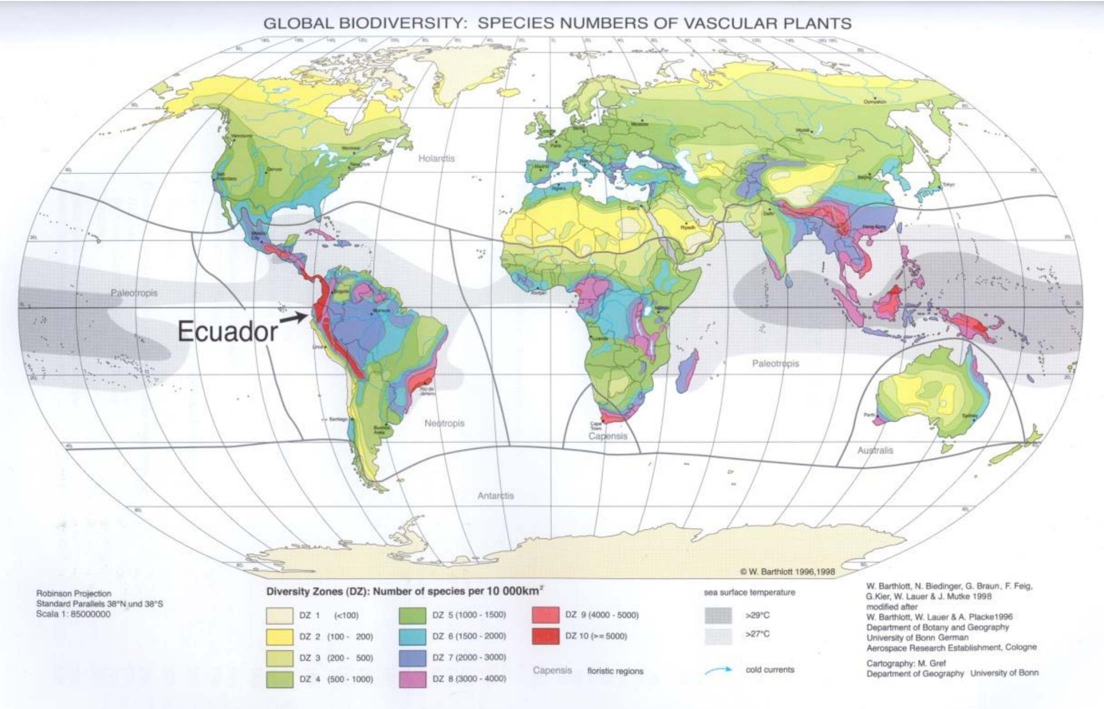
Breve história da Vegetação Neotropical

Região Neotropical:

- abrange a maior parte da América do Sul, além da América Central e sul do México.

- mais de um terço da diversidade mundial de plantas vasculares

- estimativas apontam a Região Neotropical contendo mais espécies que as floras da África e Australásia juntas.



FITODIVERSIDAD DEL MUNDO

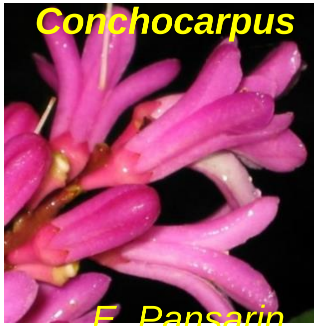
Se observa la distribución de las plantas. Lo oscuro presenta la mayor biodiversidad, como es el caso del Ecuador. Mapa del Instituto Botánico de la Universidad de Bonn "Systematik y Biodiversitat" del Profesor Barthlott.

1. Riqueza florística e diversidade de biomas.

2. Padrões espaciais e causas da diversidade específica neotropical:


Polygala

F.P. Costa


Conchocarpus

E. Pansarin

a. História da biota: 4 grandes momentos

b. Principais eventos da formação dos principais domínios fitogeográficos brasileiros

c. Padrões espaciais e processos de diversificação:

- análise de padrões espaciais observados em grupos selecionados de angiospermas; modelos explicativos

- avanços recentes: filogenias robustas; análises biogeográficas espaço-temporais.

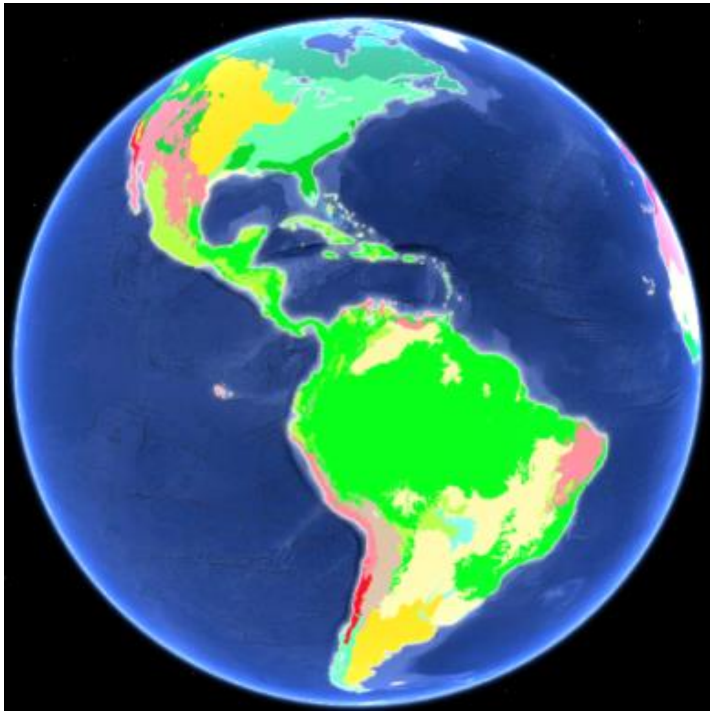

Declieuxia

G. Antar

Região NEOTROPICAL

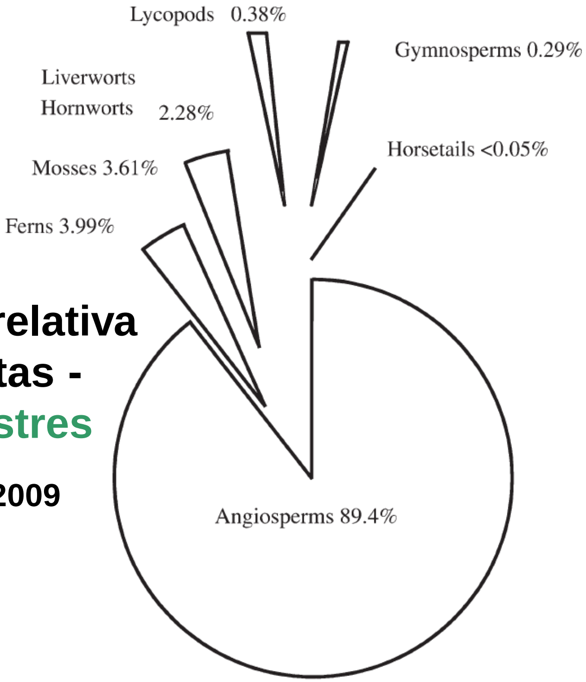
ca. 100.000 especies de plantas com sementes:
ca. 37% das espécies conhecidas

Antonelli & Sanmartín 2011

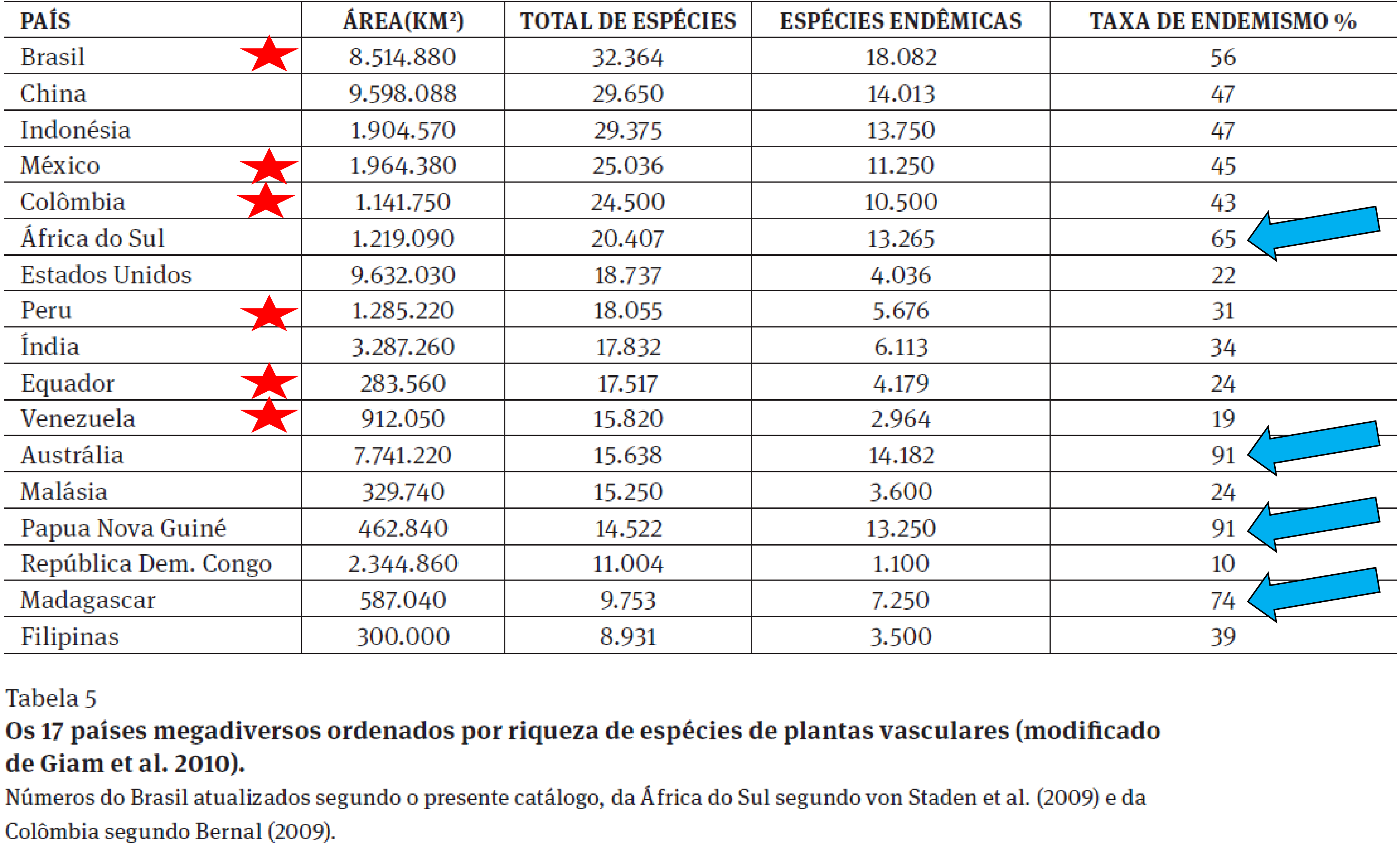


Diversidade relativa das Embriófitas - plantas terrestres

Crepet & Niklas 2009



★neotropical



PAÍS	ÁREA(KM²)	TOTAL DE ESPÉCIES	ESPÉCIES ENDÊMICAS	TAXA DE ENDEMISMO %
Brasil ★	8.514.880	32.364	18.082	56
China	9.598.088	29.650	14.013	47
Indonésia	1.904.570	29.375	13.750	47
México ★	1.964.380	25.036	11.250	45
Colômbia ★	1.141.750	24.500	10.500	43
África do Sul	1.219.090	20.407	13.265	65
Estados Unidos	9.632.030	18.737	4.036	22
Peru ★	1.285.220	18.055	5.676	31
Índia	3.287.260	17.832	6.113	34
Equador ★	283.560	17.517	4.179	24
Venezuela ★	912.050	15.820	2.964	19
Austrália	7.741.220	15.638	14.182	91
Malásia	329.740	15.250	3.600	24
Papua Nova Guiné	462.840	14.522	13.250	91
República Dem. Congo	2.344.860	11.004	1.100	10
Madagascar	587.040	9.753	7.250	74
Filipinas	300.000	8.931	3.500	39

Tabela 5

Os 17 países megadiversos ordenados por riqueza de espécies de plantas vasculares (modificado de Giam et al. 2010).

Números do Brasil atualizados segundo o presente catálogo, da África do Sul segundo von Staden et al. (2009) e da Colômbia segundo Bernal (2009).

Forzza *et al.* 2010

Ulloa-Ulloa et al. 2017: Riqueza florística nas Américas

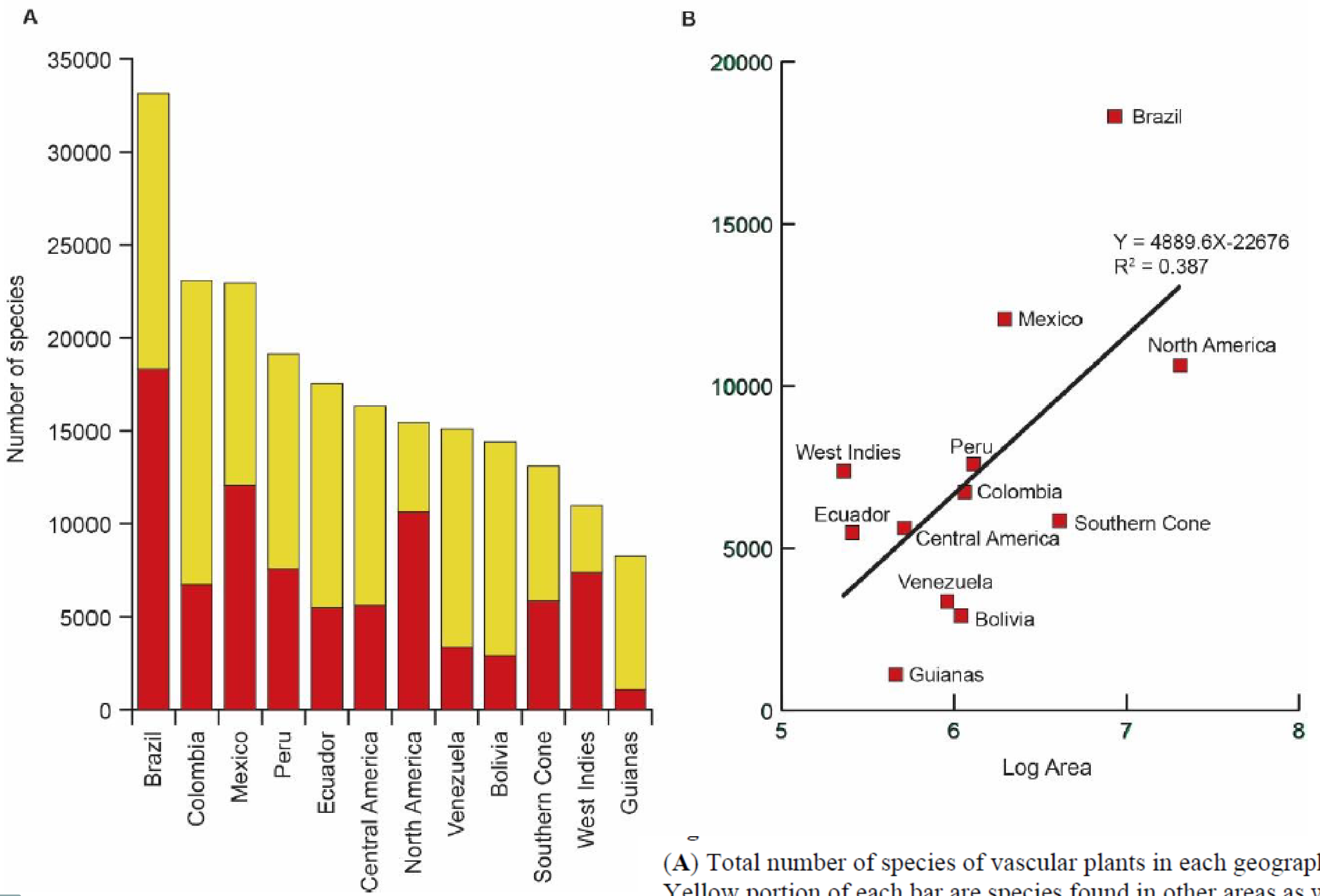
Américas abrigam 124.933 espécies de plantas vasculares,
em 6.227 gêneros e 355 famílias.
Esse total corresponde a 1/3 das espécies desse grupo.

América do Sul: 82.052 espécies, das quais 73.552 são endêmicas. Apenas 8.300 dessas espécies ocorre também na América do Norte.

A flora da América do Sul é 6% maior que a da África, cuja área é 2 x maior.

Em média, 744 espécies novas de plantas são descritas por ano.

Ulloa-Ulloa et al. 2017: Riqueza florística nas Américas



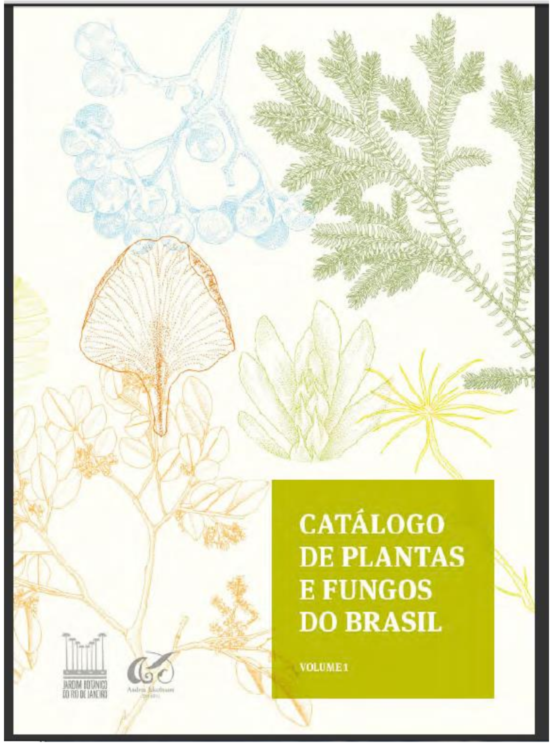
(**A**) Total number of species of vascular plants in each geographic area in the Americas. Yellow portion of each bar are species found in other areas as well. Red portion of each bar are species restricted to the area. (**B**) The number of range-restricted species as a function of log area. Larger areas tend to have more range-restricted species.

🟥 **restritas ao país**

Diversidade florística no Brasil

Após Catálogo de 2010, a Lista tem sido atualizada continuamente:

www.floradobrasil.jbrj.gov.br



CATÁLOGO
DE PLANTAS
E FUNGOS
DO BRASIL

VOLUME 1

2017: 46.403 espécies:

		endêmicas	
5.726	fungos	124	
4.751	algas	233	
1.552	briófitas	321	
1.322	samambaias e licófitas	**505**	**34.344 spp. plantas vasculares**
30	gimnospermas	2	
33.022	angiospermas	**18.581**	

Diversidade florística no Brasil

Plantas vasculares: dados de 2017:

34.344 spp - Brasil é o país de maior fitodiversidade do mundo.

18.581 spp endêmicas de angiospermas no país: proporção de endemismo de 55,9%, a maior da Região Neotropical.

www.floradobrasil.jbrj.gov.br

Ulloa et al. 2017: em média 744 espécies novas de plantas são descritas por ano nas Américas; estima-se que existam entre 3,5 e 7 mil por serem descritas no Brasil.

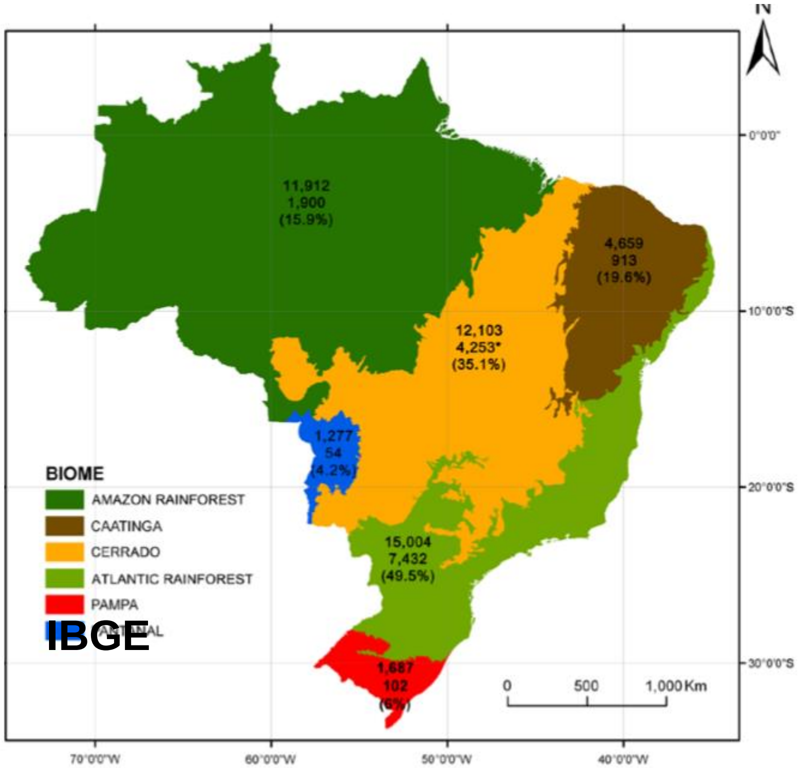


Figure 3 – Map of Brazilian biomes showing the total number of seed plant species (top number), the number of endemic species (middle number), and the percentage endemism for each biome. *Podocarpus barretoi Laubenf. & Silba is the only endemic species of Gymnosperm.

BFG (*Brazil Flora Group)* 2015

Plantas vasculares nos domínios fitogeográficos do Brasil

(dados de 2015)

Mata Atlântica: 15.004 spp., 7.432 endêmicas do país.

Cerrado: savanas mais ricas do mundo -12.103 spp. (4.253 endêmicas do país).

Amazônia: 11.912 spp. (1.900 endêmicas do país).

Florestas neotropicais (ombrófilas ou estacionais) abrigam uma biota megadiversa e única…


Amazonas, Brasil

Minas Gerais, Brasil

Vegetações mais abertas como campos de cimeira, matas montanas e nebulares …

Rio Grande do Sul, Brasil

Santa Catarina, Brasil

La Paz, Bolivia

…pradarias, estepes e campos rupestres e de altitude …


Buenos Aires, Argentina


Rio Grande do Sul, Brasil


Minas Gerais, Brasil


Espírito Santo, Brasil

…desertos e semidesertos (puna)…

La Paz, Bolivia

Tucumán, Argentina

San Juan, Argentina

Santiago, Chile

…montanhas e afloramentos rochosos …


Bahia, Brasil

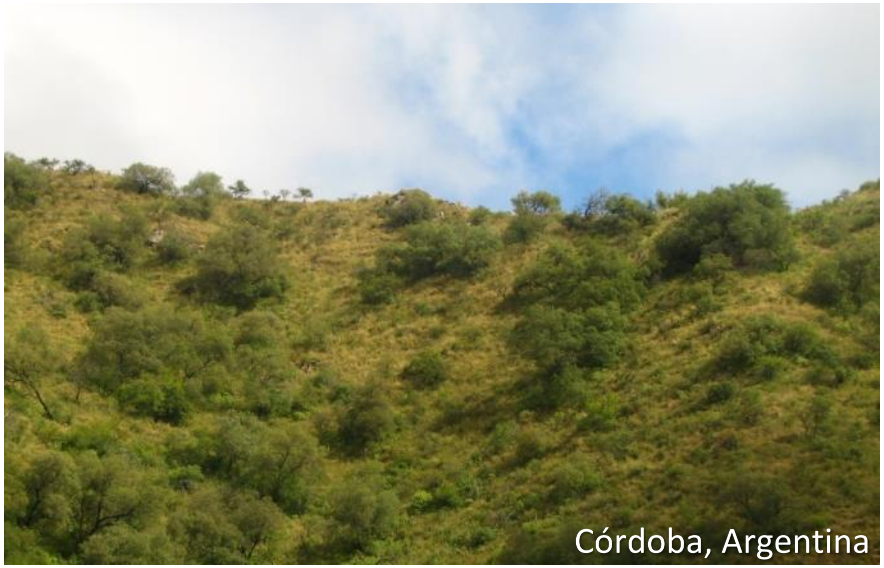

Rio de Janeiro, Brasil


Espírito Santo, Brasil


Rio Grande do Sul, Brasil

… e formações savânicas (cerrado, butiazal, espinal etc) também abrigam floras únicas com altos níveis de endemismo.

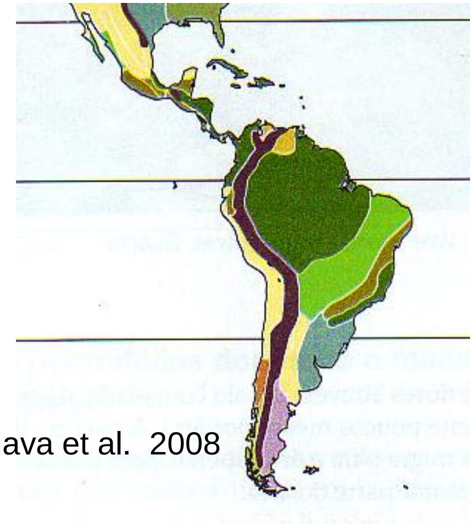

Minas Gerais, Brasil


Córdoba, Argentina


Rio Grande do Sul, Brasil


Rio Grande do Sul, Brasil

Enorme diversidade florística da Região Neotropical está intrinsecamente associada à ampla heterogeneidade ecológica do continente.



Sadava et al. 2008

Porém, a história peculiar do continente sulamericano, com eventos geológicos, climáticos e vegetacionais, foi determinante ao impulsionar a **evolução particular das linhagens de plantas do continente**.

Região Neotropical tem expressivo número de famílias endêmicas ou subendêmicas, e o maior número de gêneros endêmicos.

Muitas famílias de angiospermas, embora amplamente distribuídas pelo mundo, possuem maior riqueza na América Tropical, onde está também seu centro de endemismos.

Exemplos de endemismos de biomas neotropicais

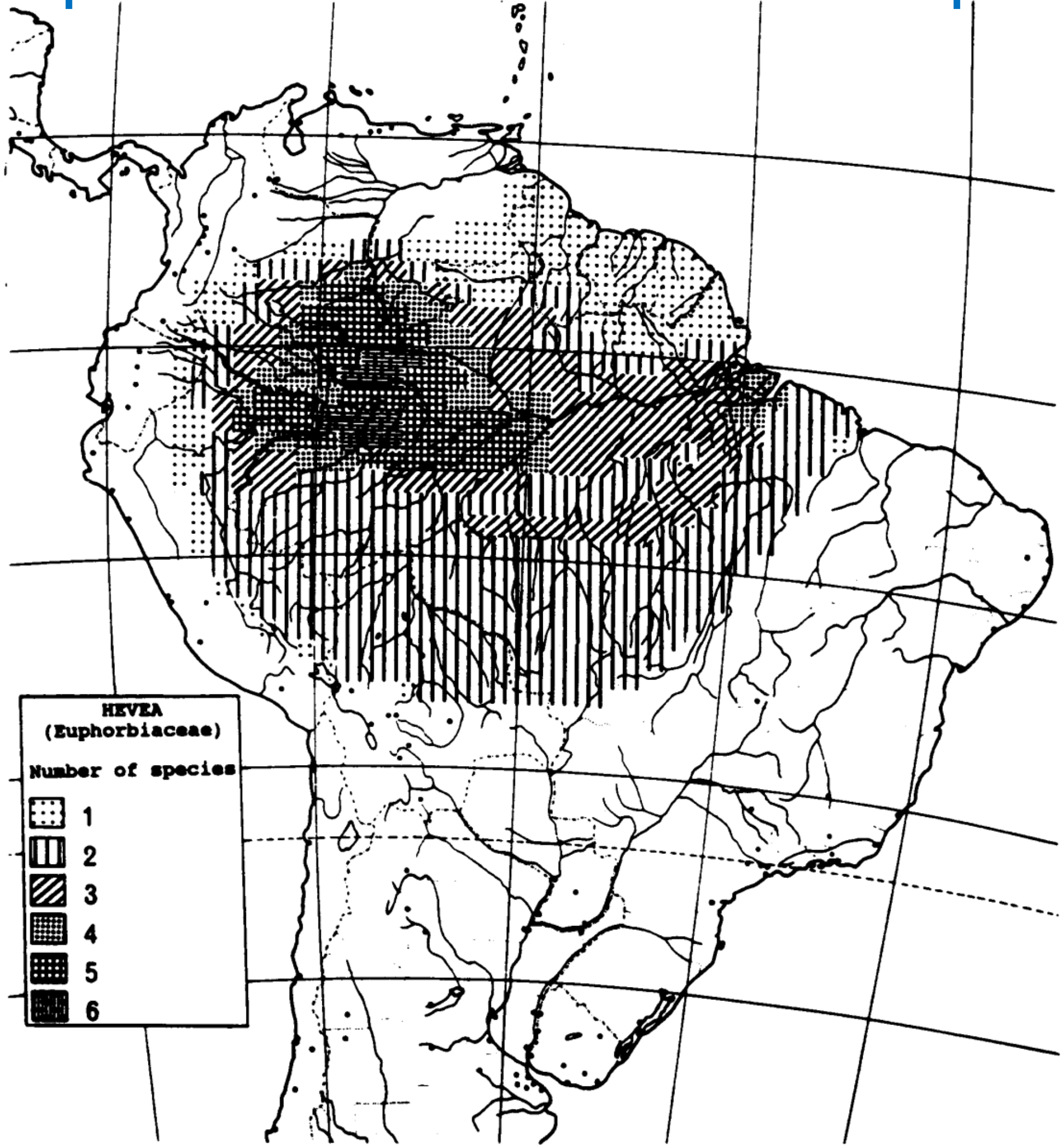
seringueira

Hevea brasiliensis

Euphorbiaceae

e...

Sagotia, Sandwithia....



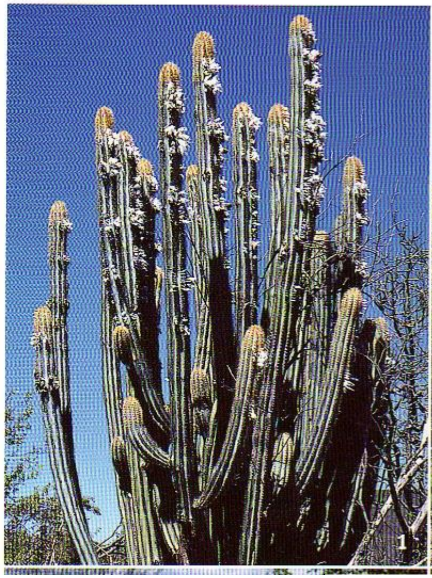
Distribution density map of species of *Hevea*

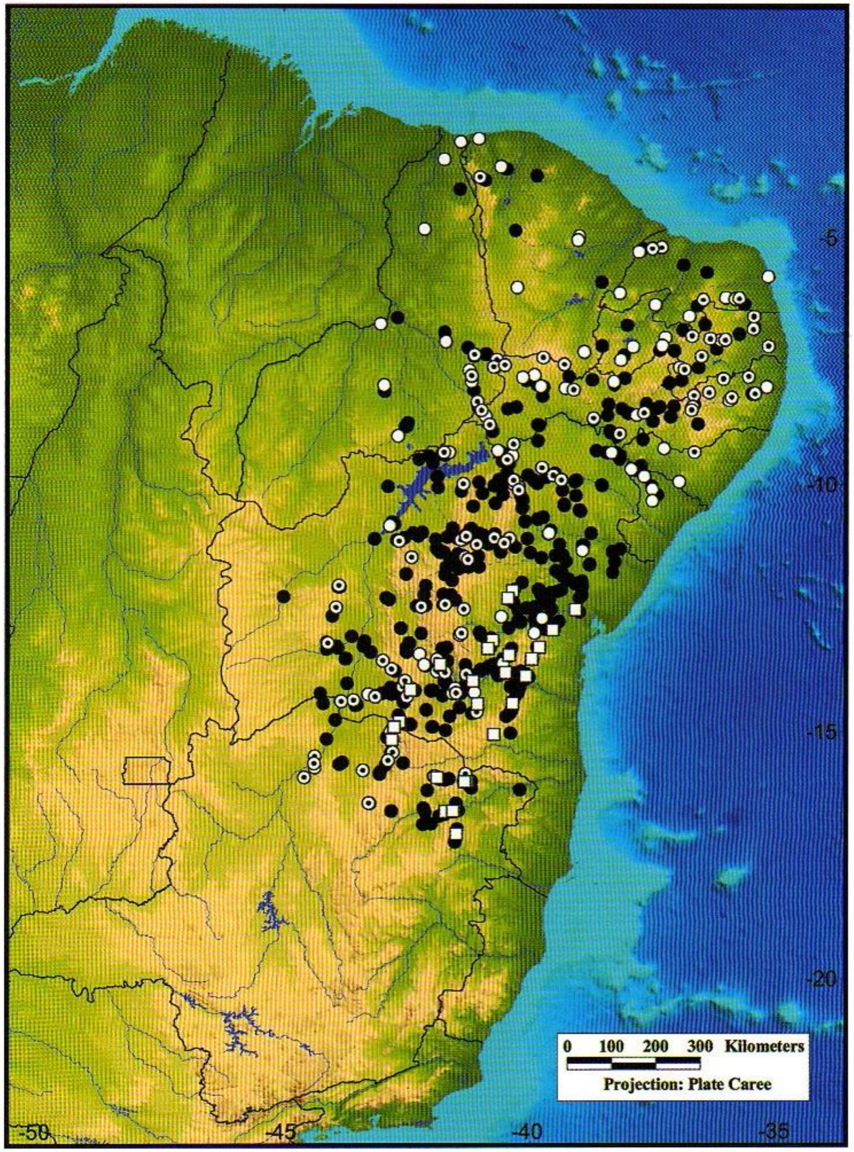
Prance 1994 in Forey *et al.*

Exemplos de endemismos de biomas neotropicais

CAATINGA - Savana estépica

Pilosocereus pachycladus Cactaceae

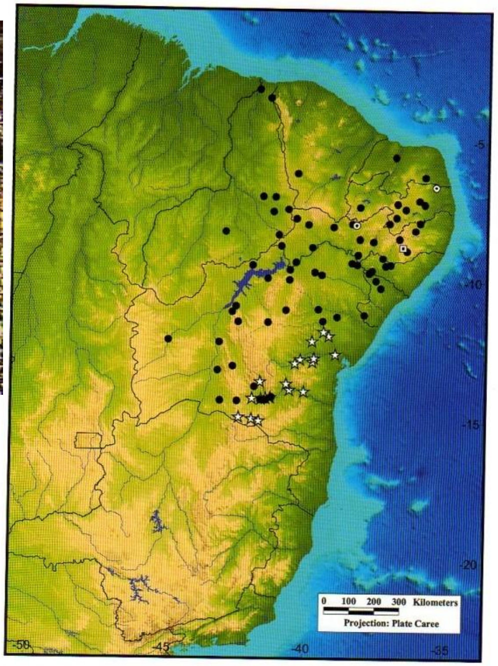




Map 3. Distribution records of taxa typical of *caatinga* and *caatinga-agreste* vegetation, distinguishing *Brasilicereus phaeacanthus* [□], *Pilosocereus gounellei* subsp. *gounellei* [○] and *P. pachycladus, sens. lat.* [⊙] (omitting a southern *campo rupestre* site) and indicating the approximate limits of the *caatinga* biome (excluding south-western *mata seca*).

Taylor & Zappi 2004

Melocactus violaceus Cactaceae

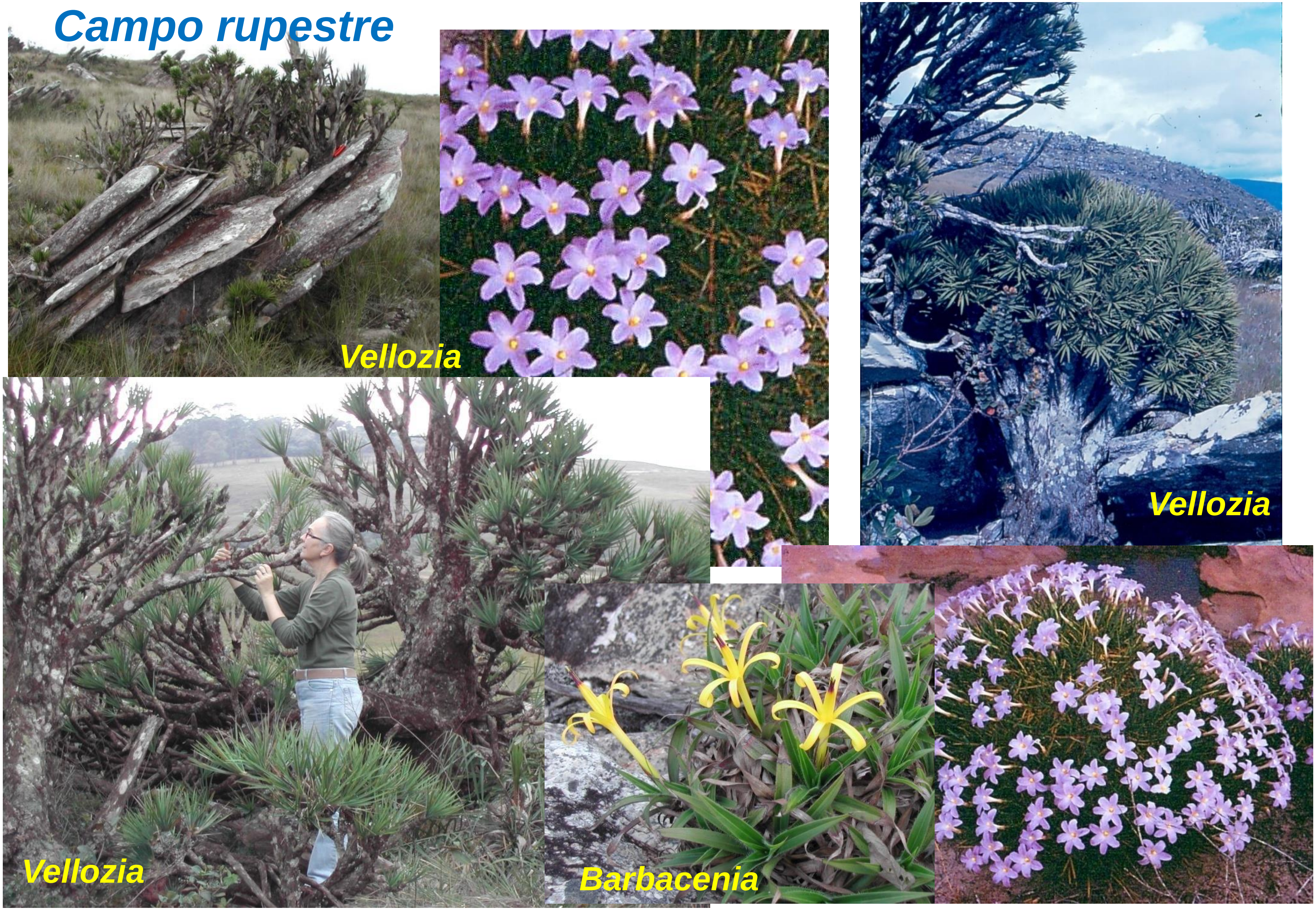


Map 45. Distribution of the MELOCACTUS VIOLACEUS Species Group (I): *M. salvadorensis* [☆], *M. zehntneri* [●] and *M. lanssensianus* [▣; ⊙ = records of comparable taxa].

Velloziaceae

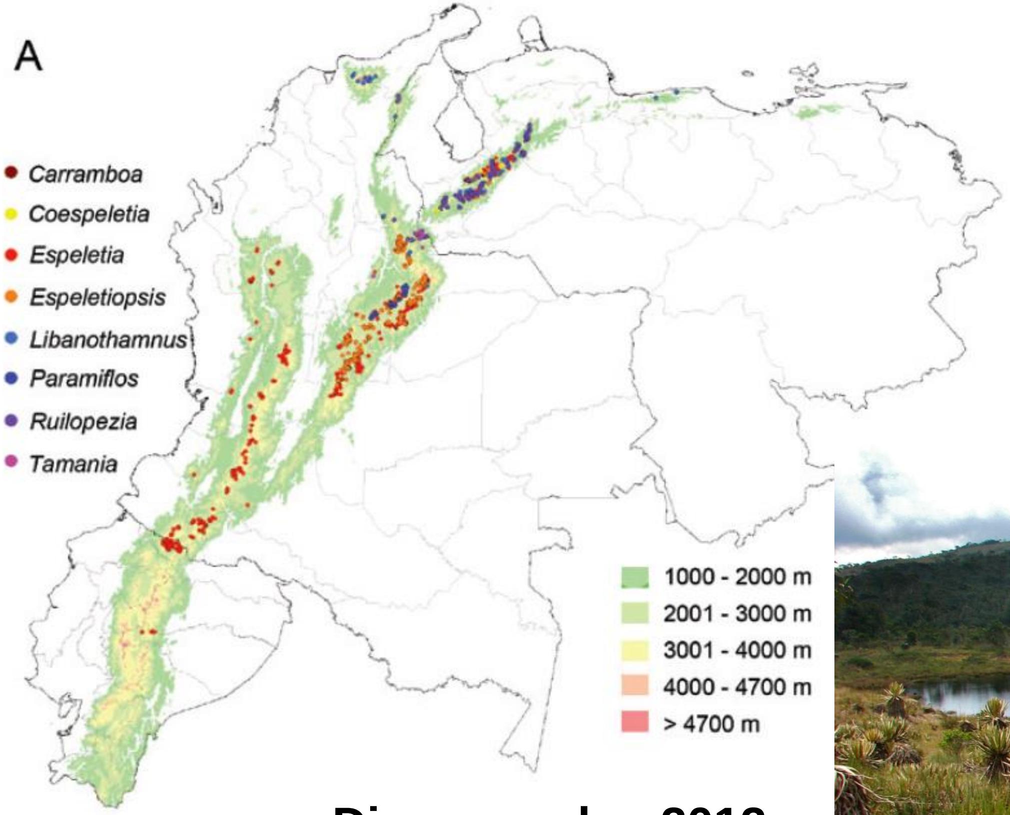
Exemplos de endemismos de biomas neotropicais

Campo rupestre



PÁRAMOS andinos
(2800 – 4700 m alt.)
Espeletiinae, ASTERACEAE

Exemplos de endemismos de biomas neotropicais

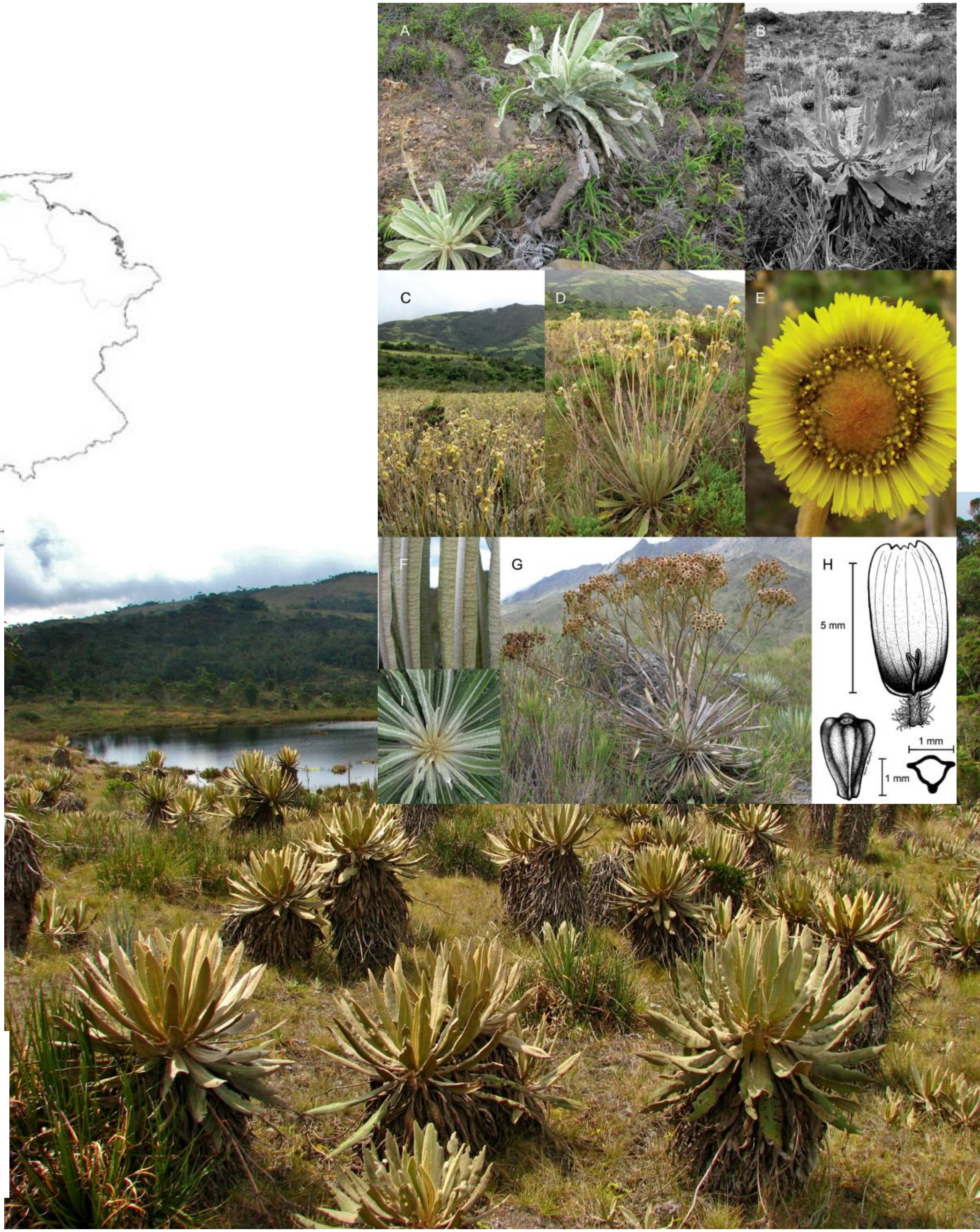


Diazgranados 2012

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae)

Mauricio Diazgranados[1,2]

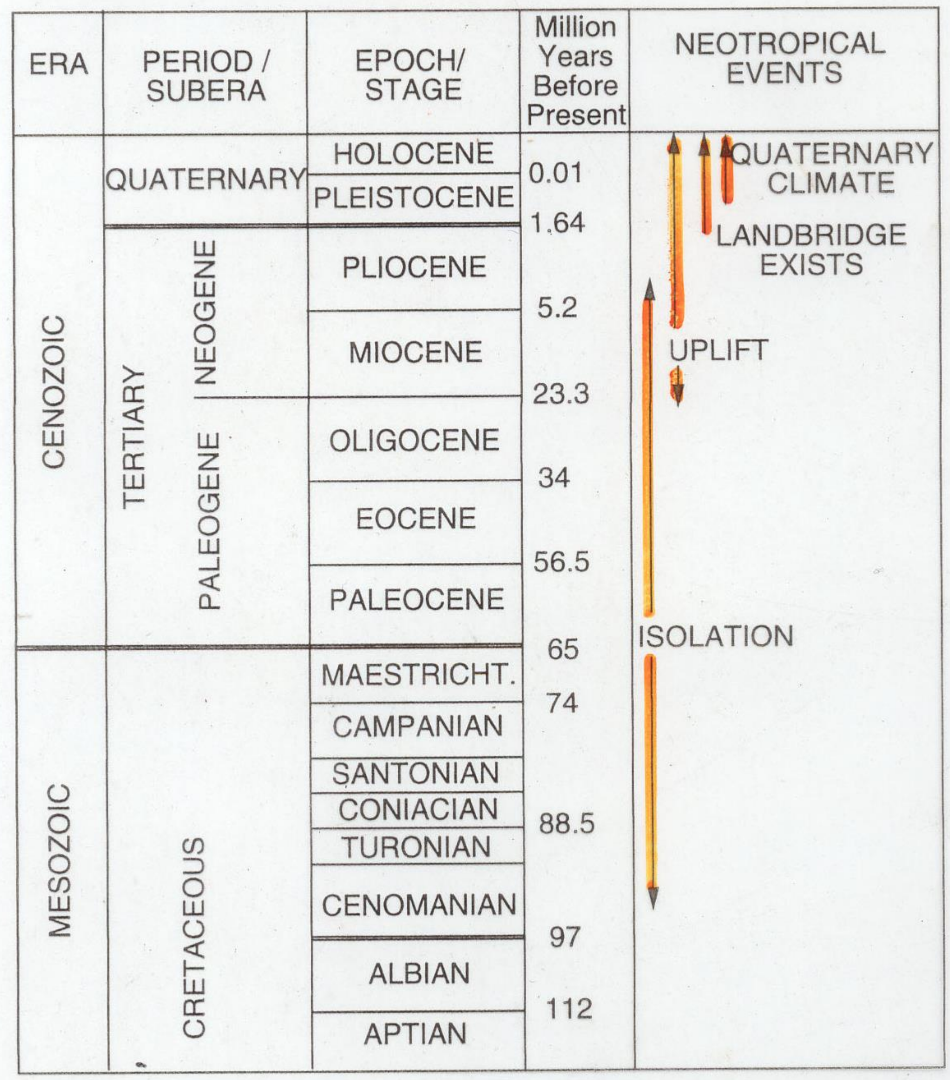


Breve história da Vegetação Neotropical

Burnham & Graham 1999

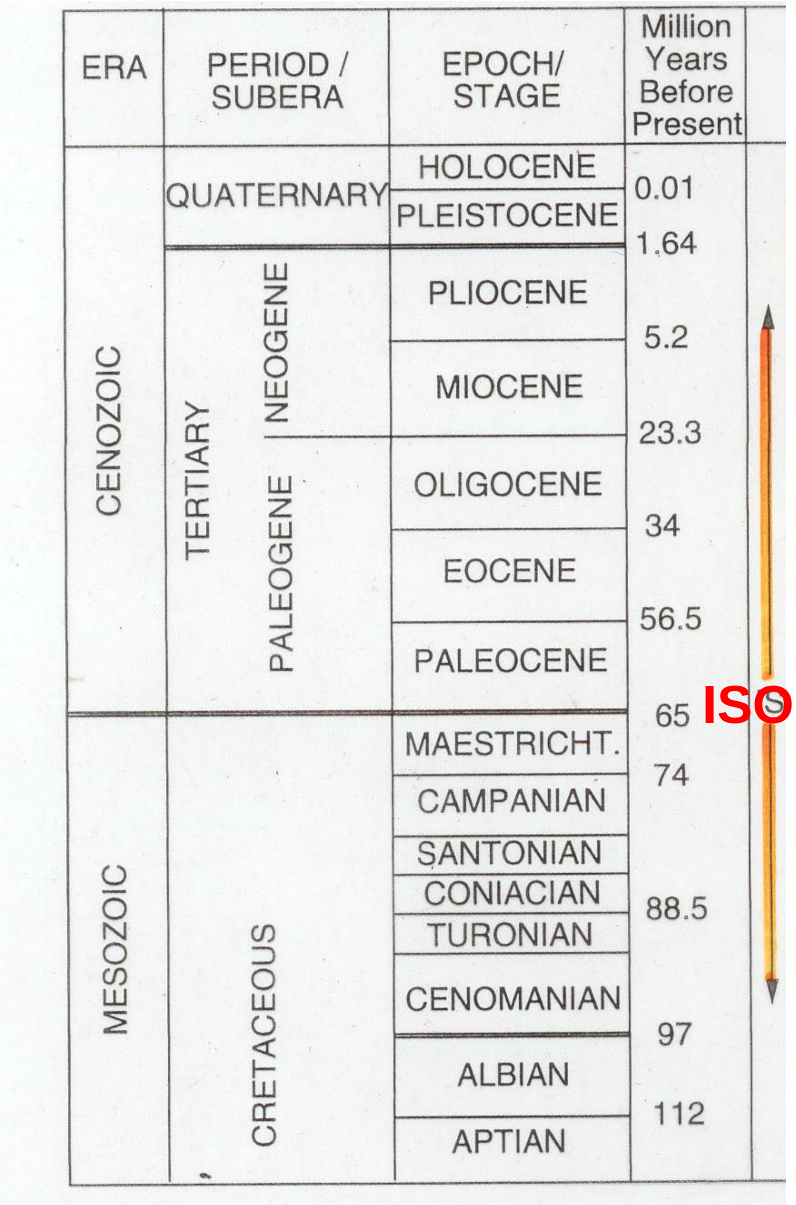
(e Graham 2011)

A PARTIAL TIME SCALE (CRETACEOUS TO PRESENT)



ERA	PERIOD / SUBERA		EPOCH/ STAGE	Million Years Before Present	NEOTROPICAL EVENTS
CENOZOIC	QUATERNARY		HOLOCENE	0.01	QUATERNARY CLIMATE
			PLEISTOCENE	1.64	LANDBRIDGE EXISTS
	TERTIARY	NEOGENE	PLIOCENE	5.2	
			MIOCENE	23.3	UPLIFT
		PALEOGENE	OLIGOCENE	34	
			EOCENE	56.5	
			PALEOCENE	65	ISOLATION
MESOZOIC	CRETACEOUS		MAESTRICHT.	74	
			CAMPANIAN		
			SANTONIAN		
			CONIACIAN	88.5	
			TURONIAN		
			CENOMANIAN	97	
			ALBIAN	112	
			APTIAN		

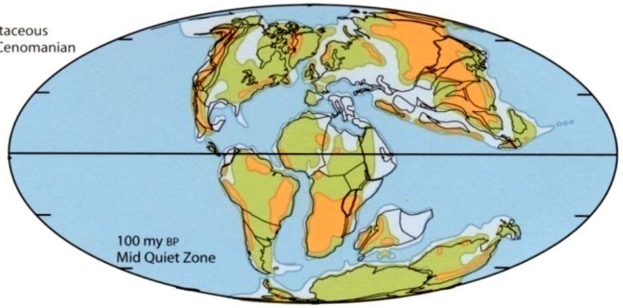
Figure 1. Time scale for the mid-Cretaceous to Present showing the four events discussed in the text. Note that the events are not temporally distinct from one another.



ERA	PERIOD / SUBERA		EPOCH/ STAGE	Million Years Before Present
CENOZOIC	QUATERNARY		HOLOCENE	0.01
			PLEISTOCENE	1.64
	TERTIARY	NEOGENE	PLIOCENE	5.2
			MIOCENE	23.3
		PALEOGENE	OLIGOCENE	34
			EOCENE	56.5
			PALEOCENE	65
MESOZOIC	CRETACEOUS		MAESTRICHT.	74
			CAMPANIAN	
			SANTONIAN	
			CONIACIAN	88.5
			TURONIAN	
			CENOMANIAN	97
			ALBIAN	112
			APTIAN	

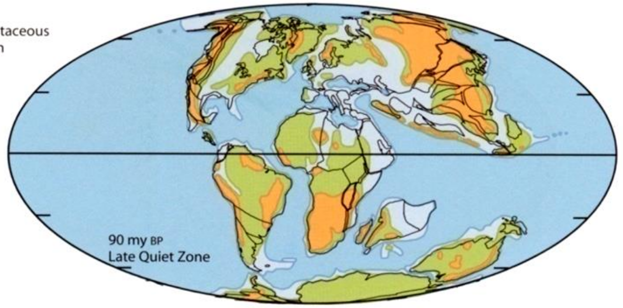
Burnham & Graham 1999

Plate 8
Mid Cretaceous
Albian-Cenomanian



Lomolino & Heaney 2004

Plate 9
Late Cretaceous
Turonian



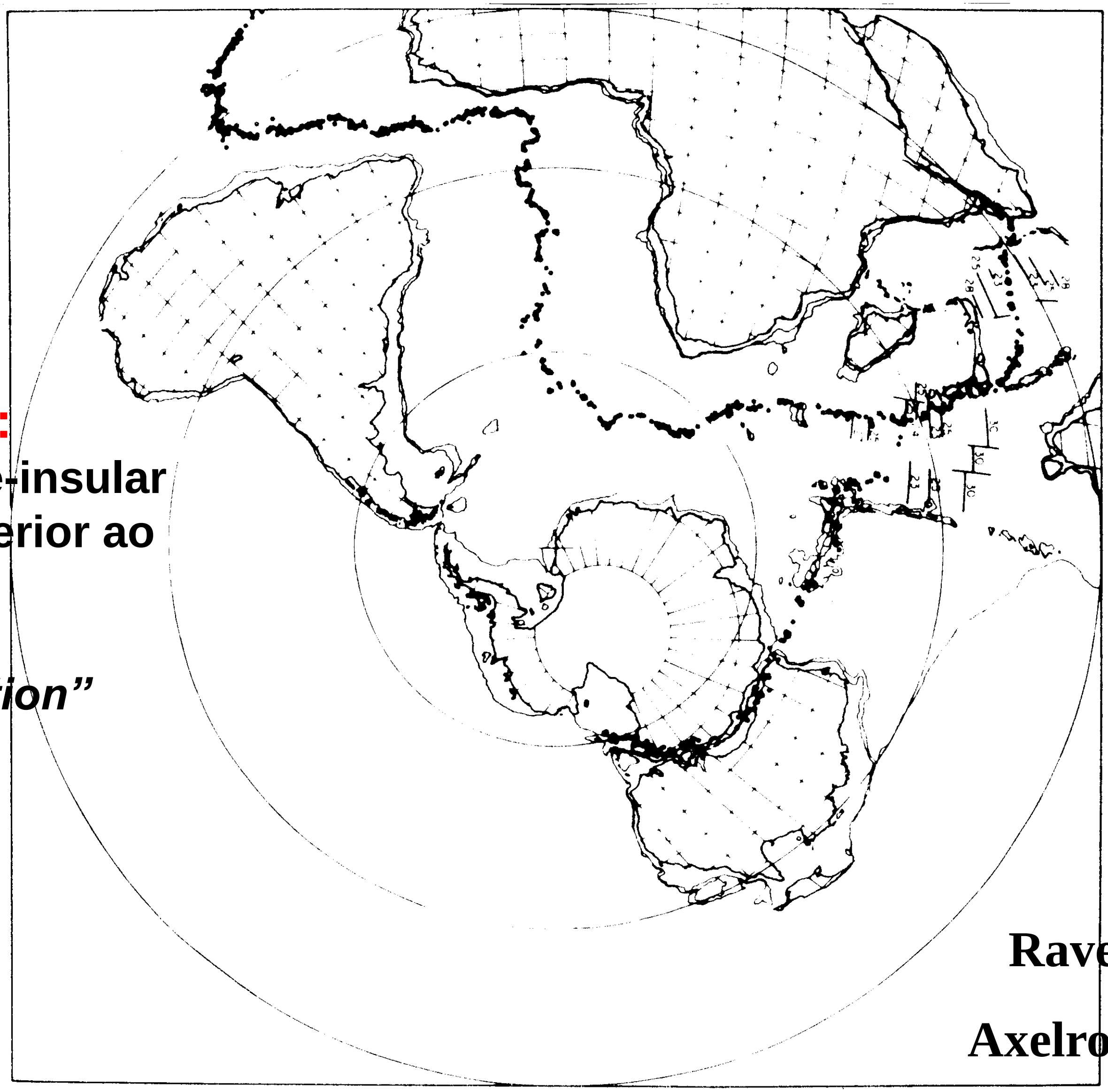
ISOLAMENTO: AS = continente-insular! imprimiu forte marca na flora neotropical

Palinofósseis e macrofósseis do Eoceno ao Mioceno = flora tropical rica!

Floras do Mioceno na Amazônia são extremamente semelhantes às atuais em diversidade (baseadas nas famílias dominantes)

ISOLAMENTO:
AS = continente-insular do Cretáceo inferior ao Plioceno!

"splendid isolation"
(Simpson 1980)

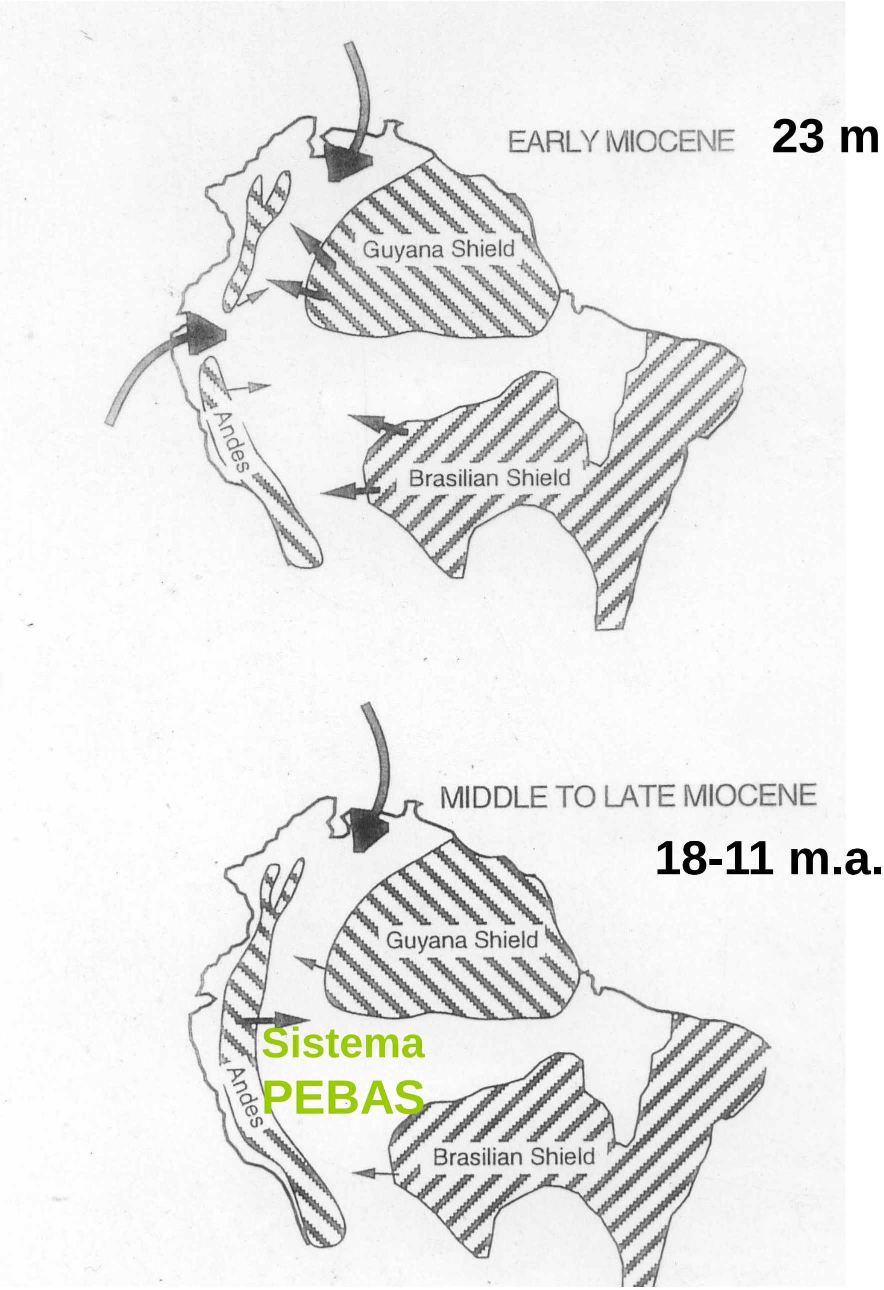


Raven & Axelrod 1974

Reconstruction showing early **Tertiary configuration of Gondwanan continents.** Dots show active plate boundaries at that time. (From Jardine & McKenzie, 1972; reprinted by permission from *Nature* 235: 22. © 1972, Macmillan Journals Ltd.)

OROGENIA

Burnham & Graham 1999



23 m.a.

18-11 m.a.

Sistema PEBAS

Configuração estabelecida há cerca de 7-2,5 Ma

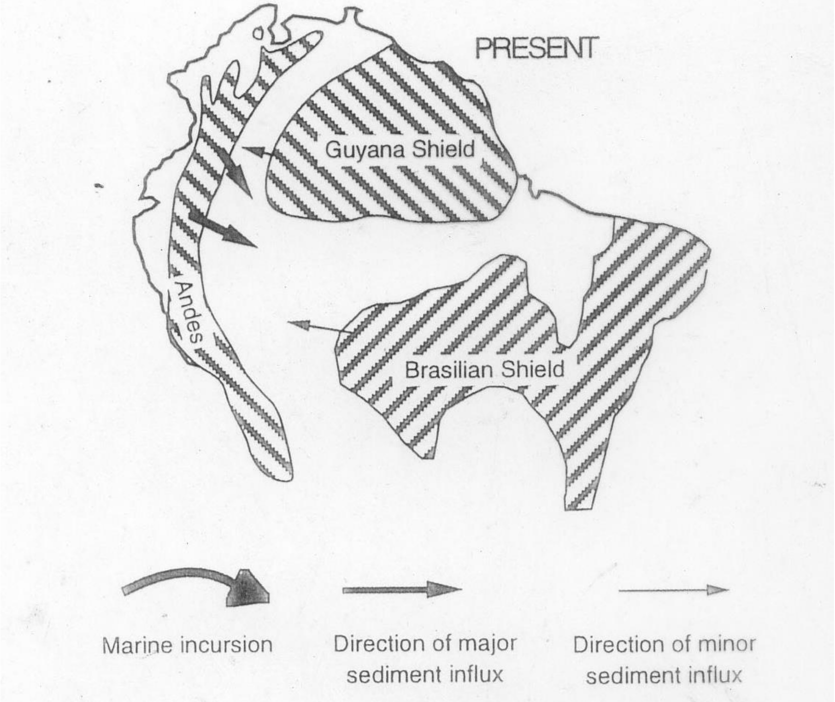


Figure 10. Major sedimentary sources, highland areas, and seaways in Early Miocene, Middle to Late Miocene, and Present South America. From Hoorn (1994b).

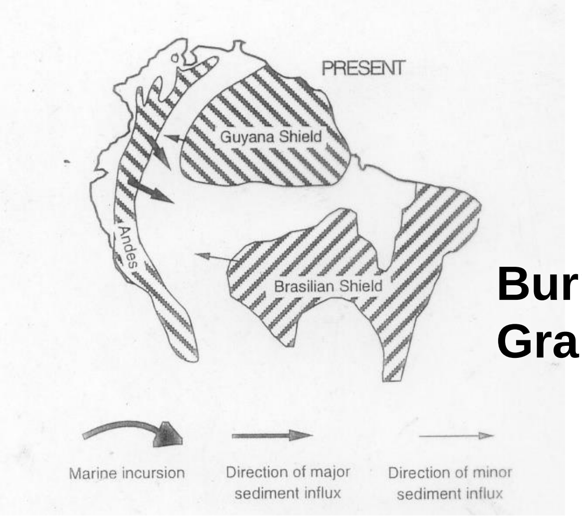
PEBAS: grande lago ou sistema fluvial com terra firme?

OROGENIA

Dados geofísicos recentes mostram
forte correlação entre soerguimento da Cadeia Andina
e o desenvolvimento e diversificação de
florestas montanas na Colômbia e Venezuela.

Orogenia afetou a geomorfologia
das terras baixas amazônicas:
cristas levantaram há 2,5 m.a.
(hoje indistintas porque erodidas)

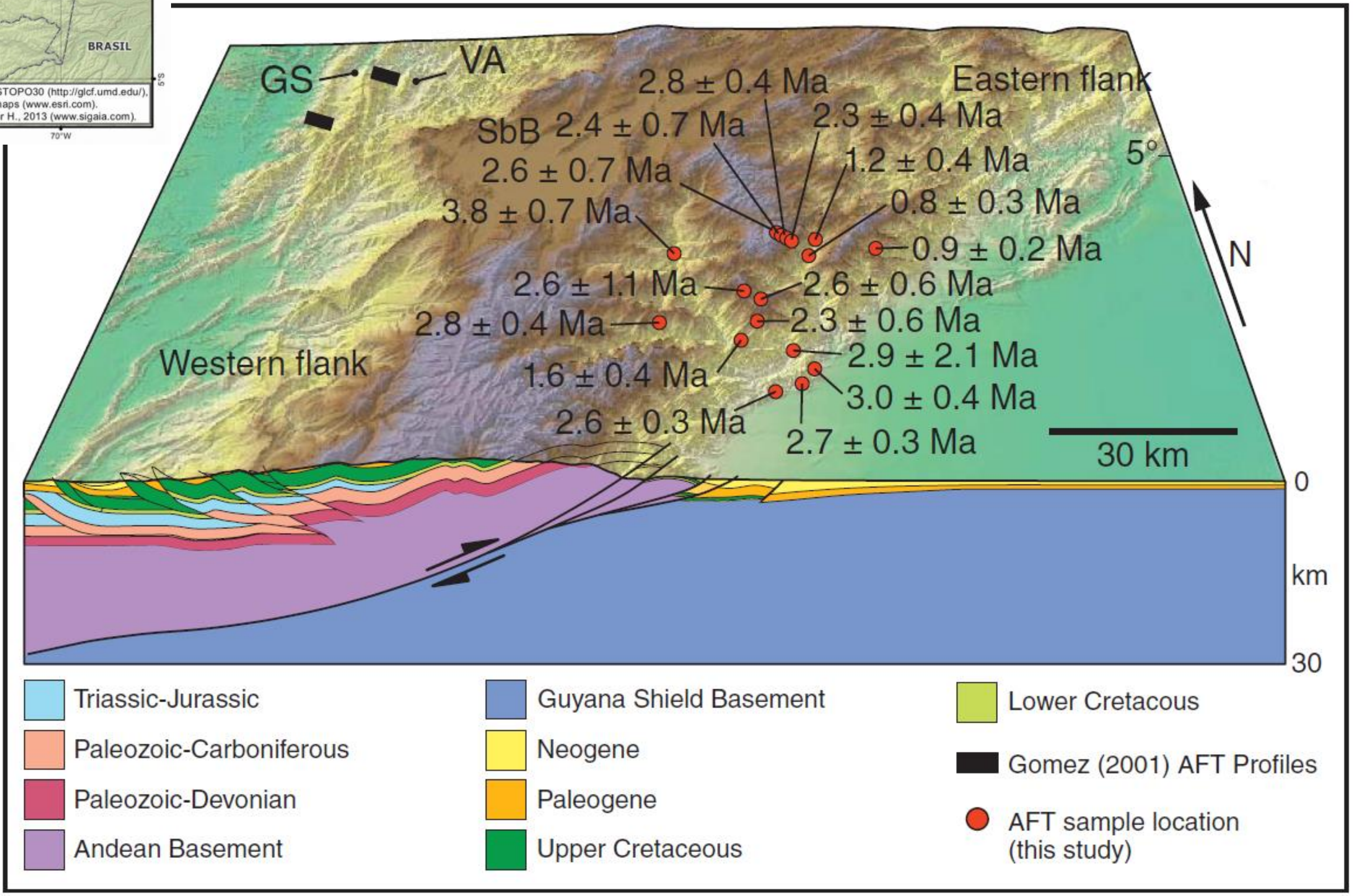
Lago?



Burnham &
Graham 1999

Climatic forcing of asymmetric orogenic evolution in the Eastern Cordillera of Colombia

Mora et al. 2008



(A) Digital elevation model of the Eastern Cordillera including the deeply dissected Eastern flank, the central flat-lying Sabana de Bogotá basin and the topographically lower western flank. GS—Guaduas syncline; VA—Villleta anticlinorium.

Houston & Hartley 2003

ANDES

Secção na Bolívia: Cordilheira Ocidental, Altiplano, Cordilheira Oriental –

Tipos e idade de rochas, falhas

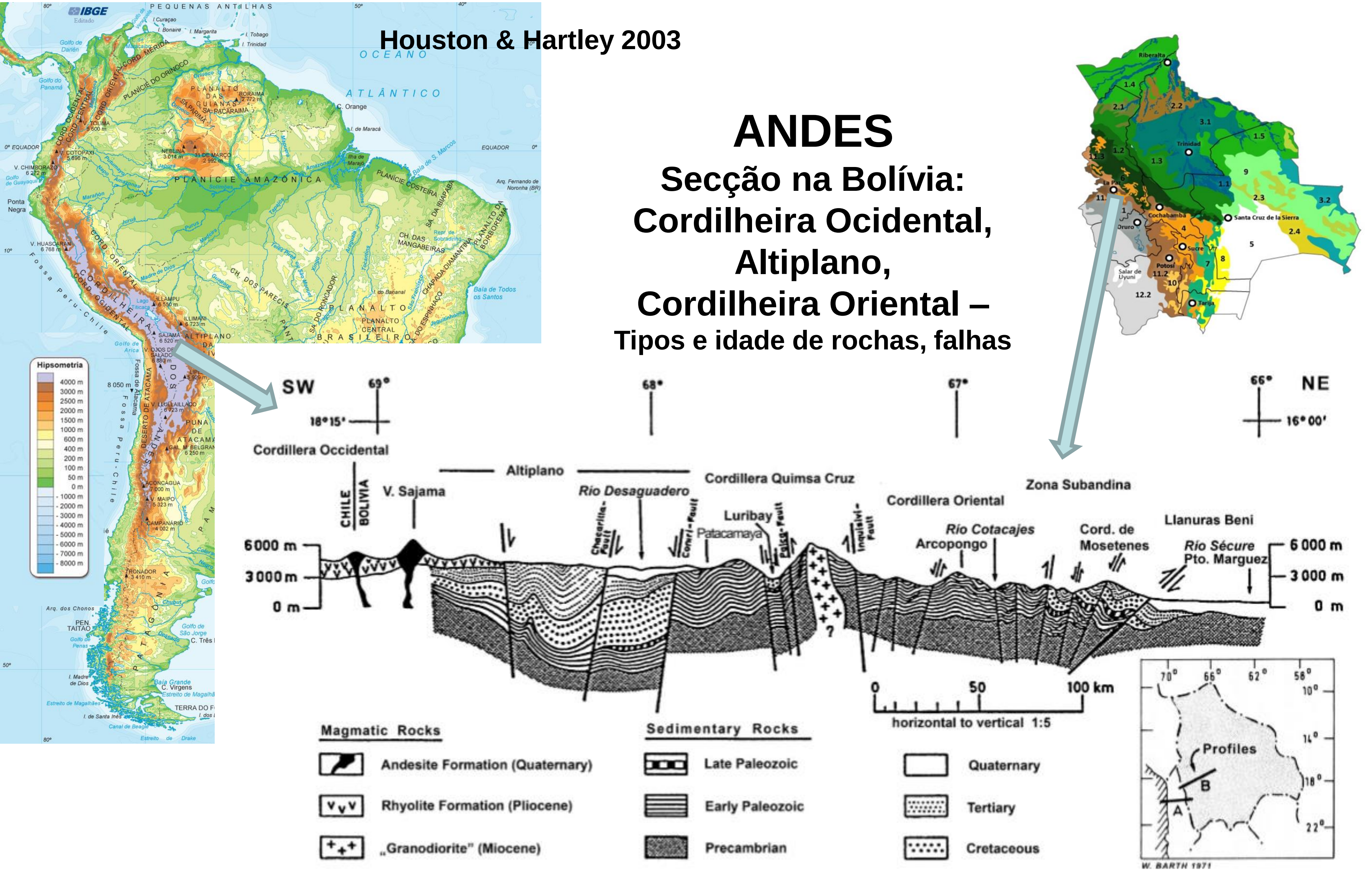
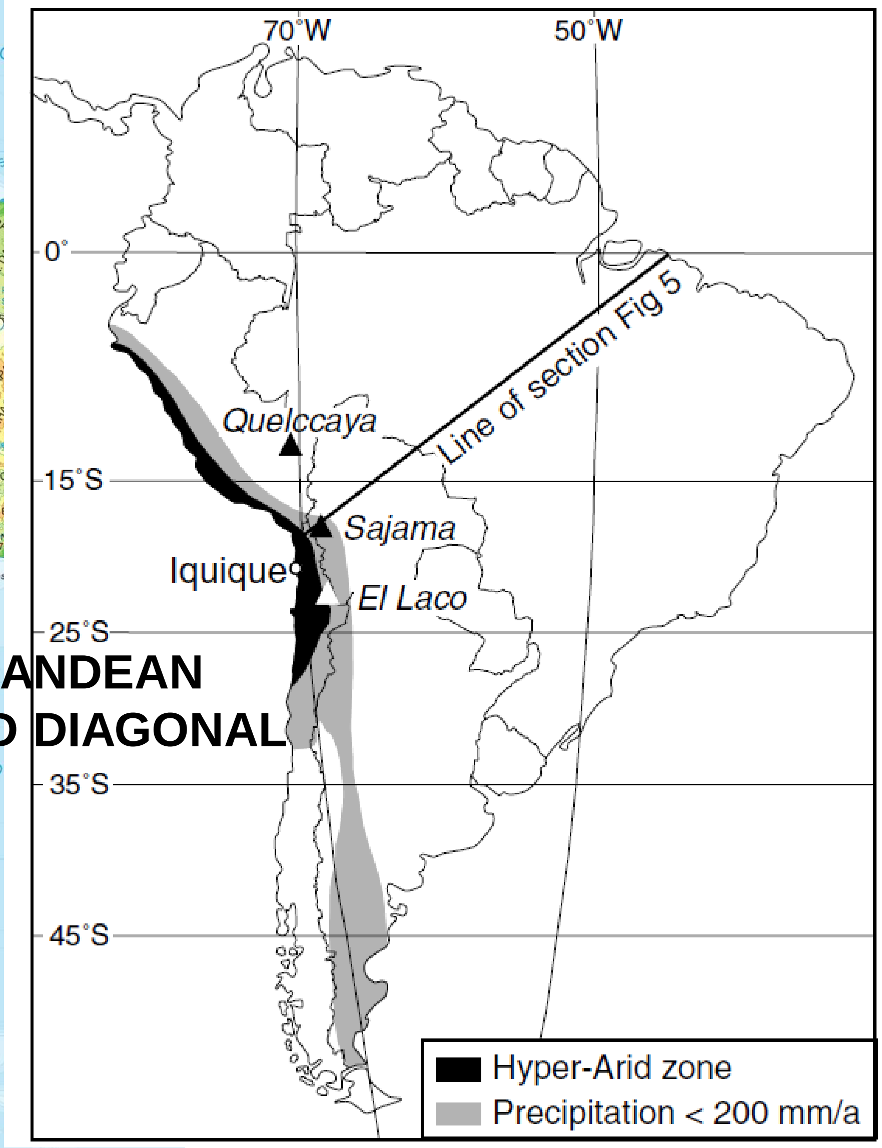


Figure 3. Sectional view of the Bolivian Andes showing approximate elevations, faults, rock types, and ages for the Western Cordillera, Altiplano, and Eastern Cordillera. Note the corrugated topography of the eastern slopes (Yungas) designated Zona Subandina on the figure. From Zeil (1979); used with permission of Borntraeger, Berlin.

Burnham 2011

THE CENTRAL ANDEAN WEST-SLOPE RAINSHADOW AND ITS POTENTIAL CONTRIBUTION TO THE ORIGIN OF HYPER-ARIDITY IN THE ATACAMA DESERT

Houston & Hartley 2003



ANDEAN ARID DIAGONAL

Montanhas são habitats com altas taxas de endemismo e de diversificação.

Filogenia estruturada geograficamente

***Cyathostegia* - Leguminosae**

Andean diversification

Pennington et al. 2010

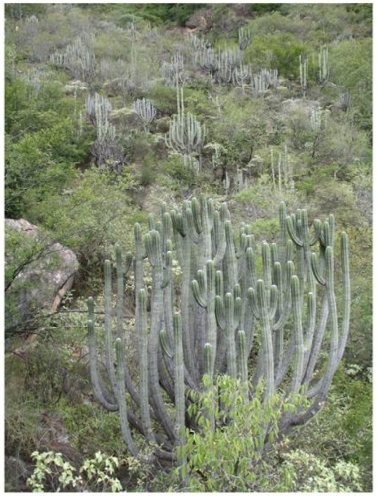
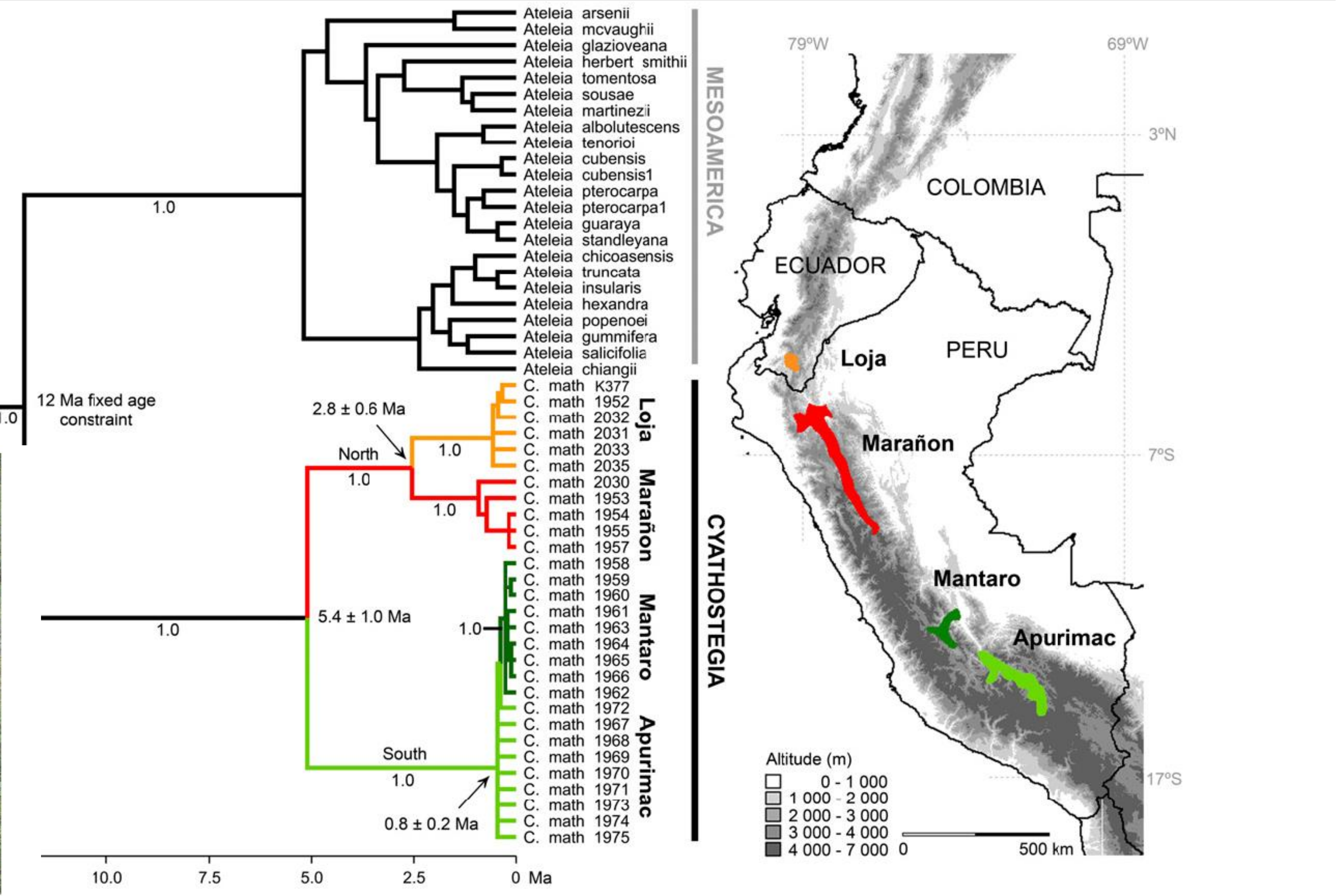
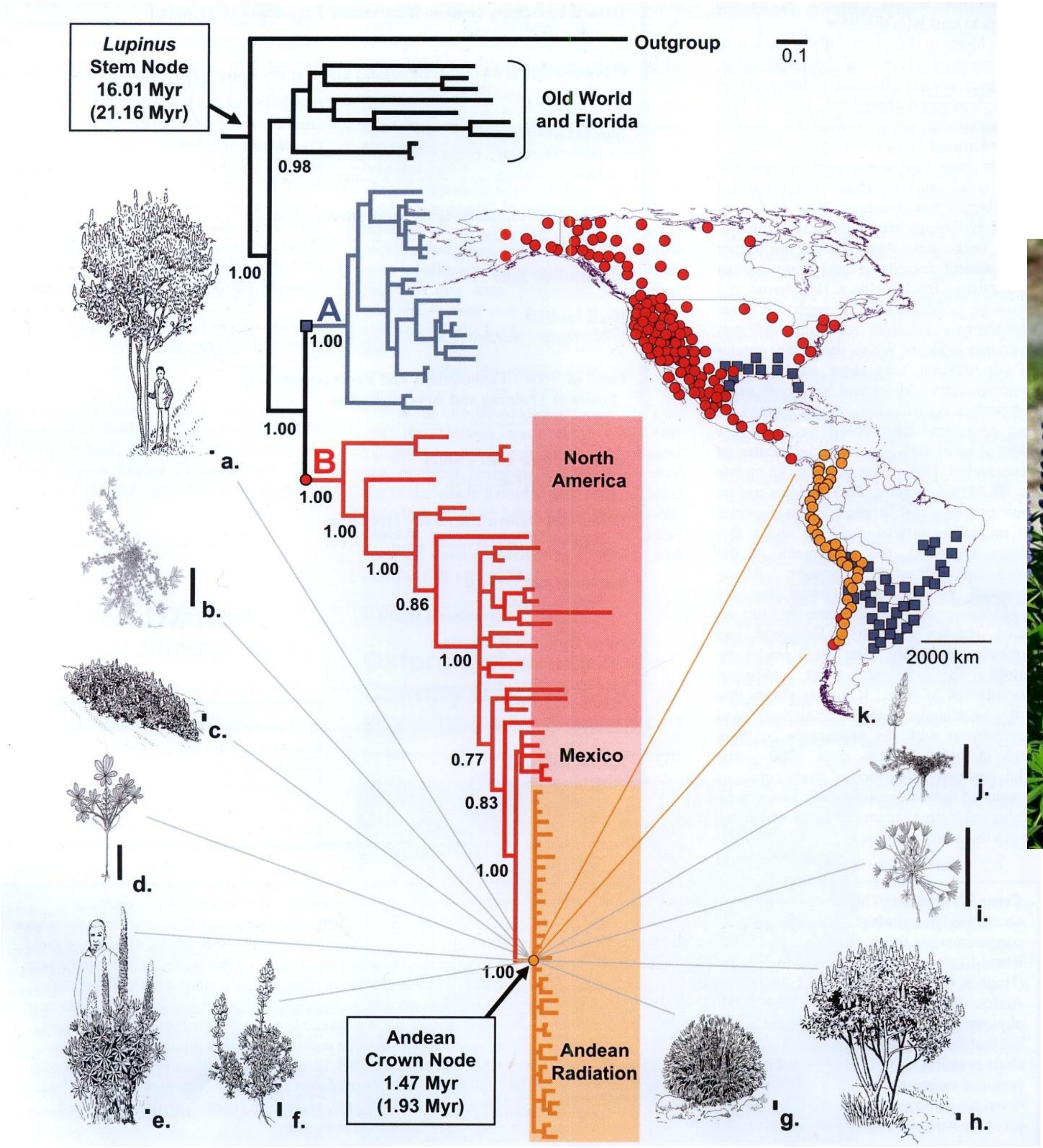


Fig. 1. Cactus-rich seasonally dry tropical forest in the Marañon valley, Peru.



n for *Cyathostegia* derived from penalized likelihood rate smoothing of a 50% majority rule Bayesian likelihood tree estimated from the ITS sequence data. Clade labels (Loja, Marañon, Mantaro, Apurimac) indicate the dry inter-Andean valleys where accessions were collected, the locations of which are shown on the map. Numbers (1.0) below branches indicate posterior probabilities.



Lupinus, Leguminosae

Hughes & Eastwood 2006

Andes: 25 m.a.

muitas spp com menos de 7 m.a.

Madriñan et al. 2013

frontiers in GENETICS

ORIGINAL RESEARCH ARTICLE
published: 09 October 2013
doi: 10.3389/fgene.2013.00192

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

Santiago Madriñán[1], Andrés J. Cortés[1,2] and James E. Richardson[1,3]*

73 dated molecular phylogenies.
The average net diversification rates of Páramo plant lineages are faster than those of other reportedly fast evolving hotspots.
Most of the speciation events that we observed in the Páramos (144 out of 177) occurred during the Pleistocene possibly due to the effects of species range contraction expansion that may have resulted from the well-documented climatic changes during that period.

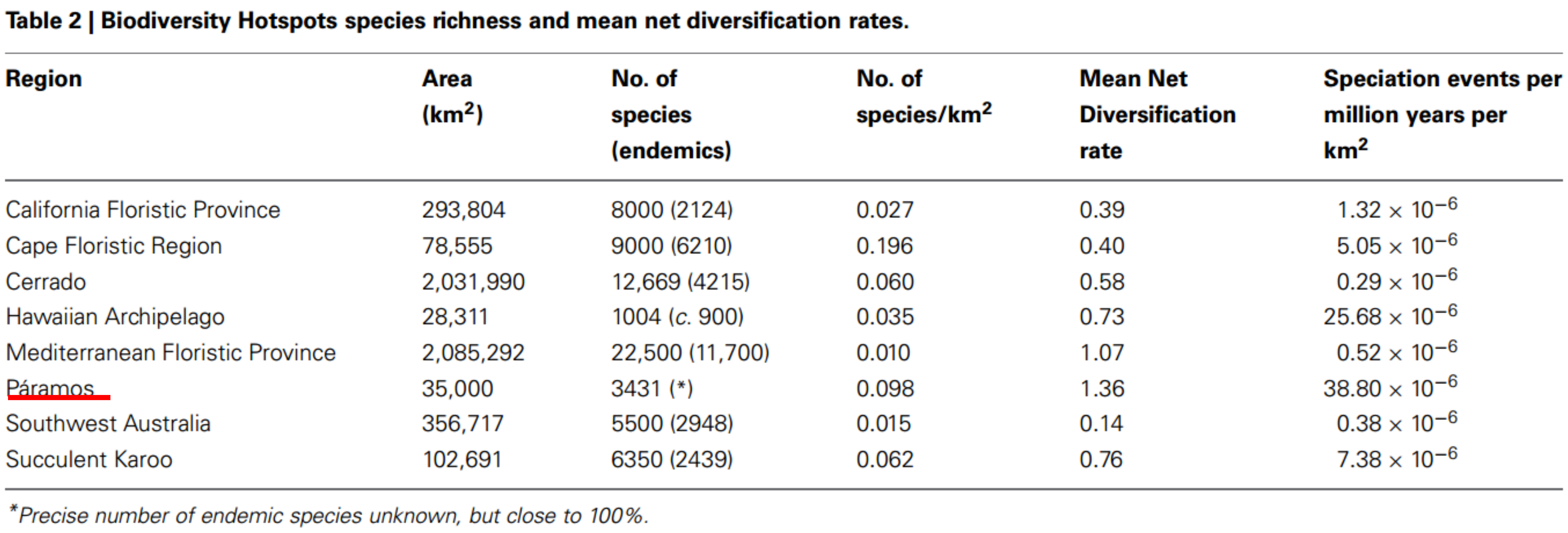


Table 2 | Biodiversity Hotspots species richness and mean net diversification rates.

Region	**Area (km^2)**	**No. of species (endemics)**	**No. of species/km^2**	**Mean Net Diversification rate**	**Speciation events per million years per km^2**
California Floristic Province	293,804	8000 (2124)	0.027	0.39	1.32×10^{-6}
Cape Floristic Region	78,555	9000 (6210)	0.196	0.40	5.05×10^{-6}
Cerrado	2,031,990	12,669 (4215)	0.060	0.58	0.29×10^{-6}
Hawaiian Archipelago	28,311	1004 (*c.* 900)	0.035	0.73	25.68×10^{-6}
Mediterranean Floristic Province	2,085,292	22,500 (11,700)	0.010	1.07	0.52×10^{-6}
Páramos	35,000	3431 (*)	0.098	1.36	38.80×10^{-6}
Southwest Australia	356,717	5500 (2948)	0.015	0.14	0.38×10^{-6}
Succulent Karoo	102,691	6350 (2439)	0.062	0.76	7.38×10^{-6}

**Precise number of endemic species unknown, but close to 100%.*

Net diversification rate: a simple estimator of Kendall (1949) and Magallón & Sanderson (2001)
$r = \ln(N) - \ln(N0)]/T$
N = standing diversity, N0 = initial diversity, here taken as = 1, T = inferred clade age.
This estimate is a pure-birth model of diversification with a constant rate and no extinction.

Escudos cristalinos proterozóicos

Escudo das Guianas

(2 bilhões de anos –formação mais antiga da Terra)

Escudo Brasileiro

(+ ou - estável nos últimos 600 m. a.)

Ambos também sofreram tectonismo no Mesozóico e no Terciário

Clapperton 1993

Generalized tectonic, structural and topographic features of South America

Topografia e batimetria da América do Sul Tropical

Hoorn et al. 2010

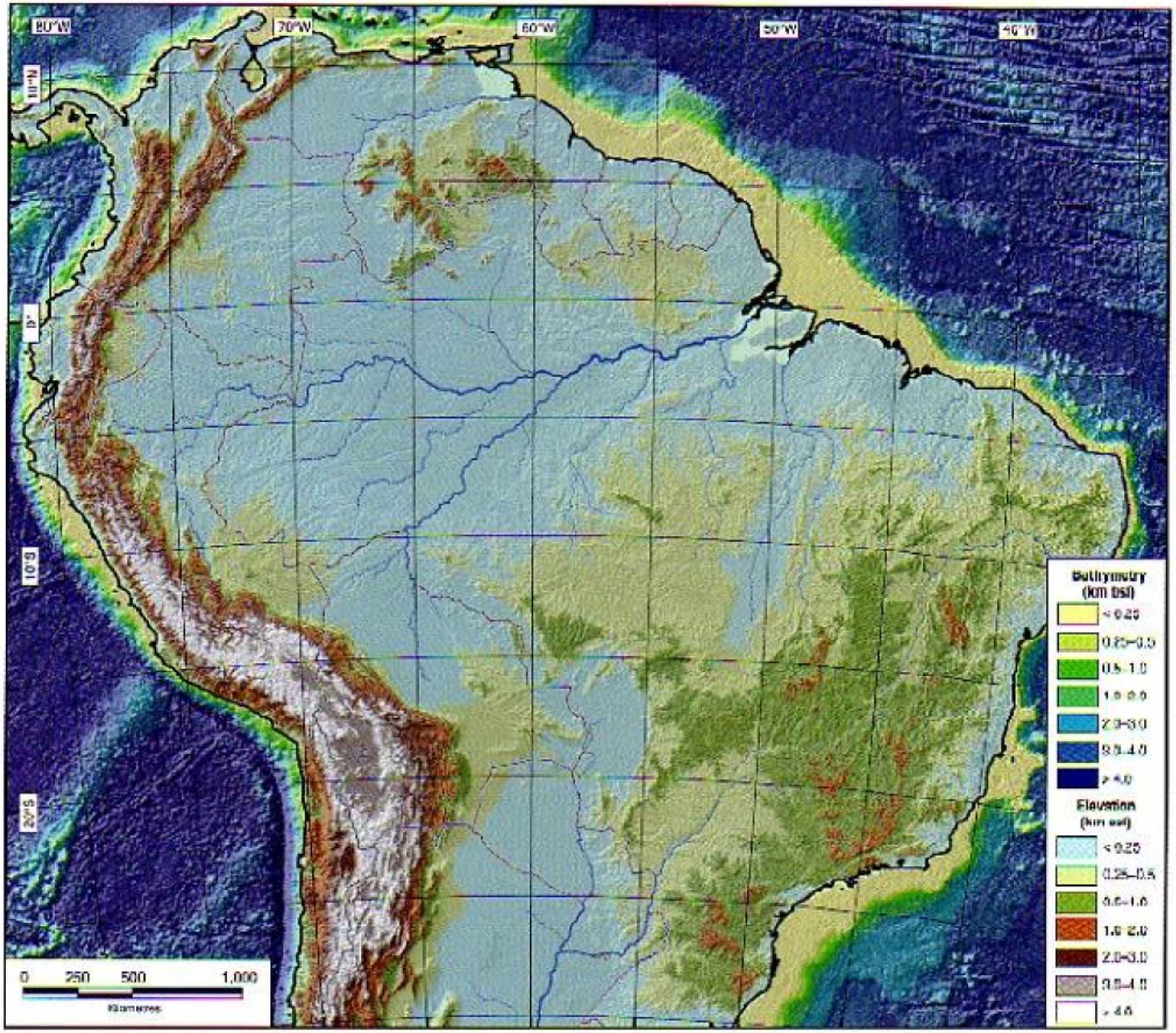
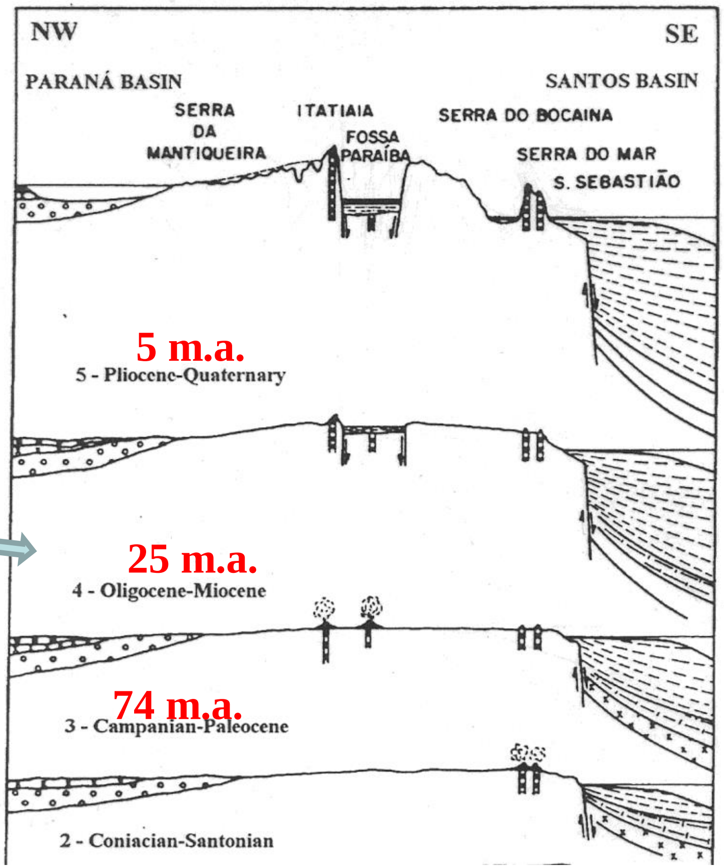


Plate 4 Shaded-relief topography and bathymetry of South America produced from ETOPO1 (Amante & Eakins 2008, ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis, National Geophysical Data Center, NESDIS, NOAA, US Department of Commerce, Boulder, CO, August 2008). Grey lines indicate national boundaries, blue lines depict rivers, with their line width proportional to drainage area. Map created by B. Bookhagen

Orogenia
no Planalto Central
e na costa Sudeste do Brasil

Costa et al. 1998

Cadeia do Espinhaço



Serra do Mar
e Serra da
Mantiqueira

Amorim & Pires 1996

Amorim & Pires 1996

Orogenia na costa Sudeste do Brasil

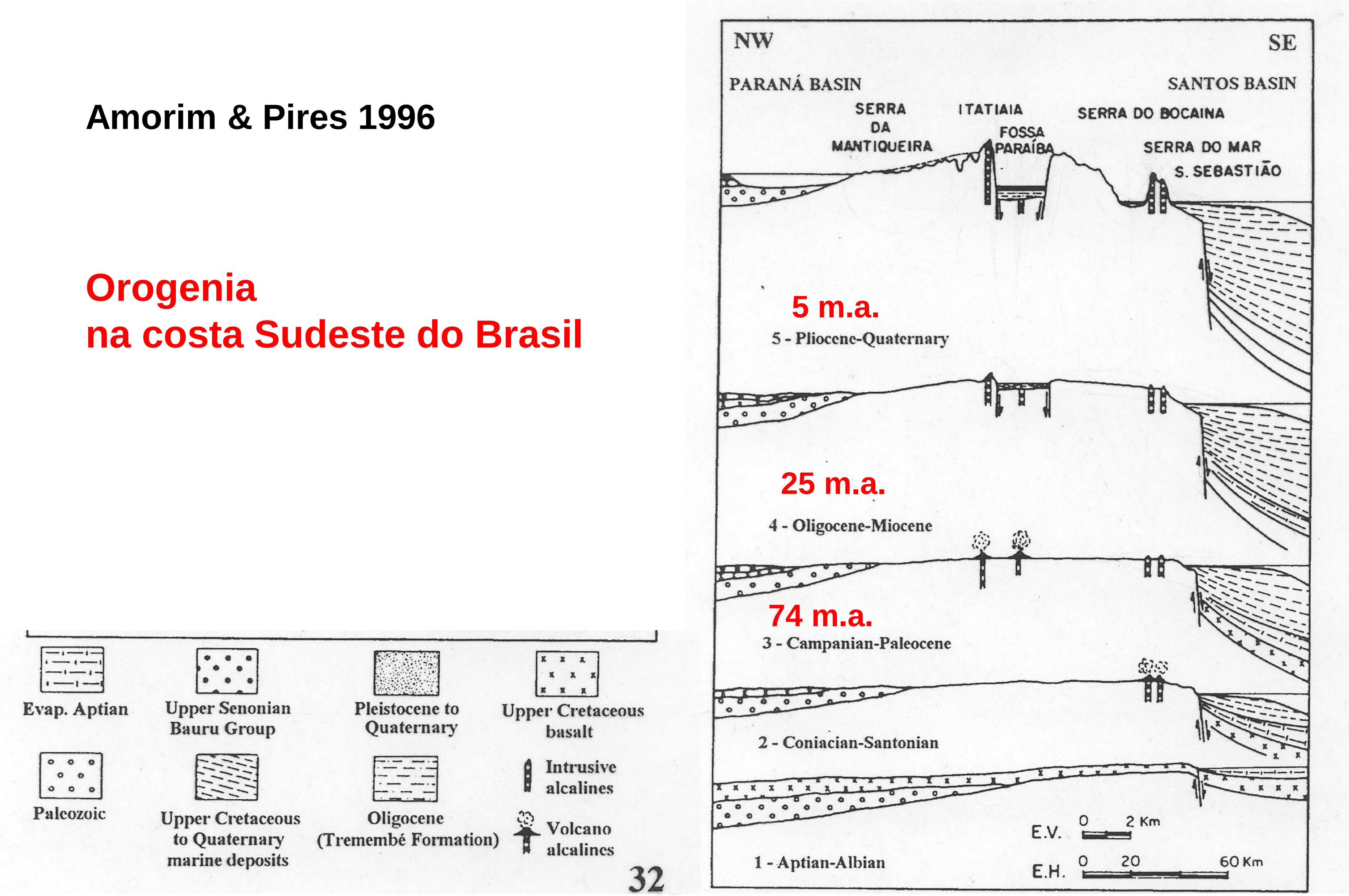


Figure 32. Middle Cretaceous-Quaternary history of a cross section southeastern Brazil. In the Campanian volcanic activity begins at the east (the Serra do Mar mountain system), with a second moutain system (Serra da Mantiqueira) arising in the Oligocene, more to the west.

ORIGEM E EVOLUÇÃO DA SERRA DO MAR

Almeida & Carneiro 1998

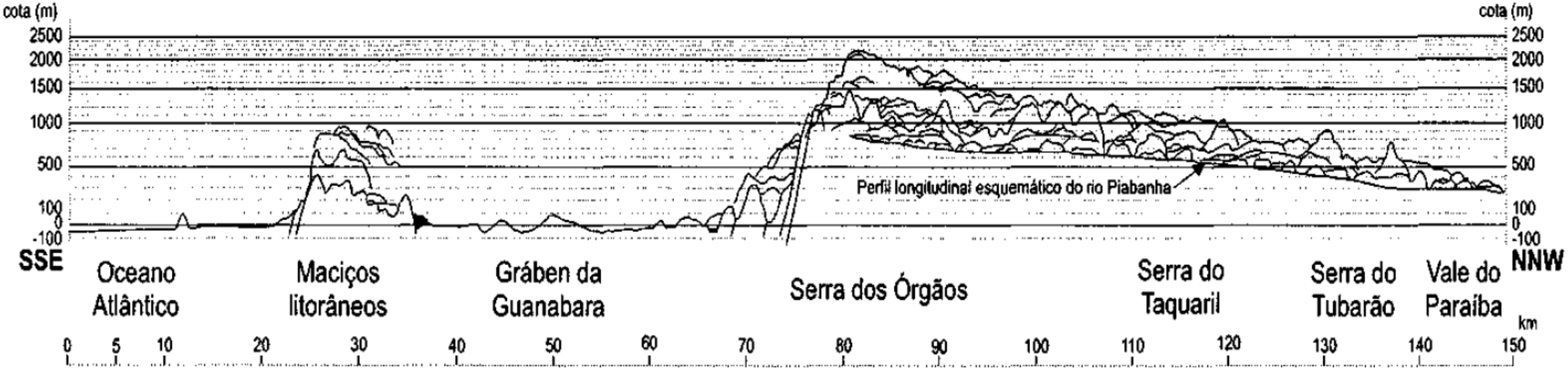


Figura 2 - Perfil esquemático transversal às estruturas geológicas da região entre o Oceano Atlântico e o Vale do Paraíba, no estado do Rio de Janeiro. A região correspondente ao Gráben da Guanabara acha-se indicada. Escala vertical logarítmica (modificado de Ruellan 1944)

CONEXÃO INTERCONTINENTAL

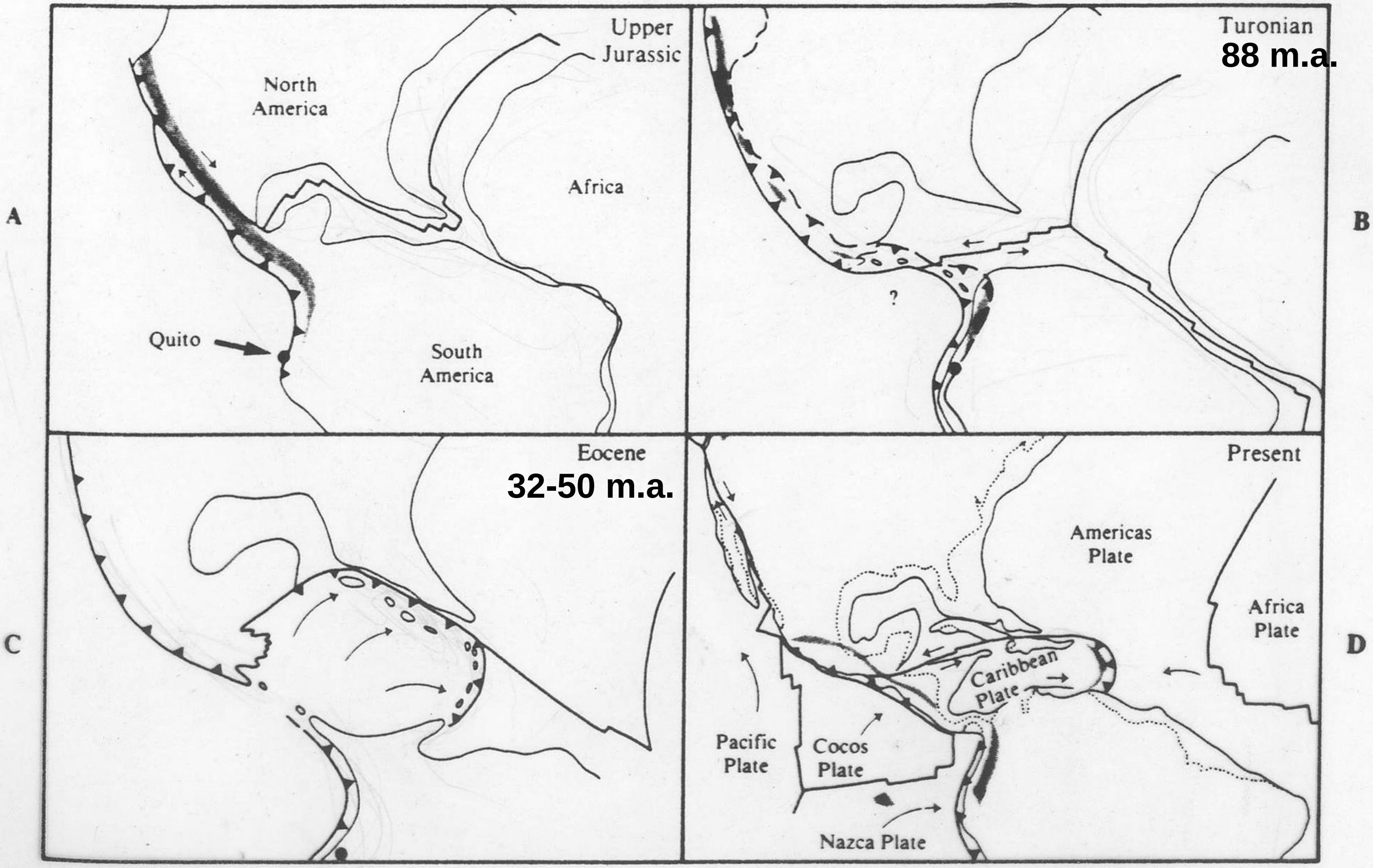


Figure 5.19
Sequential maps showing the reconstructed configuration of Central America and the Caribbean Sea relative to the nearby landmasses and oceans at various times in the past. The events described by these maps are explained in some detail in the text. (After Coney, 1982.)

Brown & Gibson 1986

CONEXÃO INTERCONTINENTAL

The role of immigrants in the assembly of the South American rainforest tree flora

Pennington & Dick 2004

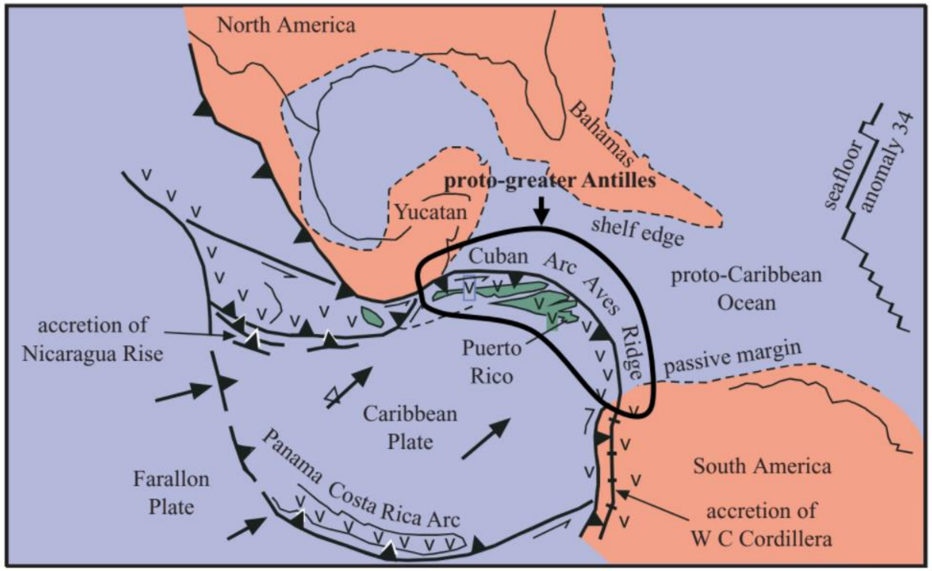


Figure 2. Campanian reconstruction of Middle America modified, with permission, from Morley (2003, fig. 6), highlighting the proto-Greater Antilles, which may have provided a filter-bridge in the Early Tertiary. Orange, thick continental crust; v symbols, volcanic arcs.

Arcos de ilhas - Cretáceo inferior

Proto-Antilhas como "ponte" até o Eoceno

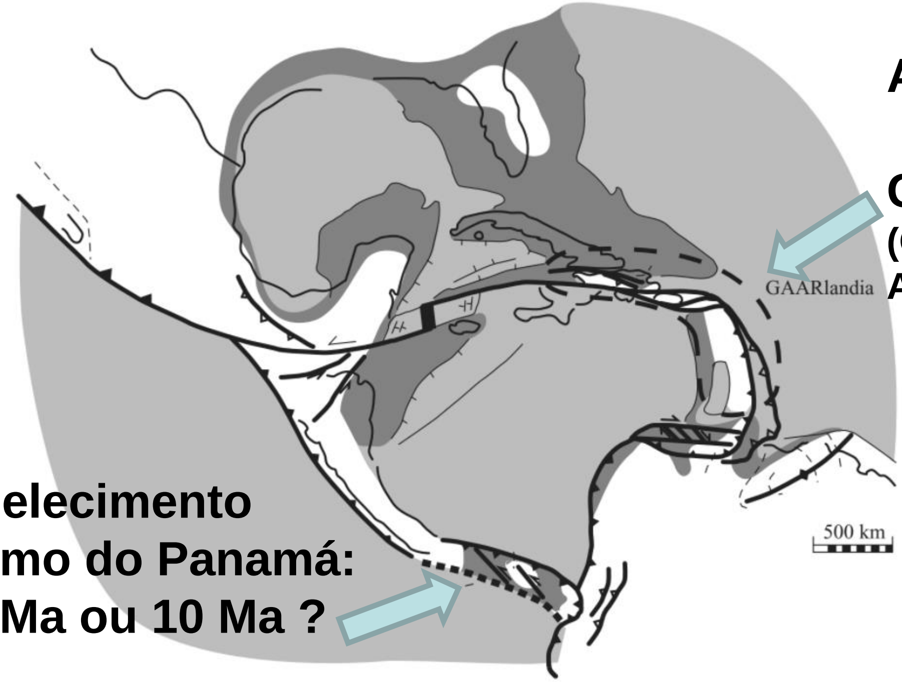


Figure 3. Caribbean tectonic reconstruction reproduced, with permission, following Pindell (1994, fig. 2.6L), highlighting the GAARlandia migration route. White, dry land and volcanic areas; dark grey, shallow water; light grey, deep water.

Alternativamente:

GAARlandia -
(Greater Antilhas + a hoje submersa Aves Ridge)

"ponte" q durou ca. 3 Ma, entre o Eoceno e Oligoceno (35-33 Ma)

Confrontar com o "isolamento esplêndido"!

Estabelecimento do istmo do Panamá: Ca. 3 Ma ou 10 Ma ?

CONEXÃO: emergência do istmo

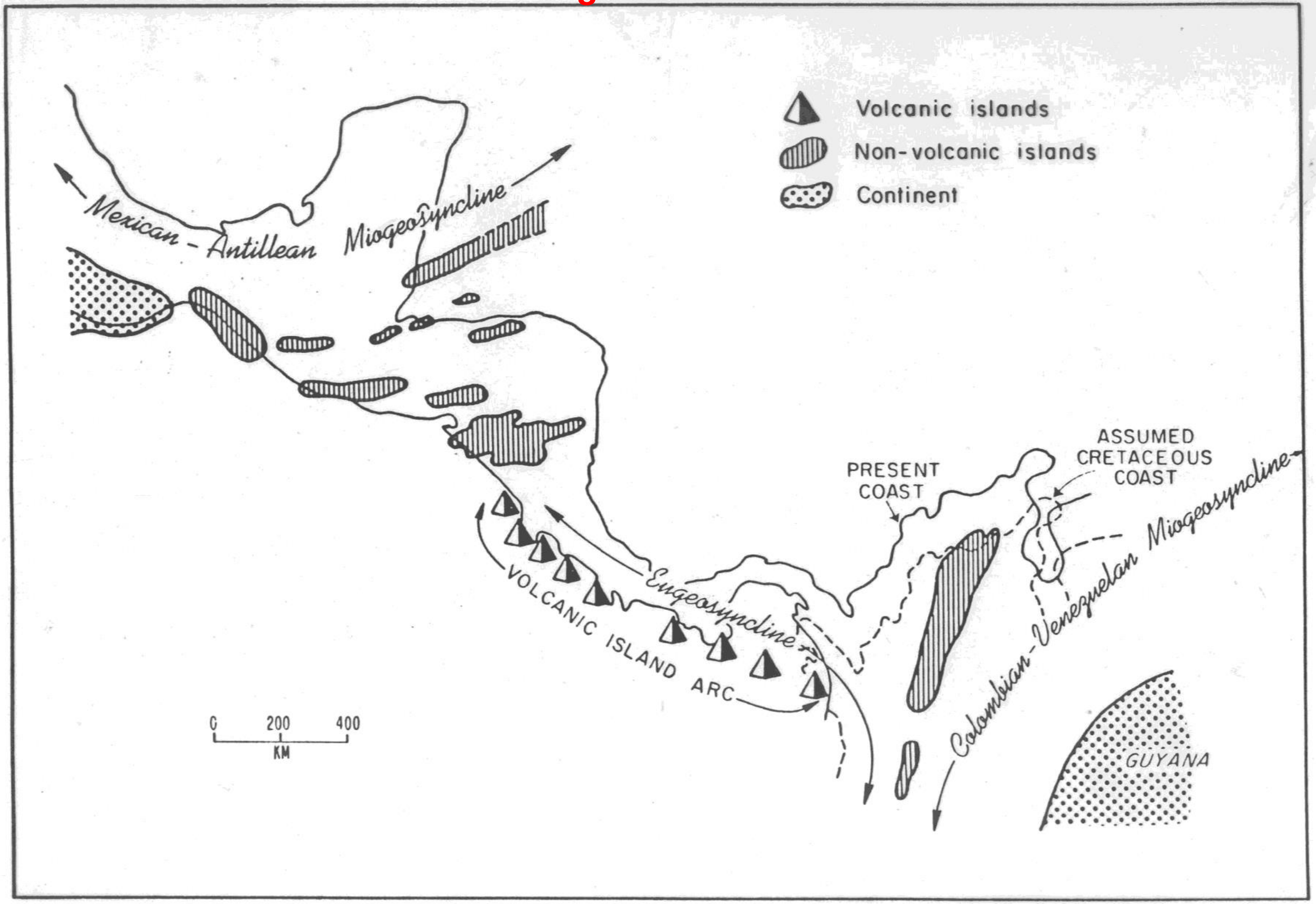


FIGURE 4. Paleogeographic relations between Central and South America in the Late Cretaceous (after Dengo, 1973).

Raven & Axelrod 1974

CONEXÃO INTERCONTINENTAL: emergência do istmo conectando AS e AC

Bacon et al. 2013

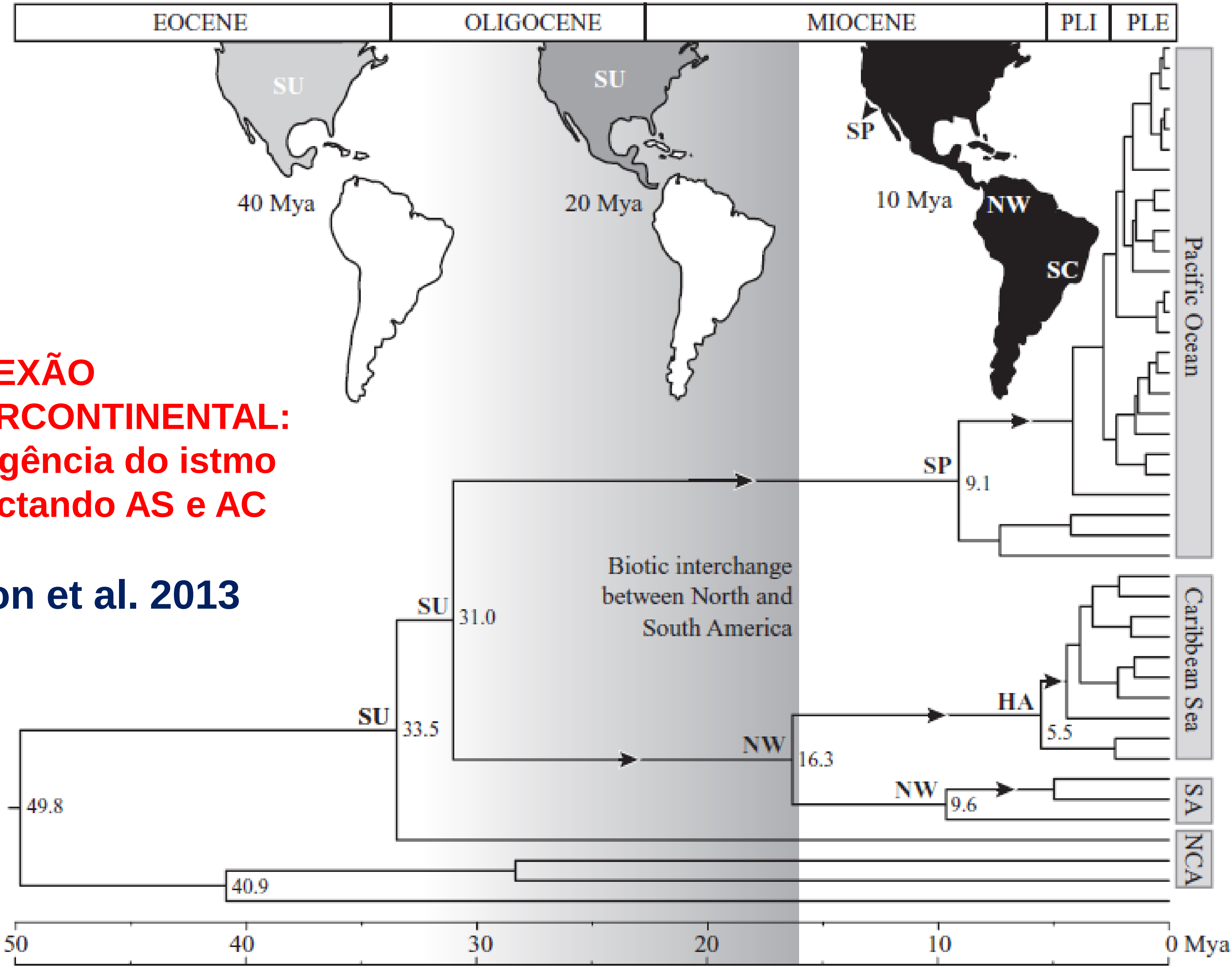


Figure 3. The most likely hypothesis of biogeographical events and diversification of Caribbean, Pacific, South American (SA) and North and Central American (NCA) lineages. Ancestral nodes are plotted against hypothetical palaeomaps of the

CONEXÃO: emergência do istmo como ponte contínua de terra (3,5 ou 10 Ma ?) fartamente documentada e demonstrada pela chegada de elementos temperados nas terras altas da AS e concomitante surgimento de táxons sul-americanos na AC.

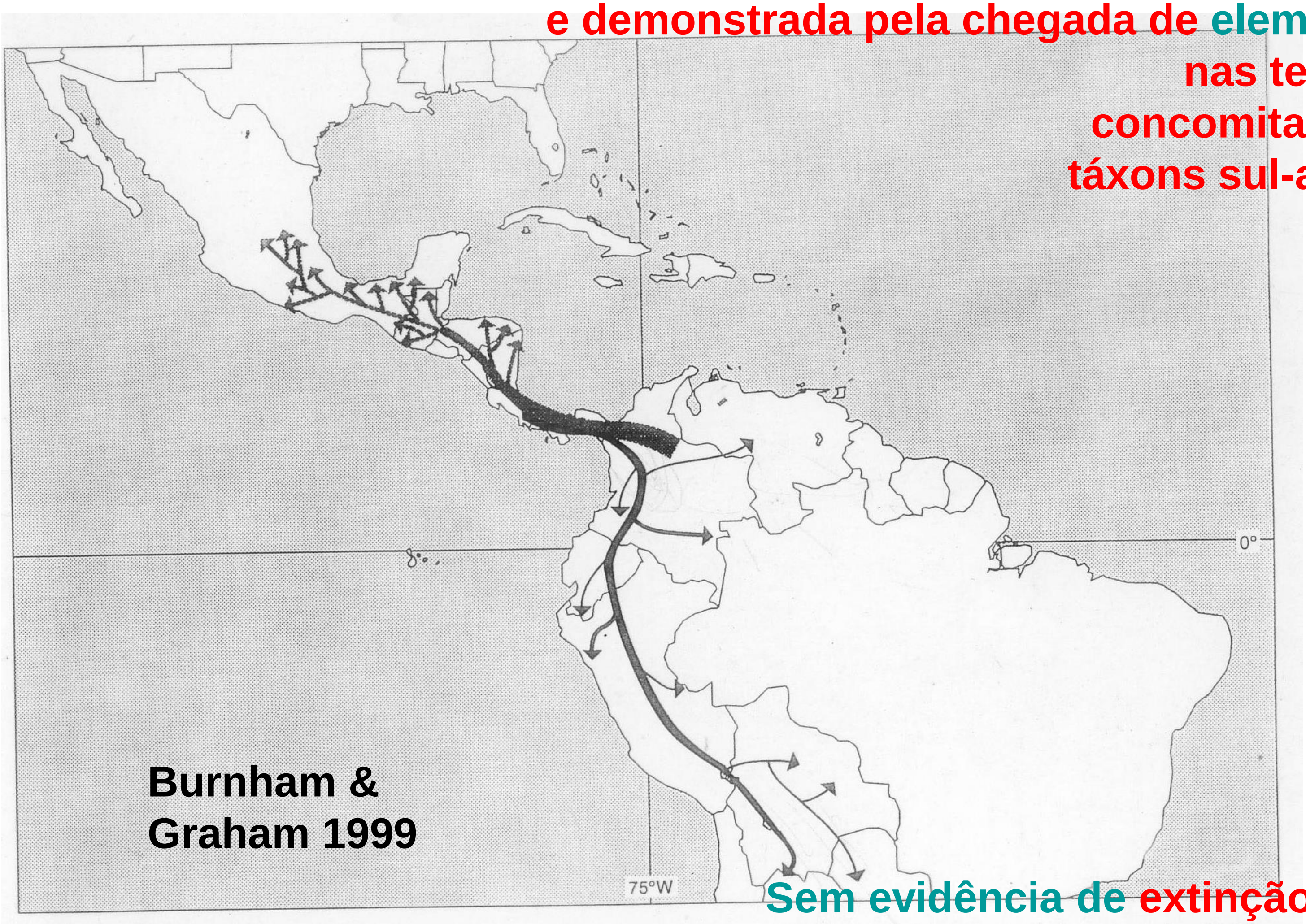


Figure 16. Woody plant migration and diversification following establishment of the Central American landbridge.

Burnham & Graham 1999

Sem evidência de extinção ou deslocamento de elementos vegetais tropicais de terras baixas pelos imigrantes do N (contraste com registro de mamíferos)

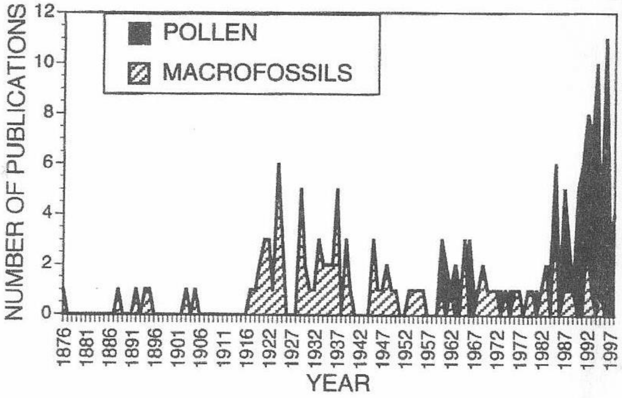


Figure 3. Publication activity in neoptropical paleobotany since 1876. Publications are coded with respect to the dominant organ reported: all macrofossils (leaves, fruits, seeds, wood) are grouped. Publications listed are primary reports of localities and fossil plant remains; no summaries or reviews are included.

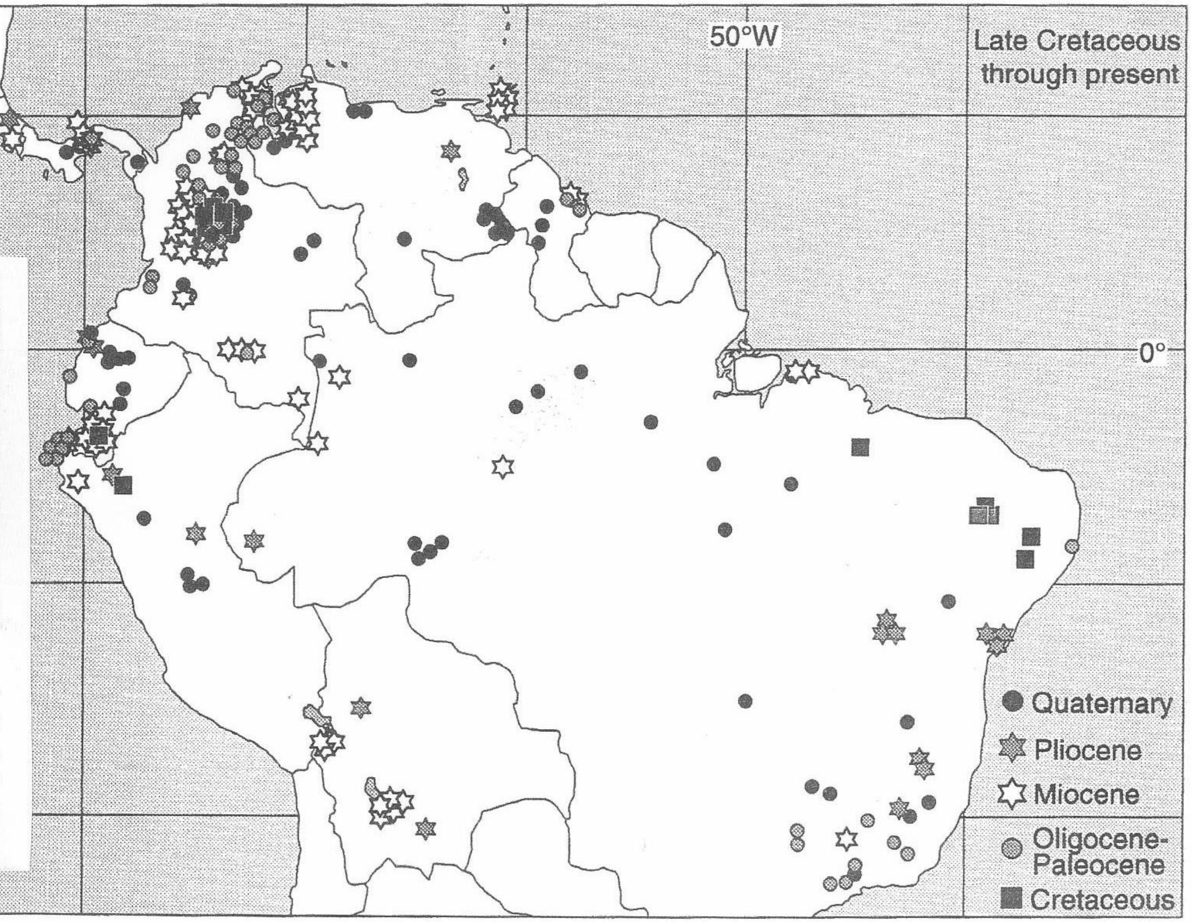


Figure 2. Distribution of published fossil plant localities in northern South America and southern Central America of Late Cretaceous to Quaternary age, referenced in Appendix 1.

**Burnham &
Graham 1999**

Gêneros gonduânicos difundindo-se para o norte

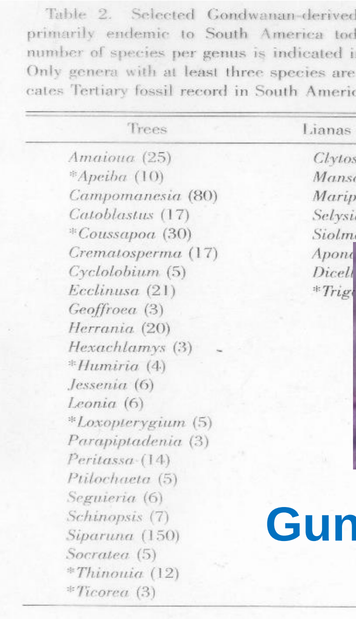


Table 2. Selected Gondwanan-derived genera, still primarily endemic to South America today. Estimated number of species per genus is indicated in parentheses. Only genera with at least three species are listed. * indicates Tertiary fossil record in South America.

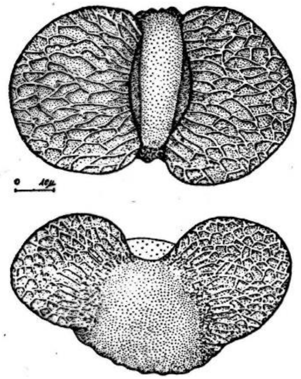
Trees	Lianas and vines
Amaioua (25)	*Clytostoma* (9)
**Apeiba* (10)	*Mansoa* (15)
Campomanesia (80)	*Maripa* (19)
Catoblastus (17)	*Selysia* (3)
**Coussapoa* (30)	*Siolmatra* (3)
Crematosperma (17)	*Apon*
Cyclolobium (5)	*Dicel*
Ecclinusa (21)	**Trig*
Geoffroea (3)	
Herrania (20)	
Hexachlamys (3)	
**Humiria* (4)	
Jessenia (6)	
Leonia (6)	
**Loxopterygium* (5)	
Parapiptadenia (3)	
Peritassa (14)	
Ptilochaeta (5)	
Seguieria (6)	
Schinopsis (7)	
Siparuna (150)	
Socratea (5)	
**Thinouia* (12)	
**Ticorea* (3)	

Drimys

Winteraceae

Gunneraceae

Gunnera



Podocarpaceae - *Podocarpus*

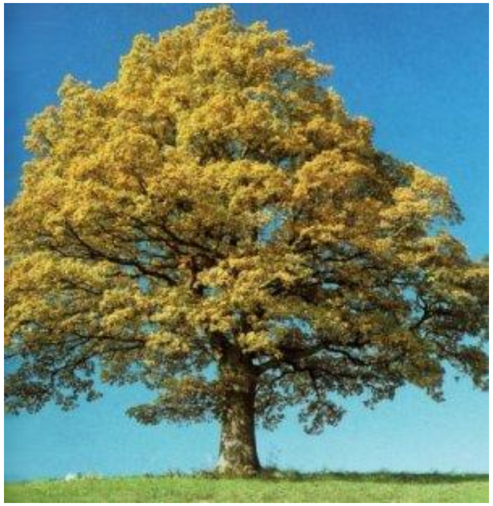
FIGURE 4. Northward extent of spread of Gondwana genera in tropical America.

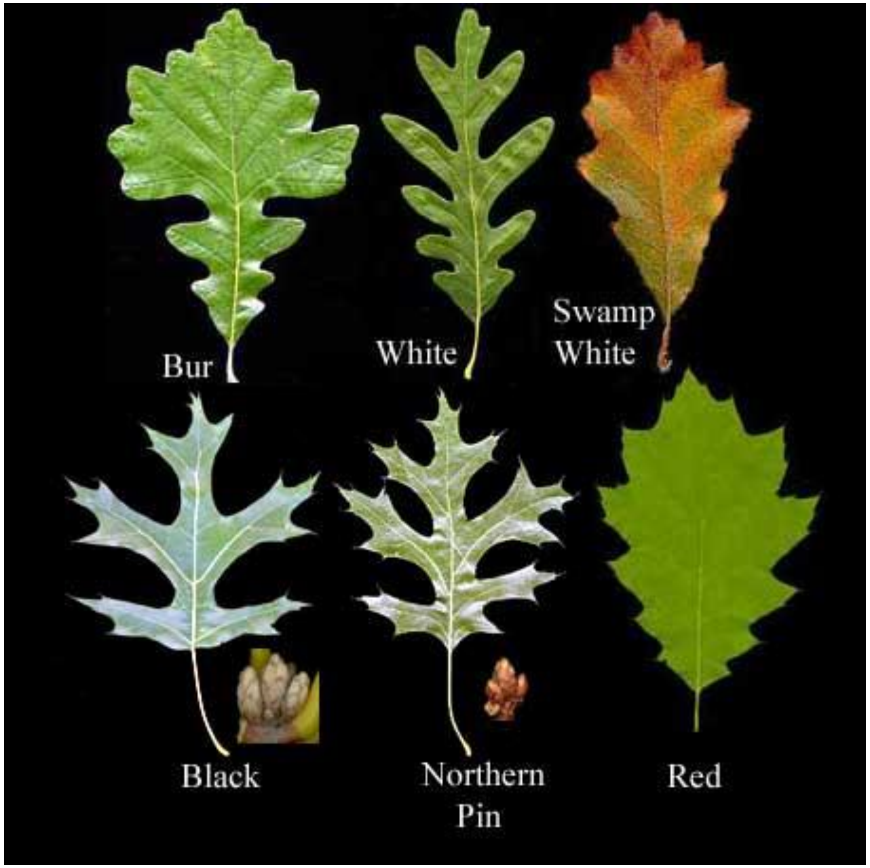
Webster in Churchill 1995

Burnham &
Graham 1999

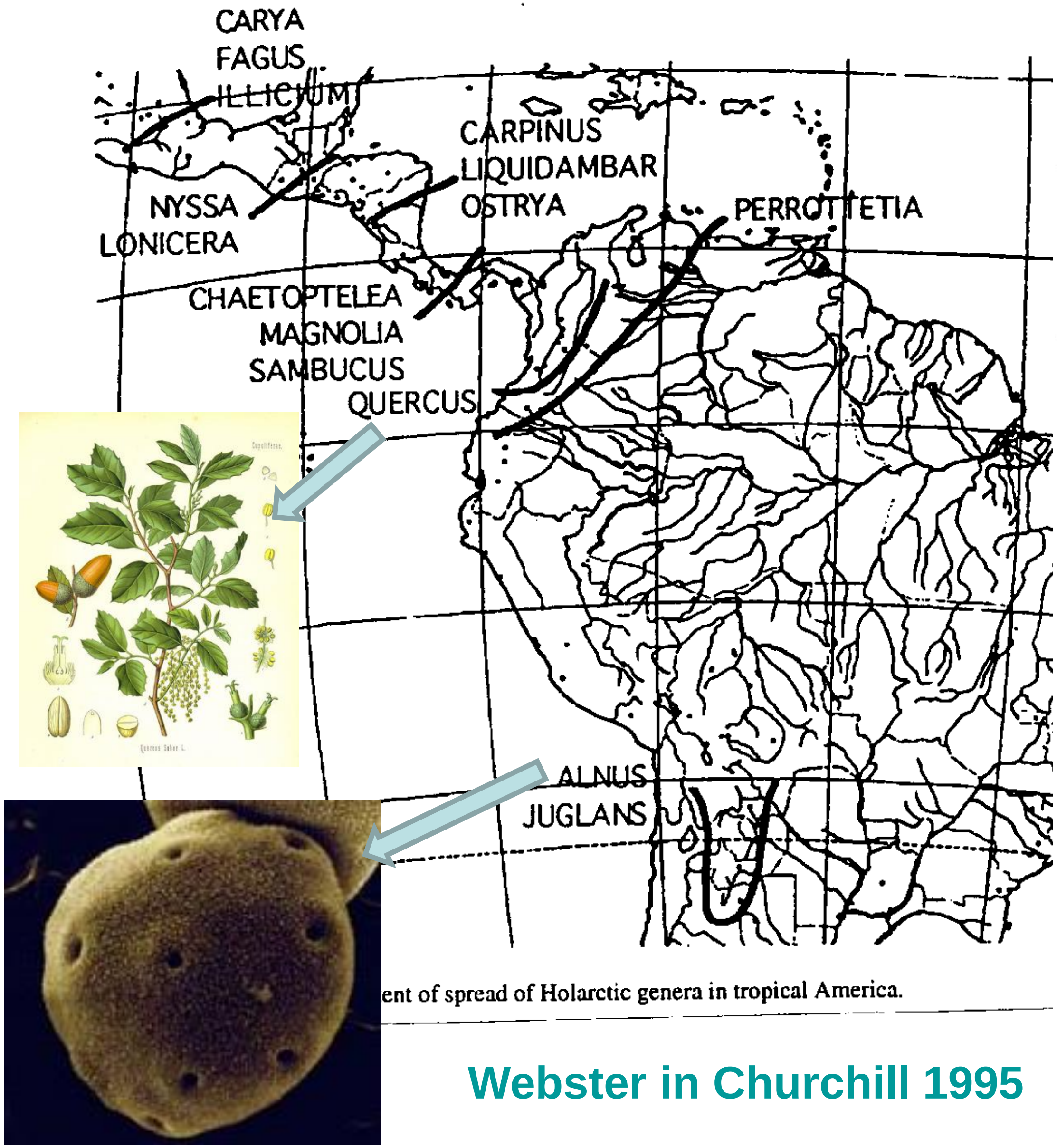
Gêneros laurasianos

Fagaceae
Quercus





Gêneros holárticos na Região Neotropical



ent of spread of Holarctic genera in tropical America.

Webster in Churchill 1995

Burnham & Graham 1999

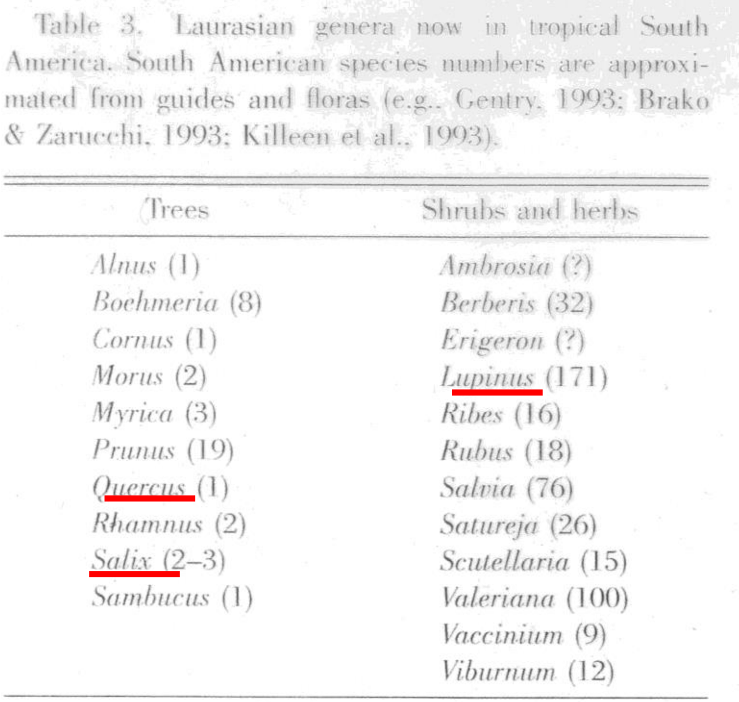


Table 3. Laurasian genera now in tropical South America. South American species numbers are approximated from guides and floras (e.g., Gentry, 1993; Brako & Zarucchi, 1993; Killeen et al., 1993).

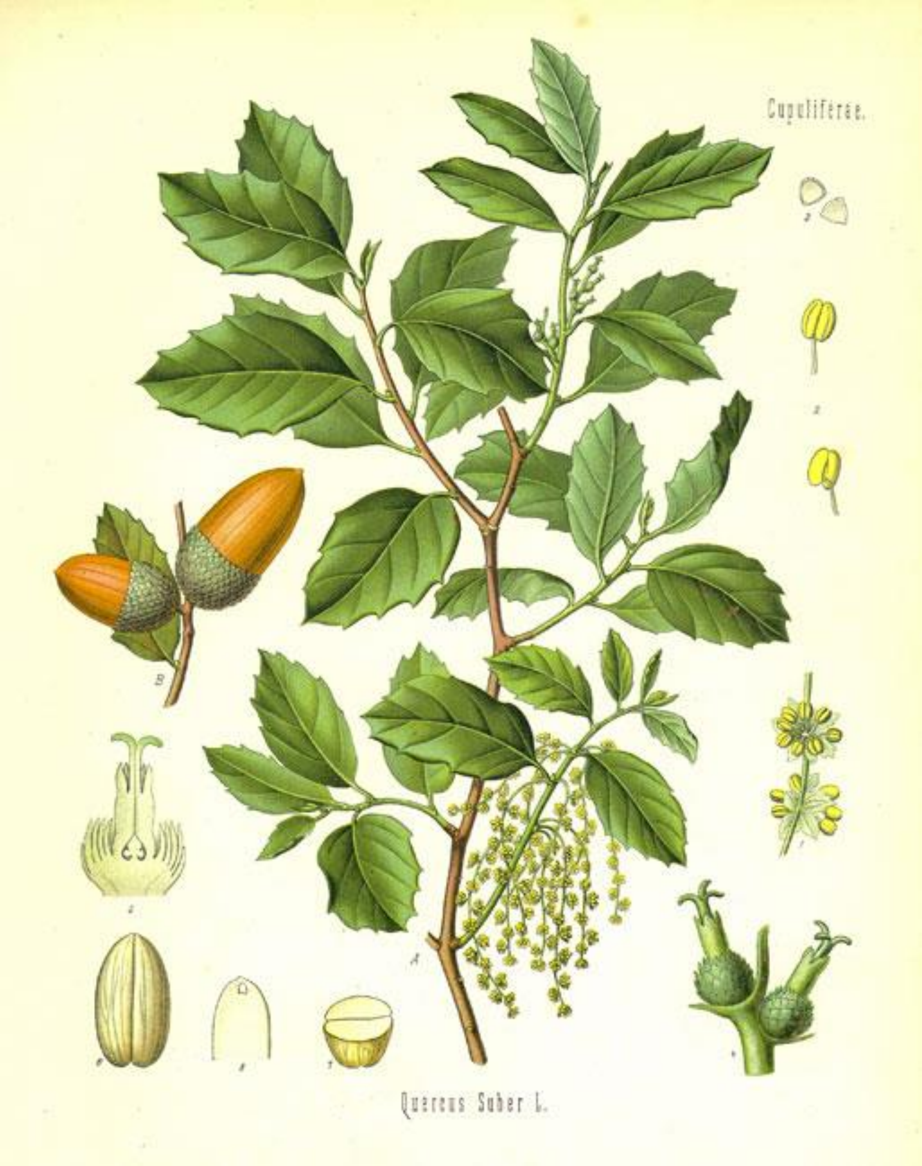
Trees	Shrubs and herbs
Alnus (1)	*Ambrosia* (?)
Boehmeria (8)	*Berberis* (32)
Cornus (1)	*Erigeron* (?)
Morus (2)	*Lupinus* (171)
Myrica (3)	*Ribes* (16)
Prunus (19)	*Rubus* (18)
Quercus (1)	*Salvia* (76)
Rhamnus (2)	*Satureja* (26)
Salix (2–3)	*Scutellaria* (15)
Sambucus (1)	*Valeriana* (100)
	Vaccinium (9)
	Viburnum (12)

Salix

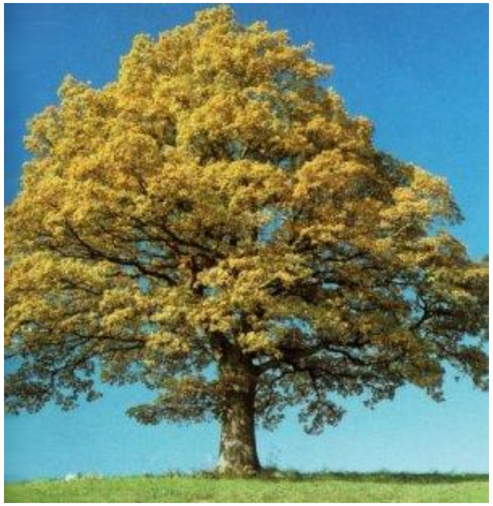
Salicaceae

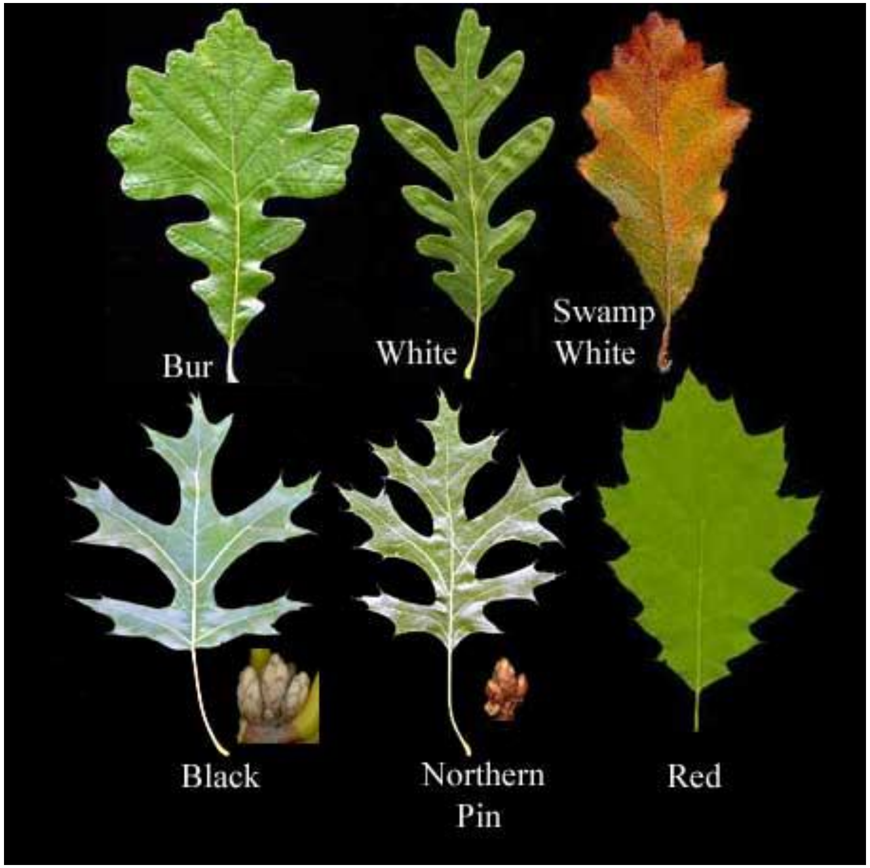
Burnham &
Graham 1999

Gêneros laurasianos



Fagaceae
Quercus





PALEOCLIMAS

Clima variou muito ao longo da história da Terra:

1. Deriva continental = mudança climática local!

Velocidade da deriva: 12 – 13 cm/ano no Cretáceo
(= mais atividade vulcânica = efeito estufa = clima quente)
depois mais lenta (2-3 cm/ano) = clima mais frio

2. GLACIAÇÕES: muitas ocorreram nos últimos bilhões de anos.

Willis & Niklas 2004

160 K. J. Willis and K. J. Niklas *The role of the Ice Ages in plant macroevolution*

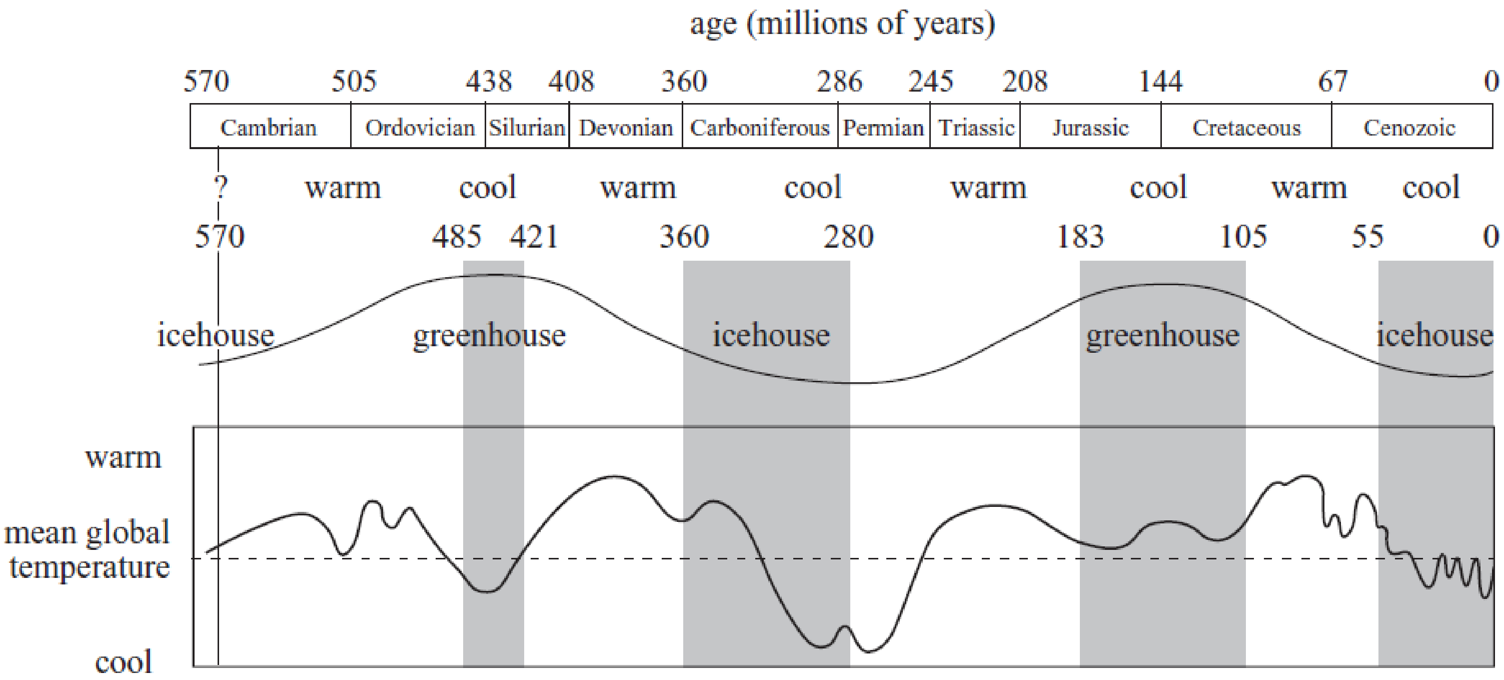


Figure 1. Climatic megacycles during the past 570 Myr (Huggett 1997; Willis & McElwain 2002). Sources for greenhouse/icehouse data from Fischer (1984), Crowley & North (1991) and Crowley (1998); warm and cold modes from Frakes *et al.* (1992); generalized temperature curve from Martin (1998).

Seward 1959 – paisagem cretácica na Groenlândia

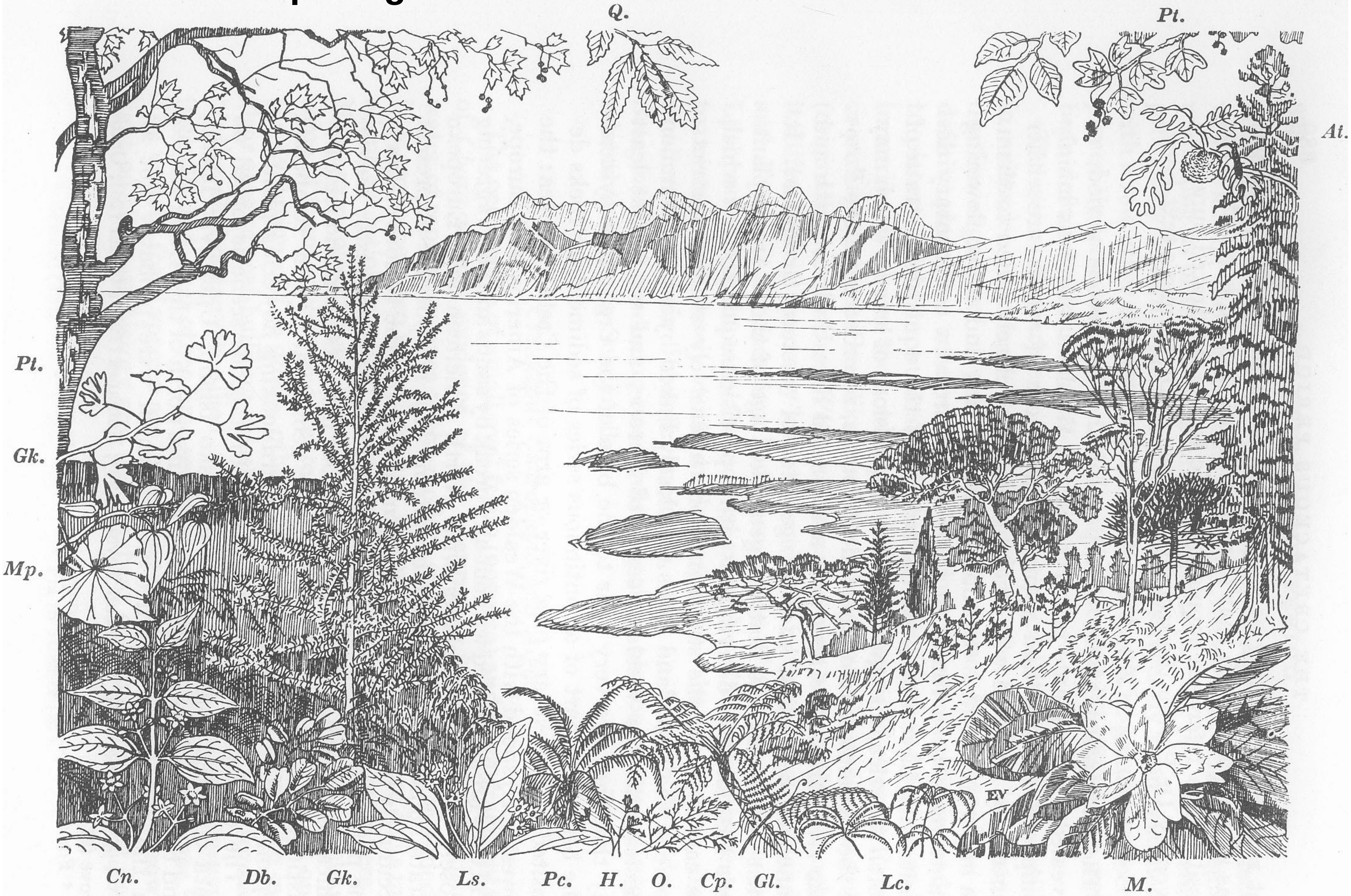


FIG. 107. A scene on the west coast of Greenland in the earlier part of the Cretaceous period. (Drawn by Mr Edward Vulliamy.) *At. Artocarpus*; *Cn. Cinnamomum*; *Cp. Cladophlebis*; *Db. Dalbergites*; *Gk. Ginkgoites*; *Gl. Gleichenites*; *H. Hausmannia*; *Lc. Laccopteris*; *Ls. Laurus*; *M. Magnolia*; *Mp. Menispermites*; *O. Onychiopsis*; *Pc. Pseudoctenis*; *Pt. Platanus*; *Q. Quercus* (oak).

Seward 1959 – paisagem oligocênica na Europa

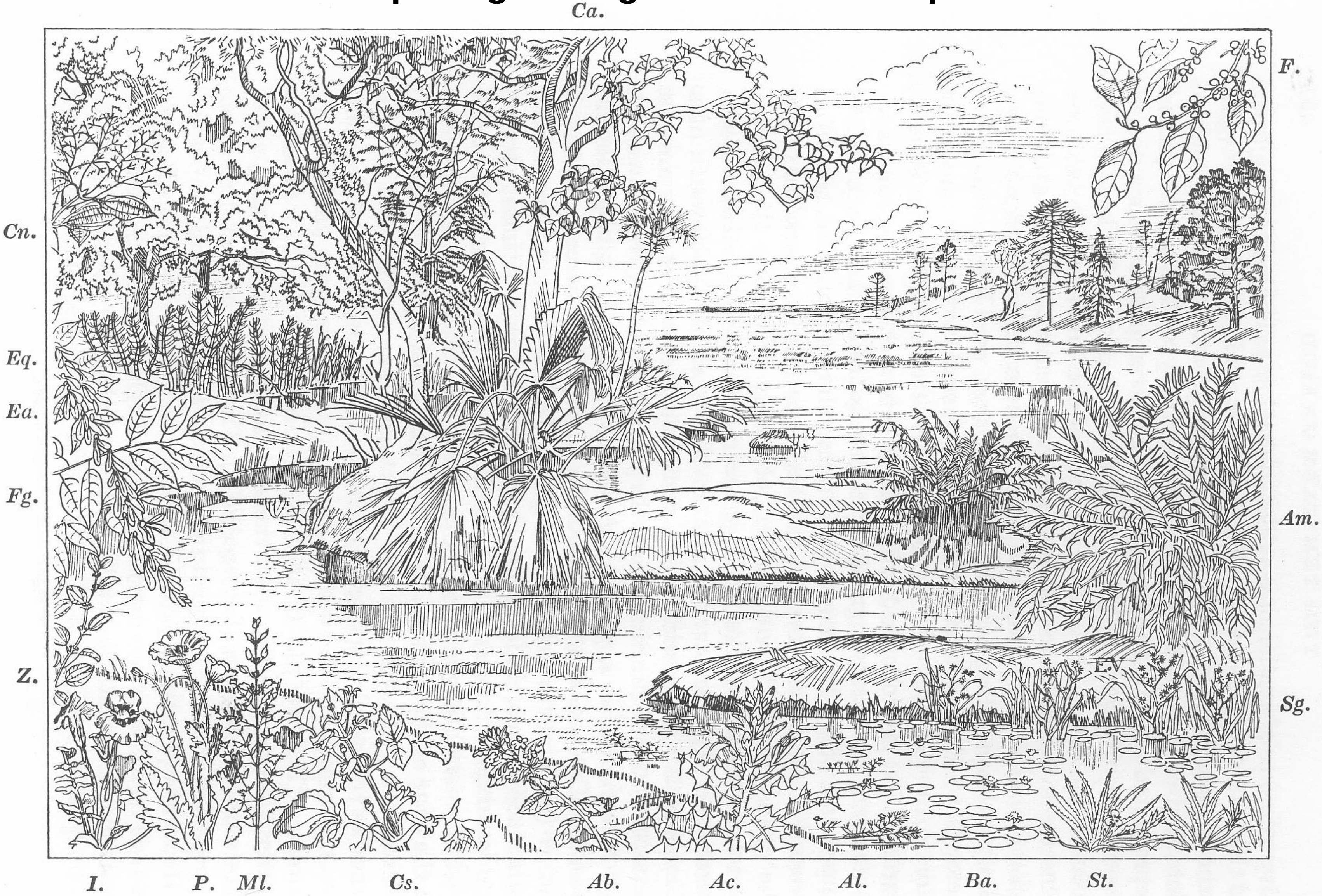


FIG. 119. Reconstruction of an Oligocene landscape in the Isle of Wight. (Drawn by Mr Edward Vulliamy.) *Ab. Abelia*; *Ac. Acanthus*; *Al. Aldrovanda*; *Am. Acrostichum*; *Ba. Brasenia*; *Ca. Catalpa*; *Cn. Cinnamomum*; *Cs. Clematis*; *Ea. Engelhardtia*; *Eq. Equisetum*; *F. Ficus*; *Fg. Fagus*; *I. Incarvillea*; *Ml. Melissa*; *P. Papaver*; *Sg. Sparganium*; *St. Stratiotes*; *Z. Zizyphus*.

Seward 1959 – paisagem quaternária na Inglaterra

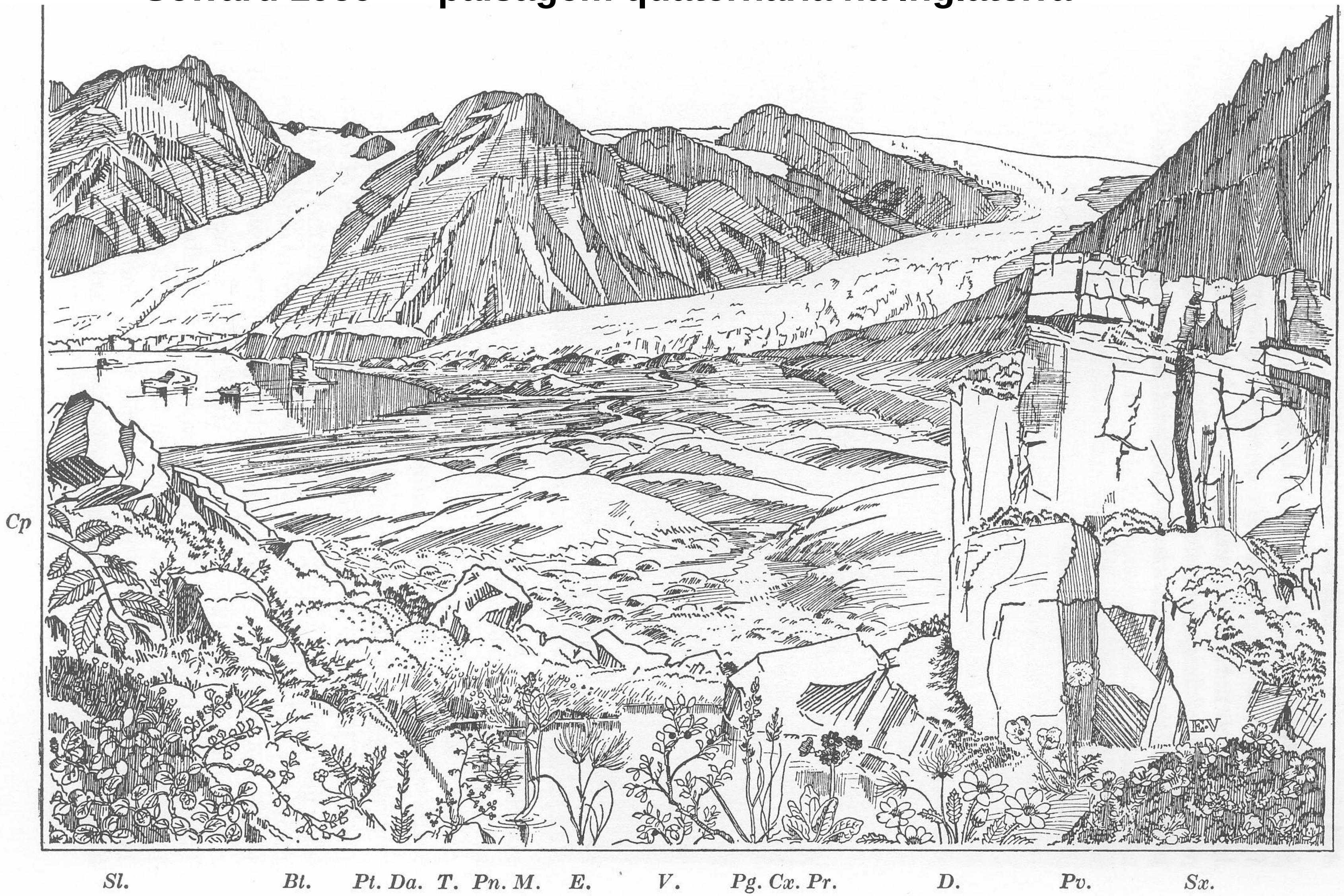


FIG. 127. An English landscape in the latter part of the Quaternary Ice Age. (Drawn by Mr Edward Vulliamy.) *Bt. Betula*; *Cp. Carpinus*; *Cx. Carex*; *D. Dryas*; *Da. Draba*; *E. Eriophorum*; *M. Menyanthes*; *Pg. Polygonum*; *Pn. Potamogeton*; *Pr. Primula*; *Pt. Potentilla*; *Pv. Papaver*; *Sl. Salix*; *Sx. Saxifraga*; *T. Thalictrum*; *V. Vaccinium*.

Glaciações pleistocênicas:

Estimativas de mudanças de temperatura por métodos quantitativos:

Ciclos de Milankovitch

Suguio 1999

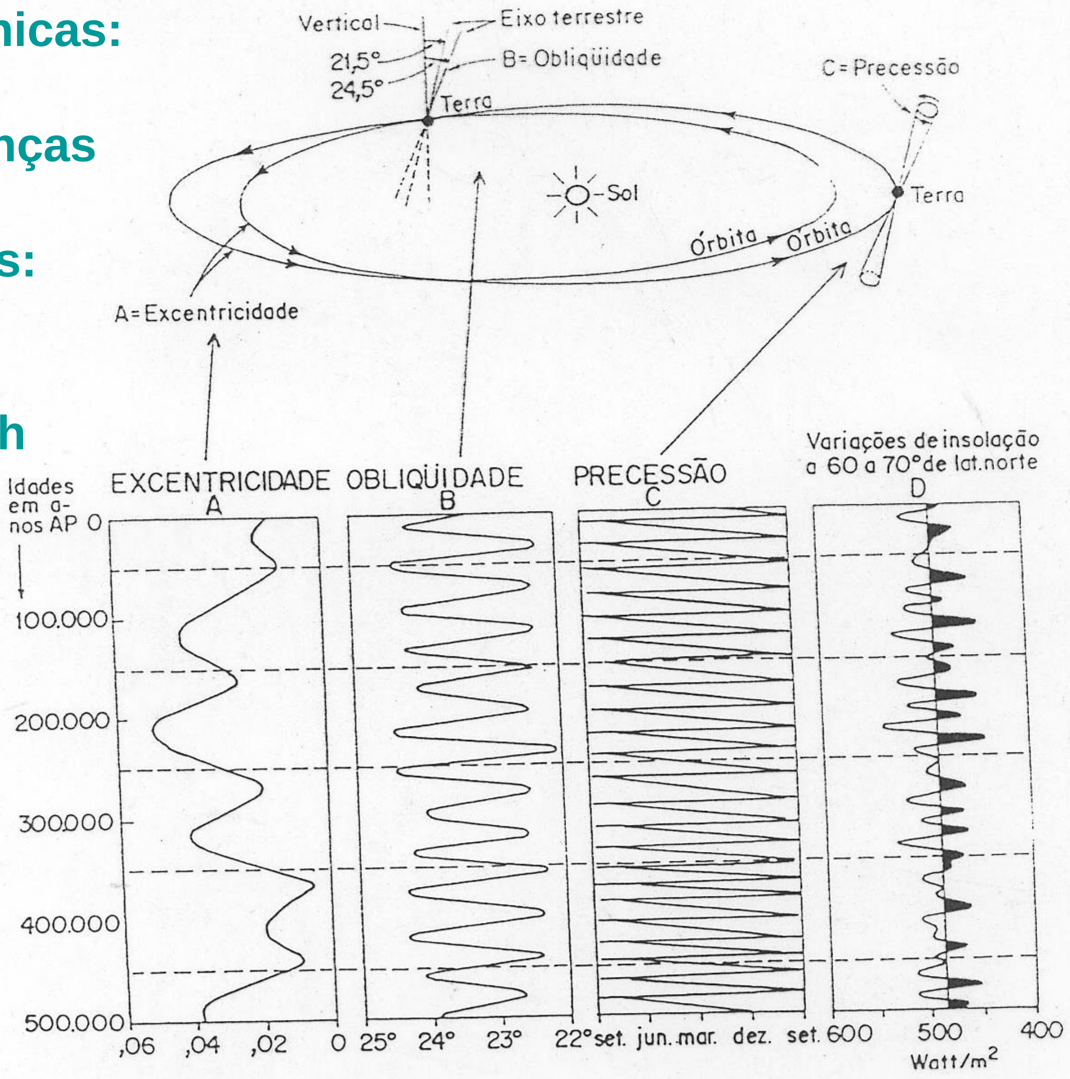


Fig. 10 - Flutuações das variáveis astronômicas calculadas por Milankovitch para os últimos 500.000 anos e as oscilações na insolação sobre a Terra em latitude norte 60 a 70°, durante o mês de julho. A = excentricidade da órbita terrestre; B = Obliqüidade da eclíptica: C = precessão de equinócios durante o periélio, quando a Terra está mais próxima do Sol. Variações de insolação: branco = períodos quentes e preto = períodos frios (Modificado de Covey, 1984 por Andersen & Borns Jr., 1994).

13

Ciclos de Milankovitch

Brown & Lomolino 1998

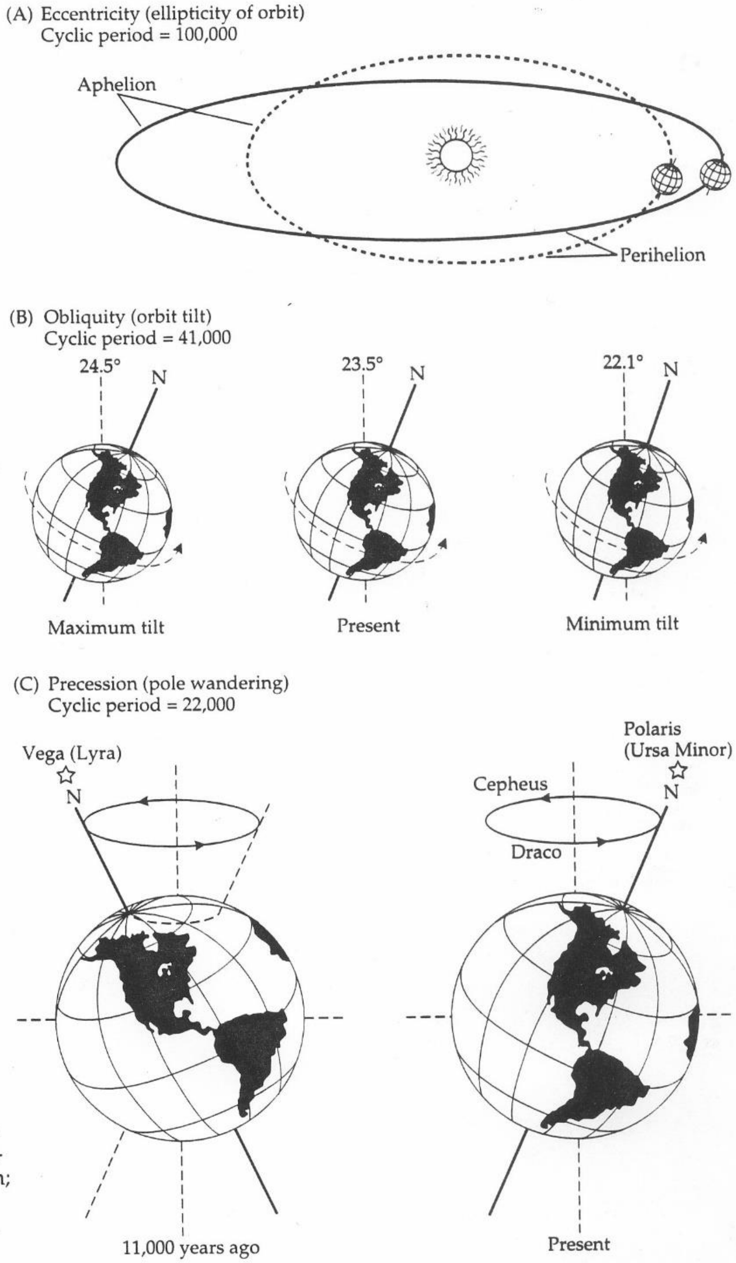


Figure 7.3 Milankovitch cycles are periodic changes in the eccentricity, obliquity, and precession of the earth's orbit. Each of these changes influences the earth's interception of solar radiation; therefore, these cycles may have been largely responsible for the glacial cycles of the Pleistocene. (After Gates 1993.)

Glaciações pleistocênicas: em média 10.000 anos cada

Métodos quantitativos em fósseis marinhos:

- **taxa de isótopos de O em $CaCO_3$**
- **razão Ca/Se**

14 Quaternary events 413

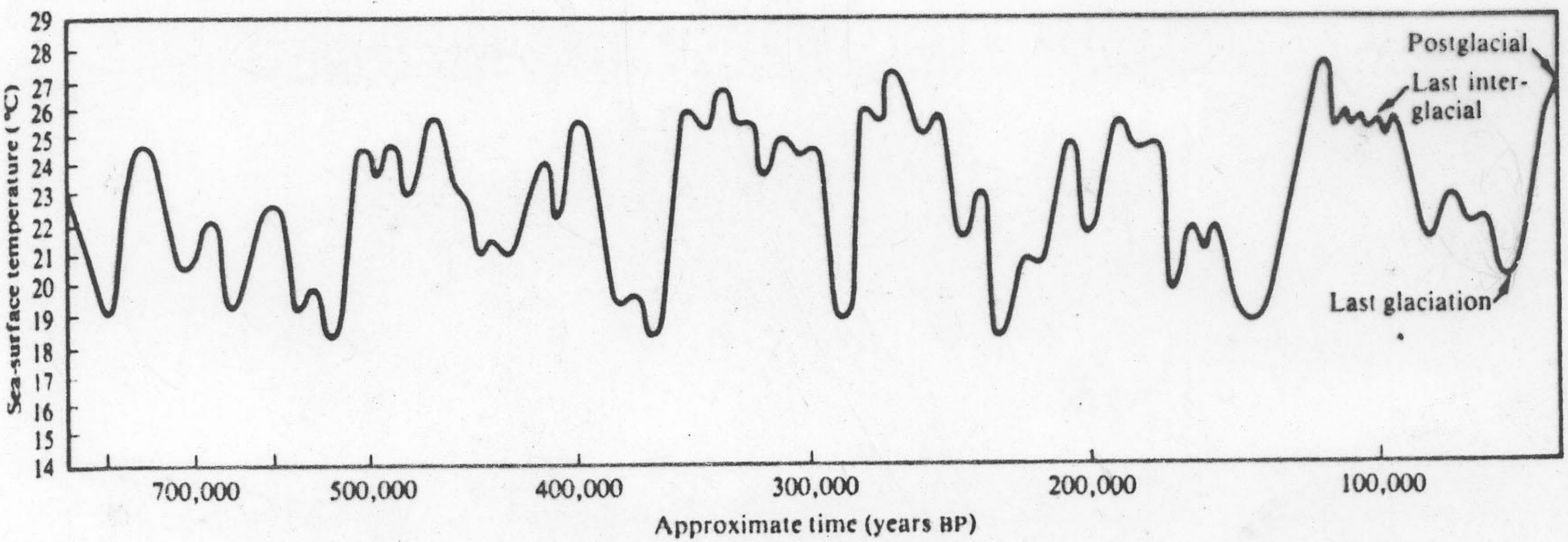


Figure 14.1
Sea-surface temperature variations at a typical tropical locality over the last 800,000 years. This pattern has been reconstructed from the $^{18}O/^{16}O$ isotope values obtained from materials in the skeletons of surface-dwelling Foraminifera deposited in deep ocean sediments. Warmer temperatures indicate interglacial periods, but not all colder water temperatures correspond to glacial episodes.

Brown & Gibson 1986

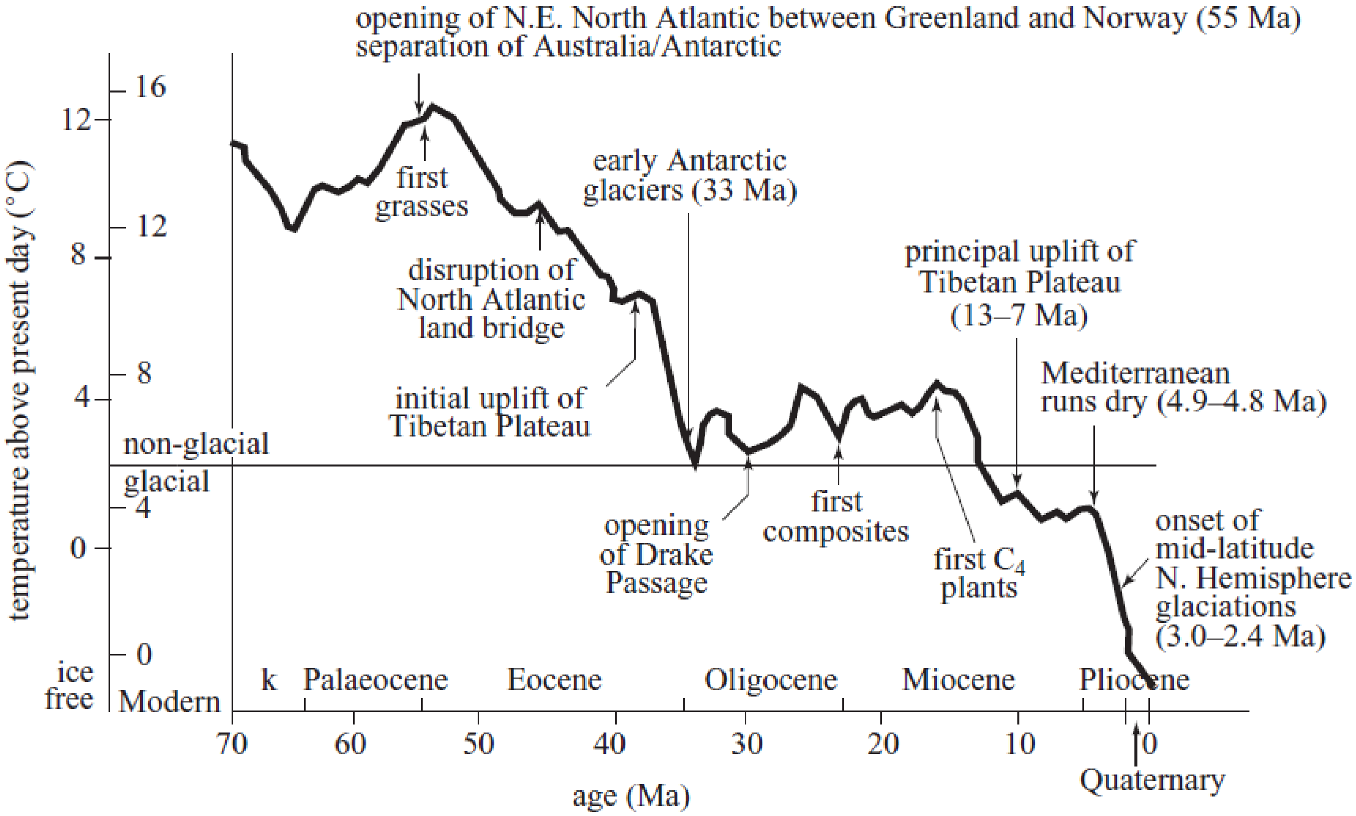


Figure 7. Temperature trends in the Tertiary, provided from oxygen isotope analysis of composite bethic foraminiferal records from Atlantic Deep Sea Drilling Program sites (Miller *et al.* 1987), where temperature is shown as degrees Celsius above present-day values. Note that the temperature scale determined from oxygen isotope analysis varies for an ice-free/modern world and that the transition between the two scales should be applied at the Eocene–Oligocene boundary (*ca.* 35 Ma). Against this temperature record are indicated major geological and botanical events during the Tertiary (from Graham (1999) and Willis & McElwain (2002)).

Glaciações pleistocênicas: em média 10.000 anos cada
Métodos quantitativos indiretos:
- taxa de 14C atmosférico inferida pelo 14C de anéis de madeiras:

-correlação negativa
da densidade estomática
com aumento de nível
de CO2 atmosférico:
d.e. reduziu 40%
em *Quercus*
nos últimos 200 anos!

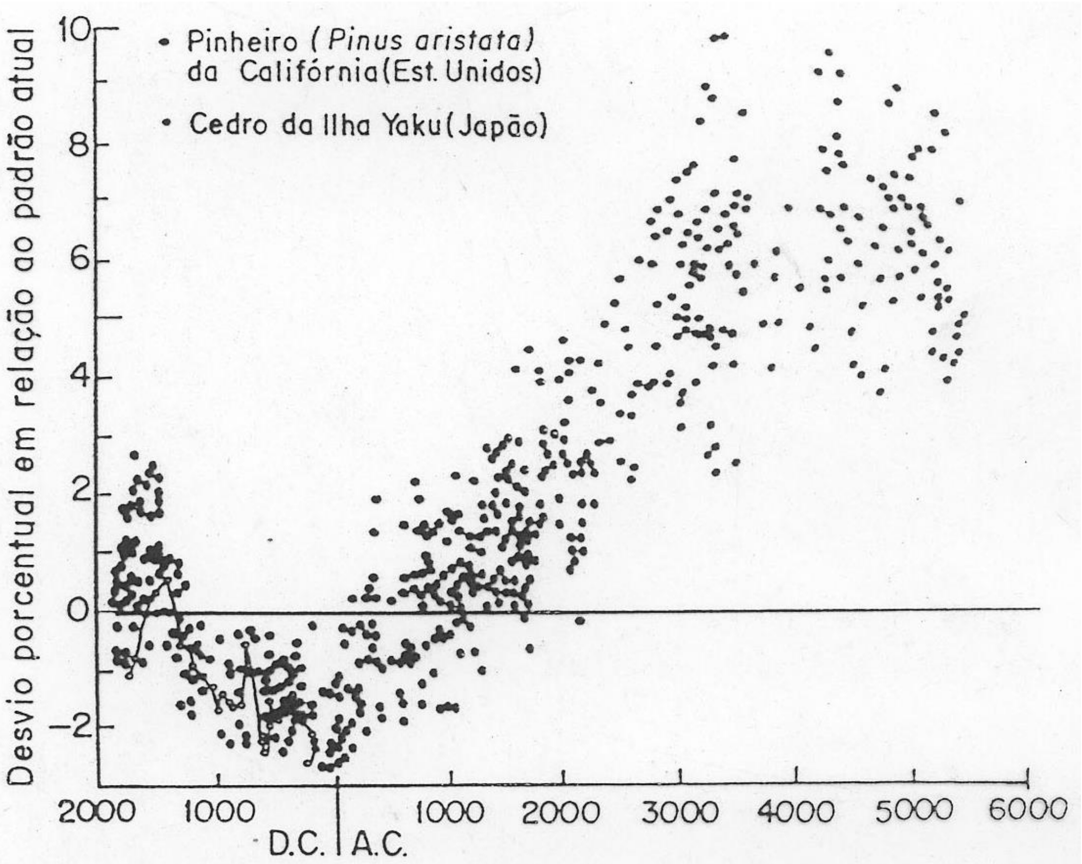


Fig. 71 - Variações das concentrações de ^{14}C na atmosfera nos últimos milhares de anos, determinadas em anéis de crescimento de árvores (Kigoshi, 1977). Cada ponto do gráfico foi obtido pela diferença entre os teores de ^{14}C em cada anel da árvore e na atmosfera, que foram consideradas constantes.

4 Glaciações pleistocênicas

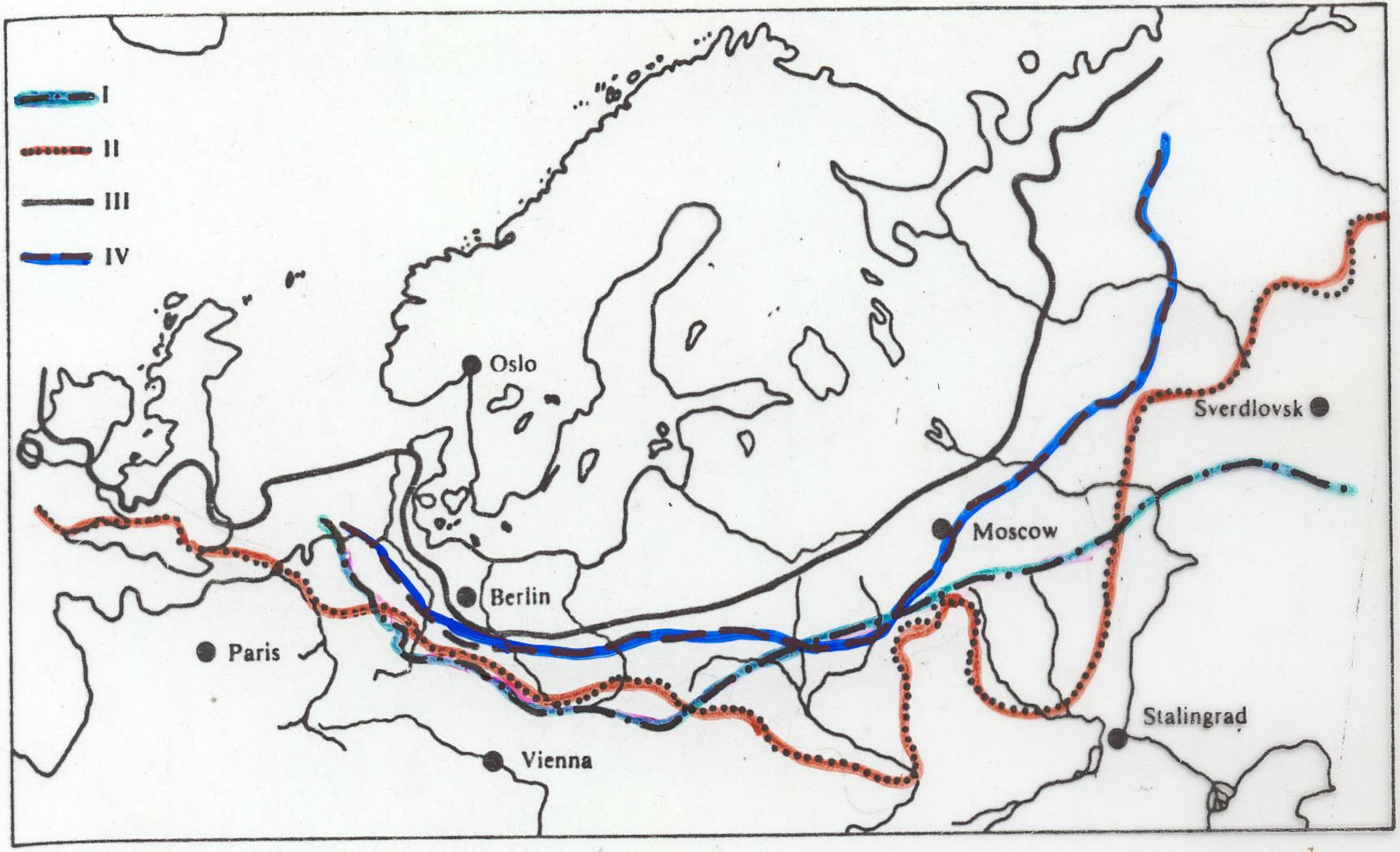
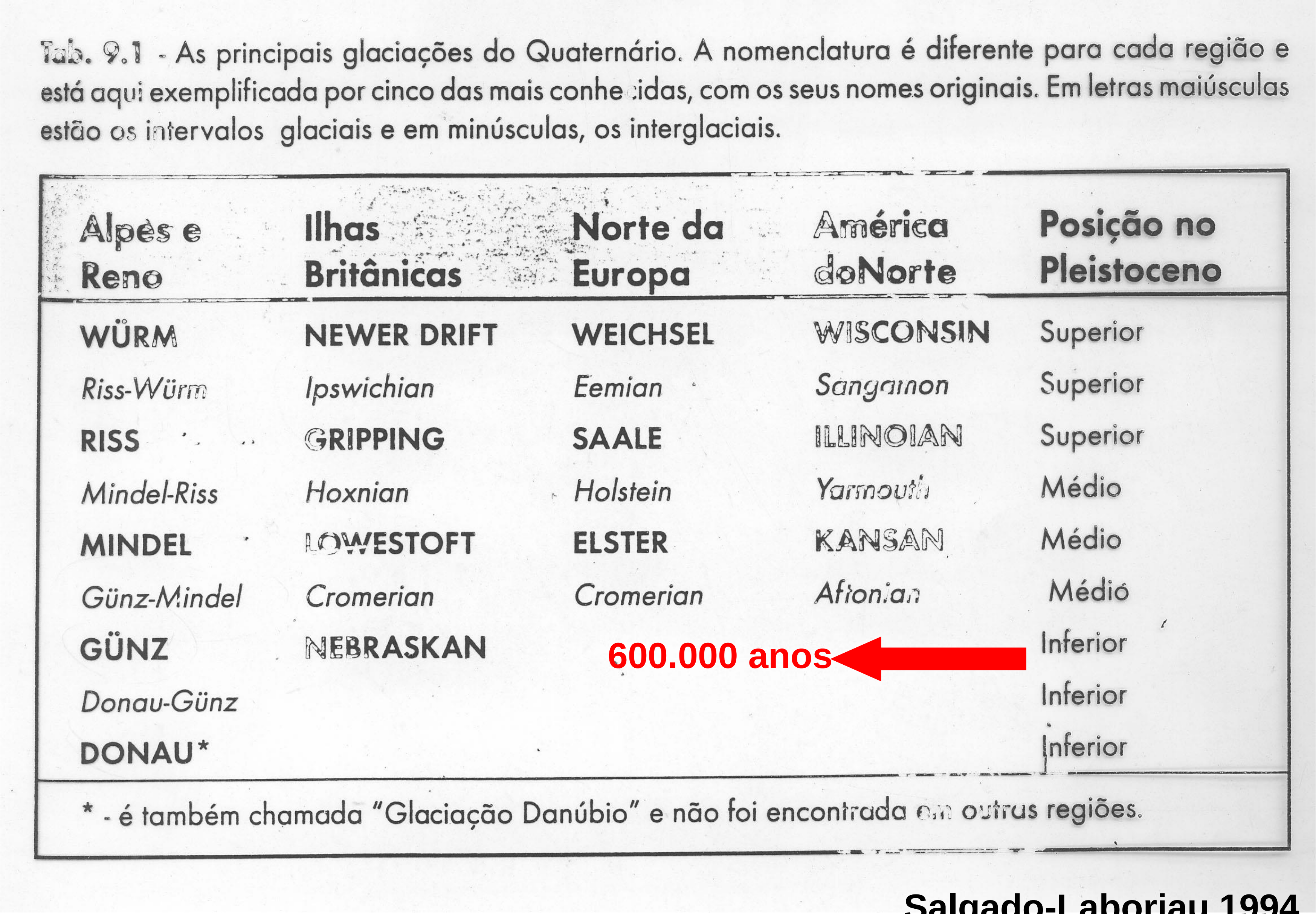


Figure 14.2
Limits of the continental ice sheets in northern Europe at various times during the Pleistocene. (After West, 1977.) The lines (I to IV) indicate the southernmost limit of the four major glacial ice sheets (oldest to youngest).



Tab. 9.1 - As principais glaciações do Quaternário. A nomenclatura é diferente para cada região e está aqui exemplificada por cinco das mais conhecidas, com os seus nomes originais. Em letras maiúsculas estão os intervalos glaciais e em minúsculas, os interglaciais.

Alpes e Reno	**Ilhas Britânicas**	**Norte da Europa**	**América doNorte**	**Posição no Pleistoceno**
WÜRM	NEWER DRIFT	WEICHSEL	WISCONSIN	Superior
Riss-Würm	*Ipswichian*	*Eemian*	*Sangamon*	Superior
RISS	GRIPPING	SAALE	ILLINOIAN	Superior
Mindel-Riss	*Hoxnian*	*Holstein*	*Yarmouth*	Médio
MINDEL	LOWESTOFT	ELSTER	KANSAN	Médio
Günz-Mindel	*Cromerian*	*Cromerian*	*Aftonian*	Médio
GÜNZ	NEBRASKAN			Inferior
Donau-Günz				Inferior
DONAU*				Inferior

* - é também chamada "Glaciação Danúbio" e não foi encontrada em outras regiões.

600.000 anos ←

Salgado-Laboriau 1994

“Pequena Era Glacial” - séc. XIII até 1750

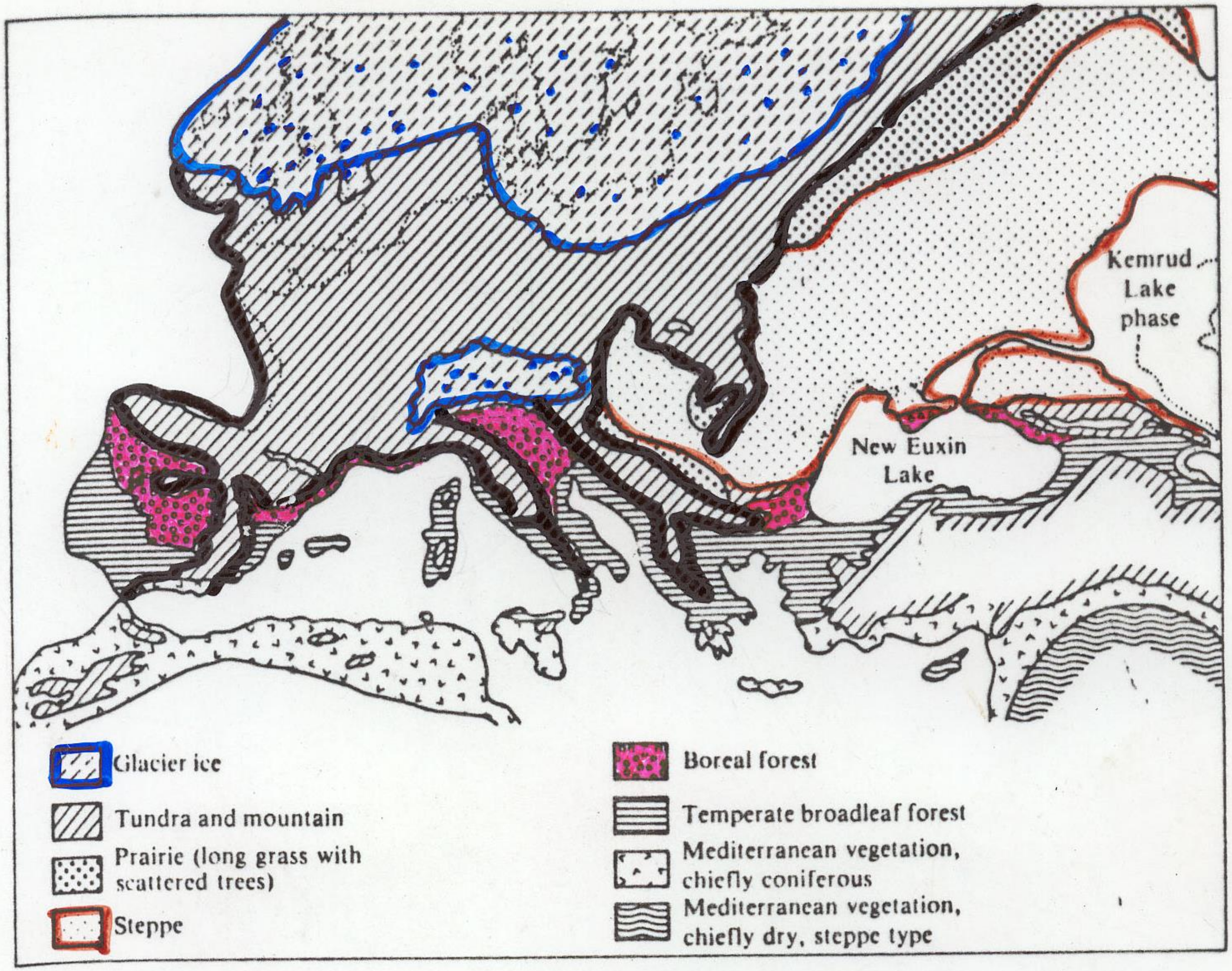


Figure 14.3
Reconstructed zones of vegetation in Europe during the Würm glacial maximum (18,000 years BP). Major vegetation types were shifted southward of their present locations by 10° to 20° of latitude, and the precursors of the Black Sea and the Caspian Sea were interconnected. (After Flint, 1971.)

Glaciação: caso mais claro de migração massiva de organismos para novas áreas continentais

Biomas deslocados de 10° a 20° para o S

Brown & Gibson 1986

Glaciação: Distribuição de saprólitos e suas idades

Cobertura nival das áreas montanas desceu para altitudes menores

Hopper 2009

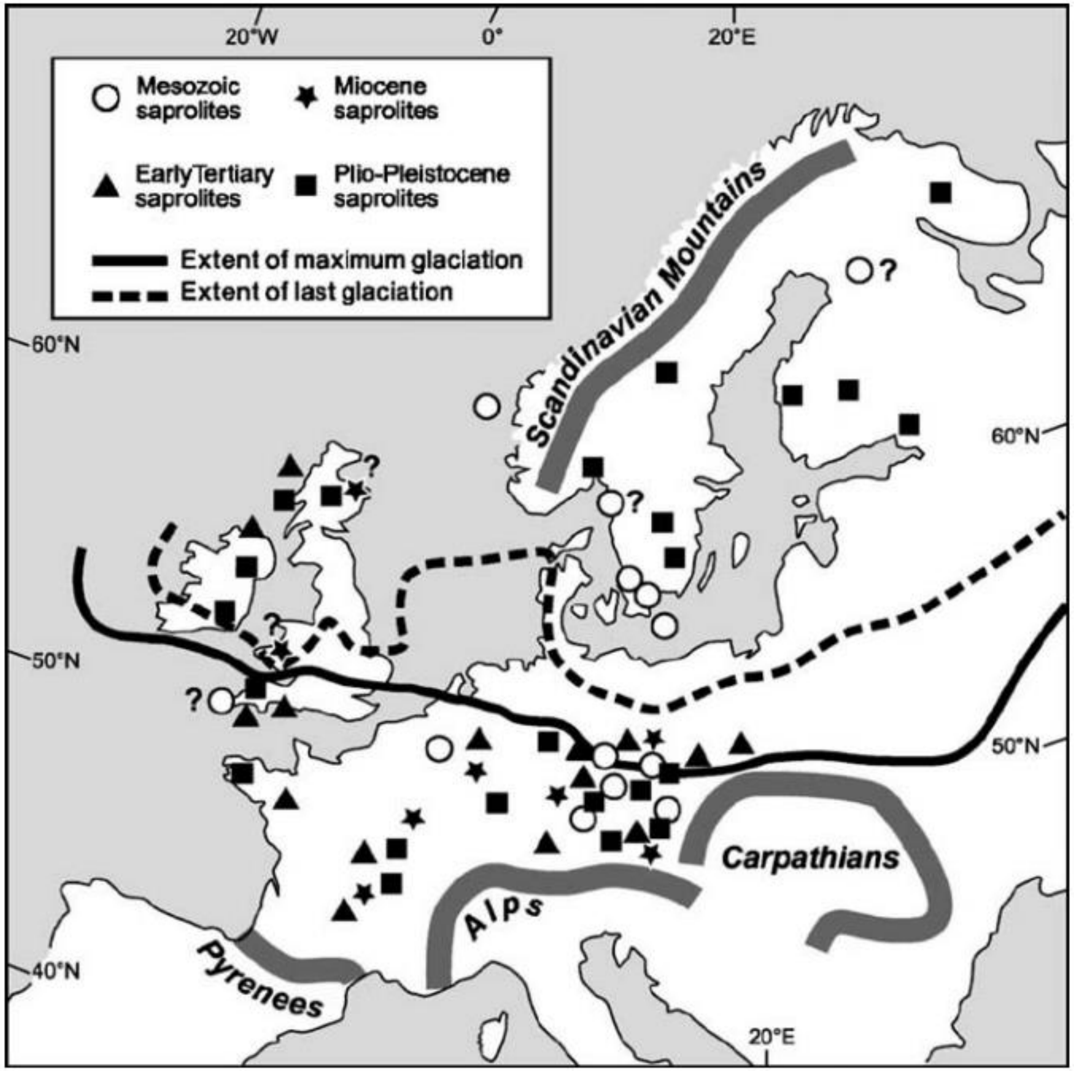
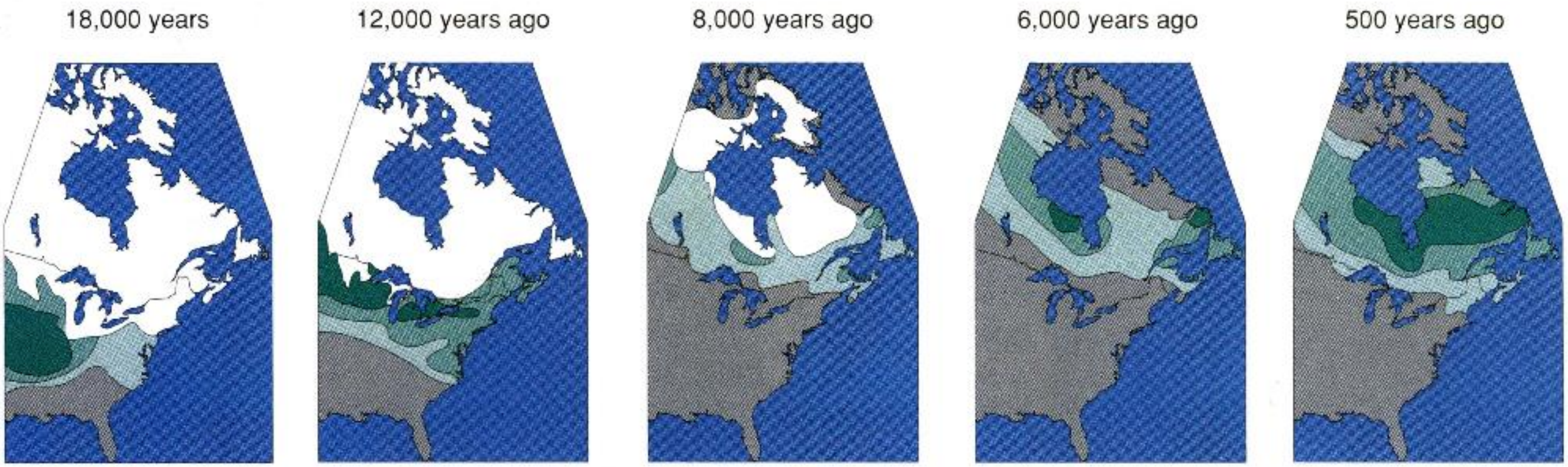
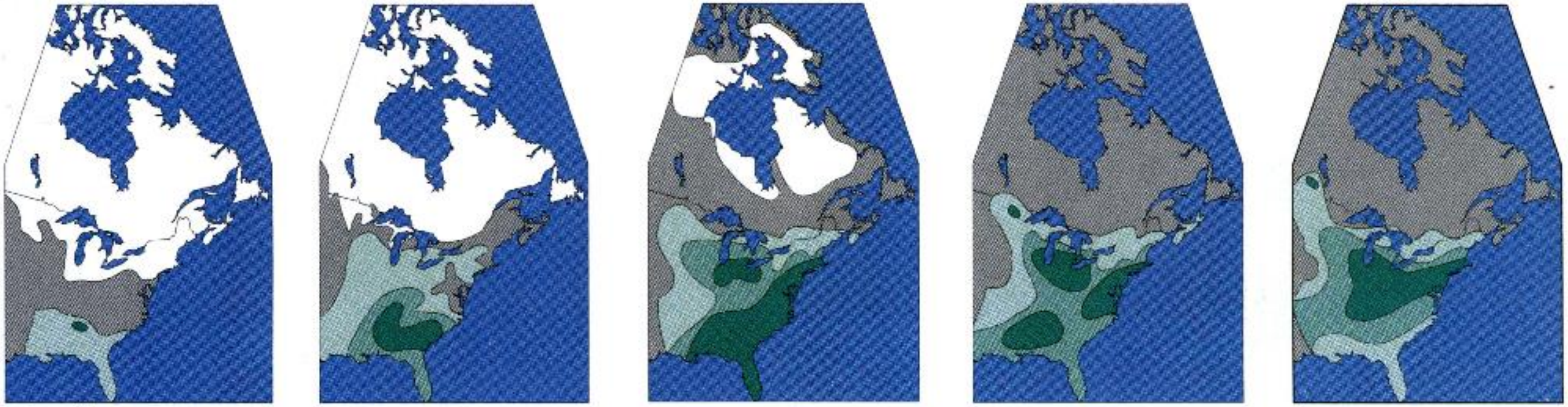


Fig. 1 European extent of maximum and last glaciation, and the distribution of relict weathering mantles (saprolites), with their most likely ages. *Question marks* indicate ages inferred from circumstantial evidence such as long-distance correlations with saprolites of known ages or morphostratigraphic dating. Excluding the Cretaceous, the Mesozoic (251–65.5 Ma) and Palaeogene or Early-Mid Tertiary (65.5–23 Ma) in Europe were generally characterised by 'tectonic stability within low relief surfaces', perhaps identical to those characterizing today's surviving OCBILs. Thus, saprolites mapped as Mesozoic or Early Tertiary with prolonged oceanic climatic buffering may well have constituted old climatically buffered infertile landscapes (OCBILs) prior to glaciation and the increased tectonism, marine inundation, uplift and extensive denudation on uplands of the Cretaceous (145.5–65.5 Ma) and Neogene (23–0 Ma). From Migoń and Lidmar-Bergström (2002), with permission



spruce pollen **pólen de *Picea***



oak pollen **pólen de *Quercus***

Figure 3. As glaciers receded from North America during the Holocene era, forests became established in their place. Pollen from sediments can be used to trace how tree species migrated northward as the climate warmed. These isopoll maps present density contours for spruce and oak pollen and show that both species moved rapidly at rates of up to one kilometer a year, their progress virtually unimpeded by large obstacles such as the Great Lakes and the Gulf of Saint Lawrence. (Adapted from Webb, Jacobson and Grimm 1987.)

▨ 5 – 20%
▨ 20 – 40%
▨ > 40%
☐ Laurentide ice sheet

Pitelka 1997

Figure 4. Schematic diagram to indicate proposed areas of refugia for temperate tree taxa in the three southern peninsulas of Europe during the last full glacial (*ca.* 100–16 ka). Evidence to support this model comes from numerous fossil pollen and plant macrofossil assemblages. (Redrawn from Willis & McElwain (2002) and references cited therein.)

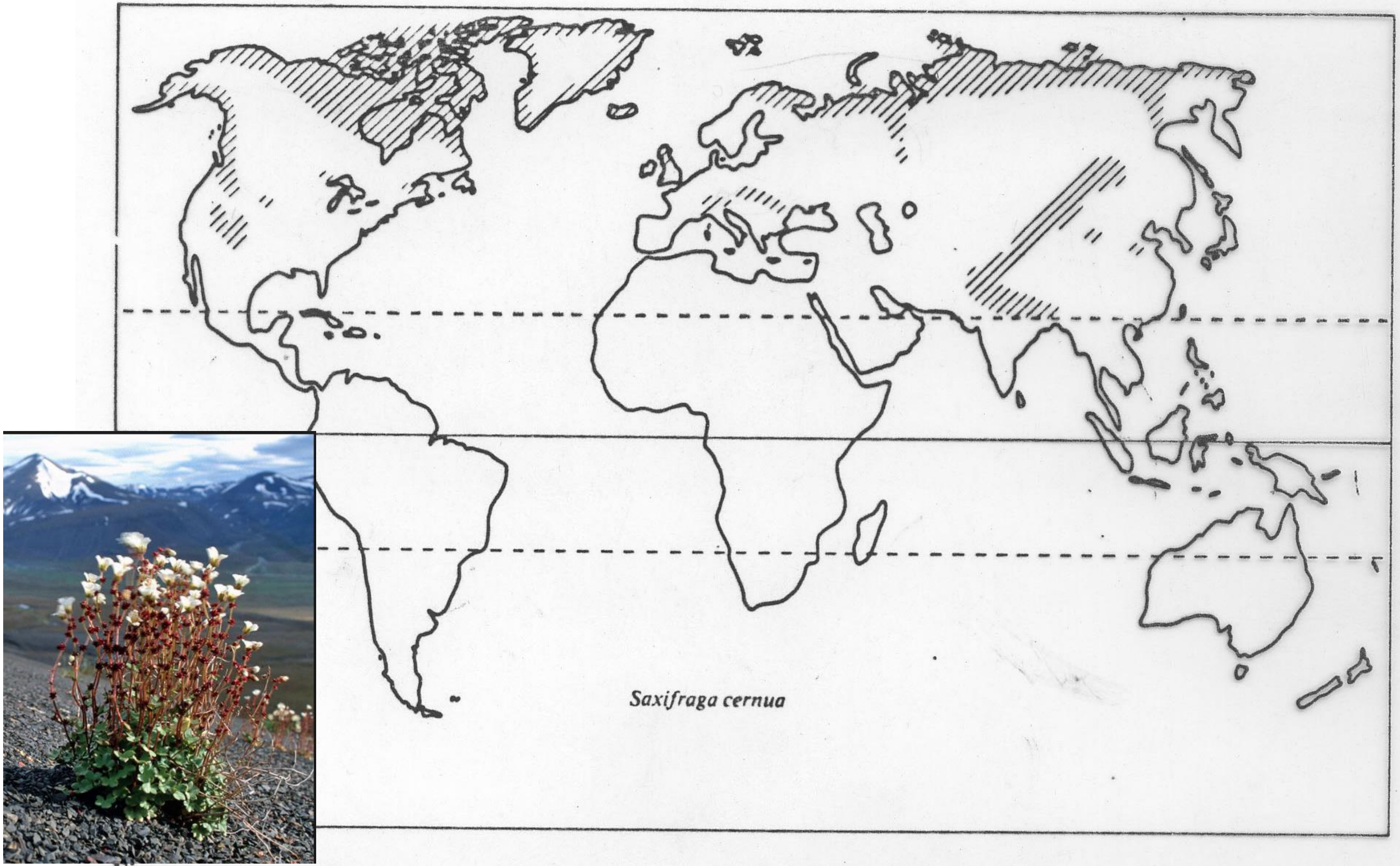


Figure 14.4
Disjunct distribution of the arctic plant *Saxifraga cernua* (Saxifragaceae) in northern and mountainous regions of the Northern Hemisphere. Like many plant and animal species, the range of this form shifted southward during glacial periods. Isolated relict populations have survived in cool climates at higher elevations since the glaciers retreated and the climate warmed. (After Hultén, 1964.)

Brown & Gibson 1986

Reconstruções de refúgios no LGM e rotas de migração pós-LGM

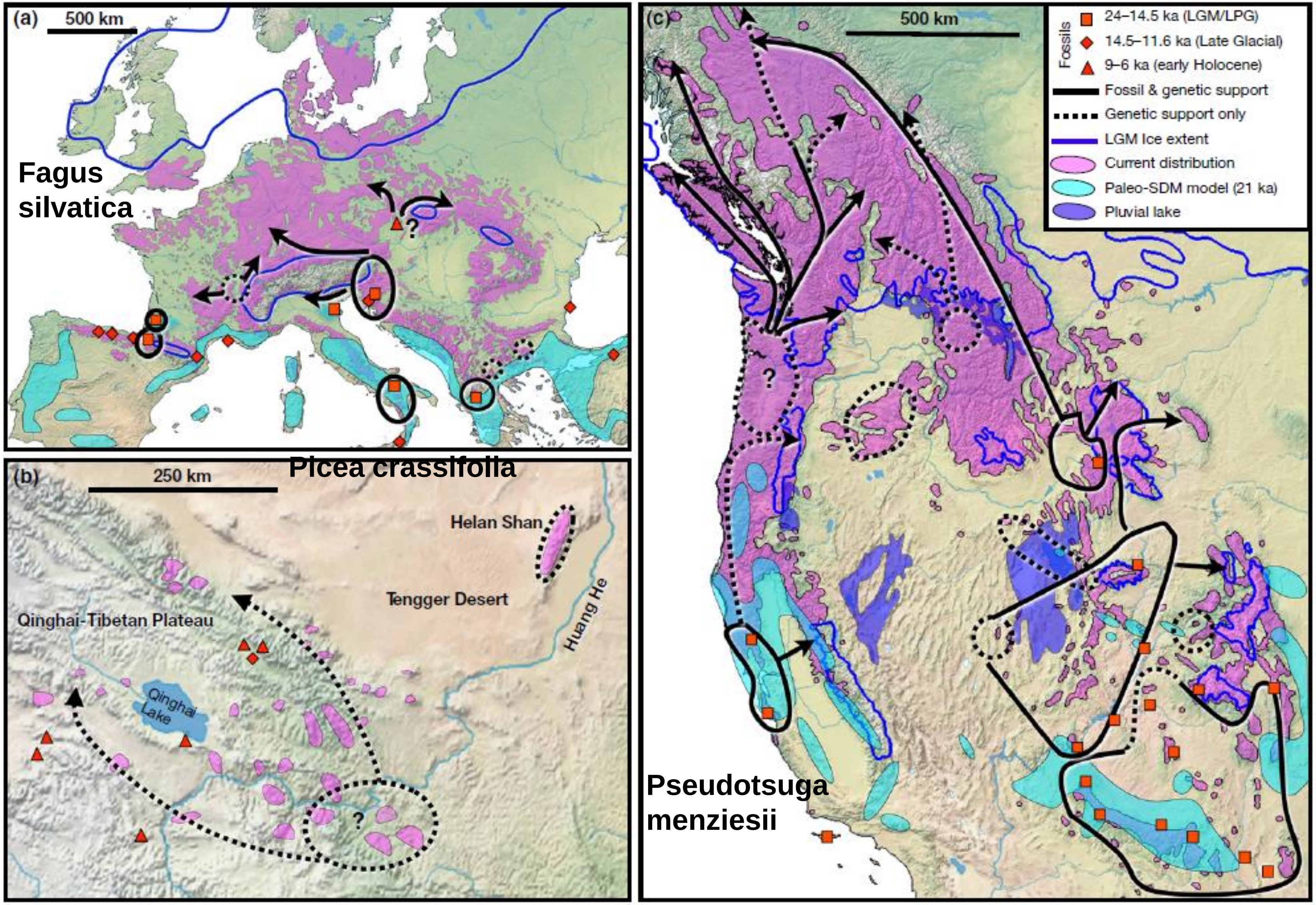
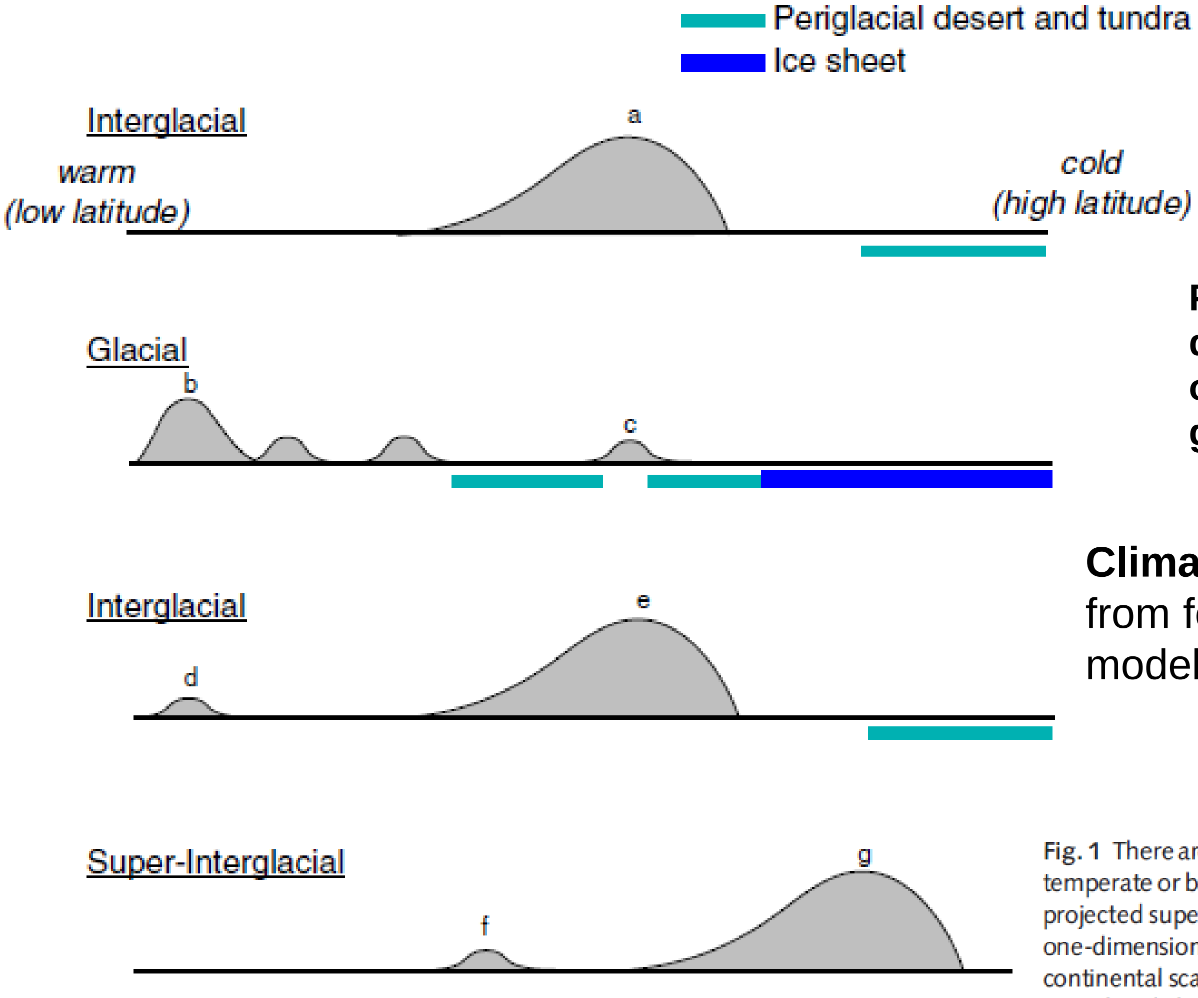


Fig. 5 Reconstructions of Last Glacial Maximum (LGM) refugia and post-LGM dispersal routes of (a) European beech (*Fagus sylvatica*), (b) Qinghai spruce (*Picea crassifolia*), and (c) Douglas-fir (*Pseudotsuga menziesii*). For fossil data, the LGM is merged with the Late Pleniglacial (LPG) period (up to 14 500 yr ago) to encompass the full period of cold and dry climate. Note that fossil locations are limited to the earliest dated fossils, and notably old or disjunct fossils that are relevant to interpreting dispersal history. Pre-LGM fossils are excluded. No paleo-species distribution modeling (SDM) exists for Qinghai spruce. Data sources are listed in the text and in the Supporting Information Notes S1. ka, thousand years.

Gavin et al. 2014



Possíveis cenários biogeográficos da resposta de espécies temperadas ou boreais a variações glaciais-interglaciais.

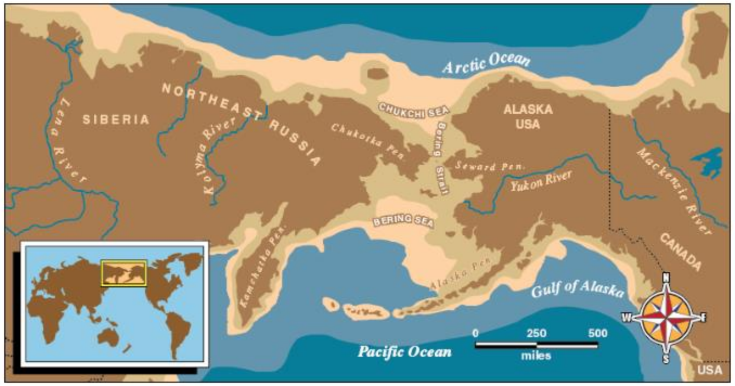
Climate refugia: joint inference from fossil records, species distribution models and phylogeography

Fig. 1 There are several possible biogeographic scenarios of the response of a temperate or boreal species to glacial–interglacial climatic variations and to a projected super-interglacial climate. These schematic diagrams represent one-dimensional views of the latitudinal distribution of a species at a continental scale. A single main distribution associated with a previous interglacial climate (a) migrated to form patchy *ex-situ* refugia (b) during a glacial period, but also possibly remained *in-situ* forming a high-latitude refugium (c) in a climatically buffered area within a mostly tundra landscape. The populations during the modern interglacial comprised climate relicts (d) and a main distribution (e) that may have been colonized by low-latitude (b) or high-latitude (c) refugia. A current area of research addresses whether such high-latitude refugia were occupied by warm-temperate species in addition to boreal species. A projected future super-interglacial, as shown here, is marked by extinction of the climate-relict population (d), establishment of a new climate-relict population (f) and poleward migration of the main distribution (g).

Gavin et al. 2014

**80% das geleiras
no Hem. Norte;
Nível do mar baixo**

Beringia
**(tundra + *Larix*
+ mamíferos)**



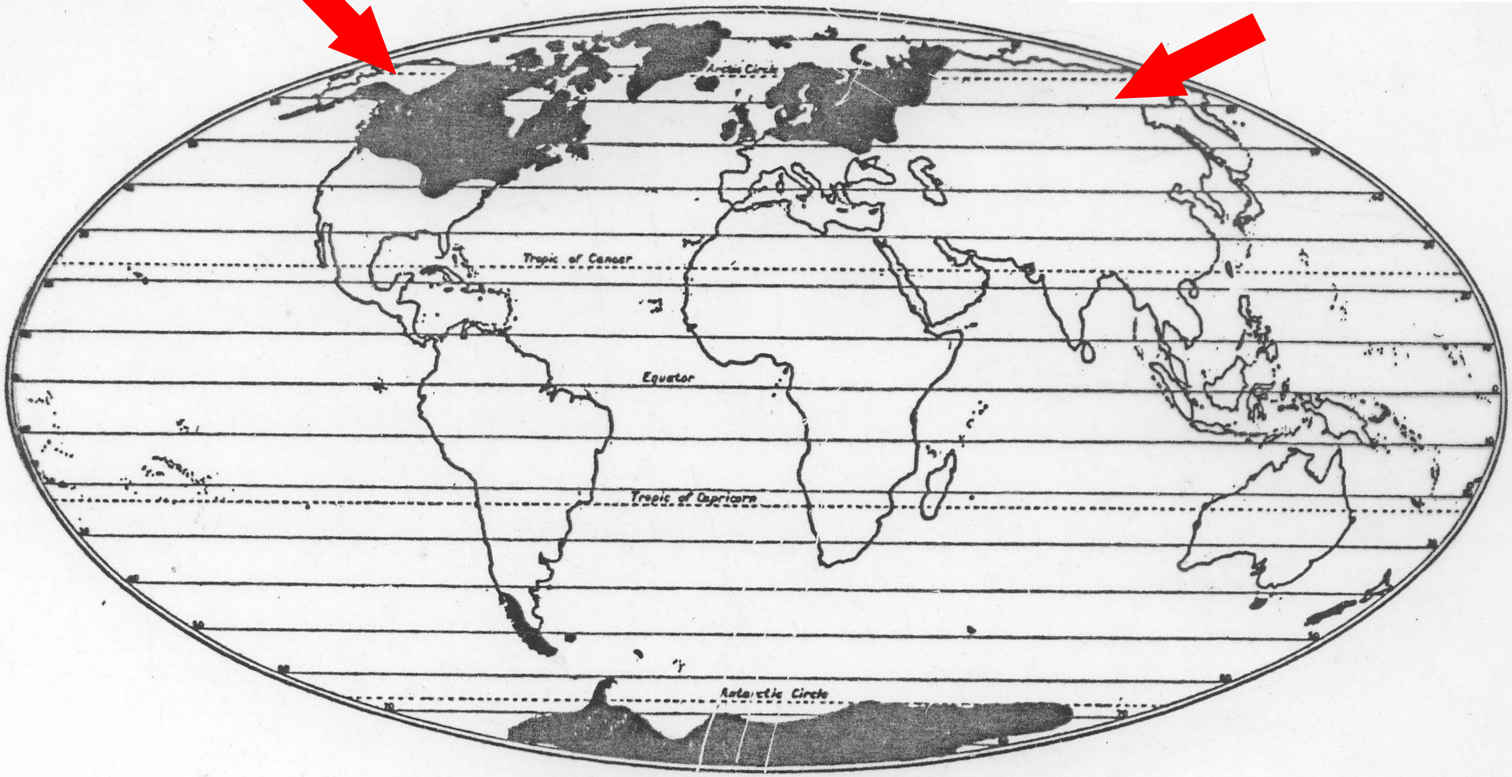


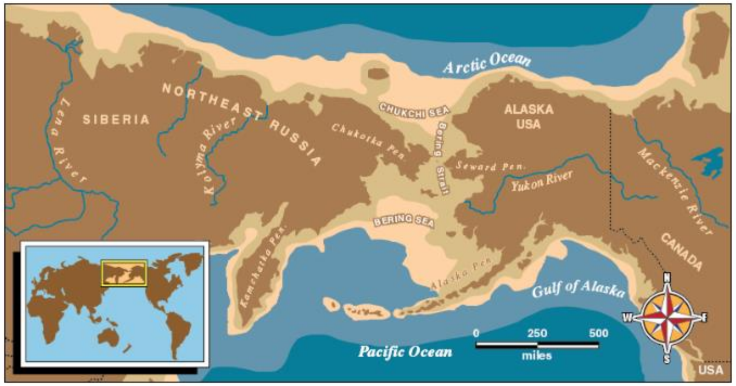
FIG. 78.—The Pleistocene Glaciation.

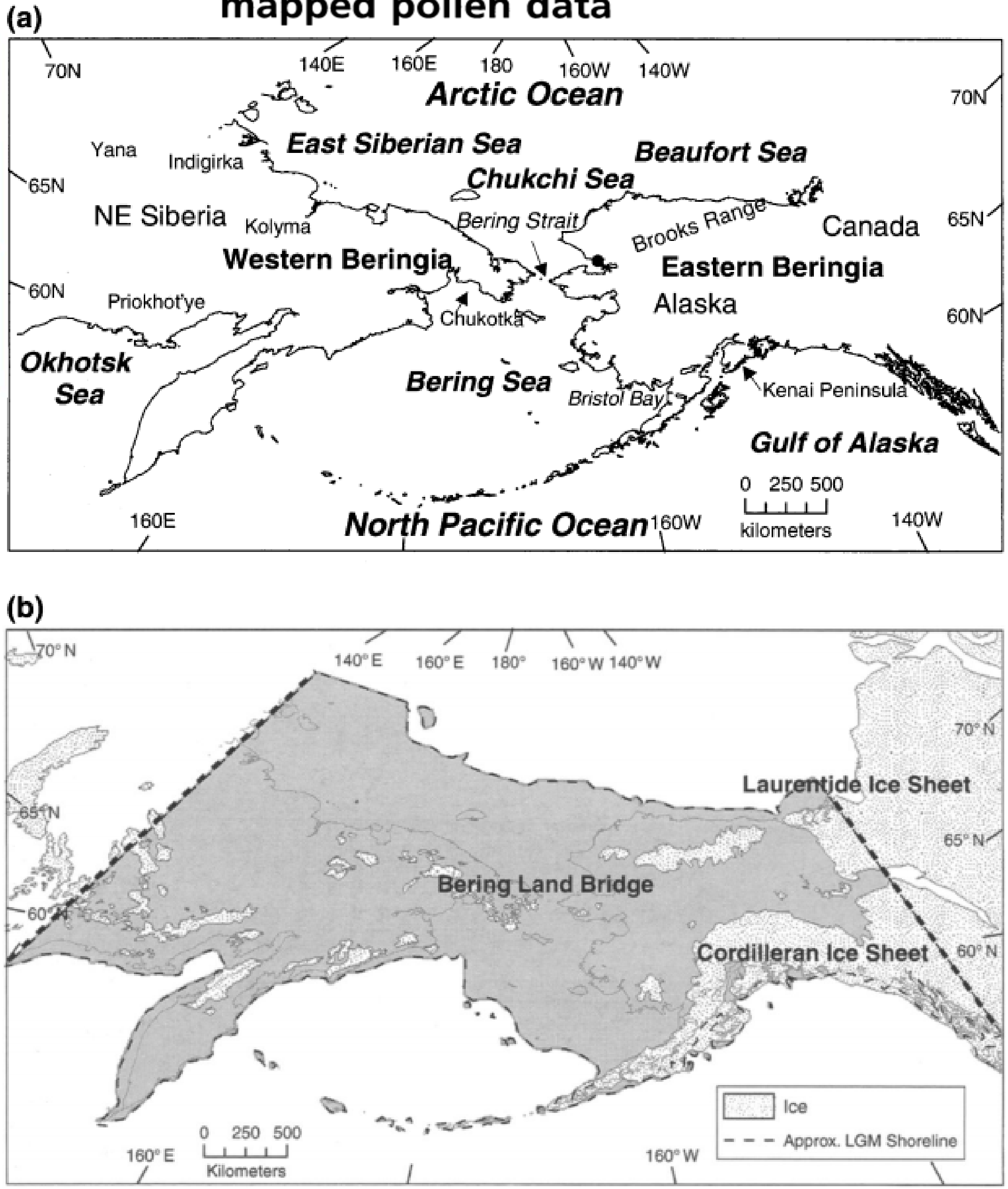
Map of the world showing, in general terms, the maximum extent of the main northern and southern ice-caps (black) during the Pleistocene. It must be remembered that the snow-line was everywhere considerably lower at that time, so that at all latitudes there were, in addition, some larger or smaller local accumulations of ice at higher altitudes. Compiled from various sources.

Geleiras da Antártida iniciaram no Mioceno

Good 1974

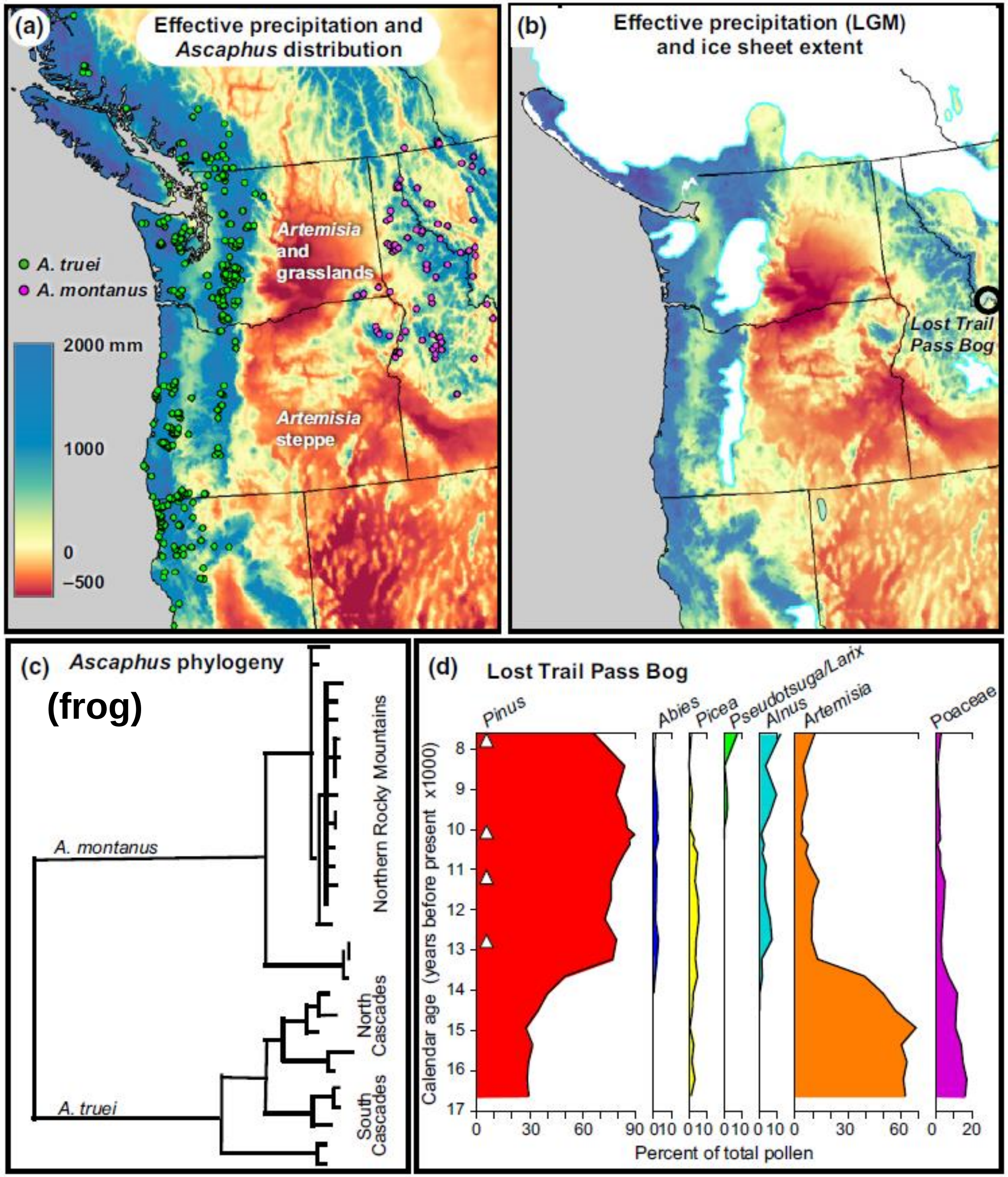
Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data





Brubaker et al. 2004

Figure 1 Map of Beringia showing geographical locations mentioned in text: (a) modern shorelines; (b) last glacial maximum shorelines (landmass shaded) and ice limits.



reconstrução paleoclimática LGM

palinodiagrama

Fig. 2 The need to bridge diverse forms of information on past species distribution is exemplified by the Clearwater Refugium of northern Idaho, USA. These figures show that some lines of evidence, but not others, support the inference of a mesic refugium in northern Idaho through the Last Glacial Maximum (LGM). (a) The distribution of the coastal and Rocky Mountain tailed frog (*Ascaphus truei* (green circles) and *A. montanus* (red circles), respectively) shows the clade's association with mountain streams in areas with high effective precipitation (annual precipitation–potential evapotranspiration) and disassociation with *Artemisia* steppe and grasslands (red areas). (b) During the LGM, the UKMO climate simulation (Johns *et al.*, 1997) predicted a slightly wetter climate compared to present and the maintenance of an arid barrier between the coast and interior, and species distribution modeling (SDM) for *Ascaphus* (not shown) showed its continued presence in Idaho and the Cascade Range (Carstens & Richards, 2007). The circle indicates the location of the pollen record in (d). (c) *Ascaphus* phylogeny from mtDNA indicating an ancient divergence of > 2 million yr between these species and suggesting the long-term isolation of the Rocky Mountain lineage (Nielson *et al.*, 2001). (d) Selected pollen taxa from a post-glacial pollen record from northern Idaho (Mehringer *et al.*, 1977). Triangles indicate radiocarbon dates. The high *Artemisia* and low tree pollen percentages in the late-glacial period (> 14 500 yr ago) suggest a vast treeless steppe of much greater extent than today, suggesting a drier regional climate than indicated by the climate simulation. The extensive *Artemisia*, specifically, indicates a habitat too cold and dry to support the mesic species in the Clearwater Refugium. It remains unknown whether fine-grained topoclimates could accommodate both lines of evidence. Taken from fig. 9 (in part) of Mehringer *et al.* (1977) and redrafted. Used with permission. Copyright Regents of the University of Colorado. See Supporting Information Notes S1 for data sources.

Gavin et al. 2014

Glaciação:

29% de toda a Terra cobertos por espessas geleiras + gelos polares (N e S) =

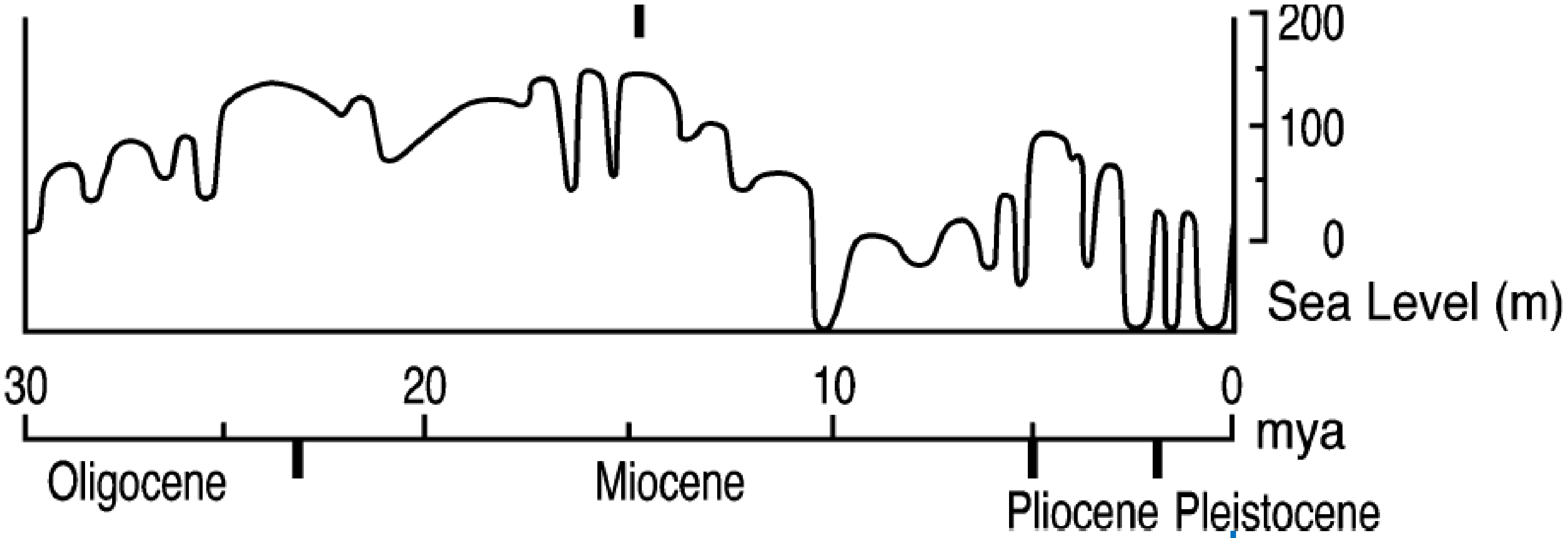
50 milhões de km3 de gelo = muita água removida do mar, cujo nível baixou: 200m?
80 a 100m?

Considerável exposição de terra unindo continentes!

Isostasia!

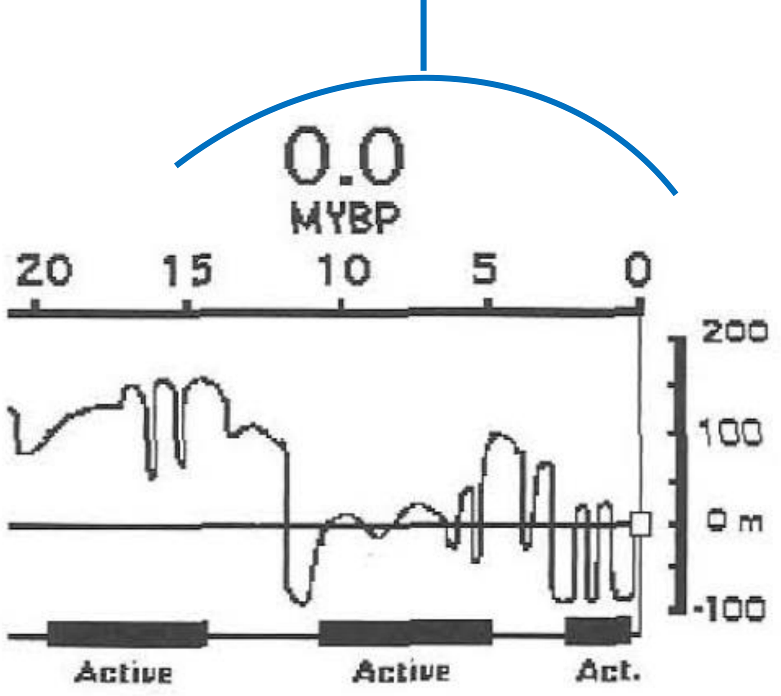
FIG. 79.—Map showing the extent of the ice advance in North America during the maximum glaciation, after Chamberlin and Salisbury.

Good 1974



Won & Renner 2006
modificado de Haq et al. 1987

Flutuações do nivel do mar do Terciário Médio ao Quaternário



Frailey 2002

Efeitos das glaciações na região Neotropical

Fig. 6. Main South American geographical areas affected by the Middle Miocene–Late Miocene marine transgression (modified from Donato et al., 2003).

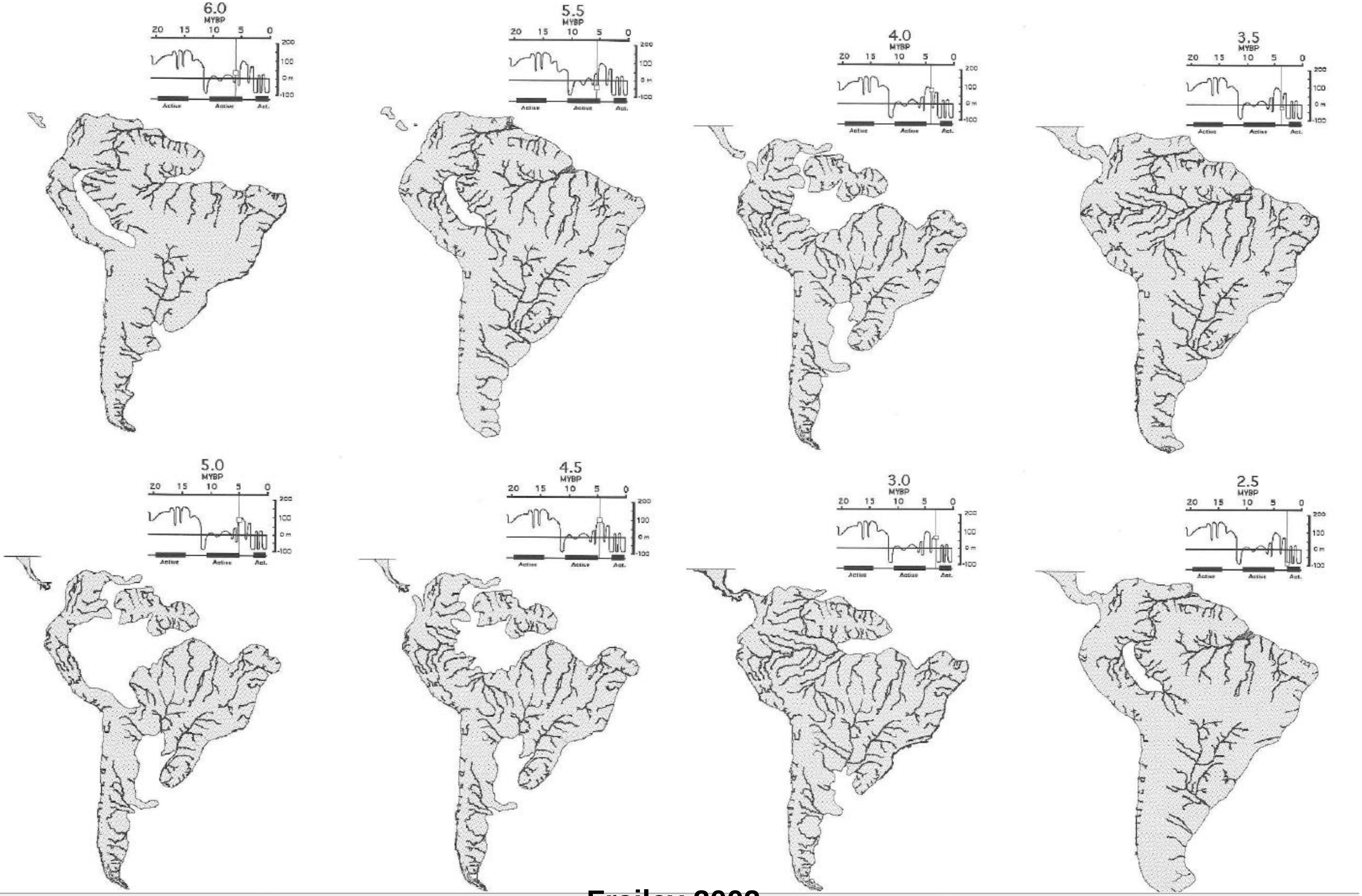
Transgressões marinhas
Mioceno Médio e Tardio

Principais áreas geográficas afetadas na América do Sul

Ortiz-Jaureguizar & Cladera 2006

cinza = terrenos emersos

Transgressões marinhas – Cenozoico - Principais áreas geográficas afetadas na América do Sul



Frailey 2002

Efeitos das glaciações na região Neotropical

Período Glacial - Interglacial:
Transgressões marinhas
Neógeno

Suguio 1999

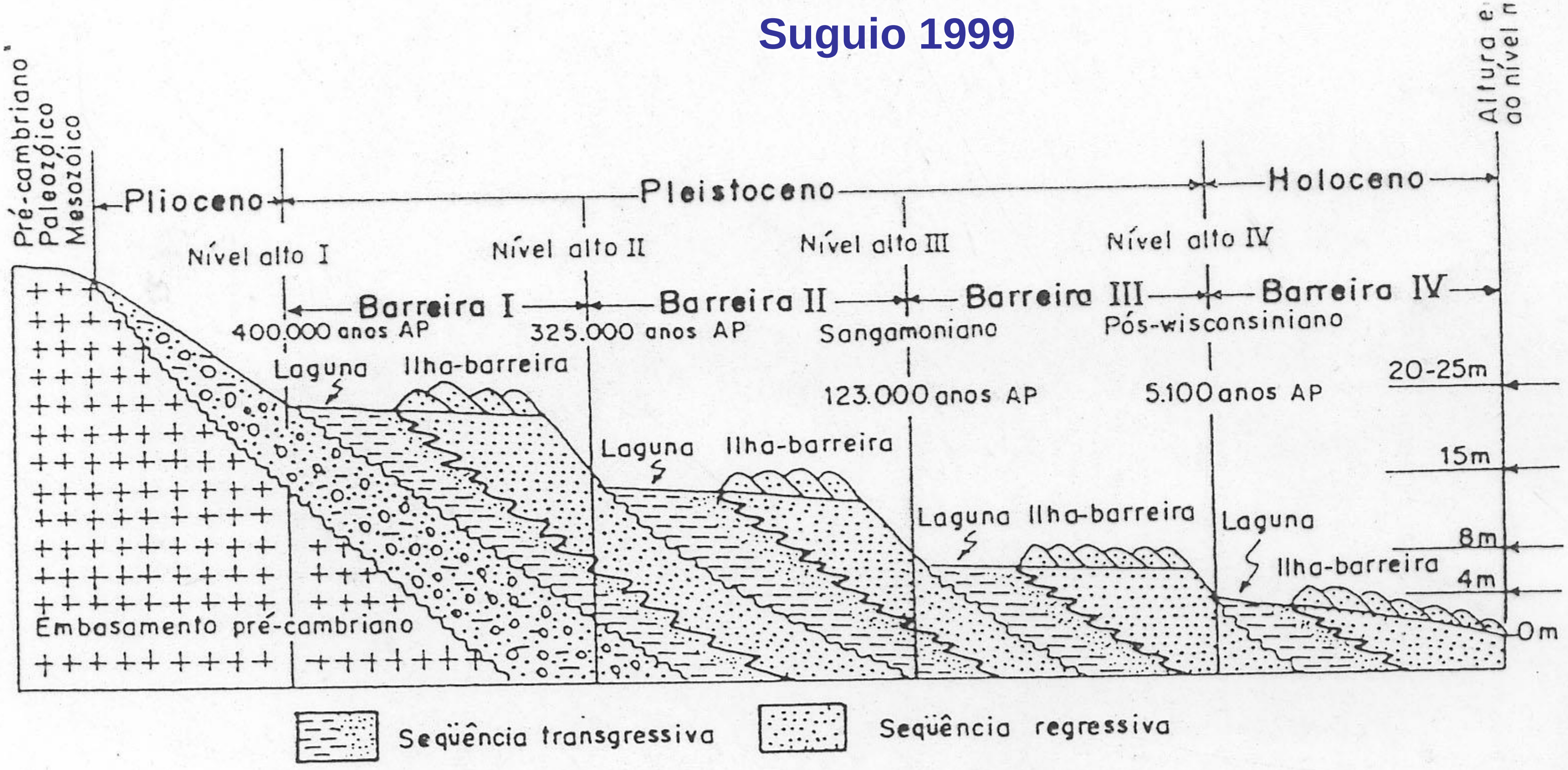


Fig. 67 - Seqüência de quatro terraços marinhos, constituindo sistemas de ilhas-barreira/lagunas, formados sob condições de níveis marinhos mais altos que o atual (Modificada de Villwock *et al.*, 1986).

Efeitos das glaciações na região Neotropical

Evidências paleopalinológicas

Andes Colombianos
Fenley 1979

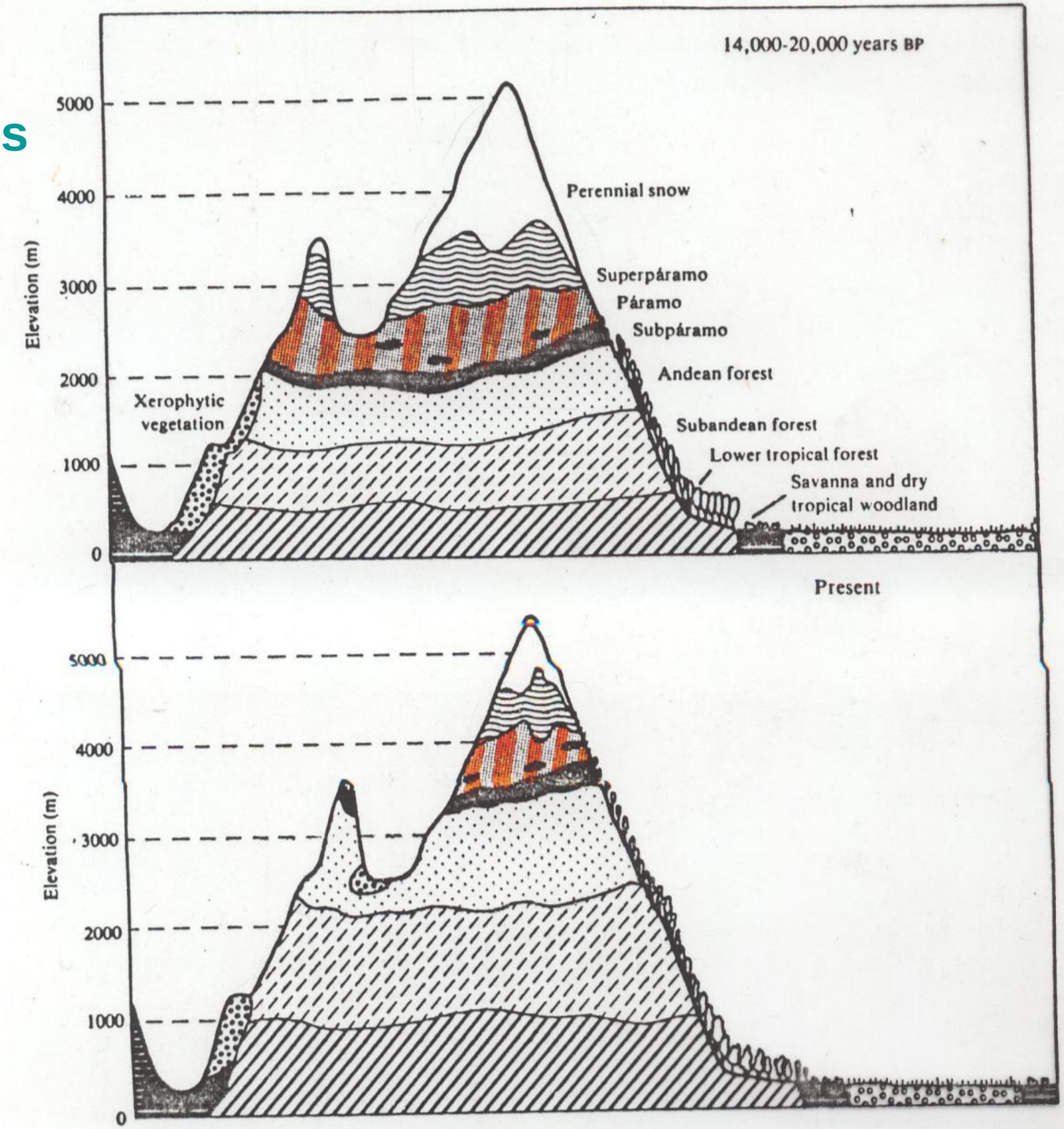
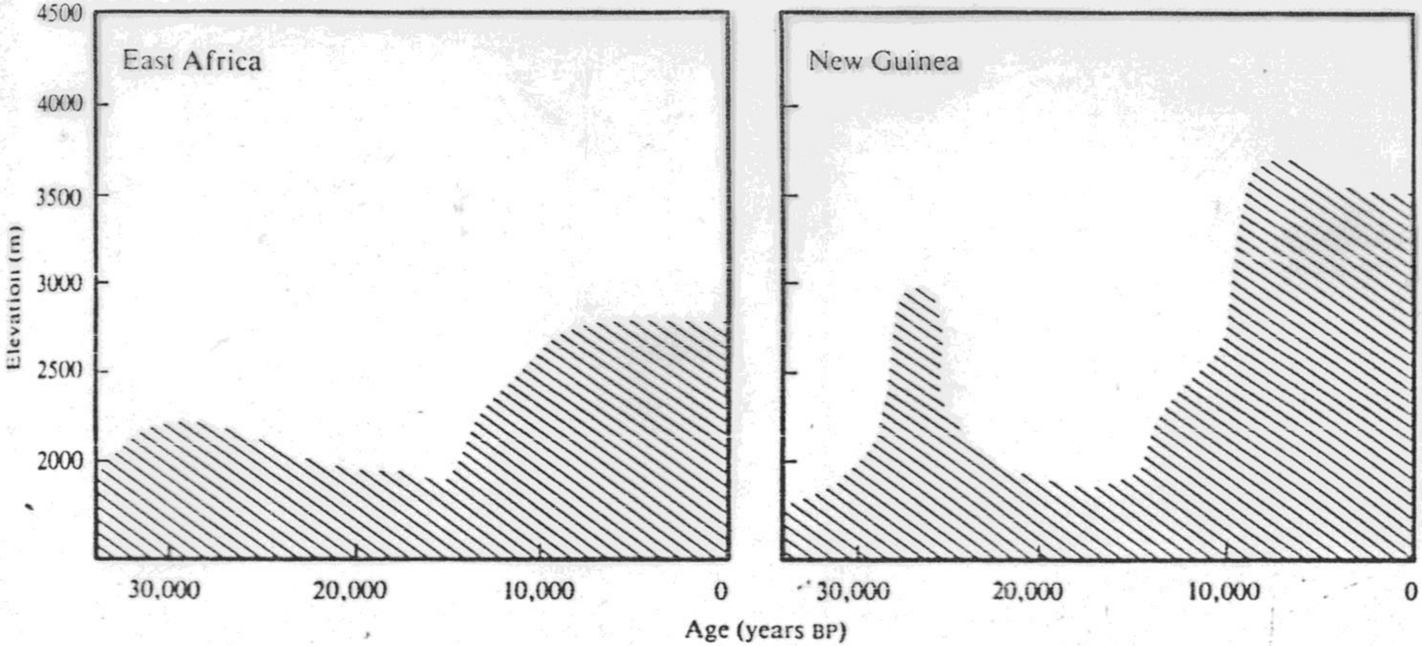


Figure 14.8
Reconstruction of the vegetation zones in the Eastern Cordillera of the Andes in Colombia during the last glacial maximum *(above)* and at present *(below)*. This is based primarily on the distribution of fossil pollen. Note that the lower zones became narrower as they shifted to lower elevations during the cooler climate of the glacial period. (After Flenley, 1979a.)

Efeitos das glaciações nos trópicos

Evidências paleopalinológicas do limite altitudinal superior das florestas tropicais 3 regiões do mundo

Fenley 1979



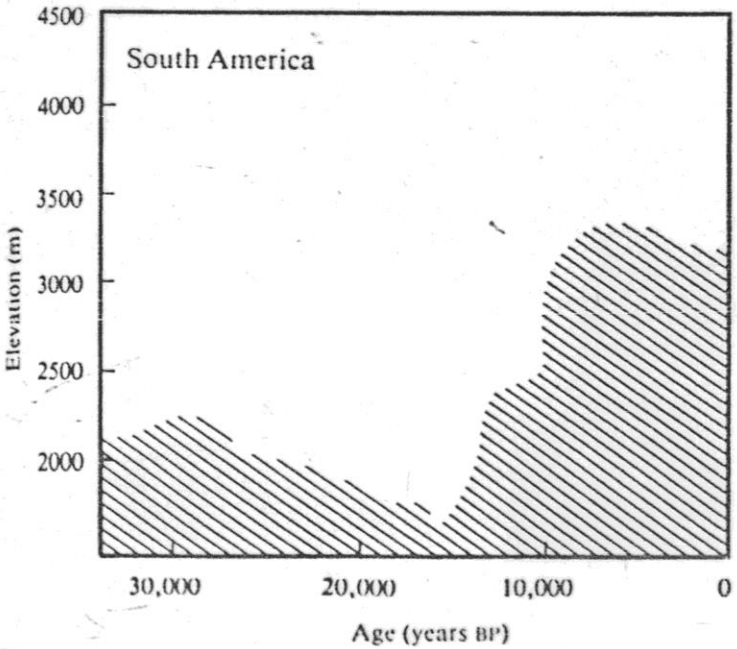


Figure 14.9
Summary of the shifts in the upper elevational limit of tropical forest in three different regions, South America, East Africa, and New Guinea, during the last 33,000 years. Note that the qualitative patterns are similar, although the exact upper elevational boundary was somewhat different in each region. (After Flenley, 1979a.)

Efeitos das flutuações paleoclimáticas nos trópicos

AFRICA
Rand Flora

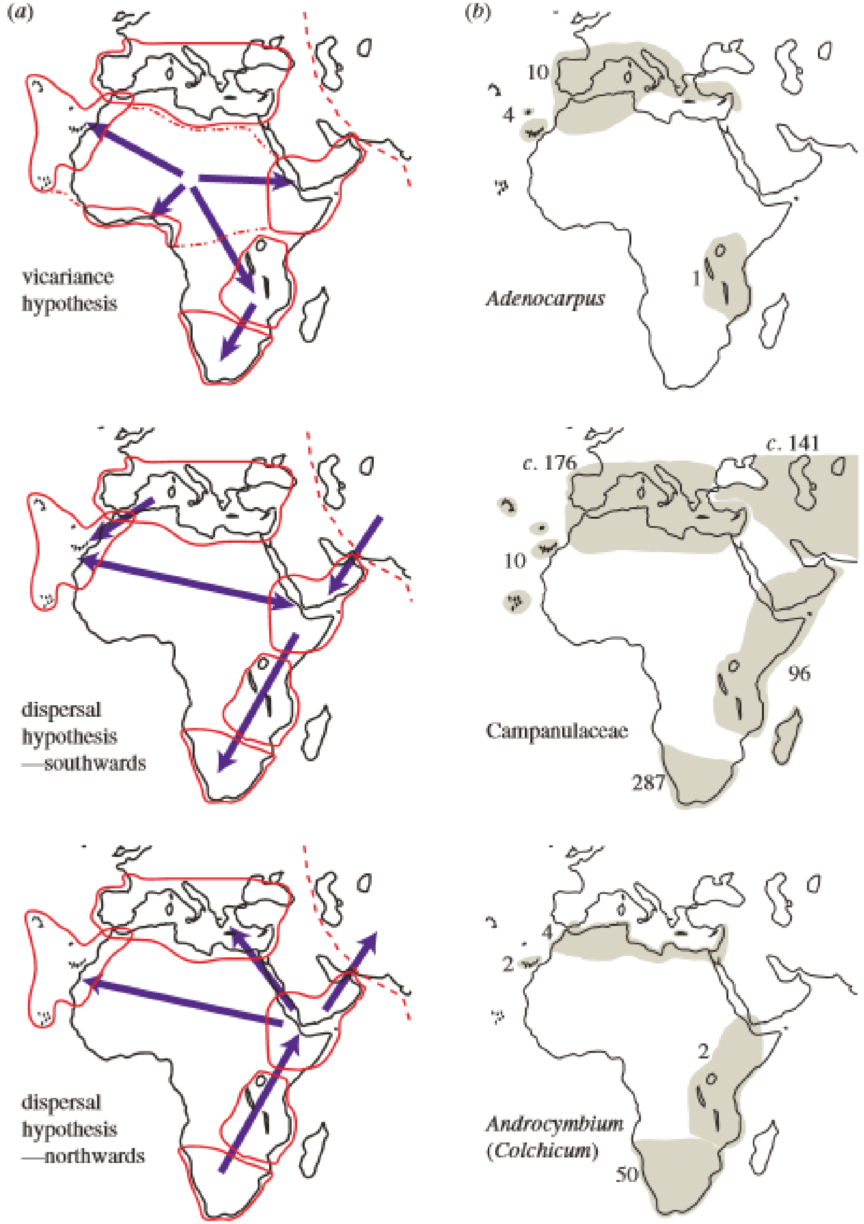


Figure 1. (*a*) The main hypotheses to explain the origin of the 'Rand Flora' pattern and (*b*) plant groups that have been argued to exemplify these hypotheses. (1) Vicariance—climatological changes lead to vicariance of a once continuous Paleogene flora. (2a) Dispersal southwards—the pattern is a consequence of immigrants from the Mediterranean region and west spreading to south Africa via eastern Africa. (2b) Dispersal northwards—the elements of the flora dispersed from south Africa to Horn of Africa region, and from there to the west and north.

Sanmartín et al. 2010

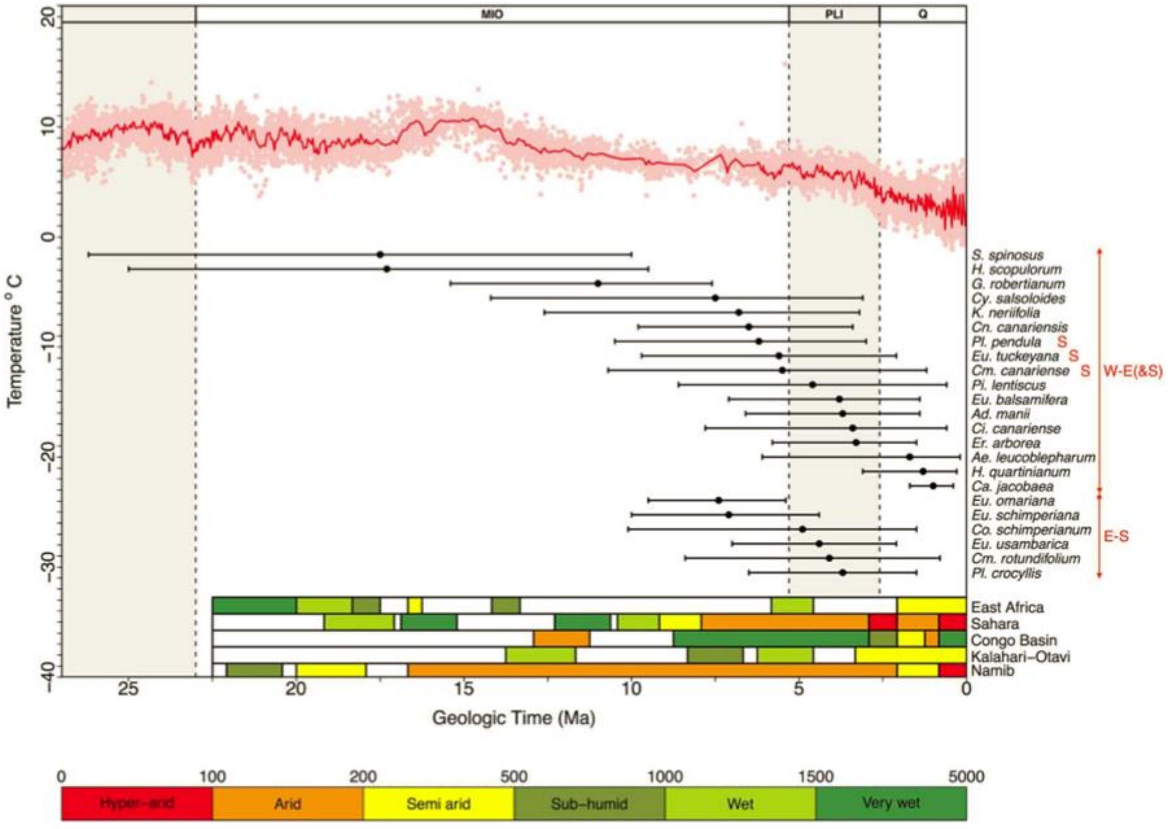
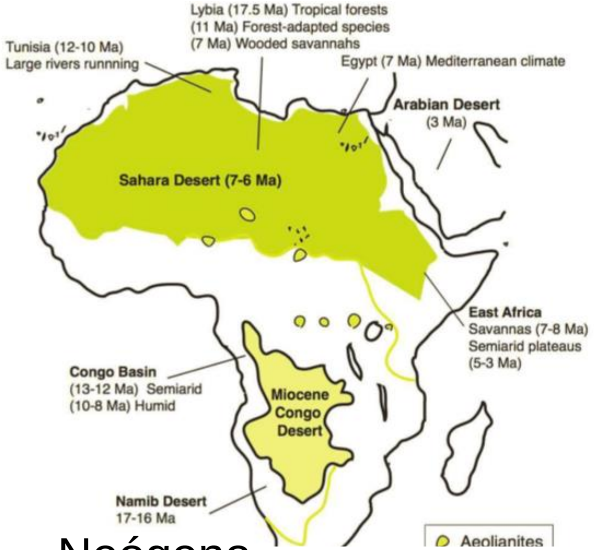
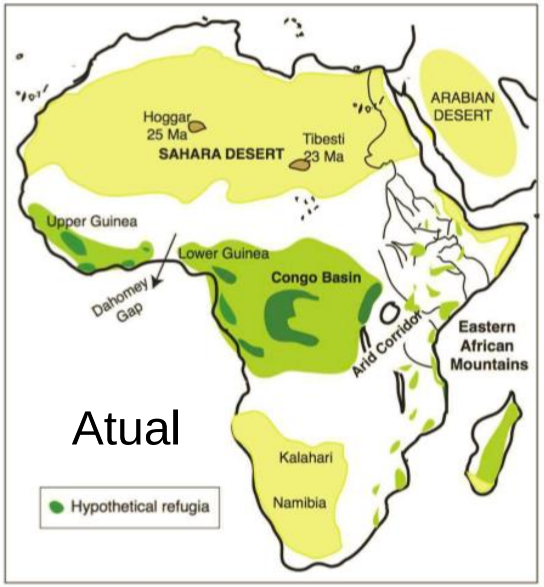


FIGURE 4 | Diagram showing estimated lineage divergence times (mean and 95% HPD confidence intervals) for Rand Flora disjunctions dated in this study and indicated in the MCC chronograms depicted in Figures S1–S17. W-E(&S): divergence times estimated between disjunct taxa distributed in Macaronesia-NW-W Africa vs. Eastern Africa (a red S indicates presence in Southern Africa); E-S: estimated divergence times between disjunct taxa distributed in southern Arabia-Eastern Africa vs. southern Africa. The red line above represents the change in global temperatures over the Cenozoic as reflected by global-deep-sea oxygen records compiled from Zachos et al. (2008); colored bars in the right bottom corner indicate climatic conditions in five regions that underwent major climate changes—either desertification or tropicalization—during the Neogene (adapted from Senut et al., 2009). Taxa names correspond to those in **Table 1**, plus two groups from the literature: *Pistacia lentiscus* and *Erica arborea* (see Discussion).



Neógeno



Atual

Pokorny et al. 2015

Disjunctions fall within the Miocene and Pliocene periods, coinciding with a major aridification trend, still ongoing, in Africa.

Age of disjunctions - related to the climatic affinities of each Rand Flora lineage: subtropical taxa dated earlier (e.g., *Sideroxylon*); those with more xeric affinities (e.g., *Campylanthus*) diverging later.

Some lineages (e.g., *Cicer*, *Campylanthus*) show a long temporal gap between stem and crown ages, suggestive of **extinction.**

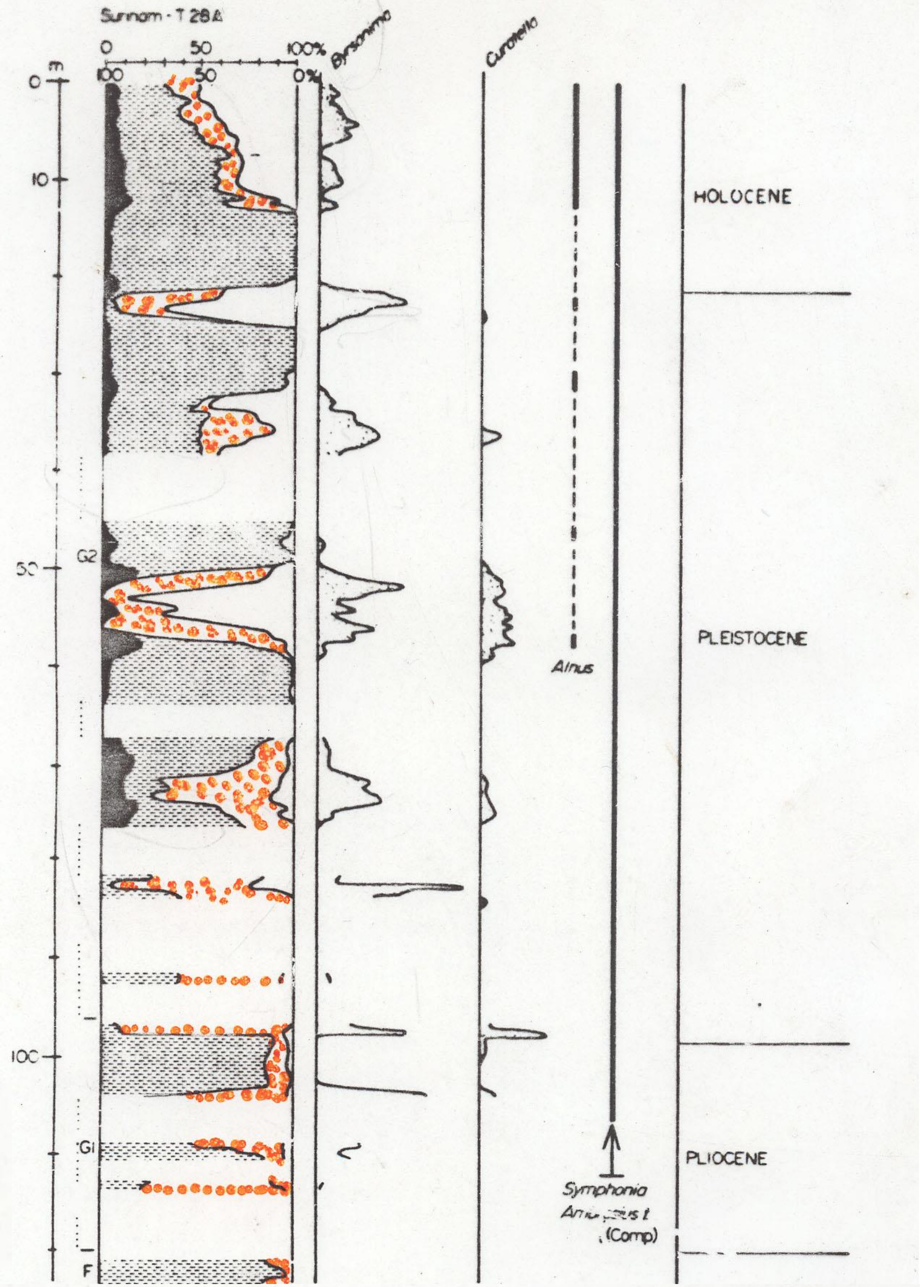
The Rand Flora pattern seems to fit the definition of **biogeographic pseudocongruence**, with the pattern arising at **different times** in response to the increasing aridity of the African continent, with interspersed periods of humidity allowing range expansions.

Efeitos das flutuações paleoclimáticas na região Neotropical

Evidências palinoestratigráficas

Suriname – 125m de sedimentos

Van den Hammen 1988



▨ Avicennia + Rhizophora

☐ Gramineae

● Other forest elements

Figure 2. Simplified pollen diagram of 125 m of Pliocene and Quaternary sediments from Alliance (Surinam). (Adapted from Wijmstra, 1969; according to Van der Hammen, 1974.)

Efeitos das flutuações paleoclimáticas na região Neotropical

Evidências palinoestratigráficas

Carajás, PA- Absy et al. 1993

palinodiagrama

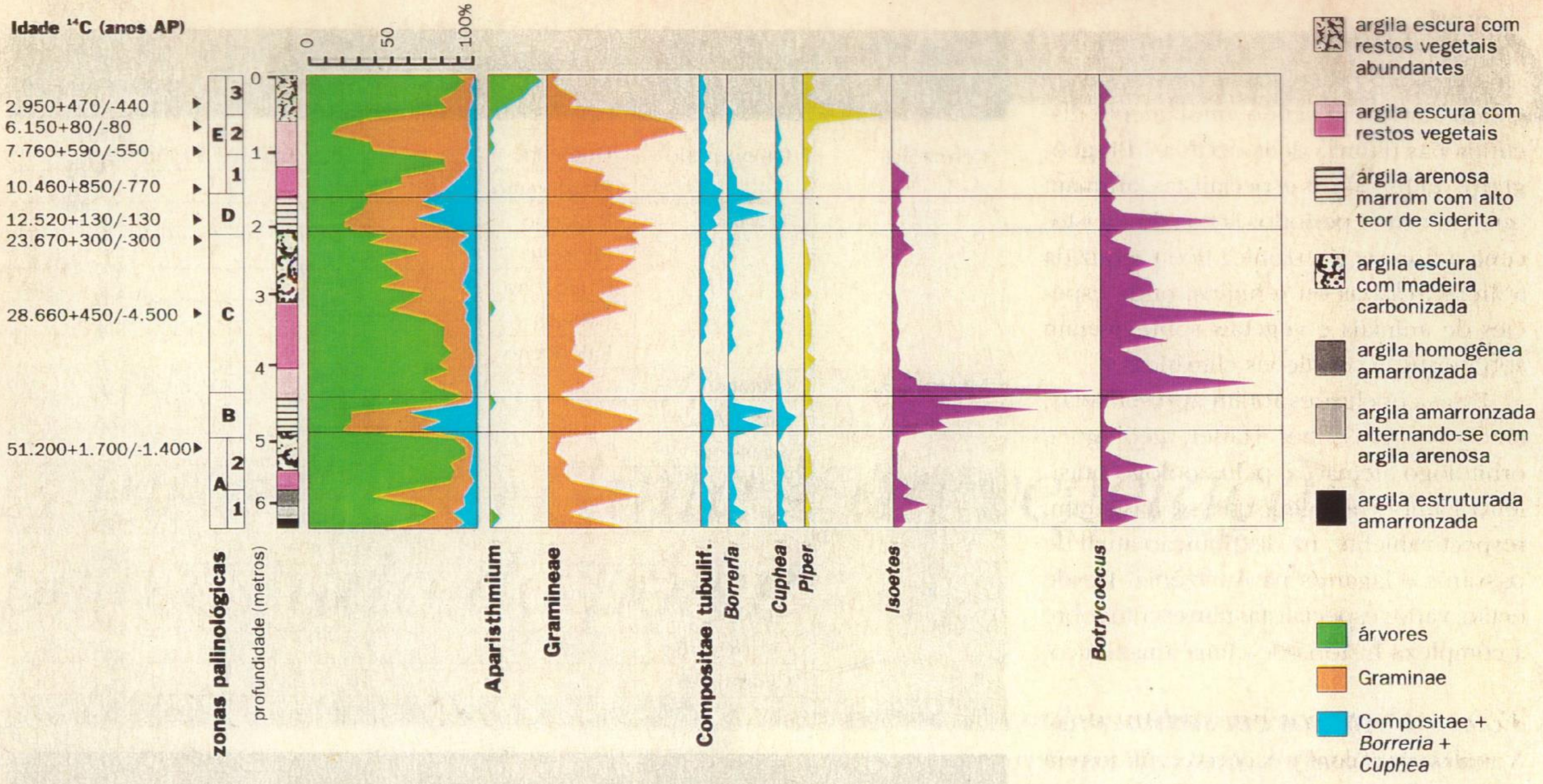


Figura 4. **Diagrama de pólen sumarizado da sondagem CSS2 em Carajás. À esquerda, estão representados os percentuais de pólen das associações das plantas indicadoras [o que são as associações das árvores, Gramineae e dos elementos de savana: Compositae +** *Borreria* **+** *Cuphea*. **À direita, as curvas individuais dos percentuais de pólen de algumas plantas. A soma de pólen usada para o cálculo da percentagem foi baseada no total de pólen dos seguintes grupos de plantas: a) árvores, b) Gramineae, c) Compositae +** *Borreria* **+** *Cuphea*.

Efeitos das flutuações paleoclimáticas na região Neotropical

Evidências paleopalinológicas

Katira, RO - Absy et al. 1993

palinodiagrama

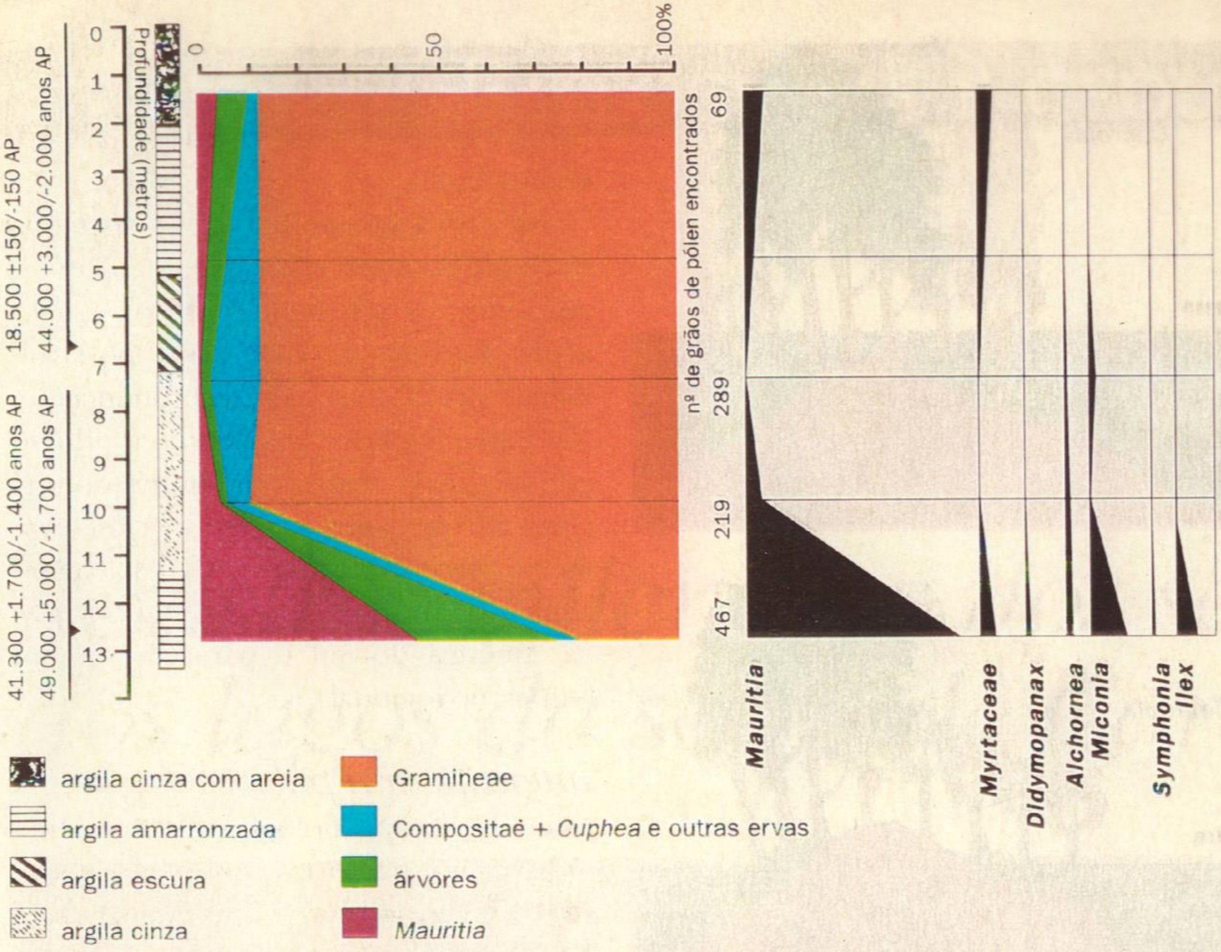


Figura 5. Diagrama de pólen sumarizado da sondagem de Katira, em Rondônia. À esquerda, estão representados os percentuais das seguintes plantas: Gramineae, Compositae + *Cuphea* e outras ervas, árvores e *Mauritia*. À direita, estão as curvas individuais das percentagens de pólen de algumas plantas. A soma de pólen usada para o cálculo das percentagens foi baseada no total de pólen dos seguintes grupos de plantas: a) Gramineae,

Figura 6. Lago estudado de Carajás.

Figura 7. Esporos de *Isoetes*, Pteridófita aquática encontrada nas amostras de sedimentos da sondagem CSS2 – Carajás, focalizados ao microscópio. Profundidade das amostras: 4,63-4,65 m.

Zonações palinoestratigráficas na América do Sul Tropical,
e táxons indicadores.

Hoorn et al. 2010, modificado de Leite 2006.

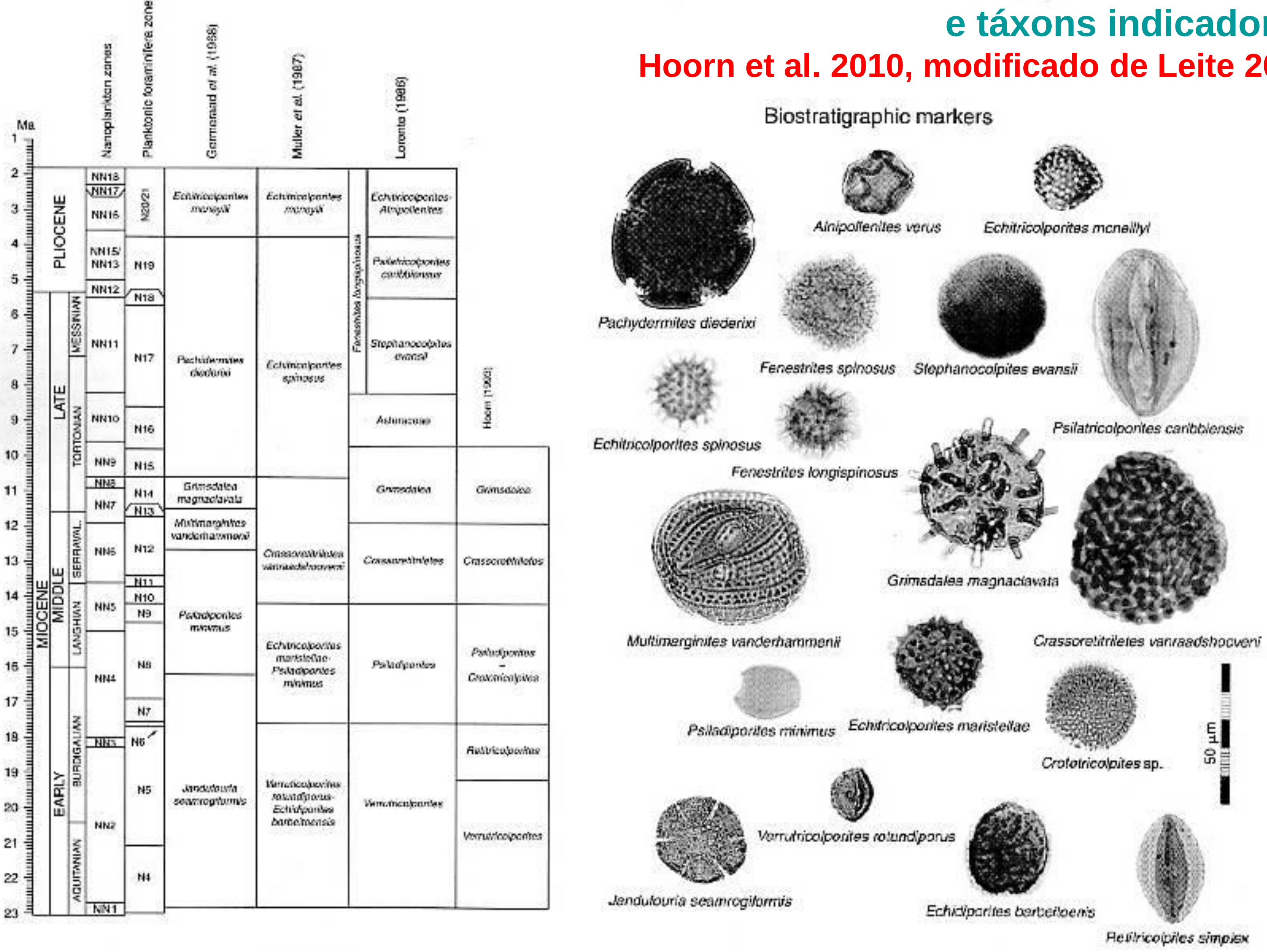


Fig. 19.2 Most important palynostratigraphic zonations for the South American tropics (modified from Leite 2006), and some of the key taxa used in the zonations.

Paisagem reconstruída da Amazônia Central - Mioceno Médio a Superior (16-7 Ma.), baseada em dados polínicos e paleoambientais.

Hoorn et al. 2010

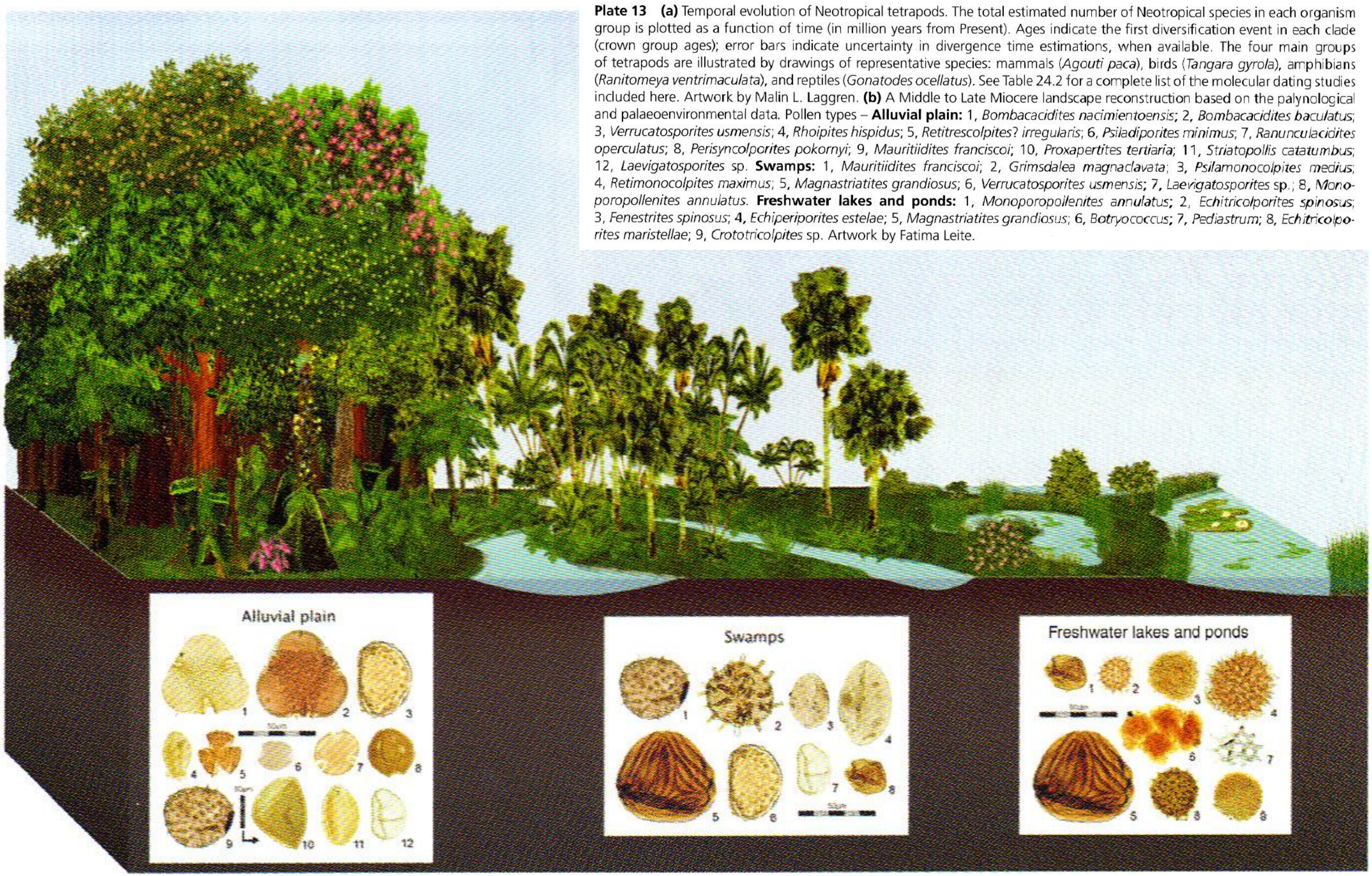
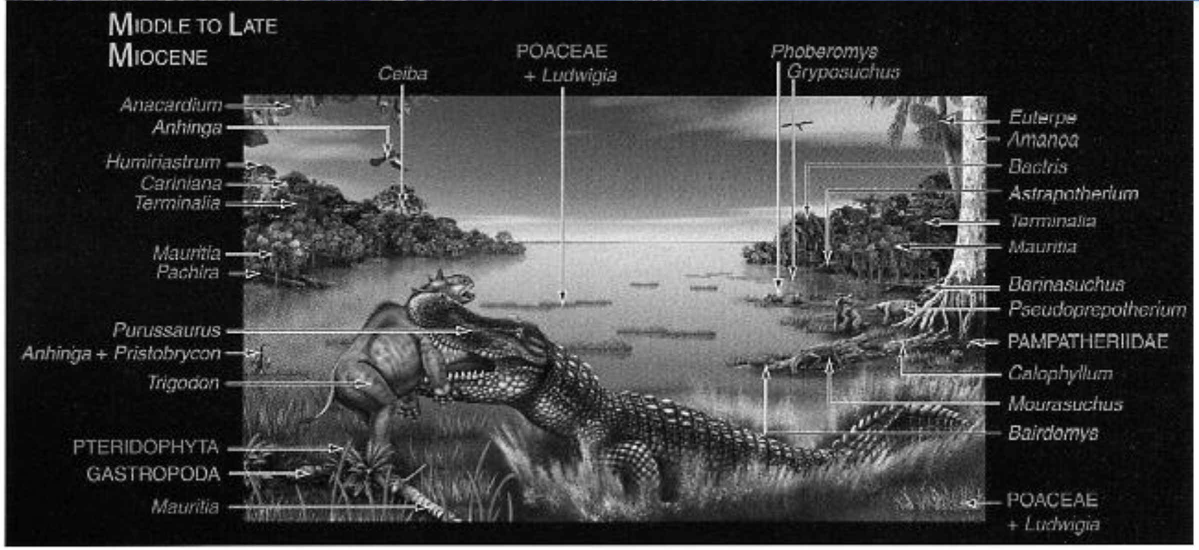


Plate 13 **(a)** Temporal evolution of Neotropical tetrapods. The total estimated number of Neotropical species in each organism group is plotted as a function of time (in million years from Present). Ages indicate the first diversification event in each clade (crown group ages); error bars indicate uncertainty in divergence time estimations, when available. The four main groups of tetrapods are illustrated by drawings of representative species: mammals (*Agouti paca*), birds (*Tangara gyrola*), amphibians (*Ranitomeya ventrimaculata*), and reptiles (*Gonatodes ocellatus*). See Table 24.2 for a complete list of the molecular dating studies included here. Artwork by Malin L. Laggren. **(b)** A Middle to Late Miocere landscape reconstruction based on the palynological and palaeoenvironmental data. Pollen types – **Alluvial plain:** 1, *Bombacacidites nacimientoensis*; 2, *Bombacacidites baculatus*; 3, *Verrucatosporites usmensis*; 4, *Rhoipites hispidus*; 5, *Retitrescolpites? irregularis*; 6, *Psiladiporites minimus*; 7, *Ranunculacidites operculatus*; 8, *Perisyncolporites pokornyi*; 9, *Mauritiidites franciscoi*; 10, *Proxapertites tertiaria*; 11, *Striatopollis catatumbus*; 12, *Laevigatosporites* sp. **Swamps:** 1, *Mauritiidites franciscoi*; 2, *Grimsdalea magnaclavata*; 3, *Psilamonocolpites medius*; 4, *Retimonocolpites maximus*; 5, *Magnastriatites grandiosus*; 6, *Verrucatosporites usmensis*; 7, *Laevigatosporites* sp.; 8, *Monoporopollenites annulatus*. **Freshwater lakes and ponds:** 1, *Monoporopollenites annulatus*; 2, *Echitricolporites spinosus*; 3, *Fenestrites spinosus*; 4, *Echiperiporites estelae*; 5, *Magnastriatites grandiosus*; 6, *Botryococcus*; 7, *Pediastrum*; 8, *Echitricolporites maristellae*; 9, *Crototricolpites* sp. Artwork by Fatima Leite.

Paisagem reconstruída da Amazônia Central – Mioceno Médio a Superior (16-7 Ma.)

Hoorn et al. 2010



Formações geológicas na Amazônia

Hoorn et al. 2010

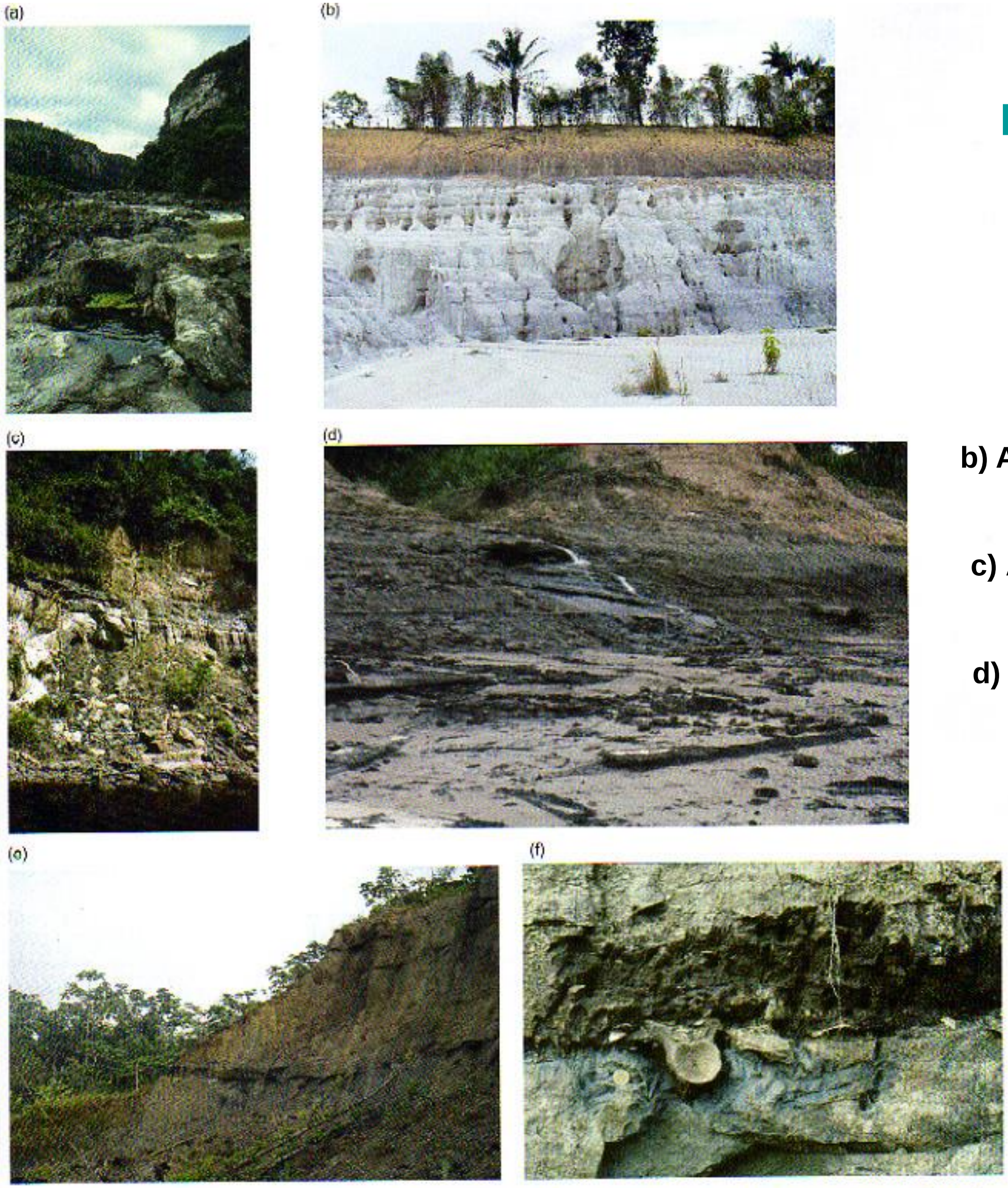


Plate 3 Geological formations in Amazonia. **(a)** Precambrian rocks (front) in contact with the Paleozoic Araracuara Formation (photo Han Overman). **(b)** Alter do Chão Formation outcrop near Manaus (photo Clauzinor da Silva). **(c)** Agua Negra, Lower Miocene, Lower Yari River area, Colombia (photo Carina Hoorn). **(d)** Paumari, Brazil; fossil wood bed from Upper Miocene strata (photo Carina Hoorn). **(e)** Los Chorros, Amazon River, Colombia, Upper Miocene (photo Carina Hoorn). **(f)** Bonebed in Los Chorros section (photo Salomon Kroonenberg).

a) Rochas precambrianas adjacentes à Formação Paleozóica Araracuara

b) Afloramento na Formação Alter do Chão, perto de Manaus

c) Água Negra, Mioceno Inferior, Rio Yari, Colômbia

d) Paumari, Brasil, madeiras fósseis em estratos do Mioceno Superior

e) Los Chorros, Rio Amazonas, Colômbia, Mioceno Superior

f) Ossos fósseis em Los Chorros, Colômbia.

Paleogeografia da Amazônia
Hoorn et al. 2010

Transição de paisagens cratônicas (A-B) para paisagens condicionadas à orogenia andina (C-F)

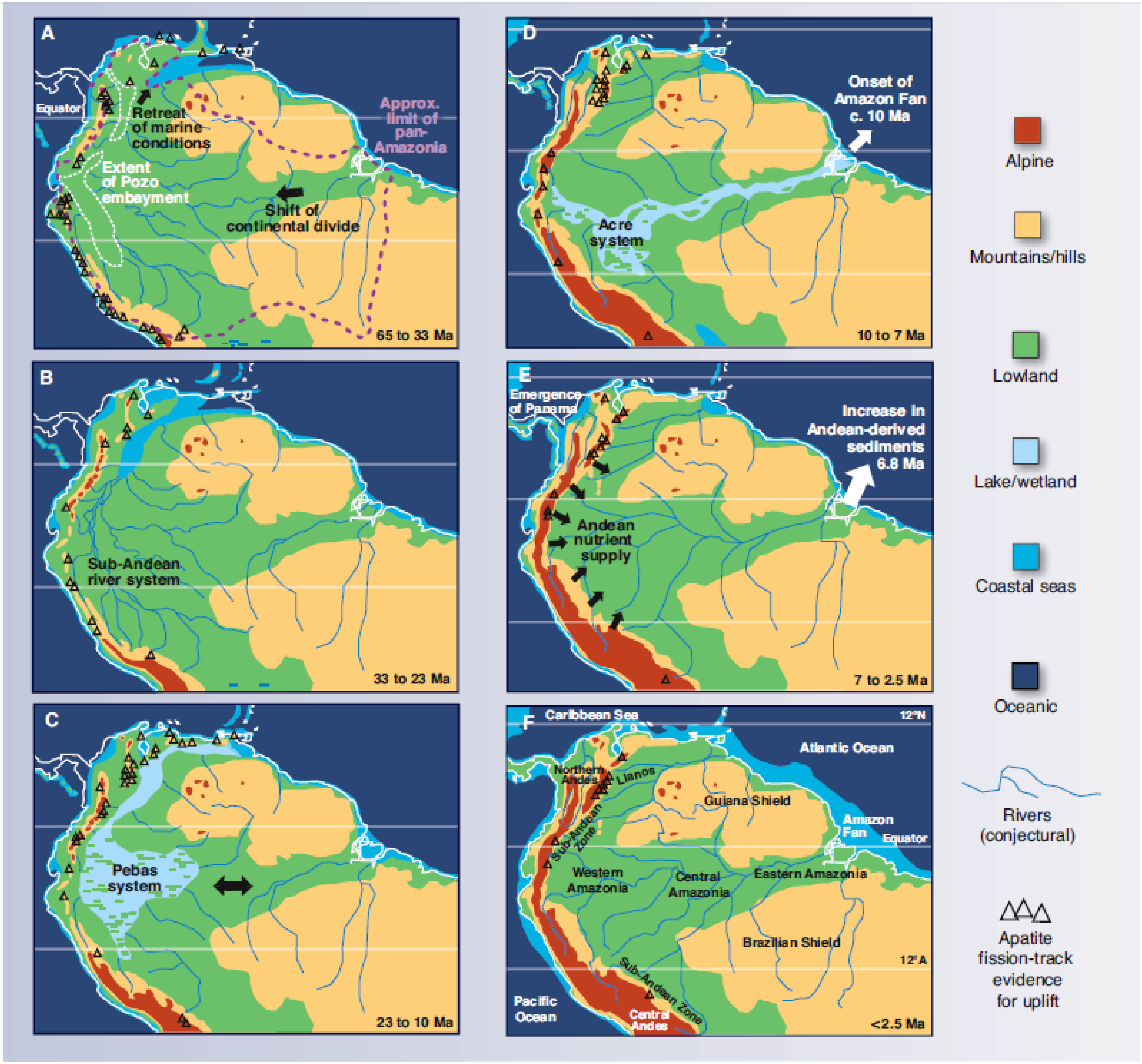


Fig. 1. Paleogeographic maps of the transition from "cratonic" (**A** and **B**) to "Andean"-dominated landscapes (**C** to **F**). (A) Amazonia once extended over most Andes (~12 Ma) and wetland progradation into Western Amazonia. (D) Uplift of the Northern Andes restricted "pan-Amazonia" and facilitated allopatric speciation

Padrões de diversidade atuais na Amazônia

Hoorn et al. 2010

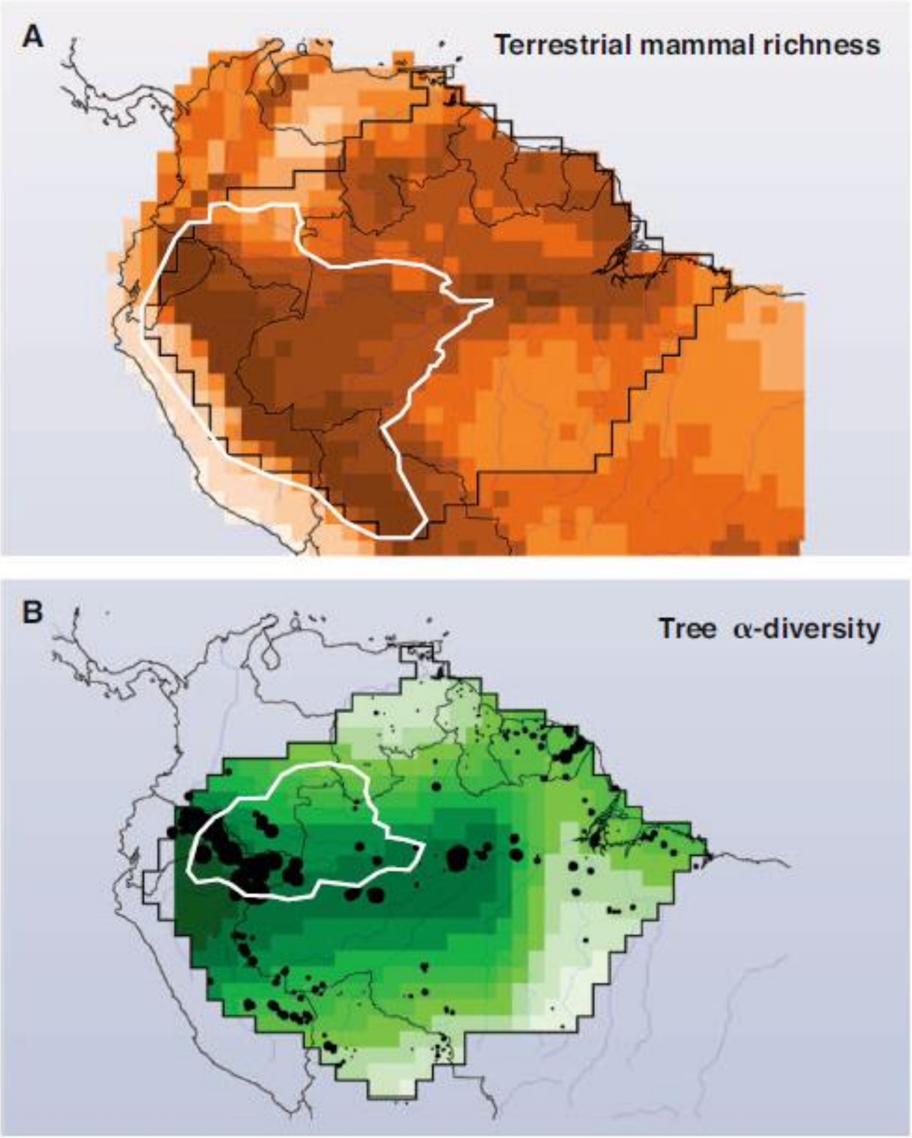


Fig. 3. Present Amazonian diversity patterns. See figs. S6 and S7 for depictions of the close relationship among Amazonian geology, soils, climate, and diversity. (**A**) Terrestrial mammal richness (range: lightest color, 2 to 10 species; darkest, 89 to 109 species) (*69*); white polygon denotes relatively rich soils (fig. S6C). (**B**) Tree α-diversity (*66*). Black dots: local tree α-diversity on 1-ha plots (*n* = 752); Fisher's α ranges from 3.6 to 300; green shades: loess spatial interpolation of 1-ha values (6 to 117); white polygon: area of least severe water shortage (see fig. S6D).

Efeitos das glaciações na região Neotropical: climas mais amenos e secos?

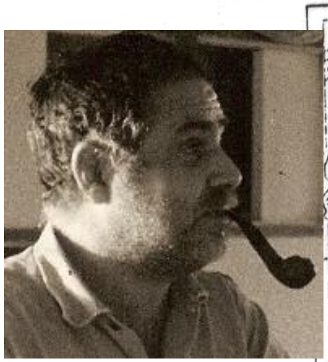


Fig. 12.- Cartes des refuges forestiers du Pléistocène proposés par différents auteurs :

A. VANZOLINI, 1970 (en noir), HAFFER, 1969 (hachuré)
B. BROWN, 1977, 1979
C. PRANCE, 1982 a.

(Granville 1992)

Evidências biológicas atuais

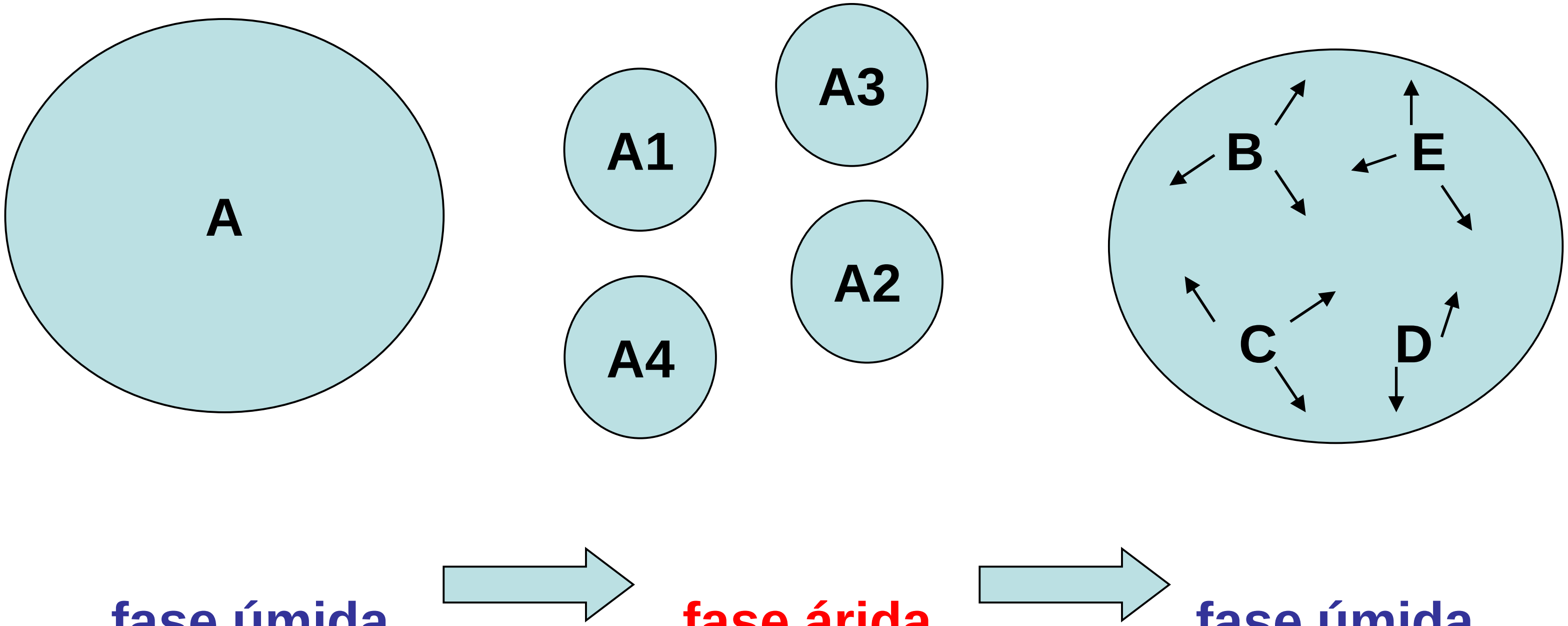
Jürgen Haffer (1932-2010)

Teoria dos Refúgios
Haffer 1969,
geólogo e ornitólogo amador,
identificou 6 centros principais
onde 150 spp de aves
estavam restritas

Padrão insular de endemismos = refúgios florestais durante períodos climáticos secos

Teoria dos Refúgios
(Haffer 1969)

fragmentação de habitat = vicariância = populações isoladas em diferenciação



fase úmida → fase árida → fase úmida

26 refúgios neotropicais de angiospermas

Prance 1982

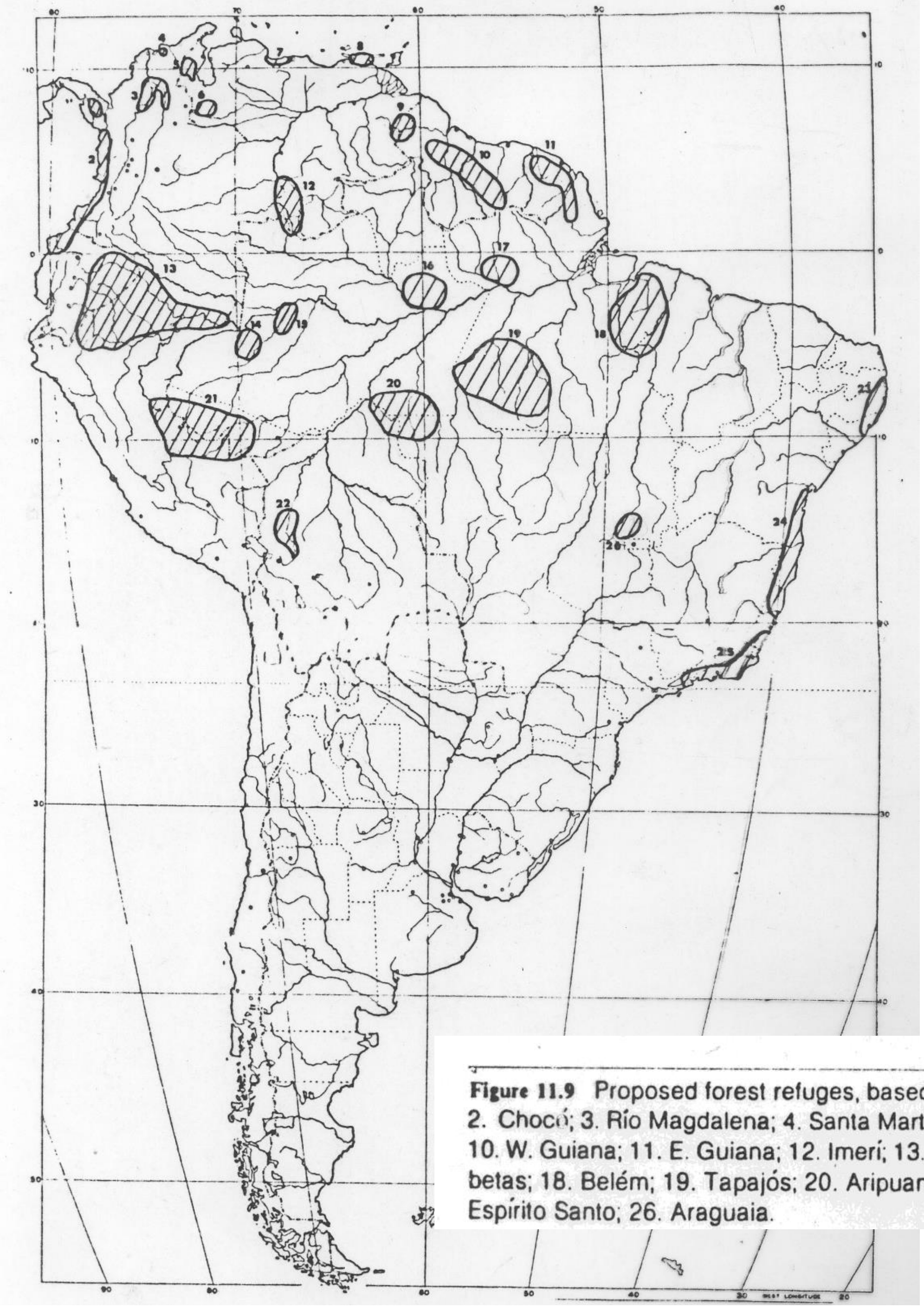
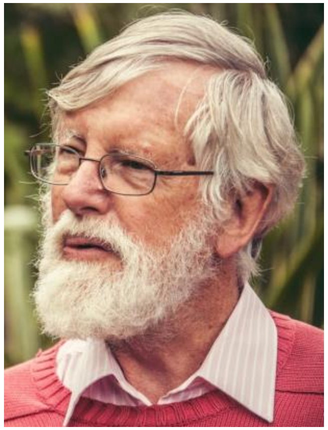


Figure 11.9 Proposed forest refuges, based on distribution of woody Angiosperm families. 1. Panama-Darién; 2. Chocó; 3. Río Magdalena; 4. Santa Marta; 5. Catatumbo; 6. Apure; 7. Rancho Grande; 8. Paria; 9. Imataca; 10. W. Guiana; 11. E. Guiana; 12. Imerí; 13. Napo; 14. São Paulo de Olivença; 15. Tefé; 16. Manaus; 17. Trombetas; 18. Belém; 19. Tapajós; 20. Aripuanã; 21. E. Peru-Acre; 22. Beni; 23. Pernambuco; 24. Bahia; 25. Rio Espírito Santo; 26. Araguaia.



Efeitos das glaciações na região Neotropical

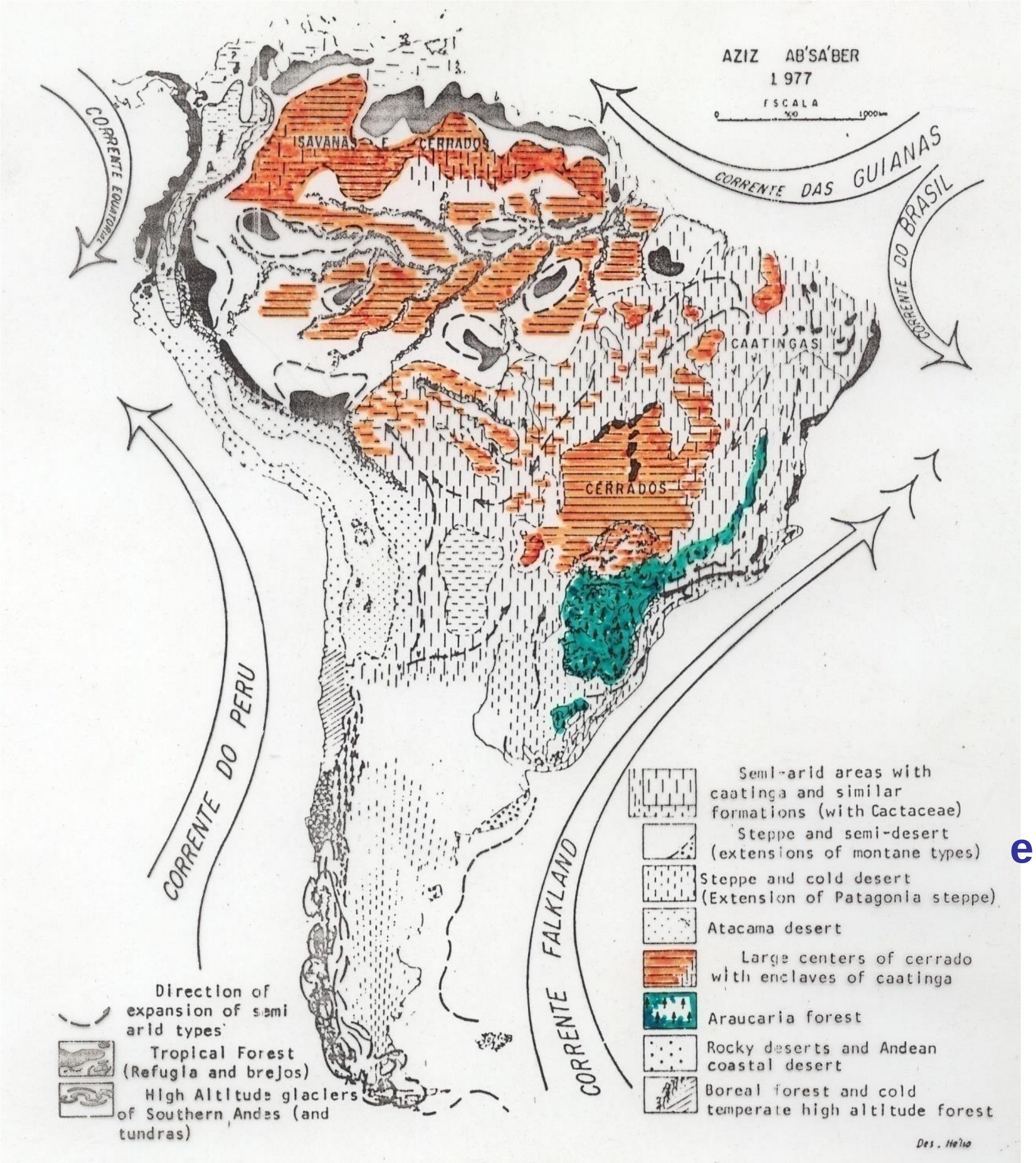


Figure 4.3 The vegetation of South America 13,000-18,000 years BP

Evidências geomorfológicas

(Teoria dos Refúgios)

“linhas-de-pedra”
em sedimentos quaternários*
refletem períodos de
umidade reduzida
com chuvas bem sazonais

*ampla ocorrência
na Amazônia e
no Planalto Central

Efeitos das glaciações na região Neotropical

Evidências geomorfológicas

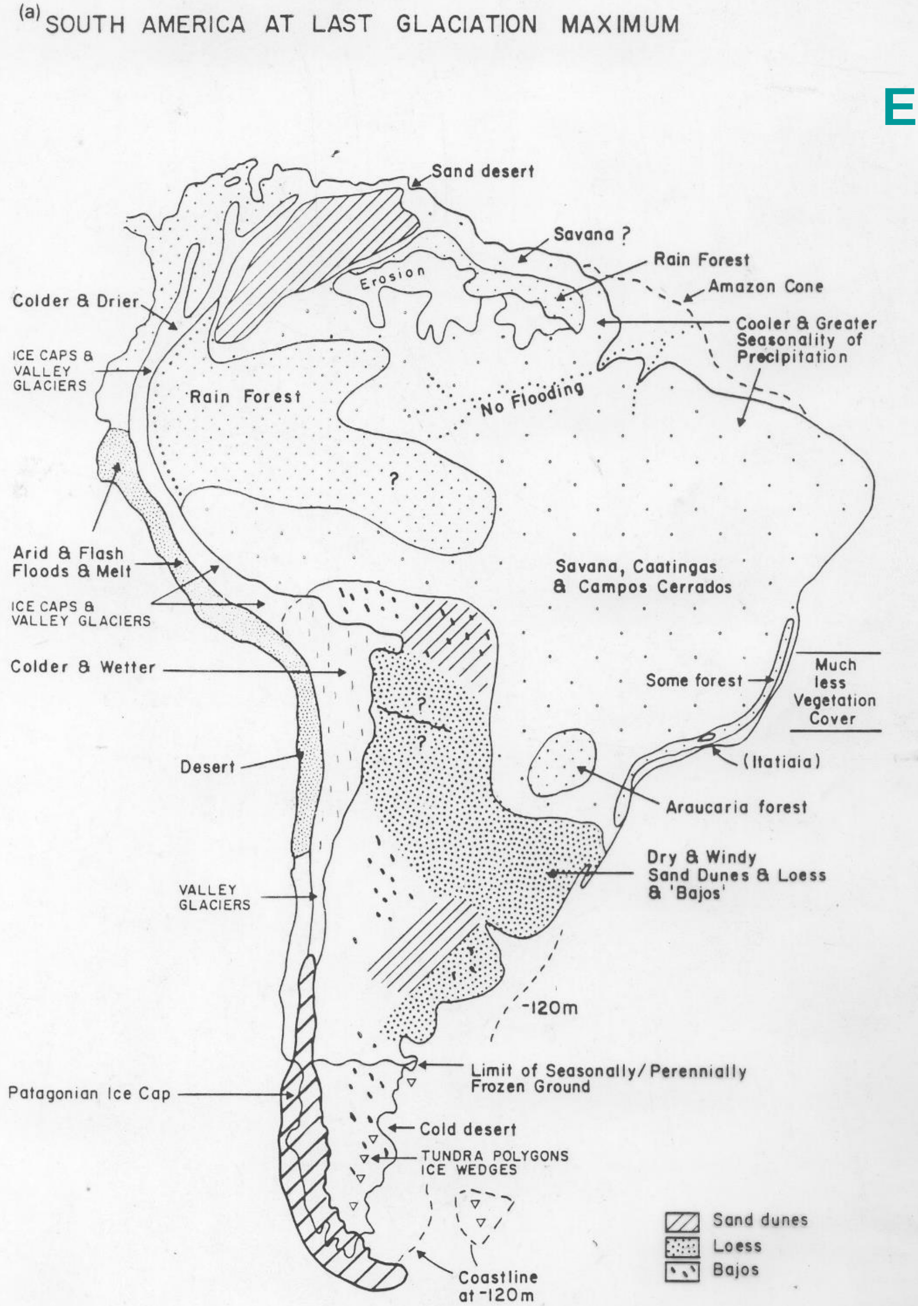


Fig. 23.10. (a) Broad distribution of various types of land surface in South America at the Last Glaciation Maximum, based on geomorphological evidence discussed in this book.

Clapperton 1993

Formações geológicas na Amazônia

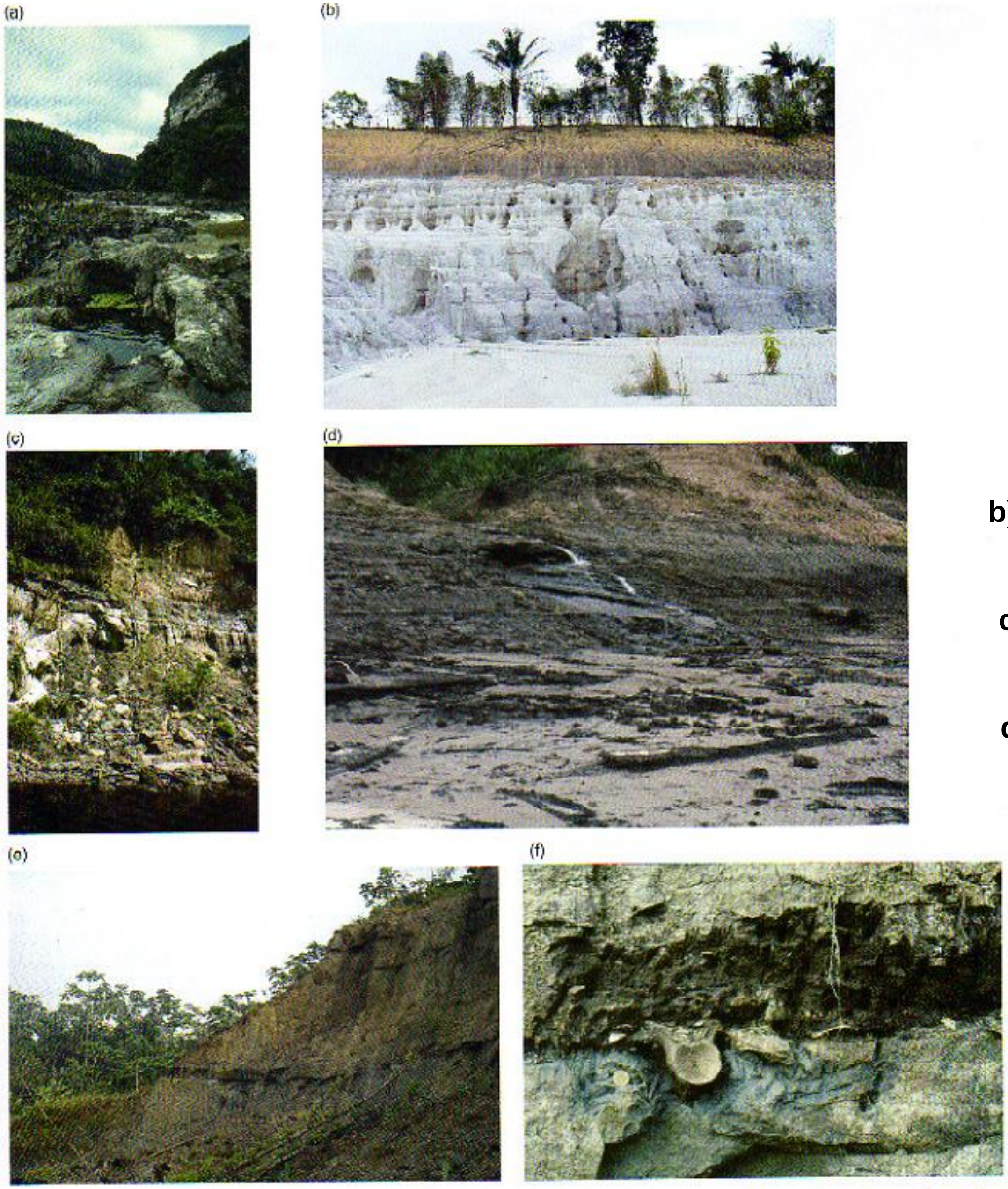


Plate 3 Geological formations in Amazonia. **(a)** Precambrian rocks (front) in contact with the Paleozoic Araracuara Formation (photo Han Overman). **(b)** Alter do Chão Formation outcrop near Manaus (photo Clauzinor da Silva). **(c)** Agua Negra, Lower Miocene, Lower Yari River area, Colombia (photo Carina Hoorn). **(d)** Paumari, Brazil; fossil wood bed from Upper Miocene strata (photo Carina Hoorn). **(e)** Los Chorros, Amazon River, Colombia, Upper Miocene (photo Carina Hoorn). **(f)** Bonebed in Los Chorros section (photo Salomon Kroonenberg).

Hoorn et al. 2010

a) Rochas precambrianas adjacentes à Formação Paleozóica Araracuara

b) Afloramento na Formação Alter do Chão, Pará

c) Água Negra, Mioceno Inferior, Rio Yari, Colômbia

d) Paumari, Brasil, madeiras fósseis em estratos do Mioceno Superior

e) Los Chorros, Rio Amazonas, Colômbia, Mioceno Superior

f) Ossos fósseis em Los Chorros, Colômbia.

mínimo glacial

presente

máximo glacial

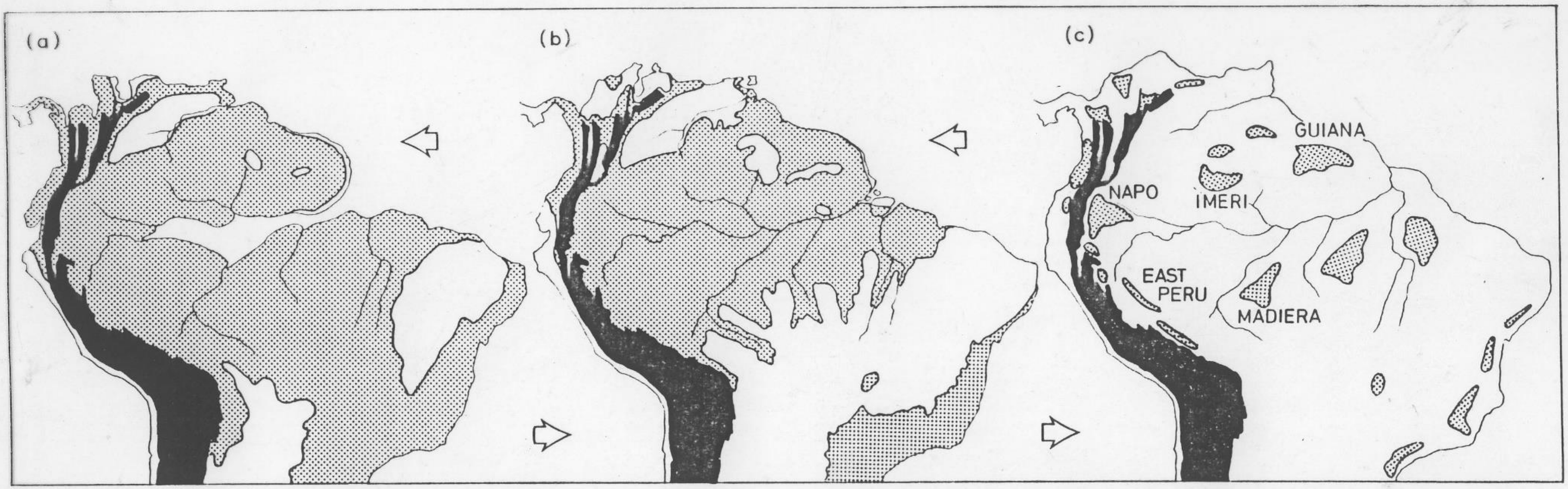


Figure 10.1 Maps of South America illustrating (a) the lowland forest configuration during glacial minima, (b) the forests at present times, and (c) the forest refuges during glacial maxima. The continental boundaries have been adjusted to reflect changing ocean levels (a) and (c). The Andes (above 1000 m) are indicated as solid black. In all maps, the general outline of the Amazon drainage is preserved so as to allow comparisons. Adapted from various sources, chiefly Dixon (1979), Haffer (1969, 1974, 1979), Hueck (1966), Lynch (1979), Schmithusen (1968), and Simpson and Haffer (1978).

Myers & Giller 1988

Períodos holocênicos secos na Amazônia:
1° a 4.000 anos, outro mais intenso há 2.100 anos e outro há 700 anos.
(Salgado-Laboriau 1994)

Críticas à Teoria dos Refúgios

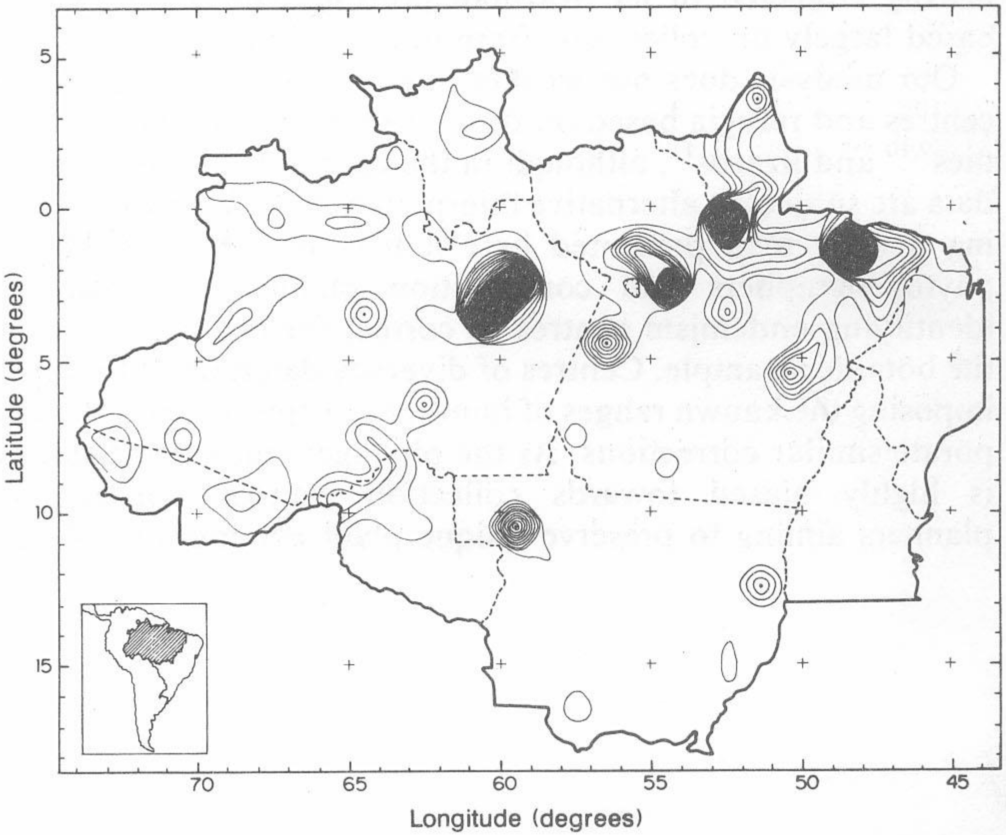


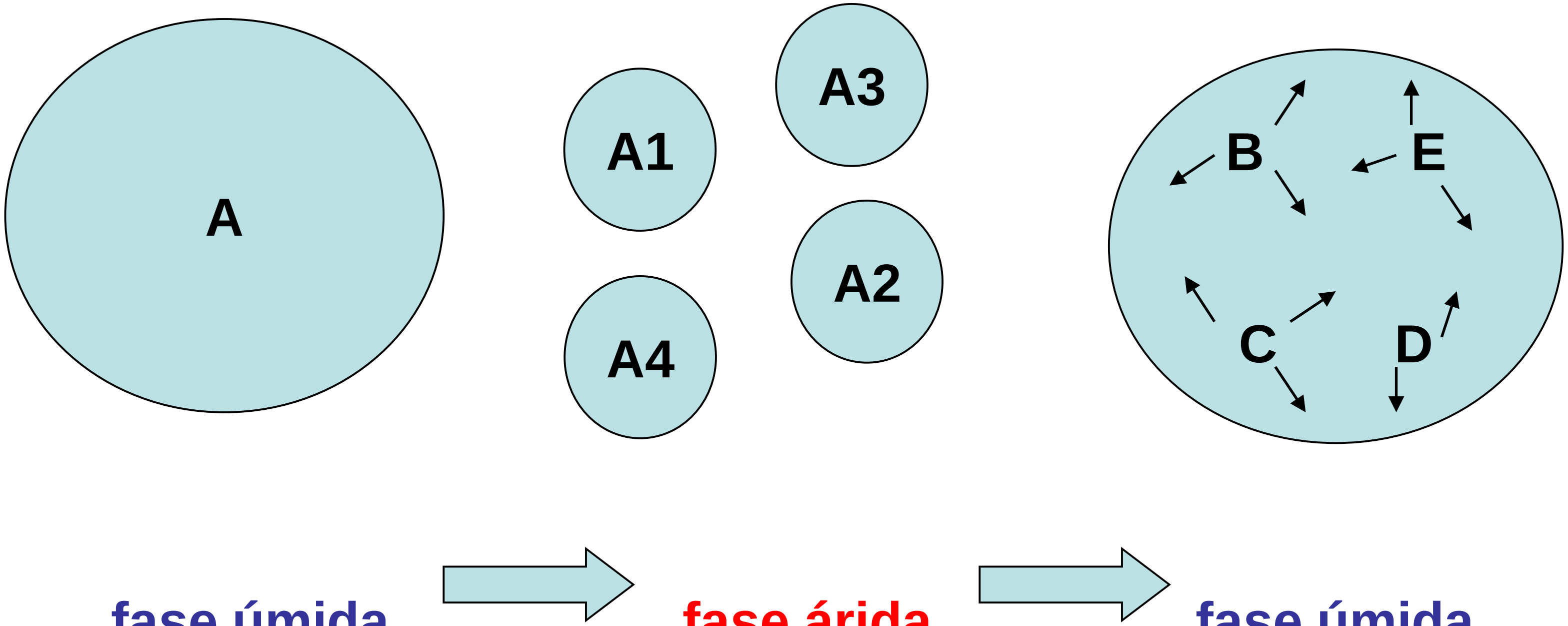
FIG. 3 Density of arborescent angiosperm collections made in Brazilian Amazonia before 1980, based on 1.0% sample from nine herbaria (National Institute for Research in the Amazon at Manaus; Goeldi Museum in Belém; Centre for Humid Tropic Research in Belém; Botanical Garden of Rio de Janeiro; National Museum in Rio de Janeiro; São Paulo Botanical Institute; University of Brasilía; New York Botanical Garden; Smithsonian Institution in Washington). Isolines represent number of specimens of genus *Inga* per degree-grid square, plotted at density intervals of five. Squares with fewer than five *Inga* do not appear on map. Density ranges from zero to 320 specimens, with peaks of 160 and 320 over Manaus and Belém, respectively. Duplicate collections deleted, leaving total sample of 2,345 specimens.

1. centros de densidade de coleta!

Nelson *et al.* 1990

Críticas à
Teoria dos Refúgios

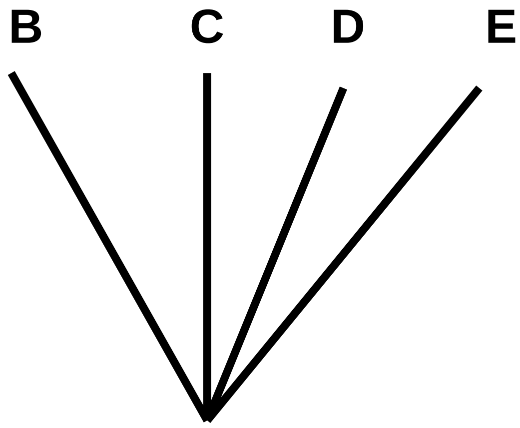
2. Cladogramas de táxons diferenciados nos refúgios deveriam apresentar padrões em politomias!



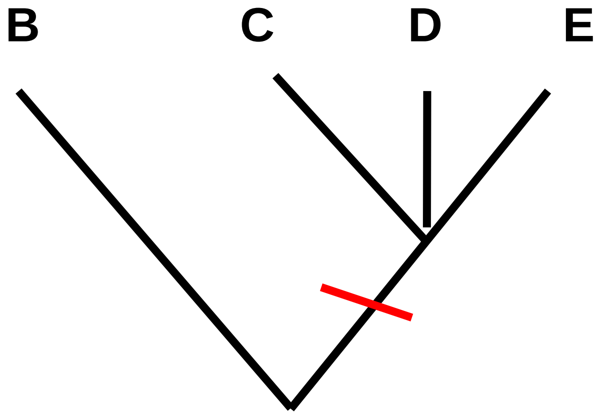
fase úmida → fase árida → fase úmida

Críticas à
Teoria dos Refúgios

2. Cladogramas de táxons diferenciados nos refúgios deveriam apresentar padrões em politomias:



esperado

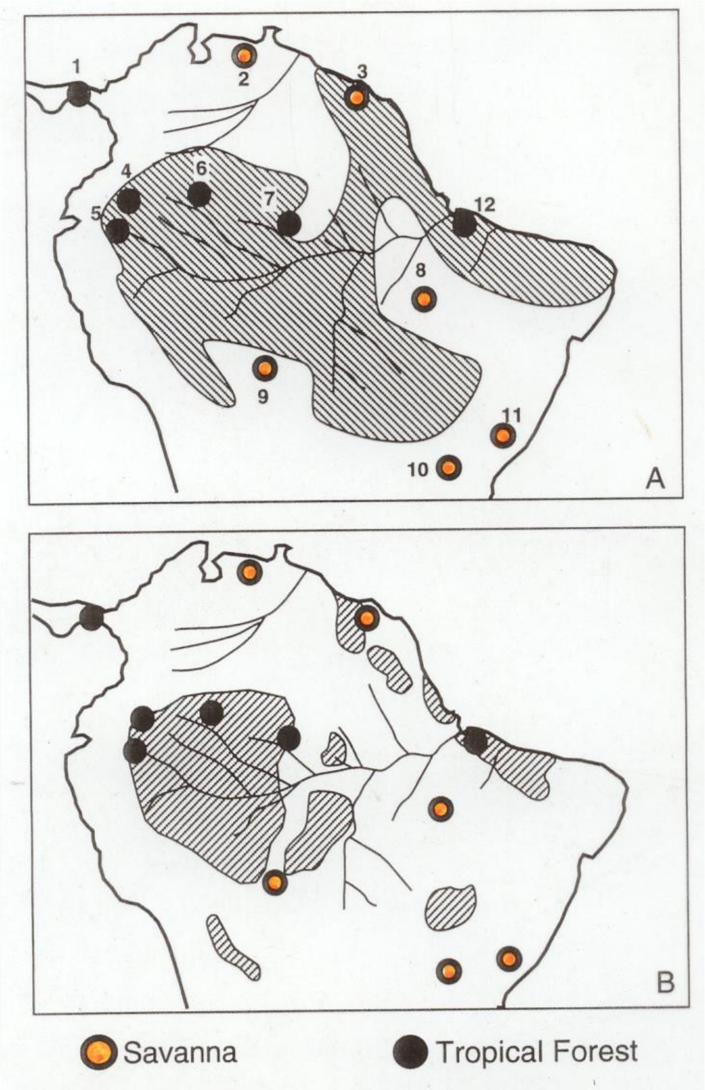


encontrado

Críticas à
Teoria dos Refúgios

3. falta de comprovação paleoestratigráfica

Burnham & Graham 1999



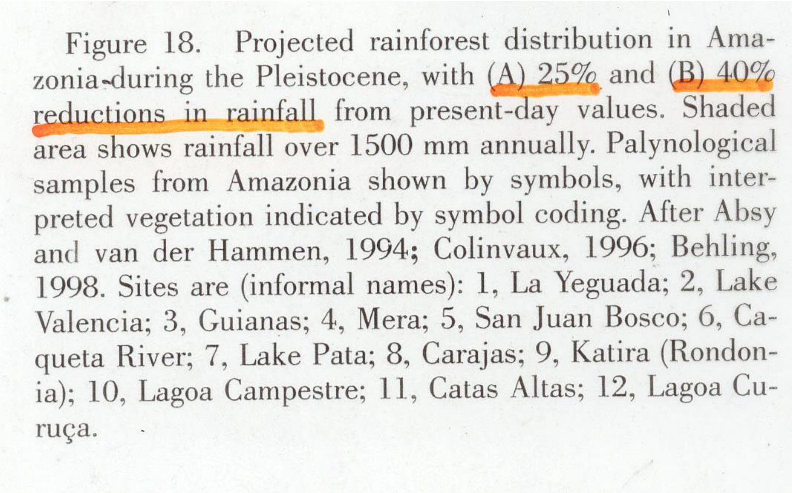
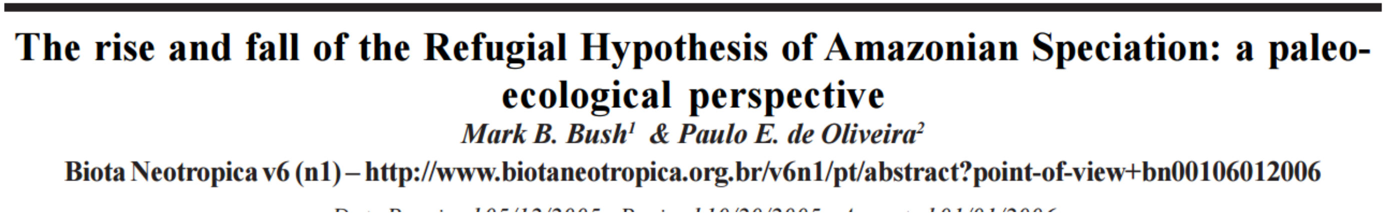


Figure 18. Projected rainforest distribution in Amazonia during the Pleistocene, with (A) 25% and (B) 40% reductions in rainfall from present-day values. Shaded area shows rainfall over 1500 mm annually. Palynological samples from Amazonia shown by symbols, with interpreted vegetation indicated by symbol coding. After Absy and van der Hammen, 1994; Colinvaux, 1996; Behling, 1998. Sites are (informal names): 1, La Yeguada; 2, Lake Valencia; 3, Guianas; 4, Mera; 5, San Juan Bosco; 6, Caqueta River; 7, Lake Pata; 8, Carajas; 9, Katira (Rondonia); 10, Lagoa Campestre; 11, Catas Altas; 12, Lagoa Curuça.



The rise and fall of the Refugial Hypothesis of Amazonian Speciation: a paleo-ecological perspective

Mark B. Bush[1] *& Paulo E. de Oliveira*[2]

Biota Neotropica v6 (n1) – http://www.biotaneotropica.org.br/v6n1/pt/abstract?point-of-view+bn00106012006

Modelos alternativos para especiação na Amazônia

Bush 1994

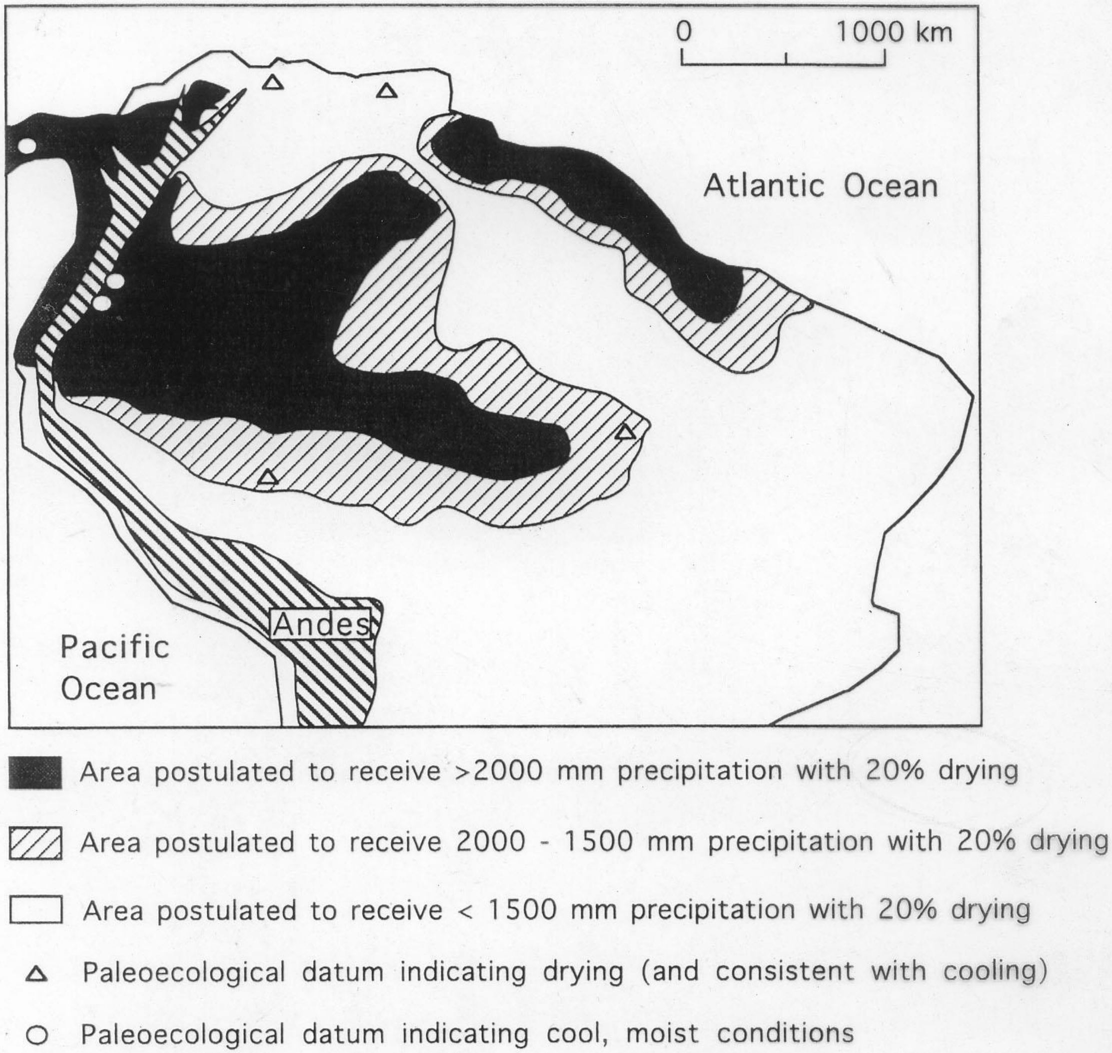


FIG. 3. Sketch map showing postulated annual precipitation to the Amazon basin with a 20% reduction in effective precipitation. Data for modern precipitation from Haffer (1987). Areas receiving less than 2000 mm of precipitation will contain floras most likely to have been affected by drought-stress. Locations of lowland paleoecological sites with records dating to the Pleistocene are shown. Paleoecological data showing drying lie within the marginal forest areas (2000–1500 mm precipitation). 1, El Valle (Bush & Colinvaux, 1990); 2, Mera (Liu & Colinvaux, 1985; Bush *et al.*, 1990); 3, San Juan Bosco (Bush *et al.* 1990); 4, Rondonia (Absy & van der Hammen, 1976); 5, Carajas (Absy *et al.*, 1991); 6, Guyana (van der Hammen, 1974); 7, Lake Valencia (Leyden, 1985).

Modelos alternativos para especiação na Amazônia

Bush 1994

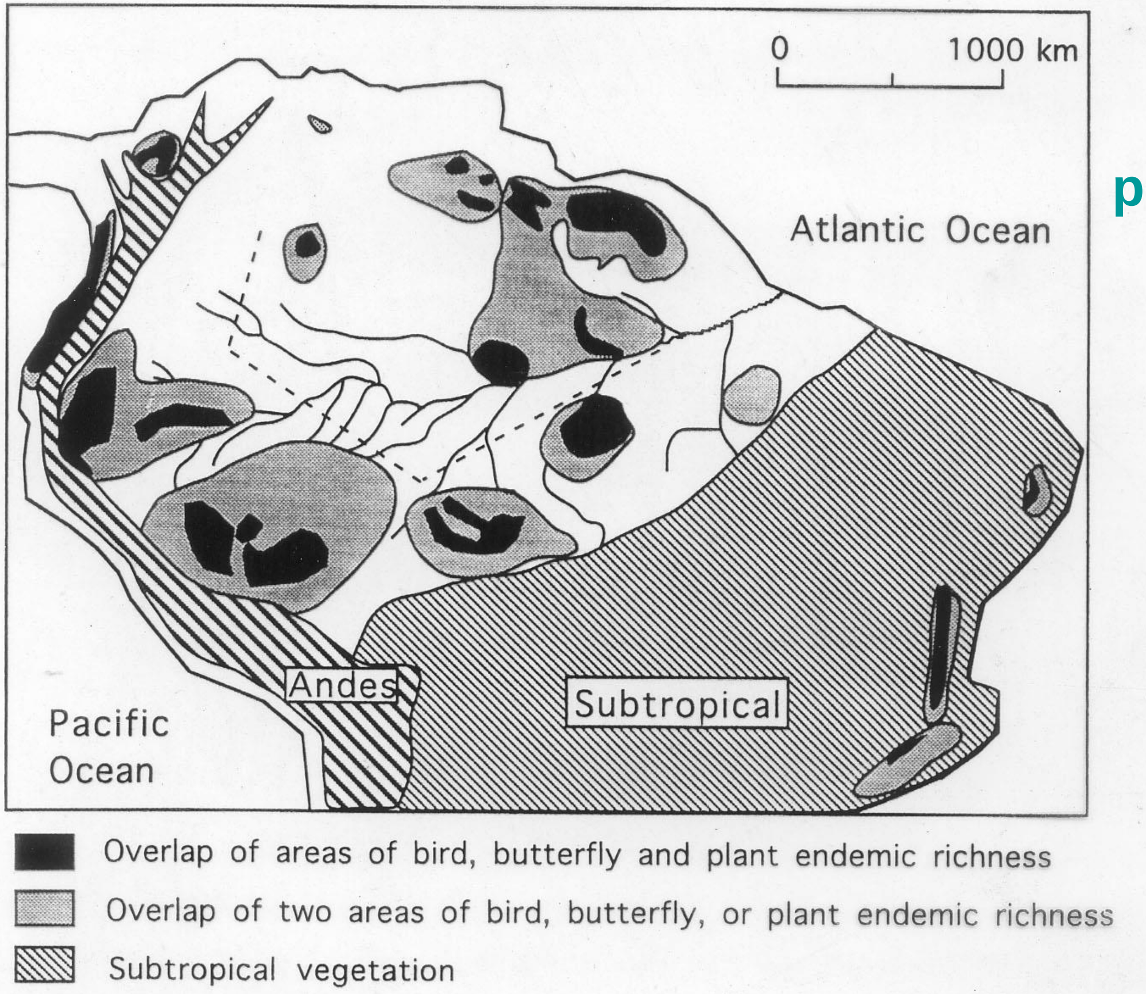


FIG. 5. Sketch map showing the location of postulated concentrations of endemic taxa based on overlapping distributions of endemic birds, butterflies and plants (after Brown, 1987b) and the northern limit of subtropical elements with a 4°C cooling. Dashed lines indicate the proposed limits of migration of Andean and subtropical elements given a 7.5°C cooling.

Modelos alternativos para especiação na Amazônia

Bush 1994

Amazonian speciation 13

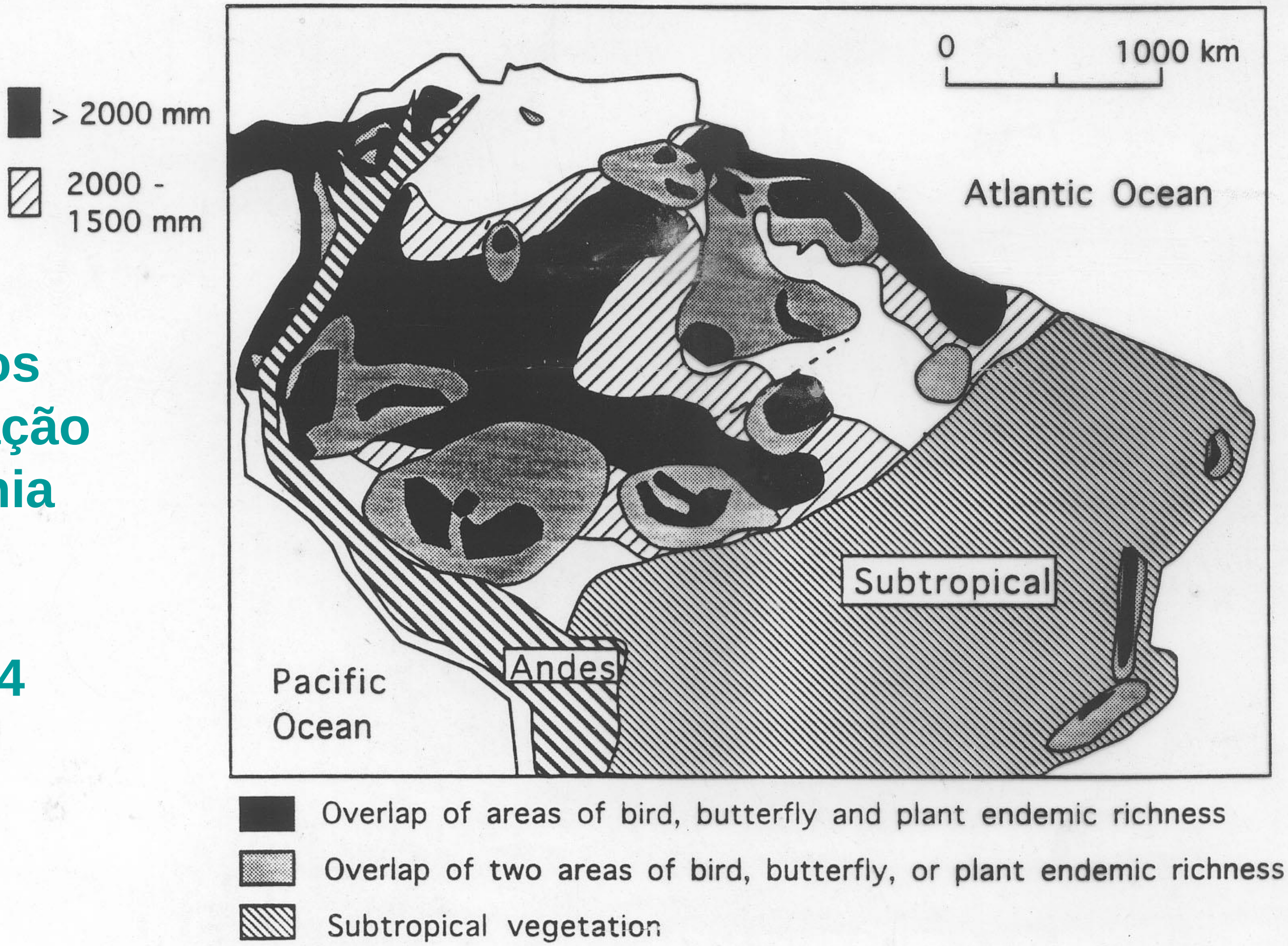


FIG. 6. Sketch map showing the location of endemic centres relative to precipitation assuming a 20% effective drying during glacial times. Endemic centres (Brown, 1987c) lie either in the marginal forest areas or within the range of migration of the Andean flora. Dashed lines indicate the proposed limits of migration of Andean and subtropical elements given a 7.5°C cooling.

Modelos alternativos paleoclimáticos na Amazônia
Lagoa da Pata (P.N. Pico da Neblina, Alto Rio Negro) Oliveira 1996

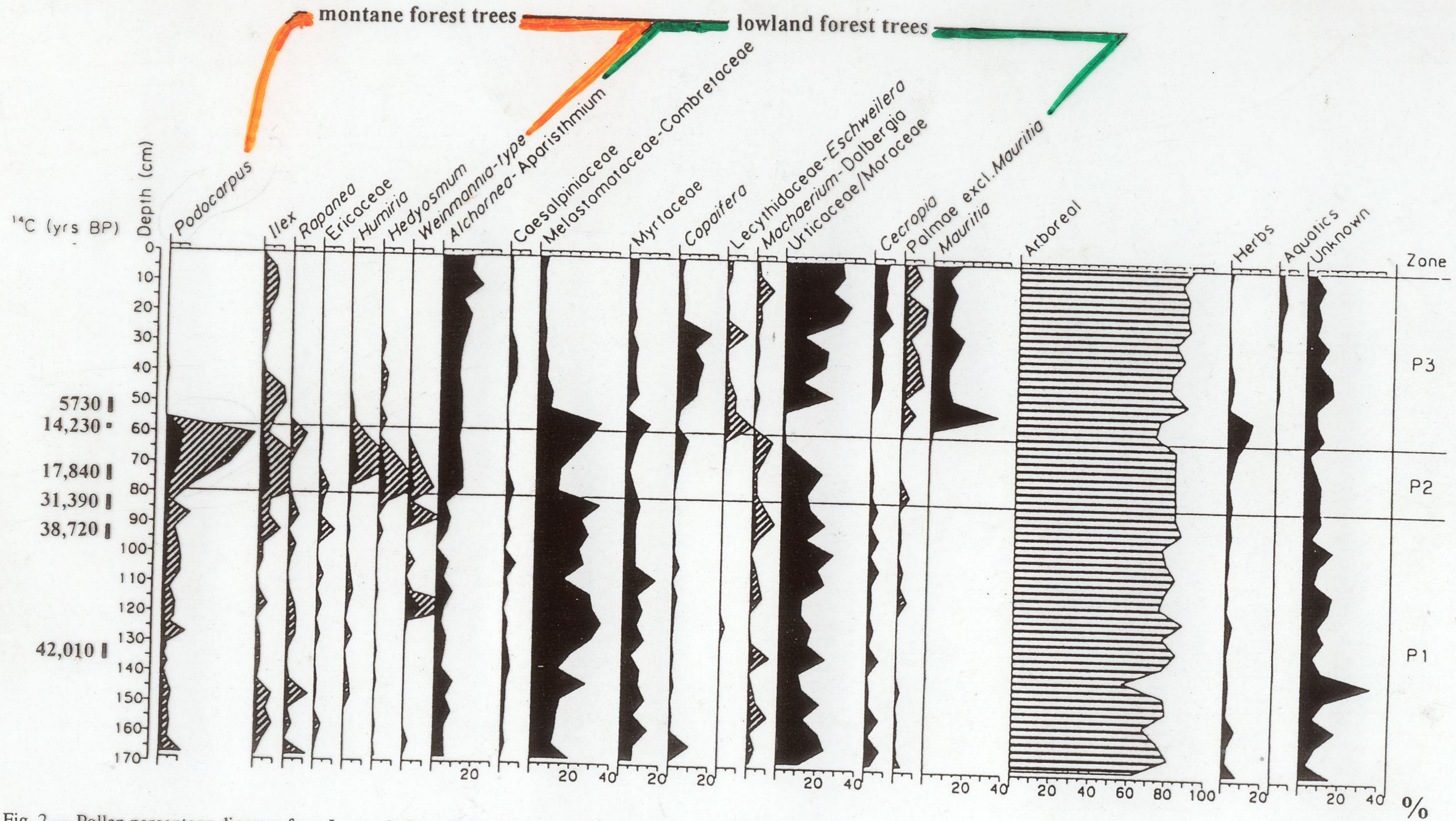
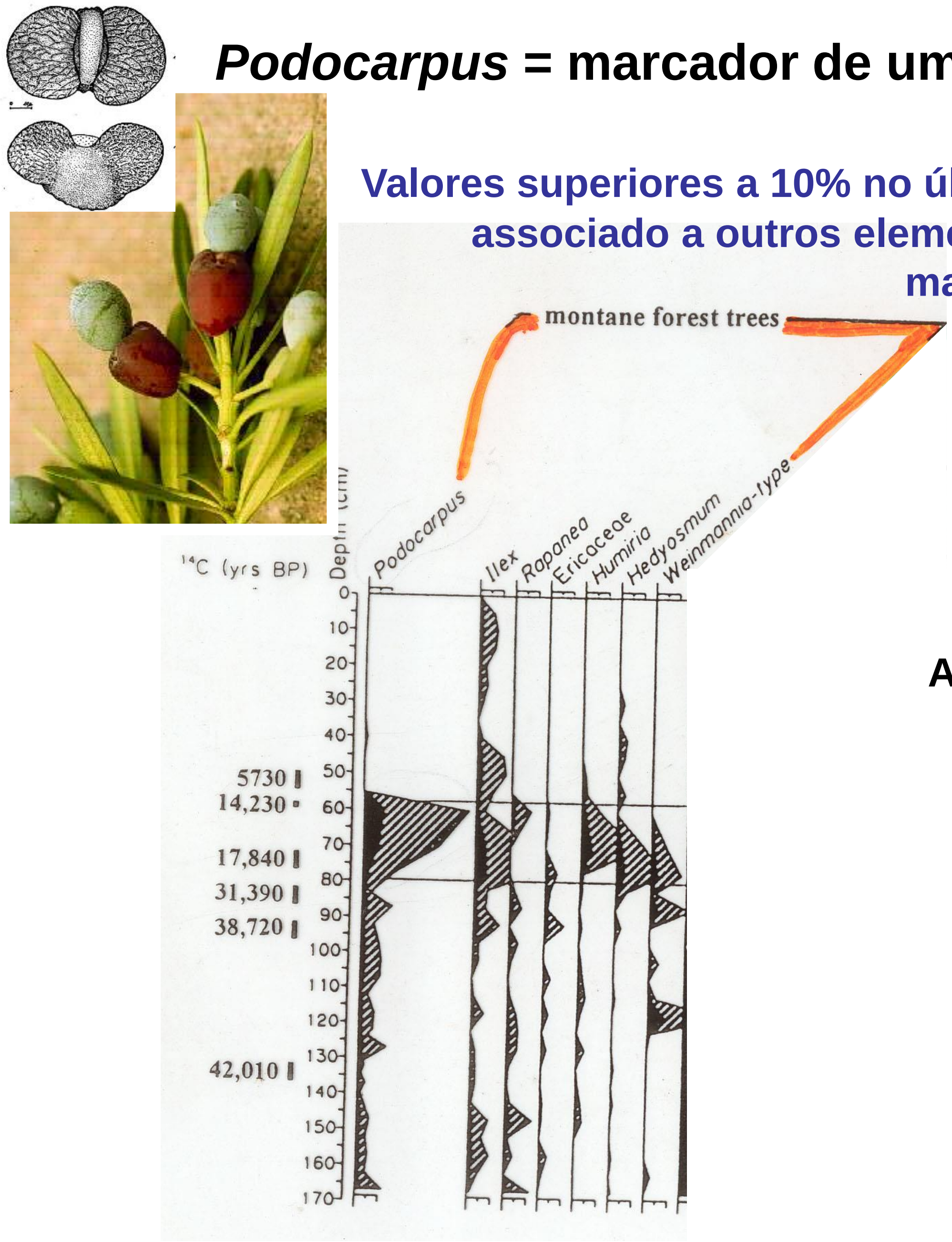


Fig. 2 — Pollen percentage diagram from Lagoa da Pata. Percentages based on Gymnosperm and Angiosperm pollen sum.

Podocarpus = marcador de umidade e temperatura mais baixa.



Valores superiores a 10% no último máximo glacial (18.000-14.000 A.P.) associado a outros elementos adaptados a temperaturas baixas, mas também a elementos de terras baixas, causando alteração na flora, mas não paleofragmentação da cobertura florestal.

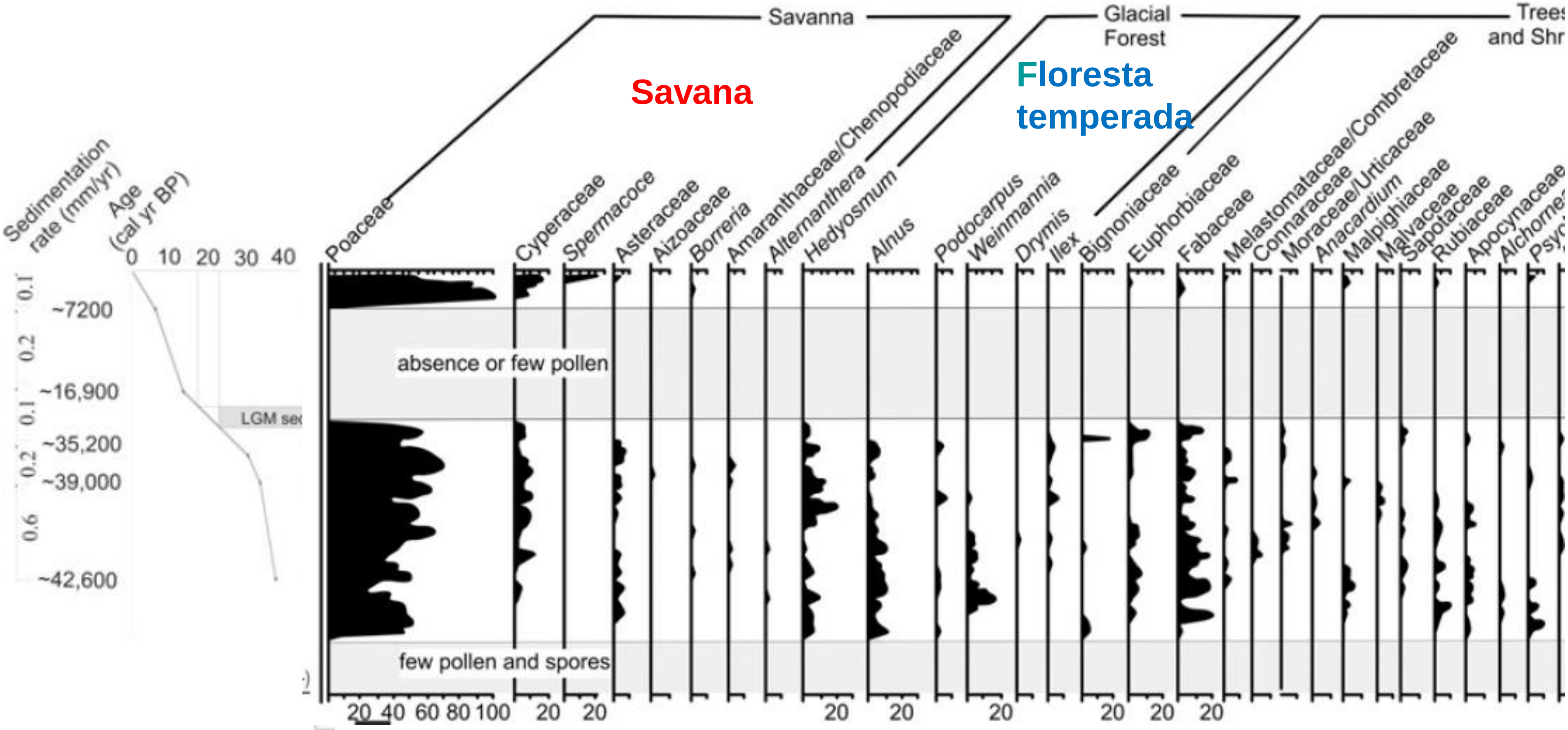
Pólen de Podocarpus desaparece nas amostras holocênicas.

Atualmente spp. de *Podocarpus* restritas a áreas montanhosas da Neblina e da Venezuela (acima de 1100m) = a expansão até 800 m durante o *umg* implica resfriamento de no mínimo 5°C (6°C?).

Oliveira 1996

Modelos alternativos paleoclimáticos na Amazônia
Humaitá, Rio Madeira (Amazônia Ocidental) Cohen et al. 2013

Alnus, Hedyosmum
Podocarpus, Drymis,
Weinmannia, Ilex



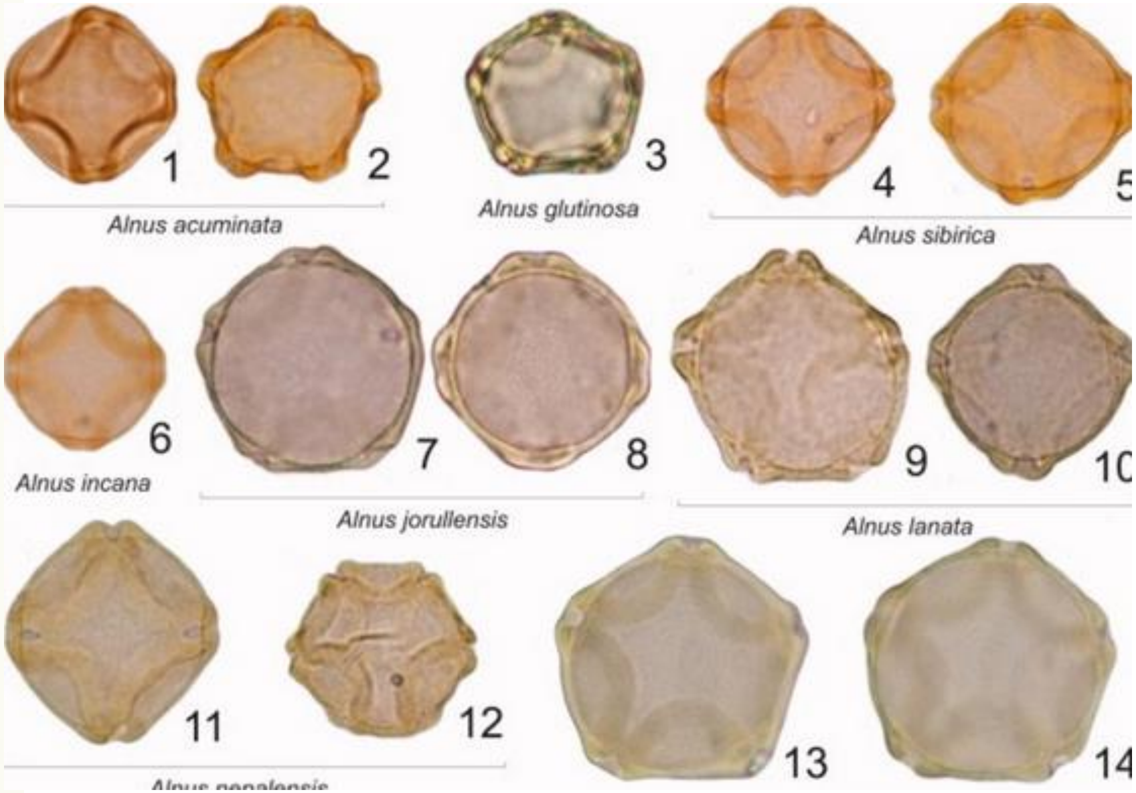
Savana

Floresta temperada

Modelos alternativos paleoclimáticos na Amazônia Humaitá - Amazônia Ocidental: Cohen et al. 2013

***Alnus glutinosa* – BETULACEAE**
delta-intkey.com

***Alnus* – pólen - Leopold et al. 2012**



Modelos alternativos paleoclimáticos na Amazônia
Humaitá - Amazônia Ocidental: Cohen et al. 2013

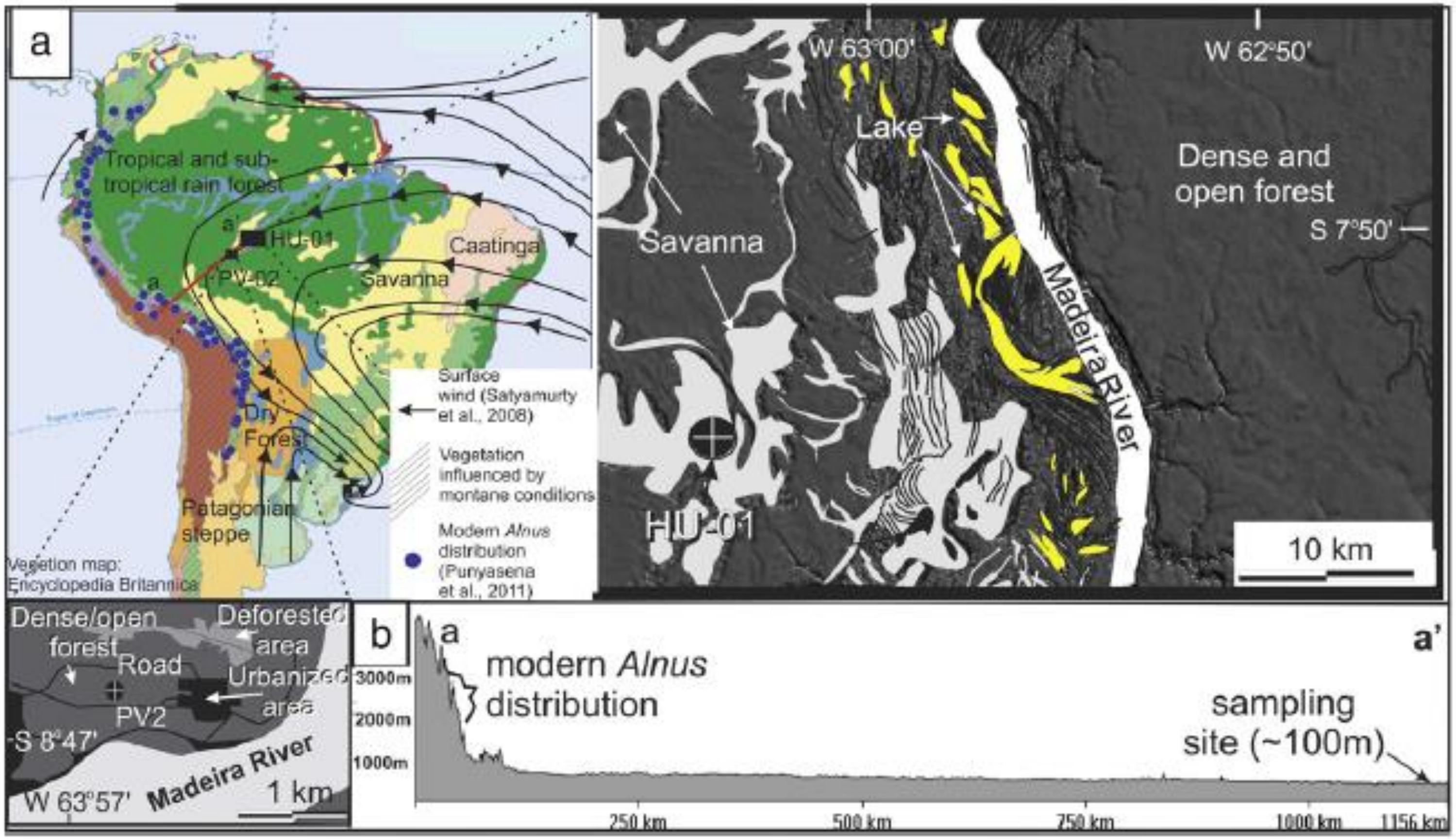


Fig. 1. a) Sediment core location, main geomorphologic features, surface wind directions, modern *Alnus* distribution, and location of vegetation units; b) topographic profile from Andes to study site.

Modelos alternativos paleoclimáticos na Amazônia

Humaitá, Rio Madeira (Amazônia Ocidental)

Modelo da evolução geomorfológica e vegetacional

Cohen et al. 2013

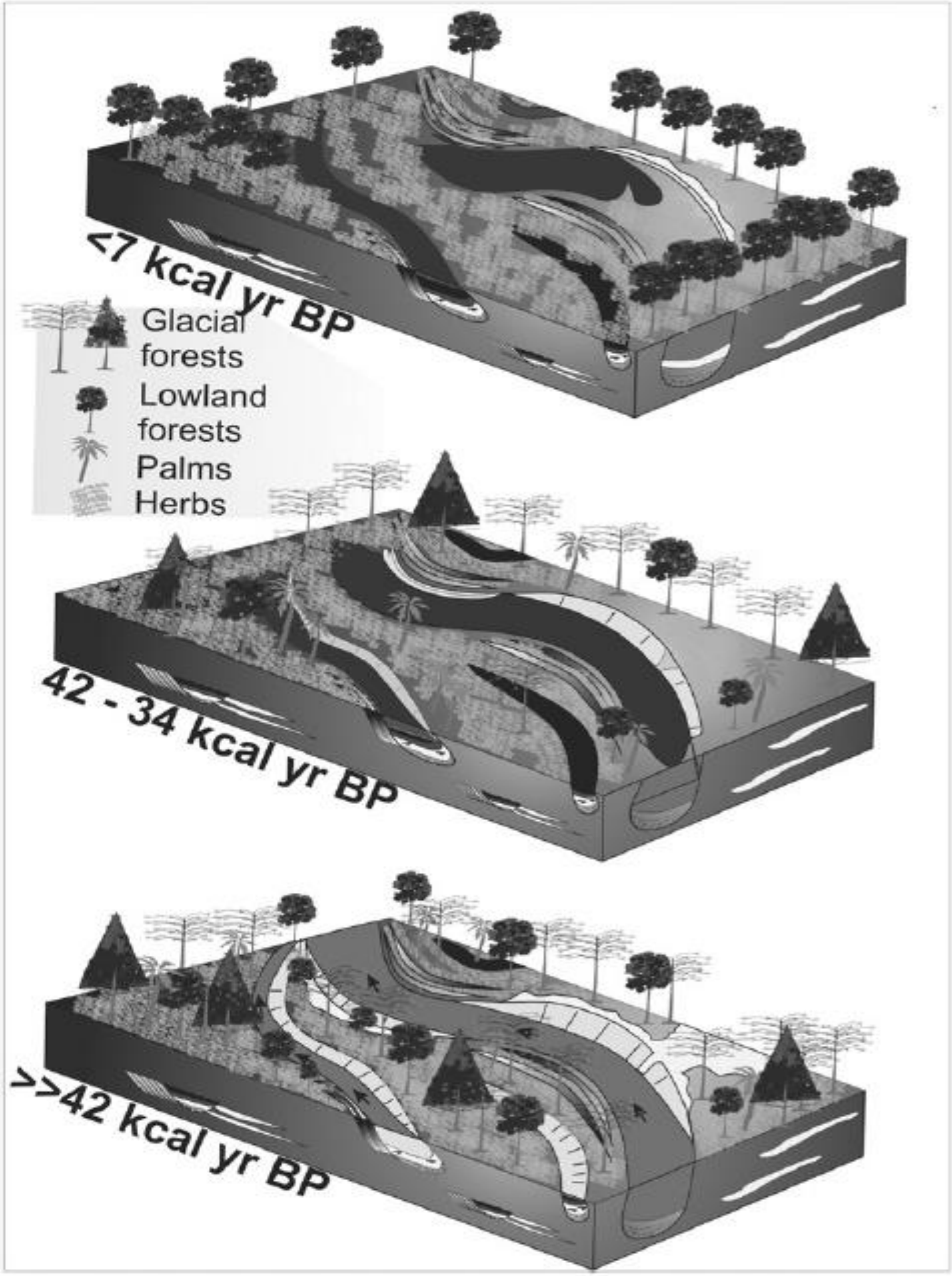


Fig. 4. Geomorphologic and vegetation evolution model for the study site.

Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum (LGM)

Mayle *et al.* 2004

palaeovegetation and independent palaeoclimatic datasets together -

dynamic vegetation model simulations

<u>Amazonia remained predominantly forested at the LGM</u>, although the combination of reduced temperatures, precipitation and atmospheric CO2 concentrations resulted in <u>forests structurally and floristically quite different from those of today</u>.

Cold-adapted Andean taxa mixed with rainforest taxa in central areas,
while dry forest species and lianas probably became important in the more seasonal southern Amazon forests and savannahs expanded at forest–savannah ecotones.

Outras contribuições interessantes:

Padrão peri-amazônico

Granville 1992

5

ESPECES FORESTIERES PERI-AMAZONIENNES

Fig. 2.- Exemples de distribution péri-amazonienne de TYPE I (Nord et Ouest) chez les Angiospermes des forêts humides de basse altitude

- ● A. *Couroupita guianensis* (d'après MORI & PRANCE, 1990) ;
- ■ B. *Brunfelsia grandiflora* subsp. *schultesii* (d'après PLOWMAN, 1979)
- ▲ C. *Swietenia macrophylla* (d'après PENNINGTON, 1981)

Padrão peri-amazônico

Granville 1992

ESPECES FORESTIERES PERI-AMAZONIENNES 7

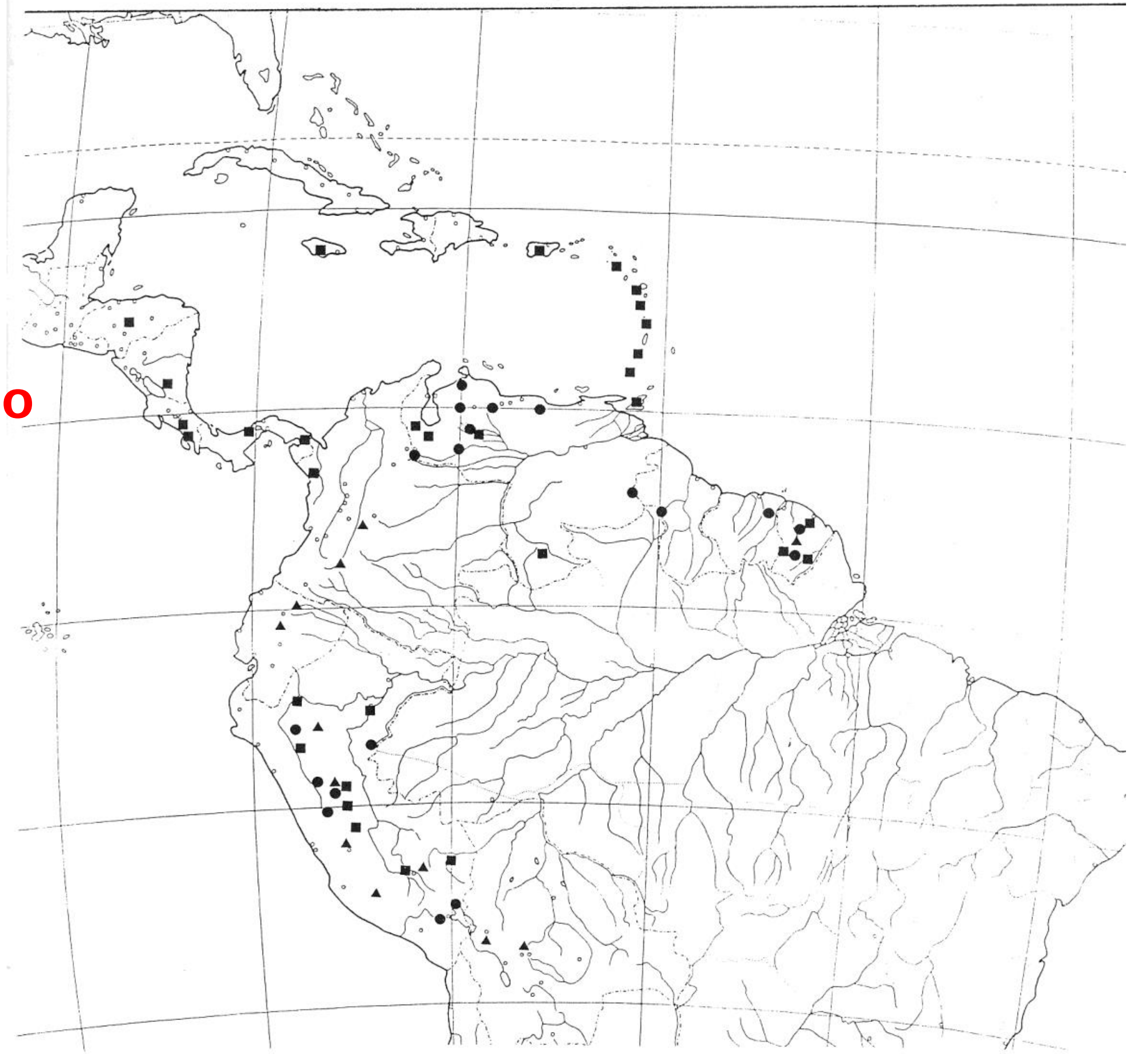


Fig. 3.- Exemples de distribution péri-amazonienne de TYPE I (Nord et Ouest) chez les Ptéridophytes des forêts humides de basse altitude (d'après CREMERS, 1990)

Padrão peri-amazônico

Granville 1992

ESPECES FORESTIERES PERI-AMAZONIENNES

11

Fig. 5.- Exemples de distribution péri-amazonienne de TYPE III (Ouest et Sud-Est) chez les Angiospermermes des forêts humides de basse altitude (d'après PRANCE, 1973)

- ● A. *Anthodiscus amazonicus* ;
- ■ B. *Cariniana estrellensis* ;
- ▲ C *Couratari macrosperma*

Padrão peri-amazônico

Granville 1992

Fig. 6.- Exemples de distribution péri-amazonienne de TYPE IV (Nord, Ouest et Sud-Est) chez les *Angiospermes* des forêts humides de basse altitude

● A. *Anartia olivacea* (d'après ALLORGE, 1985) ;
B. *Trichilia elegans* subsp. *elegans* (d'après PENNINGTON,
■ 1981) ;
▲ □ *Trichilia elegans* subsp. *richardiana* (d'après PENNINGTON, 1981) ;
C. *Banisteriopsis wurdackii* (d'après GATES, 1982)

Padrão peri-amazônico

Granville 1992

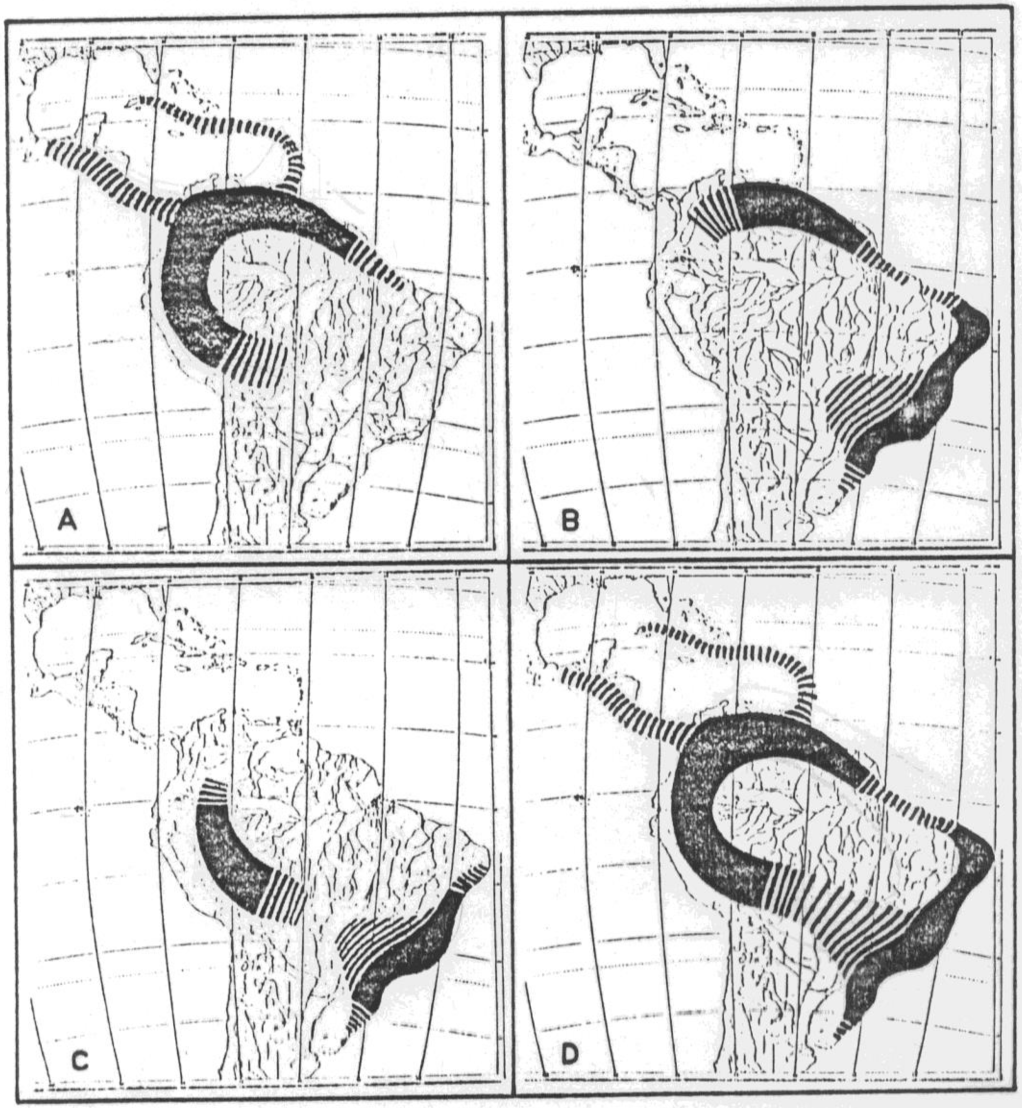


Fig. 1 - Différents types de distribution péri-amazonienne :

A. Type I : Amazonie occidentale + Amazonie septentrionale
B. Type II : Côte atlantique brésilienne + Amazonie septentrionale
C. Type III : Amazonie occidentale + côte atlantique brésilienne
D. Type IV: Amazonie occidentale + Amazonie septentrionale + côte atlantique brésilienne (+ Amazonie méridionale)

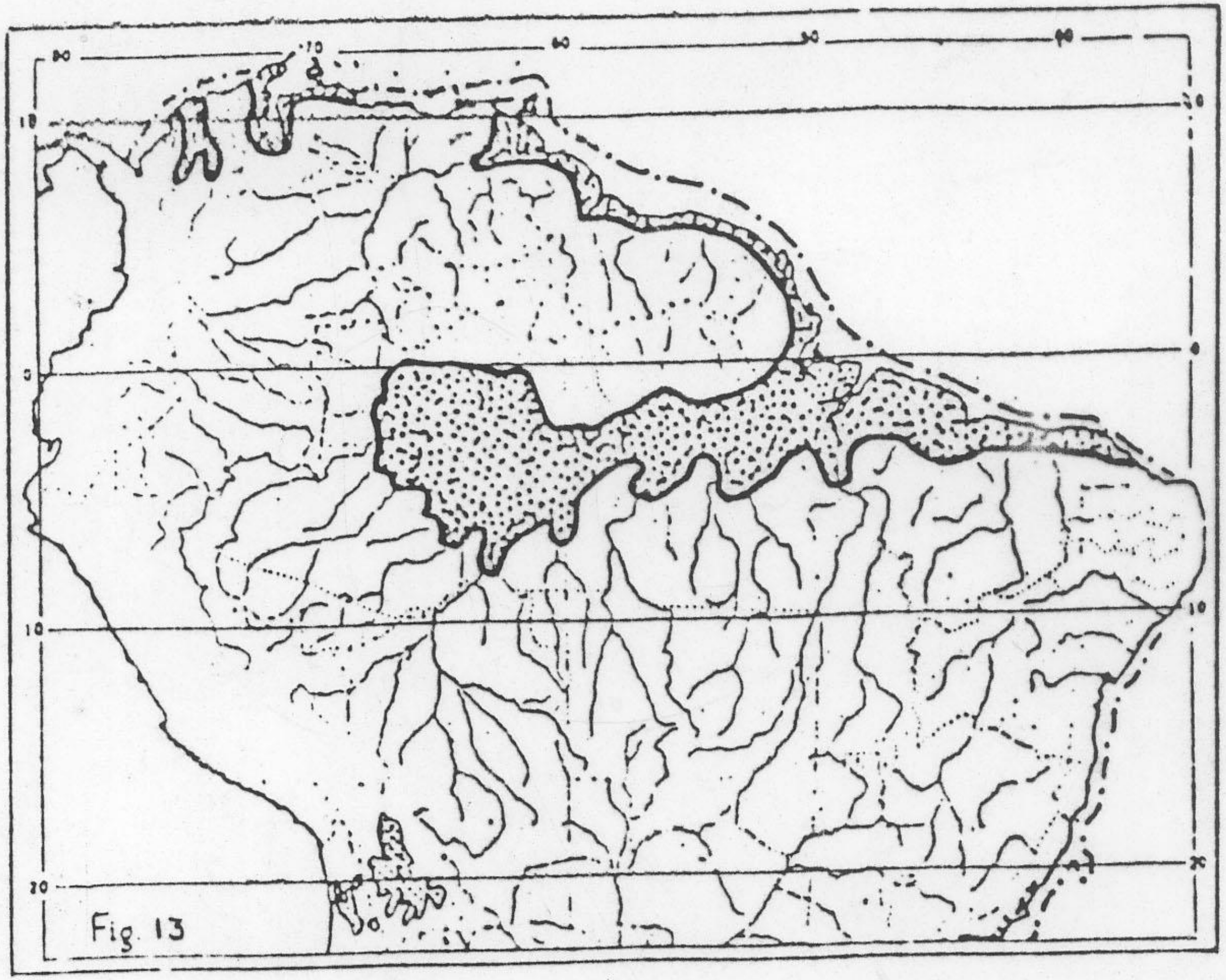


Fig. 13.- Transgression marine interglaciaire
(d'après VUILLEUMIER, 1971)

Outras contribuições interessantes:

Oliveira & Daly 1999

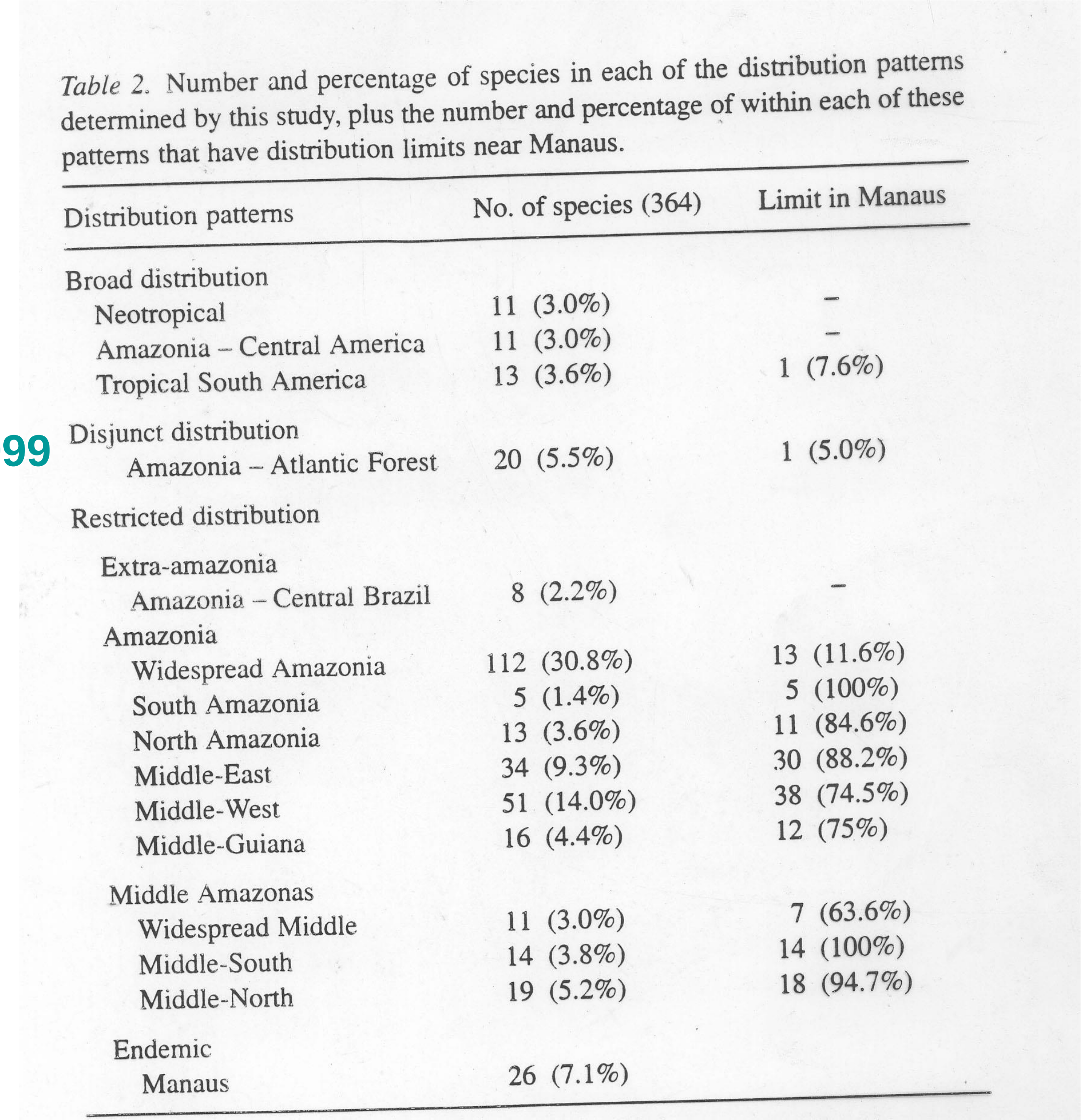


Table 2. Number and percentage of species in each of the distribution patterns determined by this study, plus the number and percentage of within each of these patterns that have distribution limits near Manaus.

Distribution patterns	No. of species (364)	Limit in Manaus
Broad distribution		
Neotropical	11 (3.0%)	–
Amazonia – Central America	11 (3.0%)	–
Tropical South America	13 (3.6%)	1 (7.6%)
Disjunct distribution		
Amazonia – Atlantic Forest	20 (5.5%)	1 (5.0%)
Restricted distribution		
Extra-amazonia		
Amazonia – Central Brazil	8 (2.2%)	–
Amazonia		
Widespread Amazonia	112 (30.8%)	13 (11.6%)
South Amazonia	5 (1.4%)	5 (100%)
North Amazonia	13 (3.6%)	11 (84.6%)
Middle-East	34 (9.3%)	30 (88.2%)
Middle-West	51 (14.0%)	38 (74.5%)
Middle-Guiana	16 (4.4%)	12 (75%)
Middle Amazonas		
Widespread Middle	11 (3.0%)	7 (63.6%)
Middle-South	14 (3.8%)	14 (100%)
Middle-North	19 (5.2%)	18 (94.7%)
Endemic		
Manaus	26 (7.1%)	

Oliveira & Daly 1999

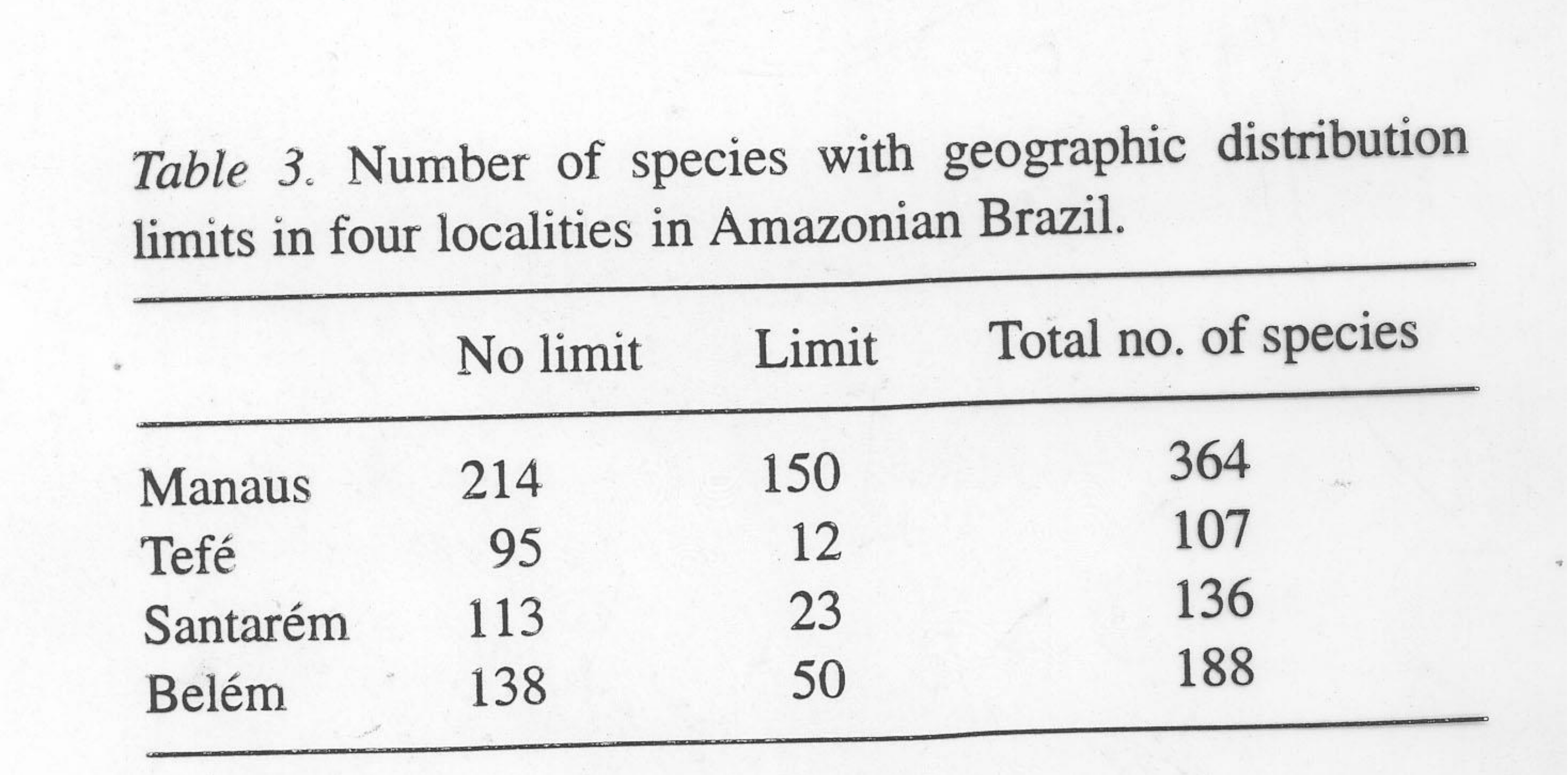


Table 3. Number of species with geographic distribution limits in four localities in Amazonian Brazil.

	No limit	Limit	Total no. of species
Manaus	214	150	364
Tefé	95	12	107
Santarém	113	23	136
Belém	138	50	188

Oliveira & Daly 1999

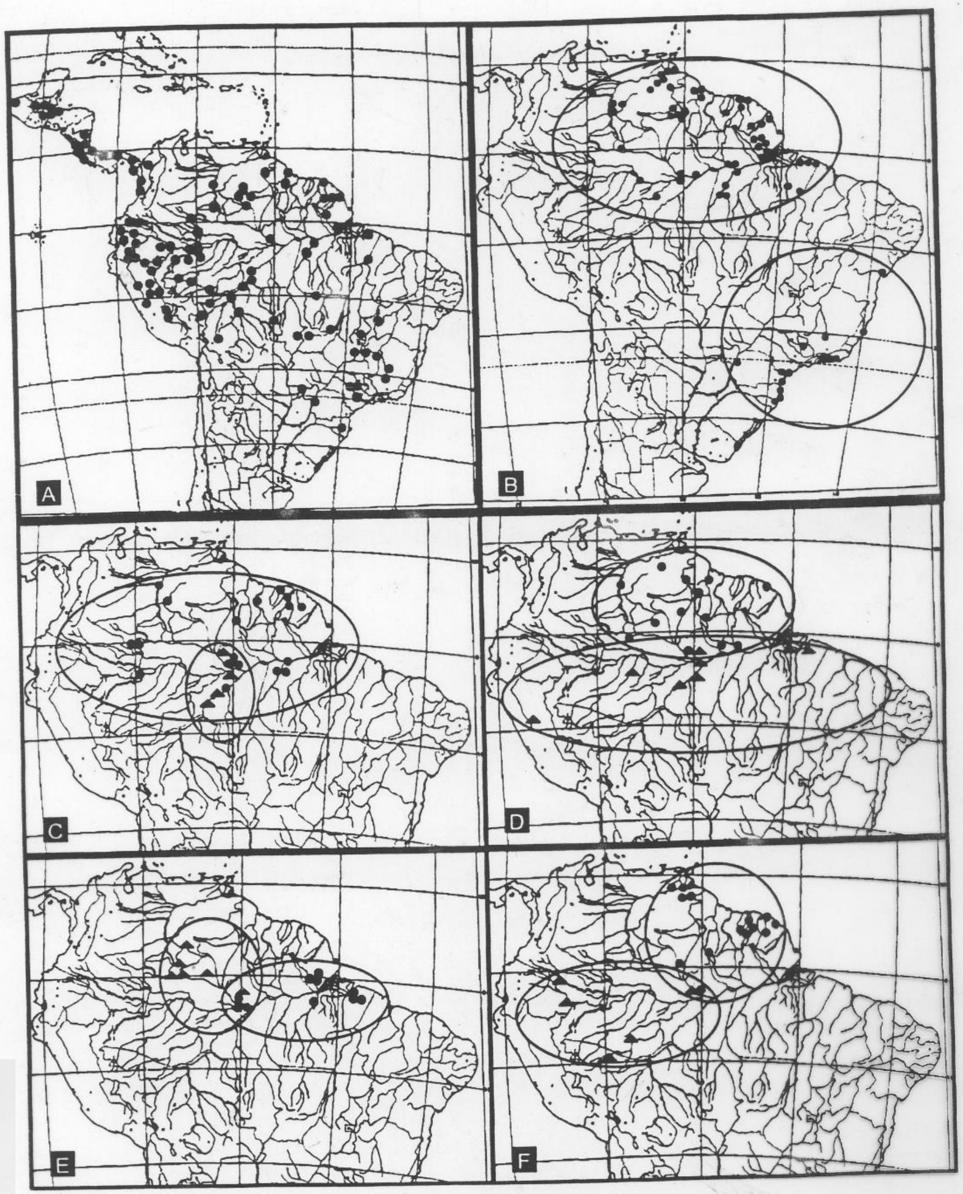


Figure 2. Principal geographic distribution patterns illustrated by selected species. A: ● *Pouteria torta*(Mart.) Radlk. – wide distribution. B: ● *Pouteria venosa* (Mart.) Baehni – Disjunct Amazonia/Atlantic Forest. C: ● *Couratari stellata* A.C.Sm. – Widespread Amazonia; ▲ *Couepia magnoliifolia* Benth. ex Hook f., Middle-South Amazonas. D: ● *Licania coriacea* Benth., North Amazonas; ▲ *Pouteria opposita* (Ducke) T.D.Penn., South Amazonas. E: ● *Couepia robusta* Huber, Middle-East Amazonas ▲ *Micropholis splendens* Gilly ex Aubrév., Middle-North Amazonas. F: ● *Eschweilera collina* Eyma, Middle Amazonas/Guianas; ▲ *Couepia macrophylla* Spruce ex Hook. f., Middle-West Amazonas.

Haffer 2001 in Vieira *et al.*

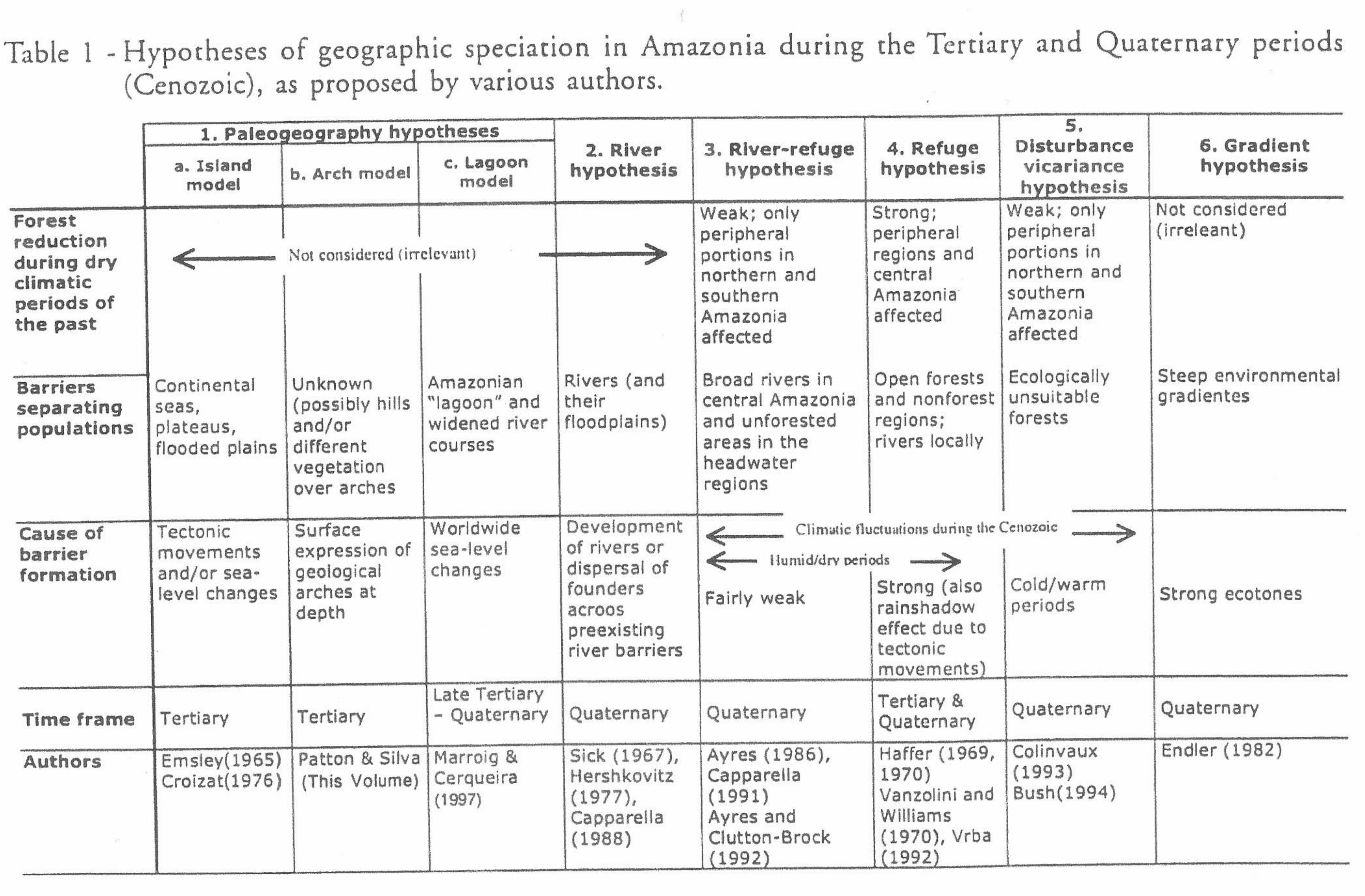
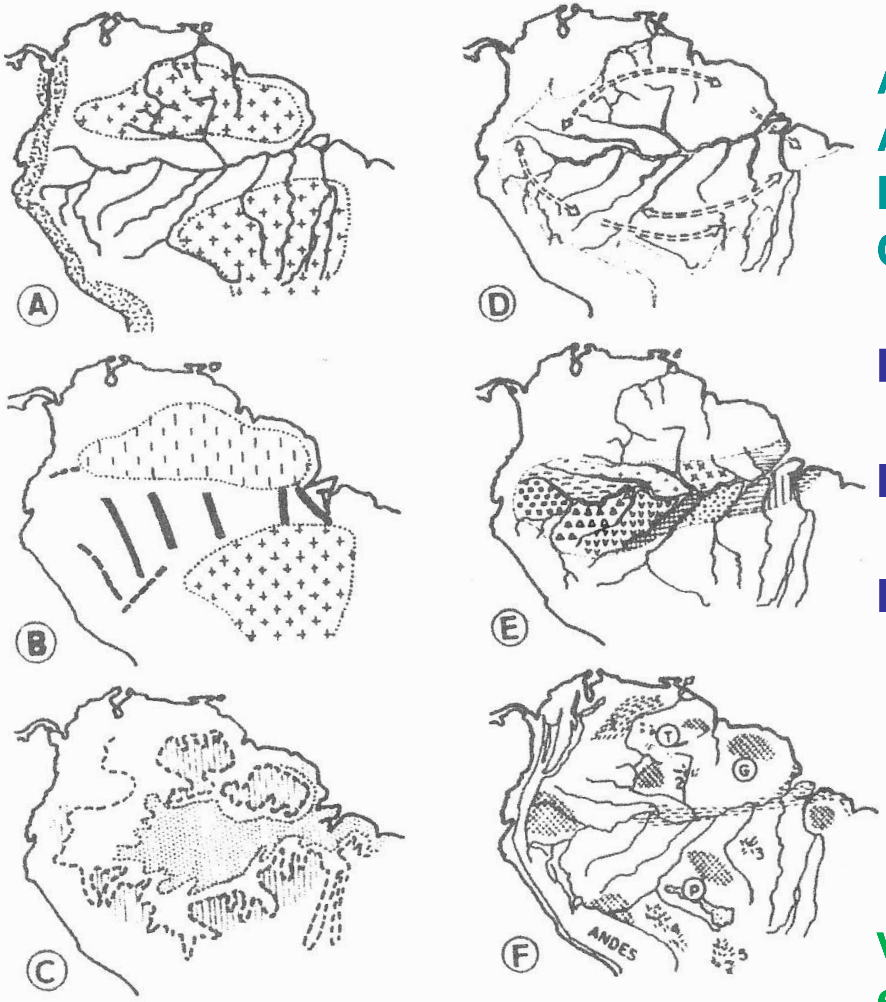


Table 1 - Hypotheses of geographic speciation in Amazonia during the Tertiary and Quaternary periods (Cenozoic), as proposed by various authors.

	1. Paleogeography hypotheses			**2. River hypothesis**	**3. River-refuge hypothesis**	**4. Refuge hypothesis**	**5. Disturbance vicariance hypothesis**	**6. Gradient hypothesis**
	a. Island model	**b. Arch model**	**c. Lagoon model**					
Forest reduction during dry climatic periods of the past	← Not considered (irrelevant) →				Weak; only peripheral portions in northern and southern Amazonia affected	Strong; peripheral regions and central Amazonia affected	Weak; only peripheral portions in northern and southern Amazonia affected	Not considered (irreleant)
Barriers separating populations	Continental seas, plateaus, flooded plains	Unknown (possibly hills and/or different vegetation over arches	Amazonian "lagoon" and widened river courses	Rivers (and their floodplains)	Broad rivers in central Amazonia and unforested areas in the headwater regions	Open forests and nonforest regions; rivers locally	Ecologically unsuitable forests	Steep environmental gradientes
Cause of barrier formation	Tectonic movements and/or sea-level changes	Surface expression of geological arches at depth	Worldwide sea-level changes	Development of rivers or dispersal of founders acroos preexisting river barriers	← Climatic fluctuations during the Cenozoic → ← Humid/dry periods → Fairly weak	Strong (also rainshadow effect due to tectonic movements)	Cold/warm periods	Strong ecotones
Time frame	Tertiary	Tertiary	Late Tertiary – Quaternary	Quaternary	Quaternary	Tertiary & Quaternary	Quaternary	Quaternary
Authors	Emsley(1965) Croizat(1976)	Patton & Silva (This Volume)	Marroig & Cerqueira (1997)	Sick (1967), Hershkovitz (1977), Capparella (1988)	Ayres (1986), Capparella (1991) Ayres and Clutton-Brock (1992)	Haffer (1969, 1970) Vanzolini and Williams (1970), Vrba (1992)	Colinvaux (1993) Bush(1994)	Endler (1982)

ver também Haffer 2008

Modelos de especiação geográfica na Amazônia



A – C. Hipóteses paleogeográficas
A. Modelo de ilha
B. Modelo dos Arcos centrais
C. Modelo do Lago

D. Modelo de Rios

E. Hipótese de Refúgios - rios

F. Modelo dos Refúgios

Haffer in Vieira *et al.* 2001

ver tb Haffer 2008:
expande a Teoria dos Refúgios
para todo o Cenozóico.

Novos dados paleoecológicos na Amazânia

Quaternário

Haffer 2008

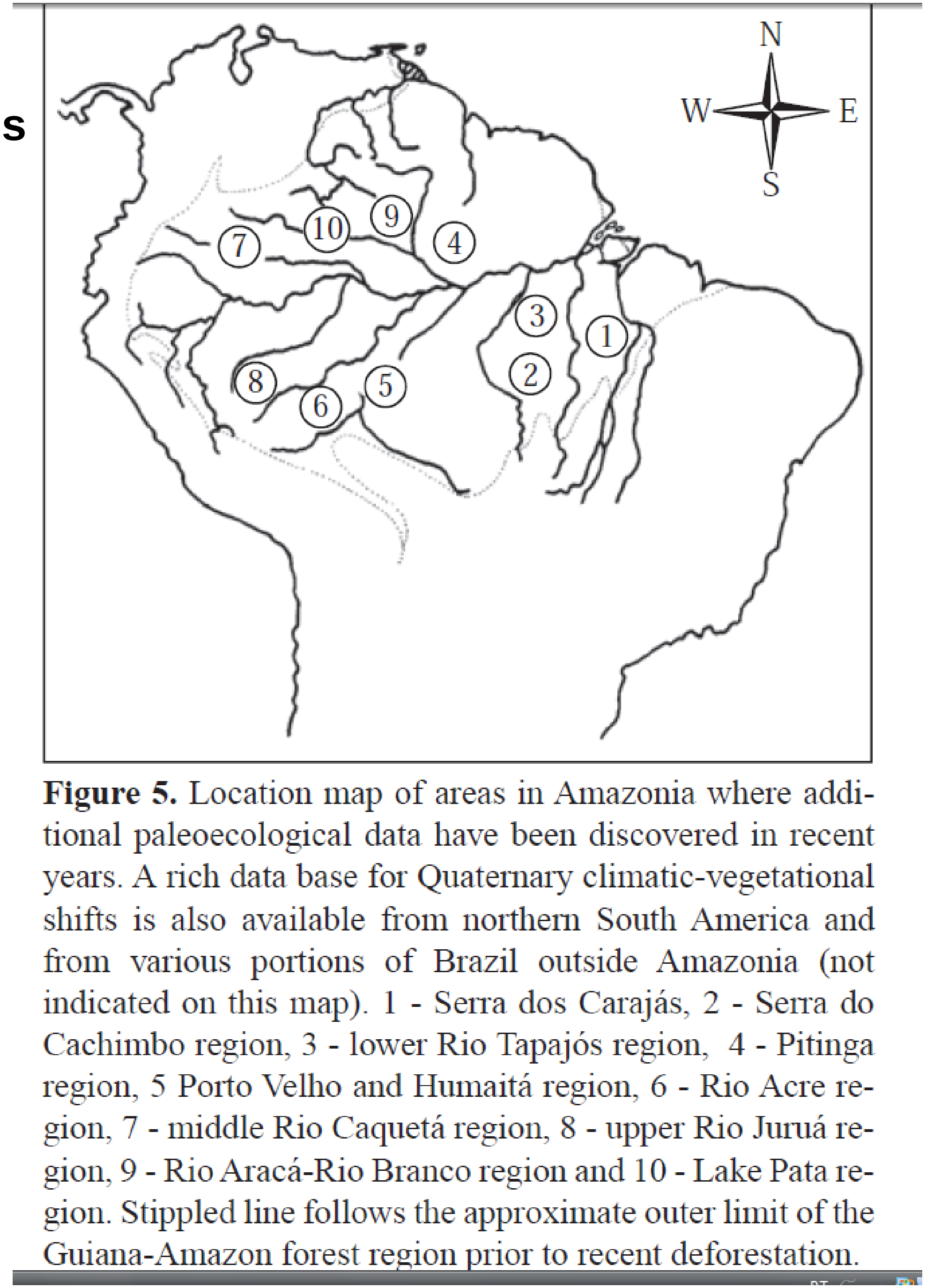


Figure 5. Location map of areas in Amazonia where additional paleoecological data have been discovered in recent years. A rich data base for Quaternary climatic-vegetational shifts is also available from northern South America and from various portions of Brazil outside Amazonia (not indicated on this map). 1 - Serra dos Carajás, 2 - Serra do Cachimbo region, 3 - lower Rio Tapajós region, 4 - Pitinga region, 5 Porto Velho and Humaitá region, 6 - Rio Acre region, 7 - middle Rio Caquetá region, 8 - upper Rio Juruá region, 9 - Rio Aracá-Rio Branco region and 10 - Lake Pata region. Stippled line follows the approximate outer limit of the Guiana-Amazon forest region prior to recent deforestation.

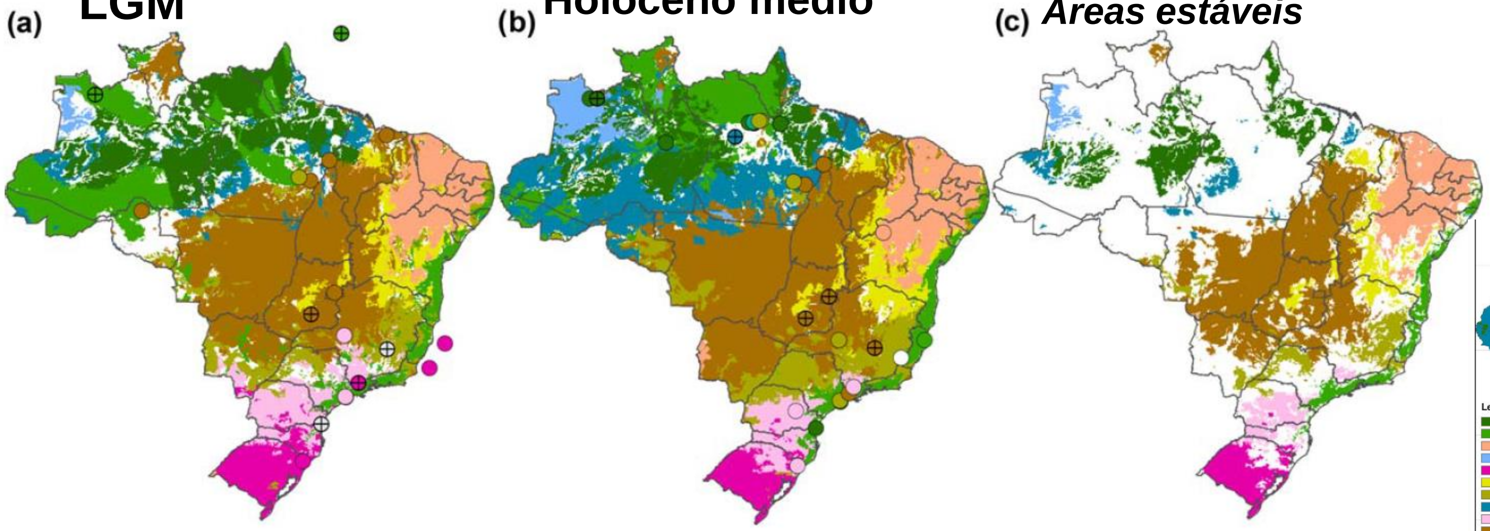
- 🟩 Equatorial forest
- 🟩 Tropical forest
- 🟧 Caatinga
- 🟦 White-sand vegetation
- 🟪 South grassland
- 🟨 Deciduous forest
- 🟨 Semideciduous forest
- 🟦 Open ombrouphylous forest
- 🟪 Mixed forest
- 🟫 Savanna

Vegetation cover of Brazil in the last 21 ka: New insights into the Amazonian refugia and Pleistocenic arc hypotheses

Main conclusions: **With regard to Haffer's hypothesis, the forests of the Amazonian lowlands retreated to refugia areas, while the colder and wetter climate of the basin created a favourable niche for another type of forest, instead of savanna.**
The advance of dry vegetation was restricted to ecotonal conditions, preventing the formation of a continuous Pleistocene arc, predicted by Prado and Gibbs's hypothesis.

Arruda et al. 2017

LGM **Holoceno médio** ***Áreas estáveis***



Atual

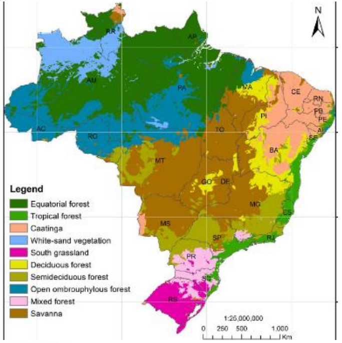


FIGURE 3 Spatial distribution of biomes at different moments in the past. Biome distribution in (a) the Last Glacial Maximum and (b) the Mid-Holocene. (c) Stability/refugia areas of the biomes based on the consensus between the two distribution scenarios and the present distribution (Figure 1). White areas on the maps indicate areas of conflict between the different general circulation models. Circles on the maps (a and b) are pollen records, whose colours represent the biome in the corresponding period. Circles marked with a cross indicate important observations at the sites. Green circle = rain forest pollen with presence of Andean species in the Last Glacial Maximum (Colinvaux et al., 1996; Haberle & Maslin, 1999) and pollen grains of herbs in the forest interior during the mid-Holocene (Mayle & Power, 2008). Brown circle = savanna pollen with evidence of flooding, similar to veredas (swamp forests; Salgado-Labouriau, Barberi, Vicentini, & Parizzi, 1998). White circle = grassland surrounded by forest in the southeast (Behling & Lichte, 1997) and grassland without Araucaria in the south (Behling & Negrelle, 2001). Blue circle = open ombrophilous or semi-deciduous forest (Irion et al., 2006). A list of the data sources is found in Supporting Information Appendix S2

Modelos alternativos para elevada taxa de especiação nas regiões tropicais

CRONOGRAMAS

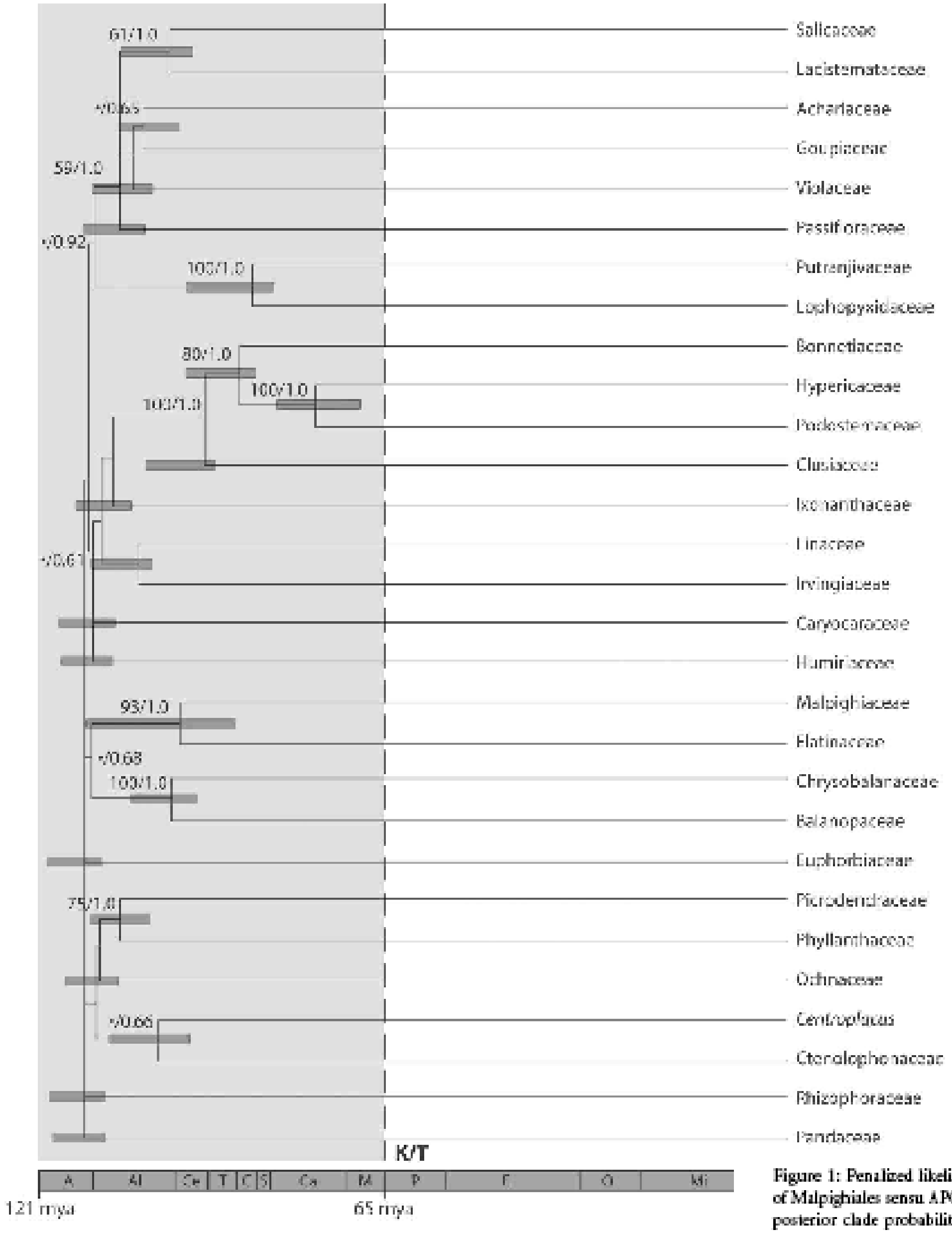


Figure 1: Penalized likelihood chronogram of Malpighiales. Figure reduced from 124-taxon data set to represent only the 28 recommended families of Malpighiales sensu APG (2003) plus the previously unplaced taxon *Centroplacus*. For outgroups and rooting see text. Bootstrap values and Bayesian posterior clade probabilities (>50%/0.50), respectively, indicated near nodes; bullet = support values ≤50%/0.50. The monophyly of Malpighiales was supported by a very high bootstrap value (100%) and posterior probability (1.0). Confidence intervals shown with shaded bars. Divergence times were calculated on this rate-smoothed topology by calibrating nodes with several minimum age constraints from macrofossil and palynological data (table 1). A maximum age constraint of 125 m.yr. was enforced for the root node based on the oldest occurrence of tricolpate pollen grains representing the eudicot clade (see text). The K/T boundary (~65 Ma) is marked with a dashed line. The origin of Malpighiales is estimated at 114 Ma. The scale bar indicates major Cretaceous and Cenozoic intervals: *A* = Aptian, *Al* = Albian, *Ce* = Cenomanian, *T* = Turonian, *C* = Coniacian, *S* = Santonian, *Ca* = Campanian, *M* = Maastrichtian, *P* = Paleocene, *E* = Eocene, *O* = Oligocene, *Mi* = Miocene, *P/P* = Pliocene/Pleistocene. For complete 124-taxon chronogram, see appendix C.

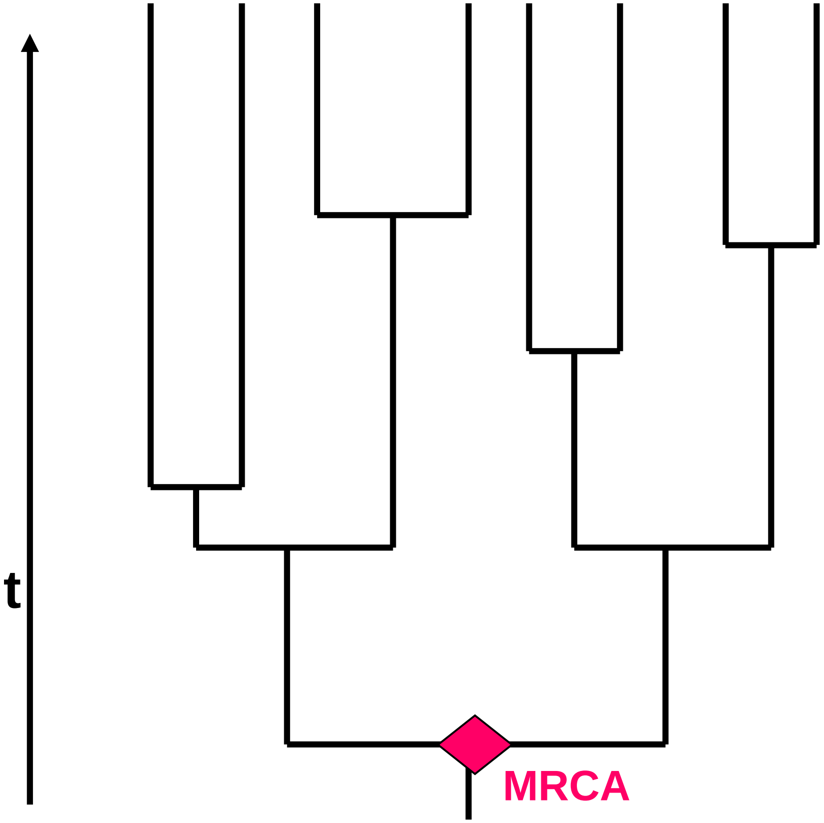
Radiação de MALPIGHIALES e origem das Florestas Tropicais Pluviais

100 m.a. ?

Davis *et al.* 2005

Modelo de MUSEU (Wallace 1878, Stebbins 1974)

numerosas substituições de nucleotídeos entre spp + topologia consistente com origem das ssp a partir do MRCA

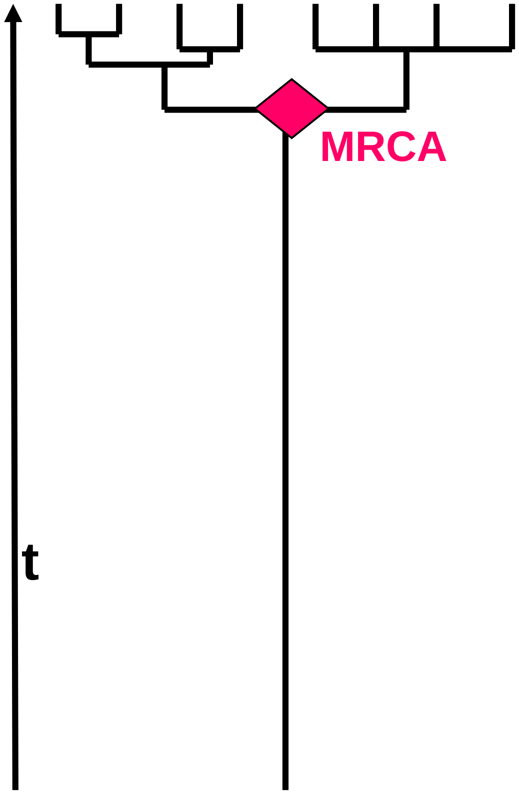


Acumulação gradual de diversidade a partir do MRCA (Ancestral Comum Mais Recente) das spp atuais: filogenia resolvida

Baixa taxa de EXTINÇÃO

Modelo de BERÇÁRIO (*cradle)* (Stebbins 1974)

poucas substituições de nucleotídeos diferenciando spp + topologia com ramos curtos a partir do MRCA onde a diversificação iniciou



Diversificação rápida e recente a partir do MRCA das spp. atuais: filogenia com baixa resolução

Alta taxa de ESPECIAÇÃO

Cronobiogeografia – permite avaliar os dois modelos

Richardson et al. 2001 - *Inga*

ITS1 e 2:

tempo de diversificação
entre 13,4 e 2,0 m.a.
(média de 5,9 m.a.)

trnL-F:

tempo de diversificação
entre 4,3 m.a. e 300.000 anos
(média 1,8 m.a.).

Patton & Silva in Vieira 2001 – mamíferos
tempo de diversificação bem mais antigo
do que se supunha.

Modelos alternativos para elevada taxa de especiação nas regiões tropicais

CRONOGRAMAS:

As IDADES de muitos clados neotropicais
inferidas pelas datações moleculares remontam
a períodos anteriores às glaciações pleistocênicas.
=
os grupos estudados eram altamente diversificados já no Terciário!

(e.g. Richardson et al. 2001;
Knapp & Mallet 2003;
Antonelli & Sanmartin 2011)

Modelos alternativos para elevada taxa de especiação nas regiões tropicais

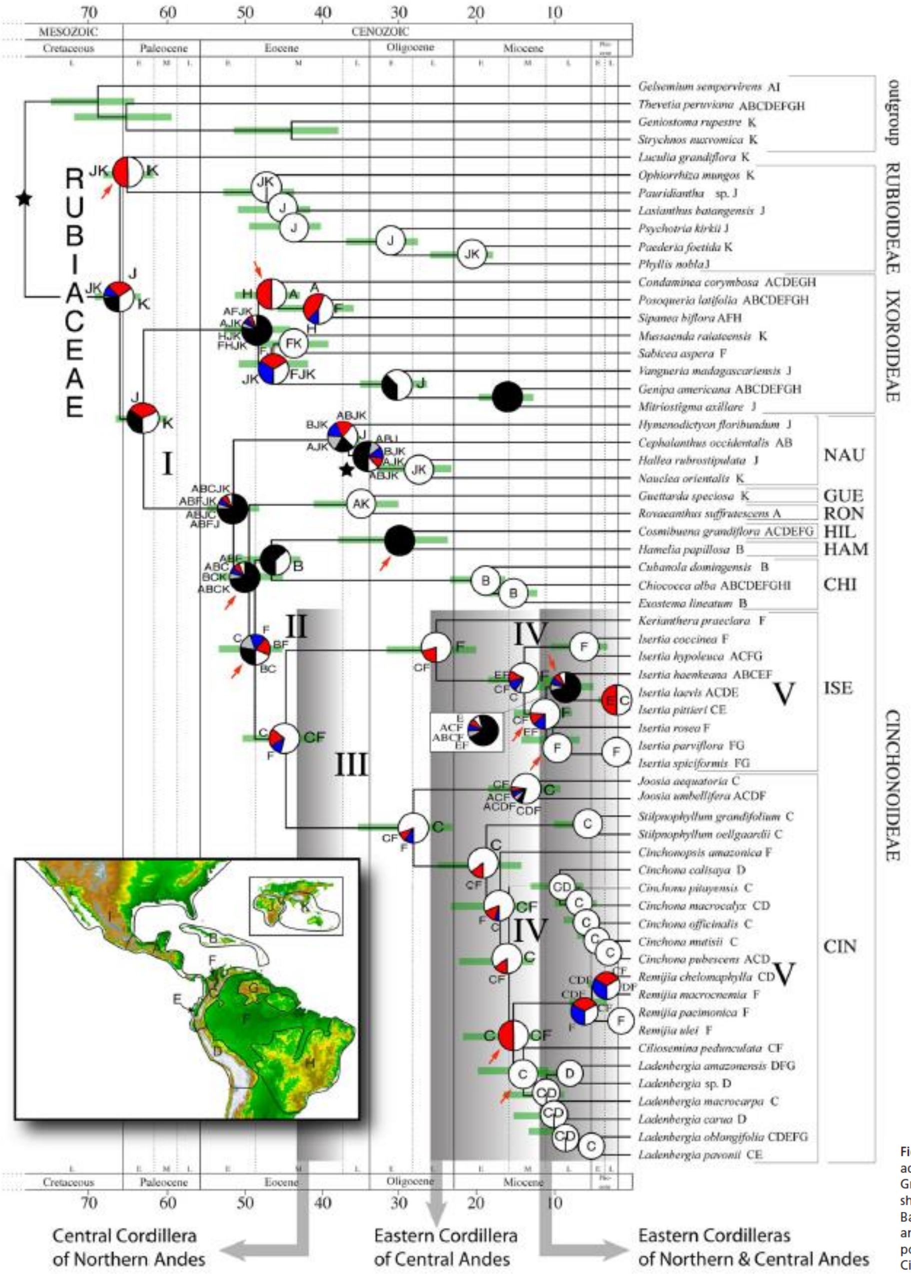
HOORN et al. 2010

Ampla revisão das evidências geológicas, fósseis e moleculares na América do Sul setentrional:
Dinâmica climática do Pleistoceno <u>não deve ser responsável</u> pela alta diversidade específica neotropical.

De Aguiar et al. 2009
Modelo de especiação nulo.

Especiação alopátrida pode <u>não ter sido o modo dominante</u> nas florestas úmidas da região Neotropical???

Cronograma combinado com análise biogeográfica das RUBIACEAE neotropicais (BEAST)



Antonelli *et al.* 2009

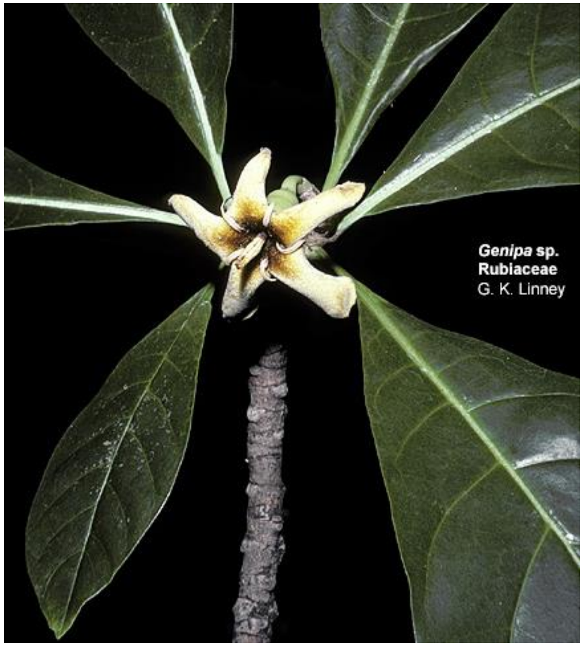


Fig. 1. Combined chronogram and biogeographic analysis of Neotropical Rubiaceae. The tree is the 50% majority-rule consensus (with compatible groups added) from the Bayesian analysis, with branches proportional to absolute ages (in millions of years) calculated from mean branch lengths of 6,000 Bayesian trees. Green bars indicate 95% confidence intervals of node ages estimated from 1,000 trees randomly sampled from the Bayesian stationary distribution. Node charts show the relative probabilities of alternative ancestral distributions obtained by integrating dispersal-vicariance analysis (DIVA) optimizations over the 1,000 Bayesian trees; the first 4 areas with highest probability are colored according to their relative probability in the following order: white > red > blue > gray; any remaining areas (usually frequencies <0.01) are collectively given with black color. Stars indicate calibration points. Red arrows indicate clades with a posterior probability <0.90. Present ranges for each species are given after the species name. Brackets identify subfamilies and tribes: CHI, Chiococceae; CIN, Cinchoneae; GUE, Guettardeae; HAM, Hamelieae; HIL, Hillieae; ISE, Isertieae; NAU, Naucleeae; RON, Rondeletieae. Shaded boxes indicate approximate periods of Andean uplift phases. The biogeographic interpretation of events I–V is summarized in Fig. 2. (*Inset*) Areas used in the biogeographic analysis. A, Central America, B, West Indies; C, Northern Andes; D, Central Andes; E, Chocó; F, Amazonia; G, The Guiana Shield; H, Southeastern South America; I, Temperate North America; J, Africa; K, Australasia. Topographic map from the National Geophysical Data Center (www.ngdc.noaa.gov).

Evolução espaço-temporal das RUBIACEAE neotropicais

Antonelli *et al.* 2009

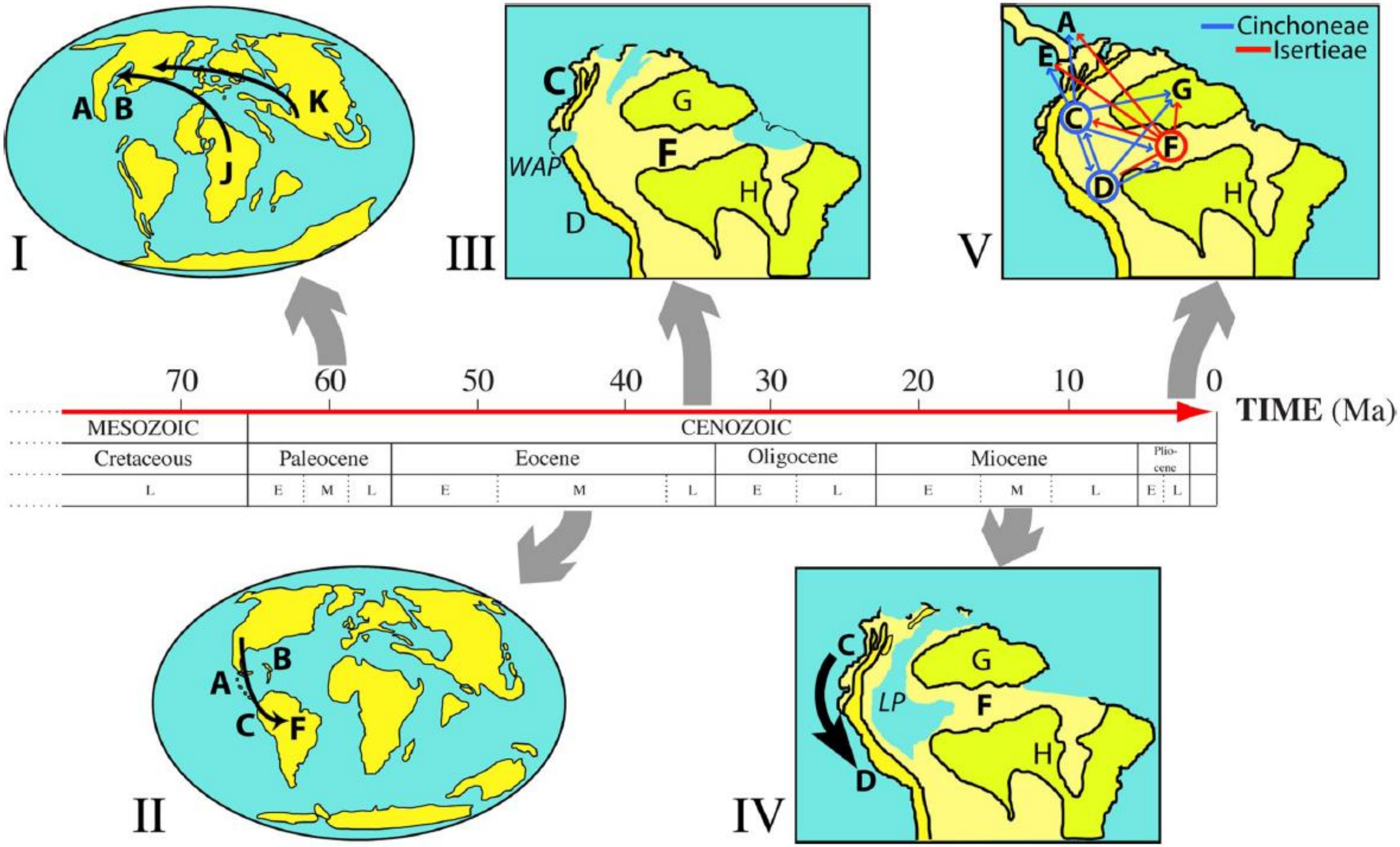


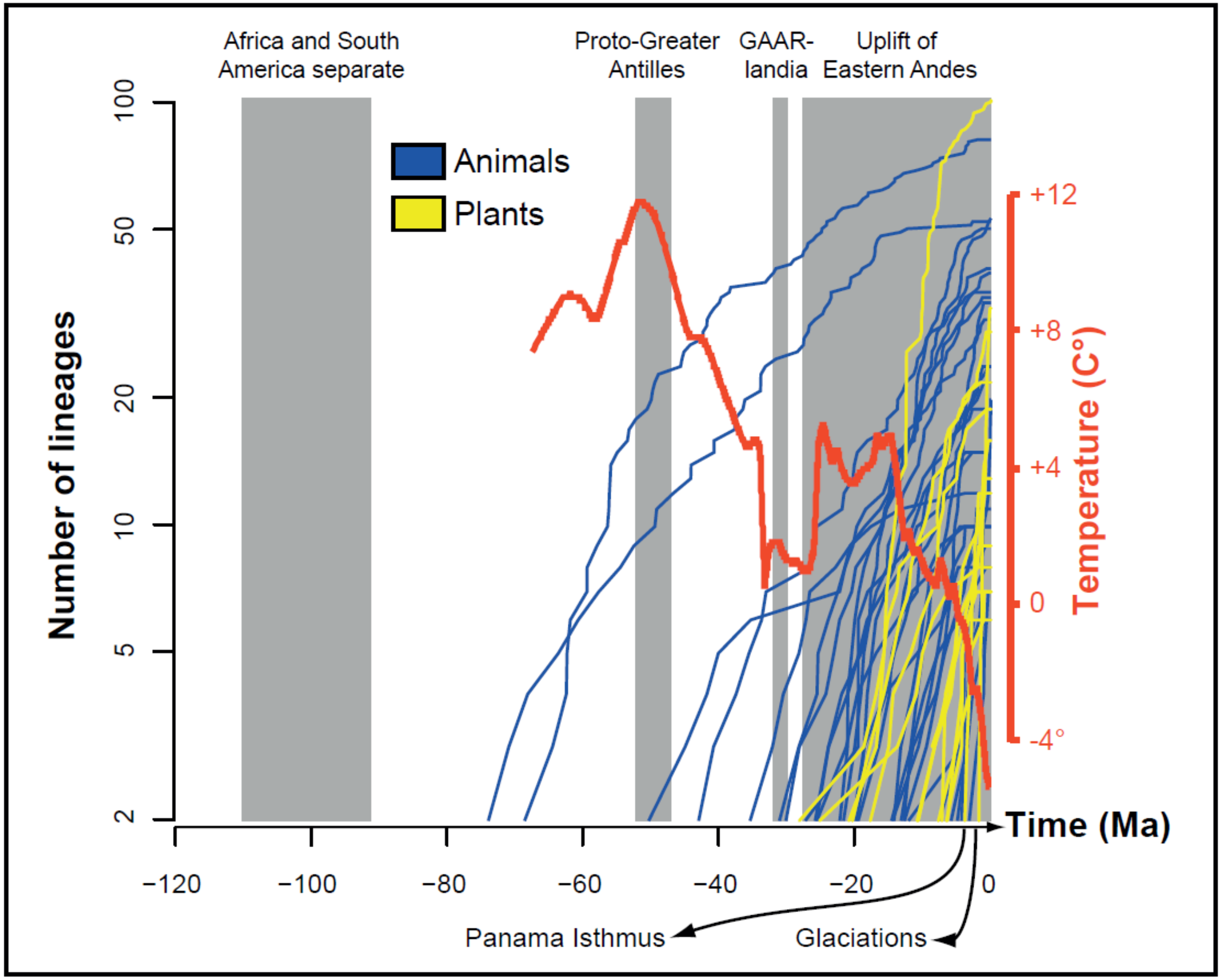
Fig. 2. Spatiotemporal evolution of the Neotropical Rubiaceae. (I) Paleocene: Rubiaceae ancestors use the boreotropical route to reach North America from the Paleotropics. (II) Early Eocene: Dispersal into South America, presumably facilitated by occasional island chains. (III) Late Eocene: North Andean and Amazonian lineages become isolated by marine incursions such as the Western Andean Portal (WAP). (IV) Middle Miocene: The gradual uplift of the Eastern Cordillera creates a huge watershed, Lake Pebas (LP). It also closes the WAP, enabling dispersal of plant lineages from the Northern to the Central Andes. (V) The Pebas system drains, promoting land dispersal of several lineages and rapid speciation of terrestrial plants in western Amazonia. Area codings as in Fig. 1. (Maps I–II are based on C. R. Scotese's PALEOMAP project (www.scotese.com); maps III–V modified from refs. 2 and 28).

Why are there so many plant species in the Neotropics?

Antonelli & Sanmartin 2011

Fig. 6. Lineage-through-time (LTT) plots for a representative sample of dated phylogenies of Neotropical organisms (from Antonelli & al., in prep.), depicting 14 plant and 30 animal phylogenies. The shaded boxes represent the approximate duration of some geological and geographic events suggested to have fostered the dispersal and radiation of Neotropical organisms. Global temperature curve from Zachos & al. (2001). GAARlandia: Greater Antilles and Aves Ridge.

14 filogenias de plantas
30 filogenias de animais



Refutam: **1. diversificação gonduânica (clados neotropicais modernos não existiam antes da separação da África da Am. Sul);**
2. dinâmica pleistocênica (maioria dos grupos já estava bem diversificada).

Rull 2007

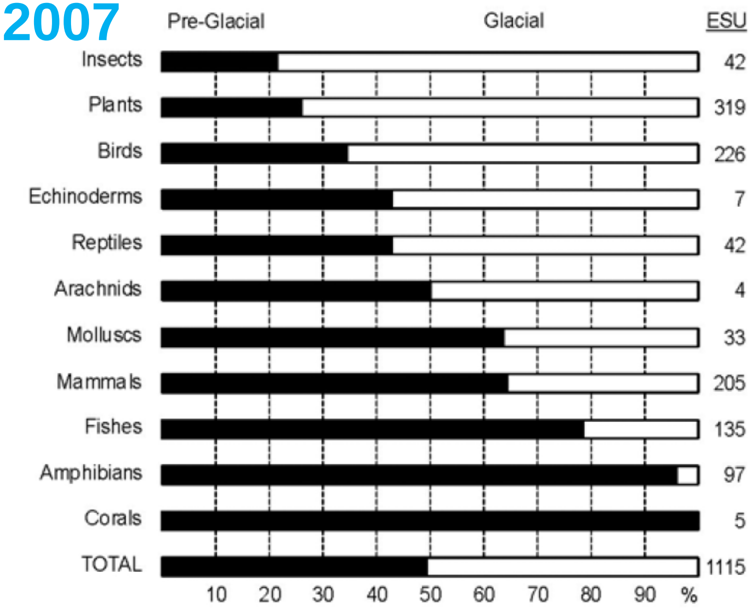
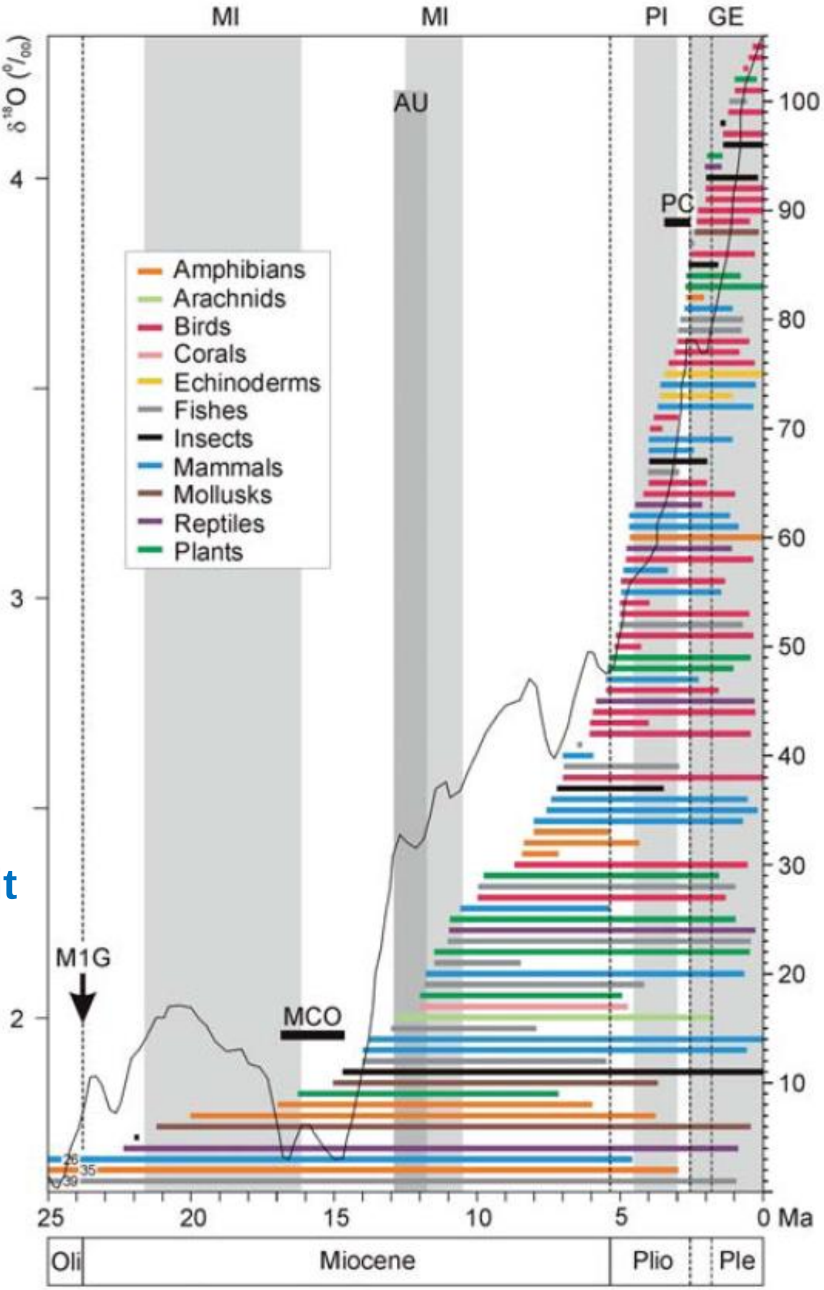


Figure 2. Percentage of ESUs originated either in the pre-Glacial (black bars) or in the Glacial (white bars) for each taxonomic group studied. The number of ESUs for each group is given in the right side. Note that the number of ESUs reported here (1115) is lower than the total number of ESUs analyzed (1404). This is due to the unavailability of quantitative age estimates for some of the ESUs considered.

ESU (Ryder 1986) – Evolutionary Significant Unit

1404 ESUs de 150 táxons (maioria gêneros)

Figure 3. Time range of ESU's divergence for each group studied. Bars represent the time interval between the origin of the older (left) and the younger (right) ESU within each group, and are sorted chronologically according to the emergence of the older ESU. Time in million years before present (my BP). Geochronological units: Oli = Oligocene, Plio = Pliocene, Ple = Pleistocene (Berggren et al., 1995). The two possibilities for the Pliocene/Pleistocene boundary are depicted (Walsh, 2006). Singular periods and events are highlighted with grey areas: GE = Glacial Epoch, PI = formation of the Isthmus of Panamá (Bartoli et al., 2005), MI = Marine incursions into the Amazon basin (Lovejoy et al., 2006), AU = Major event of north-Andean uplift (Hoorn et al., 1995). The smoothed oxygen isotope deep-sea curve (solid black line) is represented in $\delta^{18}O$ units (Zachos et al., 2001). This parameter is largely (~70%) controlled by the ice volume of Antarctica and the Northern Hemisphere, hence, it is correlated with the intensity of continental glaciation and therefore with global cooling. M1G = Miocene-1 Glaciation, MCO = Miocene Climatic Optimum, and PC = Pliocene Cooling (Zachos et al., 2001).



POLÊMICA: Neotropical species emerged primarily during the Quaternary (the last ~2 million years), favored by the alternating glacial/interglacial climates

X

older Tertiary origin linked primarily to paleogeographic changes?

Rull 2007: **thorough review of the available literature on DNA molecular dating shows that the Tertiary-Quaternary debate no longer makes sense. Indeed, the >1400 Neotropical species dated so far appeared in a continual fashion since the late Eocene/early Oligocene (~39 million years before present) to the Quaternary. Speciation rates maximized during the Plio-Pleistocene (the last ~5 million years), coinciding with a global climatic cooling.**

Paleogeographic mechanisms of speciation are relatively well known, but diversification processes linked to climate are still poorly understood. These results are important to understand the origin of present-day biodiversity patterns at both local and global scales, as well as the genetic and environmental mechanisms involved.

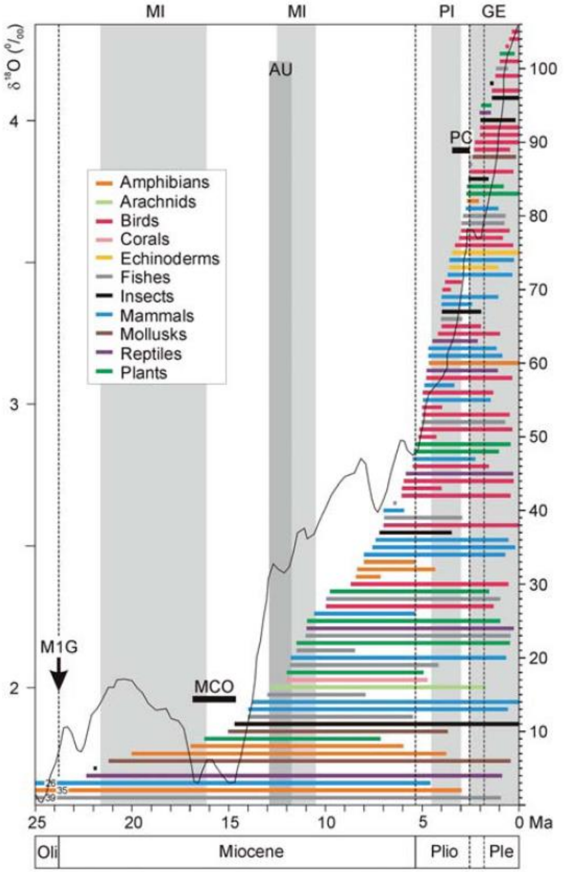


Figure 3. Time range of ESU's divergence for each group studied. Bars represent the time interval between the origin of the older (left) and the younger (right) ESU within each group, and are sorted chronologically according to the emergence of the older ESU. Time in mil-

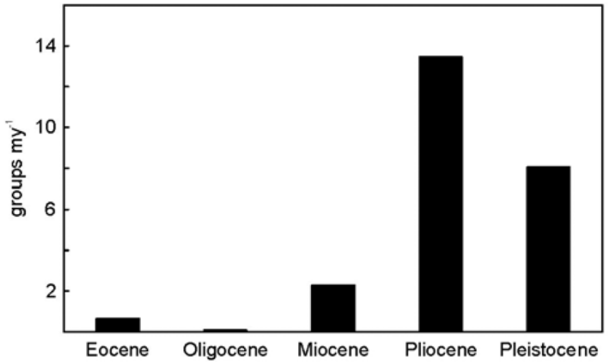


Figure 4. Speciation rates measured as the number of groups that began to diversify per million years, within each period.

Willis & Niklas 2004 The role of Quaternary environmental change in plant macroevolution: the exception or the rule?

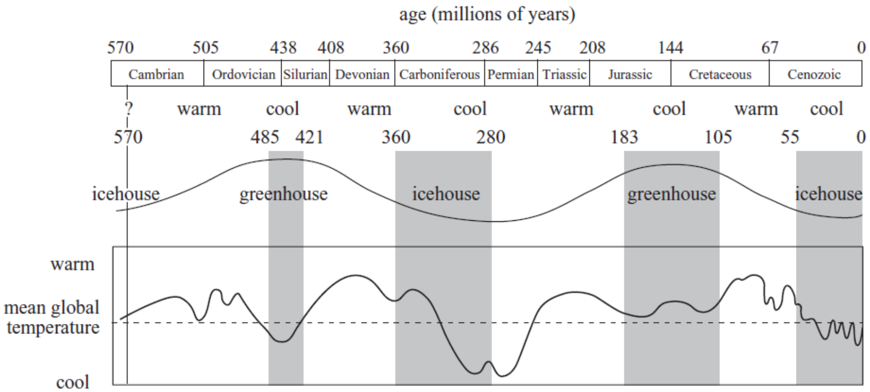


Figure 1. Climatic megacycles during the past 570 Myr (Huggett 1997; Willis & McElwain 2002). Sources for greenhouse/icehouse data from Fischer (1984), Crowley & North (1991) and Crowley (1998); warm and cold modes from Frakes *et al.* (1992); generalized temperature curve from Martin (1998).

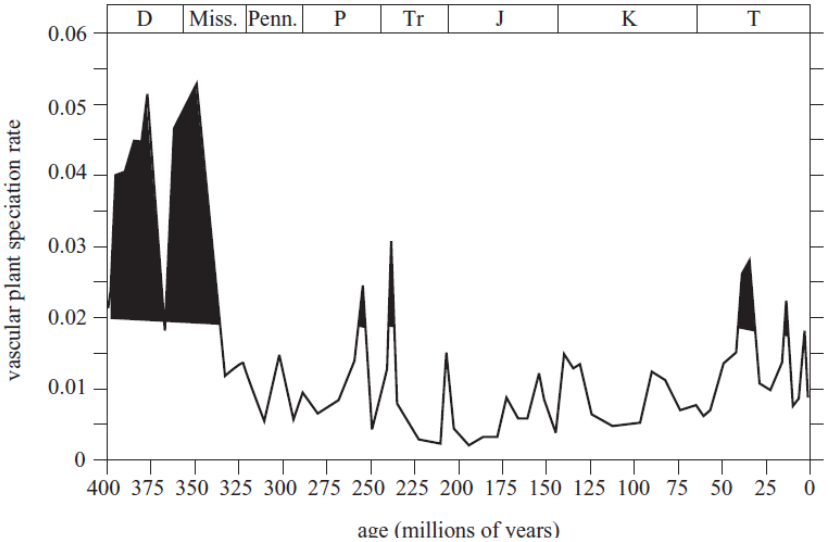


Figure 8. Speciation rate of vascular land plants over the past 400 Myr (Niklas 1997), where speciation rate is calculated as the number of new species appearing per geological stage time period per standing species diversity in each stage.

Analysis of the plant fossil record for the Quaternary (in detail) and for the past 410 Myr:

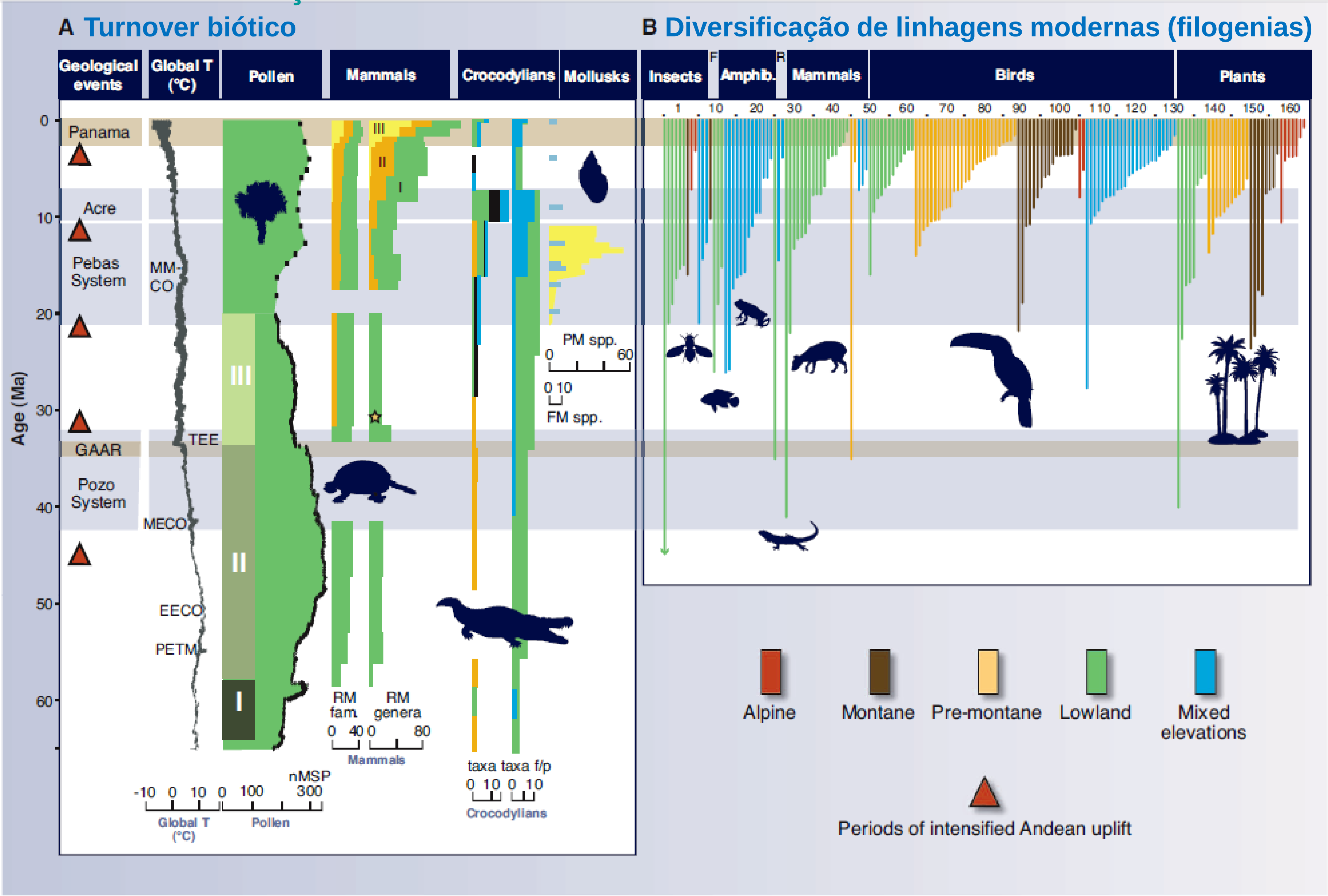
Quaternary record: it **appears that the dominant response of arborescent species during the Quaternary was extinction rather than speciation or stasis.**
By contrast, fossil record of vascular plants for the past 410 Myr indicates that speciation rates often increased during long intervals of icehouse Earth (spanning up to 50 Myr).

Therefore, longer periods of icehouse Earth than those occurring during the Quaternary may have isolated plant populations for sufficiently long periods of time to foster genomic diversification and allopatric speciation.

Additional and detailed molecular studies of extant populations of Quaternary species are required in order to determine the extent to which the 'relic' species have genomically diversified across their current populations.

Alterações bióticas na Amazônia

Hoorn et al. 2010



A Turnover biótico

B Diversificação de linhagens modernas (filogenias)

Fig. 2. Biotic changes in Amazonia through time (*23*). **(A)** The Cenozoic fossil record of the tropical lowlands reveals the timing of biotic turnover. Paleogene floral diversity (from pollen records) increased with high temperature, but in the Neogene it was unrelated and remained relatively high even under cooler

fluvial mollusk; PM, Pebasian endemic mollusk species. Crocodylians: Left column, number of species from fossil record; right column, number of caimanine species from fossil record versus number of lineages (orange, non-eusuchian crocodyliforms; green, Caimaninae; black, Gavialoidea; blue, Molecular Ecology: INVITED REVIEW AND META-ANALYSES :

Phylogeographical patterns shed light on evolutionary process in South America

Turchetto-Zolet et al. 2012

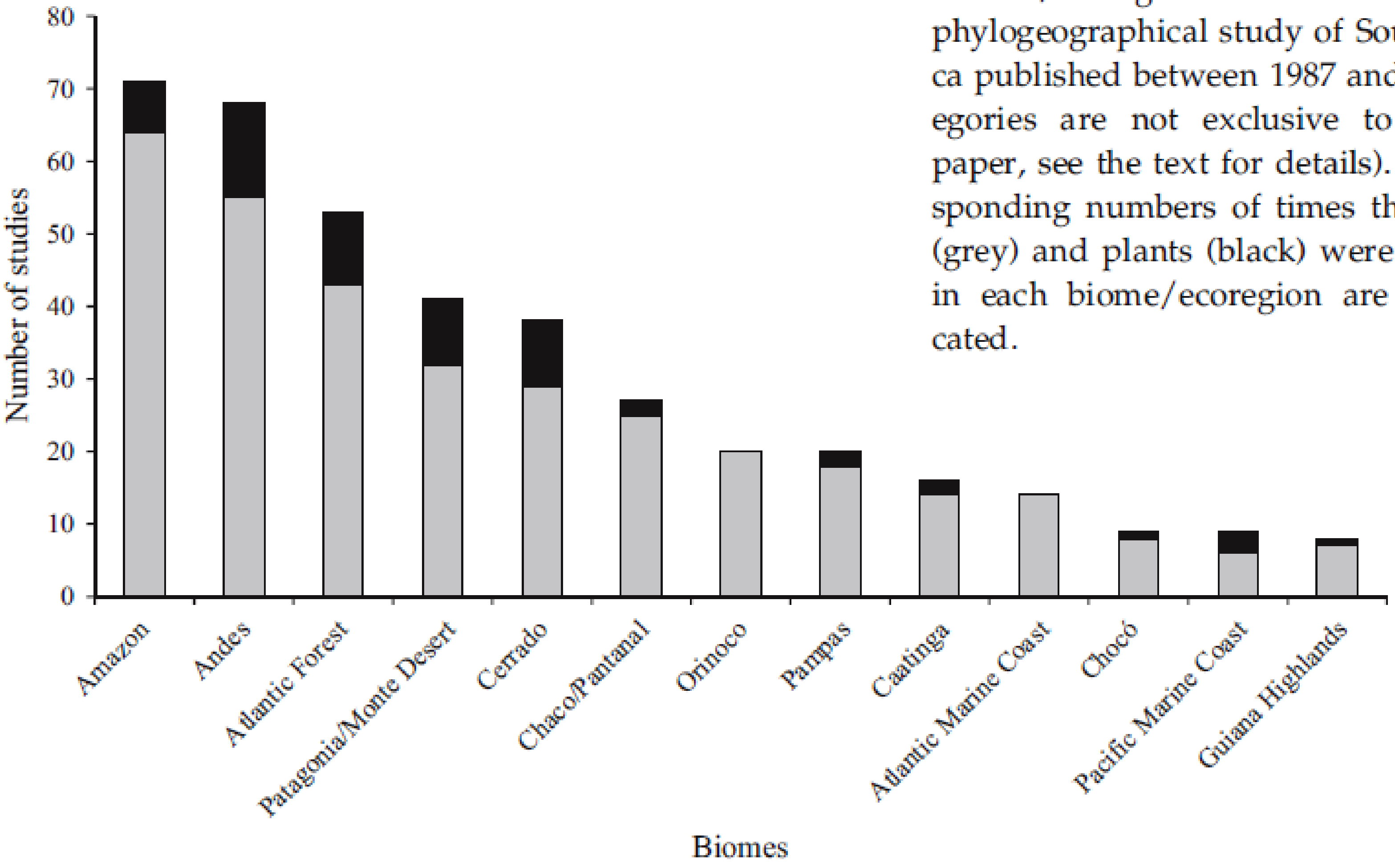


Fig. 5 Number of times that individual biomes/ecoregions were included in a phylogeographical study of South America published between 1987 and 2011 (categories are not exclusive to a certain paper, see the text for details). The corresponding numbers of times that animals (grey) and plants (black) were addressed in each biome/ecoregion are also indicated.

Molecular Ecology: INVITED REVIEW AND META-ANALYSES :

Phylogeographical patterns shed light on evolutionary process in South America

Turchetto-Zolet et al. 2012

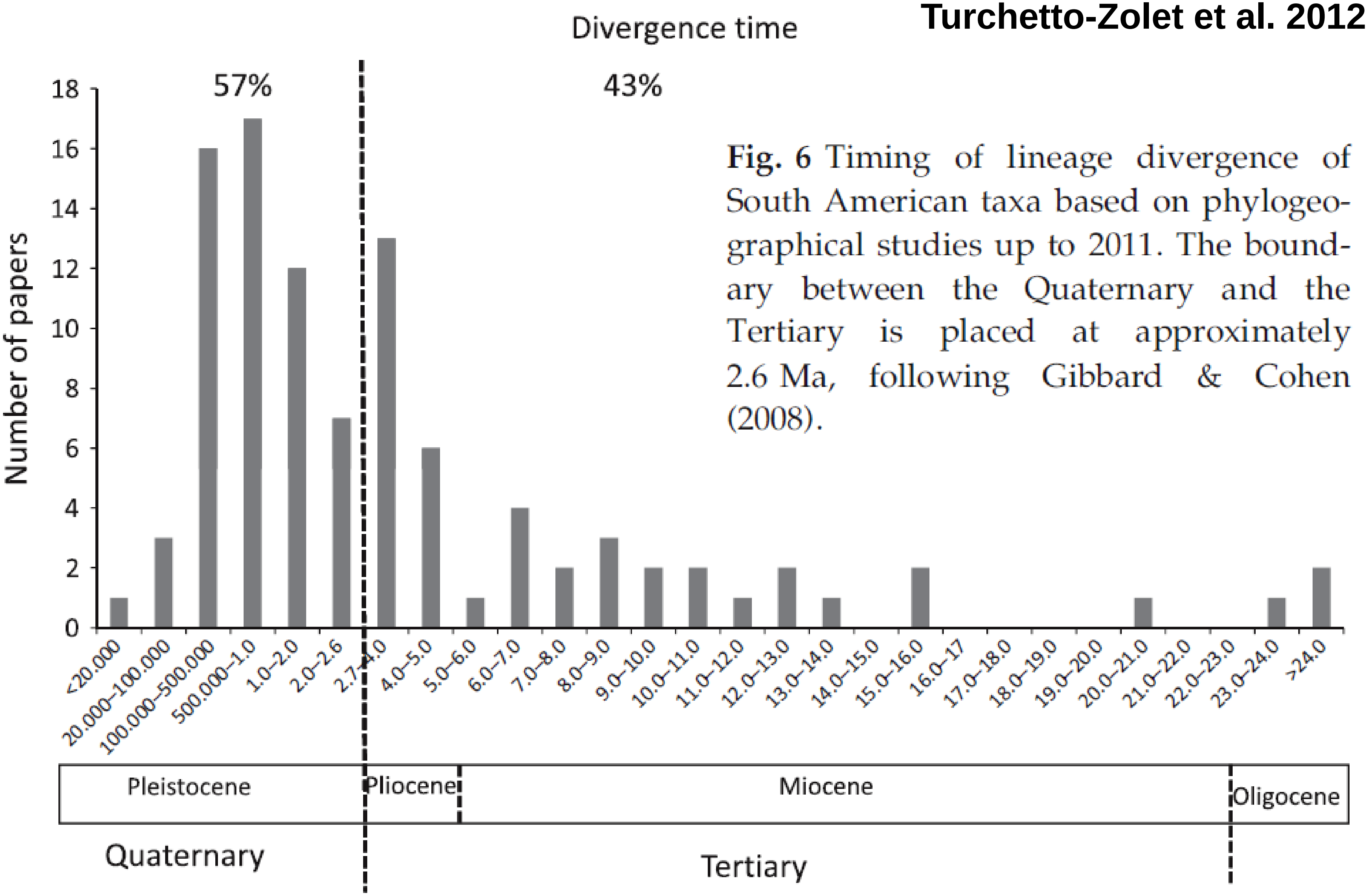


Fig. 6 Timing of lineage divergence of South American taxa based on phylogeographical studies up to 2011. The boundary between the Quaternary and the Tertiary is placed at approximately 2.6 Ma, following Gibbard & Cohen (2008).

A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years

Ribas et al. 2011

Psophia

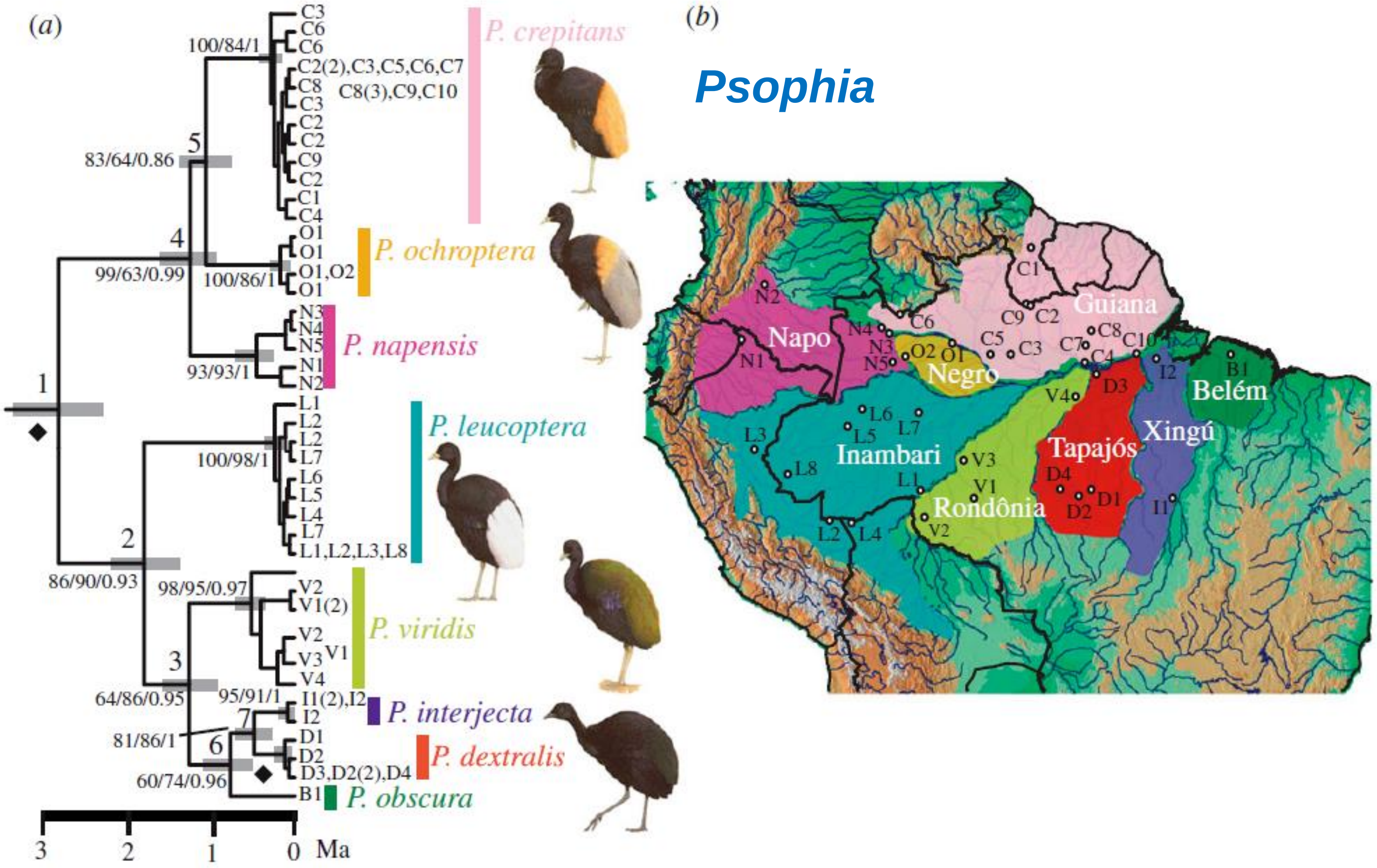


Figure 1. (*a*) Chronogram derived from a Bayesian analysis of cyt b and ND2 sequences (2181 bp) with a calibration derived from an analysis of the *RAG2* nuclear gene (table 1). Support values correspond to MP bootstrap/ML bootstrap/posterior probability. Filled diamonds indicate maximum support values (100/100/1.0) in all analyses. Bars correspond to confidence intervals. (*b*) Map showing current distribution and collection localities of samples included in the molecular analysis.

A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years

Ribas et al. 2011

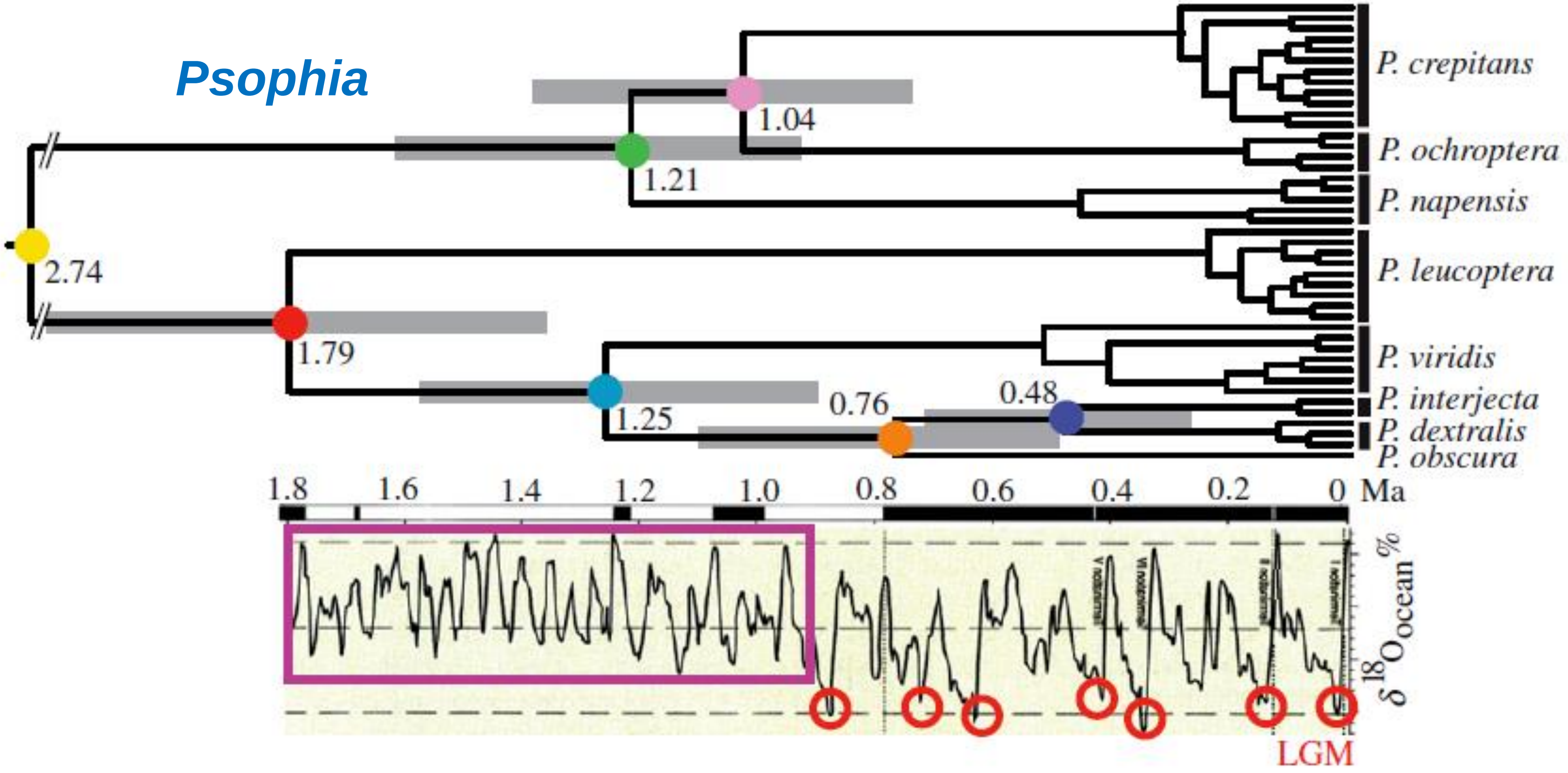
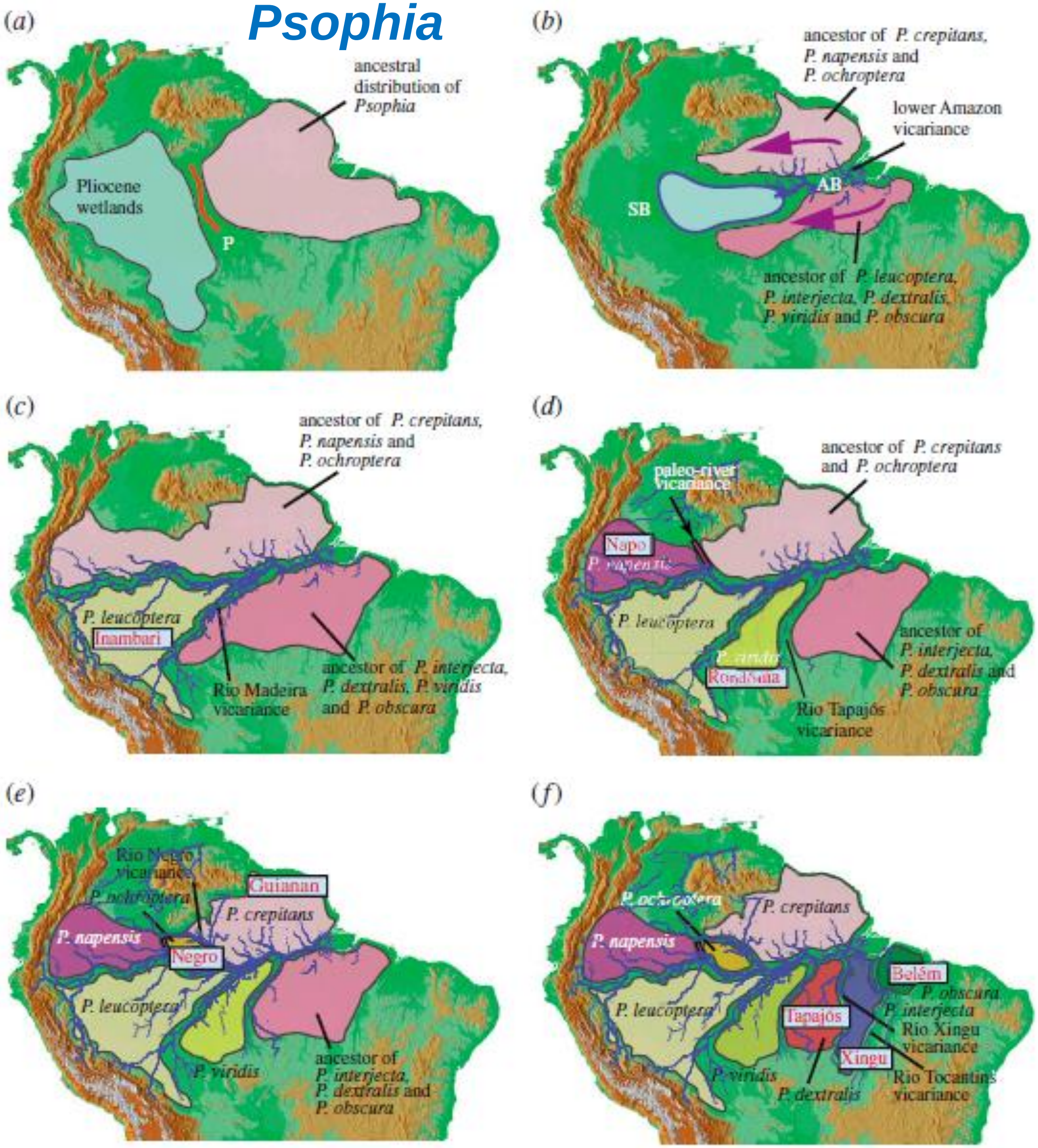


Figure 2. The mean age of speciation events (coloured dots) for lineages of *Psophia* calculated from genetic dating analysis plotted against the Quaternary climate curve derived from δ^{18}O (modified from 70) provides a phylogenetic test of the refuge hypothesis. The estimated age of the youngest species-pair, *P. interjecta* and *P. dextralis* (dark blue dot), indicates that the two species existed in their respective rainforest areas of endemism through four major glacial cycles (red circles), including the LGM. The next youngest speciation event, giving rise to *P. obscura* and the ancestor of *P. dextralis* + *P. interjecta* (orange dot), was prior to two additional cold cycles. Prior to approximately 1.0 Ma, in the '41 kyr world', climate was warmer and sensitivity to orbital forcing was lower (purple box; see text), hence orbital cycling would have been more unlikely to have created refuges at this time. The species history of *Psophia* is a falsifying instance of the refuge hypothesis inasmuch as they persisted throughout Amazonian wet forest areas of endemism during multiple glacial cycles.

Psophia



c. 3,0-2,7 m.a.

c. 2,7-2 m.a.

c. 2-1 m.a.

c. 1,3-0.8 m.a.

c. 1-0,7 m.a.

c. 0,8-0,3 m.a.

Ribas et al. 2011

Figure 3. A palaeobiogeographic model for terrestrial environments of Amazonia for the last 3.0 Myr based on the evolutionary history of the trumpeters (*Psophia*) and geological data (see main text). Historical distributions are estimated from specimen locations (electronic supplementary material, figure S1). Rivers and their tributaries are depicted as in the present, but their palaeopositions may have differed. Indicated ages of river drainages are interpretable as ages of isolating events, not necessarily of river entrenchment. (*a*) Approximately 3.0–2.7 Ma: western lowland Amazonia is a large interconnected wetland/lake/river

Neogene origins and implied warmth tolerance of Amazon tree species - Dick et al. 2012

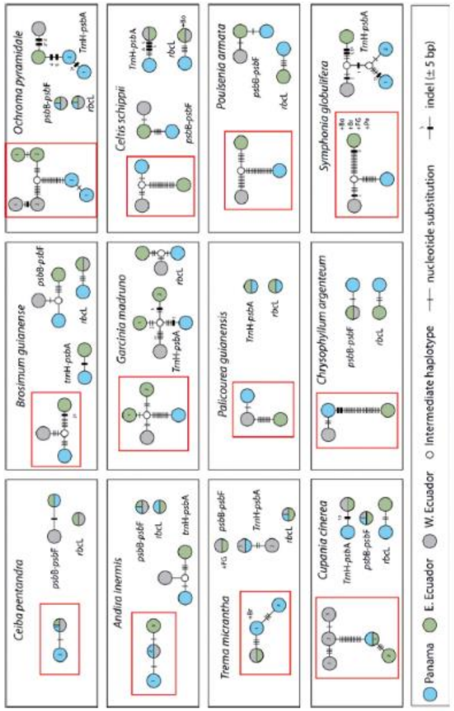


Figure 2. Haplotype networks for nuclear ITS and chloroplast DNA sequence data. Circles represent haplotypes, colors are geographic locations; hatch marks represent mutational steps. ITS haplotypes are bounded by red rectangles. Additional geographic representation of some haplotypes is indicated by country abbreviations: Bolivia (Bo), Brazil (Br), French Guiana (FG), and Peru (Pe).

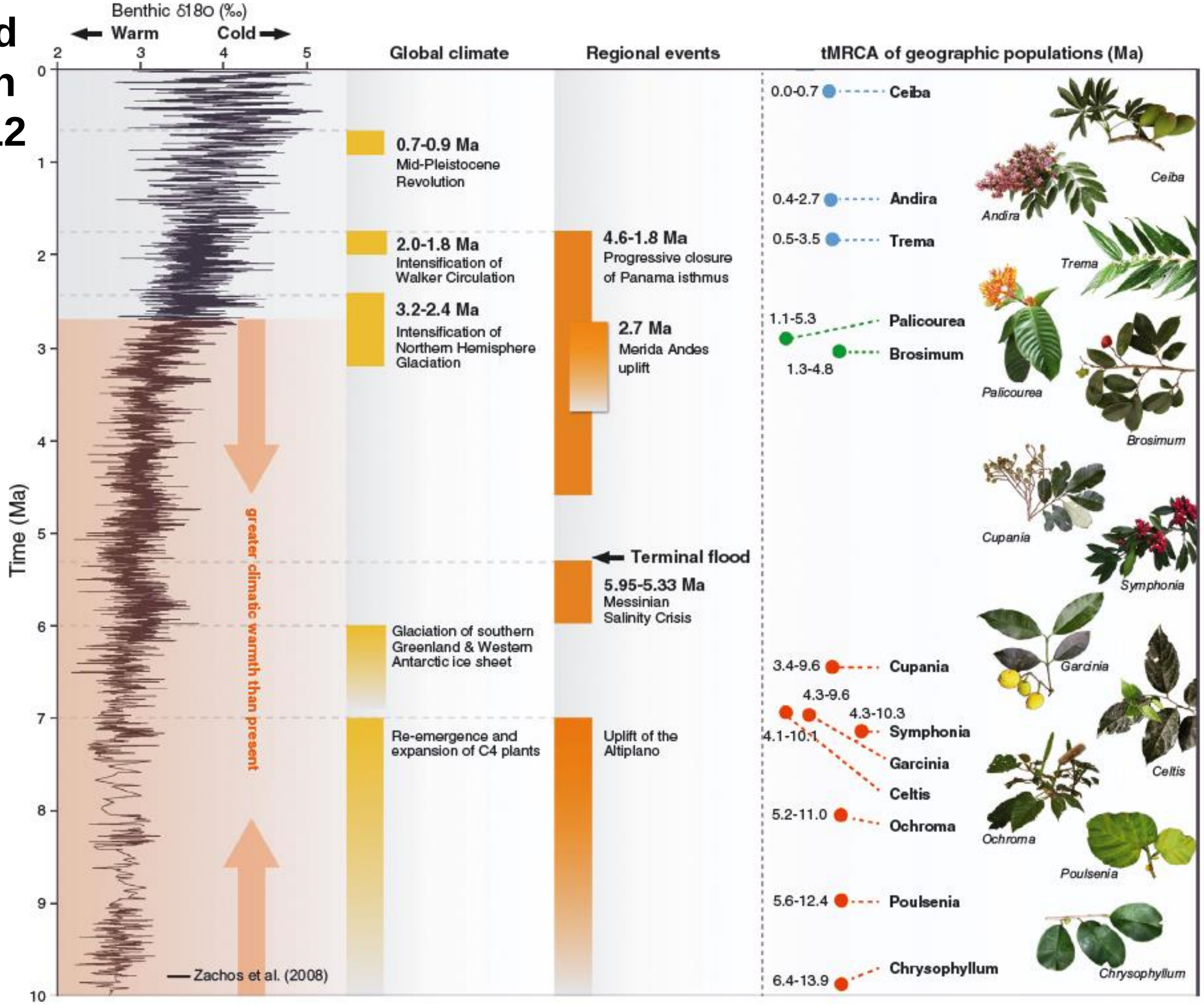


Figure 3. tMRCA of geographic lineages and relevant corresponding surface air temperatures (Zachos et al. 2008) and climatic and geological events. Mean tMRCA estimates are shown in colored circles (Pleistocene blue, Pliocene green, Miocene red) accompanied by upper and lower 95% HPD intervals. Large vertical arrows indicate period in which average surface air temperatures were warmer than present. Tree photographs were provided by Center for Tropical Forest Sciences.

Comparative phylogeographic analyses: 9 of 12 widespread Amazon tree species have Pliocene or earlier lineages (>2.6 Ma), with seven dating from the Miocene (>5.6 Ma) and three >8 Ma.
The remarkably old age of these species suggest that Amazon forests passed through warmth similar to 2100 levels and that, in the absence of other major environmental changes, near-term high temperature-induced mass species extinction is unlikely.

Outras florestas tropicais úmidas neotropicais: “refúgios” na Mata Atlântica” ?

Thomas *et al.* 1998.

Neotropical forest expansion during the last glacial period challenges refuge hypothesis

Leite et al. 2016

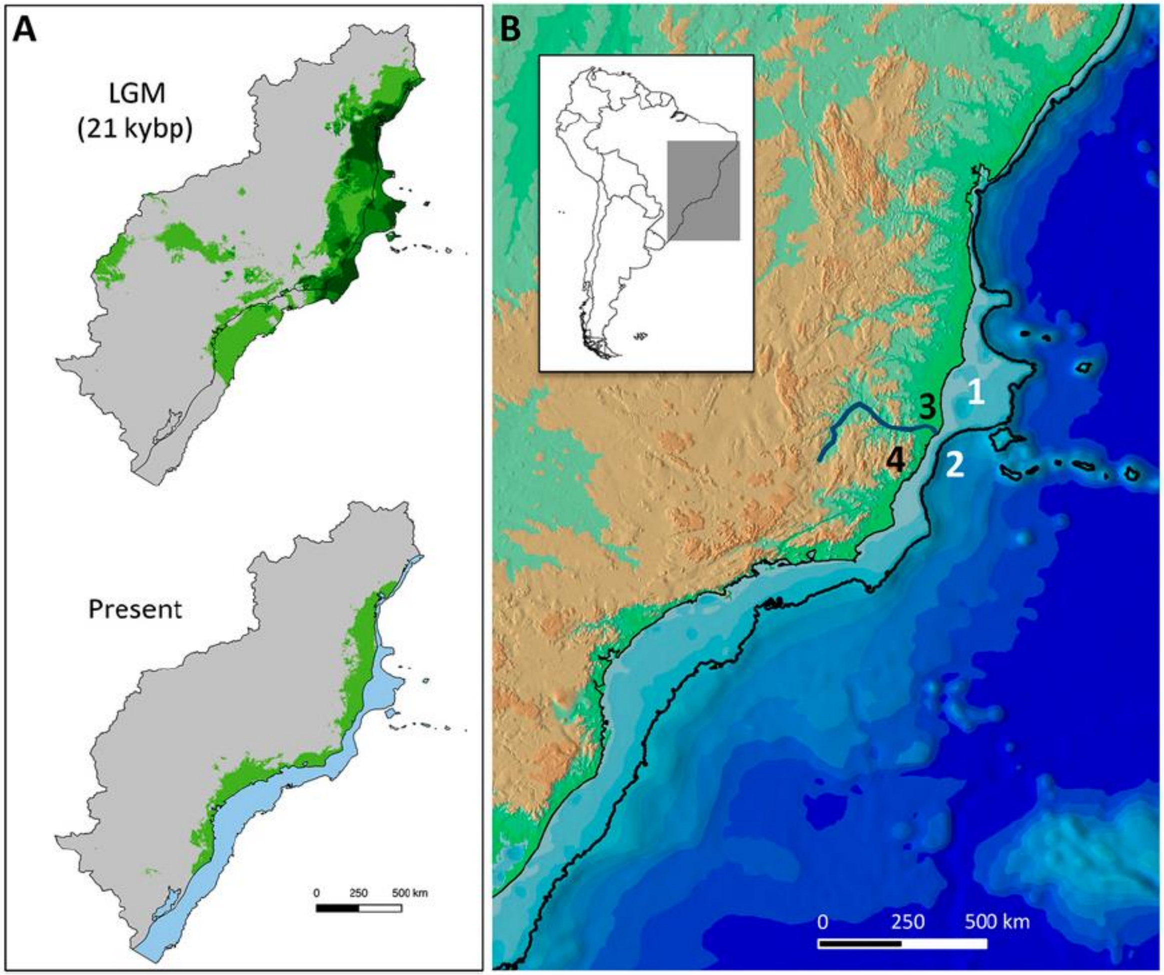


Fig. 3. Connections between the Brazilian continental shelf and the Atlantic Forest. (*A*) Projected extent of suitable broadleaf evergreen rainforest areas (green) during the last glacial maximum (LGM) and the present. The LGM map shows the overlap of three models (dark green), two models (medium green), and one model (light green). Suitable areas for rainforest on the continental shelf during the LGM (green) are submersed in the present (blue). (*B*) Topographic map of the eastern Brazilian coast emphasizing the continental shelf (light blue, bounded by the −150 m isobath) and four key features mentioned in the text: the Abrolhos Bank (site 1), Tubarão Bight (site 2), Doce River (site 3), and Espírito Santo Mountains (site 4). The lowlands (<500 m) are represented in green, the highlands (>500 m) in orange, and ocean depth increases progressively toward darker blue areas.

Neotropical forest expansion during the last glacial period challenges refuge hypothesis

Leite et al. 2016

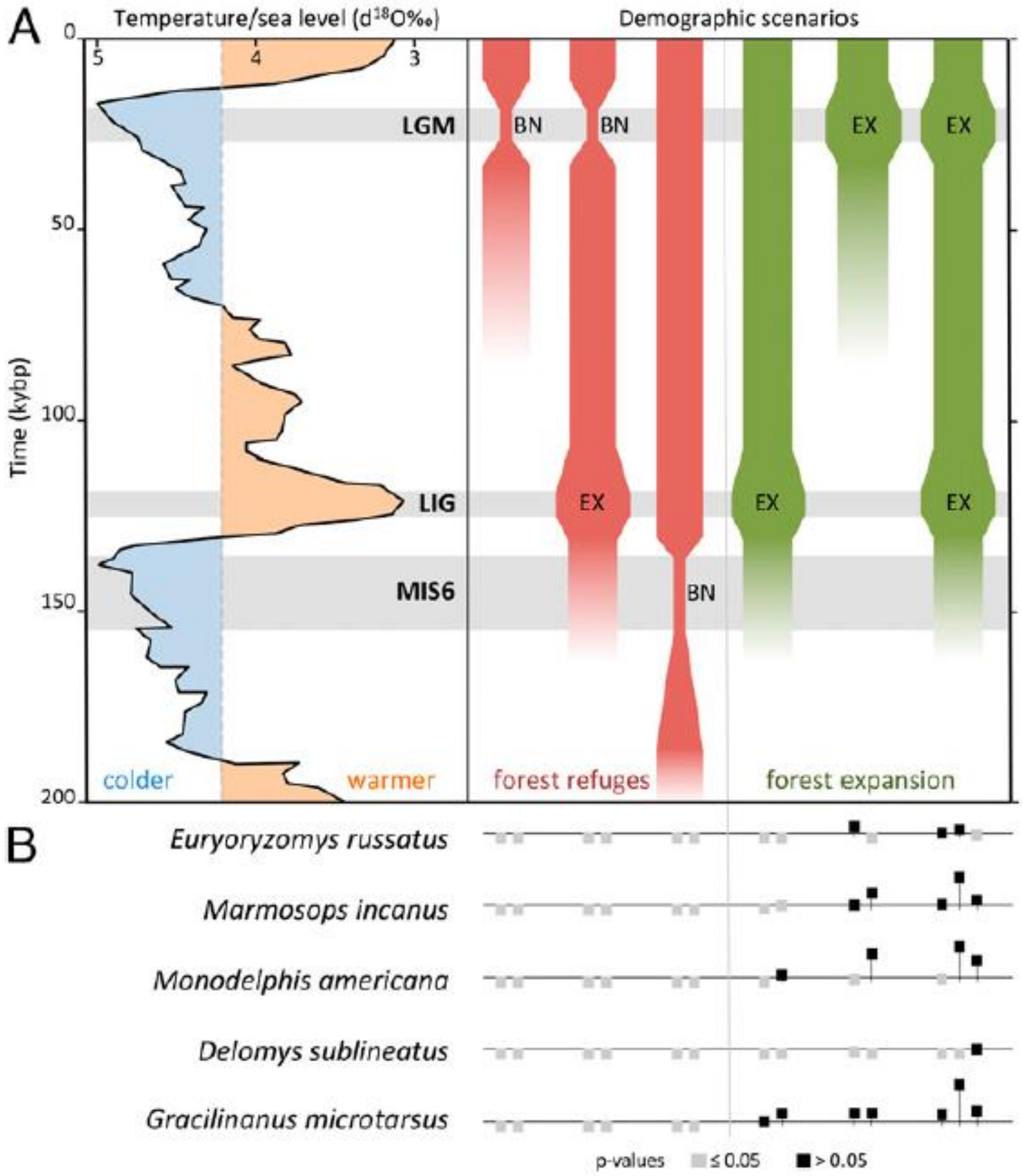
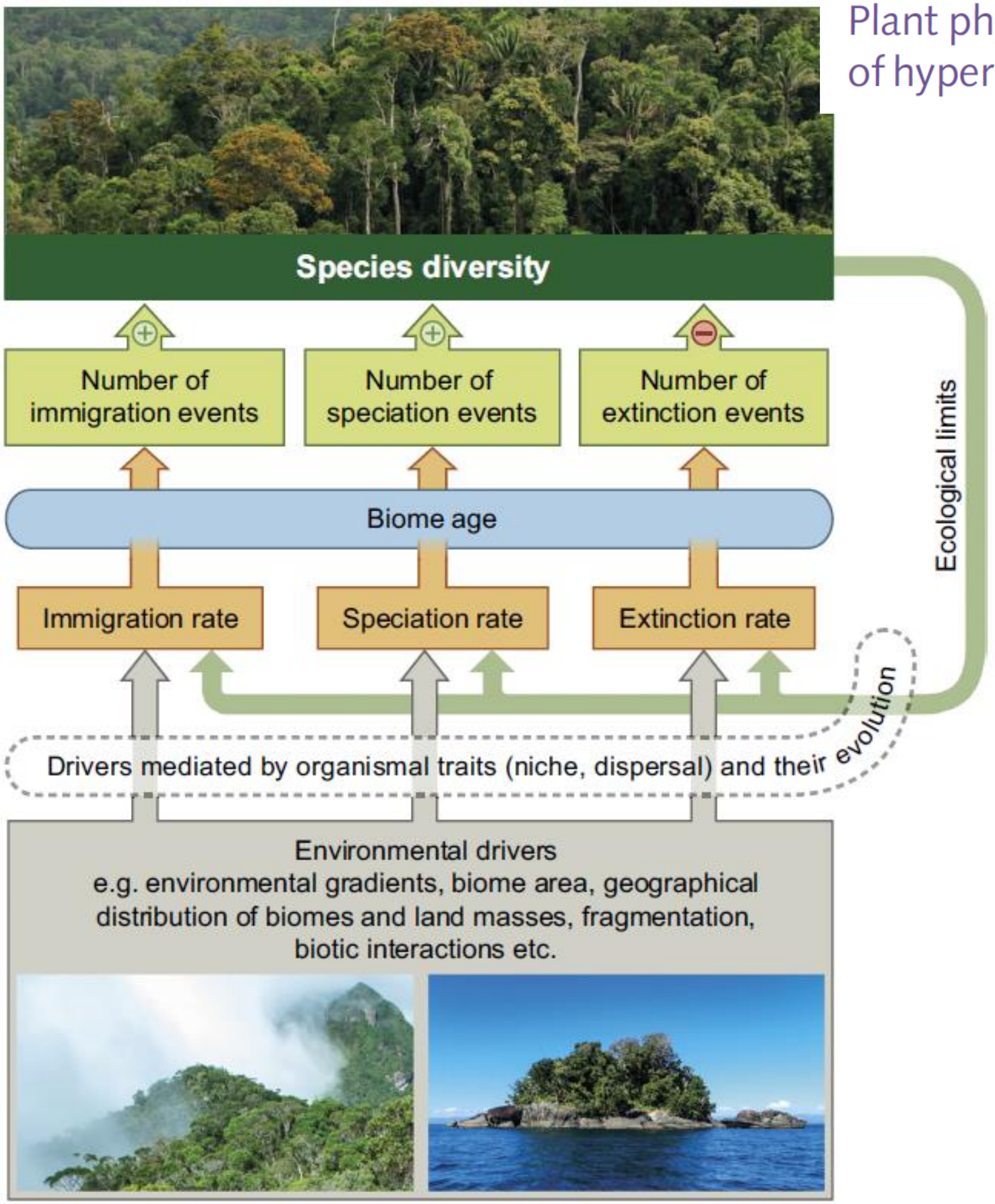


Fig. 2. Species responses to demographic scenarios of forest refuges (red) and forest expansion (green) during climatic oscillations from 200 kybp. (*A*) Benthic d^{18}O records reflecting changes in seawater temperature and ice volume (7), and corresponding demographic scenarios of population bottleneck (BN) and/or expansion (EX) in different periods: last glacial maximum (LGM), last interglacial (LIG), and penultimate glacial maximum (MIS6). (*B*) Results of the coalescent simulations for each species, confirming population expansions during both LGM and LIG. The horizontal line represents the threshold *P* value (0.05) for each species. Scenarios resulting in *P* values at or below this level were rejected (gray), and those above this level were not rejected (black). See Fig. S1 for additional scenarios tested and rejected.

Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome

Eiserhardt et al. 2017



Species diversity

⊕ Number of immigration events

⊕ Number of speciation events

⊖ Number of extinction events

Biome age

Immigration rate

Speciation rate

Extinction rate

Ecological limits

Drivers mediated by organismal traits (niche, dispersal) and their evolution

Environmental drivers
e.g. environmental gradients, biome area, geographical distribution of biomes and land masses, fragmentation, biotic interactions etc.

Photos: W. J. Baker

Fig. 3 A framework of hypotheses regarding the origin of tropical rainforest (TRF) species diversity. The immediate determinants of species diversity are events of speciation, extinction and immigration into a biome (green boxes). The number of those events depends on the age of the biome and its clades (blue), and the rates at which speciation, extinction and immigration happen (yellow). These rates may depend on the environment (grey, e.g. if the environmentally defined area of a biome is large, extinction is thought to be less frequent and speciation more frequent than in smaller biomes; Fine & Ree, 2006), and the way in which rates respond to the environment depends on the intrinsic properties of species. A special case of environmental determination of rates is 'ecological limits', where the outcome of the diversification process (i.e. species diversity itself) is thought to exert a feedback effect on rates, increasing extinction or decreasing speciation/immigration (dark green arrow).

Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome

Eiserhardt et al. 2017

Modelos

“Berçário” **“Museu”** **Modelo misto**

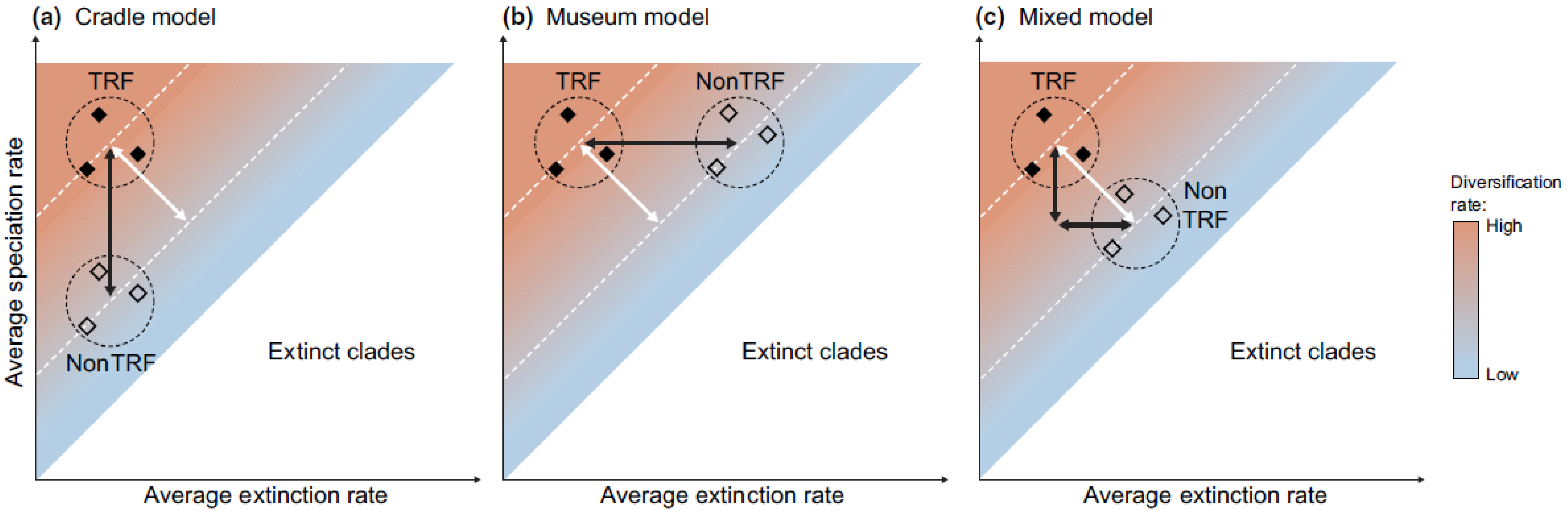

(a) Cradle model (b) Museum model (c) Mixed model

Fig. 4 Separating the roles of extinction and speciation in the evolution of tropical rainforest (TRF) species diversity requires a large sample of TRF (closed diamonds) and nonTRF (open diamonds) clades. Using well-sampled species-level phylogenies, overall speciation rate and extinction rate can be estimated for each clade, and analysed across clades (de Vos *et al.*, 2015). Assuming that TRF clades have a higher diversification rate than nonTRF clades (white arrows and lines), i.e. high TRF species richness is not exclusively a result of age or immigration, three scenarios are possible. In (a), only speciation rates (*y*-axis), but not extinction rates (*x*-axis), are significantly different; this corresponds to the ‘cradle’ scenario of Stebbins (1974) (see Section II). In (b), only extinction rates are significantly different, corresponding to Stebbins’ ‘museum’. However, high diversification rates may also be a result of a combination of higher speciation and lower extinction (mixed model, c).