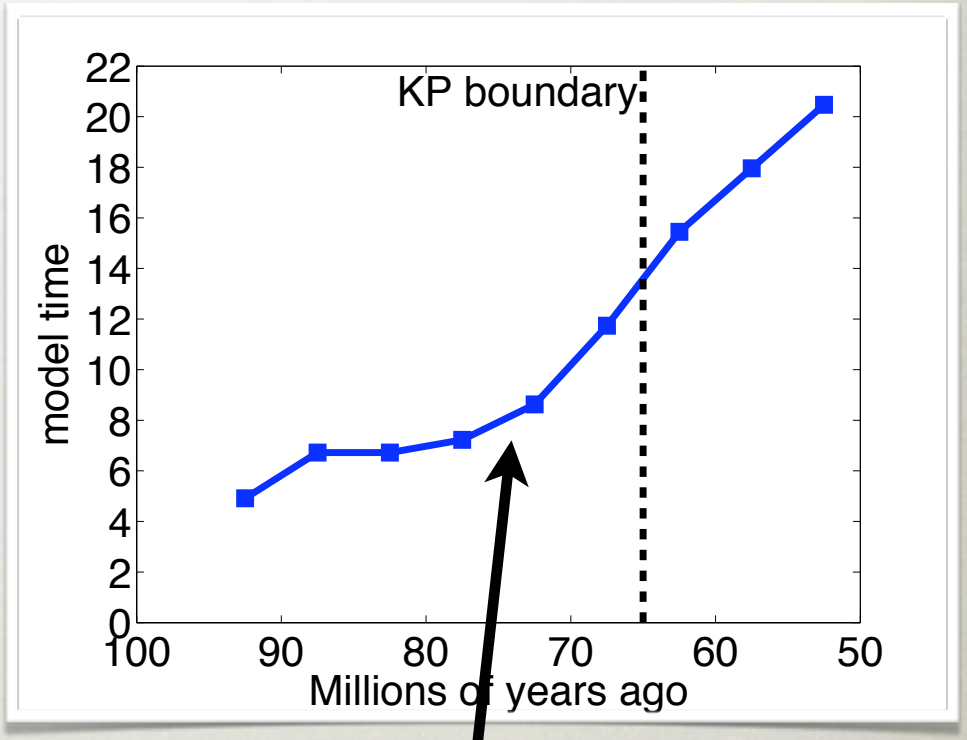
data from Alroy (2000)

# Size Diversification

**model dynamics**




**model time**




agrees with molecular-clocks for genetic diversification

# Thursday

Southern Right whale (photo credit: Brian Skerry)