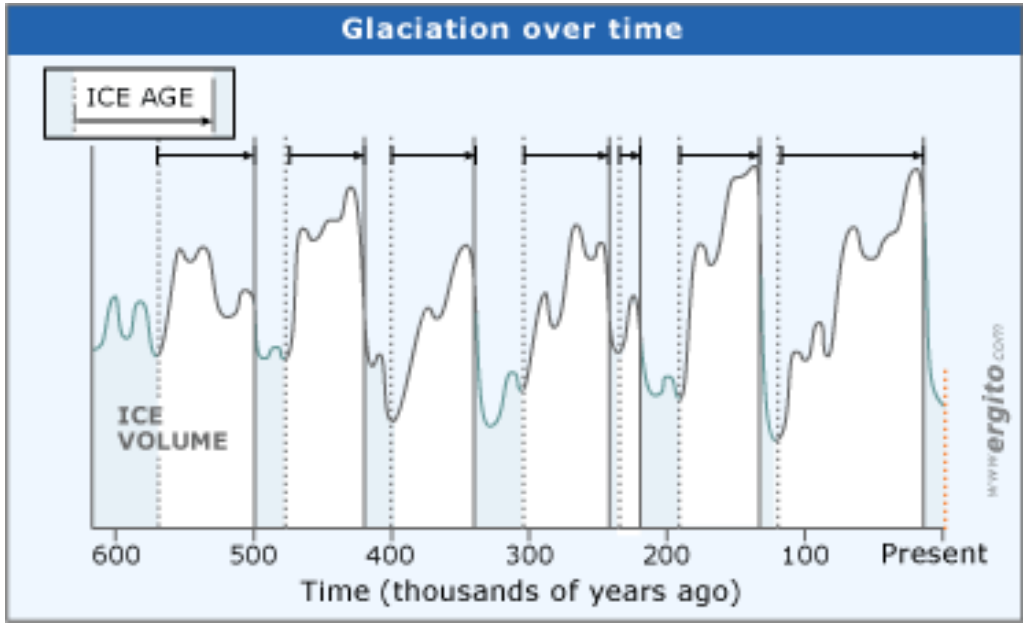

Tropical Rainforests
in the Pleistocene
Thomas Krahn

Tropical Rainforests in the Pleistocene



- tropics stable during Pleistocene?
- 1° C temperature drop based on 1976 CLIMAP study of warm vs. cold loving forams (vs. 10° C in North Atlantic)

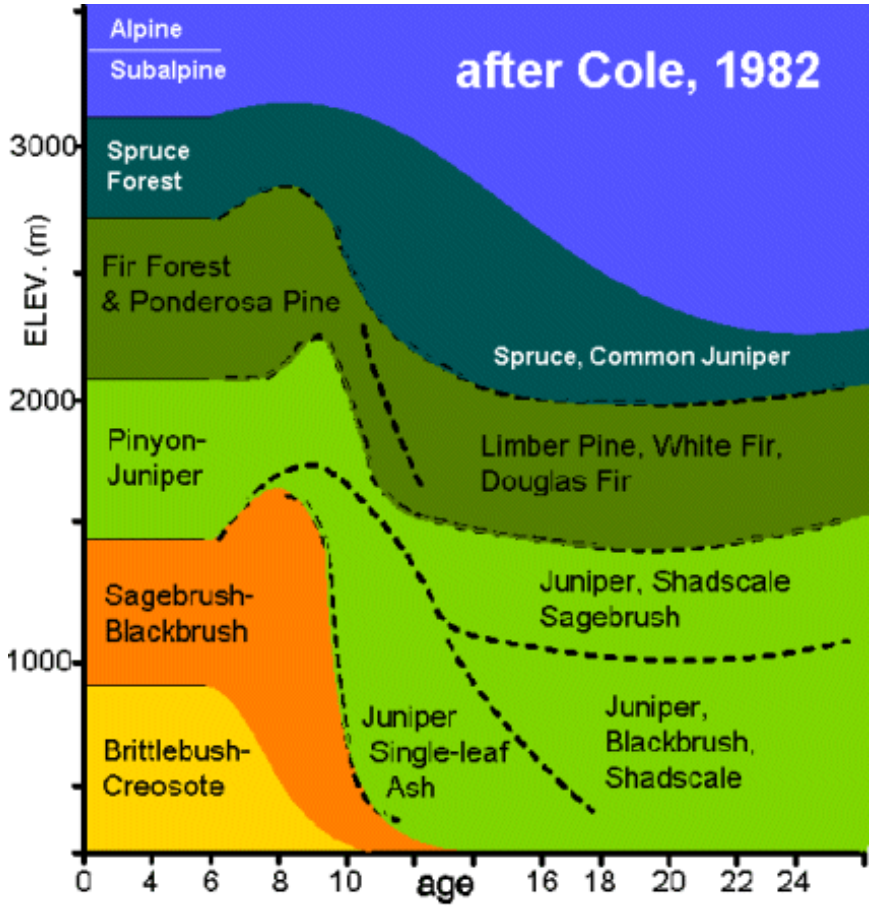
Tropical Rainforests in the Pleistocene

Pollen analysis of Mauna Loa cores over the last 40,000 years (Hotchkiss 2001)

Paleothermometers have since pointed to colder and drier tropics

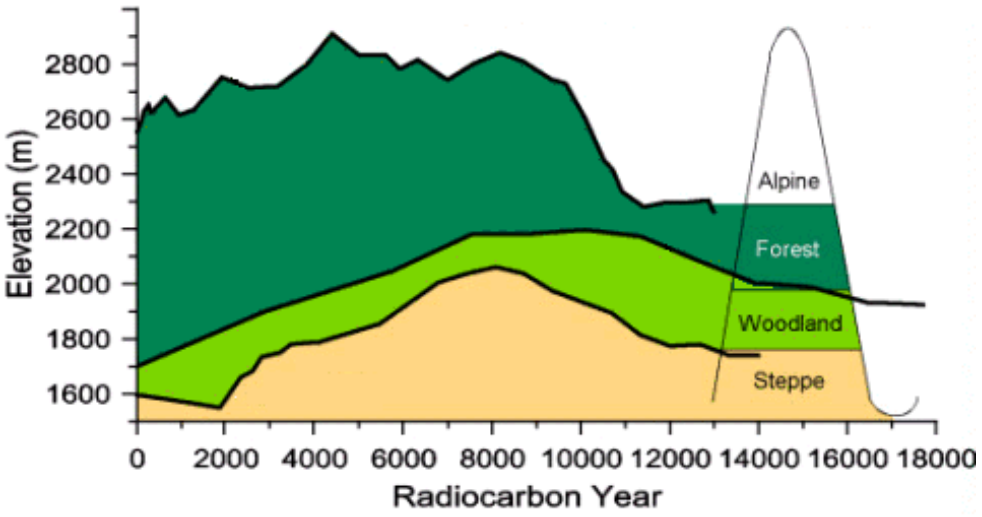
- pollen analysis points to 4-6° C cooling in Pleistocene (Hawaii, Bolivia)
- snow line altitudes in Andean and Hawaiian mountains show lowering during Pleistocene
- various chemical signatures ($CaCO_3$, noble gases in water)
- re-analysis of 1976 CLIMAP data indicates 3-4° C drop

Tropical Rainforests in the Pleistocene



Grand Canyon elevation shifts

- vegetation zones in mountains shifted down and up during glacial - interglacial cycles
- well characterized events in temperate montane systems



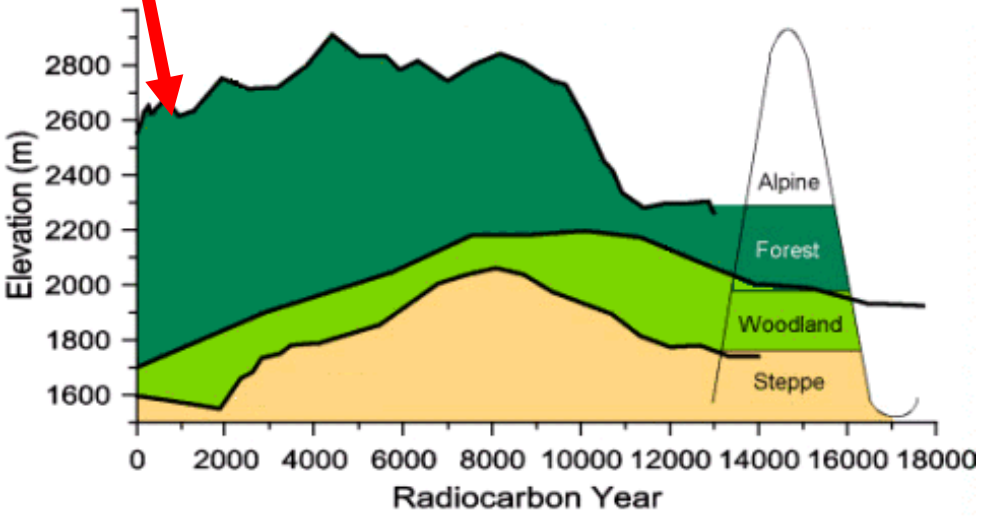
North Great Basin elevation shift

Tropical Rainforests in the Pleistocene

"Nowhere to go but up"

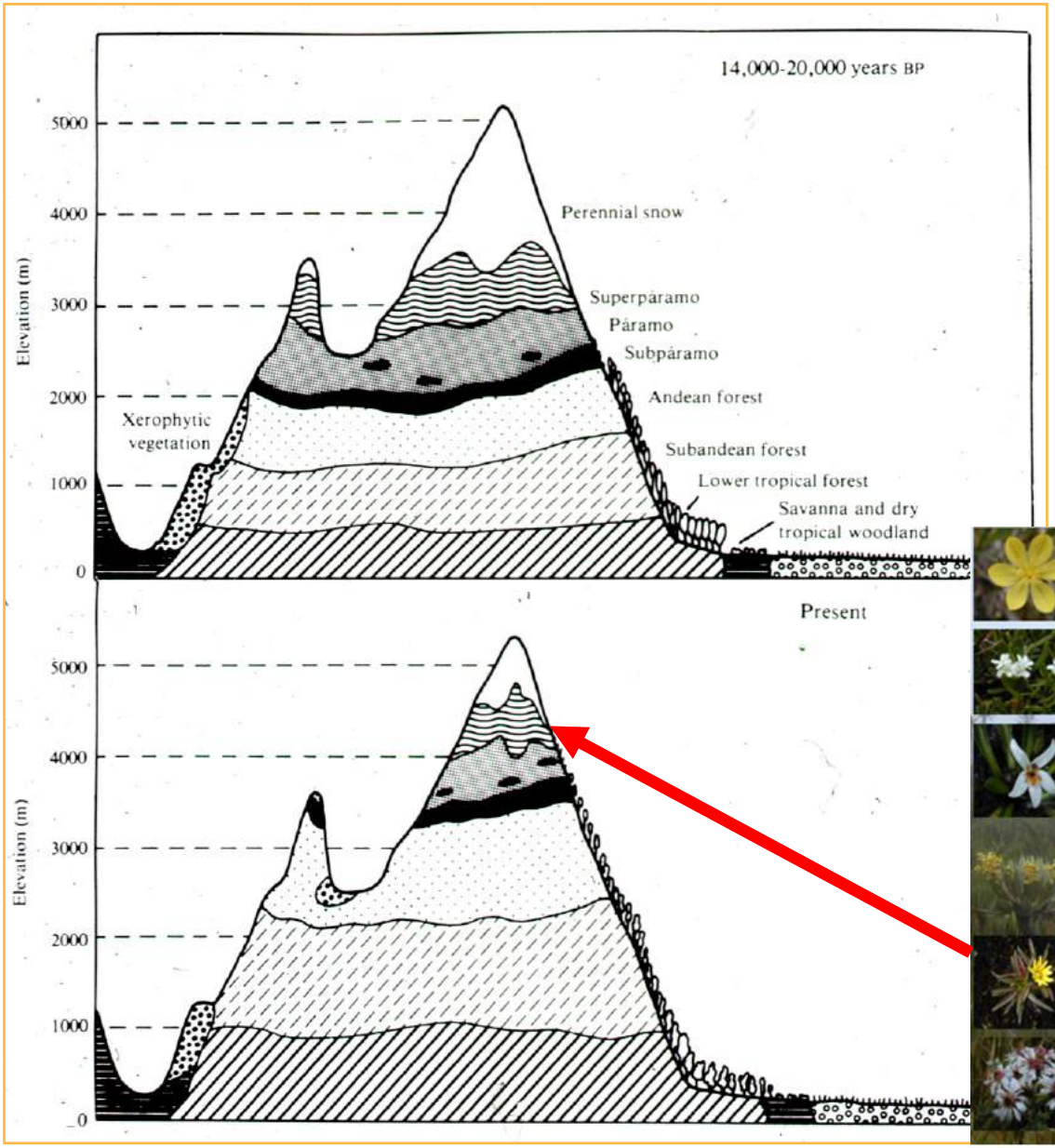
Core habitat is receding upwards in elevation and will shift 750 km NW under conservative climate estimates

- vegetation zones in mountains shifted down and up during glacial - interglacial cycles
- well characterized events in temperate montane systems



North Great Basin elevation shift

Tropical Rainforests in the Pleistocene

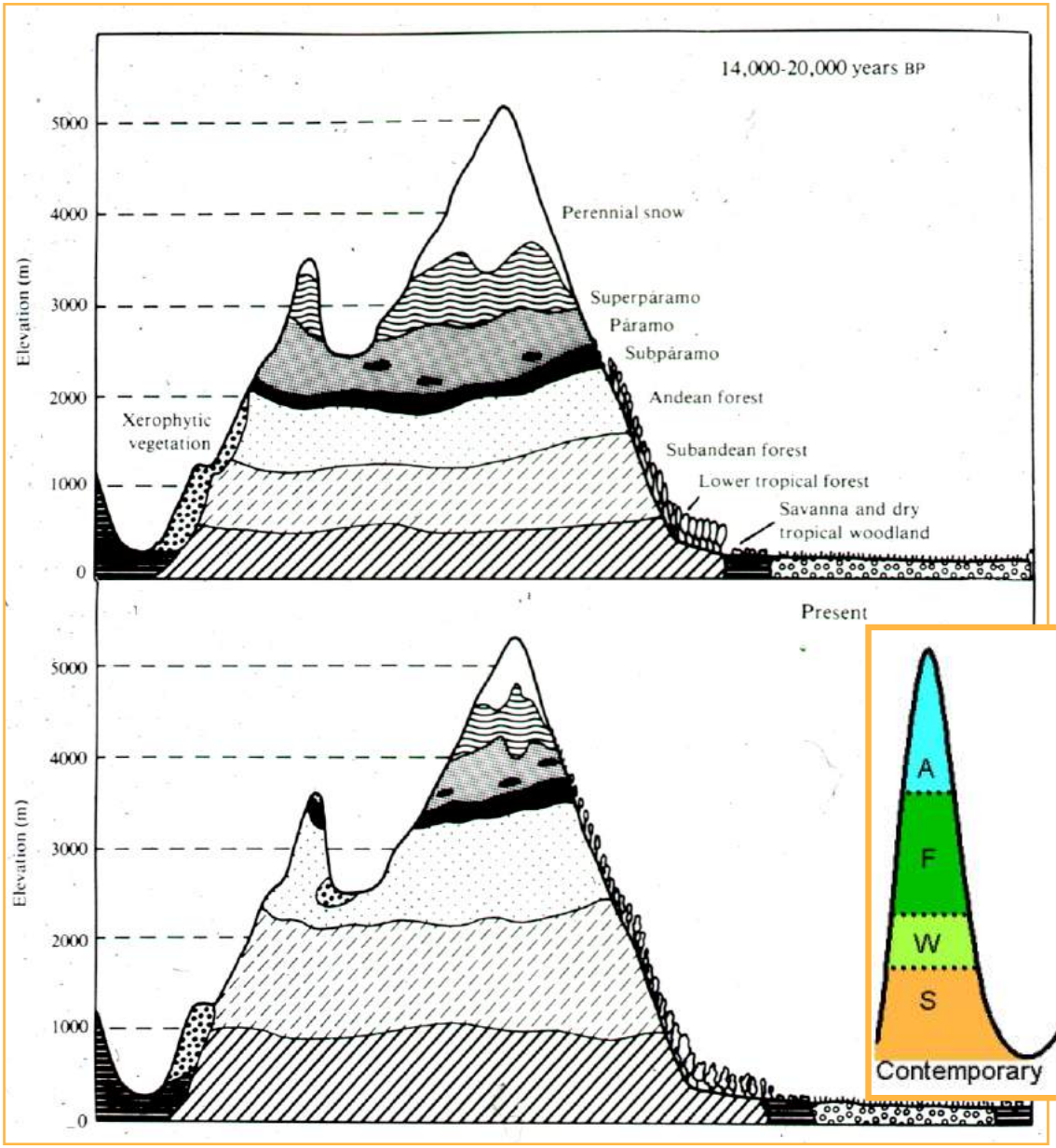


- palynological data for Central and South America mountains indicate similar shifts (repeatedly?) during Pleistocene and Holocene

Páramo is the world's fastest evolving and coolest biodiversity hotspot

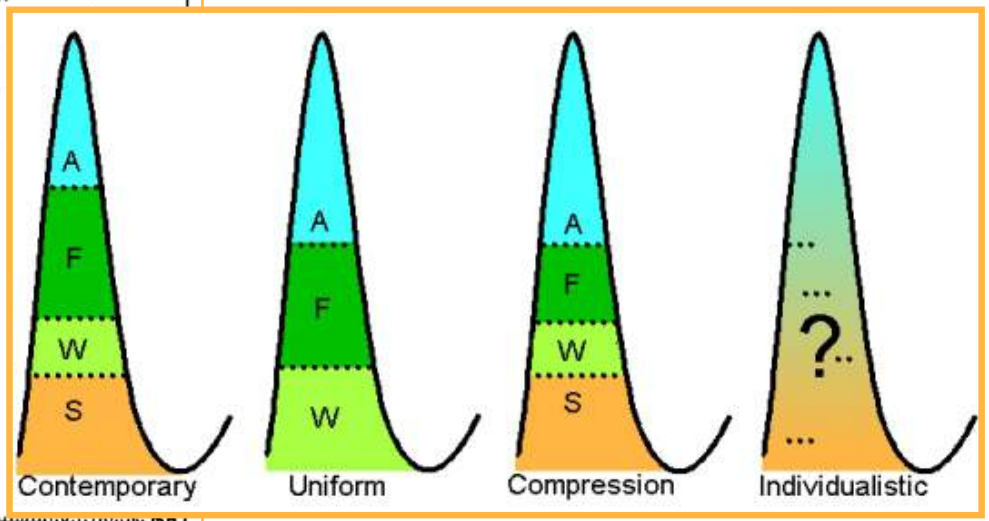
Paramo – risk of extinction?

Tropical Rainforests in the Pleistocene



- palynological data for Central and South America mountains indicate similar shifts (repeatedly?) during Pleistocene and Holocene

- *how* zones shifted is still debated



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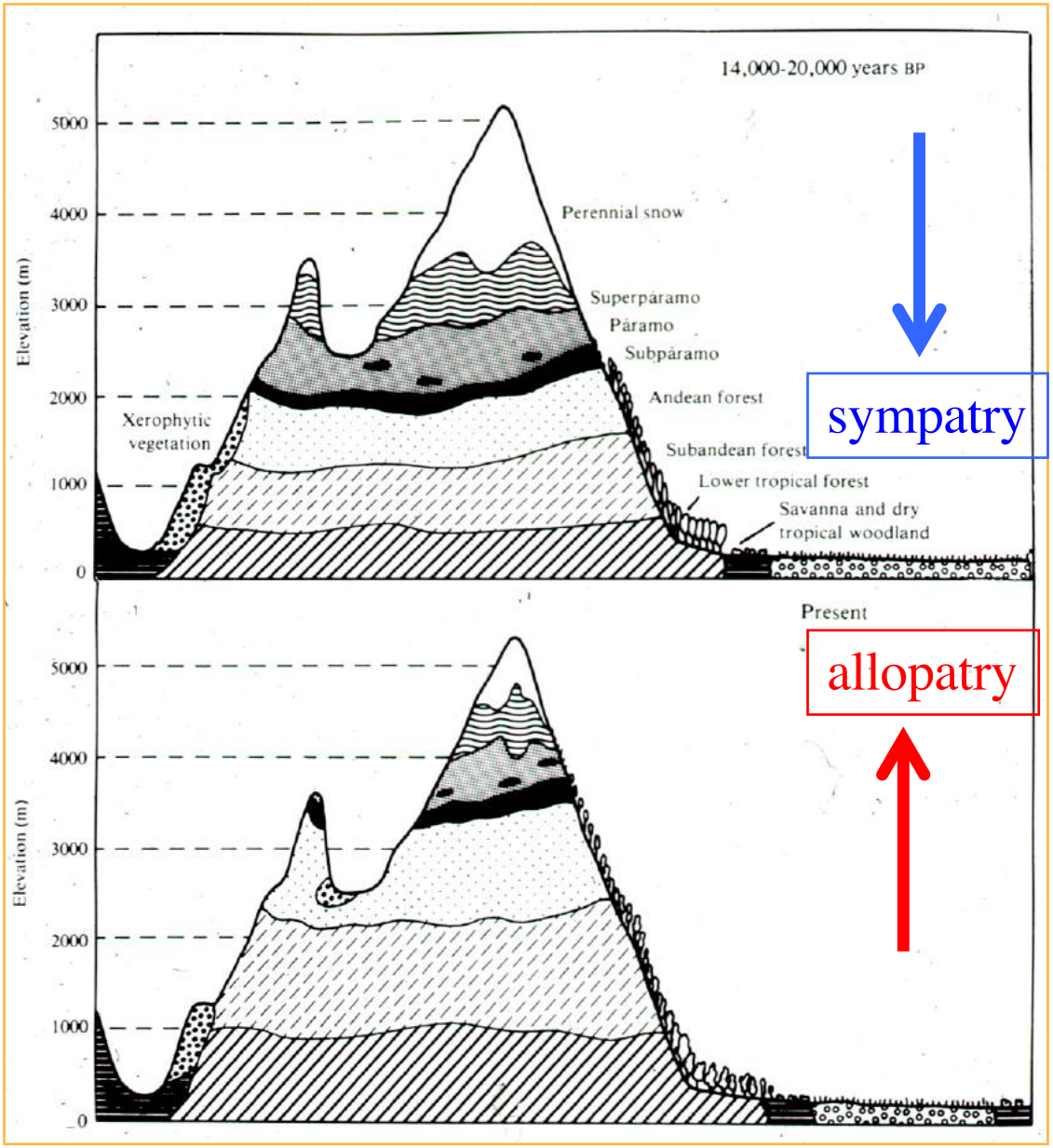
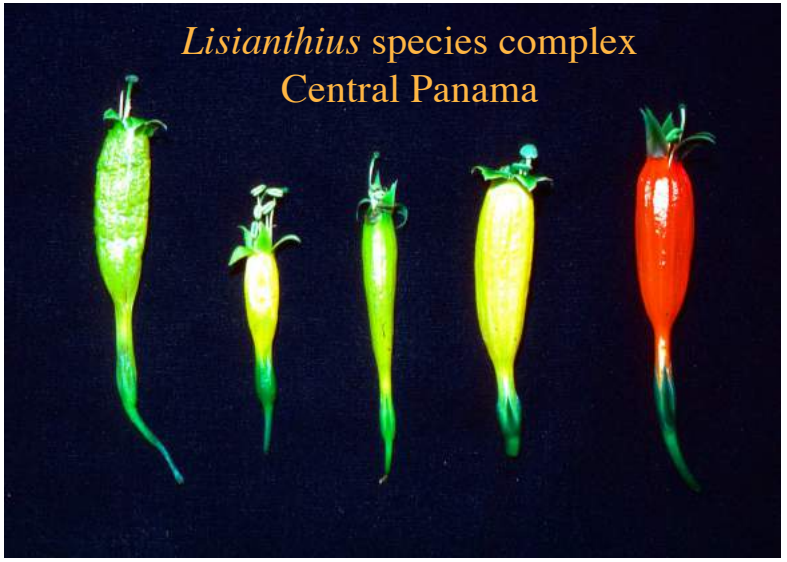


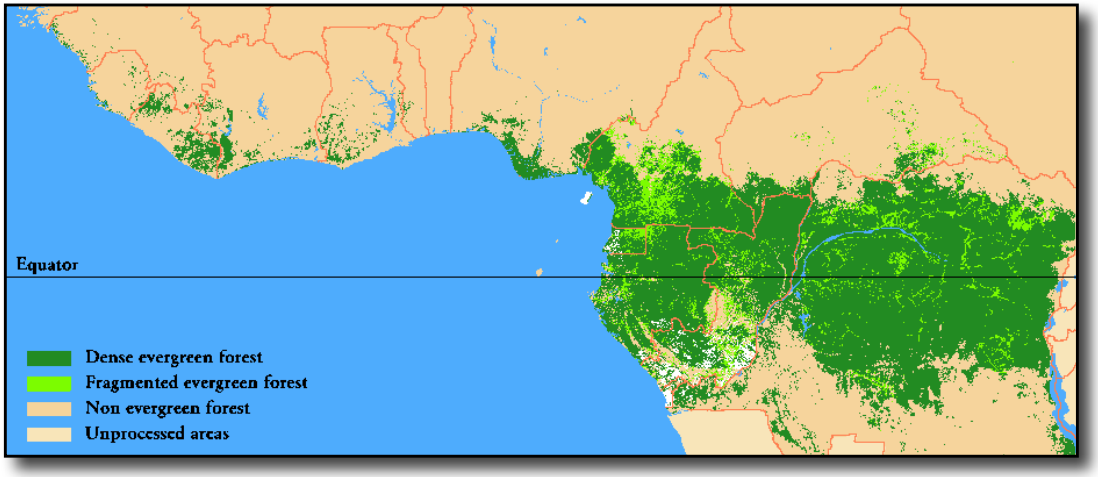
- repeated shifts probably presented montane species with cycles of *sympatry in glacials* and *allopatry in interglacials* — speciation pump in e.g. paramo species or cloud forest species



Tropical Rainforests in the Pleistocene

Evidence is pointing to cooler tropics during glacials

But what impact on the biogeography of tropical lowland plants and animals?



Tropical Rainforests in the Pleistocene

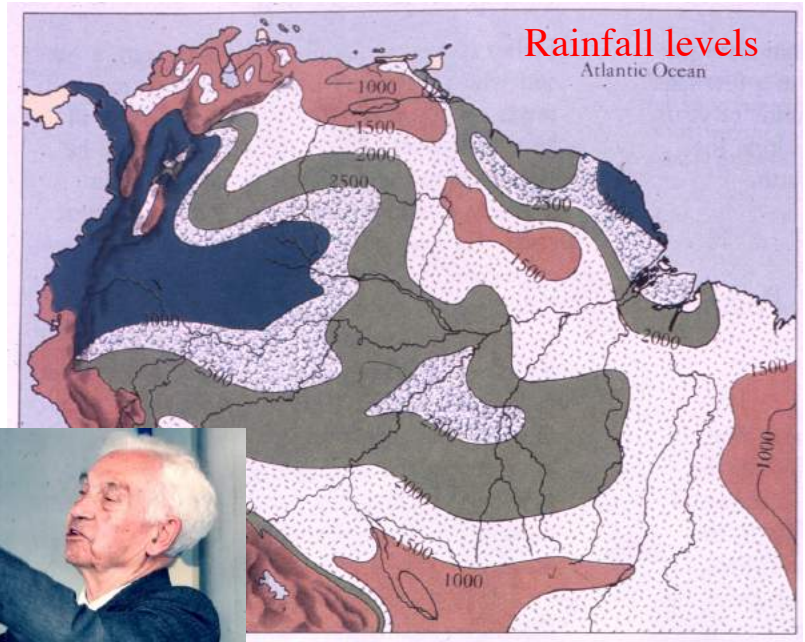
— the Refugia Hypothesis

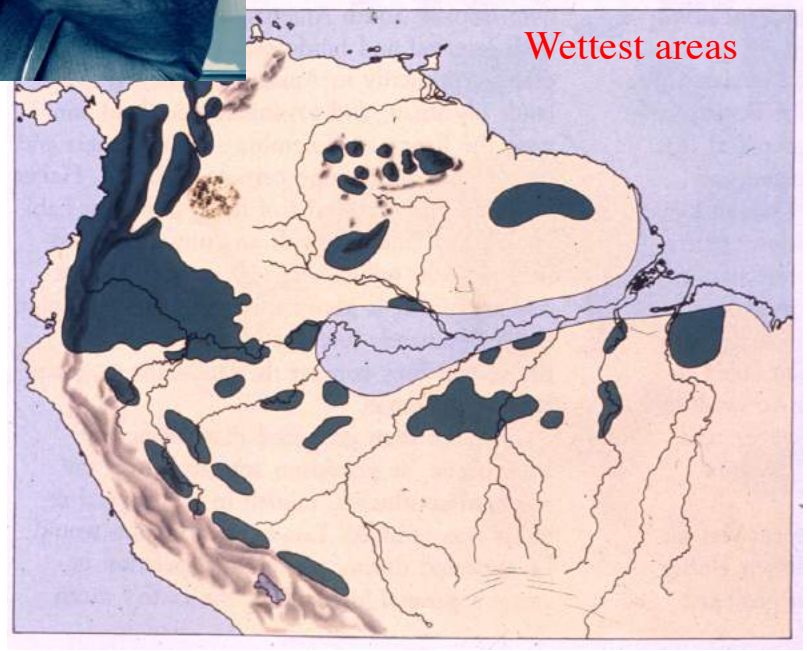
Jurgen Haffer, geologist and "birder," proposed "Refugia" hypothesis in 1969 (*Science*, July 11)

- observed that present distribution of rainfall over South America gives rise to both forested and non-forested areas

- and that areas > 1500 mm rainfall linked with present day centers of diversity and biogeographical patterns of distribution

Tropical Rainforests in the Pleistocene





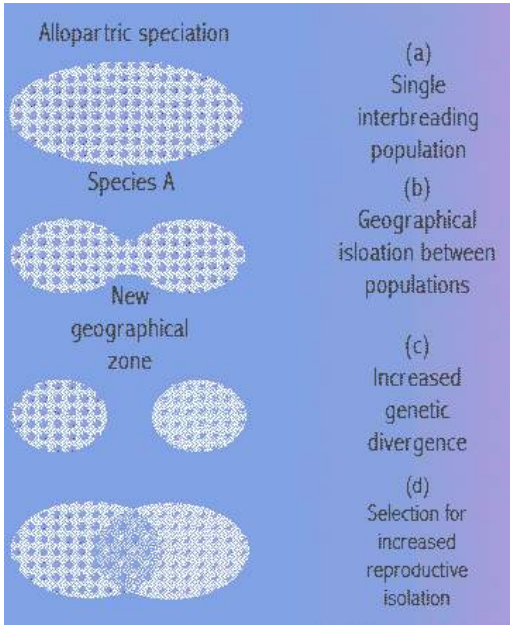
— the Refugia Hypothesis

Jurgen Haffer, geologist and "birder," proposed "Refugia" hypothesis in 1969 (*Science*, July 11)

- Hypothesis: Speciation of birds in the Amazon had been produced by cycles of expansion and contraction of forest environments during the Pleistocene

- During glacial periods, reduced temperature and humidity in the lowlands of South America left relatively small "islands" - refuges - of tropical rainforests surrounded by xeric habitats

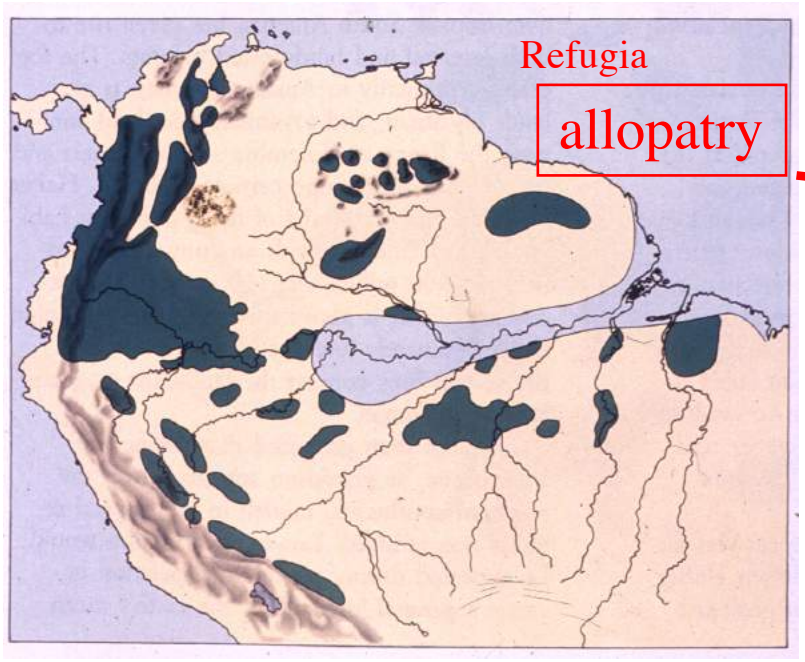
Tropical Rainforests in the Pleistocene



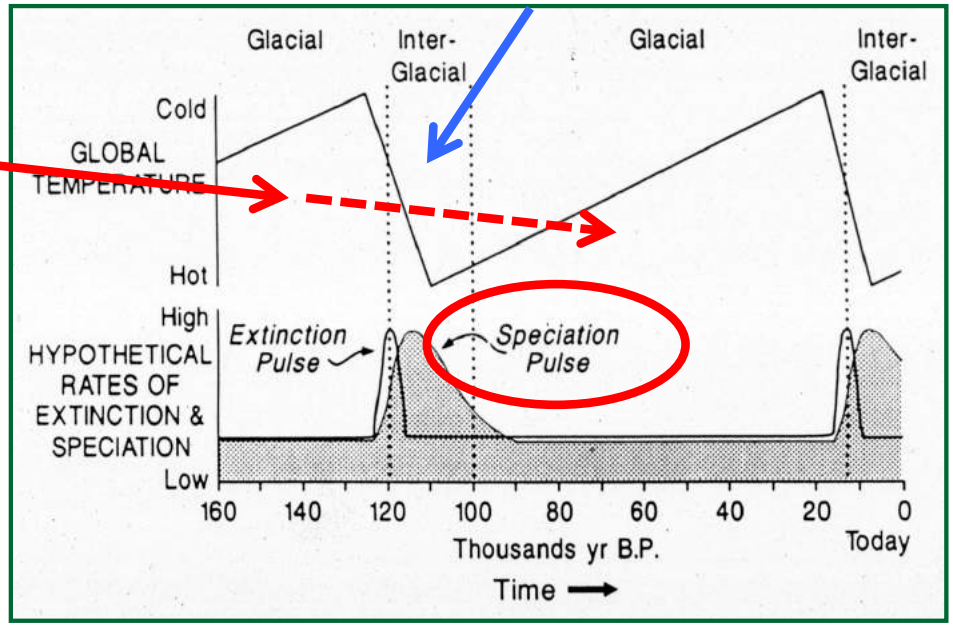
— the Refugia Hypothesis

Jurgen Haffer, geologist and "birder," proposed "Refugia" hypothesis in 1969 (*Science*, July 11)

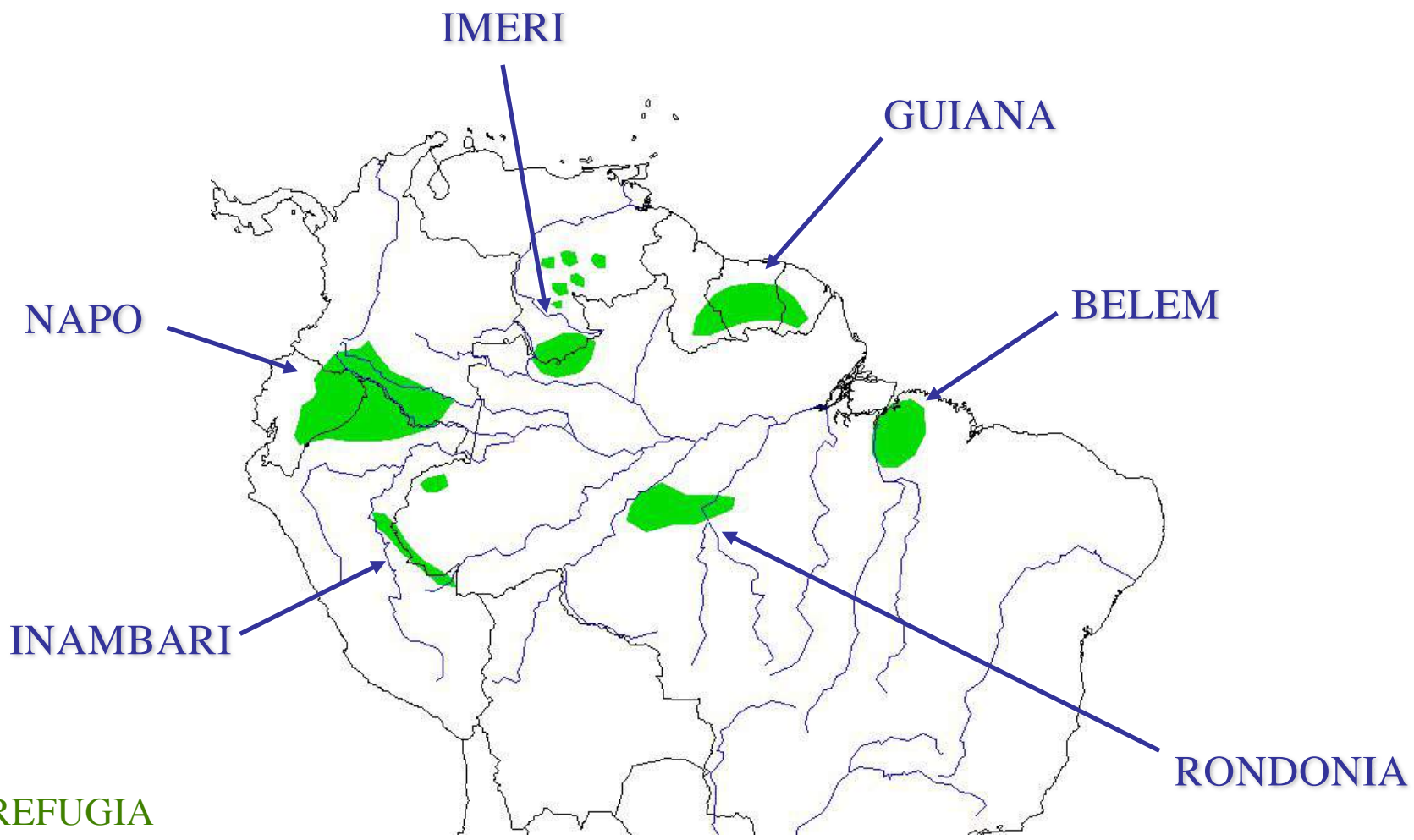
- allopatric speciation would lead to "species pump"



sympatry



Tropical Rainforests in the Pleistocene



THE REFUGIA

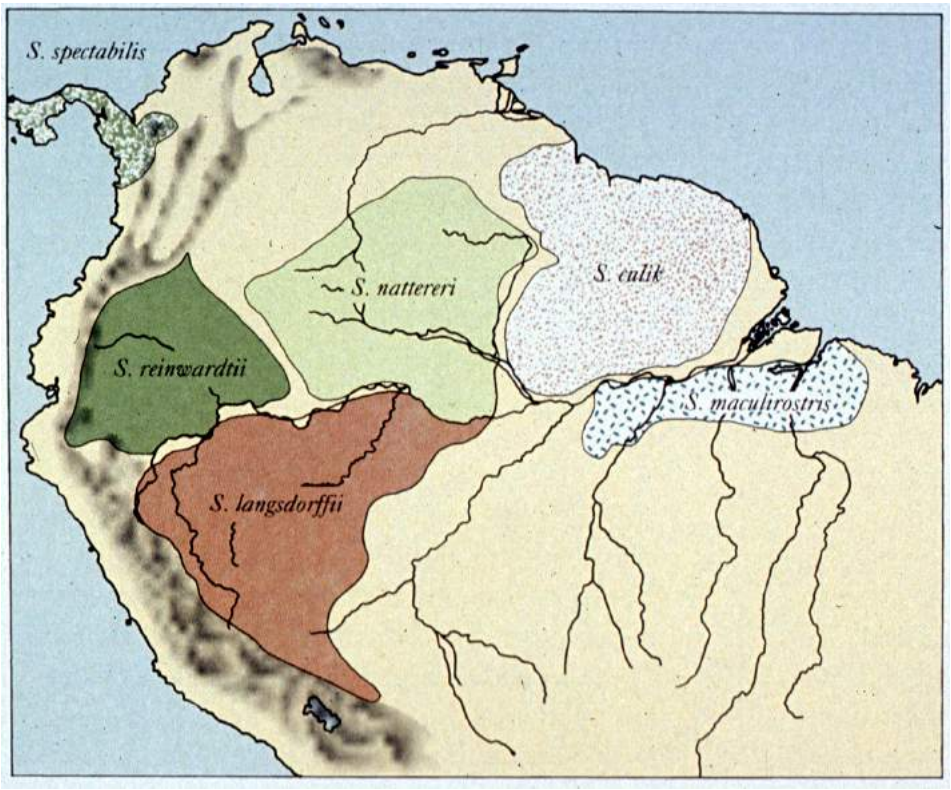
Haffer, J. 1969. Speciation in Amazonian forest birds

Tropical Rainforests in the Pleistocene

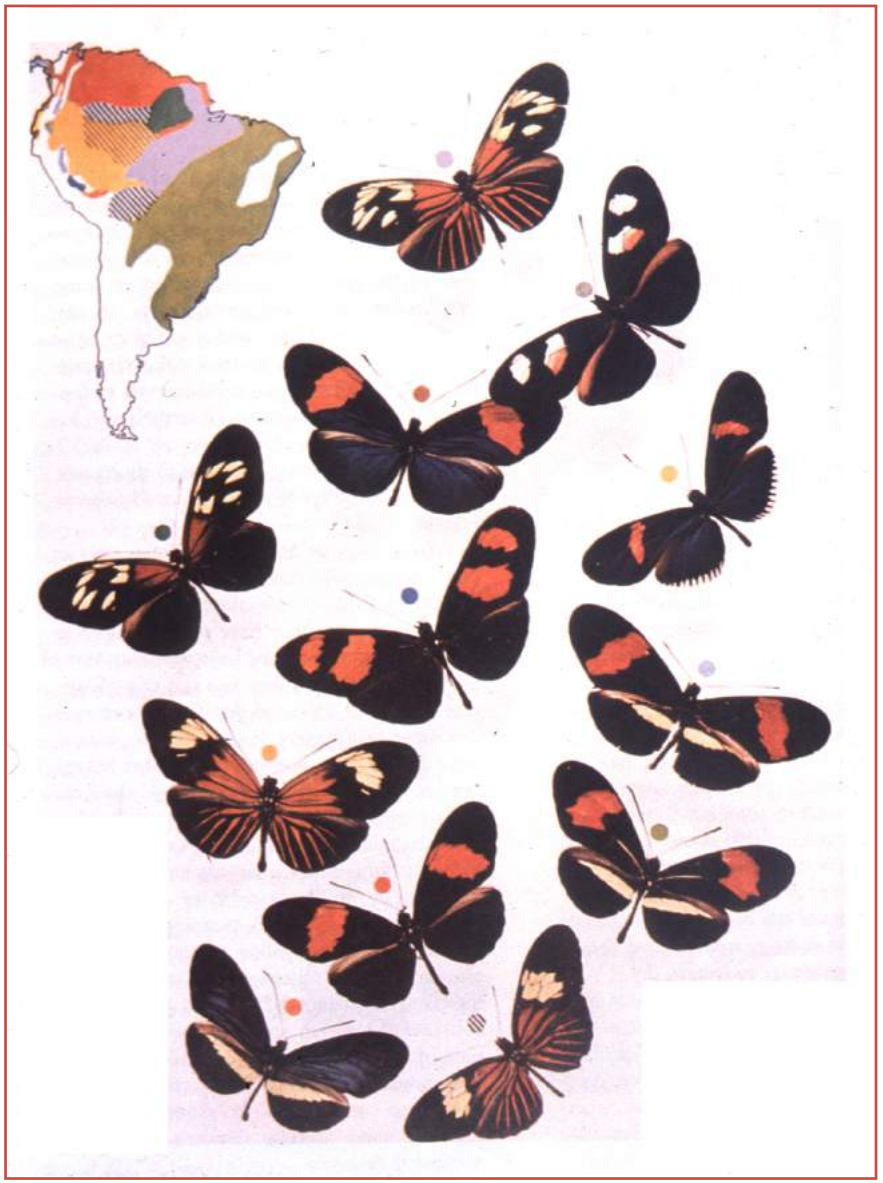
Toucan "sibling species" in Amazon basin

— the Refugia Hypothesis

- recent speciation of birds in the Amazon fits his model
- species centered over these proposed "tropical forest refugia"



Tropical Rainforests in the Pleistocene



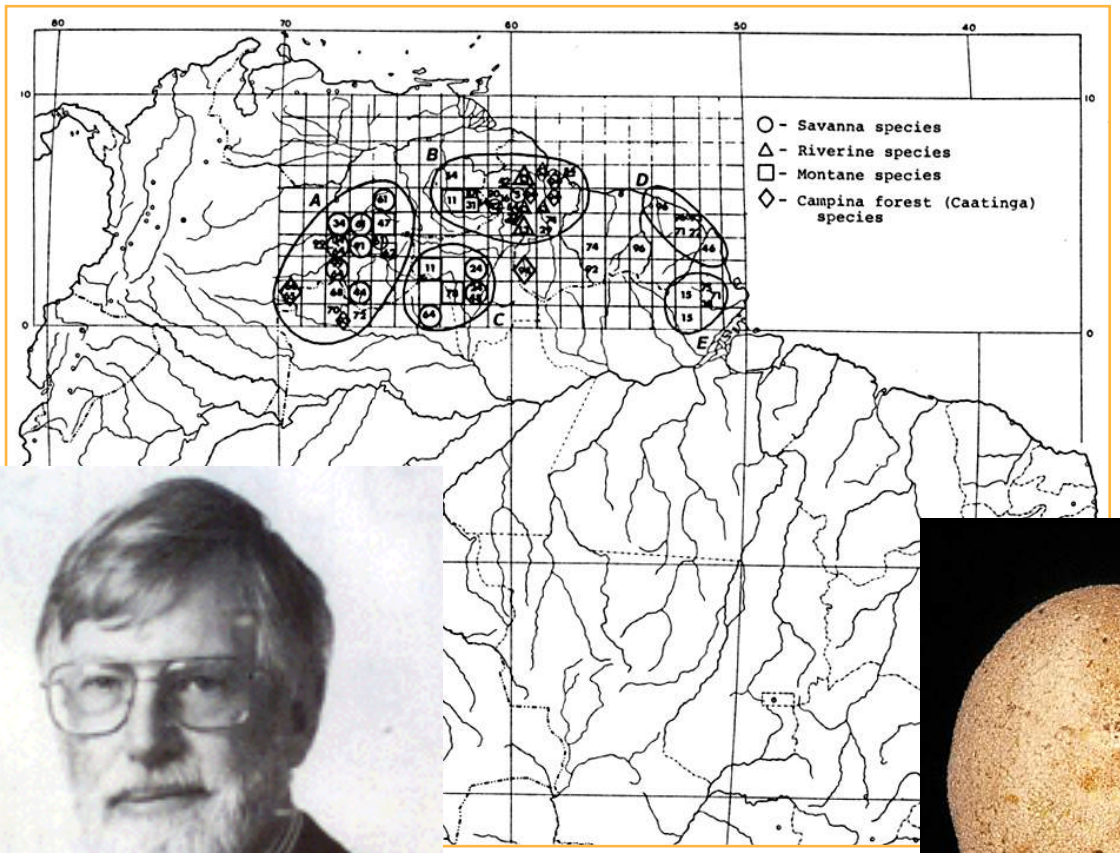
— the Refugia Hypothesis

• pictured-winged Heliconid butterflies suggested same pattern of correlation of sibling species and tropical forest refugia

Tropical Rainforests in the Pleistocene

— the Refugia Hypothesis

• Sir Ghillean Prance provided many examples of Amazonian plant taxa that supported the "tropical forest refugia" hypothesis



Distribution of Chrysobalanaceae in wet tropical forests

Tropical Rainforests in the Pleistocene

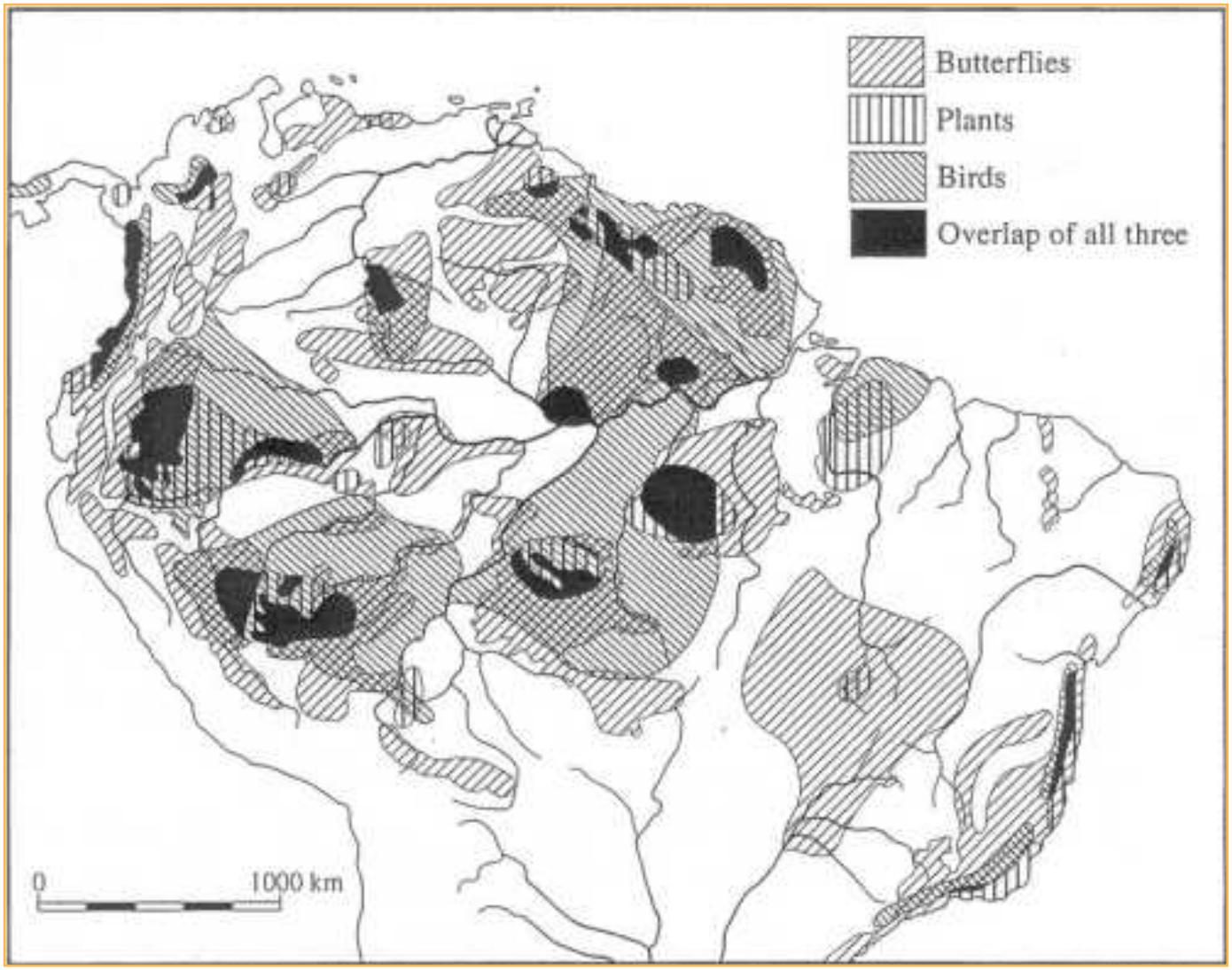
— the Refugia Hypothesis

- Sir Ghillean Prance provided many examples of Amazonian plant taxa that supported the "tropical forest refugia" hypothesis

- Prance proposed 26 refugia based on plants alone

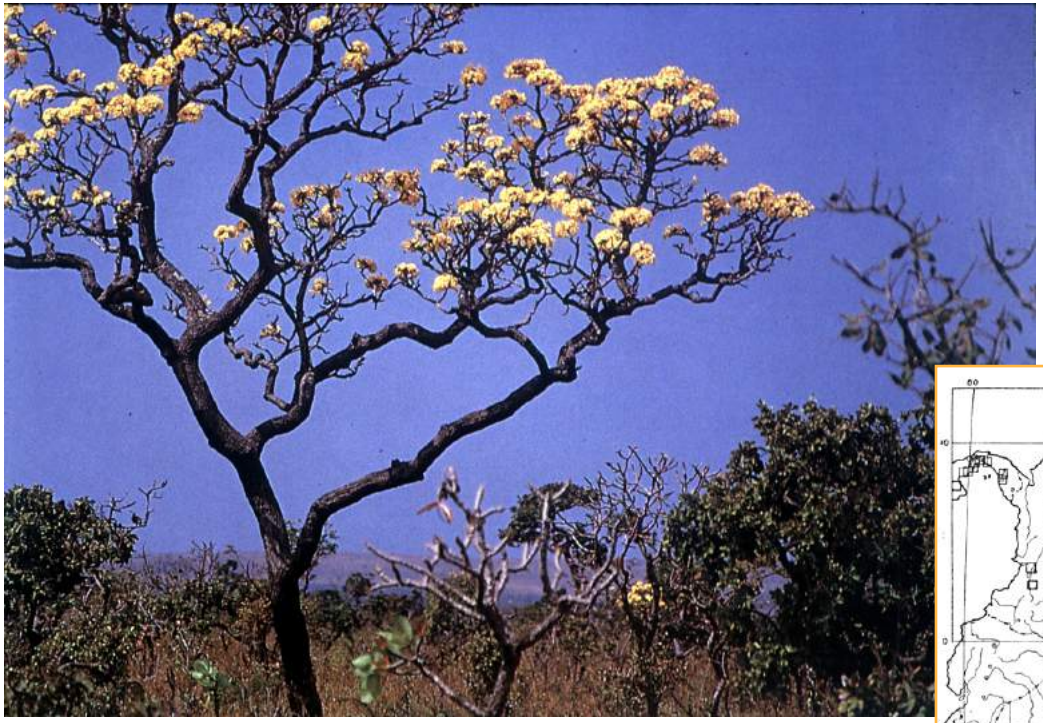
Plant "tropical forest refugia" based on centers of plant diversity are correlated with areas of wet conditions during dry periods

Tropical Rainforests in the Pleistocene



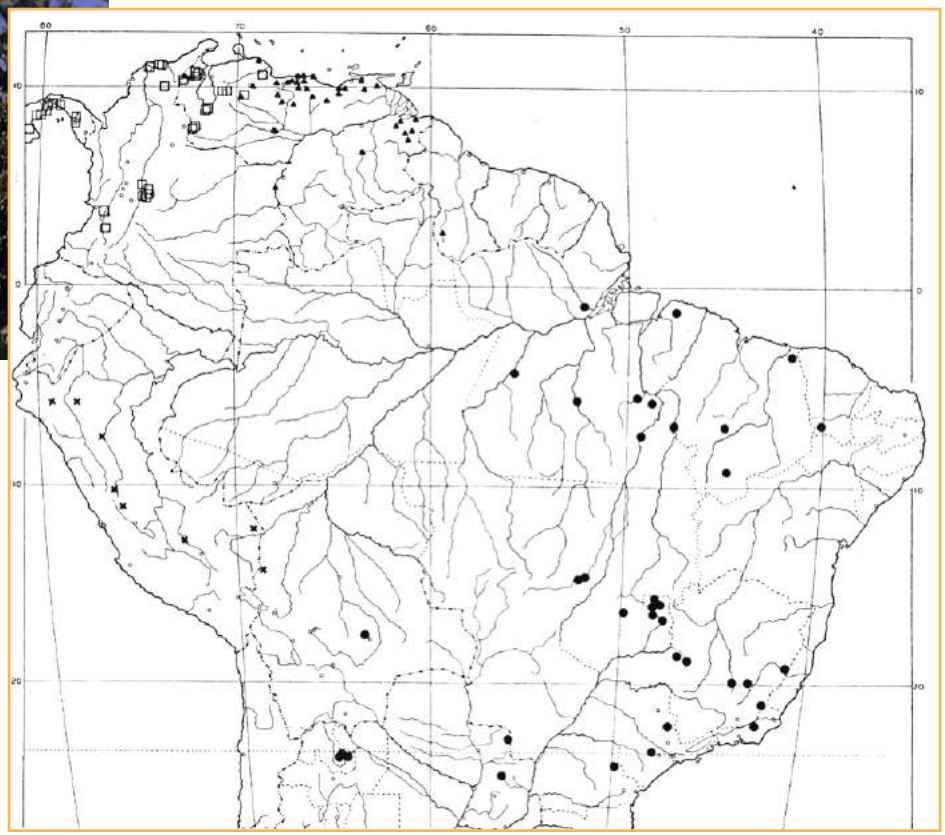
The elegance of the model was the congruent refugial maps for butterflies, frogs, lizards, and families of plants

Tropical Rainforests in the Pleistocene



Tabebuia ochracea
(Bignoniaceae)

Distribution of this savanna tree



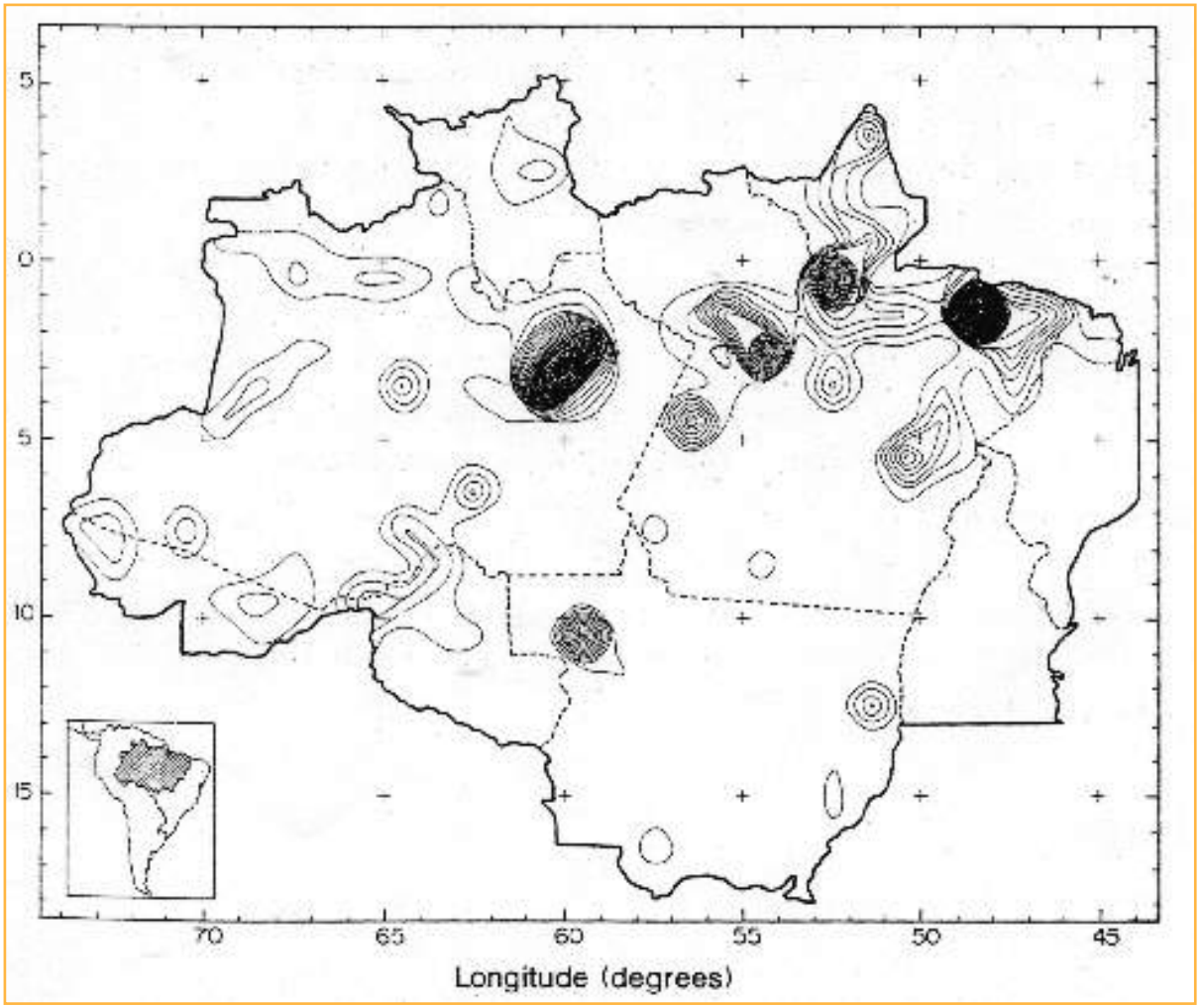
- "Reverse refugia" were also found for savanna trees like *Tabebuia*

- Savanna refugia were in areas <1500 mm rainfall

Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model

- collecting data biased for refugia areas – "museum model"

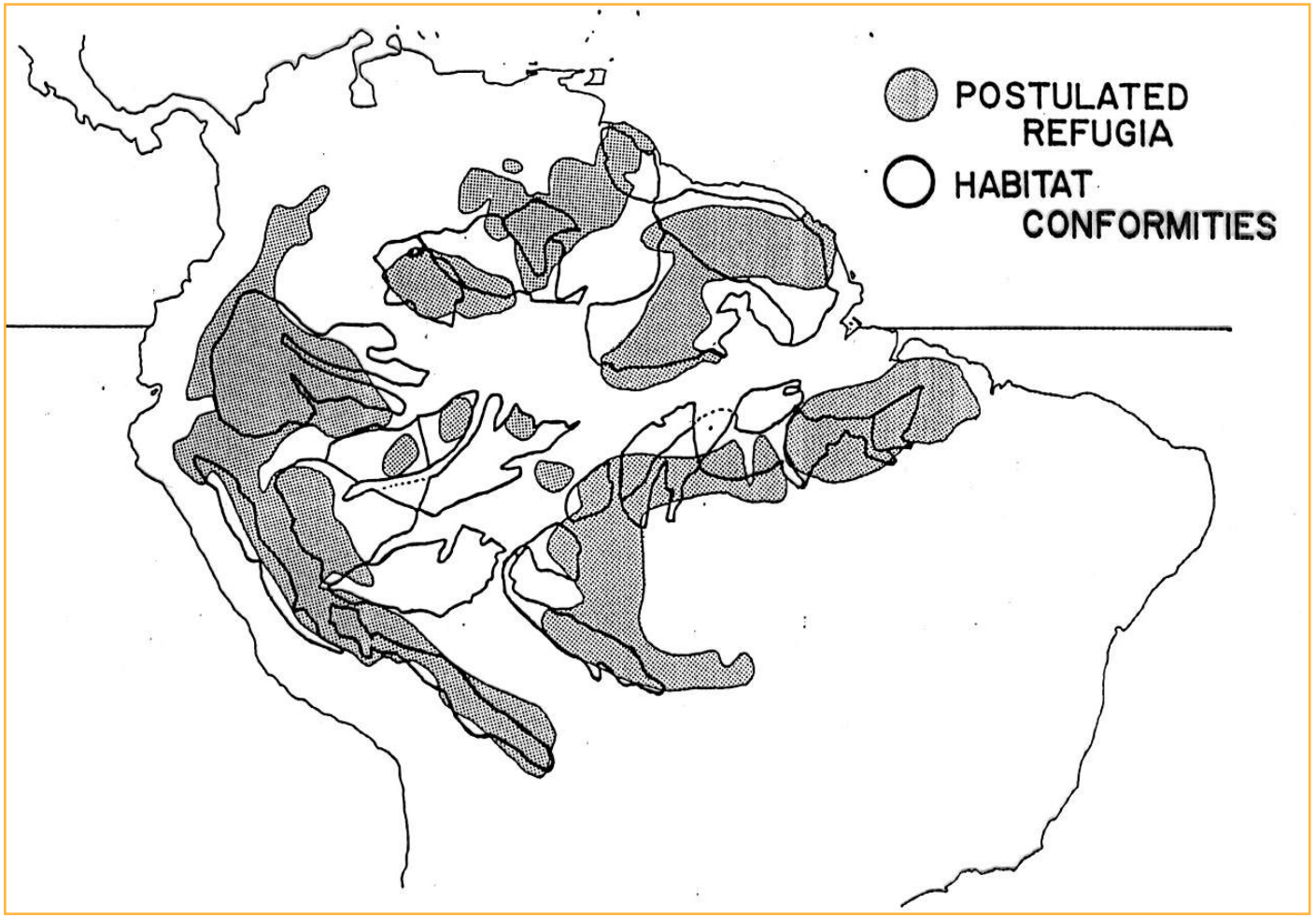


Collecting intensity of plant taxa used in the construction of refugial arguments

Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model

- ecological reasons for concentration of species in putative "refugia"
  - soil
  - local climate
  - vegetation type
  - rainfall
  - geology
  - river boundaries



Coincidence of range of major zones of habitat uniformity and postulated refugia

Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model

Palynological Evidence

Colinvaux *et al*. 1996

(One site in north-western Amazon)

"Western Amazon was forested in the Pleistocene as it is now"

Hoorn C. 1997

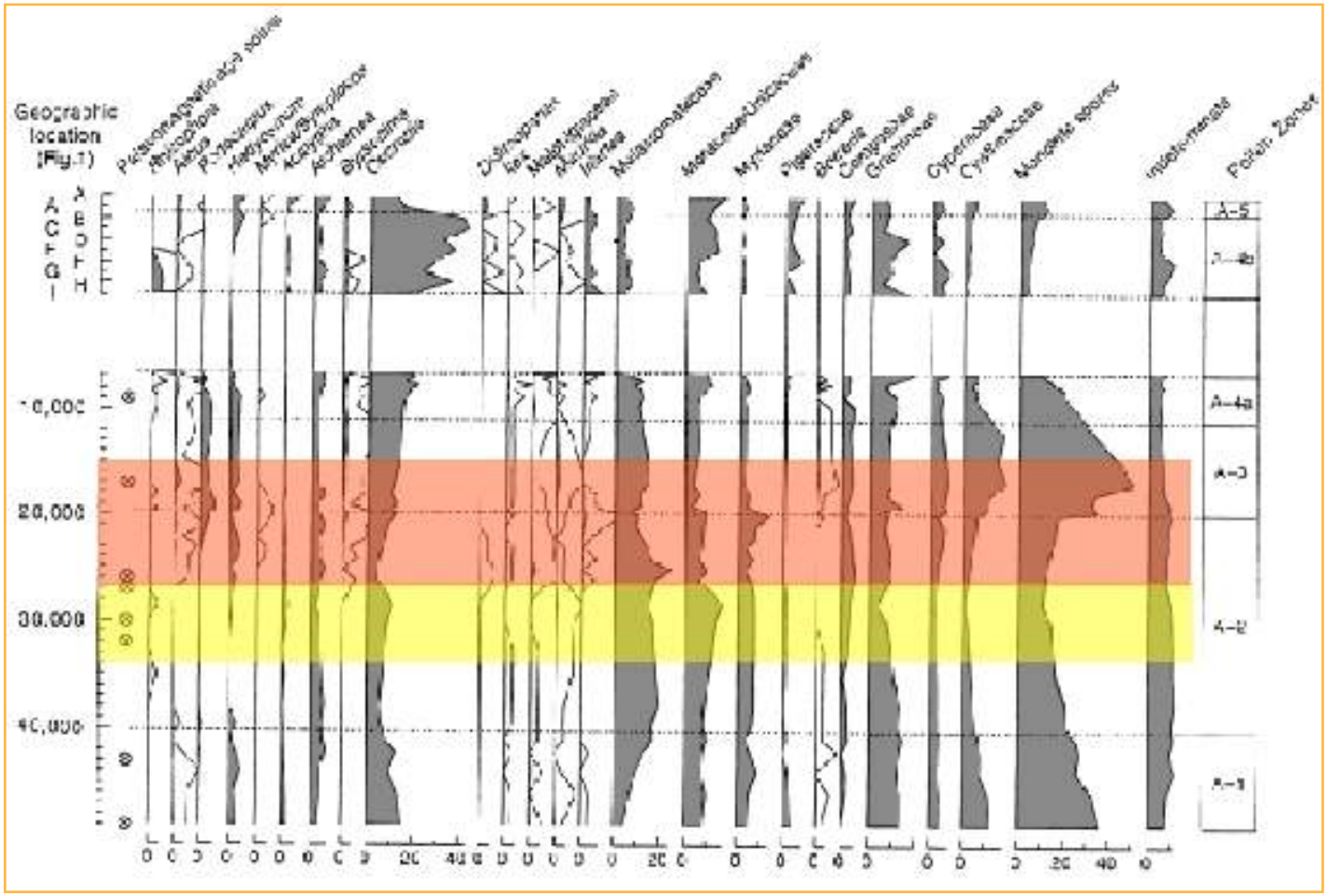
(Amazon Fan)

"Palynological data give no indication of major vegetational changes in the drainage basin" (of the Amazon)

Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model

- Sediment cores from the Amazon fan provide an insight on the past vegetation of Amazonia at the scale of that landscape and do not support the assumption that large areas of savanna replaced forest

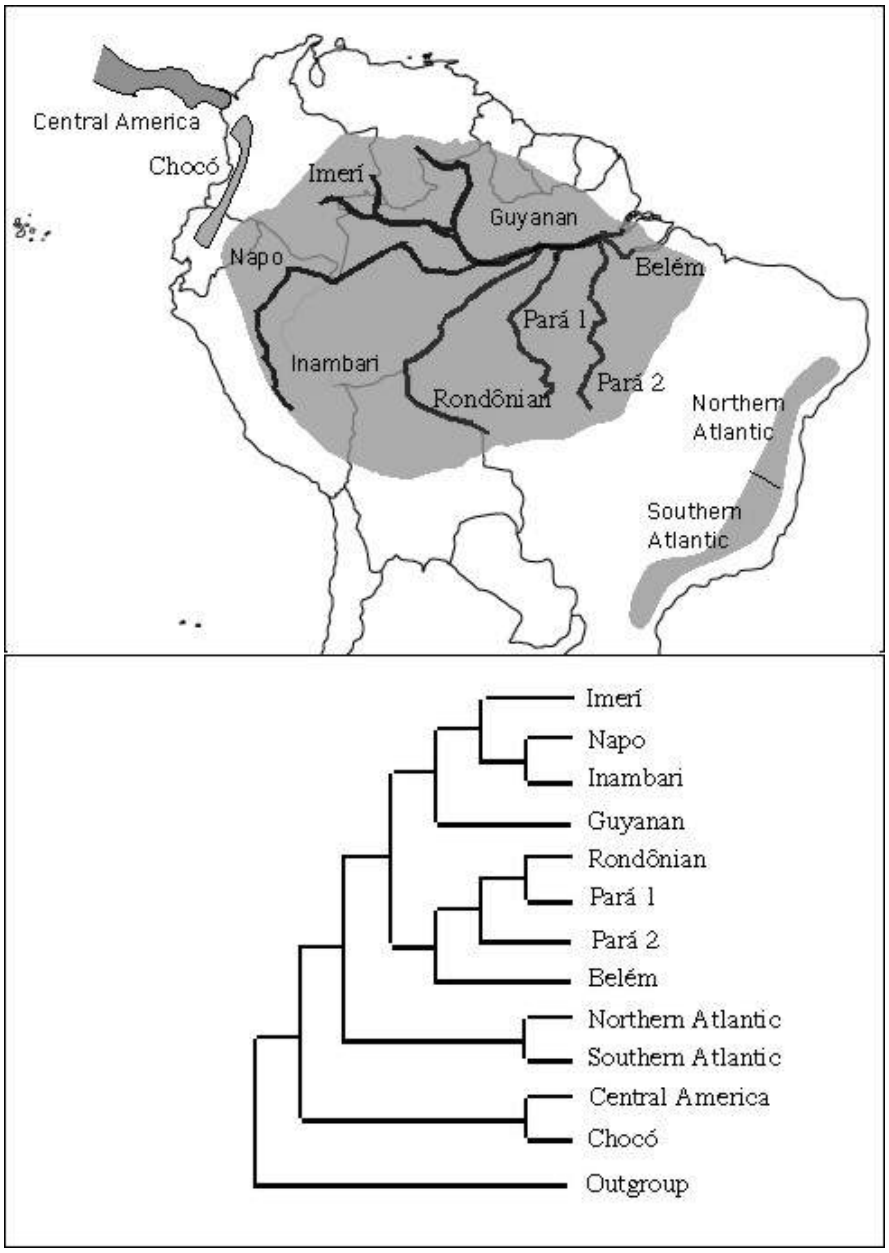


Pollen data from modern Amazonian river muds (upper panel) and from ice age deposits of the Amazon Fan

Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model

- Phylogeographic analysis of Amazonian birds based on DNA does not support Refugia model based on either proximity of refugia in area cladogram nor recency of speciation
- clocks indicate Pre-Pleistocene events!



Tropical Rainforests in the Pleistocene

Opposition to the Refugia Model — the winner?

A paradigm to be discarded: Geological and paleoecological data falsify the HAFFER & PRANCE refuge hypothesis of Amazonian speciation

Colinvaux PA, Irion G, Rasanen ME, Bush MB, de Mello JASN

Amazoniana-Limnologia et Oecologia Regionalis Systemae Fluminis Amazonas16 (3-4): 609-646 [2001]

Abstract:
All geological data from Amazonian landforms imply continuous humid weathering throughout late Tertiary and Quaternary times, with all claims for arid land processes shown to be in error. Sand dunes exist only where thick deposits of sand prevent stable vegetative cover. A ground truth survey shows that proposed dune fields in the Pantanal do Mato Grosso do not in fact exist and that dunes in Pantanal Setentrional continue to be active. All available Amazonian pollen data, without exception and including new data, imply biome stability: no pollen data suggest increased coverage of savanna in glacial times, claims to the contrary being demonstrably in error. Amazonian climate is not monolithic, with secular climatic changes across the basin not in phase. New evidence shows that vegetation response to lowered temperatures, lowered CO, and fluctuating dry seasons produced by MILANKOVITCH forcing resulted only in population changes within plant communities without biome replacements. Diversity between habitats within the forest provides vicariance for alternative evolutionary models. The "aridity with refuges paradigm" now impedes Amazonian research and should be discarded.

Paul Colinvaux

Amazon Expeditions: My Quest for the Ice-Age Equator

Yale Univ Press, 2008

Tropical Rainforests in the Pleistocene

Gracious losers?

Climatic forcing of evolution in Amazonia during the Cenozoic: On the refuge theory of biotic differentiation

Haffer J, Prance GT

Amazoniana-Limnologia et Oecologia Regionalis Systemae Fluminis Amazonas16 (3-4): 579-605 [2001]

Abstract:

The refuge theory postulates that extensive patches of humid rainforests persisted during dry periods of the Tertiary and Quaternary, especially near areas of surface relief in peripheral portions of Amazonia, where many extant species and subspecies of plants and animals probably originated. The humid 'refugia' may have been separated by various types of savanna and dry forests as well as other intermediate vegetation types of seasonally dry climates. The number and size of refugia during different dry periods remain unknown. Biogeographic evidence for the former existence of forest refugia include areas of endemism and sharply defined contact zones between species and subspecies of Amazonian forest birds and other animals which represent zones of conspicuous biogeographic discontinuity in a continuous forest environment.

Alternative models of barrier formation in Amazonia leading to allopatric speciation include the river hypothesis, river-refuge hypothesis, canopy-density hypothesis, disturbance-vicariance hypothesis, museum hypothesis and various paleogeography hypotheses, some aspects of which may be applicable to certain periods in the evolution of the biota.

Tropical Rainforests in the Pleistocene

Good read!

[see lecture webpage for pdf]

Refuting Refugia?

Sandra Knapp and James Mallet

According to Charles Darwin, the origin of species was "the mystery of mysteries" (*1*). If so, then the Neotropical (Central and South American) forests, which harbor more plant species than the tropics of Asia and Africa combined (*2*), are the most mysterious of all. On page 122 of this issue, Wilf *et al.* (*3*) show that this massive diversification was active by the early Eocene, 52 million years ago. High plant species diversity in the Neotropics is clearly ancient.

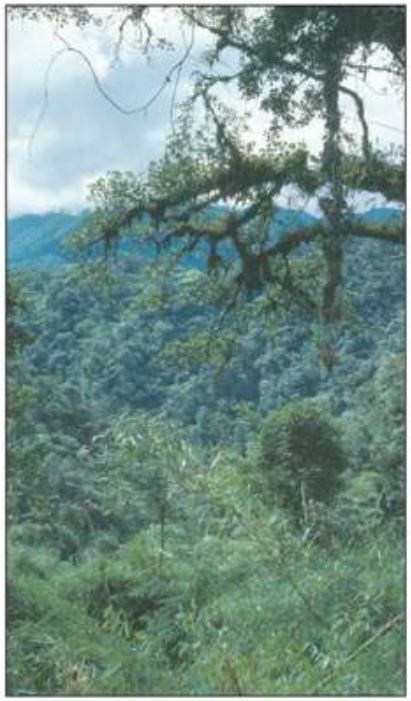
Many biologists in the mid-20th century assumed that speciation occurred only in geographically separated populations. South America, with its continuous belt of rainforest and superfluity of species, might seem to contradict the idea of such "allopatric" speciation. In the 1960s, biologists applied the temperate-zone model of ice-age refugia to explain this enigma, rather than reevaluating the central role of allopatry in speciation theory (*4*).

It had long been recognized that animal and plant ranges must have contracted while ice-sheets spread over the Northern Hemisphere. General cooling, sea-level reductions, and the locking up of much of the planet's water in greatly extended polar ice caps are thought to have caused extensive aridity worldwide. Fossil sand dunes, pollen samples from sediment in high-elevation lake-beds, and "stone lines" (strata suggesting periods of high erosion expected during arid periods) all suggested that arid climates may have prevailed in the Neotropics during much of the Pleistocene (1.64 million to 10,000 years ago).

Modern geographic patterns of differentiation and speciation across the Neotropical forest also hinted at past allopatry. If, during dry periods, rainforest became restricted to refuges scattered across tropical America, the allopatry deemed necessary for speciation could have occurred in waves throughout the Pleistocene. This "refugium theory" was proposed to explain both geographic variation within species and overall high species diversity (*4*).

From the 1970s, the Neotropical refugium model accumulated many critics. If natural selection drives speciation, then gene flow will not affect diversification in areas that are much larger than the per-generation dispersal range of individuals; thus, "parapatric" speciation (geographic speciation while populations remain in contact, or "isolation by distance") is as plausible as allopatric speciation (*5*). Furthermore, the geographic ranges of Amazonian birds may require no historical refugium explanation because random placement produces similar distributions (*6*). An analysis

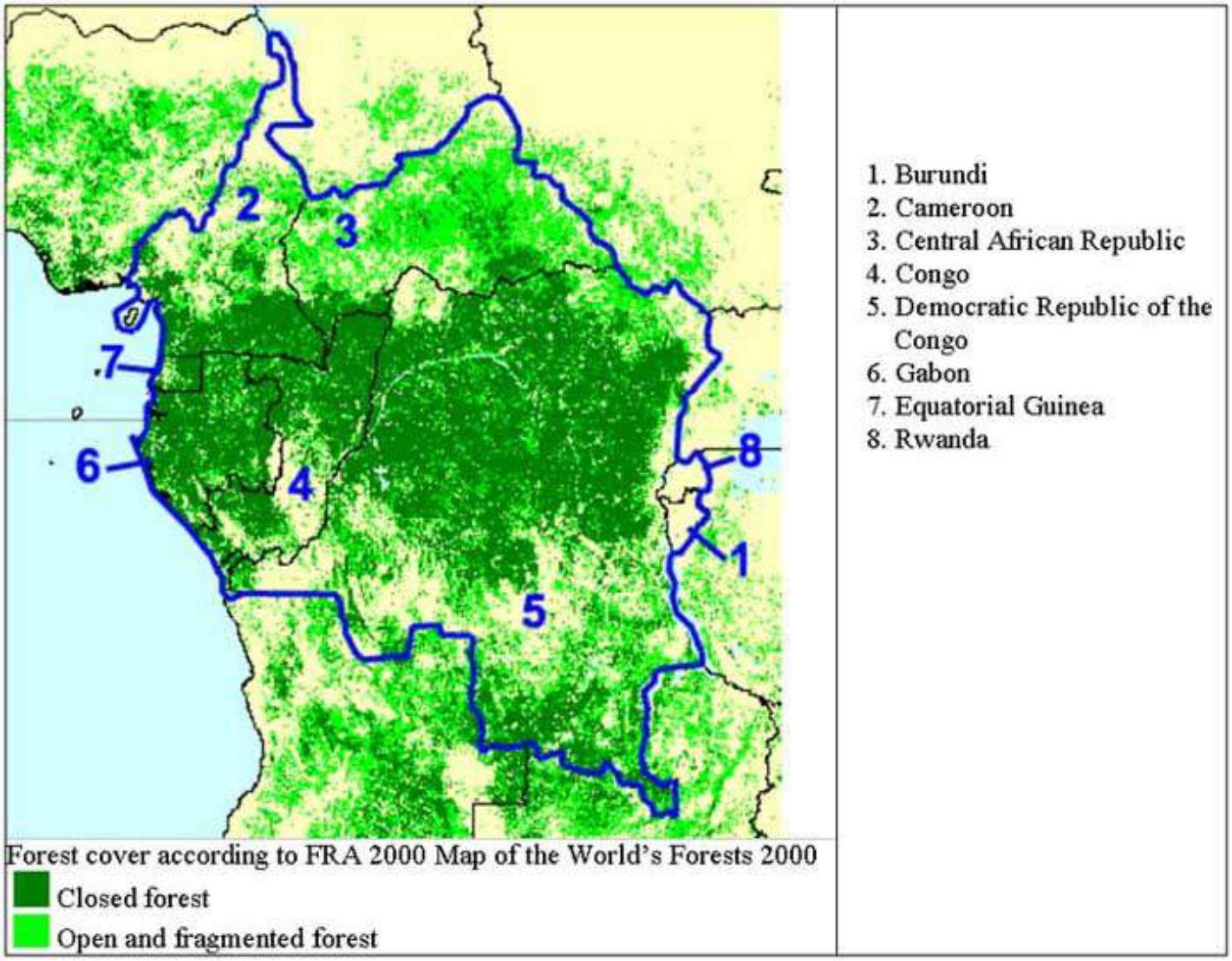
S. Knapp is in the Department of Botany, The Natural History Museum, London SW7 5BD, UK. E-mail: s.knapp@nhm.ac.uk J. Mallet is in the Department of Biology, University College London, London NW1 2HE, UK. E-mail: j.mallet@ucl.ac.uk



Where do all the species come from? The diversity of the vast Neotropical rainforests has spawned numerous theories of origin, mostly based on climate change during the Pleistocene.

Tropical Rainforests in the Pleistocene

- But the debate does NOT go away – especially in African tropics!



Tropical Rainforests in the Pleistocene

MOLECULAR ECOLOGY

Molecular Ecology (2011) **20**, 131–142 doi: 10.1111/j.1365-294X.2010.04919.x

Insights into the biogeographical history of the Lower Guinea Forest Domain: evidence for the role of refugia in the intraspecific differentiation of *Aucoumea klaineana*

CÉLINE BORN,*† NADIR ALVAREZ,‡ DOYLE McKEY,† SIMON OSSARI,* ELISABETH JEAN WICKINGS,* MARTINE HOSSAERT-McKEY† and MARIE-HÉLÈNE CHEVALLIER†§

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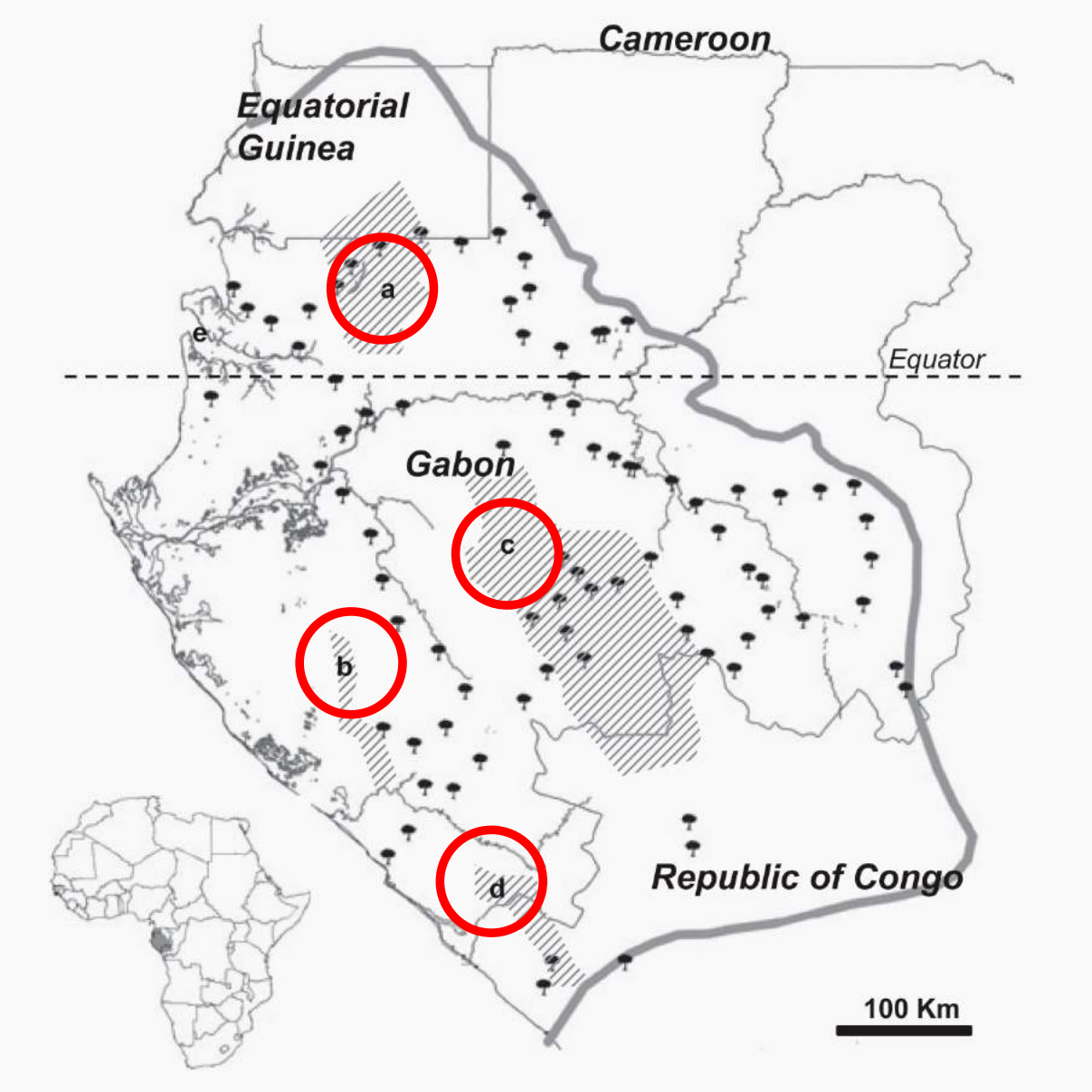

- sampling across the region including 4 postulated upland forest refugia

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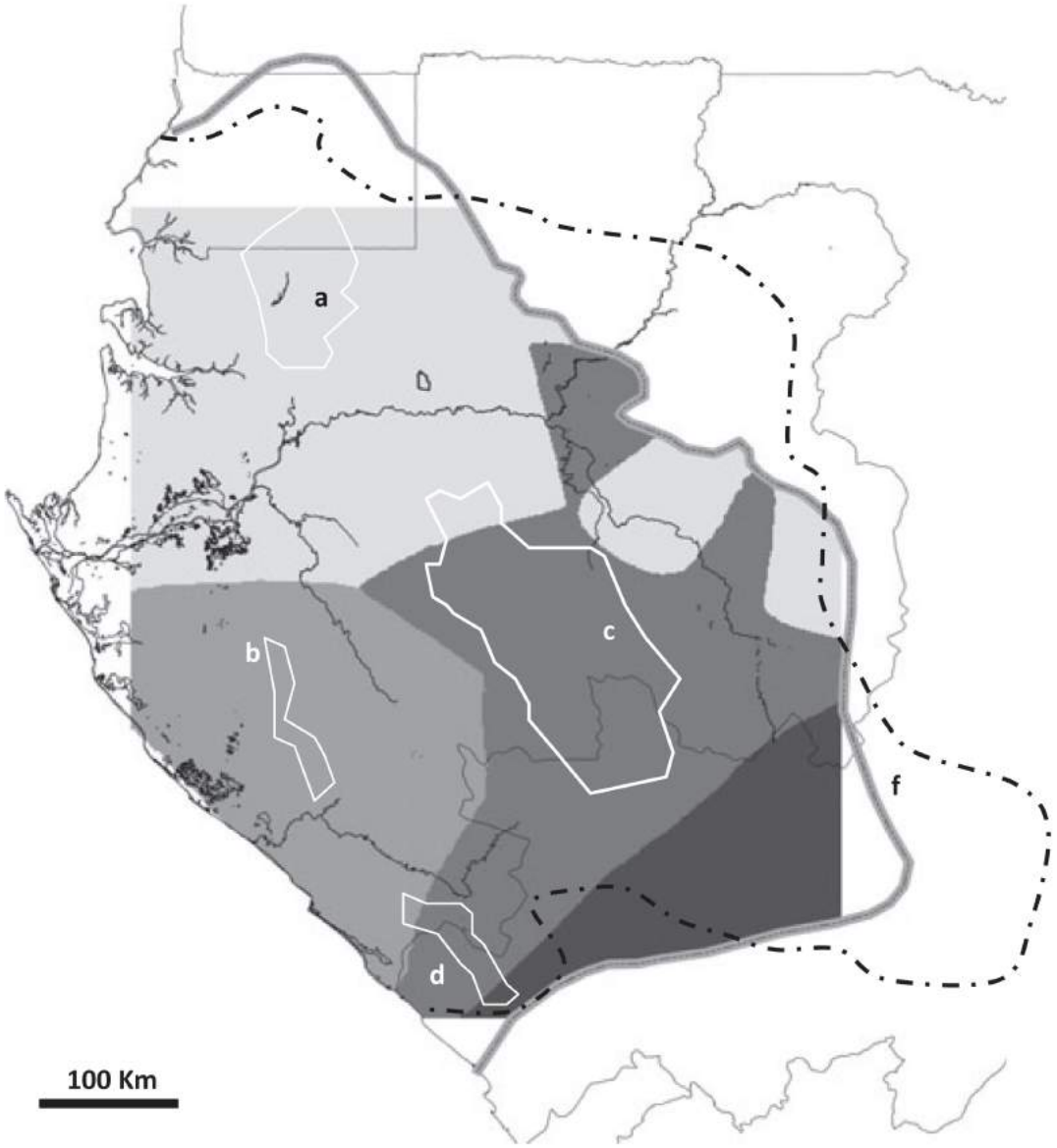

- Bayesian clustering using 10 microsatellite loci identify 4 genetic groups

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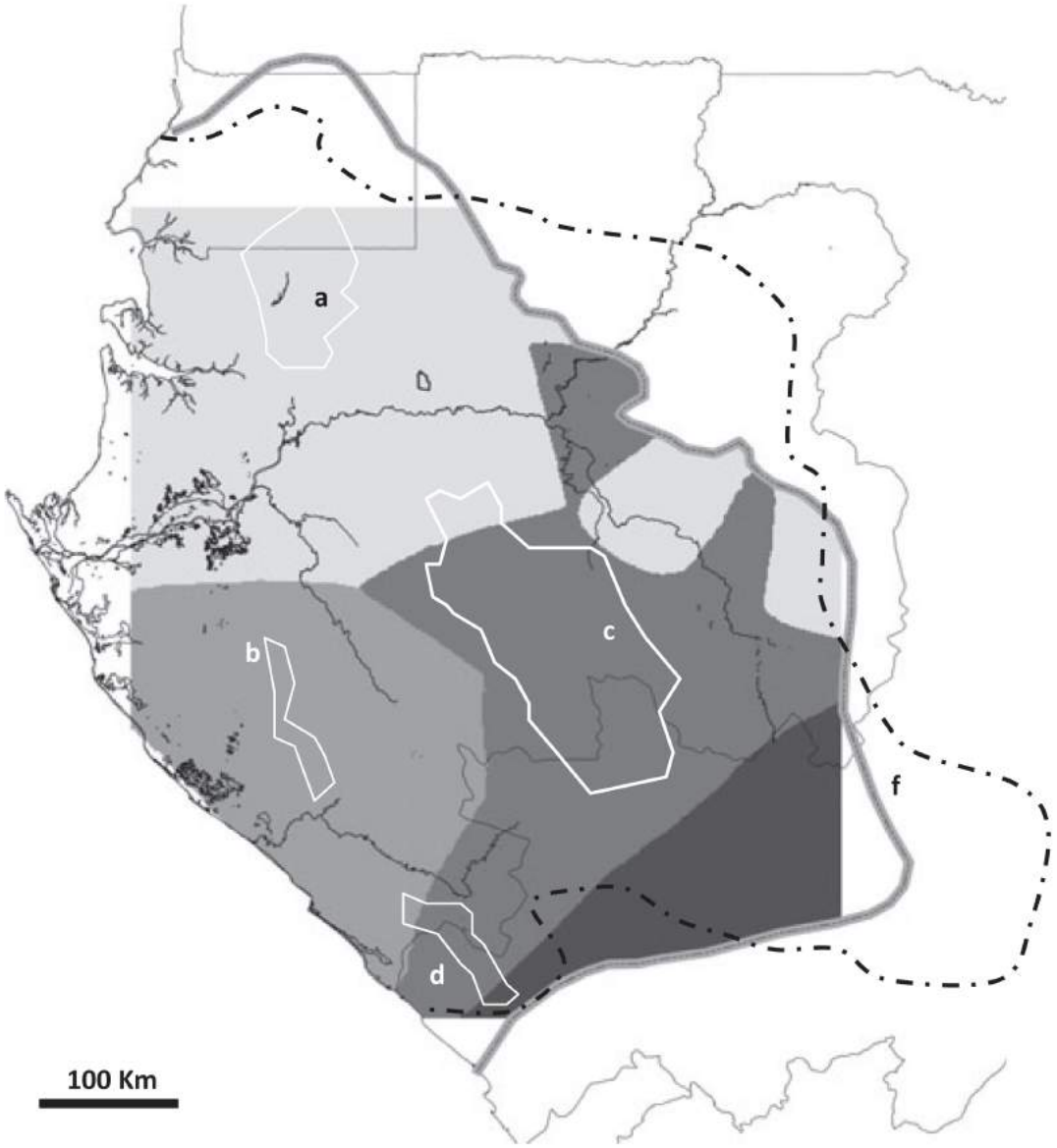


- Bayesian clustering using 10 microsatellite loci identify 4 genetic groups

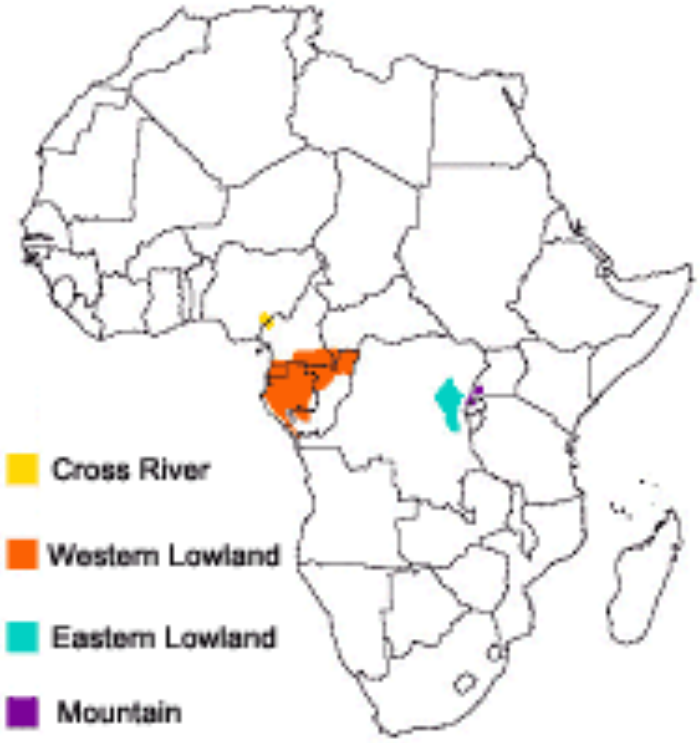
- Distributions match that of forest refugia postulated from patterns of species richness and endemism

- Results cannot be explained on the basis of present-day ecological conditions

Tropical Rainforests in the Pleistocene

The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa

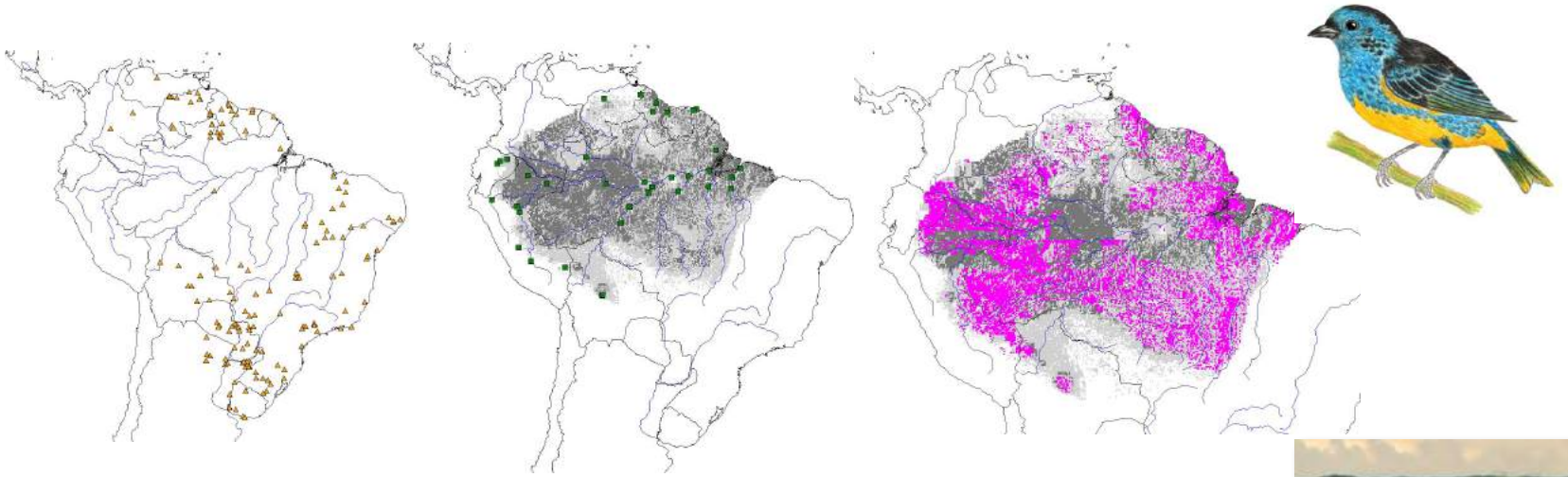
Nicola M. Anthony*†‡, Mireille Johnson-Bawe§, Kathryn Jeffery†¶, Stephen L. Clifford§, Kate A. Abernethy§¶, Caroline E. Tutin§¶, Sally A. Lahm‖, Lee J. T. White**, John F. Utley*, E. Jean Wickings§, and Michael W. Bruford†



- Similar study done with mtDNA and nuclear DNA on 4 subspecies of African gorillas

Tropical Rainforests in the Pleistocene

New biogeographic tests — Pleistocene history of Amazonian birds
as reconstructed by Ecological Niche Modeling

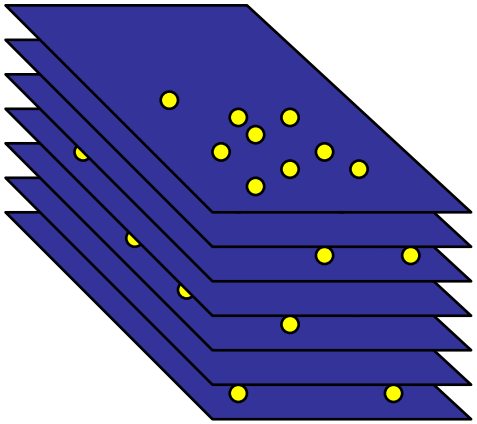


Elisa Bonaccorso

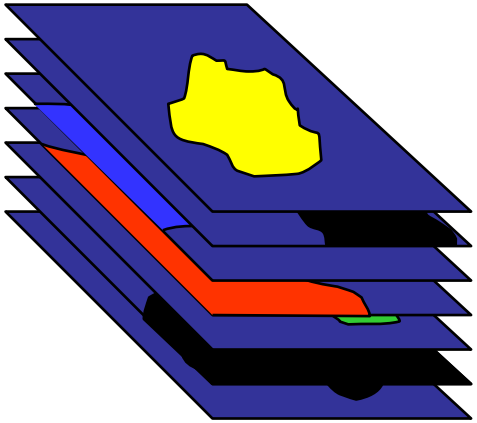
The University of Kansas &
Universidad Tecnológica Indoamérica –
Quito, Ecuador

Ecological Niche Modeling: GARP (MaxEnt now used)

Collection locality data

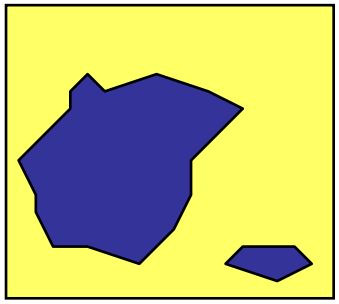


Ecological data

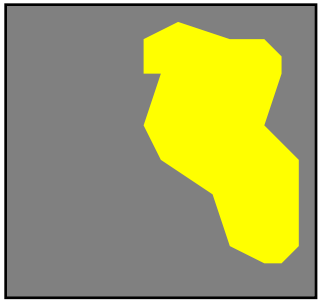


GARP

Genetic Algorithm
of Rule-set
Prediction



Distributional
prediction in the present

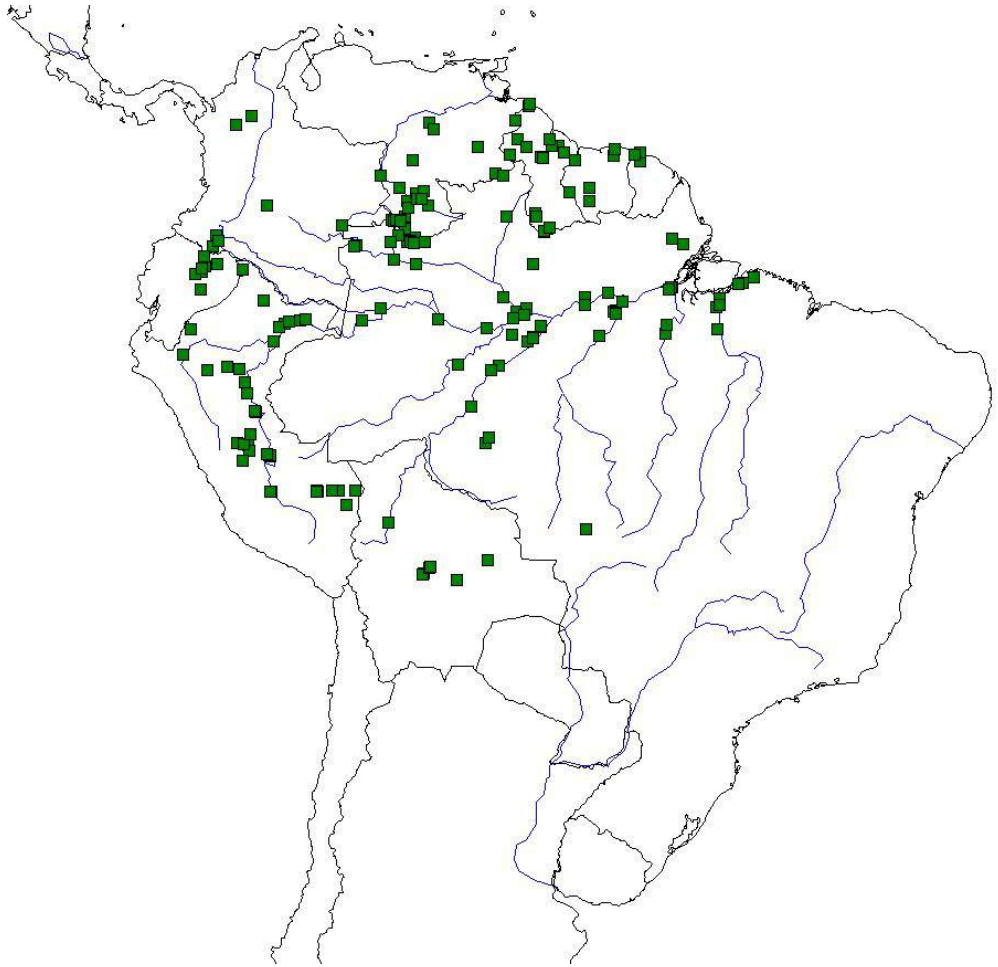


Projection to past scenario

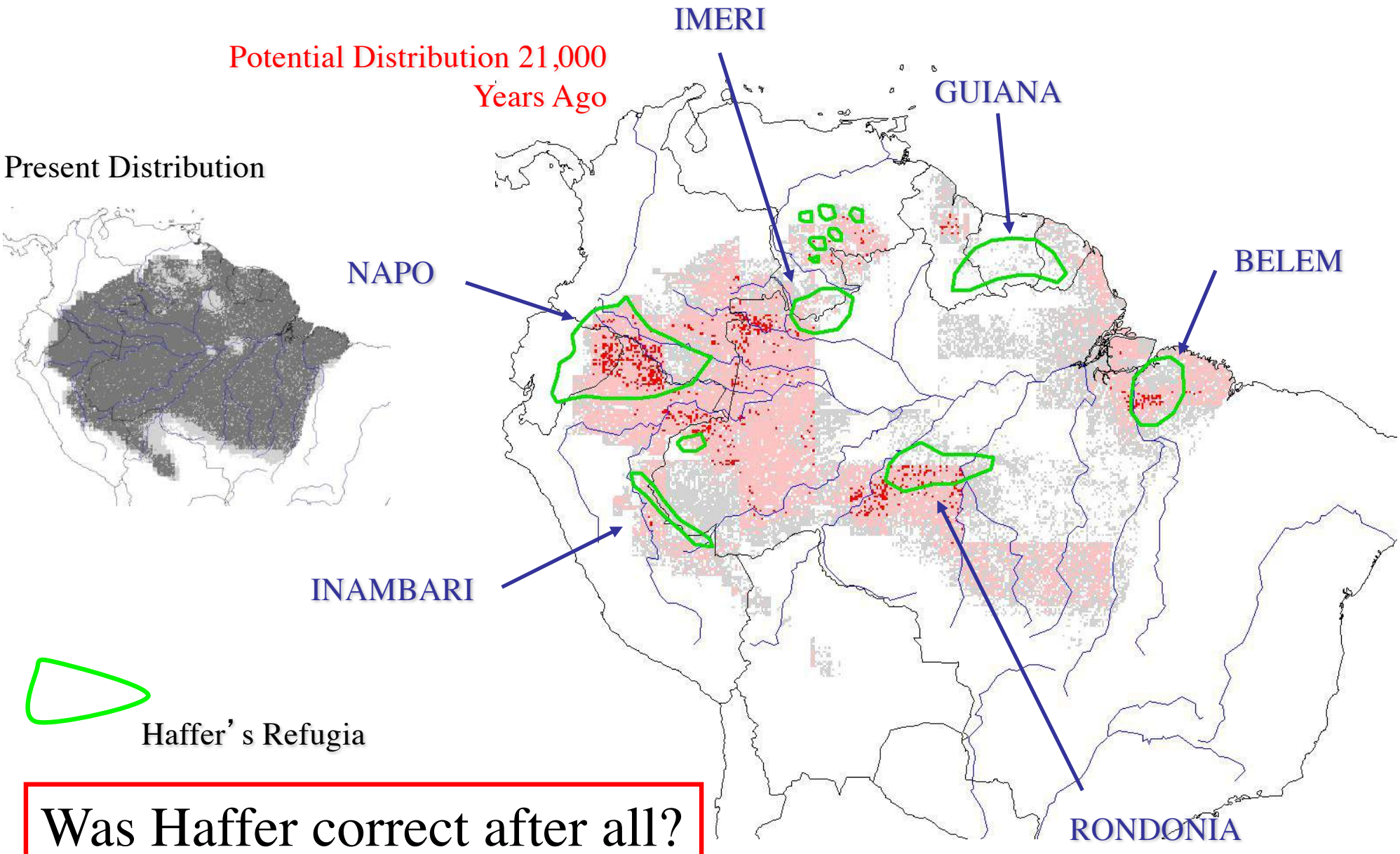
Data Set – rainfall, temperature, elevation

Forest species

Campephilus rubricollis
Formicarius colma
Phylidor pyrrhodes
Automolus infuscatus
Pipra coronata
Tangara mexicana



Forest: All Species



Was Haffer correct after all?