

# Lecture 7: Where and when: historical biogeography

**Jadranka Rota and Niklas Wahlberg**

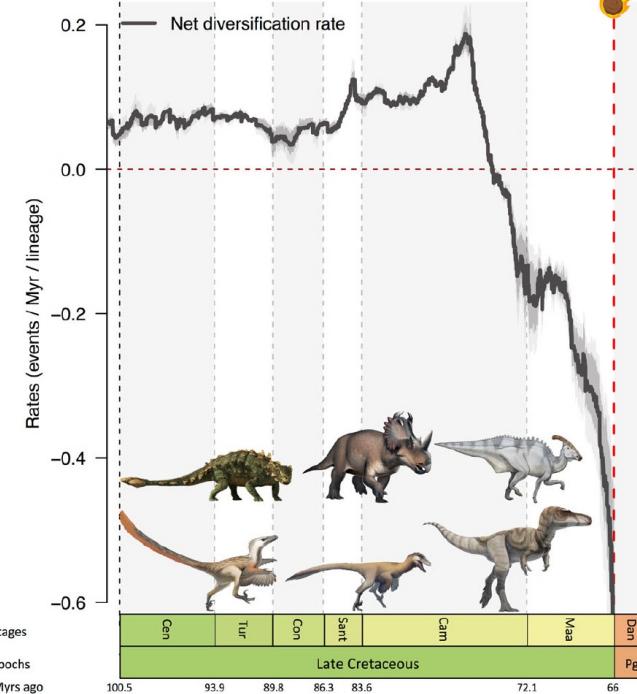
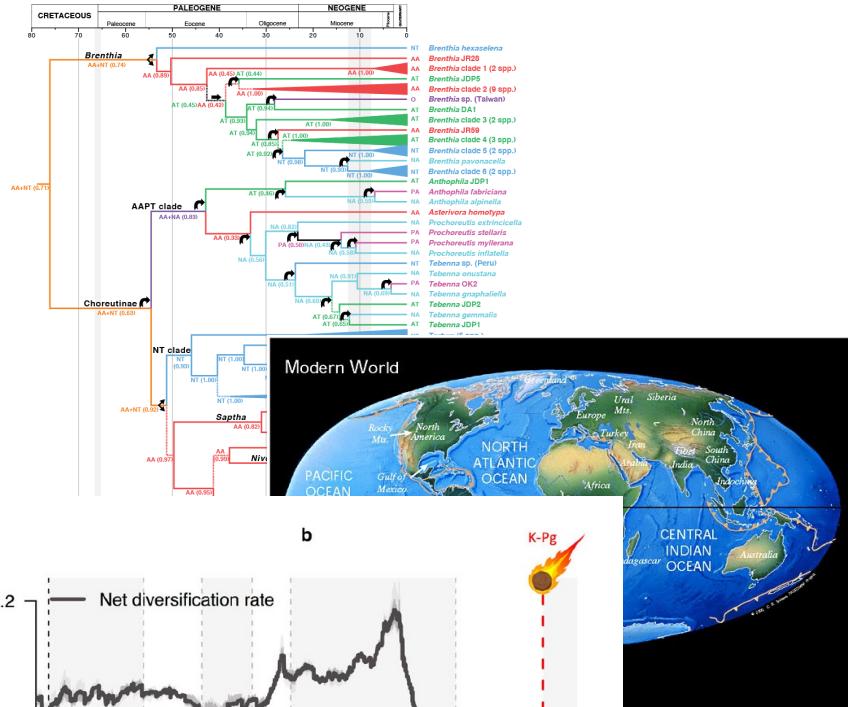
**Systematic Biology Group**

**Department of Biology**

**Lund University**

# Where and when?

- When: Timing of divergence
  - When did a group of organisms diverge from their sister group? When did much of today's biodiversity appear?
- Where: Historical biogeography
  - Where did a group of organisms originate? How did they achieve their current distribution?
- How: Diversification dynamics
  - How did a group of organisms come to have its extant diversity?



From Condamine et al. 2021

# Where did it all happen?

## Introduction to historical biogeography



**Isabel Sanmartín Bastida**

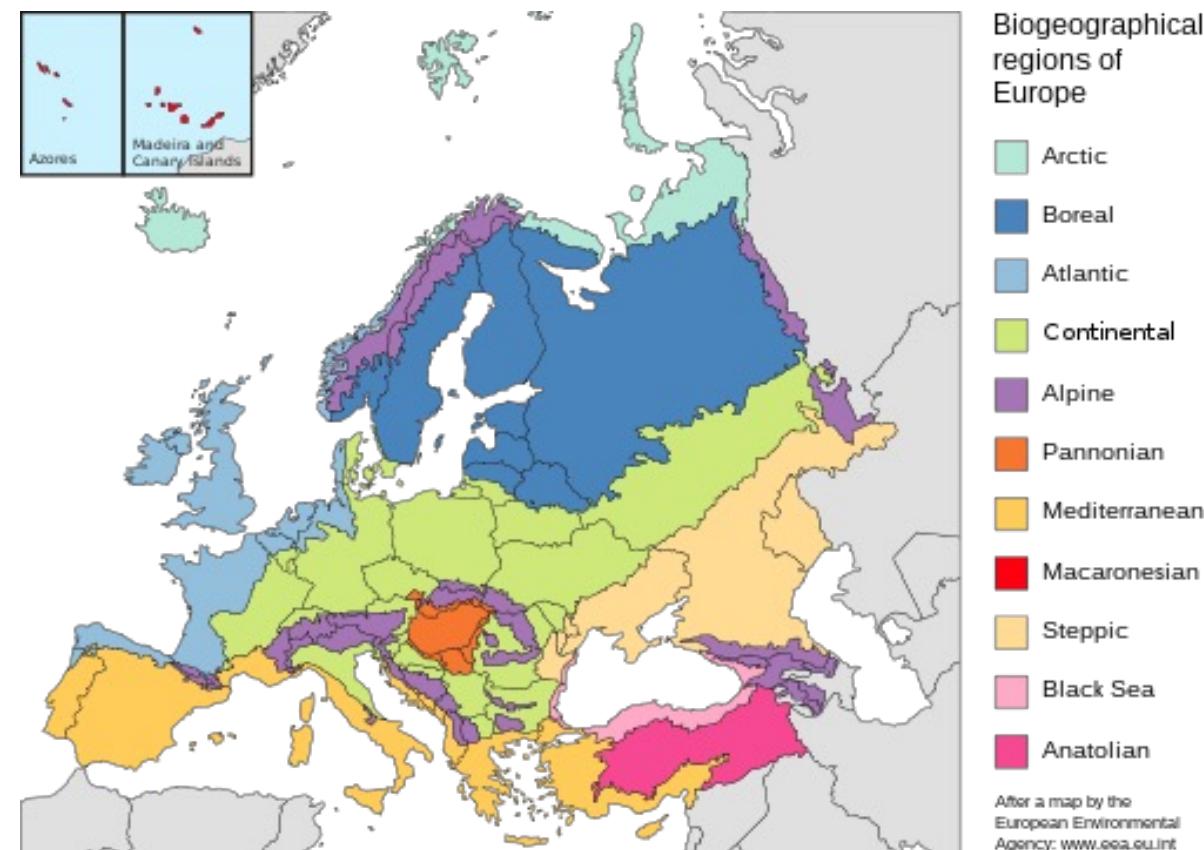
Investigadora científica | Vicedirección de Cultura Científica

Especialidad: Biogeography. Modeling the distribution of life on Earth, past and present

Some slides thanks to Isabel Sanmartín, Real Jardin Botanico, Madrid,  
<https://scholar.google.com/citations?user=zDmFP60AAAAJ&hl=en>)

# Biogeography

- **Study of species distribution in space and time**
- **Phytogeography (plants) and zoogeography (animals)**
- **Historical biogeography**
  - Inference of past distributions and processes that led to today's distribution
  - Time scale: millions of years
- **Phylogeography**
  - At the level of populations (intraspecific level)
  - Time scale: tens of thousands of years



Júlio Reis, CC BY-SA 3.0 via Wikimedia Commons

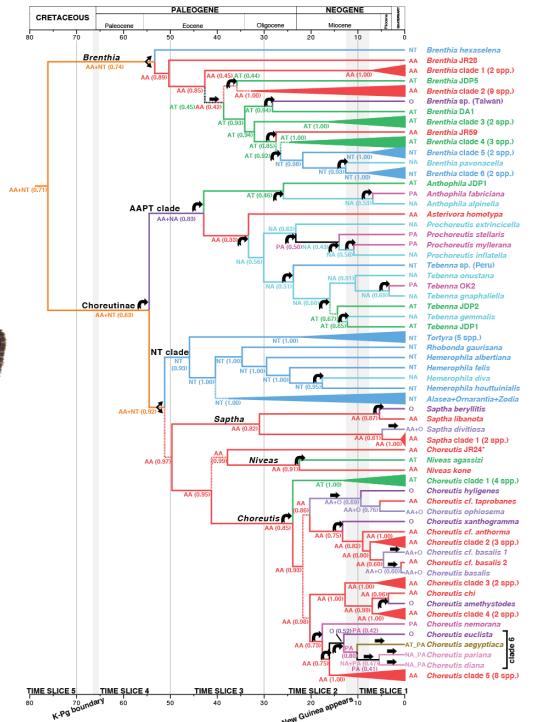
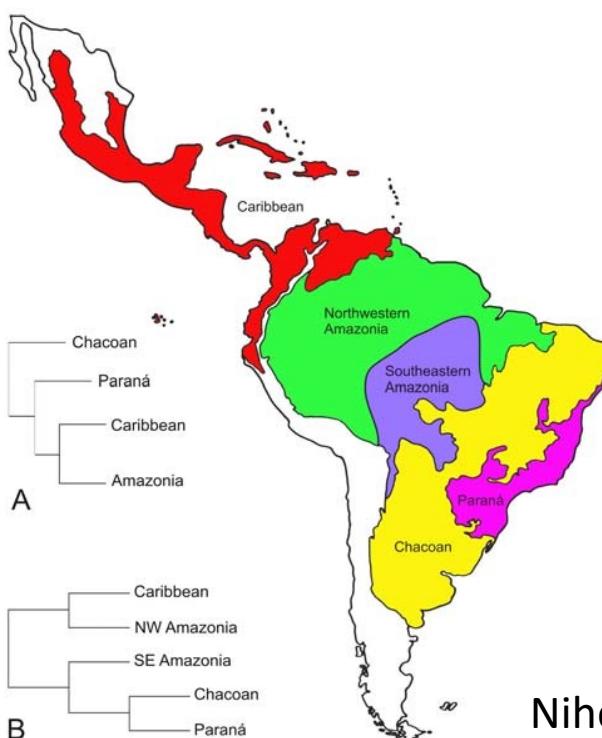
Biogeographical regions of Europe

Arctic
Boreal
Atlantic
Continental
Alpine
Pannonian
Mediterranean
Macaronesian
Steppic
Black Sea
Anatolian

After a map by the European Environmental Agency: [www.eea.eu.int](http://www.eea.eu.int)

# Historical biogeography

- Taxon biogeography
  - Focus on inferring the area of origin, past distribution, and the various processes that led to current distribution
- Area biogeography
  - Focus on a specific area and how this area came to have its current community

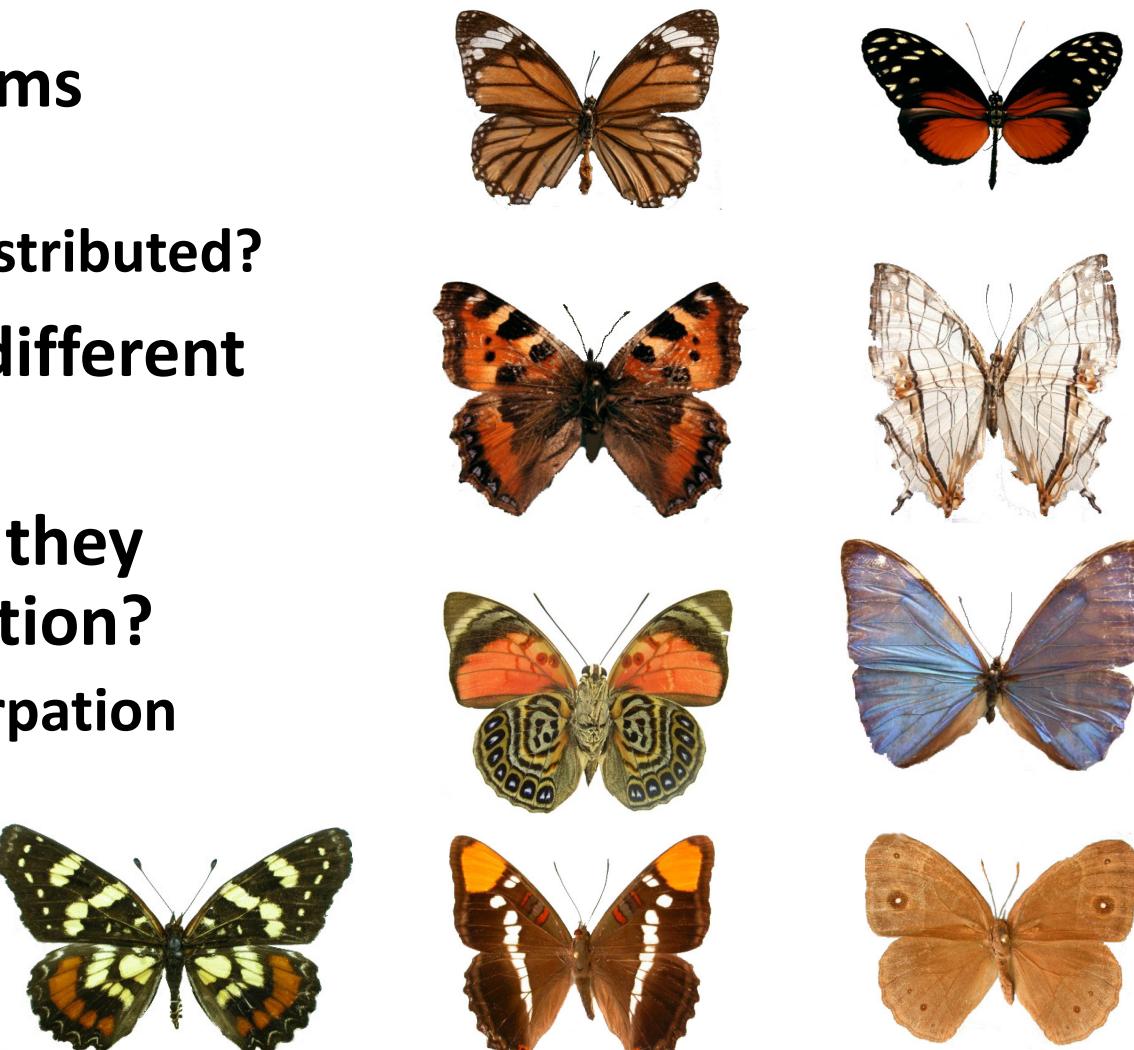


Rota et al. 2016

Nihei & De Carvalho 2007

# Historical biogeography of taxa

- Where did a group of organisms originate?
  - Where were their ancestors distributed?
- When did they first come to different areas?
- Through which processes did they achieve their current distribution?
  - E.g., vicariance, dispersal, extirpation



# Historical biogeography of areas

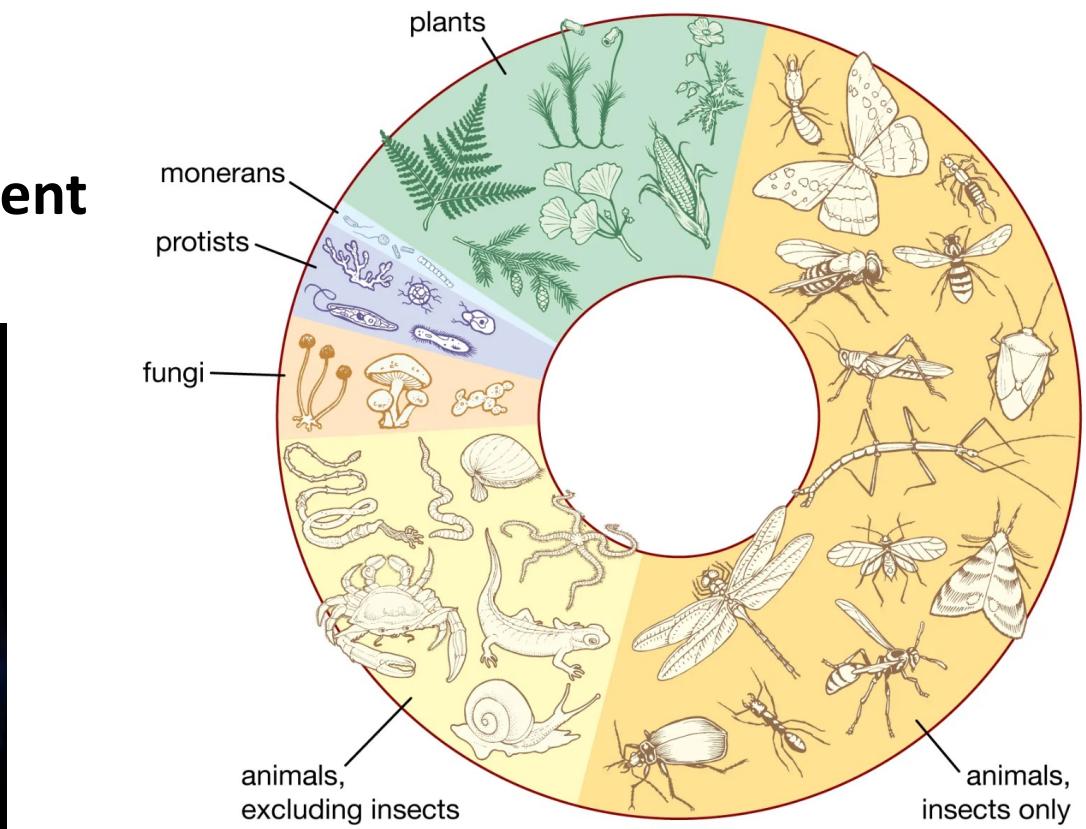
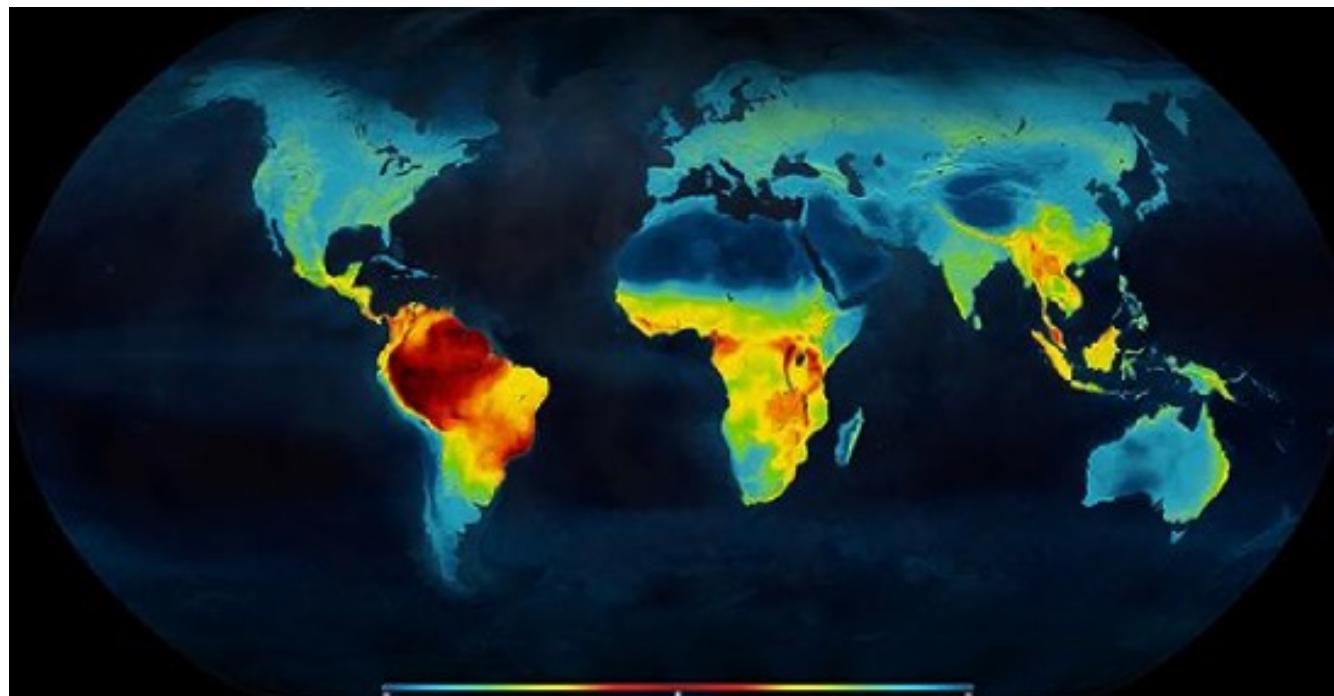
- How was a particular community assembled?
- Is there a common explanation for similar disjunct distributions?
  - Disjunct distribution = when one taxon is distributed in two or more non-continuous areas
- What is the role of geographical barriers to dispersal?
- Can we explain differential diversity in different areas?



Wikipedia

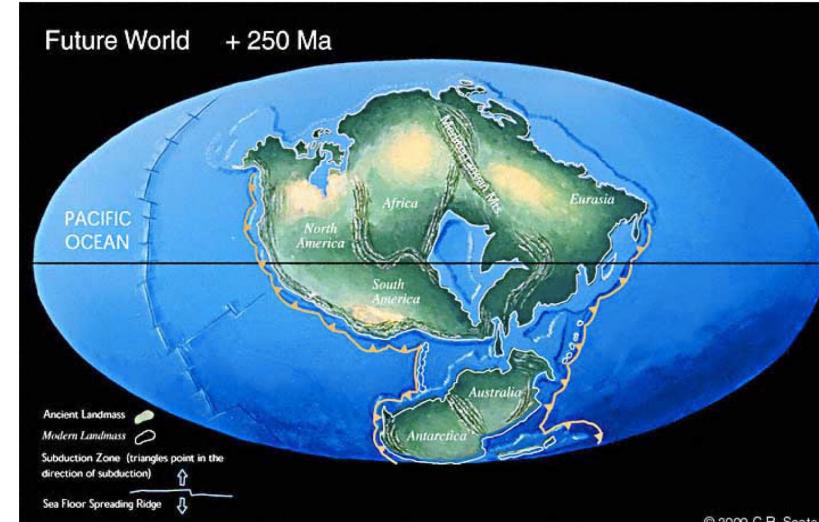
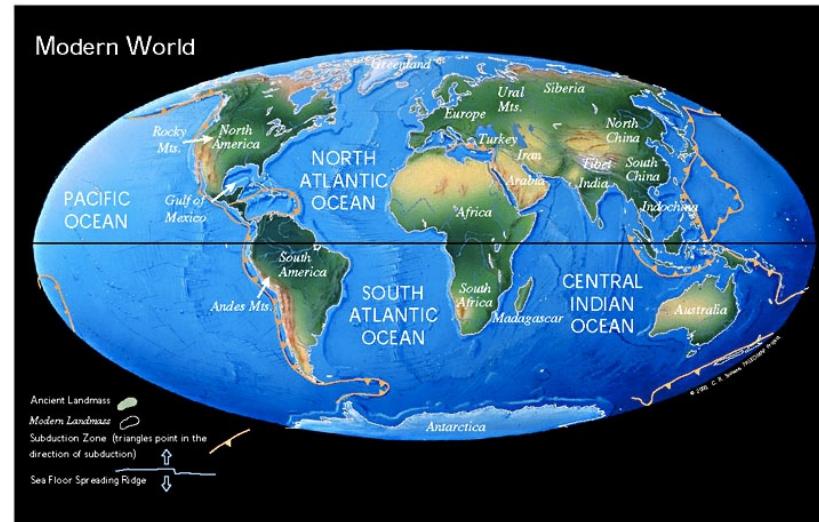
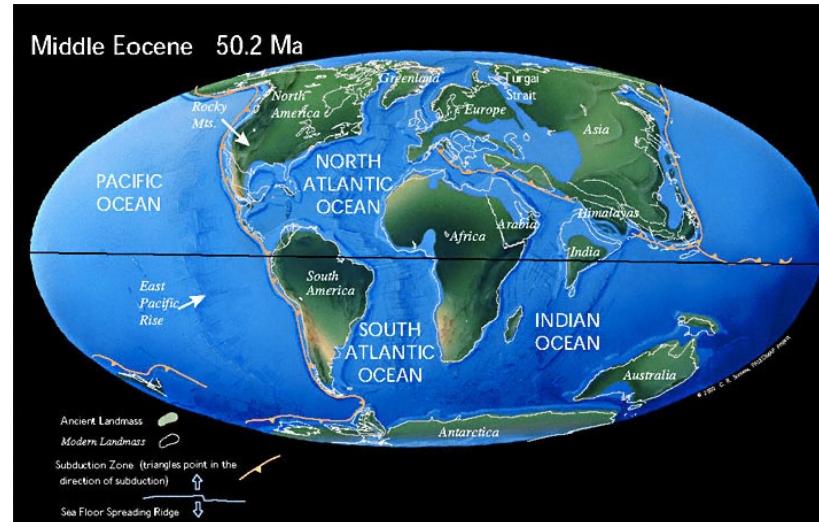
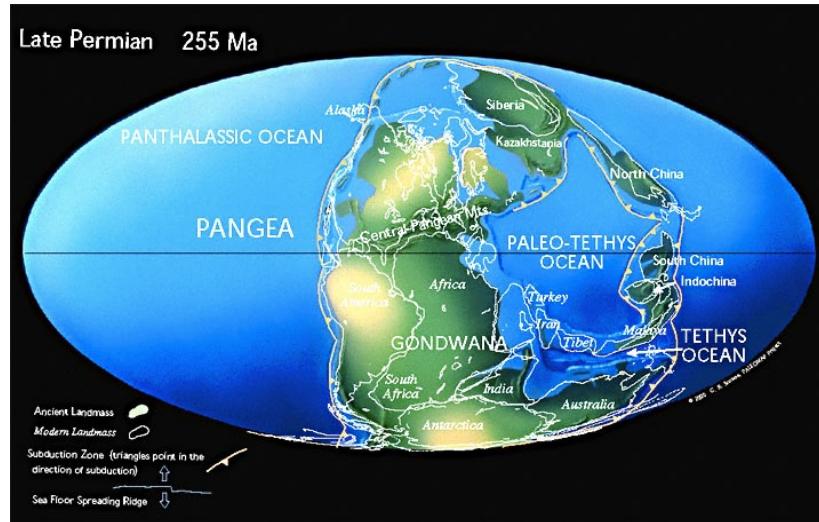
# Global diversity

- Unevenly distributed
  - Across lineages
  - Across areas – e.g. latitudinal diversity gradient



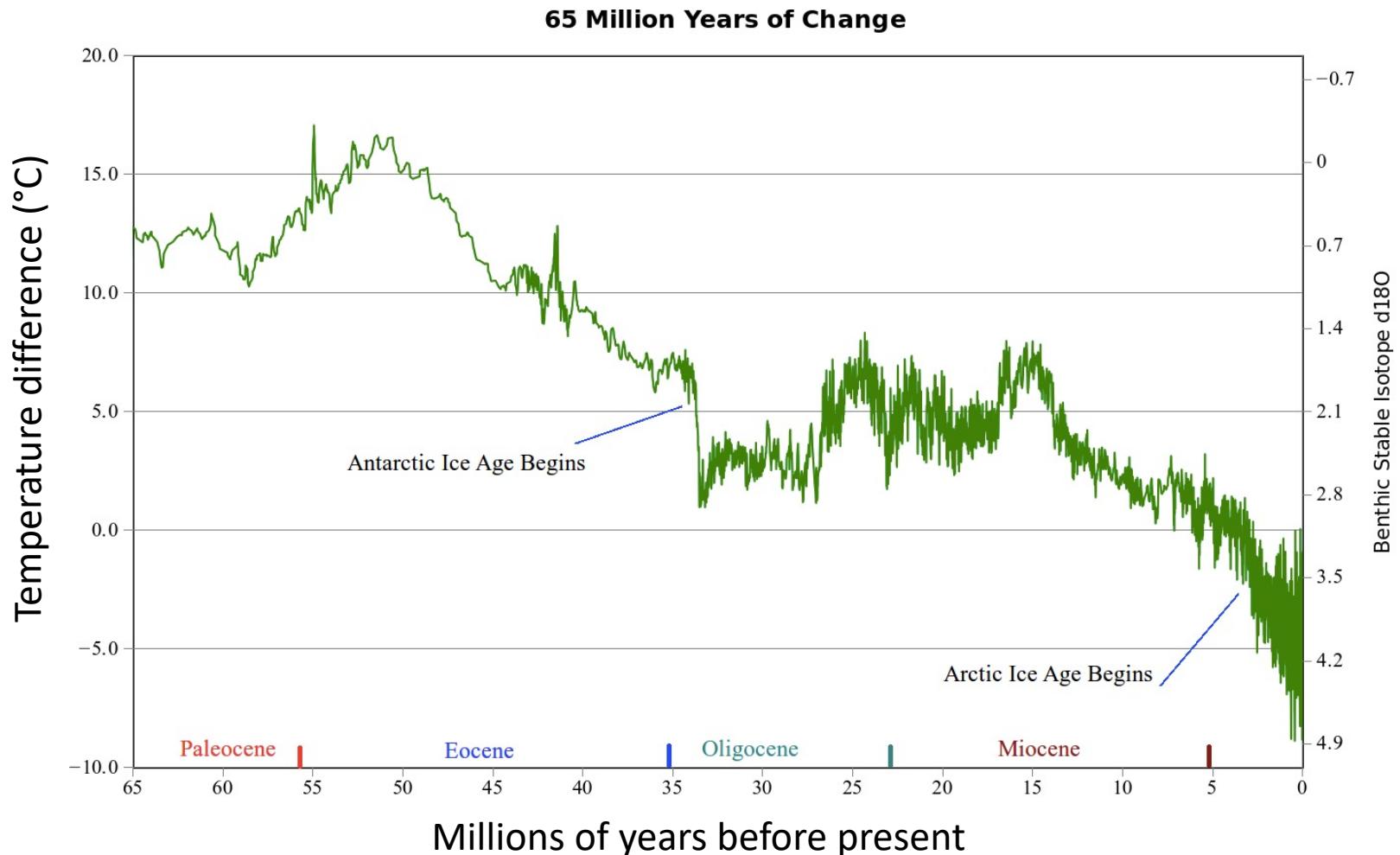
© Encyclopædia Britannica, Inc.

# A changing geology

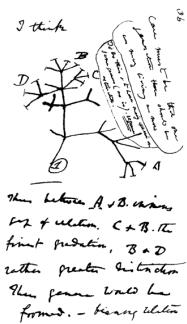


- Plate tectonics
  - Accepted as theory since 1960s

# A changing climate

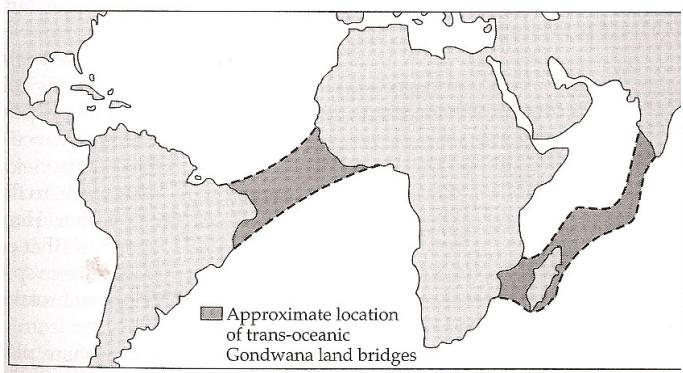


# Phylogenetic biogeography

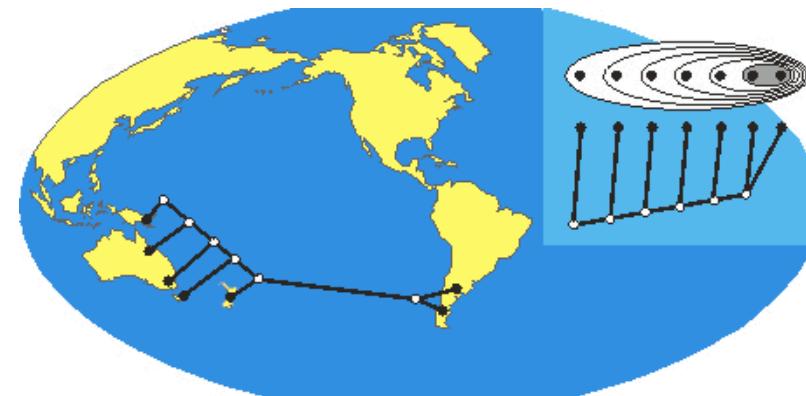


**Evolution in space and time**

Charles Darwin (1859):  
“species migrate from  
centers of origin and  
later evolve into new  
species by natural  
selection”



John Dalton Hooker (1860) – species  
migrated through landbridges now vanished

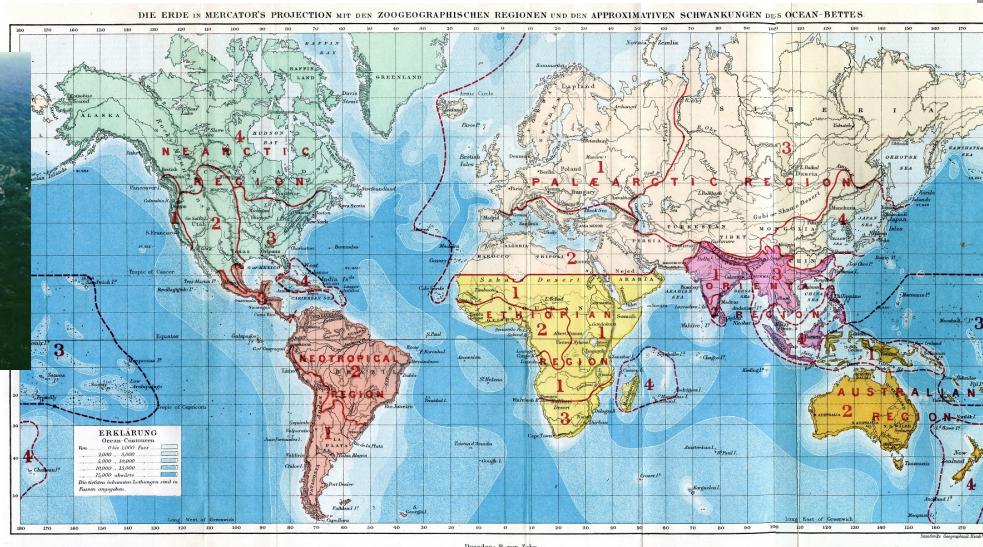


“The branching order of  
lineages in a phylogeny  
contain information about  
their geographic origins”

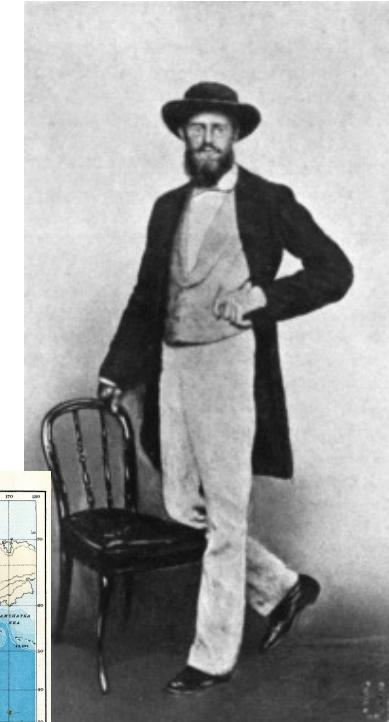
Phylogenetic biogeography  
(Hennig, 1966; Brundin 1966)

# Alfred R. Wallace (1823–1913)

- Co-Developer “Theory of Evolution by Natural Selection” with Charles Darwin
- Great Explorer
- The “father” of Biogeography

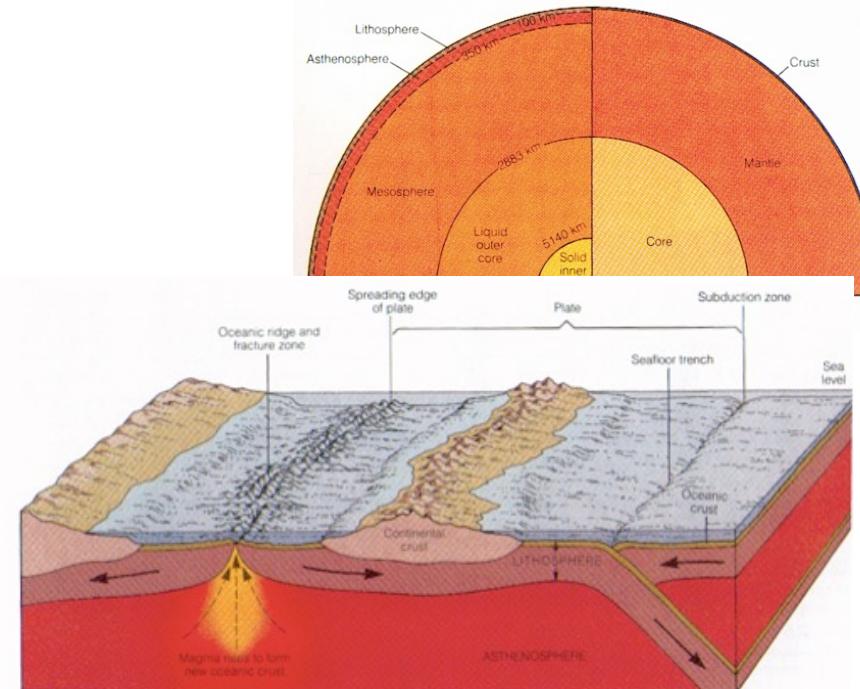
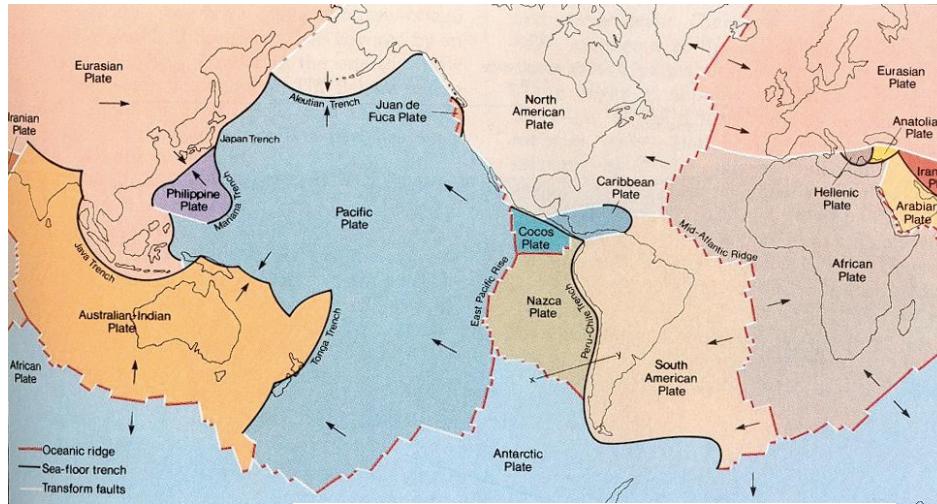


(Zoo) Biogeographic regions: Wallace's line



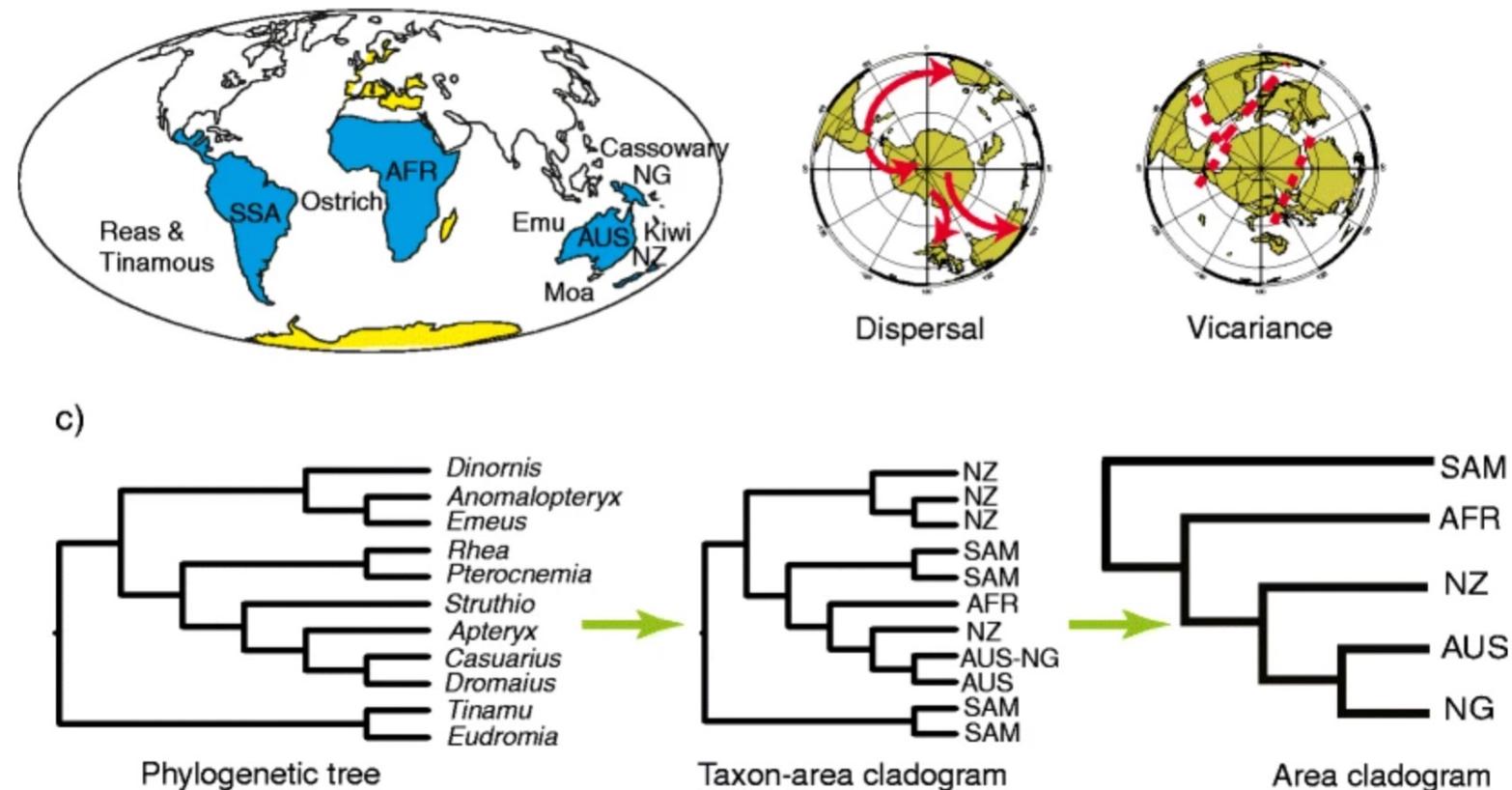
# Plate tectonics

- 1960s: Theory of Plate tectonics
  - Geologic composition of Earth
  - Tectonic supercycle
  - Lithosphere divided into plates that slide over mantle



# Brief history of historical biogeography

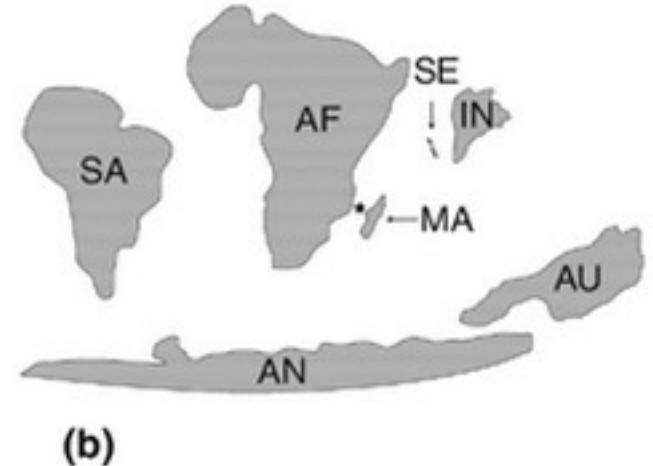
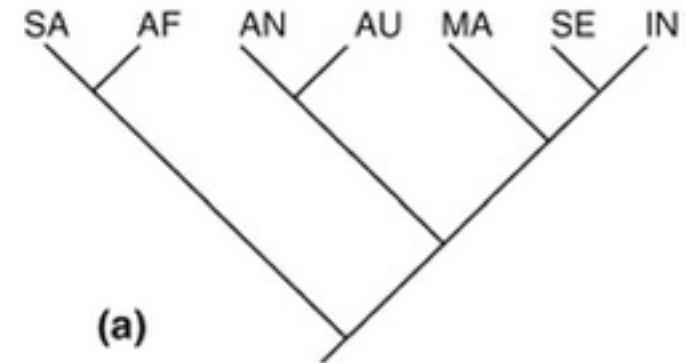
- Dispersal – thought to be the only way that species ranges could change
- As plate tectonics accepted, vicariance invoked
- Looking for vicariance in different groups of organisms was the dominant way to study historical biogeography



Biogeographic history of the ratite birds (ostriches, emus, reas, etc.).  
From Sanmartín 2012: Fig. 1  
Yellow: fossil remains; blue: current distribution

# Pattern-based methods

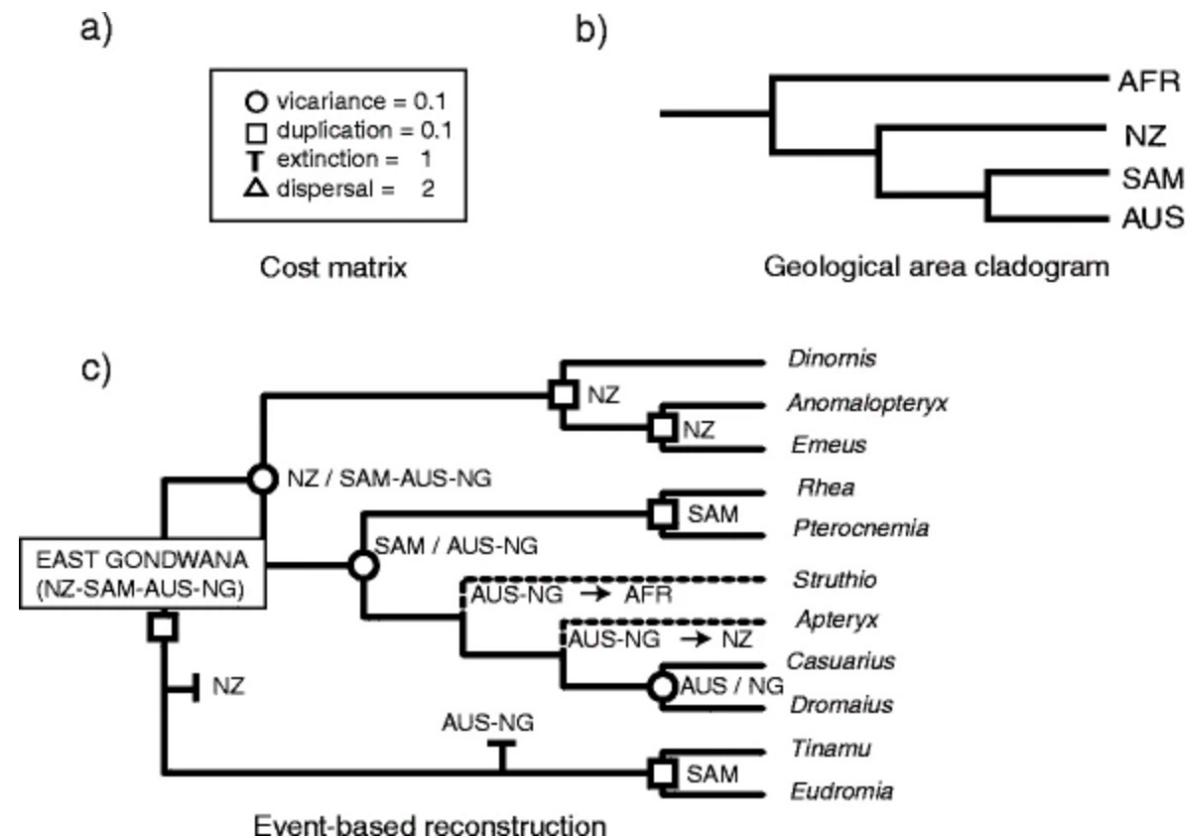
- Compare taxa in a given set of areas
- Search for similar patterns (common history = vicariance)
- Explain differences with dispersal/extinction
- Founder: Lars Brundin, Syst. Zool. 1972
- Taxon-area cladogram
  - Areas of distribution used to replace species/group names in the tree
  - Trying to find common patterns of divergence based on areas across different groups of organisms



Example from Sparks & Smith 2005 Syst. Biol.

# Event-based methods

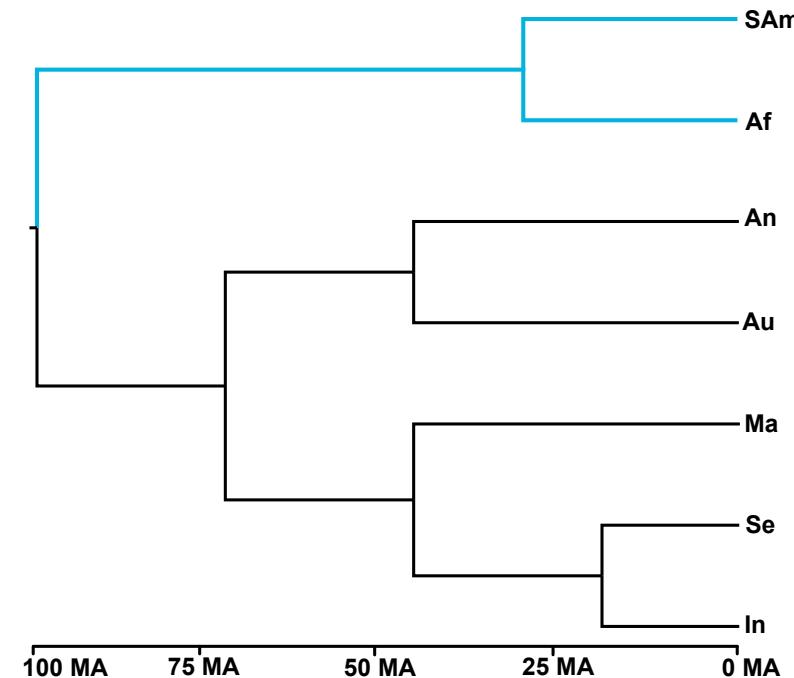
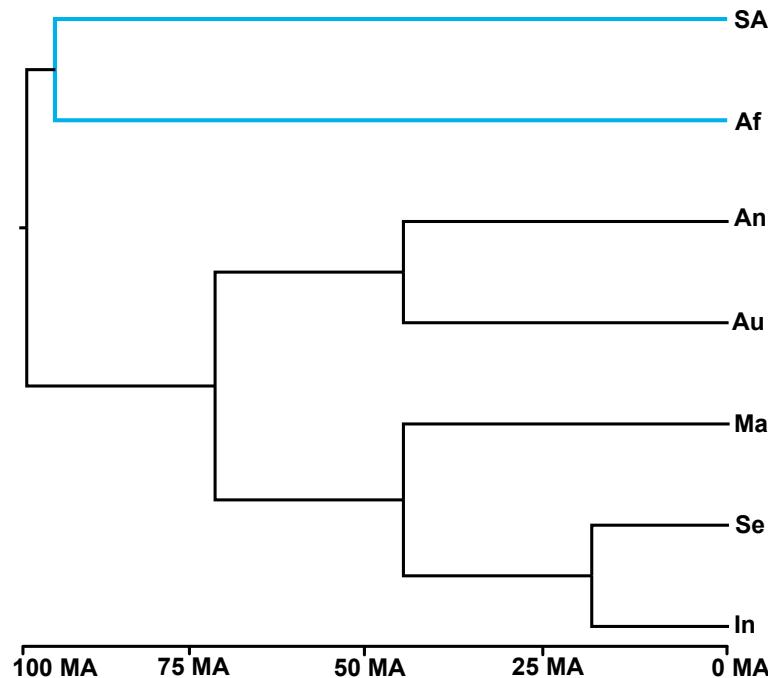
- Focused on assigning cost or probability to the main events
  - Vicariance (splitting of a range)
  - Duplication (inheritance of a range)
  - Dispersal (addition of an area)
  - Extinction (loss of an area)

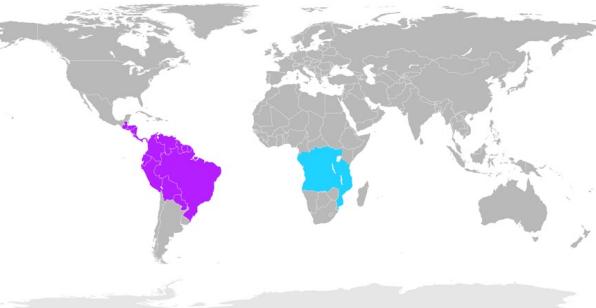


Event-based reconstruction of the biogeographic history of ratites.  
From Sanmartín 2012: Fig. 3

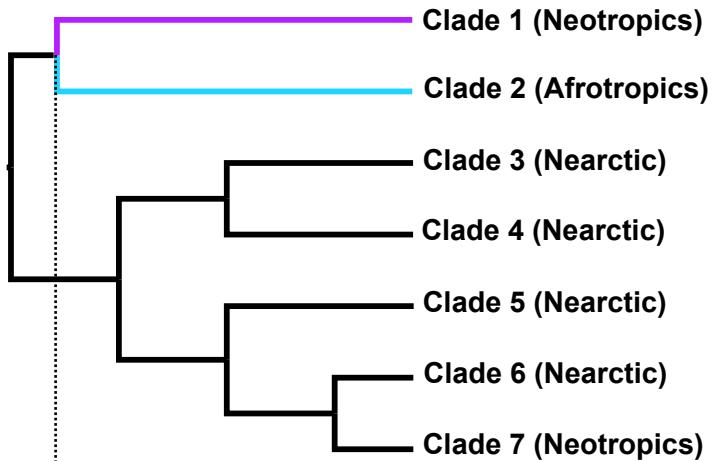
# Problems with early approaches

- Times of divergence were not considered
- Vicariance assumed even when dispersal could be the explanation

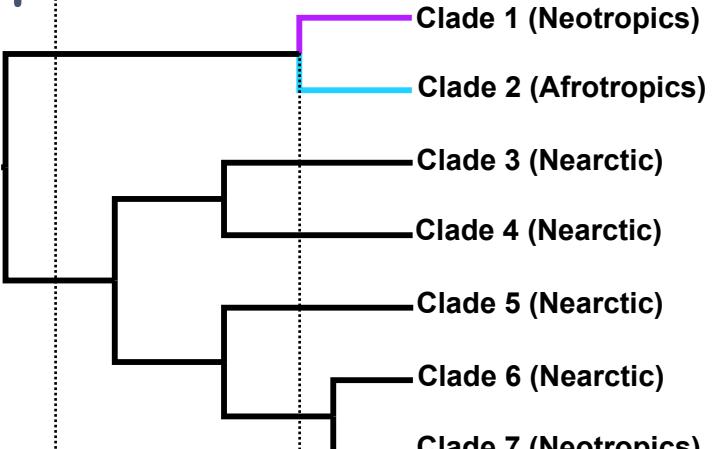




## Vicariance scenario

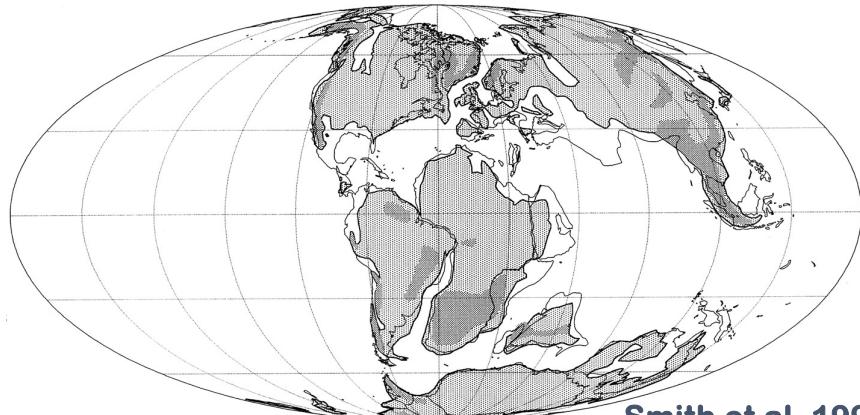


# Dispersal scenario



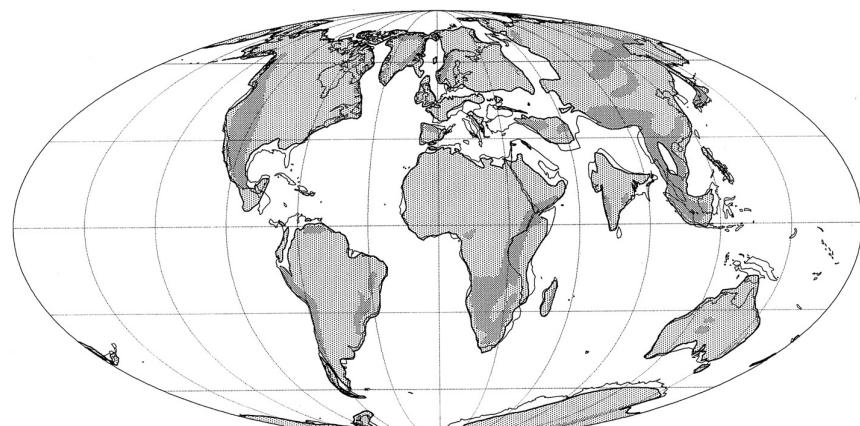
120 90 60 30 0 Millions years ago (MA)

# Position of continents 120 MA

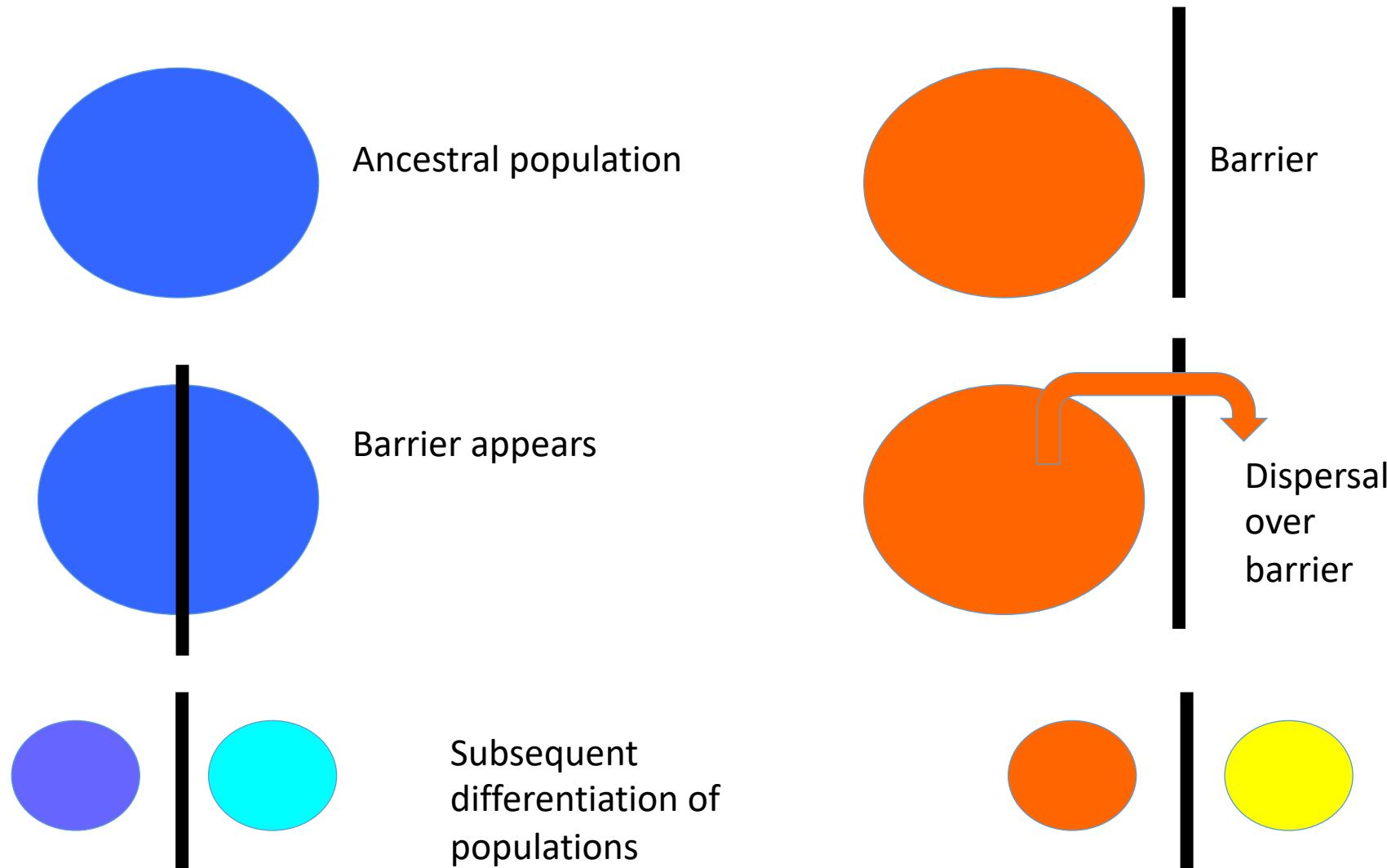


Smith et al. 1994

## Position of continents 40 MA



# Vicariance vs. dispersal



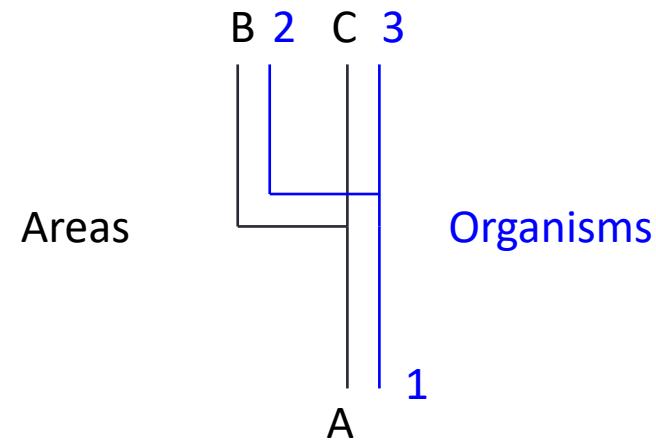
# Event-based biogeography

- Explicitly incorporate biogeographic processes into the analysis (event-based approach)
- Each type of process is assigned a cost inversely related to its likelihood
- The optimal biogeographic reconstruction is the one that minimises the total cost of the implied events (most parsimonious solution)

# Biogeographic processes

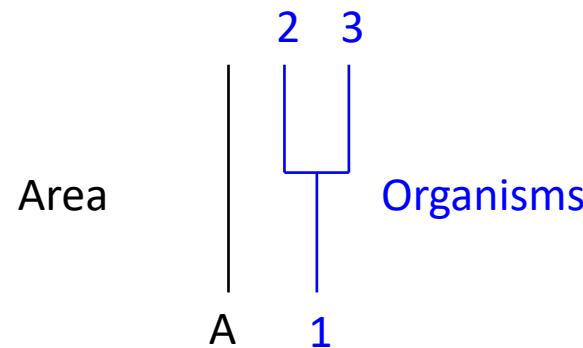
- **Vicariance**
- **Dispersal**
  - Range expansion for a species
  - Can be associated with speciation
- **Extinction**
  - Partial (local extirpation in a subset of areas), a.k.a. range contraction
  - Full (lineage extinction)
- **Duplication**
  - Speciation within an area
- **Long distance dispersal and establishment (LDDE)**
  - A.k.a. founder event

# Vicariance



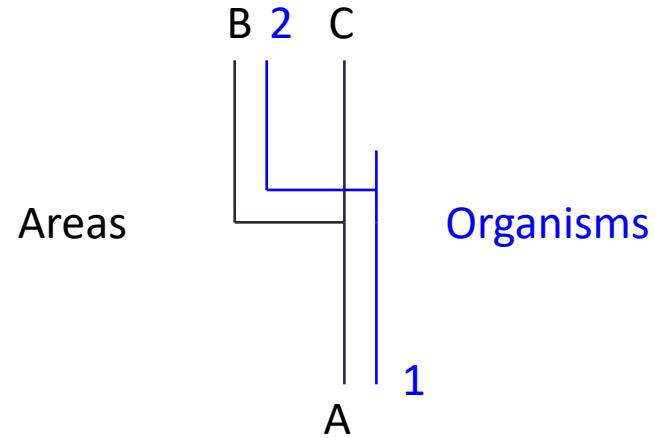
- Area A split into areas B and C
- Allopatric speciation in response to a general dispersal barrier

# Duplication



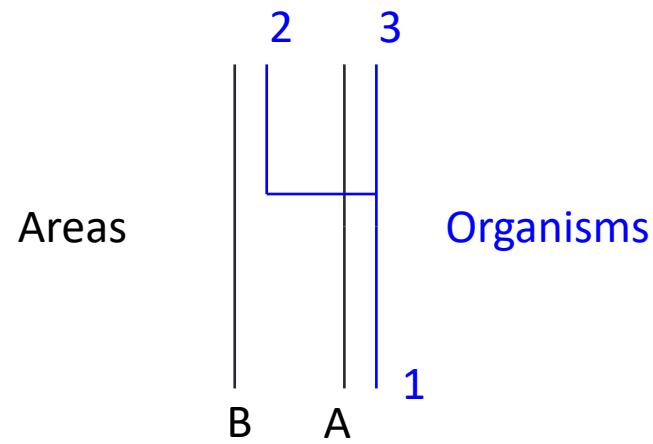
- Diversification within area
- Sympatric speciation or allopatric speciation in response to temporary dispersal barrier

# Local extinction



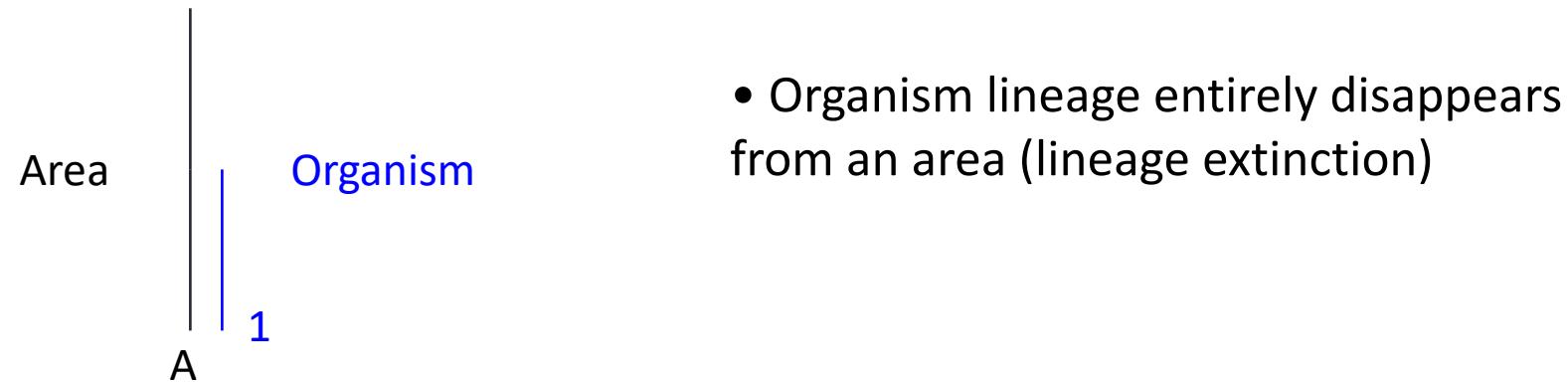
- Organism disappears from one area where it was predicted to occur (after a vicariance event)

# Dispersal (partial)

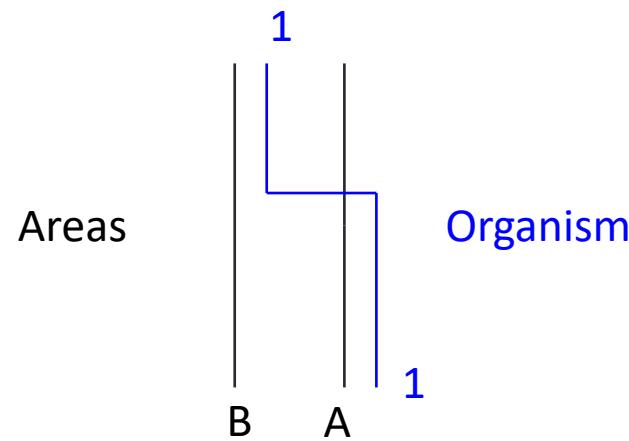


- colonization of a new area across a pre-existent barrier giving rise to new species (allopatric speciation)
- "speciation-coupled dispersal"

# Extinction (complete)



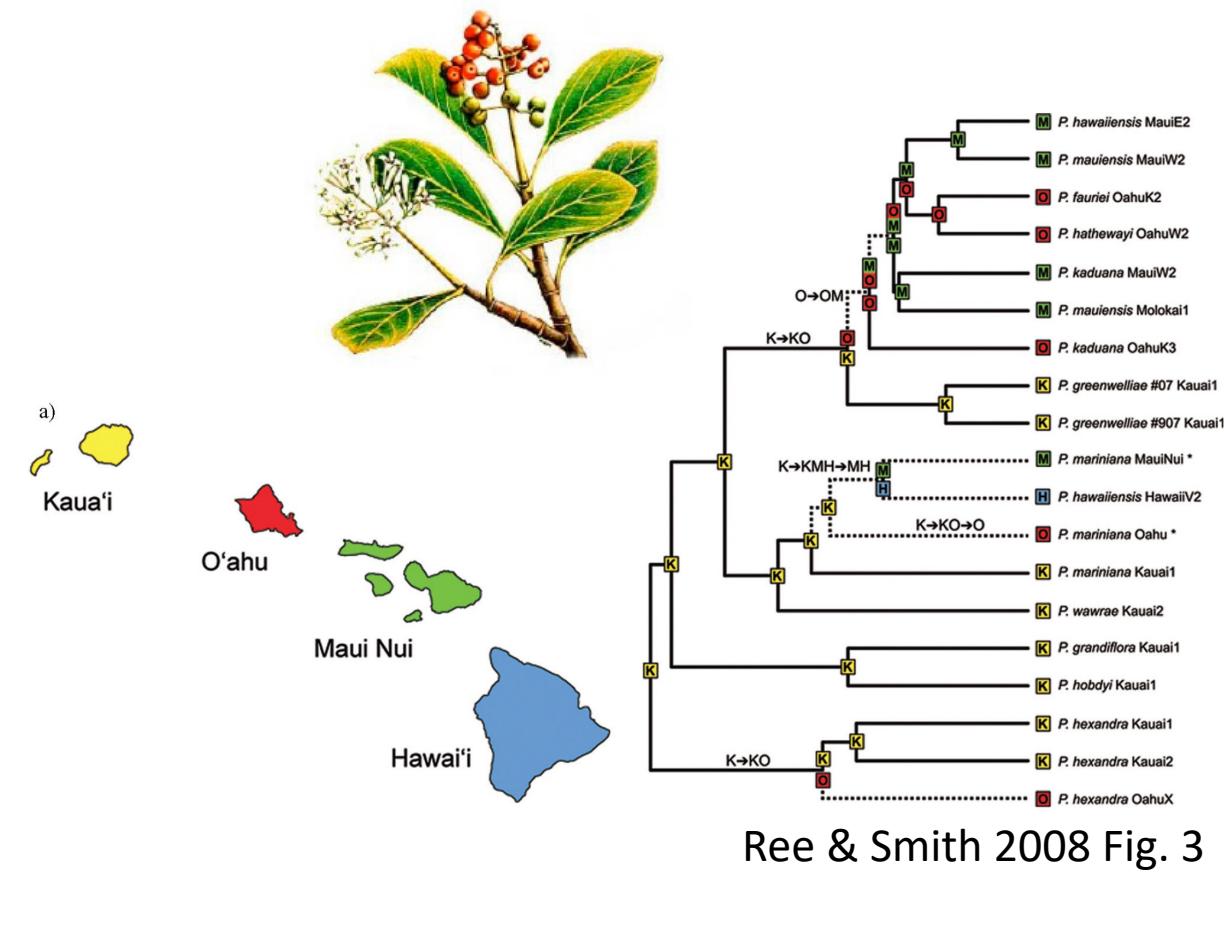
# Dispersal (complete)



- Lineage switches from one area to another
- No speciation

# Parametric historical biogeography

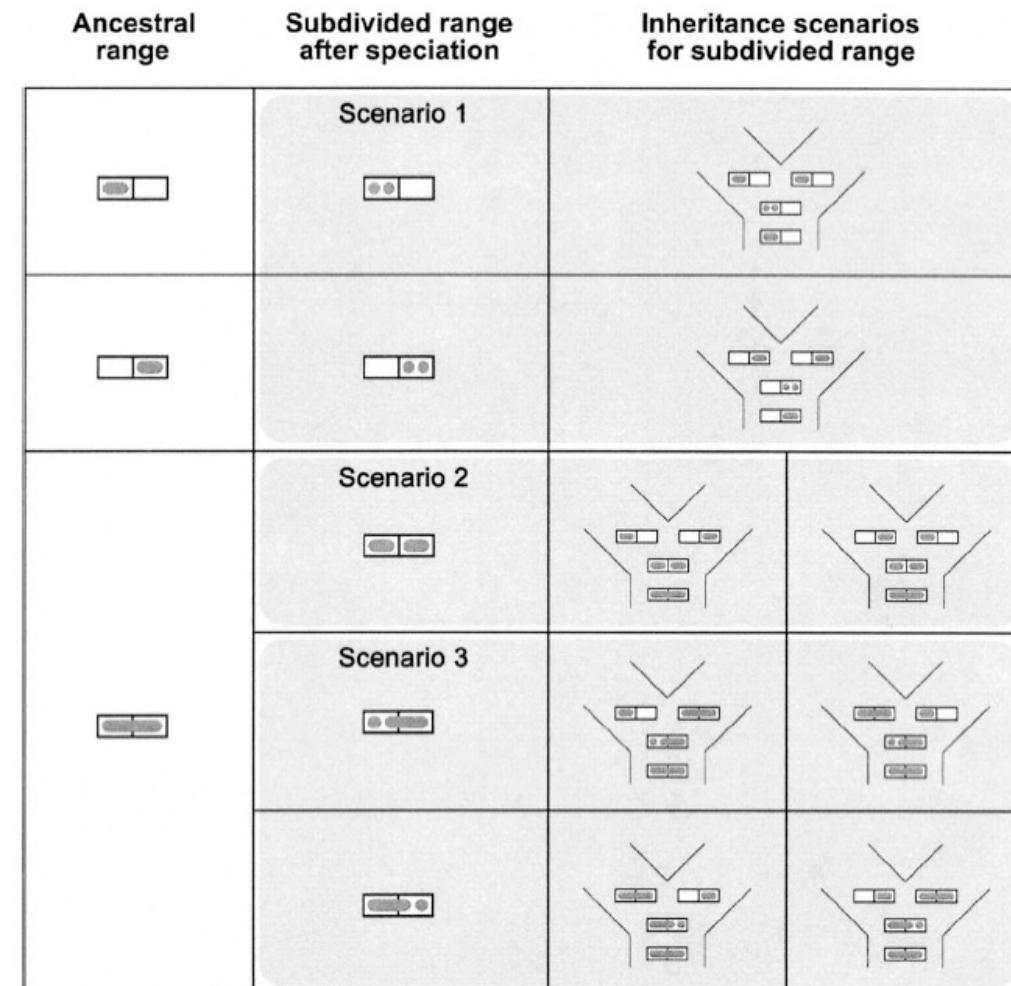
- Modern probabilistic approaches (model-based)
  - Incorporation of lineage divergence times
  - External sources of evidence
    - Past climate and geography
    - Fossil record
    - Ecological niche
  - Rate of different processes is estimated from the data (parameters in an ML model)
- Dispersal-Extinction-Cladogenesis (DEC) - first parametric approach (Ree et al. 2005)
- First implemented in program Lagrange, additional programs since then (e.g. BioGeoBEARS by Matzke 2014)



# Dispersal-Extinction-Cladogenesis (DEC)

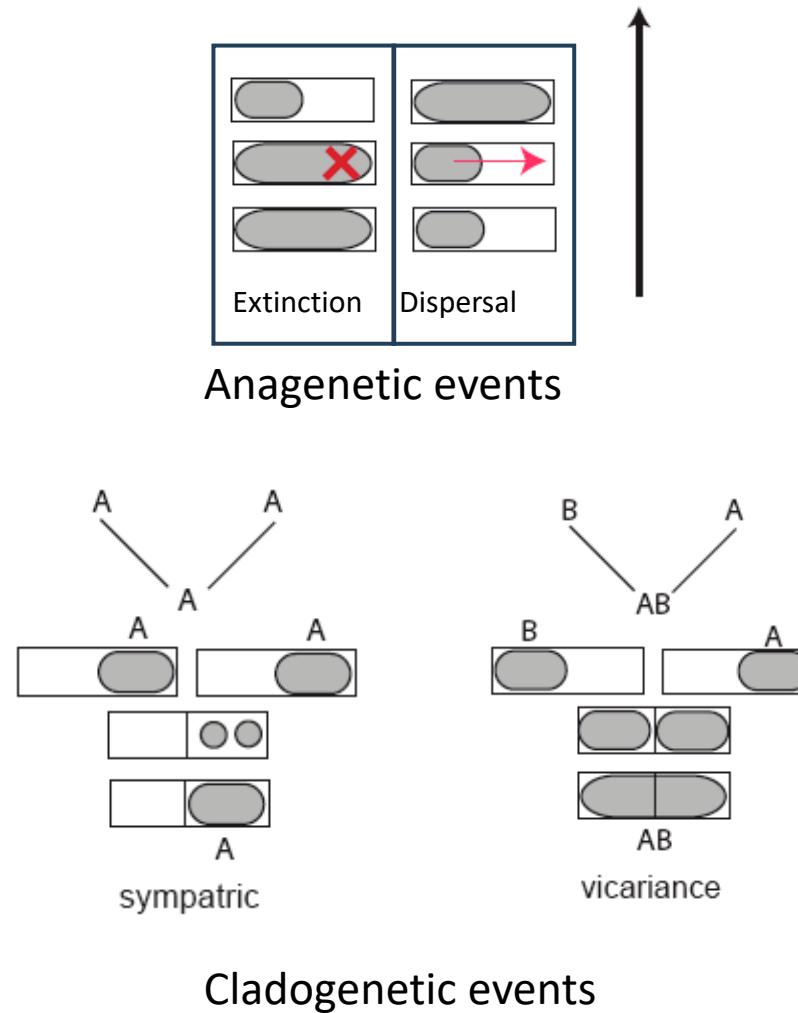
Ree et al. 2005: Evolution

ML reconstruction of ancestral area



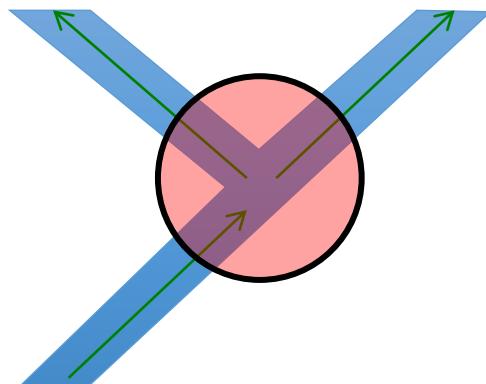
# Dispersal-Vicariance optimization

- **Distributions** described in terms of unit areas
- **Anagenetic events** (internodes): dispersal - extinction (+1)
- **Cladogenesis: speciation** can only have two effects on distributions:
  - **Speciation within a unit area:** both descendants occur in the same unit area as their immediate ancestor
  - **Vicariance:** the distribution of the ancestor is divided into two mutually exclusive sets of unit areas

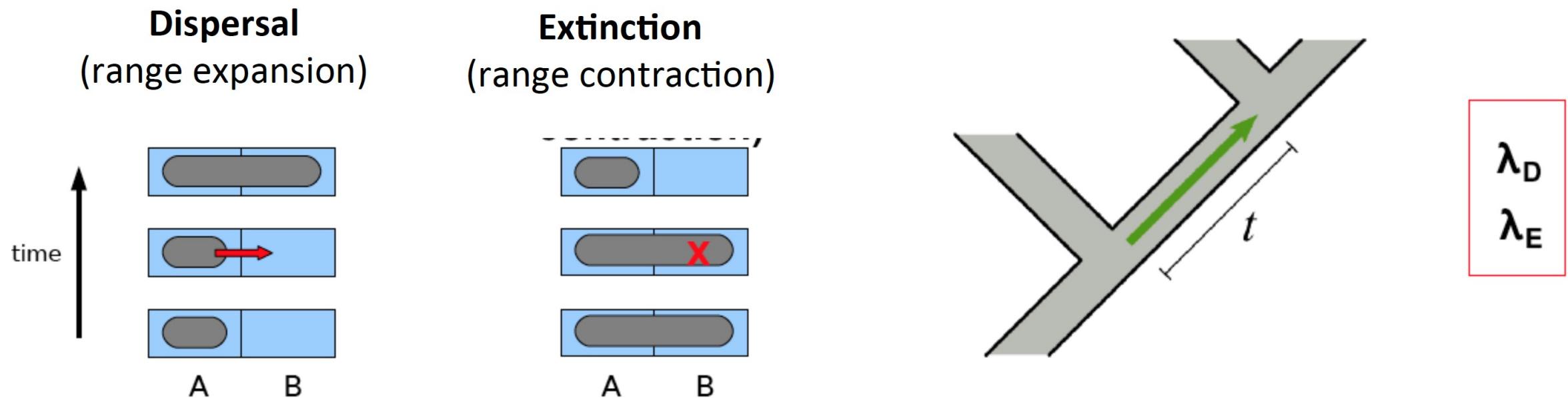


# Anagenesis vs. cladogenesis

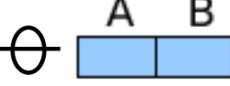
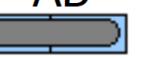
- Anagenesis: dispersal and local extinction along a branch
- Cladogenesis: range subdivision and inheritance at speciation



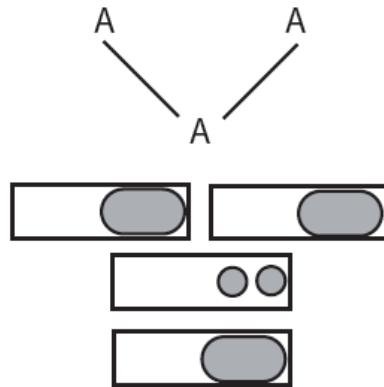
# Anagenetic range evolution



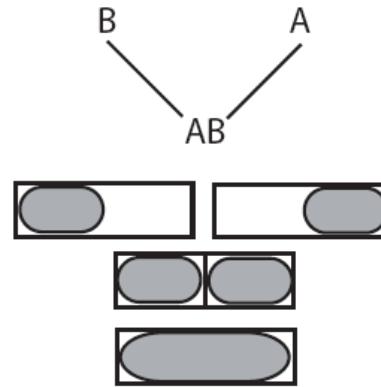
# Range transition probabilities ( $P$ ) from dispersal and extinction rates ( $Q$ )

		A	B				
		A	$\lambda_D$				
		B	$\lambda_D$				
dispersal rates							
extinction rates			$\lambda_E$	$\lambda_E$			
Range of descendant							
		$\emptyset$		A	B	AB	
							
		$\emptyset$	A B	---	0	0	0
			$\lambda_E$	---	0	$\lambda_D$	
			$\lambda_E$	0	---	$\lambda_D$	
		AB		0	$\lambda_E$	$\lambda_E$	---
Symmetric dispersal and extinction rates (2 parameters)							

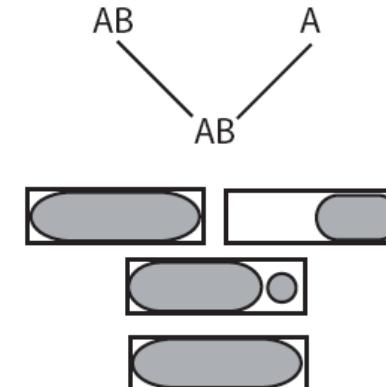
# Cladogenesis (range inheritance scenarios)



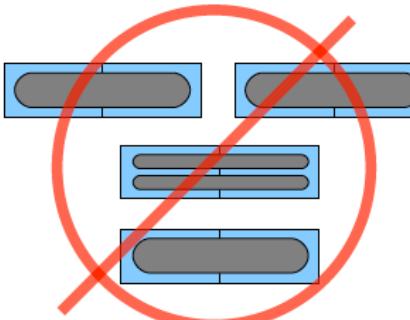
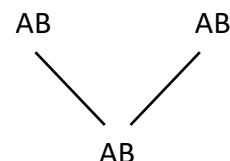
sympatric



vicariance

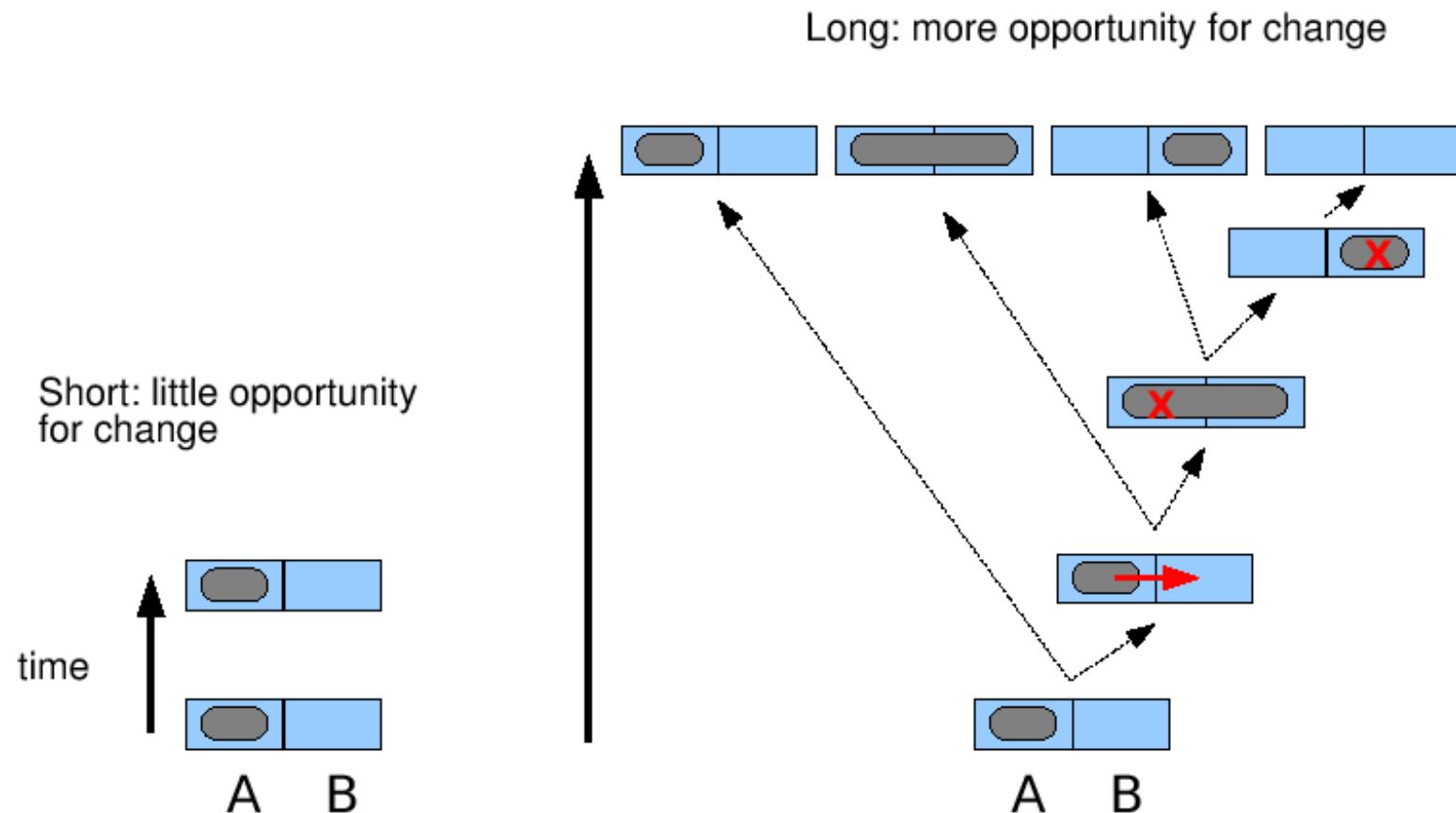


peripheral isolate



**Widespread ranges  
cannot be identically  
inherited! Biologically  
unrealistic**

# Branch length matters!

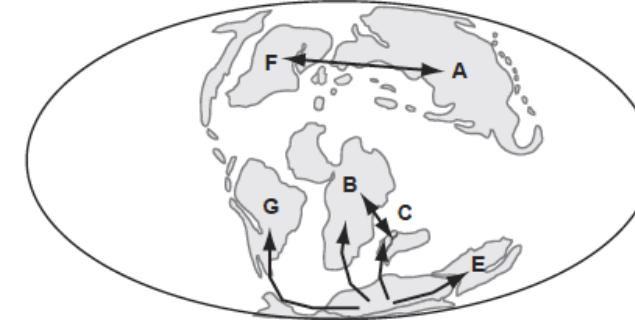


# DEC (Dispersal-Extinction-Cladogenesis)

- Model components

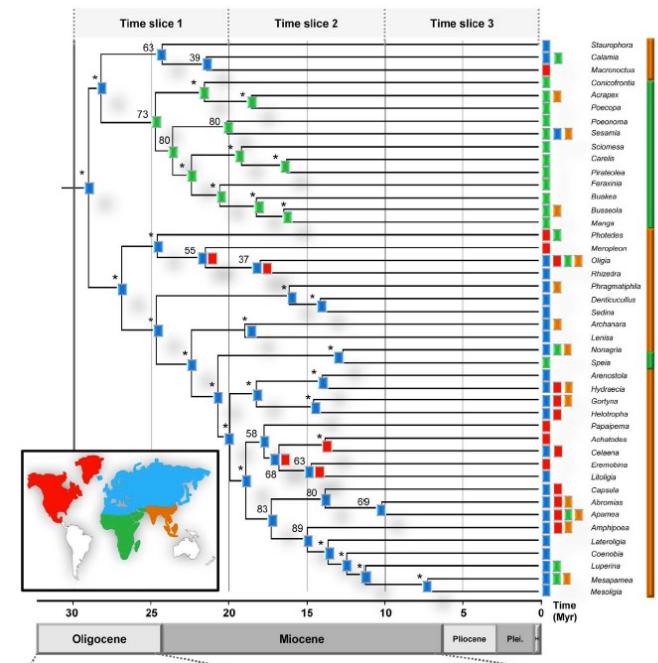
- Paleogeographic component (a set of areas with connections – dispersal routes – between pairs of areas)
  - Can change over time (using “time slices”)
- Phylogeny with branch lengths calibrated to give lineage divergence times = time-calibrated tree

(a) Time slice 1: before 80 Ma



	A	B	C	D	E	F	G
A	1	0.01	0.01	0.01	0.01	1	0.01
B	0.01	1	1	0.01	1	0.01	1
C	0.01	1	1	0.01	1	0.01	1
D	0	0	0	0	0	0	0
E	0.01	1	1	0.01	1	0.01	1
F	1	0.01	0.01	0.01	0.01	1	0.01
G	0.01	1	1	0.01	1	0.01	1

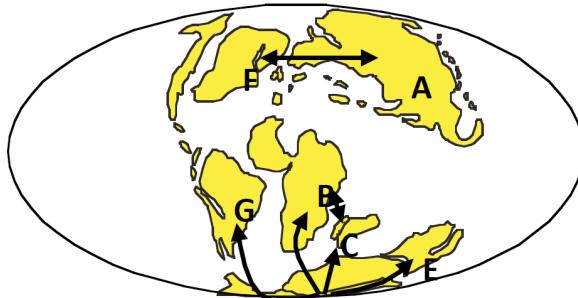
Buerki et al. 2011 J. Biogeo.



Toussaint et al. 2012 PLoS One

# Time-stratified model

- Paleogeographic model
  - Connectivity among areas modeled as discrete time slices
  - Rates of dispersal scaled according to availability of paleogeographic connections - landbridges, wind-ocean currents, etc.
  - Reflecting change in dispersal opportunities over time

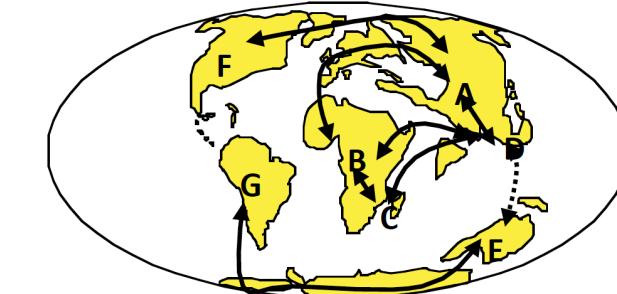


Before 80 Ma

	A	B	C	D	E	F	G
A	1	0	0	0	0	1	0
B	0	1	1	0	1	0	1
C	0	1	1	0	1	0	1
D	0	0	0	0	0	0	0
E	0	1	1	0	1	0	1
F	1	0	0	0	0	1	0
G	0	1	1	0	1	0	1

Before 60 Ma

	A	B	C	D	E	F	G
A	1	0	0	1	0	1	0
B	0	1	1	0	1	0	0
C	0	1	1	0	0	0	0
D	1	0	0	1	0	0	0
E	0	0	0	0	1	0	1
F	1	0	0	0	0	1	1
G	0	0	0	0	1	1	1



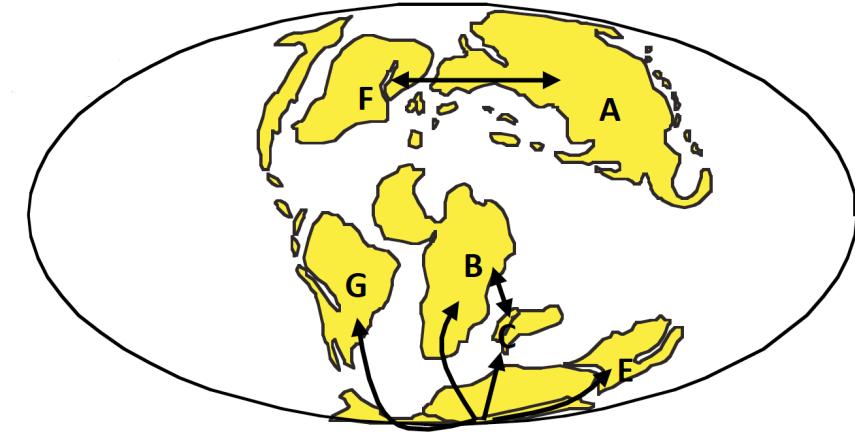
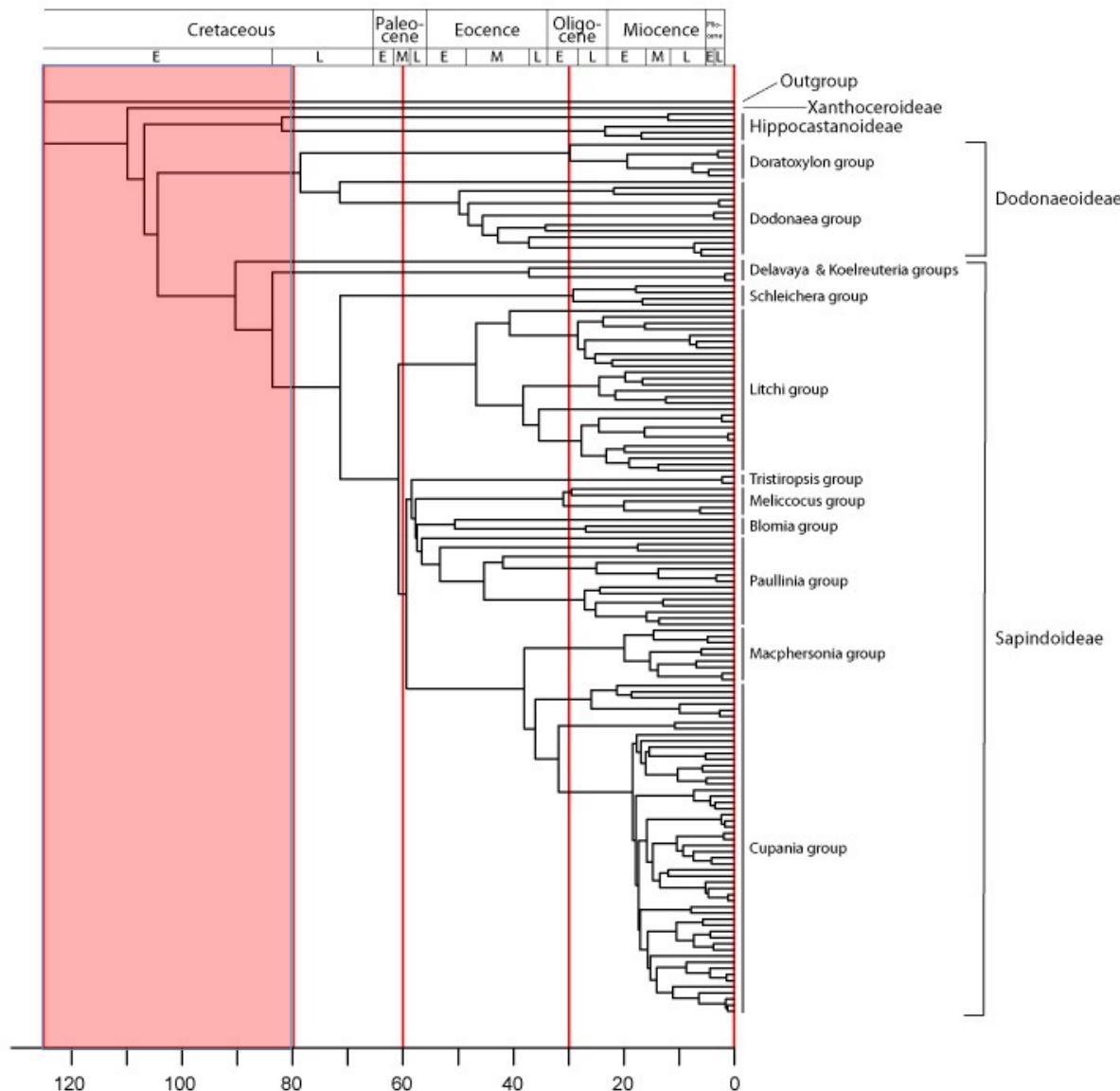
Before 30 Ma

	A	B	C	D	E	F	G
A	1	1	0	1	0	1	0
B	1	1	1	1	0	0	0
C	0	1	1	1	0	0	0
D	1	1	1	1	0.5	0	0
E	0	0	0	0.5	1	0	1
F	1	0	0	0	0	1	0
G	0	0	0	0	1	0	1

30-0 Ma

	A	B	C	D	E	F	G
A	1	1	0	1	0	1	0
B	1	1	1	1	0.5	0	0.5
C	0	1	1	1	0.5	0	0
D	1	1	1	1	1	0	0
E	0	0.5	0.5	1	1	0	0.5
F	1	0	0	0	0	1	1
G	0	0.5	0	0	0.5	1	1

# Time slice I: before 80 MA

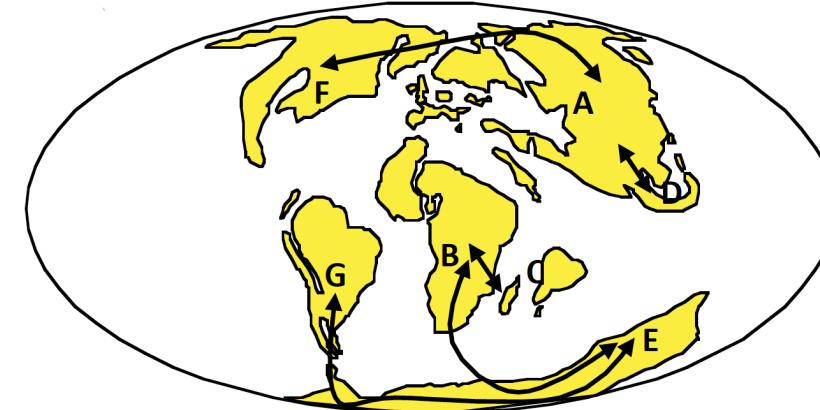
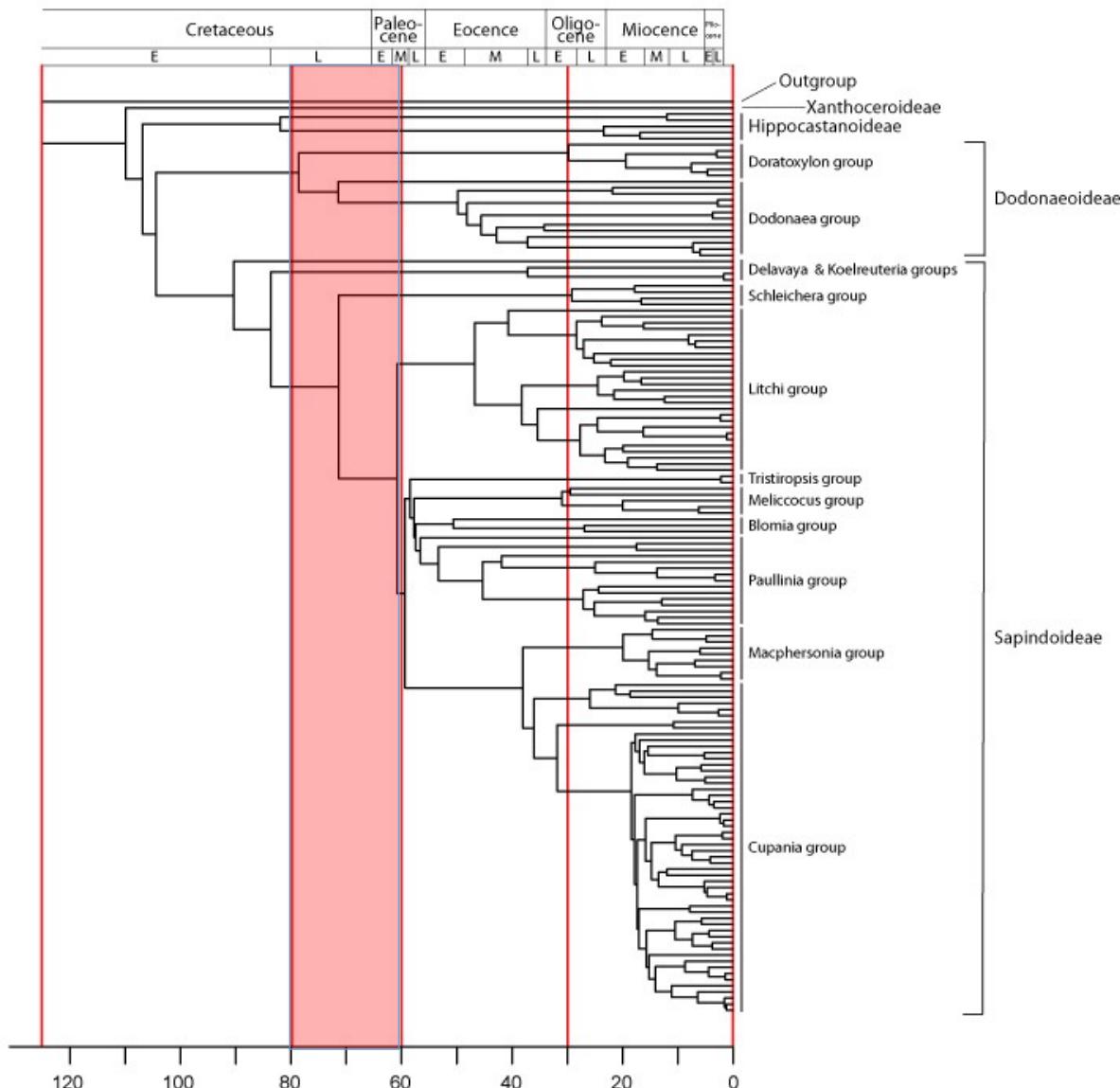


	A	B	C	D	E	F	G
A	1	0	0	0	0	1	0
B	0	1	1	0	1	0	1
C	0	1	1	0	1	0	1
D	0	0	0	0	0	0	0
E	0	1	1	0	1	0	1
F	1	0	0	0	0	1	0
G	0	1	1	0	1	0	1

At that time SE Asia  
was not in place

Images from I. Sanmartín

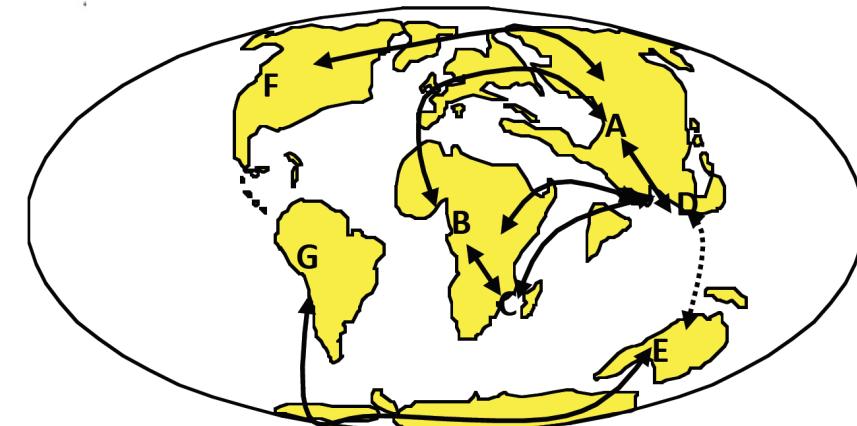
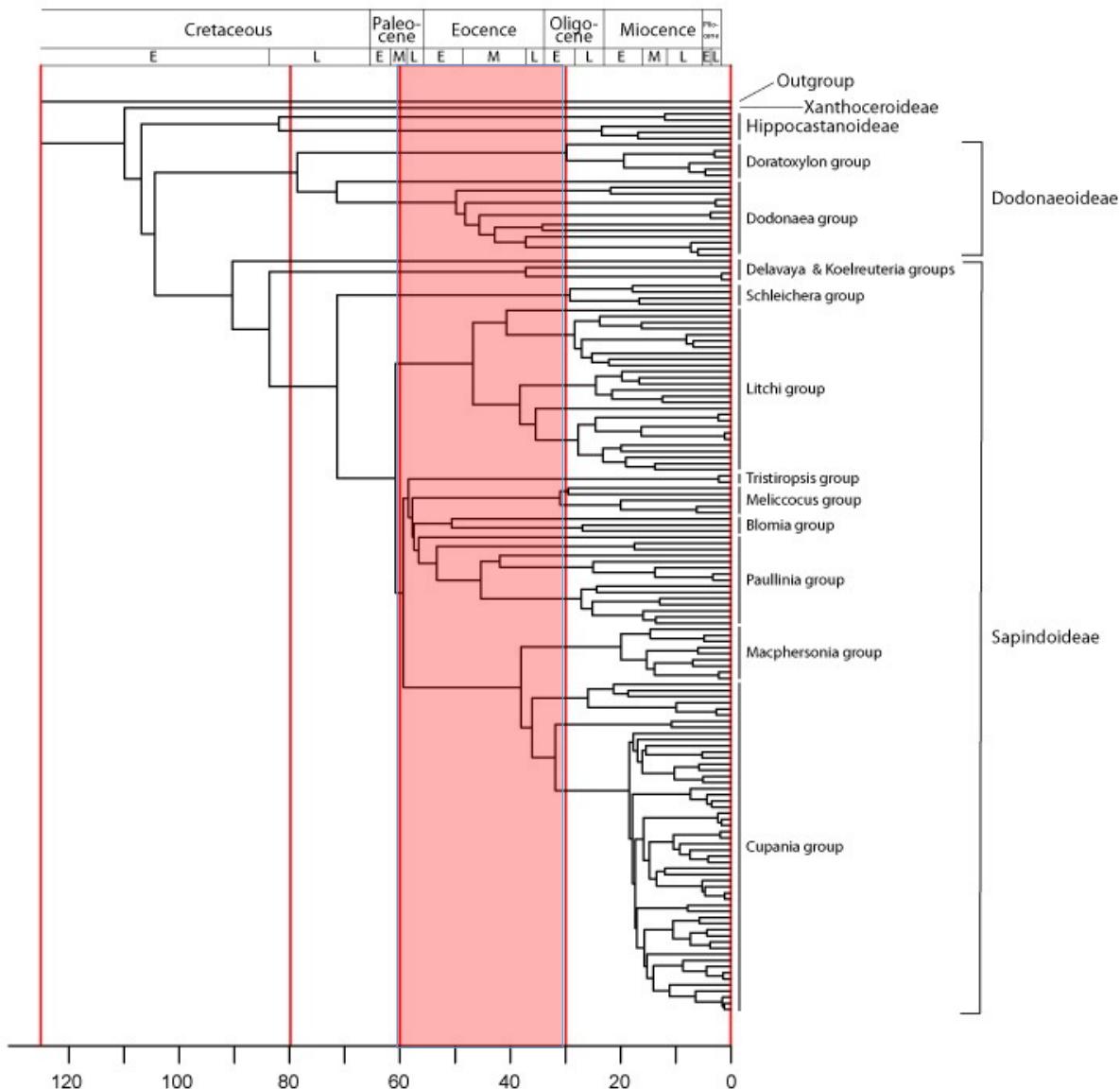
# Time slice II: 80–60 MA



	A	B	C	D	E	F	G
A	1	0	0	1	0	1	0
B	0	1	1	0	1	0	0
C	0	1	1	0	0	0	0
D	1	0	0	1	0	0	0
E	0	0	0	0	0	1	0
F	1	0	0	0	0	1	1
G	0	0	0	0	1	1	1

“proto-SE Asia”: SE Malaysian Peninsula + SW Borneo  
(Metcalfe, 1998)

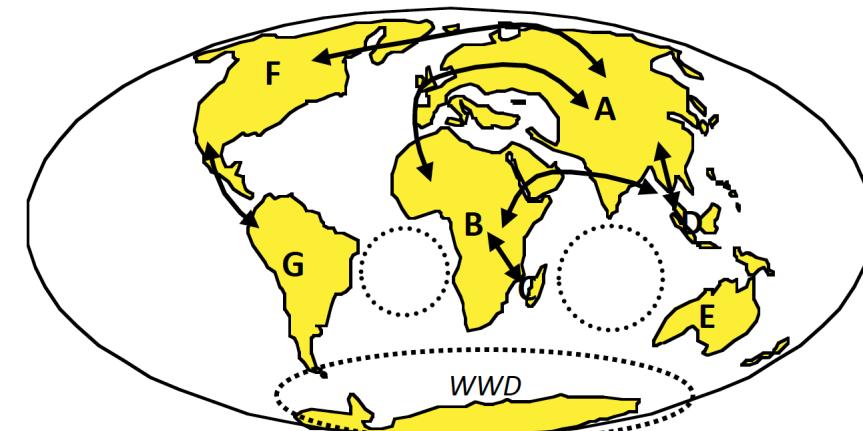
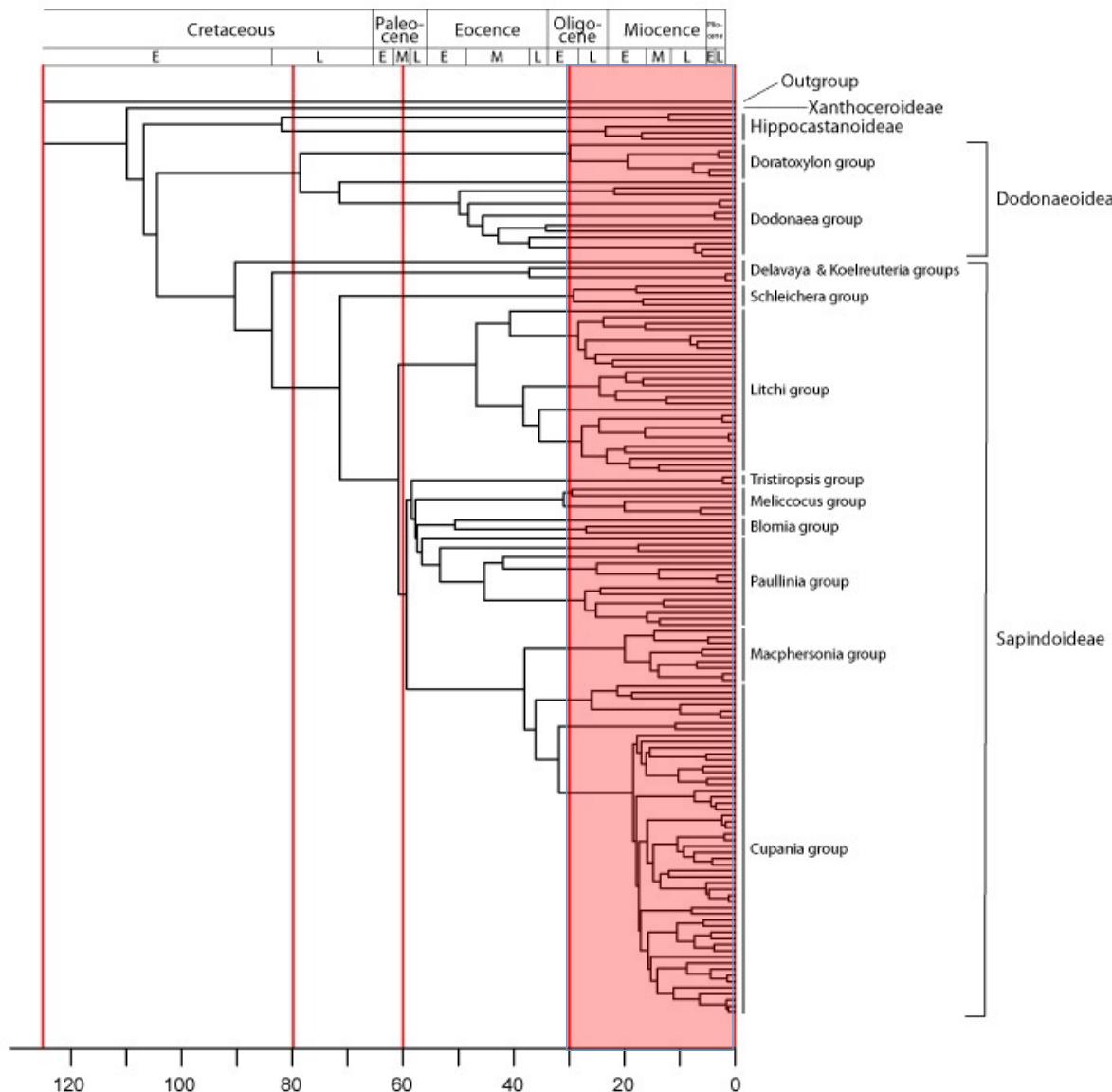
# Time slice III: 60–30 MA



	A	B	C	D	E	F	G
A	1	1	0	1	0	1	0
B	1	1	1	1	0	0	0
C	0	1	1	1	0	0	0
D	1	1	1	1	0.5	0	0
E	0	0	0	0.5	1	0	1
F	1	0	0	0	0	1	0
G	0	0	0	0	1	0	1

**Break up of Gondwana**  
Collision AFR - EURASIA

# Time slice IV: 30–0 MA



	A	B	C	D	E	F	G
A	1	1	0	1	0	1	0
B	1	1	1	1	0.5	0	0.5
C	0	1	1	1	0.5	0	0
D	1	1	1	1	1	0	0
E	0	0.5	0.5	1	1	0	0.5
F	1	0	0	0	0	1	1
G	0	0.5	0	0	0.5	1	1

**West Wind Drift**  
Equatorial Currents

# Advantages of DEC

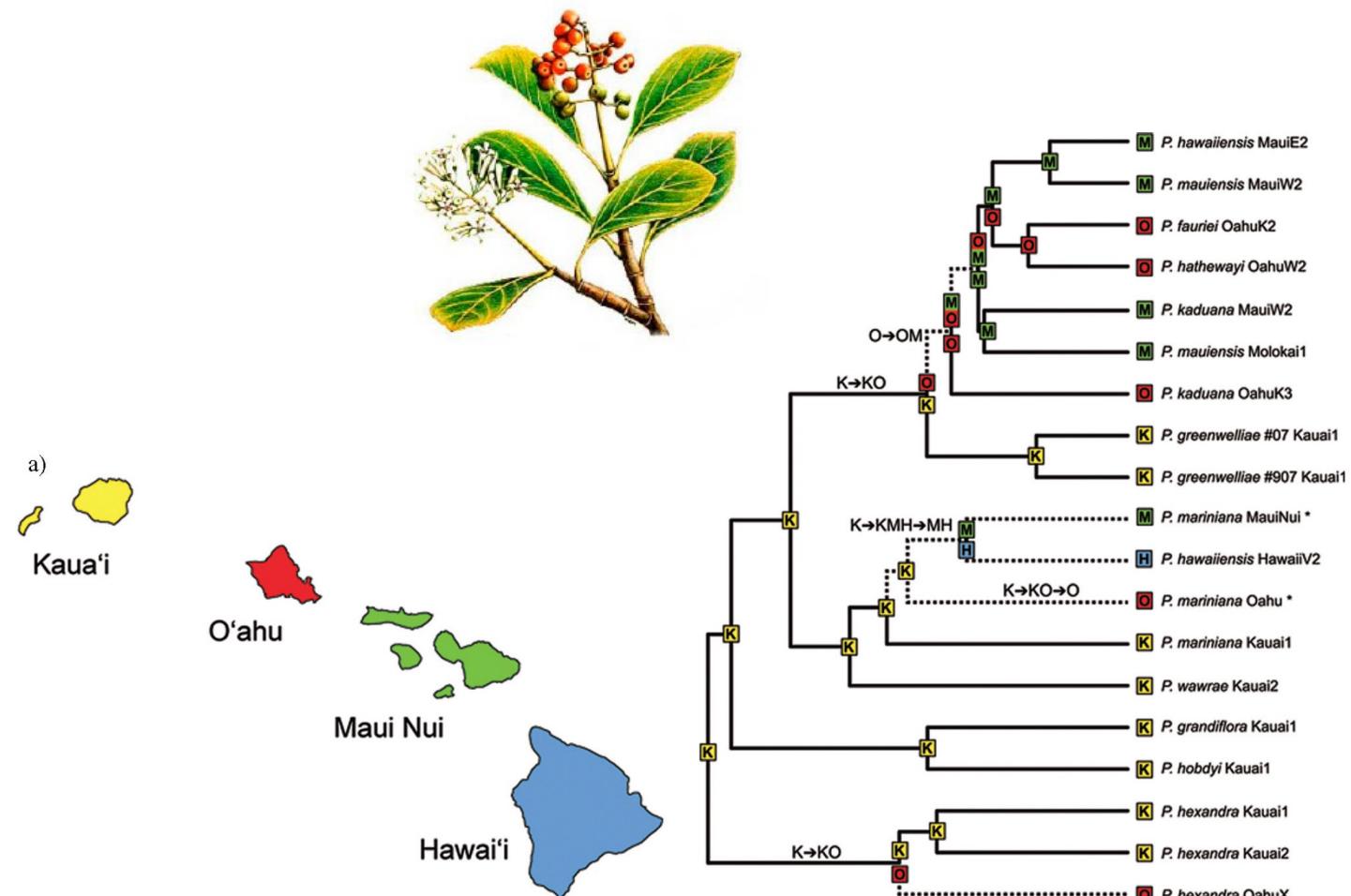
- Does not favour a particular scenario
- Incorporates available biological and geological information
- Enables hypothesis testing in a statistical framework (maximum likelihood)
  - Comparison of different models corresponding to different hypotheses
  - Identifying the best-fitting model
- In Bayesian framework, estimation of parameters over every possible tree topology and combination of branch lengths
  - Incorporation of uncertainty inherent in phylogenetic inference and timing of divergence analysis

# Limitations of DEC

- Balancing the complexity of biogeographic models against the amount of data
  - The issue of overparameterization
- The more areas in the model, the more possible ranges and parameters that need to be estimated
- Important to use alternative sources of evidence to decrease the size of the parameter matrix
  - E.g. not allow certain ranges because they weren't geographically adjacent during some time period
  - Or not allow certain transitions between geographic states
- Like other modelling approaches, we can only compare a certain set of models
  - Our best model could still be pretty far from the truth

# Case study: Hawaiian *Psychotria*

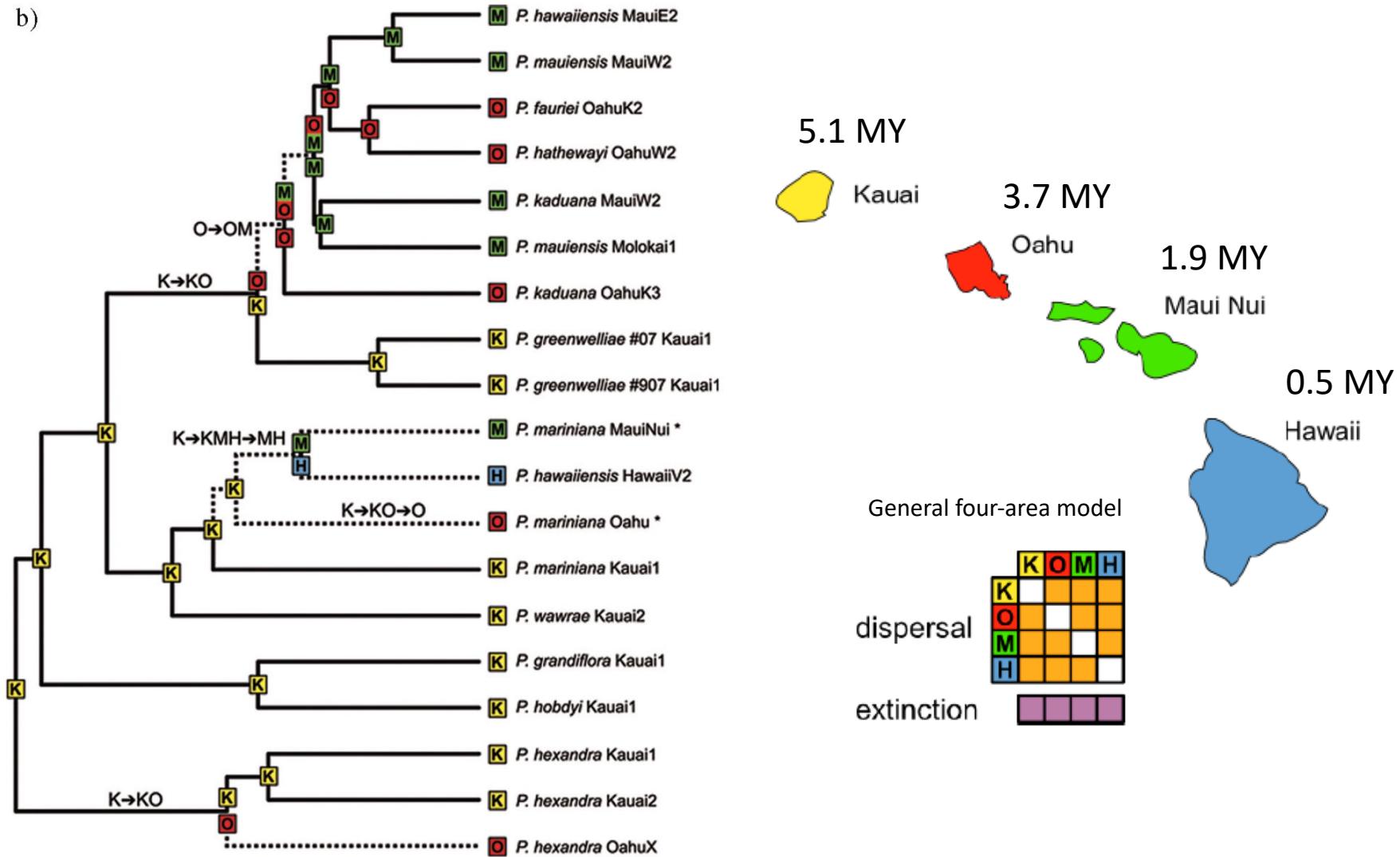
- Family Rubiaceae, 1582 spp. described
- One of the largest plant genera
- Pantropical distribution
- Radiation in Hawaii
  - 11 species, 19 populations
- Study by Nepokroeff et al. 2003
- DEC model applied by Ree & Smith 2008



# Questions about Hawaiian *Psychotria*

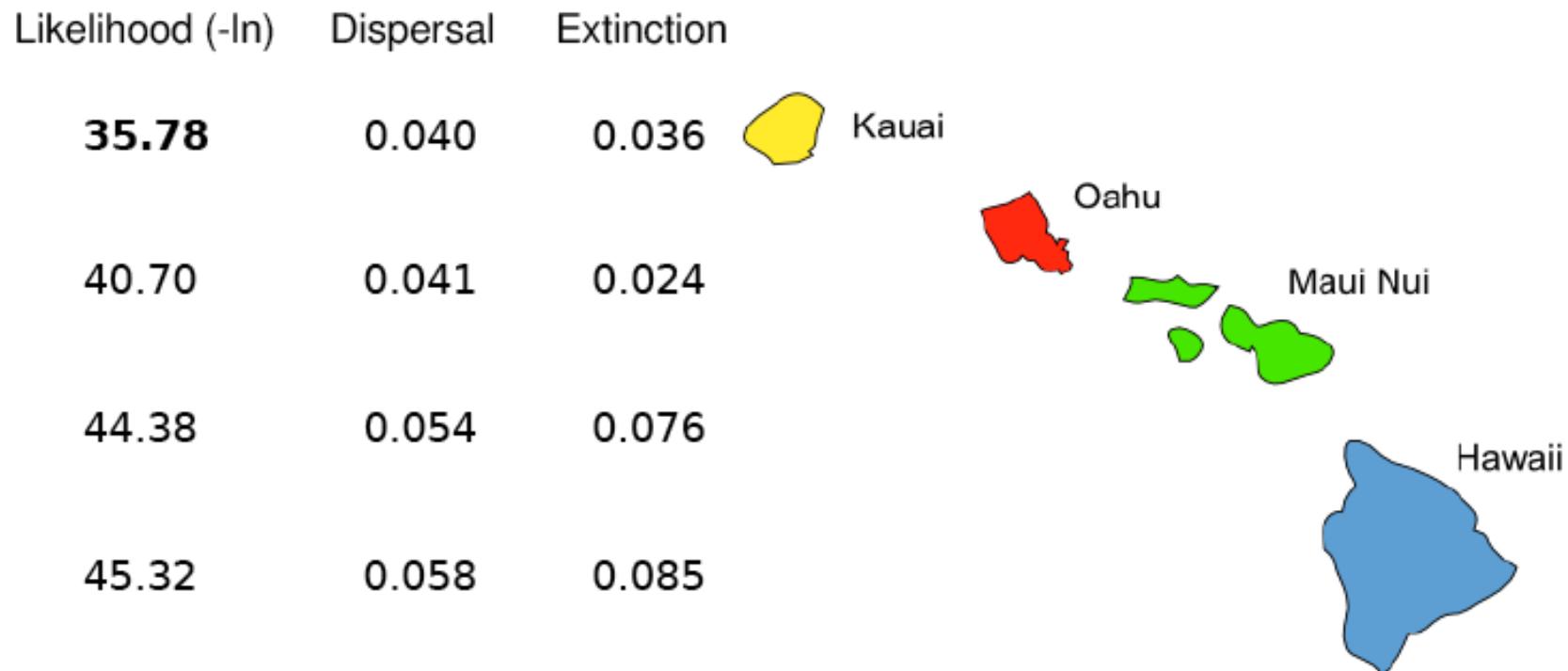
- Which island was most likely colonized by the ancestor of the clade?
- The relative degree of within-area versus between-area lineage divergence following dispersal?
  - i.e., the extent to which dispersal leads to cladogenesis
- Whether simpler models, e.g. those allowing only dispersal between adjacent islands were favored over the general model?
- One of the objectives: compare inference between models with and without temporal constraints
  - Ages of Hawaiian islands well known

# 19 populations, phylogram, single-area endemics



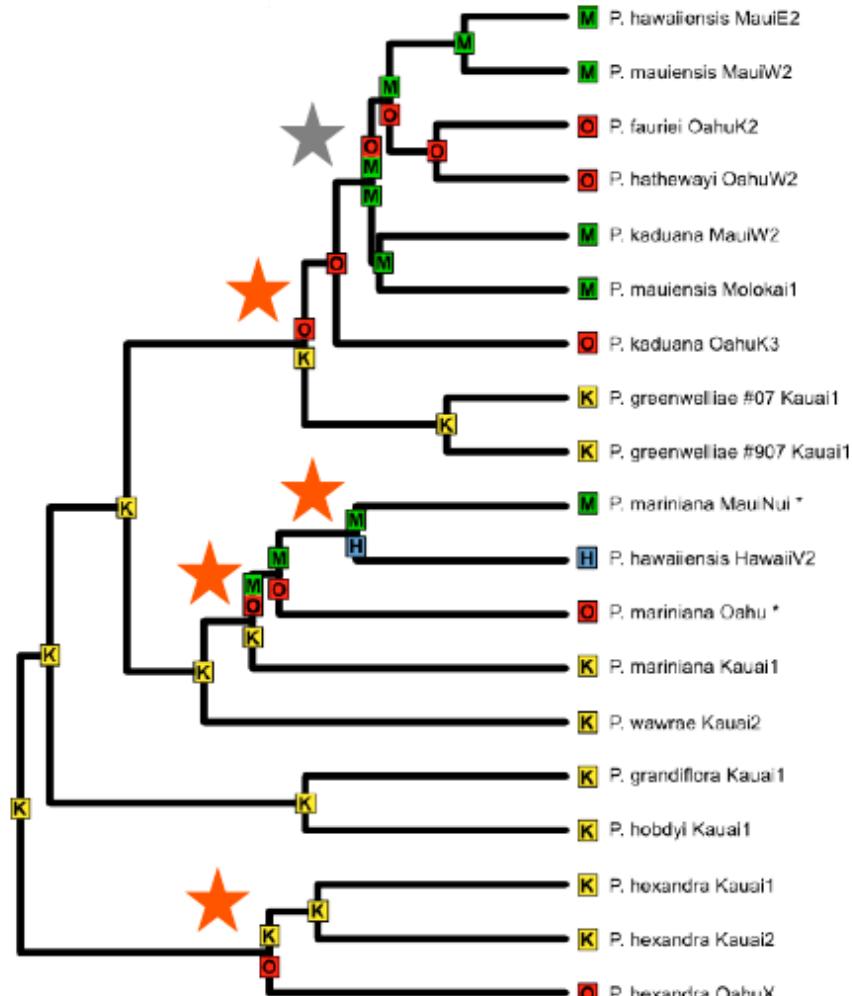
# Likelihoods of area colonization

For each island at the root, optimize dispersal and extinction rates and compare likelihoods



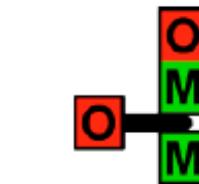
# Ancestral ranges, dispersal, and lineage divergence

- For each internal node, compare likelihoods of ancestral range scenarios
- Re-optimize dispersal and extinction rates
- 5 dispersal events; only 1 not associated with lineage divergence (speciation)



Modified from slide by I. Sanmartín

# Ancestral ranges, dispersal, and lineage divergence



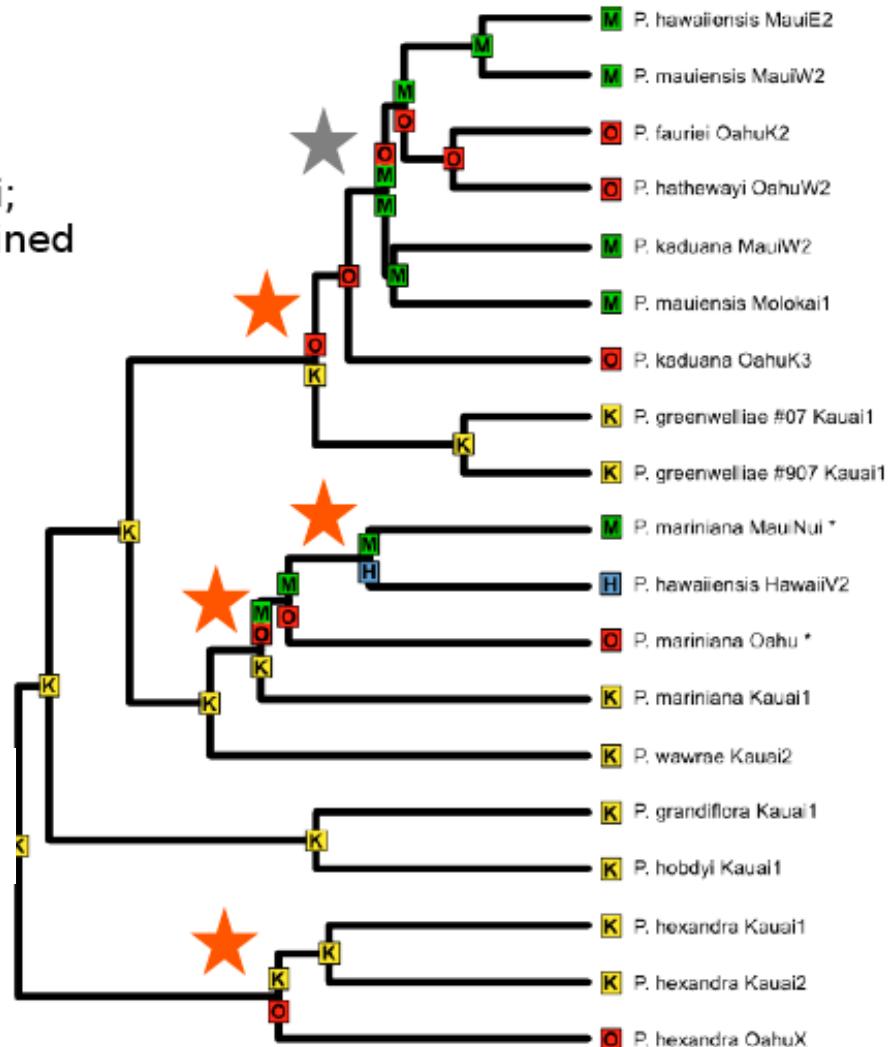
dispersal to Maui;  
divergence within Maui;  
widespread range retained



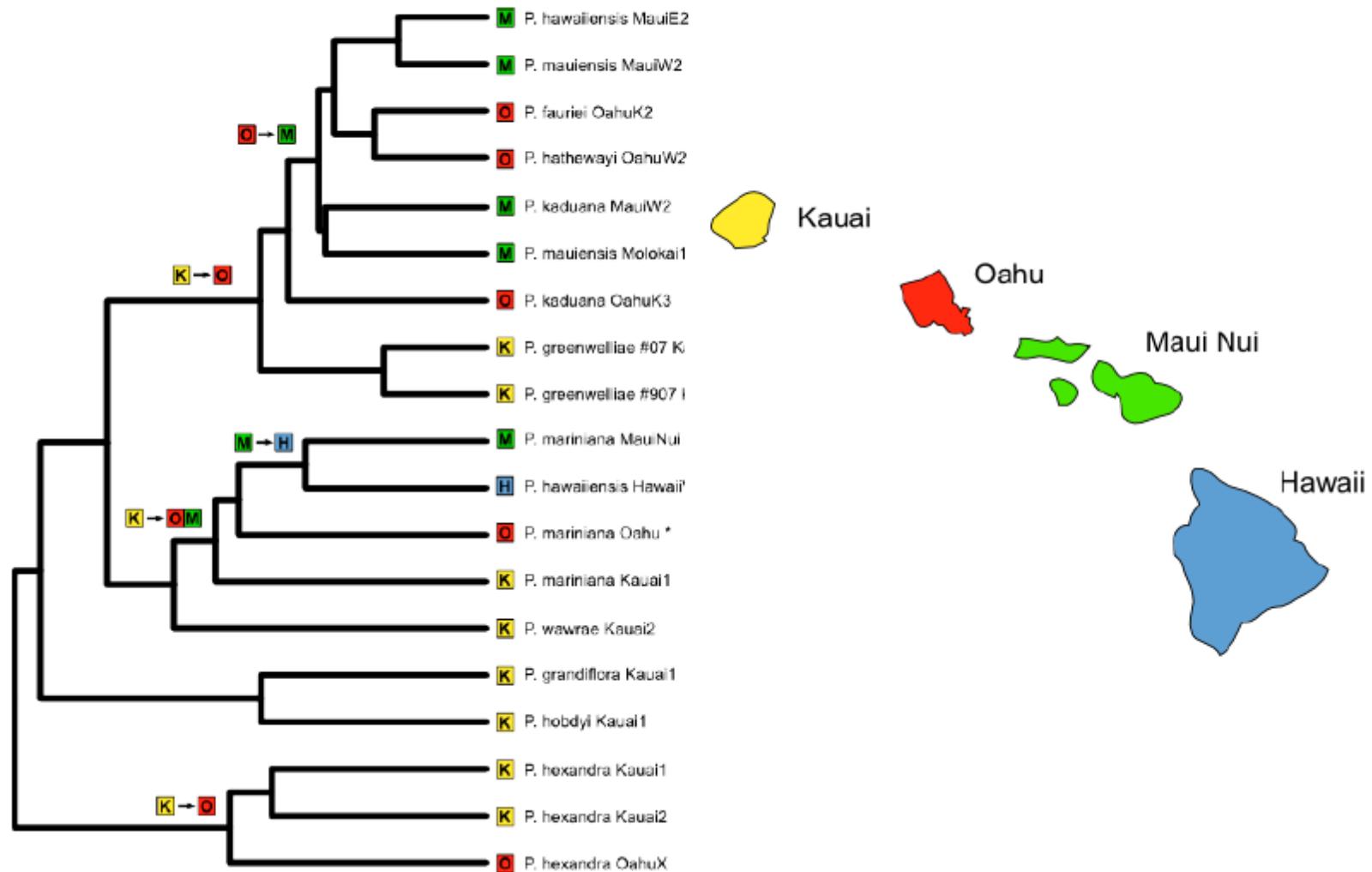
dispersal to Oahu followed  
by "vicariant" speciation;  
cladogenesis by dispersal



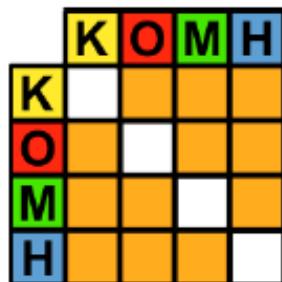
dispersal event associated  
with lineage divergence



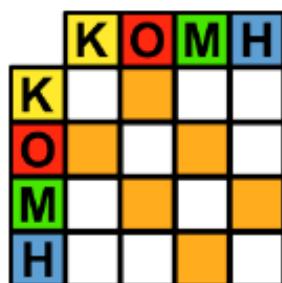
# Directional dispersal model favored?



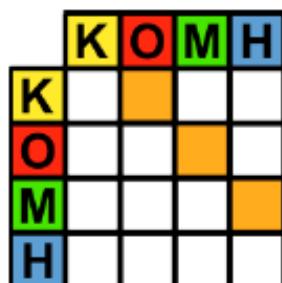
# Simplified 4-area model: linear dispersal



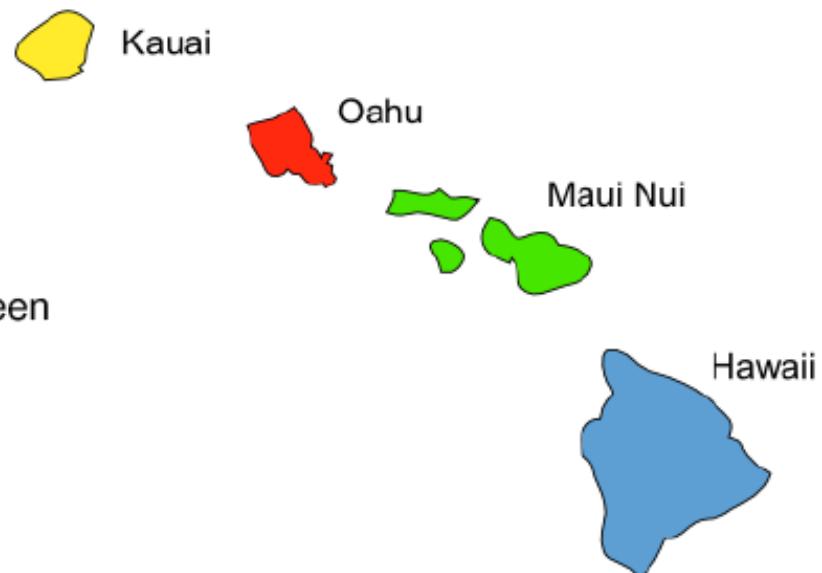
dispersal between  
all islands possible



linear dispersal only between  
adjacent islands

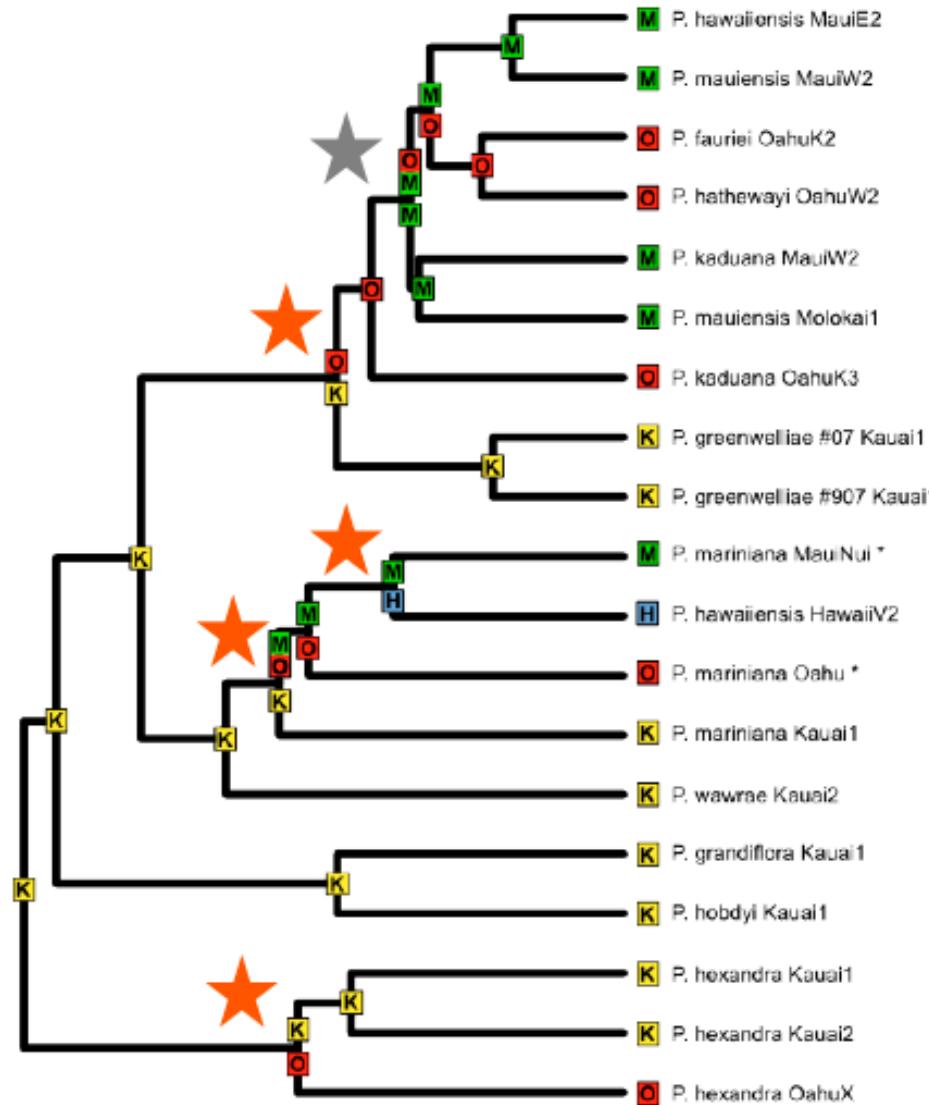


linear, directional dispersal only to adjacent younger islands

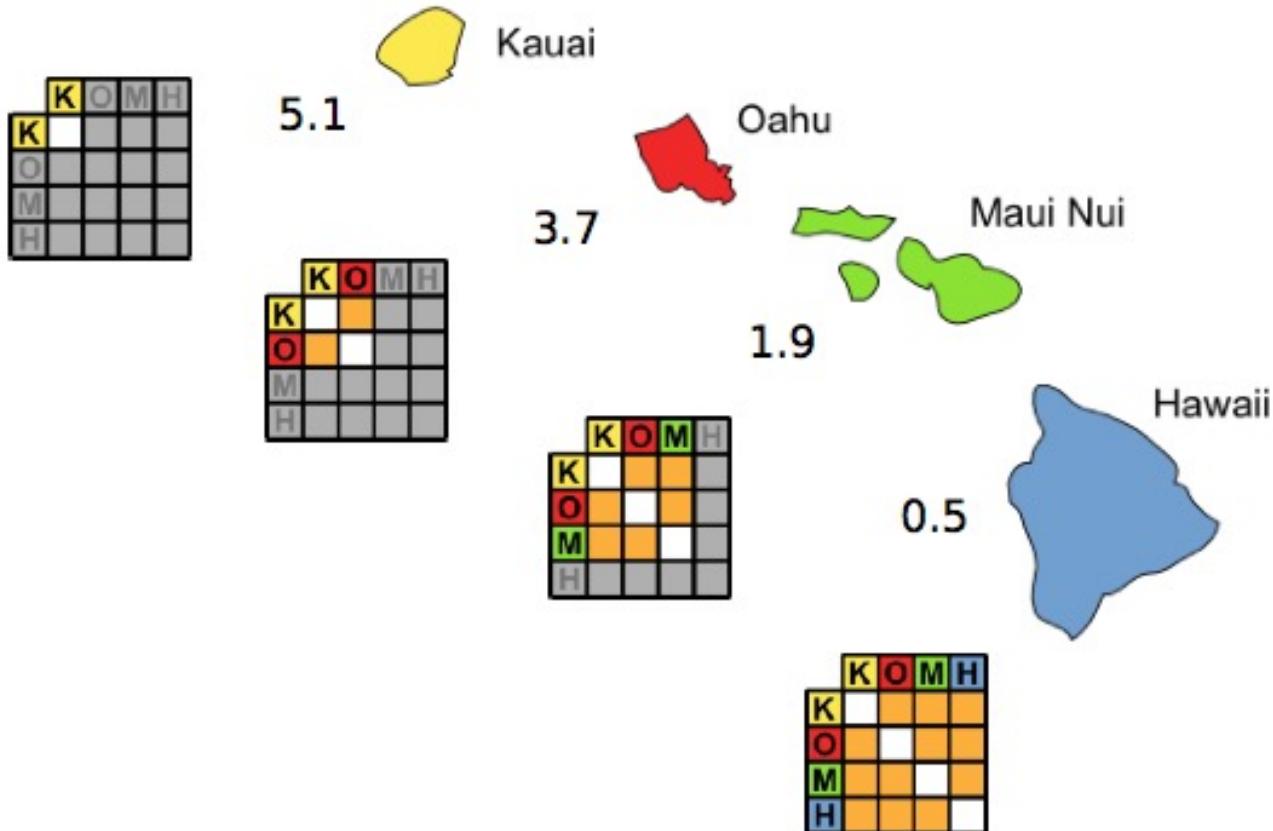


# Hawaiian *Psychotria*: likelihood inferences

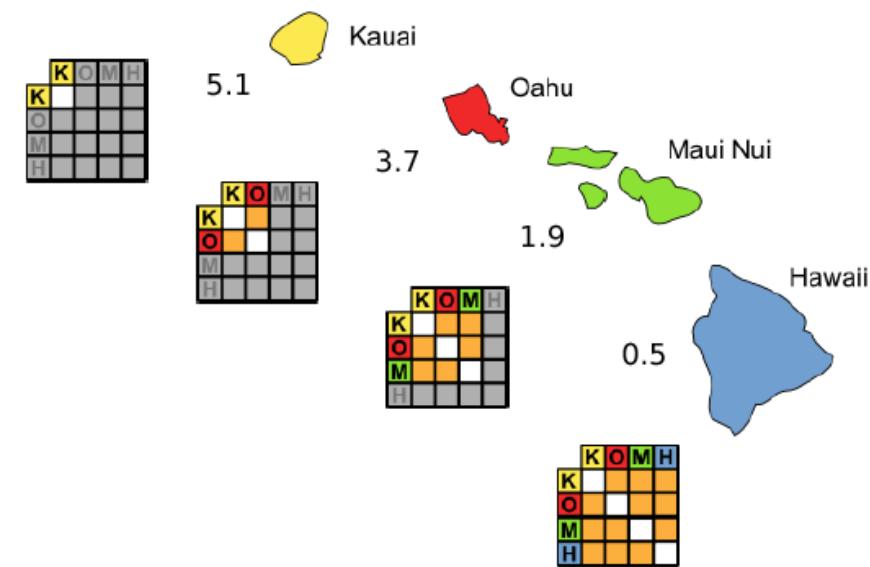
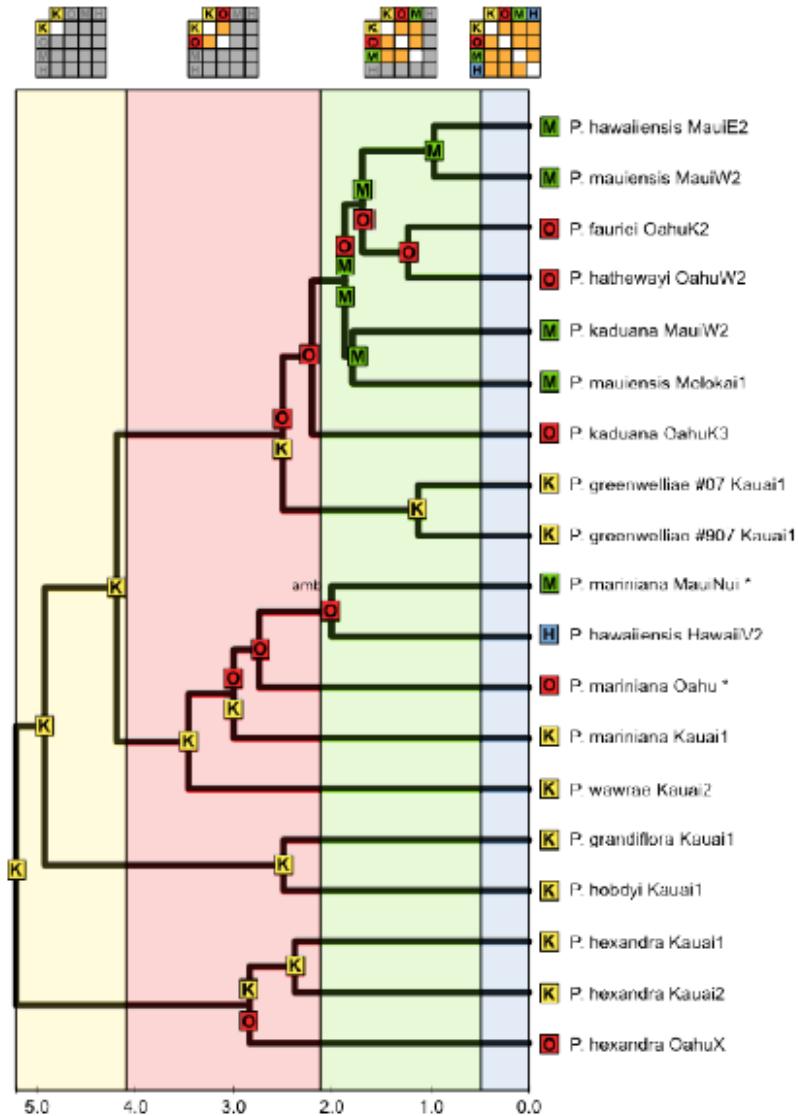
- Kauai strongly favored as area of colonization
- Direction of inferred dispersal is from older to younger islands
- 4 out of 5 inferred dispersal events associated with lineage divergence
- Simpler models (small contiguous ranges, linear directional dispersal) fit the data better than more general models



# Area connections (dispersal opportunities) through time



# Time connections

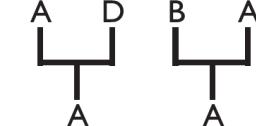
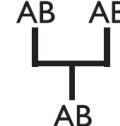
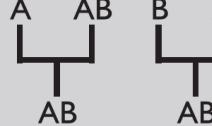
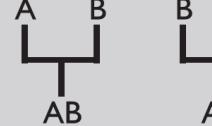
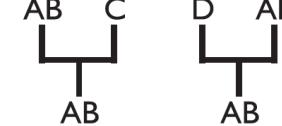
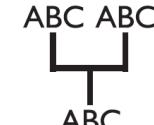
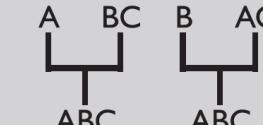
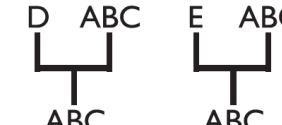
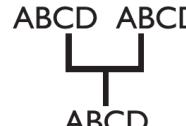


# Dispersal-extinction-cladogenesis (DEC) models in BioGeoBEARS

All events modelled by  
BioGeoBEARS

Events allowed by  
LAGRANGE

## Types of speciation and example descendant ranges:

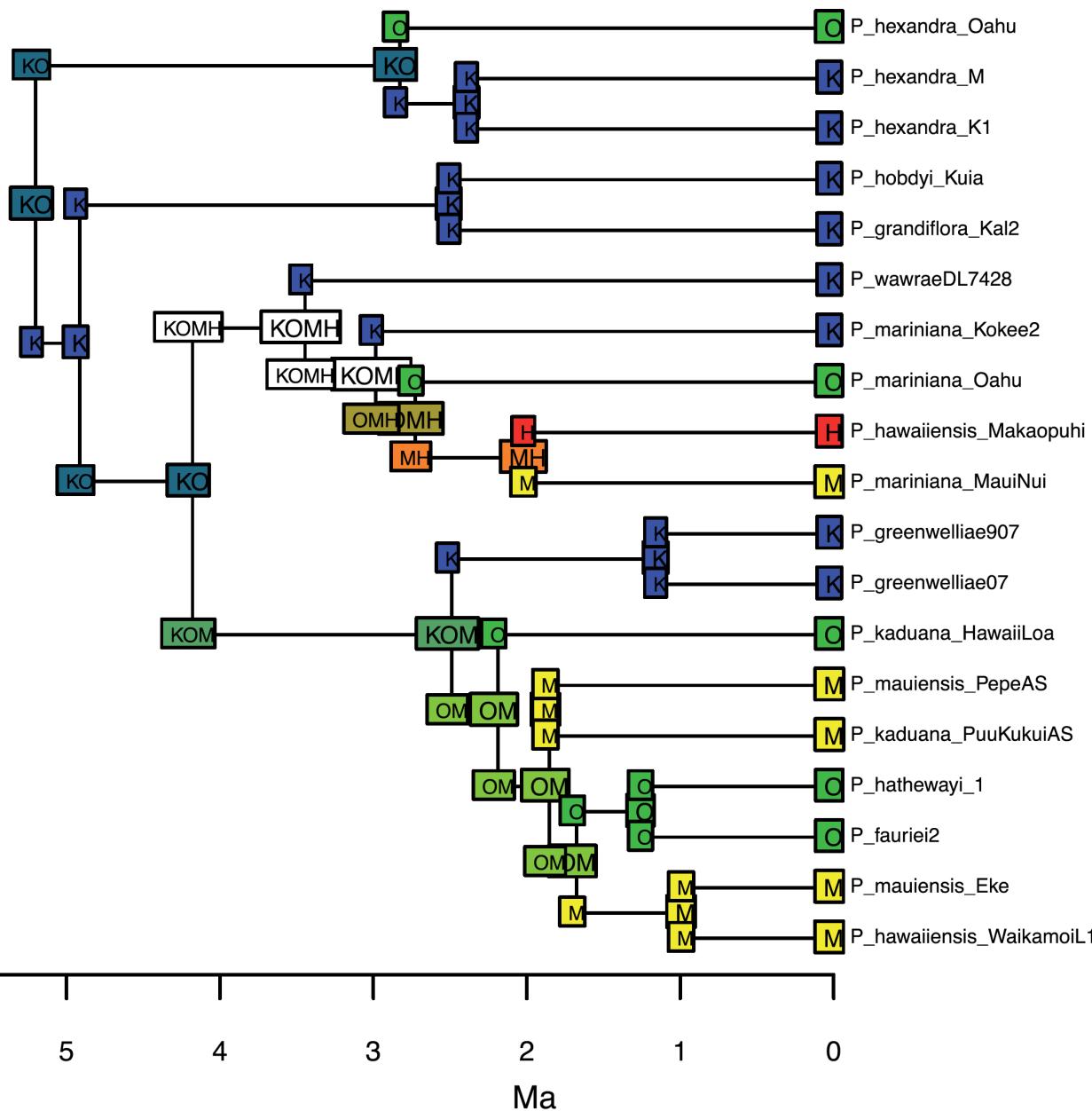
Ancestral ranges	Sympatric (range copying)	Sympatric (subset)	Vicariance	LDDE event
A		--	--	
AB				
ABC				
ABCD				

# DEC+j: modelling of LDDEs

- DEC+j = Long distance dispersal and establishment events allowed (so-called jump dispersal or founder-event speciation)
  - Cladogenetic range inheritance scenario
- Conceptual flaw of DEC:
  - Cladogenetic events (unlike anagenetic) are not modelled as probabilistic with respect to time
  - This artificially inflates the contribution of the cladogenetic events to the likelihood
  - Underestimation of anagenetic, time-dependent range evolution
- Leads to DEC+j almost always being better fit to data than DEC
  - These two models are not comparable

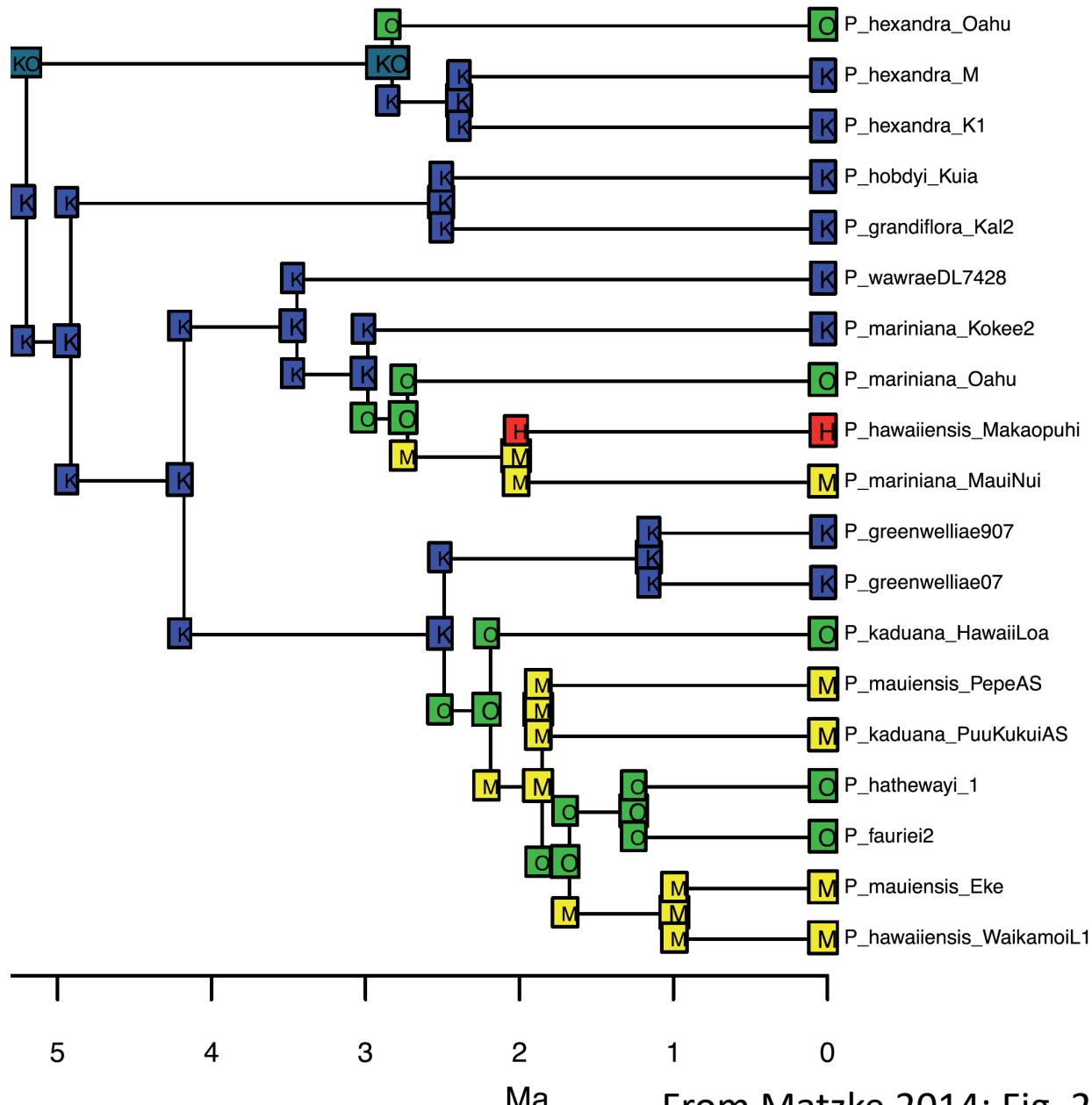
### BioGeoBEARS DEC on Psychotria M0\_unconstrained

anstates: global optim, 4 areas max. d=0.035; e=0.028; j=0; LnL=-34.5

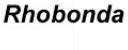


### BioGeoBEARS DEC+J on Psychotria M0\_unconstrained

anstates: global optim, 4 areas max. d=0; e=0; j=0.114; LnL=-20.9



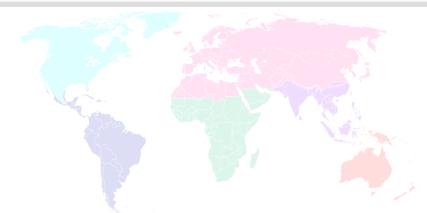
From Matzke 2014: Fig. 2

1.00  
100Brenthia  AA, AT, NA, NT, O1.00  
100Anthophila  AT, NA, PA1.00  
100Prochoreutis  NA, NT, PA1.00  
100Caloreas  NA, NT1.00  
100Tebenna  AA, AT, NA, NT, O, PA1.00  
100Saptha  AA, O1.00  
100Tortyra  NA, NT1.00  
100Zodia  NT1.00  
100Alasea  NT1.00  
100Rhbonda  NT1.00  
100Hemerophila  NA, NT1.00  
100Ornaranthia  NA, NT1.00  
100Choreutinae sp.  AA

0.2

# Historical biogeography of metalmark moths (Choreutidae)

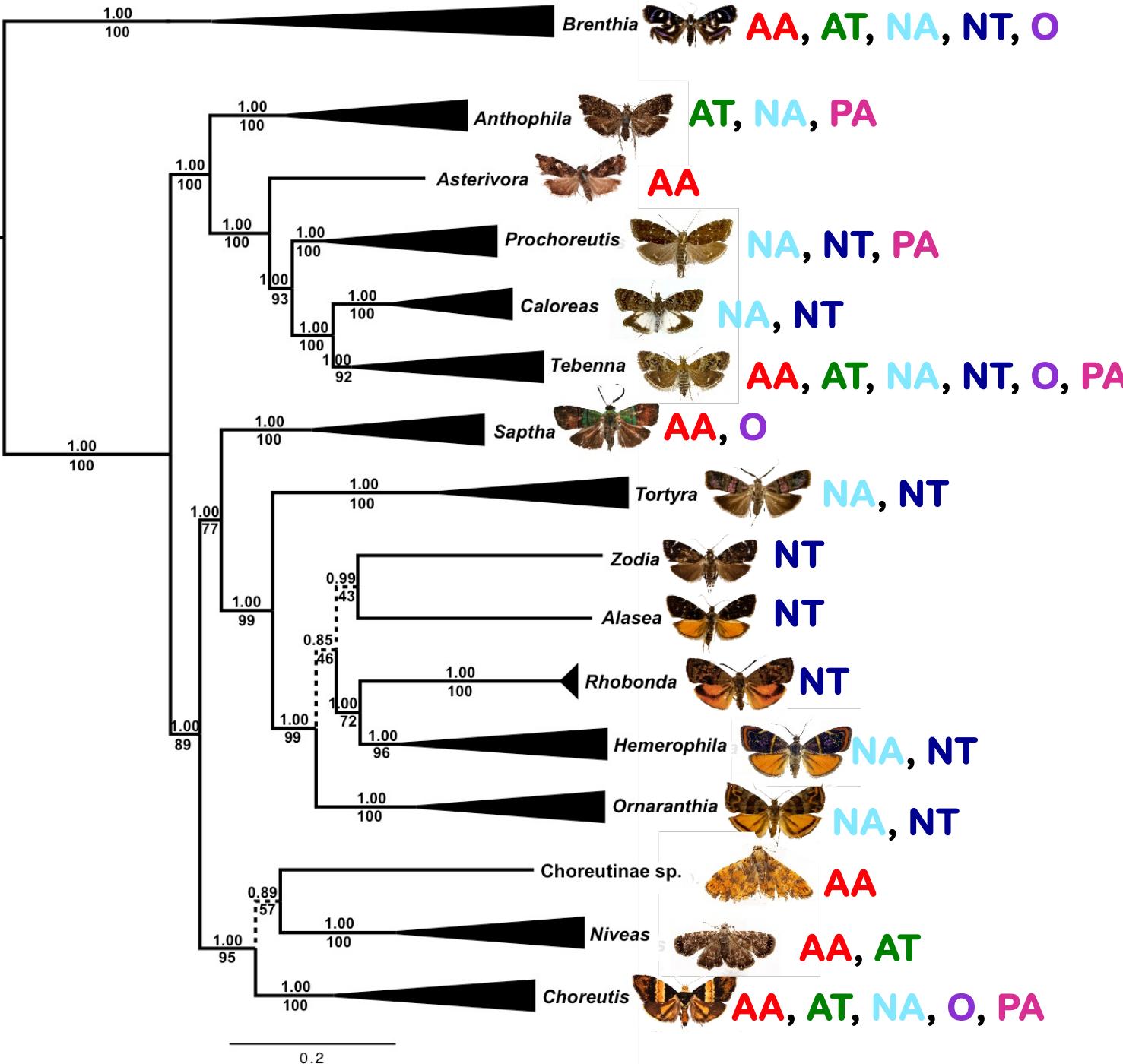
**AA:** Australasian  
**AT:** Afrotropical  
**NA:** Nearctic  
**NT:** Neotropical  
**O:** Oriental  
**PA:** Palaearctic



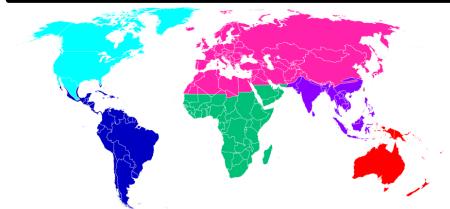
**Vicariance or dispersal?**

If dispersal, must have been long distance.

Time-calibrated tree needed!



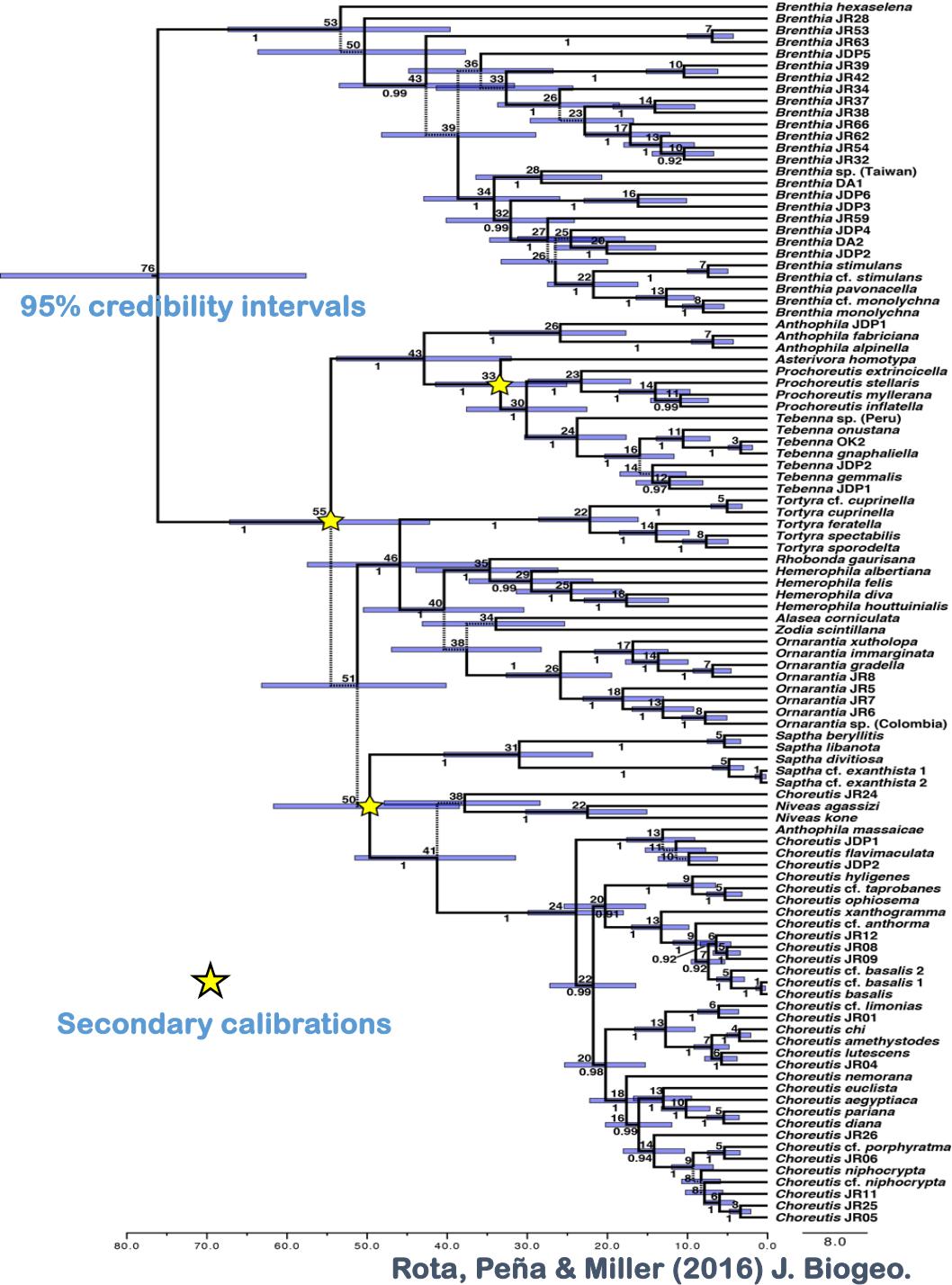
**AA: Australasian**  
**AT: Afrotropical**  
**NA: Nearctic**  
**NT: Neotropical**  
**O: Oriental**  
**PA: Palaearctic**

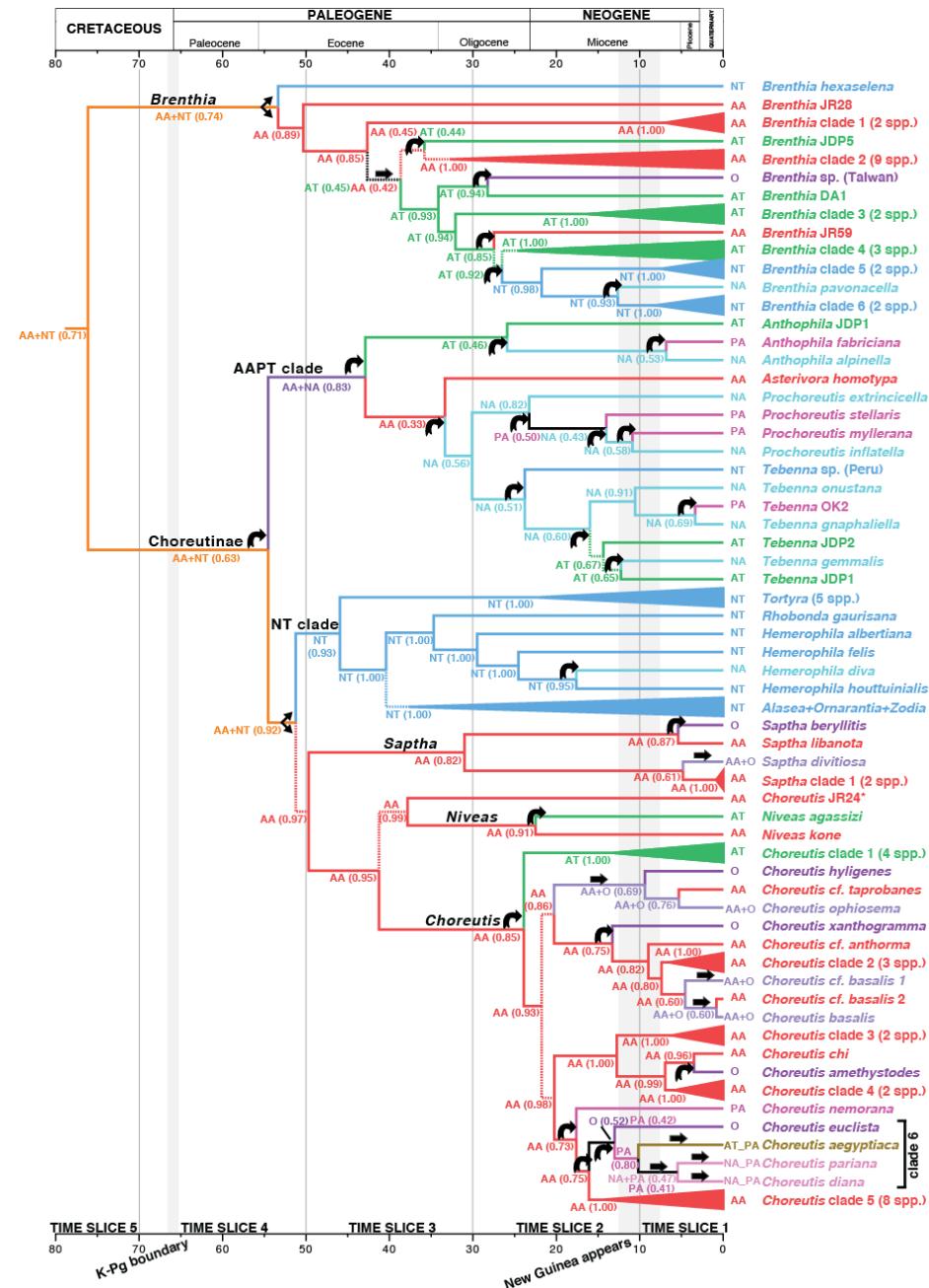


**Vicariance or dispersal?**  
**If dispersal, must have been long distance.**  
**Time-calibrated tree needed!**

# Time-calibrated tree

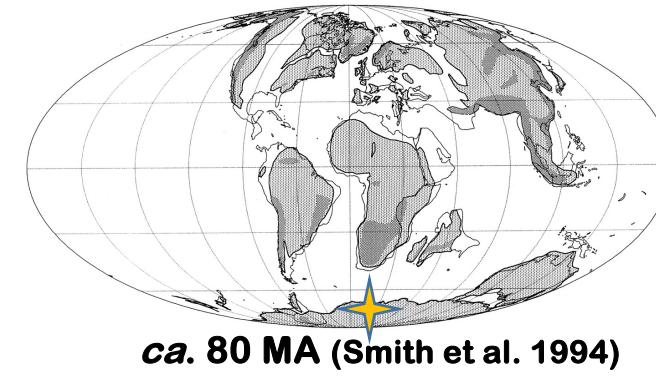
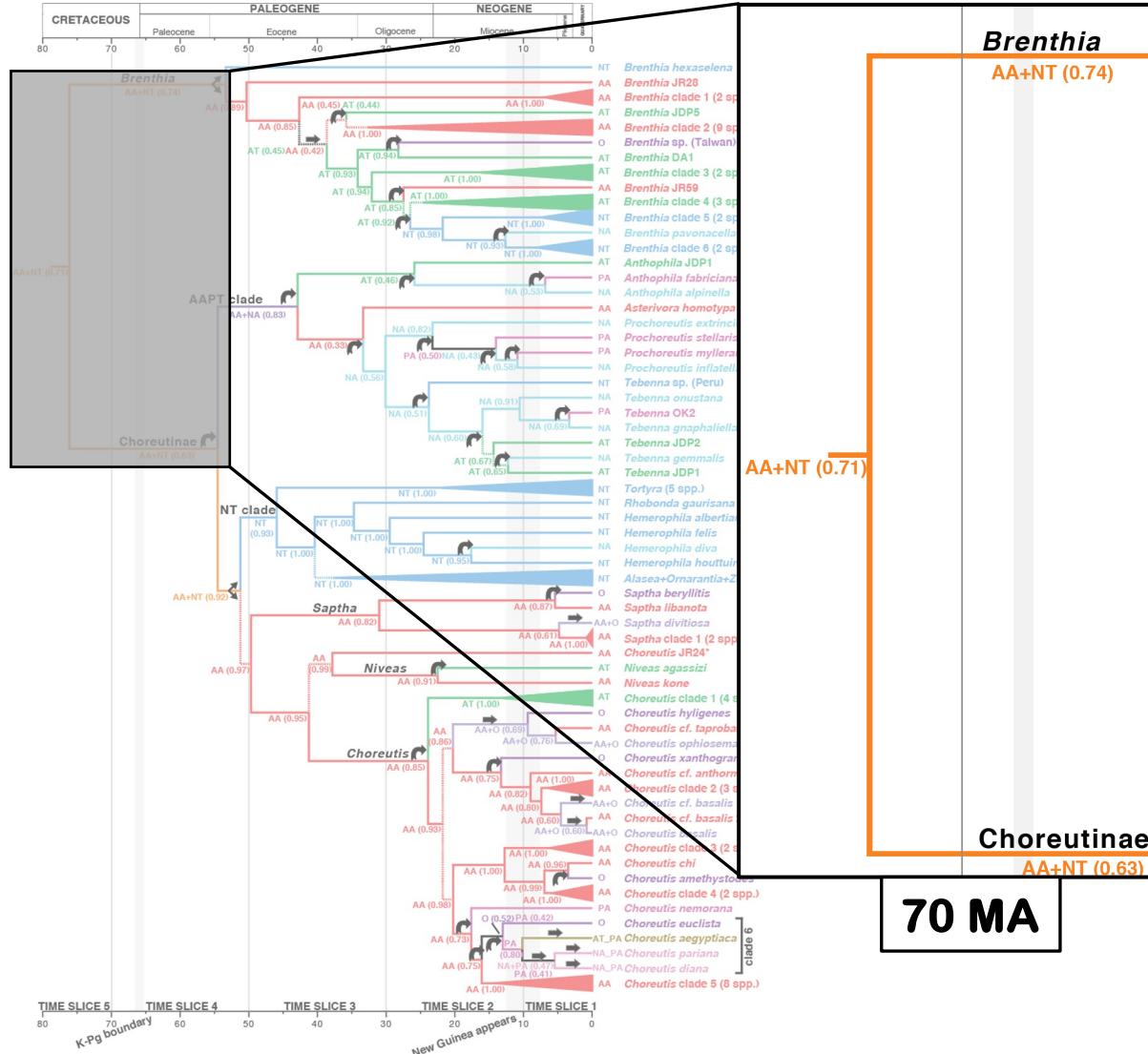
- Time calibration: three secondary calibration points from an all-Lepidoptera study (Wahlberg et al. 2013)
- BEAST (Drummond et al. 2002)





- Ancestral range estimation using BioGeoBEARS (Matzke 2014)
  - World divided into six biogeographic regions:  
**AA: Australasian**, AT: Afrotropical, **NA: Nearctic**, NT: Neotropical, O: Oriental, PA: Palaearctic
  - Time divided into slices linked to position of continents
  - Events inferred:
    - ➡ LDDE
    - ➡ Range expansion (dispersal)
    - ➡ Vicariance

# Area of origin: weak signal



**ca. 80 MA (Smith et al. 1994)**

## Legend

AA: Australasian

## AT: Afrotropical

NA: Nearctic

## NT: Neotropical

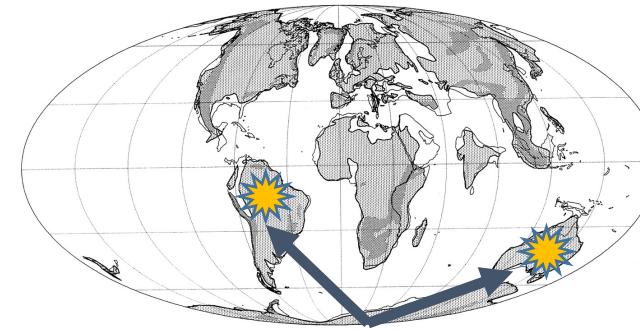
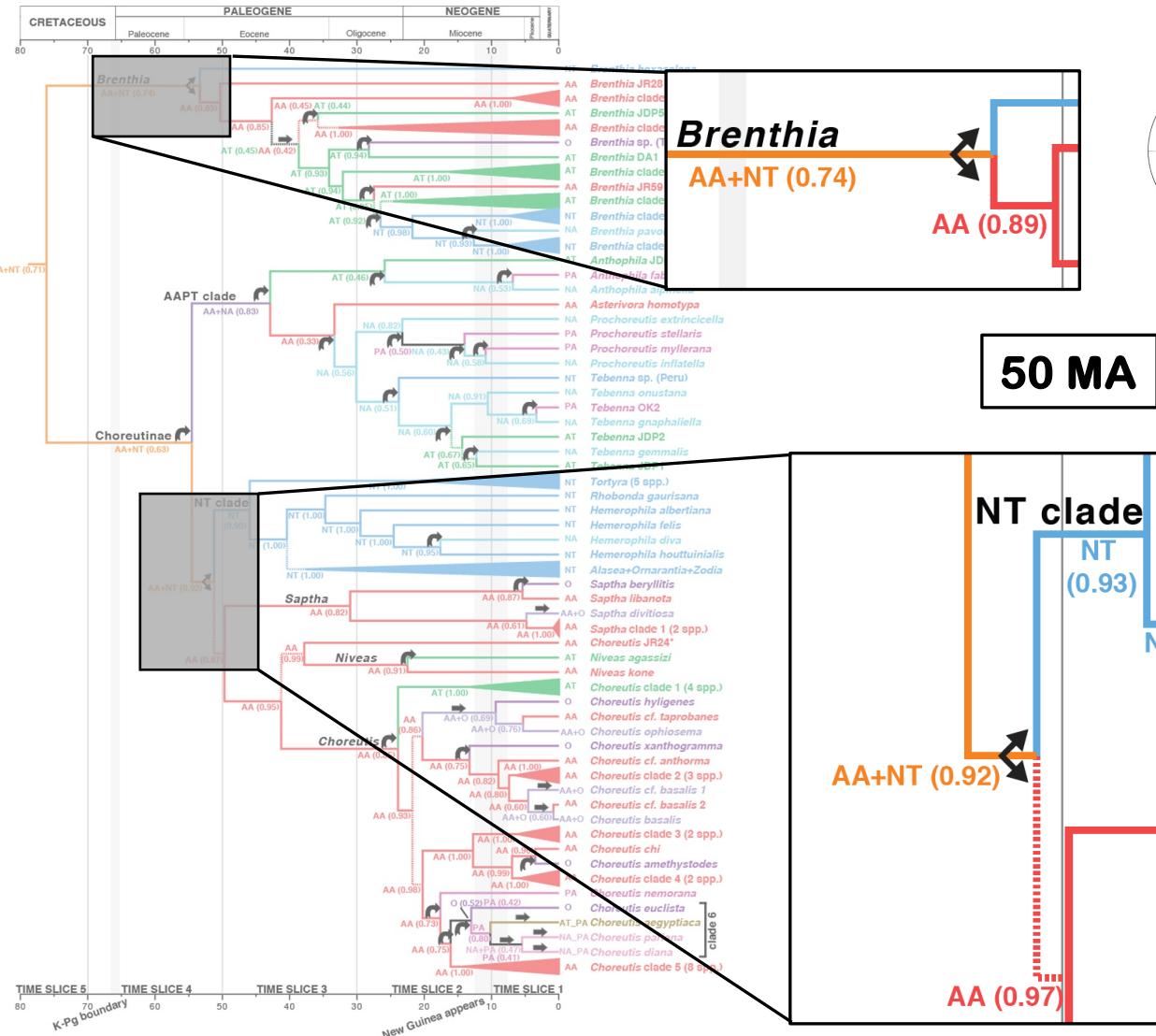
## O: Oriental

PA: Palaeartic

## LDDE (founder event)

- range expansion  
(dispersal)
- ↖ vicariance

# Vicariance events

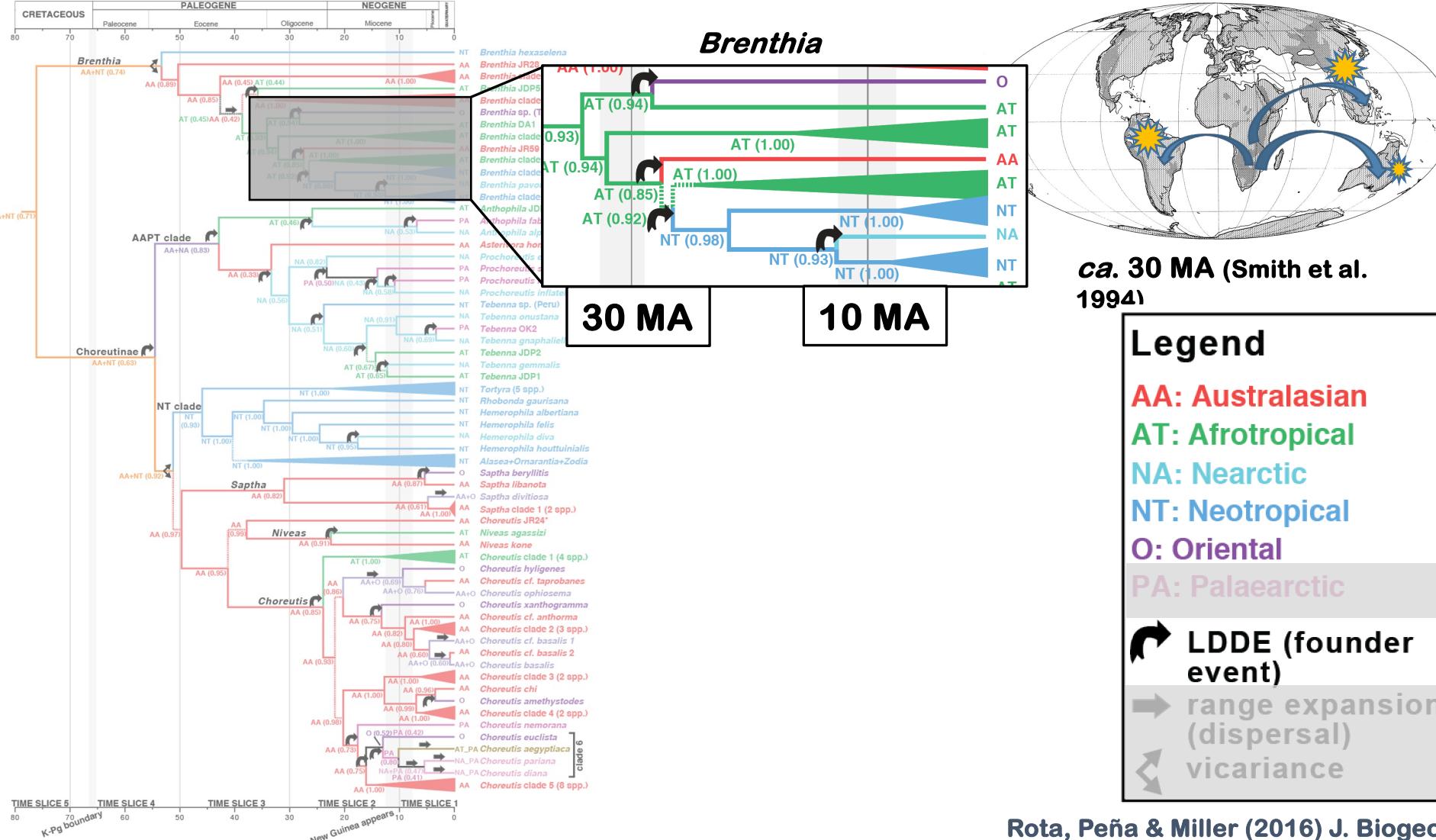


ca. 50 MA (Smith et al. 1994)

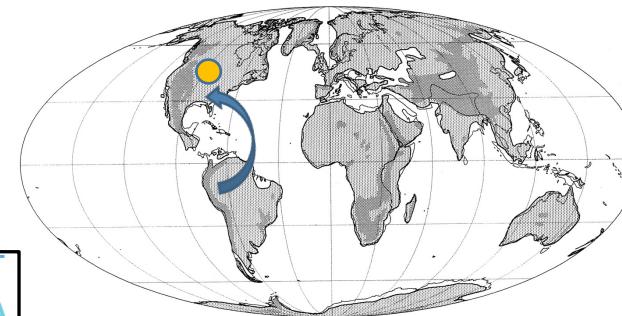
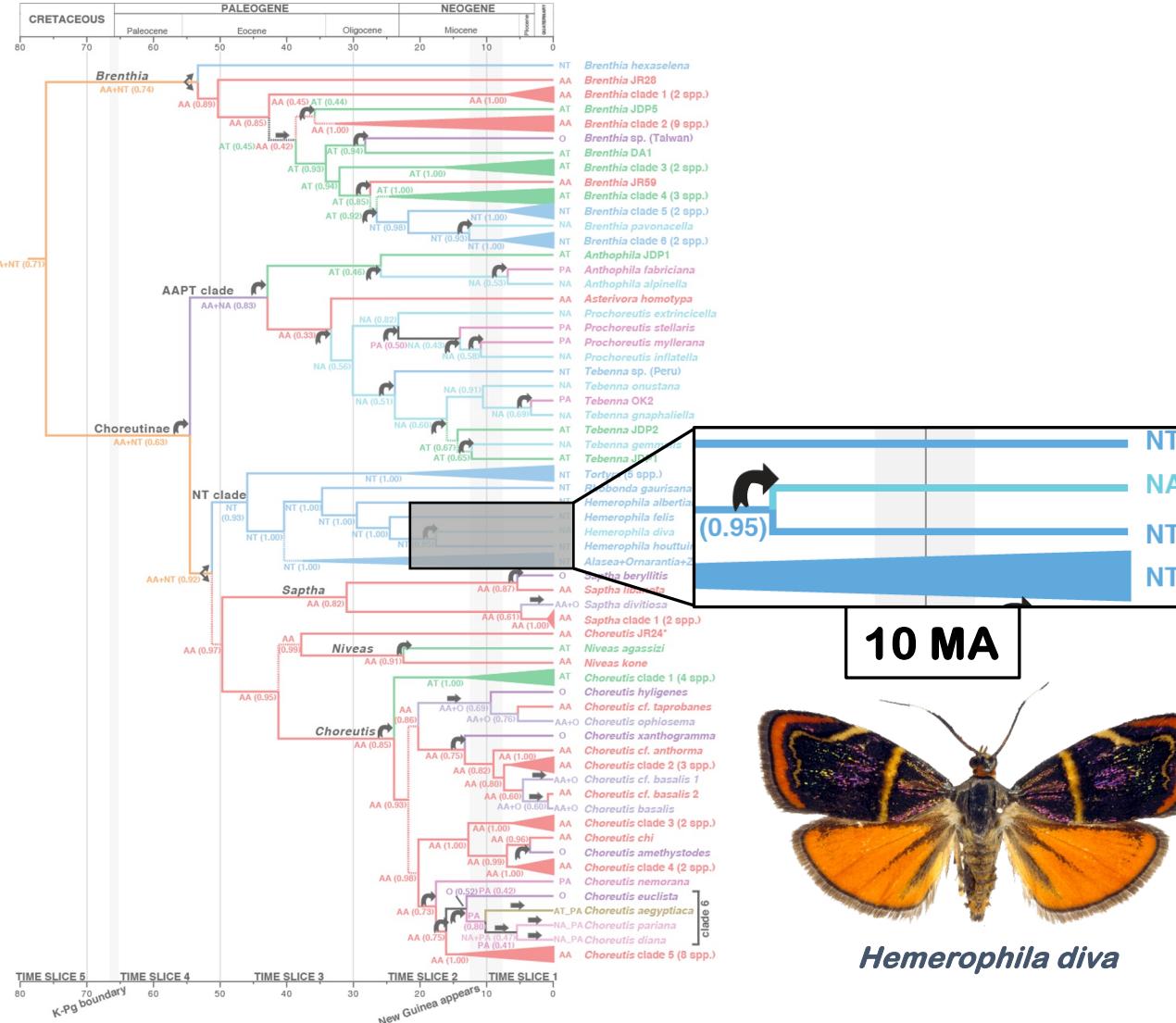
## Legend

- AA: Australasian
- AT: Afrotropical
- NA: Nearctic
- NT: Neotropical
- O: Oriental
- PA: Palaearctic
- ➡ LDDE (founder event)
- ➡ range expansion (dispersal)
- ↔ vicariance

# Crossing oceans: LDDE events out of Africa



# From the Neotropics to the Nearctic



**ca. 20 MA (Smith et al. 1994)**

## Legend

## **AA: Australasian**

AT: Afrotropical

NA: Nearctic

NT: Neotropical

NT: Neotropical

C. Oriental  
PA: Palaeartic

LDDE (founder event)

→ range expansion  
(dispersal)

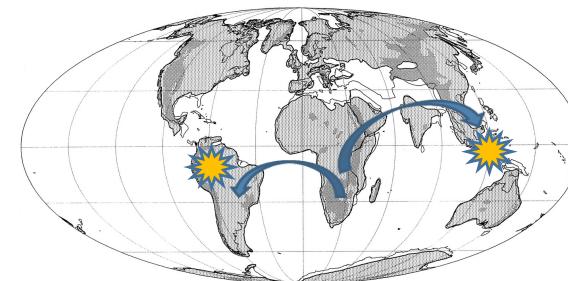
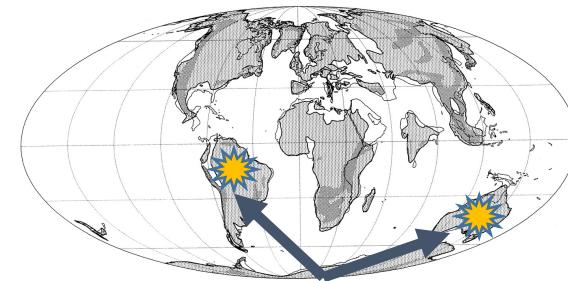
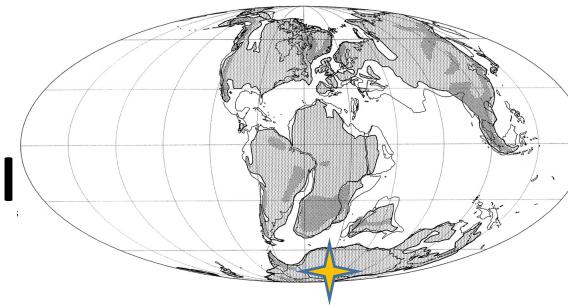
(dispersal)  
vicariance



### *Hemerophila diva*

# Historical biogeography conclusions:

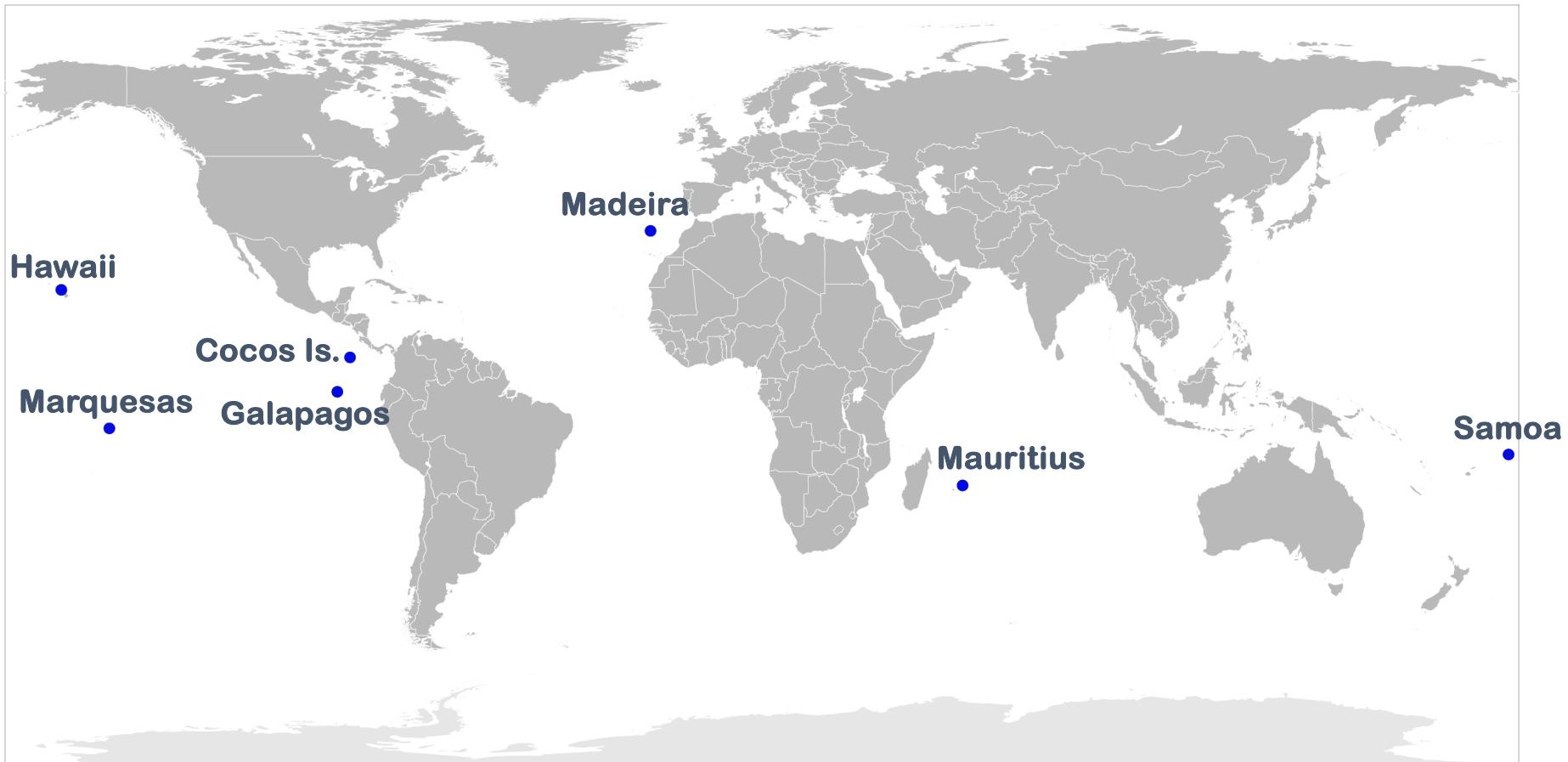
- **Area of origin of metalmark moths**
  - Probably Australasia + Neotropics, signal weak – high uncertainty
- **Vicariance important in the early history**
  - Two vicariances before 50 MA
- **LDDEs**
  - Happened many times, throughout the history, but how?



# Microlepidopterans present on oceanic islands



**Metalmark moths (Choreutidae)**



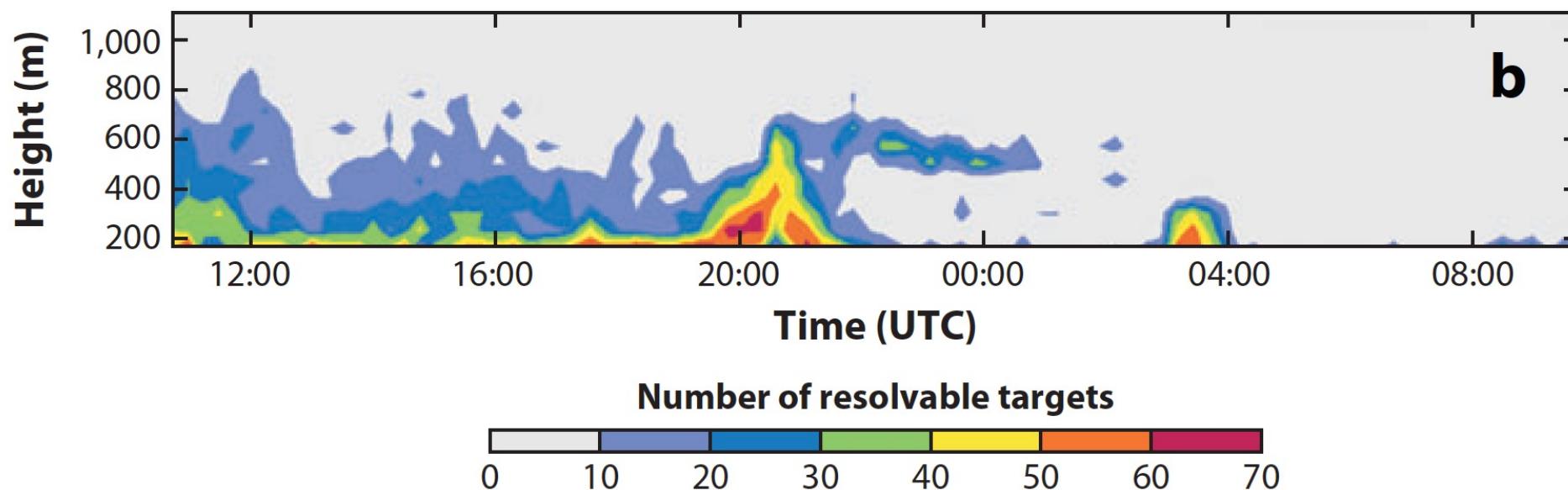
# How did choreutids cross oceans?

- Insects can use thermal uplifts and fast, high altitude air currents and they do it *en masse* (Hu et al. 2016)
  - Use of vertical-looking entomological radar or VLR (Fig. 1a Chapman et al. 2011)



# How did choreutids cross oceans? (cont.)

**Data from a vertical-looking entomological radar or VLR (Fig 1b, Chapman et al. 2011)**



**Time/height plot of insect numbers recorded by a VLR (England, 2003)**

# How did choreutids cross oceans? (cont.)

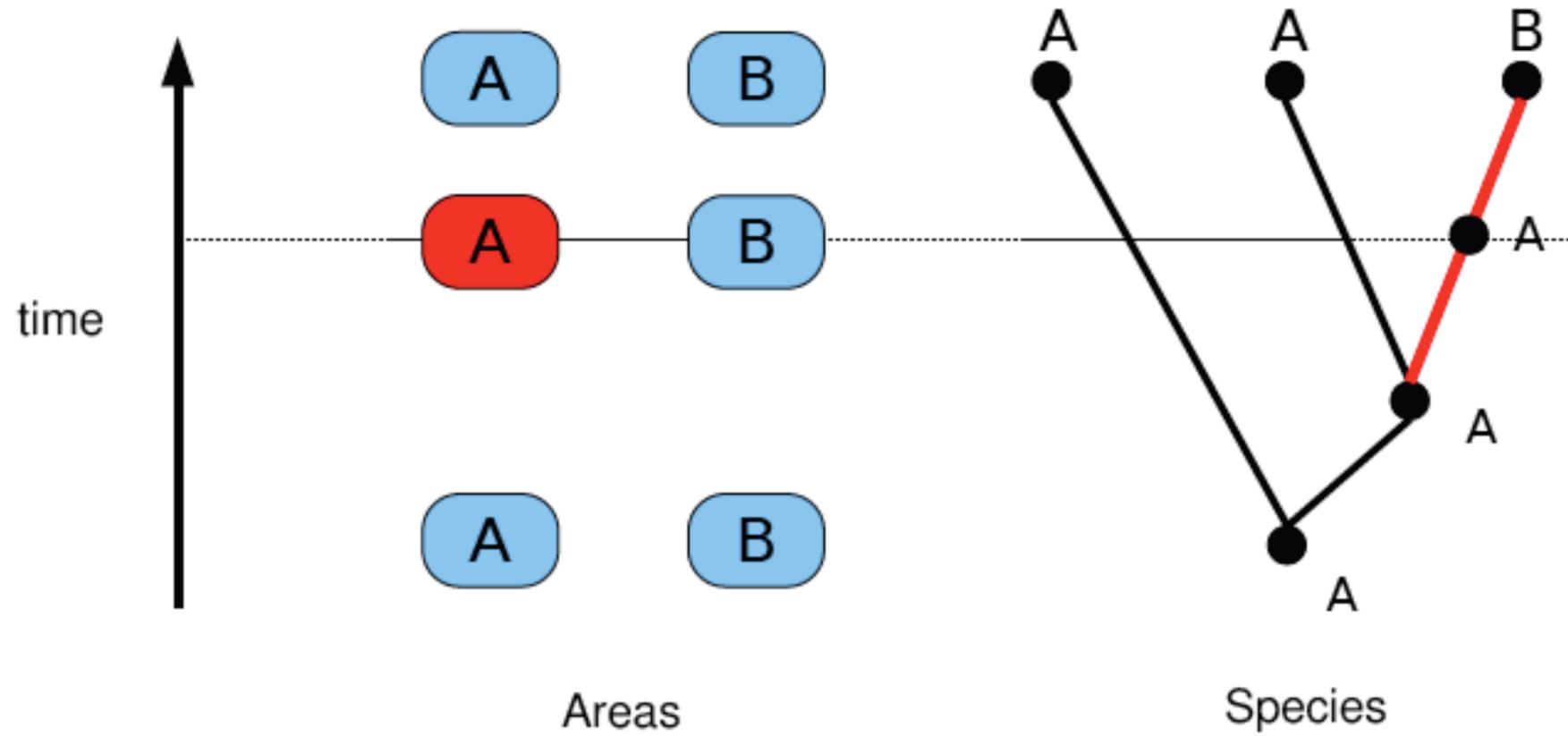
- All major insect orders have ability to use these atmospheric conditions
  - Evolved independently multiple times (Gatehouse 1997, Chapman & Drake 2010)
  - Atmospheric conditions also used by microinsects (Geerts & Miao 2005a,b)
  - Consistent with trapping results by ships and airplanes over oceans (Miller 1996)

# And what about establishment?

- Important host plant family for **Choreutidae**: Moraceae, especially *Ficus*
- *Ficus* has circumtropical distribution
- **Choreutidae** – specialists at the host plant genus level



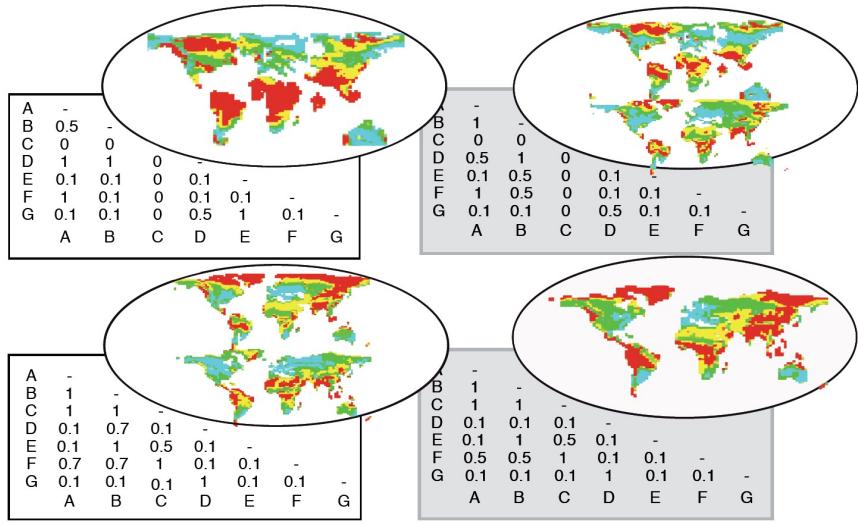
# Incorporation of the fossil record



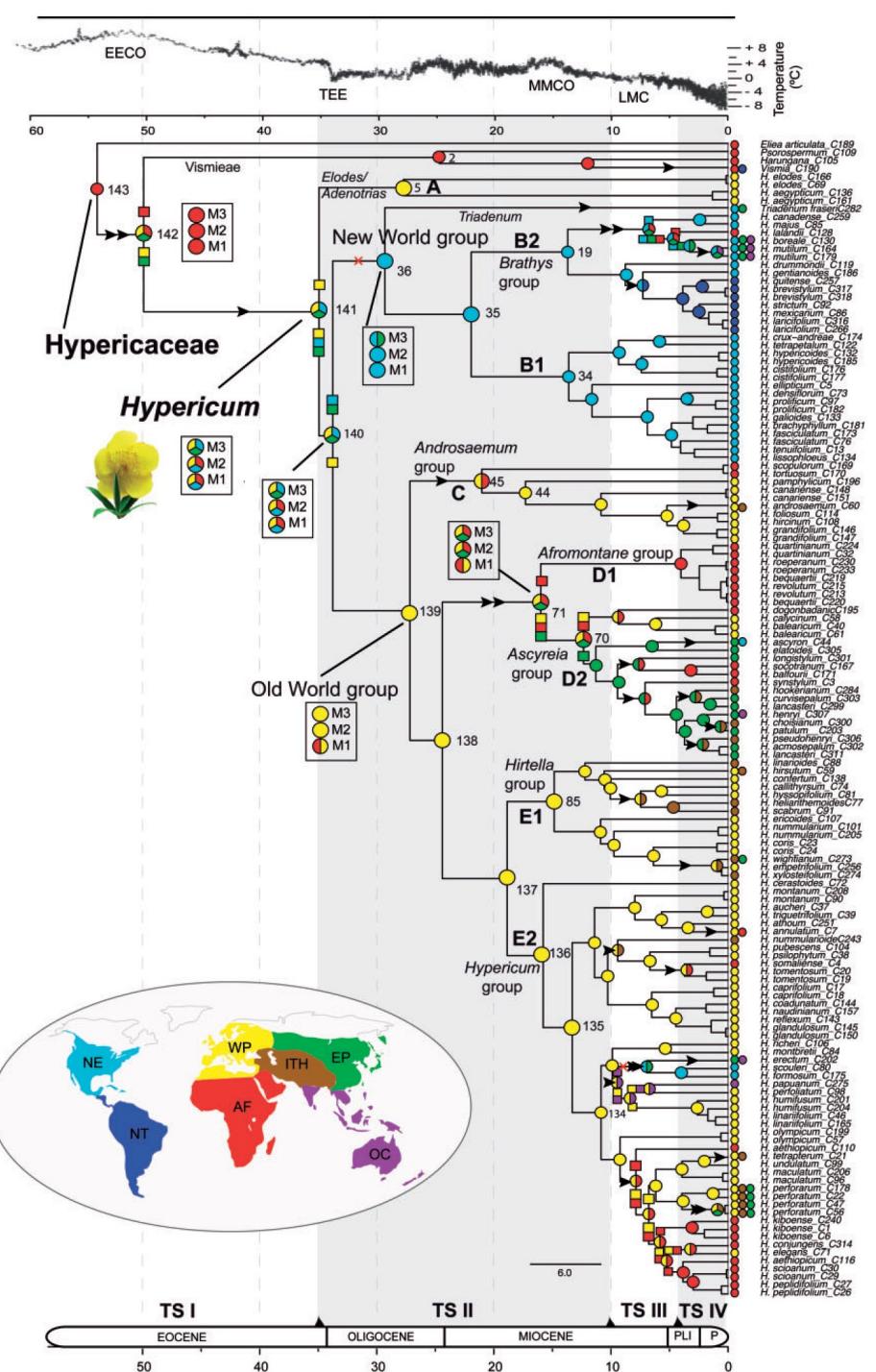
Fossils provide direct evidence of ancestral ranges

# Integrating fossil-based information into biogeographic analysis

1) Constrain inference of ancestral ranges according to fossil record and paleogeography.

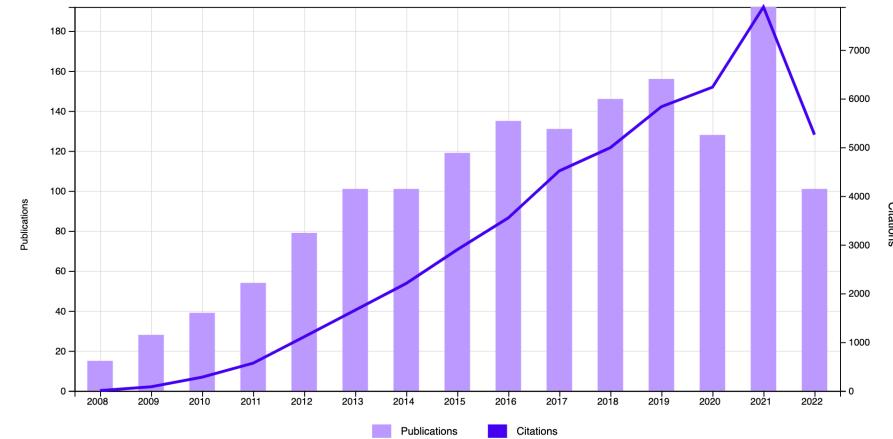


2) Use ancestral climatic niches to inform on potential dispersal routes and barriers (ecological connectivity).

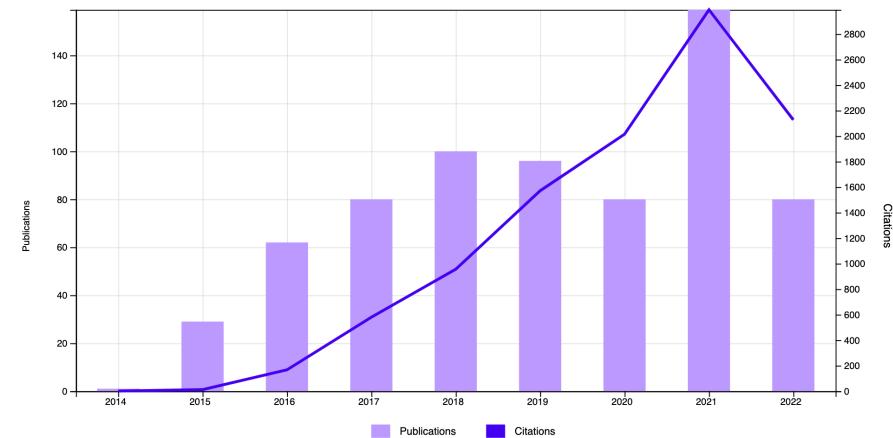


# Active area of research

- Incorporation of diversification models in which speciation and extinction rates are range dependent (GEOSS model - Goldberg, Lancaster, Ree 2011)
  - E.g. lineages with wider ancestral ranges -> higher rate of speciation and lower rate of extinction
- Fully Bayesian approaches also possible – inference of phylogeny, ancestral range, and diversification dynamics at the same time (RevBayes – Höhna S. et al. 2016. *Syst. Biol.* 65: 726-736)



Web of Science citation record for Ree & Smith 2008: 1558 (from Oct 2022)



Web of Science citation record for Matzke 2014: 692 (from Oct 2022)

# Some relevant literature

- **Goldberg EE, Lancaster LT, Ree RH (2011) Systematic Biology 60: 451-465.**  
<https://doi.org/10.1093/sysbio/syr046>
- **Matzke N (2014) Systematic Biology 63: 951-970.**  
<https://doi.org/10.1093/sysbio/syu056>
- **Ree RH, Moore BR, Webb CO, Donoghue MJ (2005) Evolution, 59: 2299-2311.** (<https://doi.org/10.1111/j.0014-3820.2005.tb00940.x>)
- **Ree RH, Smith SA (2008) Systematic Biology 57: 4-14.**  
<https://doi.org/10.1080/10635150701883881>
- **Ree RH, Sanmartín I (2018) Journal of Biogeography 45: 741-749.**  
<https://doi.org/10.1111/jbi.13173>
- **Sanmartín I (2012) Evolution: Education and Outreach 5: 555-568.**  
<https://doi.org/10.1007/s12052-012-0421-2>