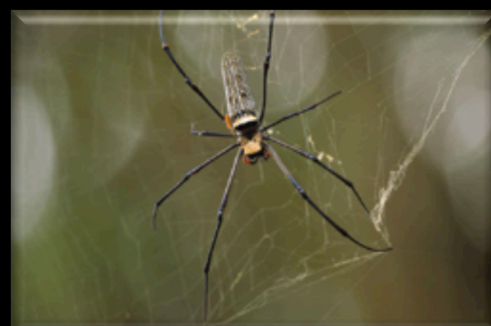
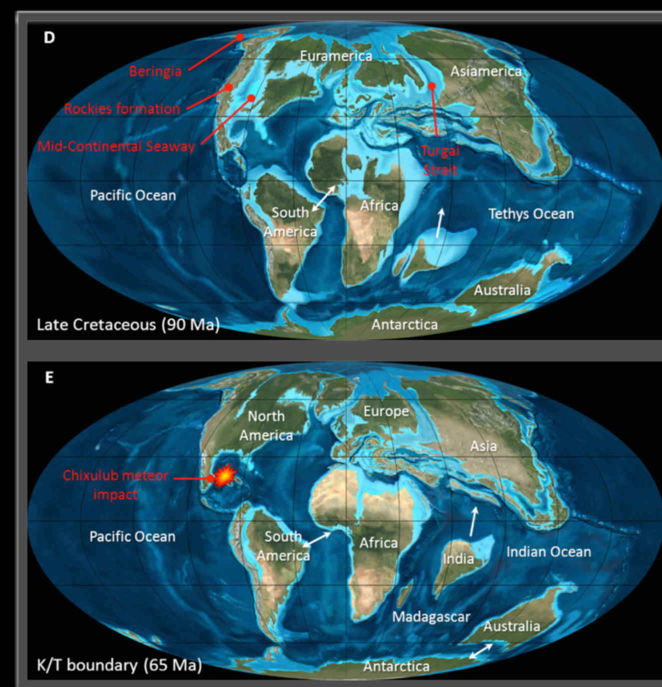
Paris,
February 27, 2013

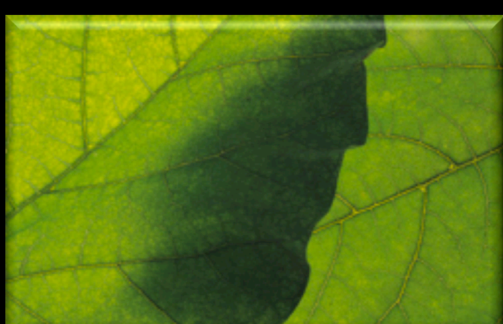
Macroevolutionary perspectives to environmental change

Fabien Condamine

CNRS, UMR 7641 Centre de Mathématiques Appliquées (Ecole Polytechnique)







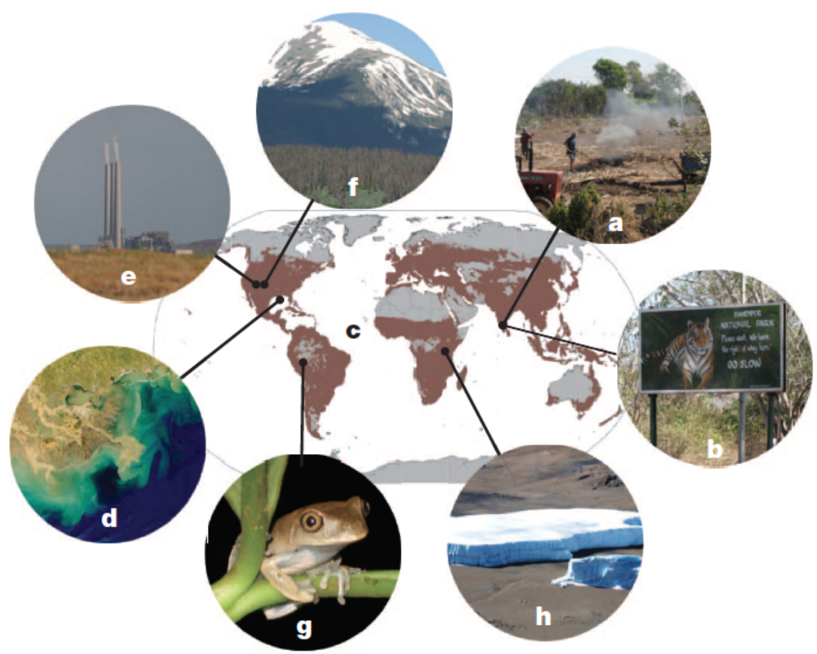
Human activities are generating major environmental changes

REVIEW

doi:10.1038/nature11018

Approaching a state shift in Earth's biosphere

Anthony D. Barnosky[1,2,3], Elizabeth A. Hadly[4], Jordi Bascompte[5], Eric L. Berlow[6], James H. Brown[7], Mikael Fortelius[8], Wayne M. Getz[9], John Harte[9,10], Alan Hastings[11], Pablo A. Marquet[12,13,14,15], Neo D. Martinez[16], Arne Mooers[17], Peter Roopnarine[18], Geerat Vermeij[19], John W. Williams[20], Rosemary Gillespie[9], Justin Kitzes[9], Charles Marshall[1,2], Nicholas Matzke[1], David P. Mindell[21], Eloy Revilla[22] & Adam B. Smith[23]

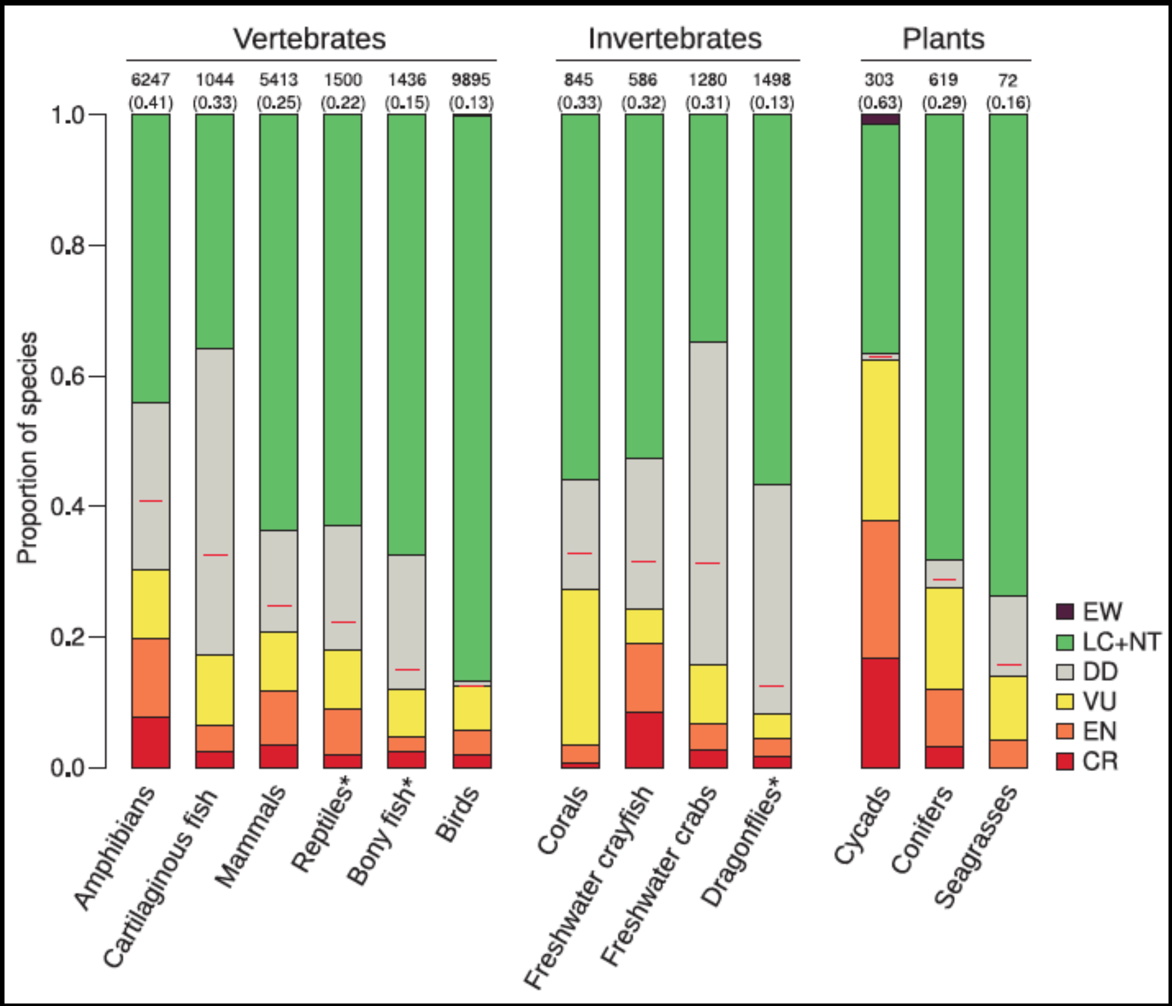


Ex.
- global warming
- habitat loss
- hunting
- increased UV-radiation
- overexploitation
- pollution

➡ This exerts high pressure on ecosystems and biodiversity

Barnosky et al. 2012 – Nature

Species in all groups are threatened by extinctions



Amphibians = 41%

Corals = 33%

Cycads = 63%

Hoffmann et al. 2010 – Science

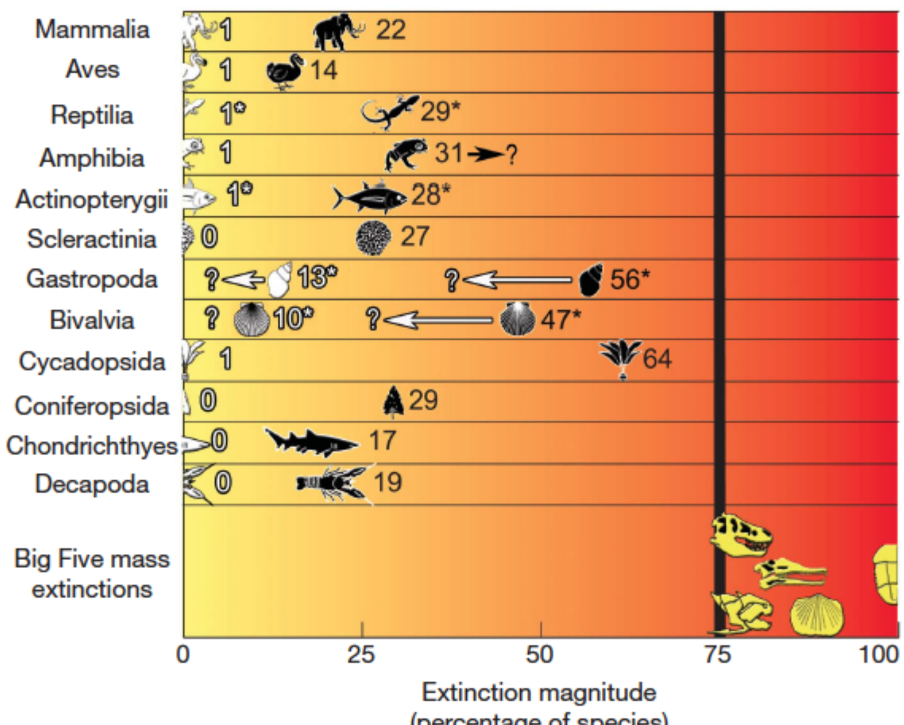
Paleontologists think we are entering a 'mass extinction'

REVIEW

doi:10.1038/nature09678

Has the Earth's sixth mass extinction already arrived?

Anthony D. Barnosky[1,2,3], Nicholas Matzke[1], Susumu Tomiya[1,2,3], Guinevere O. U. Wogan[1,3], Brian Swartz[1,2], Tiago B. Quental[1,2]†, Charles Marshall[1,2], Jenny L. McGuire[1,2,3]†, Emily L. Lindsey[1,2], Kaitlin C. Maguire[1,2], Ben Mersey[1,4] & Elizabeth A. Ferrer[1,2]



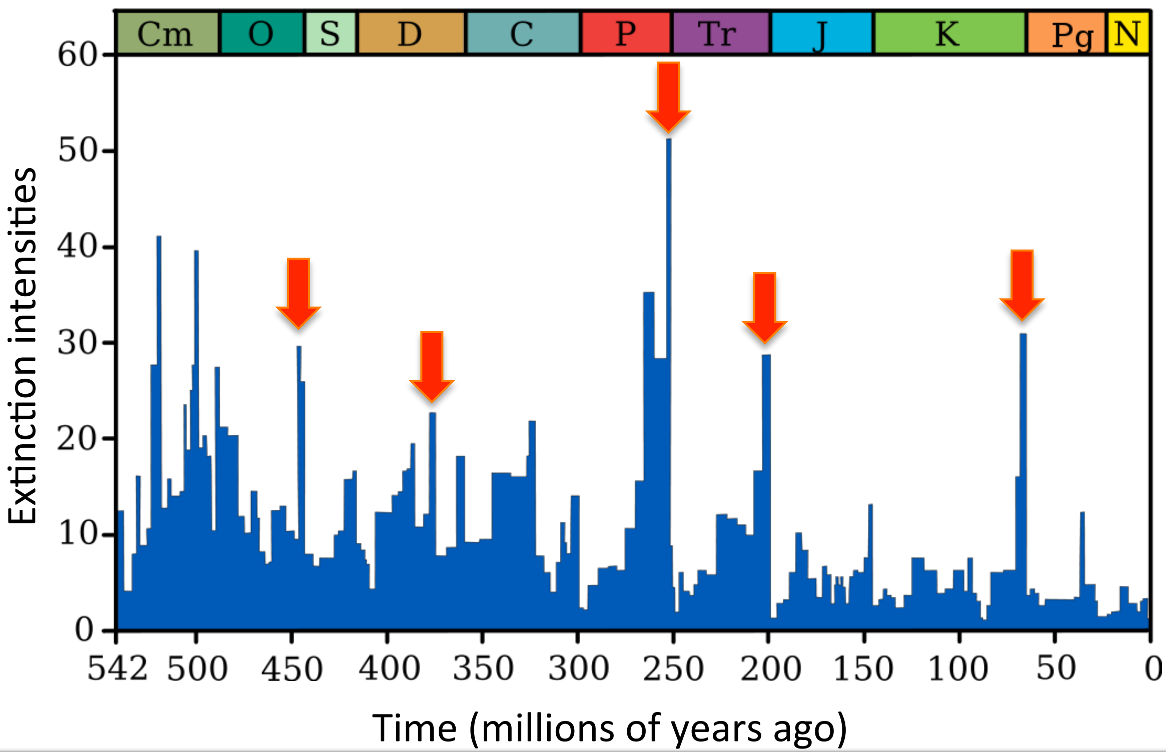
- ✓ **Mass extinctions** = times when the Earth loses 75% of its species in geologically short interval

Barnosky et al. 2011 – Nature

This is not the first time that Earth experiences mass extinctions

Mass Extinctions in the Marine Fossil Record

Abstract. *A new compilation of fossil data on invertebrate and vertebrate families indicates that four mass extinctions in the marine realm are statistically distinct from background extinction levels. These four occurred late in the Ordovician, Permian, Triassic, and Cretaceous periods. A fifth extinction event in the Devonian stands out from the background but is not statistically significant in these data. Background extinction rates appear to have declined since Cambrian time, which is consistent with the prediction that optimization of fitness should increase through evolutionary time.*



- ✓ Occurred only 5 times in the past 542 million years ('Big Five')

Ex.

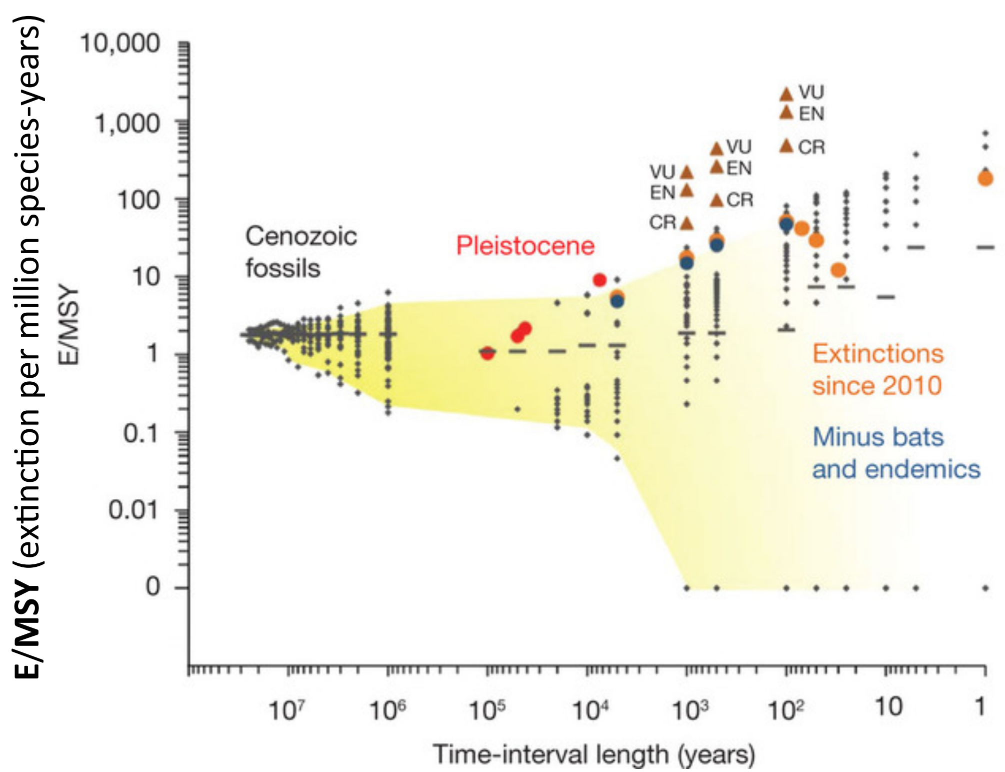
Most drastic event was **252 Ma (end-Permian)** with **80-96% species loss**

Raup & Sepkoski 1982 – Science

Current biodiversity crisis results from a decoupling between speciation and extinction

Has the Earth's sixth mass extinction already arrived?

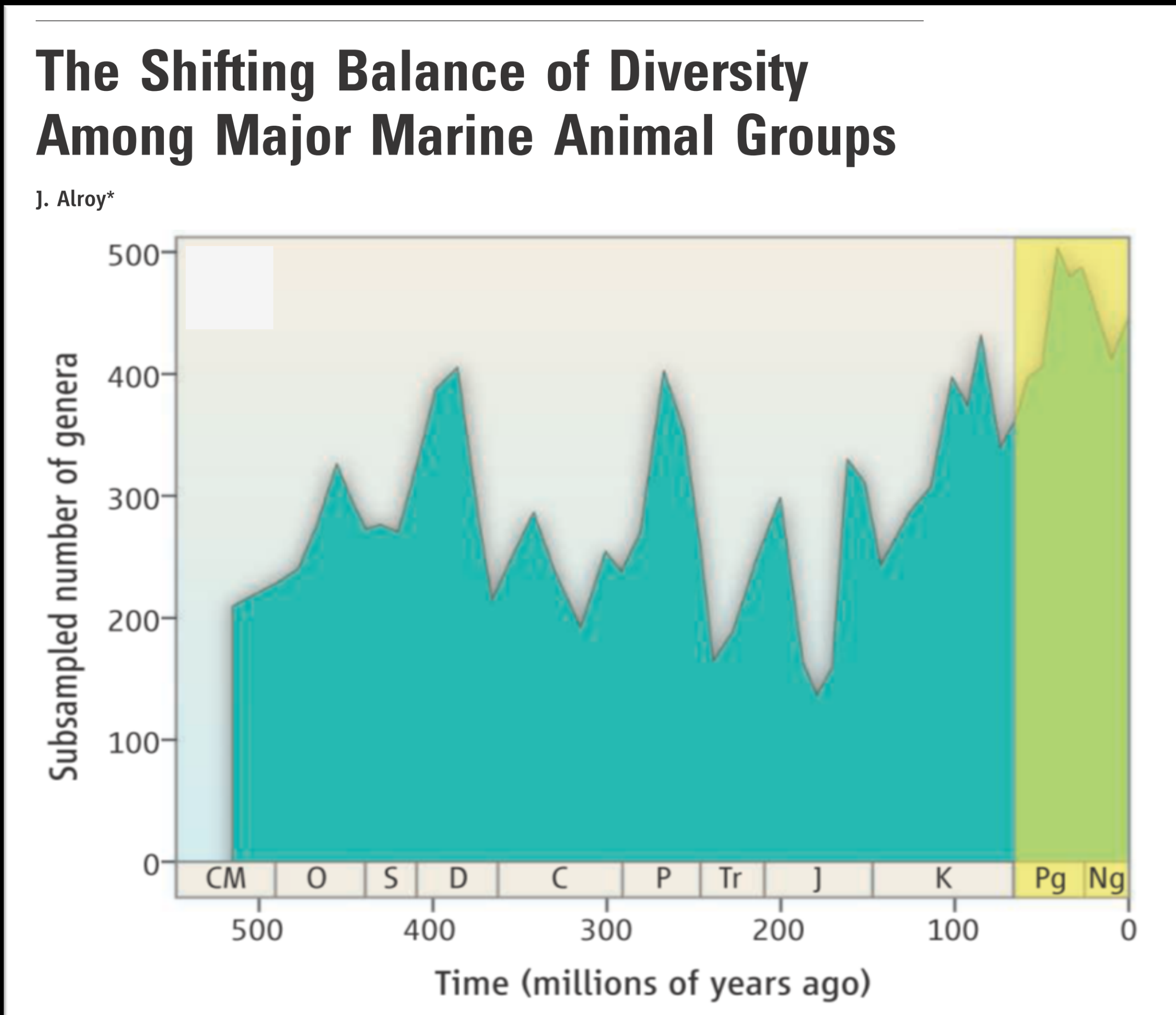
Anthony D. Barnosky[1,2,3], Nicholas Matzke[1], Susumu Tomiya[1,2,3], Guinevere O. U. Wogan[1,3], Brian Swartz[1,2], Tiago B. Quental[1,2]†, Charles Marshall[1,2], Jenny L. McGuire[1,2,3]†, Emily L. Lindsey[1,2], Kaitlin C. Maguire[1,2], Ben Mersey[1,4] & Elizabeth A. Ferrer[1,2]



- ✓ Current extinction rates are higher than in the fossil record
- ✓ Species go extinct **1000 times faster**

Barnosky et al. 2011 – Nature

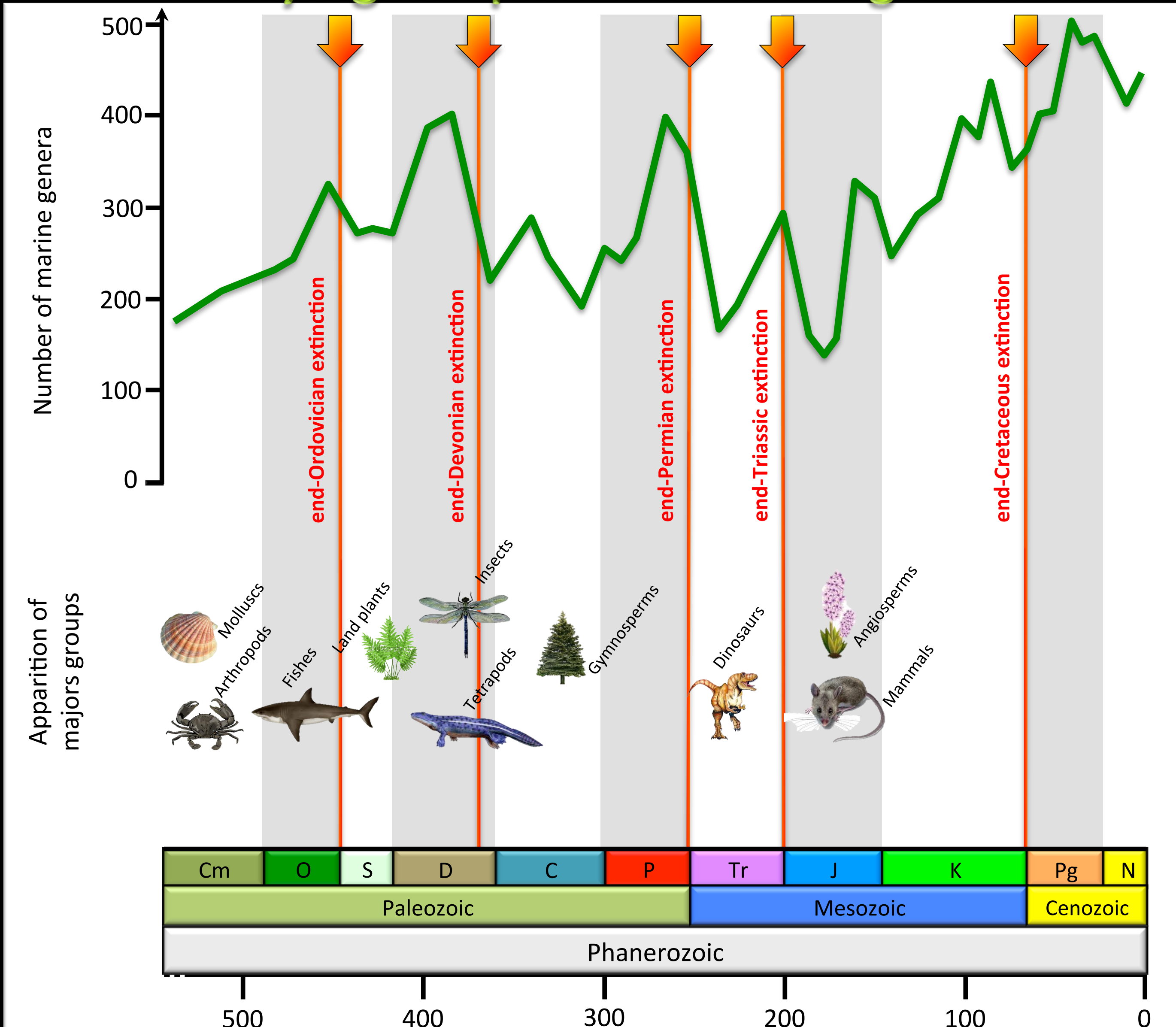
To understand the current biodiversity crisis, we need to understand its past long-term dynamics



- ✓ Historically done with the **marine fossil record**
- ✓ **Direct evidence** of diversity dynamics through time

Alroy 2010 – Science

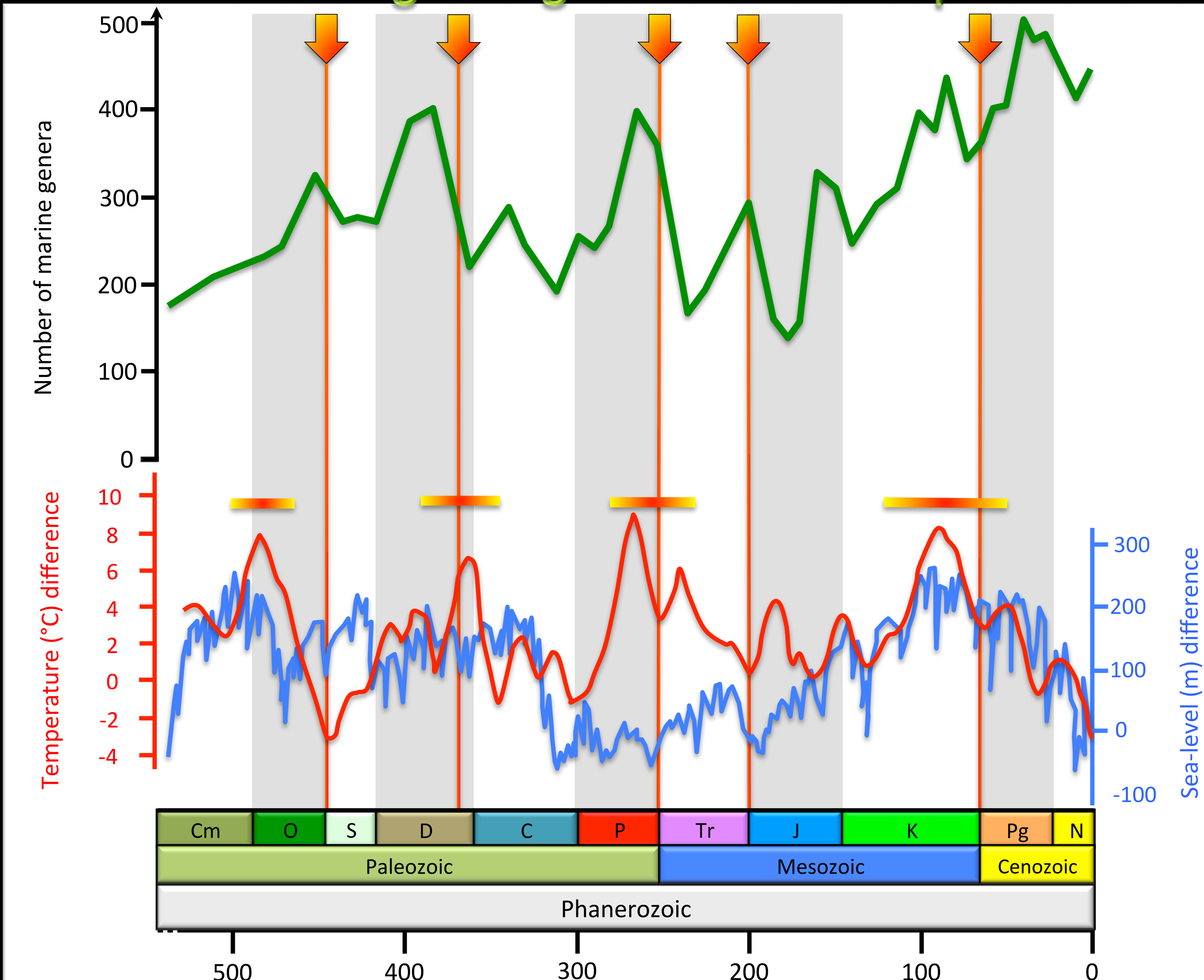
Studying the past can shed light on the current crisis



✓ Originations **but also** **extinctions** **are part of the history of life**

Condamine et al. 2013 – Ecol. Letters

Evaluating background and exceptional extinctions

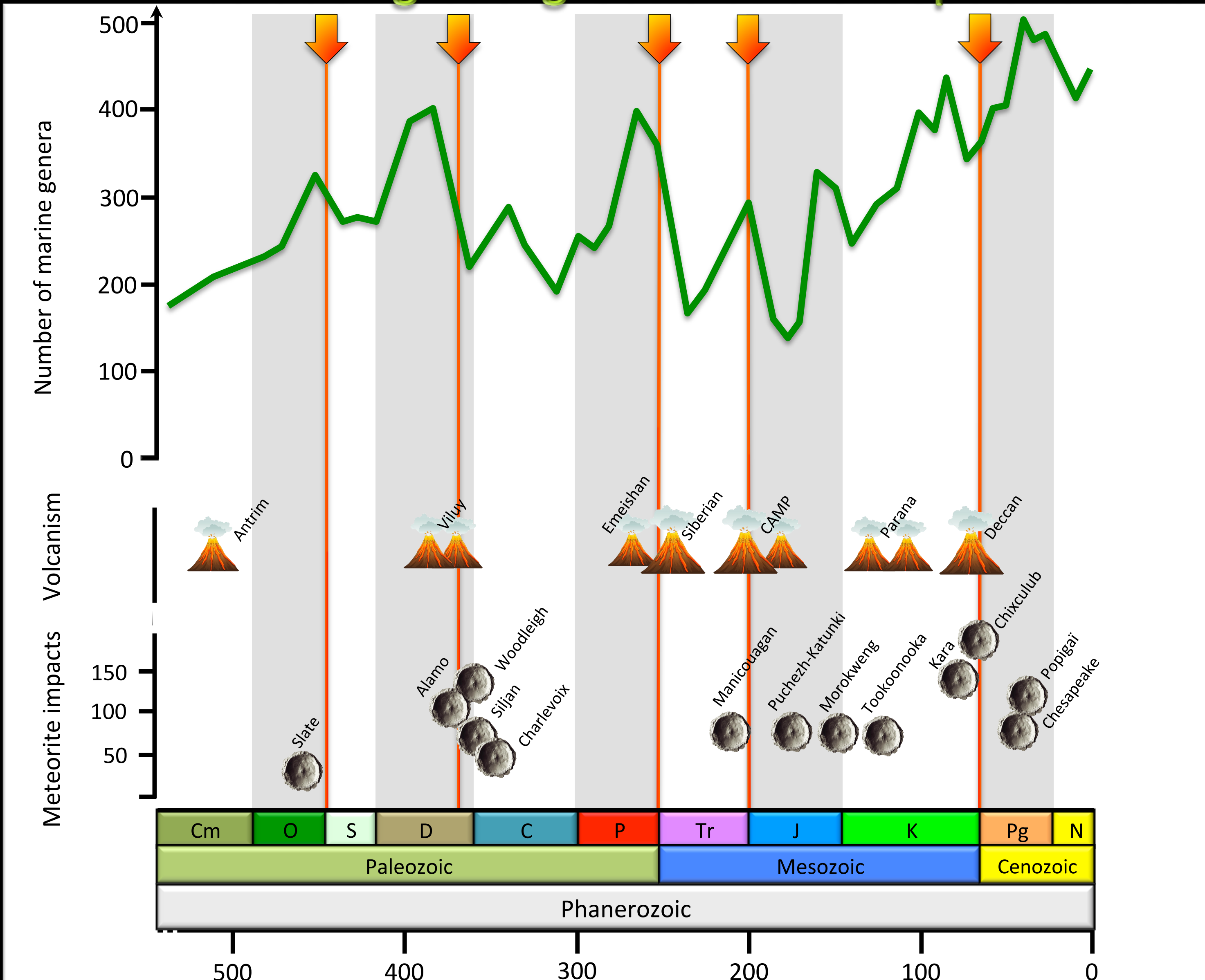


✓ To better:

Understand causes of extinction due to climatic changes

Condamine et al. 2013 – Ecol. Letters

Evaluating background and exceptional extinctions



✓ To better:

Understand causes of extinction due to geological changes

Condamine et al. 2013 – Ecol. Letters

Profusion of evidence from the marine fossil record

Michael Benton

Shanan Peters

ARTICLE

Diversification and Extinction in the History of Life

M. J. Benton

Speciation

REVIEW

The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time

Michael J. Benton

nature geoscience REVIEW ARTICLE

PUBLISHED ONLINE: 27 MAY 2012 | DOI: 10.1038/NGEO1475

The timing and pattern of biotic recovery following the end-Permian mass extinction

Zhong-Qiang Chen[1] and Michael J. Benton[2*]

Geologic constraints on the macroevolutionary history of marine animals

Shanan E. Peters*

Department of Geological Sciences and Museum of Paleontology, University of Michigan, 1109 South Geddes Road, Ann Arbor, MI 48104

Edited by W. A. Berggren, Woods Hole Oceanographic Institution, Woods Hole, MA, and approved July 15, 2005 (received for review March 30, 2005)

nature Vol 454 | 31 July 2008 | doi:10.1038/nature07032

LETTERS

Environmental determinants of extinction selectivity in the fossil record

Shanan E. Peters[1]

LETTER

doi:10.1038/nature11815

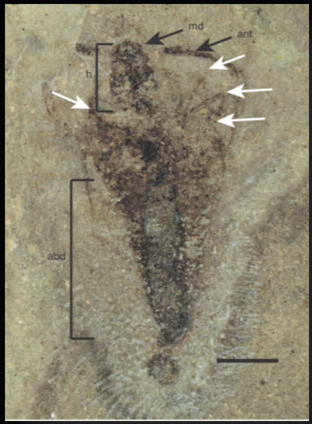
Oceanographic controls on the diversity and extinction of planktonic foraminifera

Shanan E. Peters[1], Daniel C. Kelly[1] & Andrew J. Fraass[1]†

Benton 1995 – Science
Benton 2009 – Science
Chen & Benton 2012 – Nature Geosci.

Peters 2005 – PNAS
Peters 2008 – Nature
Peters et al. 2013 – Nature

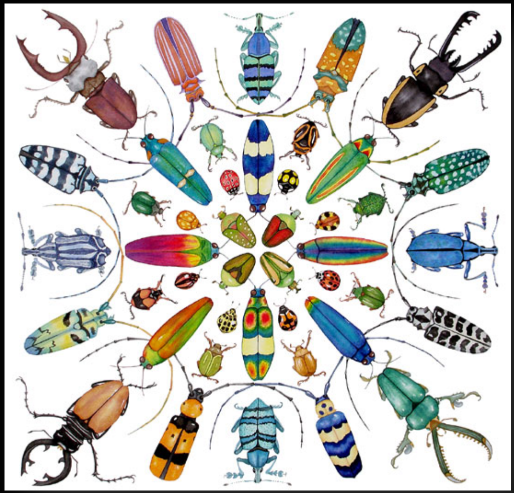
But the picture from the fossil record is not exhaustive



Fossil record is:
- Biased
- Incomplete
- Uneven

Many groups lack a suitable fossil record

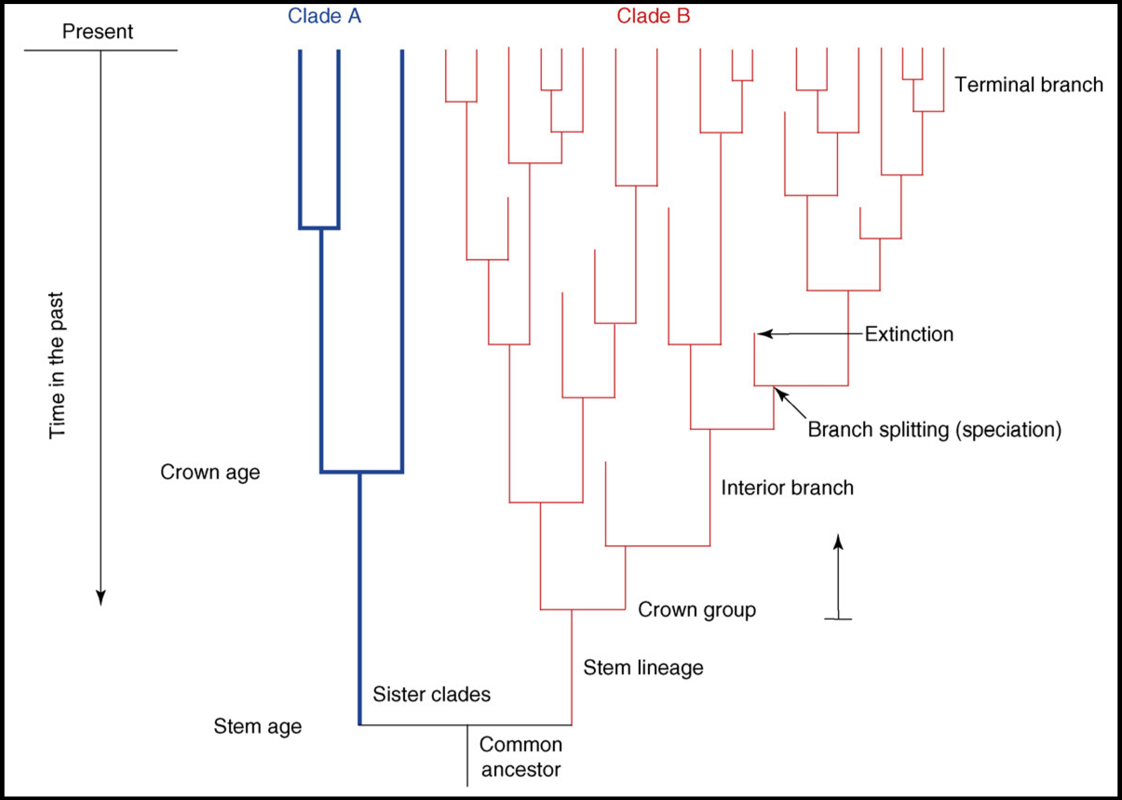
e.g., insects, plants, birds…

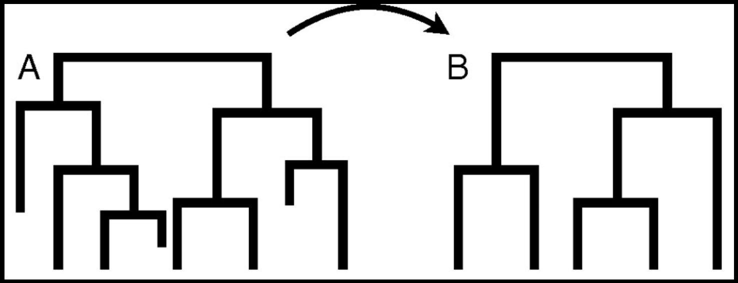


We need **more data** to better understand diversity dynamics in relation with environmental changes

Phylogenetic approaches to diversification

➡ Using relationships between extant species and their divergence times

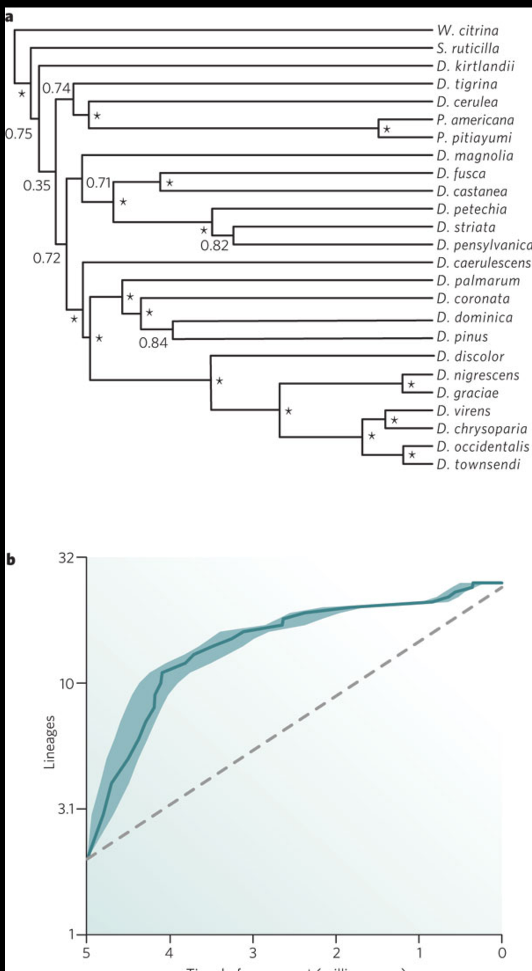


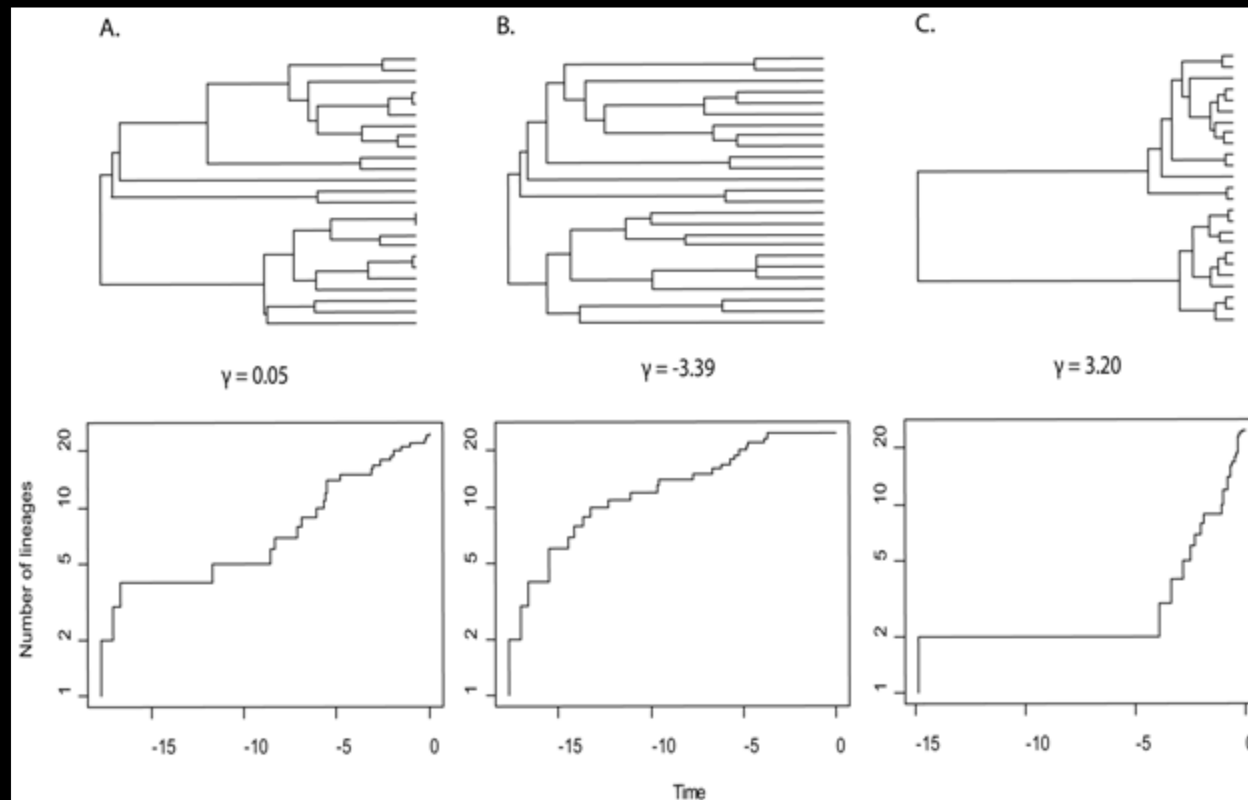


Ricklefs 2007 – TREE

Phylogenetic approaches to diversification

➡ Phylogenies can be converted into **lineages-through-time (LTT) plot**





Reznick & Ricklefs 2009 – Nature

Phylogenetic approaches to diversification

ECOLOGY LETTERS

Ecology Letters, (2013) doi: 10.1111/ele.12062

IDEA AND PERSPECTIVE

Macroevolutionary perspectives to environmental change

Fabien L. Condamine[1] Jonathan Rolland[1] and Hélène Morlon[1]

Abstract

Predicting how biodiversity will be affected and will respond to human-induced environmental changes is one of the most critical challenges facing ecologists today. Here, we put current environmental changes and their effects on biodiversity in a macroevolutionary perspective. We build on research in palaeontology and recent developments in phylogenetic approaches to ask how macroevolution can help us understand how environmental changes have affected biodiversity in the past, and how they will affect biodiversity in the future. More and more paleontological and phylogenetic data are accumulated, and we argue that much of the potential these data have for understanding environmental changes remains to be explored.

Keywords

Biodiversity, birth–death models, diversification rates, extinction, fossils, global change, mass extinctions, paleoenvironment, speciation.

Ecology Letters (2013)

Macroevolutionary perspectives to environmental change

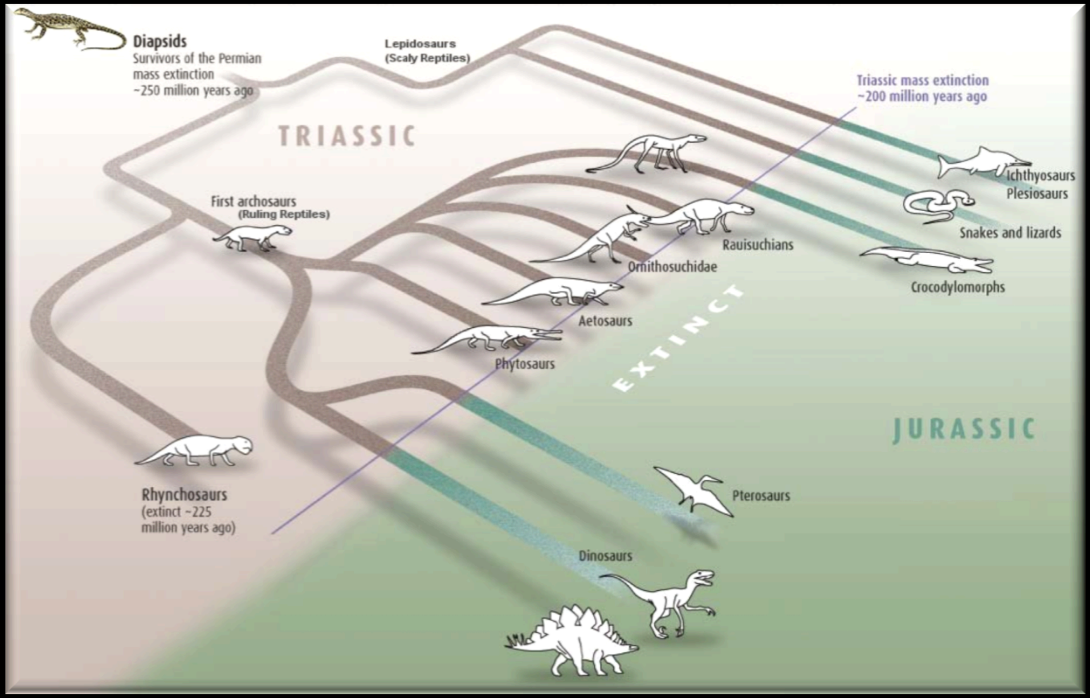
1 – Mass extinctions and recovery in relation to environmental change

2 – Background speciation and extinction in relation to environmental change

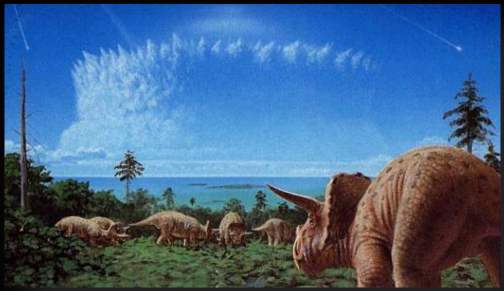
3 – Vulnerability and evolutionary potential

4 – Limitations and Perspectives

Mass extinctions and recovery in relation to environmental change



Why studying mass extinctions?



➡ Four main reasons:

1. Useful to estimate **when** mass extinctions occurred

2. Useful to estimate **how many** species were lost (extinction intensity)

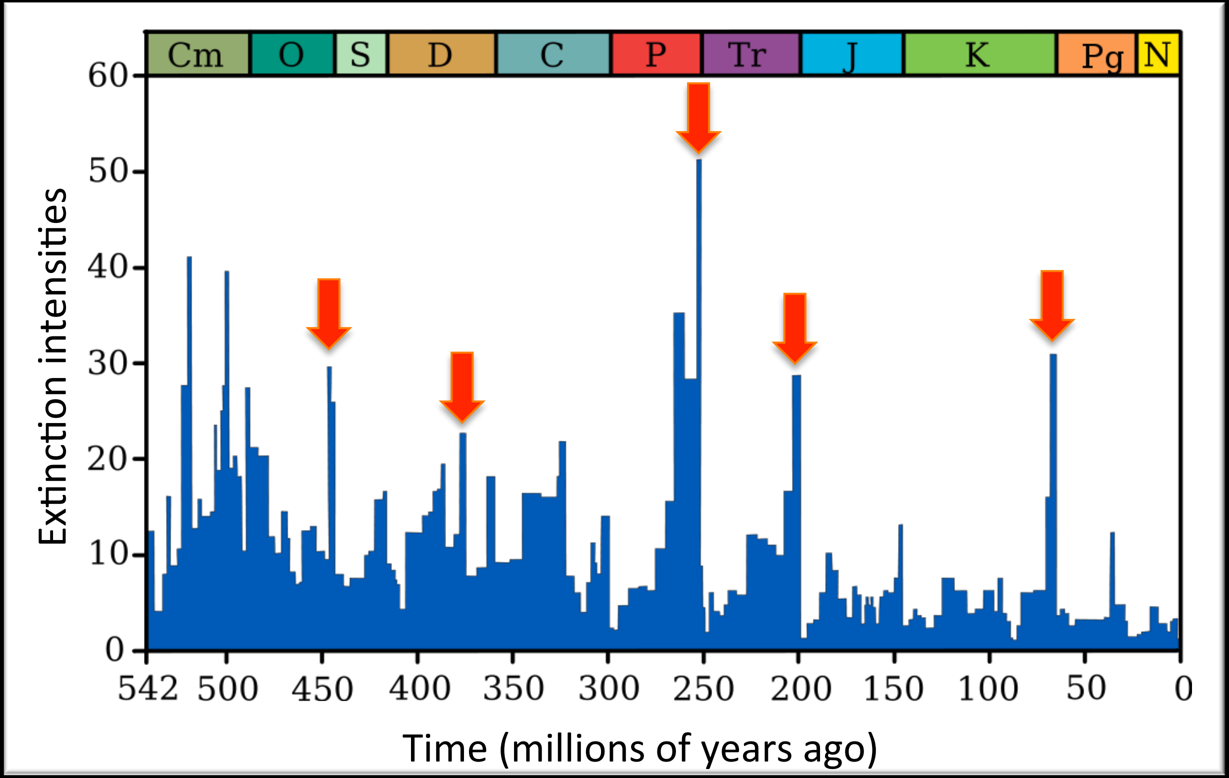
3. Useful to estimate **which clades** were impacted and what traits were associated with extinction (extinction selectivity)

4. Useful to estimate at **which level** of extinction biodiversity was able to recover

To find the causes of mass extinctions

Detecting mass extinctions in the fossil record

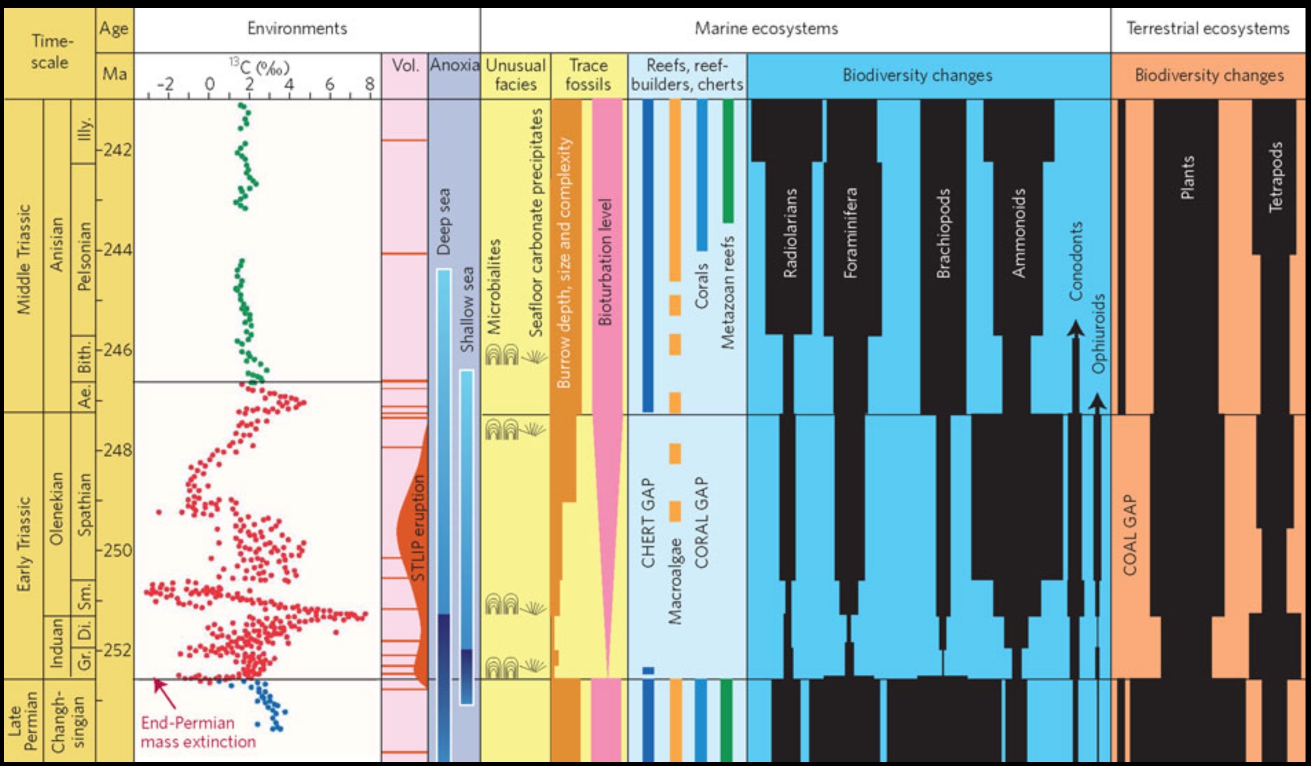
Paleontologists idenitified five mass extinctions:



- **443 Ma** with 86% species loss
- **359 Ma** with 75% species loss
- **252 Ma** with 95% species loss
- **201 Ma** with 80% species loss
- **66 Ma** with 76% species loss

Detecting mass extinctions in the fossil record

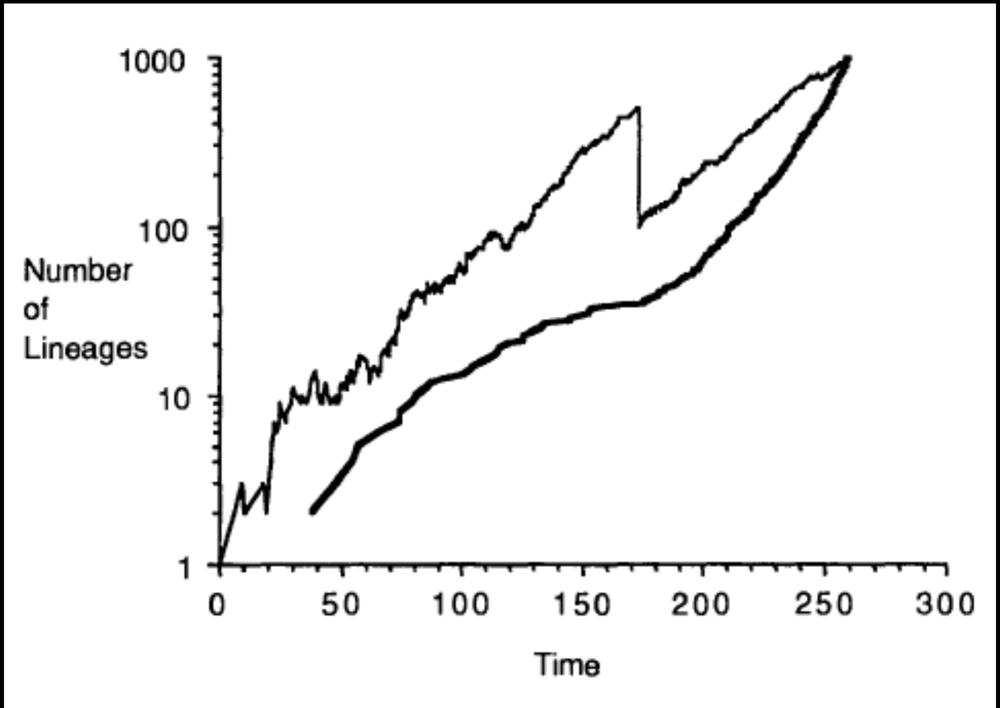
➡ Paleontologists can study the causes of mass extinctions



Chen & Benton 2012 – Nature Geosci.

Detecting mass extinctions in phylogenies

➡ Theoretically possible to detect mass extinction in phylogenies



- ✓ **Birth-death model** can model the process of tree growth
- ✓ Adding a **punctual event** that remove a part of the species give a **LTT interrupted by a plateau**

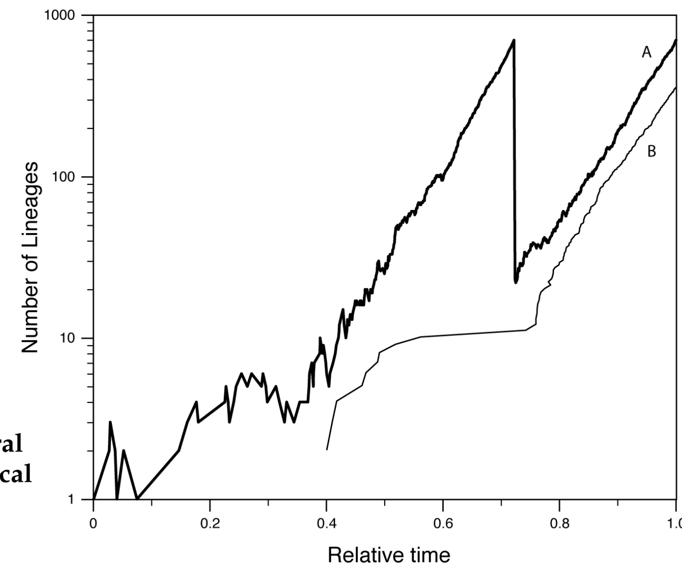
Harvey et al. 1994 – Evolution

Detecting mass extinctions in phylogenies

➡ Few studies tested whether mass extinction can be found in phylogenies

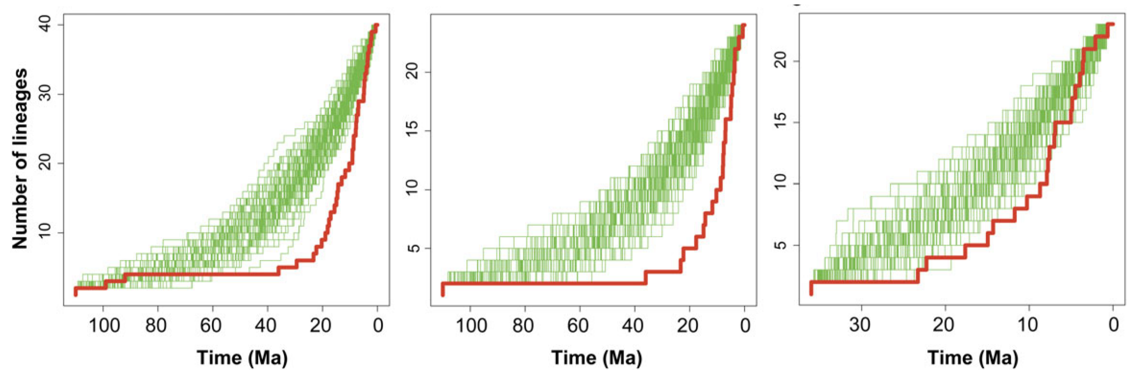
EXPLOSIVE RADIATION OR CRYPTIC MASS EXTINCTION? INTERPRETING SIGNATURES IN MOLECULAR PHYLOGENIES

Michael D. Crisp[1,2] and Lyn G. Cook[3,4]



Mass Extinction, Gradual Cooling, or Rapid Radiation? Reconstructing the Spatiotemporal Evolution of the Ancient Angiosperm Genus *Hedyosmum* (Chloranthaceae) Using Empirical and Simulated Approaches

Alexandre Antonelli[1,2,*] and Isabel Sanmartín[3]

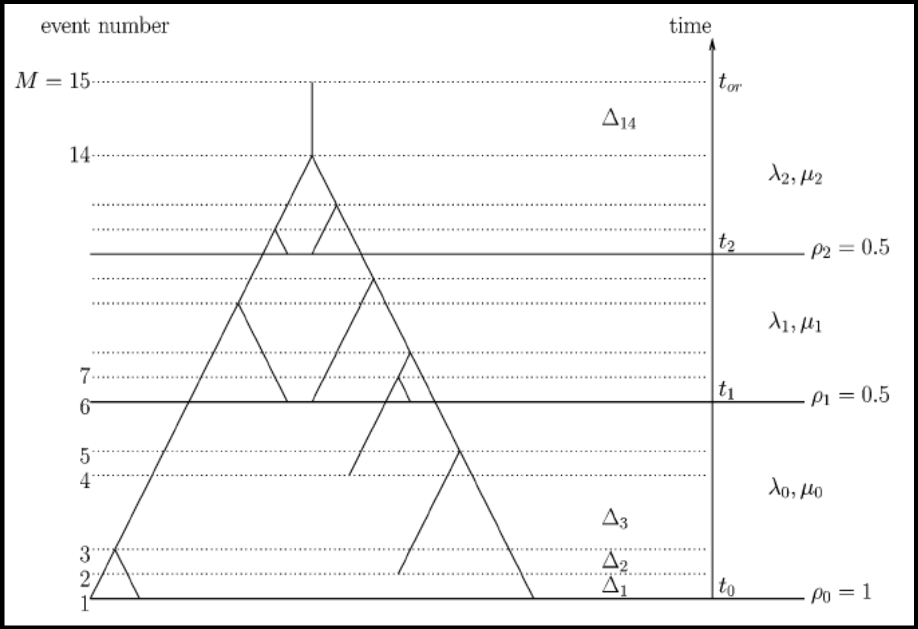


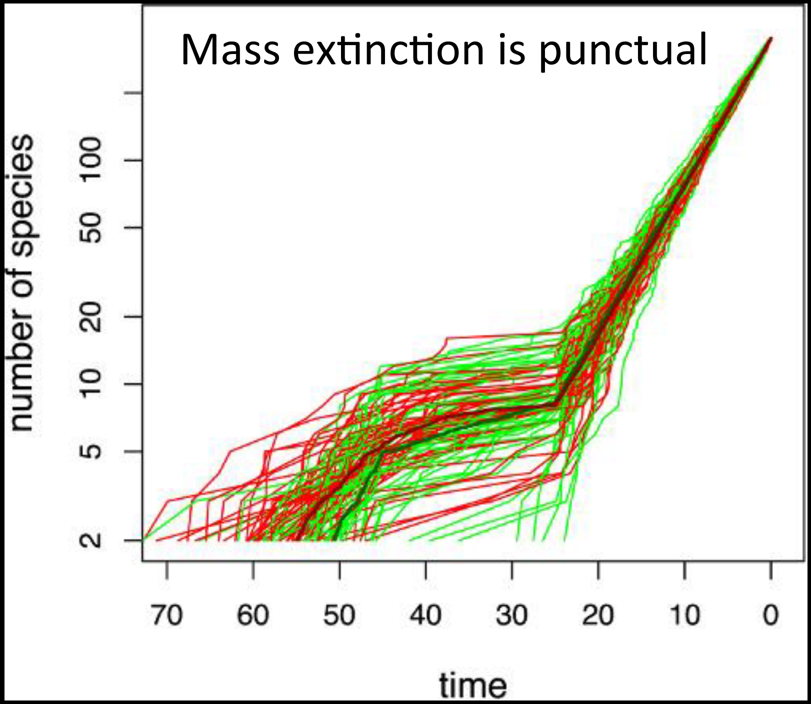
Cook & Crisp 2009 – Evolution
Antonelli & Sanmartín 2011 – Syst. Biol.

Detecting mass extinctions in phylogenies

➡ New methods (TreePar) have been developped to address this issue

Episodic birth-death process



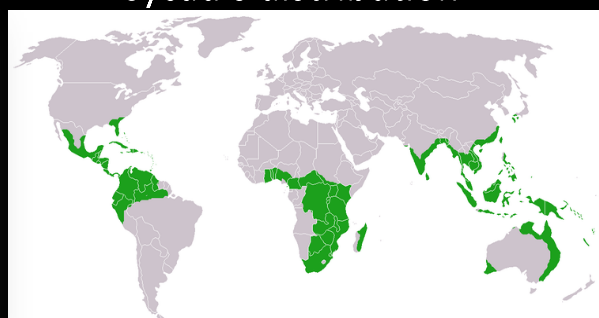


Stadler 2011 – Syst. Biol.

Case study: the **Cycads**, an ancient group of seed plants

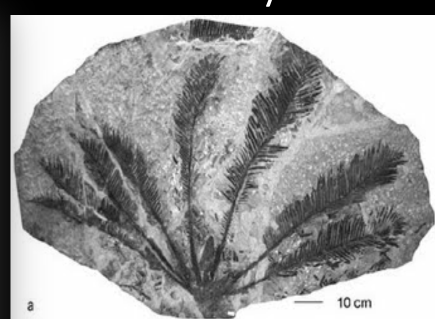
- 300 palm-like species, distributed in all tropical regions
- Appeared *ca.* 270 Ma, survived to three mass extinctions
- 63% of threatened species (IUCN's Red List)

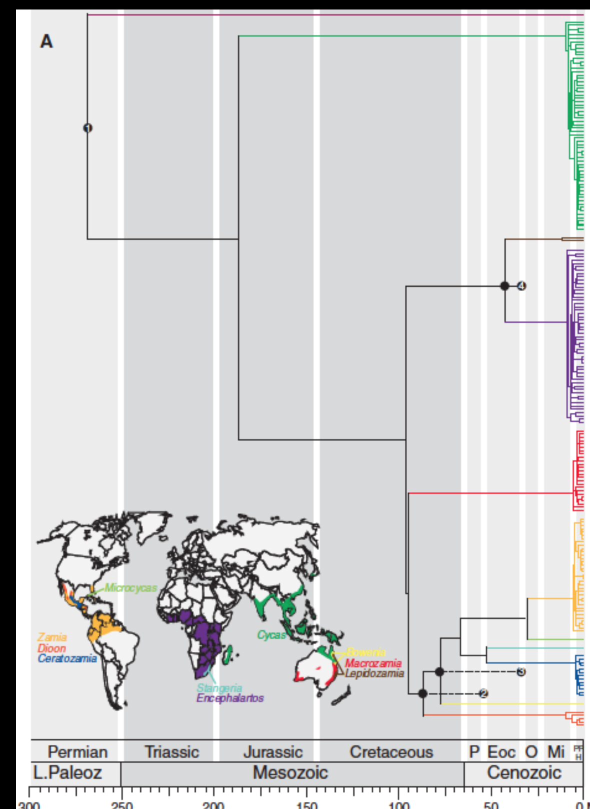
Cycad's distribution



EW: *Encephalartos woodii*

Triassic cycad





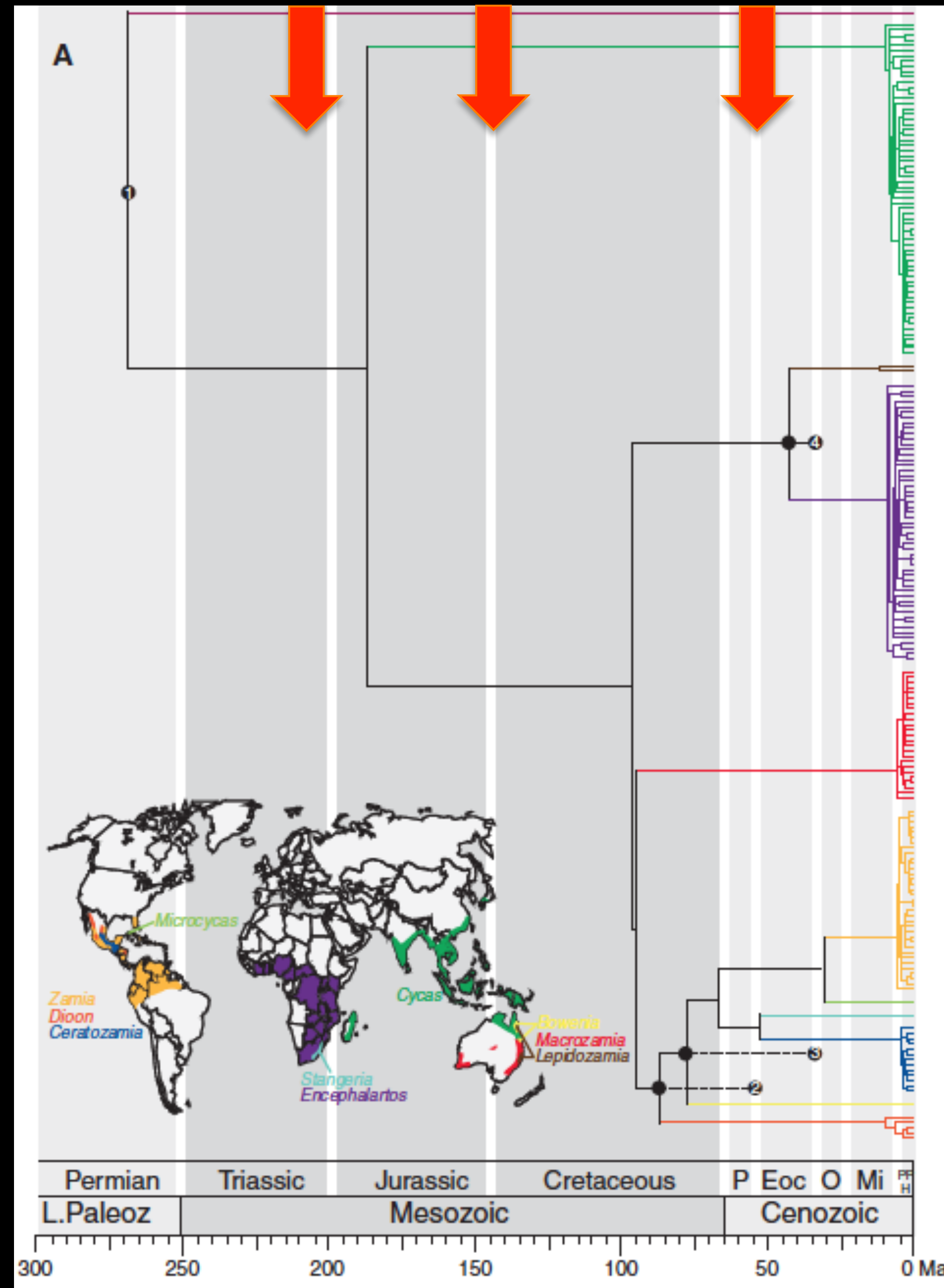
Nagalingum et al. 2011 – Science

Using the method **TreePar**

First ME is congruent with a known ME in the fossil record at **205 Ma** (Triassic-Jurassic)

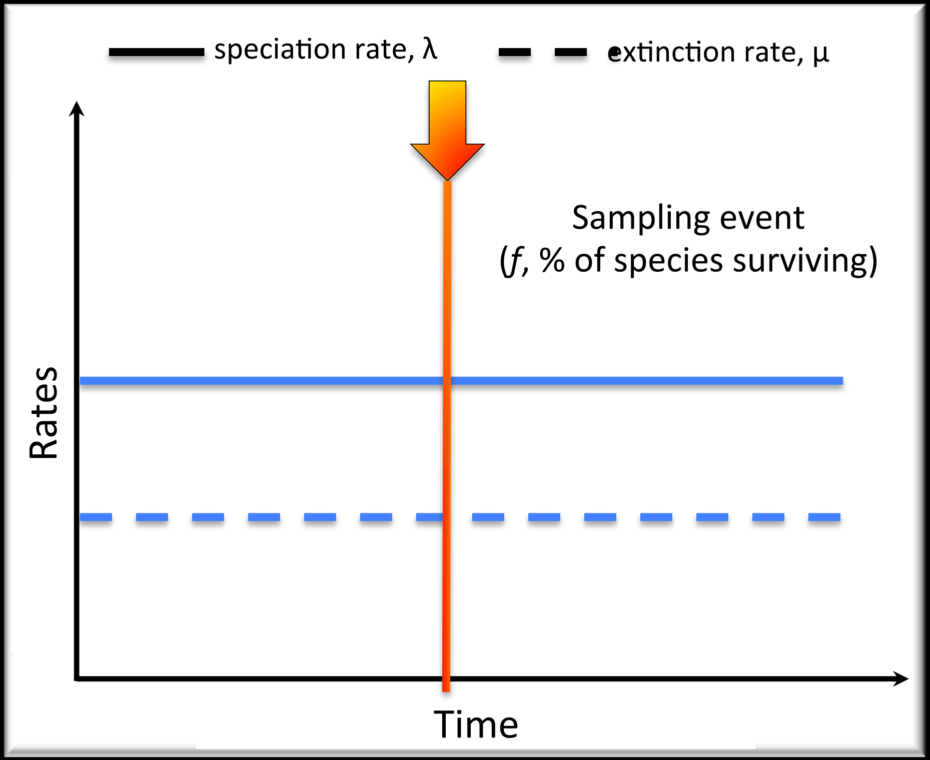
Second is a lesser ectinction event known from the fossil record at **135 Ma** (Jurassic-Cretaceous)

Third is in the Cenozoic at **58 Ma** and congruent with a global warming of climate



Problem with detecting mass extinctions in phylogenies

➡ Speciation model with mass extinction and model with a stasis phase = same LTT plots

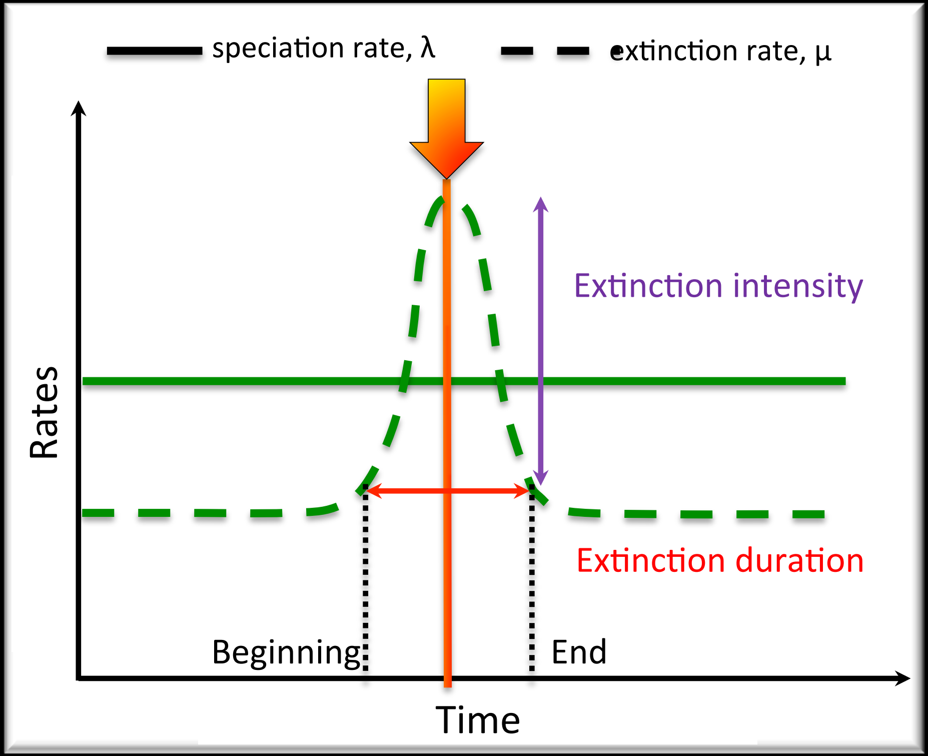


- ✓ **Mass extinction** modelled as an instantaneous event
- ✓ **Classic rate shifts** are instantaneous too
- ✓ **Hard to distinguish** between the two scenarios
- ✓ Same rates **before and after** the event

Stadler 2011 – Syst. Biol.

Problem with detecting mass extinctions in phylogenies

➡ Mass extinctions have not necessary a short time duration



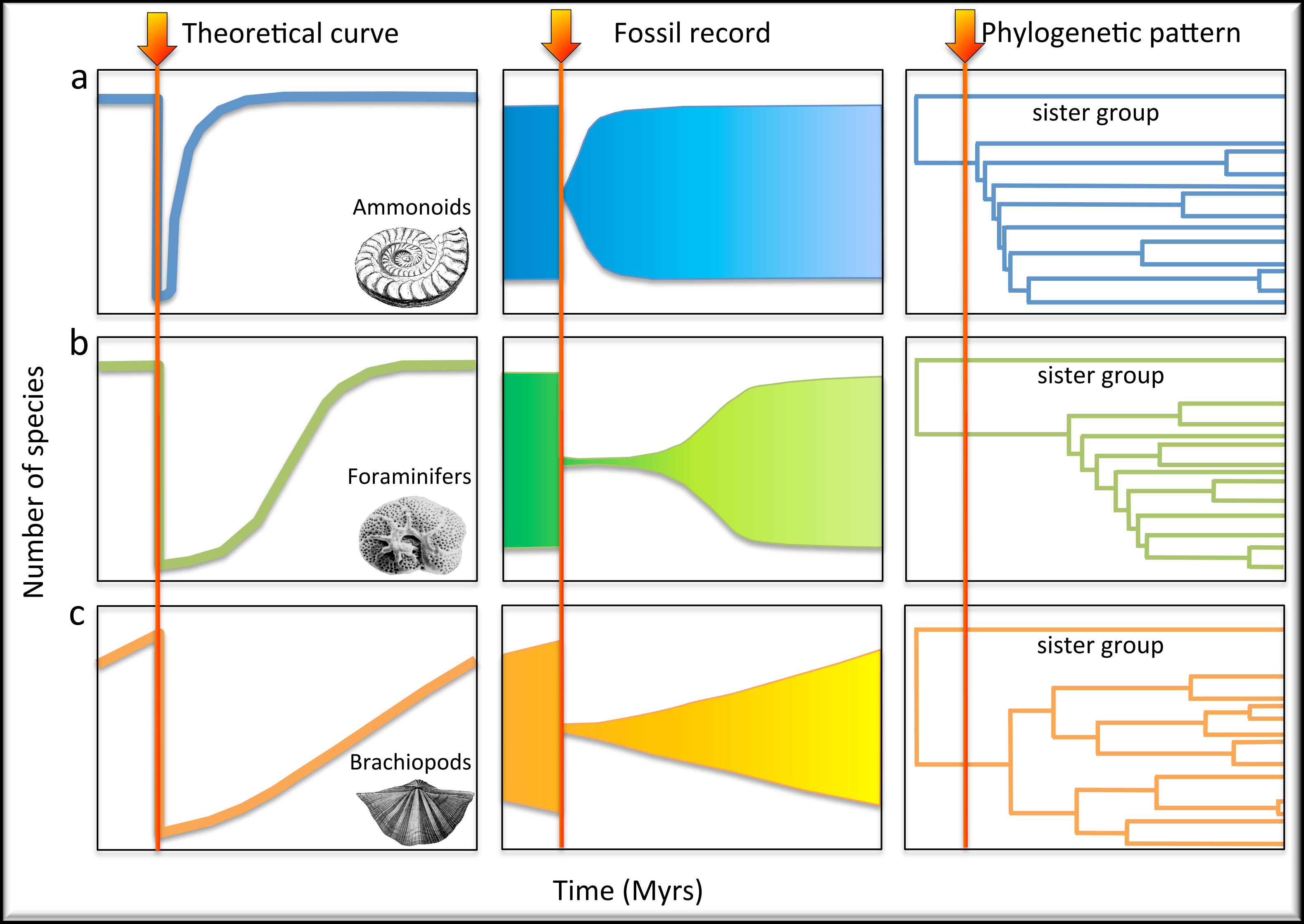
- ✓ Taking into account duration of the event
- ✓ Modelling extinction with continuous forms

Or:

- ✓ Background and mass extinction events **modelled within the same framework**
- ✓ Mass extinctions = extremes of a background **continuum of intensities and duration**

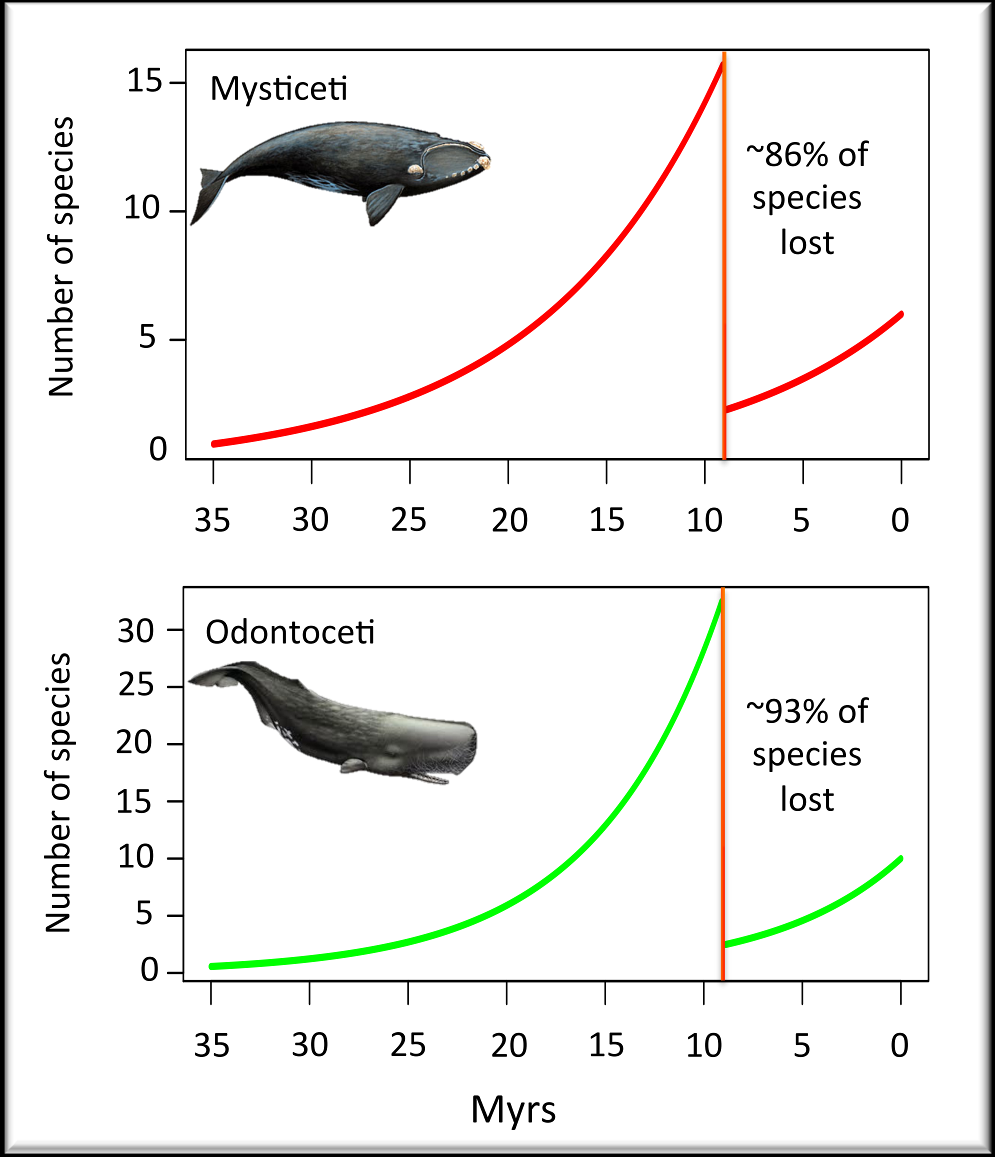
Condamine et al. 2013 – Ecol. Letters

Recovery after mass extinctions



Condamine et al. 2013 – Ecol. Letters

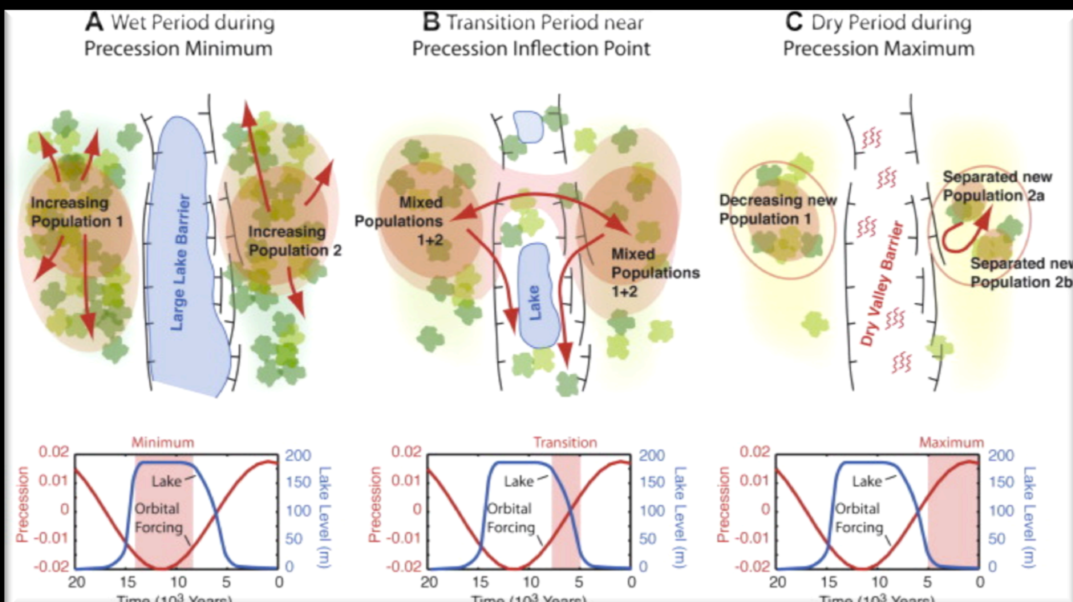
Recovery after mass extinctions



- ✓ **Mass extinctions (9 Ma)** associated with high species loss (86-93%)
- ✓ Clades did not recover after suggesting a **'time-for-speciation' recovery**

Condamine et al. 2013 – Ecol. Letters

Background speciation and extinction in relation to environmental change



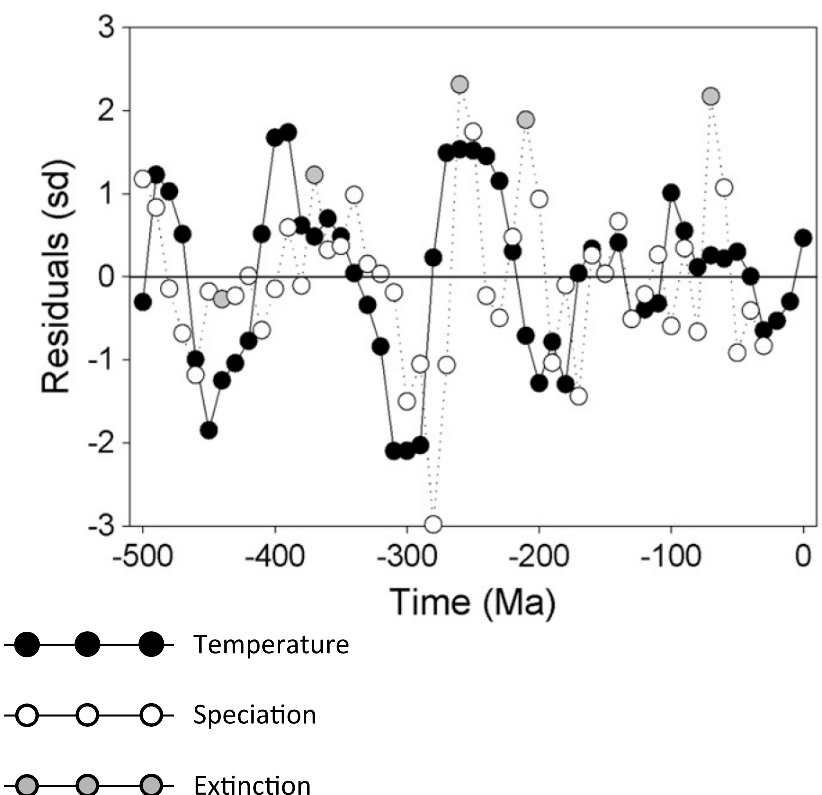
What does the fossil record teach us?

Biodiversity tracks temperature over time

Peter J. Mayhew[a,1], Mark A. Bell[b], Timothy G. Benton[c], and Alistair J. McGowan[b]

[a]Department of Biology, University of York, York YO10 5DD, United Kingdom; [b]School of Geographical and Earth Sciences, University of Glasgow, Glasgow G12 8QQ, United Kingdom; and [c]Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, United Kingdom

Edited by David Jablonski, The University of Chicago, Chicago, IL, and approved July 30, 2012 (received for review January 18, 2012)

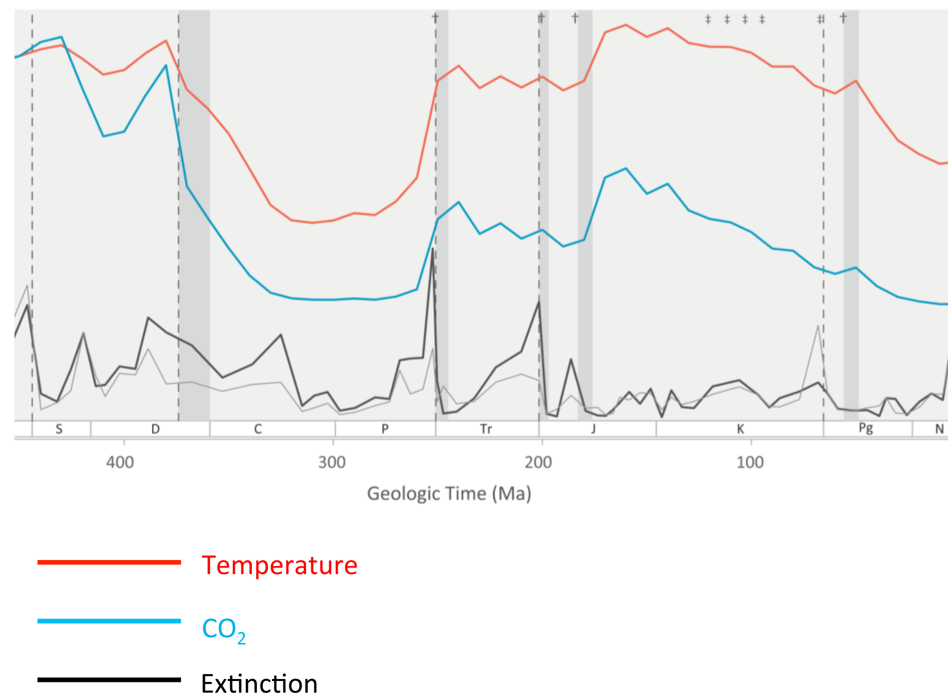


Mayhew et al. 2012 – PNAS

Review
Cell PRESS

Extinctions in ancient and modern seas

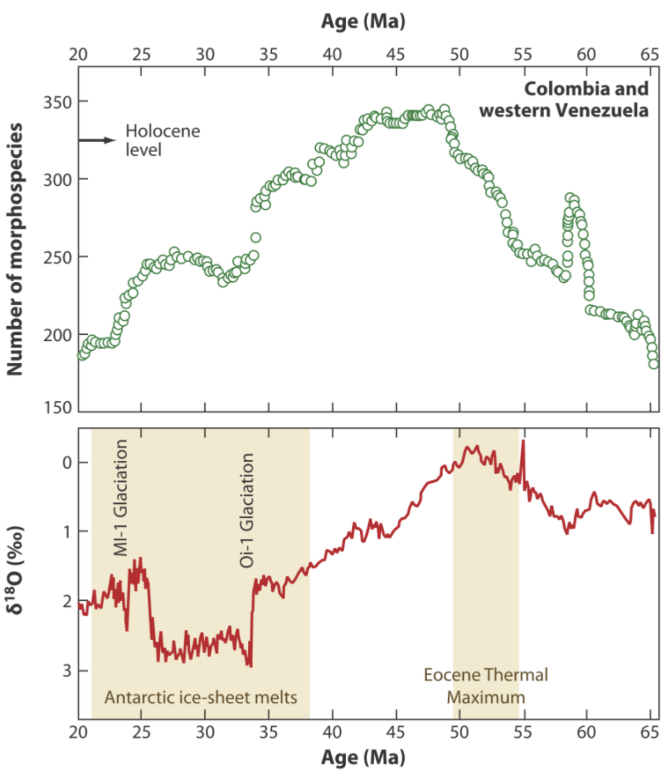
Paul G. Harnik[1], Heike K. Lotze[2], Sean C. Anderson[3], Zoe V. Finkel[4], Seth Finnegan[5], David R. Lindberg[5,6], Lee Hsiang Liow[7], Rowan Lockwood[8], Craig R. McClain[1], Jenny L. McGuire[1,9], Aaron O'Dea[10], John M. Pandolfi[11], Carl Simpson[12], and Derek P. Tittensor[2,13,14]



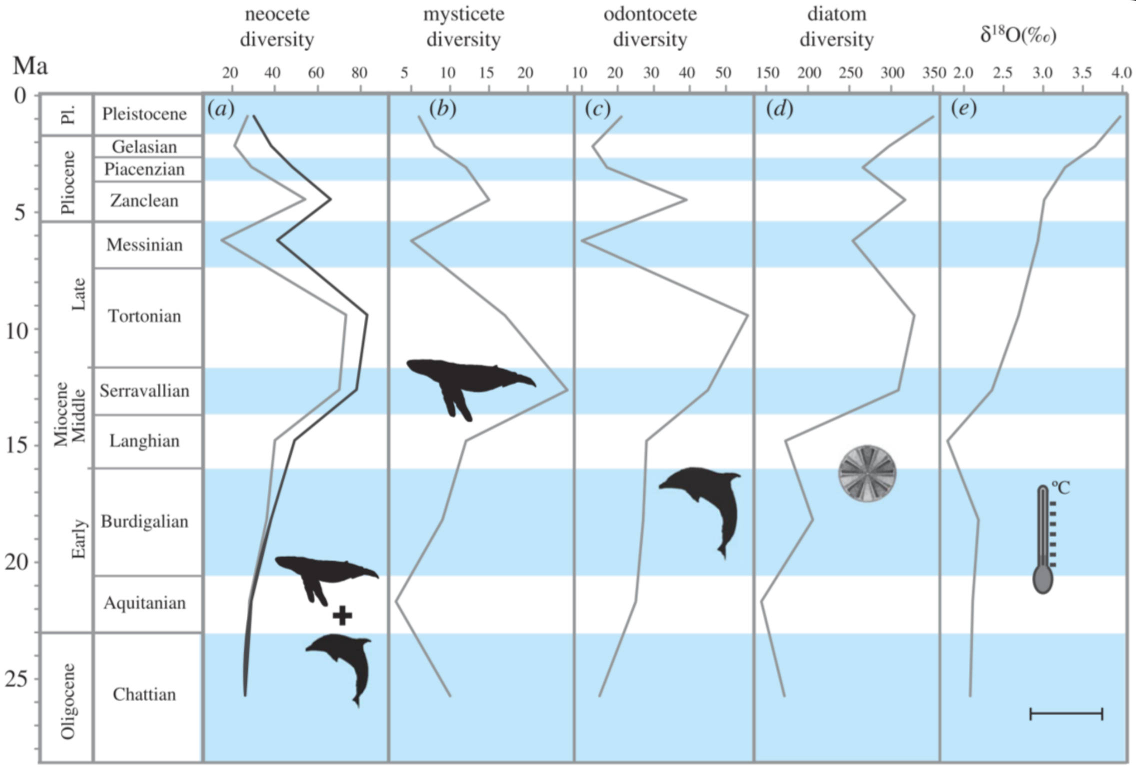
Harnik et al. 2012 – TREE

What does the fossil record teach us?

"Good correlation between diversity fluctuations and changes in global temperature, suggesting that climate change may be directly driving the diversity pattern."

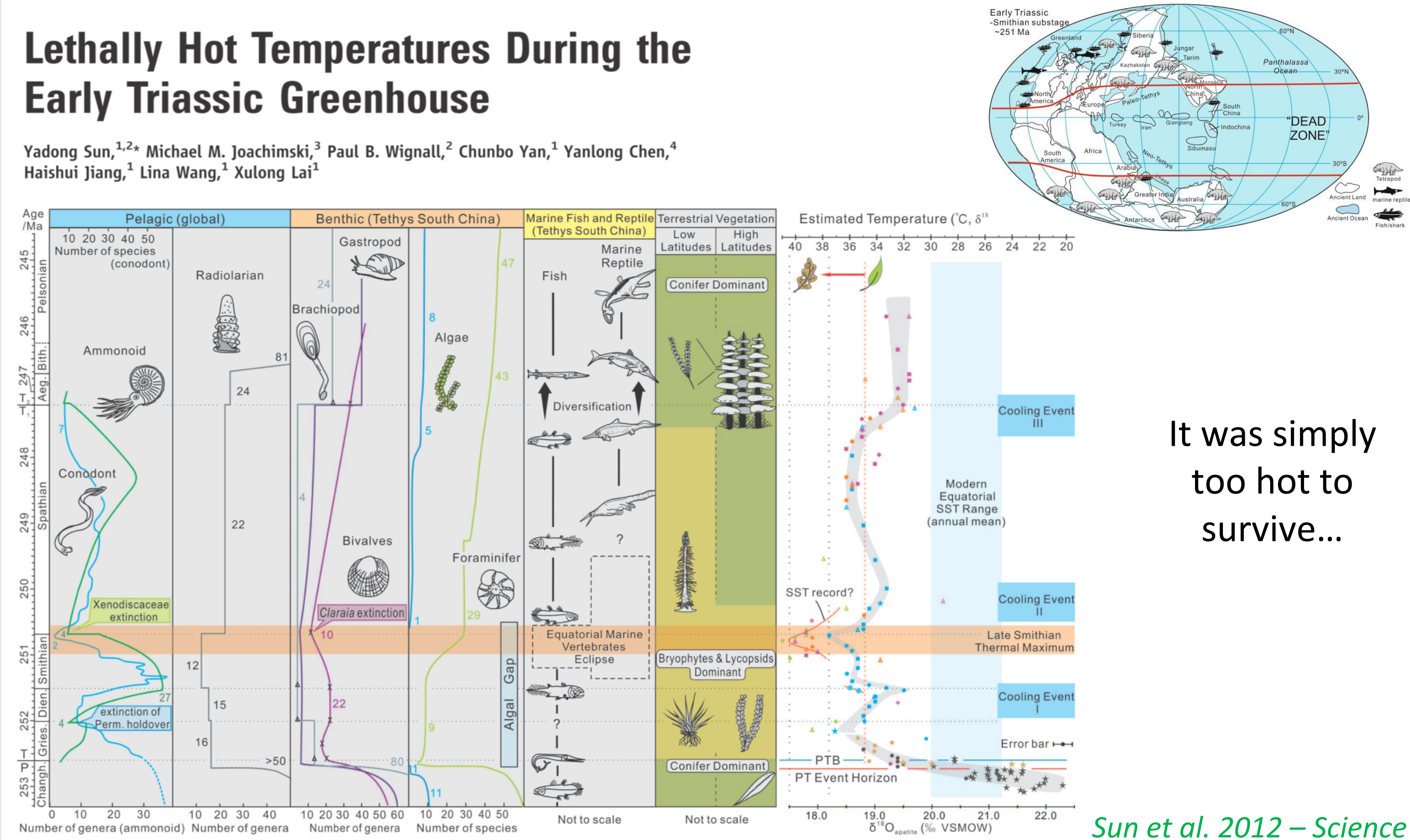


Jaramillo et al. 2006 – Science



Marx & Uhen 2010 – Science

What does the fossil record teach us?



It was simply too hot to survive…

Sun et al. 2012 – Science

Phylogenetic approaches

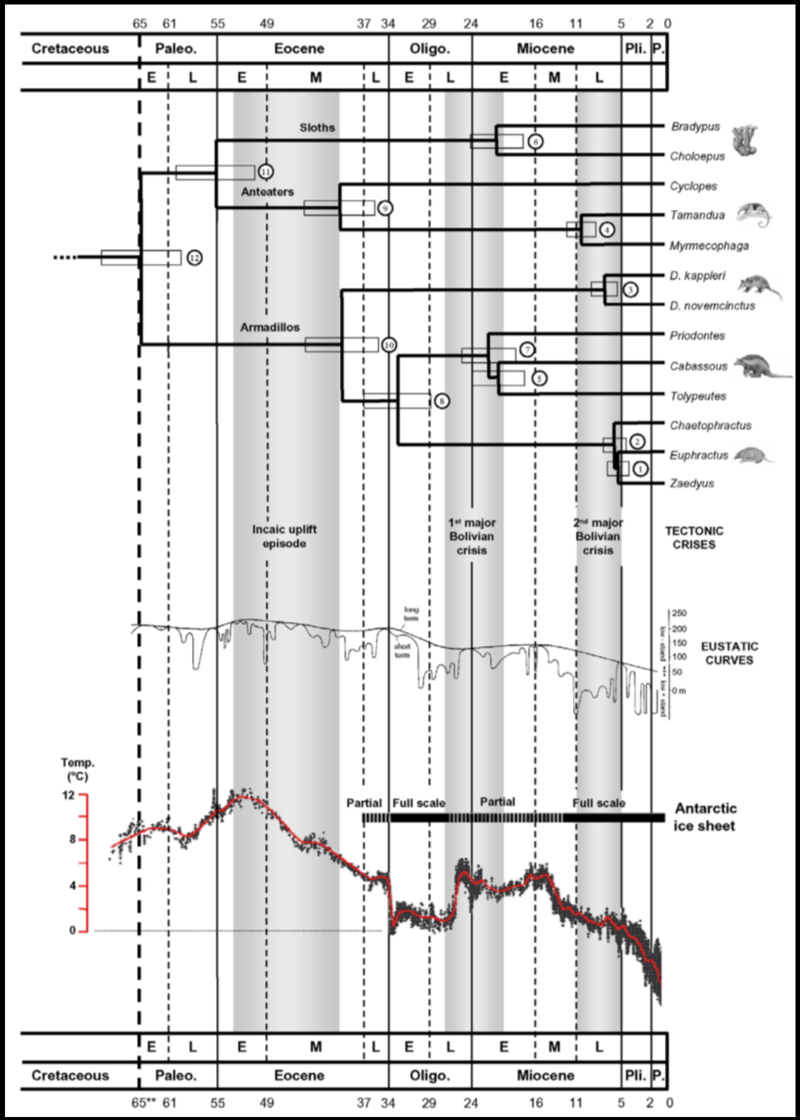
➡ Several approaches exist to assess the impact of climate

1. Comparing phylogenies with paleoclimatic curves

2. Fitting birth-death model at specific climatic event

3. Using trait-dependent diversification models

1. Comparing phylogenies with paleoclimatic curves



Delsuc et al. 2004 – BMC Evol. Biol.

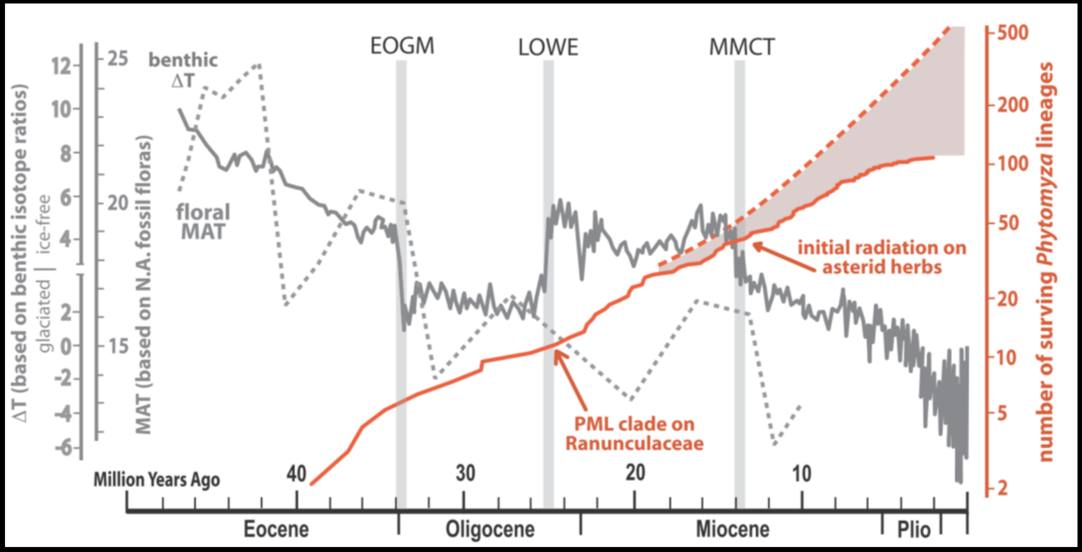
- ✓ Idea: Visually searched for correlations between phylogenetic events and specific climate changes
- ✓ Drawback: highly correlative and speculative approach

2. Fitting birth-death model at specific climatic event

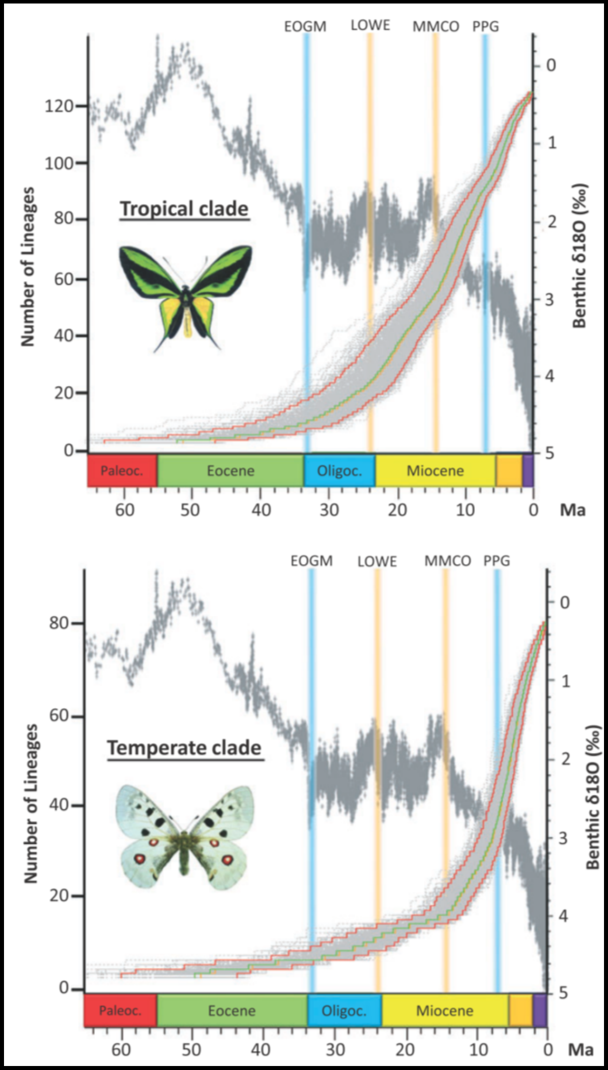
a. We know **periods of climate changes** in the history

b. **Compare** a one-rate BD model vs. 2-rates BD model

c. **Shift time** is the climatic event (e.g. cooling event)



Winkler et al. 2009 – PNAS



Condamine et al. 2012 – Ecol. Letters

3. Using trait-dependent diversification models

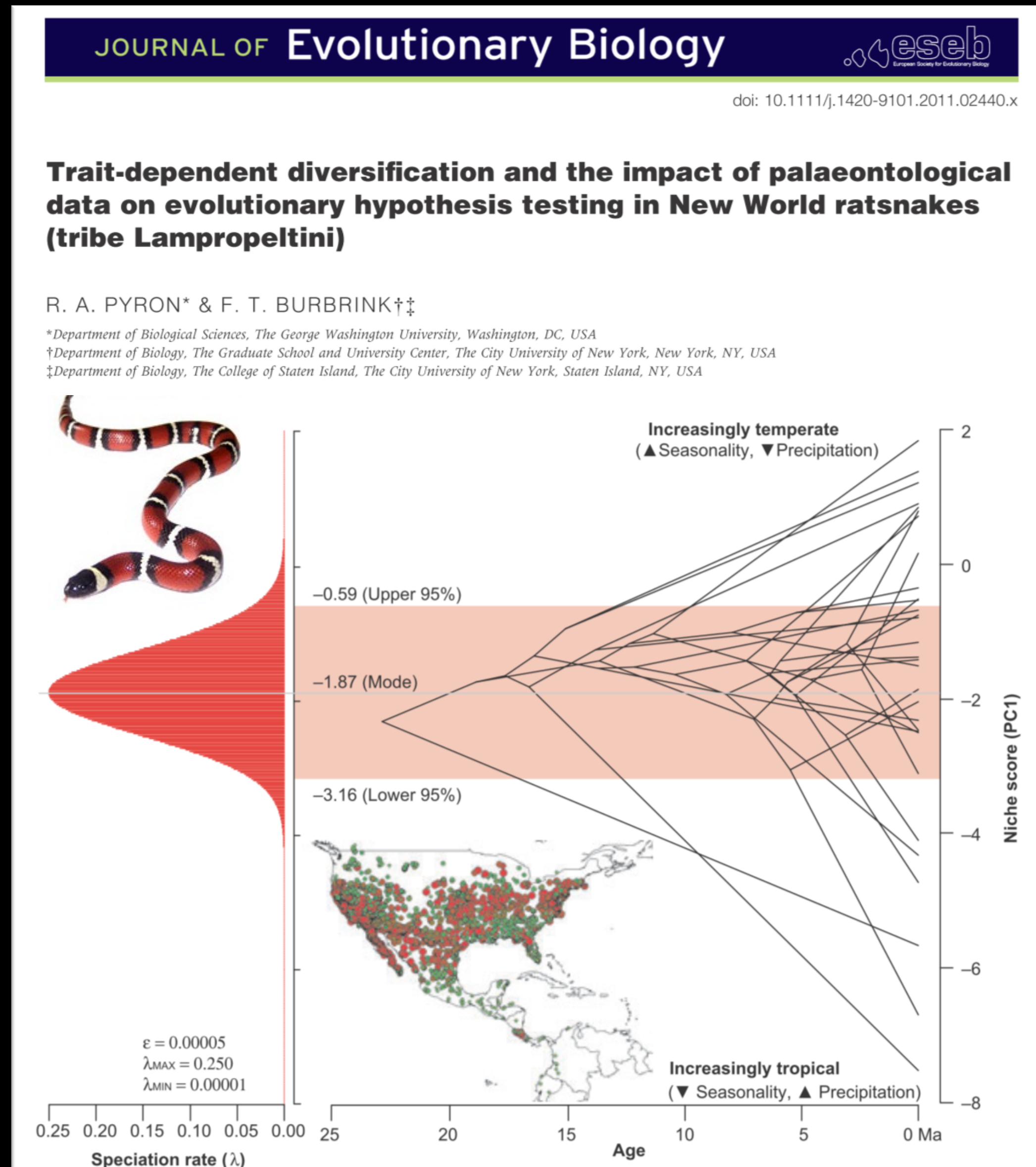
a. Inferring functional dependence of speciation and extinction rates on a character

b. Characters may be either **binary** (presence/absence) or **quantitative** (temperature)

BiSSE (Maddison et al. 2007 – Syst. Biol.)
QuaSSE (FitzJohn 2010 – Syst. Biol.)

c. Compare several functional dependences (sigmoid, hump-shaped)

Pyron & Burbrink 2012 – J. Evol. Biol.


JOURNAL OF Evolutionary Biology

doi: 10.1111/j.1420-9101.2011.02440.x

Trait-dependent diversification and the impact of palaeontological data on evolutionary hypothesis testing in New World ratsnakes (tribe Lampropeltini)

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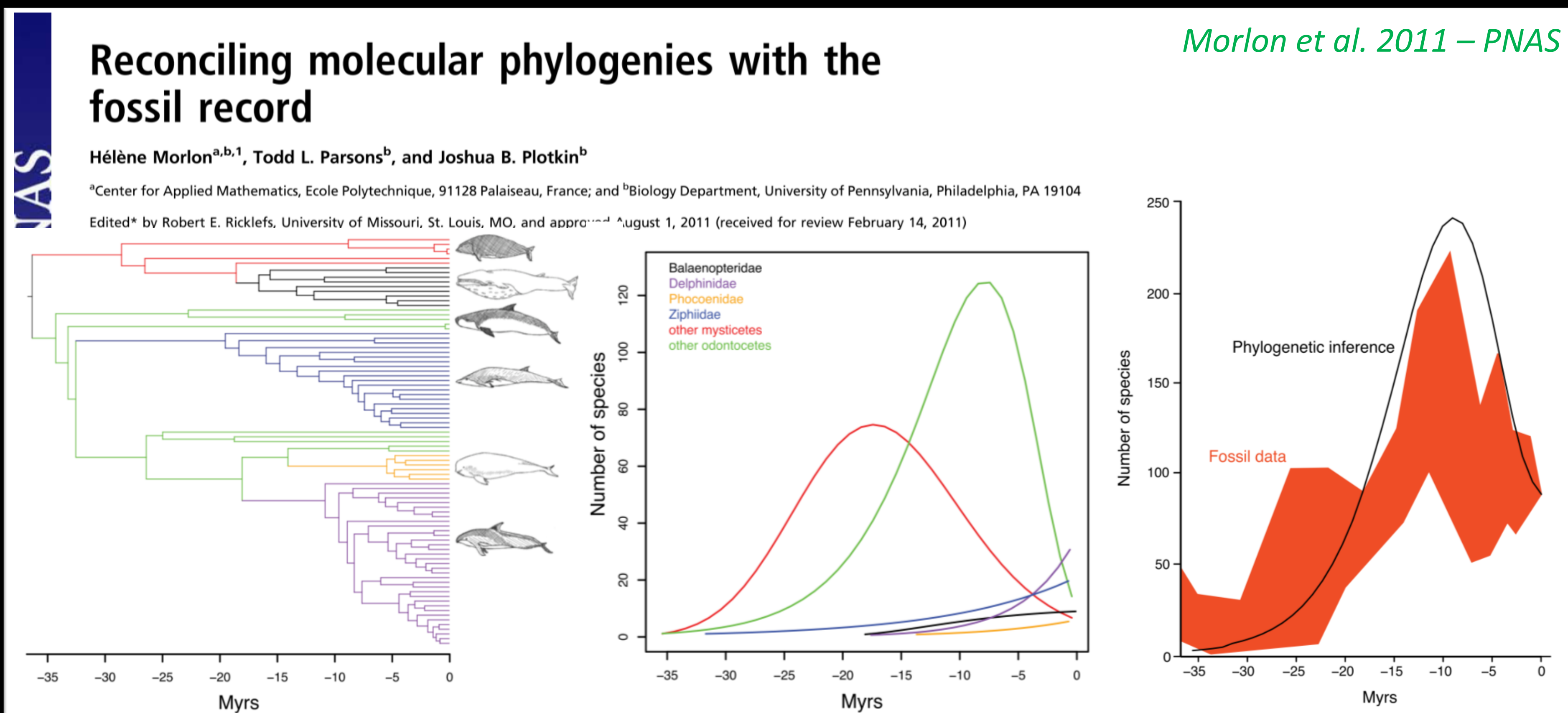
A new approach incorporating paleotemperature data

1 – Approach based on a time-dependent diversification model

- Speciation and extinction rates can **vary trough time**
- Extinction rate **can exceed** that of speciation
- Only a **fraction of extant species** are sampled



A new approach incorporating paleotemperature data

1 – Approach based on a time-dependent diversification model

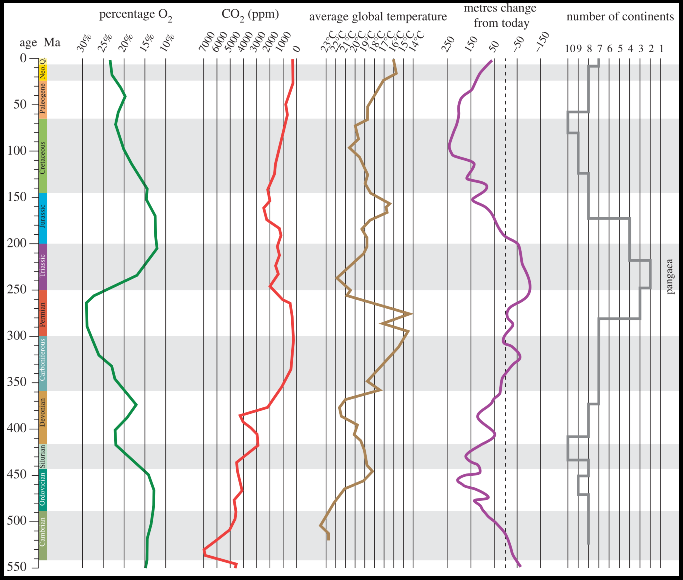
- Speciation and extinction rates can **vary trough time**
- Extinction rate **can exceed** that of speciation
- Only a **fraction of extant species** are sampled

Morlon et al. 2011 – PNAS

In addition

2 – It allows speciation and extinction rates to **also depend on an external variable, itself depending on time:**

- Temperature
- Sea level
- Atmospheric carbon concentration
- Number of continents
- *… any external variable you want*



Benton 2010 – PTRSB

A new approach incorporating paleotemperature data

Equations of speciation and extinction rates depending on time and environmental variable *(E(t))*

$$\tilde{\lambda}(t) = \lambda\left(t, E_1(t), E_2(t), \ldots, E_k(t)\right)$$

$$\tilde{\mu}(t) = \mu\left(t, E_1(t), E_2(t), \ldots, E_k(t)\right)$$

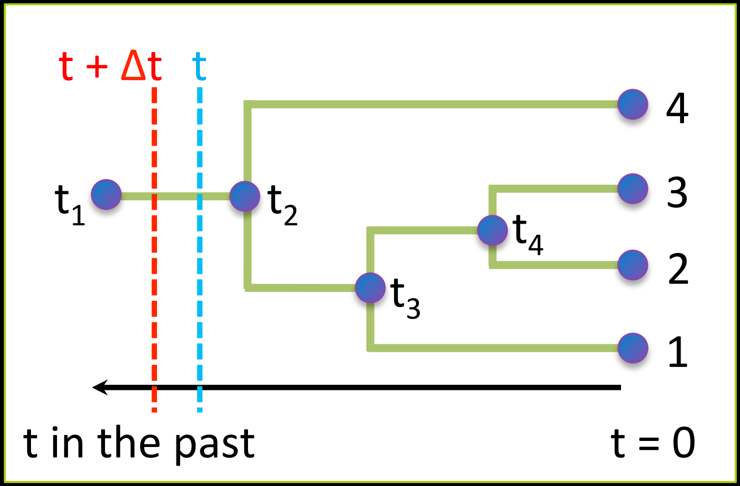
The new exact Likelihood expression of the model with time-varying speciation and extinction rates and incomplete sampling

$$L(t_1, \ldots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^{n} \tilde{\lambda}(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)}$$

A new approach incorporating paleotemperature data

- Time is **measured from the present to the past**

- **$t = 0$** denotes the present, and t increases into the past
- **t_1** denotes the first time at which the ancestral species came into existence
- **t_2** is the time of the most recent common ancestor of the sampled species
- **$\{t_2, t_3, \ldots, t_n\}$** denote the times of branching events in the phylogeny, with **$t_1 > t_2 > \ldots > t_n$**



A new approach incorporating paleotemperature data

$$L(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1)\prod_{i=2}^{n} \tilde{\lambda}(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)}$$

probability that *n* species are sampled today

A new approach incorporating paleotemperature data

$$L(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1) \prod_{i=2}^{n} \tilde{\lambda}(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)}$$

$\Psi(t_2,t_1)$, the probability that a lineage survives from t_1 to t_2 and leaves one descendant lineage at time t_2:

$$\Psi(t_2,t_1) = e^{\int_{t2}^{t_1} \tilde{\lambda}(u)-\tilde{\mu}(u)du} \left[1 + \frac{\int_s^{t_1} e^{\int_0^{\tau} \tilde{\lambda}(\sigma)d\sigma} \tilde{\lambda}(\tau)d\tau}{\frac{1}{f} + \int_0^{t2} e^{\int_0^{\tau} \tilde{\lambda}(\sigma)d\sigma} \tilde{\lambda}(\tau)d\tau} \right]^{-2}$$

A new approach incorporating paleotemperature data

$$L(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1) \prod_{i=2}^{n} \tilde{\lambda}(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)}$$

probability of a speciation event at time t_i

In which, $\mathbf{s_{i,1}}$ and $\mathbf{s_{i,2}}$ denote the times at which the descendant lineages introduced themselves branch at time t_i

A new approach incorporating paleotemperature data

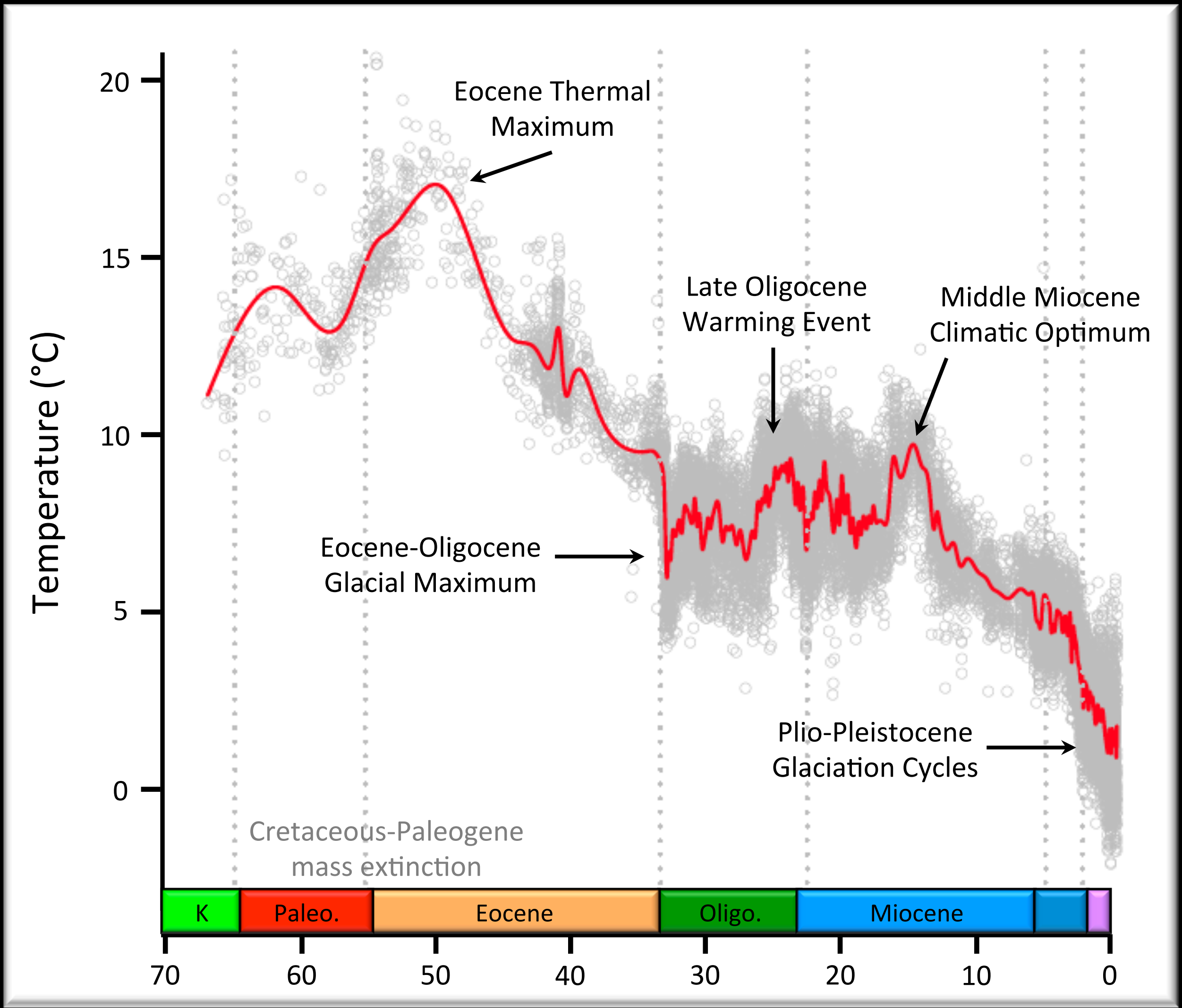
$$L(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1)\prod_{i=2}^{n} \tilde{\lambda}(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)}$$

$1 - \Phi(t_1)$, the probability that the subclade did not go extinct

$\Phi(t)$, the probability that a lineage alive at time t has no descendant in the sample:

$$\Phi(t) = 1 - \frac{e^{\int_0^t \tilde{\lambda}(u)-\tilde{\mu}(u)du}}{\frac{1}{f} + \int_0^t e^{\int_0^s \tilde{\lambda}(u)-\tilde{\mu}(u)du}\,\tilde{\lambda}(s)ds}$$

Case study with Cetacea



Tested with an **exponential dependence** of speciation on temperature given by:

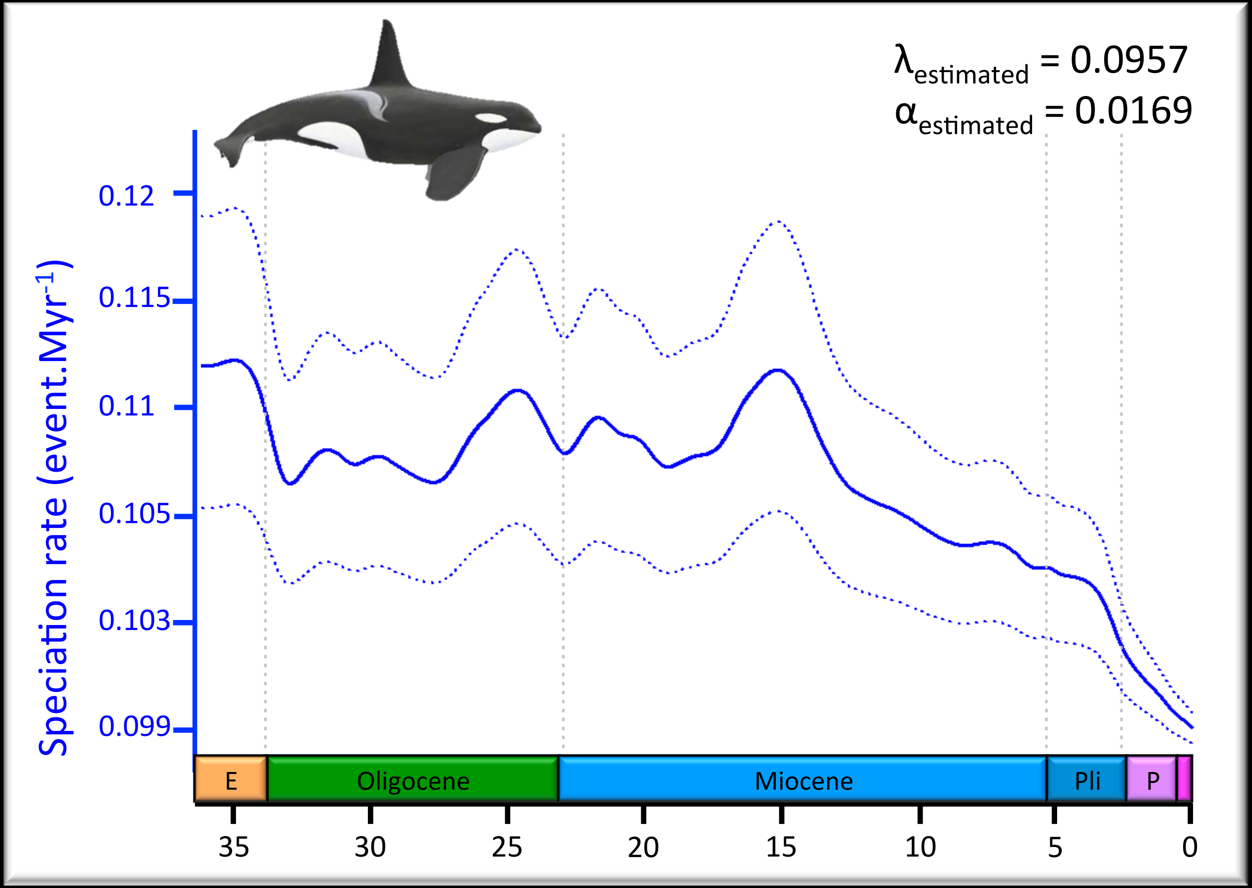
$$\widetilde{\lambda}(t) = \lambda_0 e^{\alpha T(t)}$$

Positive α indicate that higher temperatures **enhance** speciation

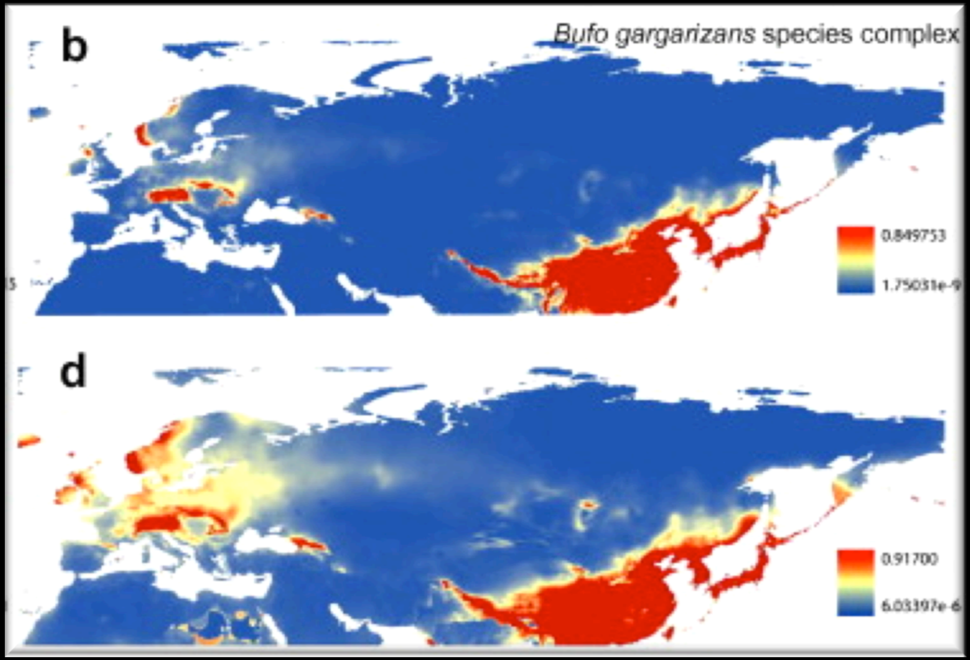
Negative α indicate that higher temperatures **hamper** speciation

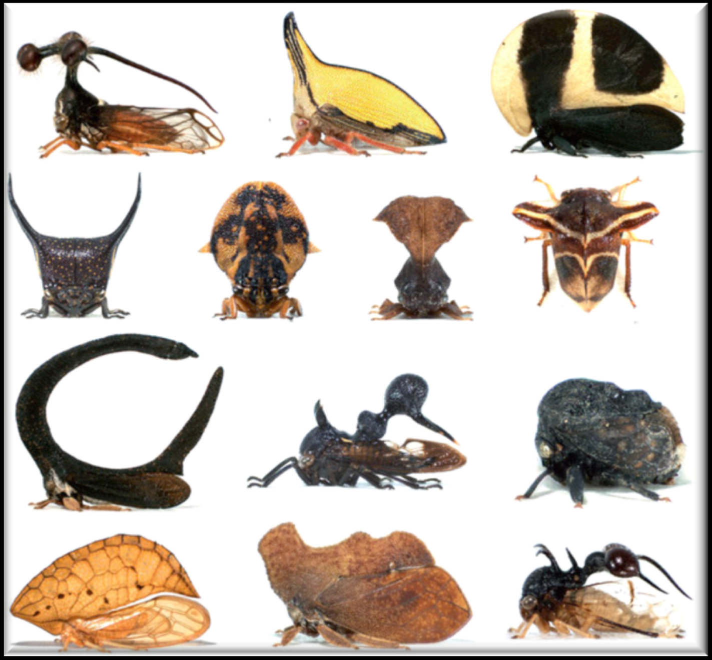
Case study with Cetacea

The relationship between speciation rate and temperature estimated with the approach is $\lambda(T) = 0.0957e^{0.0169T}$, suggesting a positive dependence of speciation rates on temperature

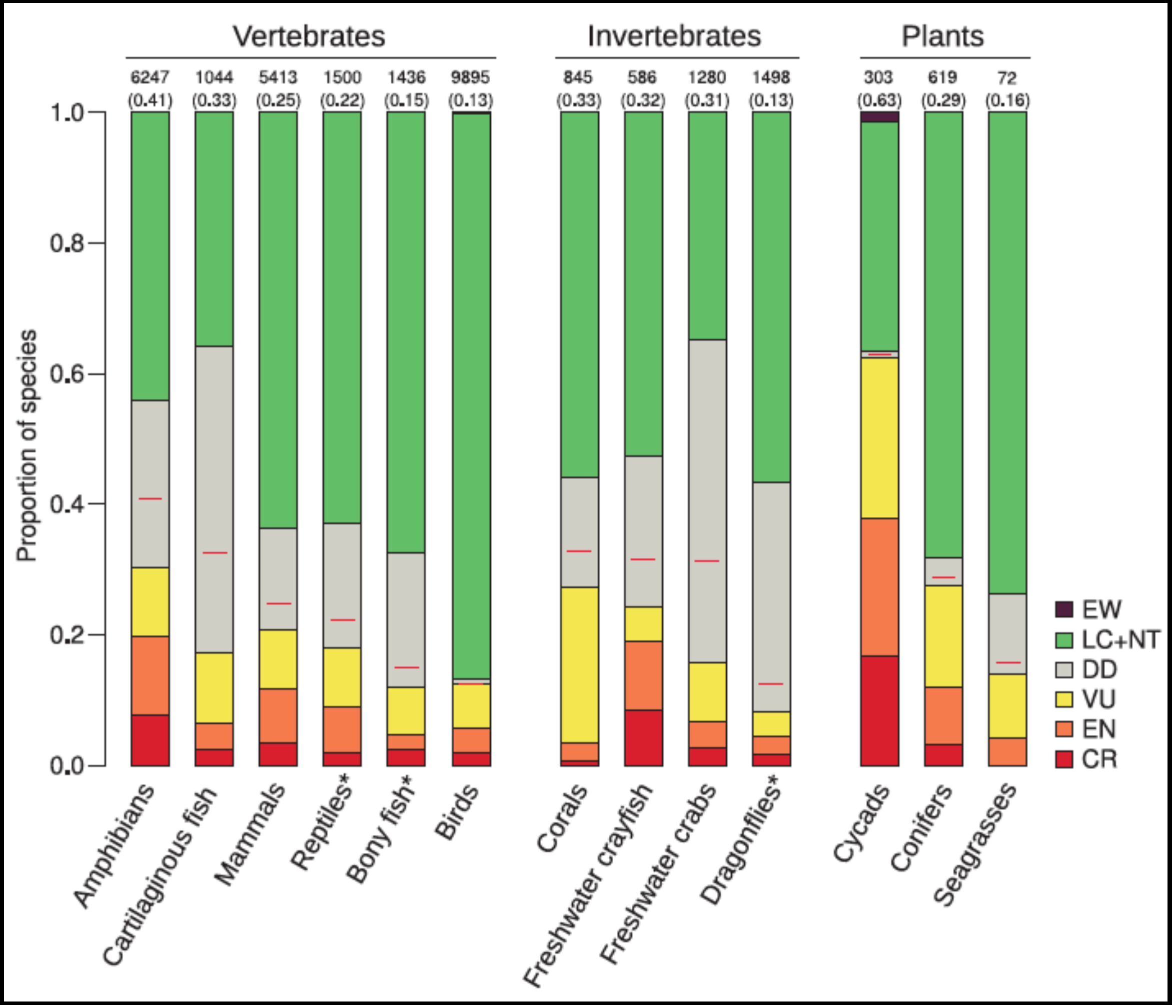


Vulnerability and evolutionary potential



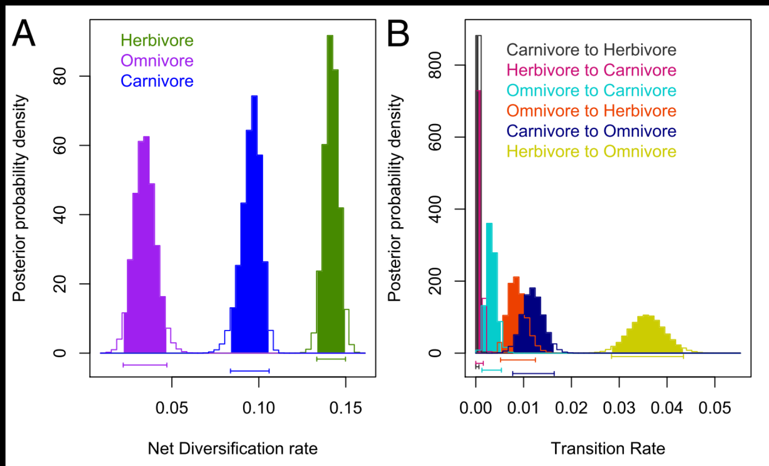


Clades are more threatened by extinctions than others



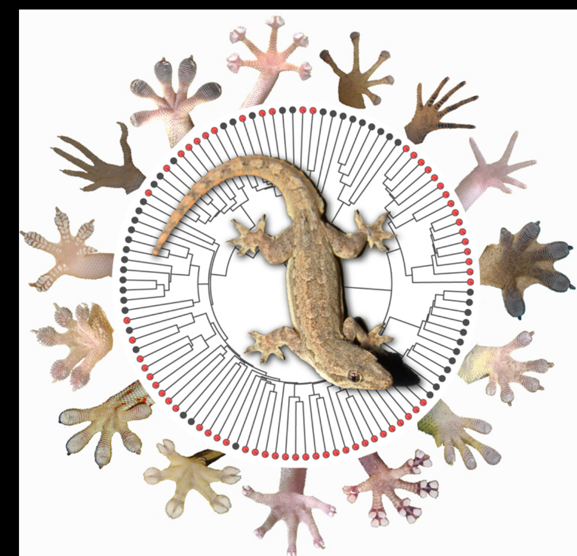
Hoffmann et al. 2010 – Science

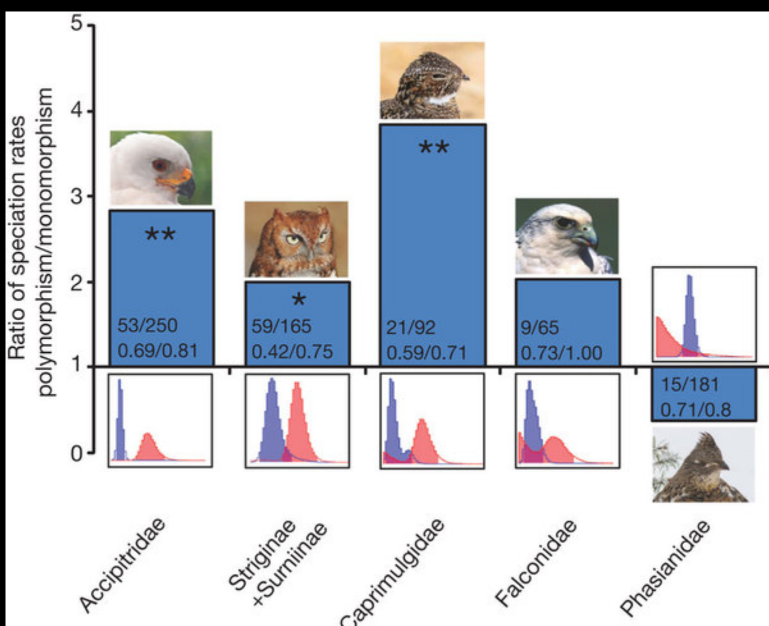
Evaluating vulnerability and evolutionary potential of lineages



Trophic strategy

Morphological character

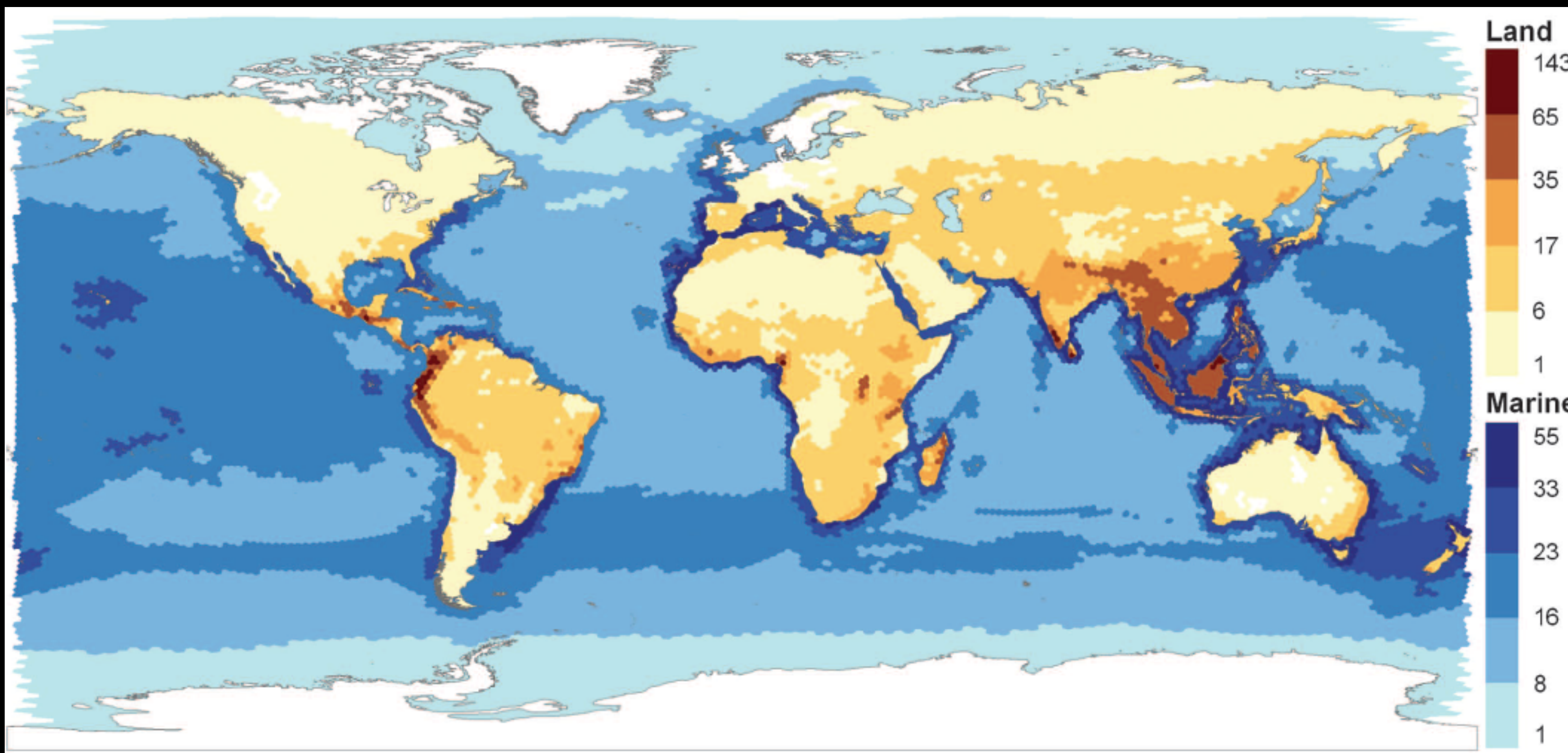




Colour polymorphism

Goldberg et al. 2010 – Science
Gamble et al. 2012 – PLoS One
Hugall & Stuart-Fox 2012 – Nature
Price et al. 2012 – PNAS

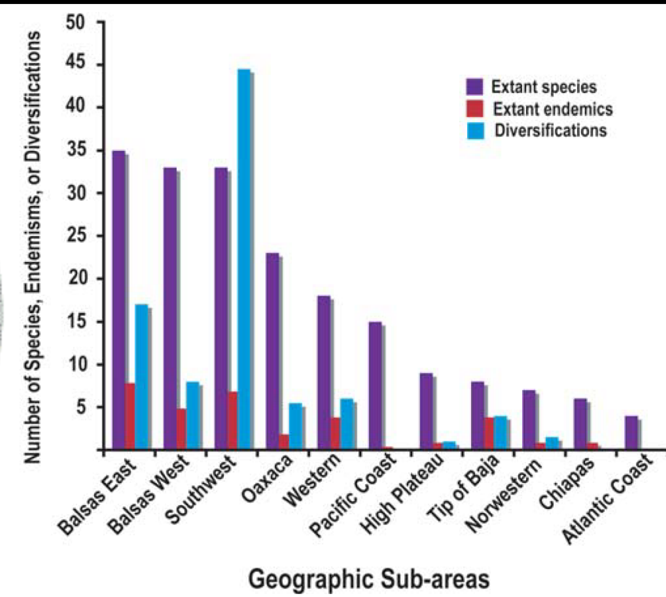
Regions are more threatened by extinctions than others



Hoffmann et al. 2010 – Science

Conservation policies focus on biodiversity hotspots

… But areas of high diversity are not necessarily areas of high diversification

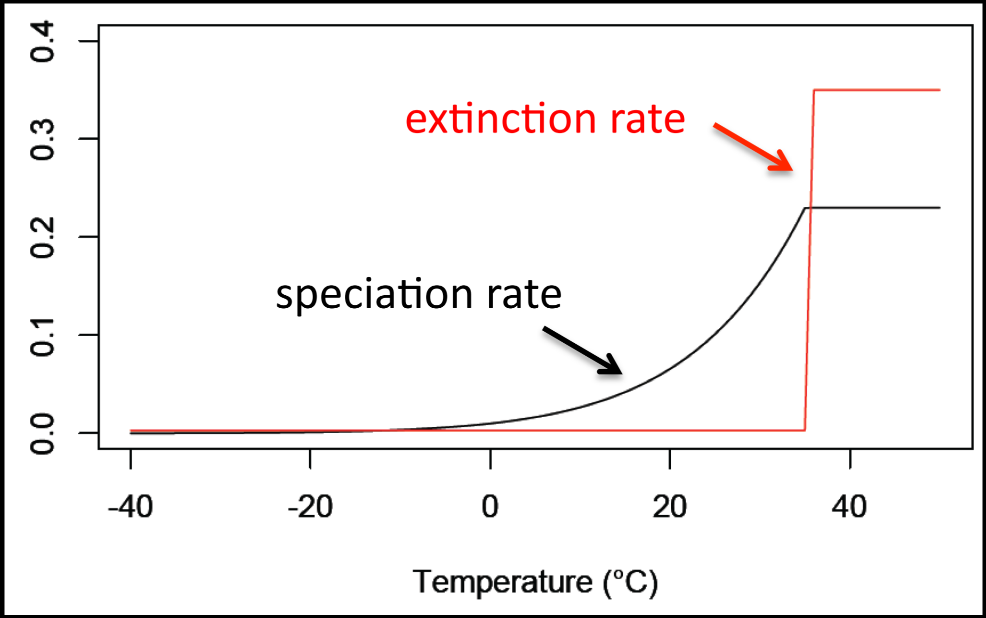


Myers et al. 2000 – Nature   *Beccera & Venable 2008 – PLoS One*

Evaluating vulnerability and evolutionary potential of regions

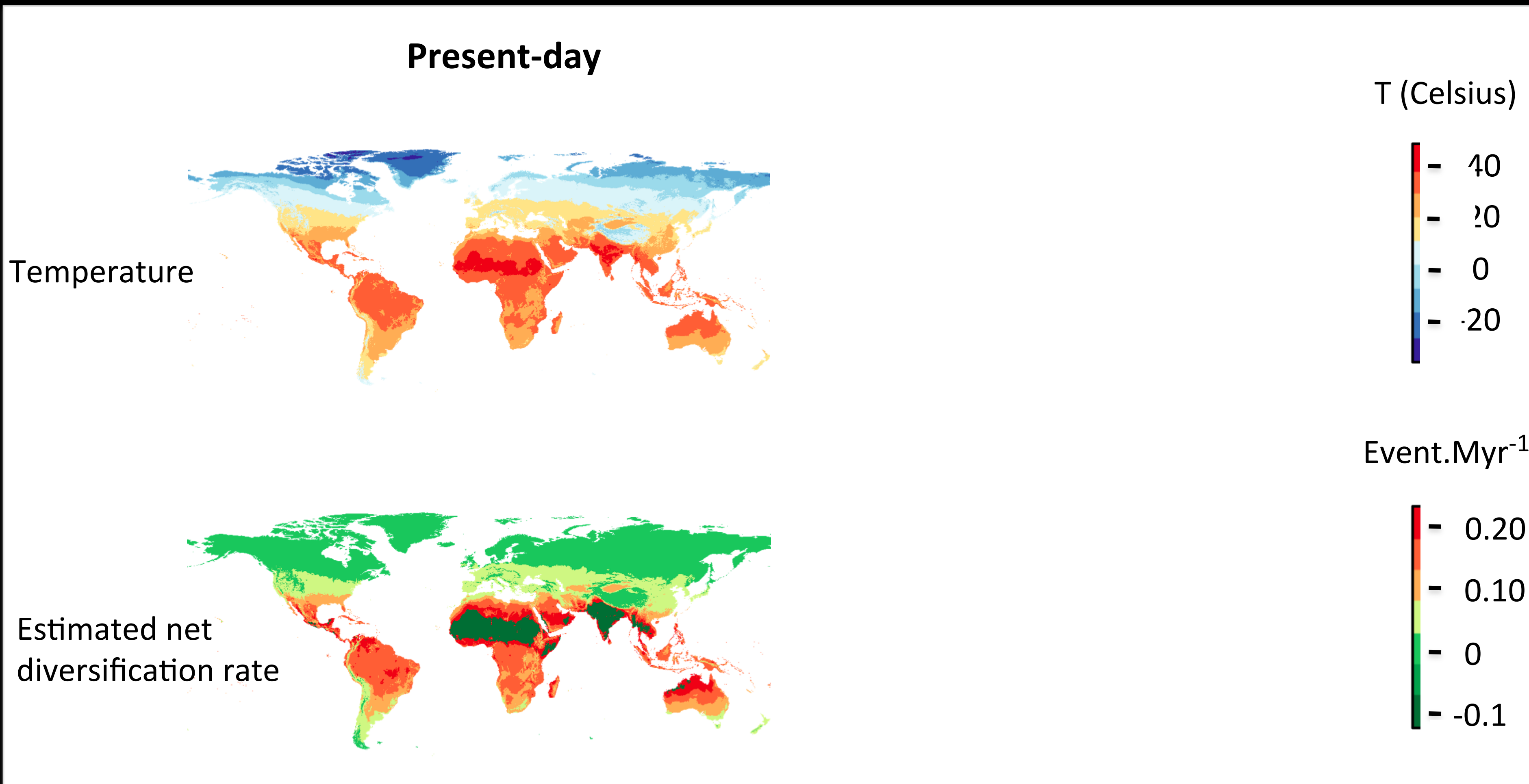
➡ Using phylogenetic approaches (trait-dependent diversification model like QuaSSE)

Possible to estimate the functional dependence of diversification rates on environmental variables:



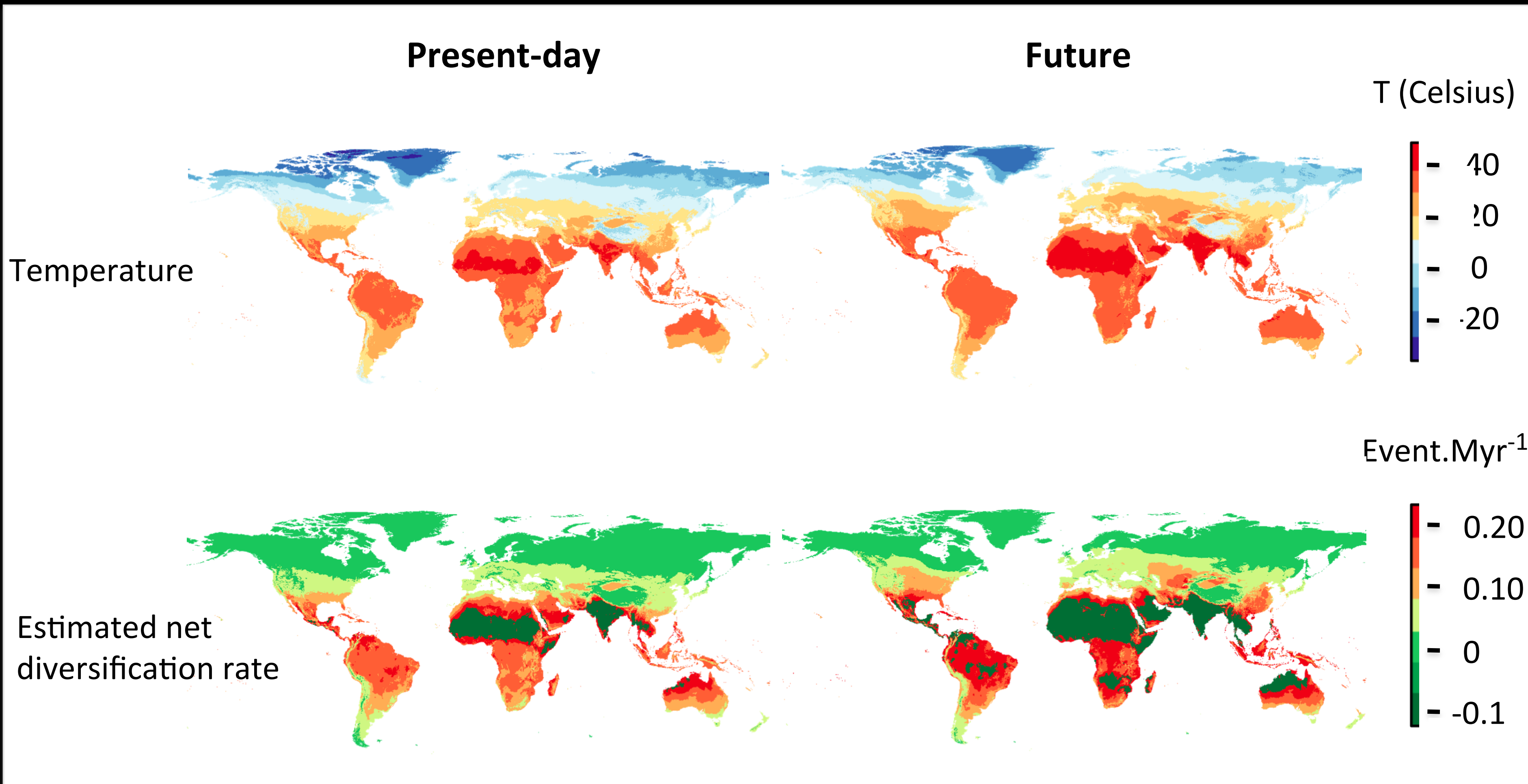
Evaluating vulnerability and evolutionary potential of regions

Map **current environmental variables** and associated diversification rate

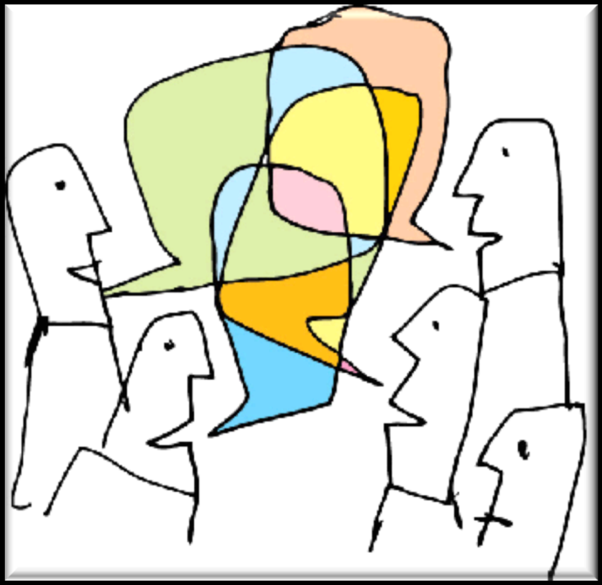


Evaluating vulnerability and evolutionary potential of regions

Map **future (2080) environmental variables** and associated diversification rate



Limitations and Perspectives



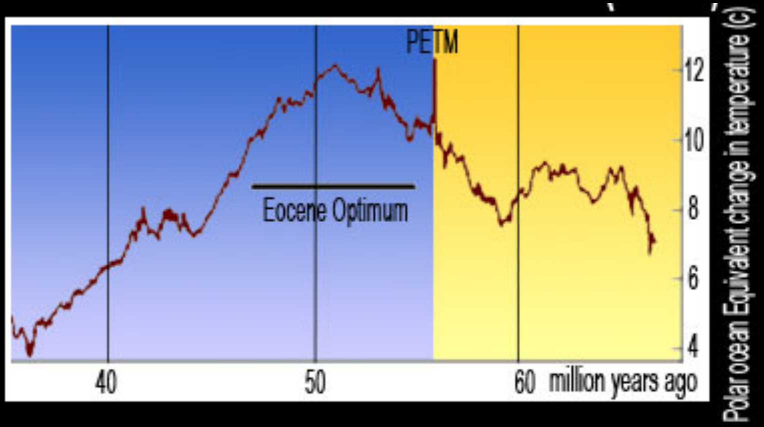
Past versus current environmental changes

- ✓ Keep in mind that what happened in the past is different from what happen today
- ✓ Environmental changes are faster than in the past:

Ex.

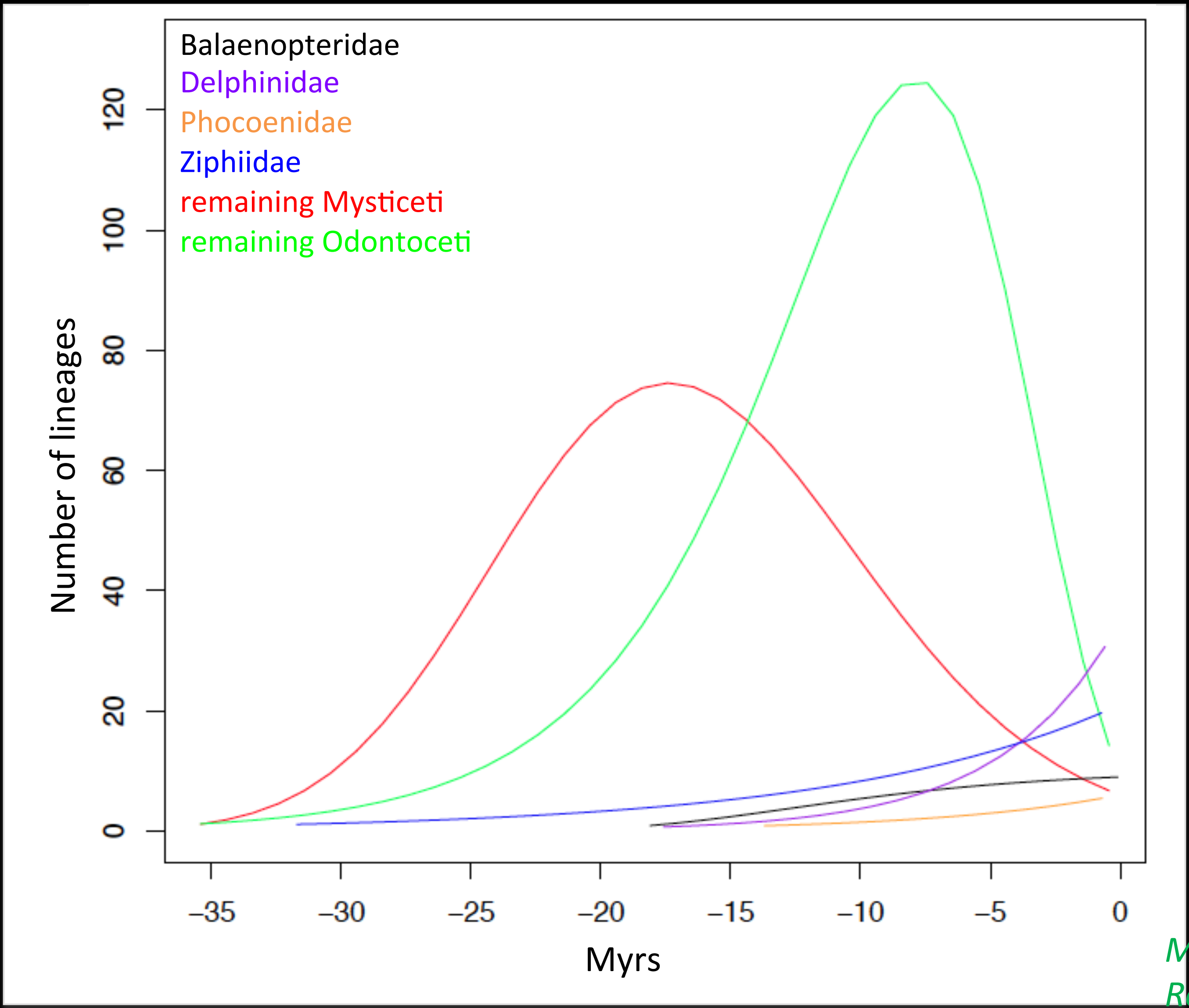
- Habitat loss (bolide impacts) were instantaneous => similar to deforestation today?

- Climate changes were usually on long-term period but … see the PETM at 56 Ma



Global temperatures have increased by 0.0074 °C per year, which is much faster than the 0.0003 °C per year increase within 20 000 years during one of the PETM

Are macroevolutionary estimates relevant to conservation?



Morlon et al. 2011 – PNAS
Rolland et al. 2012 – Biol. Letters

Comparing current extinction risks to past extinction rates

Clades with **negative diversification rates** (diversity decline) have **high current extinction risk**

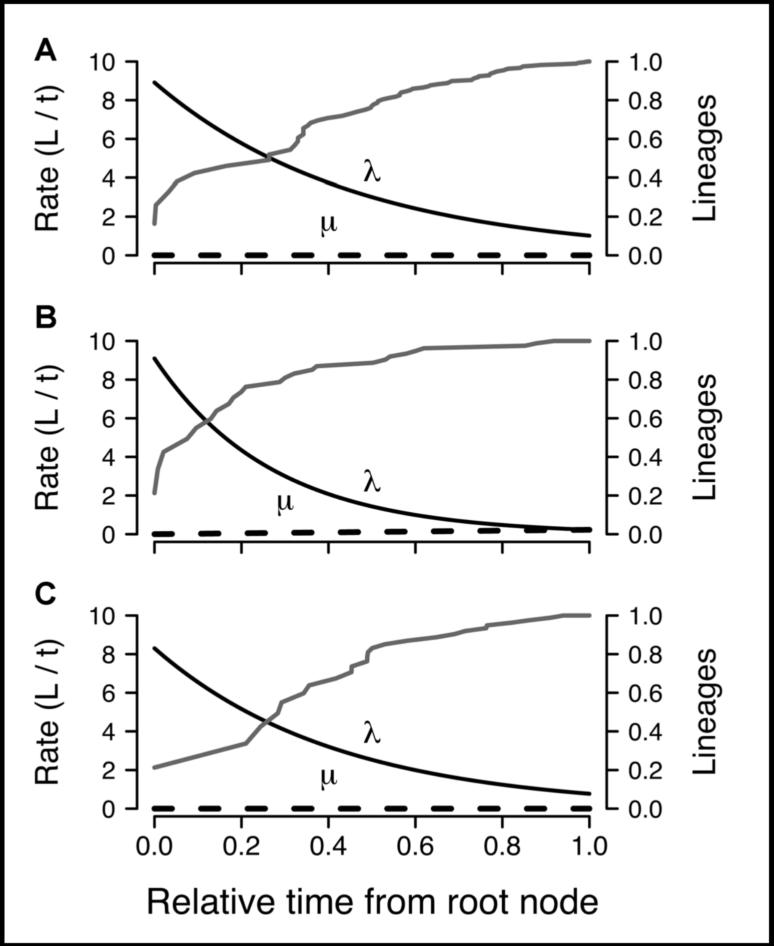
Clades	Net diversification rates at present		% of threatened	
Balaenopteridae	0.02		25	
Delphinidae	0.224	0.119	13.9	20.4
Phocoenidae	0.141	(±0.085)	42.9	(±0.18)
Ziphiidae	0.093		0.0	
other mysticetes	**-0.528**	**-0.703**	**33.3**	**50**
other odontocetes	**-0.877**	**(±0.247)**	**66.7**	**(±0.23)**

Suggest a **phylogenetic conservatism of extinction**

Some biological attributes (body size) that confer risk are conserved

Estimating extinction rates using phylogenies

For many groups there are **low extinction rates** which is unrealistic given the fossil record



- Integrating **phylogenies** and the **fossil record** in time-dependent model (Morlon et al. 2011 – PNAS)
- Work in collaboration with Tiago Quental (U. Sao Paulo, Brazil)

Rabosky & Lovette 2008 – Evolution
Quental & Marshall 2010 – TREE
Didier et al. 2012 – JTB

Conclusion

1. Phylogenies can be used to **understand past diversity dynamics and how they were influenced by environmental**
2. Phylogenies provide an **additional tool to predict** how diversity dynamics may be influenced by environmental change in the future
3. The **causes** of current extinctions **may be different** from what happened in the past and they are orders of magnitude higher
4. We have **little power to understand the past**, and we will have even **less to predict the future**
5. There are many caveats but the **full potential of phylogenies** in global change biology and conservation has **yet to be explored**

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and many more…

Thanks for your attention