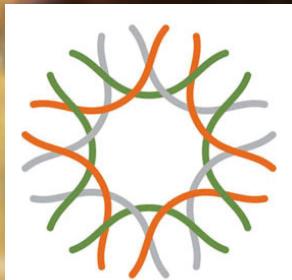


# Historical biogeography and biodiversity dynamics of Ponerine ants

Maël DORÉ

European IUSSI Congress  
July 10<sup>th</sup> 2024



CALIFORNIA  
ACADEMY OF  
SCIENCES

Photo credits: F. Brassard



# Ponerinae Subfamily

Top 3 ant subfamily for **diversity**  
with 50 genera and ca. **1,400 species**

Predatory ants: include the **trap-jaw ants**  
(*Anochetus*, *Odontomachus*)

High diversity of **mandible shapes**  
related to **diet specialization**

Plesiomorphic robust morphology

Include the **largest ant species**:  
*Dinoponera gigantea*



Formicinae  
3,300 sp.  
22%

Myrmicinae  
7,200 sp.  
48%

**Ponerinae**  
**1,400 sp.**  
**10%**

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Photo Credits: Magdalena Sorger

# Ponerinae Subfamily

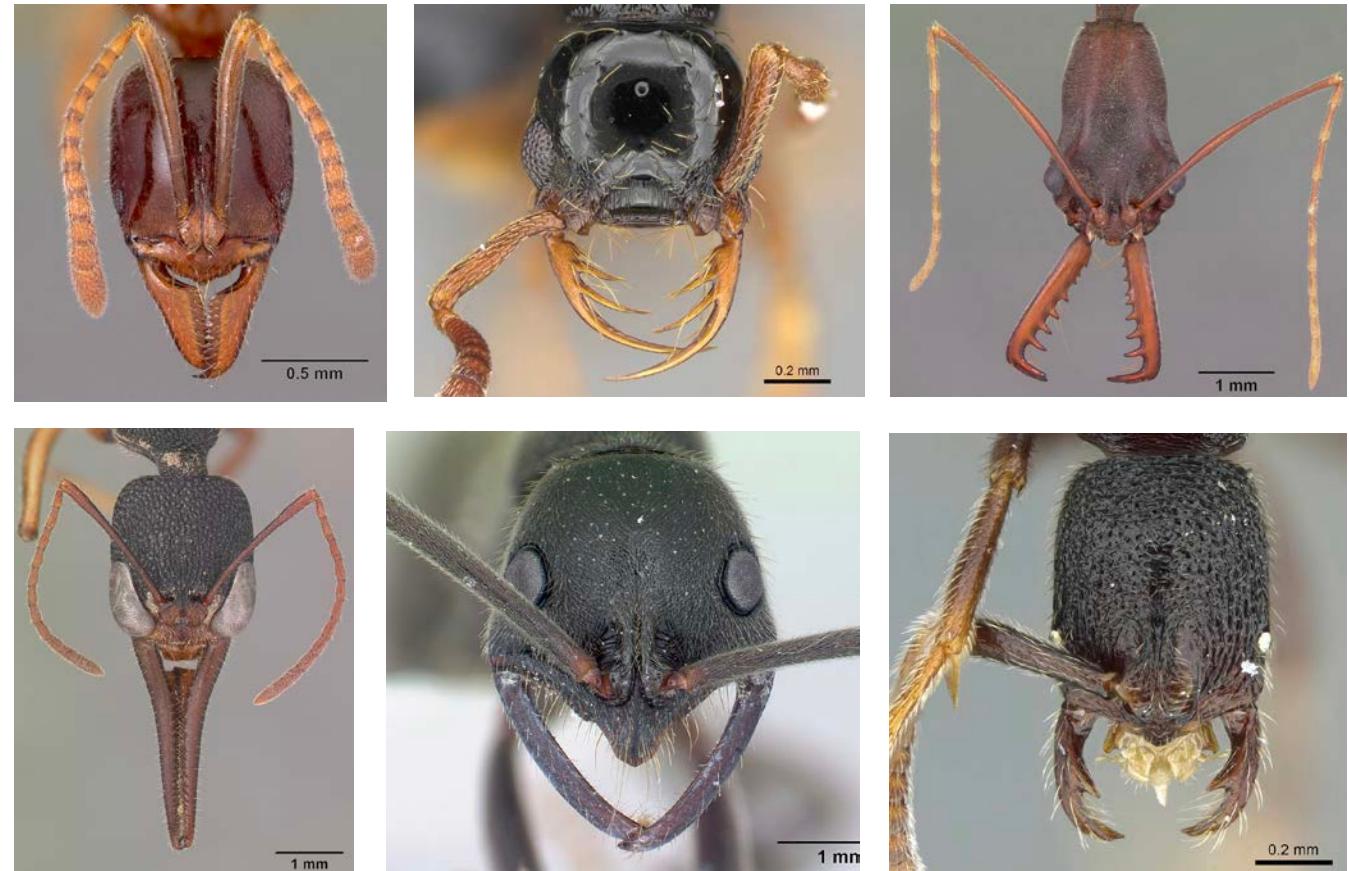
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Source: AntWeb

# Ponerinae Subfamily

Photo Credits: Tatyana Kolesnikova

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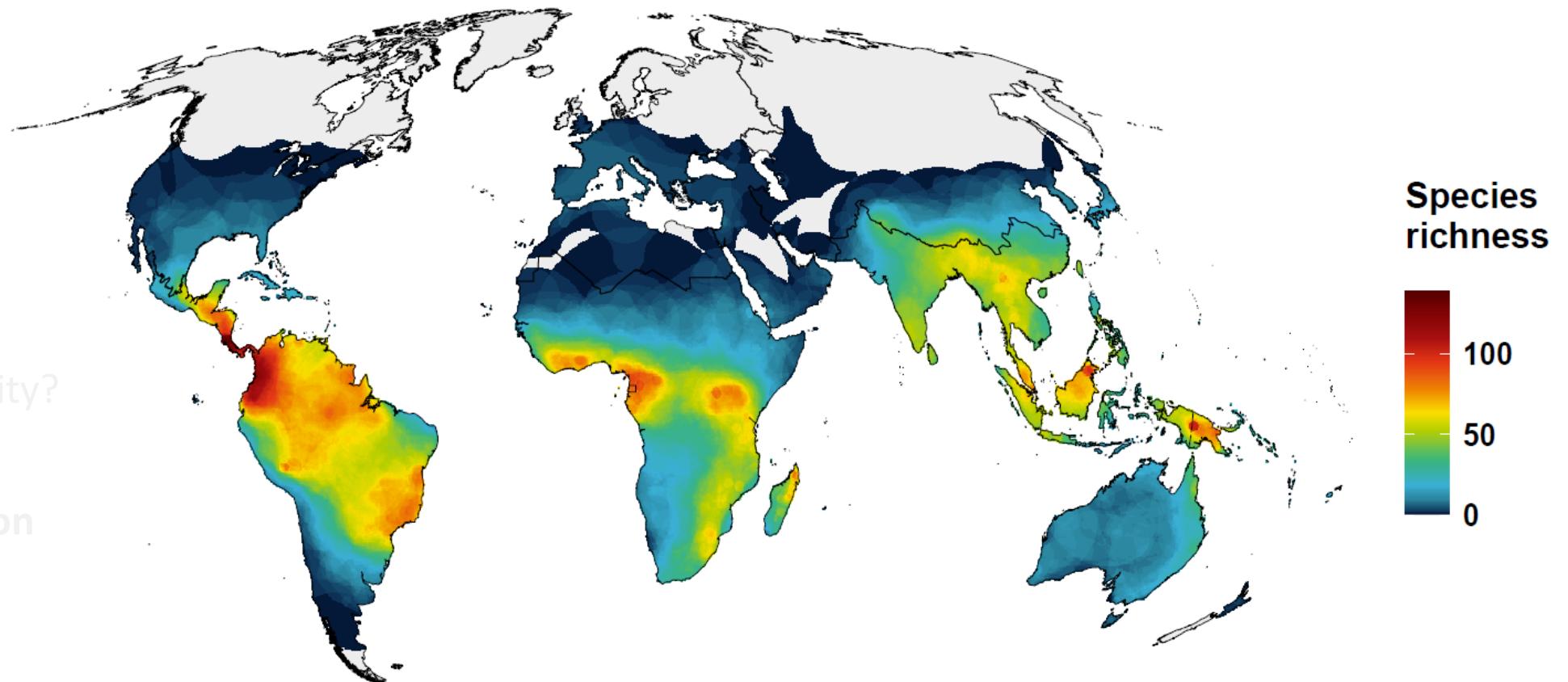


*Dinoponera gigantea* in Belem, Brazil  
Up to 40 mm

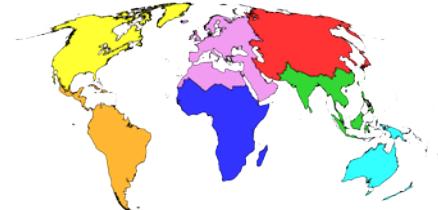
# Current diversity

## Species richness of Ponerinae ants

1/ Origin of the clade?

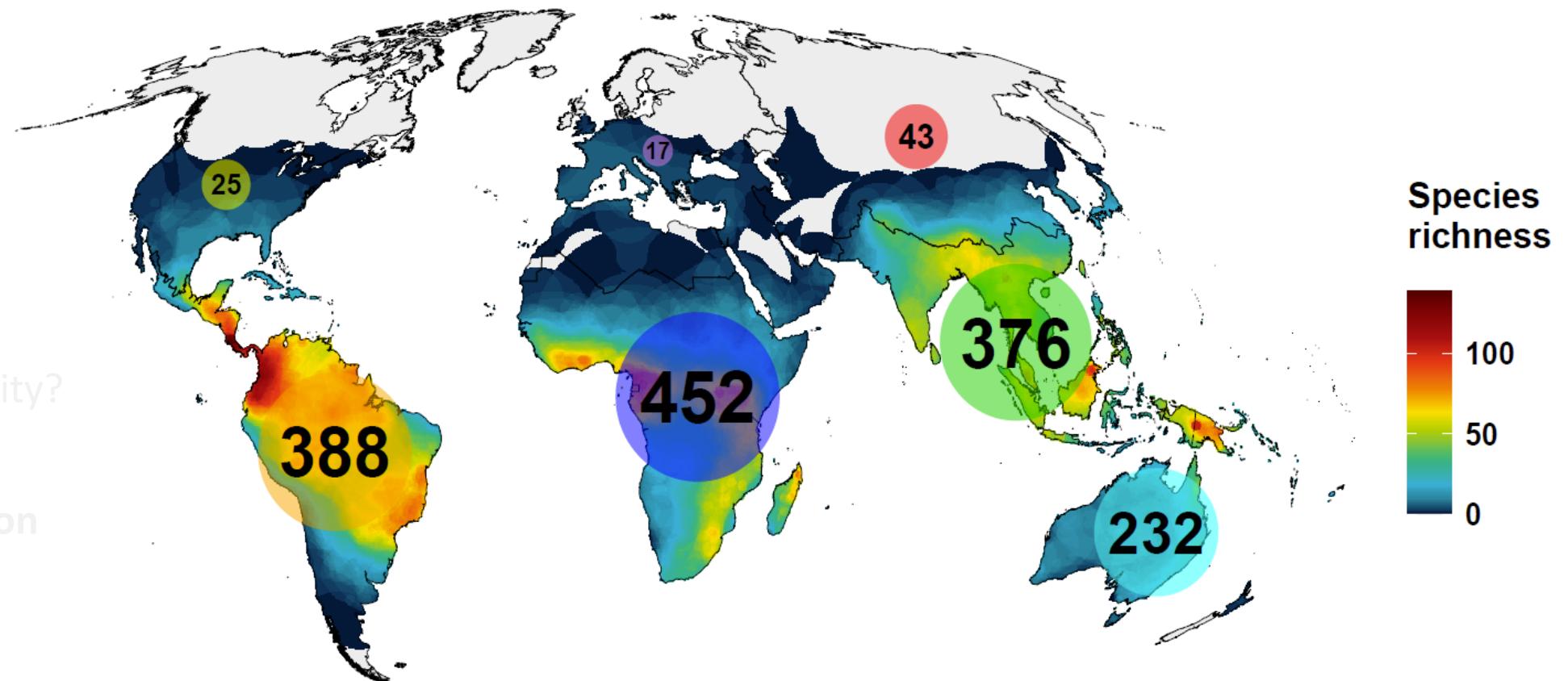


# Current diversity



## Species richness of Ponerinae ants

1/ Origin of the clade?



2/ Source of diversity?

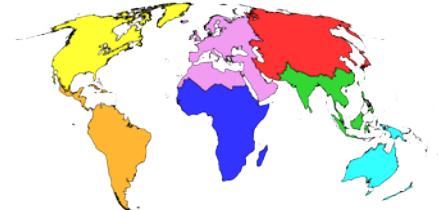
*In situ* diversification

vs.

Dispersal

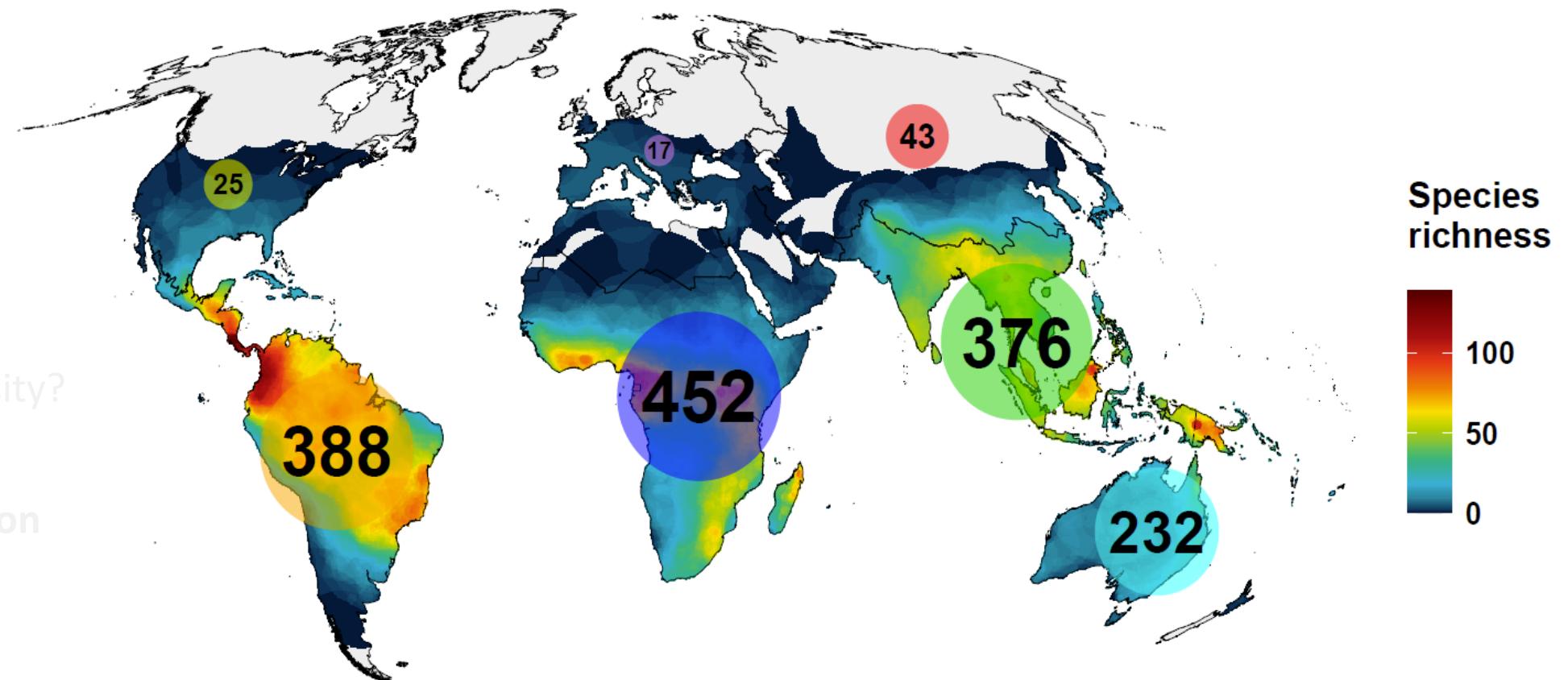
Doré et al., *in prep.*

# Current diversity

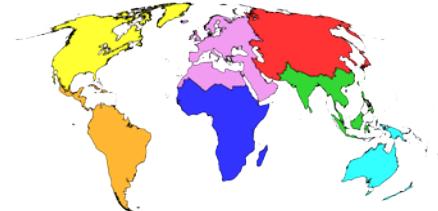


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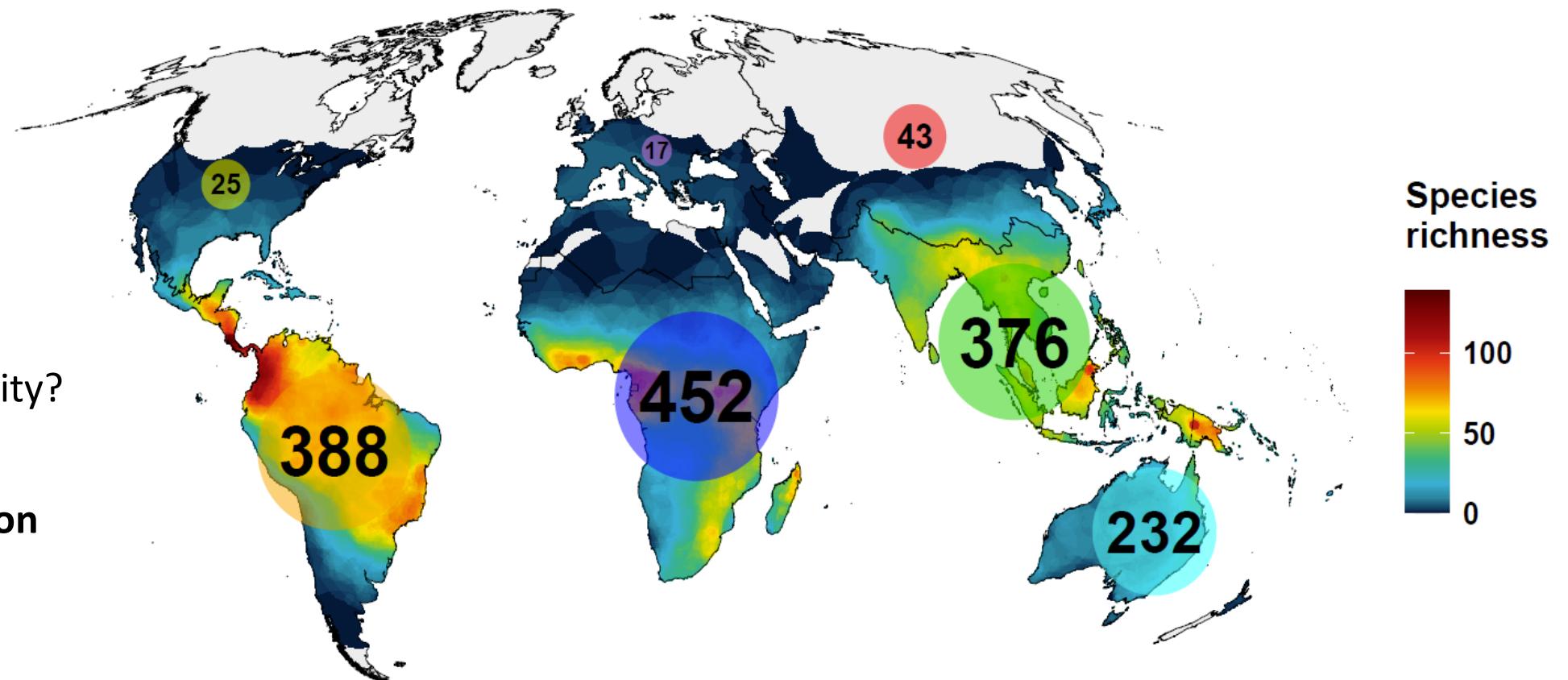


# Current diversity



## Species richness of Ponerinae ants

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# Phylogenomic methods

Doré et al., *in prep.*

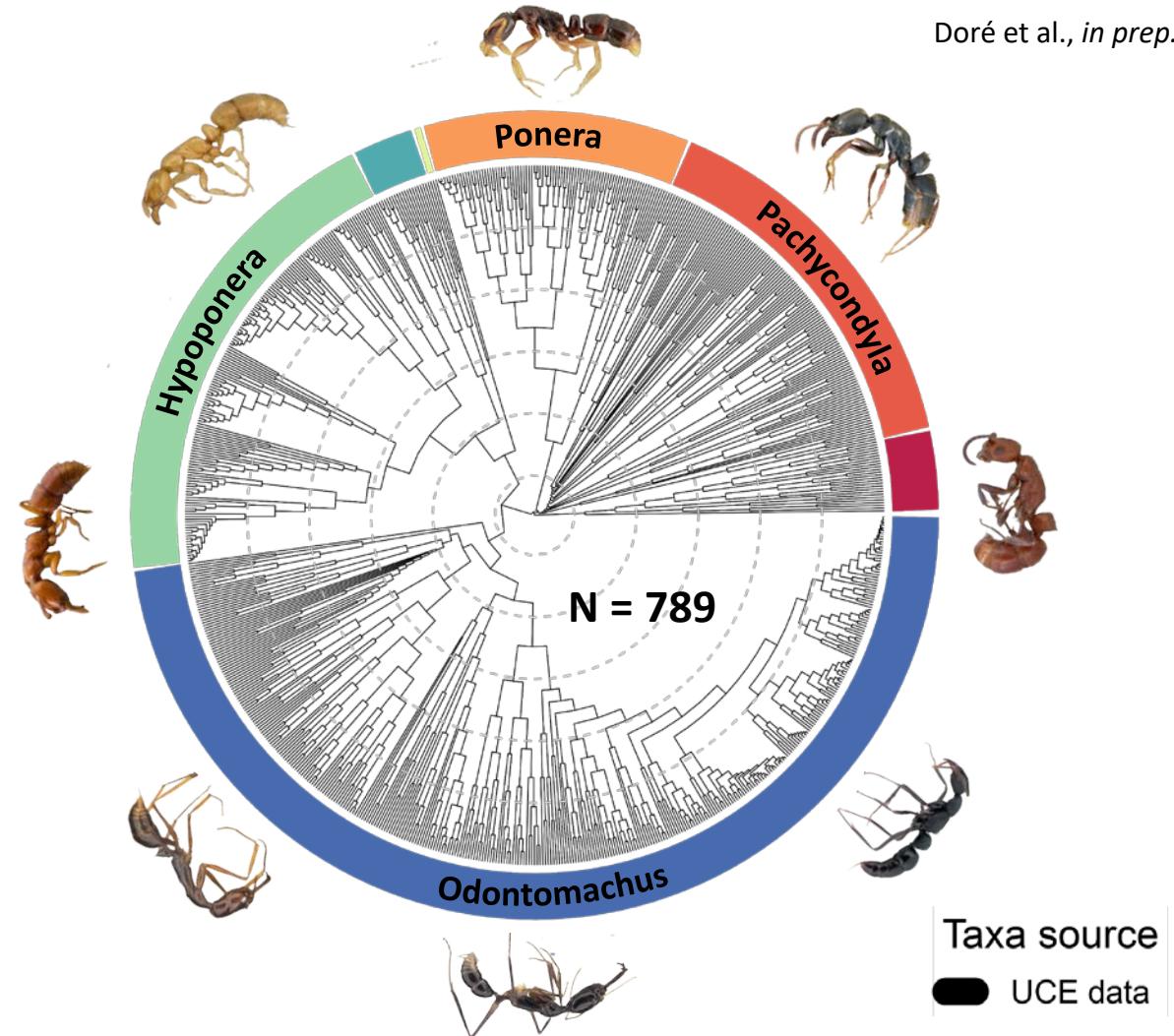
**Taxa sampling:** 789 species (51.4%)  
among all 50 Genera (100%)

Molecular data: 2,365 **UCE loci** = 1.05 M sites

Phylogenetic inferences: ML in **IQ-Tree**  
with **SWSC partitioning**

**Sensitivity analyses:**  
Inference method x Loci filtering x  
Partitioning scheme

**Grafting of missing species:**  
Impute all 745 valid species with no UCE data using  
available taxonomic and geographic information



**New species-level phylogeny  
for Ponerinae**

# Phylogenomic methods

Doré et al., *in prep.*

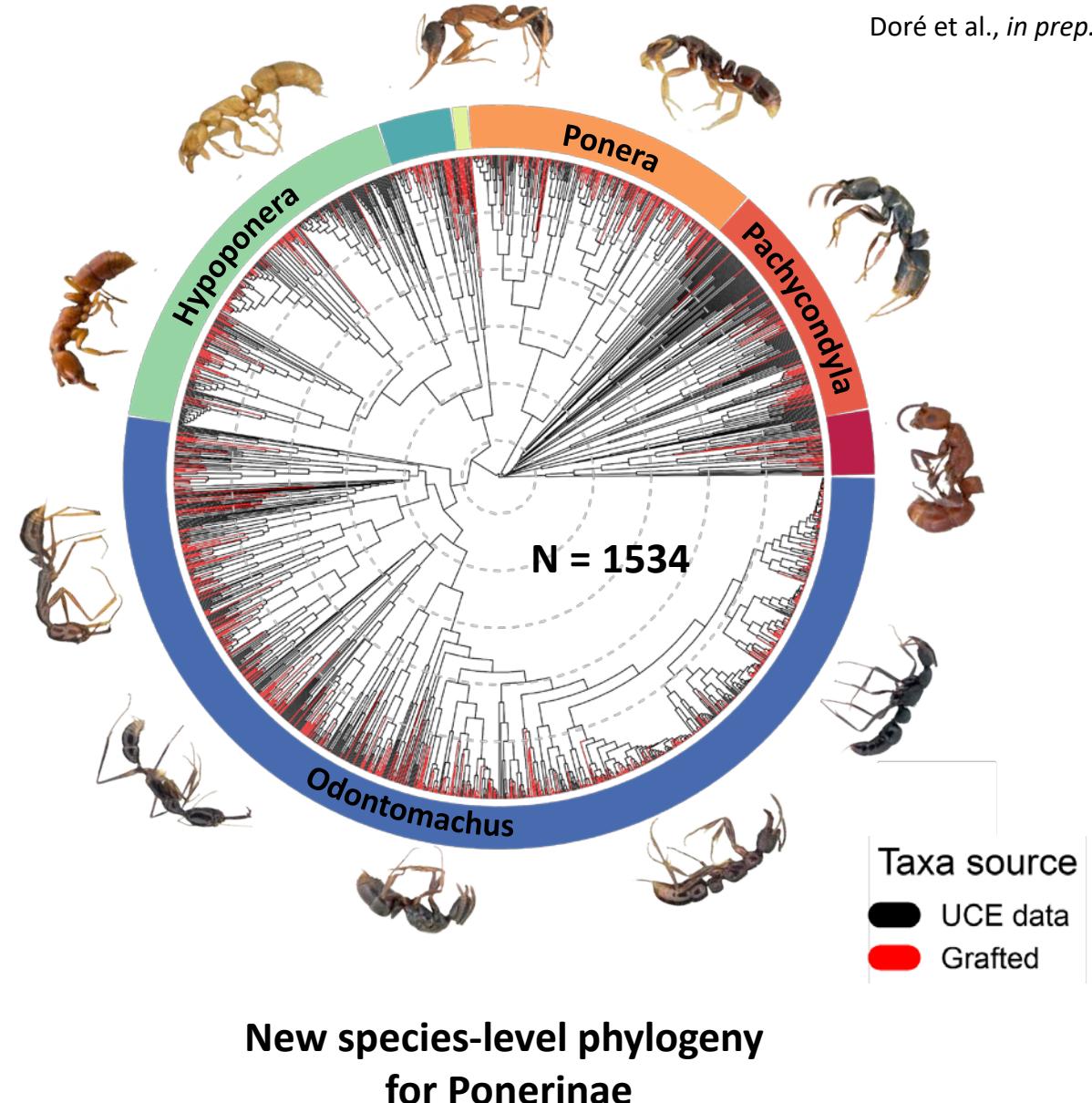
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# Biogeographic data

## Occurrence sources:

- AntWeb (62,301 records)
- GABI/AntMap (93,557 records)

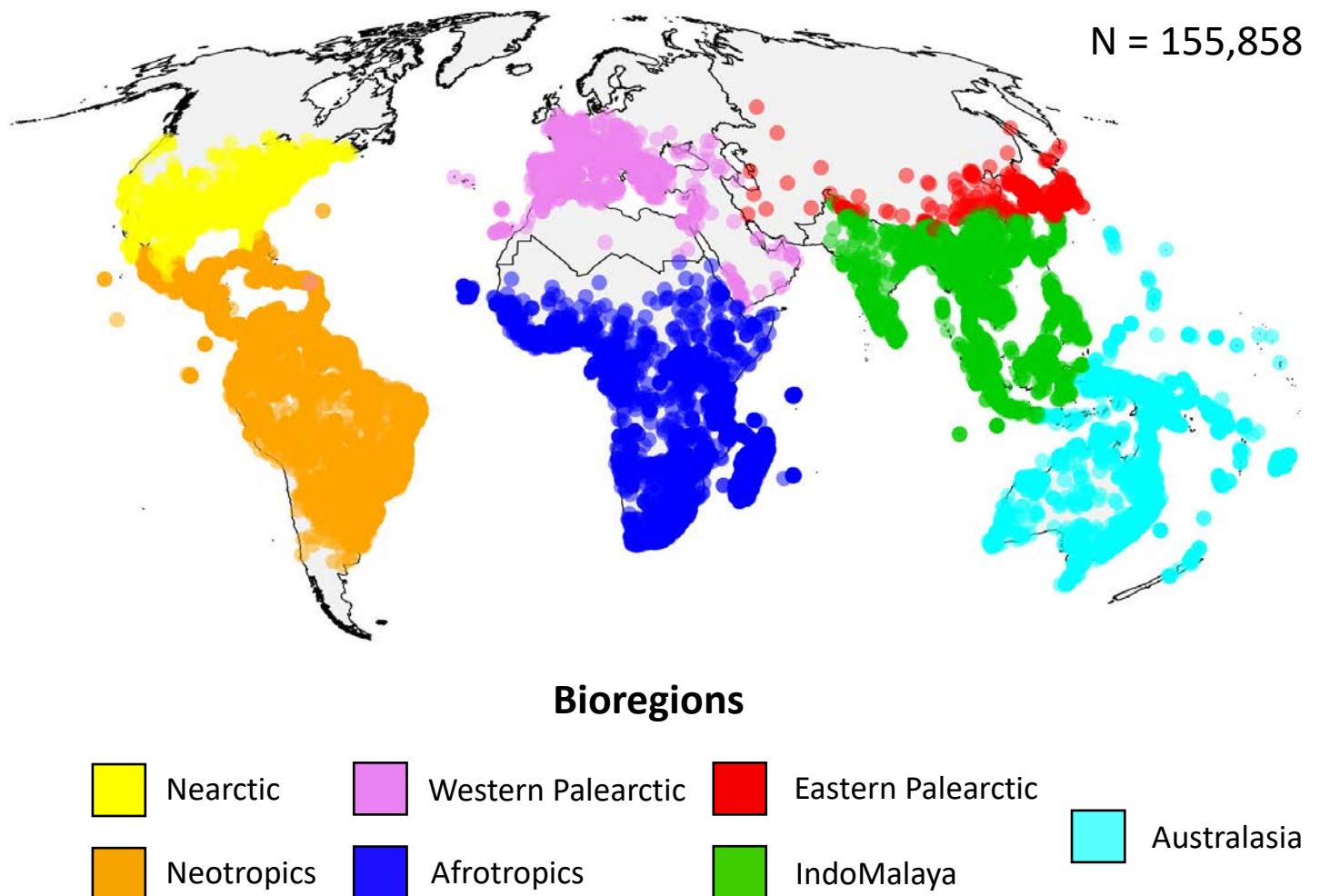
## Bioregions as defined in AntWeb

## Data curation:

- Automatic and visual checks
  - *CoordinateCleaner* (Zizka et al., 2019)
- Geogazeeting
  - *geoBoundaries* (Runfola et al., 2020)
- Accuracy estimates

Final database: 155,858 records

- 105,574 records from GPS
- 50,284 records from locality



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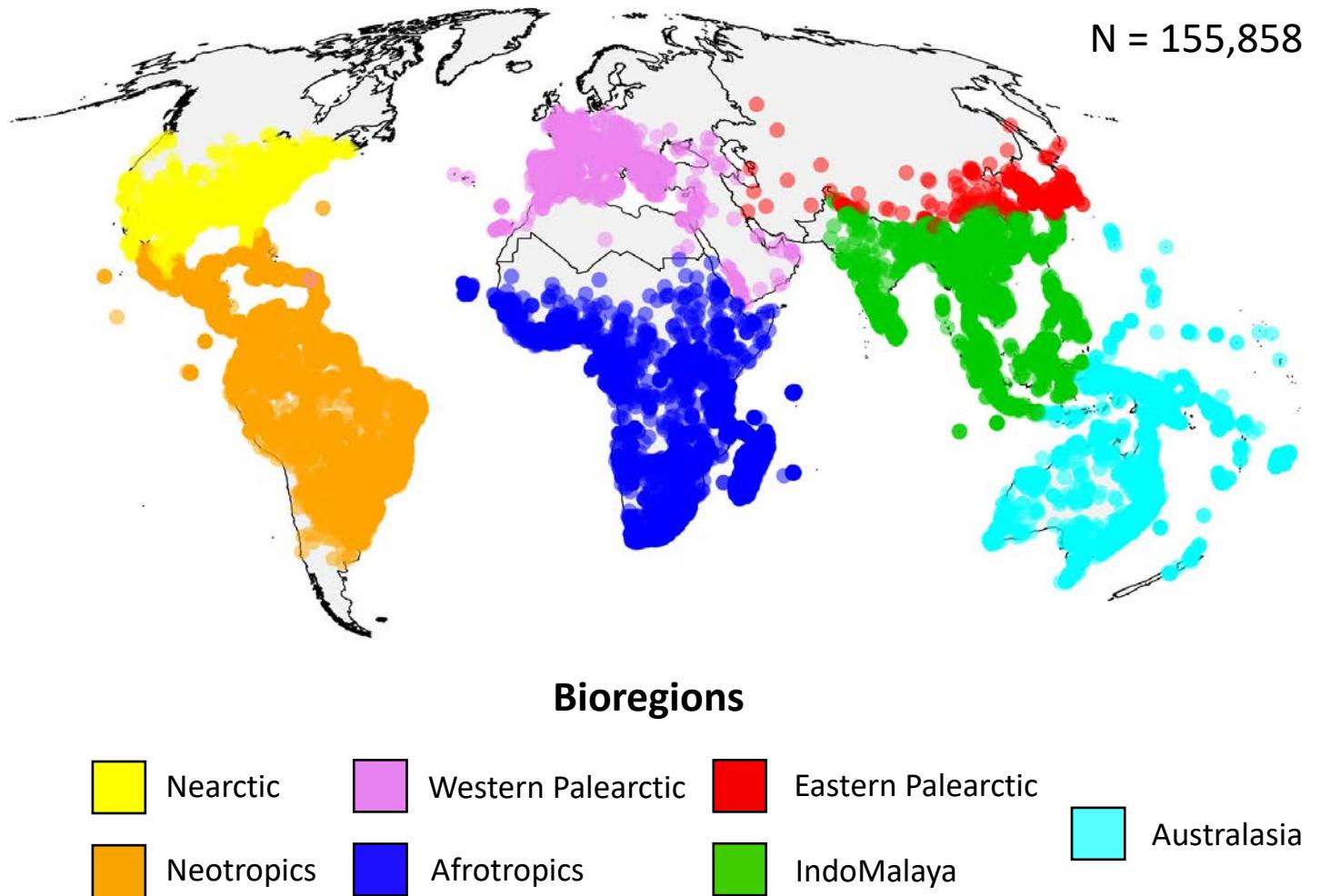
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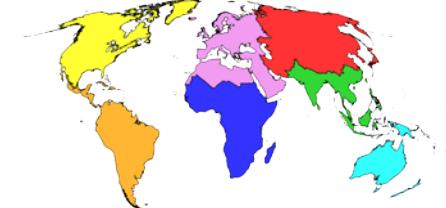
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- 50,284 records from **locality**



# Biogeographic methods



## BioGeoBEARS framework:

- DIVALIKE, DEC, DIVALIKE + J, DEC + J
- Model selection based on AICc
- Best model = **Time-stratified DEC + J**

## Model of continental connectivity

## Ancestral Range Estimates (ARE):

- Marginal likelihoods of node ranges

## Biogeographic Stochastic Mapping (BSM):

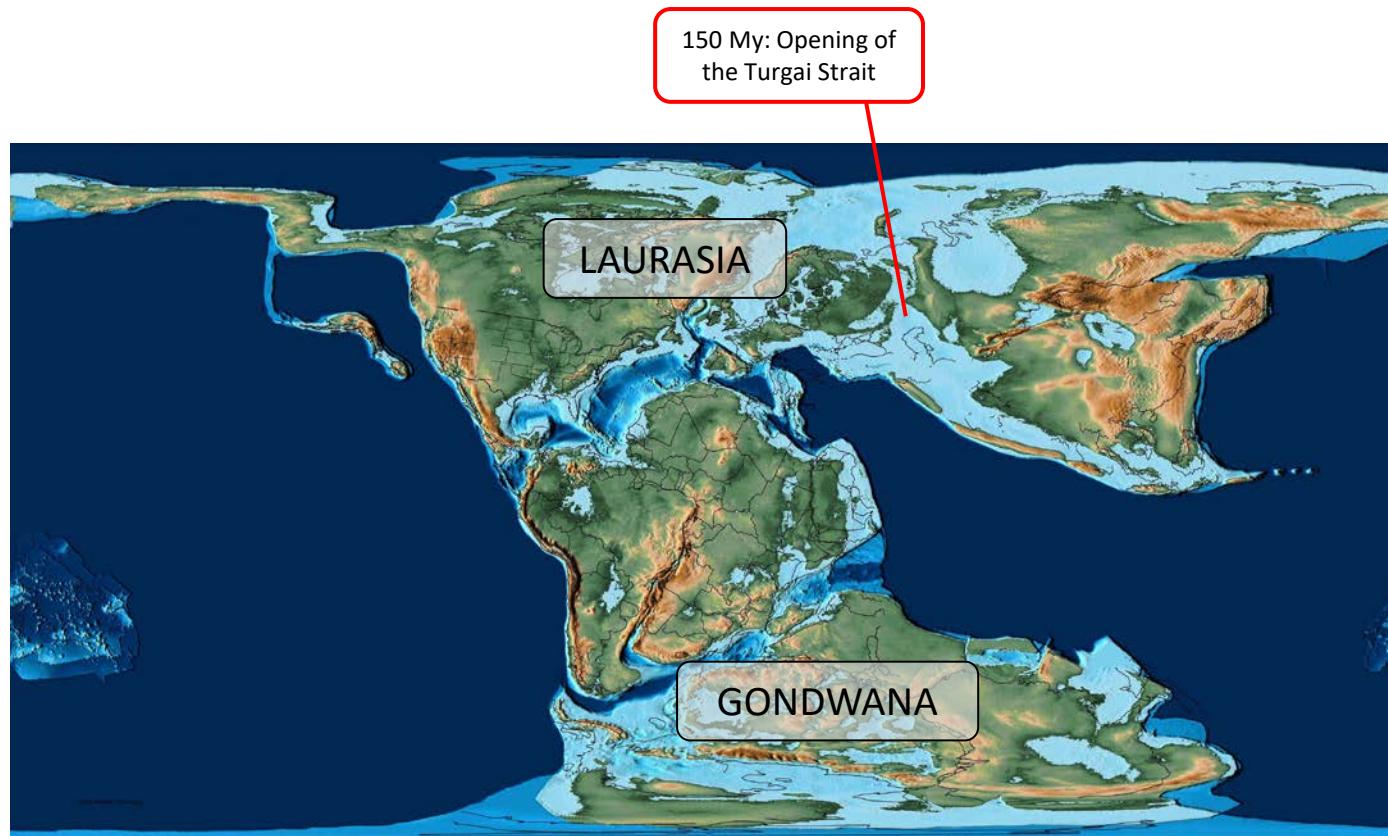
- Simulation of **biogeographic histories** compatible with ancestral ranges estimates
- Summary statistics across 1000 BSM

## Model comparison

	DEC+J	DIVALIKE+J	DIVALIKE	DEC
logLk	-2154	-2205	-4391	-4467
# params	3	3	2	2
AICc	4313	4416	8787	8939
Δ AICc	0	103	4474	4626
Akaike weights	100 %	0 %	0 %	0 %
d	0.007	0.008	0.030	0.024
e	0.000	0.000	0.019	0.020
y	0.994	0.991	1.000	1.000
v	0.994	0.991	1.000	1.000
s	0.994	-	-	1.000
j	0.019	0.018	-	-

Doré et al., *in prep.*

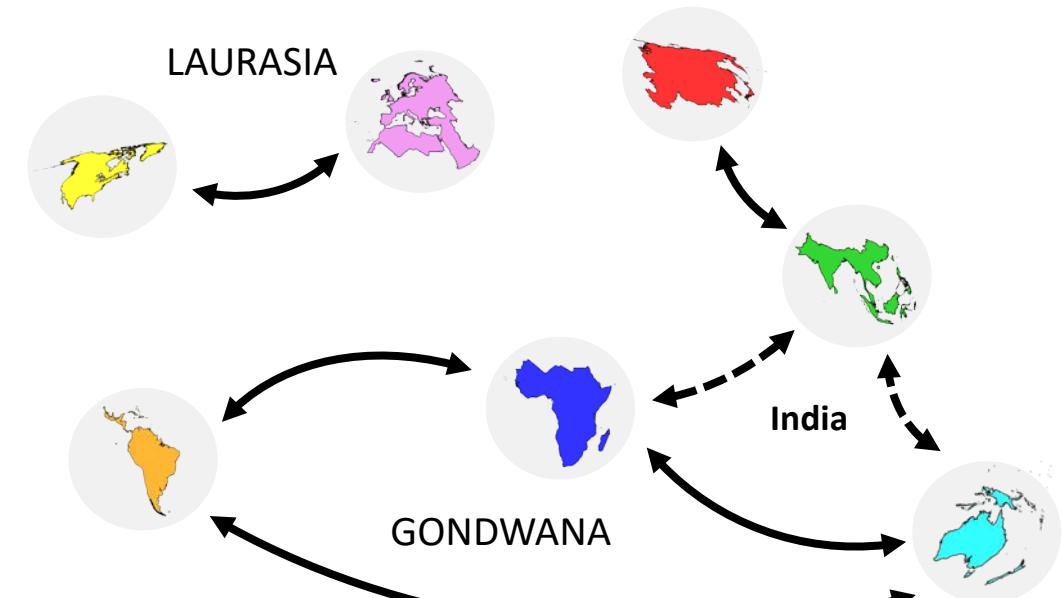
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese

Early Cretaceous

145.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

55.8

33.9

23.0

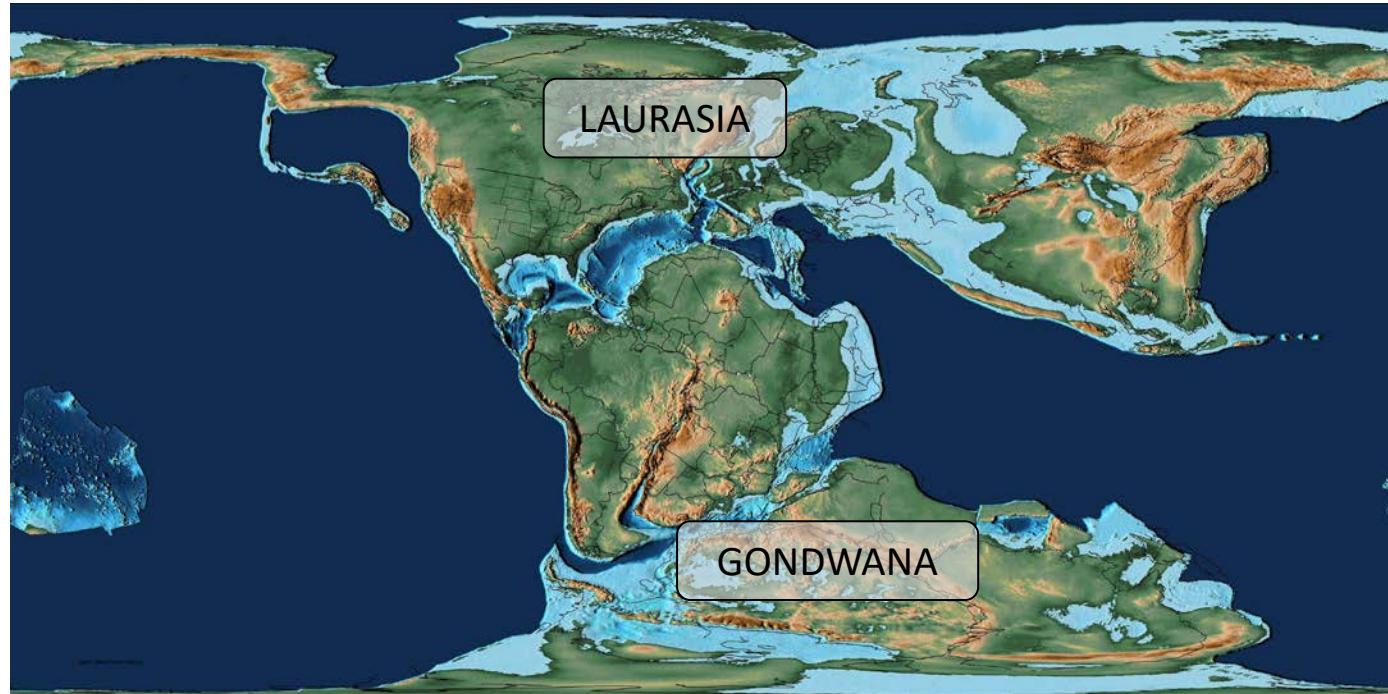
5.3

0

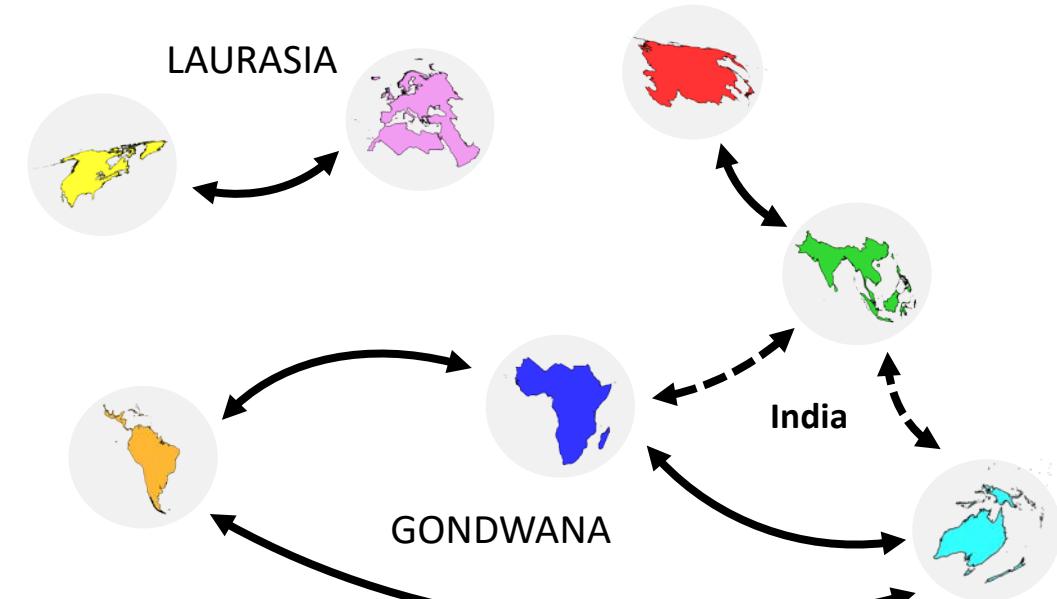
# Biogeographic methods

Early Cretaceous

140.0 My

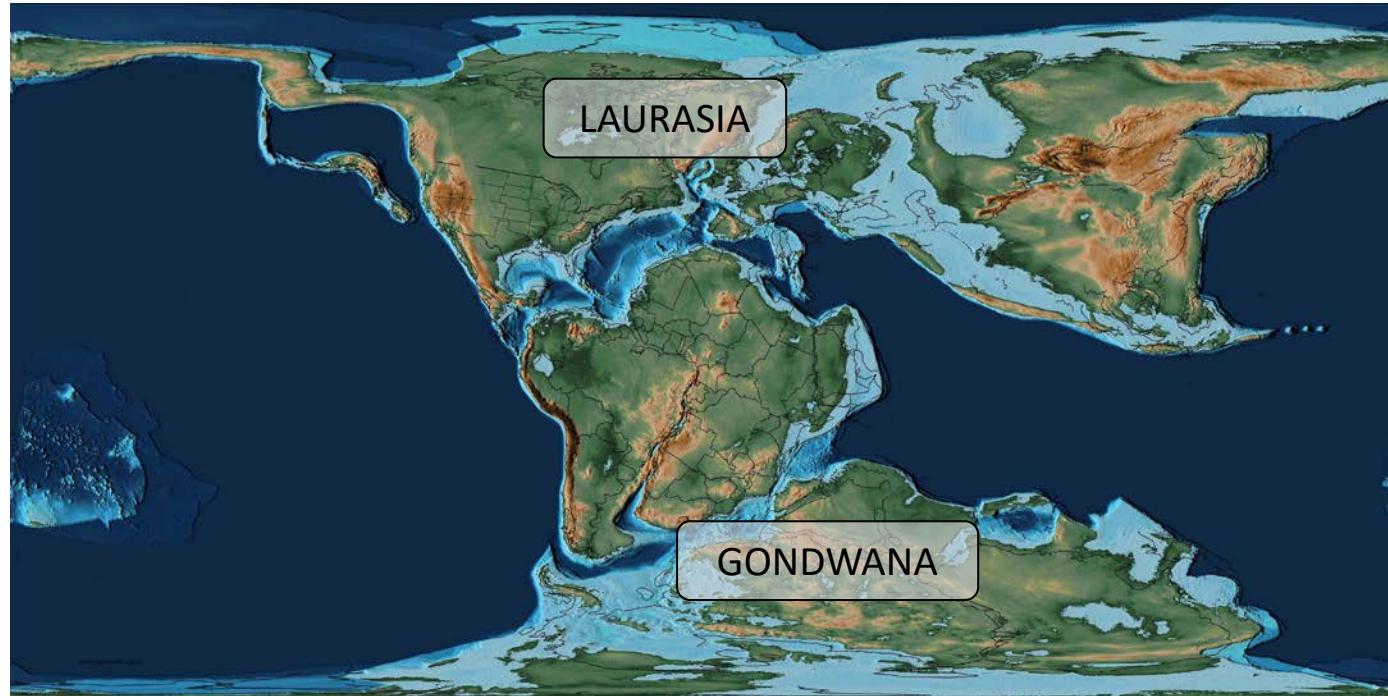


Source: PALEOMAP Project by C. Scotese

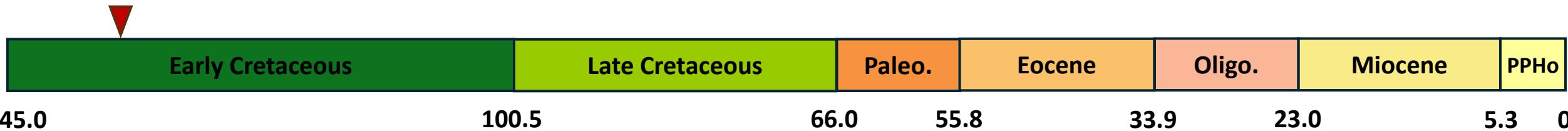
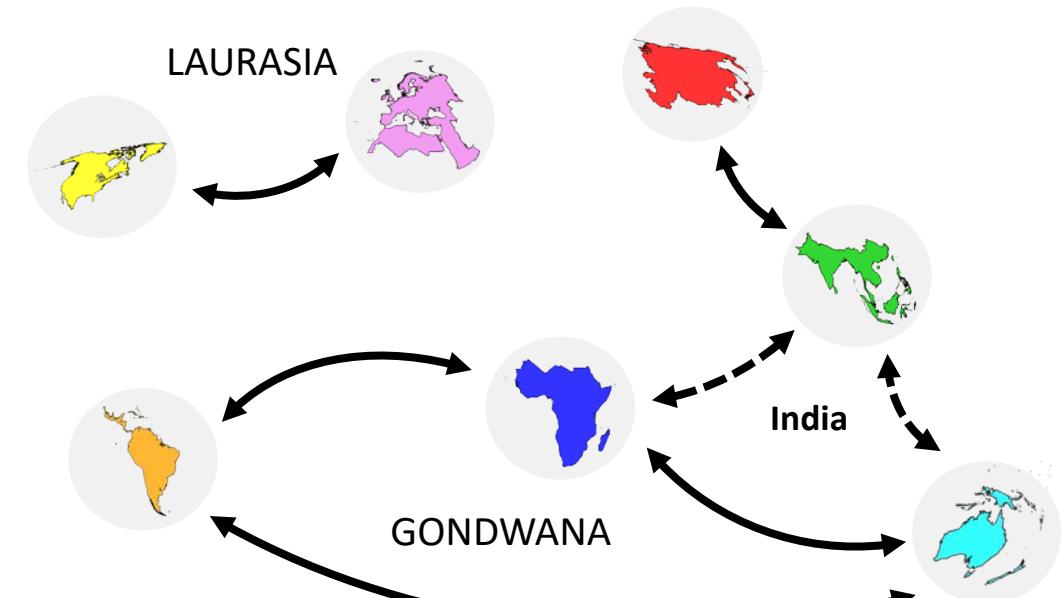


# Biogeographic methods

Early Cretaceous  
135.0 My

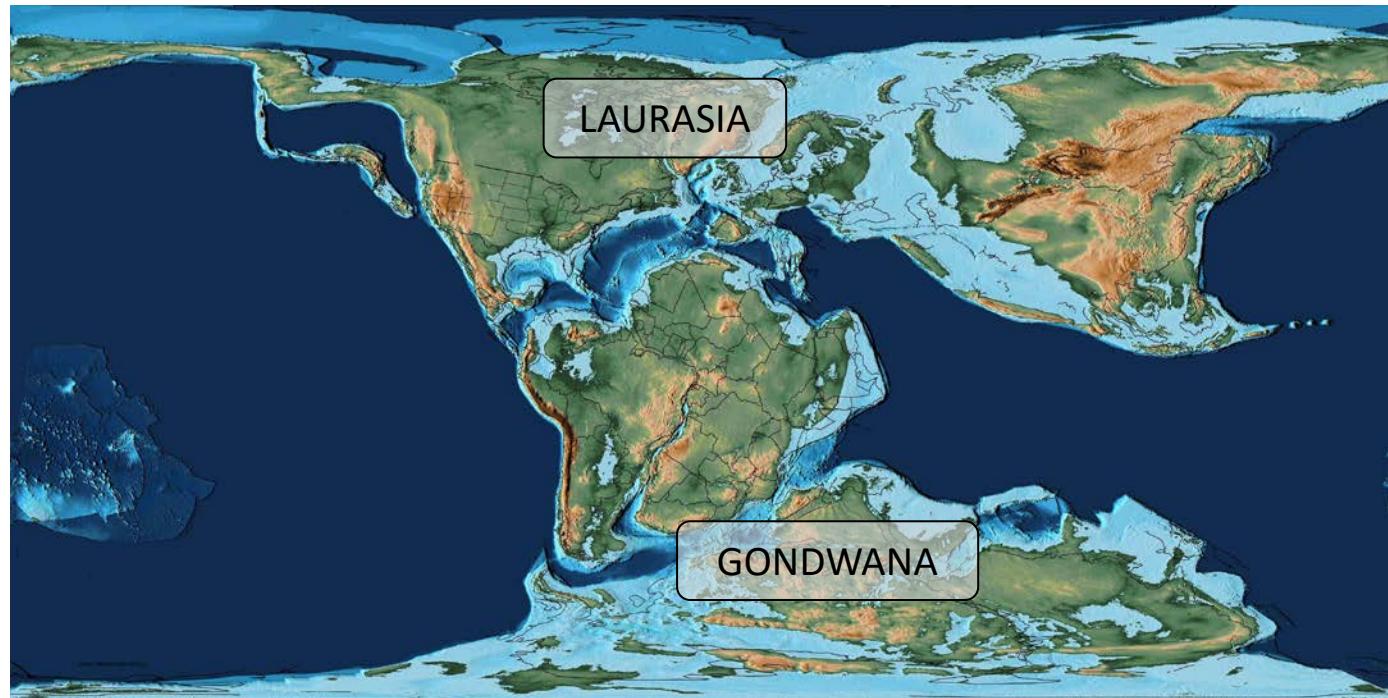


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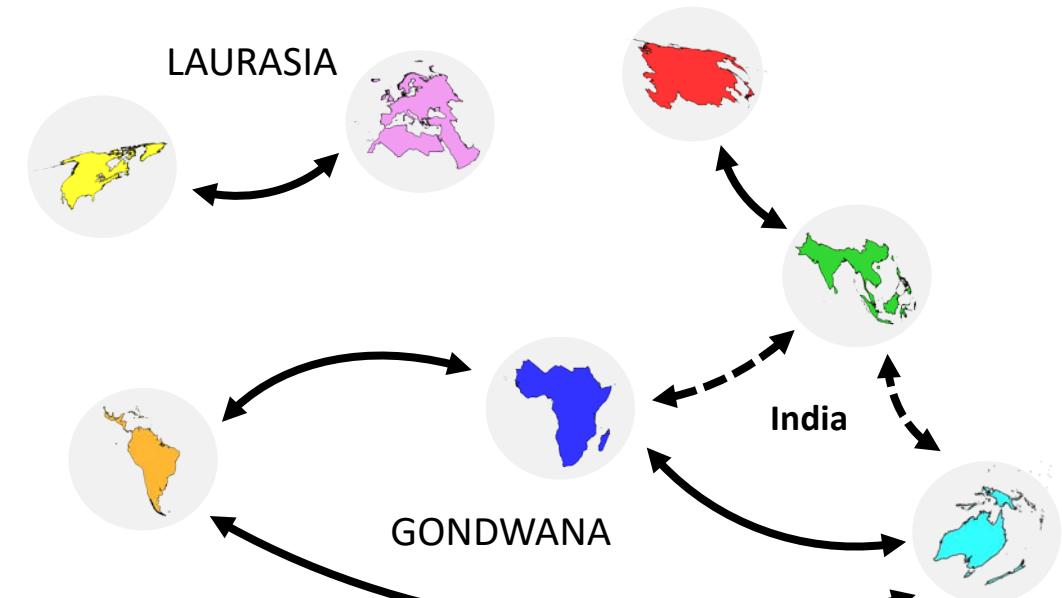


# Biogeographic methods

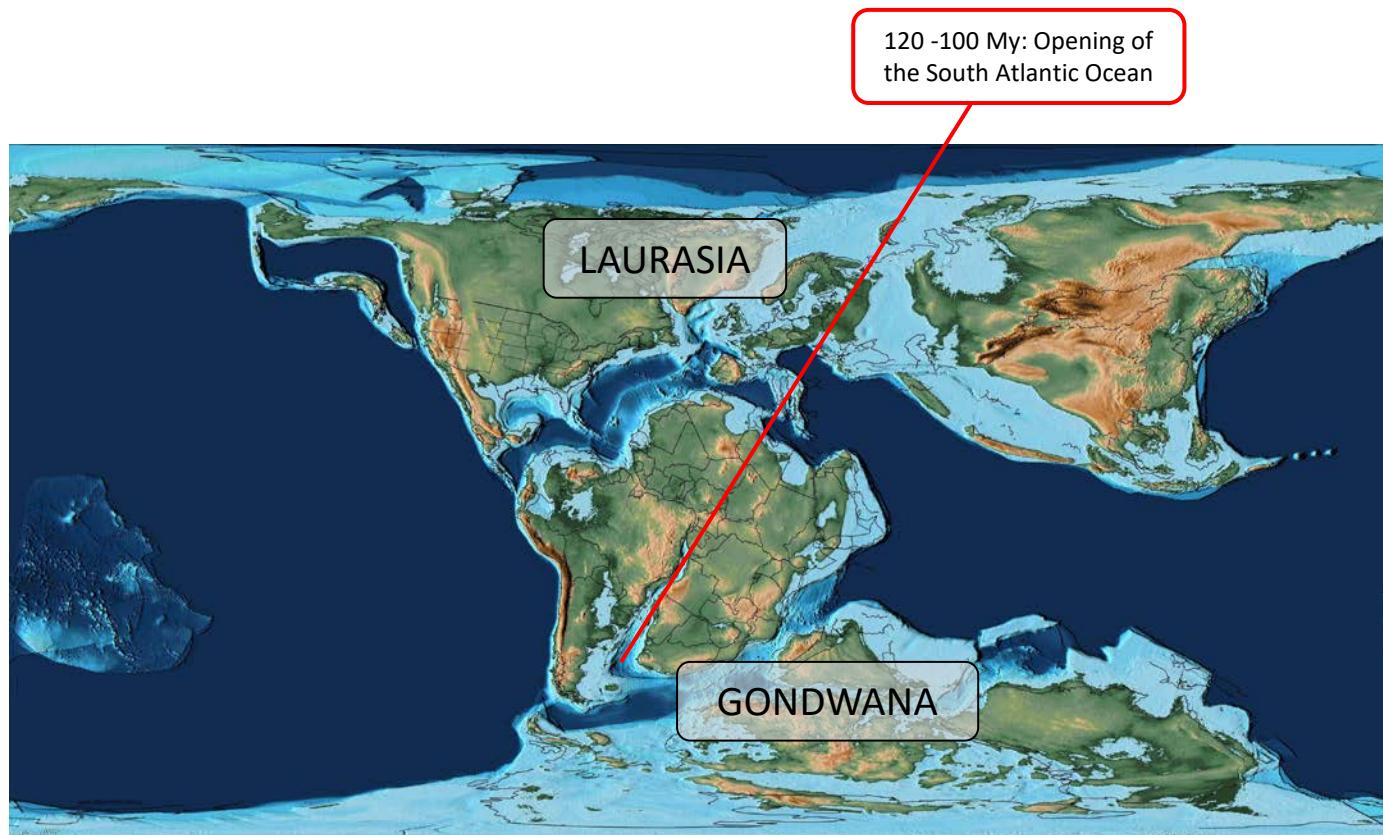
Early Cretaceous  
130.0 My



Source: PALEOMAP Project by C. Scotese



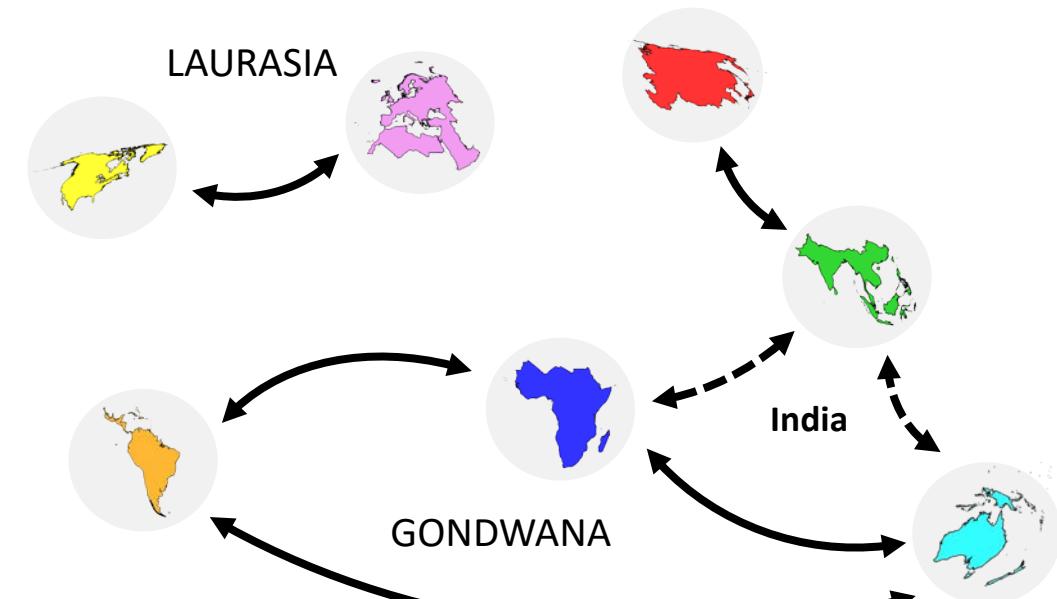
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Early Cretaceous

125.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

55.8

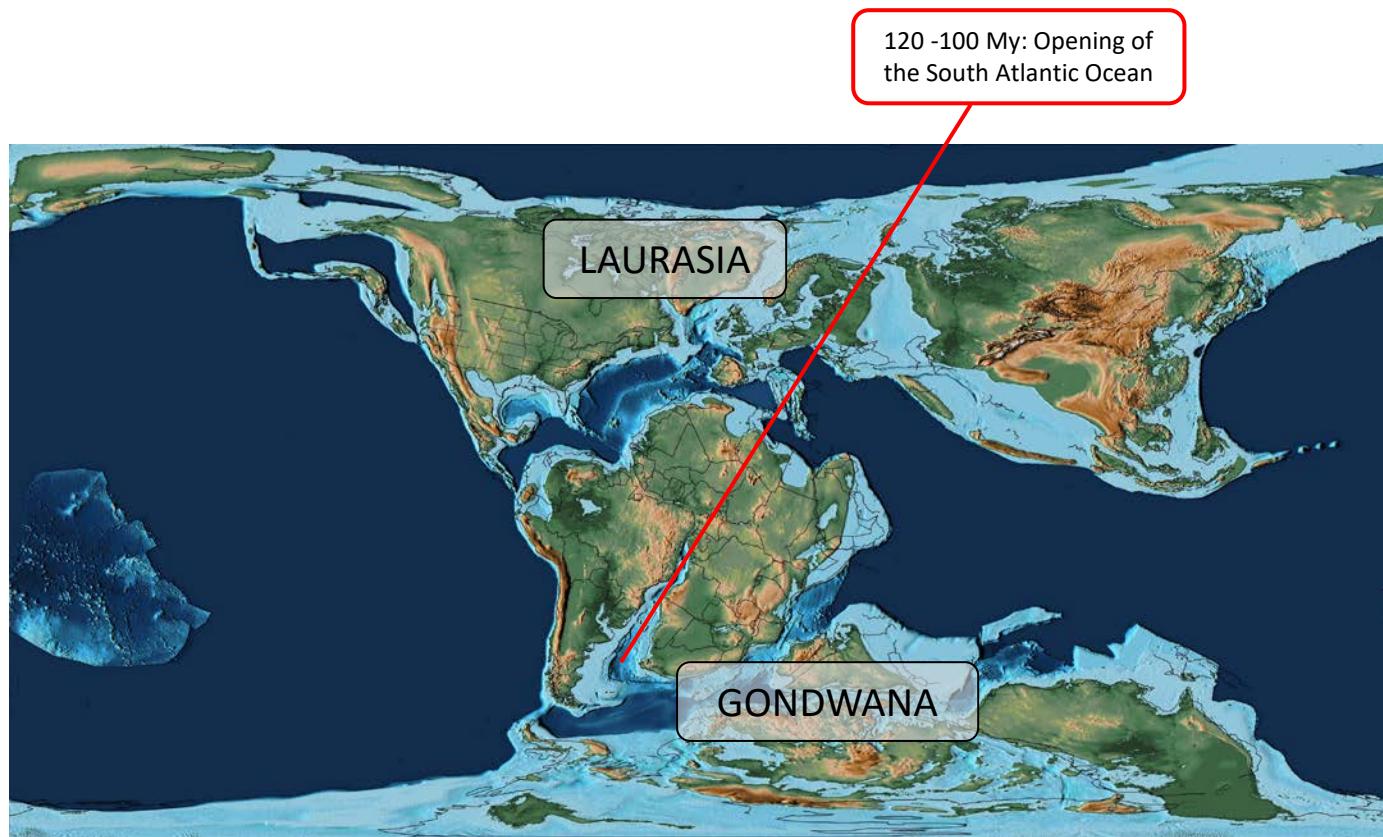
33.9

23.0

5.3

0

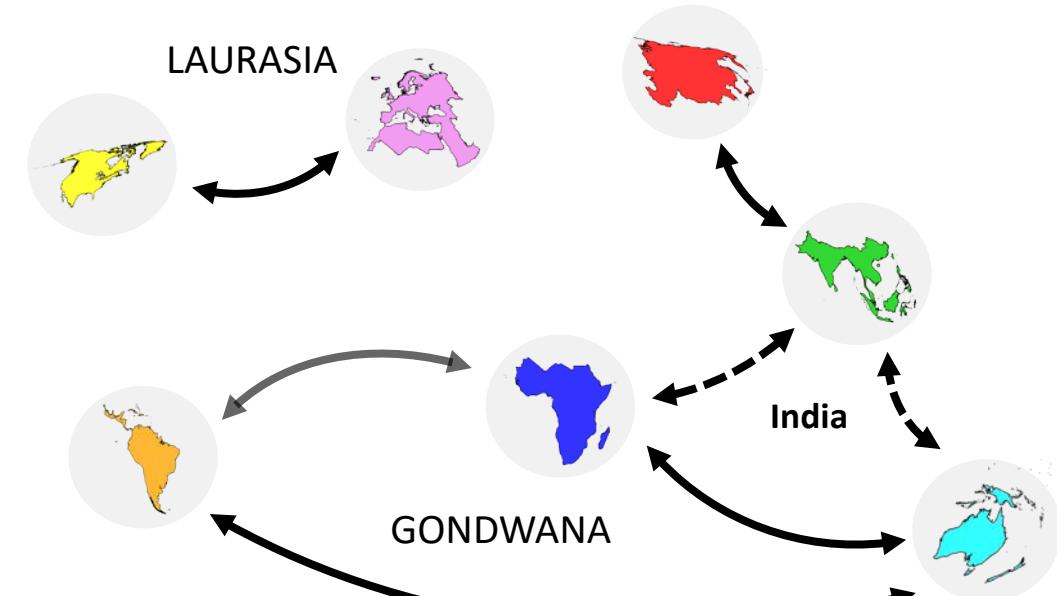
# Biogeographic methods



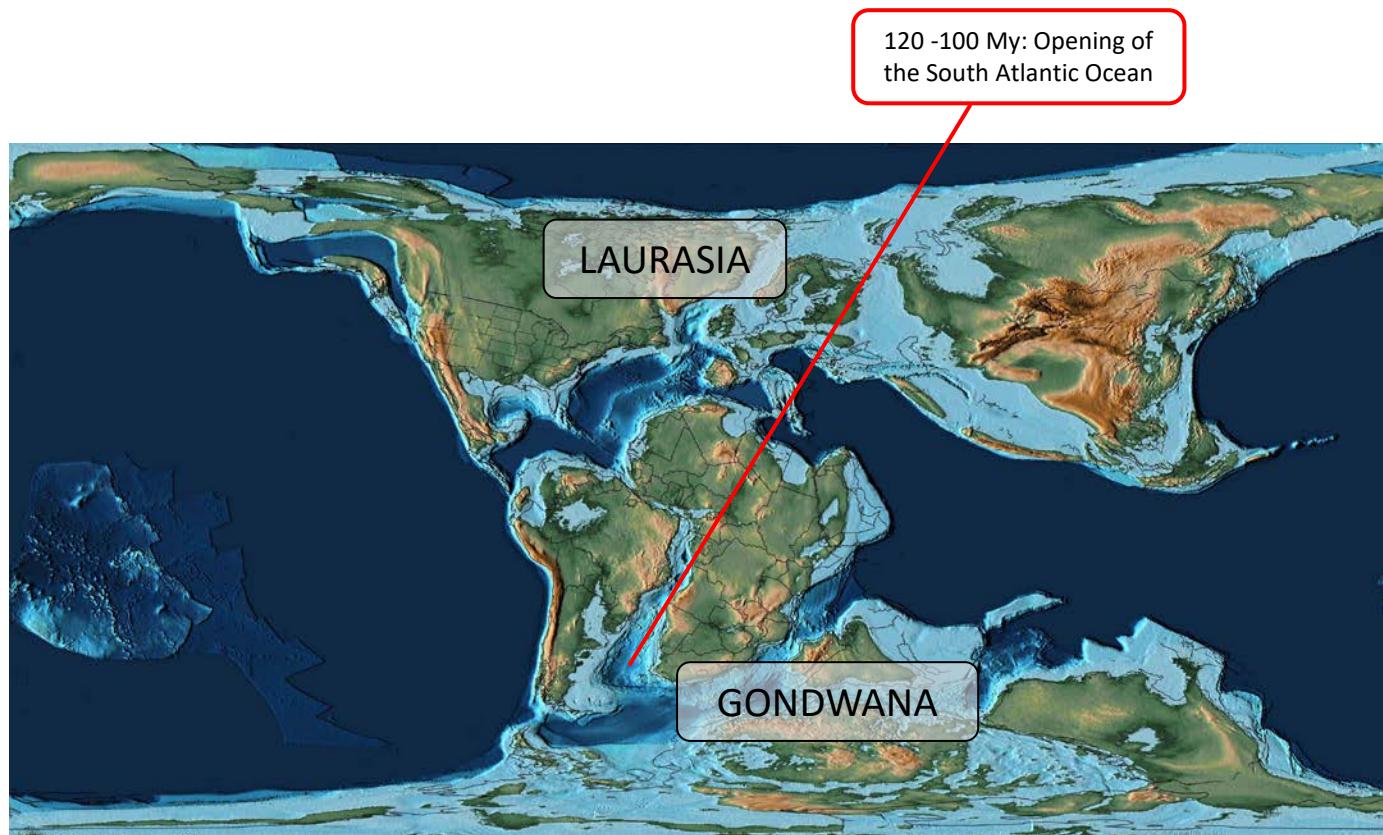
Source: PALEOMAP Project by C. Scotese



Early Cretaceous  
120.0 My

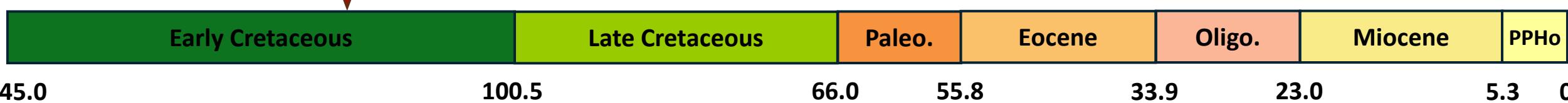
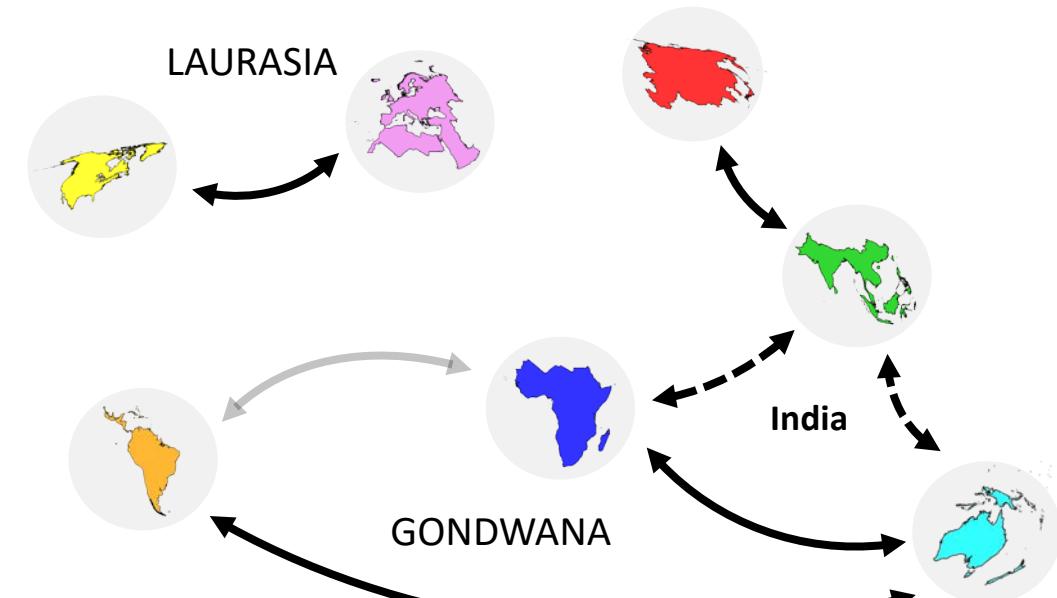


# Biogeographic methods

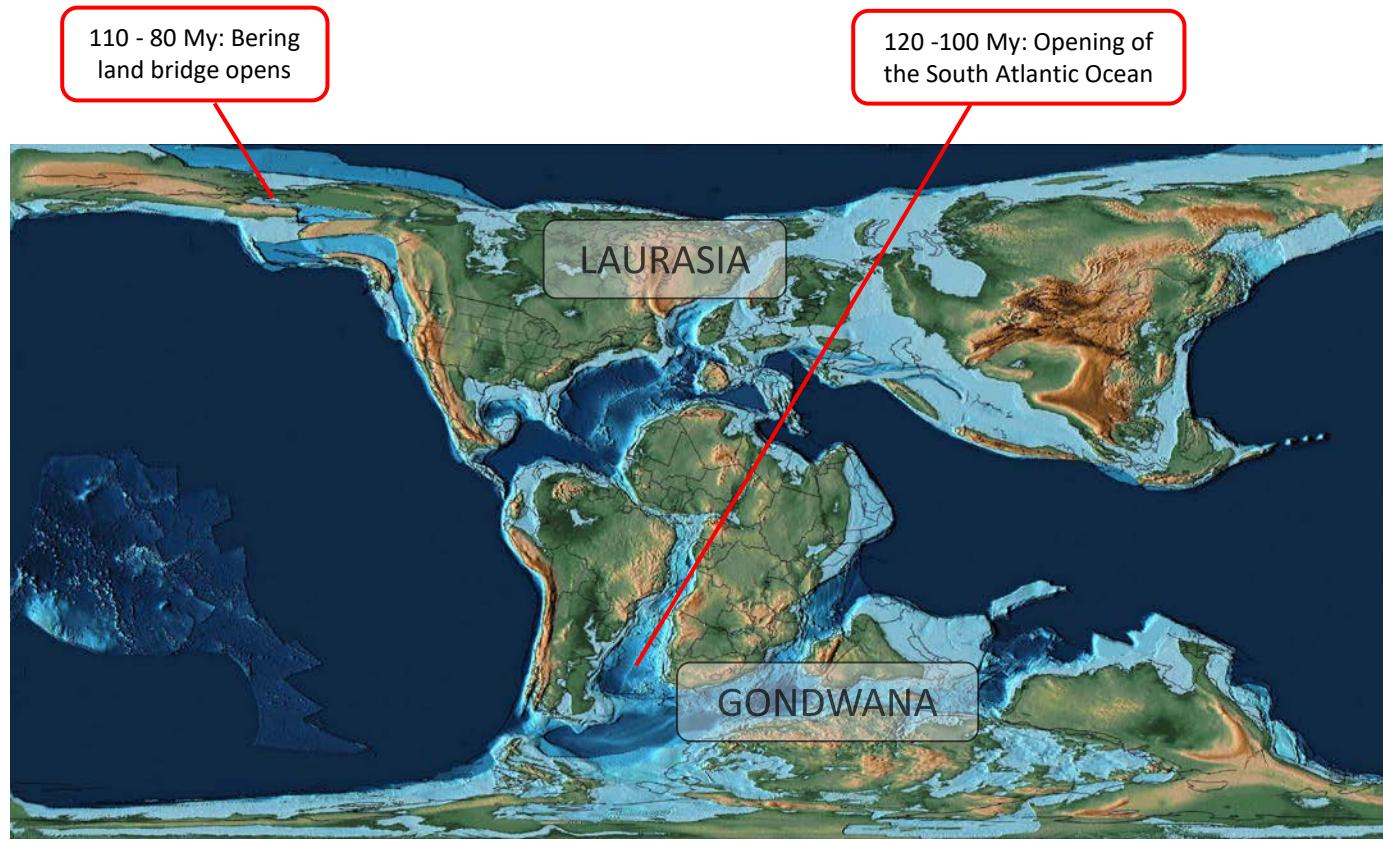


Source: PALEOMAP Project by C. Scotese

Early Cretaceous  
115.0 My



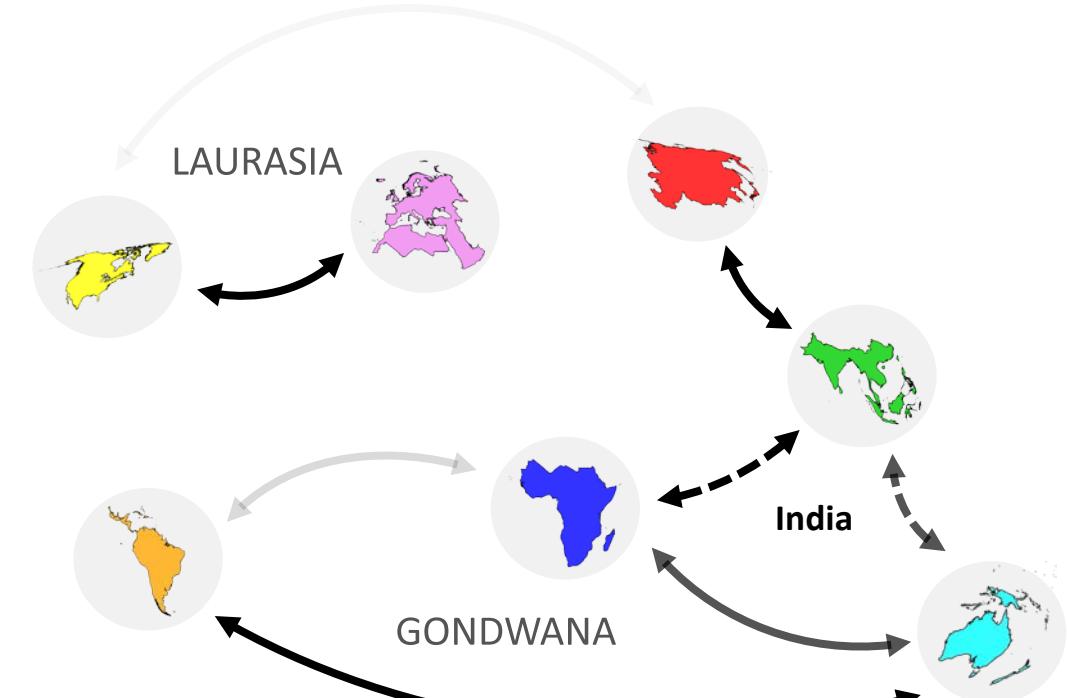
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese

Early Cretaceous

110.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

55.8

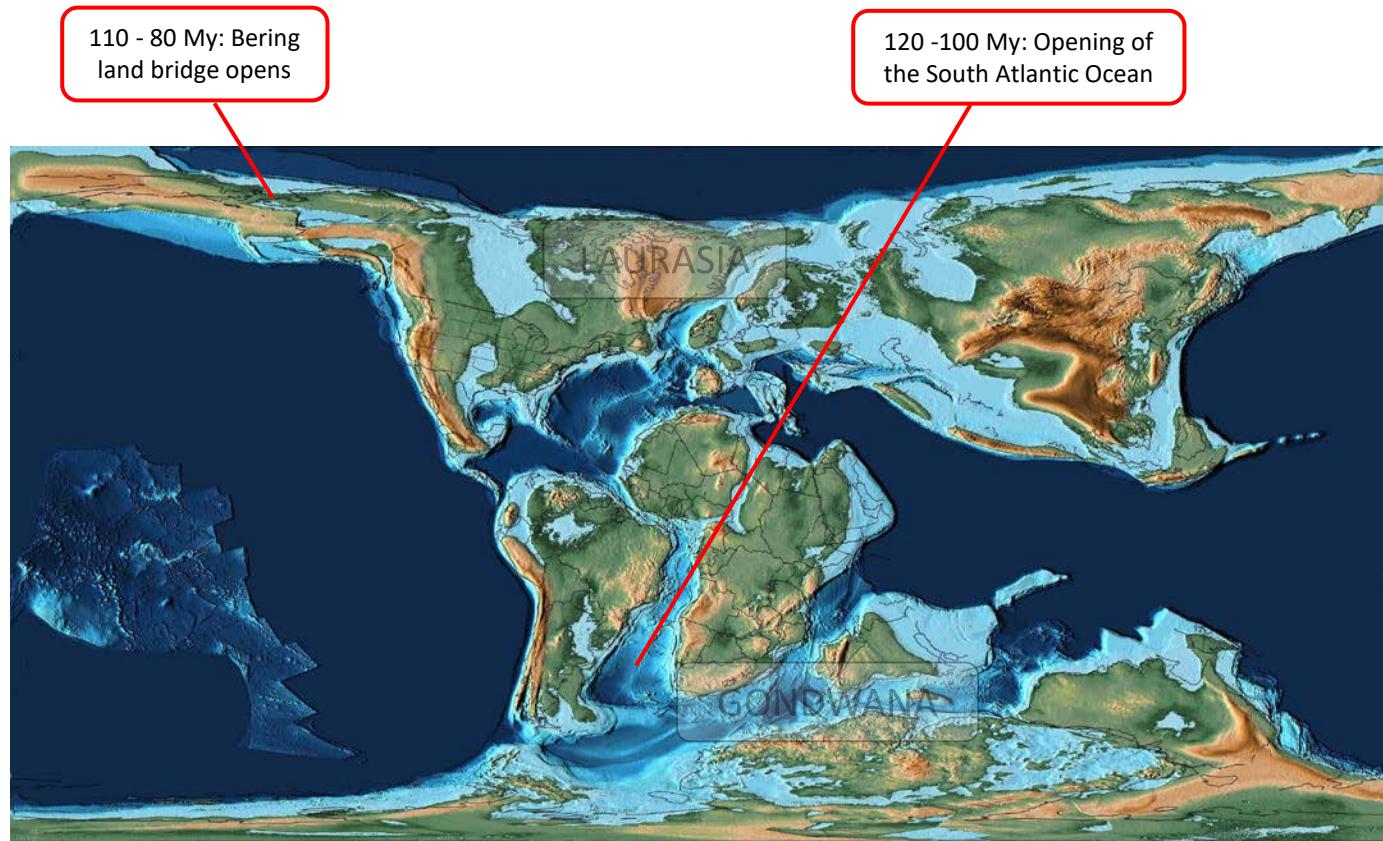
33.9

23.0

5.3

0

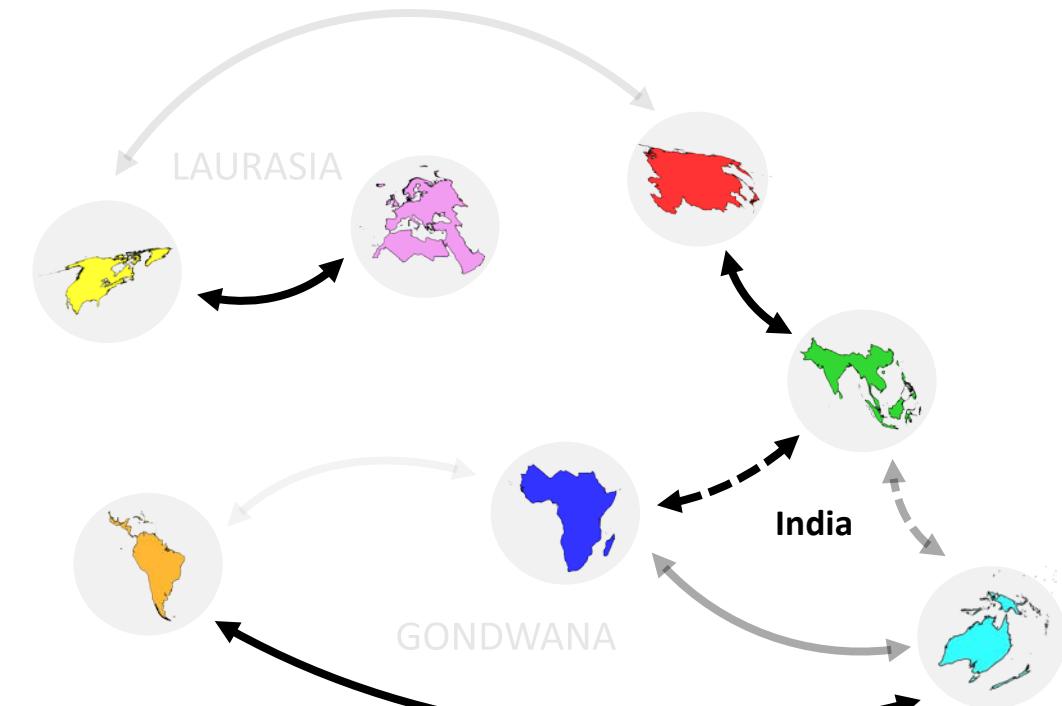
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese

Early Cretaceous

105.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

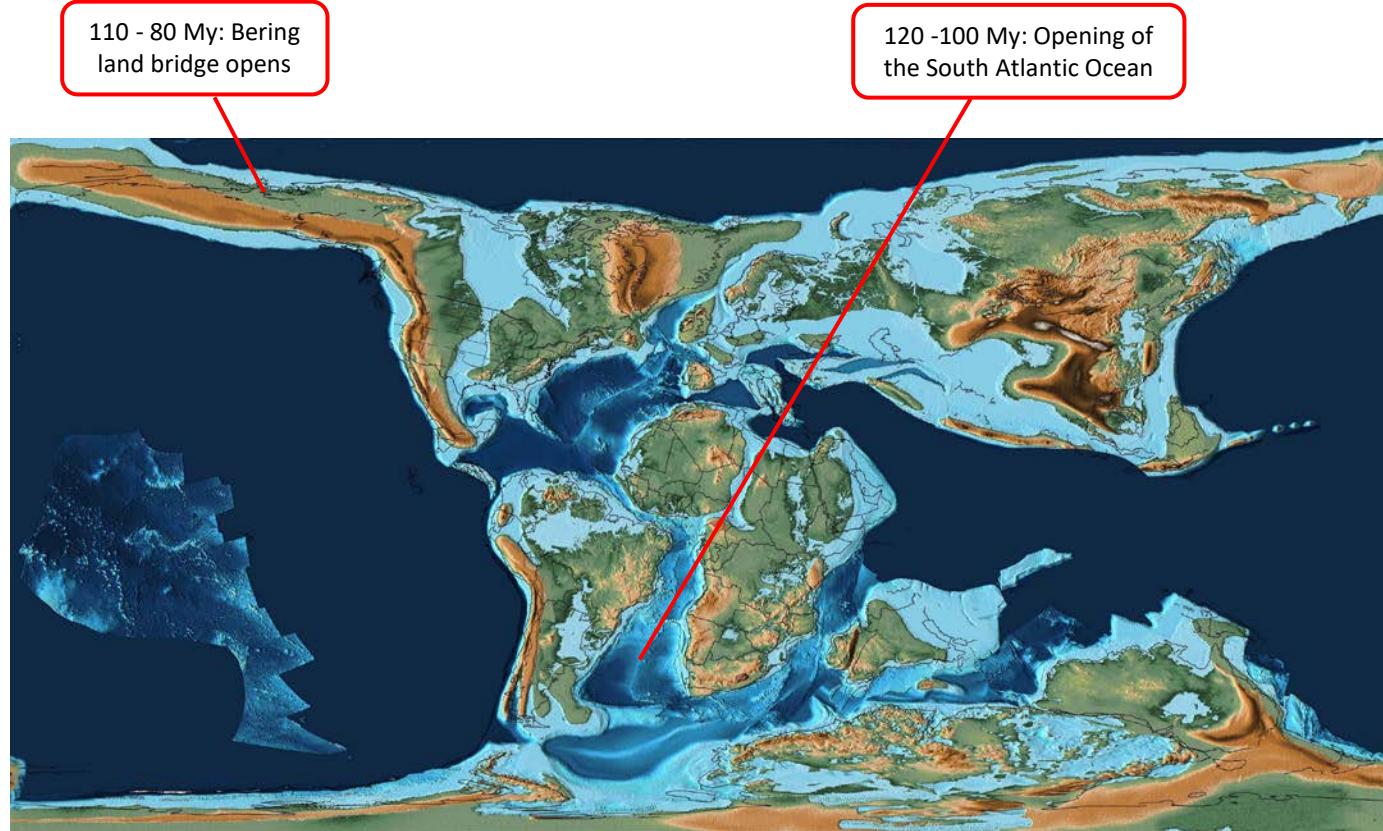
55.8

33.9

23.0

5.3 0

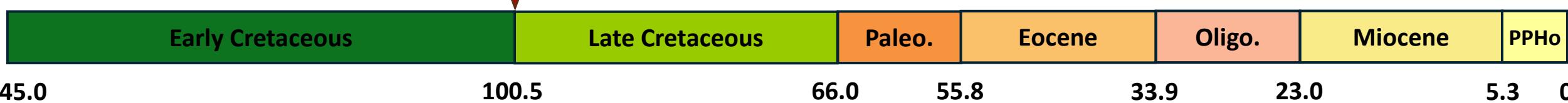
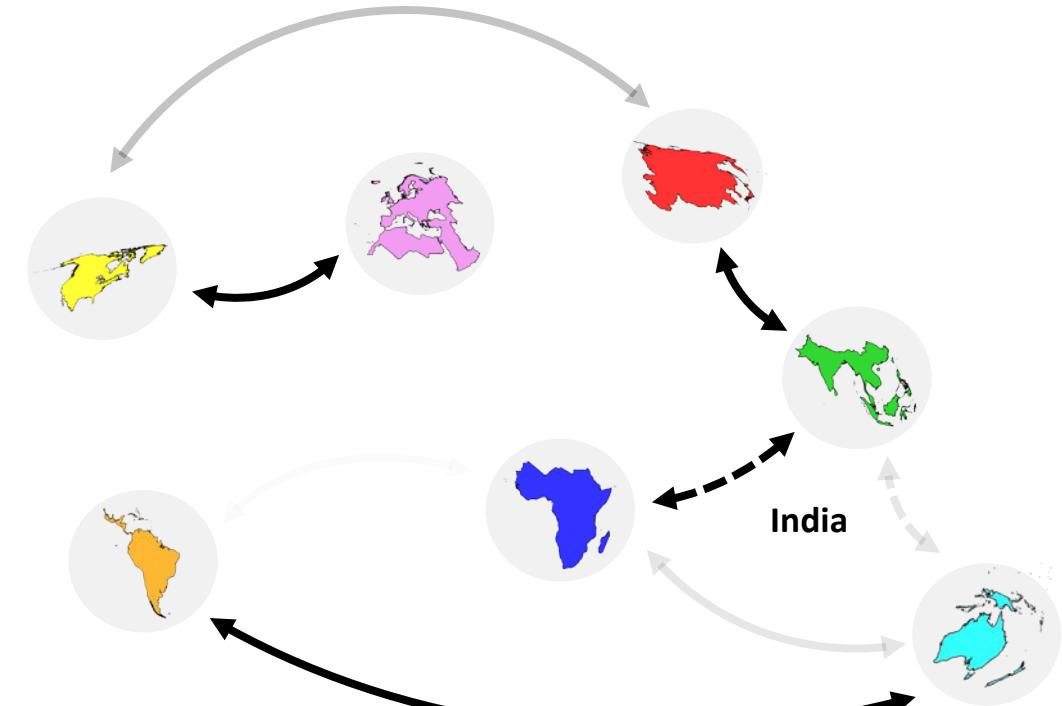
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese

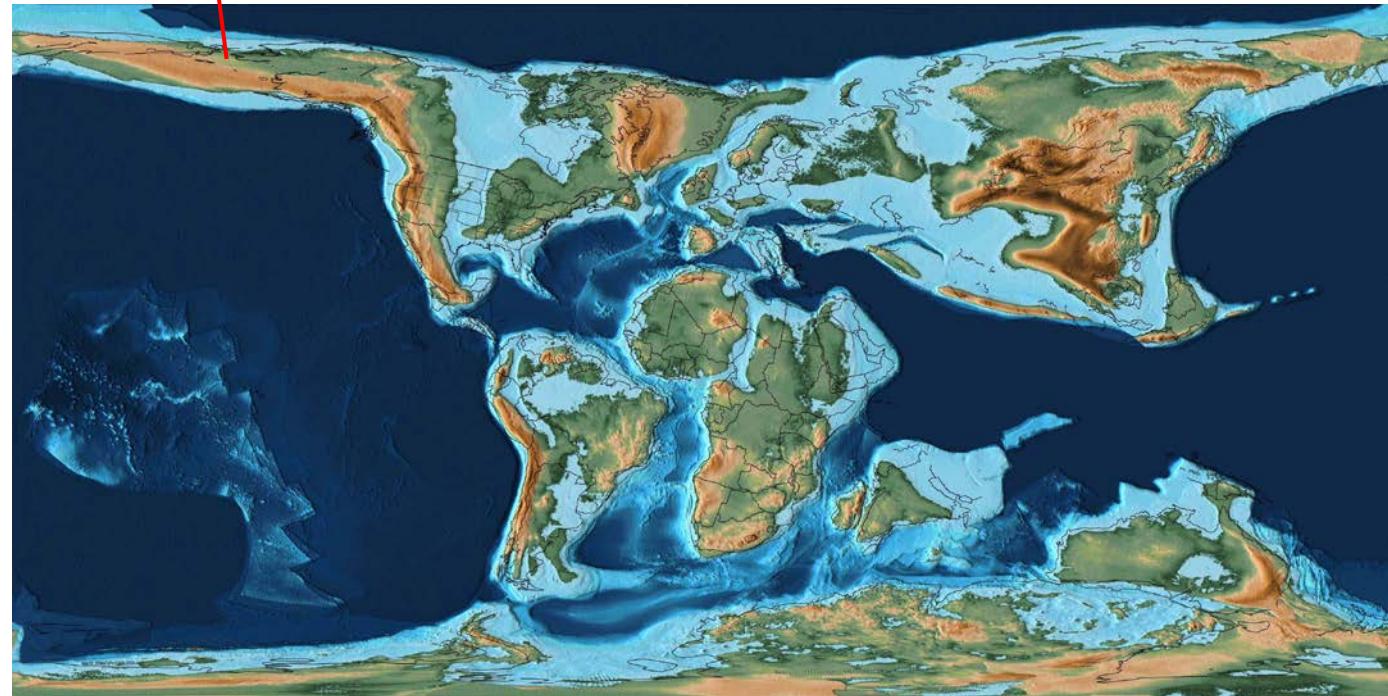
Early to Late Cretaceous

100.5 My



# Biogeographic methods

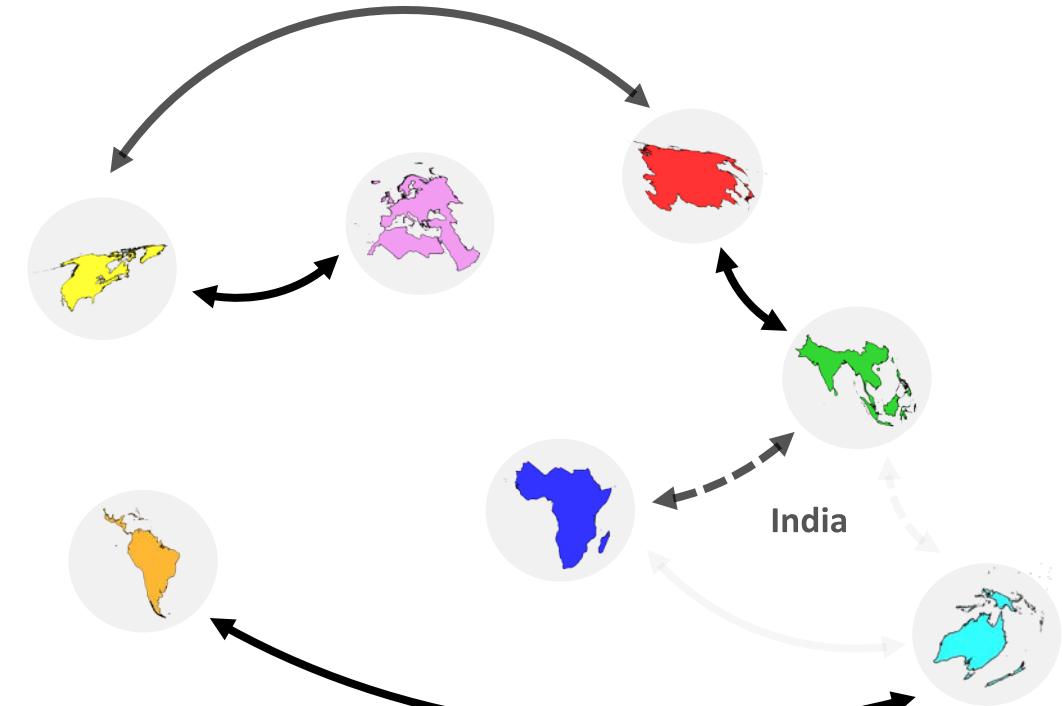
110 - 80 My: Bering land bridge opens



Source: PALEOMAP Project by C. Scotese

Late Cretaceous

95.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

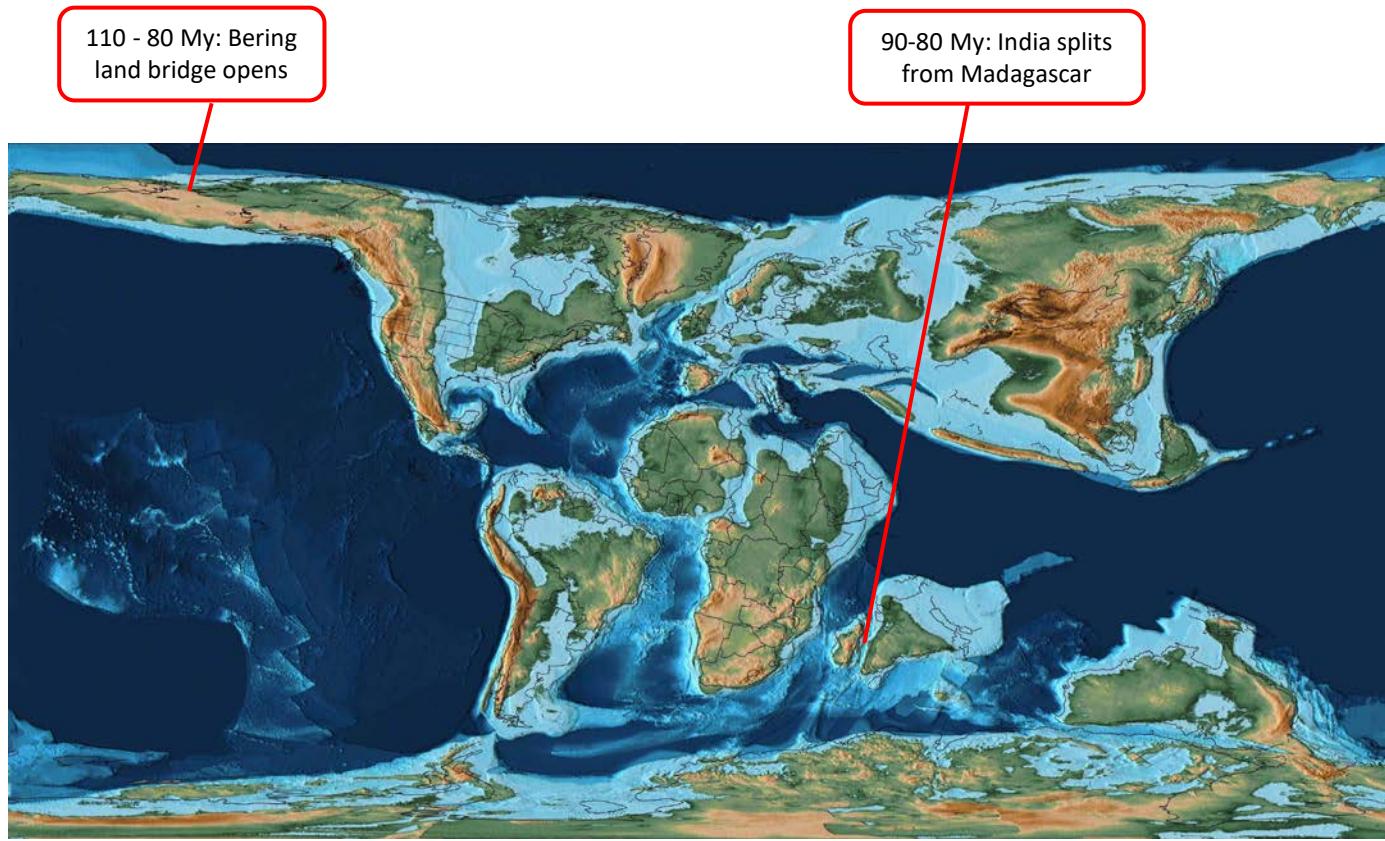
55.8

33.9

23.0

5.3 0

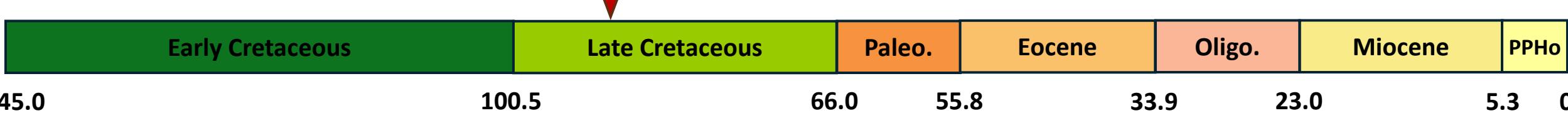
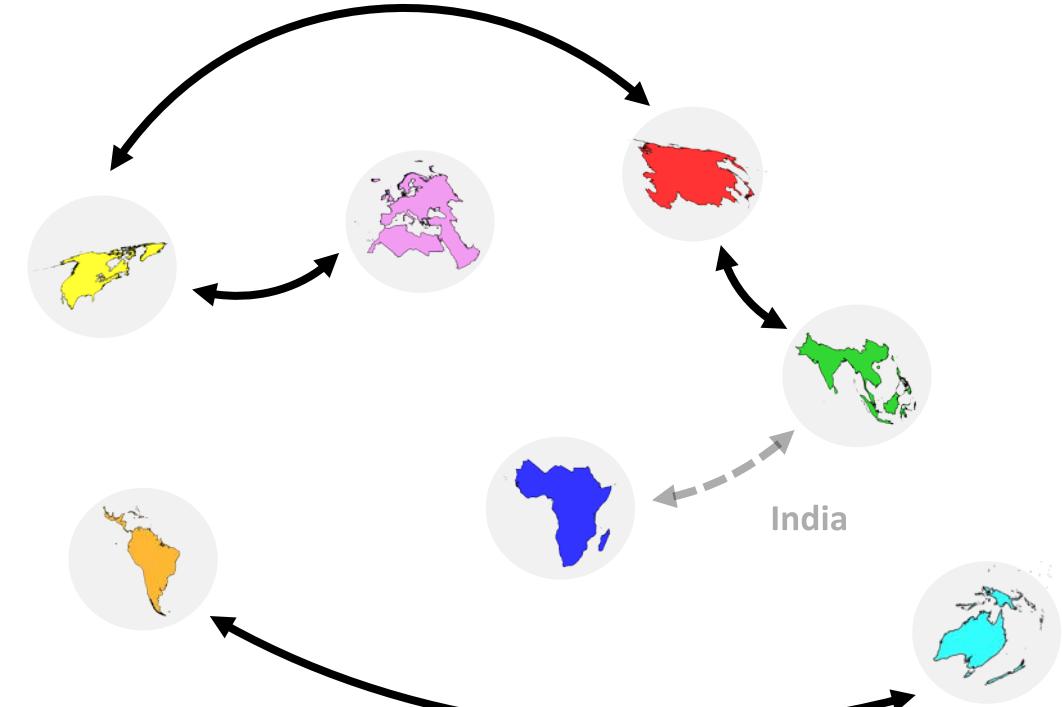
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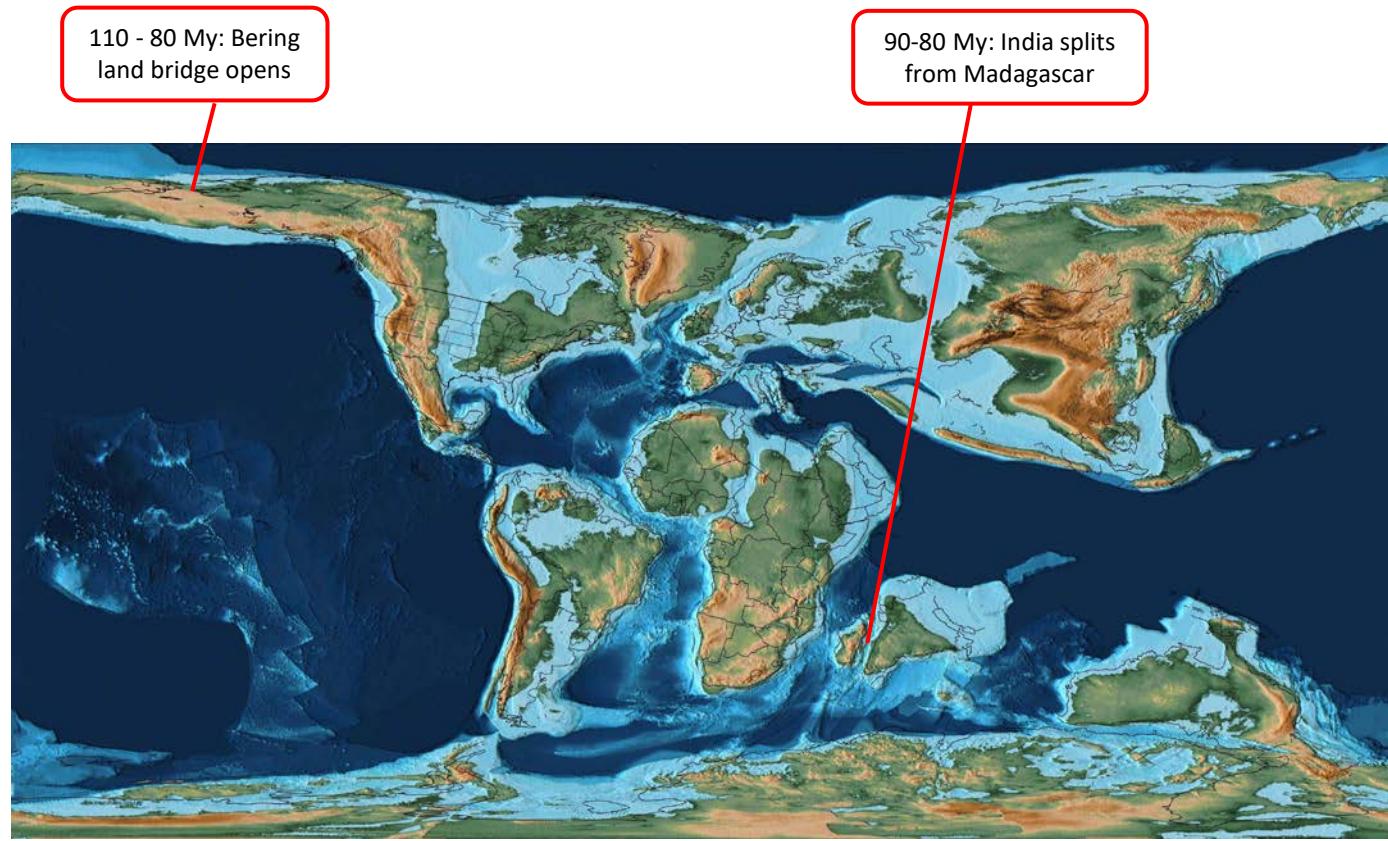
Source: PALEOMAP Project by C. Scotese

Late Cretaceous

90.0 My



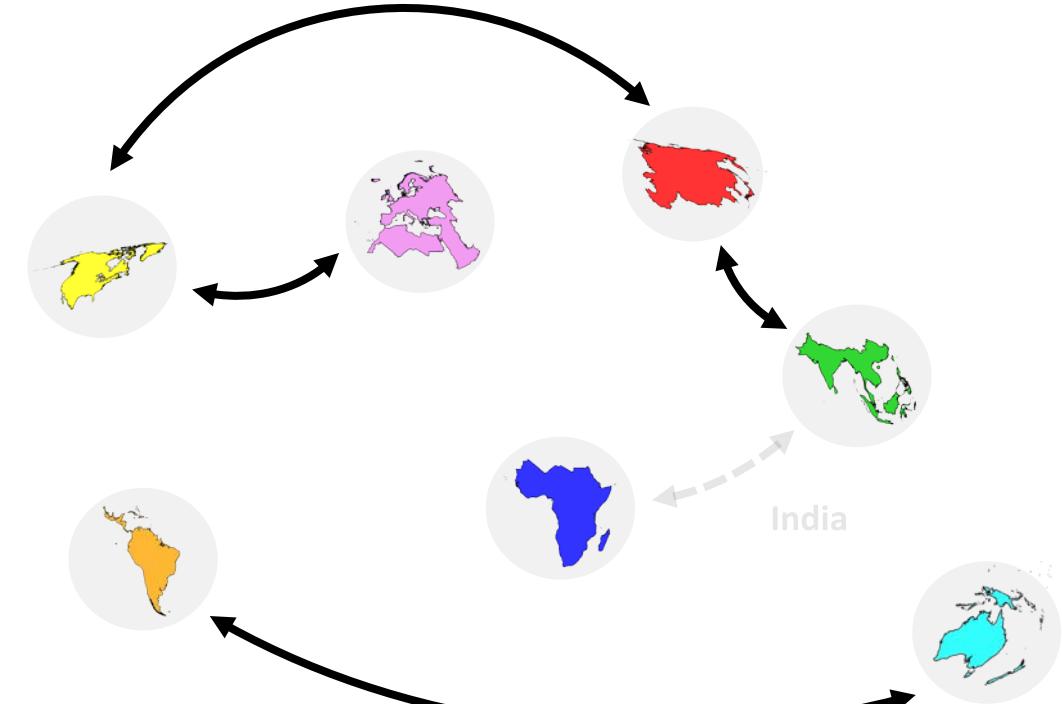
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Source: PALEOMAP Project by C. Scotese

Late Cretaceous

85.0 My



Early Cretaceous

Late Cretaceous

Paleo.

Eocene

Oligo.

Miocene

PPHo

145.0

100.5

66.0

55.8

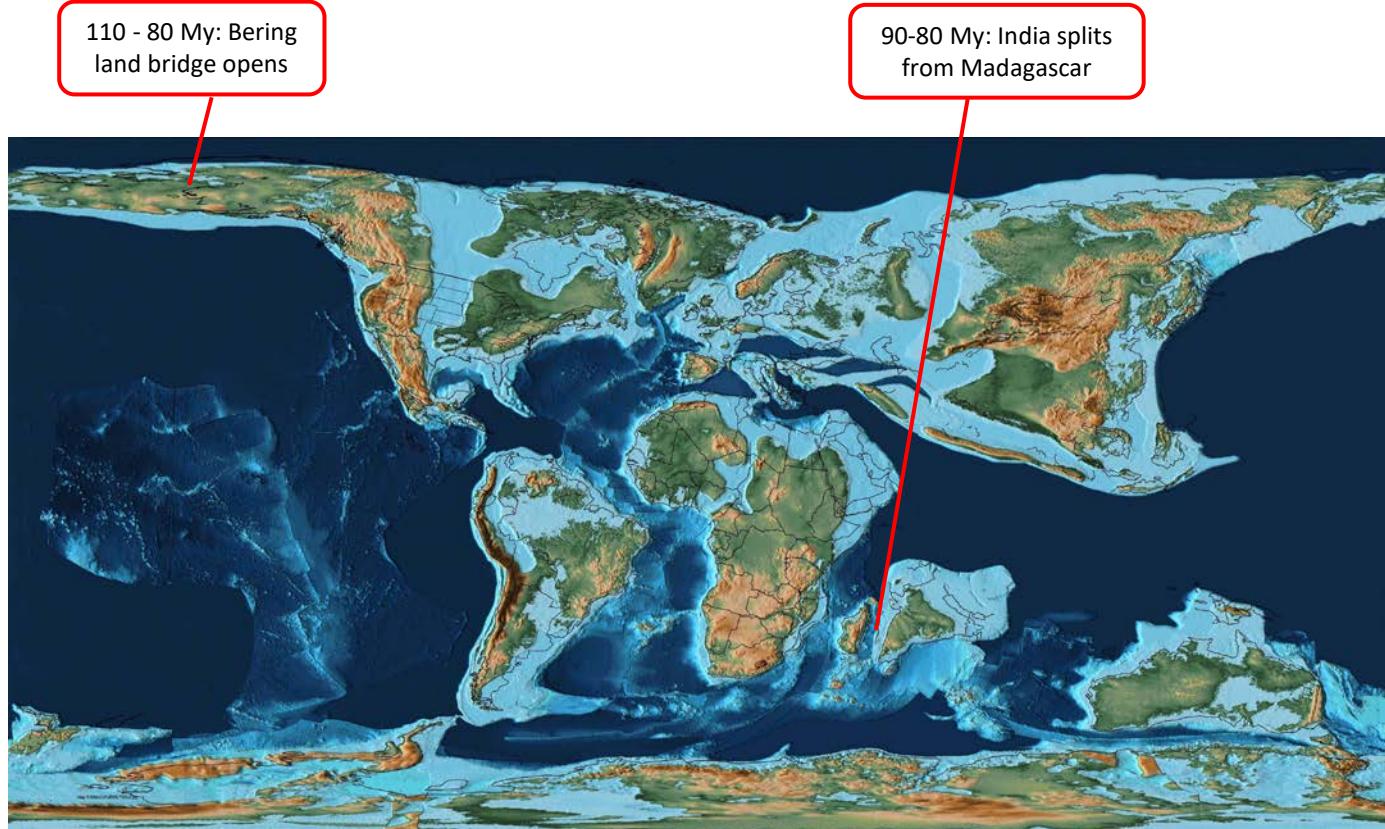
33.9

23.0

5.3

0

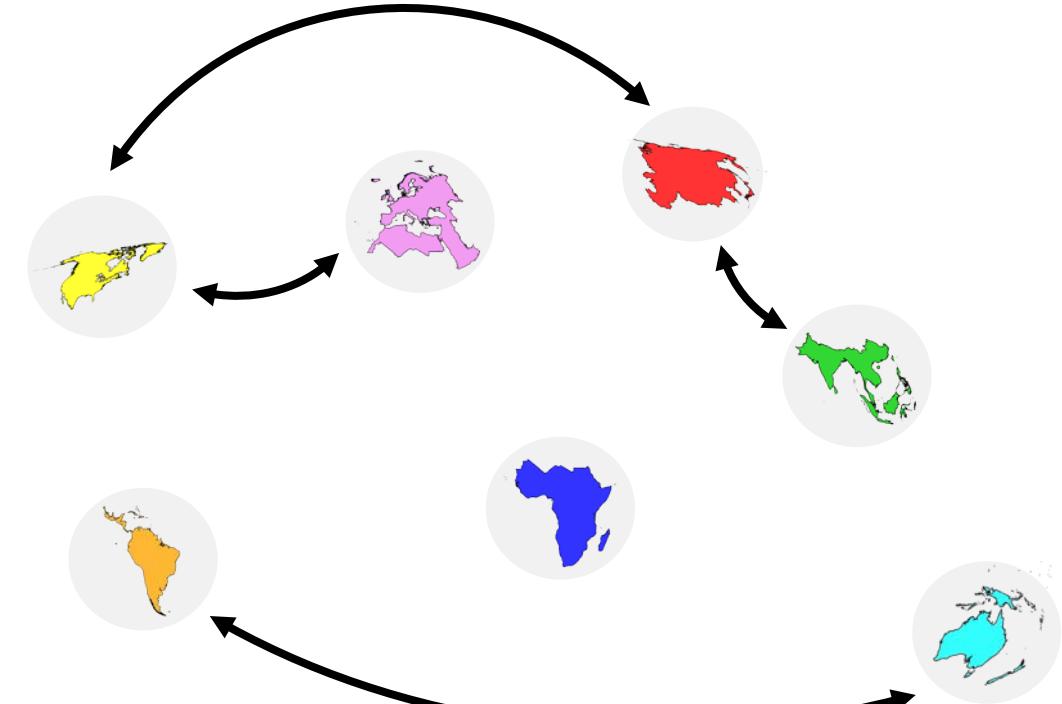
# Biogeographic methods



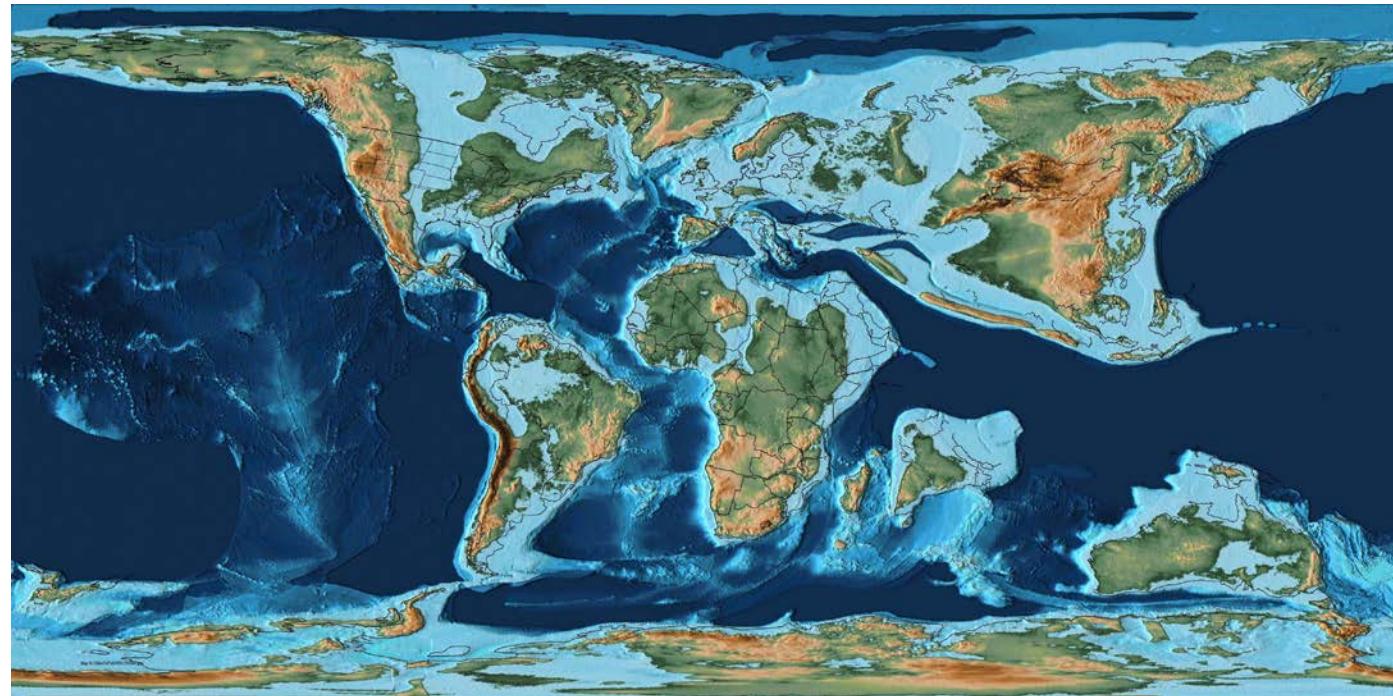
Source: PALEOMAP Project by C. Scotese

Late Cretaceous

80.0 My

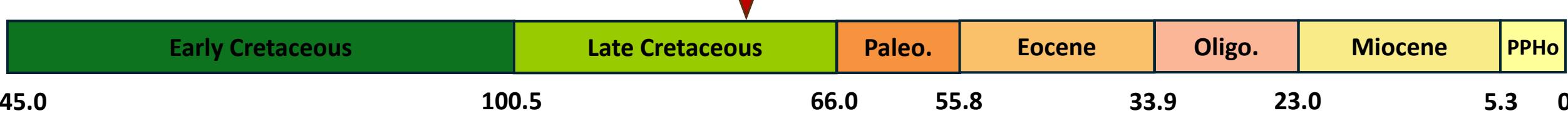
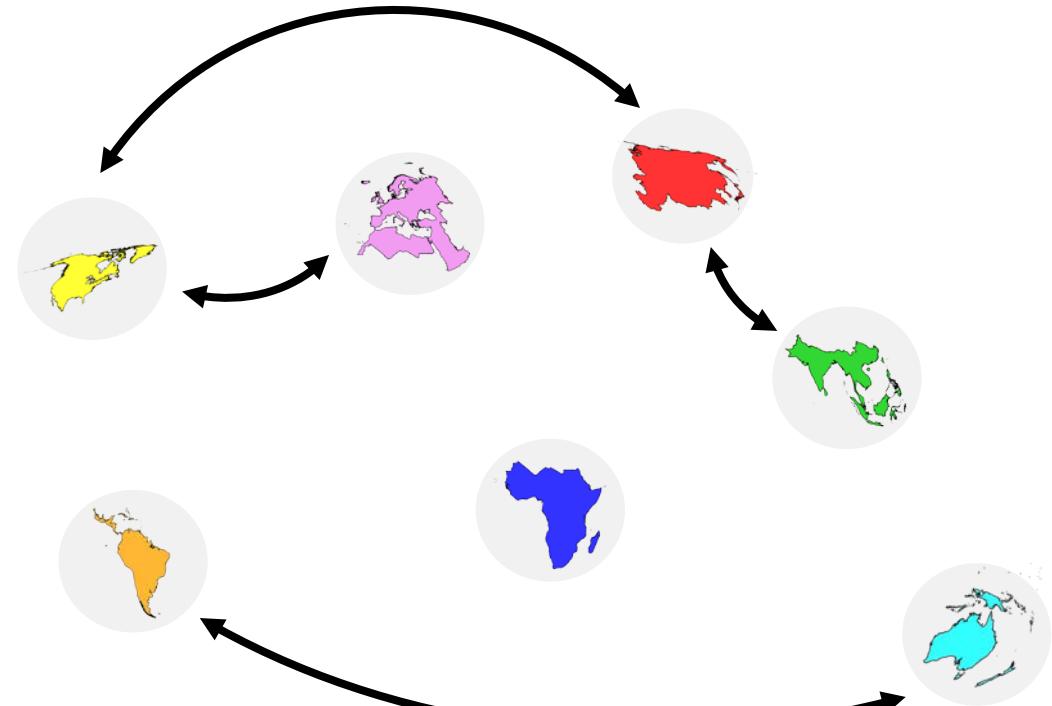


# Biogeographic methods

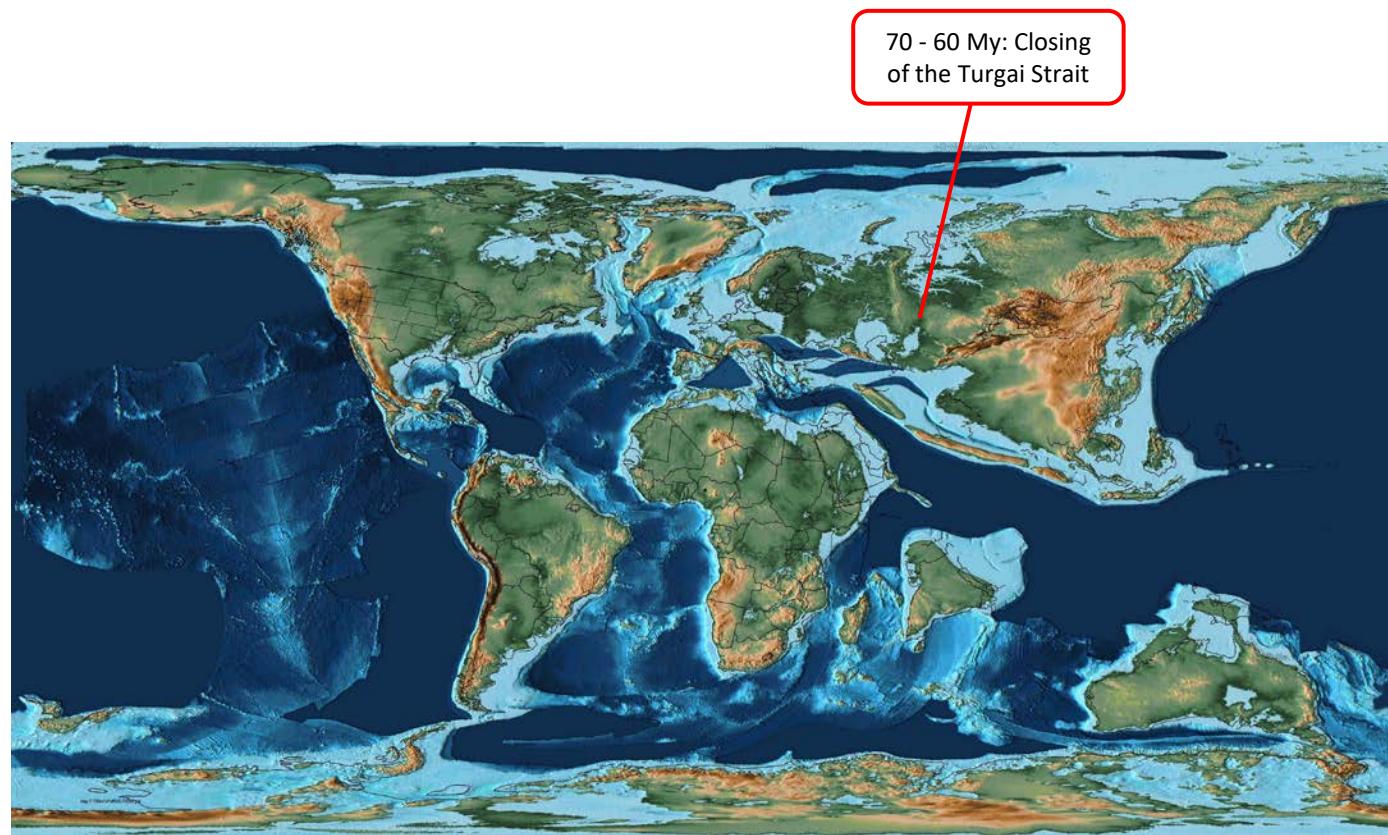


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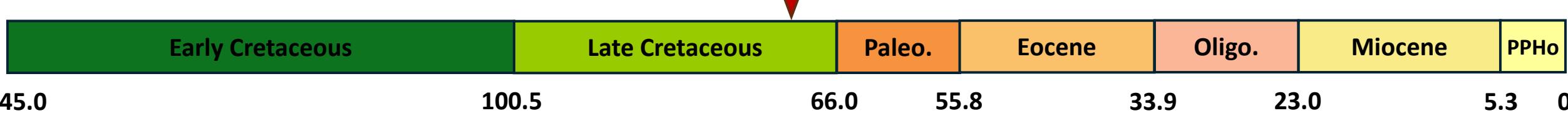
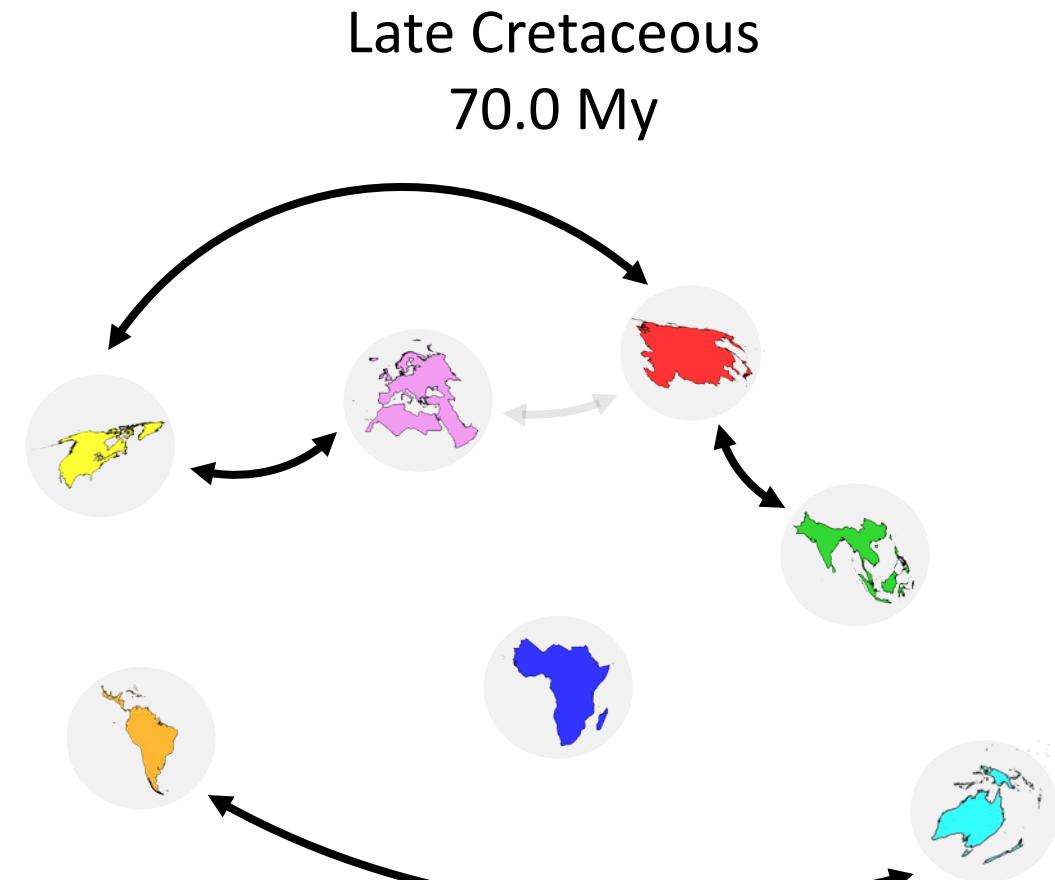
Late Cretaceous  
75.0 My



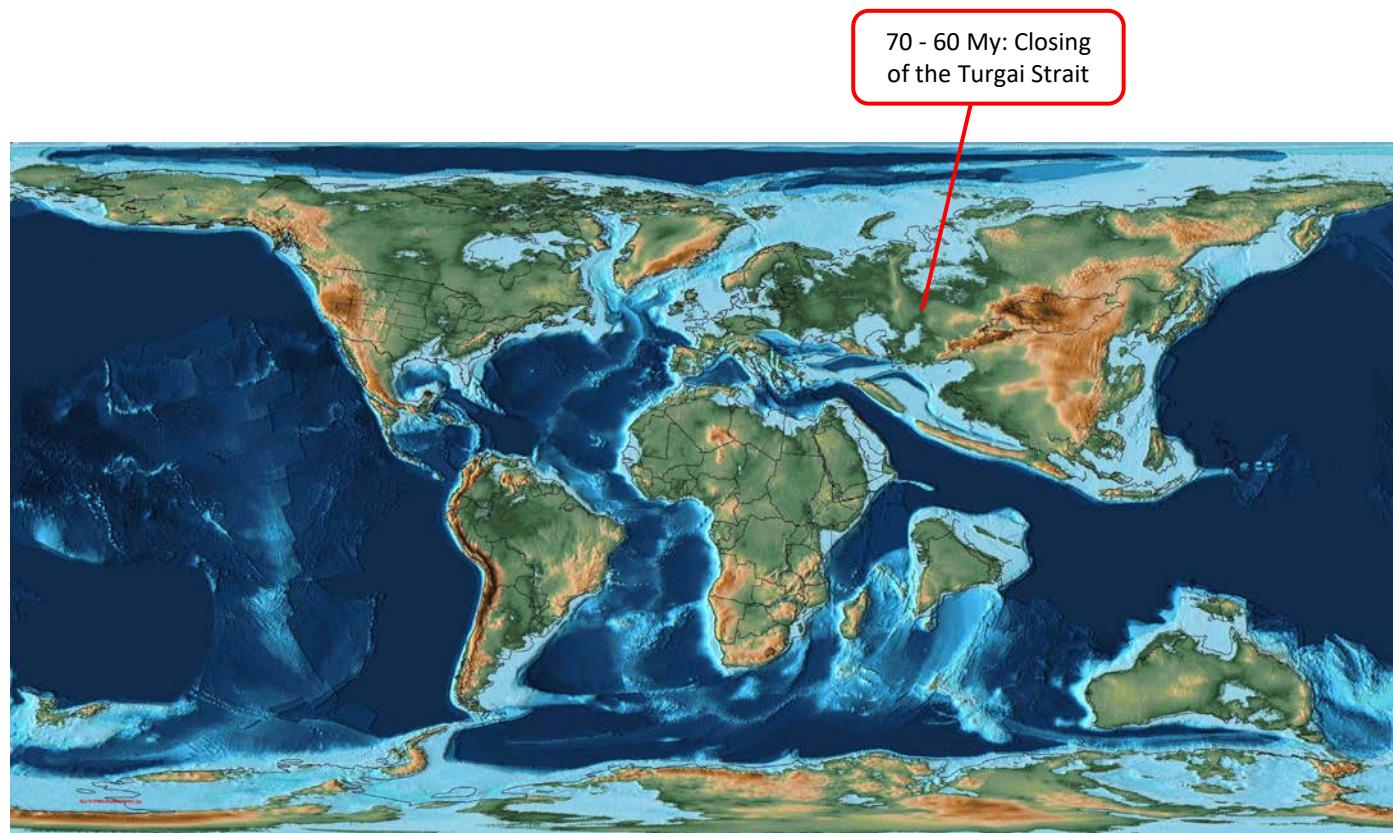
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese



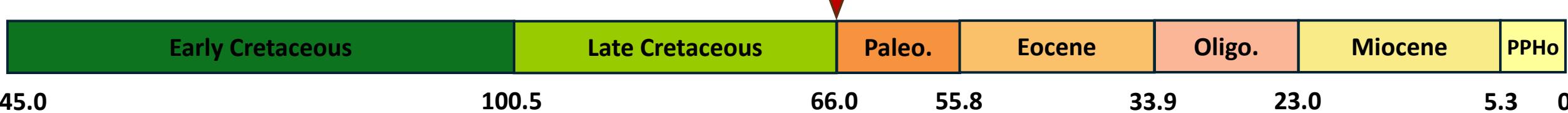
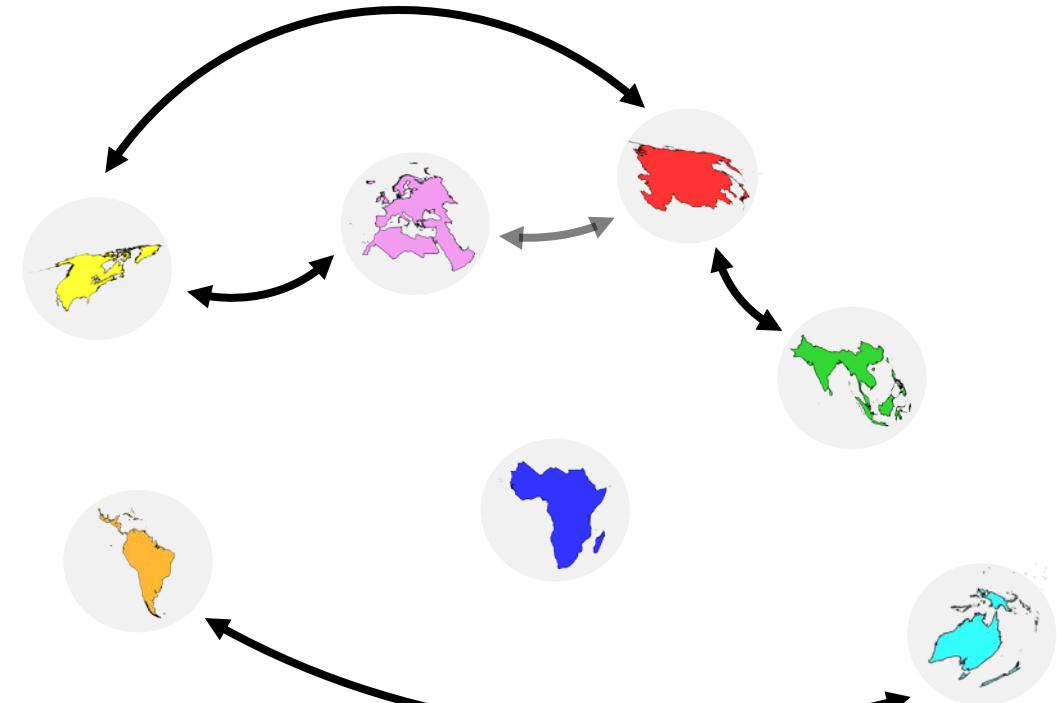
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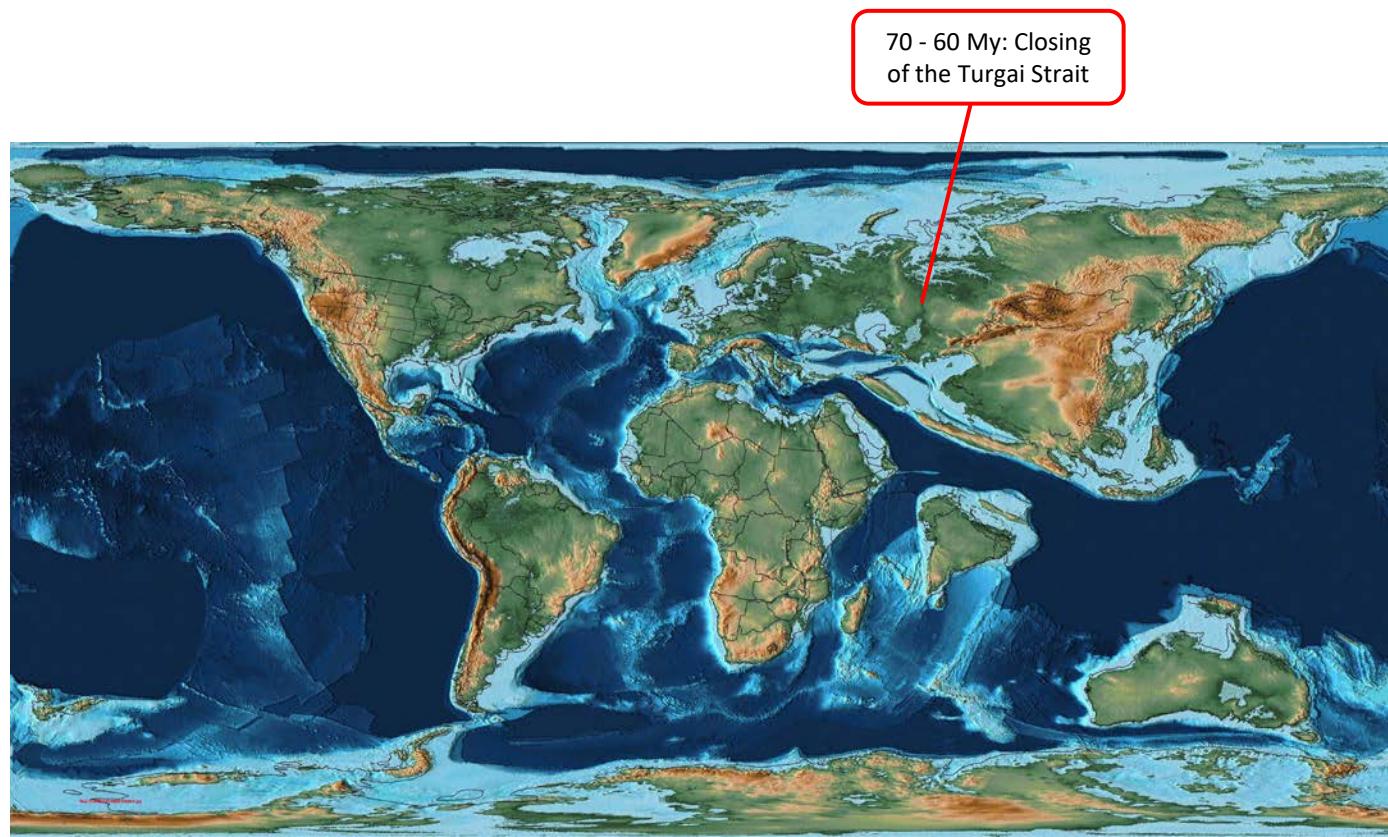
Source: PALEOMAP Project by C. Scotese

Late Cretaceous to Paleocene

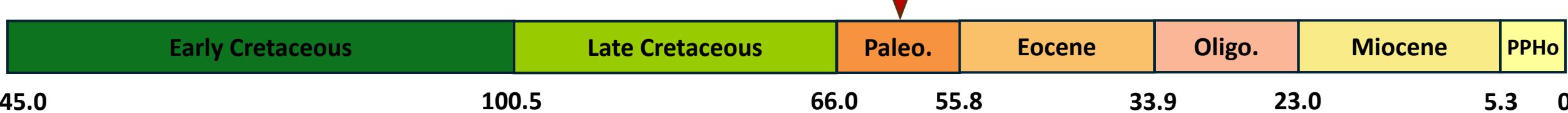
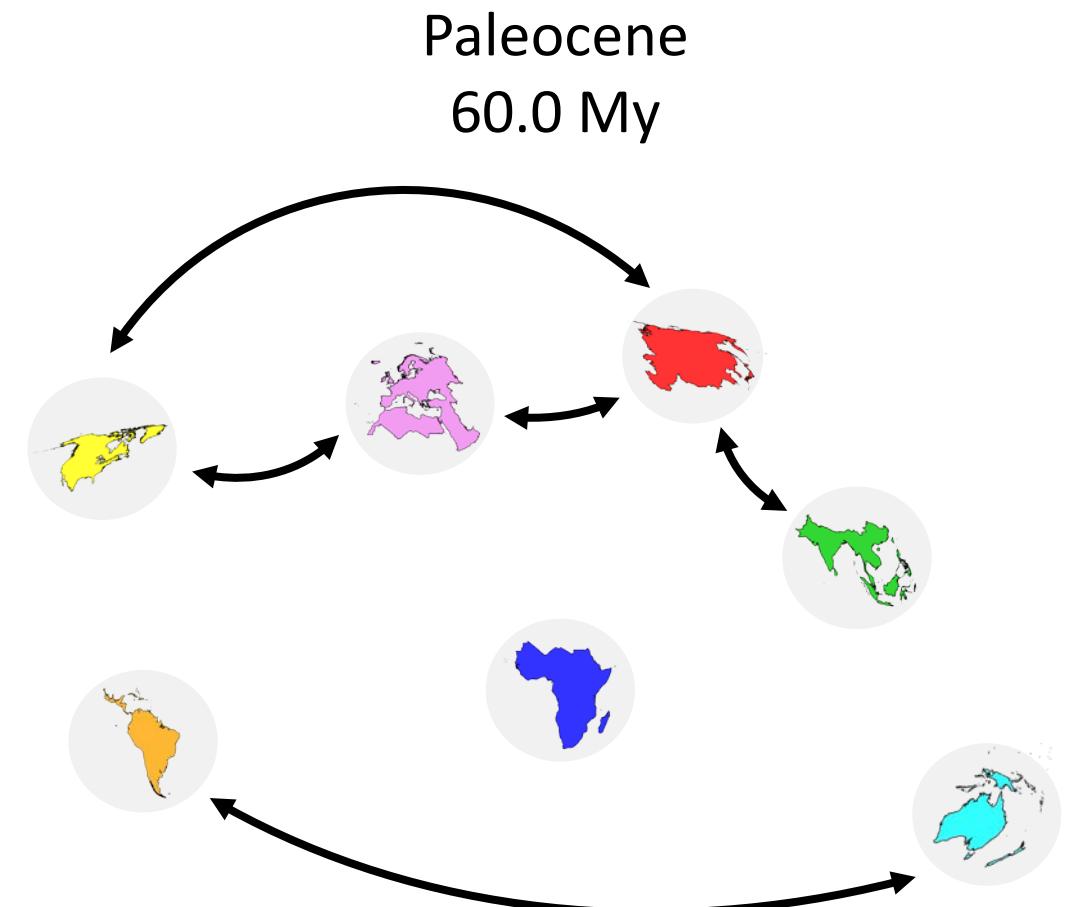
66.0 My



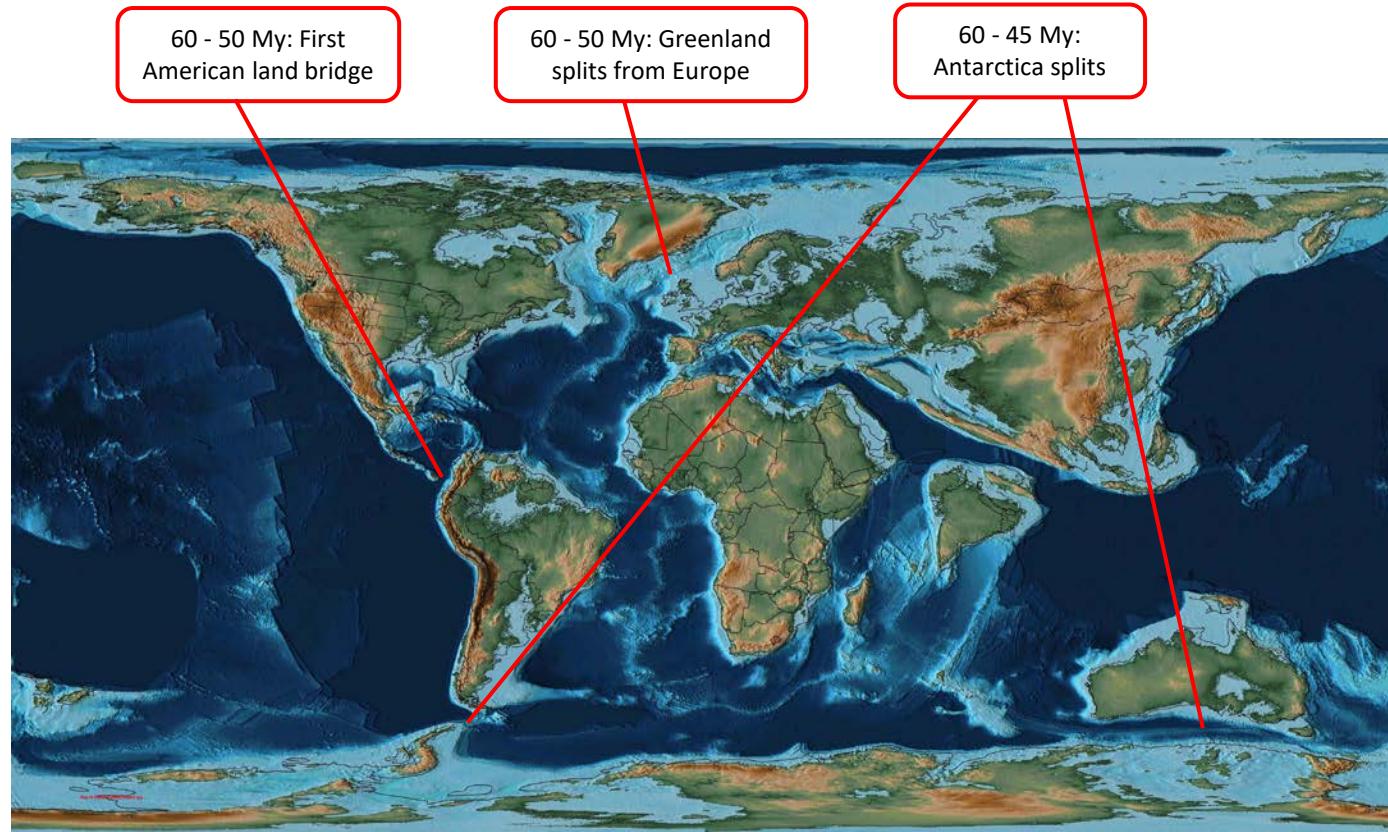
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese



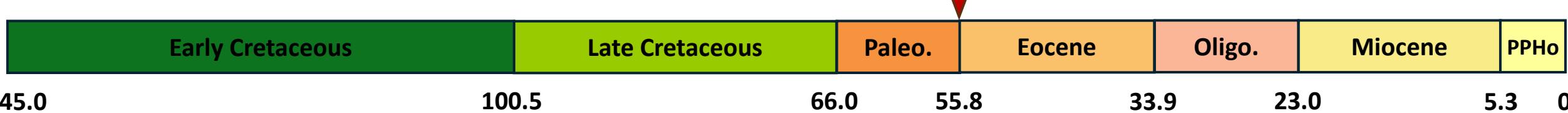
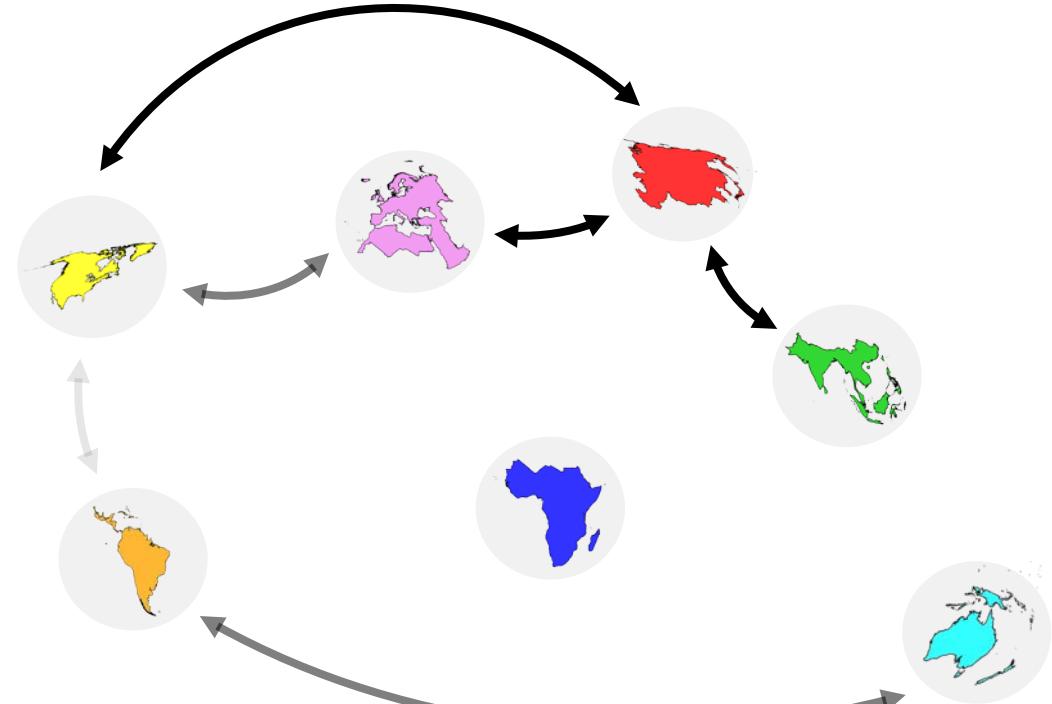
# Biogeographic methods



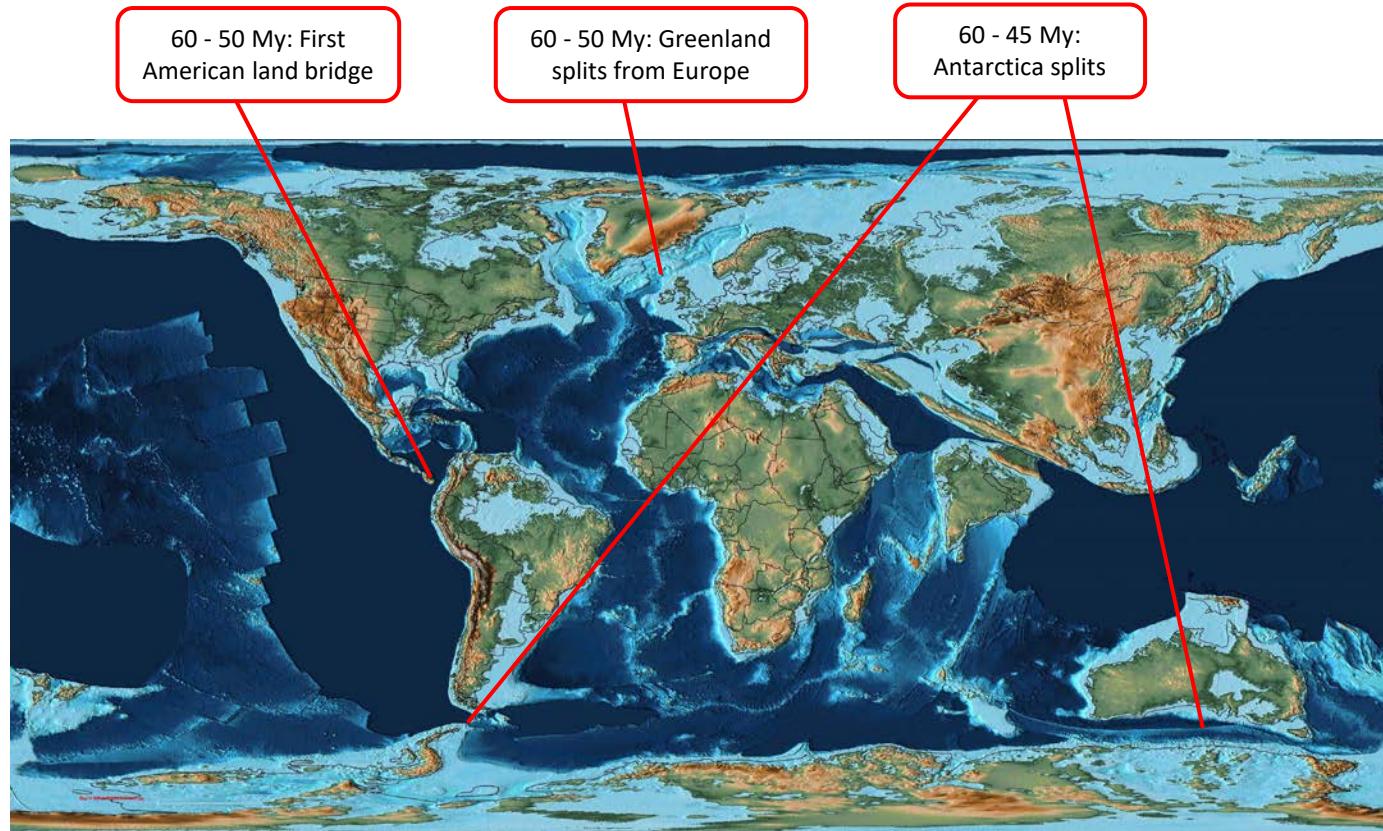
Source: PALEOMAP Project by C. Scotese

Paleocene to Eocene

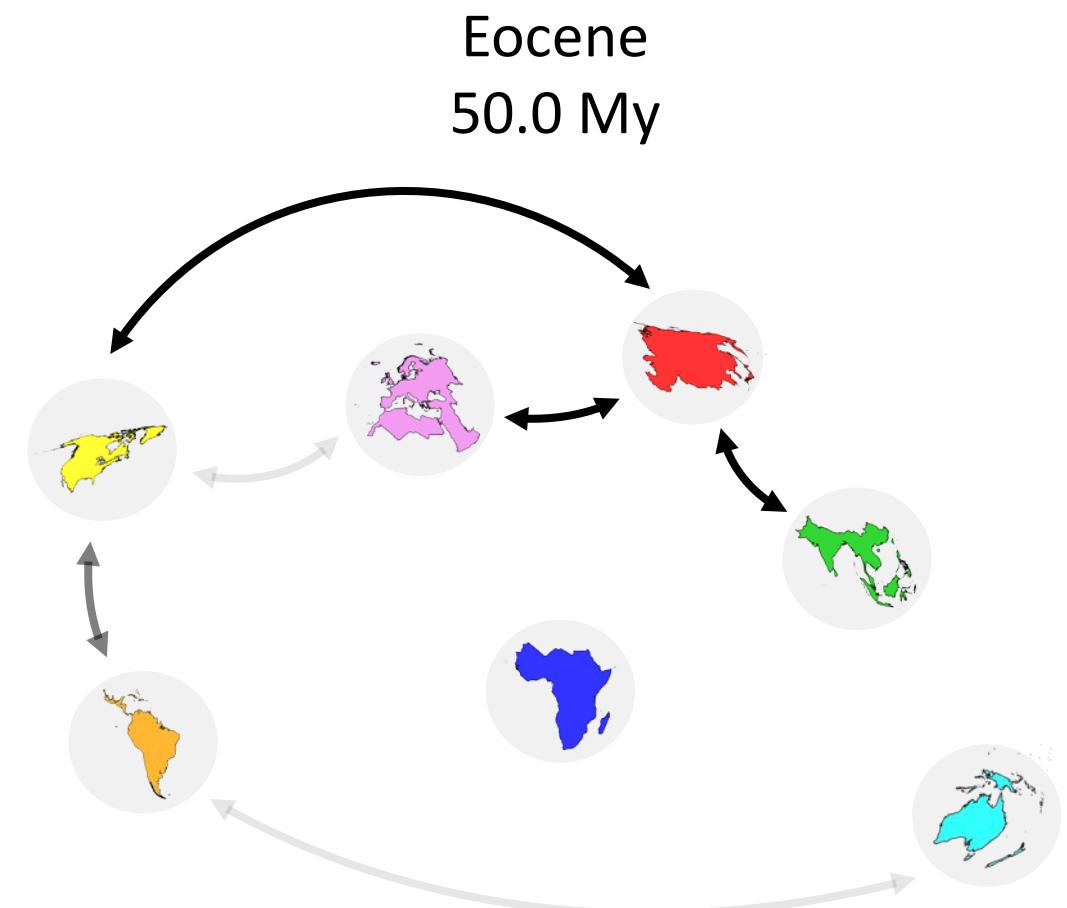
55.8 My



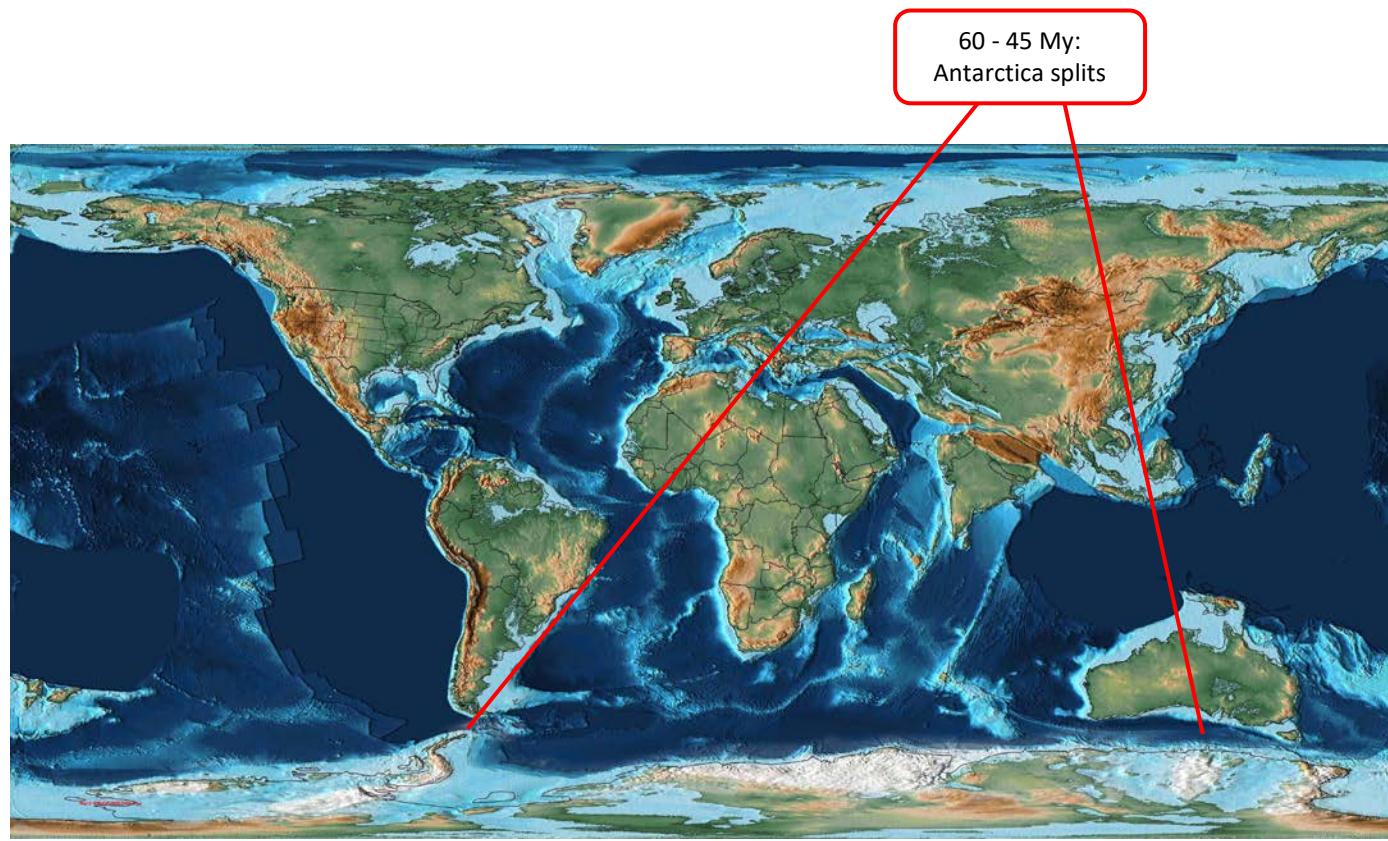
# Biogeographic methods



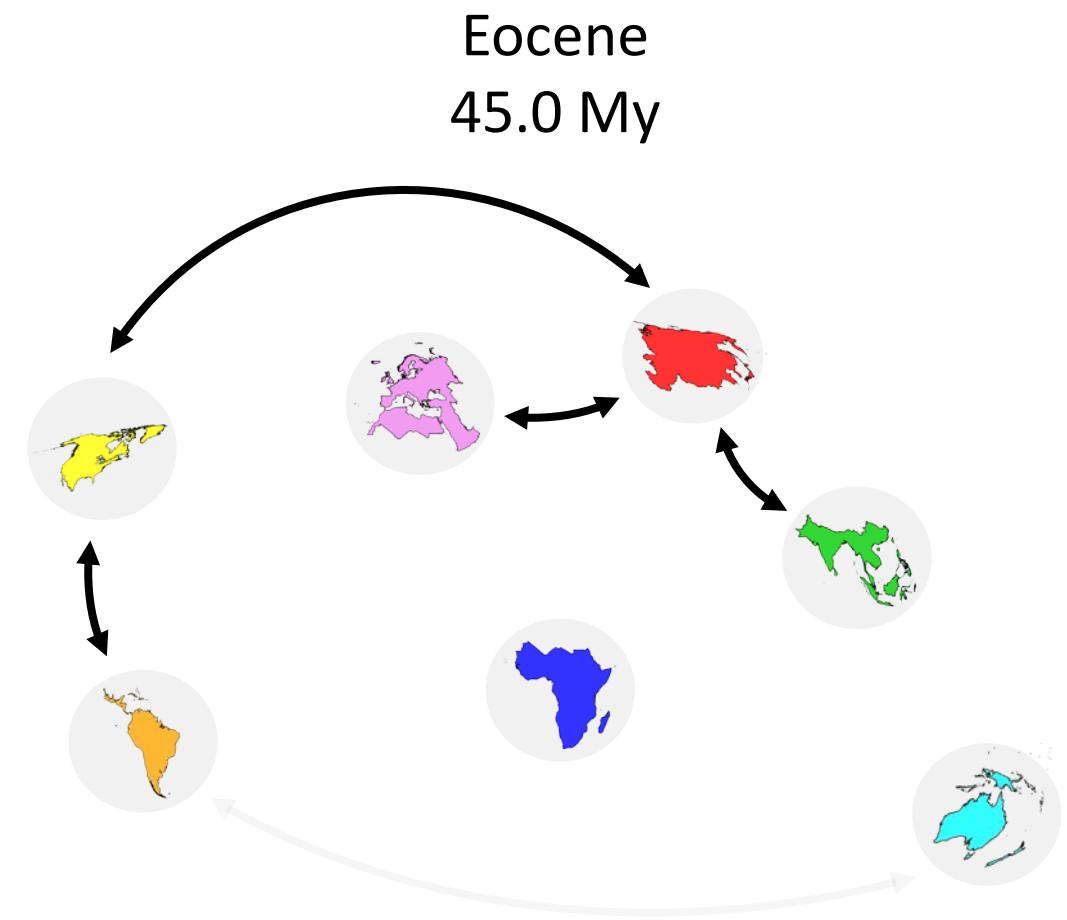
Source: PALEOMAP Project by C. Scotese



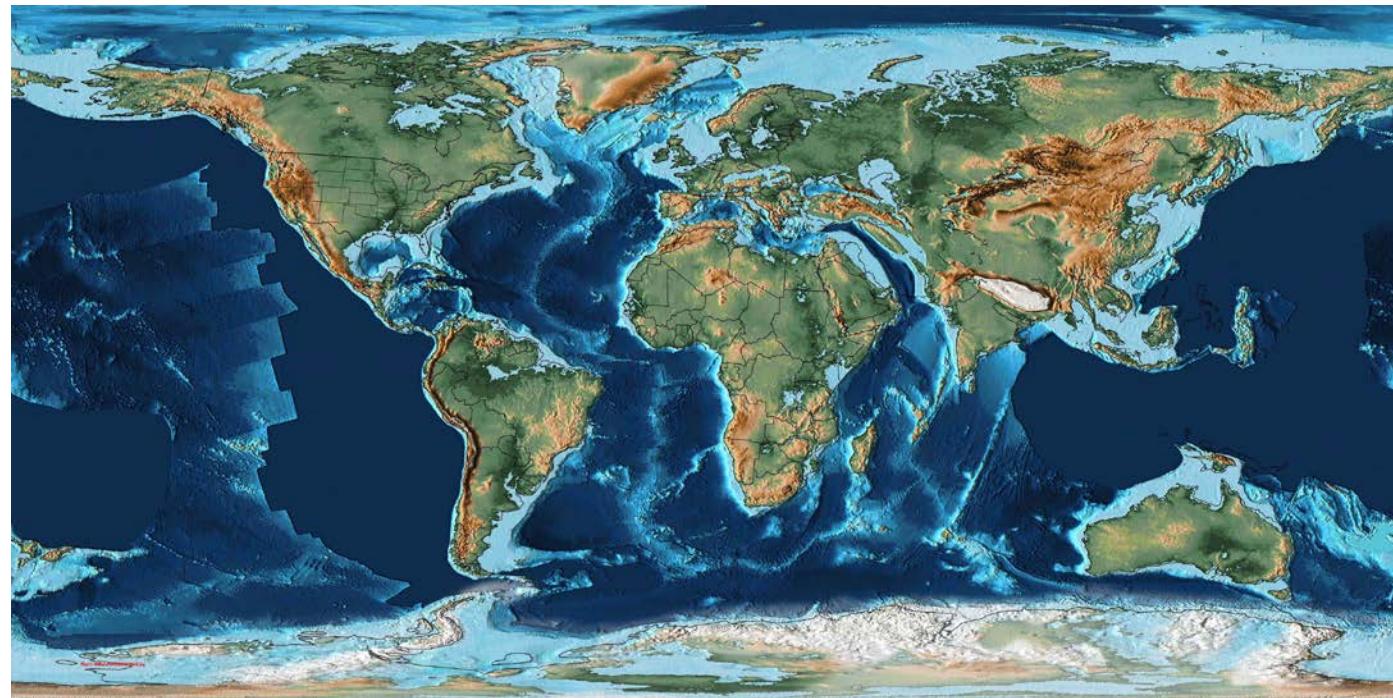
# Biogeographic methods



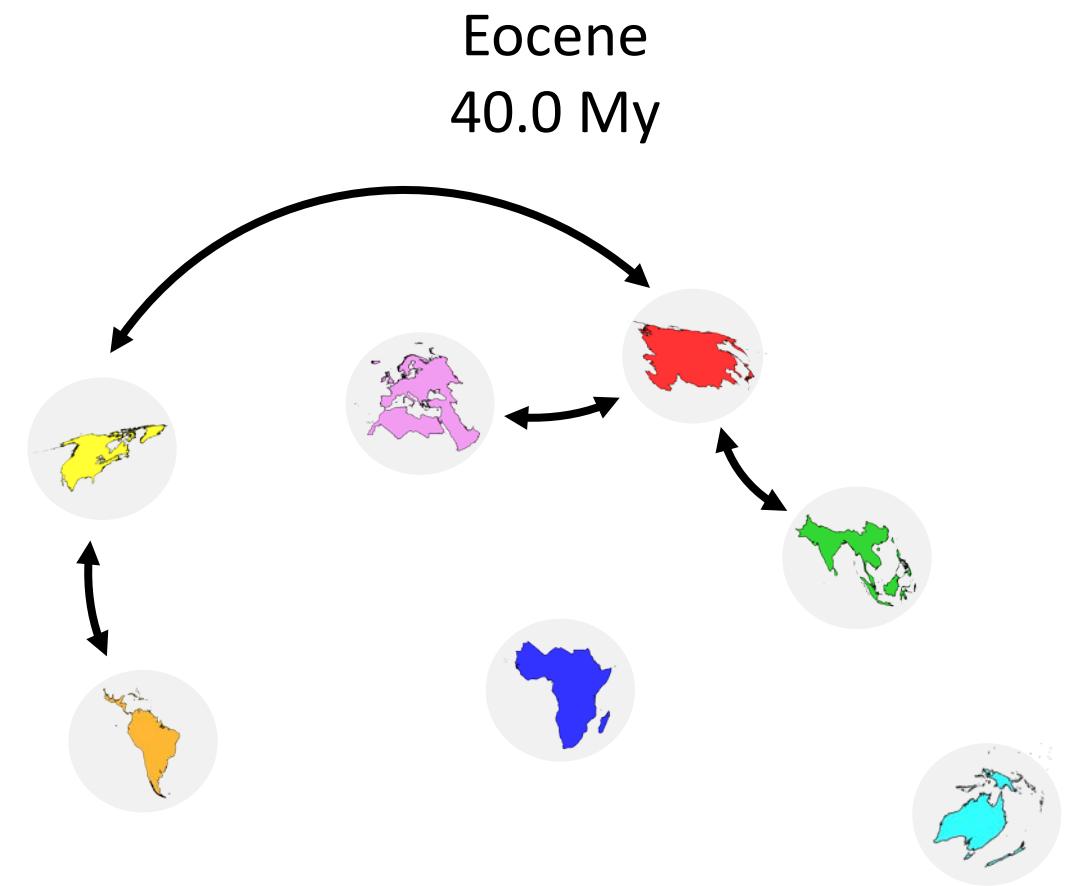
Source: PALEOMAP Project by C. Scotese



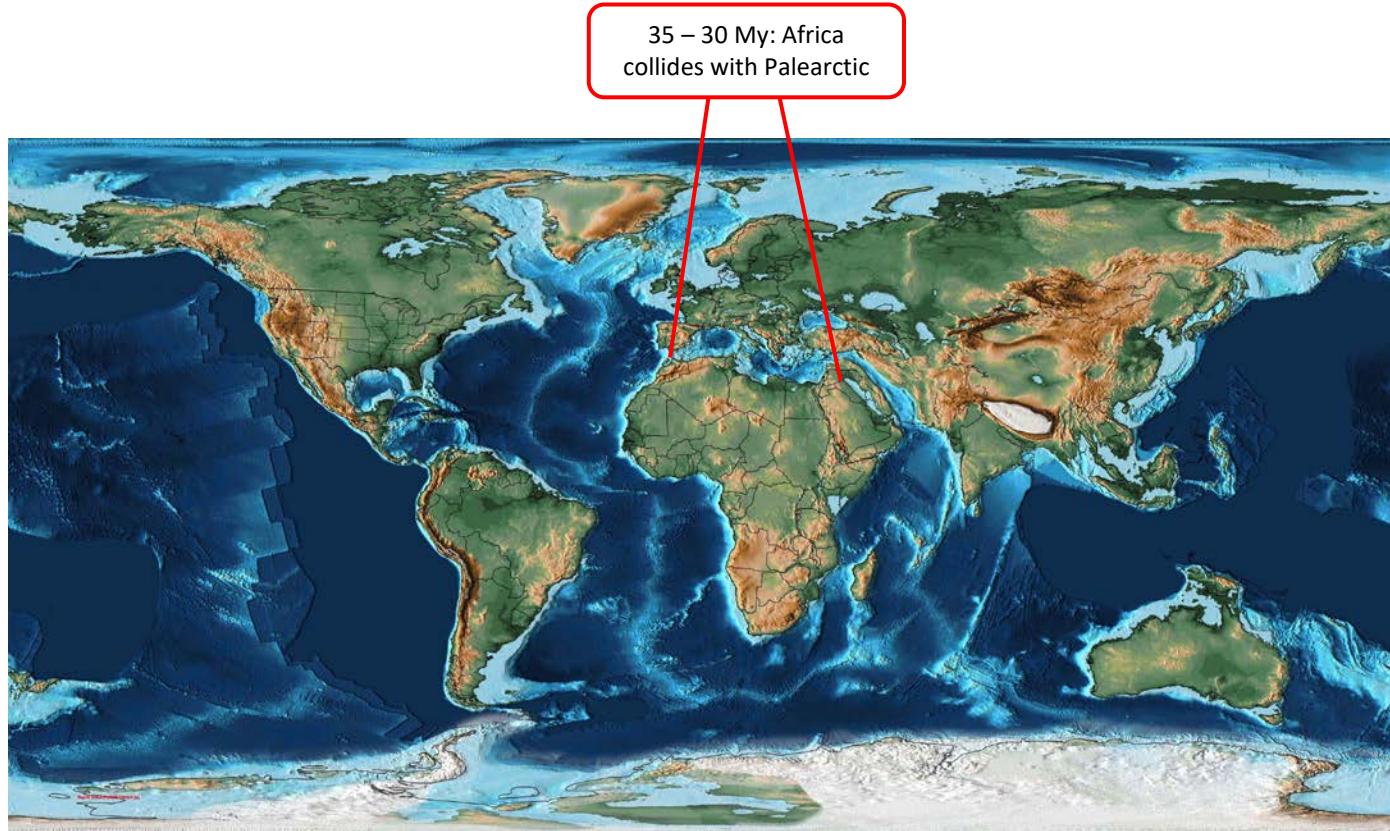
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese



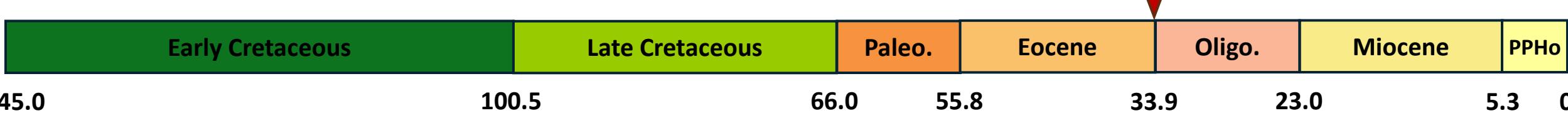
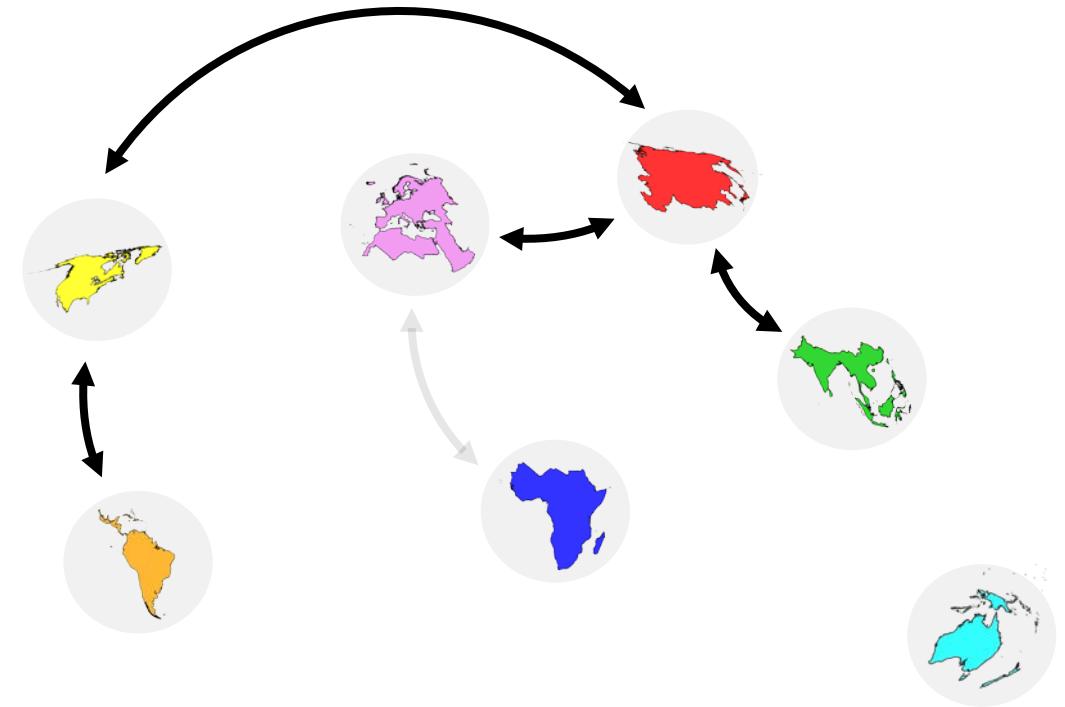
# Biogeographic methods



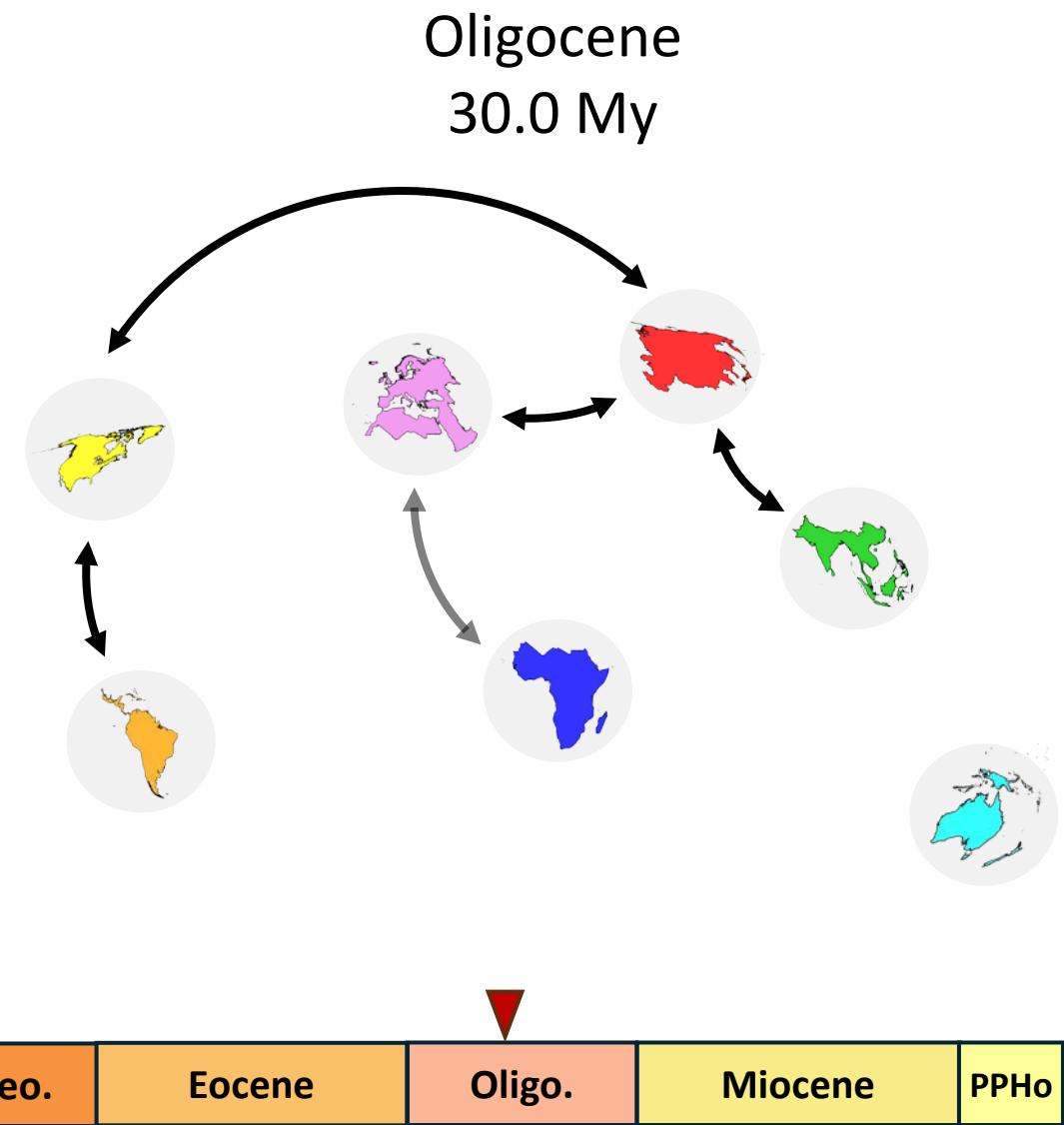
Source: PALEOMAP Project by C. Scotese

Eocene to Oligocene

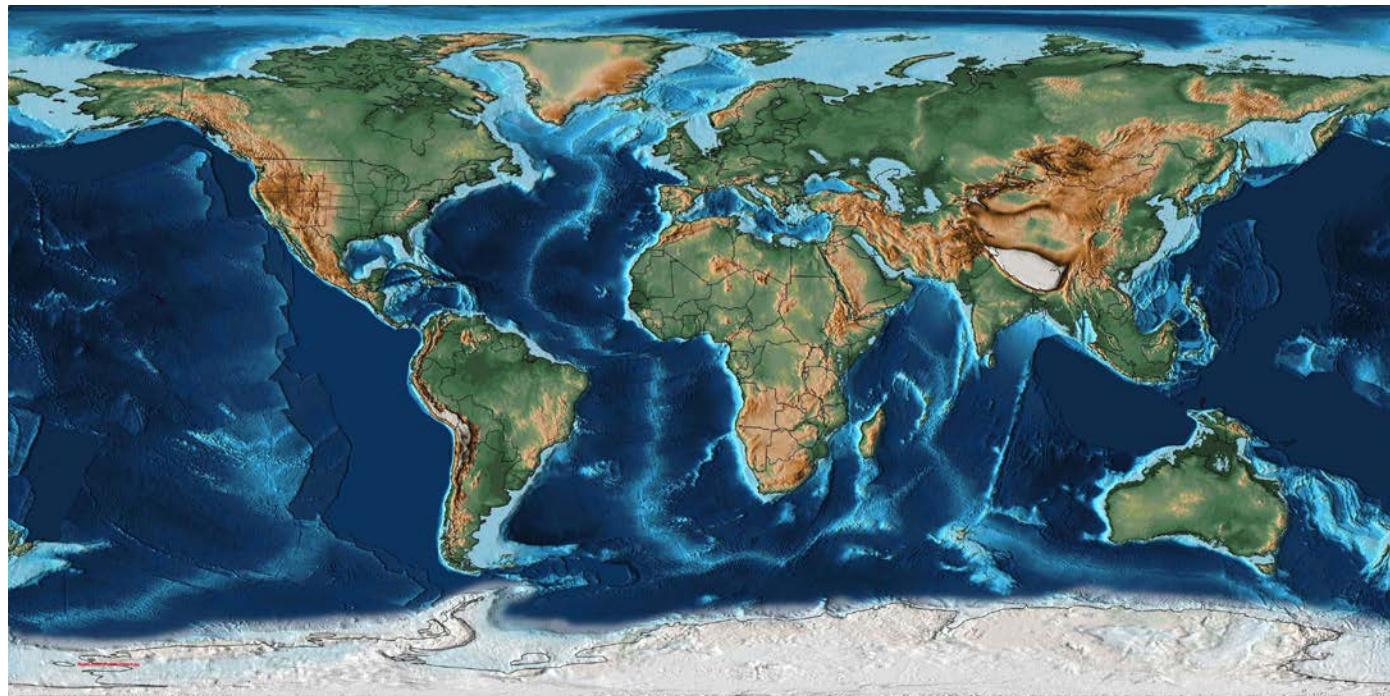
33.9 My



# Biogeographic methods



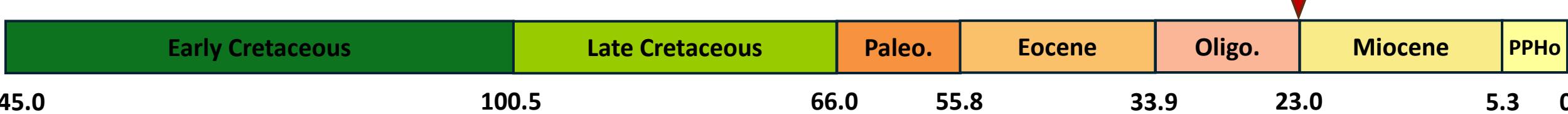
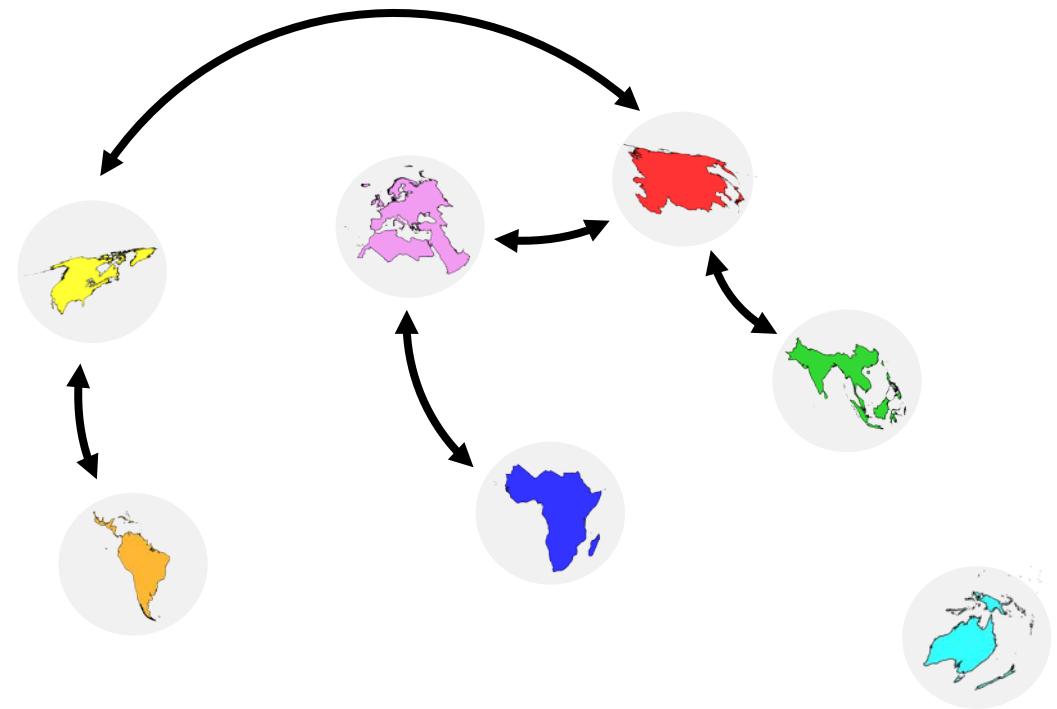
# Biogeographic methods



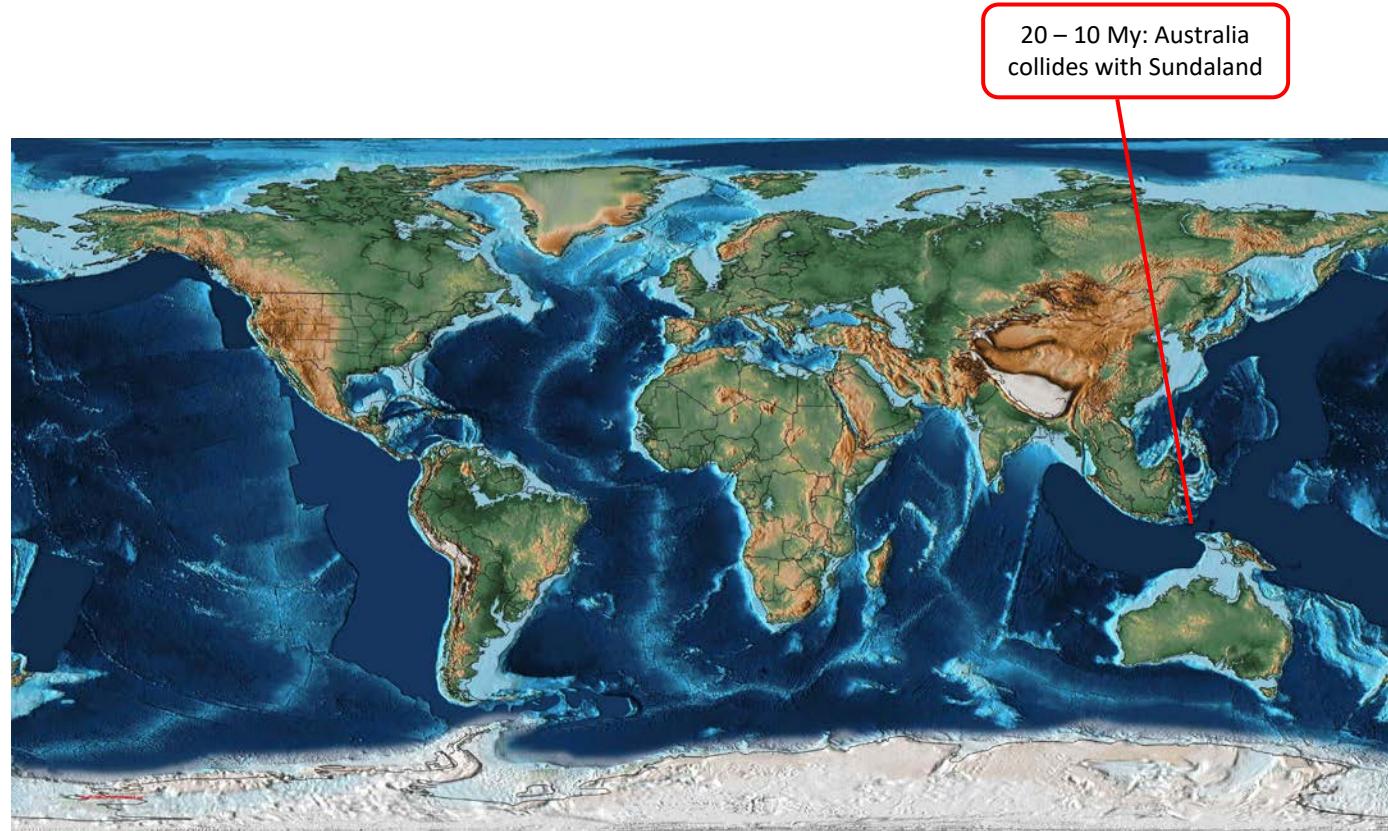
Source: PALEOMAP Project by C. Scotese

Oligocene to Miocene

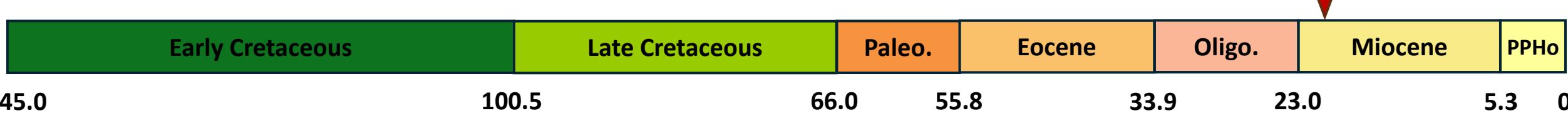
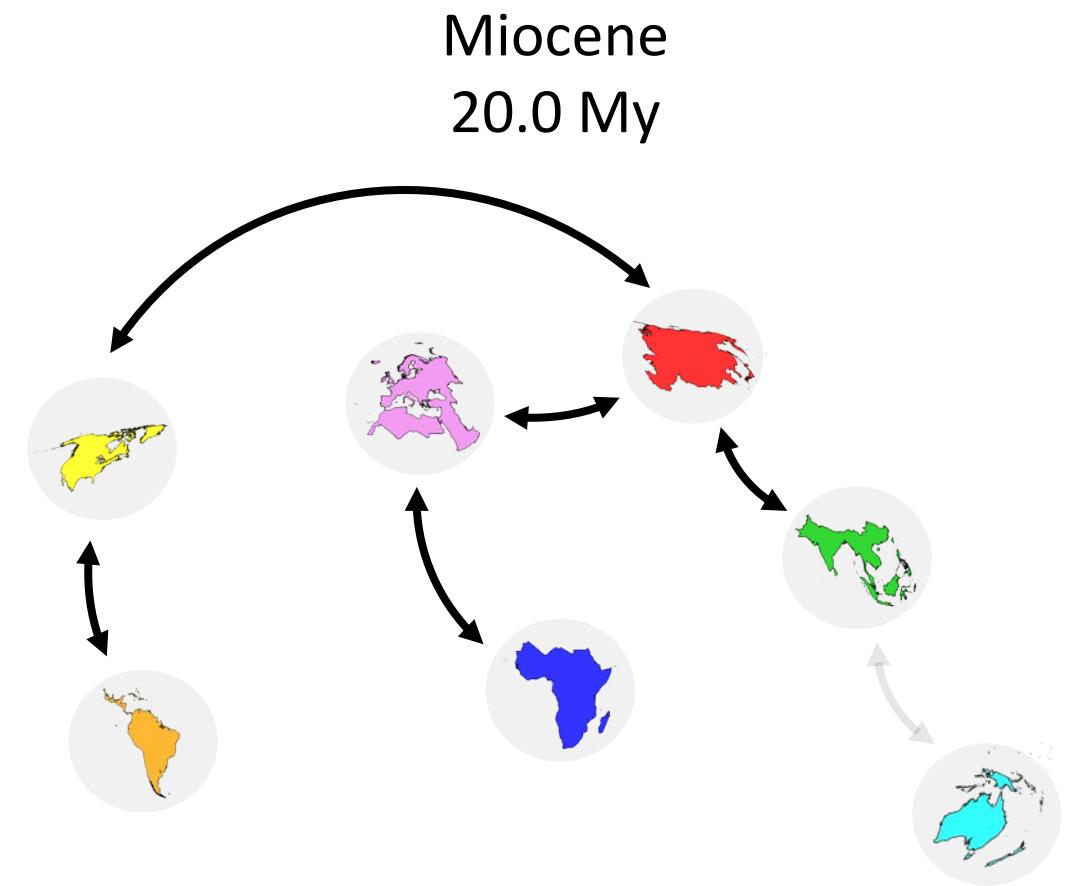
23.0 My



# Biogeographic methods



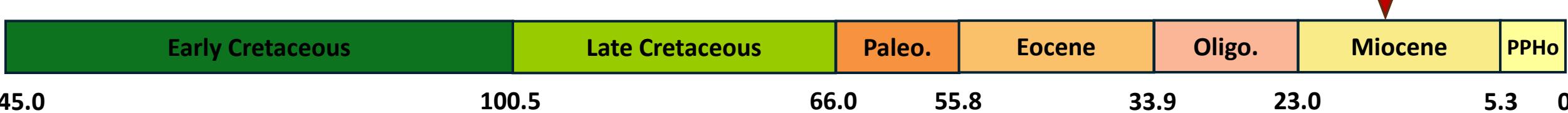
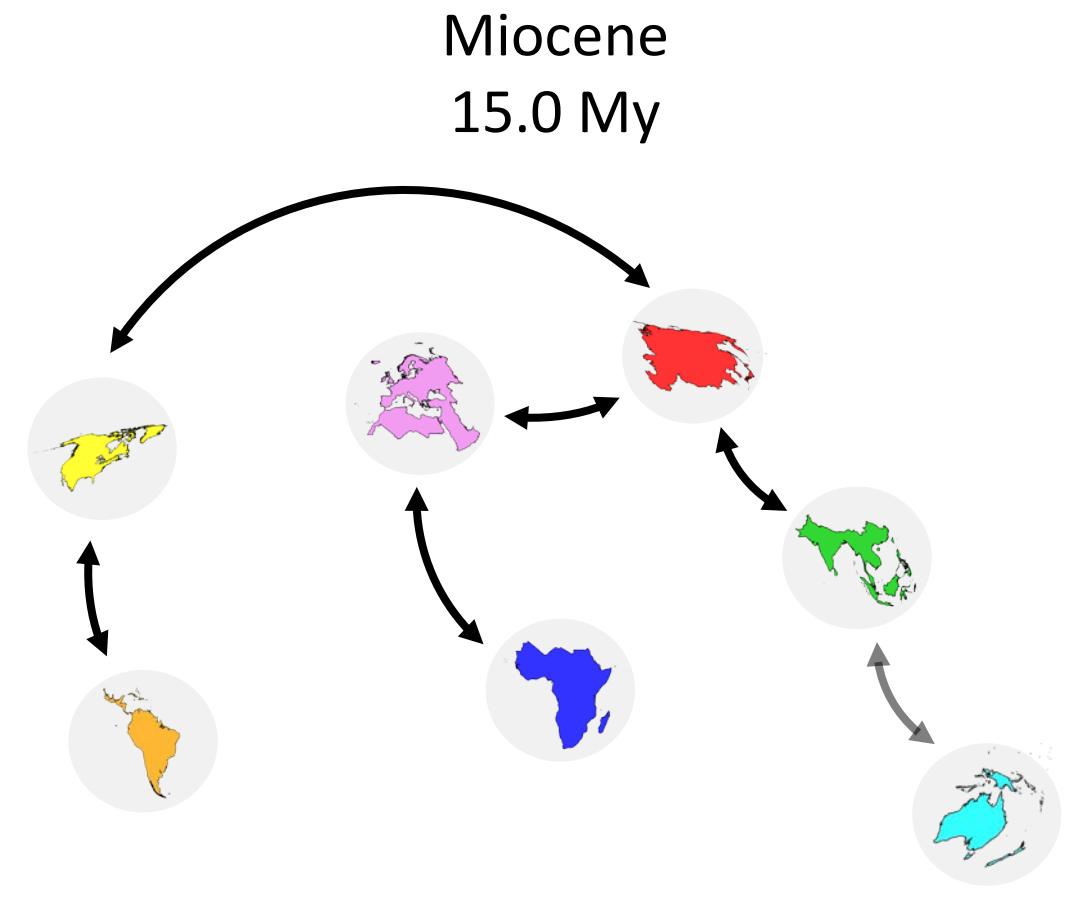
Source: PALEOMAP Project by C. Scotese



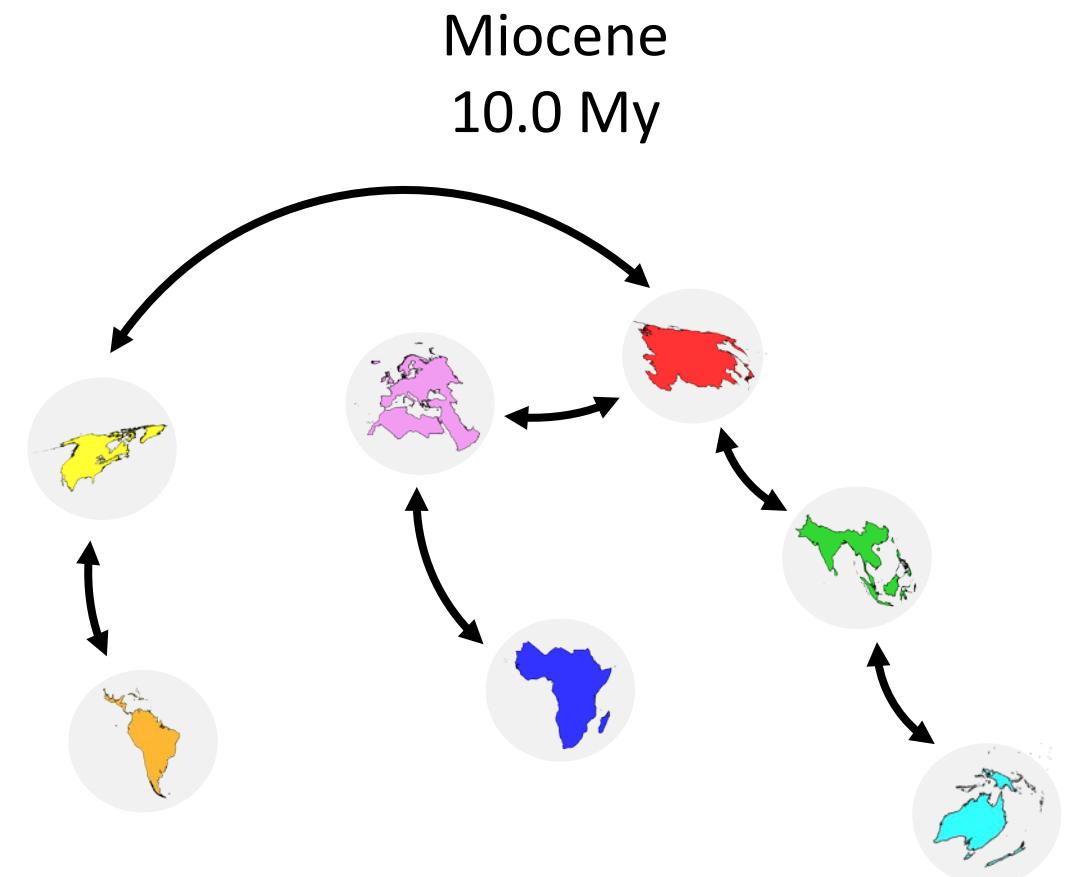
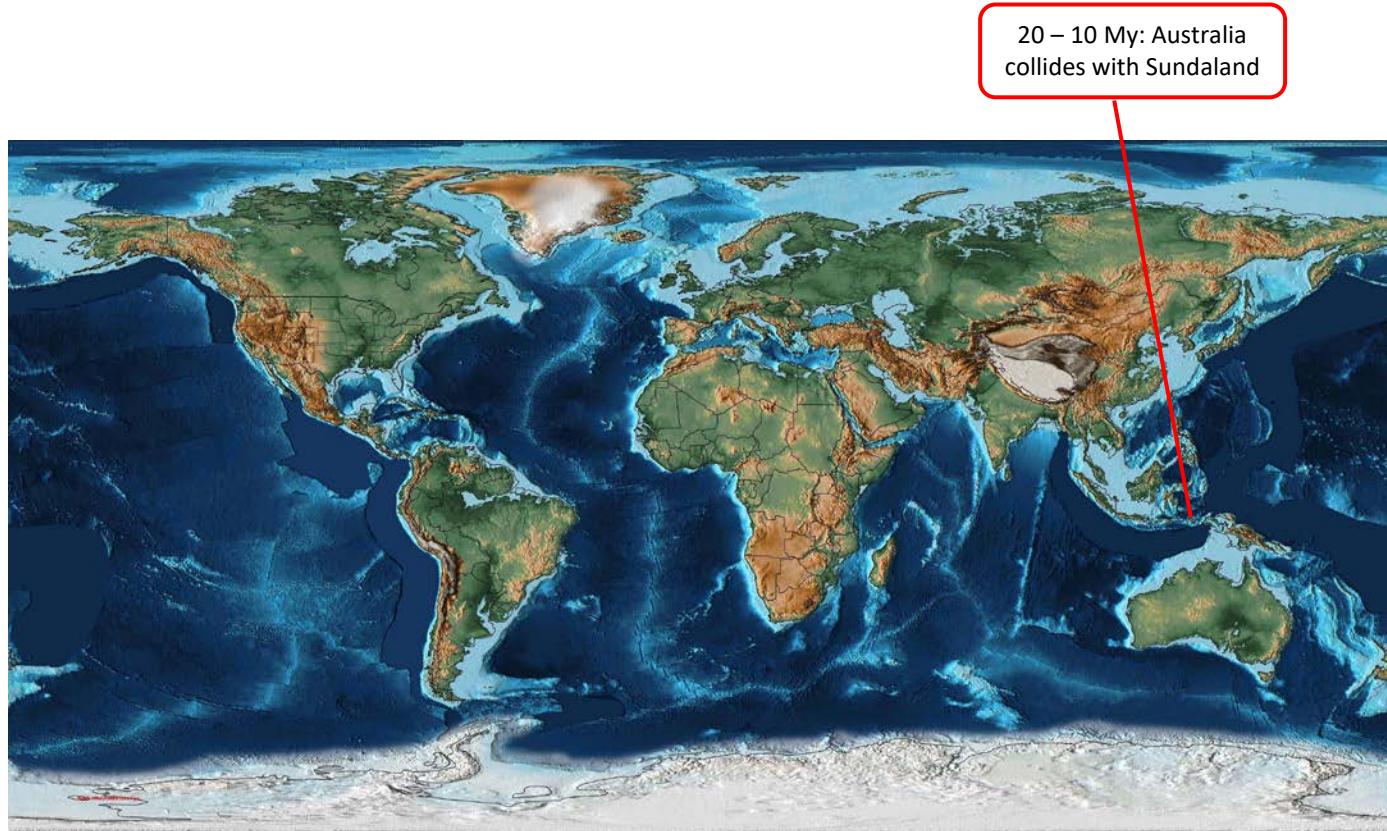
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese



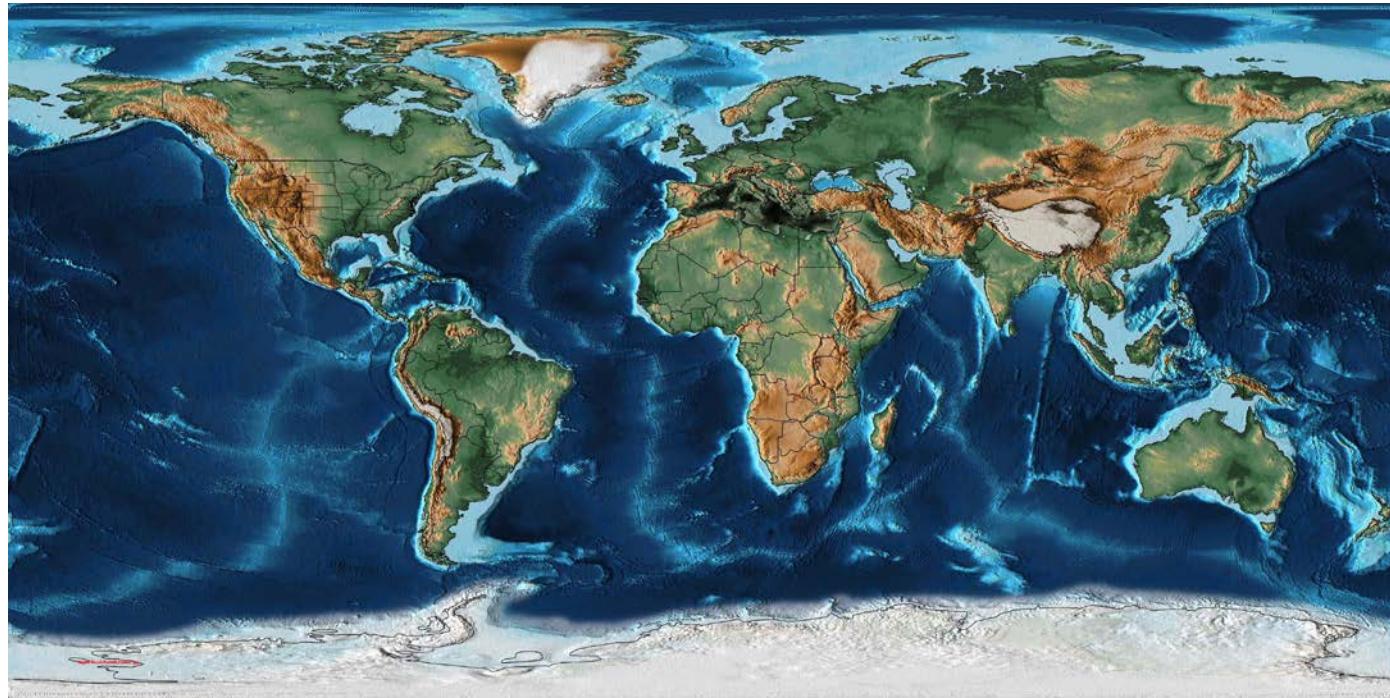
# Biogeographic methods



Source: PALEOMAP Project by C. Scotese

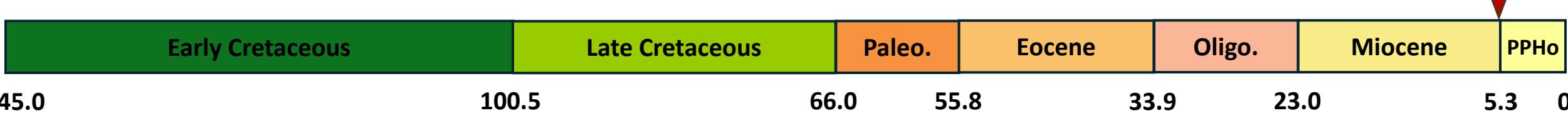
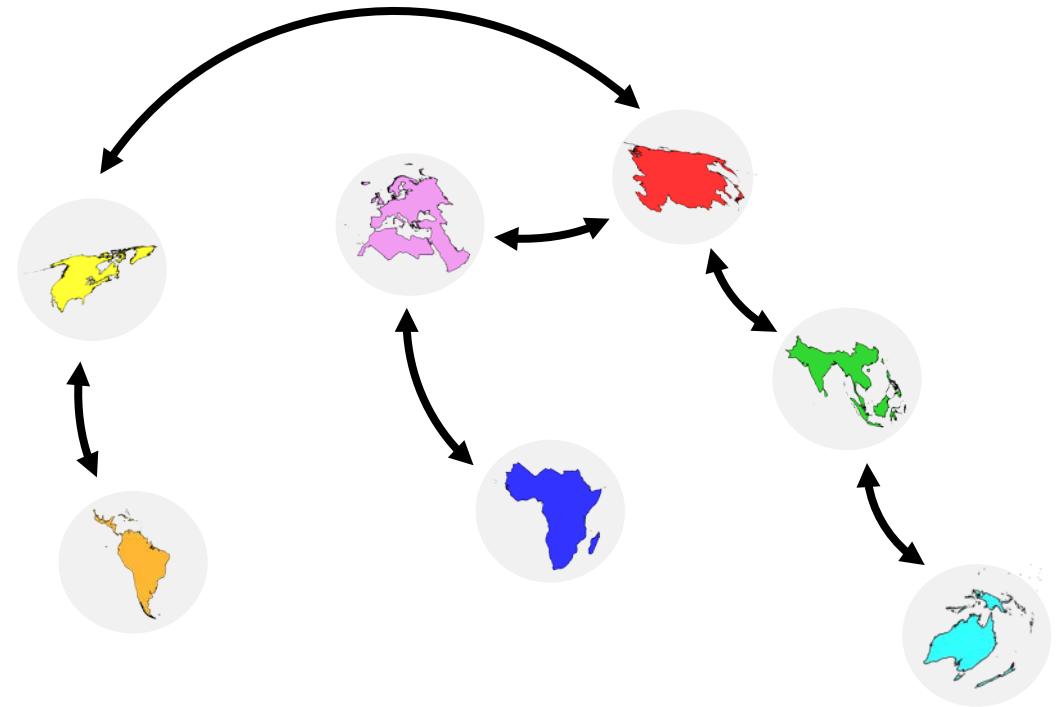


# Biogeographic methods

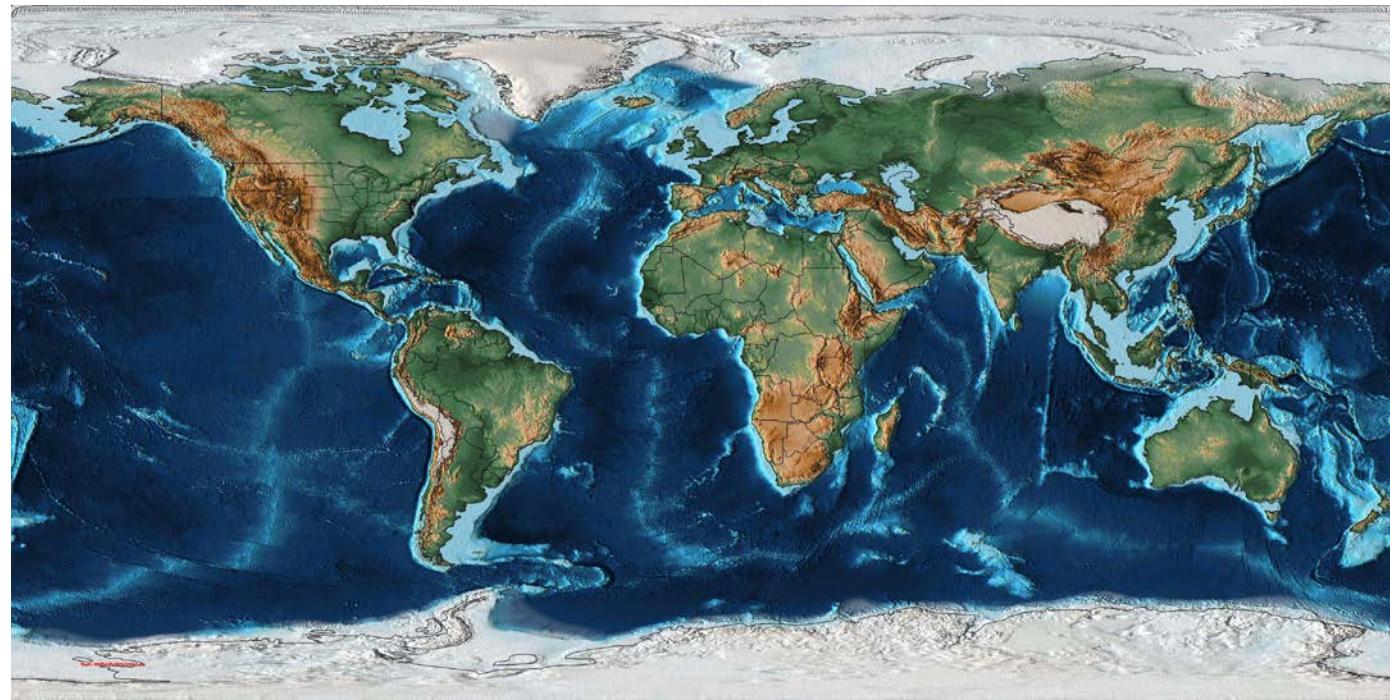


Source: PALEOMAP Project by C. Scotese

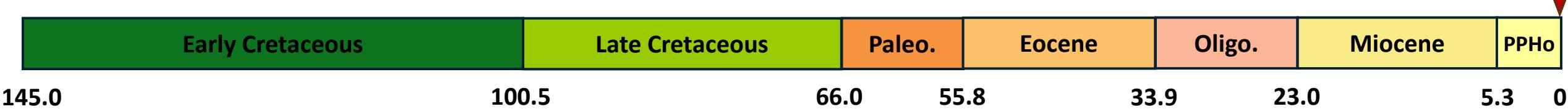
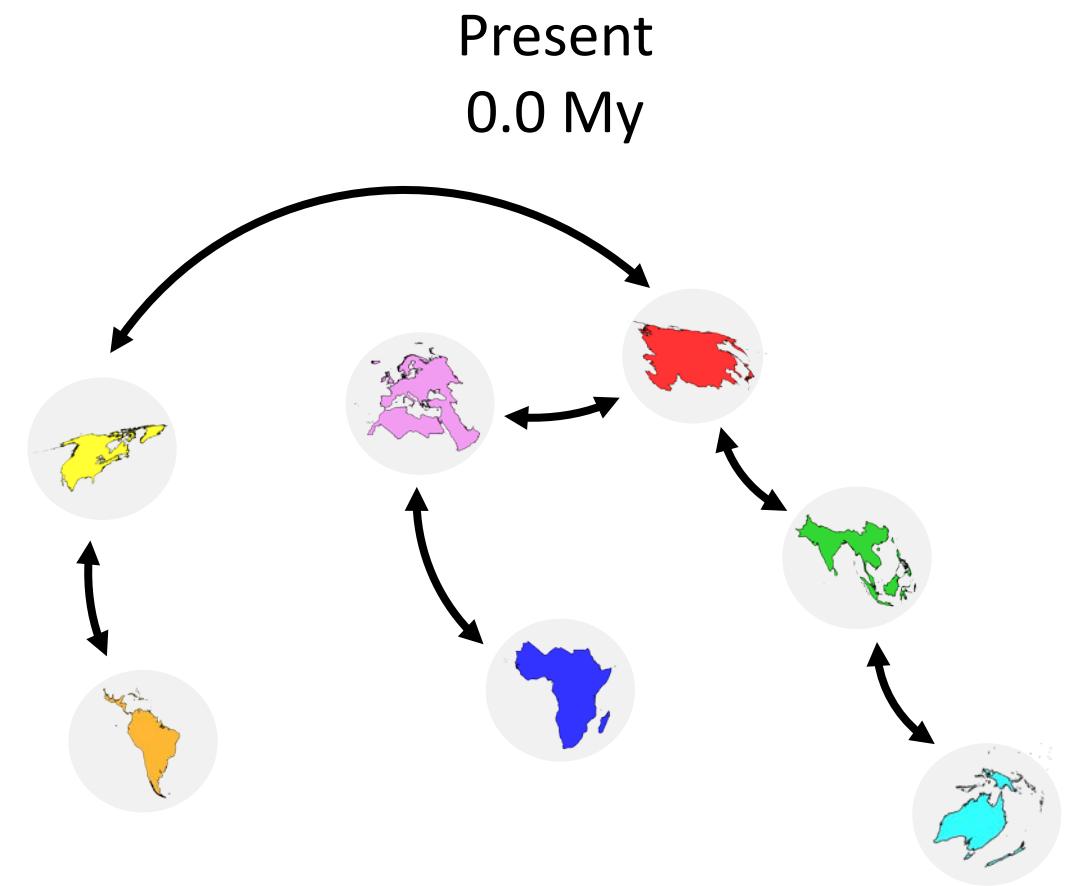
Miocene to Plio-Pleisto-Holocene  
5.3 My



# Biogeographic methods



Source: PALEOMAP Project by C. Scotese



# Biogeographic methods



## BioGeoBEARS framework:

- DIVALIKE, DEC, DIVALIKE + J, DEC + J
- Model selection based on AICc
- Best model = **Time-stratified DEC + J**

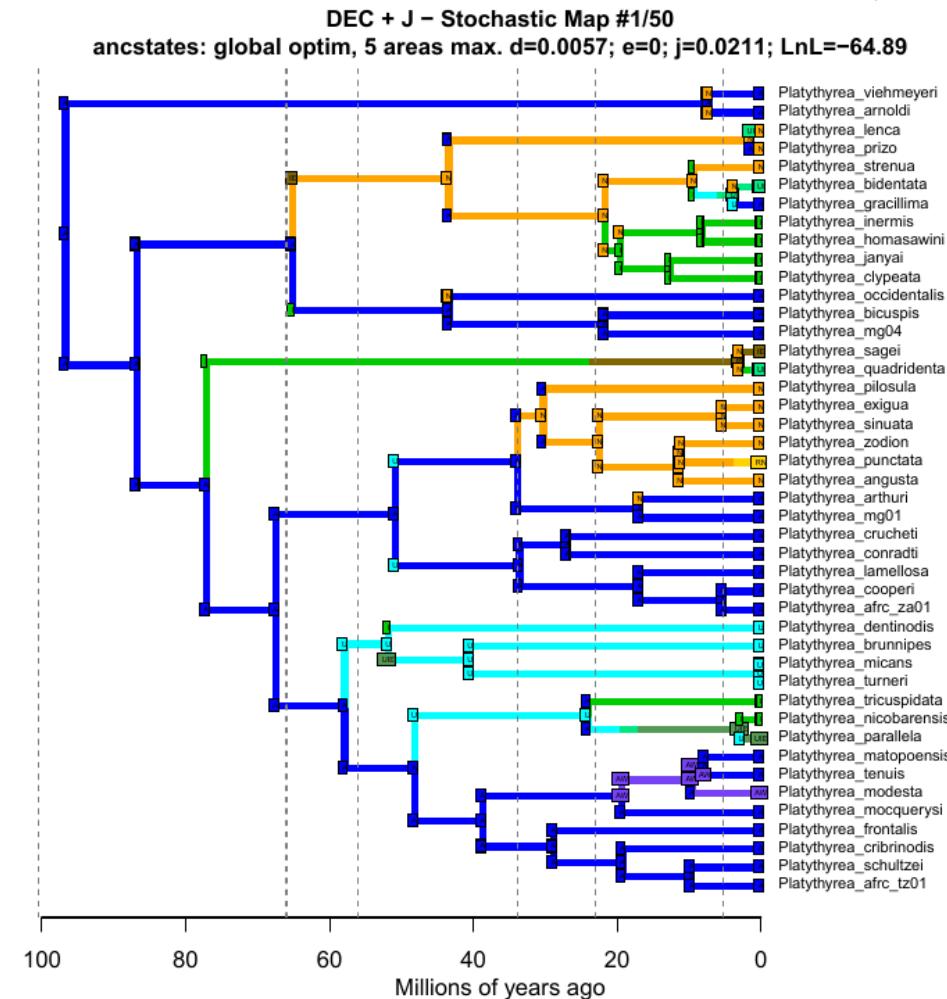
## Model of continental connectivity

## Ancestral Range Estimates (ARE):

- Marginal likelihoods of node ranges

## Biogeographic Stochastic Mapping (BSM):

- Simulation of **biogeographic histories** compatible with ancestral ranges estimates
- Summary statistics across 1000 BSM



# Origins of clades

Overall picture:

- Some important **regional radiations**
- Many **independent colonizations**

Origins of S&S clades:

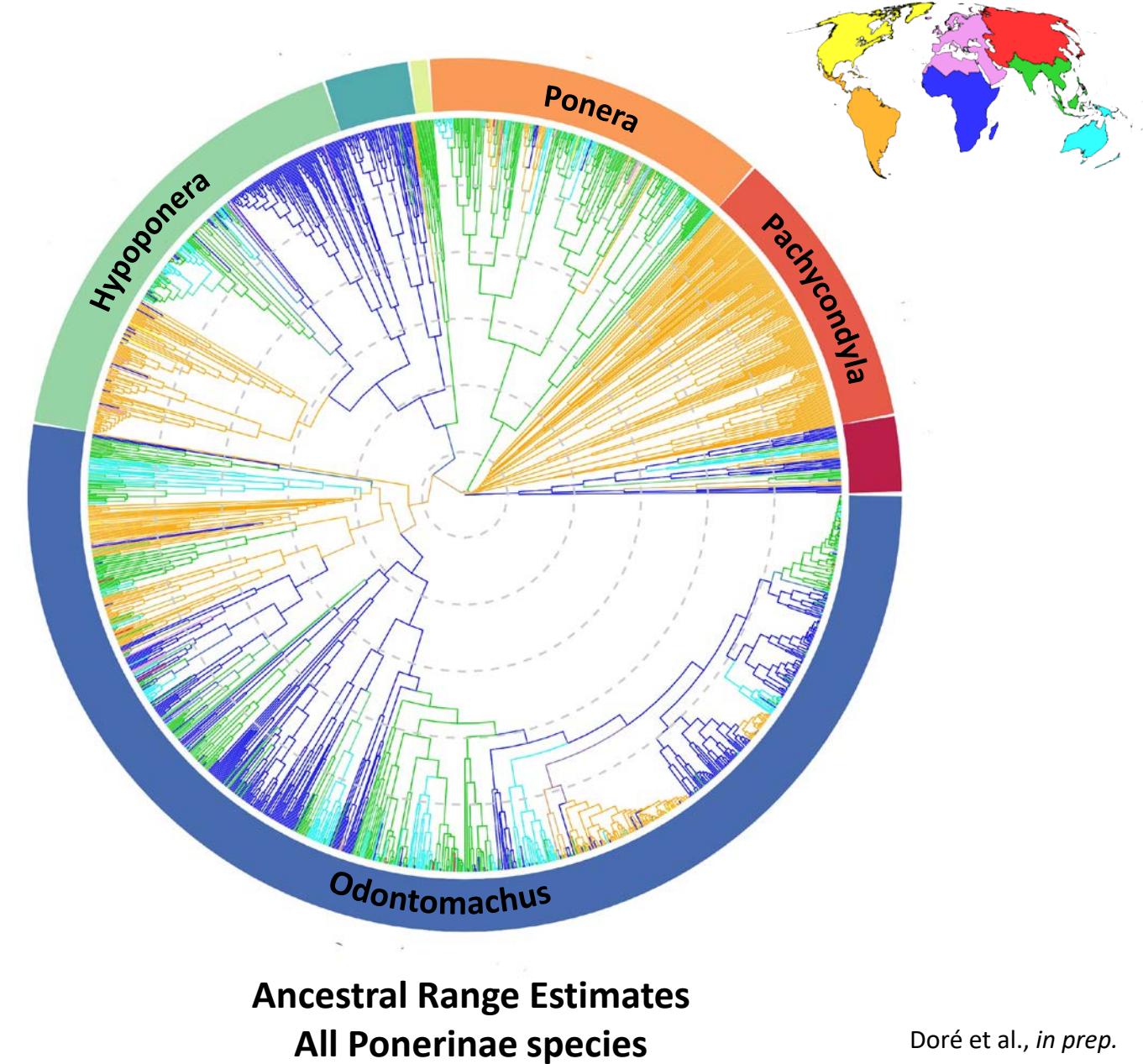
- **Afrotropics:** Platytherea, Plectroctena, Hypoponera
- **Neotropics:** Pachycondyla, Odontomachus
- **IndoMalaya:** Ponera, Harpegnathos

Origin of Ponerinae:

Afrotropics + Neotropics [ + Indo(Malaya) ]

=

Gondwana



Doré et al., *in prep.*

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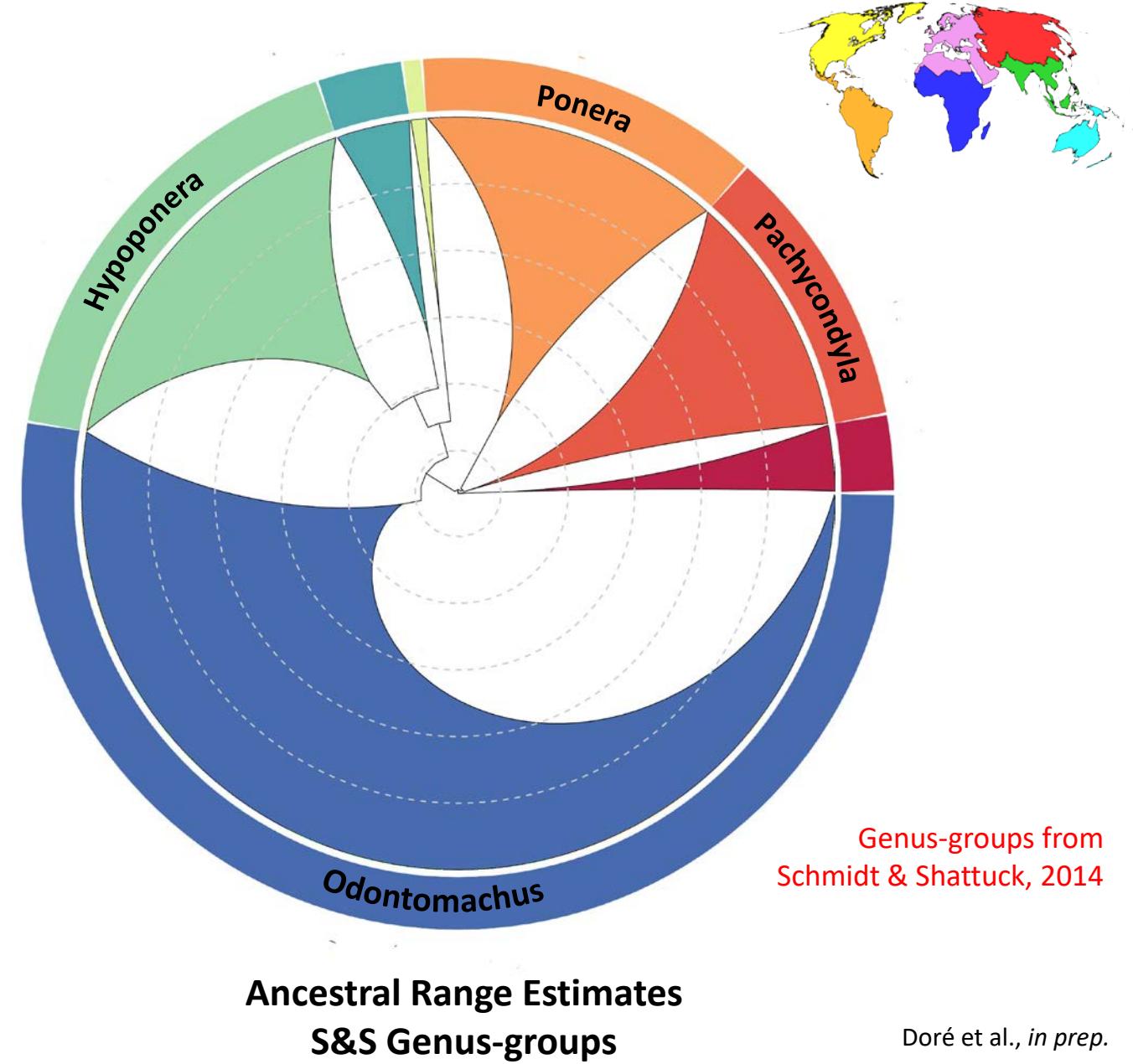
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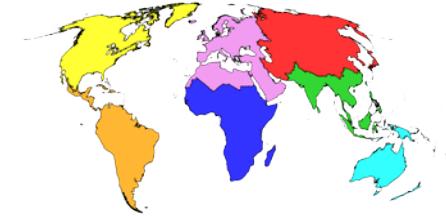
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=

Gondwana



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Origins of S&S clades:

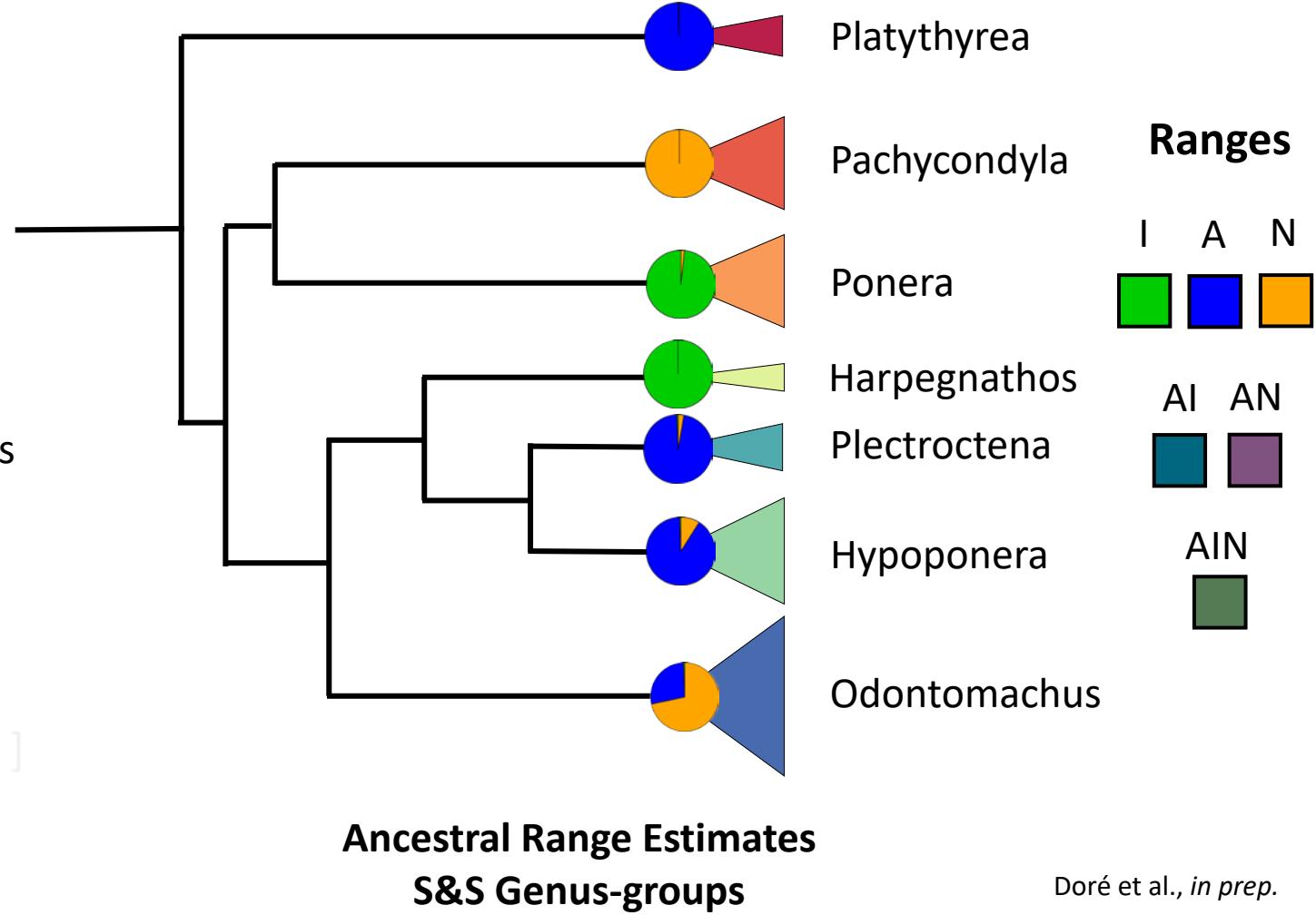
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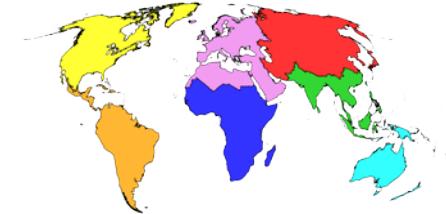
=

Gondwana



Doré et al., *in prep.*

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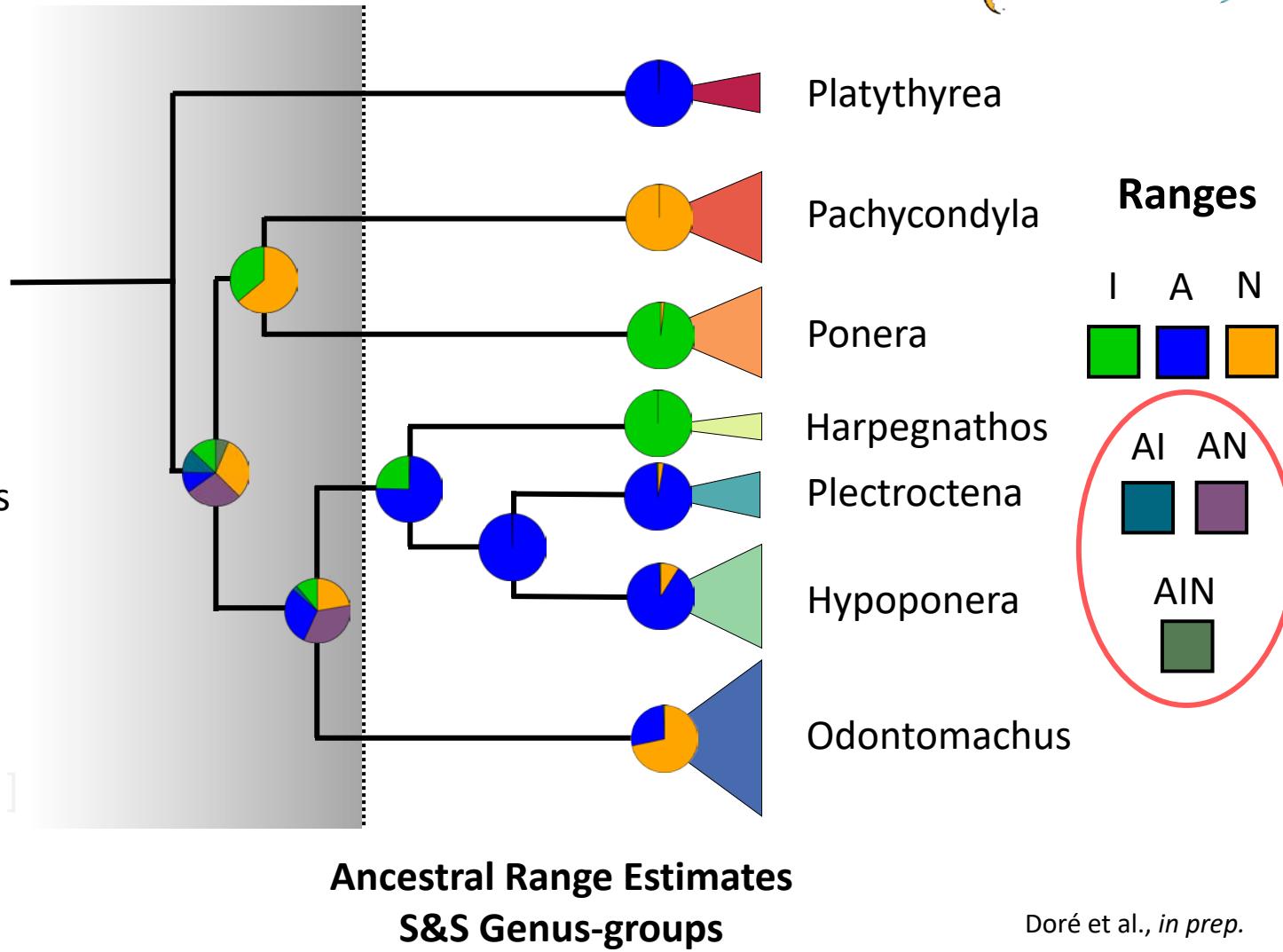
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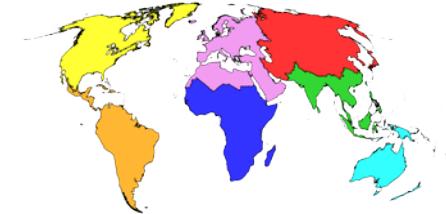
Afrotropics + Neotropics [ + Indo(Malaya) ]

=  
Gondwana

Gondwana split



# Origins of clades



Overall picture:

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- **Afrotropics**: Platythyrea, Plectroctena, Hypoponera
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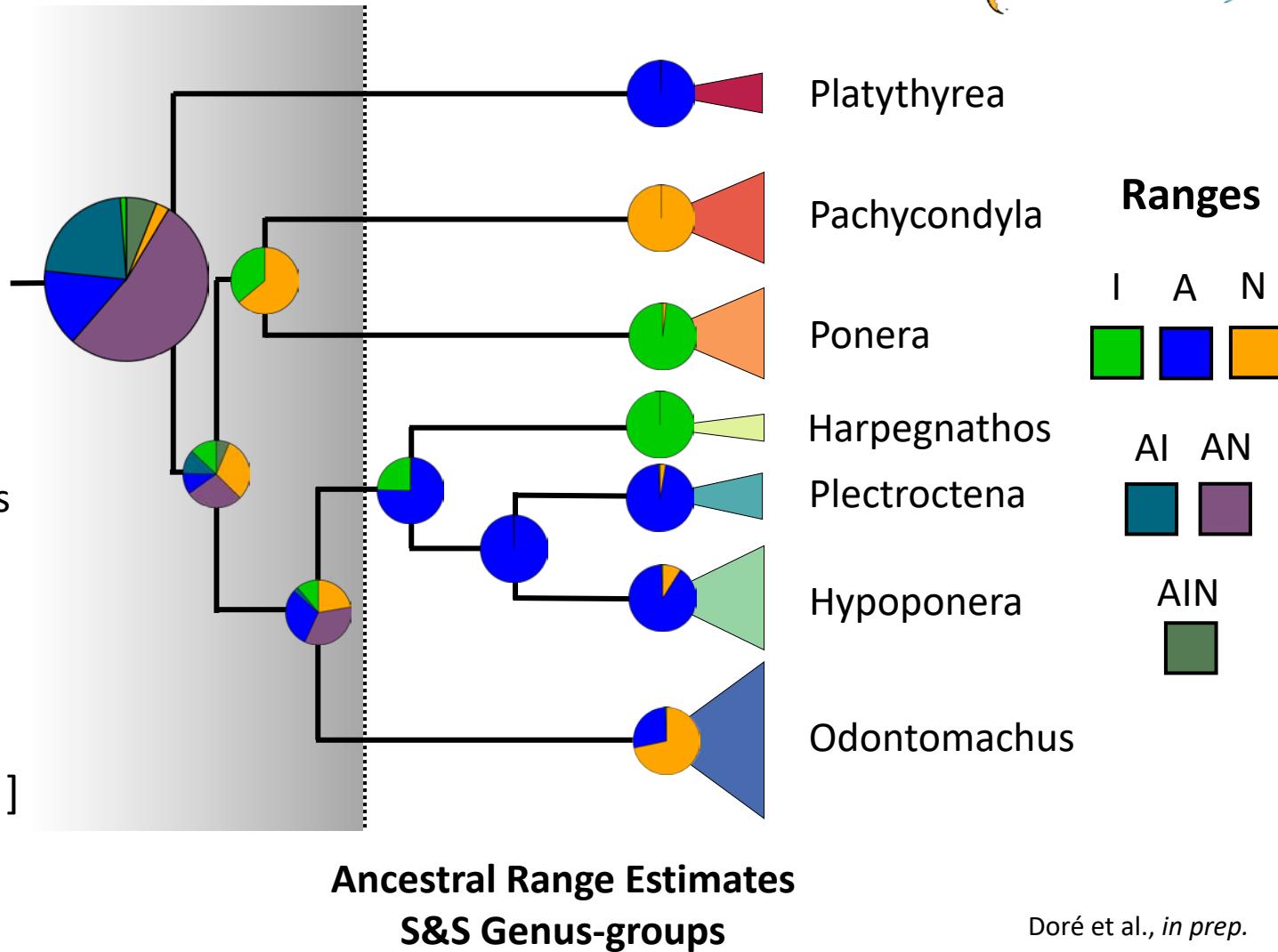
Origin of Ponerinae:

**Afrotropics + Neotropics [ + Indo(Malaya) ]**

=

**Gondwana**

Gondwana split

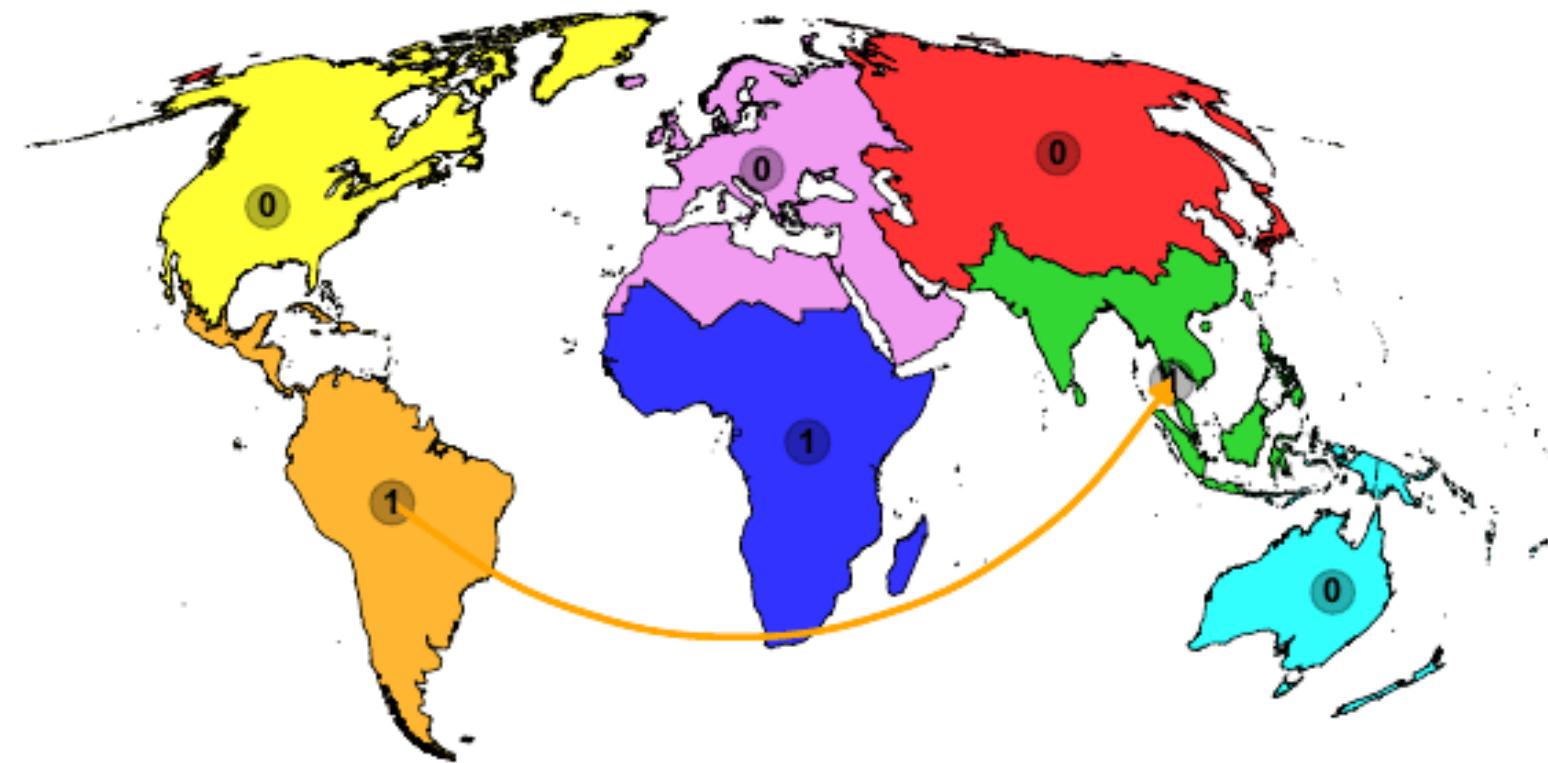


Doré et al., *in prep.*

# Dispersal events in time



## Dispersal events between bioregions 113–108 My



### Bioregions

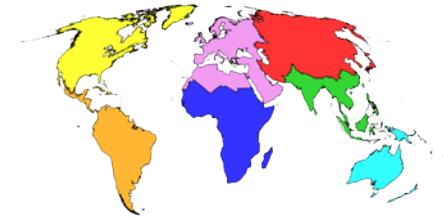
Blue	Afrotropics
Cyan	Australasia
Green	Indomalaya
Yellow	Nearctic
Orange	Neotropics
Red	Eastern Palearctic
Pink	Western Palearctic

### Dispersal events

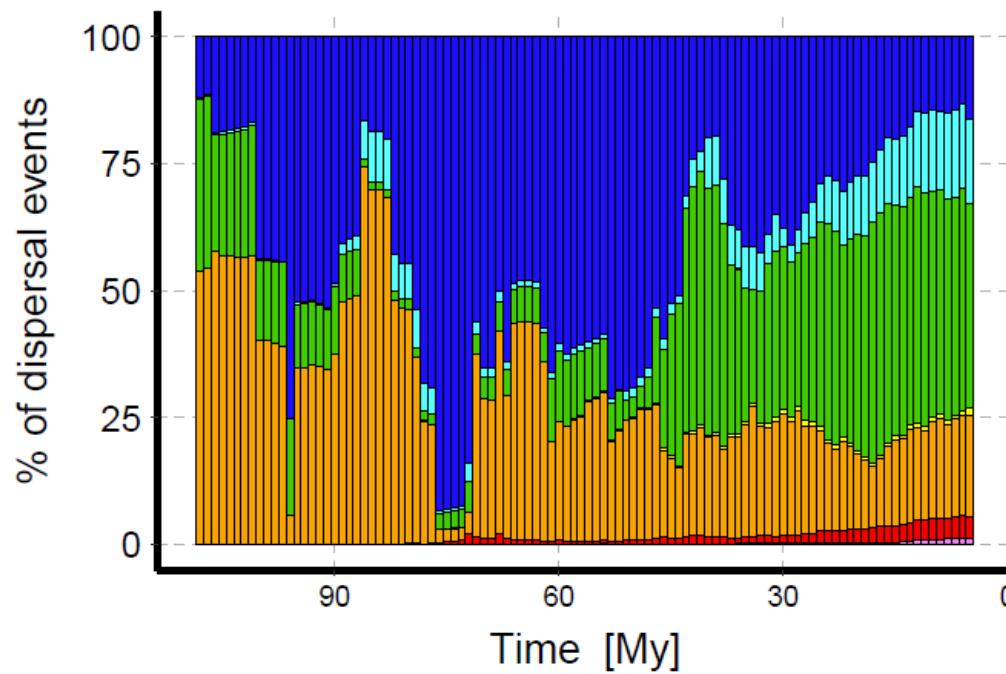
- 1
- 15
- 40

Doré et al., *in prep.*

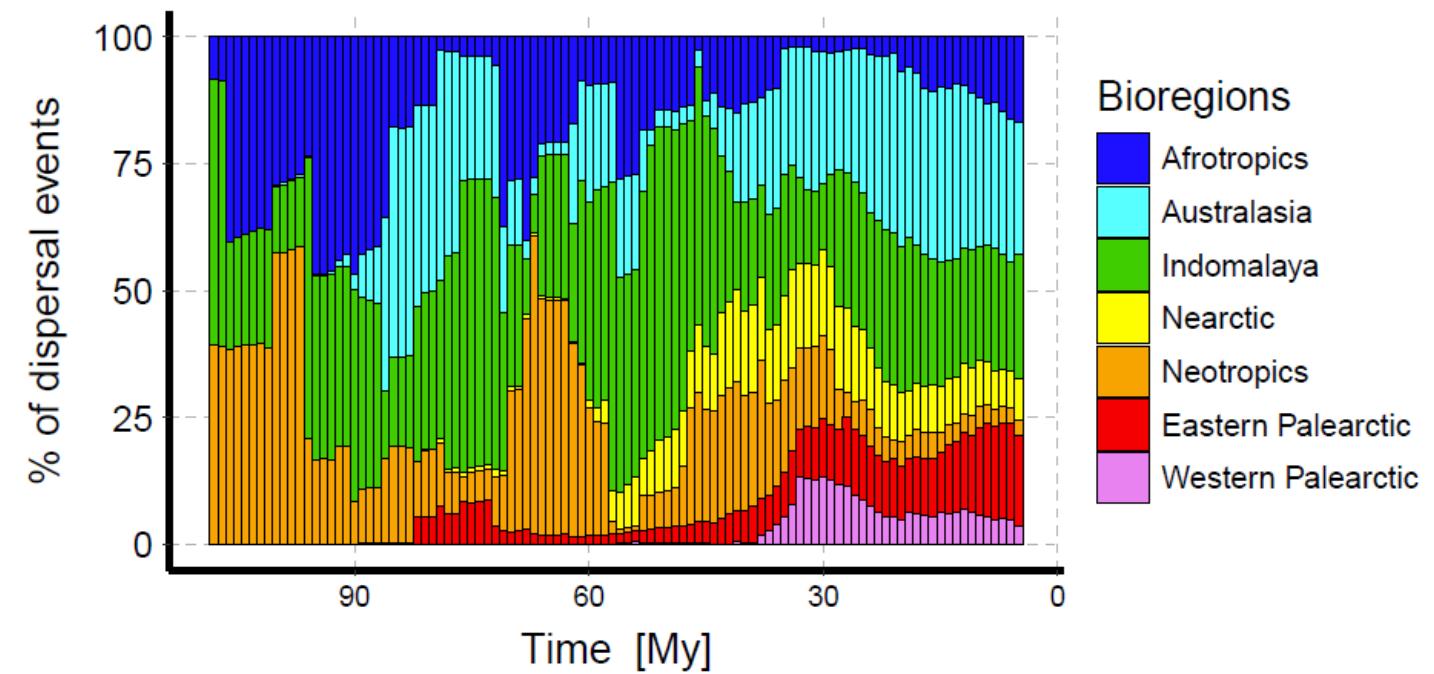
# Dispersal events in time



Dispersal events  
per Source bioregions

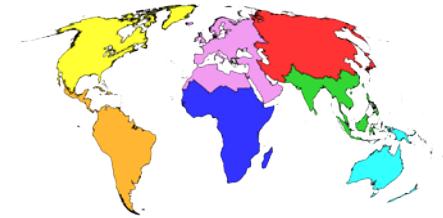


Dispersal events  
per Destination bioregions

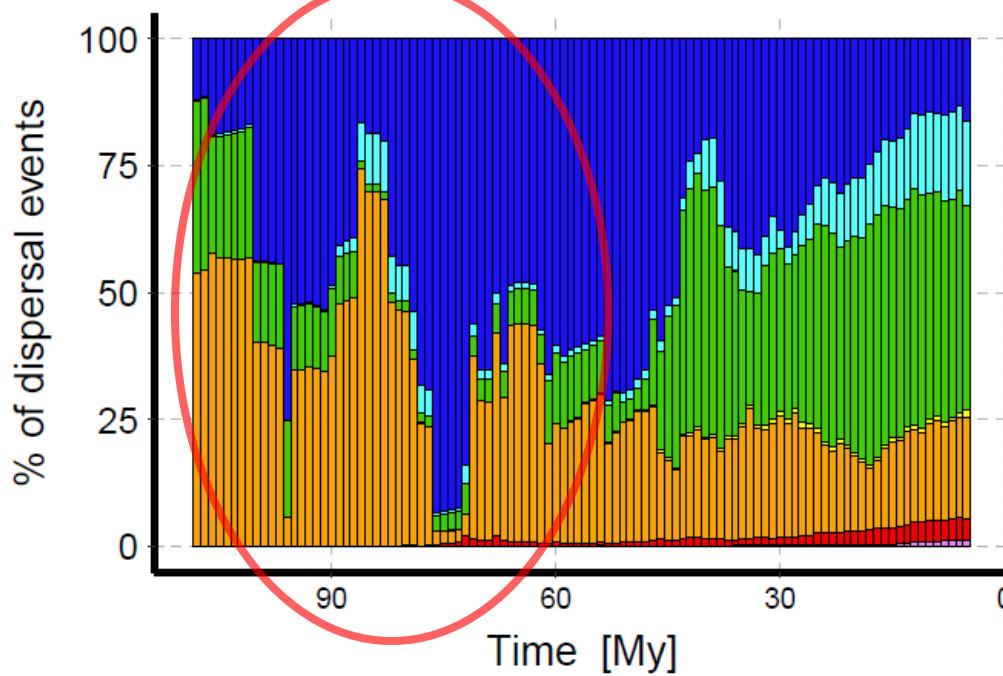


Doré et al., *in prep.*

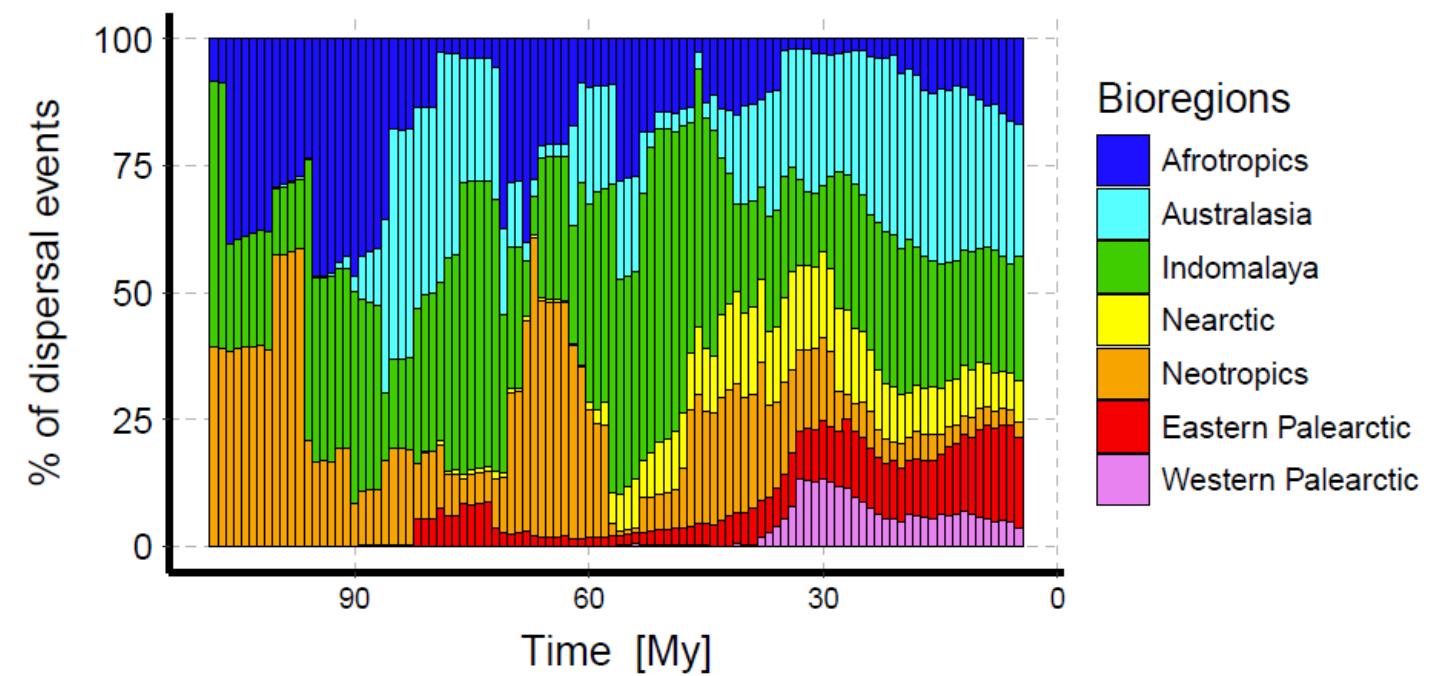
# Dispersal events in time



Dispersal events  
per Source bioregions

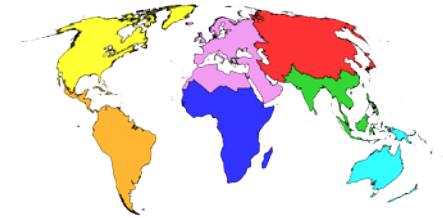


Dispersal events  
per Destination bioregions

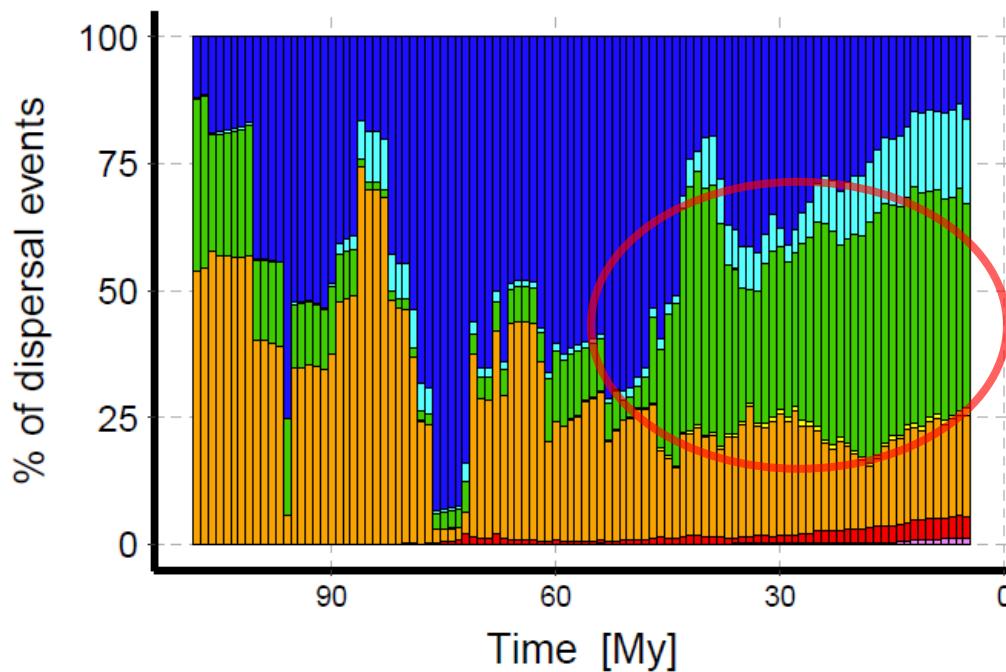


Doré et al., *in prep.*

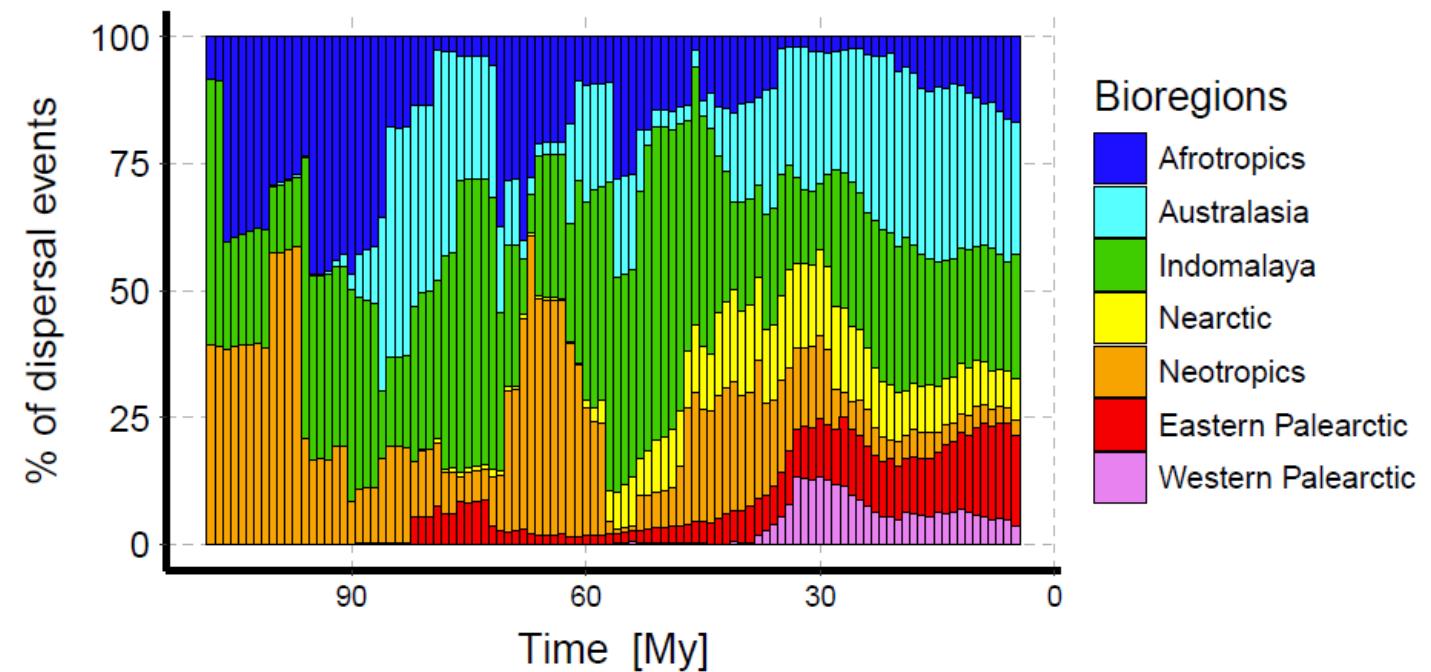
# Dispersal events in time



Dispersal events  
per Source bioregions

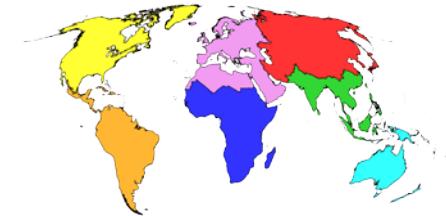


Dispersal events  
per Destination bioregions

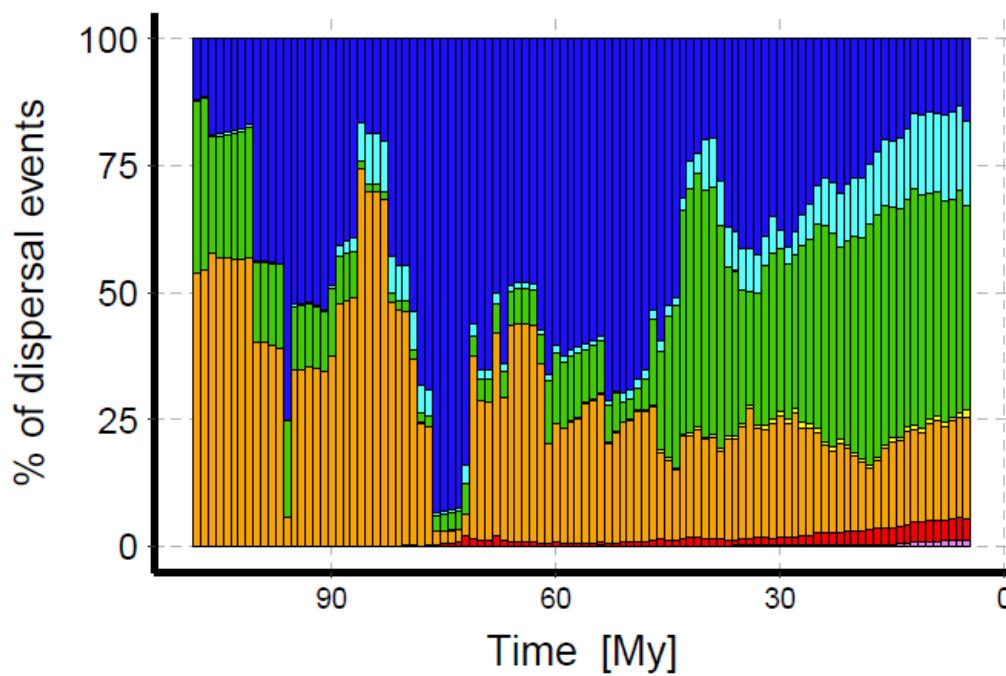


Doré et al., *in prep.*

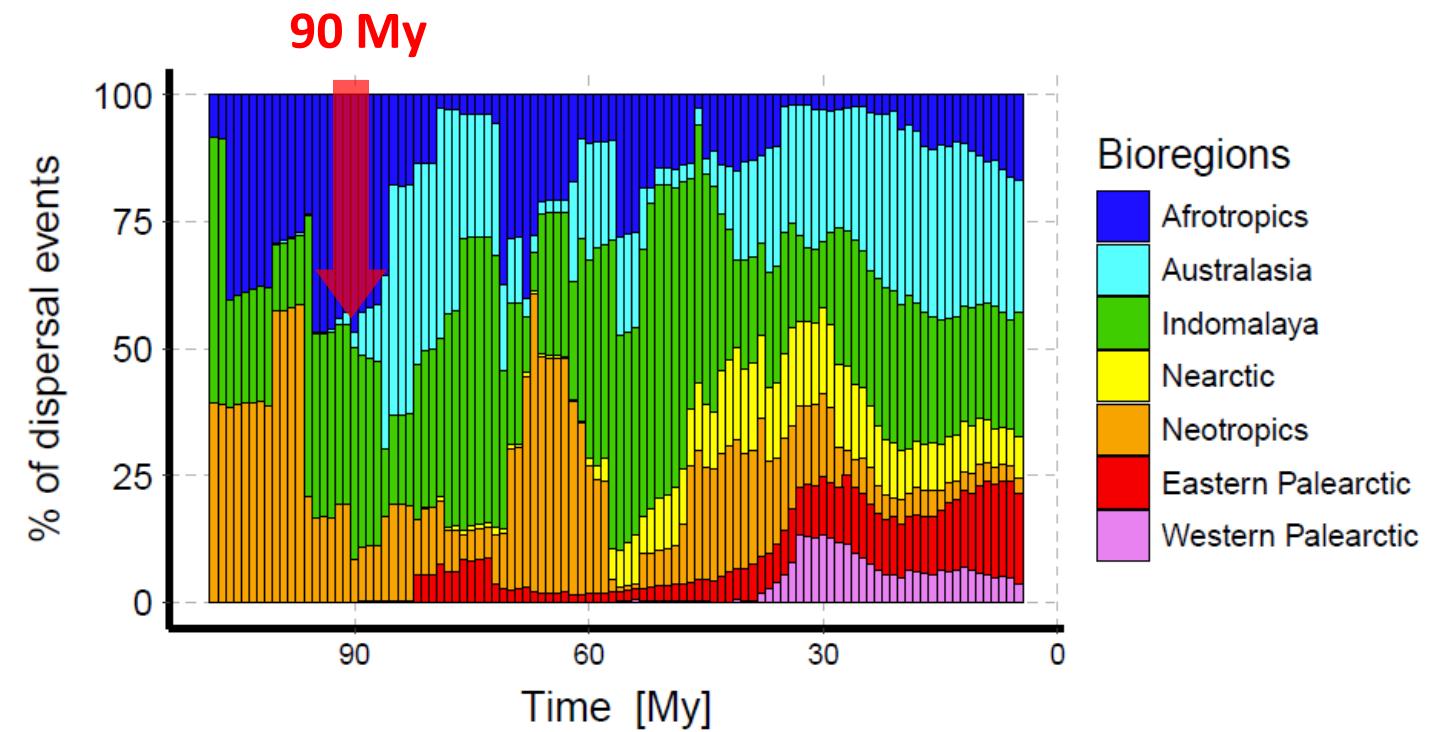
# Dispersal events in time



Dispersal events  
per Source bioregions

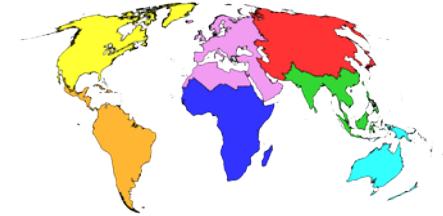


Dispersal events  
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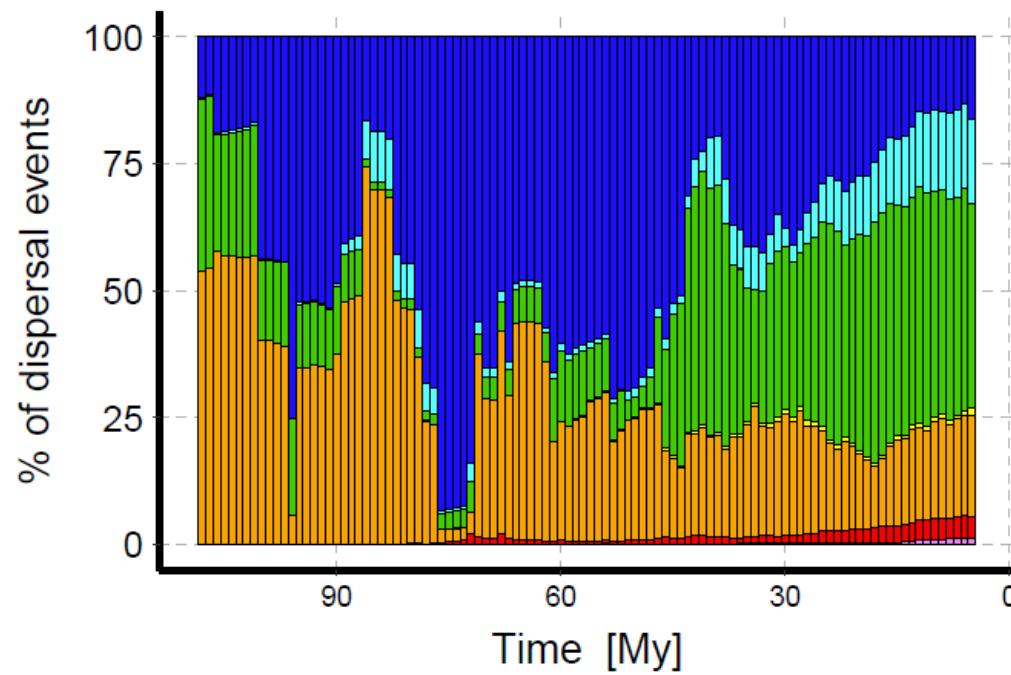


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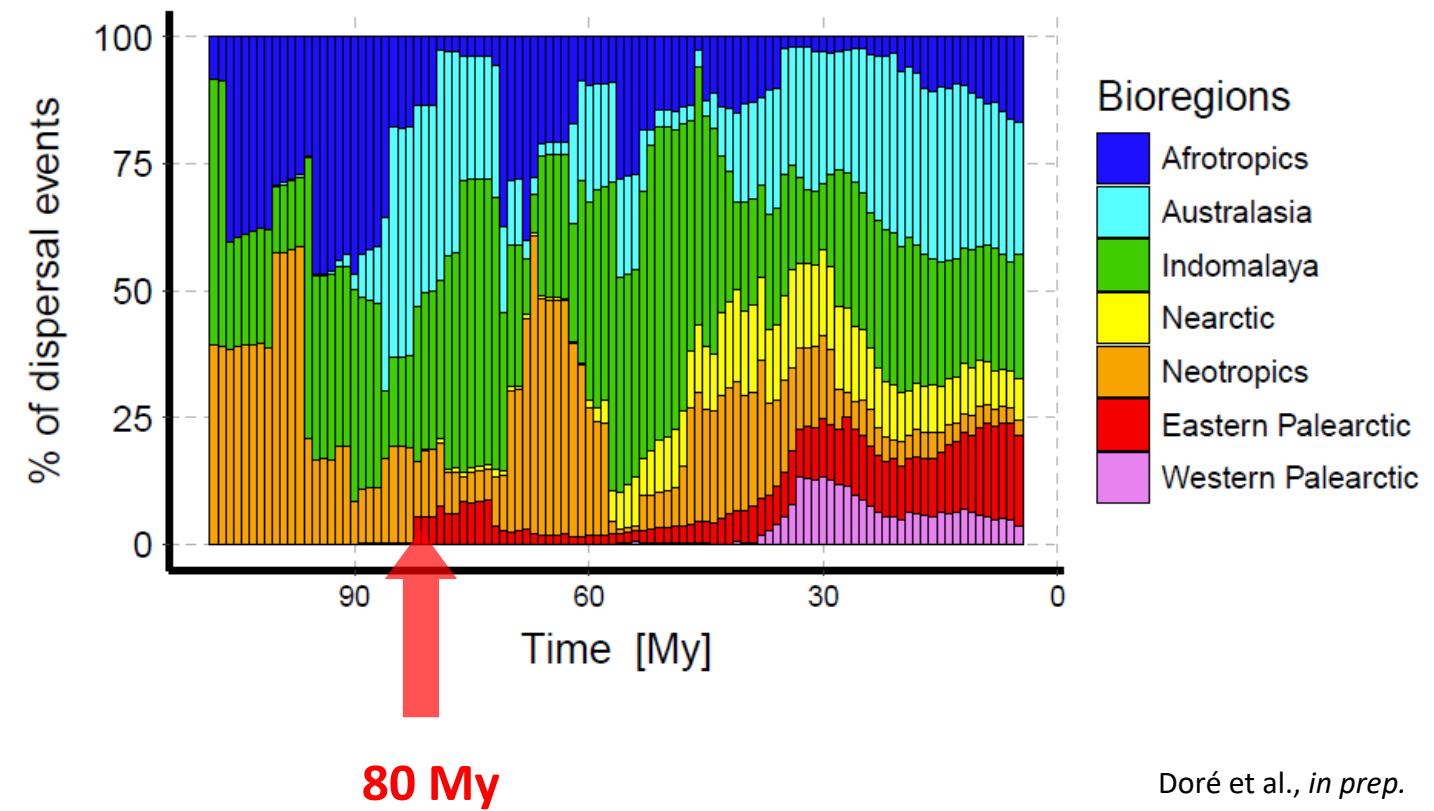
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Dispersal events  
per Source bioregions

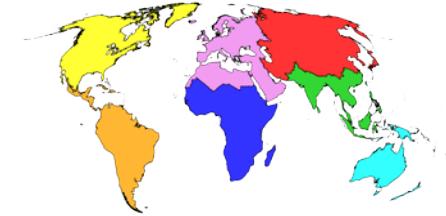


Dispersal events  
per Destination bioregions

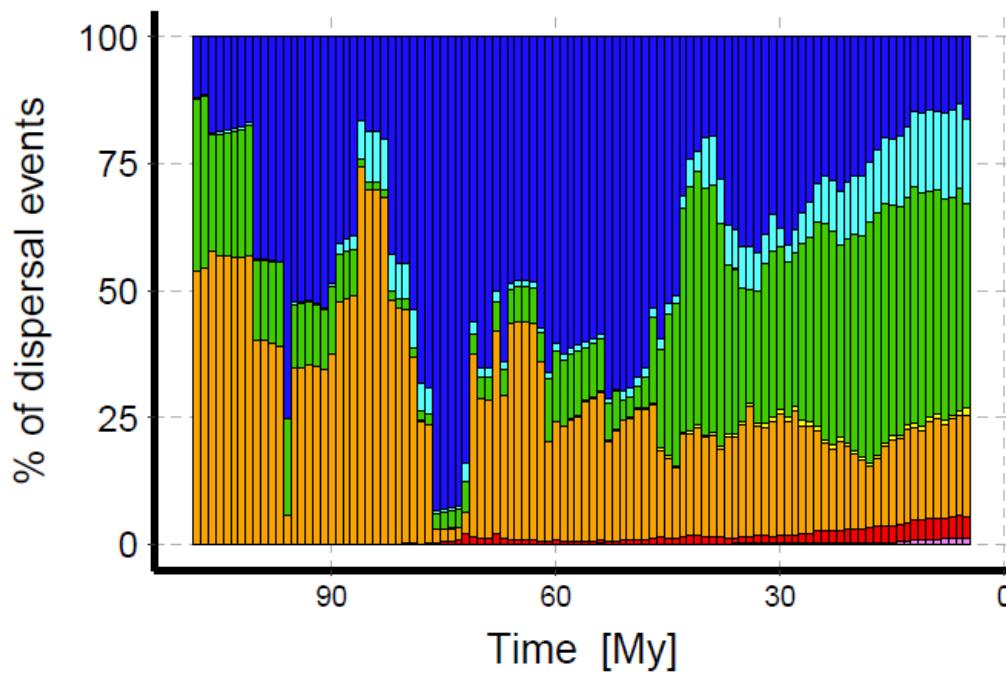


Doré et al., *in prep.*

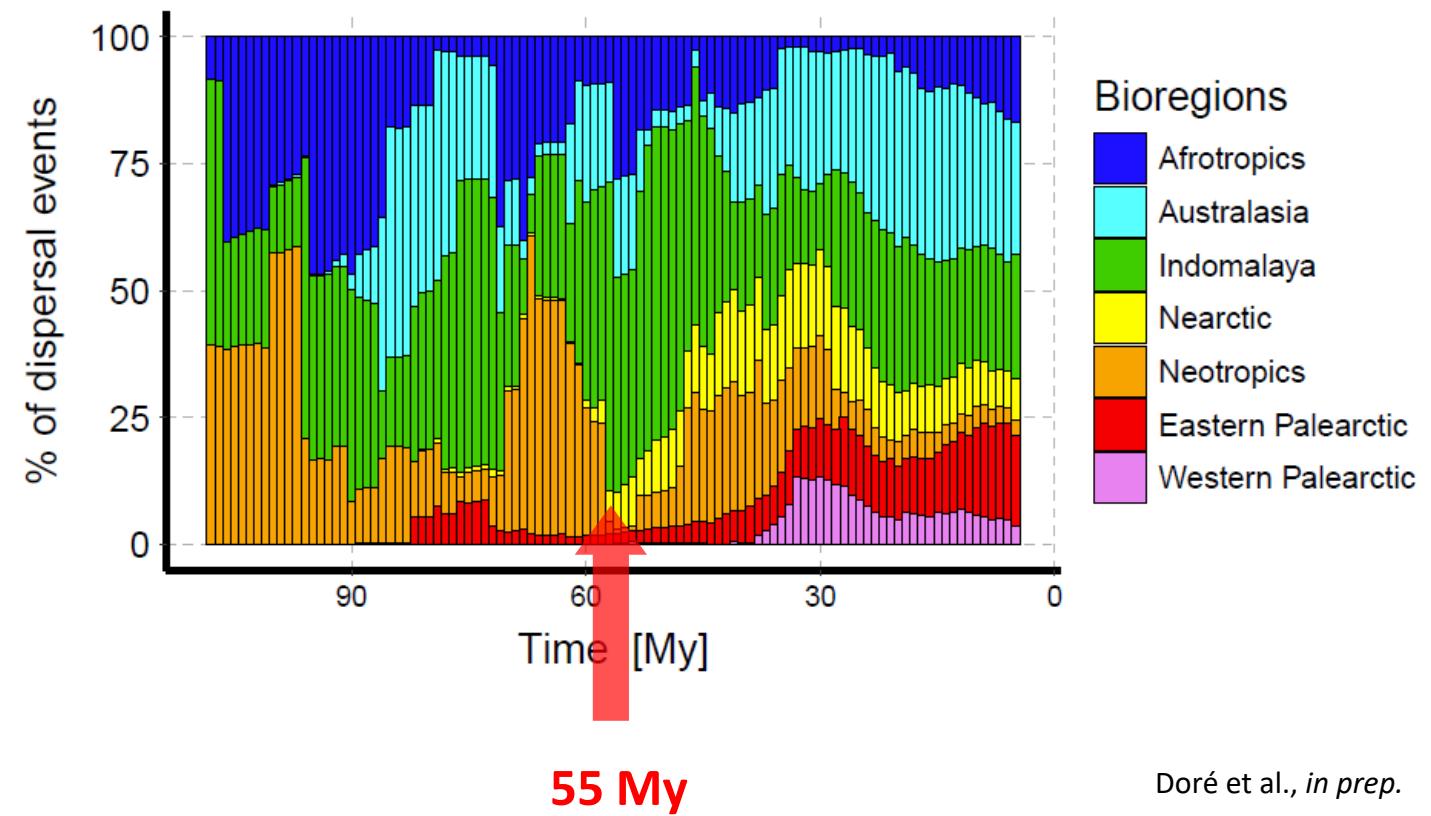
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Dispersal events  
per Source bioregions

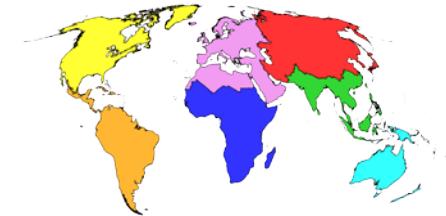


Dispersal events  
per Destination bioregions

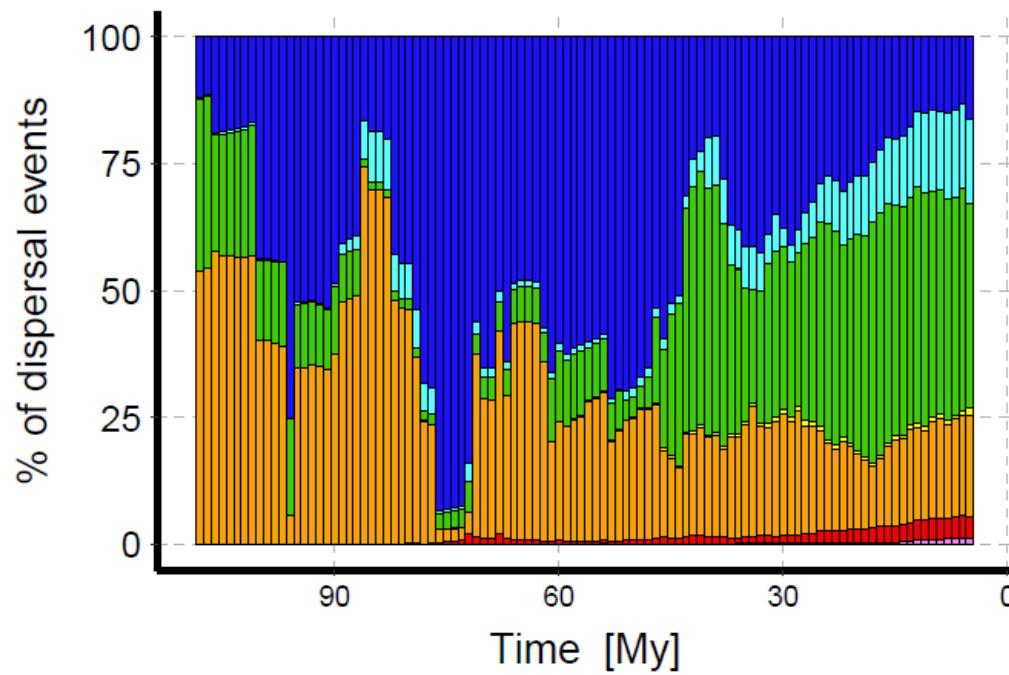


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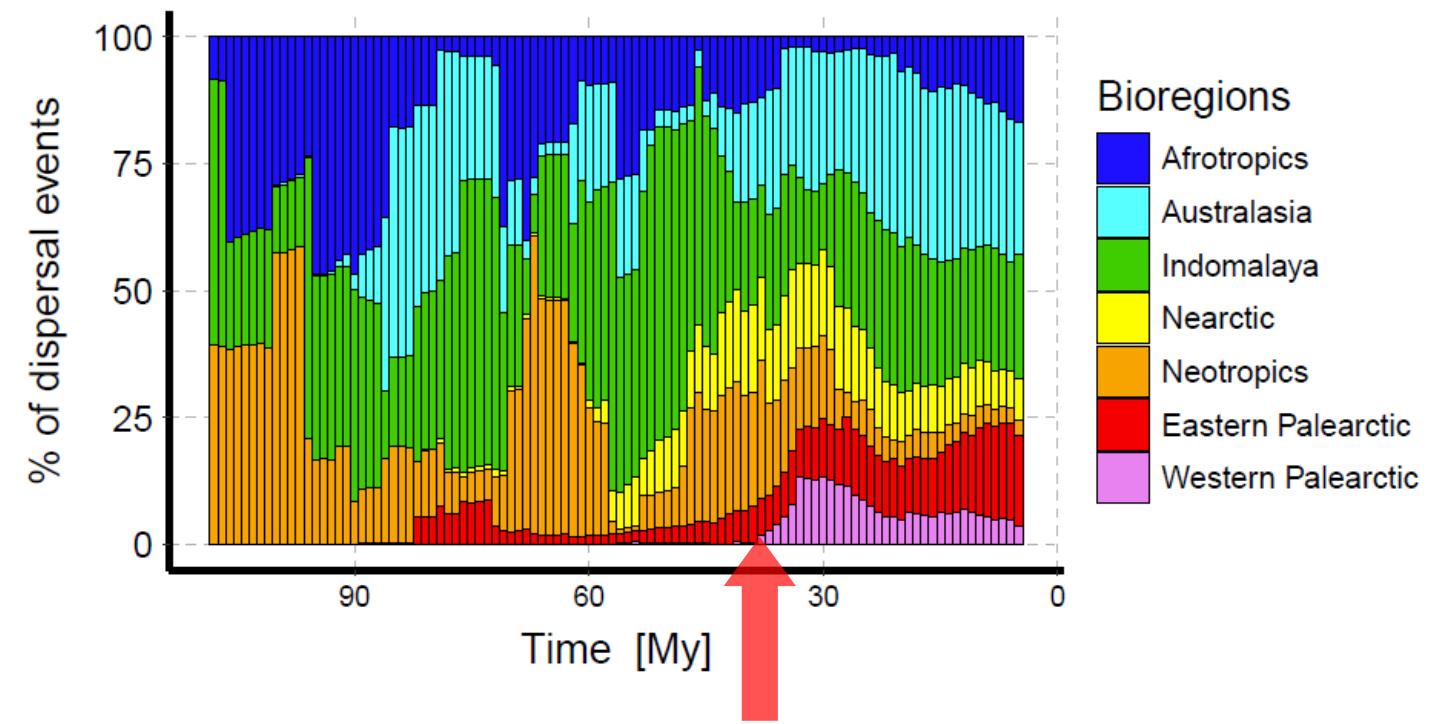
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Dispersal events  
per Source bioregions



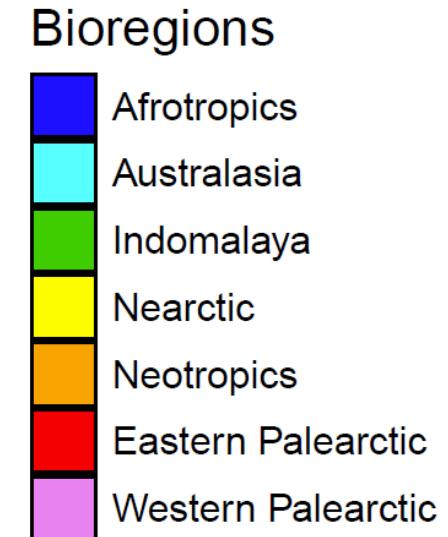
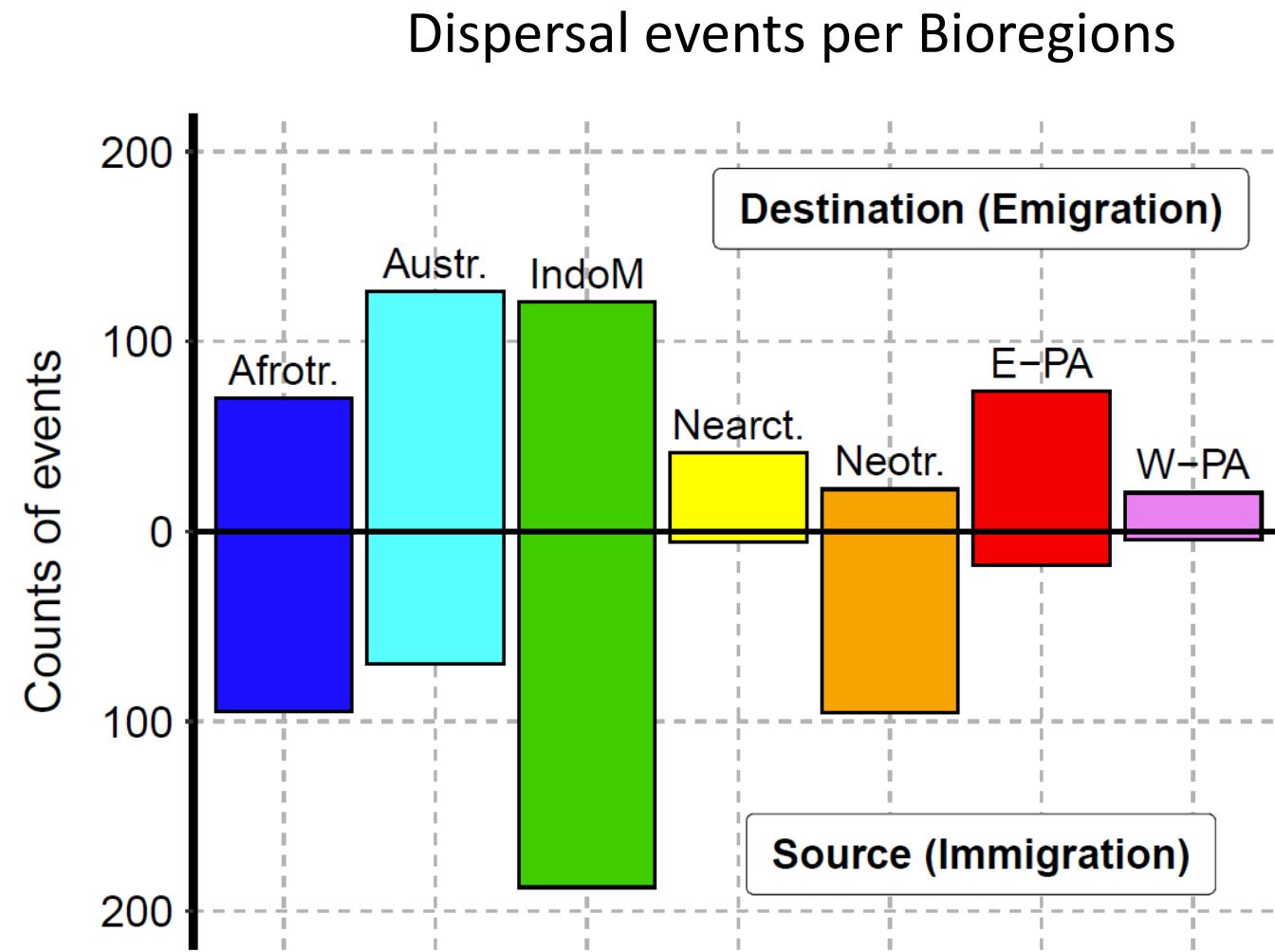
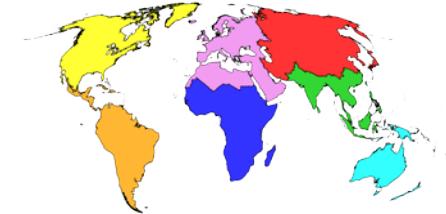
Dispersal events  
per Destination bioregions



35 My

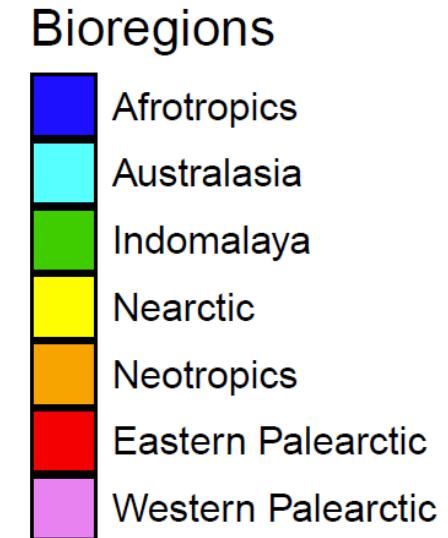
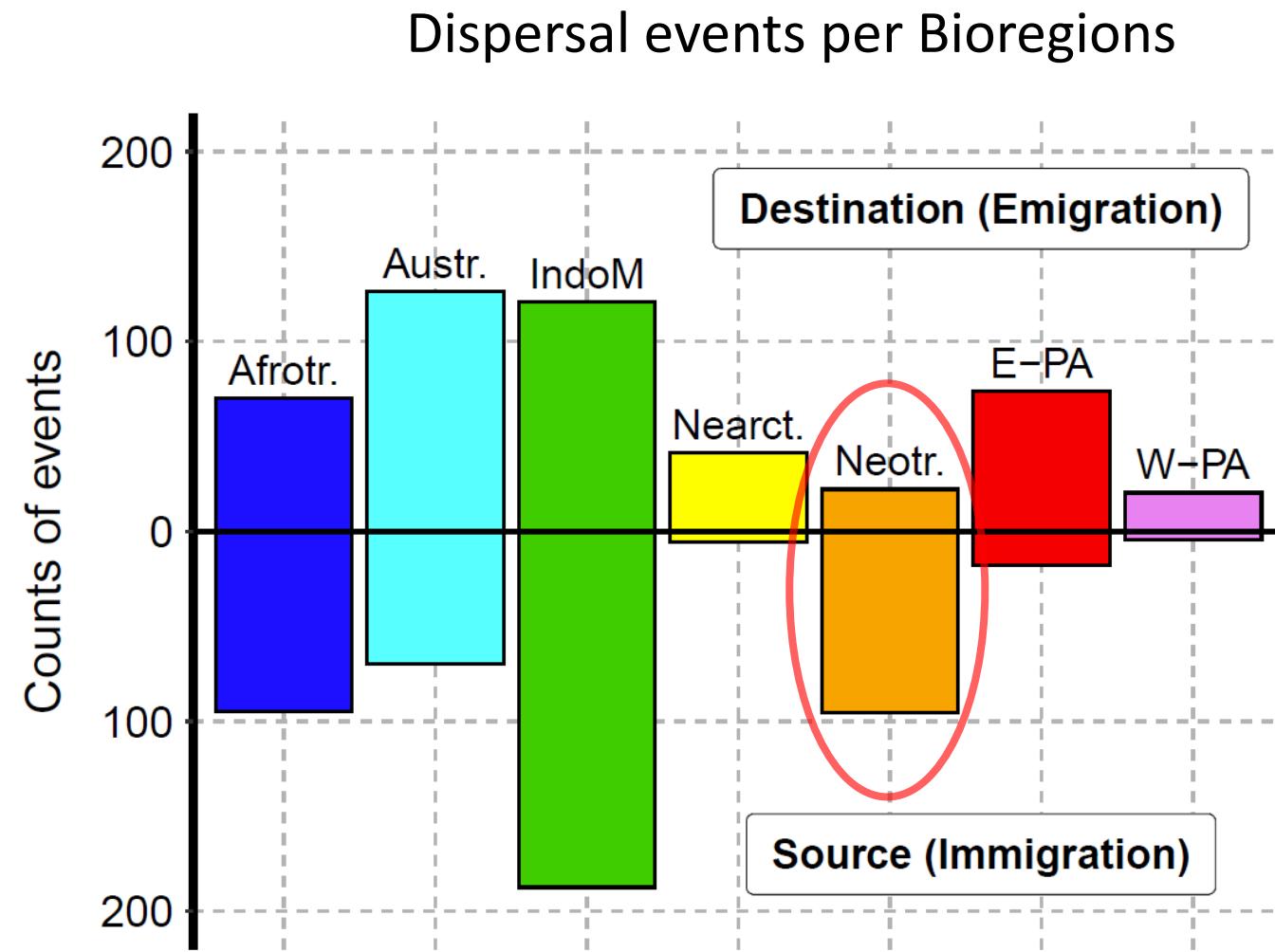
Doré et al., *in prep.*

# Macroevolutionary sources & sinks



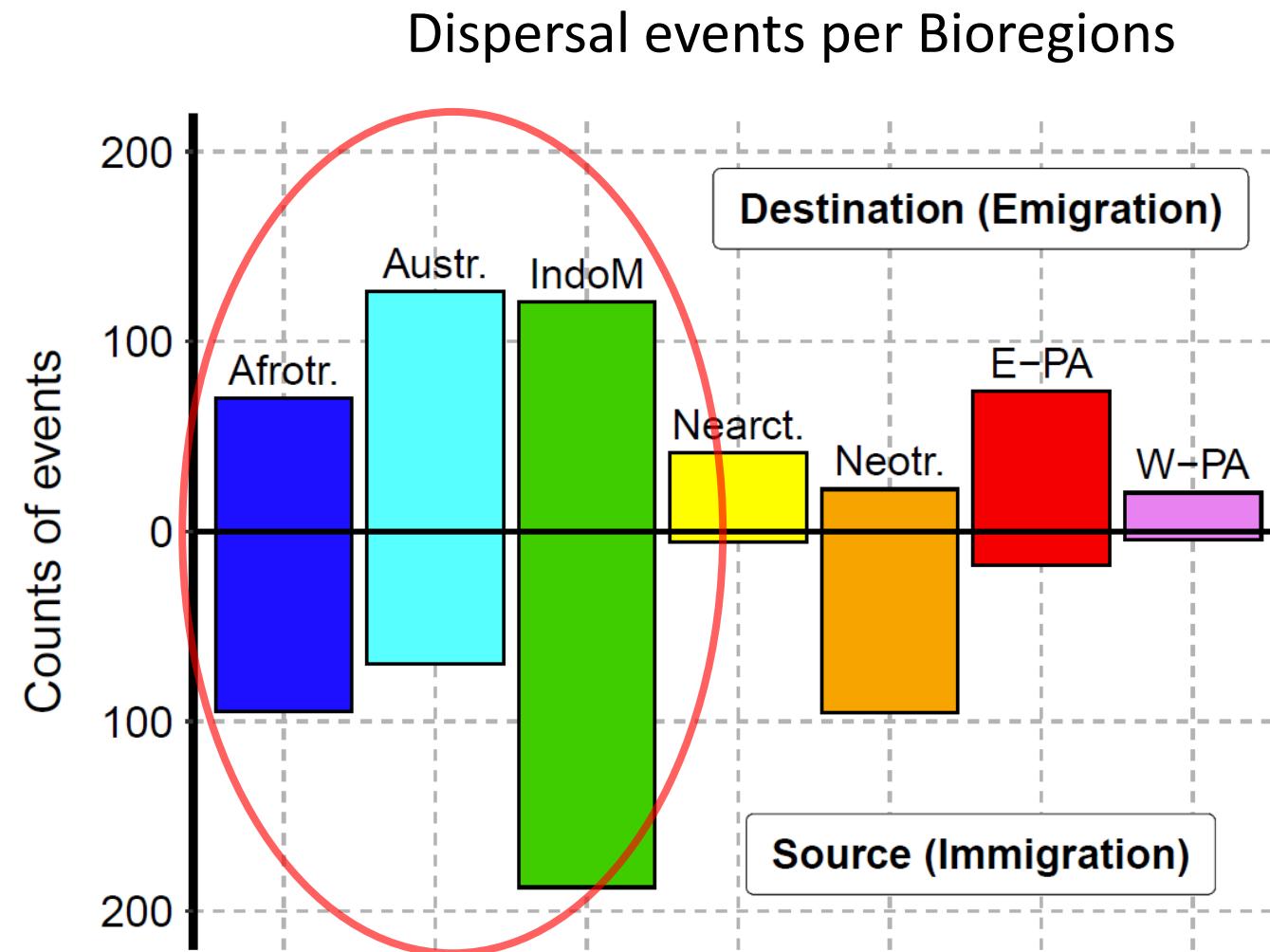
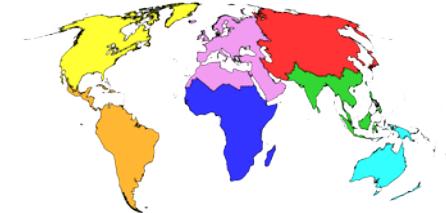
Doré et al., *in prep.*

# Macroevolutionary sources & sinks



Doré et al., *in prep.*

# Macroevolutionary sources & sinks

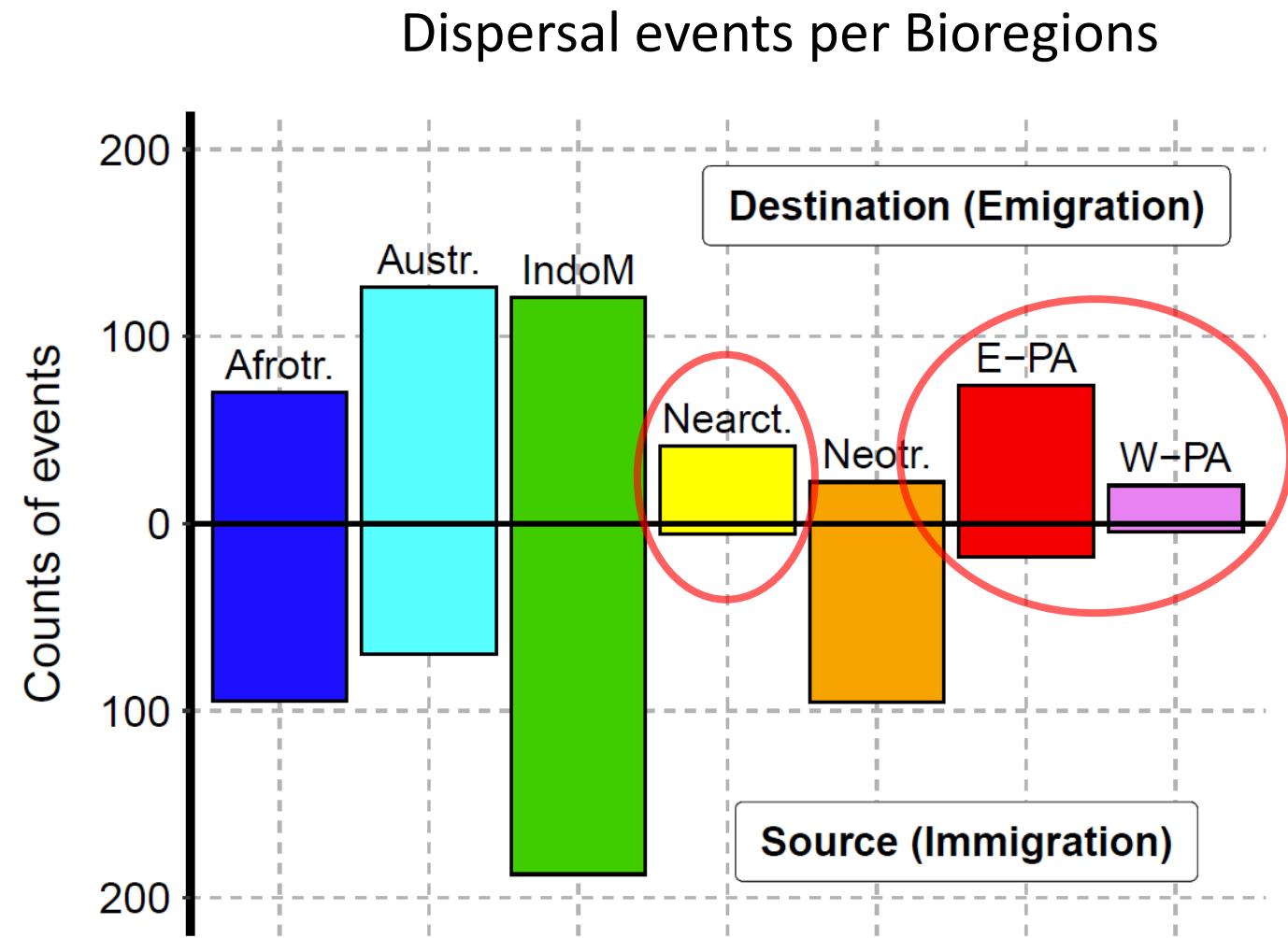
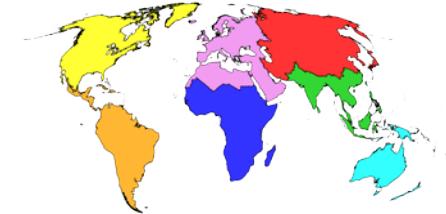


Bioregions

Afrotropics
Australasia
Indomalaya
Nearctic
Neotropics
Eastern Palearctic
Western Palearctic

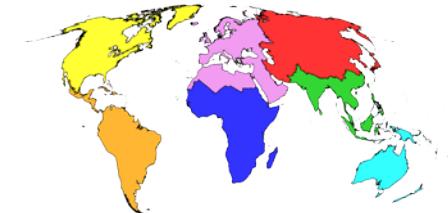
Doré et al., *in prep.*

# Macroevolutionary sources & sinks

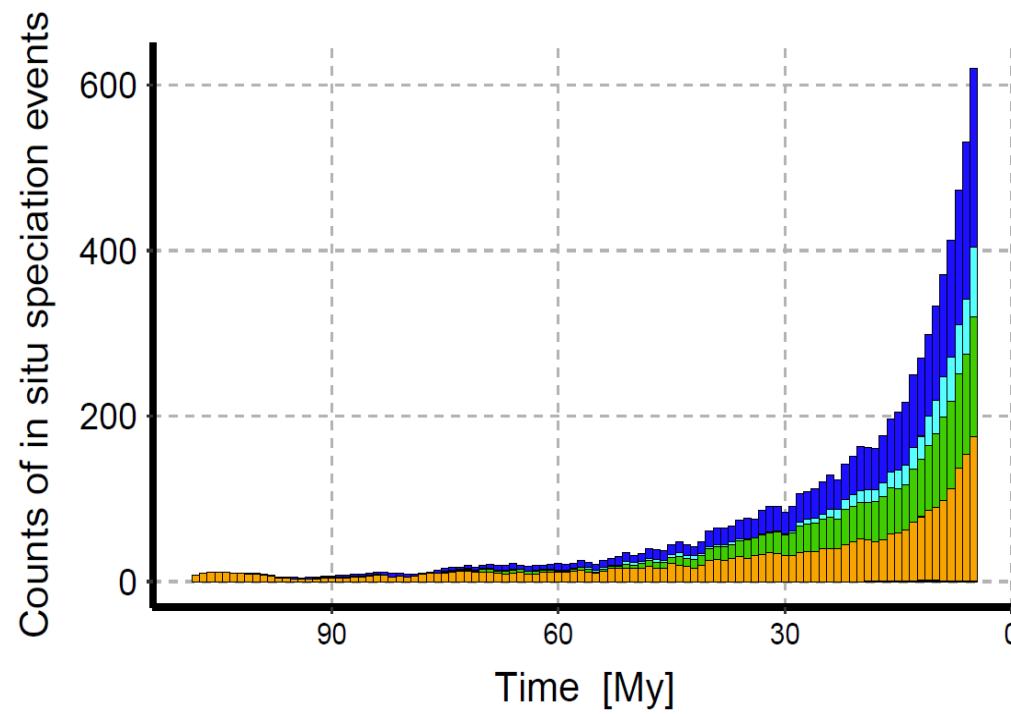


Doré et al., *in prep.*

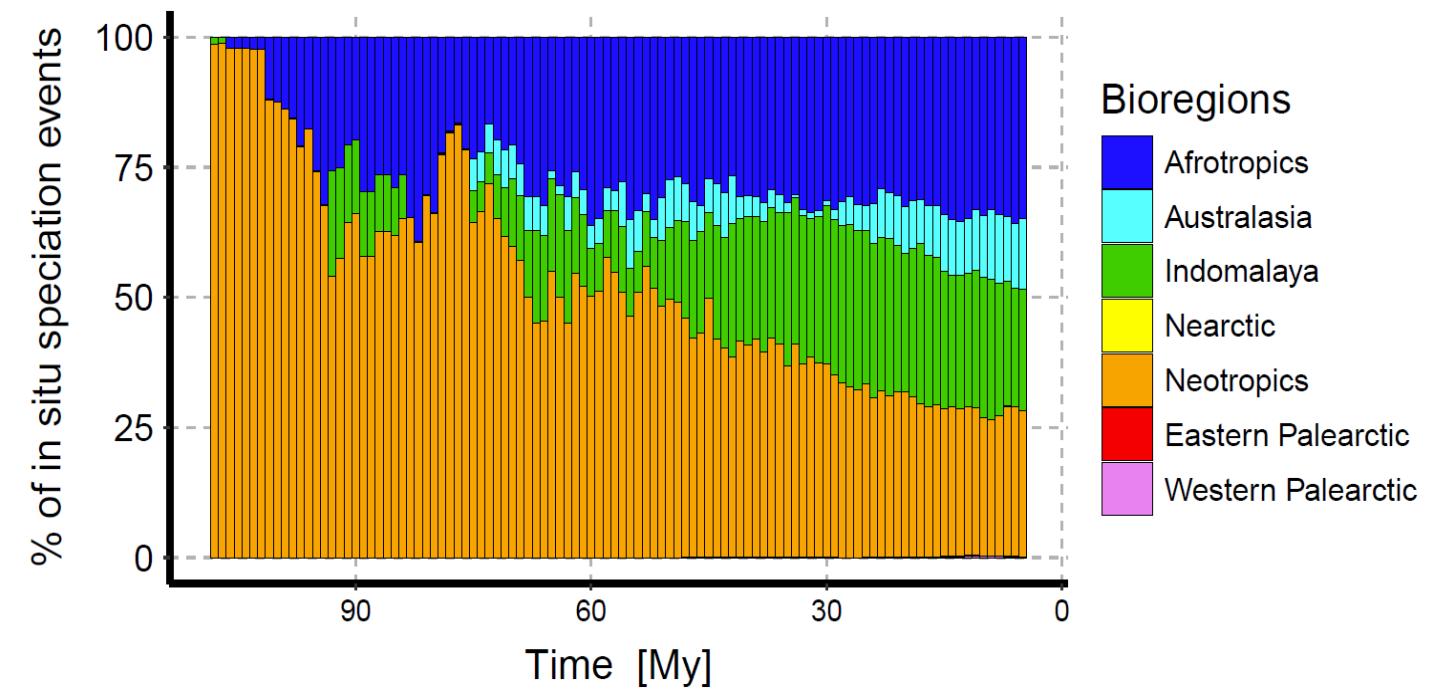
# *In situ* diversification in time



Counts  
*in situ* speciation events  
per Bioregions

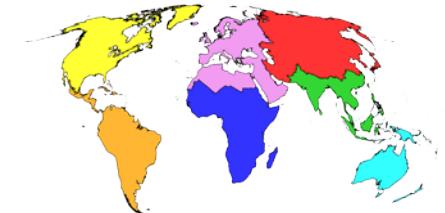


Percentages  
*in situ* speciation events  
per Bioregions

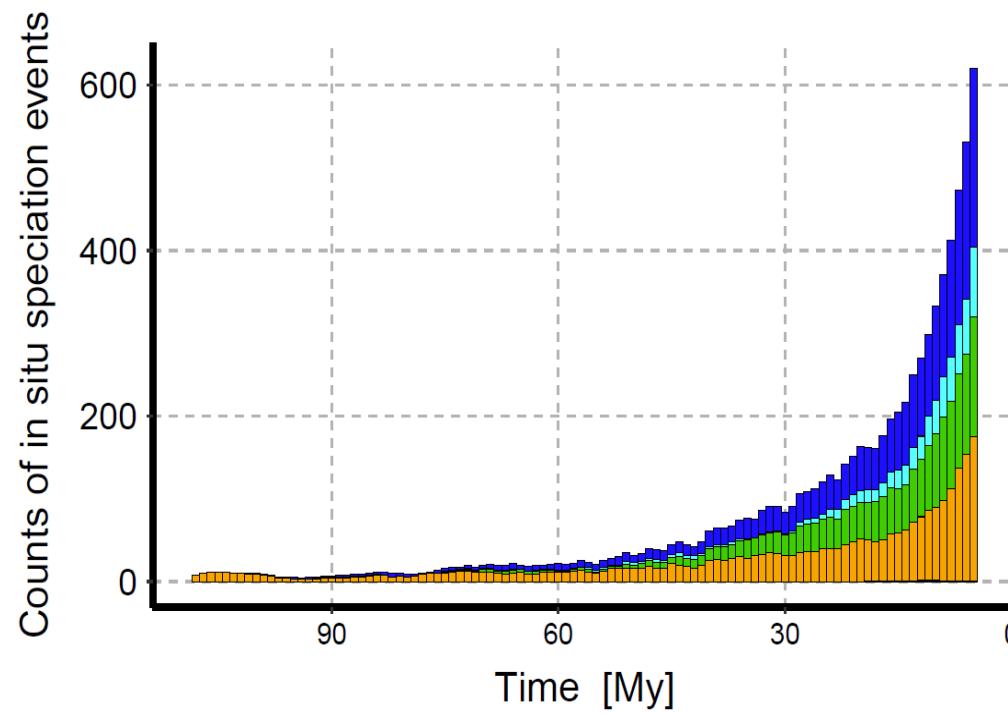


Doré et al., *in prep.*

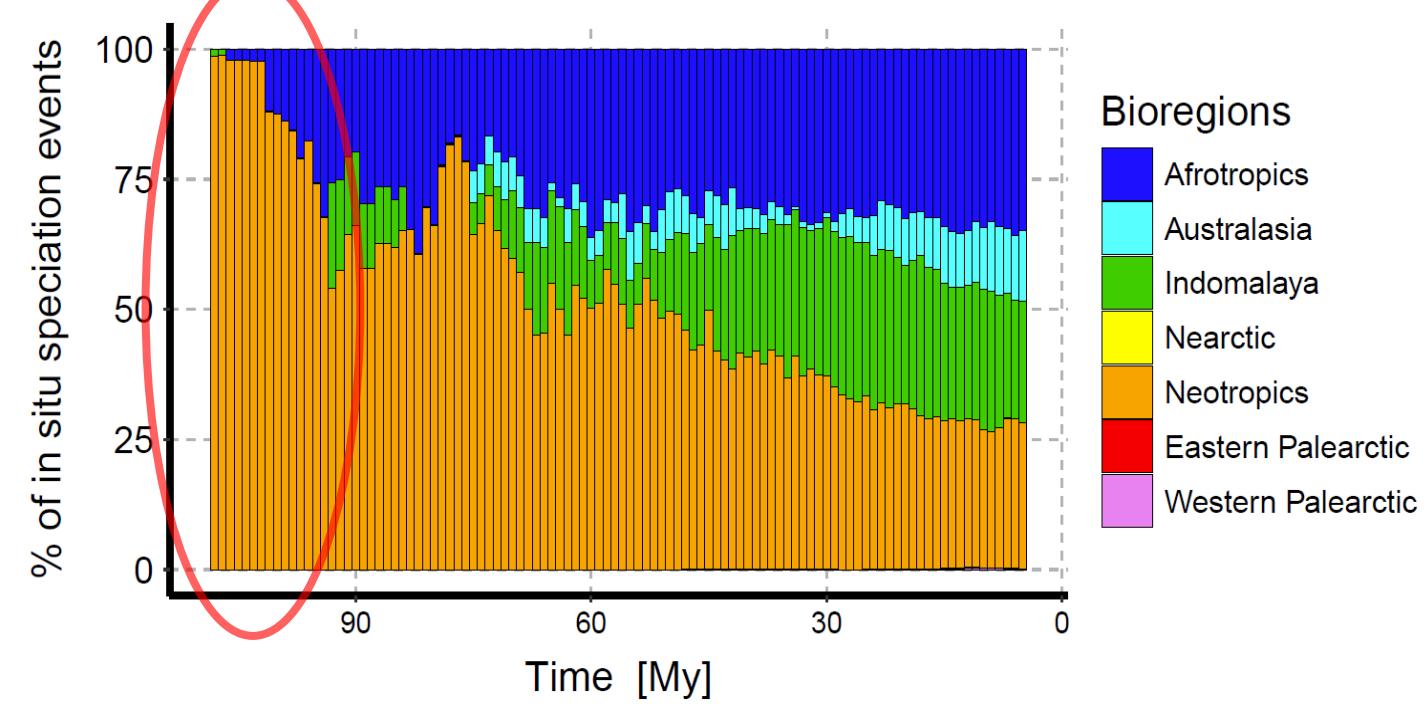
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Counts  
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Percentages  
*in situ* speciation events  
per Bioregions

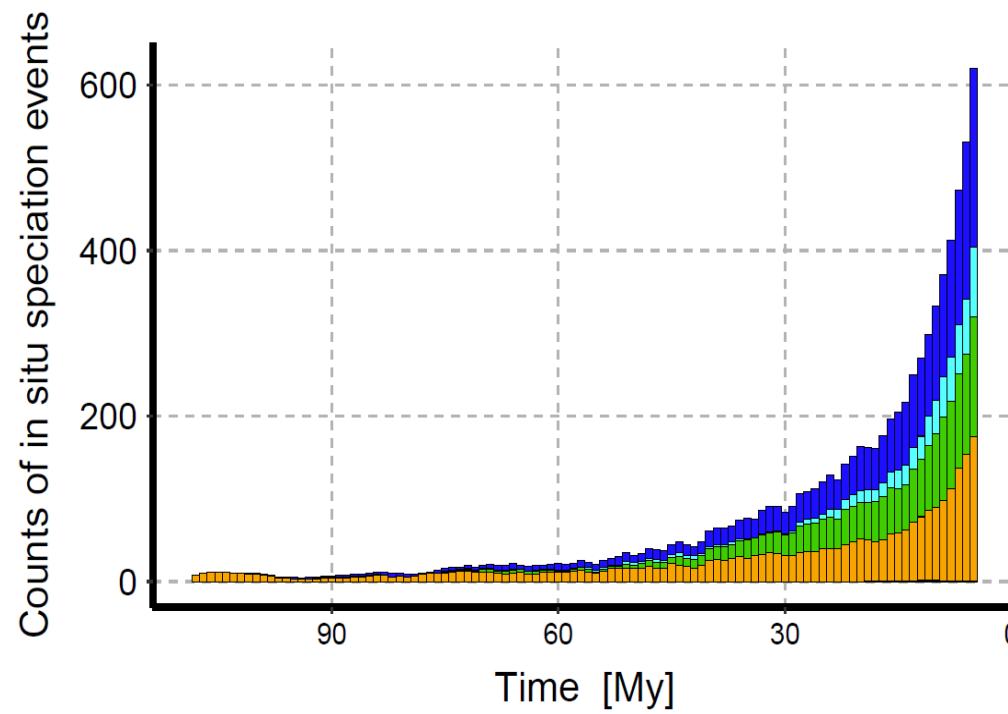


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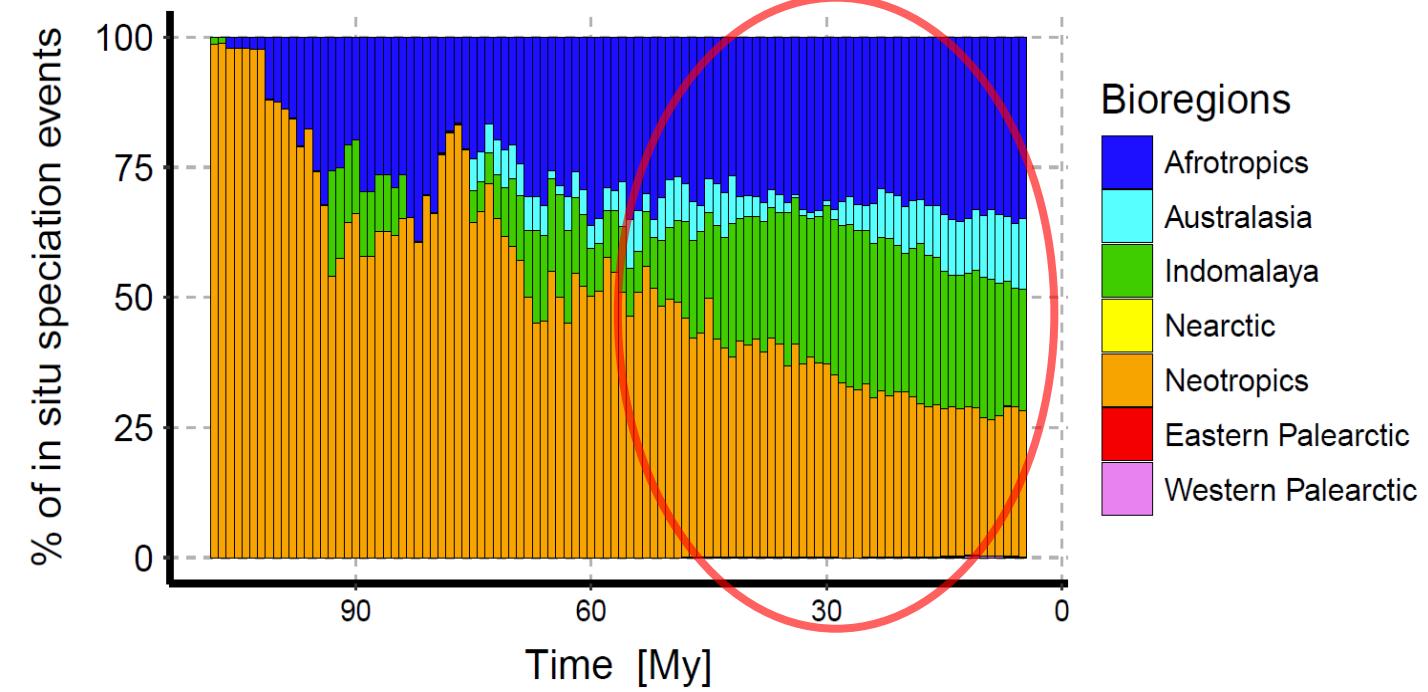
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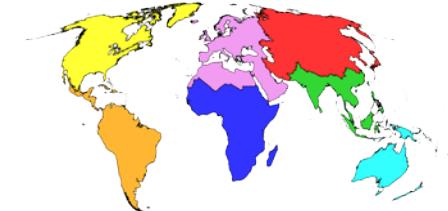


Percentages  
*in situ* speciation events  
per Bioregions

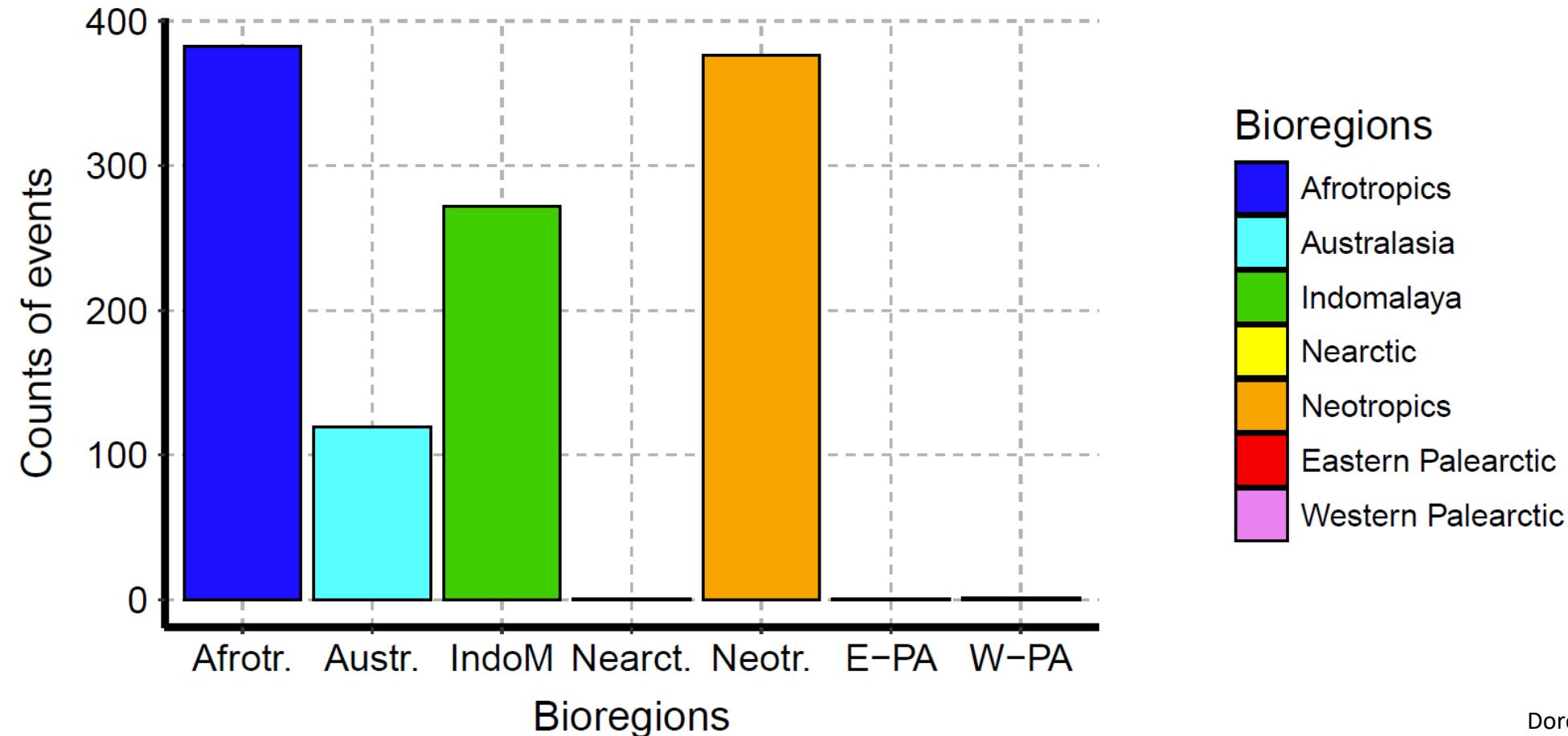


Doré et al., *in prep.*

# Overall *in situ* diversification

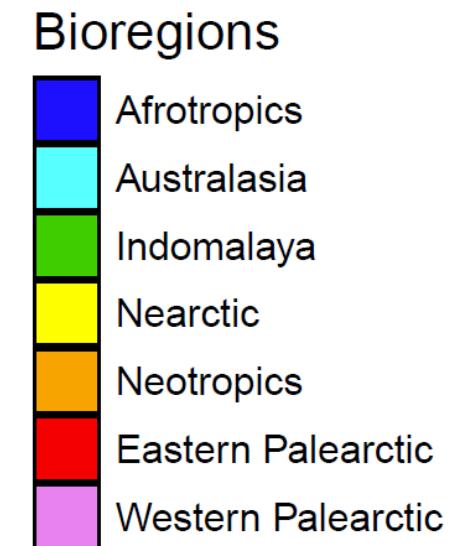
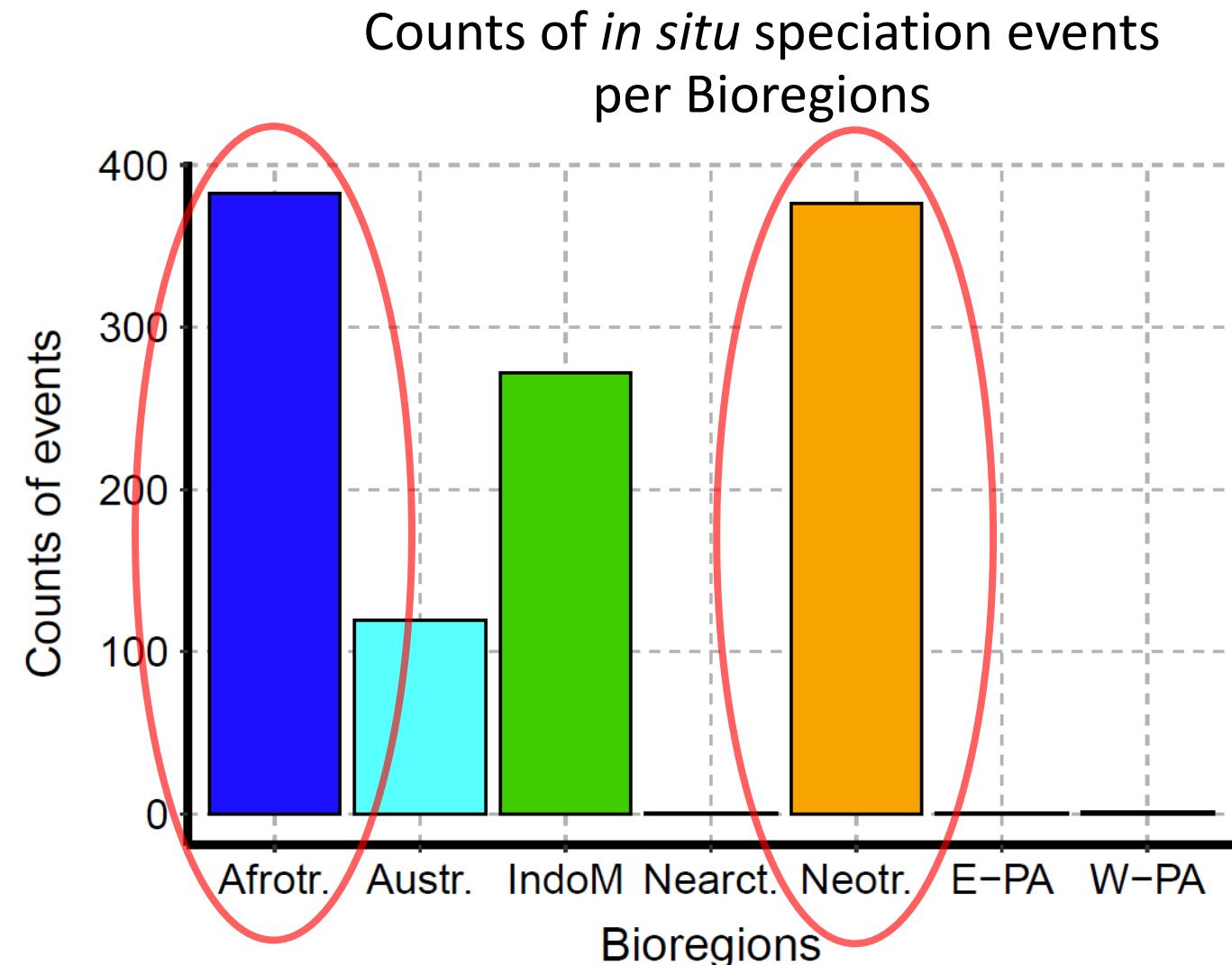


Counts of *in situ* speciation events  
per Bioregions



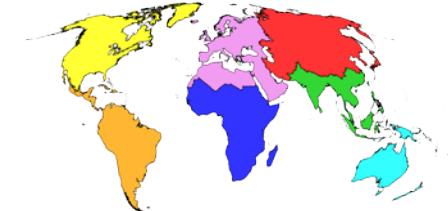
Doré et al., *in prep.*

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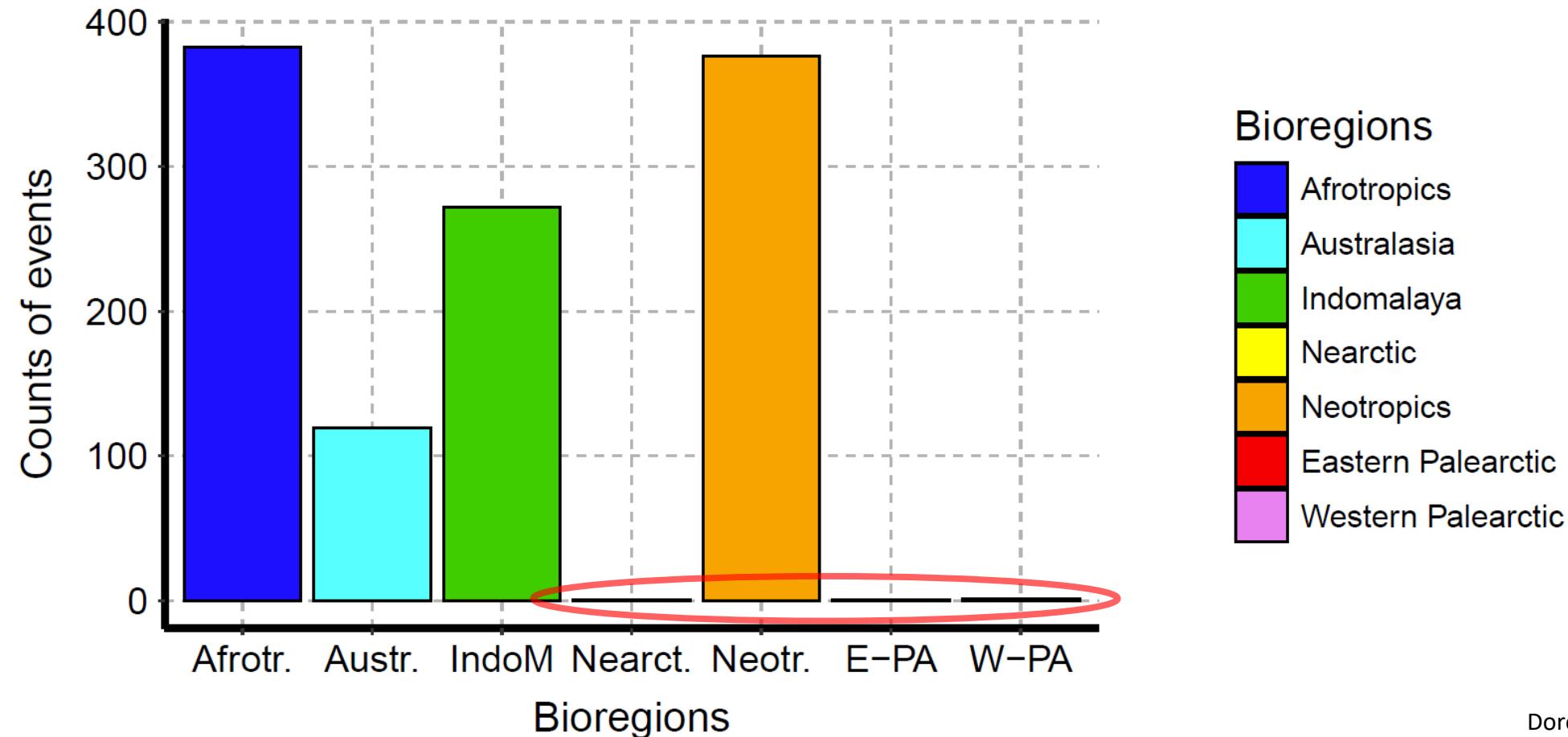


Doré et al., *in prep.*

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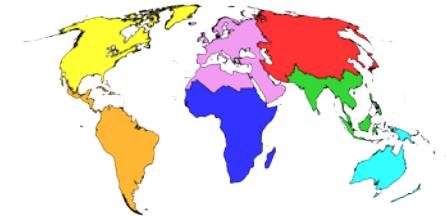


Counts of *in situ* speciation events  
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Doré et al., *in prep.*

# Conclusions



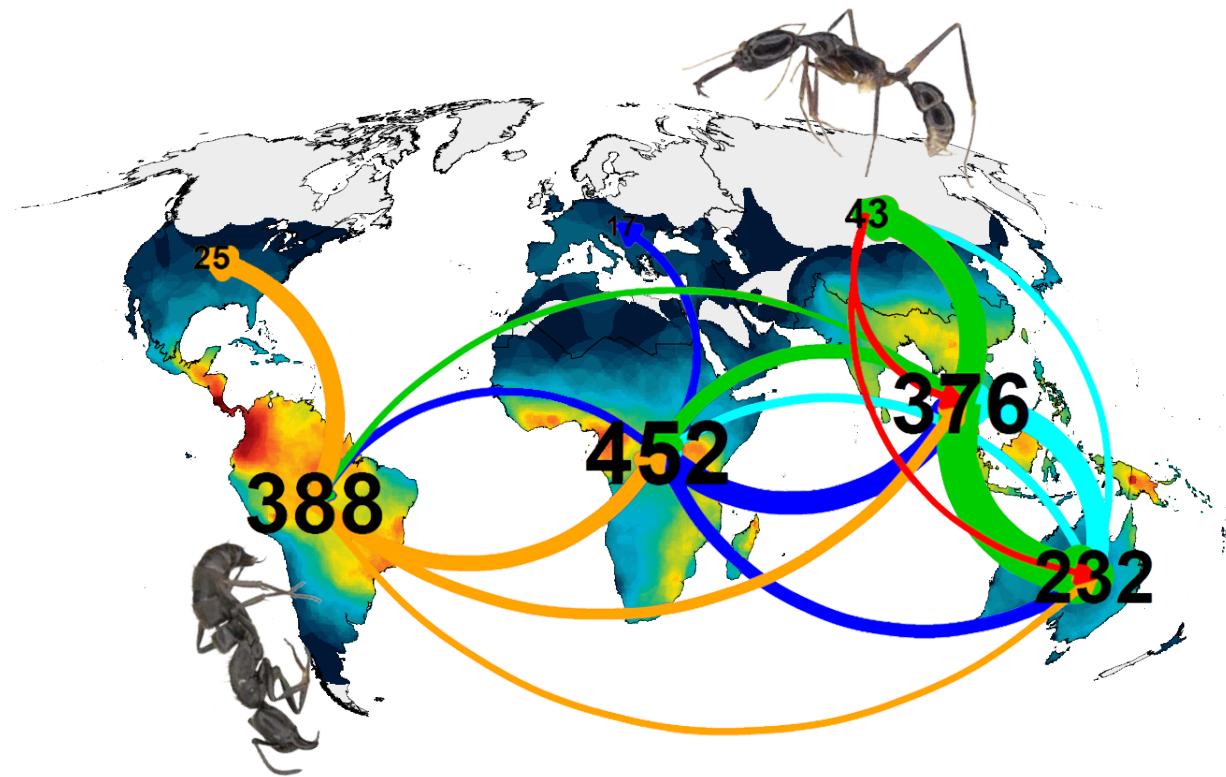
Origin in **Gondwana**  $\approx$  110-120 My

Macroevolutionary sources/sinks:

- Source = Neotropics
- Sinks = Holarctic = Palearctic + Nearctic
- Centers = Afrotropics/IndoMalaya/Australasia

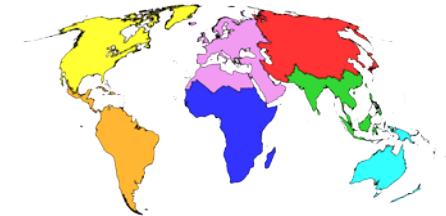
Mechanisms?

- Tropical **niche conservatism**
- Early diversification and **niche occupation** in Neotropics limits further immigration



Doré et al., *in prep.*

# Conclusions



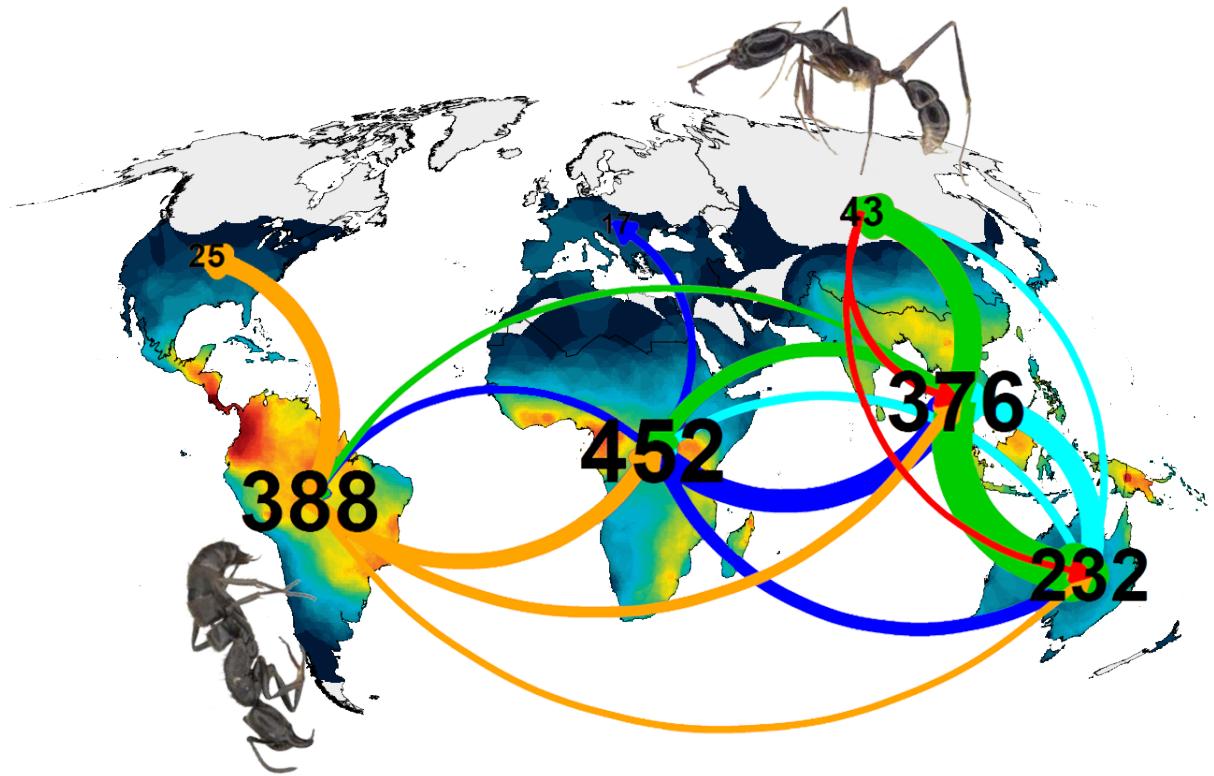
Origin in **Gondwana** ≈ 110-120 My

Macroevolutionary sources/sinks:

- **Source** = **Neotropics**
- **Sinks** = Holoarctic = **Paleartic + Nearctic**
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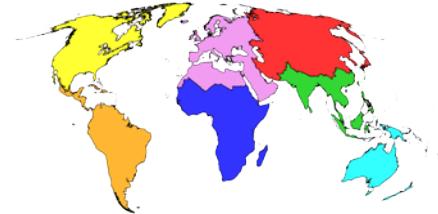
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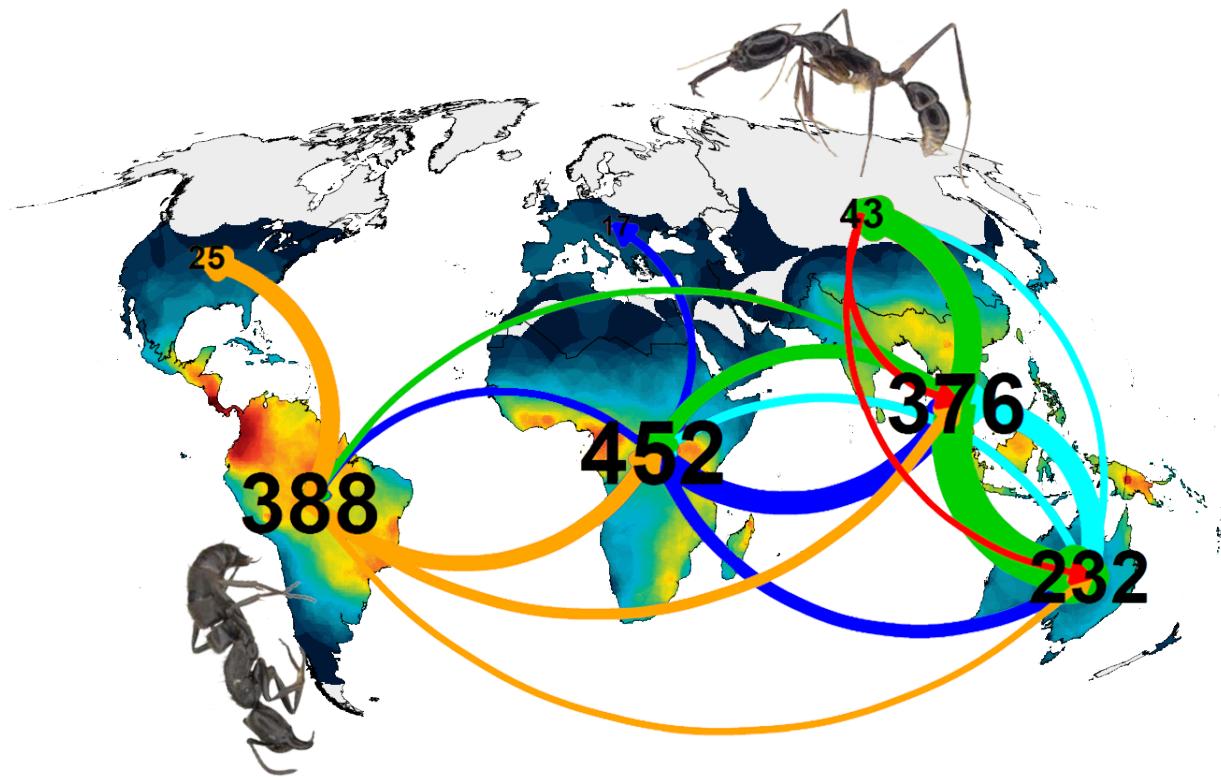
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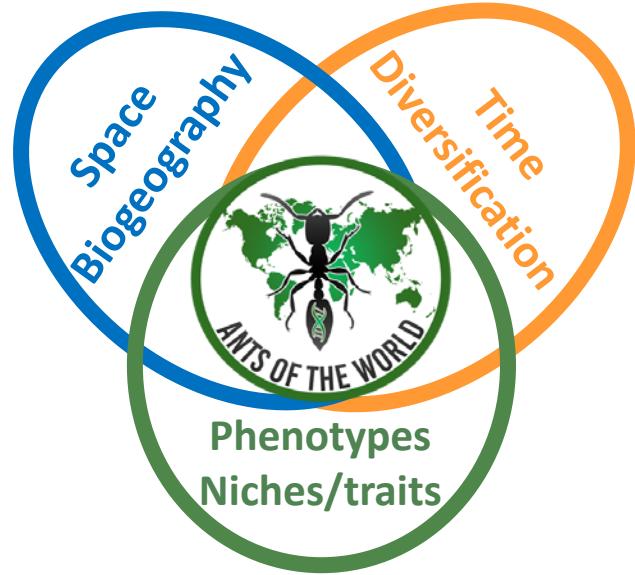
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Doré et al., *in prep.*

# Perspectives



## Climatic niche evolution:

- Is evolution repeating itself? Compare the **filling of the niche** across bioregions

## Morphology & Diversification:

- Do **key morphological innovations** trigger diversification uplifts?



## ANTS OF THE WORLD

DEB-1932467, DEB-1932062, DEB-2019431

Bonnie Blaimer



Marek Borowiec



Gabi Camacho



Jack Longino



Michael Branstetter



Brian Fisher



Phil Ward





SCAN ME

# Questions?



Photo credits: F. Brassard

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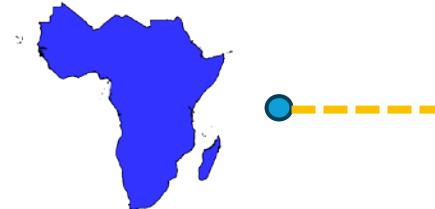
# Grafting missing taxa

**Backbone UCE phylogeny:** 789 species (51.4%)

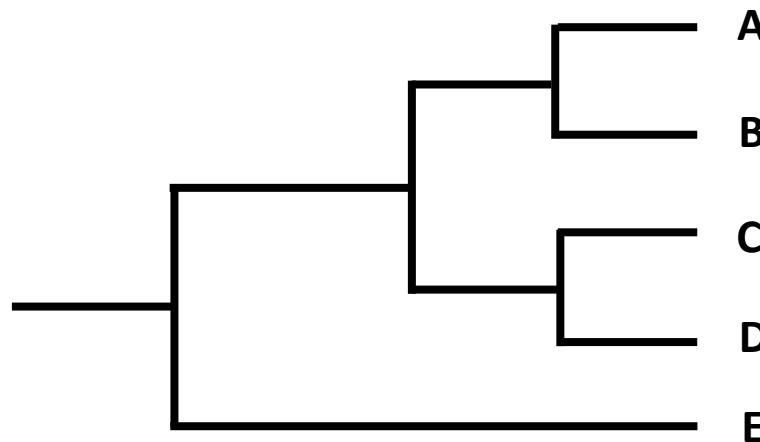
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Missing taxa  
from Afrotropics



Step 2: Define divergence time



Step 3: Randomize and repeat

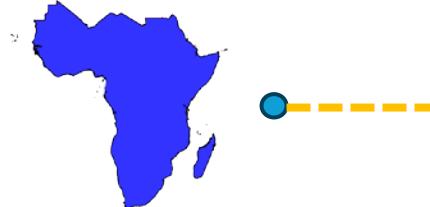
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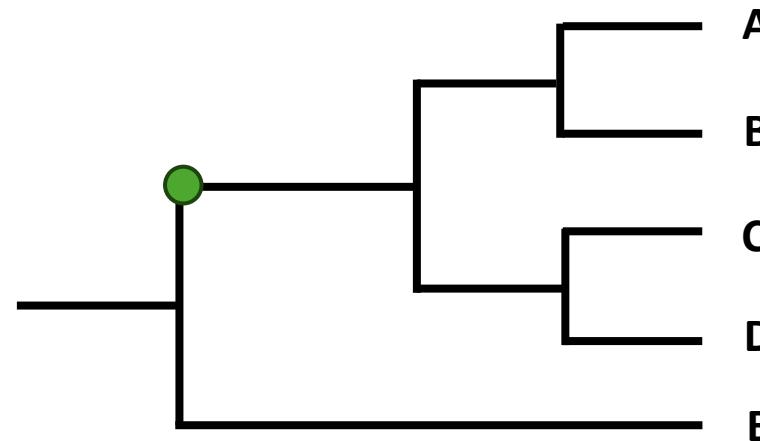
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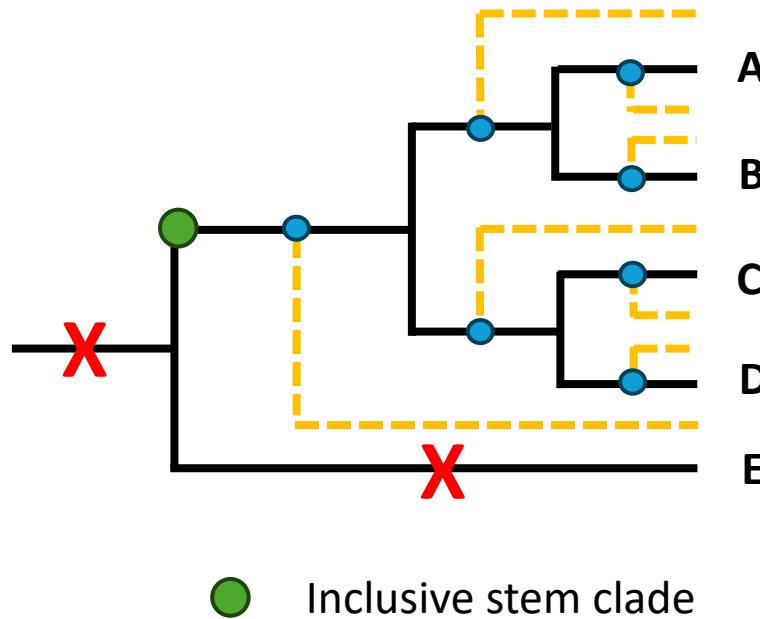
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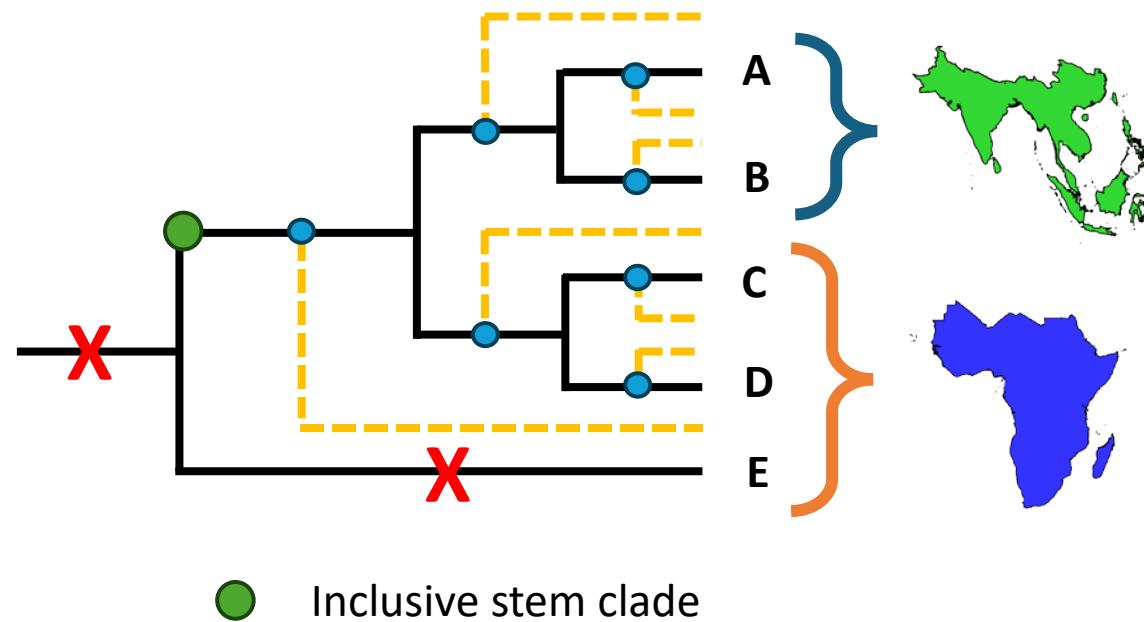
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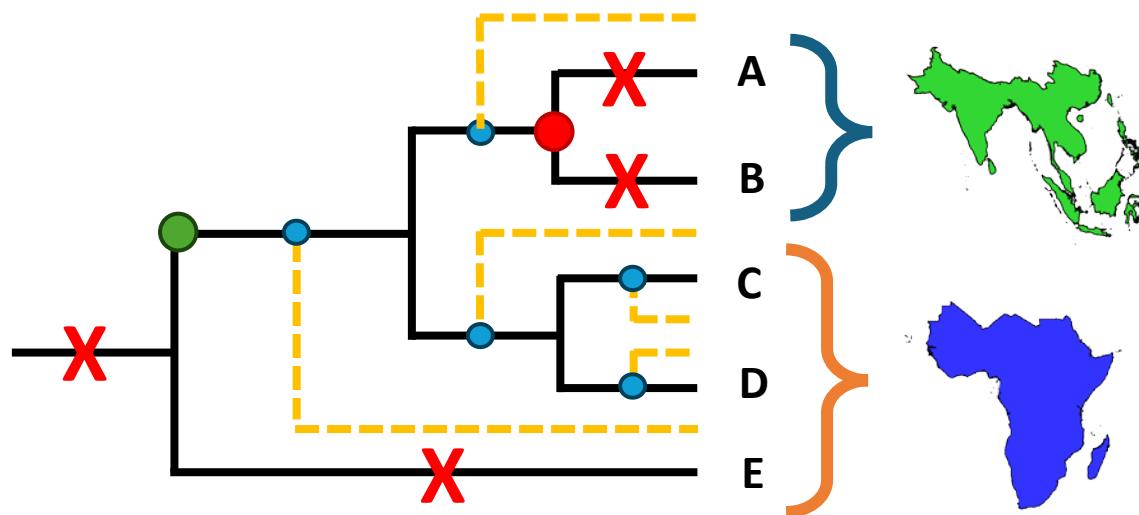
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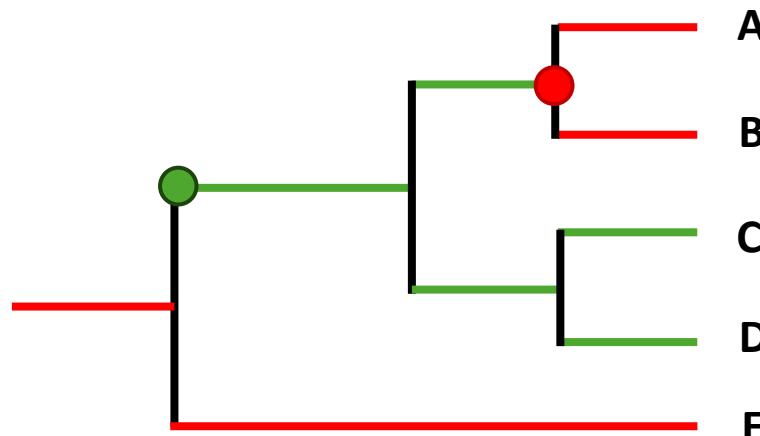
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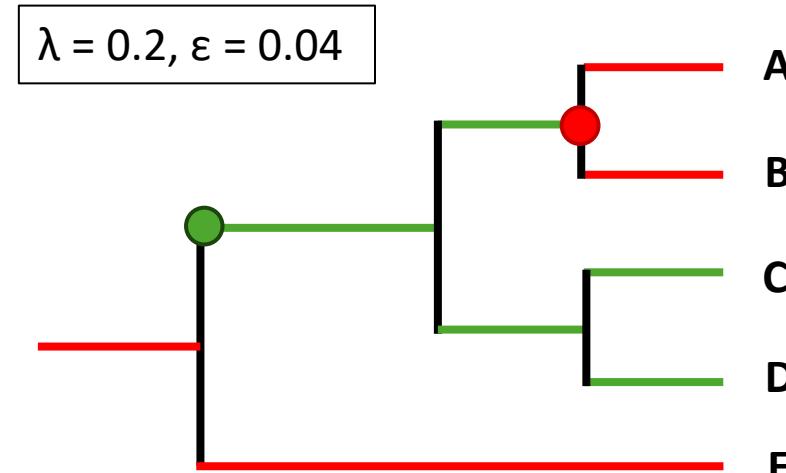
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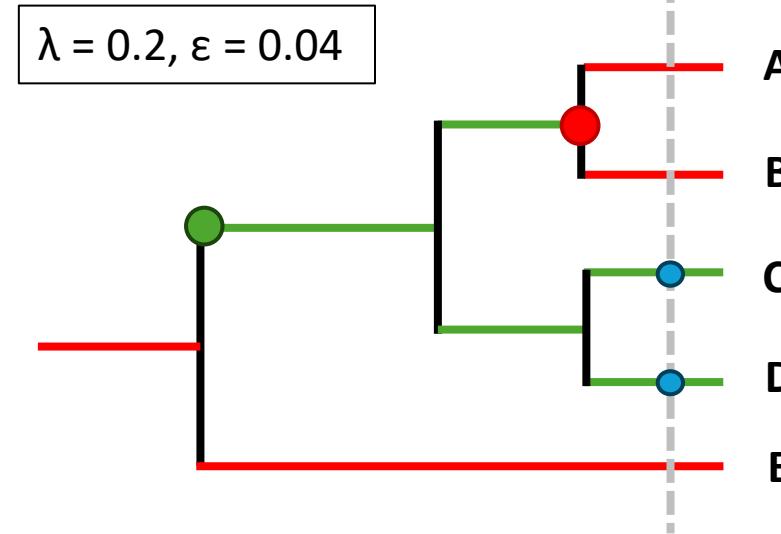
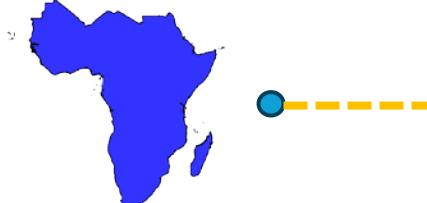
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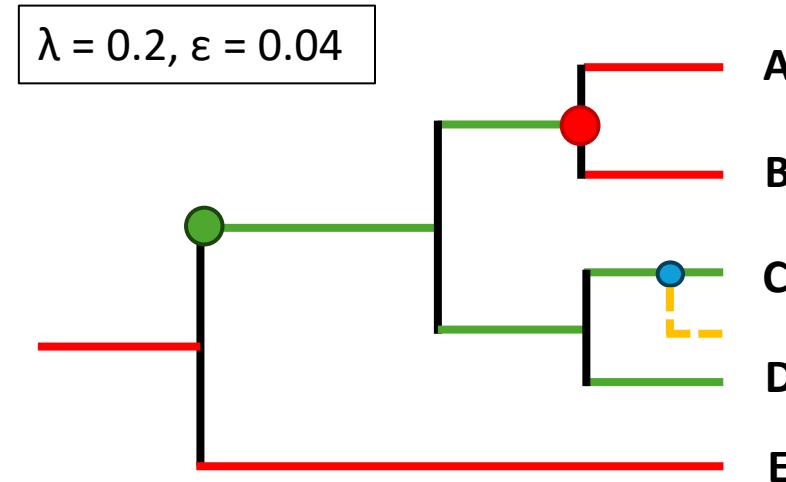
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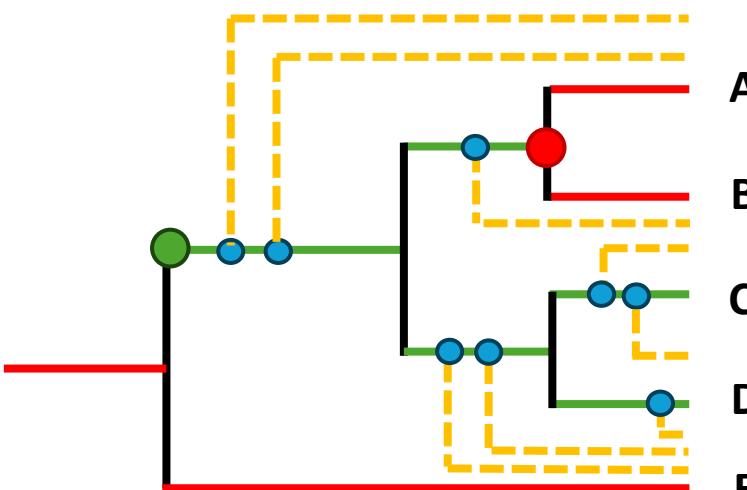
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x 1000

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# Biogeographic curation

**Data sources:** GABI v1.0 / Antmaps.org (93,568 records) and AntWeb (62,292 records)

**Goal:** Curate occurrence coordinates to use them for **biogeographic** inferences, **climatic niche** evolution, **diversity maps**, **latitudinal** and **elevation** gradient analyses, ...

- 1/ **Automatic detection** of potential errors
- 2/ **Manual checking** of outliers:
- 3/ **Retrieve occurrences** from administrative locations

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# Automatic detection

Detect ‘classic’ errors: *CoordinateCleaner* package (Zizka et al., 2019)

- Fall in **water**
- Fall in **wrong country**
- Coordinates as country **centroid**
- Coordinates as country **capital**
- In **institutions’ collections**

Detect outliers: need expert evaluation

- 1000 km min **distance**
- With less than 25% of coordinates in a single **bioregion**
- **Interactive maps** can be made available for **tricky cases** to evaluate
- **Conservative approach** = remove all outliers

# Automatic detection

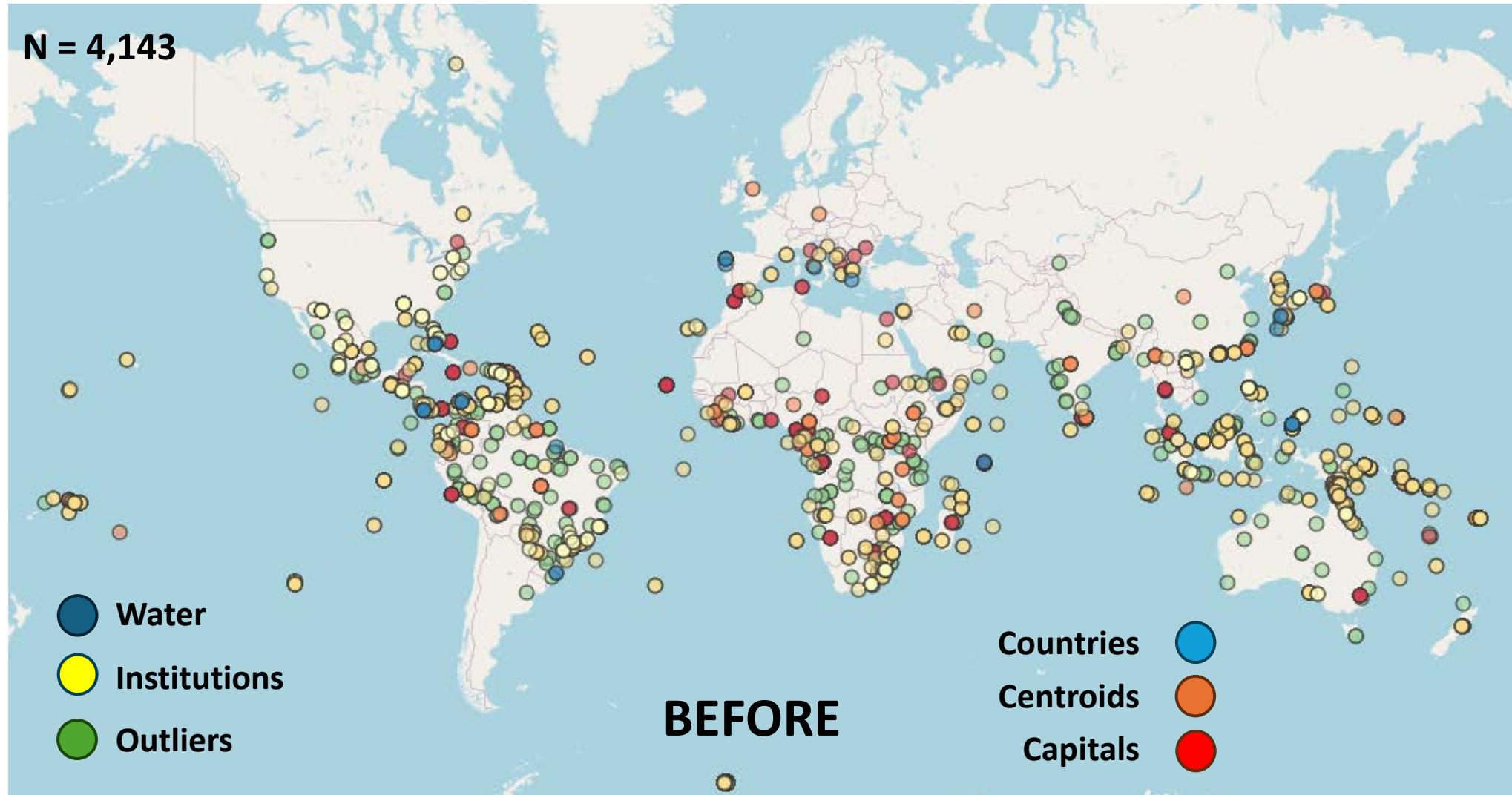
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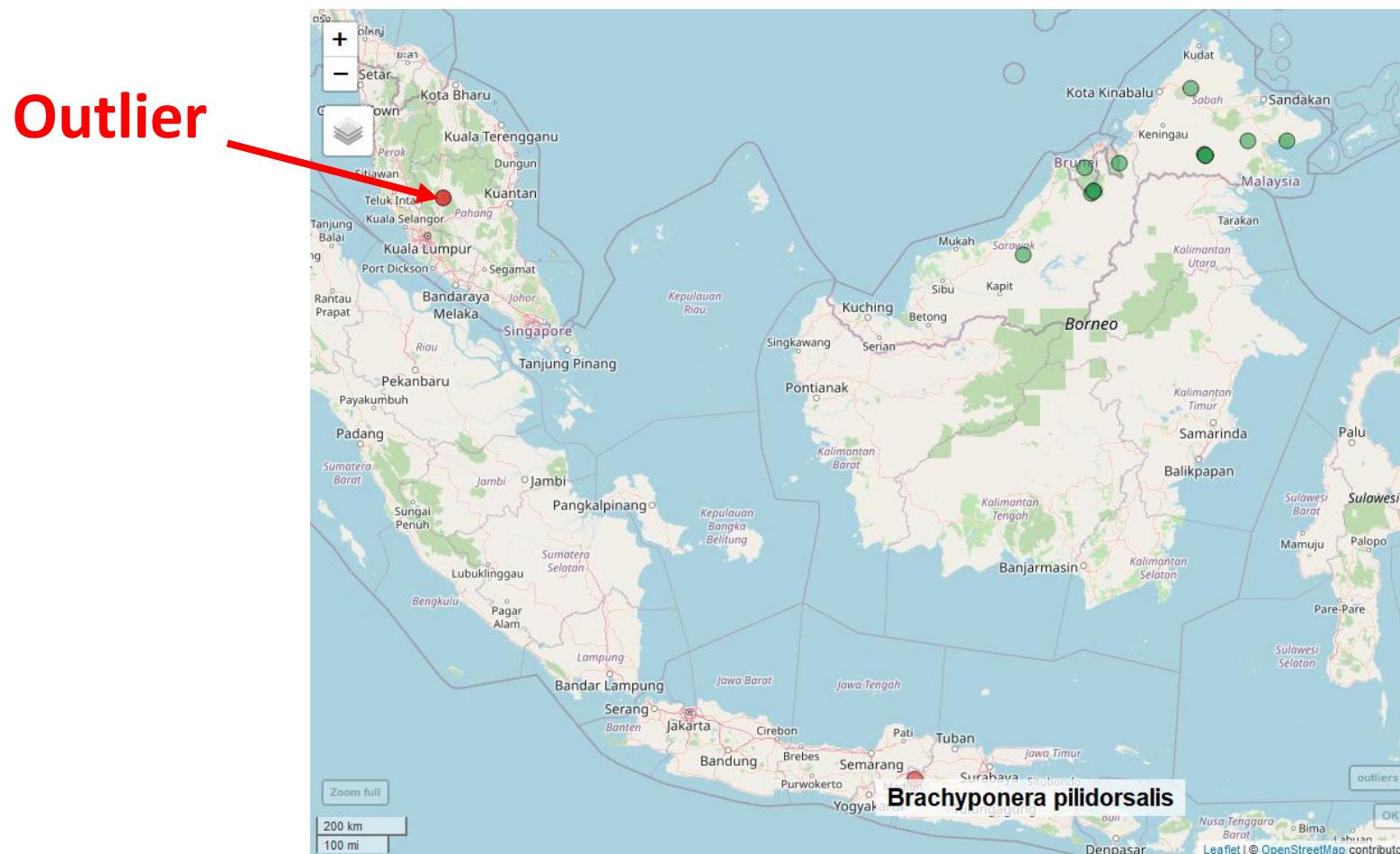
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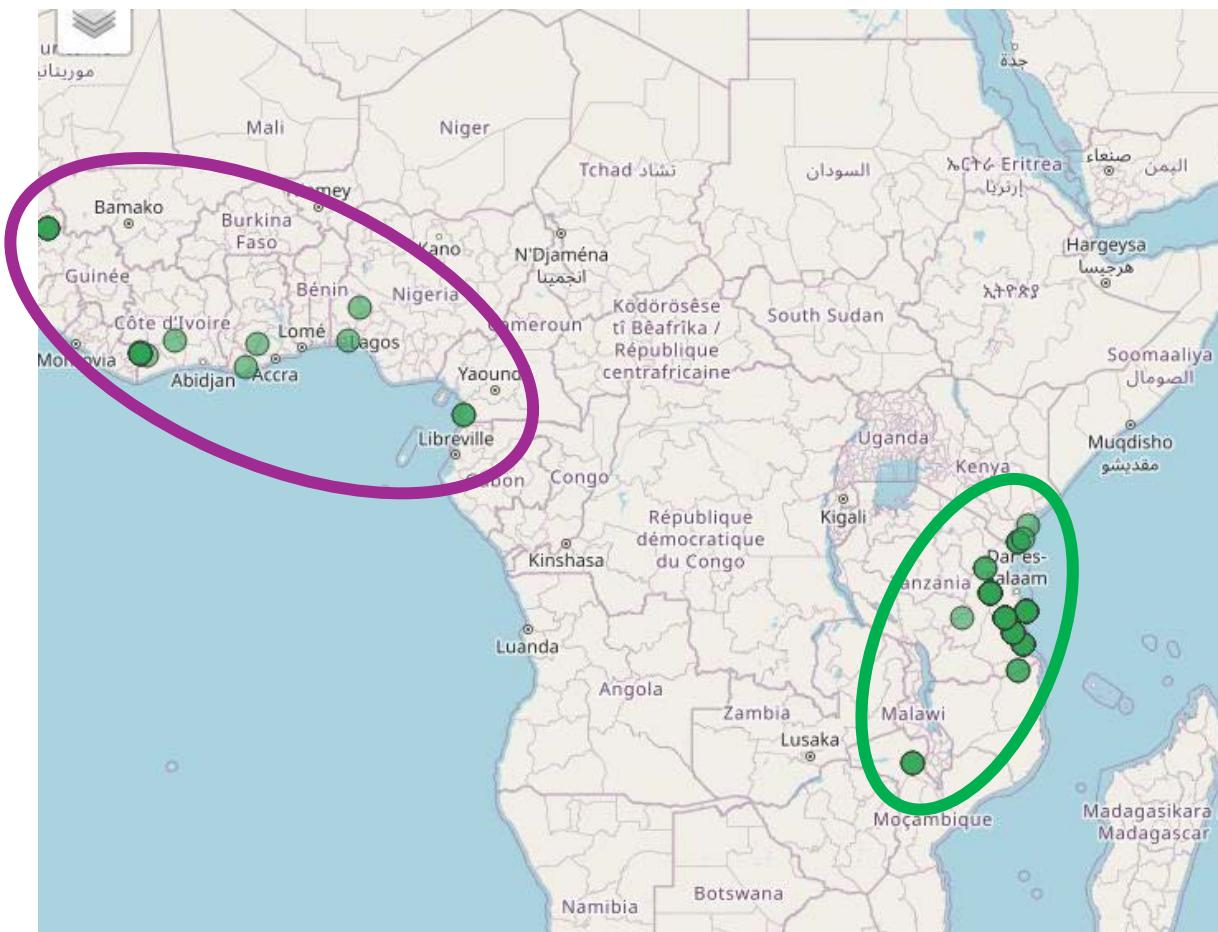
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# Manual checking of outliers



Example of distance outlier detection

# Manual checking of outliers



Example of limits of outlier detection  
Case of recently split taxa

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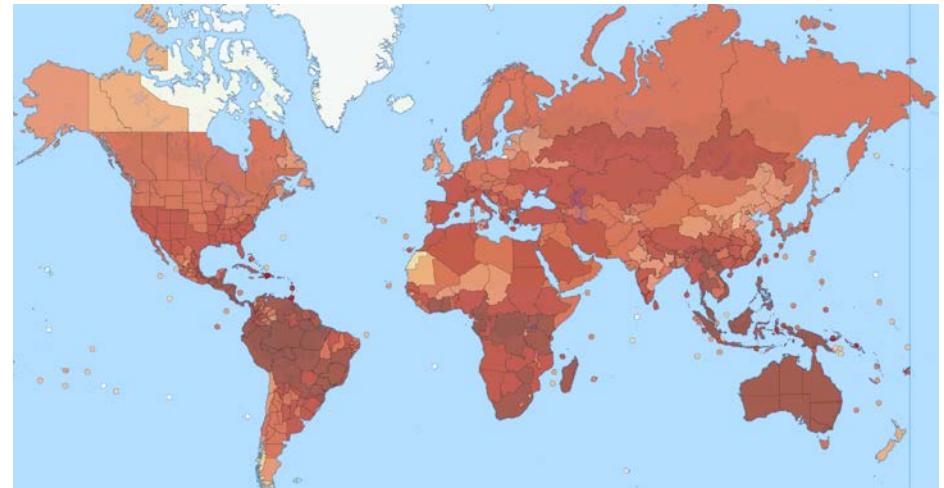
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# Retrieve occurrences

## Data sources:

- AntWeb: 2,372 occurrences  
**without coordinates** (3.8%)
- GABI: 47,972 occurrences  
**without coordinates** (51.2% !)



GABI/AntMaps = bentity2 system

Solution: Draw them at random in **geounit** when known

- Quantify **uncertainty** to allow filtering = area of the geounit

Challenge: **Homogenize** geographic unit systems

- Convert to a new curated system: **GeoBoundaries**  
(Runfola et al., 2020)



AntWeb = Geographic Names Server (GNS)

Point data, but no polygons available?!

# Retrieve occurrences

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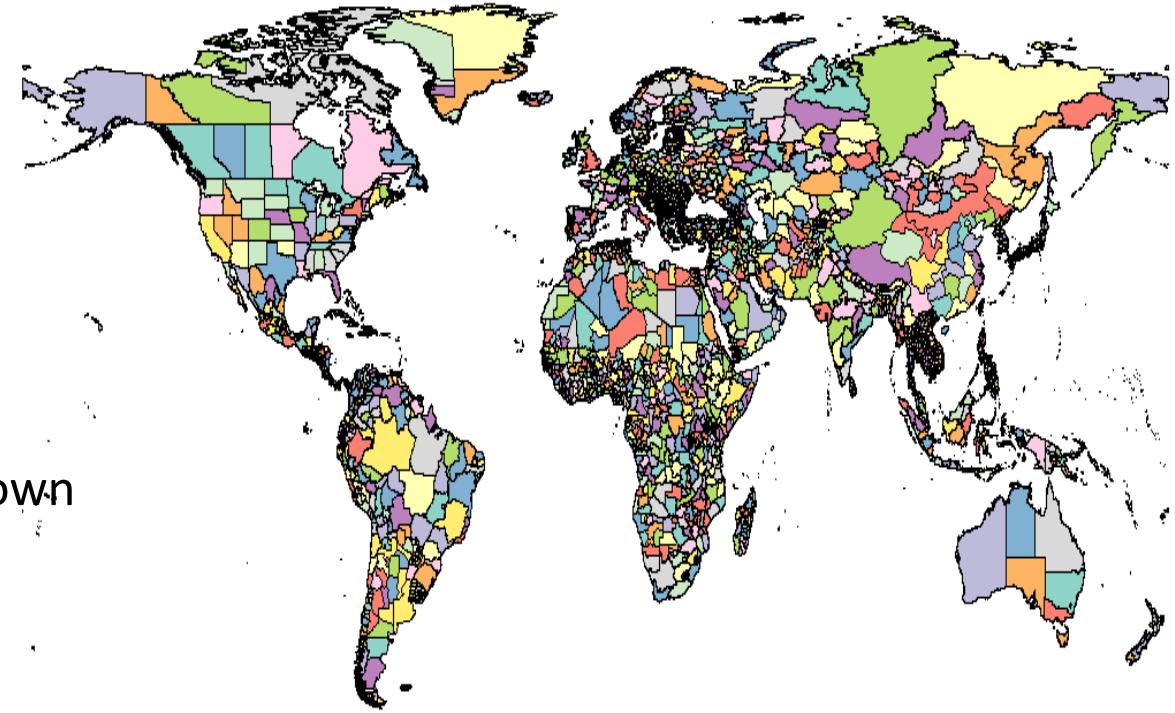
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**GeoBoundaries**

GeoLab, William & Mary College  
3,223 adm1 polygons

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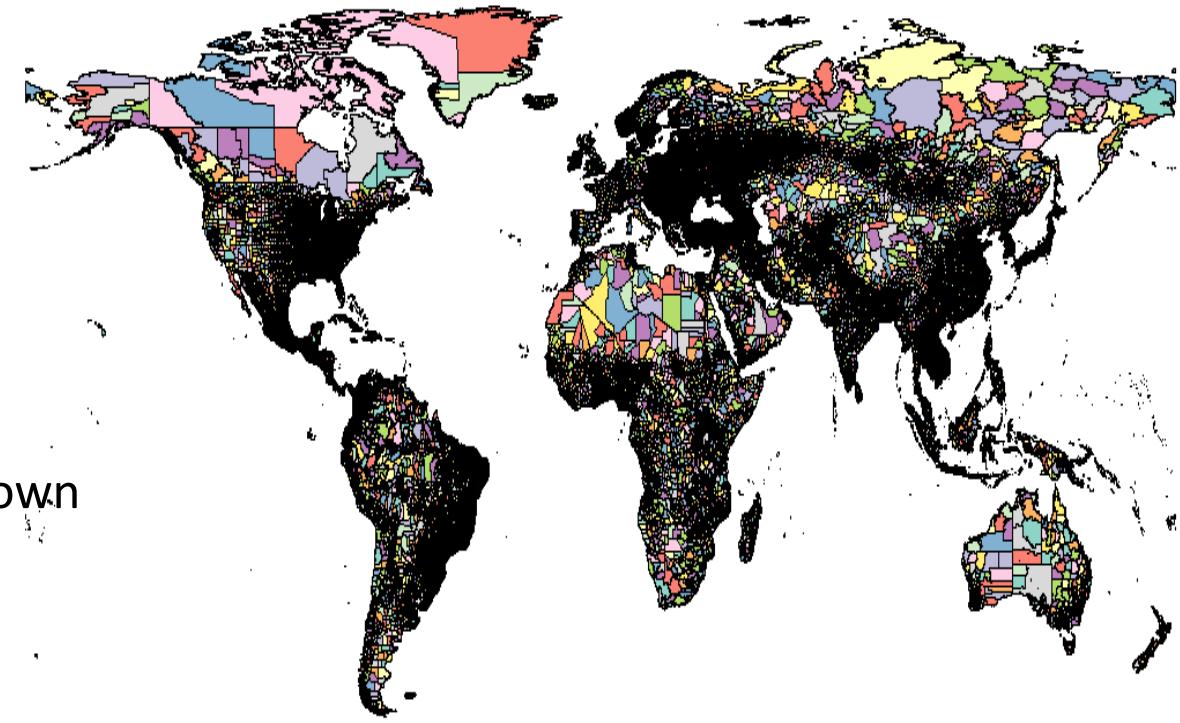
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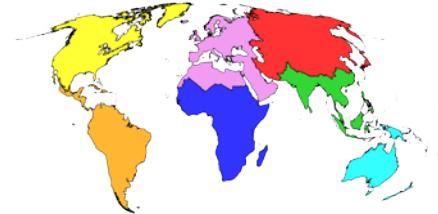
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## GeoBoundaries

GeoLab, William & Mary College  
3,223 adm1 polygons  
**49,476 adm2 polygons**

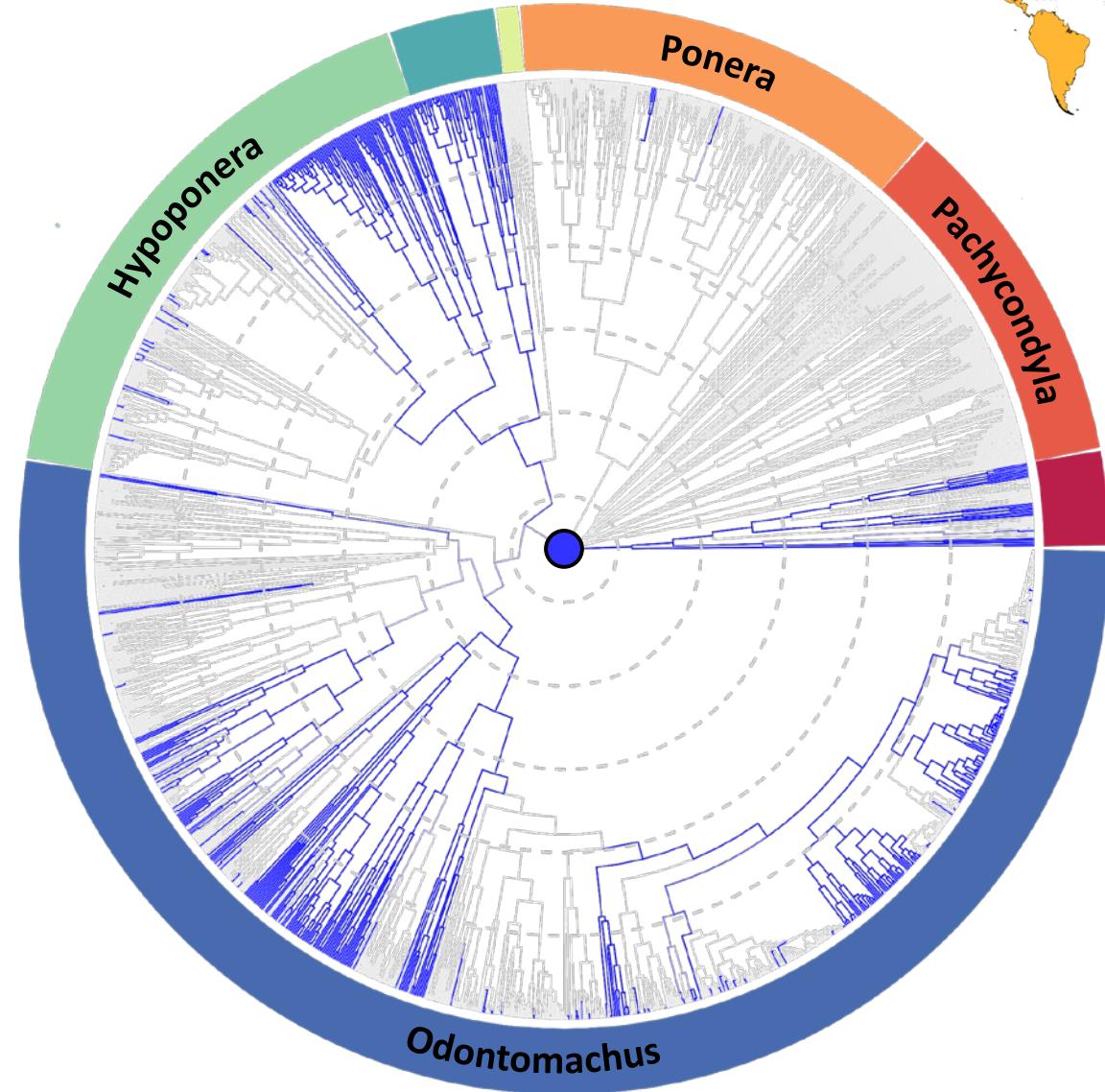
# Origins in bioregions



## Afrotropics

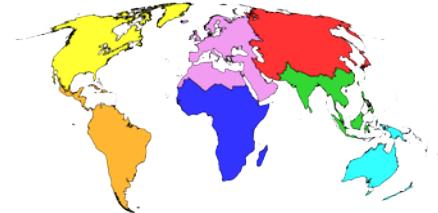
Current richness = **452 sp.**

First colonization = **113 My?**



Doré et al., *in prep.*

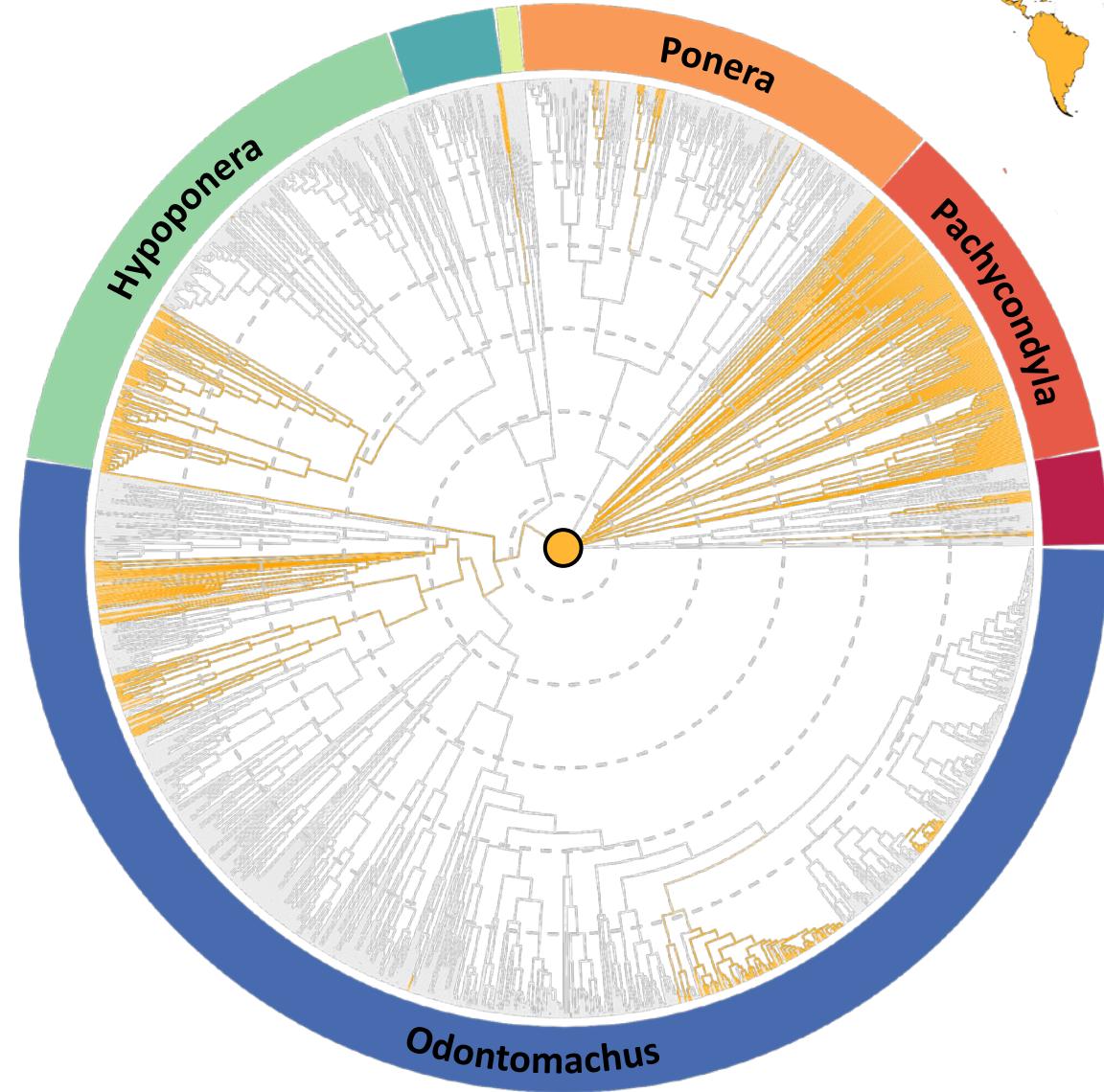
# Origins in bioregions



## Neotropics

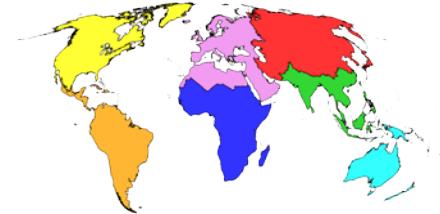
Current richness = **388 sp.**

First colonization = **113 My?**



Doré et al., *in prep.*

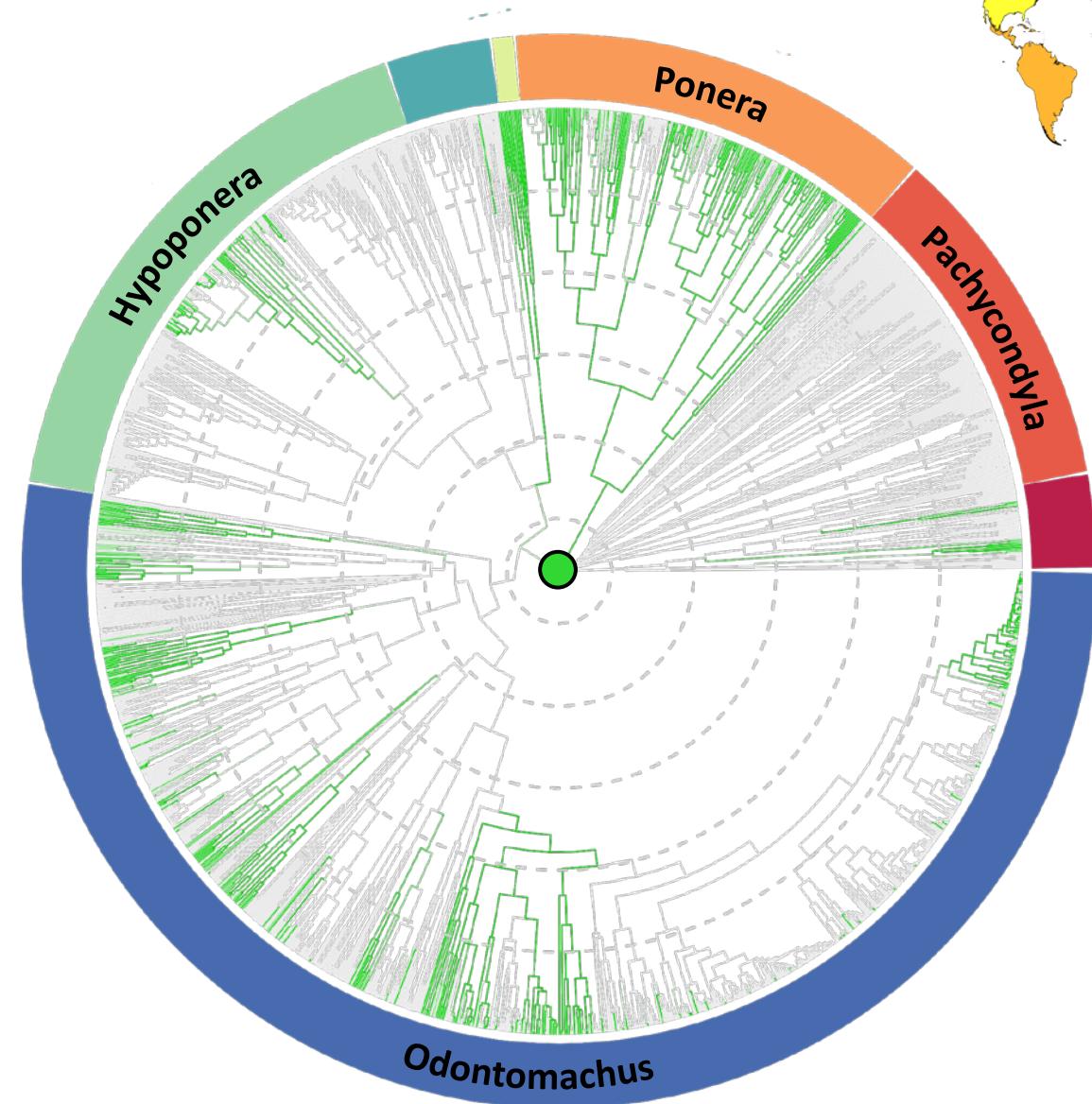
# Origins in bioregions



## IndoMalaya

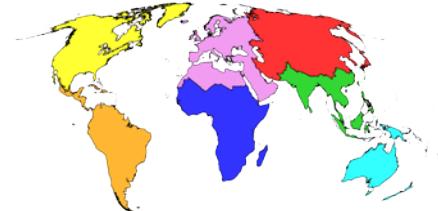
Current richness = **376** sp.

First colonization = **113** My?



Doré et al., *in prep.*

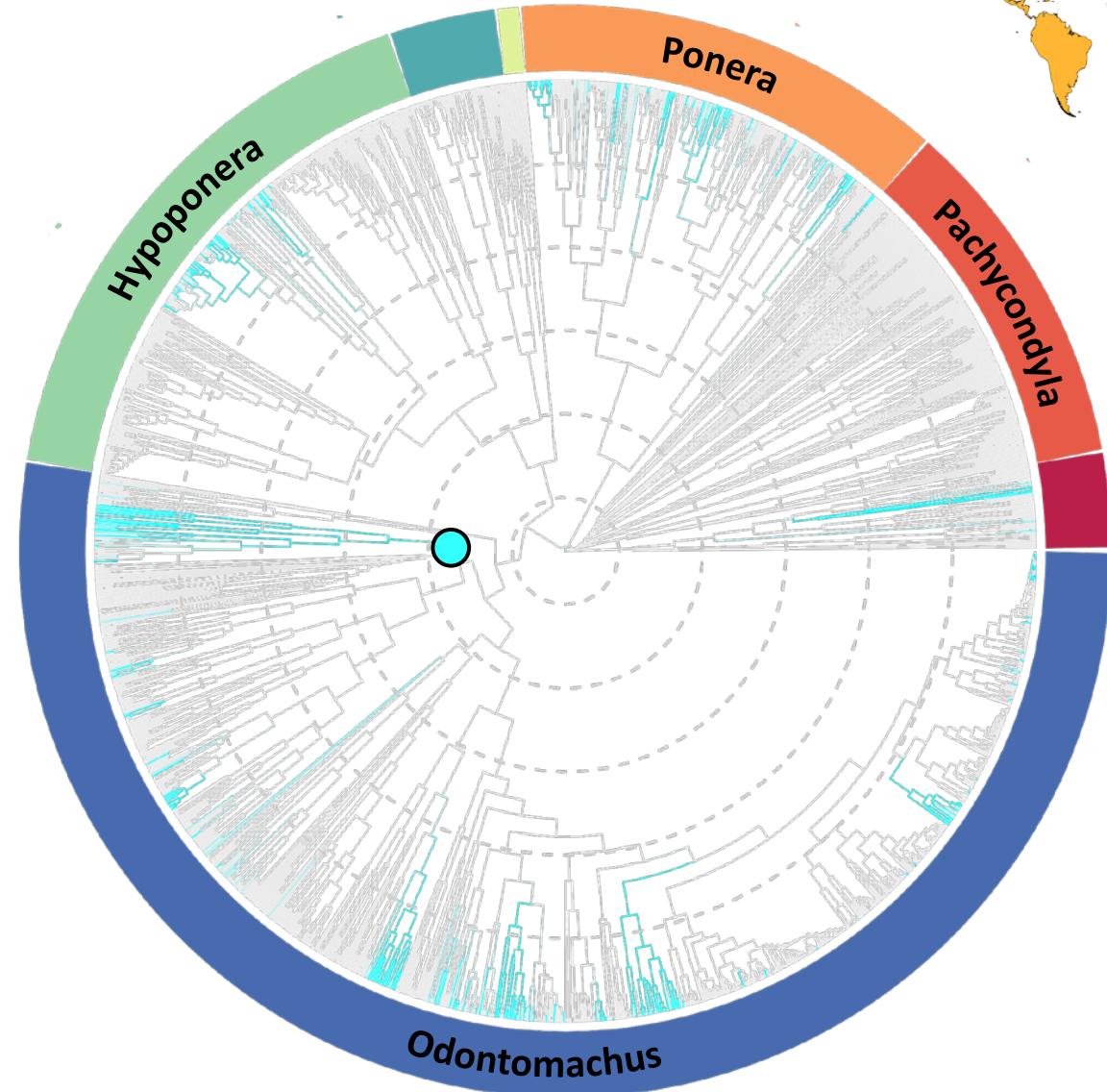
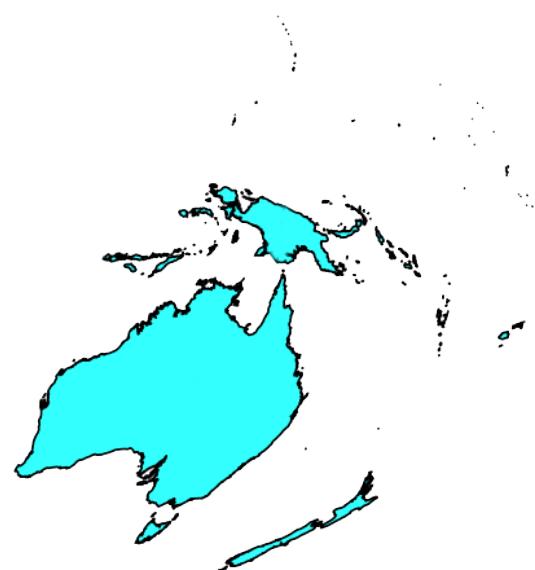
# Origins in bioregions



## Australasia

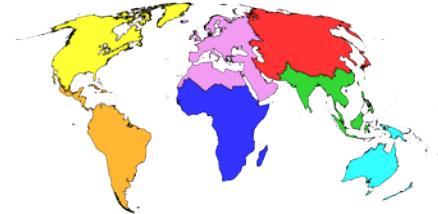
Current richness = **232** sp.

First colonization = **90 My?**



Doré et al., *in prep.*

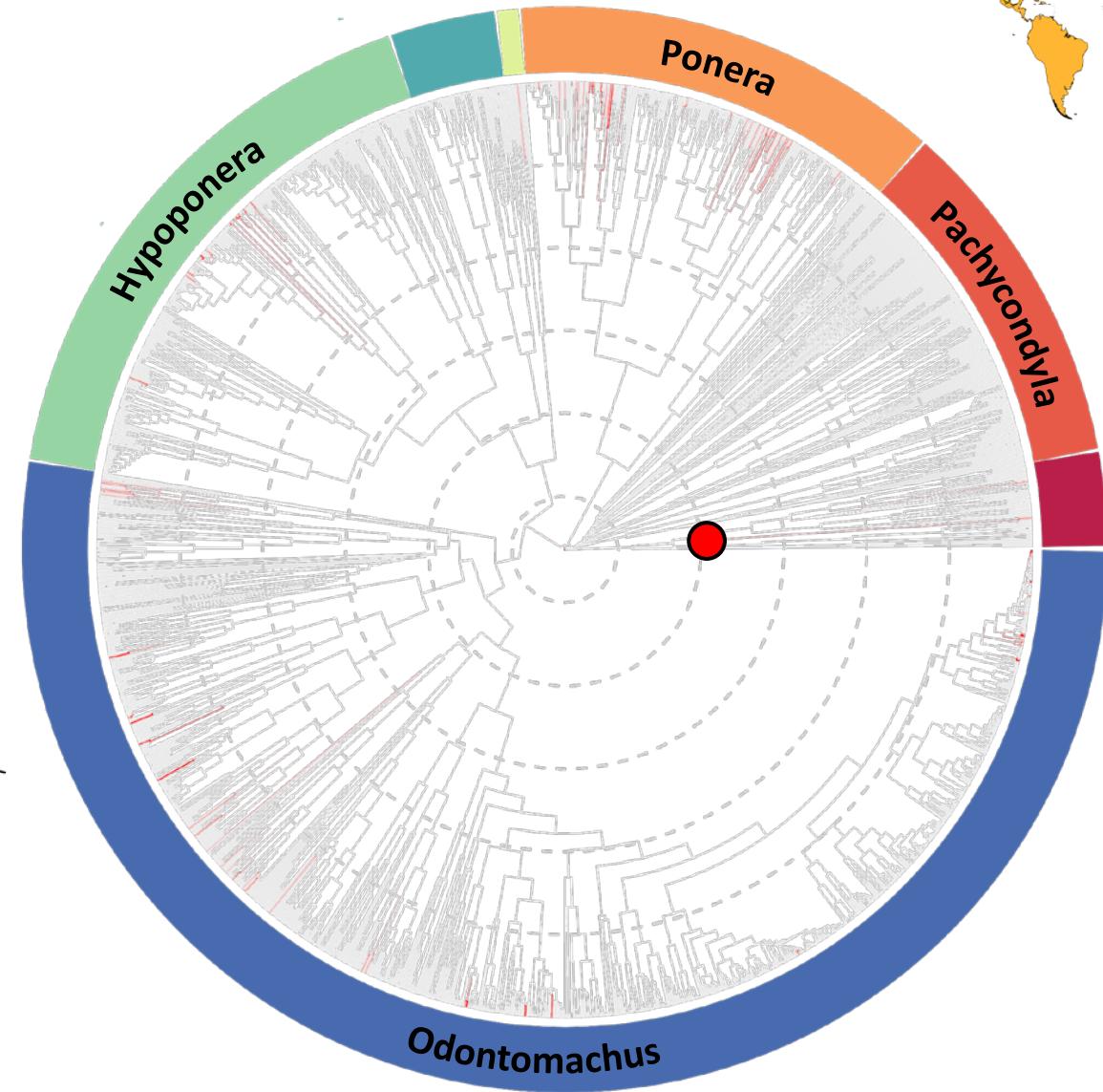
# Origins in bioregions



## Eastern Palearctic

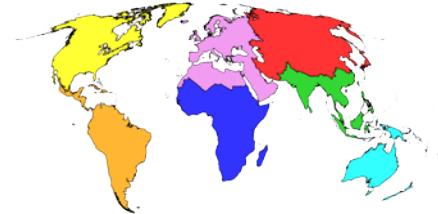
Current richness = **43 sp.**

First colonization = **80 My?**



Doré et al., *in prep.*

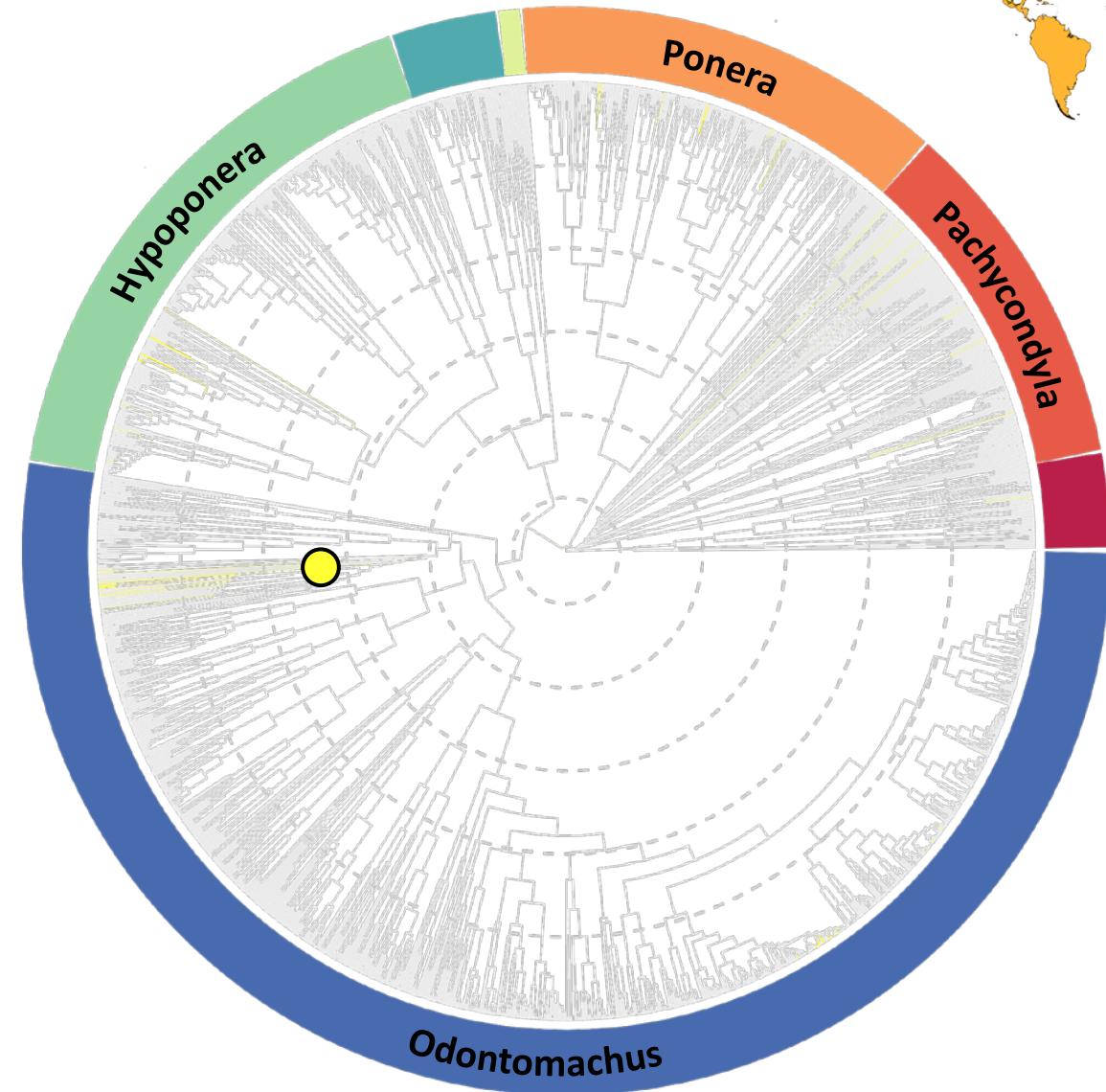
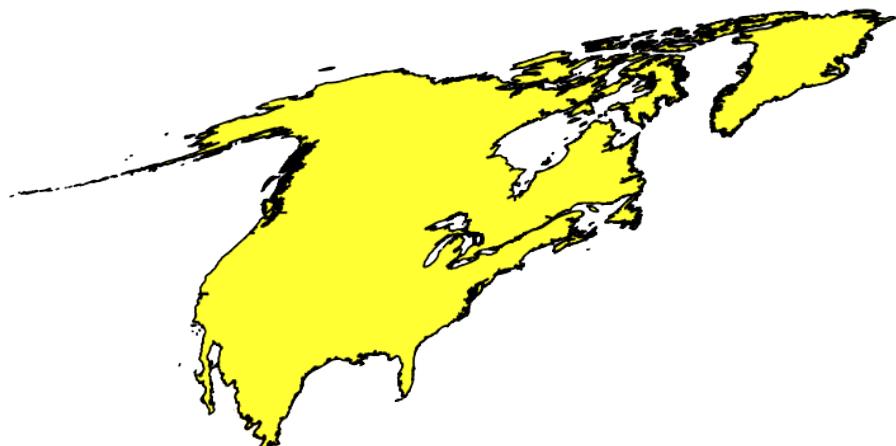
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Nearctic

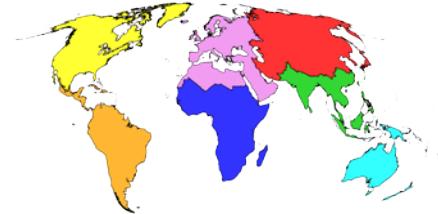
Current richness = **25 sp.**

First colonization = **55 My?**



Doré et al., *in prep.*

# Origins in bioregions



## Western Palearctic

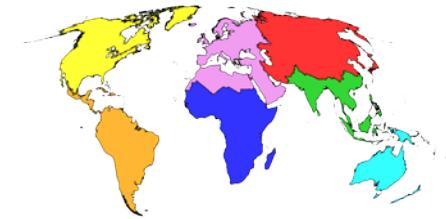
Current richness = **17 sp.**

First colonization = **35 My?**

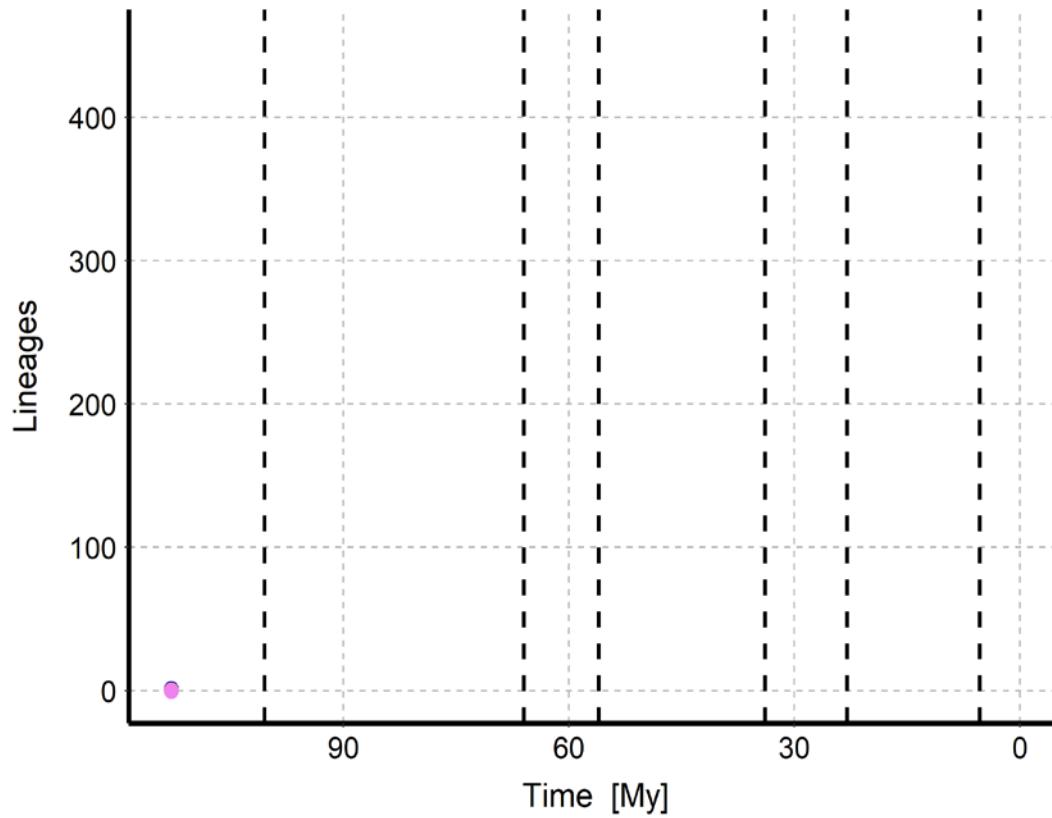


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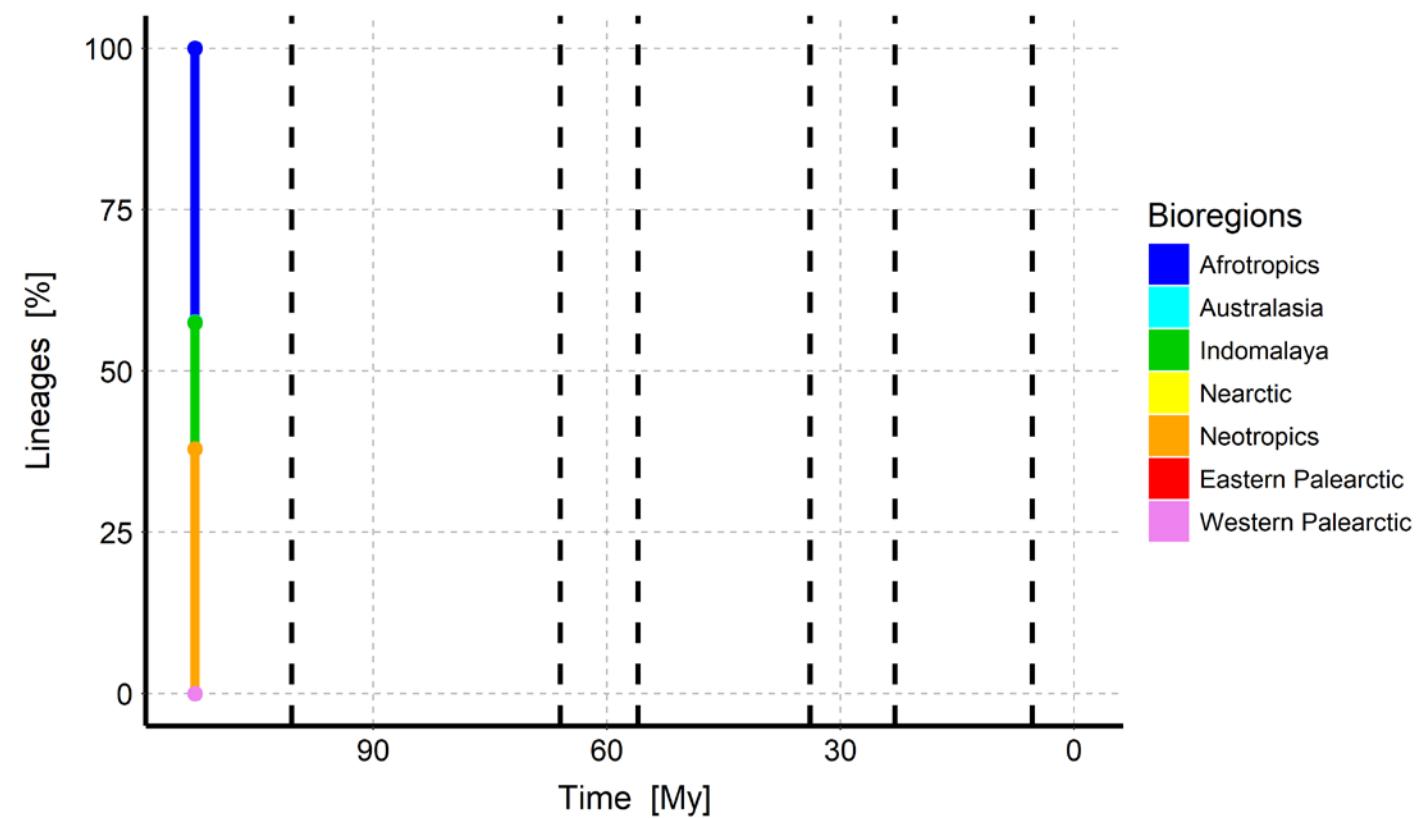
# Lineages through time



LTT per bioregion  
Time: 113 My ago

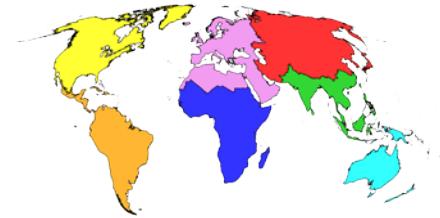


LTT per bioregion  
Time: 113 My ago

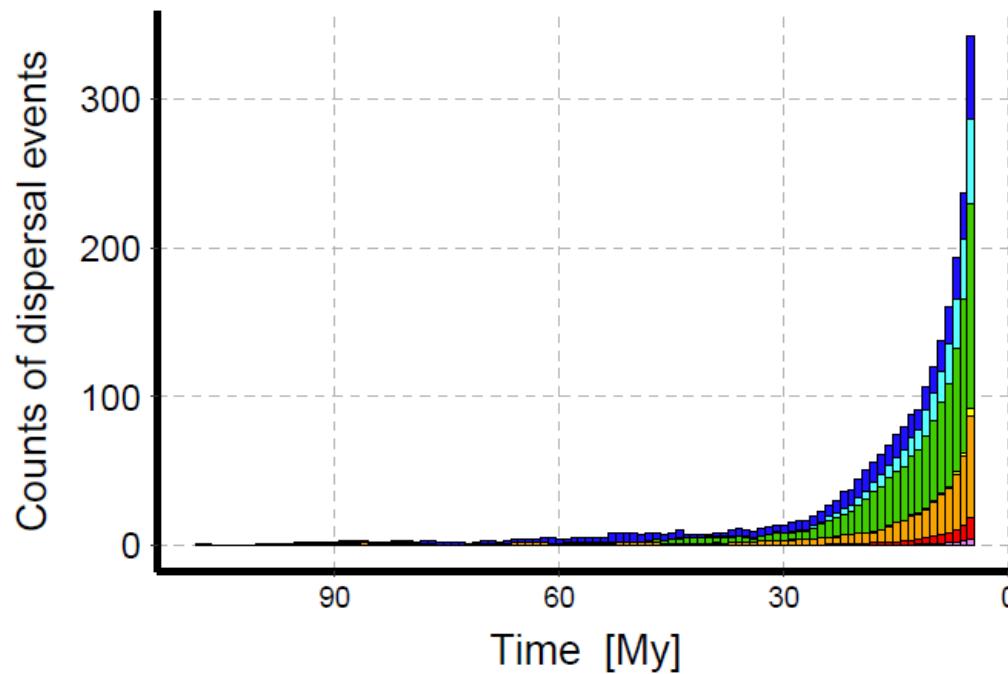


Doré et al., *in prep.*

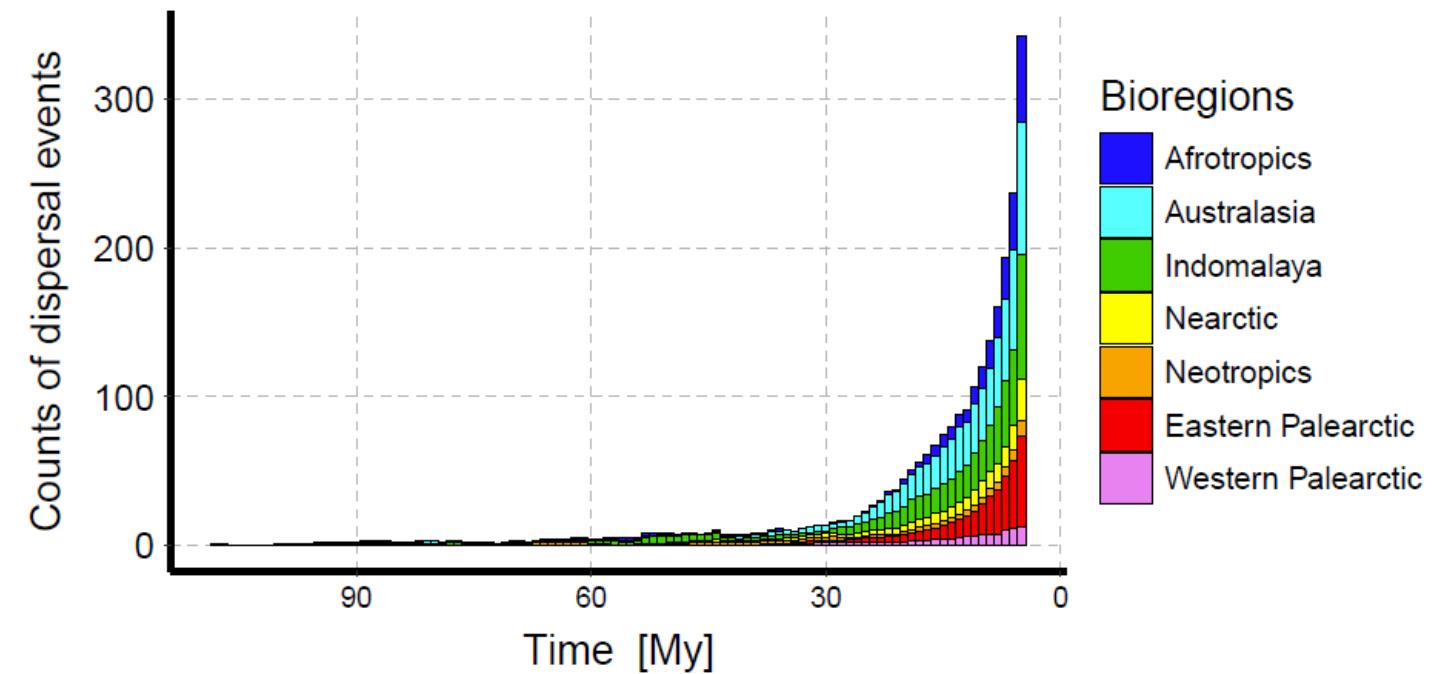
# Dispersal events in time



Dispersal events  
per Source bioregions

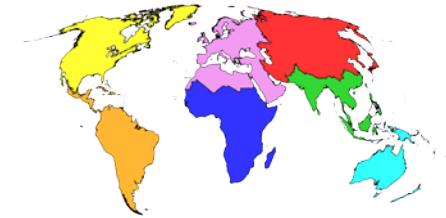


Dispersal events  
per Destination bioregions

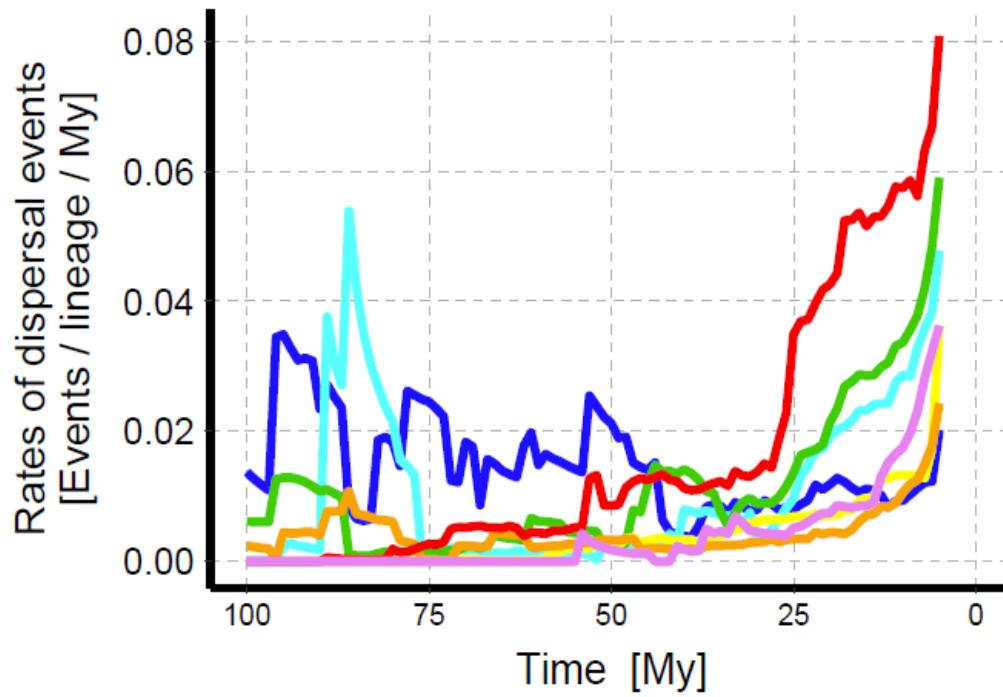


Doré et al., *in prep.*

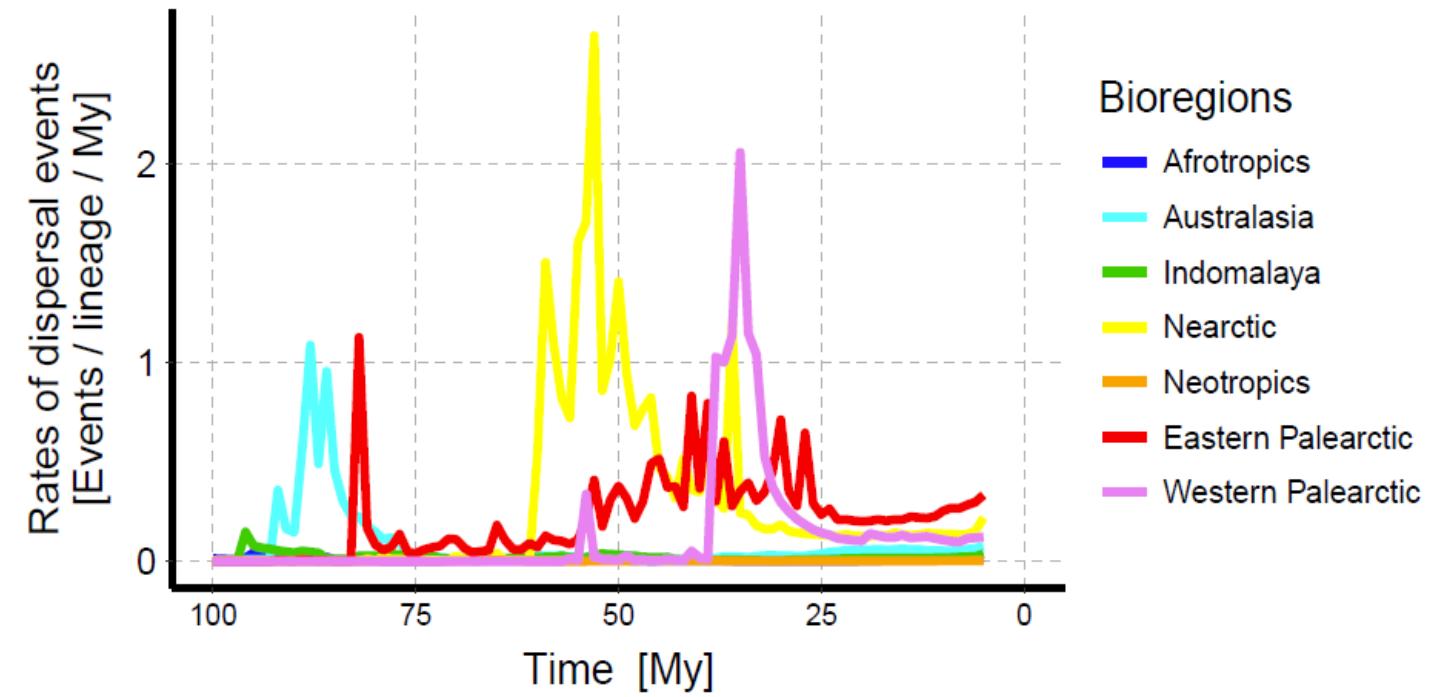
# Dispersal events in time



Rates of dispersal events  
per Source bioregions

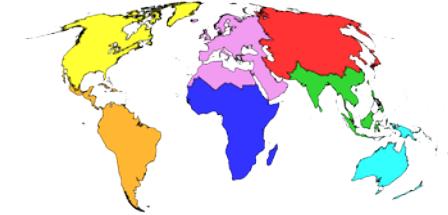


Rates of dispersal events  
per Destination bioregions

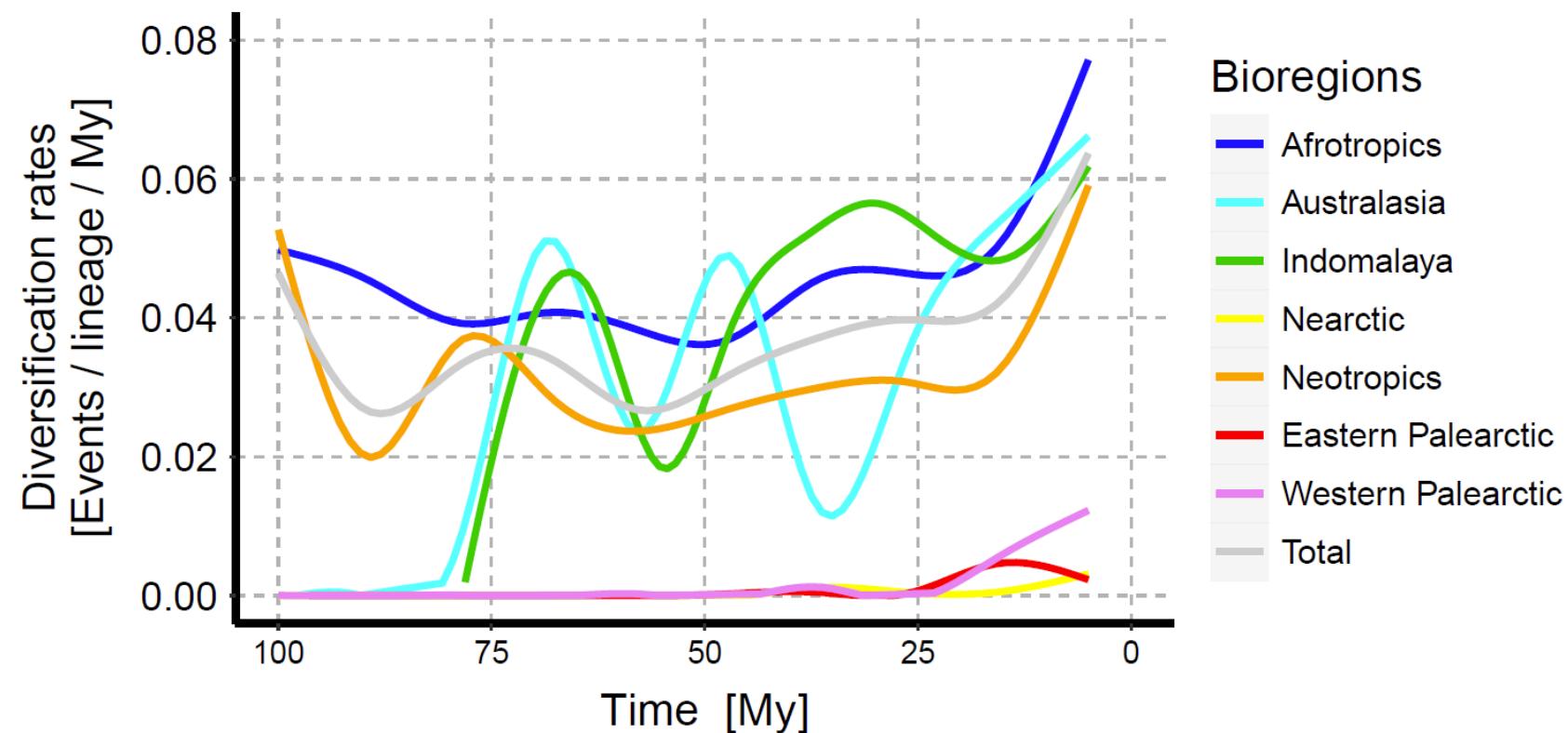


Doré et al., *in prep.*

# *In situ* diversification in time

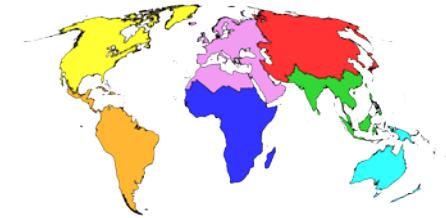


Rates of *in situ* speciation events  
per Bioregions

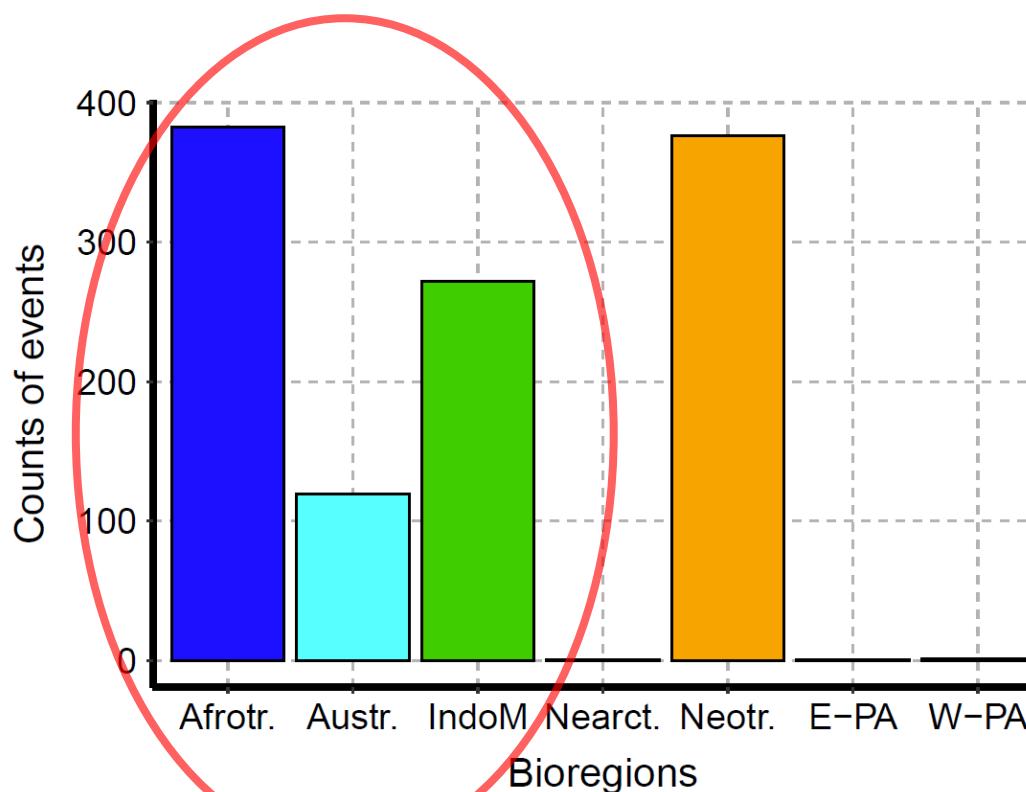


Doré et al., *in prep.*

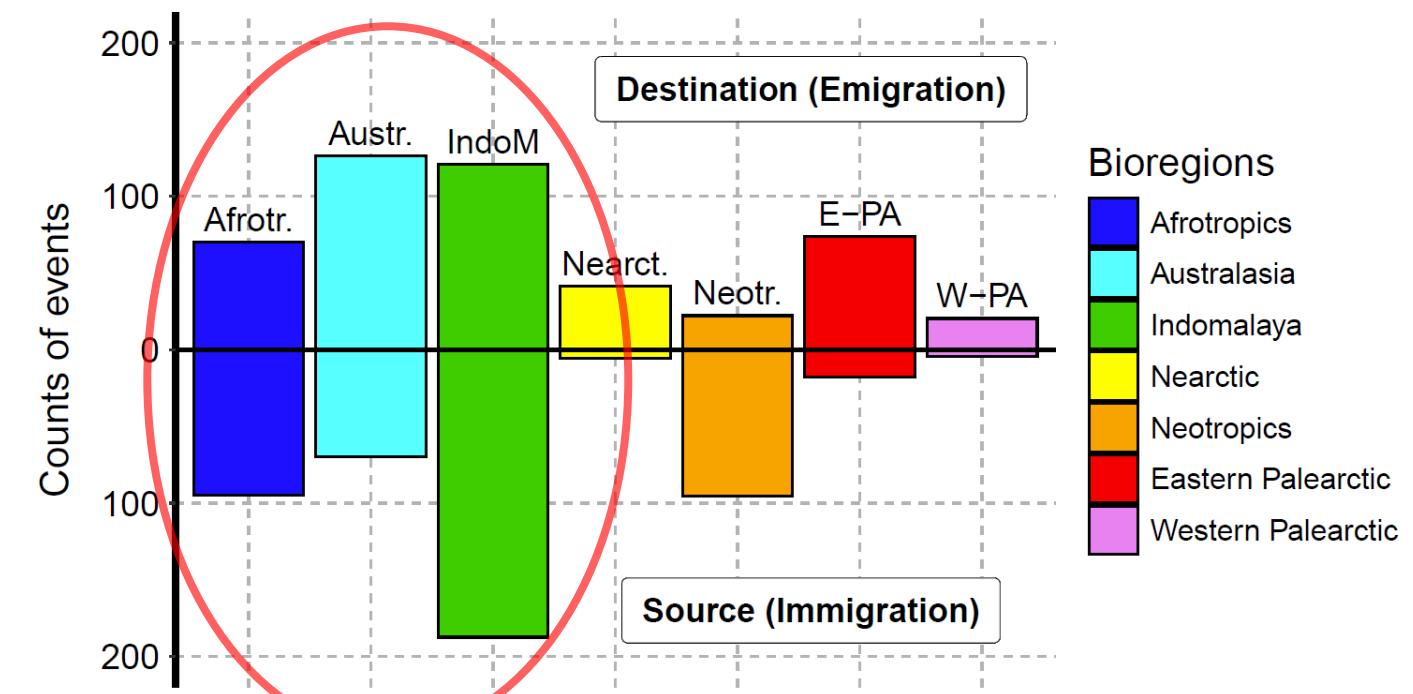
# Origin of diversity



*In situ* diversification  
per Bioregions

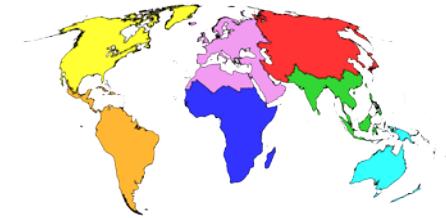


Dispersal events  
per Bioregions

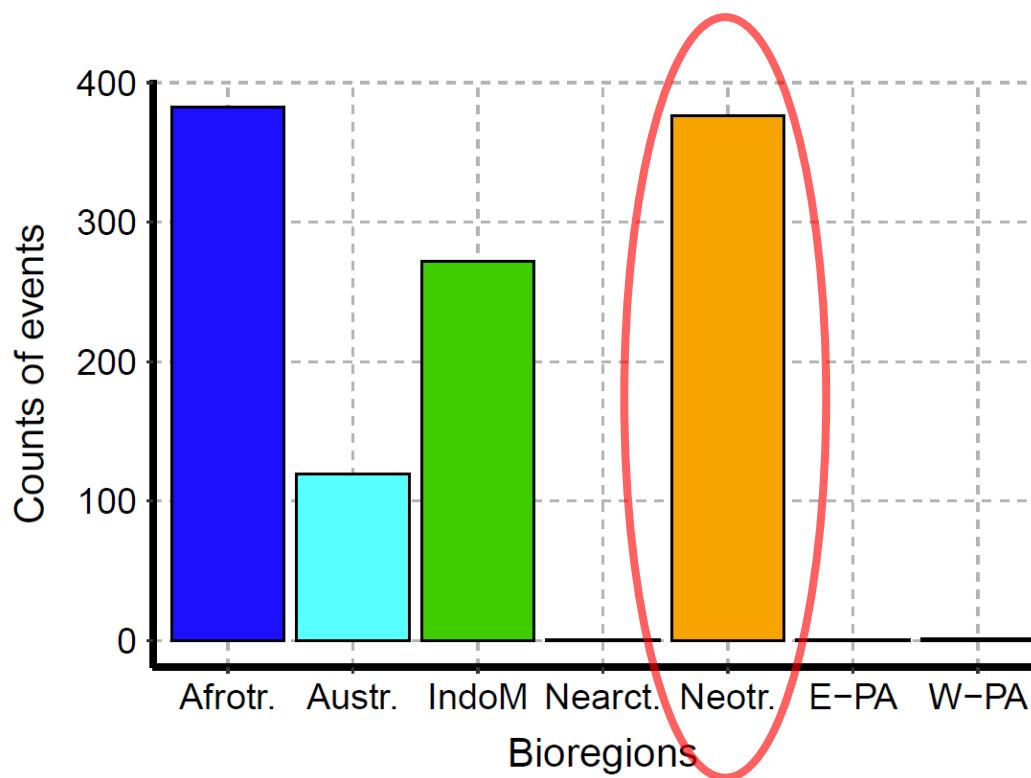


Doré et al., *in prep.*

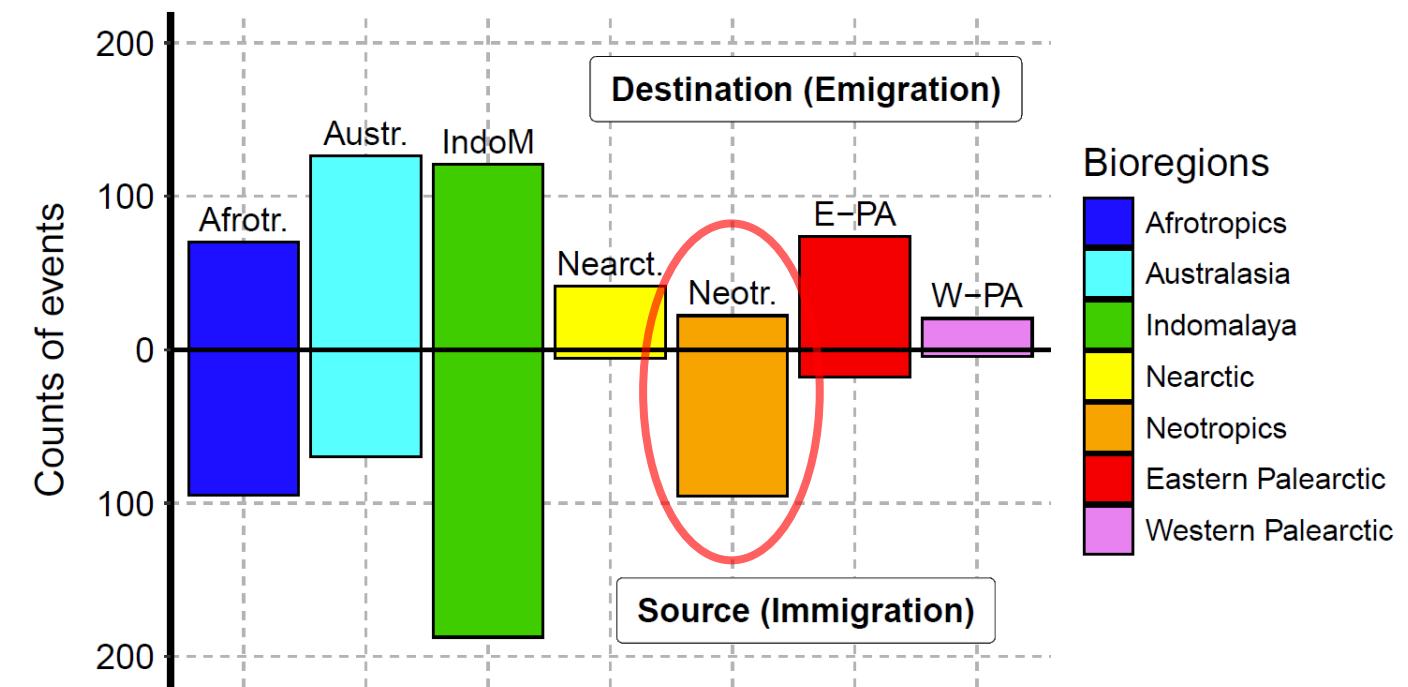
# Origin of diversity



*In situ* diversification  
per Bioregions

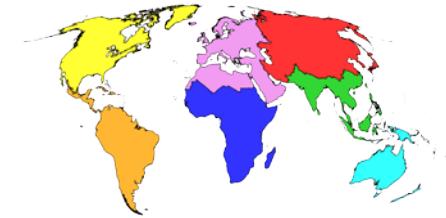


Dispersal events  
per Bioregions

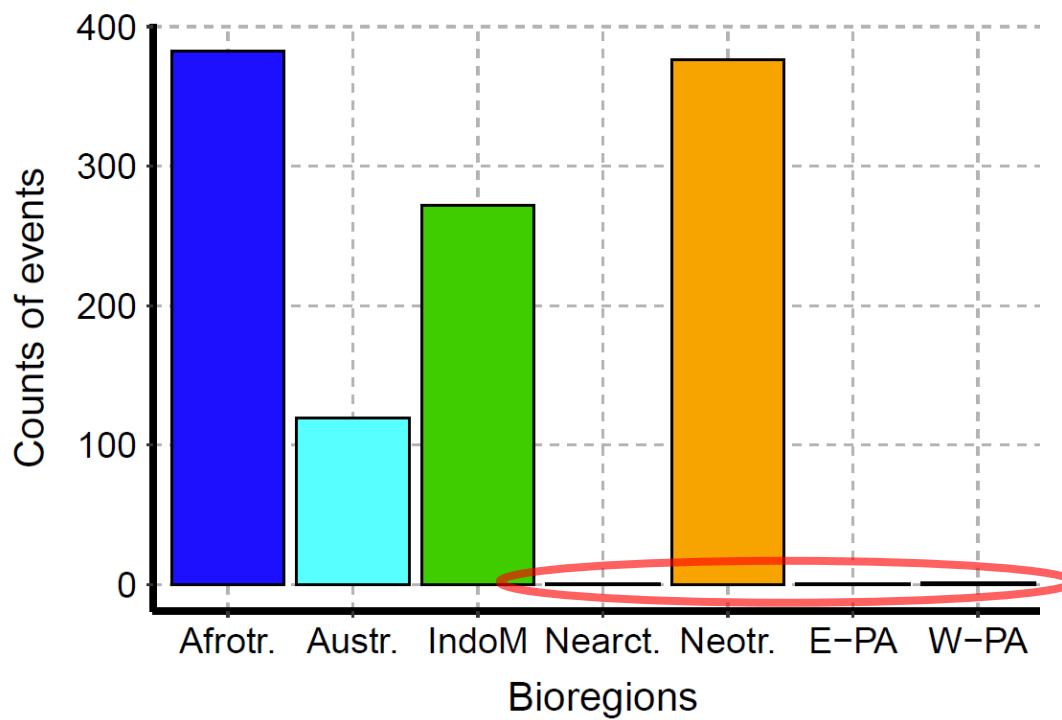


Doré et al., *in prep.*

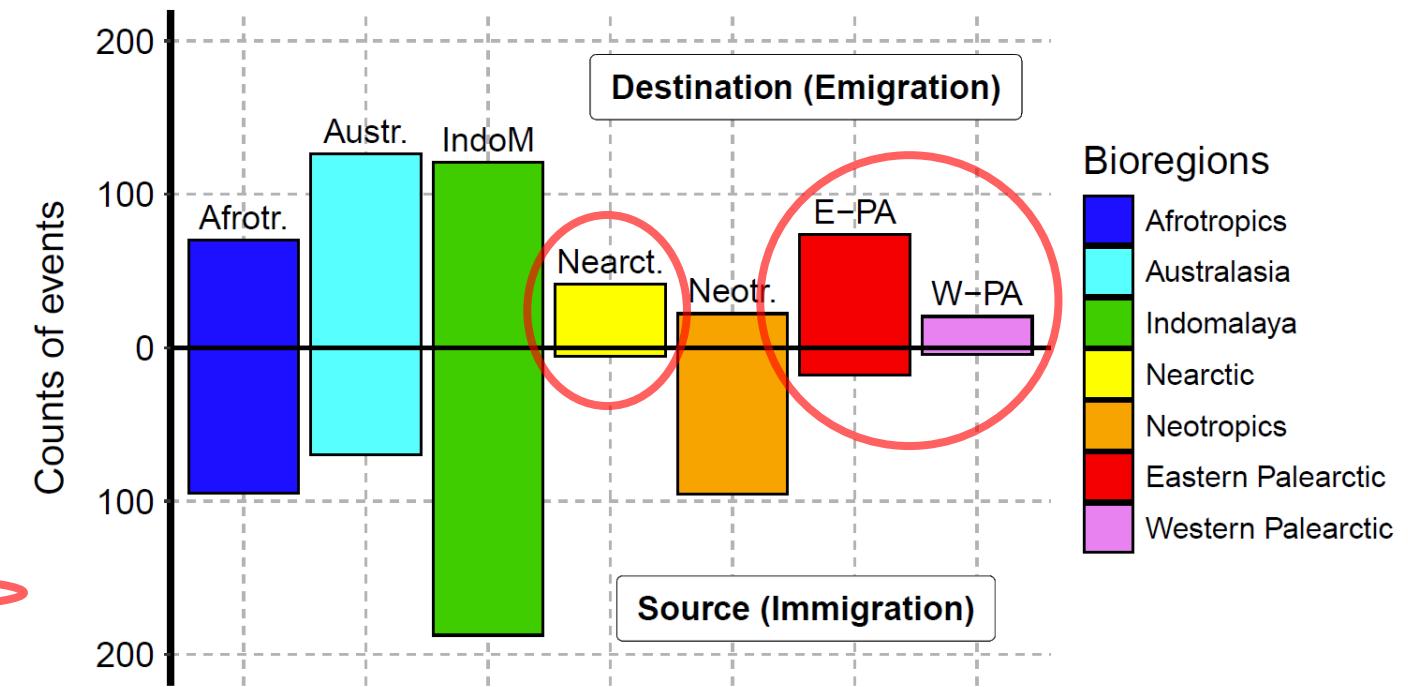
# Origin of diversity



*In situ* diversification  
per Bioregions

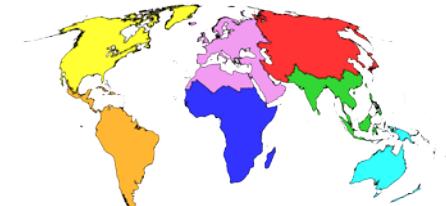


Dispersal events  
per Bioregions



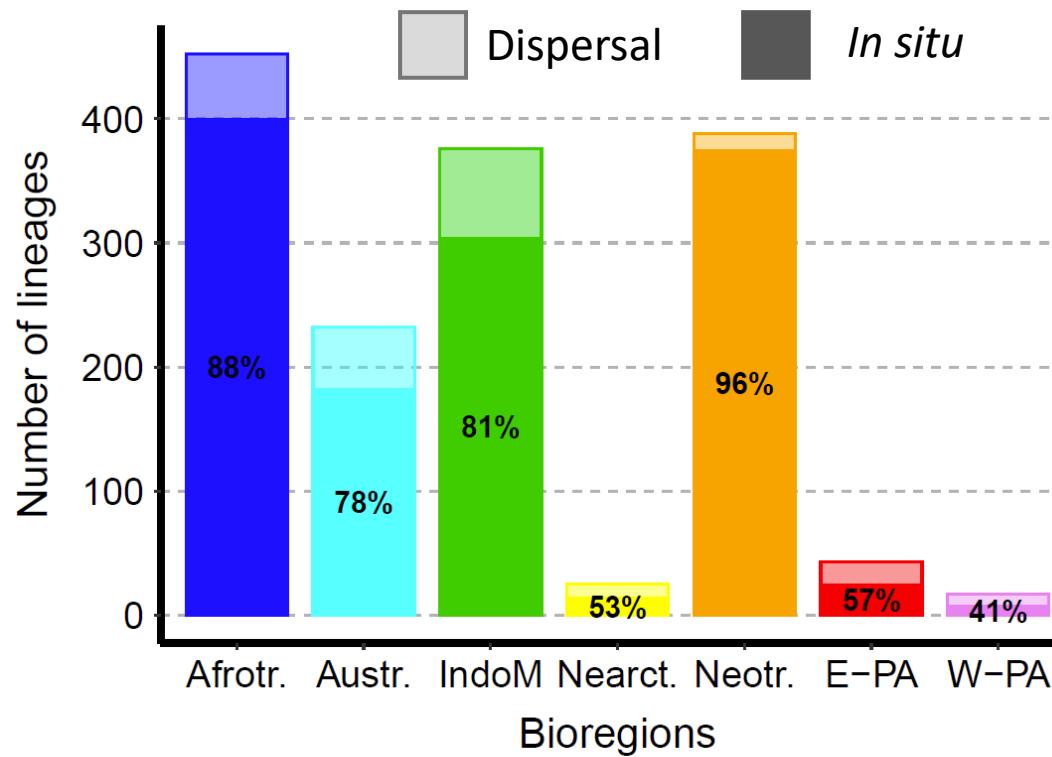
Doré et al., *in prep.*

# Origin of diversity

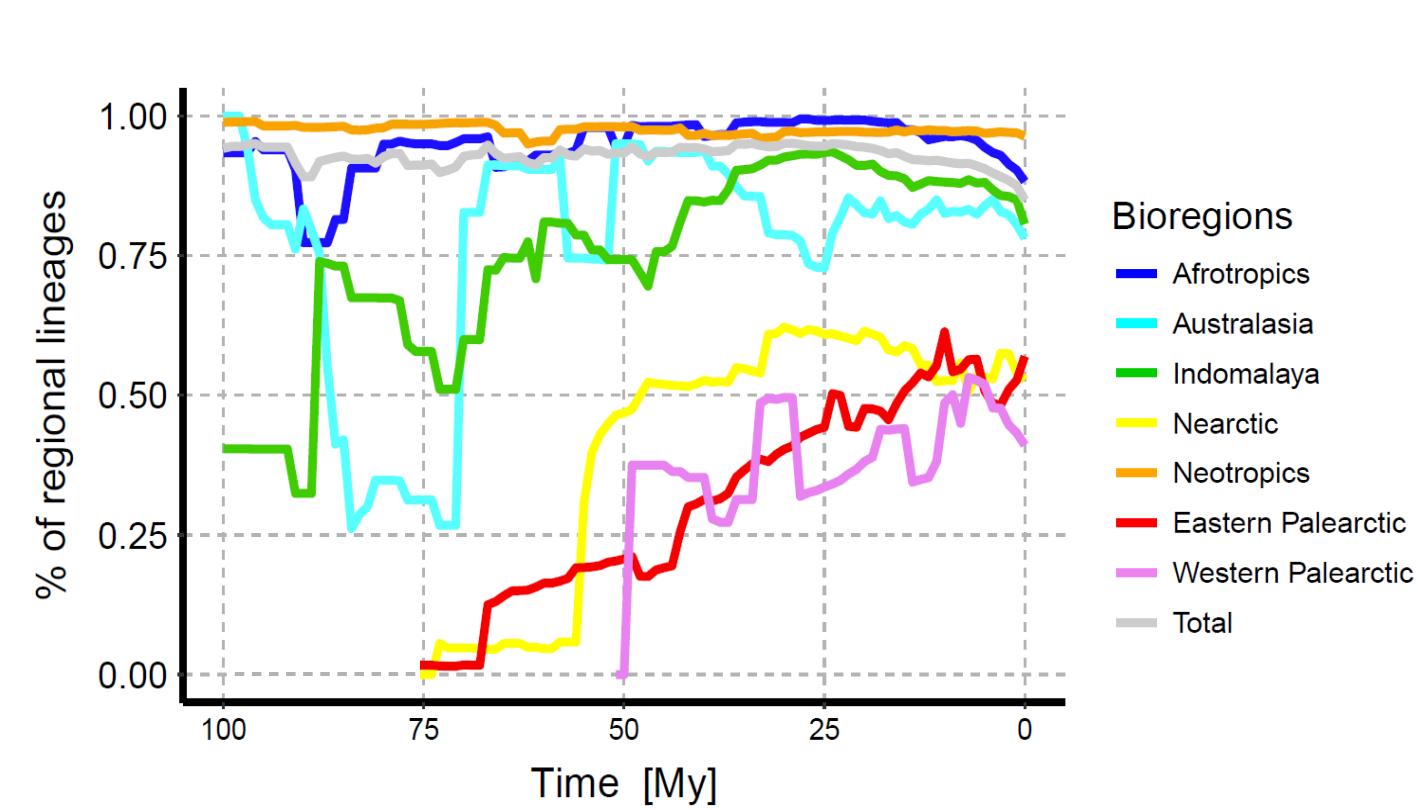


Lineage origins per Bioregions

Now

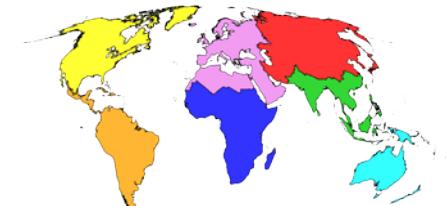


Across time

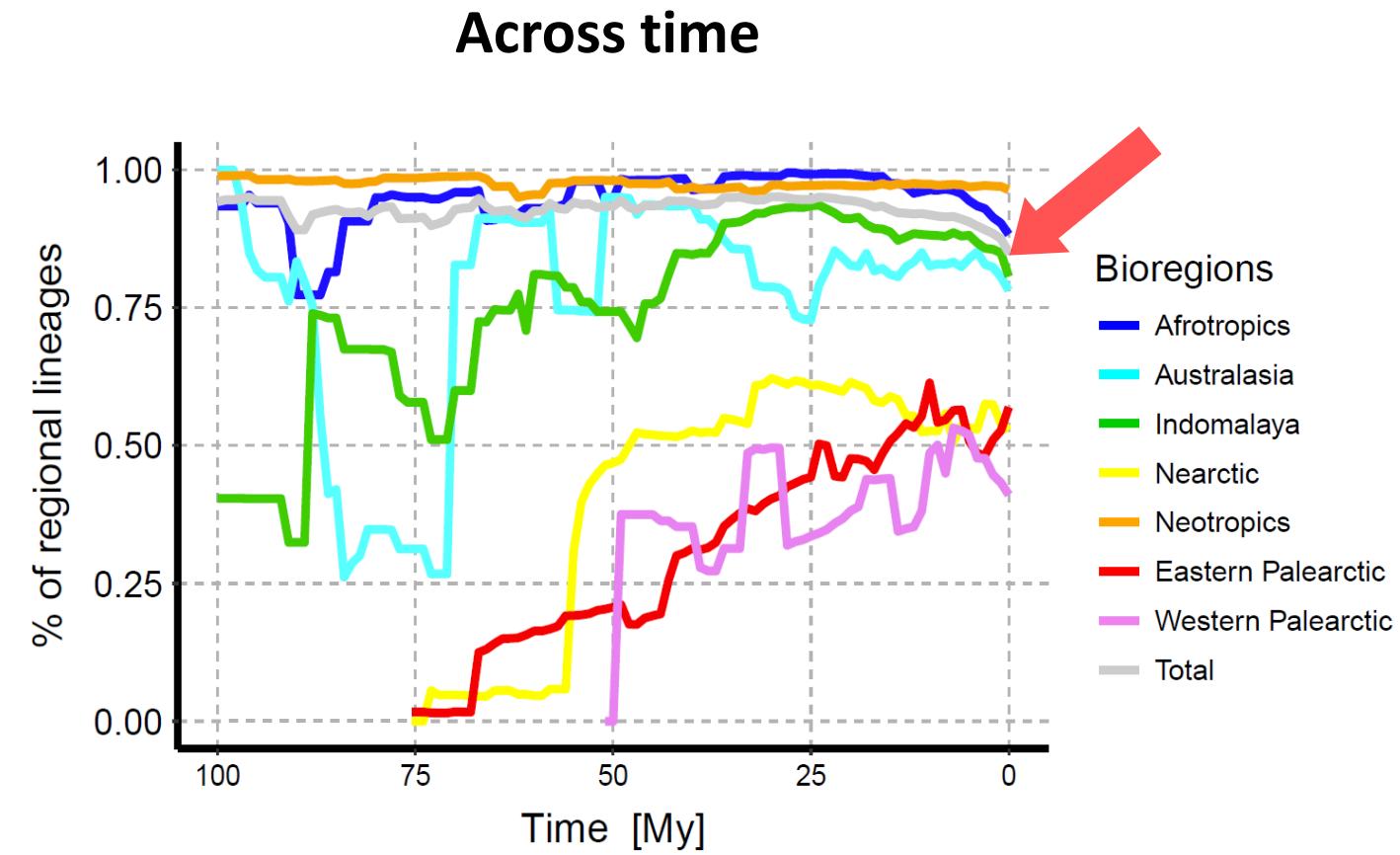
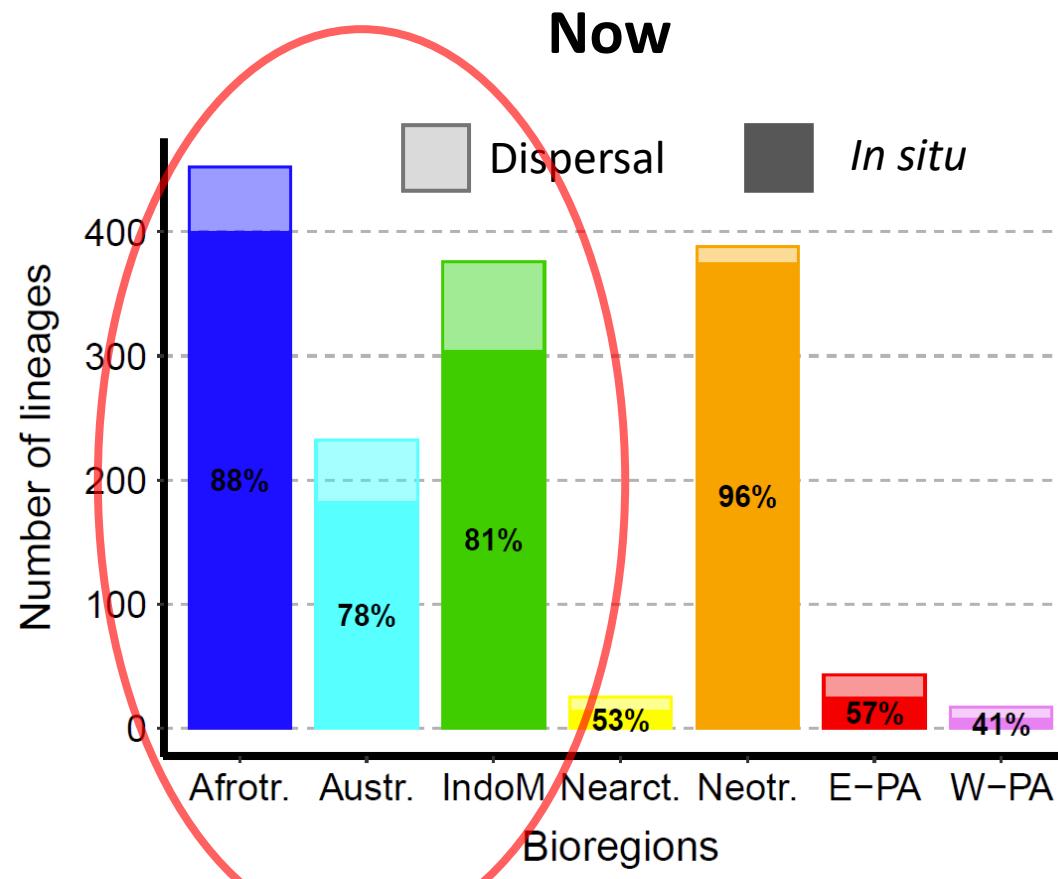


Doré et al., *in prep.*

# Origin of diversity

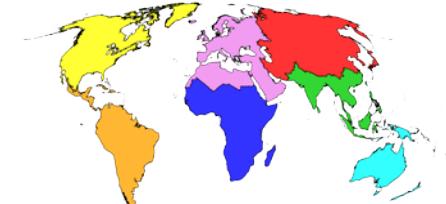


Lineage origins per Bioregions

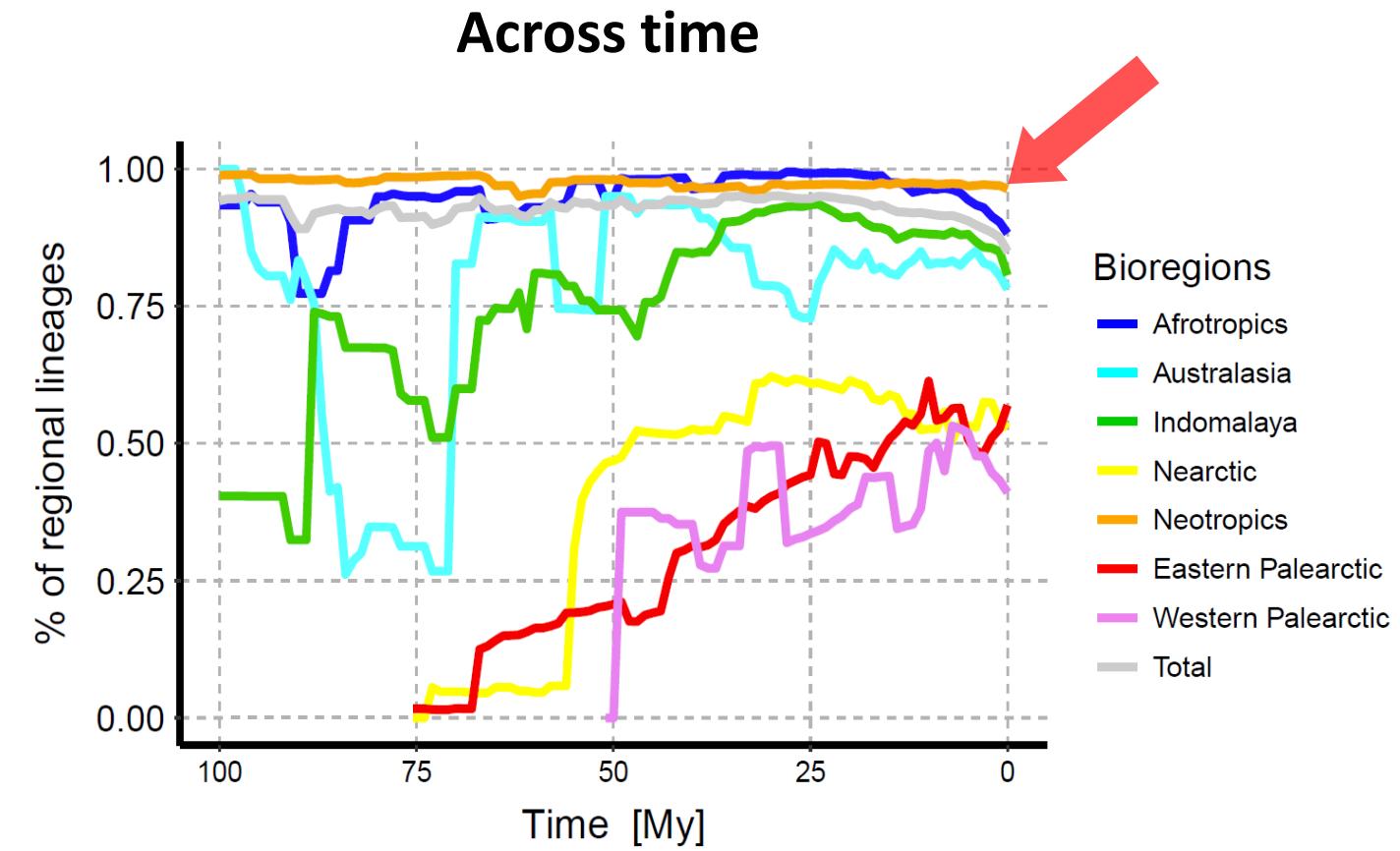
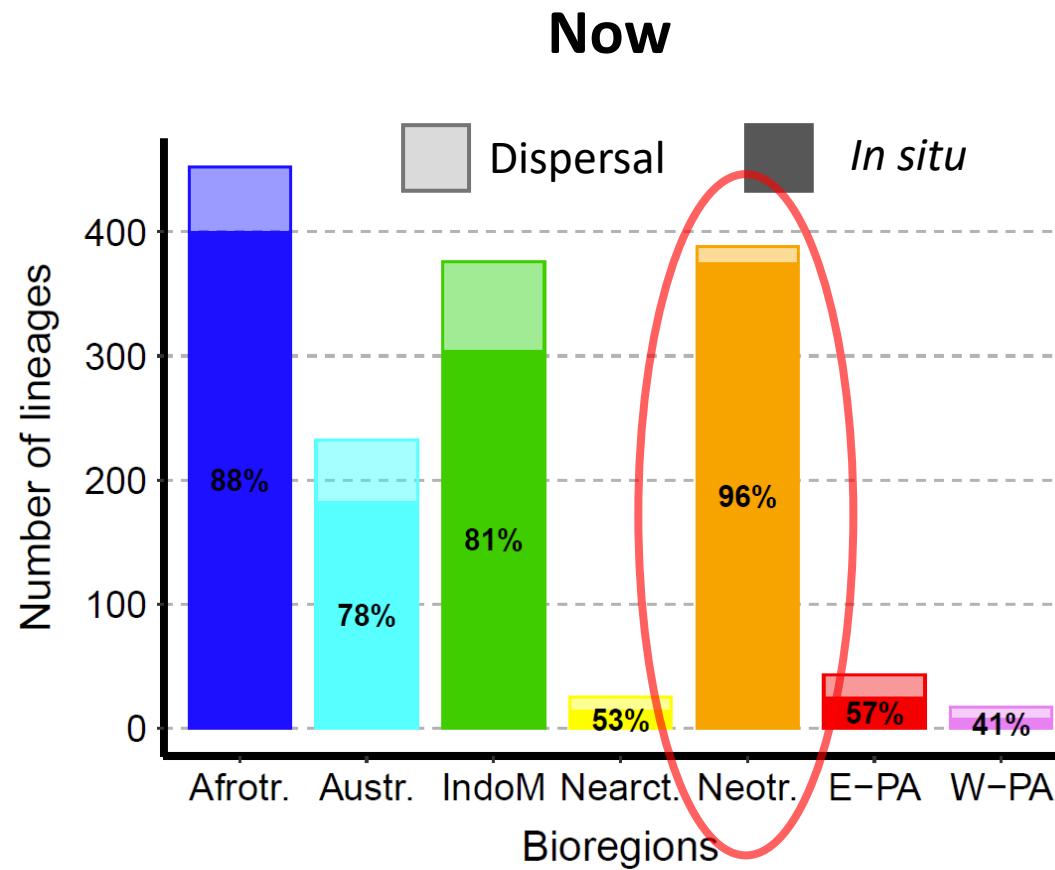


Doré et al., *in prep.*

# Origin of diversity



Lineage origins per Bioregions



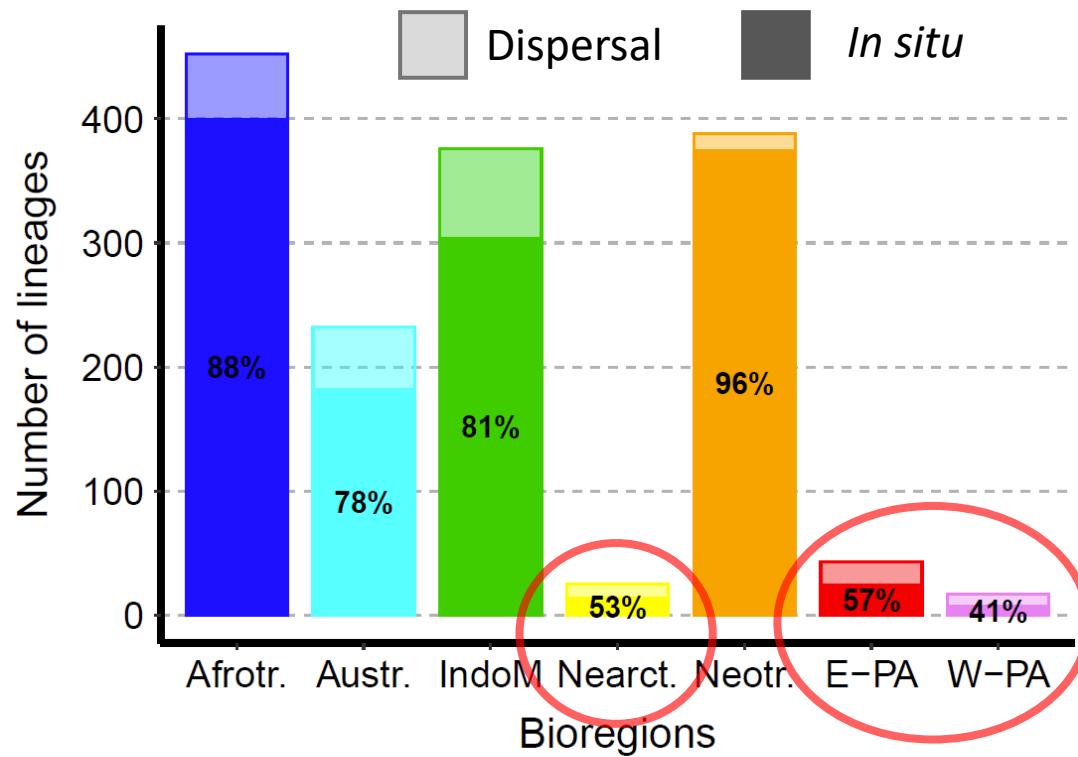
Doré et al., *in prep.*

# Origin of diversity

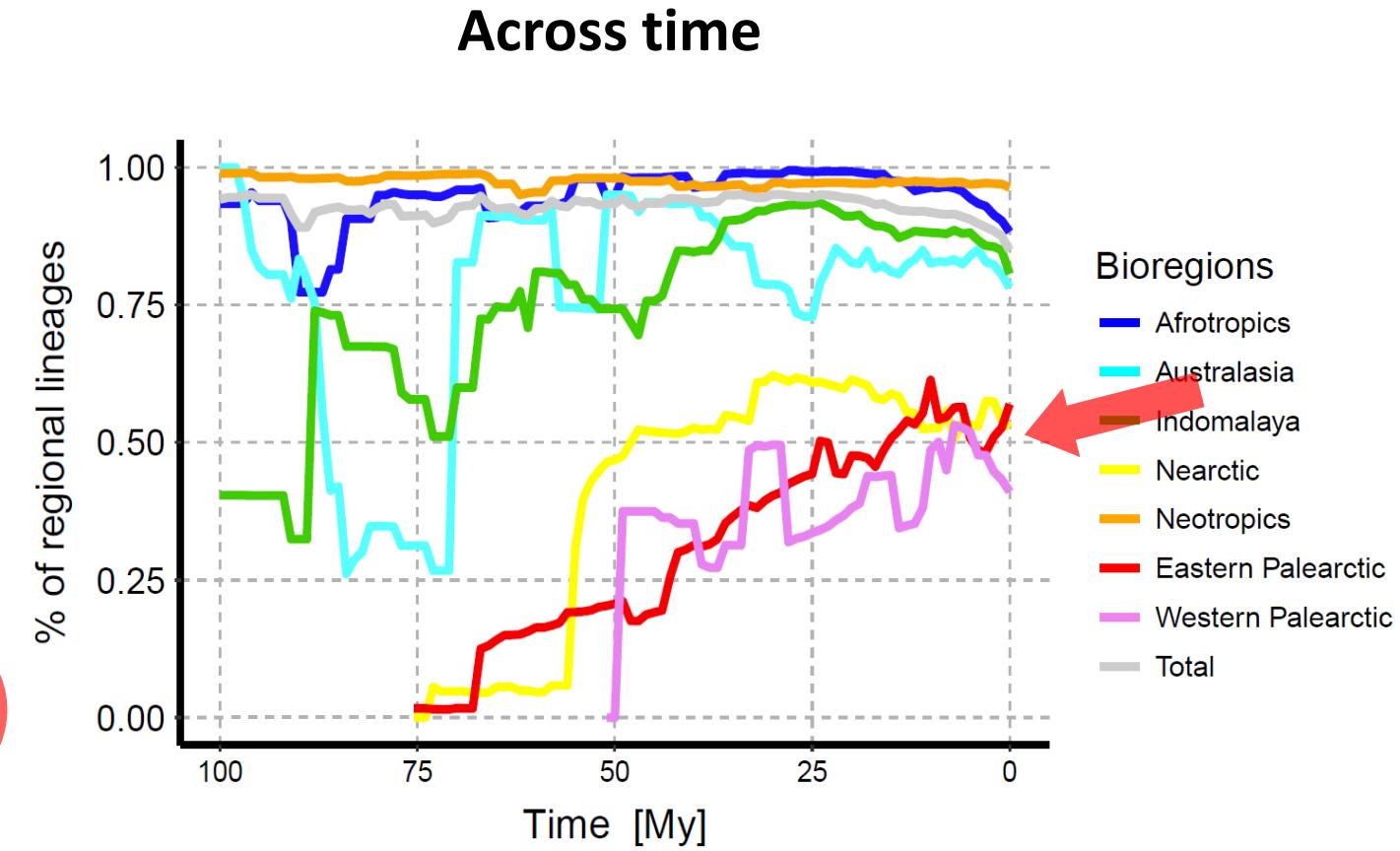


Lineage origins per Bioregions

Now



Across time



Doré et al., *in prep.*

# Conclusions



Origin in **Gondwana** ≈ 110-120 My

Timing of first colonizations:

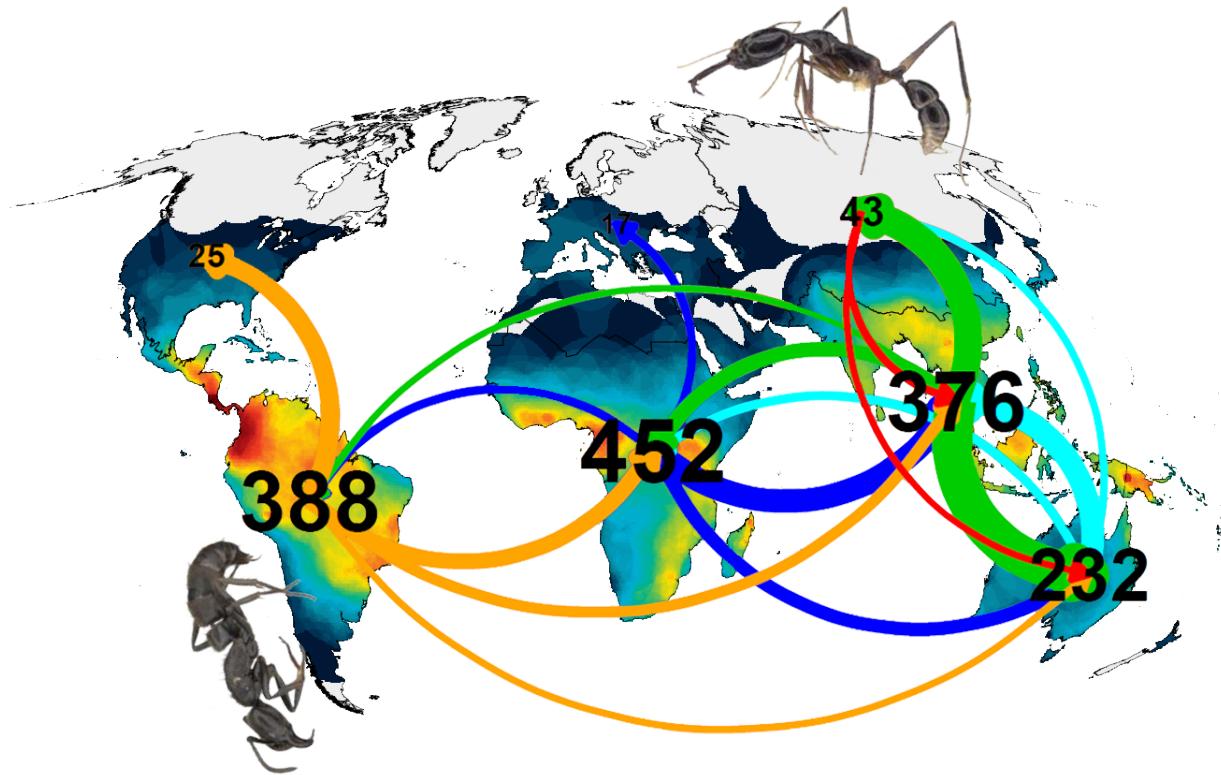
- **Eastern Palearctic** from (Indo)Malaya = 80 My
- **Nearctic** from Neotropics = 55 My
- **Western Palearctic** from Afrotropics = 35 My

Dispersal dynamics:

- Early sources: **Neotropics** + **Afrotropics**
- Overall/Recent source: **IndoMalaya**

Diversification dynamics:

- Early source: **Neotropics**
- Overall/Recent sources: **Afrotropics** + **IndoMalaya**



Doré et al., *in prep.*