Spatio-temporal evolution of the genus *Hypericum* (Hypericaceae): the strategy of the marathon runner

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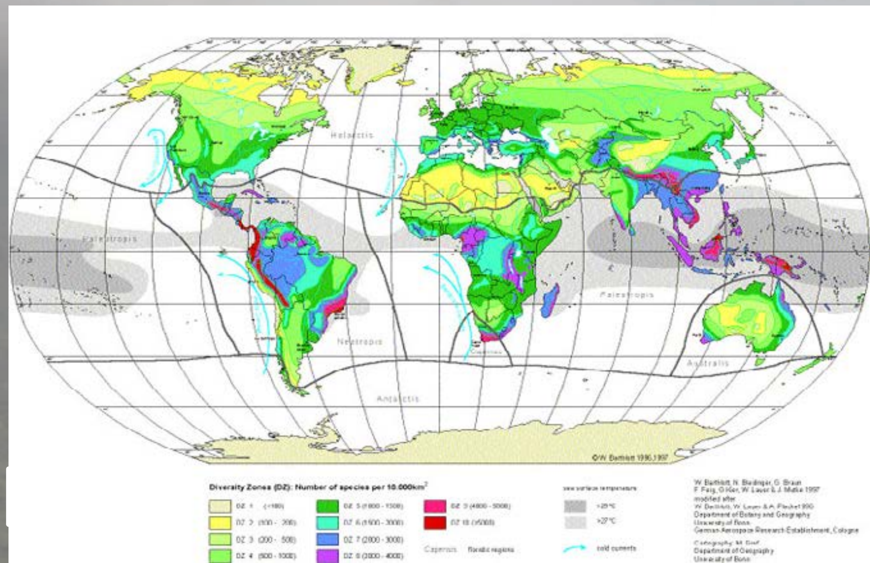
BIODIVERSITY is not **evenly** distributed

Across lineages

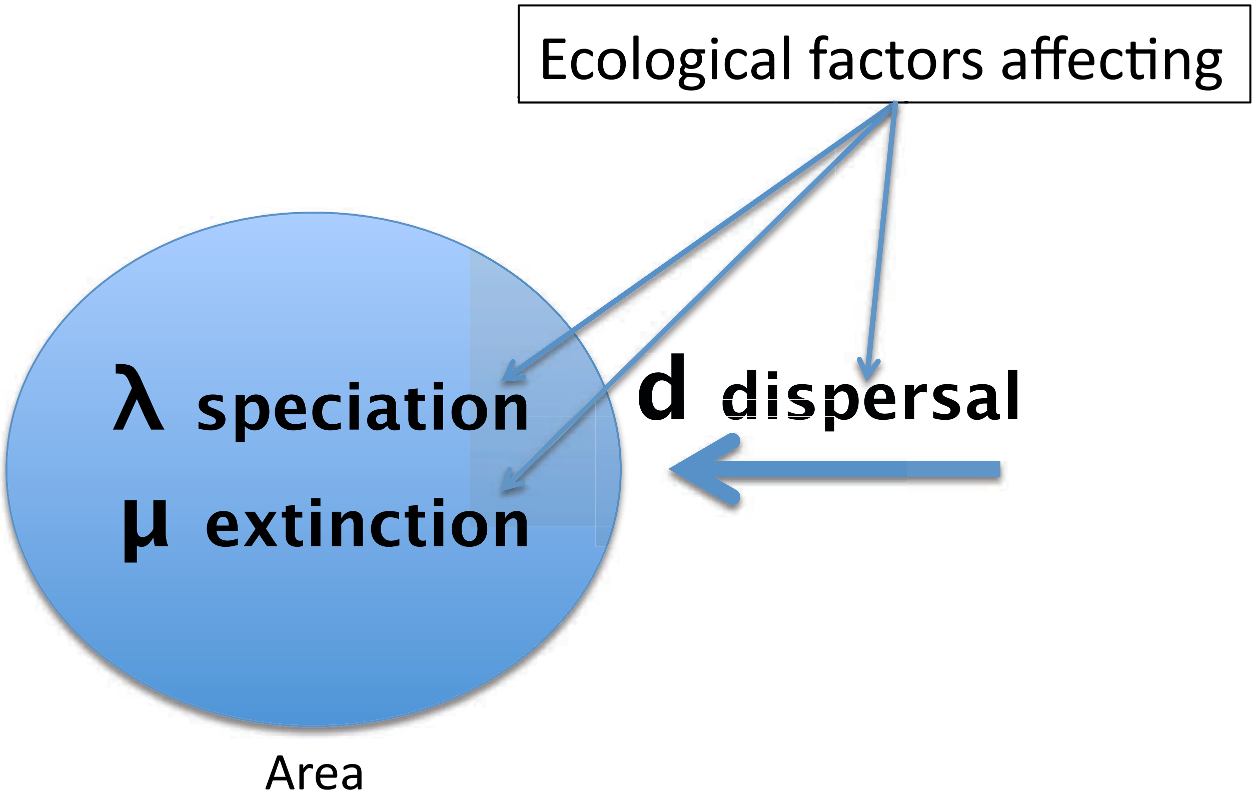
Euphorbia >2000 spp
Canarina 3 spp

Across regions
e.g. Latitudinal Diversity Gradient



Barthlott et al. (1999). Acta Botanica Fennica

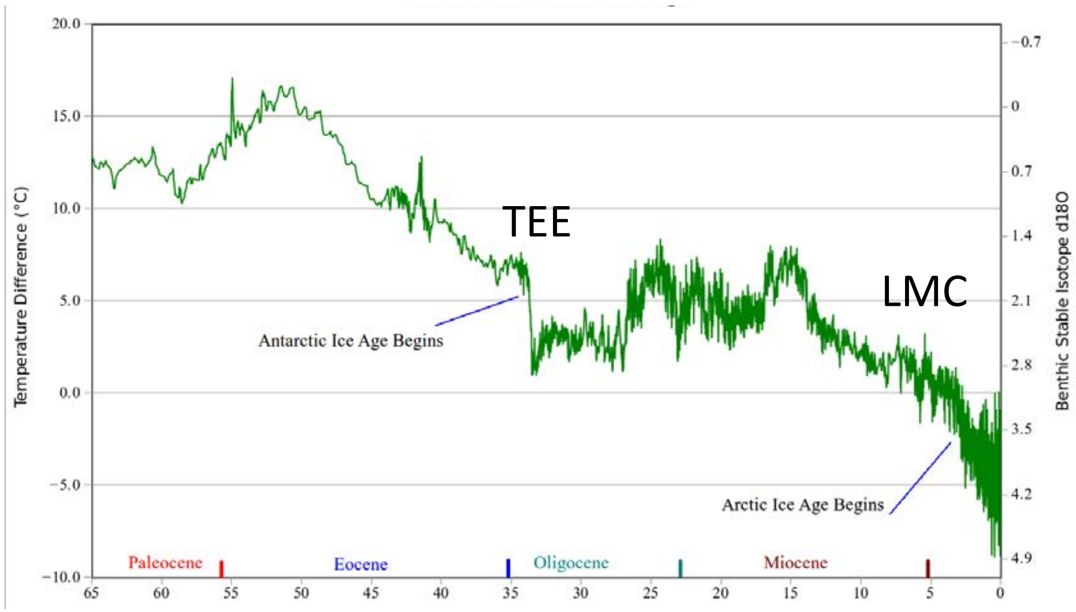
MECHANISMS REGULATING DIVERSITY

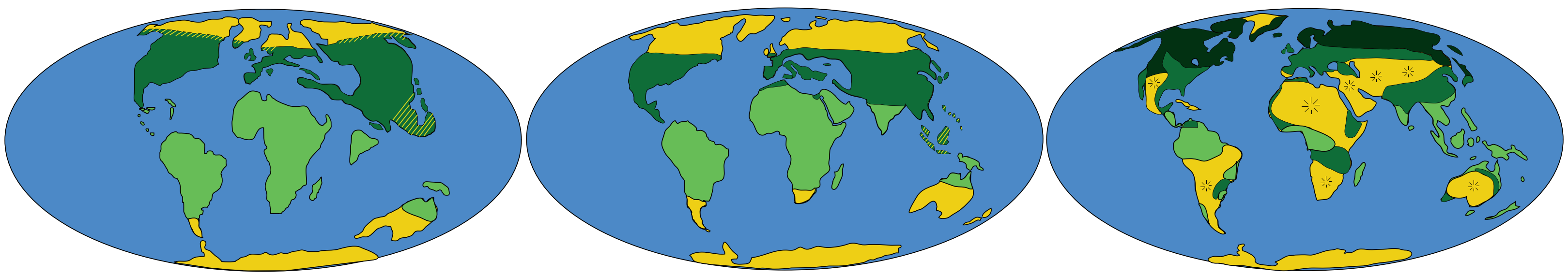


Diversity patterns arise as the interplay of **ecologic** and **evolutionary processes** (speciation, extinction, dispersal) acting through time

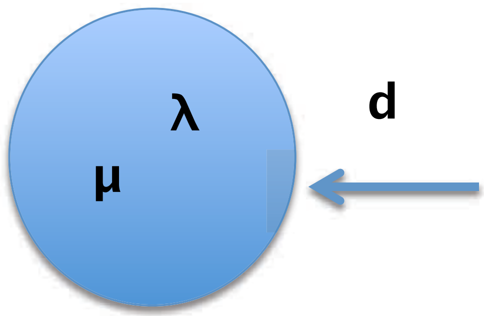
Wiens 2013

CENOZOIC GLOBAL CHANGE





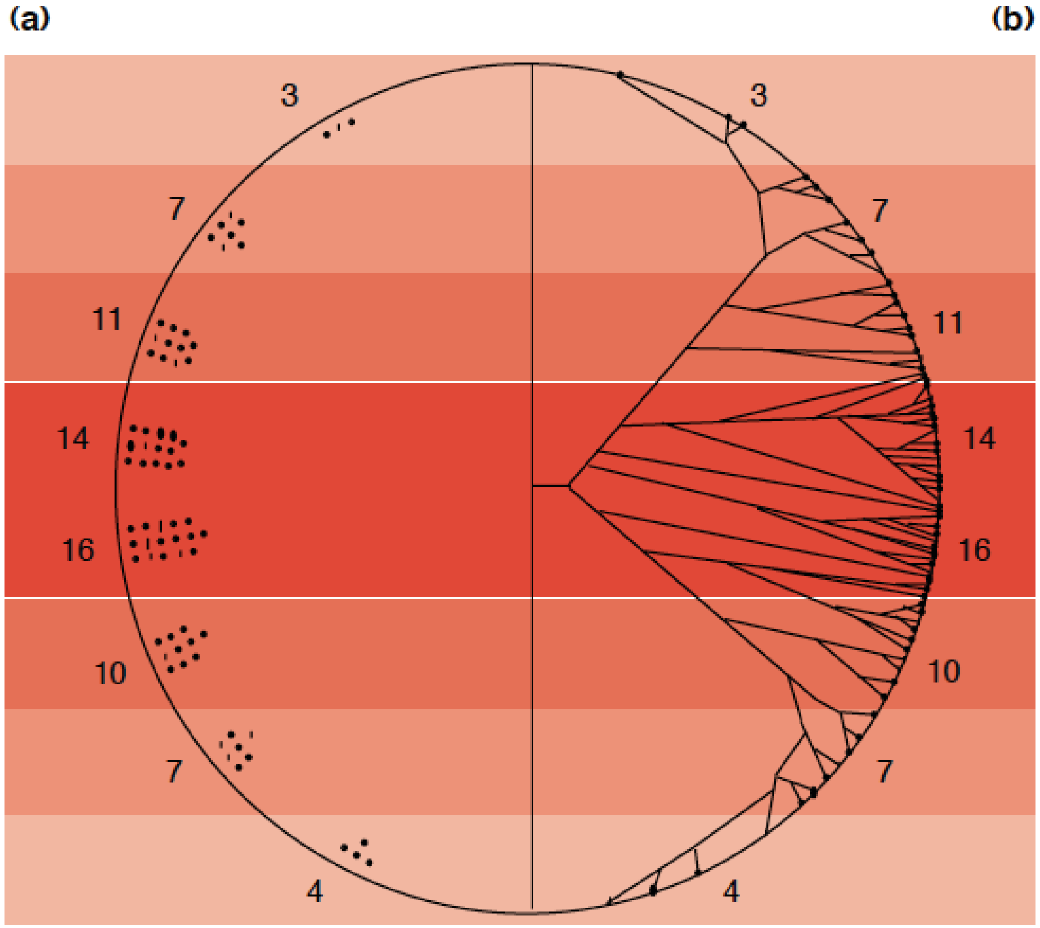
VEGETATION RESPONSE TO CLIMATE CHANGE



μ – **extinction** or **restriction to refuges**
d – **migration**
λ – **adaptation**

NICHE CONSERVATISM
Plants tend to preserve their ancestral niche preferences

Tropical Conservatism Hypothesis:
Few taxa has made the transition from tropical to temperate biomes

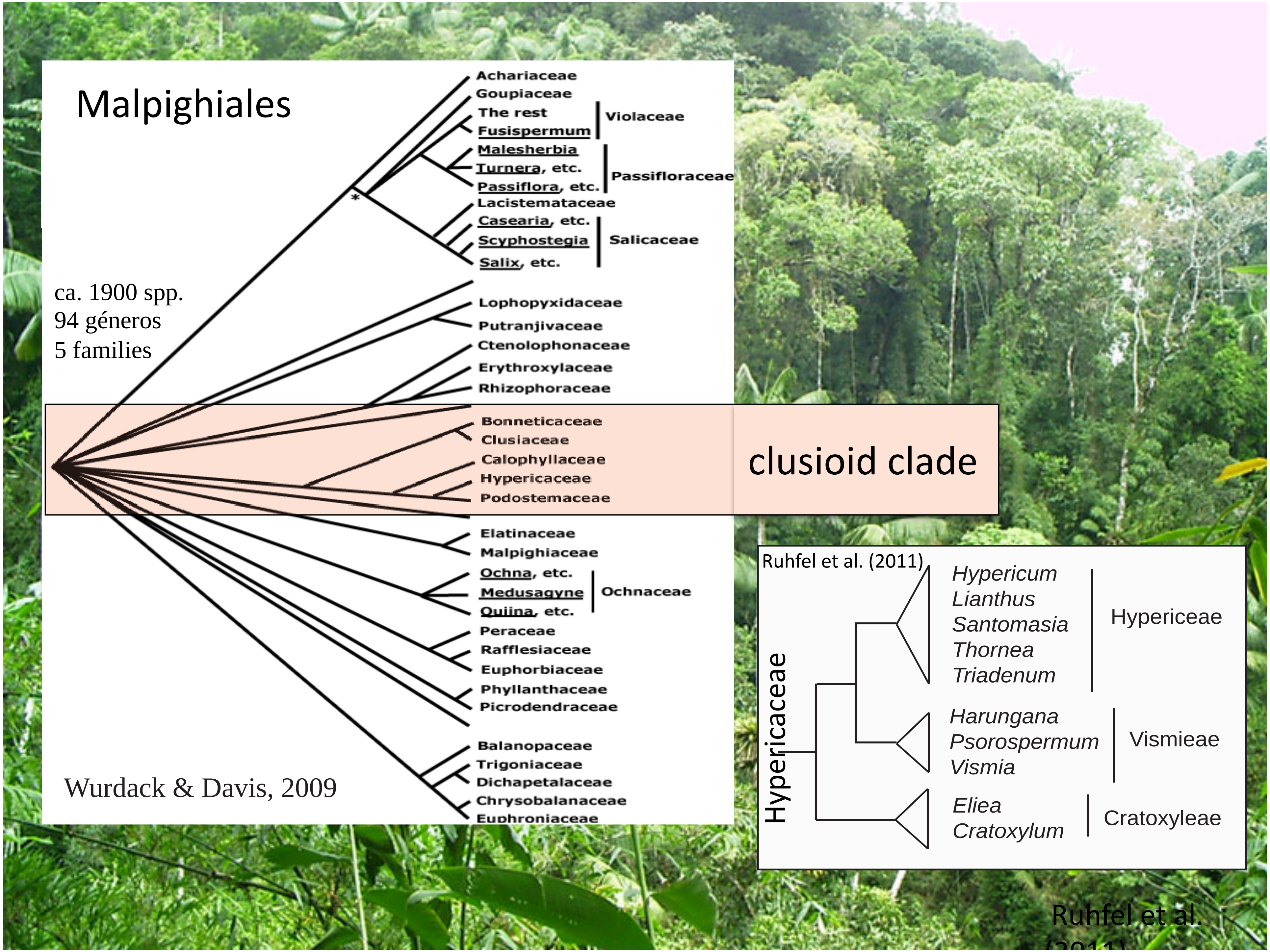


Wiens & Donoghue (2008)

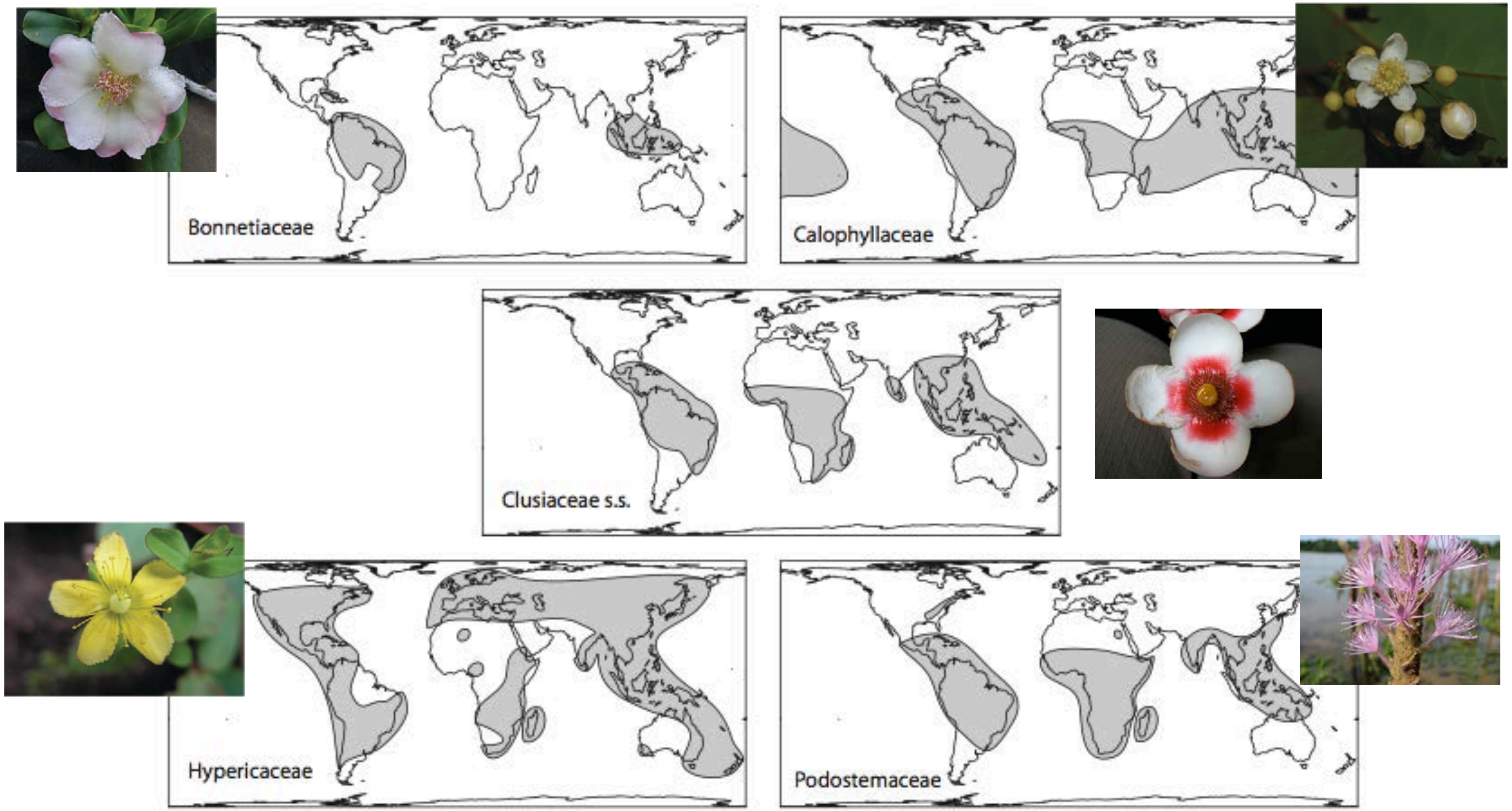
GENERAL OBJECTIVE

Understand the effect of **abiotic factors** (climate, geologic change) on the mechanisms generating and maintaining biological diversity: ***speciation and extinction***, ***niche dynamics*** and ***biogeographic processes***

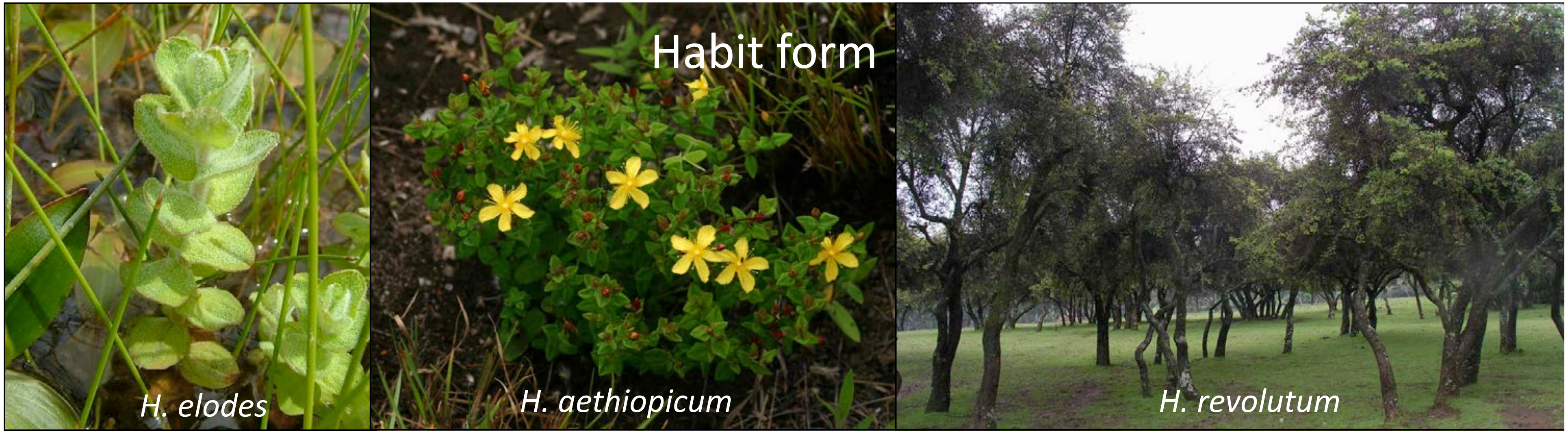
Hypericum

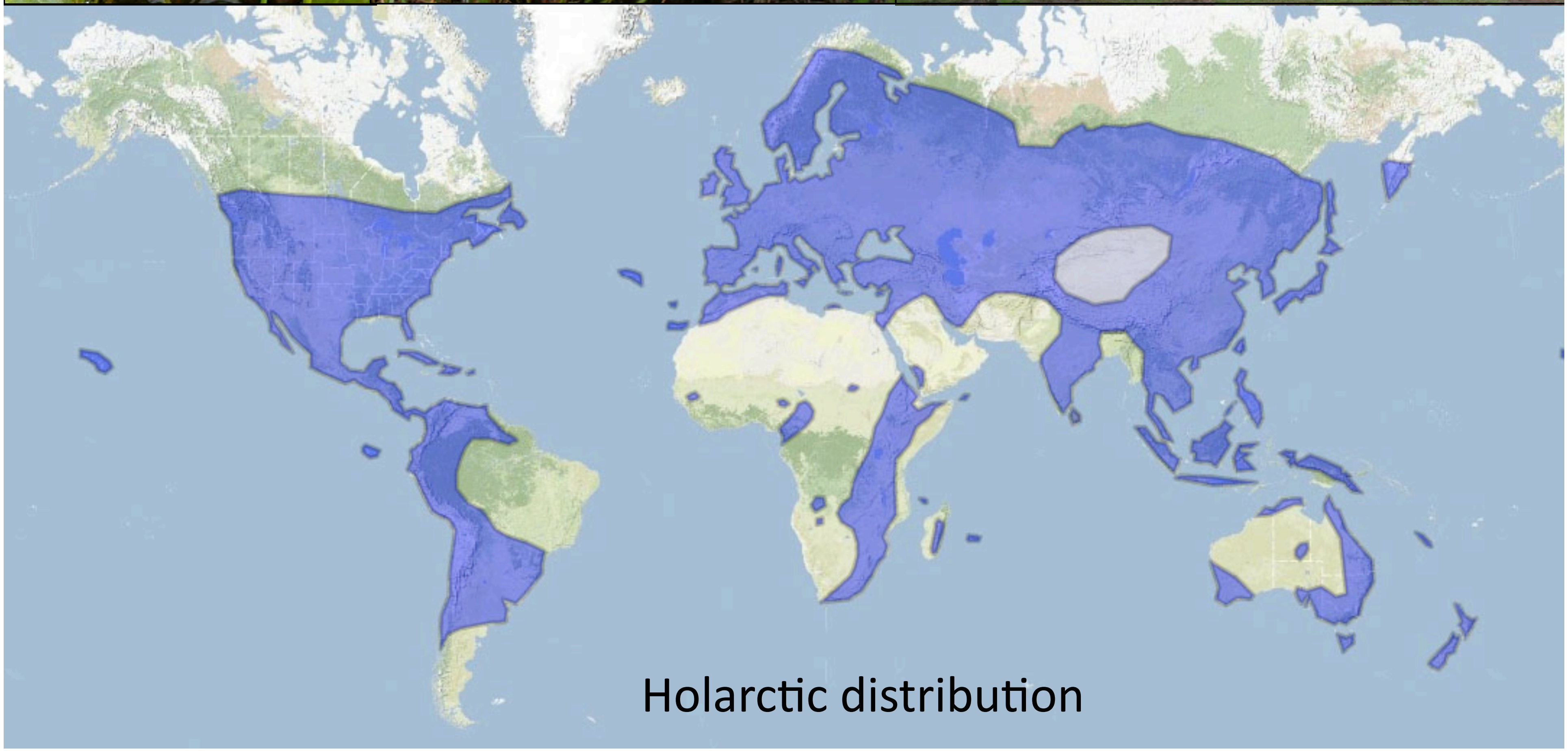

Malpighiales
ca. 1900 spp.
94 géneros
5 families
Achariaceae
Goupiaceae
The rest
Fusispermum
Violaceae
Malesherbia
Turnera, etc.
Passiflora, etc.
Passifloraceae
*
Lacistemataceae
Casearia, etc.
Scyphostegia
Salix, etc.
Salicaceae
Lophopyxidaceae
Putranjivaceae
Ctenolophonaceae
Erythroxylaceae
Rhizophoraceae
Bonneticaceae
Clusiaceae
Calophyllaceae
Hypericaceae
Podostemaceae
clusioid clade
Elatinaceae
Malpighiaceae
Ochna, etc.
Medusagyne
Quiina, etc.
Ochnaceae
Peraceae
Rafflesiaceae
Euphorbiaceae
Phyllanthaceae
Picrodendraceae
Balanopaceae
Trigoniaceae
Dichapetalaceae
Chrysobalanaceae
Euphroniaceae
Wurdack & Davis, 2009
Ruhfel et al. (2011)
Hypericaceae
Hypericum
Lianthus
Santomasia
Thornea
Triadenum
Hypericeae
Harungana
Psorospermum
Vismia
Vismieae
Eliea
Cratoxylum
Cratoxyleae
Ruhfel et al.

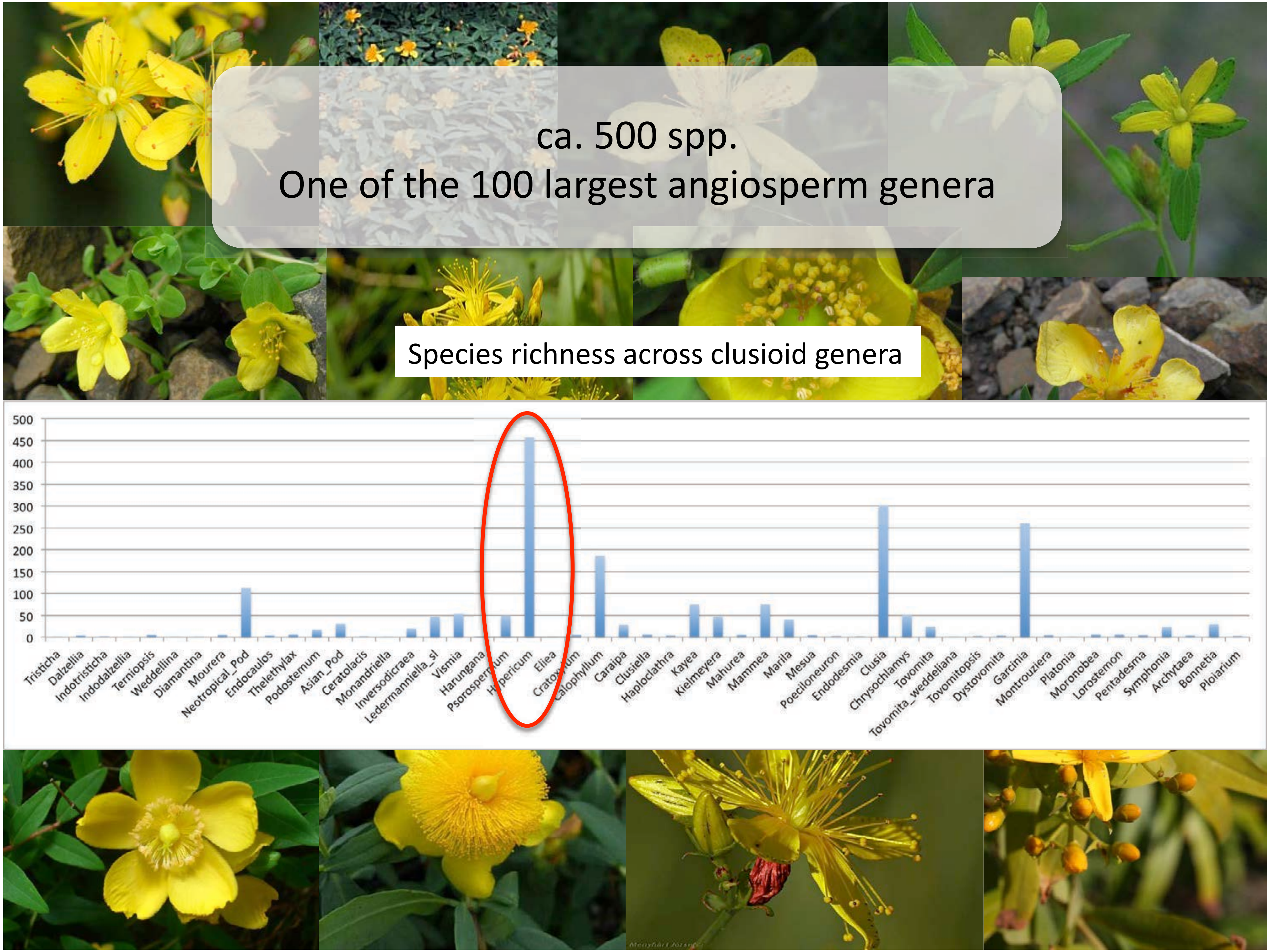
clusioid clade



Ruhfel (2011)

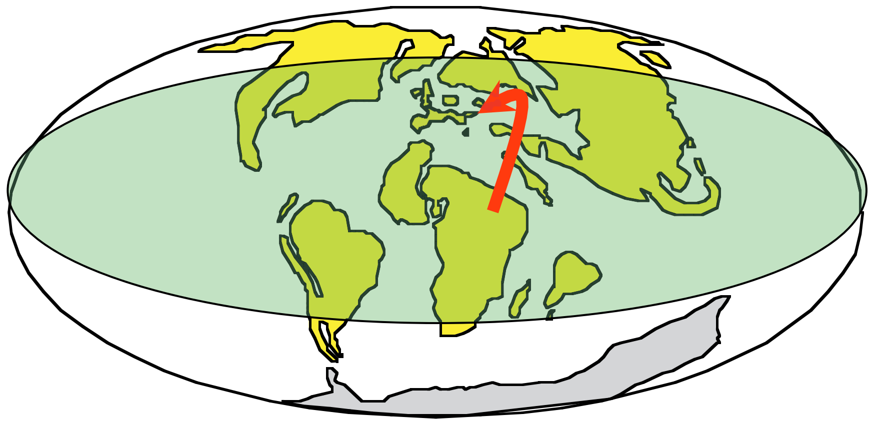

Habit form
H. elodes
H. aethiopicum
H. revolutum


Holarctic distribution


ca. 500 spp.
One of the 100 largest angiosperm genera
Species richness across clusioid genera
500
450
400
350
300
250
200
150
100
50
0
Tristicha
Dalzellia
Indotristicha
Indodalzellia
Terniopsis
Weddellina
Diamantina
Mourera
Neotropical_Pod
Endocaulos
Thelethylax
Podostemum
Asian_Pod
Ceratolacis
Monandriella
Inversodicraea
Ledermanniella_sl
Vismia
Harungana
Psorosper um
H pericum
Eliea
Cratox um
Calophyllum
Caraipa
Clusiella
Haploclathra
Kayea
Kielmeyera
Mahurea
Mammea
Marila
Mesua
Poeciloneuron
Endodesmia
Clusia
Chrysochlamys
Tovomita
Tovomita_weddeliana
Tovomitopsis
Dystovomita
Garcinia
Montrouziera
Platonia
Moronobea
Lorostemon
Pentadesma
Symphonia
Archytaea
Bonnetia
Ploiarium

Why *Hypericum*?

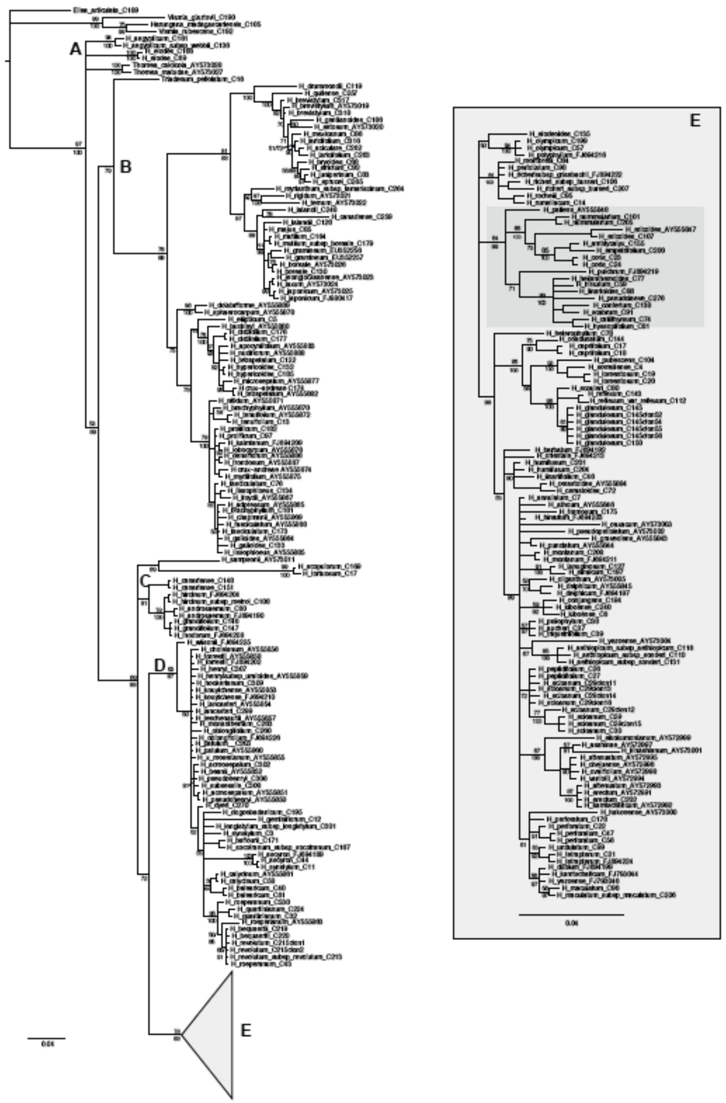
Exceptional within the clusioid clade
- 1. Temperate distribution
- 2. Herbaceous habit form
- 3. High species richness



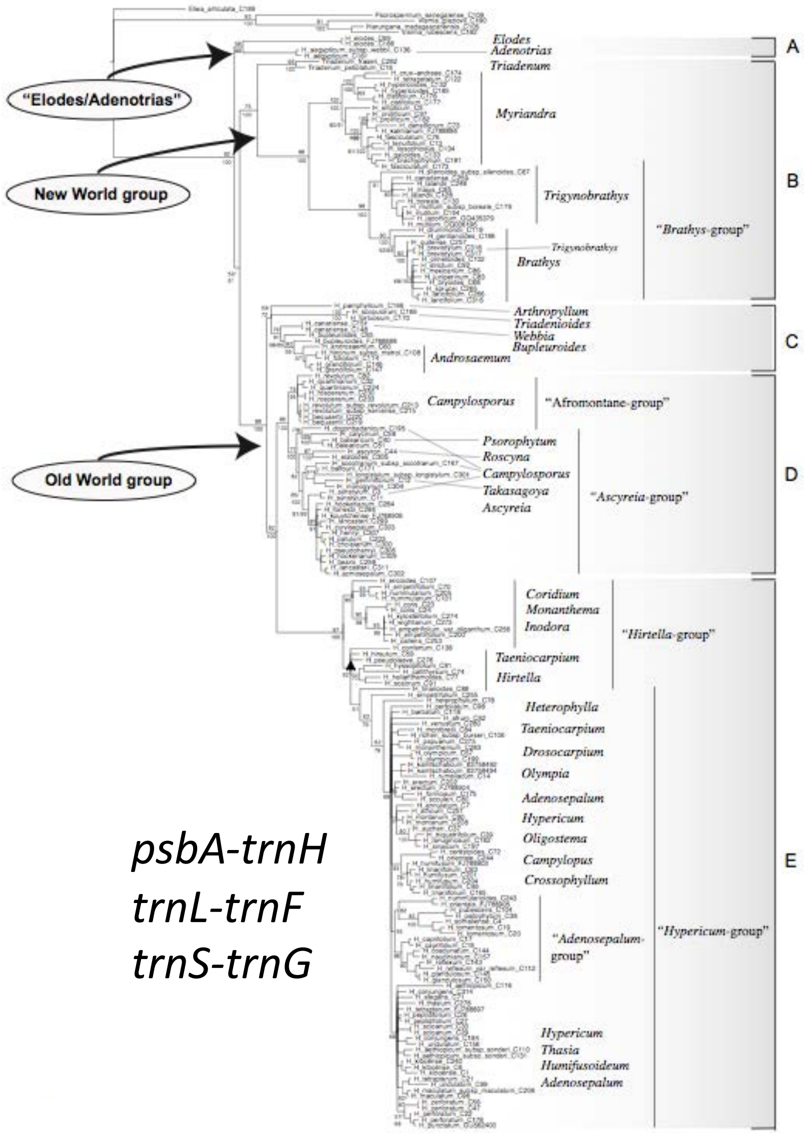
***Hypericum* is one of few plant taxa that succeeded in the transition from tropical to temperate biomes (Donoghue, 2008)**

Which factors and processes have shaped *Hypericum* distribution and diversity patterns through time?

Phylogenetic relationships



ITS 252 specimens

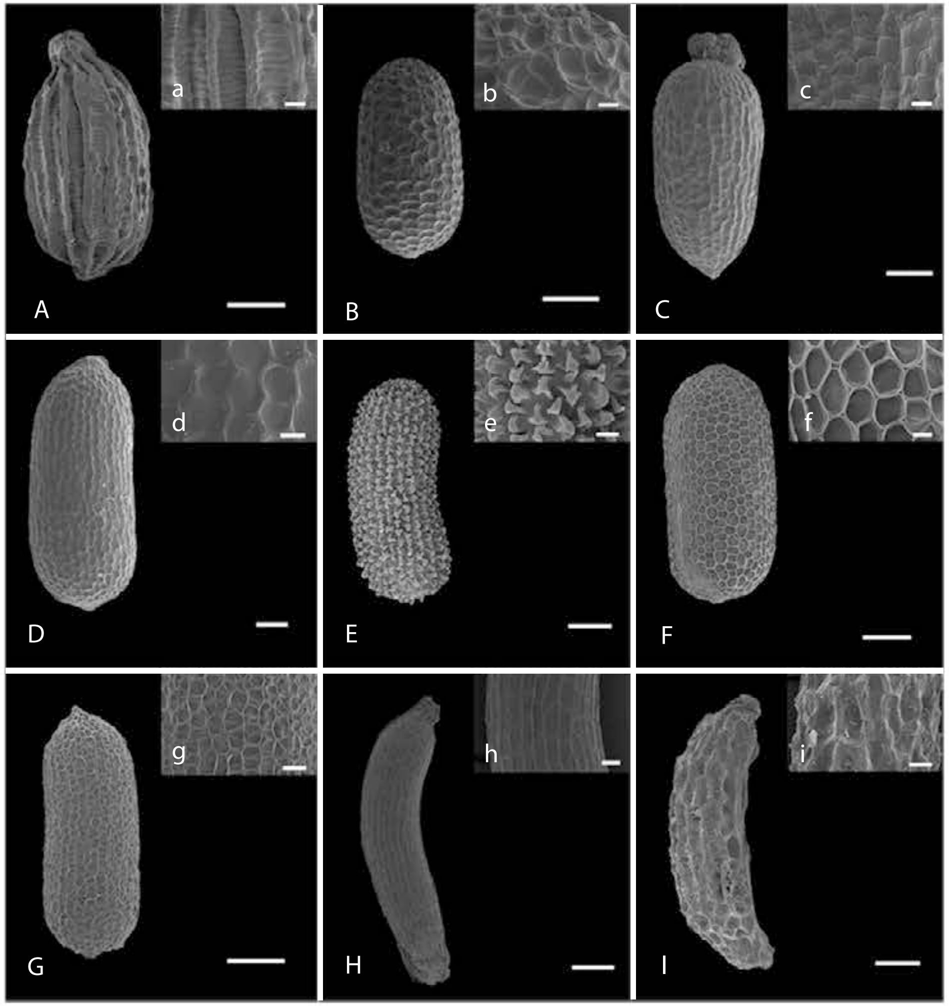


psbA-trnH
trnL-trnF
trnS-trnG

cpDNA 186 specimens

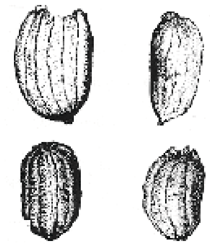
Hypericum Fossil record

Extant



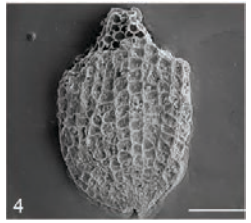
Extinct

H. antiquum



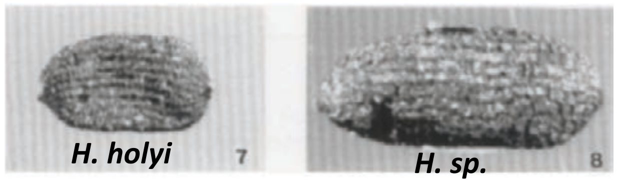
Arbuzoba (2005). L Eocene Siberia

H. septestum

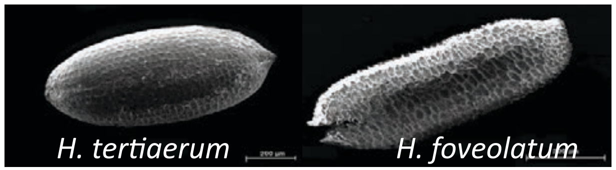


Teodoris (2003). E Miocene Czech

Nikitin (2006). Lower Oligocene Siberia

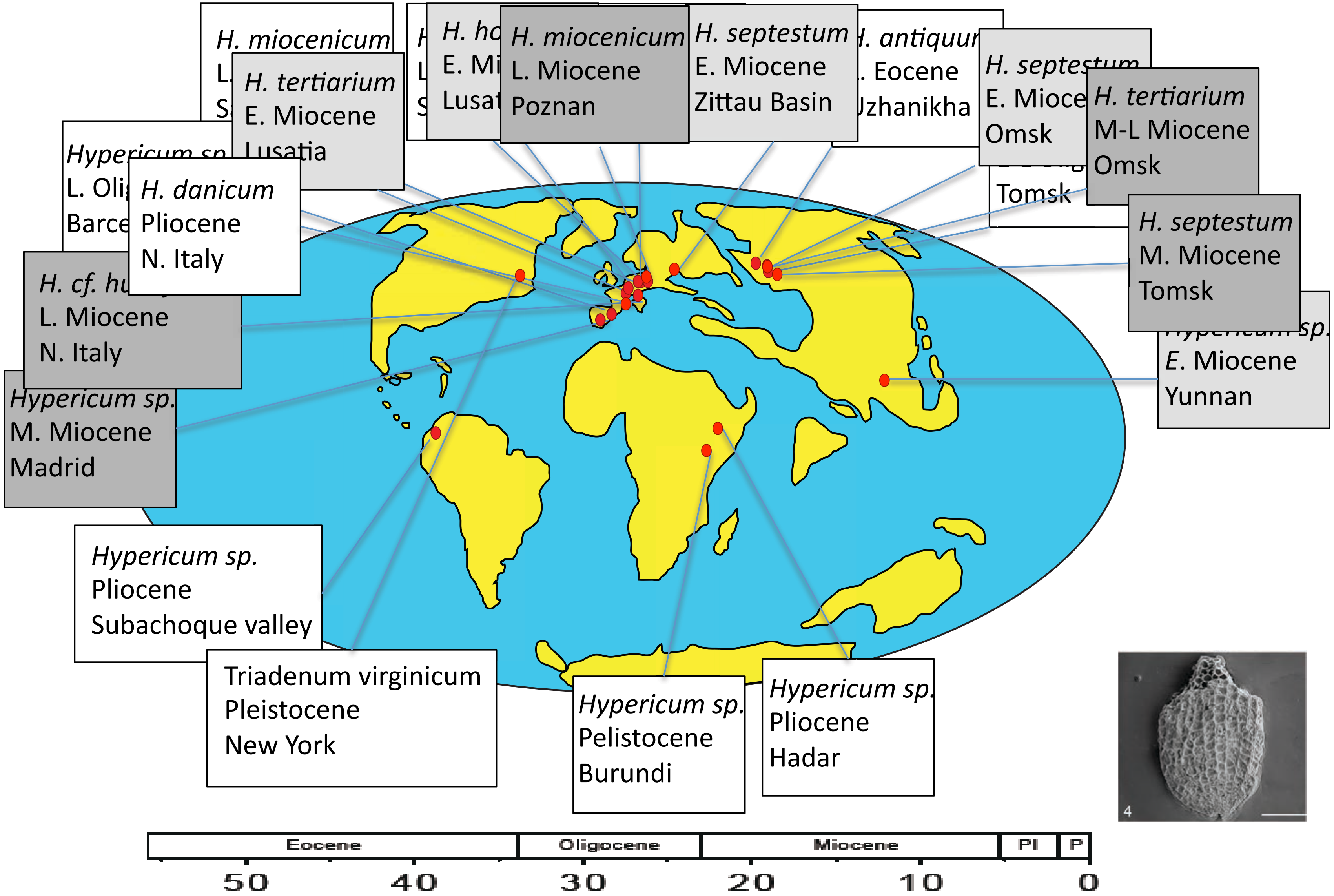


Van der Burgh (1987). Miocene Germany



Velichkevich & Zastawniak (2003). Pliocene Belarus

FOSSIL OCCURRENCES



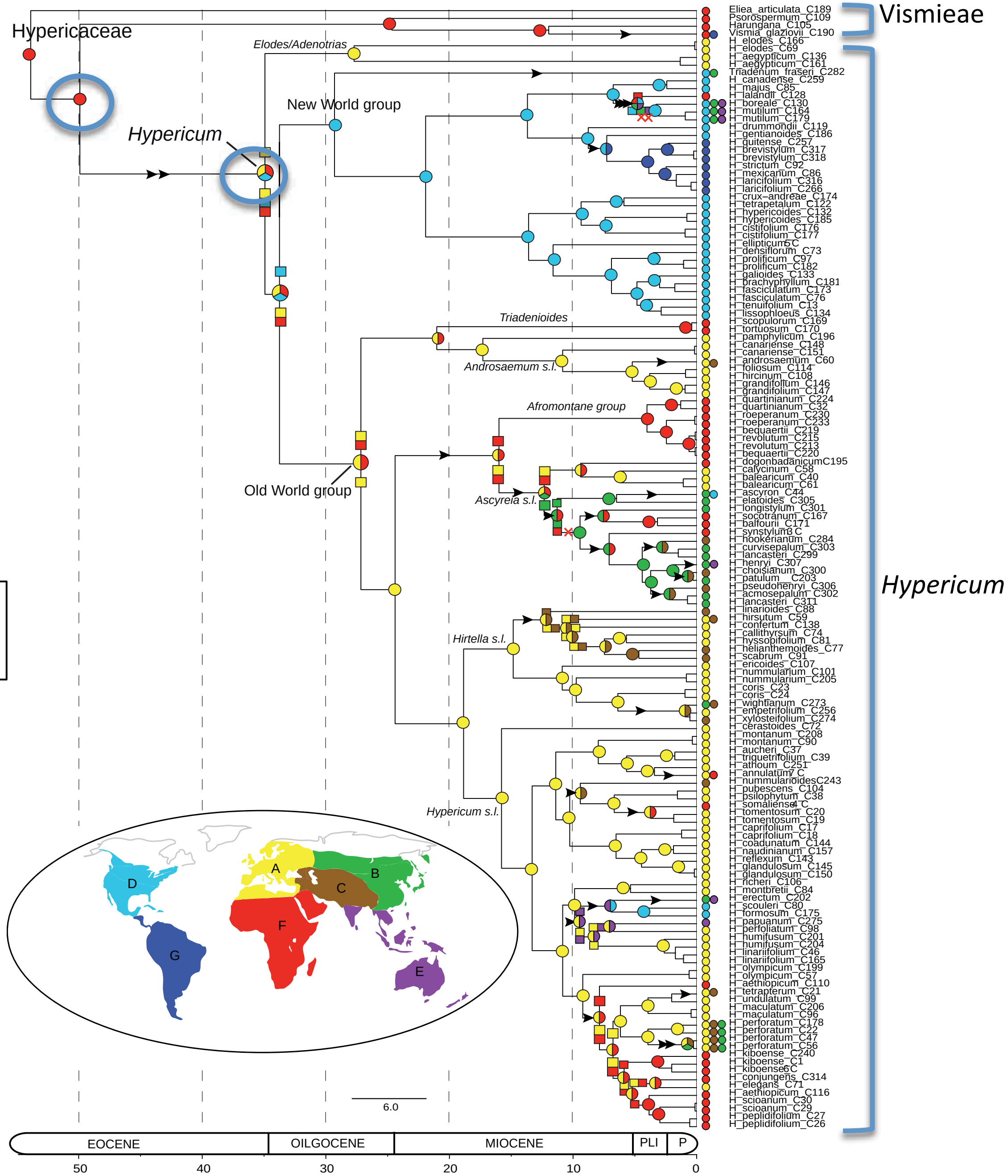
Spatio-temporal evolution

of *Hypericum*

BIOGEOGRAPHIC ANALYSIS

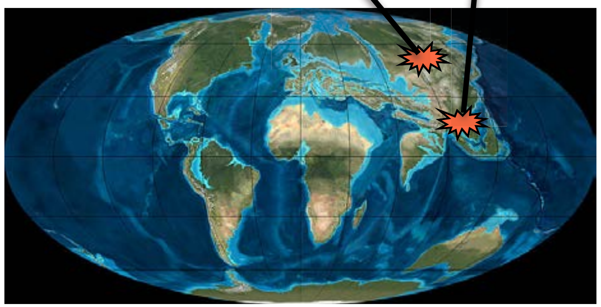
Dispersal-Extinction-Cladogenesis

- *Hypericum* ancestors distributed in Africa, North America and Western Palearctic

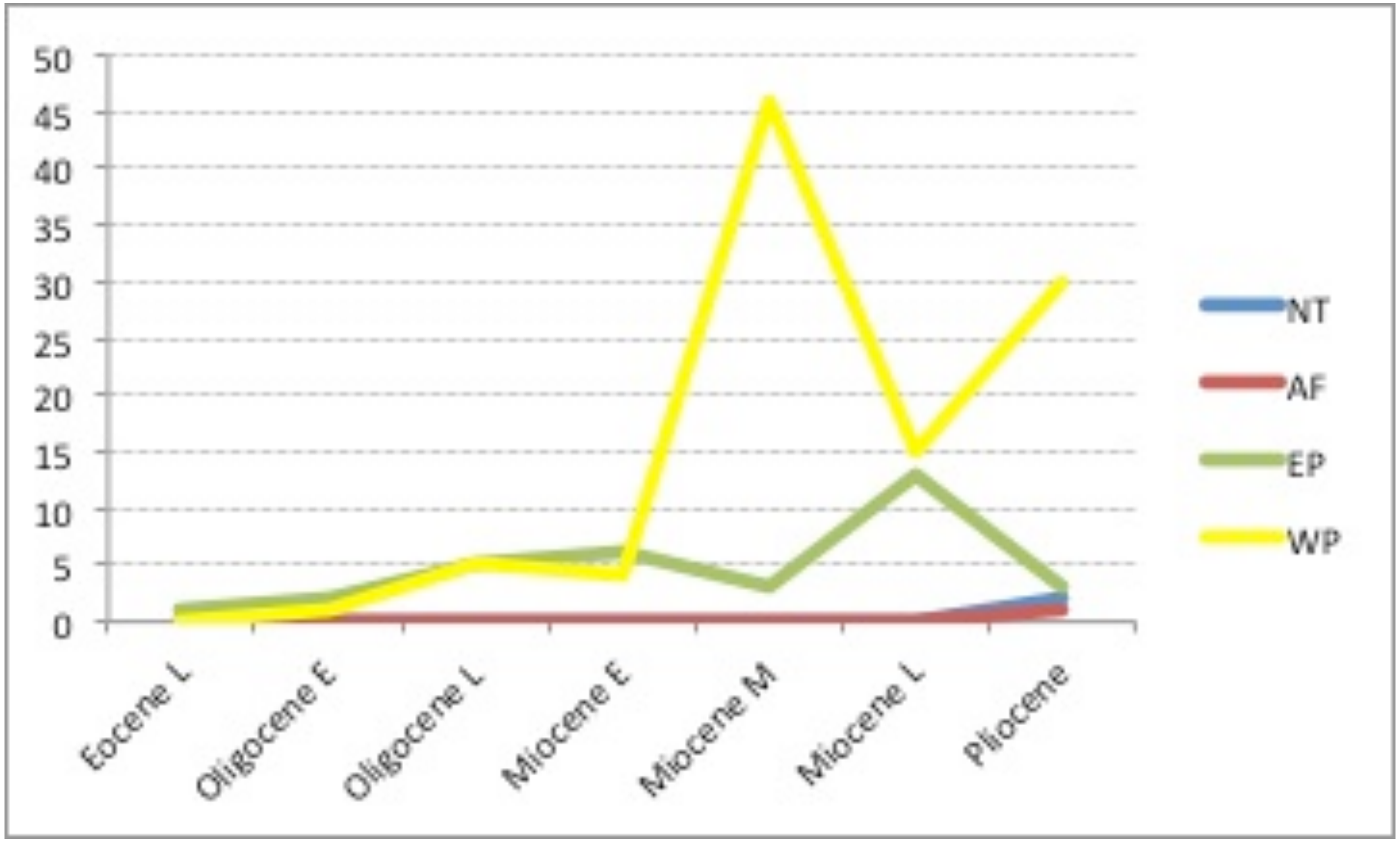


H. sp. Early-Middle Miocene, area B

H. antiquum, Late Eocene, area B

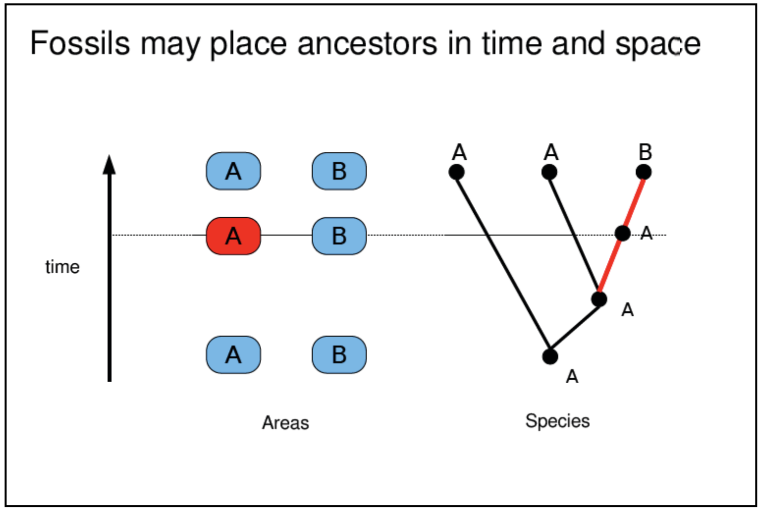


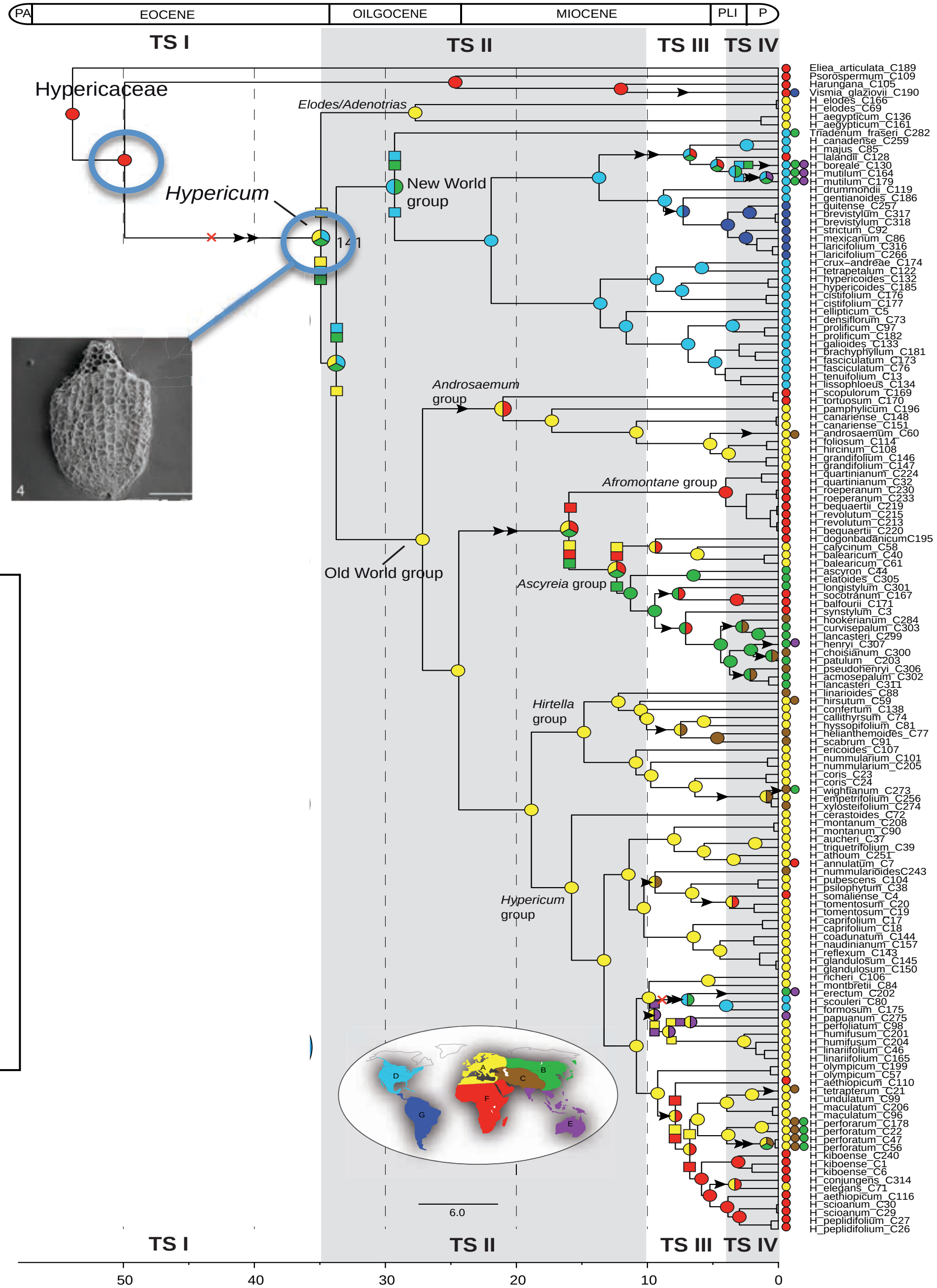
Number of *Hypericum* fossils through time and across biogeographic regions



FOSSILS PLACE ANCESTORS IN SPACE AND TIME

DEC model incorporating fossil range constrictions

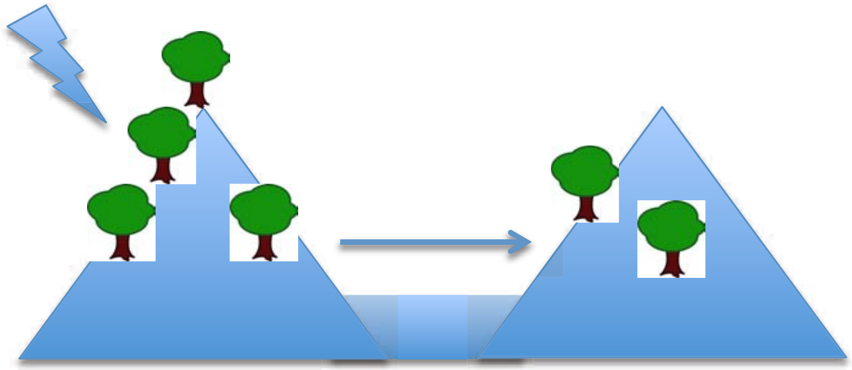


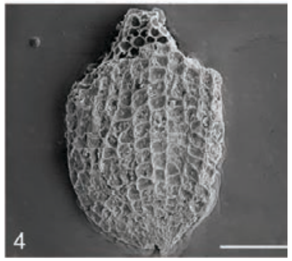


ANCESTRAL ECOLOGICAL PREFERENCES IN *HYPERICUM*

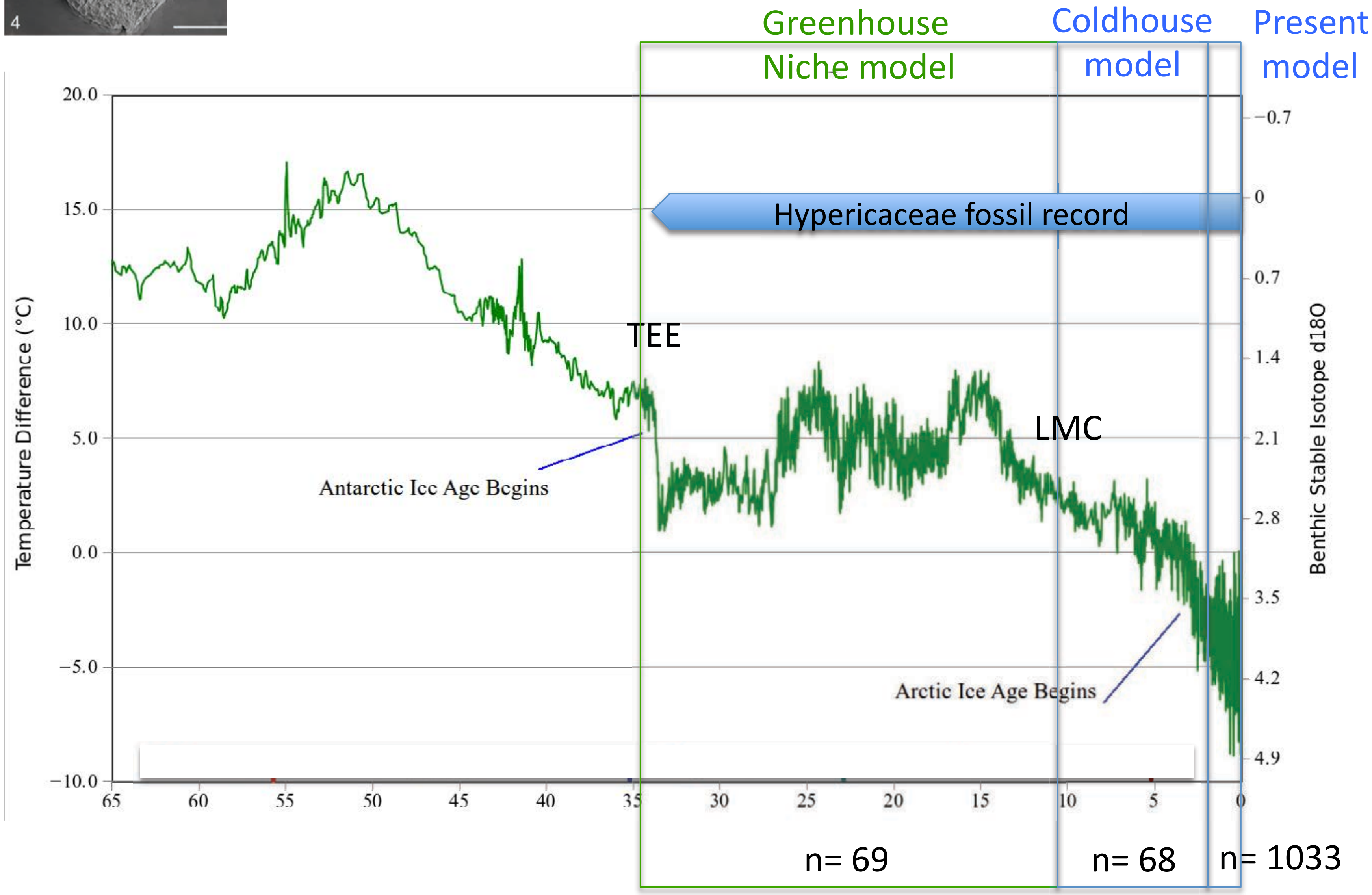
Fossils not only provide temporal and spatial information, but also inform us on the ancestral ecological preferences (niche) of the organisms

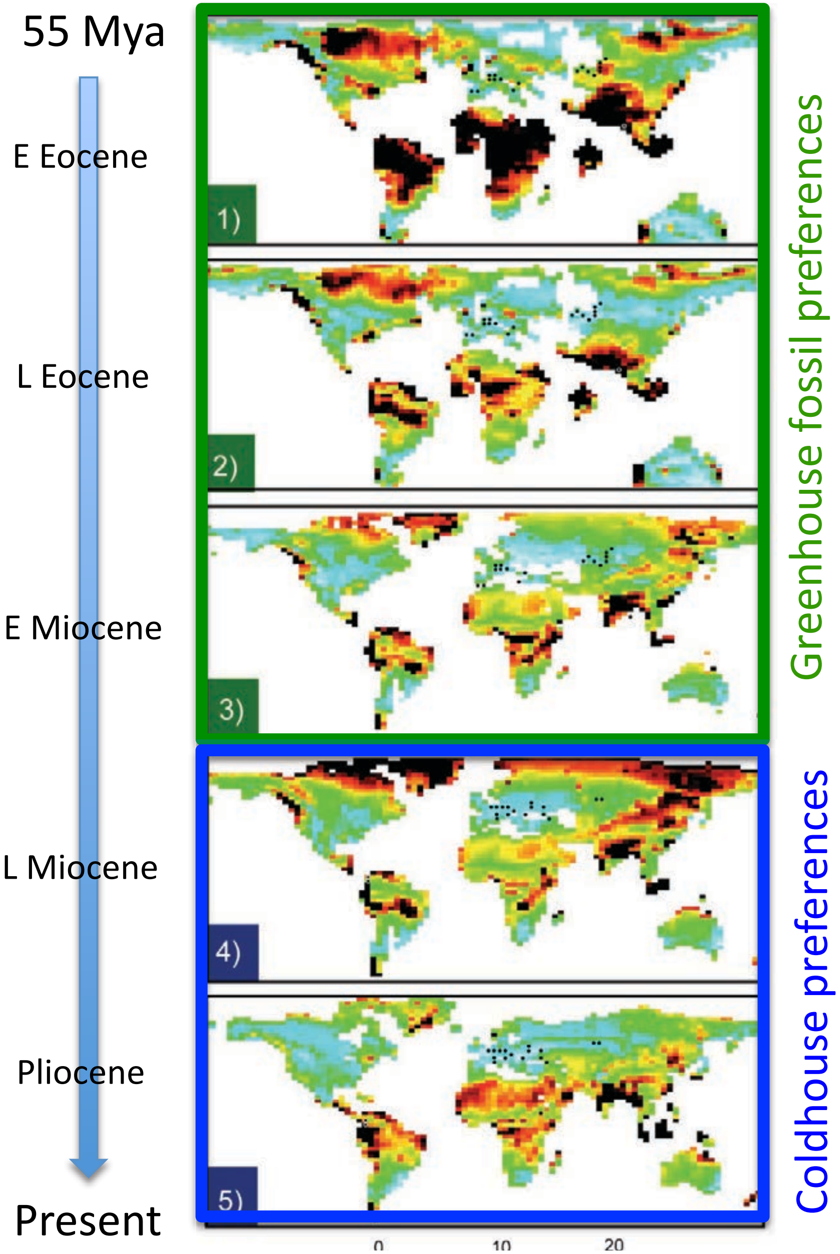
Geological connection is not the only requirement for a group to disperse





FOSSIL-BASED NICHE MODELLING

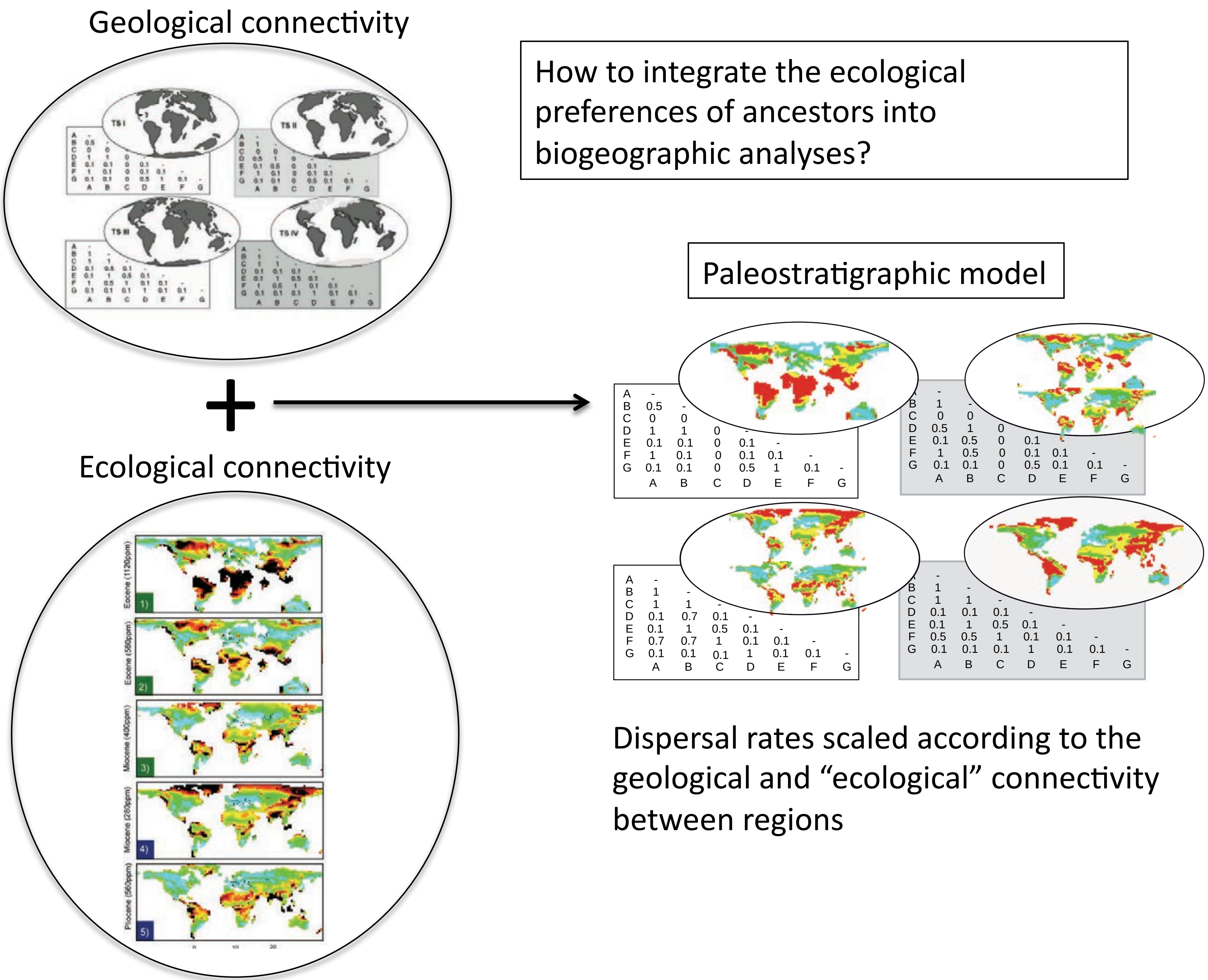




PAST POTENTIAL DISTRIBUTION FOR EXTINCT LINEAGES

- Southern region of the **Northern Hemisphere** always favourable
- **Southern Hemisphere** also favourable but equatorial regions barriers of dispersal
- **Beringia** always favourable except during the Miocene
- **Pliocene** was a very favourable period

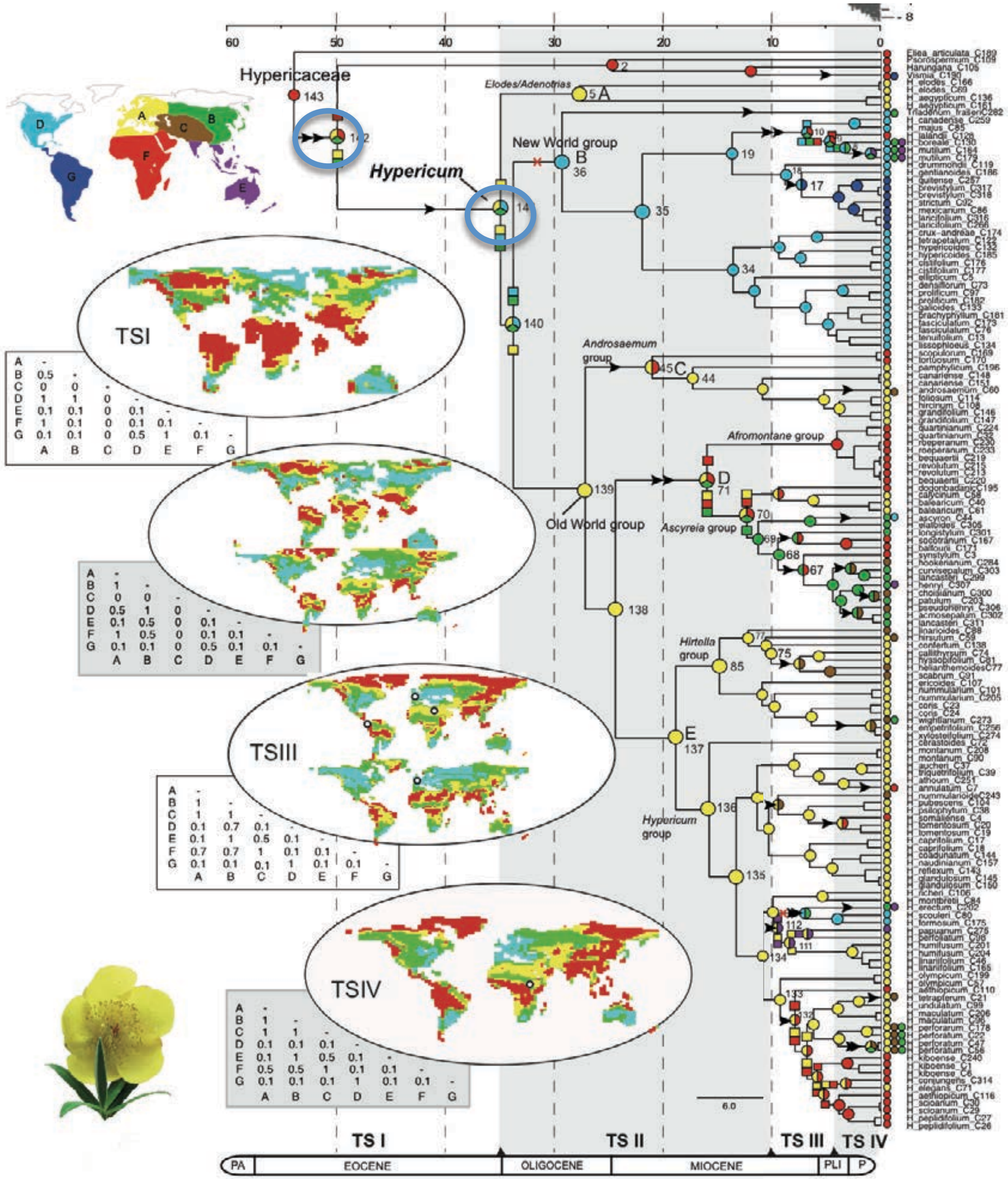
Ecological favourability of the world through time


Geological connectivity
How to integrate the ecological preferences of ancestors into biogeographic analyses?
Paleostratigraphic model
Ecological connectivity
Dispersal rates scaled according to the geological and “ecological” connectivity between regions

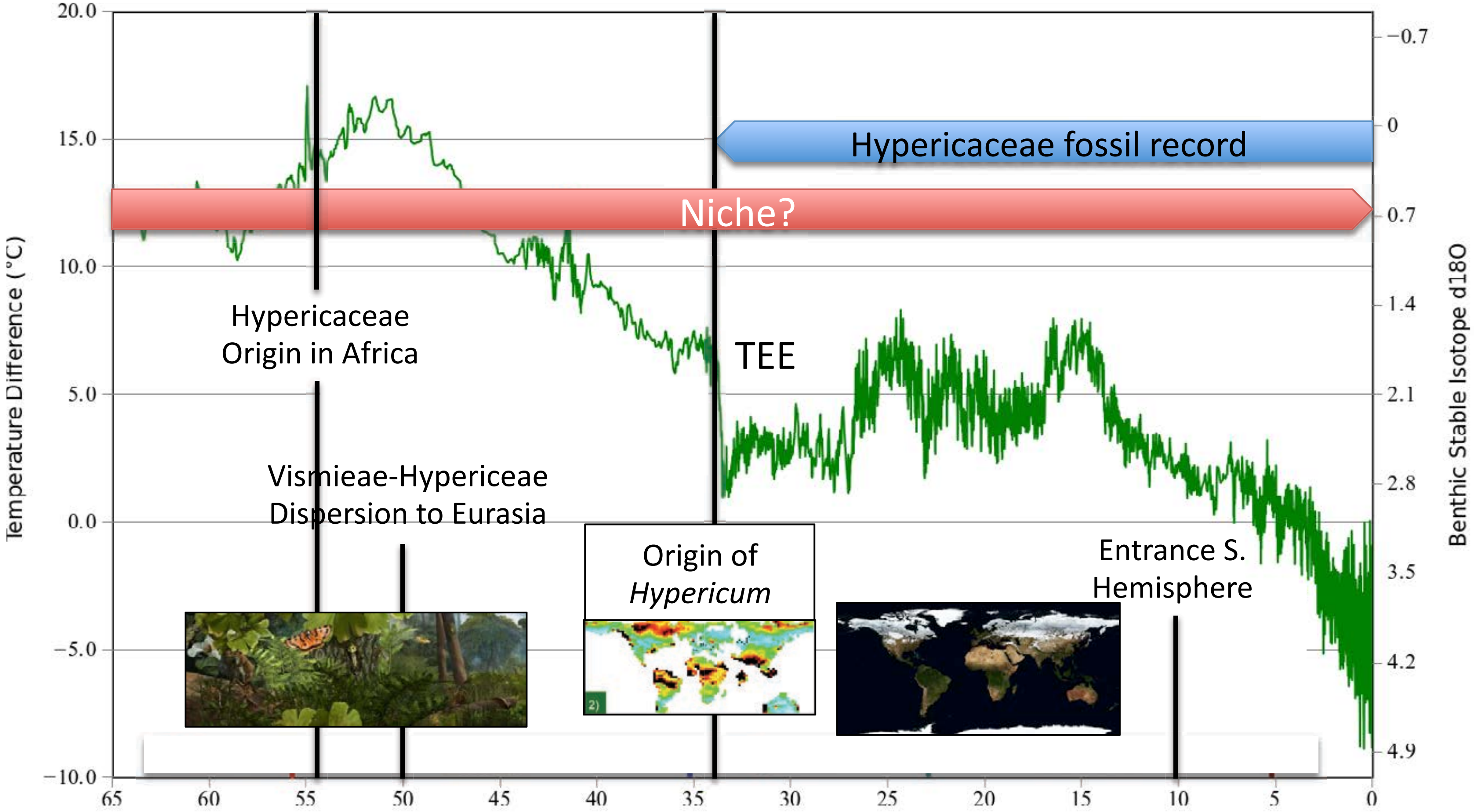
INTEGRATIVE BIOGEOGRAPHIC ANALYSIS

Geological connections
"Ecological" connections
Fossil ranges
Extant evidence

- **Colonization of the Holarctic by *Hypericum* stem lineages** (Vismeae-Hypericeae ancestor)
- ***Hypericum* ancestors distributed across the Holarctic** (crown lineage)



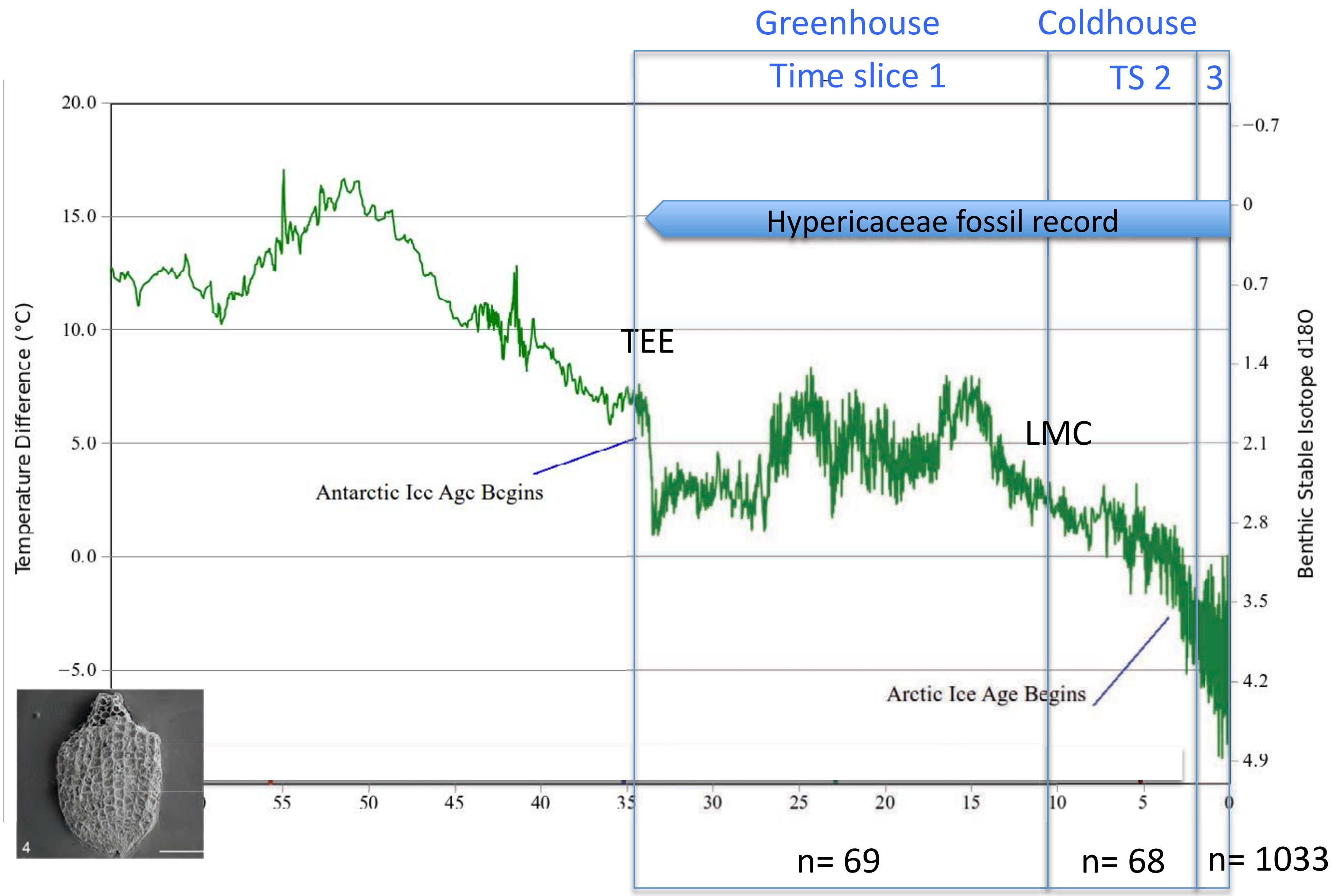
How *Hypericum* survived the TEE?



How *Hypericum* survived the TEE?

Evolutionary novelties in *Hypericum*

FOSSIL-BASED NICHE MODELLING



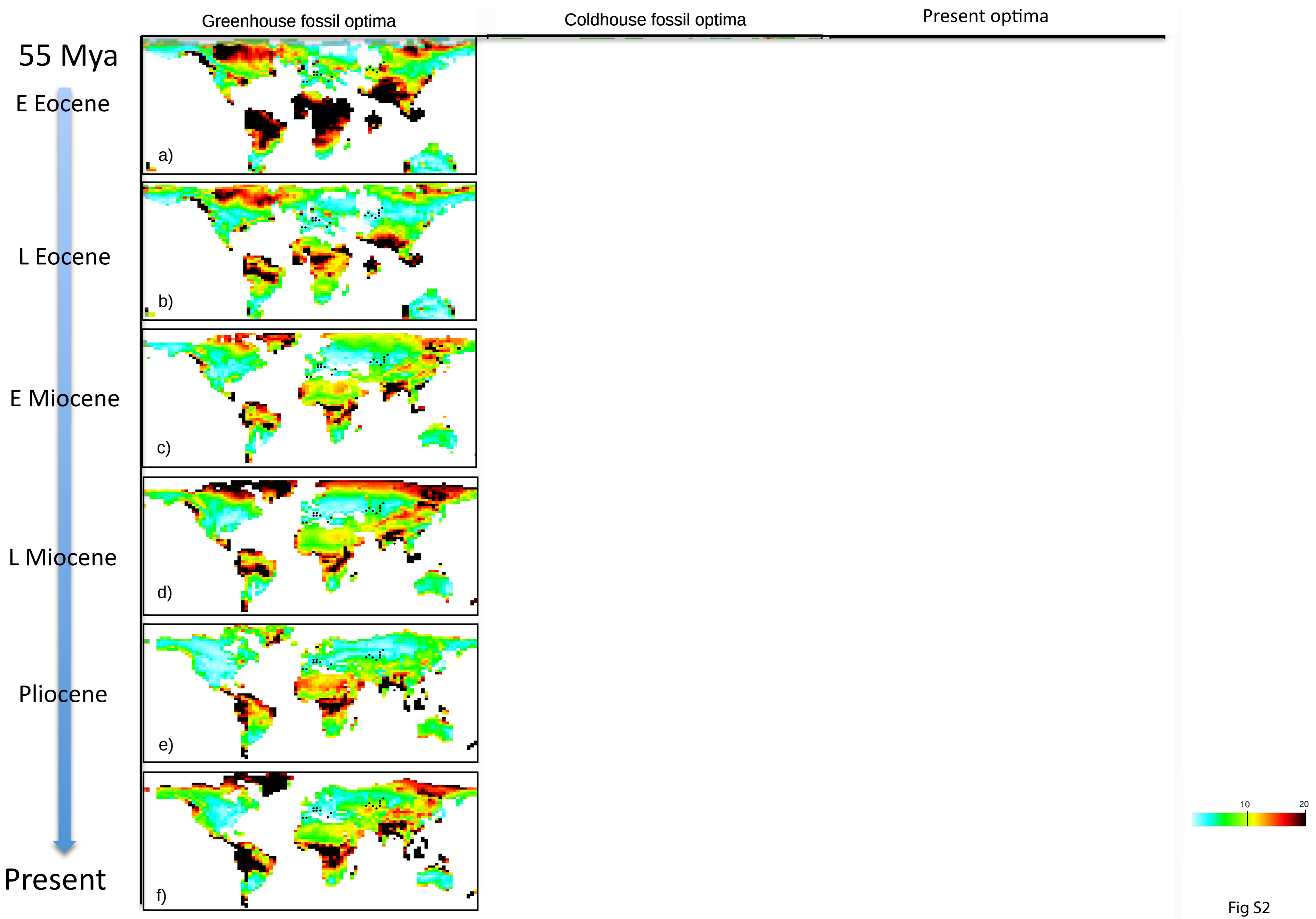

Greenhouse fossil optima
Coldhouse fossil optima
Present optima
55 Mya
E Eocene
L Eocene
E Miocene
L Miocene
Pliocene
Present
a)
b)
c)
d)
e)
f)
10
20

Fig S2

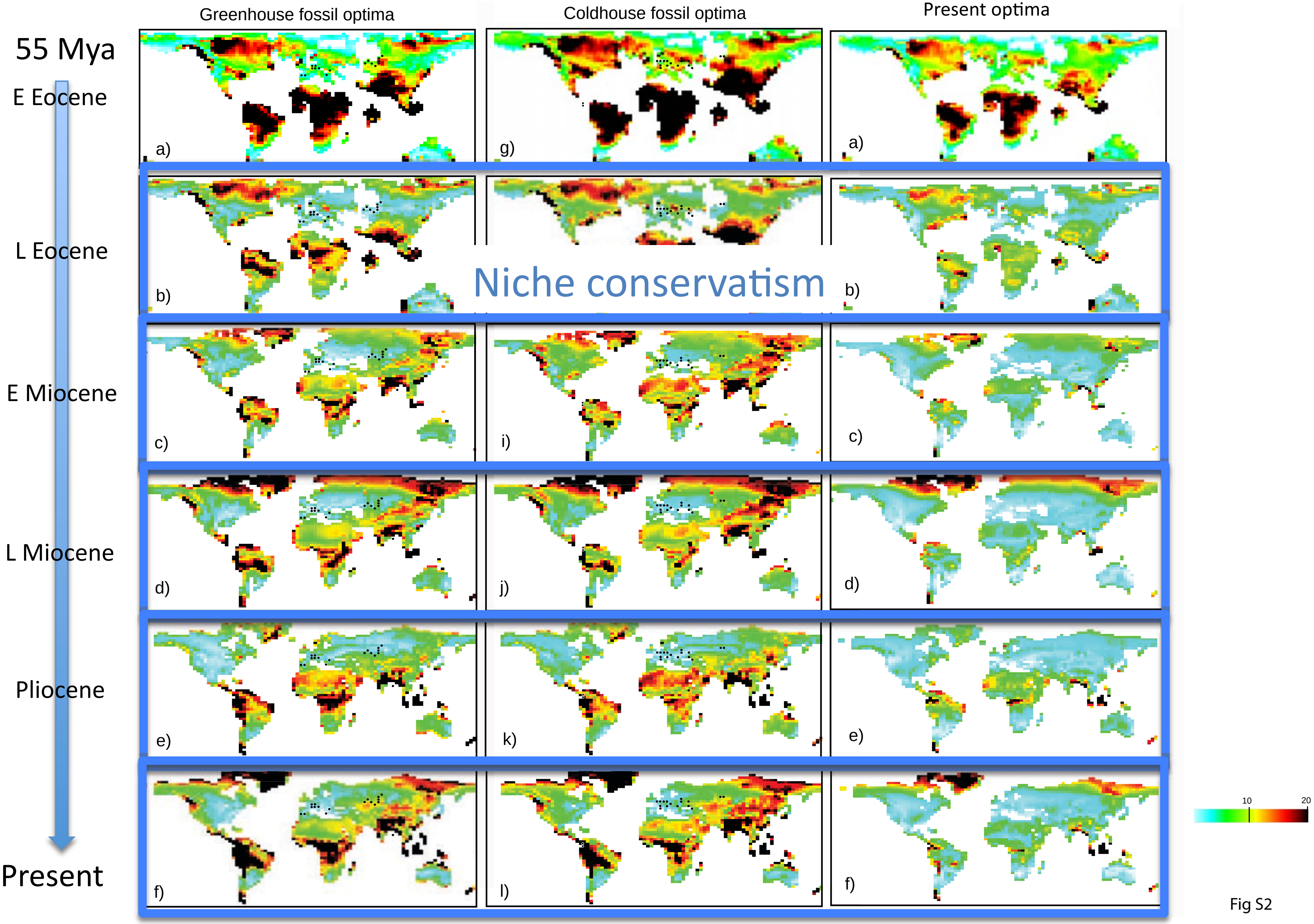
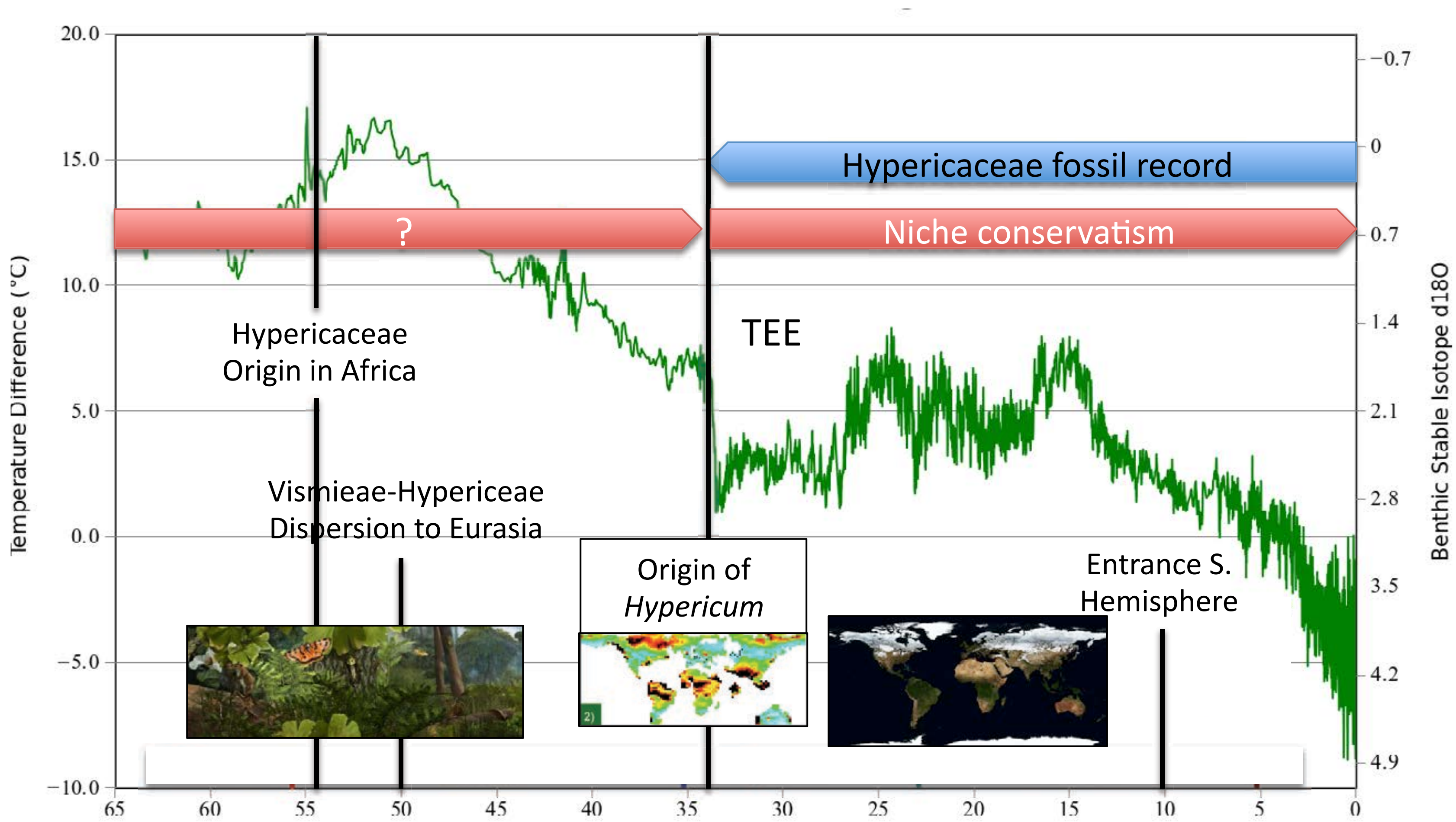
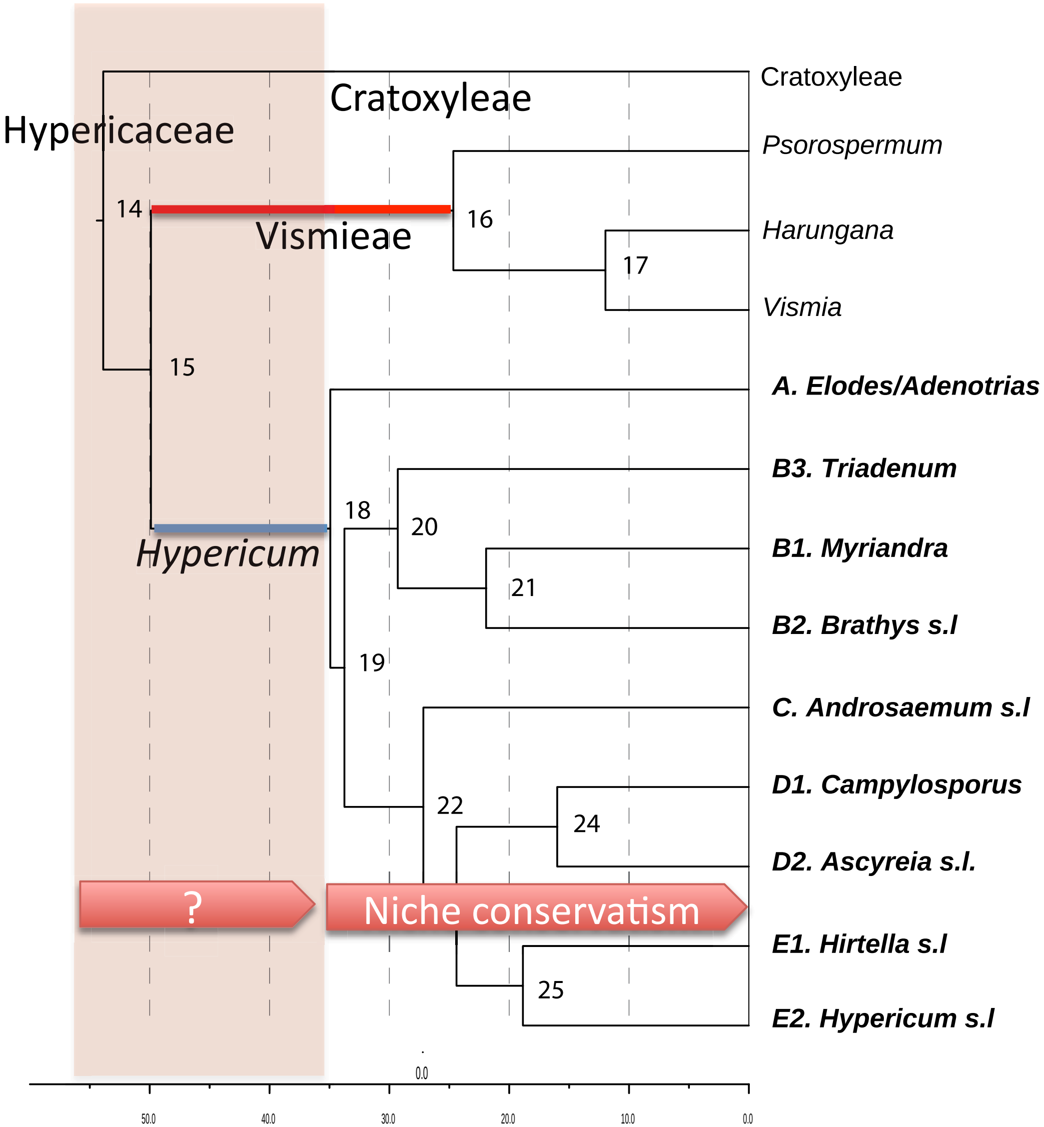

Greenhouse fossil optima
Coldhouse fossil optima
Present optima
55 Mya
E Eocene
L Eocene
E Miocene
L Miocene
Pliocene
Present
Niche conservatism
a)
b)
c)
d)
e)
f)
g)
i)
j)
k)
l)
a)
b)
c)
d)
e)
f)
10
20

Fig S2

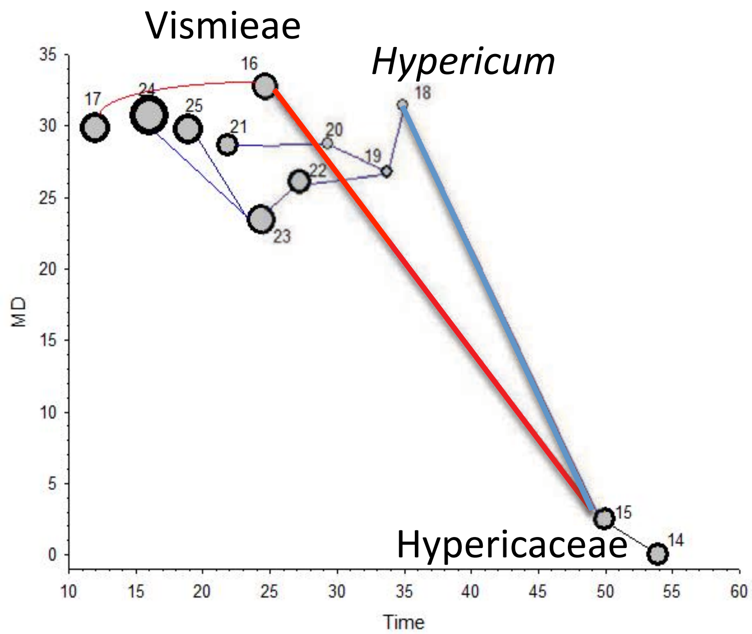
How *Hypericum* survived the TEE?



ANCESTRAL PREFERENCES IN HYPERICACEAE

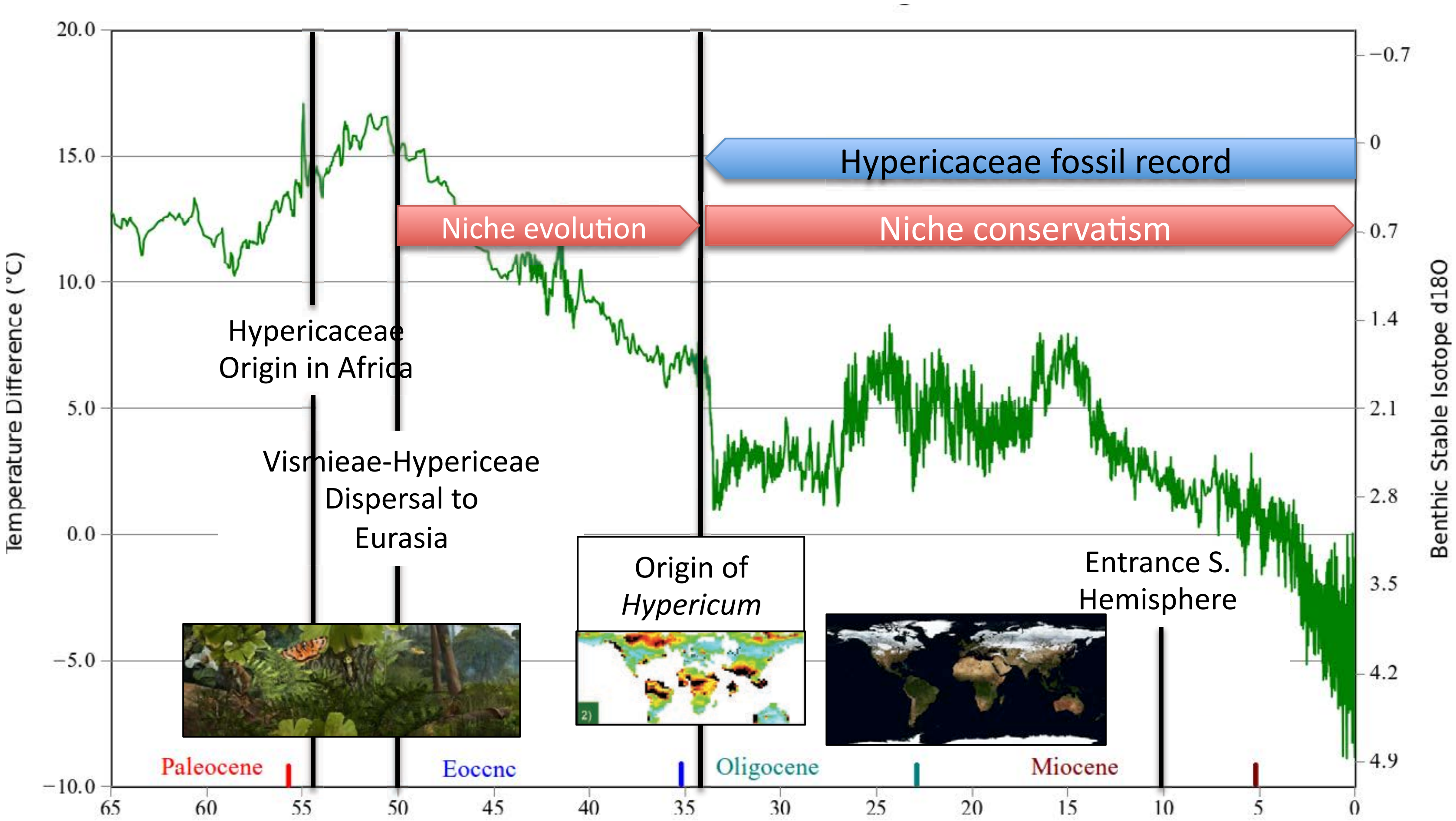


7 continuous variables, 3812 locations, Brownian model (Schluter, 1997)



Niche evolution occurred between Hypericaceae ancestors and *Hypericum* (50-35 Ma) and Vismieae ancestors

How *Hypericum* survived the TEE?



Drivers of diversification

Which were the factors explaining the extraordinary species richness of *Hypericum* compared to other clusioid genera?

We tested two hypotheses:

“<u>key-innovation diversification</u>” hypothesis (KID)

“adaptive breakthroughs” allowed the genus to diversify rapidly.

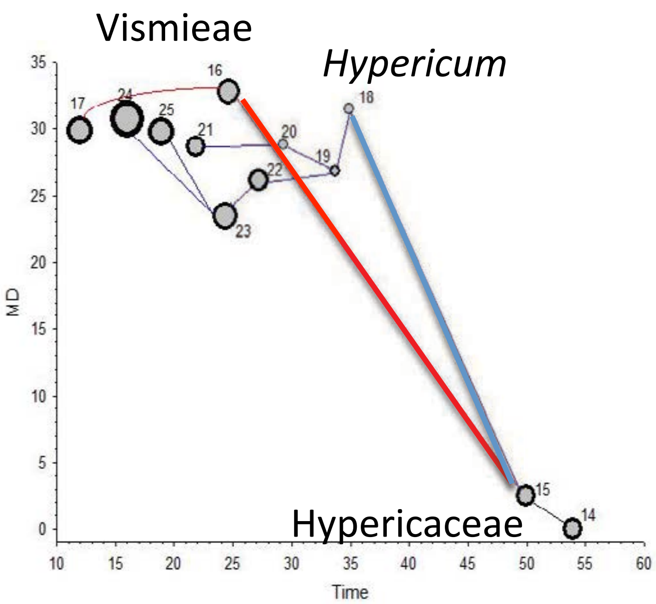
a) Ecological innovation: a change in climatic tolerances to deal with the new temperature regimes in the Holarctic
b) Morphological change: the appearance of the herbaceous habit

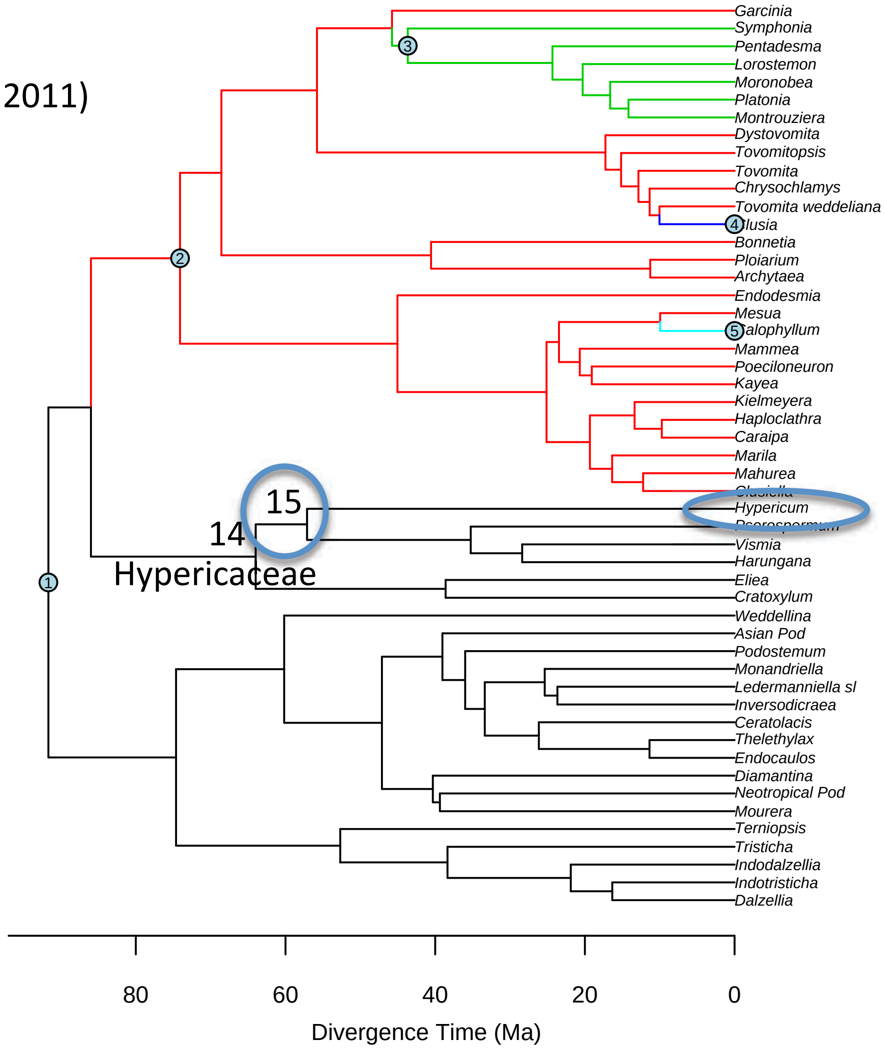
“<u>time-to-speciation effect</u>” hypothesis (TSE)

The present large diversity of *Hypericum* can be explained by the genus old age and a steady accumulation of species through time, rather than “rapid bursts of diversification”.

CHANGES IN DIVERSIFICATION ACROSS CLADES
Macroevolutionary Birth-Death models

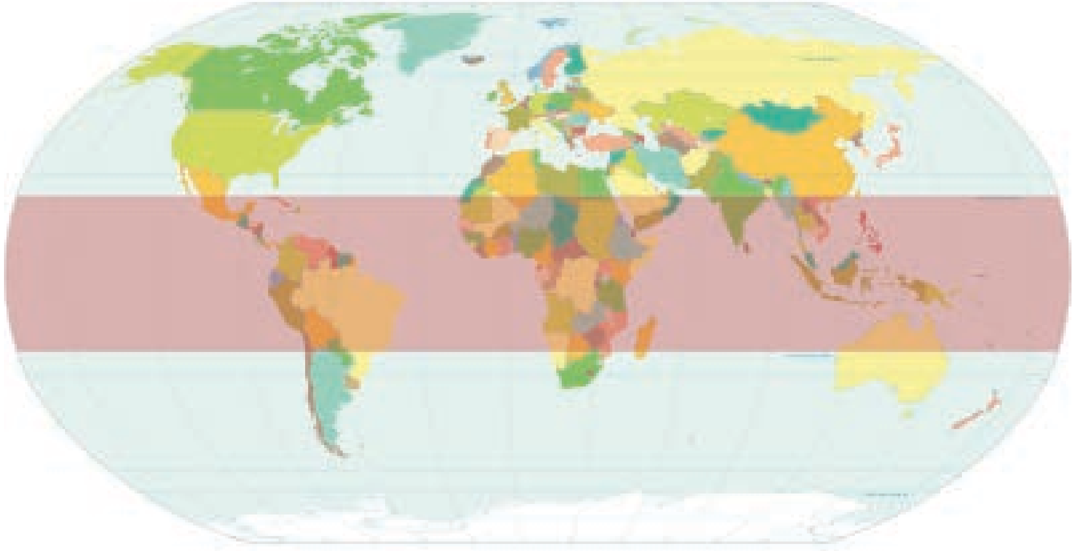
BEAST dating: clusioid clade (Ruhfel *et al.*, 2011)





MEDUSA 5 rate-shift model: Rate variation across clades

TRAIT-DEPENDENT DIVERSIFICATION



Tropical/non tropical

GeoSSE speciation constrained model

$\lambda T = \lambda NT$ equal speciation
$\mu T > \mu NT$ diff. extinction

vs.

Herb/non-herb

BiSSE model

($p > 0.05$)


Key innovations **did not promote** diversification in *Hypericum*. The age of the group and the steady accumulation of lineages better explain diversity pattern in the group (**TSE hypothesis**). But they could have contributed to decrease the **extinction risk** in a changing environment.

Mechanisms generating phytophagous insects large-scale diversity patterns: global changes versus biotic adaptations

A. Sánchez Meseguer, A. Coeur d'Acier, E. Jousselin

Montpellier, 2014

INRA SCIENCE & IMPACT
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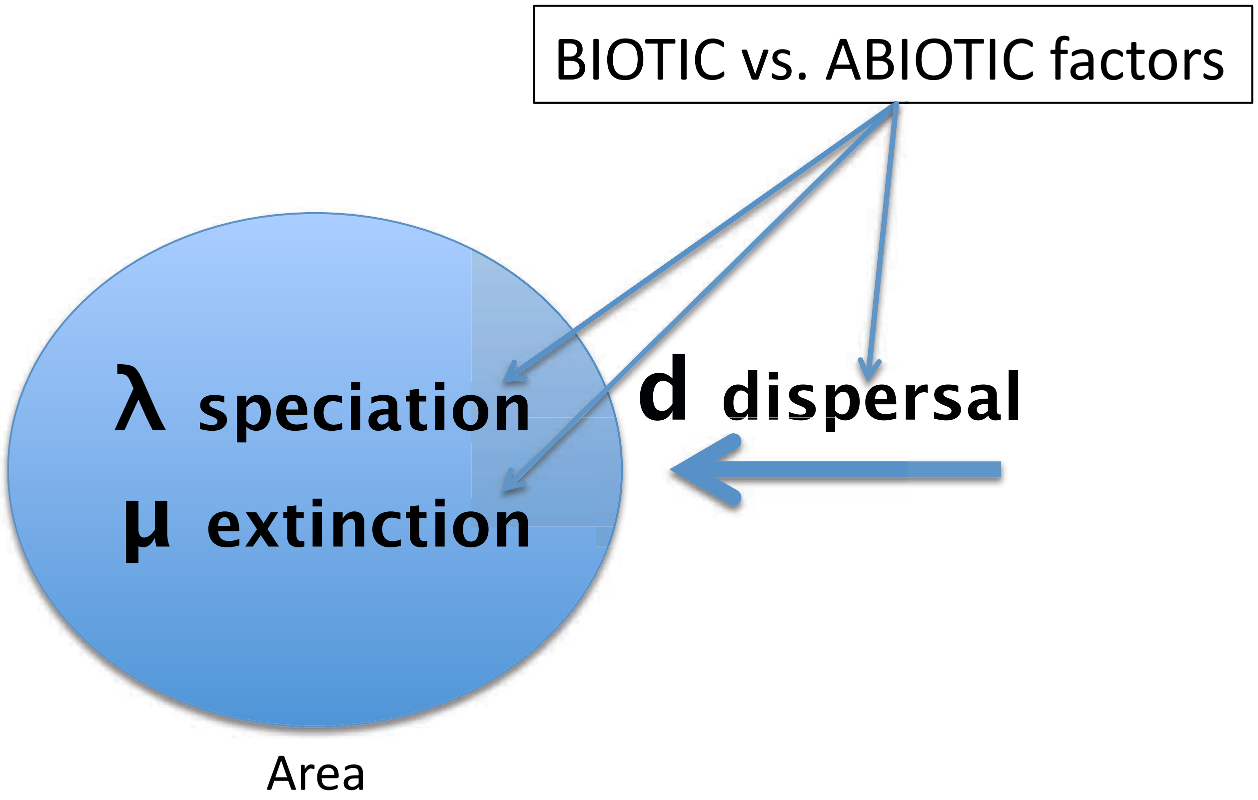
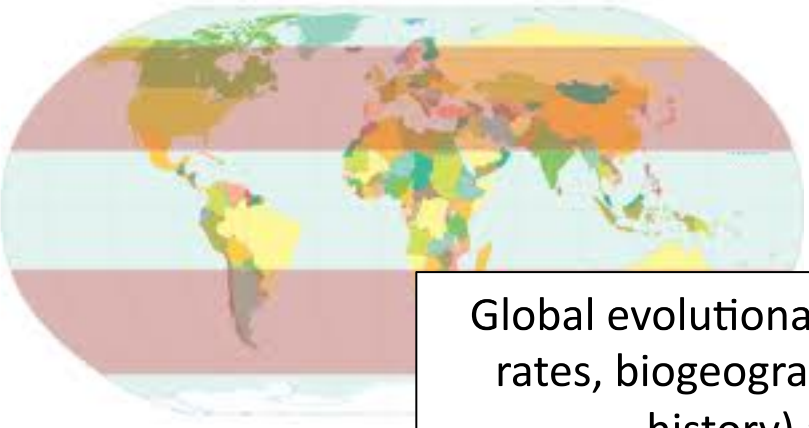
MECHANISMS REGULATING DIVERSITY

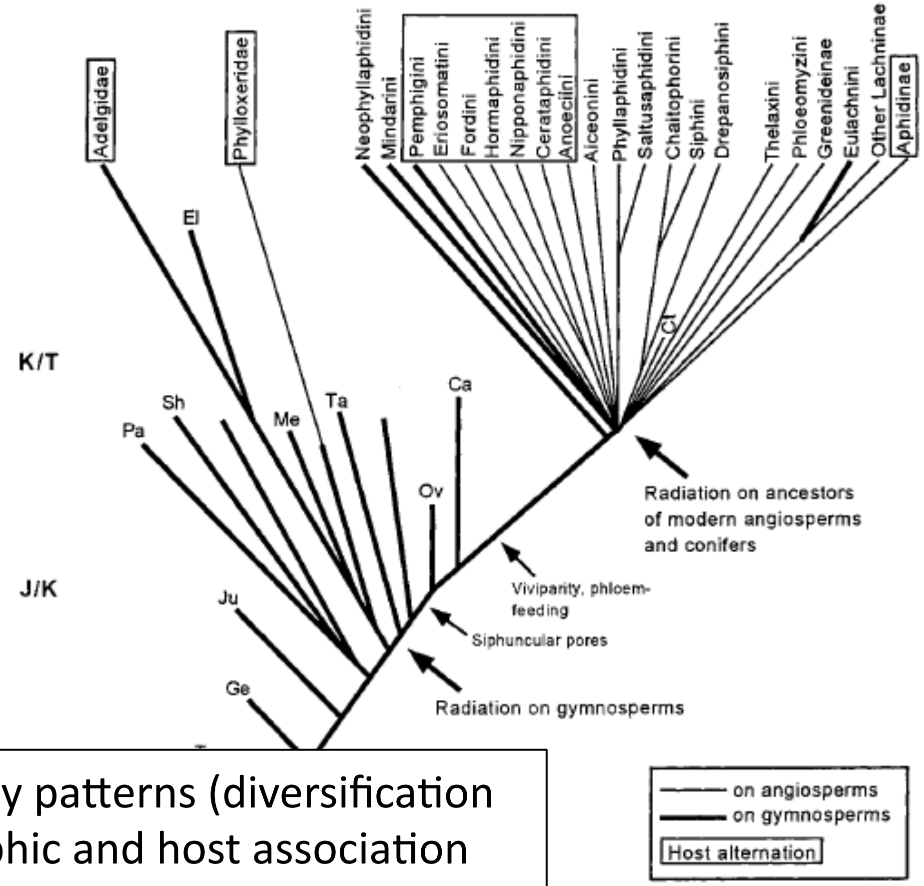


Wiens 2013

Aphids

- Aphids ca. 4000 sp. in temperate regions
- Specific association with plants
- Rapid radiation favoured by specialization on plants





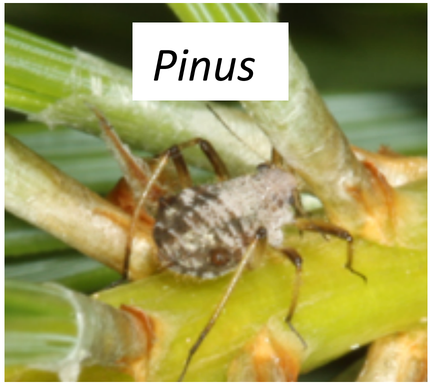
Global evolutionary patterns (diversification rates, biogeographic and host association history) are poorly known

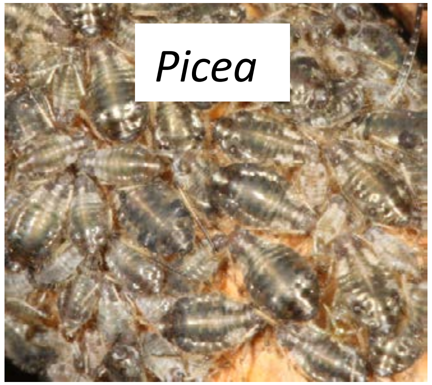
VonDohlen & Moran 2000

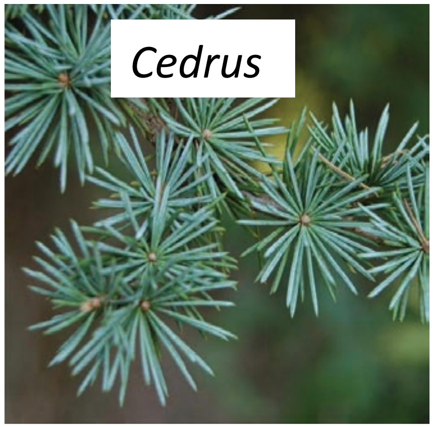
Cinara (Aphididae)

HOST ASSOCIATION

Trophic adaptation and host-shifts thought to be the main driver in its diversification (Heie 1987)



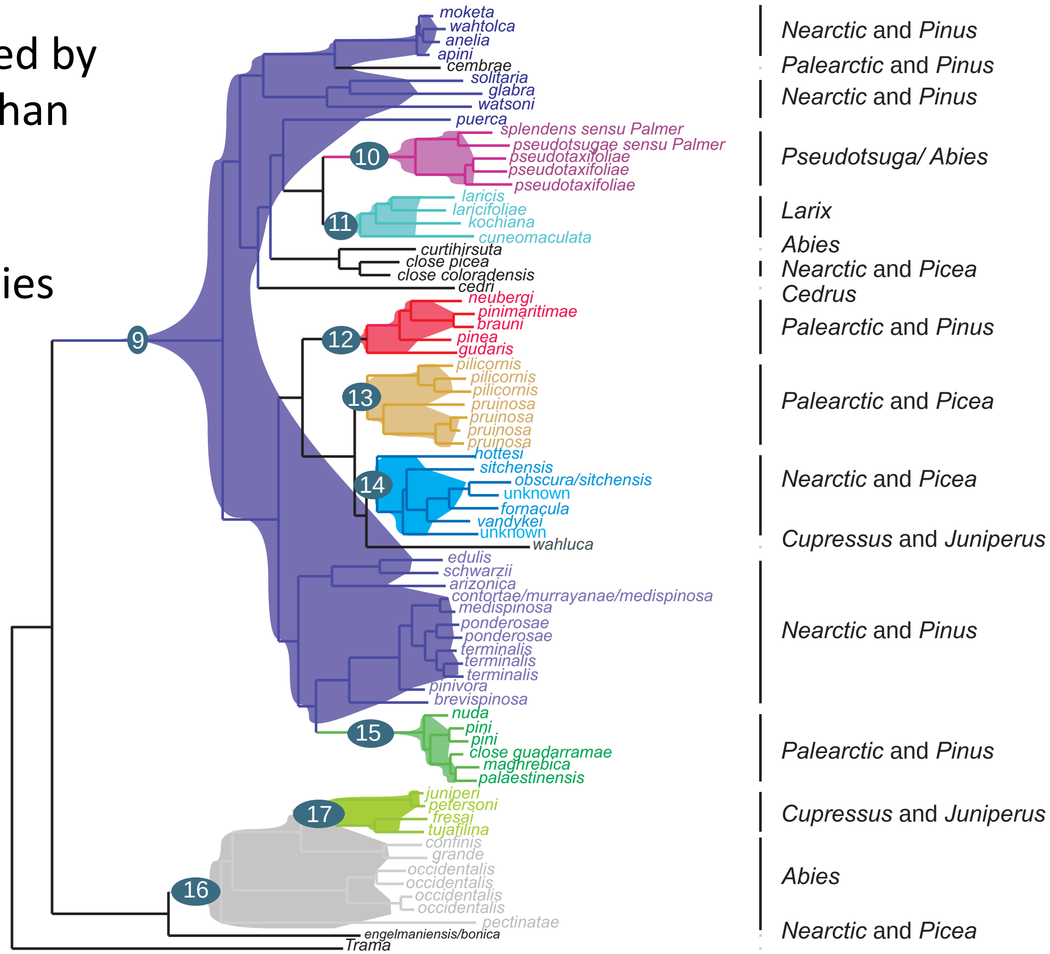




Is speciation driven by host association?

Few speciation events accompanied by host switch (Host shifts are rarer than expected by chance)

Geographic overlap between species increases with time since the divergence



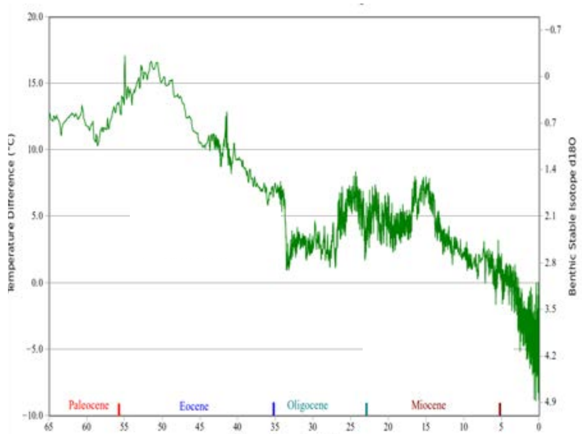
Jousselin et al., 2013

GENERAL OBJECTIVE

Study the drivers of diversification in *Cinara,* telling apart the contribution of **biotic** (species interactions) versus **abiotic factors** (climate, geologic change) on the mechanisms generating and maintaining diversity

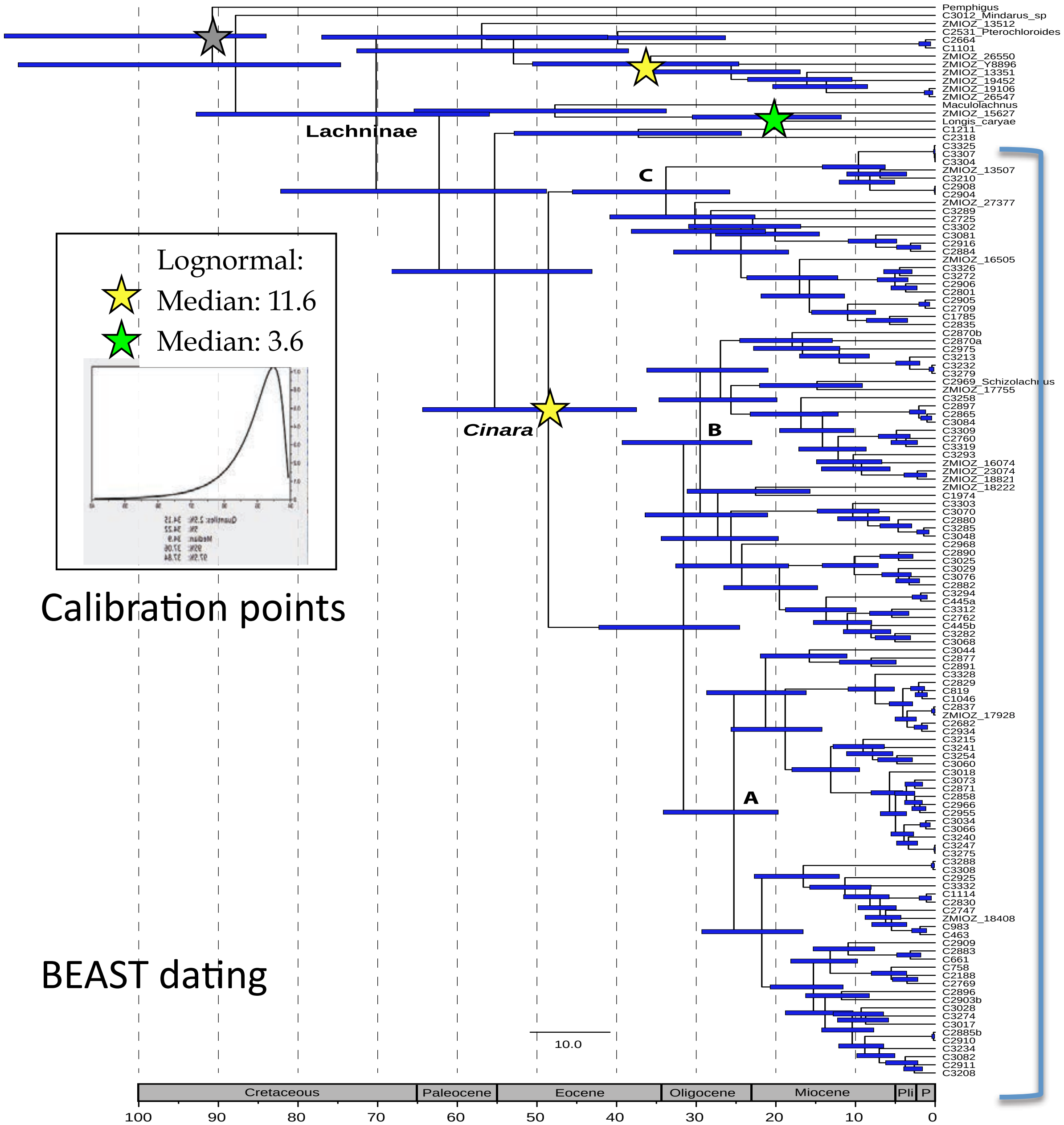
biotic interactions vs. abiotic pressures

Trophic association with conifers (host)



Abiotic pressures through the Cenozoic

Cinara age

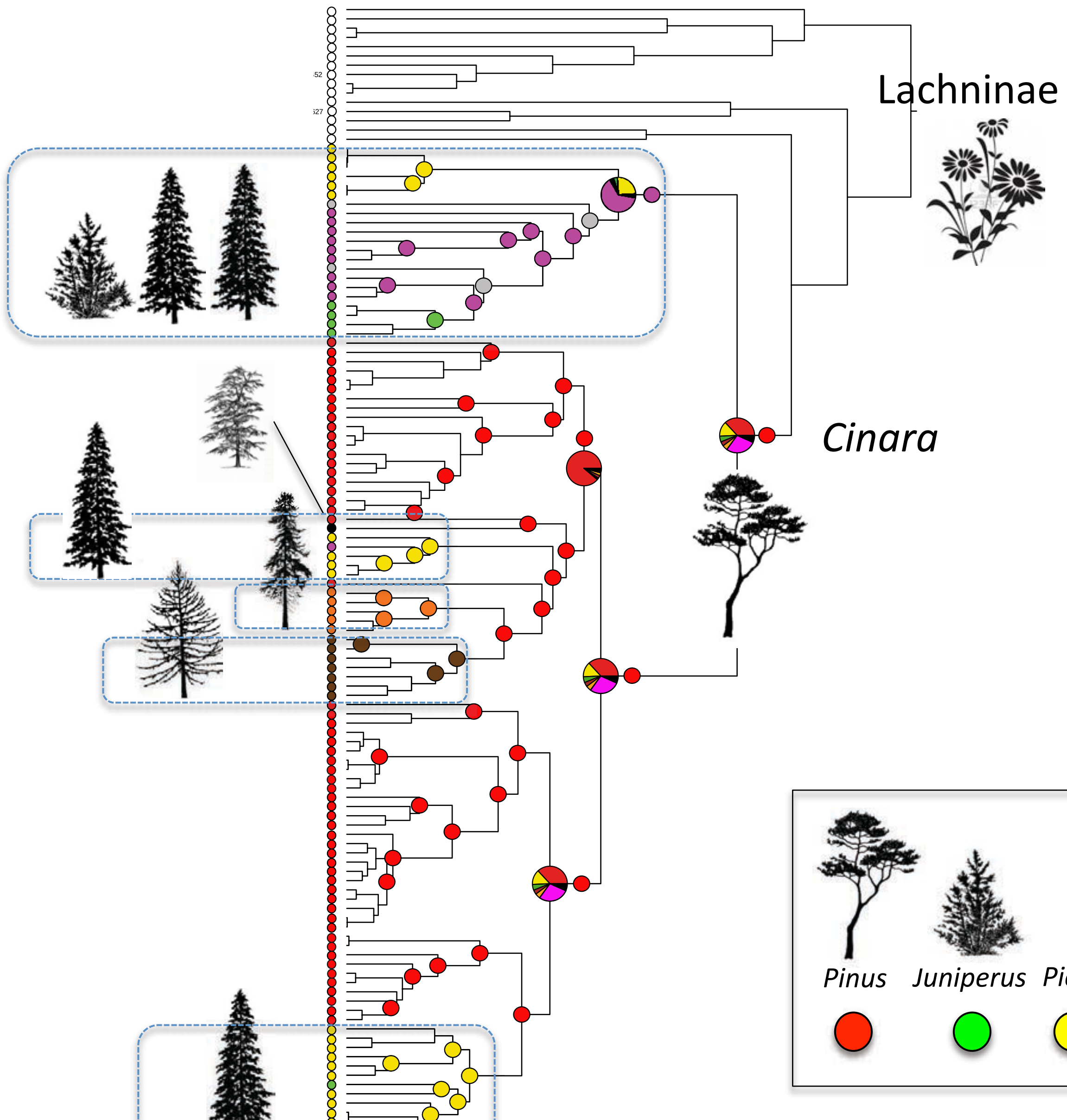


Calibration points

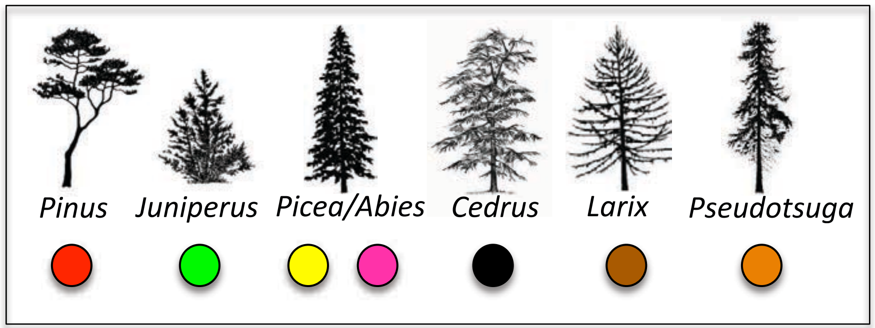
BEAST dating

Cinara

Ancestral Host Reconstruction

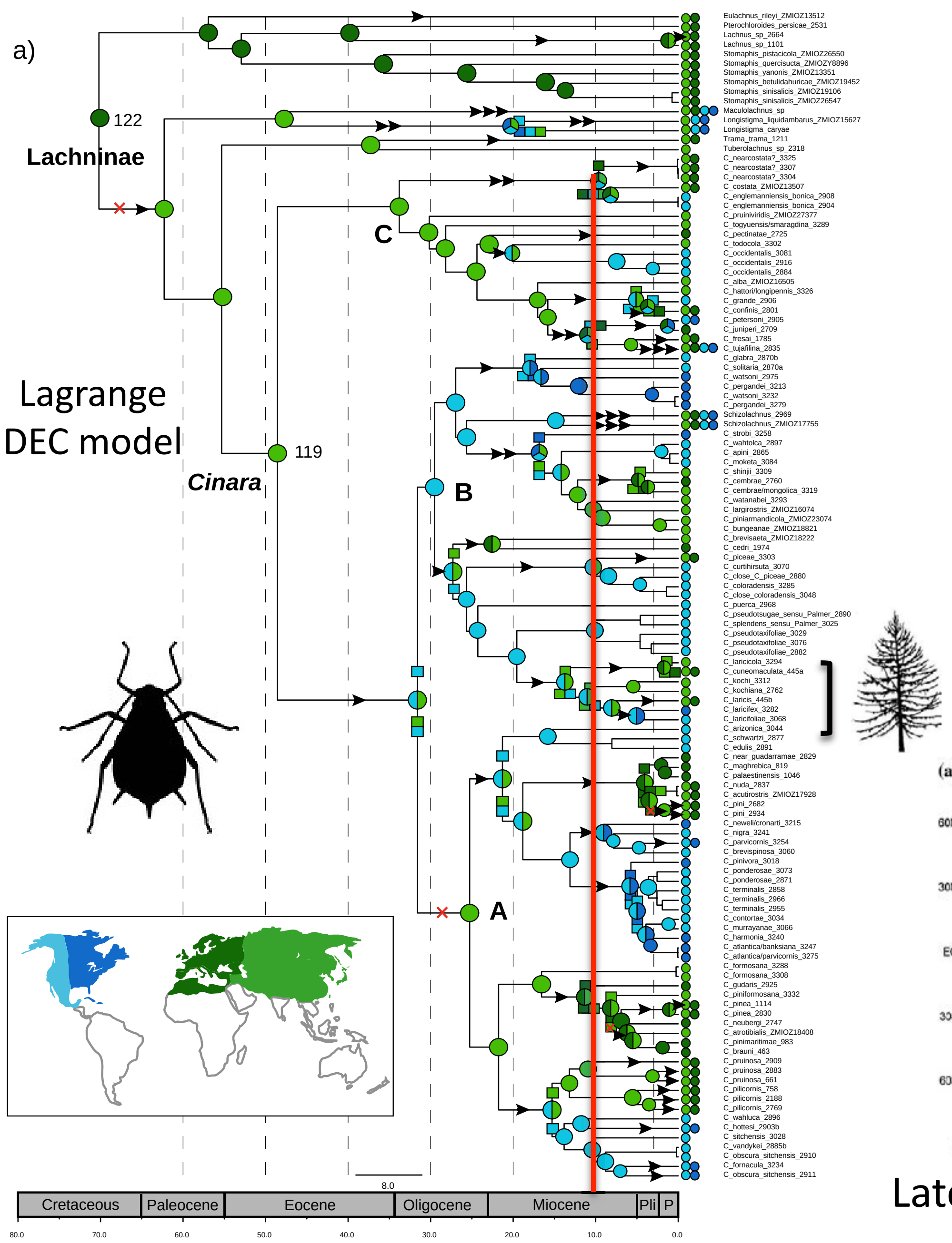


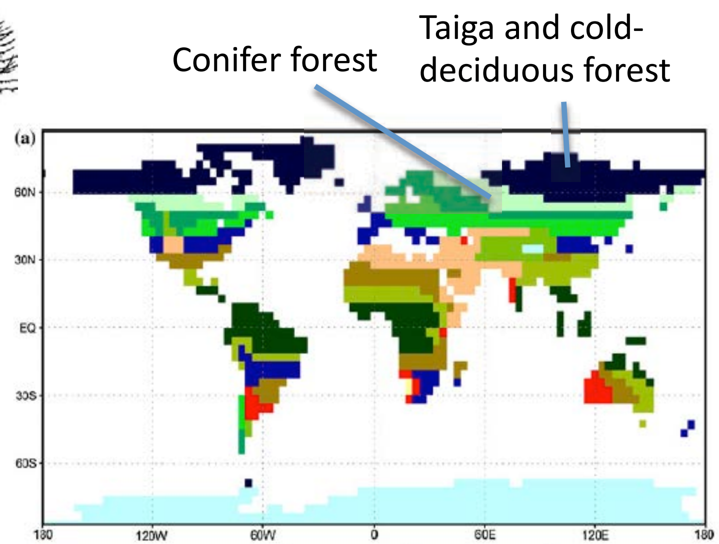
Strong host genus conservatism
(few host-genus switches)



Bayesian ASR in *BayesTrait* and ML ASR, MK1 model

Biogeographic history

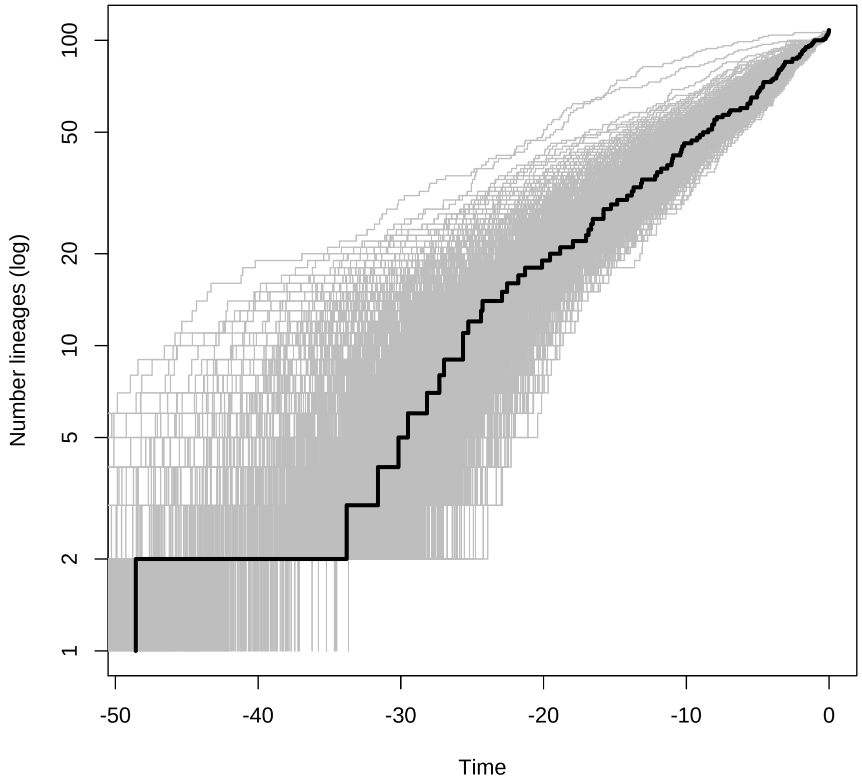




Late Miocene vegetation (Schnek et al. 2012)

Diversification Dynamics

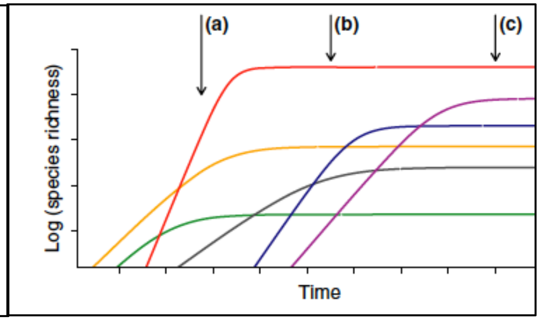
Macroevolutionary Birth-Death models



- Diversification **rates in *Cinara*** (r=0.09) are **significantly higher than in Lachninae** (r=0.04, p>0.05)

- **Constant diversification** since the crown diversification of *Cinara* to the present (*Laser*, *TreePar*)

Does not follow the adaptive radiation prediction



Project objectives

1. Reconstruct the evolutionary history of *Cinara*: time of origin, biogeographic history, ancestral host association and diversification dynamics
2. Reconstruction of the evolutionary history of the conifer host to asses congruence between biogeographic histories and diversification trajectories of *Cinara* and their hosts.

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