



# The imprint of climate in phylogenetic trees: a global analysis on the diversification of Tetrapod families

**Théo Pannetier**

Study carried out in the *Phylogénie et Évolution Moléculaires* at the ISEM,  
under the supervision of Fabien Condamine



### Drivers of diversity :

Two concurrent hypothesis

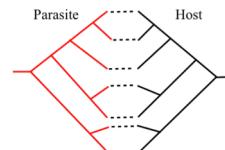
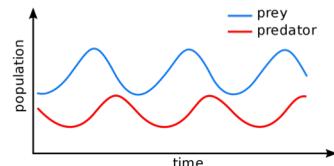
Benton 2009 – Science



### Red Queen

*Diversification process driven by biotic factors*

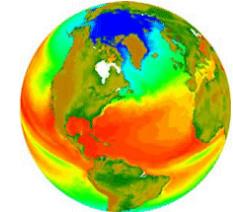
→ Effects through biotic interactions



### Court Jester

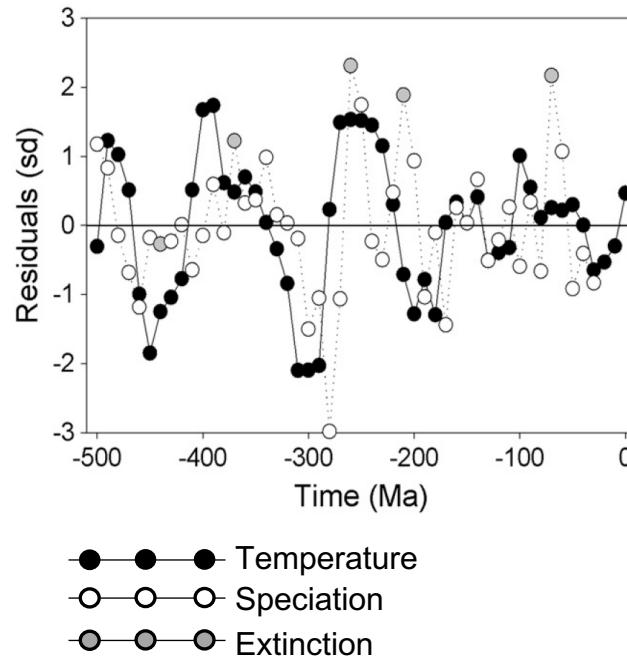
*Diversification process driven by abiotic factors*

→ Effects through the environment



Temperature → Climate

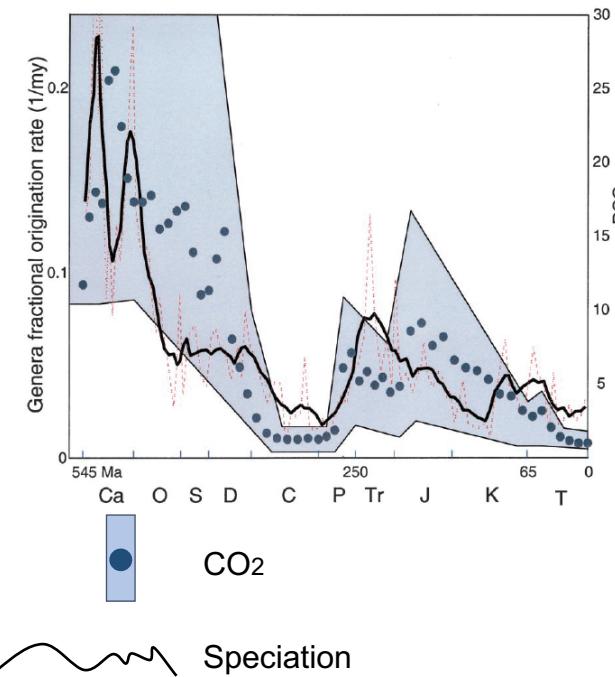
Biodiversity tracks temperature over time



Mayhew et al. 2012 – PNAS

CO<sub>2</sub> → Climate

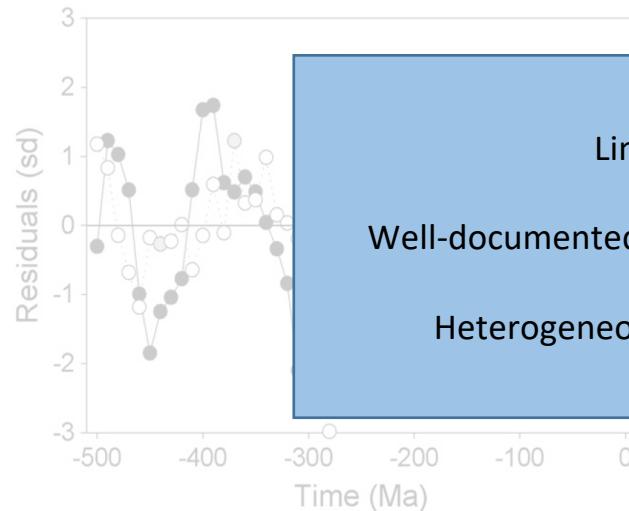
Documenting a significant relationship between macroevolutionary origination rates and Phanerozoic pCO<sub>2</sub> levels



Cornette et al. 2002 – PNAS

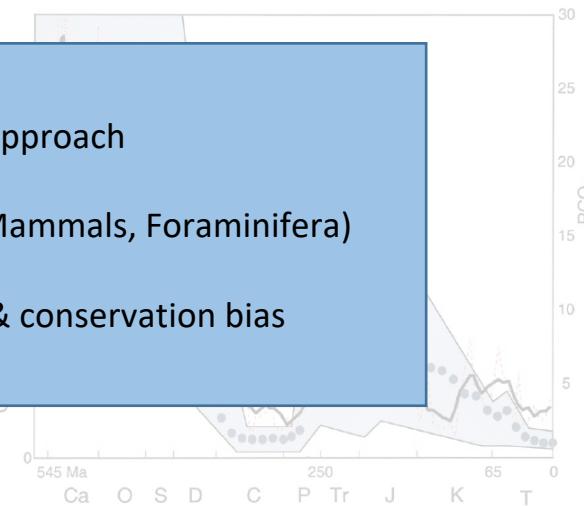
## Temperature → Climate

Biodiversity tracks temperature over time



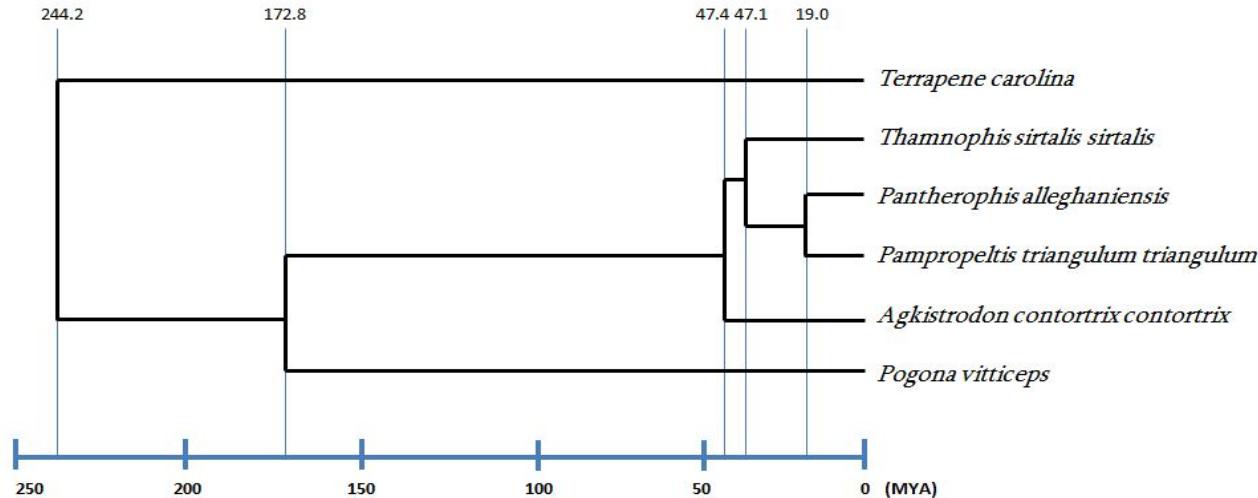
## $\text{CO}_2 \rightarrow \text{Climate}$

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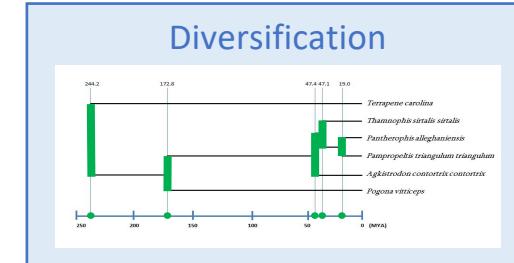
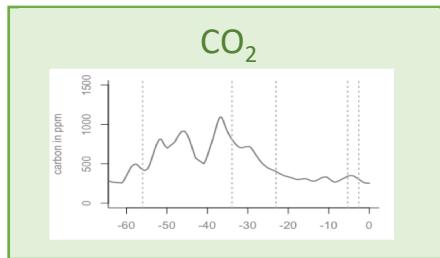
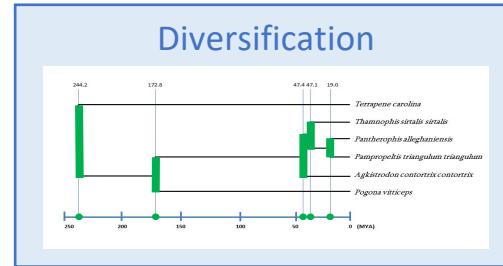
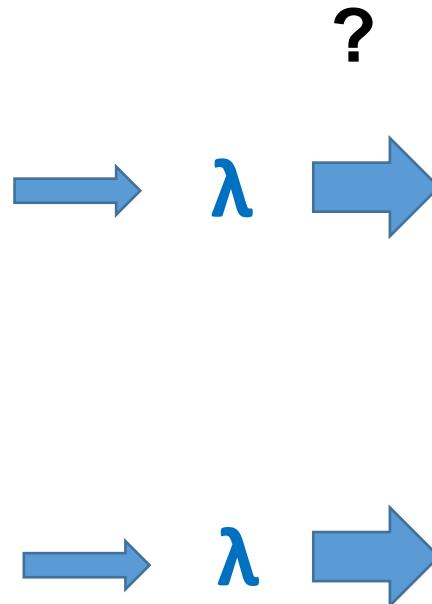
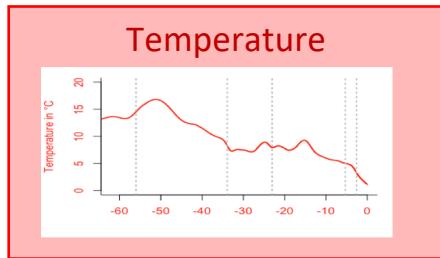


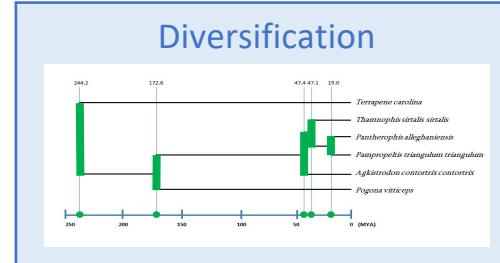
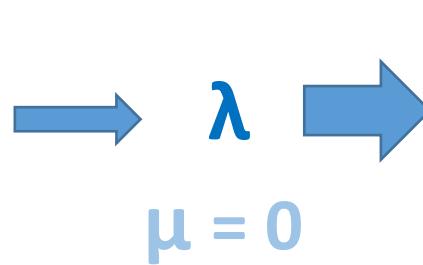
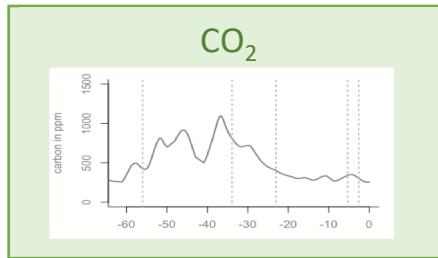
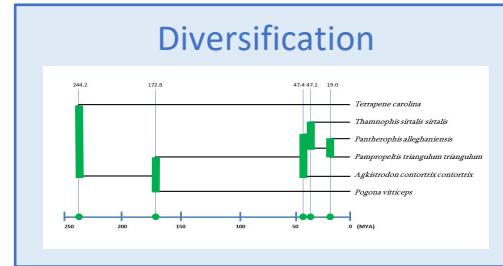
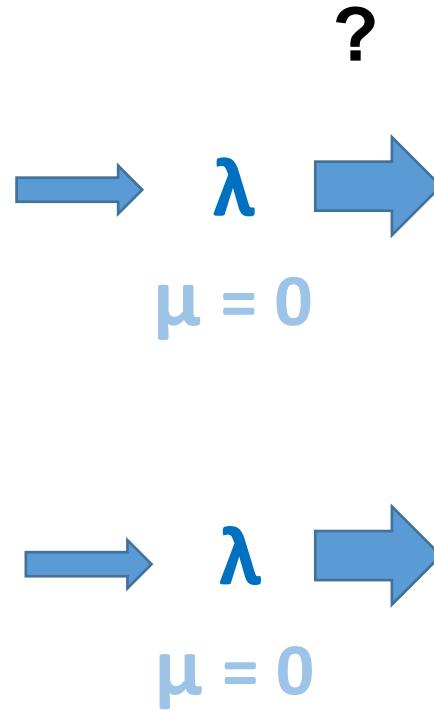
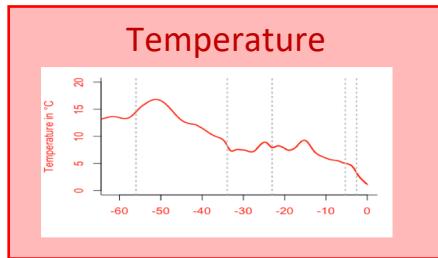
Another source of information available : molecular phylogenies

$$\text{Diversification} = \text{Speciation} (\lambda) - \text{Extinction} (\mu)$$



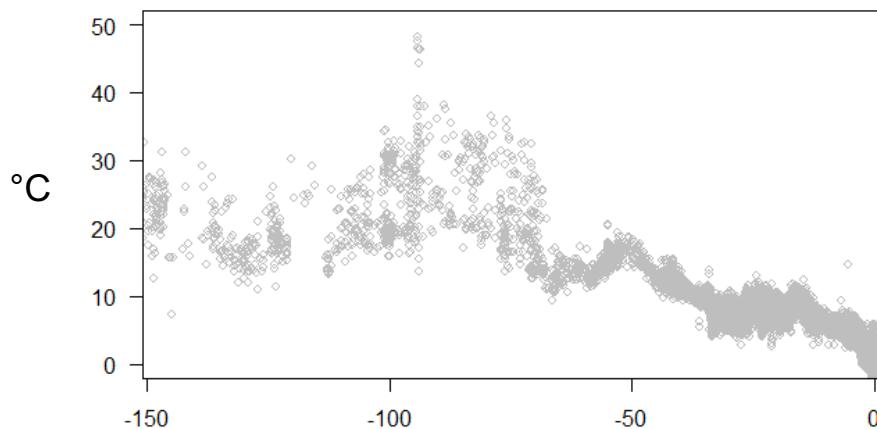
Diversification rate can be inferred from branch lengths



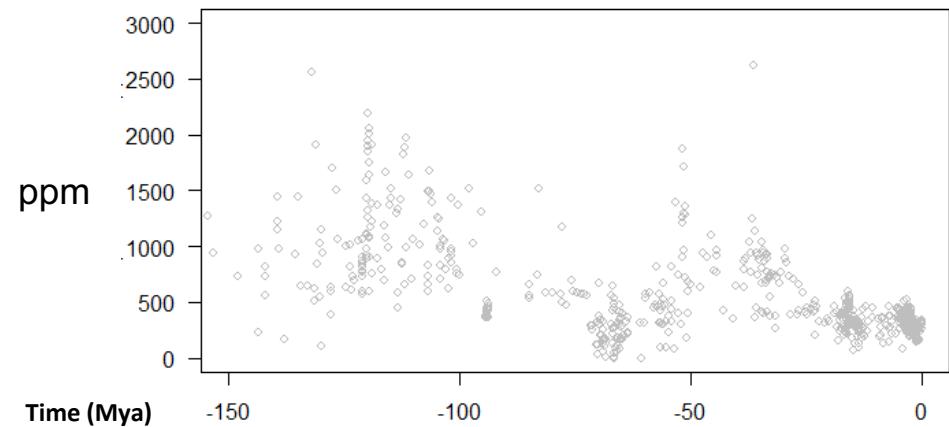


## Climatic data obtained from two datasets covering the whole 500 Mya

Global temperature



Atmospheric CO<sub>2</sub>



Zachos et al. 2008 – Nature

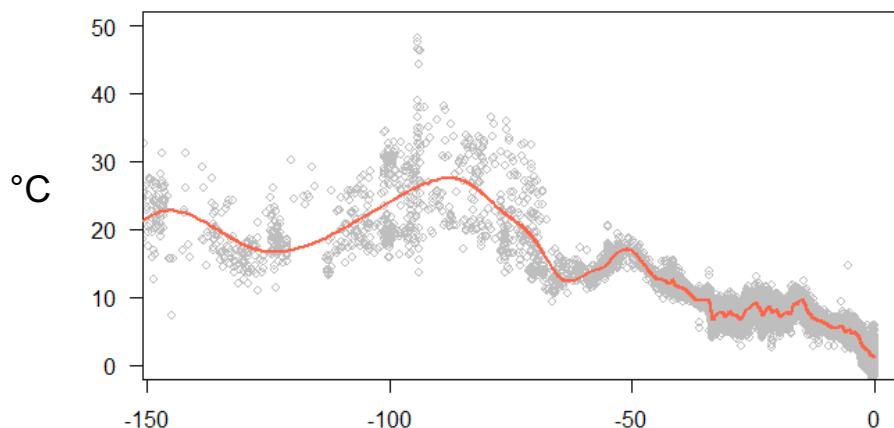
Prokoph et al. 2008 – Earth-Sci. Rev.

Cramer et al. 2011 – J. Geophys. Res.

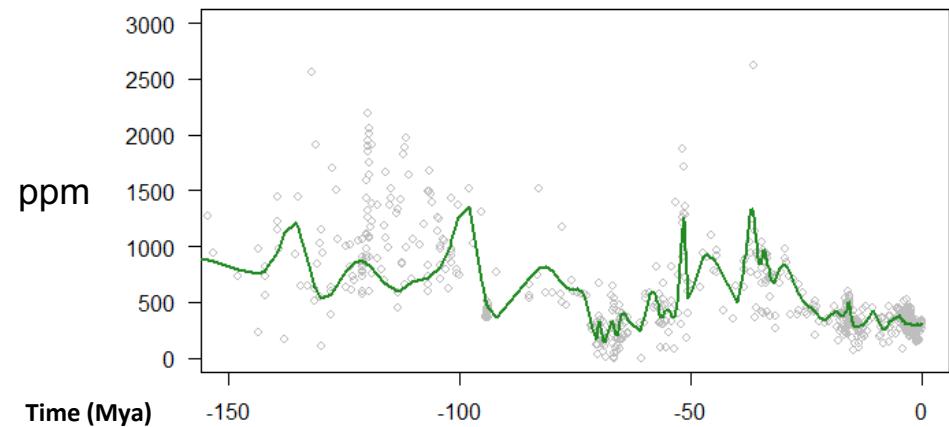
Foster et al. 2017 – Nat. Comm.

## Climatic data obtained from two datasets covering the whole 500 Mya

Global temperature



Atmospheric CO<sub>2</sub>



Discrete data points →

Continuous curve

Zachos et al. 2008 – *Nature*

Prokoph et al. 2008 – *Earth-Sci. Rev.*

Cramer et al. 2011 – *J. Geophys. Res.*

Foster et al. 2017 – *Nat. Comm.*

## Dated phylogenies for the six main clades of Tetrapods

| Clade      | Number of species | Taxon sampling | Authors                        | Number of families |
|------------|-------------------|----------------|--------------------------------|--------------------|
| Crocodylia | 25                | 100%           | Oaks (2011)                    | 1                  |
| Aves       | 11 000            | 99%            | Jetz et al. (2012)             | 129                |
| Testudines | 330               | 91%            | Rodrigues & Diniz-Filho (2016) | 7                  |
| Mammalia   | 5 500             | 99%            | Bininda-Emonds et al. (2007)   | 66                 |
| Squamates  | 10 500            | 41%            | Zheng & Wiens (2016)           | 14                 |
| Amphibia   | 7 700             | 37%            | Pyron (2014)                   | 15                 |

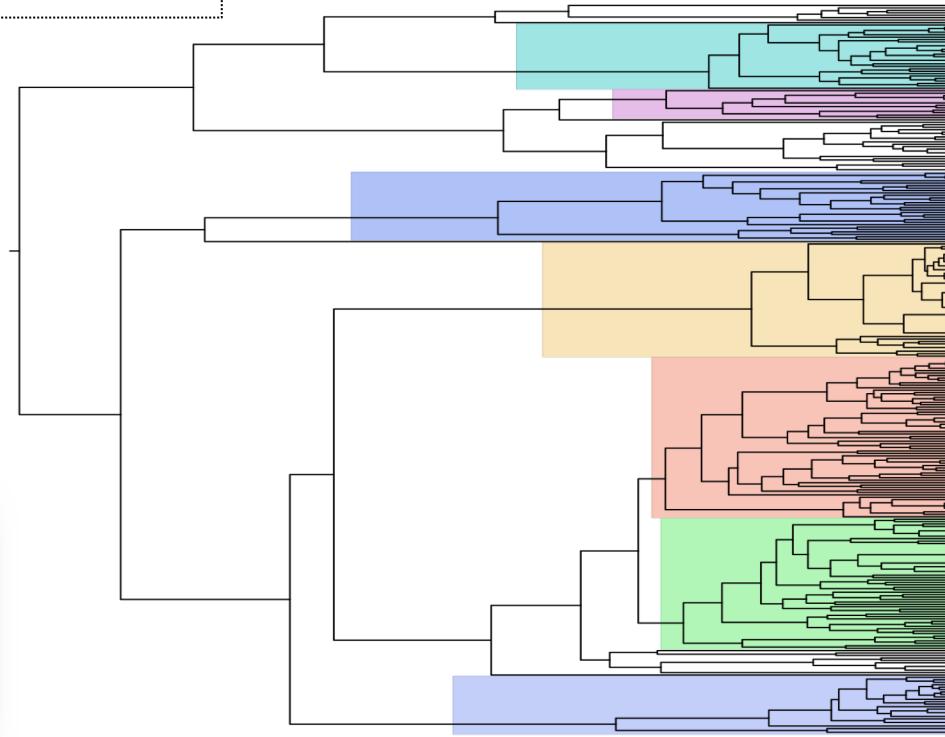
## Exemple with Testudine phylogeny (turtles & tortoises)

Criterions for inclusion in the sample:

- 1) At least 10 spp
- 2) At least 60 % of the taxa

**Testudines**

Trionychidae

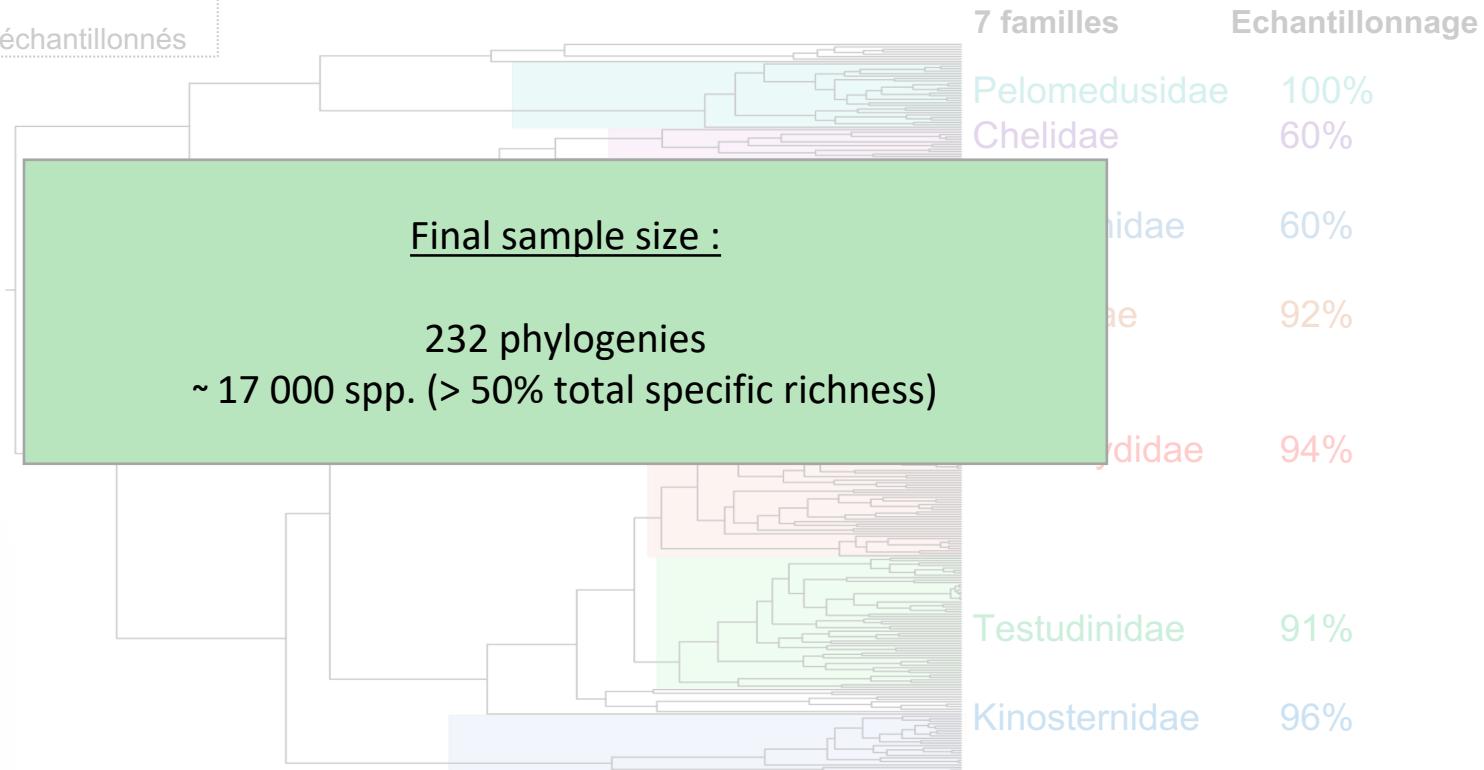


| 7 families    | Sampling |
|---------------|----------|
| Pelomedusidae | 100%     |
| Chelidae      | 60%      |
| Trionychidae  | 60%      |
| Emydidae      | 92%      |
| Geoemydidae   | 94%      |
| Testudinidae  | 91%      |
| Kinosternidae | 96%      |

## Exemple avec la phylogénie des Testudines (tortues)

Extraction des familles avec :

- 1) Au moins 10 espèces
- 2) Au moins 60% des taxons échantillonnés



Trionychidae



## Four speciation models were tested on each phylogeny

Constant model

$$\lambda(t) = \lambda$$

Speciation rate constant & independent

Time-dependent model

$$\lambda(t) = \lambda \times e^{\alpha t}$$

Speciation rate increases/decreases through time

Temperature-dependent model

$$\lambda(t) = \lambda \times e^{\alpha T^\circ(t)}$$

Speciation rate is function of temperature

CO<sub>2</sub>-dependent model

$$\lambda(t) = \lambda \times e^{\alpha CO_2(t)}$$

Speciation rate is function of a CO<sub>2</sub>

Four speciation models were tested on each phylogeny

Constant model

$$\lambda(t) = \lambda$$

Time-dependent model

$$\lambda(t) = \lambda \times e^{\alpha t}$$

Temperature-dependent model

$$\lambda(t) = \lambda \times e^{\alpha T^\circ(t)}$$

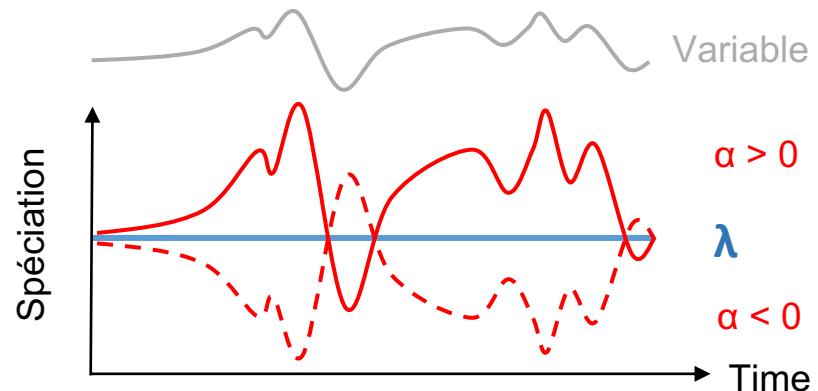
$\text{CO}_2$ -dependent model

$$\lambda(t) = \lambda \times e^{\alpha \text{CO}_2(t)}$$

Two parameters :

$\lambda$  « background » speciation rate

$\alpha$  strength and sense of the dependency



## Quatre types de modèles de spéciation testés sur chaque phylogénie

Modèle constant

$$\lambda(t) = \lambda$$

Modèle température

$$\lambda(t)$$

Modèle température

$$\text{Température } \lambda(t) = \lambda \times e^{\alpha T^\circ(t)}$$

Modèle CO<sub>2</sub>-dépendant

$$\text{CO}_2 \quad \lambda(t) = \lambda \times e^{\alpha \text{CO}_2(t)}$$

Deux paramètres:

$\lambda$  correspond à un taux de spéciation sous-jacent

Parameter optimisation → **Maximum likelihood**

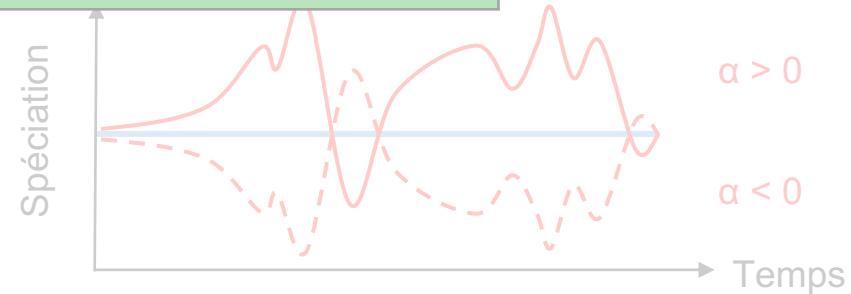
Model selection → **AIC**

le signe de  
l'effet

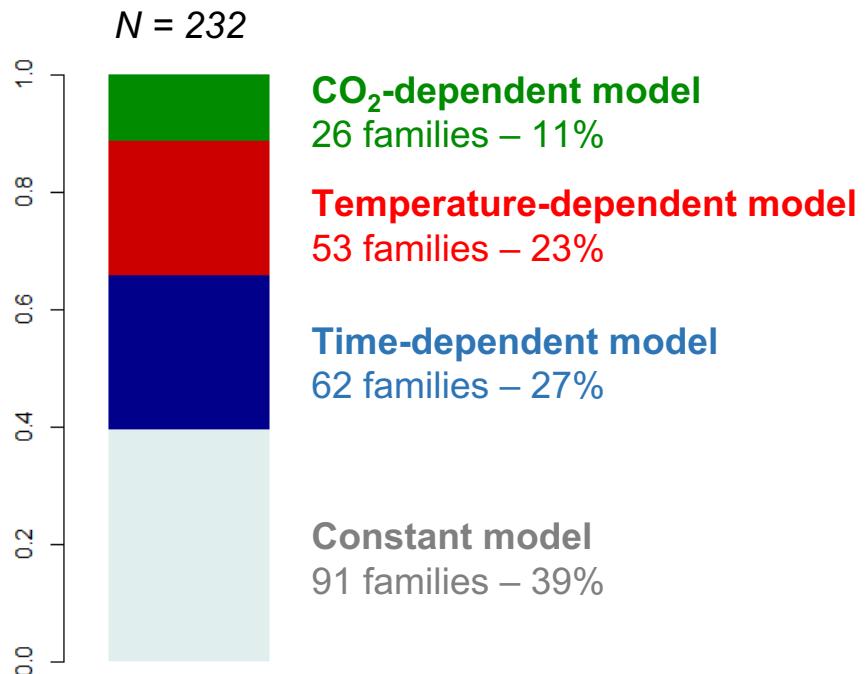
Variable

$\alpha > 0$

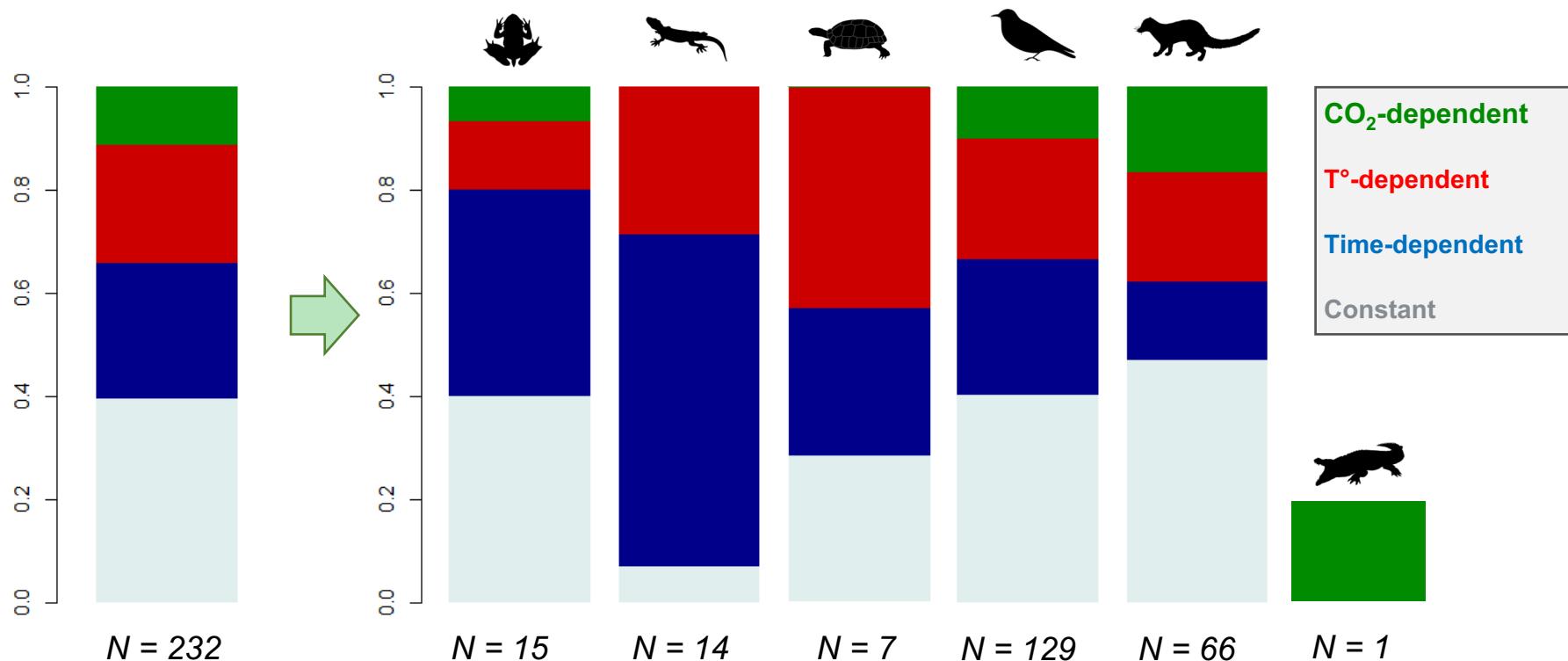
$\alpha < 0$



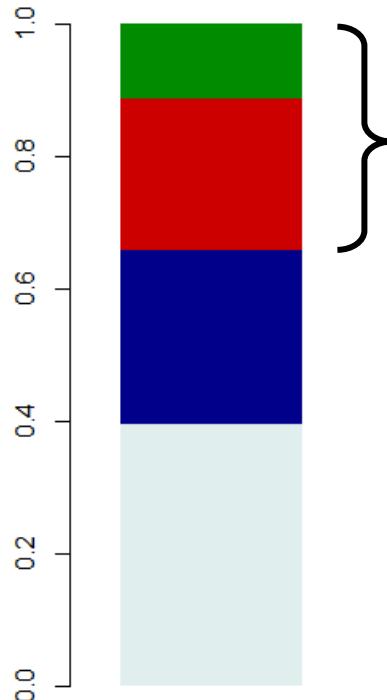
### Overall results for the 232 families



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# DISCUSSION



**34% of families:** speciation rate variations best explained by climatic variations  
(CO<sub>2</sub> & temperature)

## 1 - Signal of climate : rule or exception ?

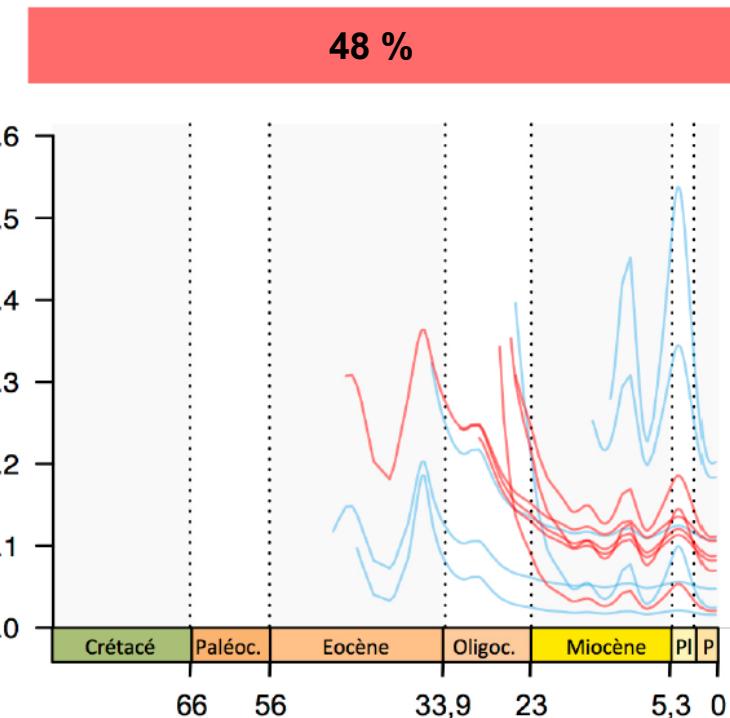


Signal found in the 6 main clades of living tetrapods

# RESULTS

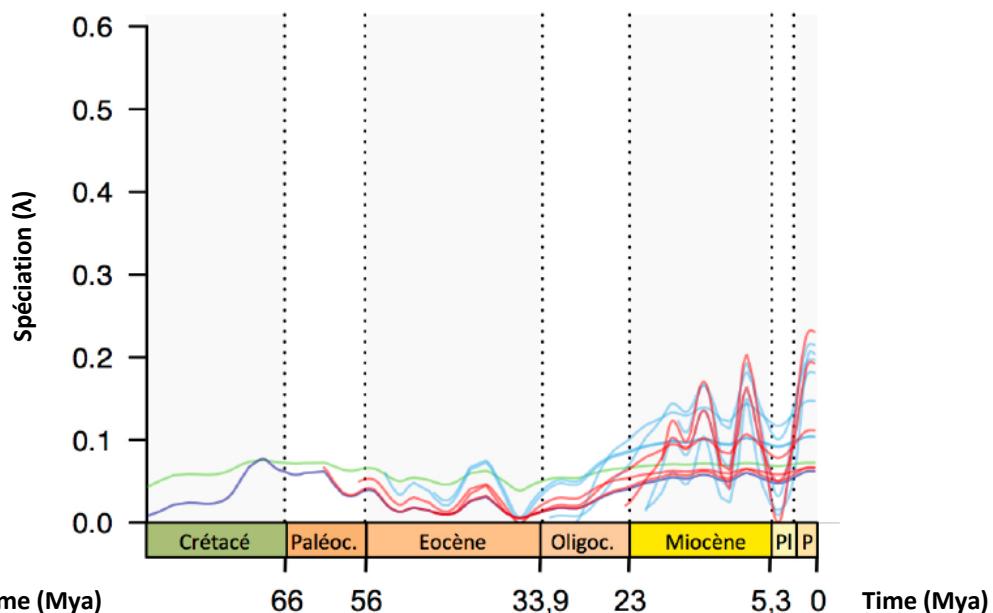
## CO<sub>2</sub>-dependent speciation

Positive correlation  $\alpha > 0$



48 %

Negative correlation  $\alpha < 0$



52 %



13



0



2



11



1

# RESULTS

## Temperature-dependent speciation

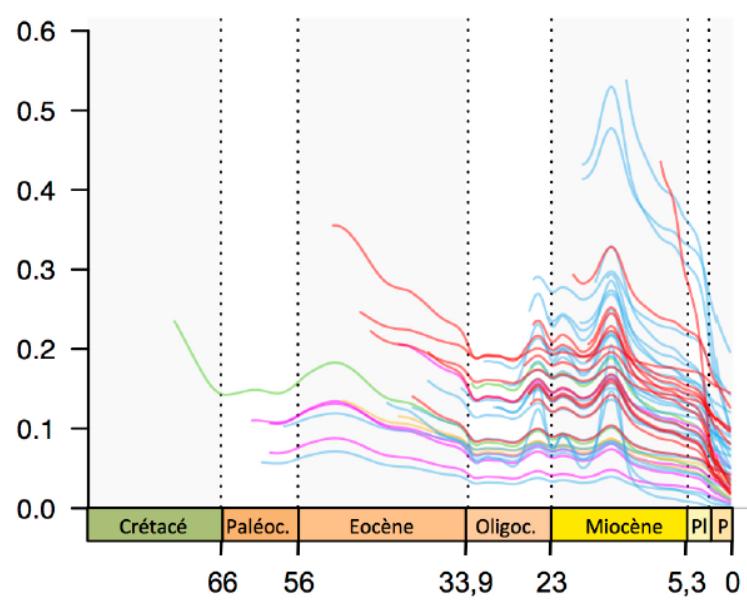
Positive correlation  $\alpha > 0$

Negative correlation  $\alpha < 0$

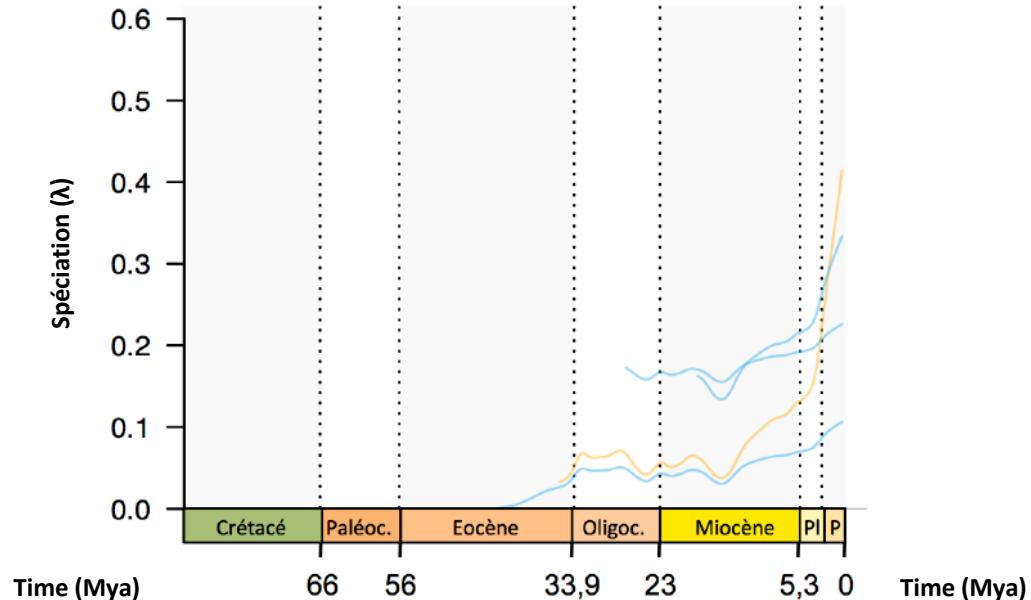
92 %

8 %

Spéciation ( $\lambda$ )



Spéciation ( $\lambda$ )



## 2 - Do warm climates promote or inhibit speciation ?

Positive  
correlation

92 %

8 %

Negative  
correlation

Speciation rate increases as temperature increases

# DISCUSSION

## 2 - Do warm climates promote or inhibit speciation ?

Positive correlation

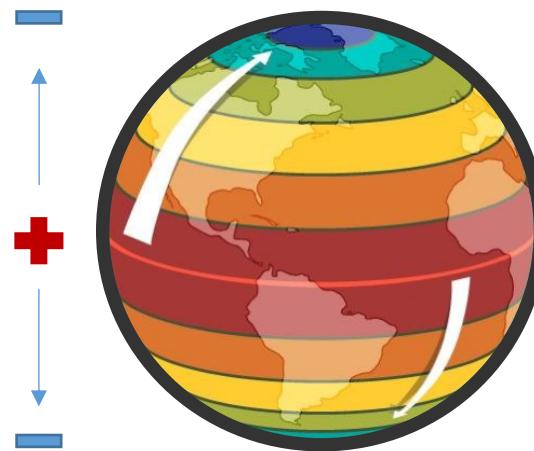
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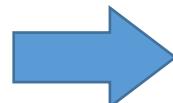
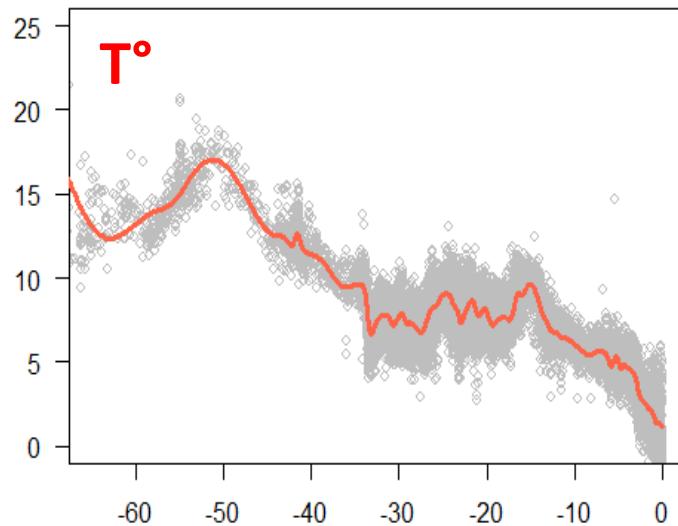
Speciation rate increases as temperature increases

**Latitudinal gradient of diversity**

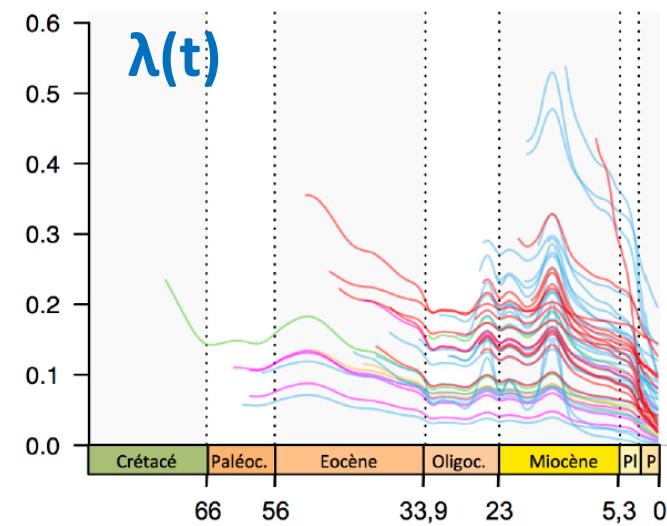


## Speciation rate increases as temperature increases

Global cooling  
over the Cenozoic



Speciation slowdown



## Speciation slowdown often inferred from phylogenies

Phillimore & Price 2008 – PLoS Biol.  
Glor 2010 – AREES  
Rabosky 2013 – AREES  
Moen & Morlon 2014 – TREE

### Some hypotheses

#### Diversity-dependent speciation

*Etienne et al. 2012 Proc. R. Soc. B*

As niches fill over time there are less opportunities for speciation

#### Protracted speciation

*Rosindell et al. 2010 – Ecol. Lett.*

Underestimated speciation at present due to ongoing speciation events

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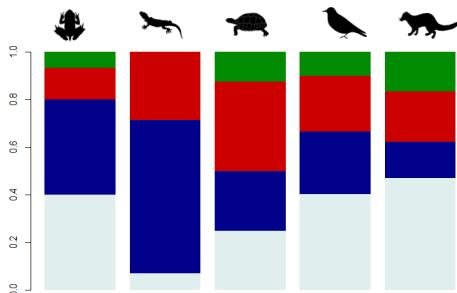
Underestimated speciation at present due to ongoing speciation events

#### T°-dependent speciation ?

Speciation has decreased as a result of global cooling

# CONCLUSIONS

Good proportion of Tetrapod phylogenies best explained by climate-dependent models of speciation



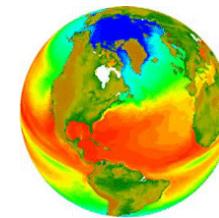
Link found in each of the 6 clades



Families of animals with diverse habitats and ecologies

Support for a role of **climate as a driver** of diversification

- What lies behind the observed correlation ?
- Importance relative to other factors ?



# CONCLUSIONS

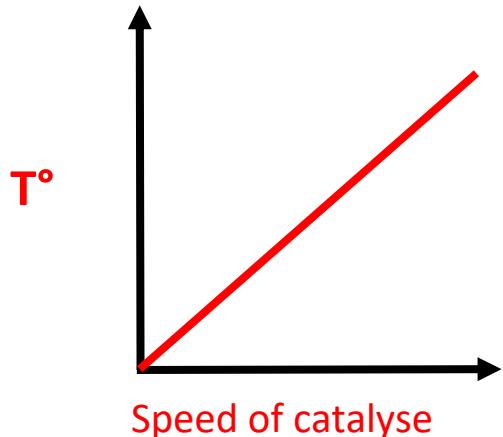


**Thank you  
for listening !**



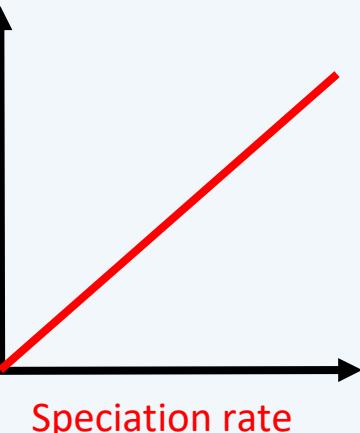
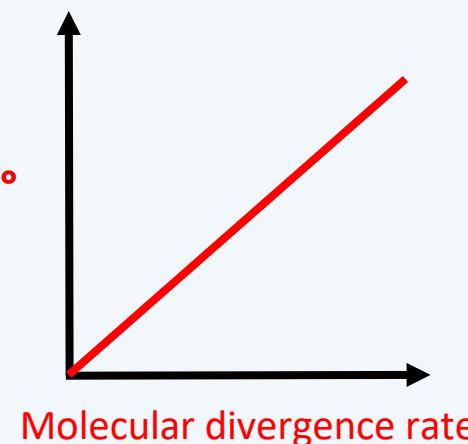
## Hypothesis for a causation ?

Metabolic theory



Kinetic effects of temperature on rates of genetic divergence and speciation

Andrew P. Allen<sup>\*†</sup>, James F. Gillooly<sup>‡</sup>, Van M. Savage<sup>§</sup>, and James H. Brown<sup>\*†||</sup>

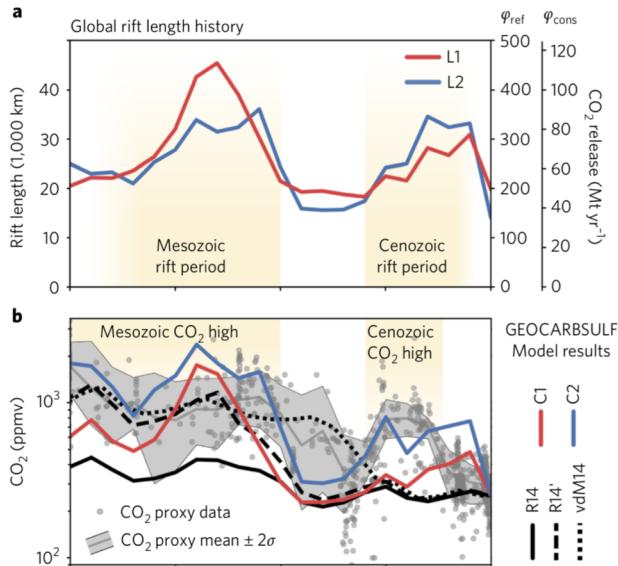


# SUPPLEMENTS

## Hypothesis for a correlation ?

### Potential links between continental rifting, CO<sub>2</sub> degassing and climate change through time

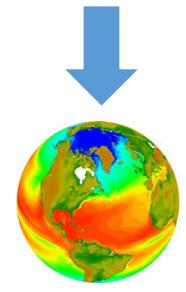
Sascha Brune<sup>1,2\*</sup>, Simon E. Williams<sup>3</sup> and R. Dietmar Müller<sup>3,4</sup>



Resources



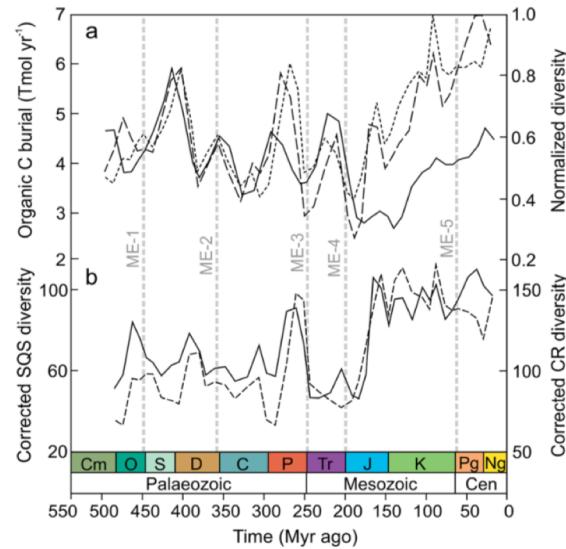
Tectonics



CO<sup>2</sup>

### Trophic and tectonic limits to the global increase of marine invertebrate diversity

Pedro Cermeño<sup>1</sup>, Michael J. Benton<sup>2</sup>, Óscar Paz<sup>1</sup> & Christian Vérard<sup>3</sup>

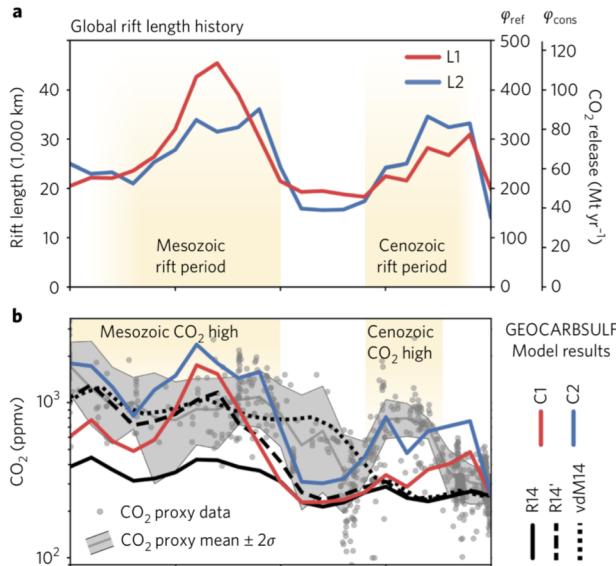


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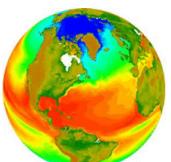
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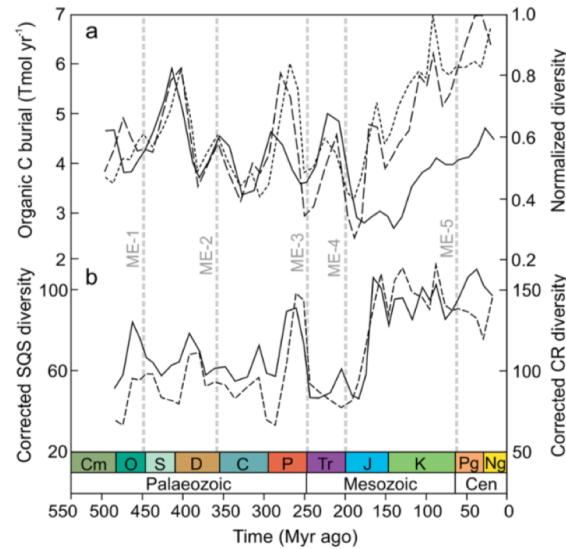
Tectonics

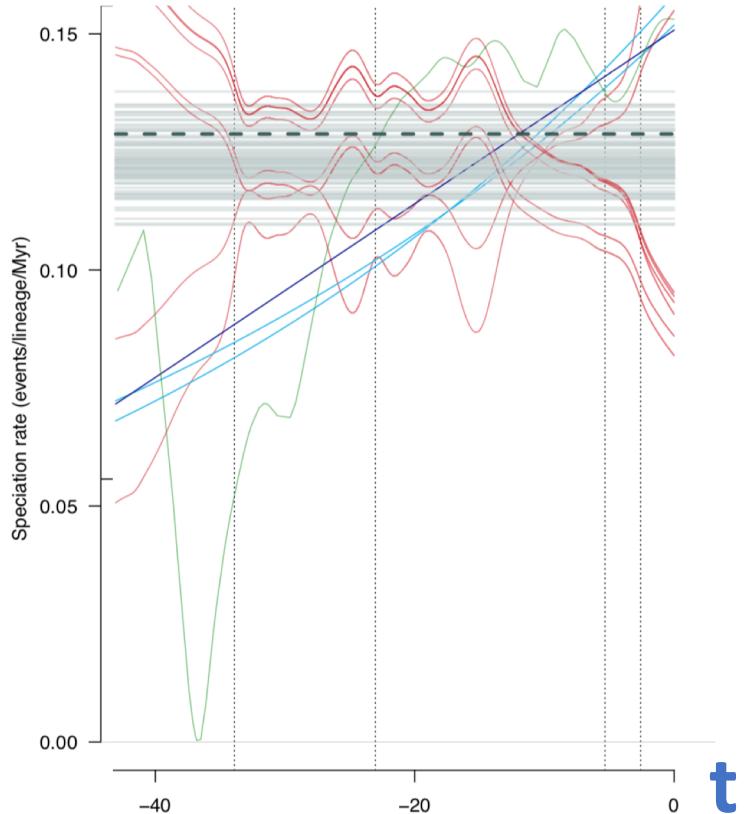
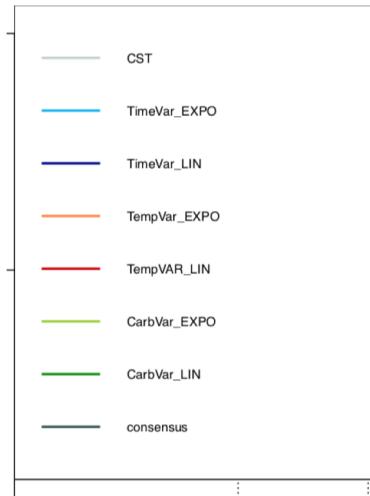


CO<sup>2</sup>

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$\lambda(t)$ 

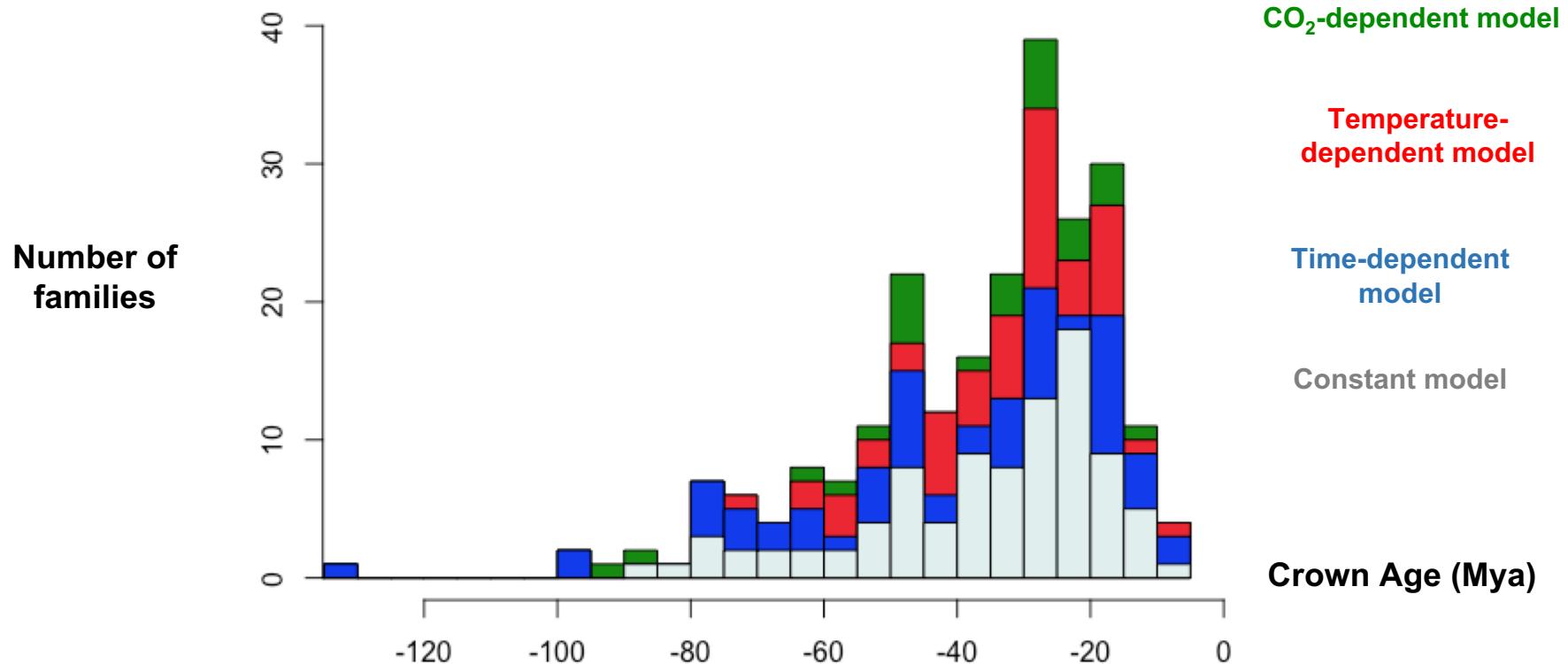
Strigidae

Best models selected for  
100 post probability trees  
from Jetz et al. 2012

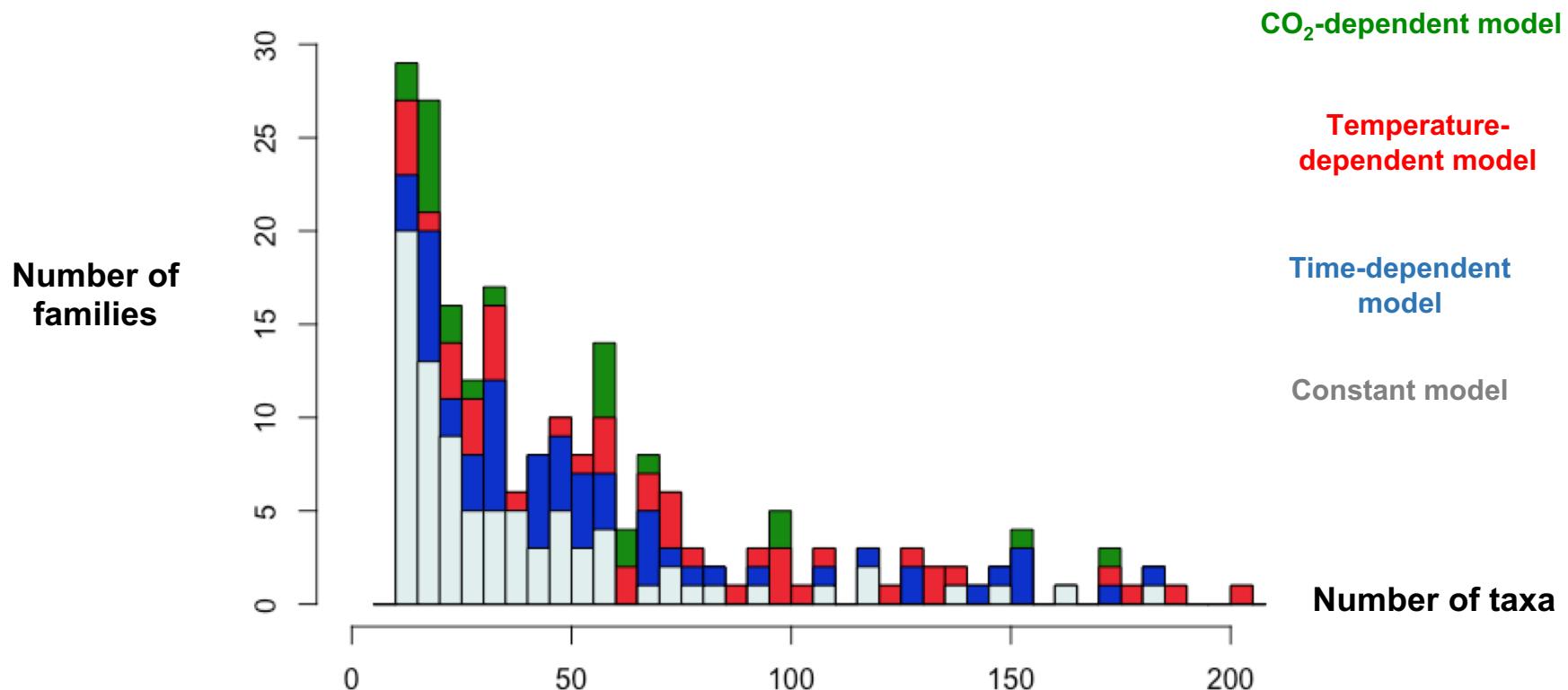
— — — Consensus tree



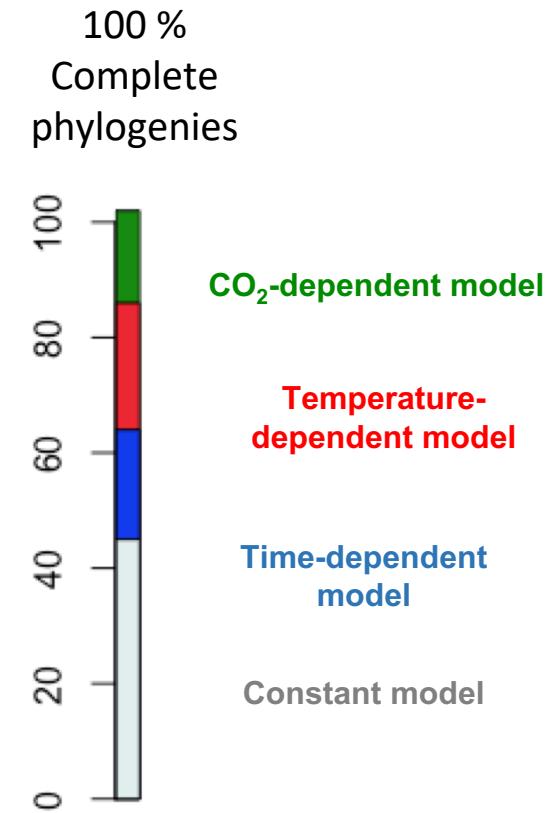
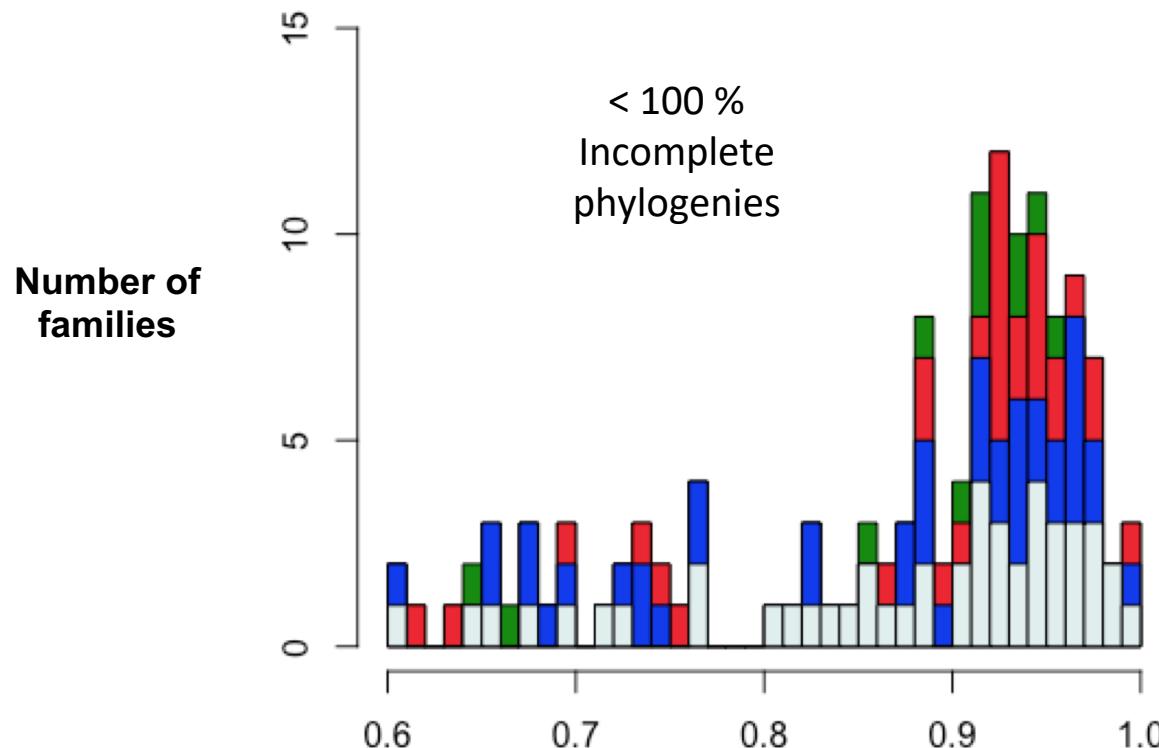
## Selected models and age of phylogenies



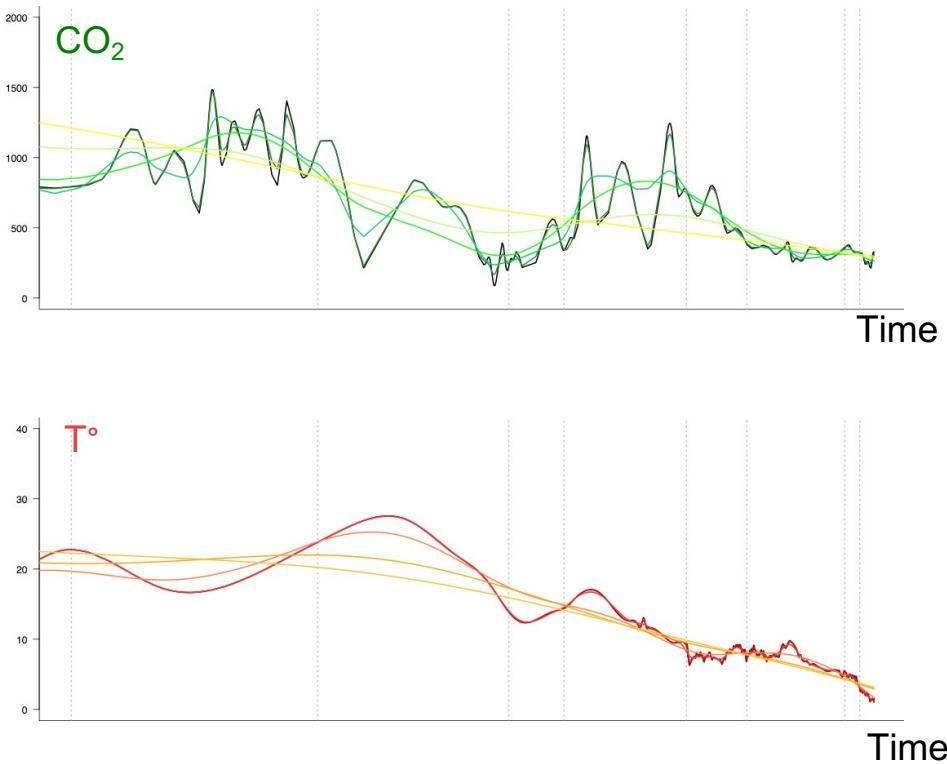
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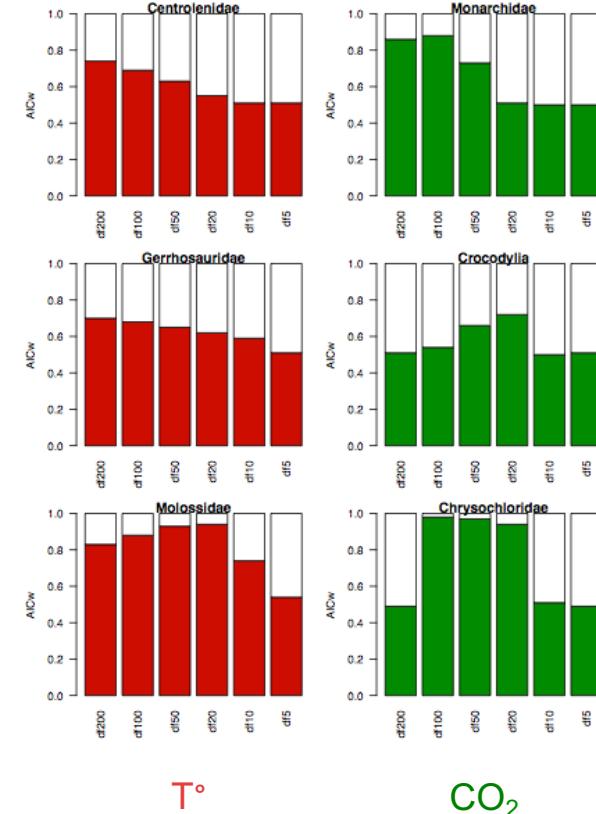
## Selected models and completeness of phylogenies



# SUPPLEMENTS

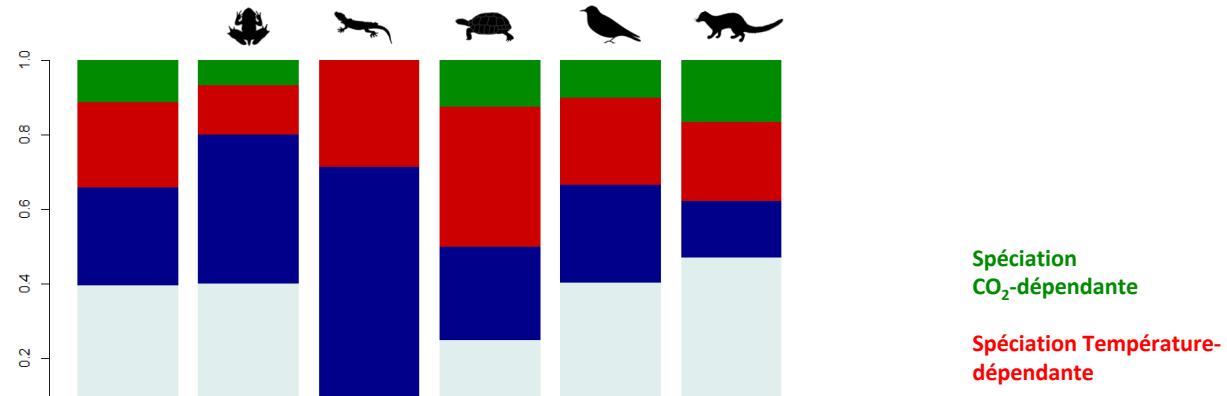


High resolution → Poor resolution

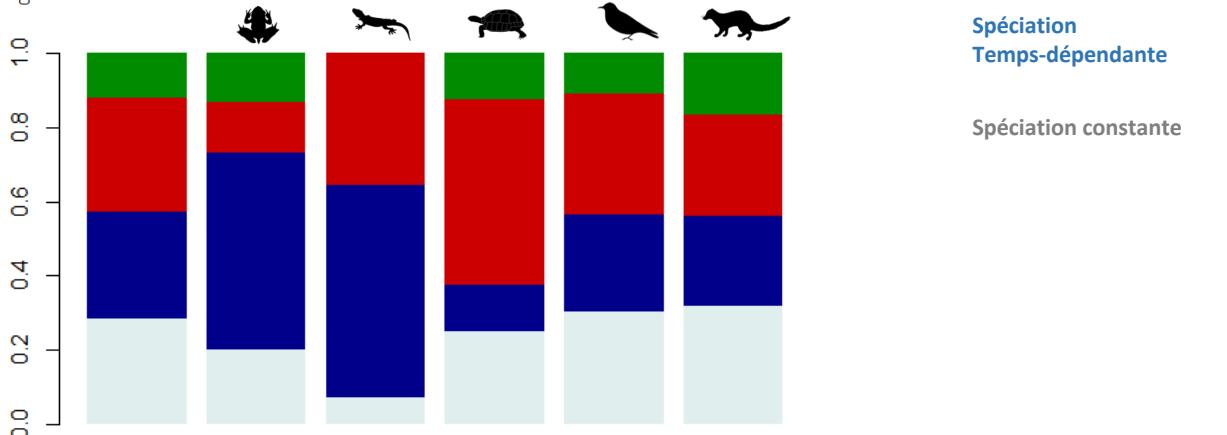


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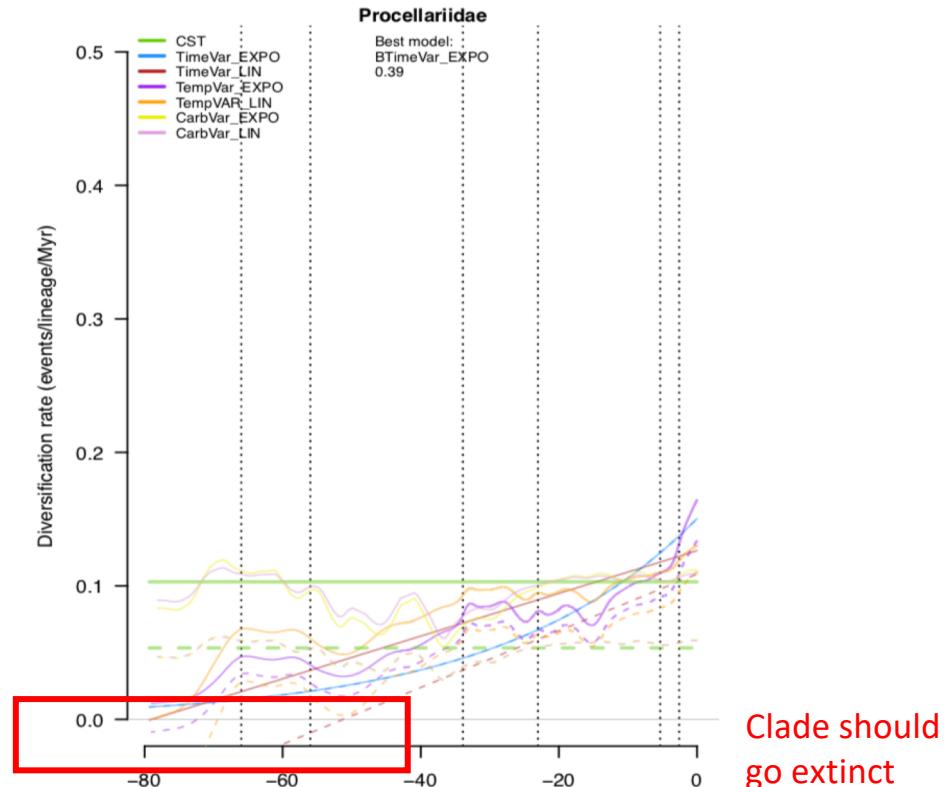
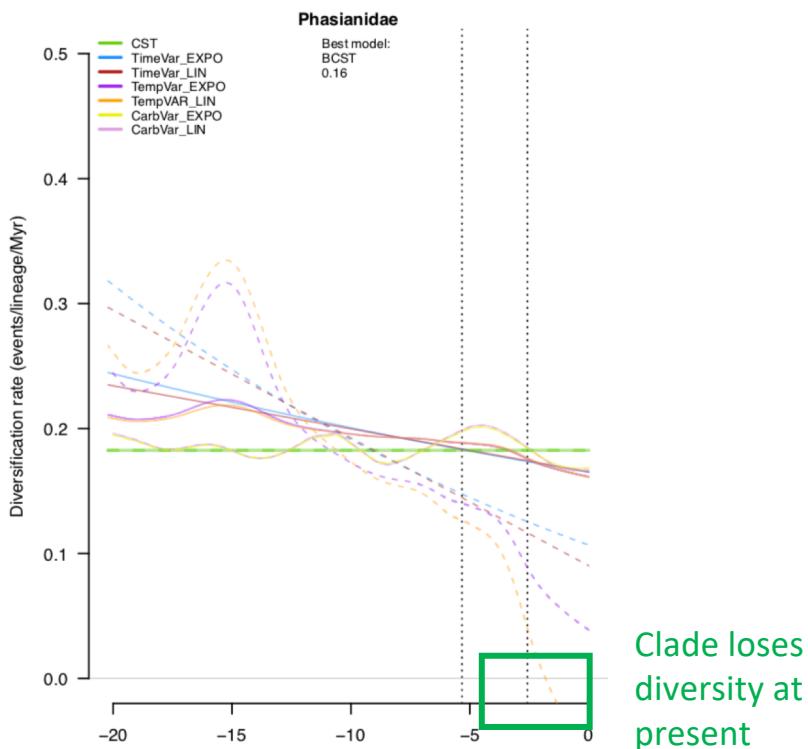
Speciation only



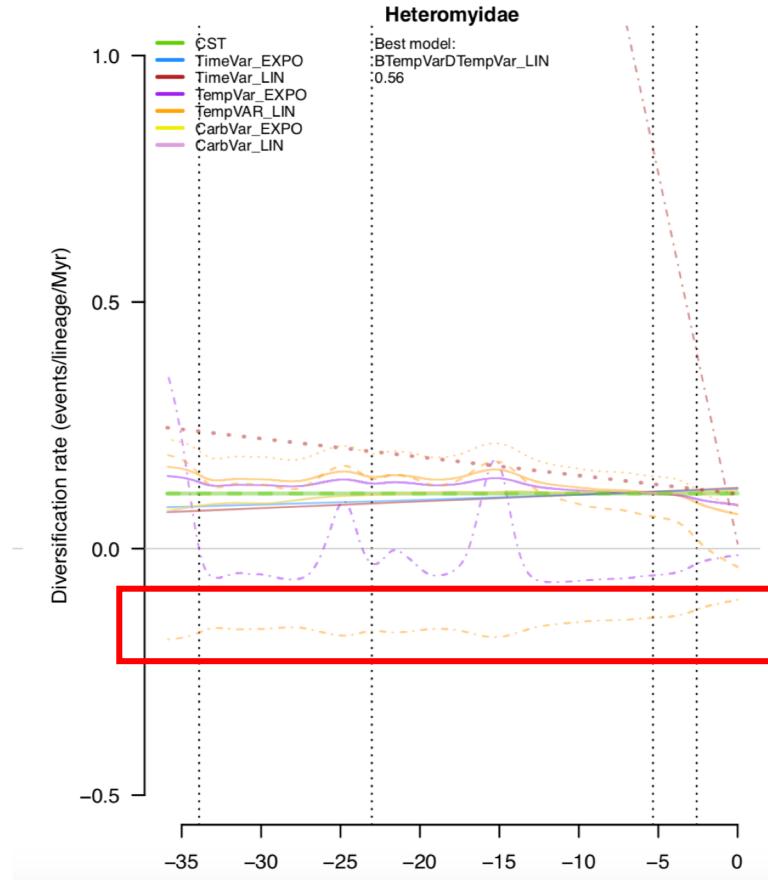
Speciation + Extinction



## Negative diversification (extinction > speciation)

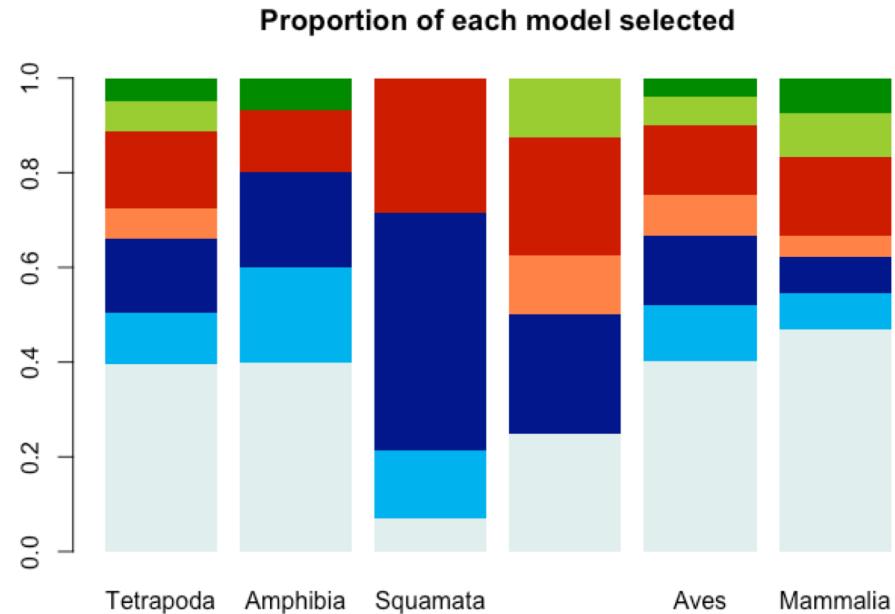


# SUPPLEMENTS



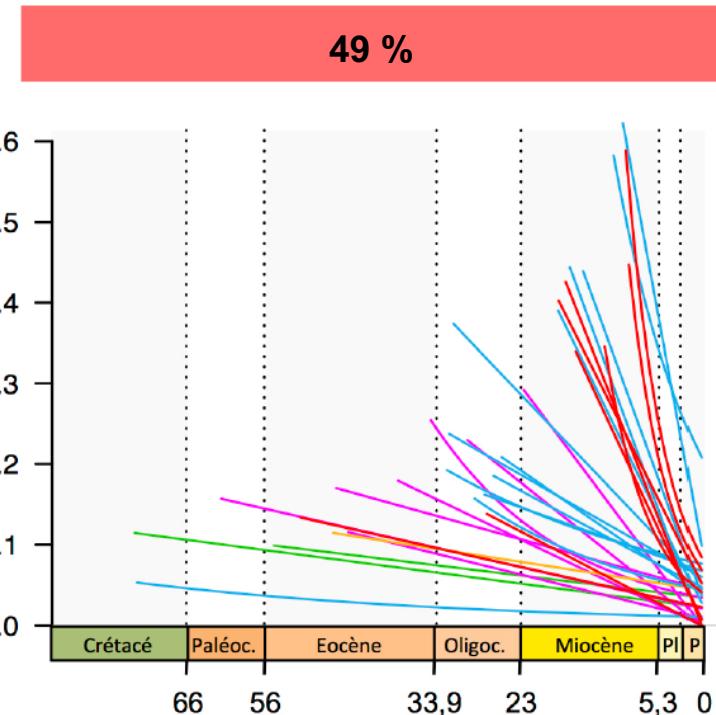
Support for a model with negative diversification over all the history of the clade !

Deep shade → exponential model  
Light shade → linear model

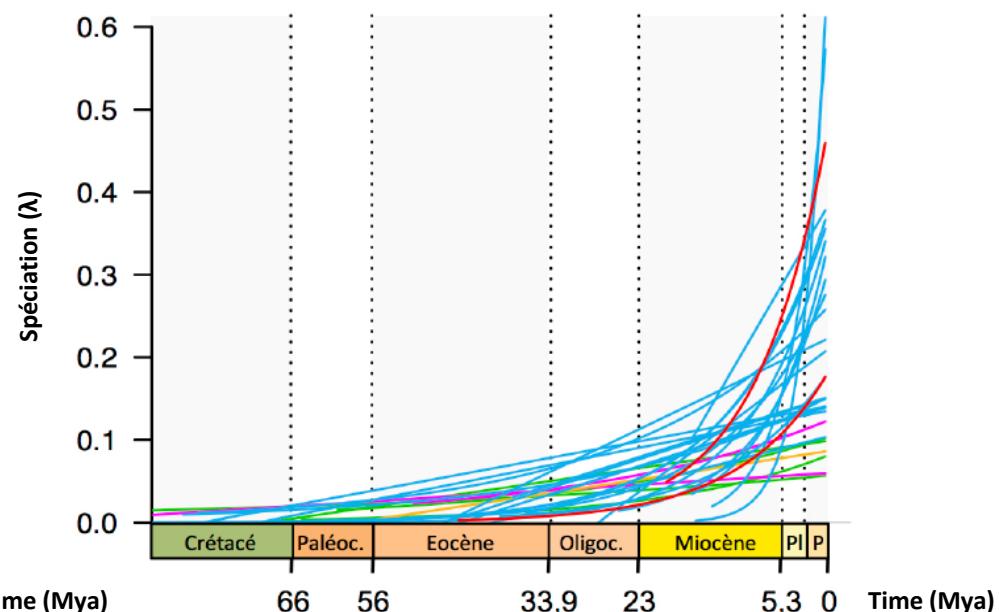


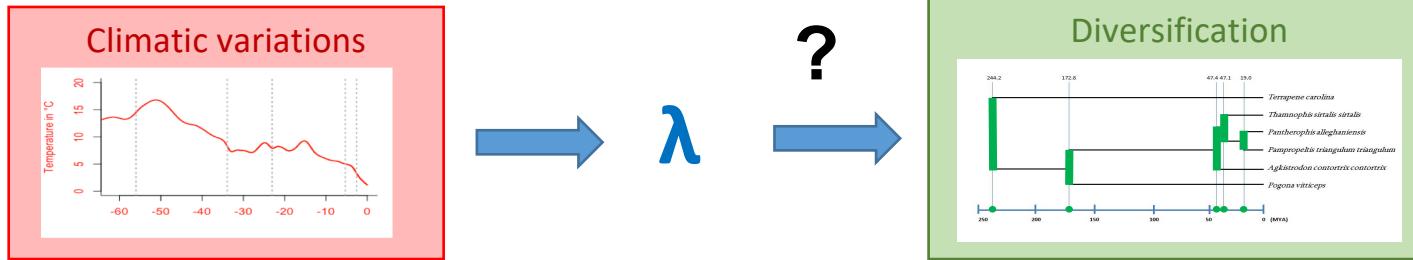
# SUPPLEMENTS

Positive correlation  $\alpha > 0$



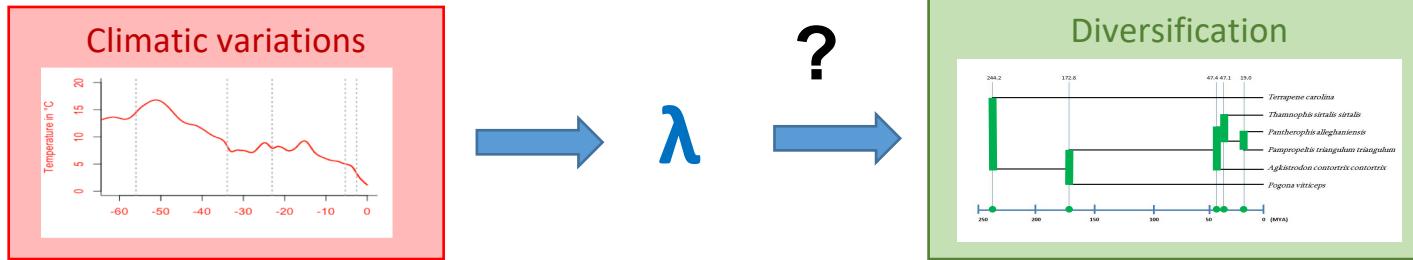
Negative correlation  $\alpha < 0$





### Hypothesis tested on Tetrapod families





## Main questions

- 1 ) Signal of climate : rule or exception ?
- 2 ) Do warm/cold climates promote or inhibit speciation ?