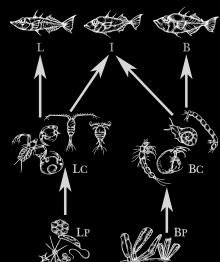
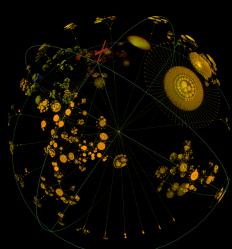


Causes and Effects of Adaptive Radiation



Luke J. Harmon
University of Idaho

Causes and Effects of AR

- Introduction: Filling the adaptive zone
- Part I: Fish as pond “sunglasses”
- Part II: The delayed rise of present-day... everything
- Conclusion: A paradox in reverse

Introduction: Filling the adaptive zone



Simpson 1953

Introduction: Filling the adaptive zone



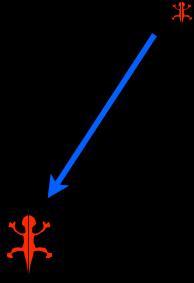
Photos by A. Hendry

- Adaptive Radiation:
- The evolution of ecological disparity within a rapidly multiplying lineage

Schlüter 2001

A Model of Adaptive Radiation

- Species enters a new adaptive zone
- Rates of diversification are initially high due to ecological opportunity
- Those rates slow through time



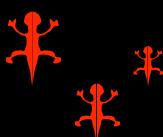
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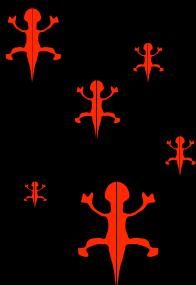
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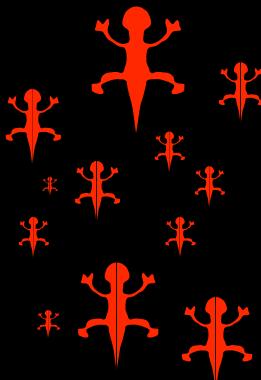
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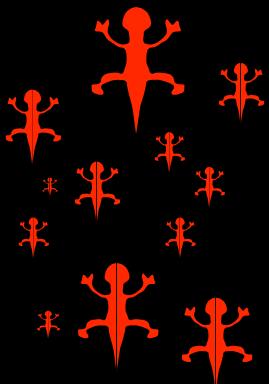
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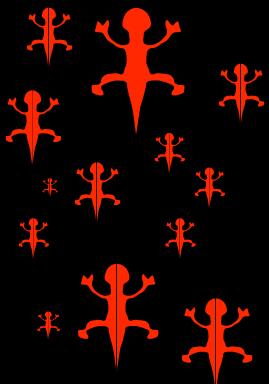
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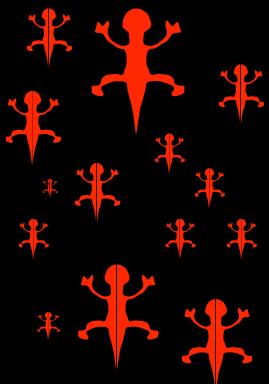
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A Model of Adaptive Radiation

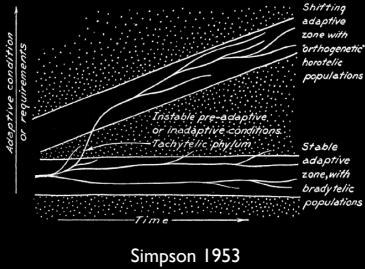
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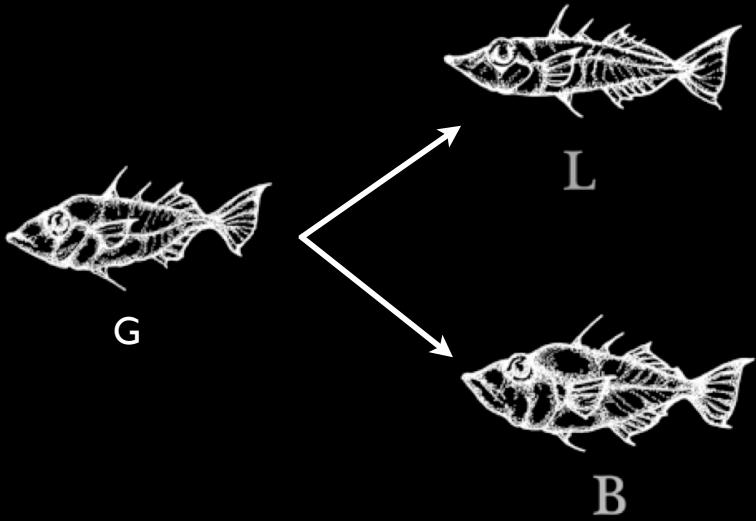
Causes and Effects of AR

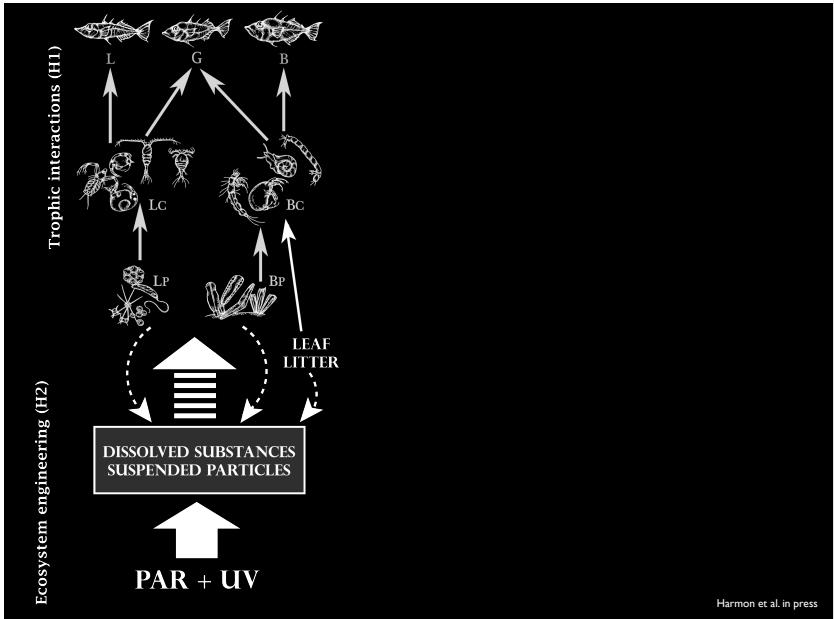
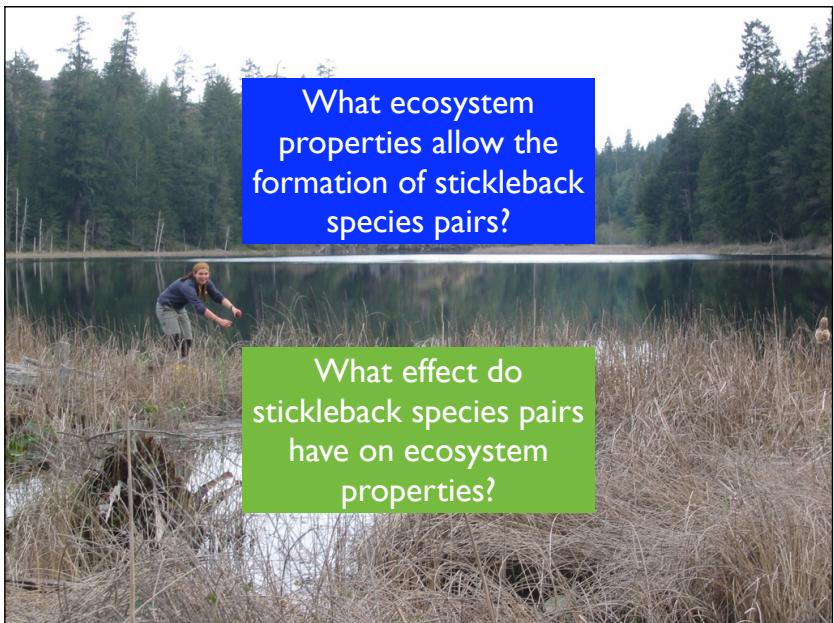
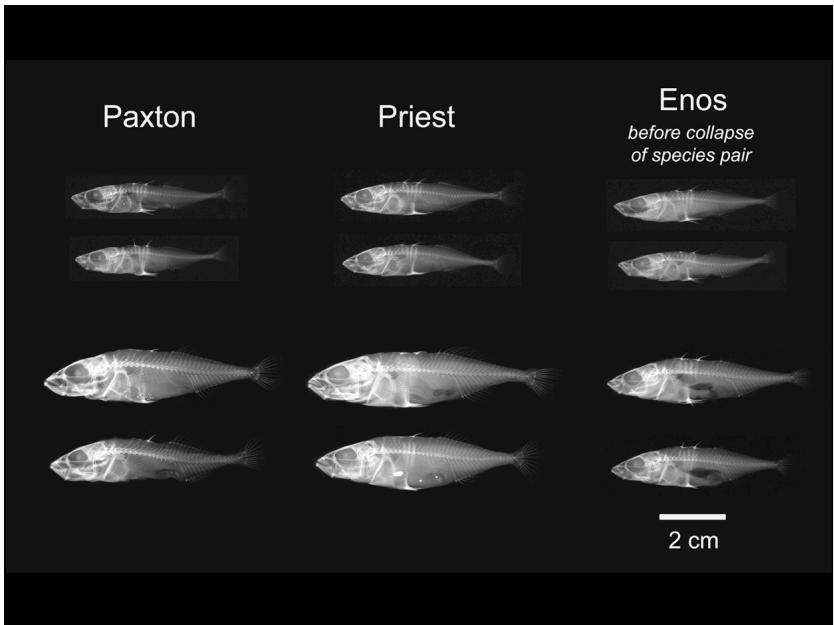
- Introduction: Filling the adaptive zone
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Does diversification matter?



- Most focus on the effects of the environment on adaptive radiation
- Might diversification, from one species to many, affect ecosystems and how they function?





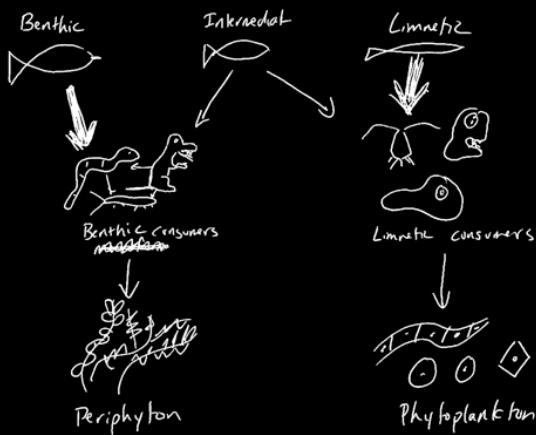
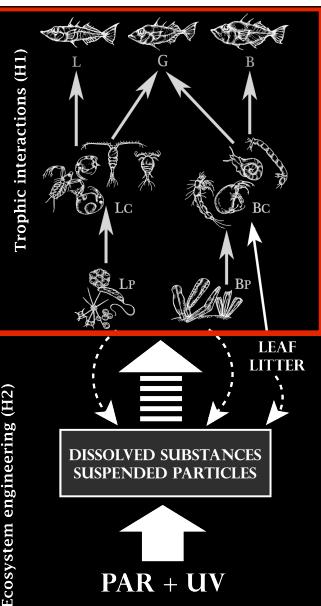


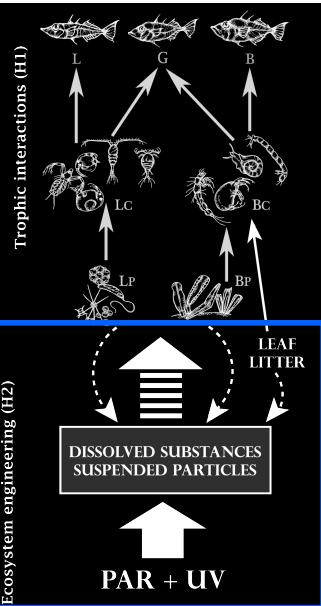
Figure 1. Hypothesized trophic structure of mesocosms.



Hypothesis 1: Trophic interactions

- The strength of species effects will increase through the course of adaptive radiation
- Trophic cascades will increase in magnitude as generalists evolve into multiple specialists

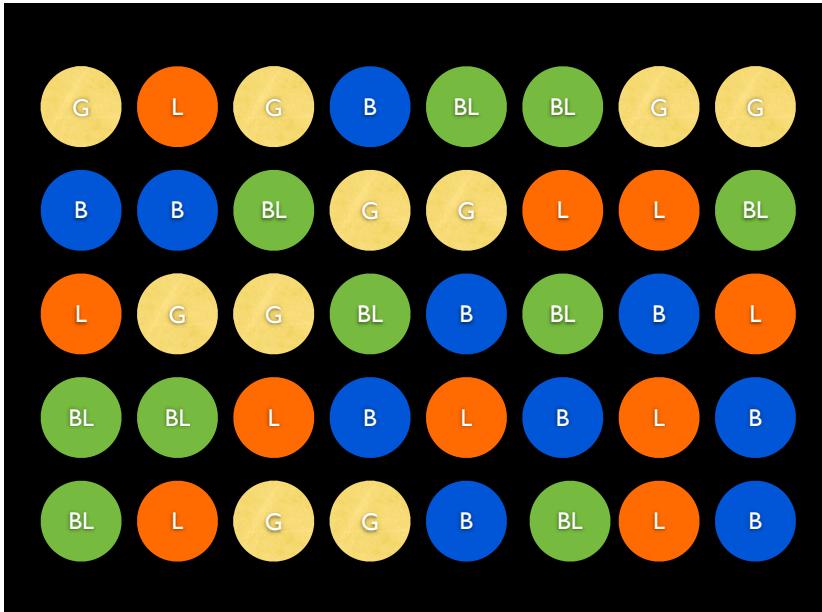
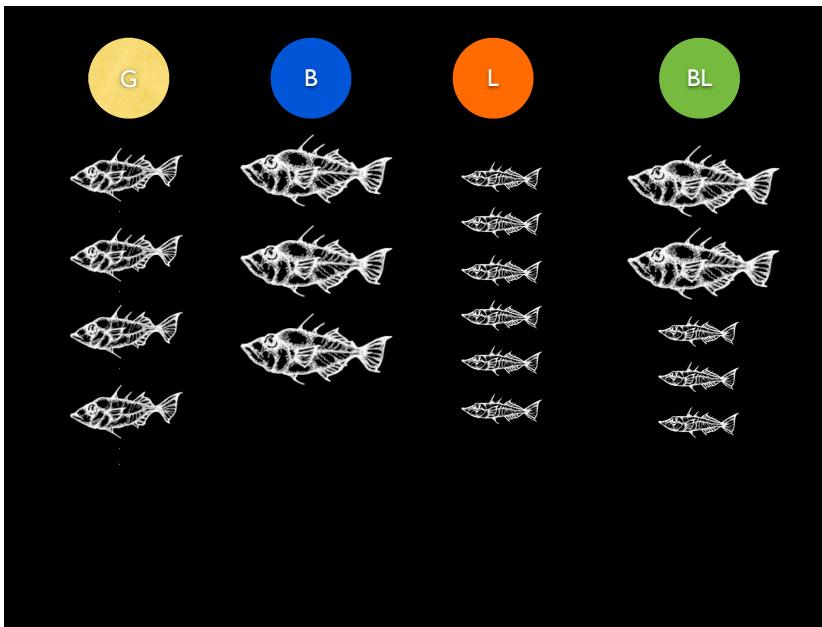
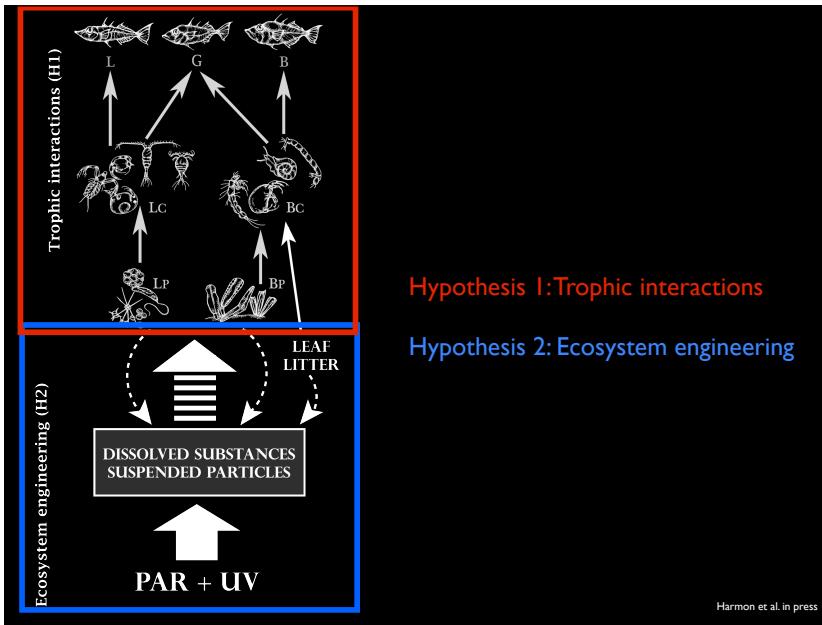
Harmon et al. in press

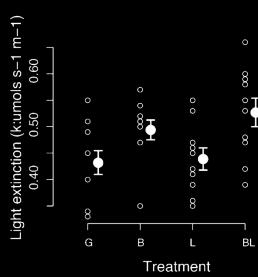
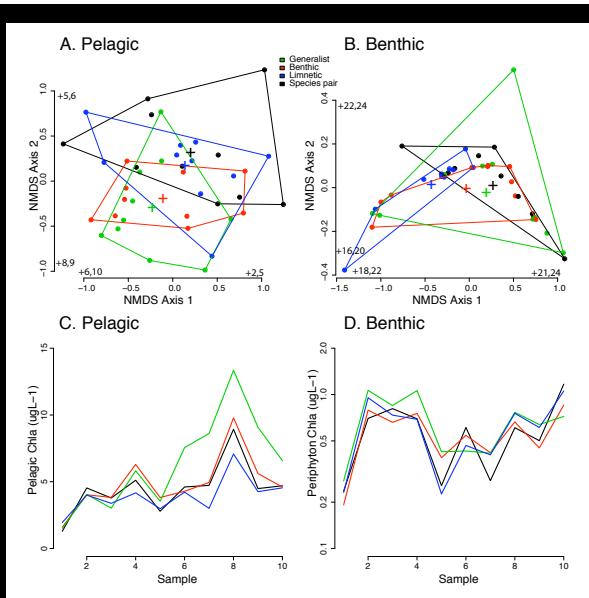


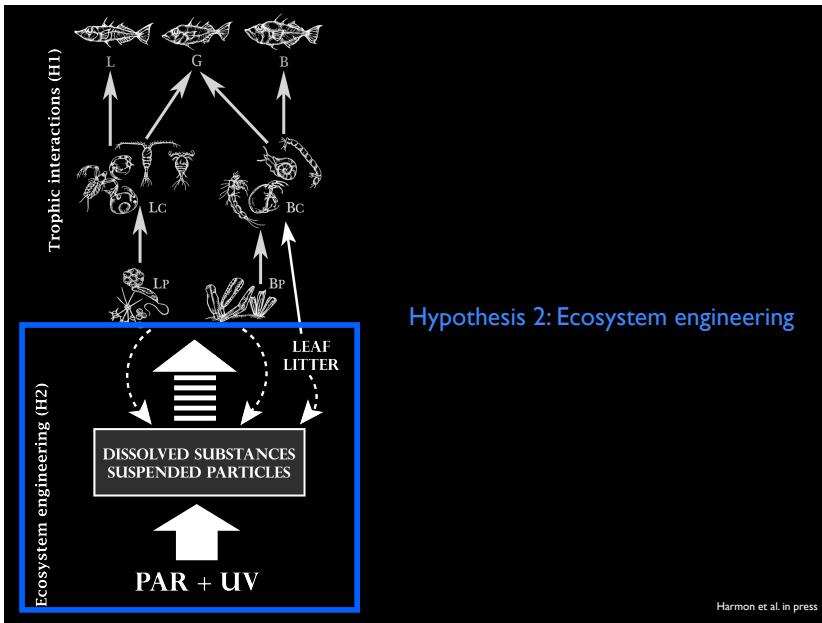
Hypothesis 2: Ecosystem engineering

- Species' effects will depend on how they alter their environment
- Effects will depend on species composition but in complex ways

Harmon et al. in press





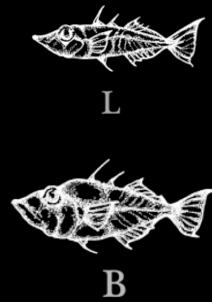


Hypothesis 2: Ecosystem engineering

Harmon et al. in press

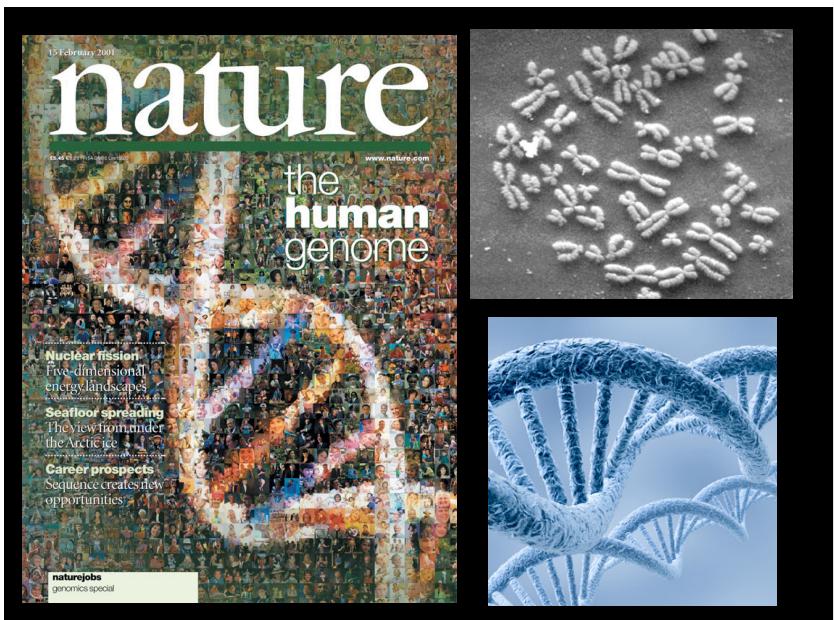
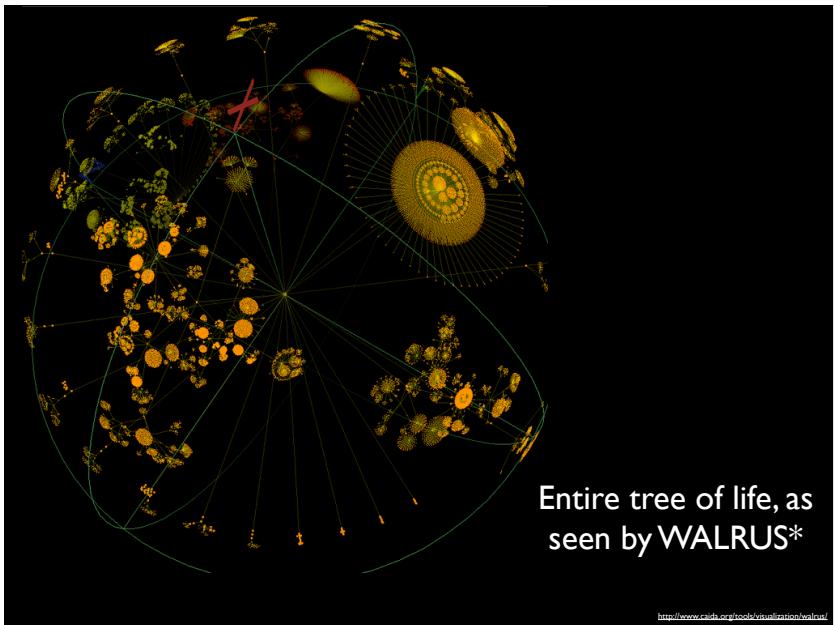
Does diversification matter?

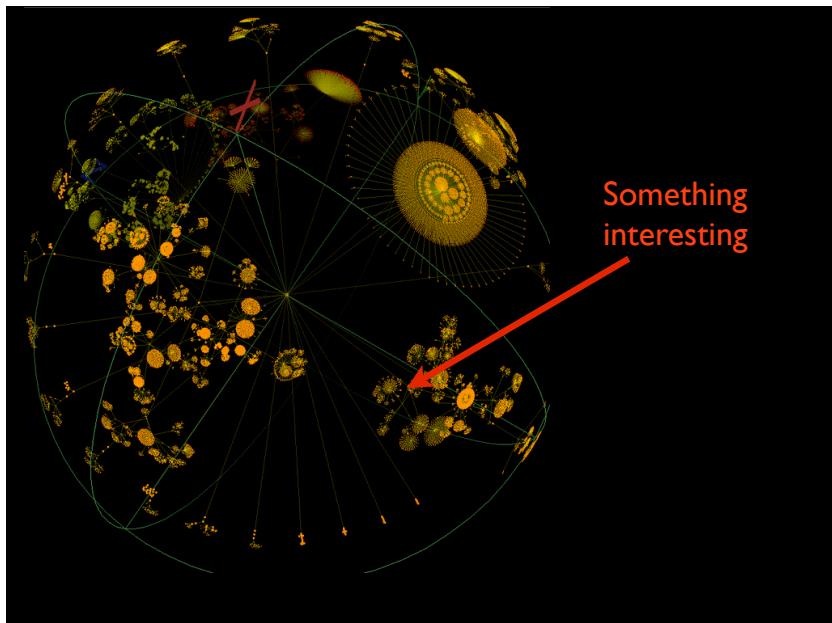
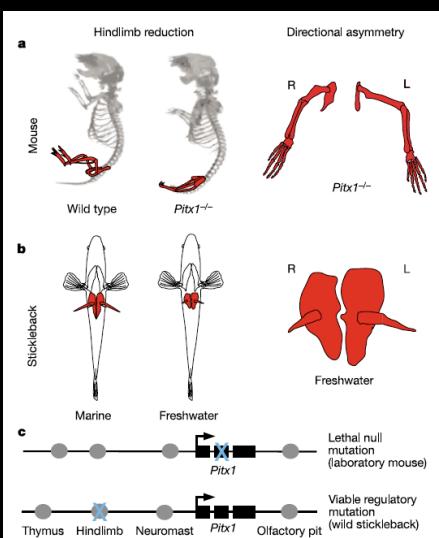
- Diversification matters for ecosystems
- Rapid radiation can have tremendous effects on ecosystem function



Causes and Effects of AR

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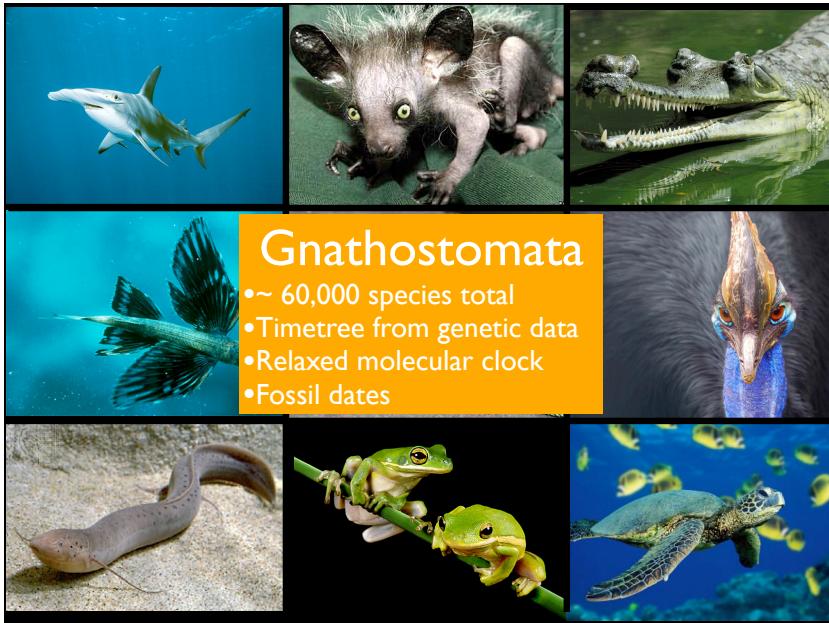




Locating Adaptive Radiations in the ToL

- What are the average rates of speciation and extinction across the tree of life?
- Can we identify groups that stand out against this background?

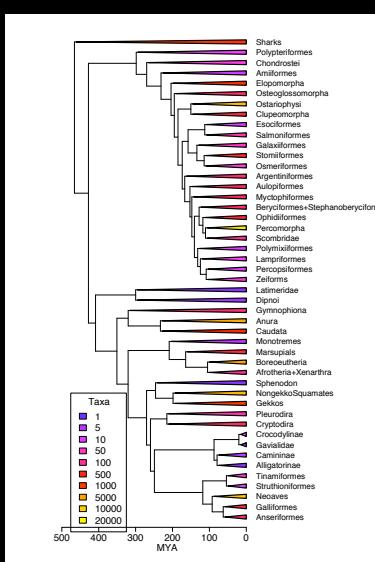
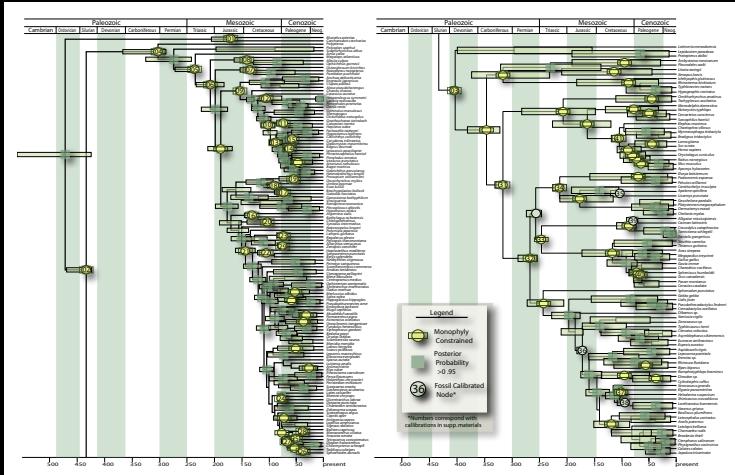


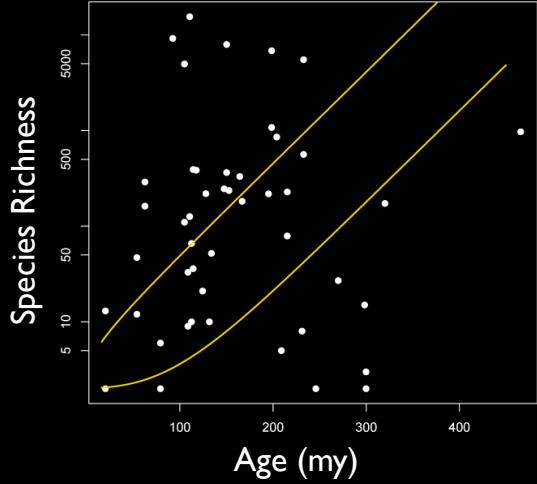
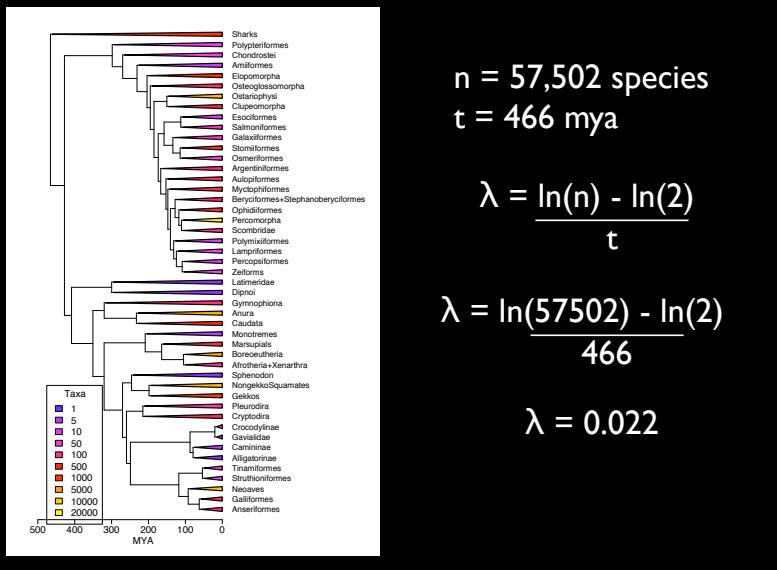
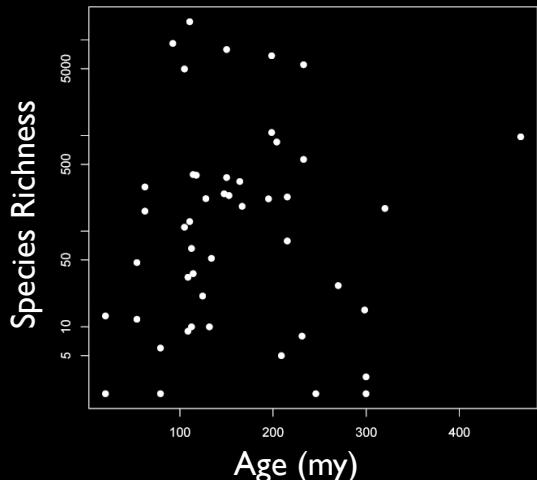


Gnathostomata

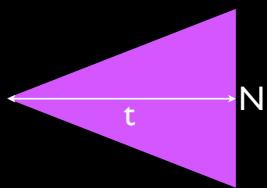
- ~ 60,000 species total
- Timetree from genetic data
- Relaxed molecular clock
- Fossil dates

Sharks, Fish... and Tetrapods



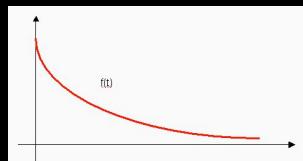


Combining Phylogenetic and Taxonomic Data



Combining Phylogenetic and Taxonomic Data

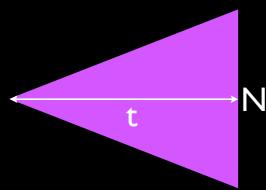
- Phylogenetic branch lengths
- Intervals between speciation events are waiting times
- Under pure-birth model, these are drawn from an exponential distribution



Exponential distribution

Combining Phylogenetic and Taxonomic Data

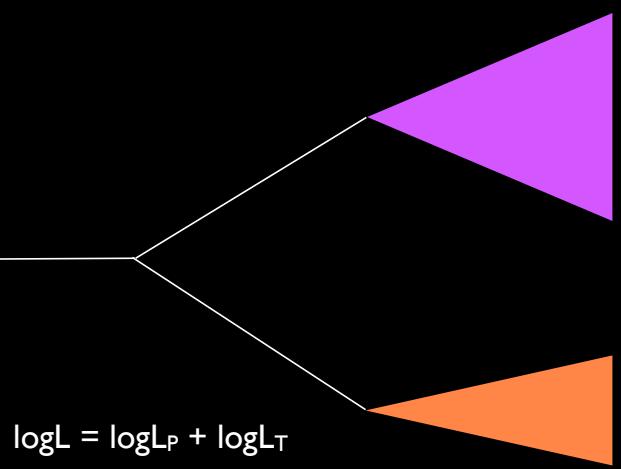
- Use clade diversity (N), age (t), rates of speciation (λ), extinction (μ)
- Diversity drawn from a particular distribution



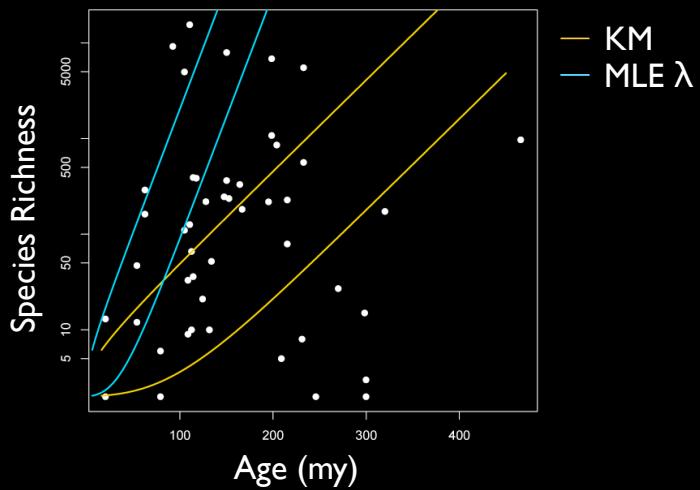
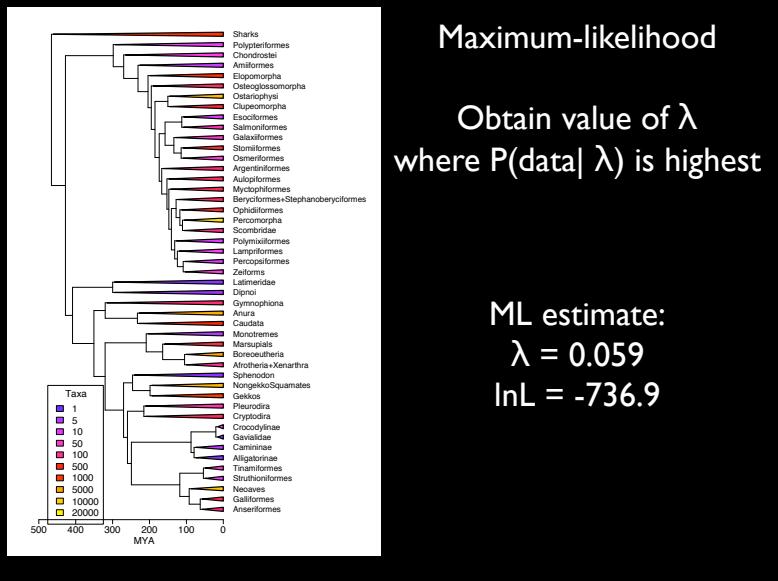
$$\text{Prob}[N(t) = 0] = \alpha_r^r, \text{ and}$$
$$\text{Prob}[N(t) = i] = \sum_{j=0}^{\min(i,r)} \binom{a}{j} \binom{a+i-j-1}{1} \times \alpha^{a-j} \beta^{i-j} (1-\alpha-\beta)^j, \quad (i \geq 1),$$

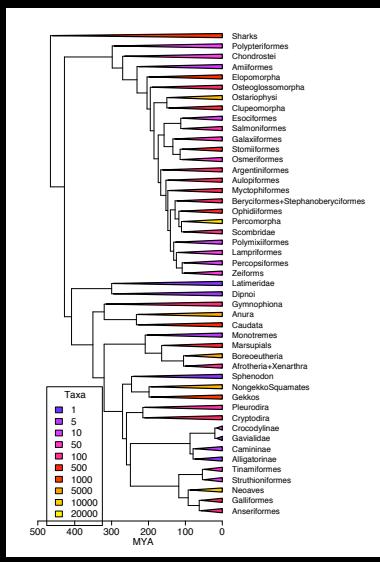
where

$$\alpha_r = \epsilon \beta_r \quad \text{and} \quad r = \lambda - \mu$$
$$\beta_r = \frac{e^{rt} - 1}{e^{rt} - \epsilon} \quad \epsilon = \mu/\lambda$$



Rabosky et al. 2007





Maximum-likelihood

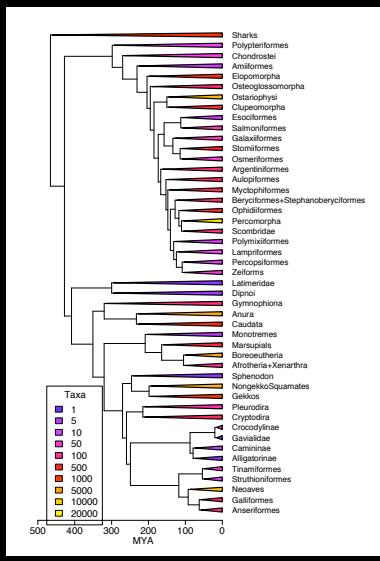
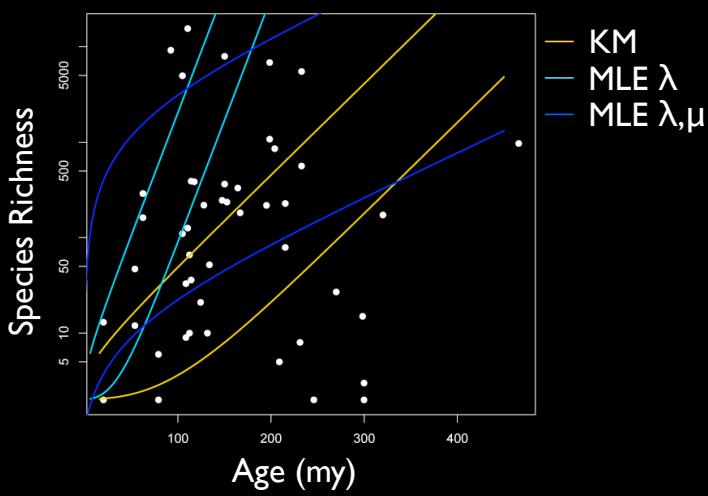
Obtain value of λ and μ
where $P(\text{data} | \lambda, \mu)$ is highest

ML estimates:

$$\lambda = 5.1$$

$$\mu = 5.0$$

$$\ln L = -578$$



Which Clades Stand Out?

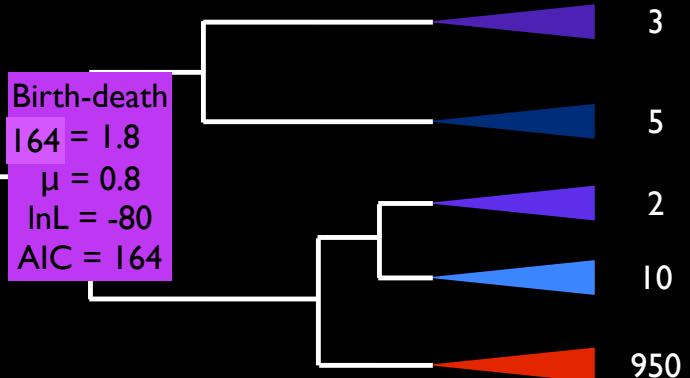
- Given the overall model, which clades stand out as having distinct patterns of diversification?
- Can we identify the “adaptive radiations” and the “living fossils”?

MEDUSA method

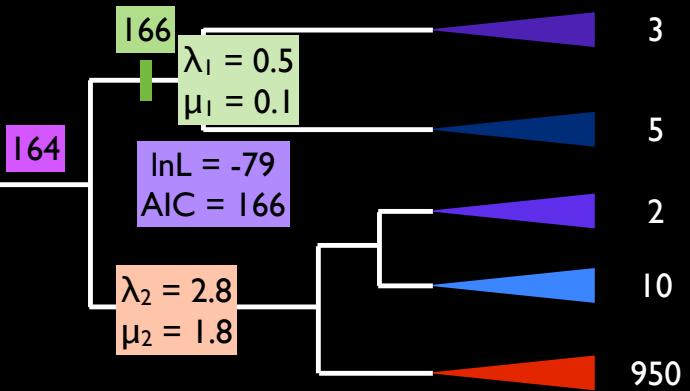
Modeling
Evolutionary
Diversification
Using
Stepwise
AIC



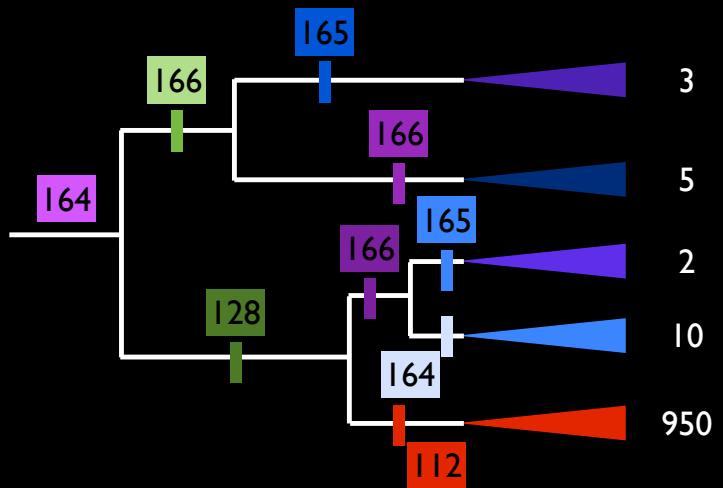
MEDUSA method



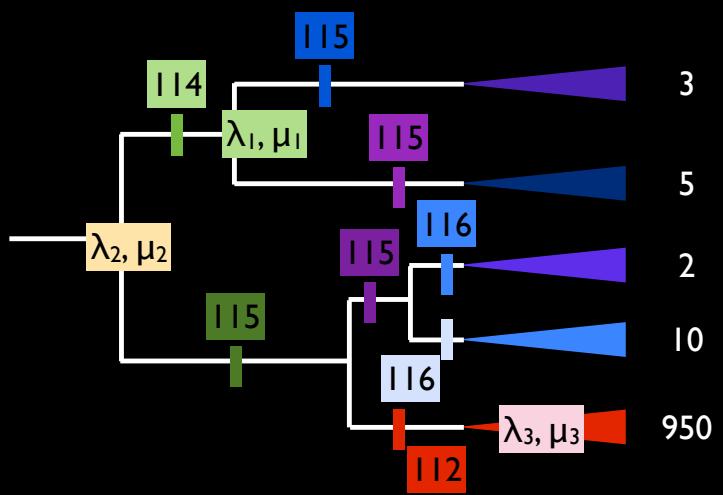
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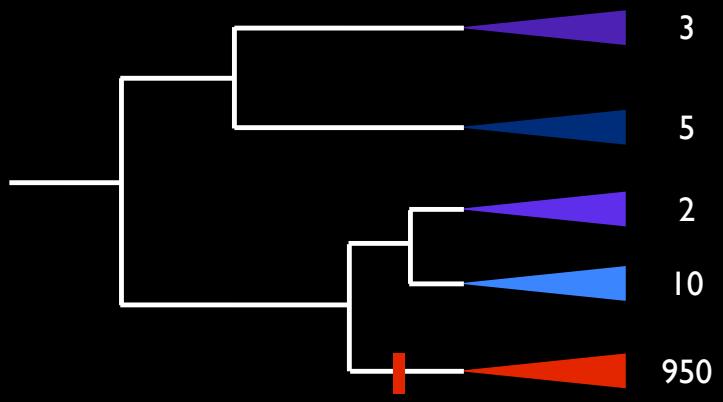
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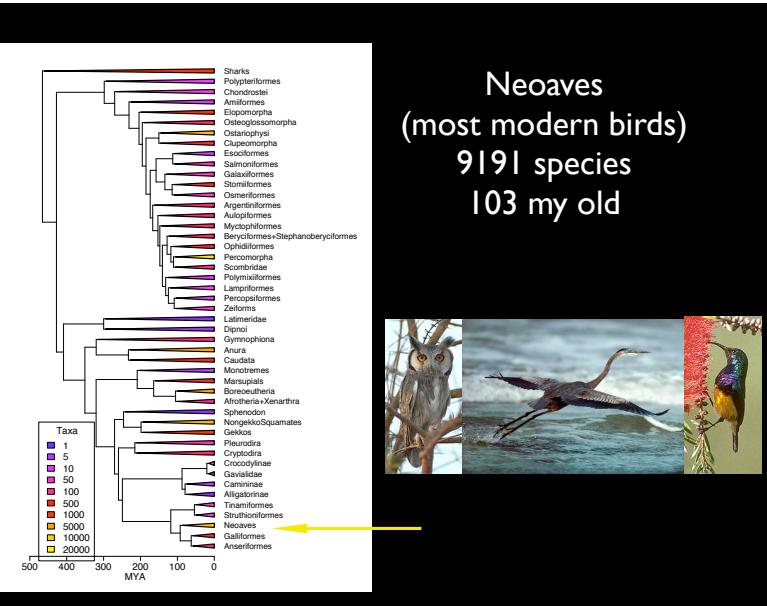
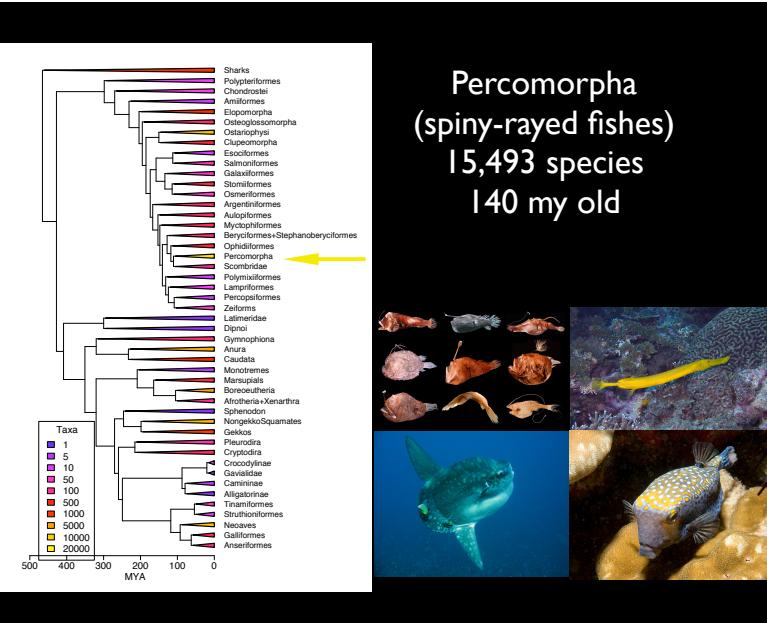
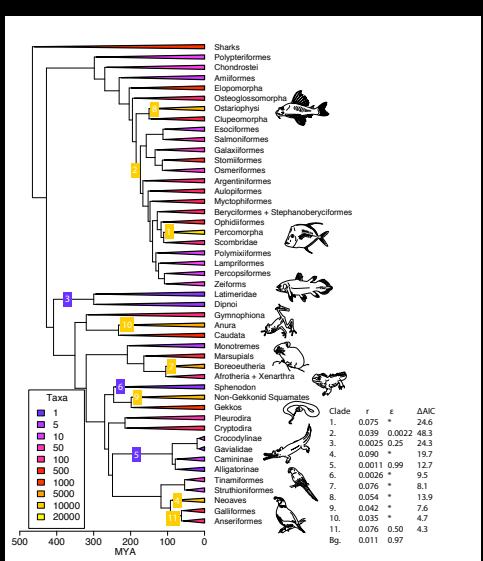


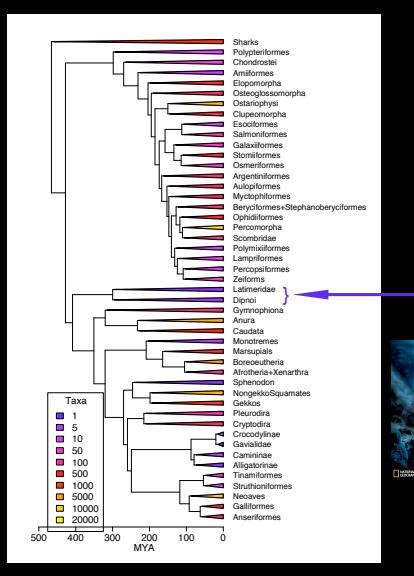
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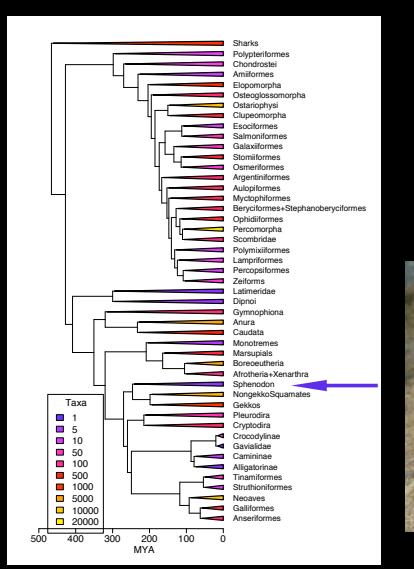
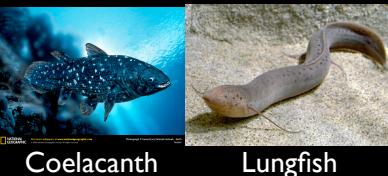
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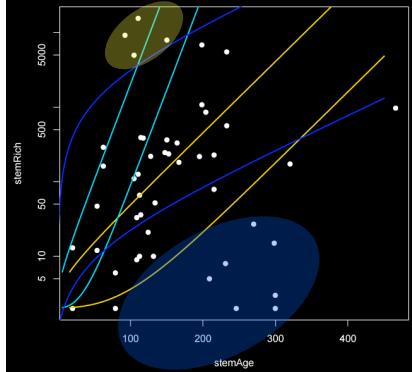
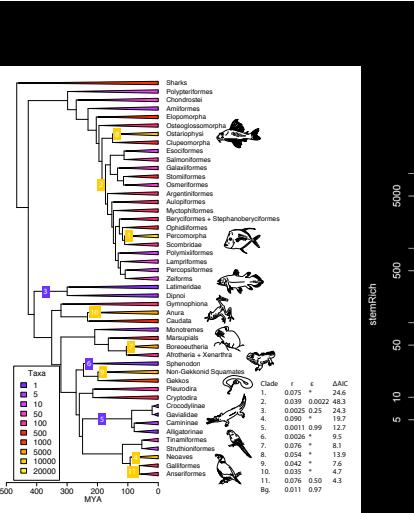




**Latimeridae (Coelacanth)
+ Dipnoi (Lungfish)**
 $3+2=5$ species
421 my old

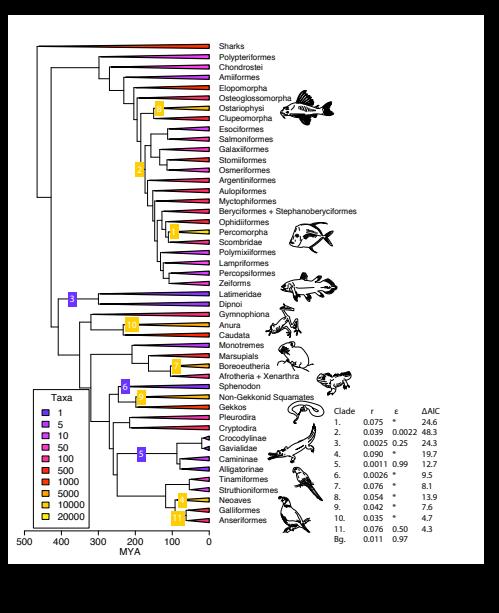


**Sphenodon
(tuatara)**
2 species
248 my old



Delayed rise:

Most diverse groups have relatively depauperate sister clades that share common “key characters”



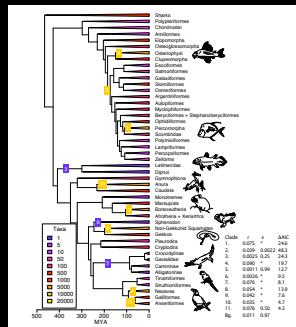
Living Fossils

- Old, depauperate groups are the real mystery
- Greatly reduced speciation and extinction required for long periods of time



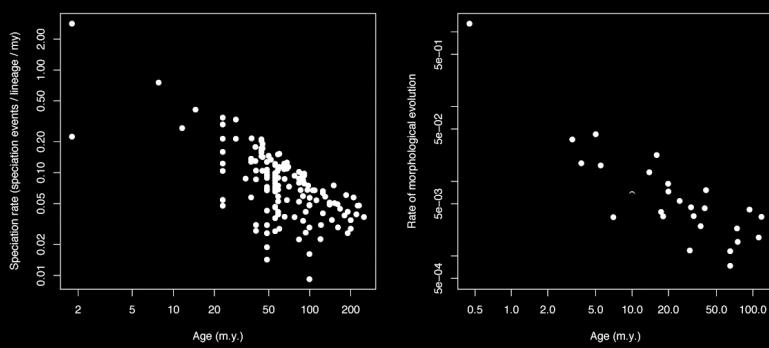
The “delayed rise”

- There have been high turnover rates through the history of this large clade
- Groups often experience a “delayed rise” following evolution of key characters
- Living fossils are a deep mystery in macroevolution



Causes and Effects of AR

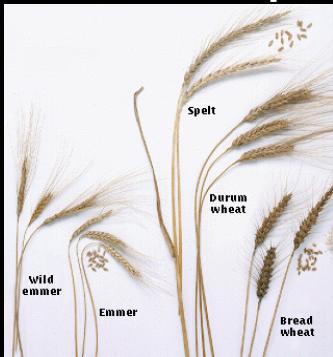
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Paradox of Macroevolution?

- Scaling of rates through time is evidence that common models of evolution (Brownian motion, pure birth) are wrong
- Both speciation and phenotypic change appear extremely rapid when we look closely
- Why is there so *little* diversity on the earth?

Implications



Domestication



Evolution of Resistance

Acknowledgements

- Harmon, Alfaro, Losos, and Schluter labs
 - NCEAS and NESCent
 - Various funding sources

