

Breve história da Vegetação Neotropical

parte II

1. Riqueza florística e diversidade de biomas.

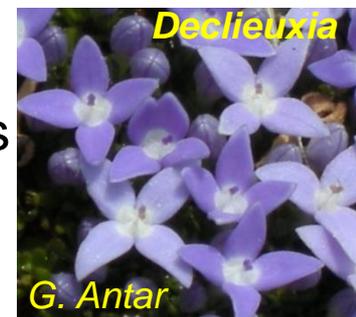
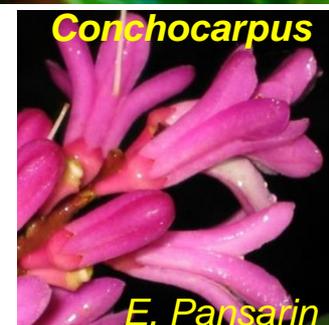
2. Padrões espaciais e causas da diversidade específica neotropical:

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.



Breve história da Vegetação Neotropical

parte II

Burnham & Graham 1999;
Graham 2011

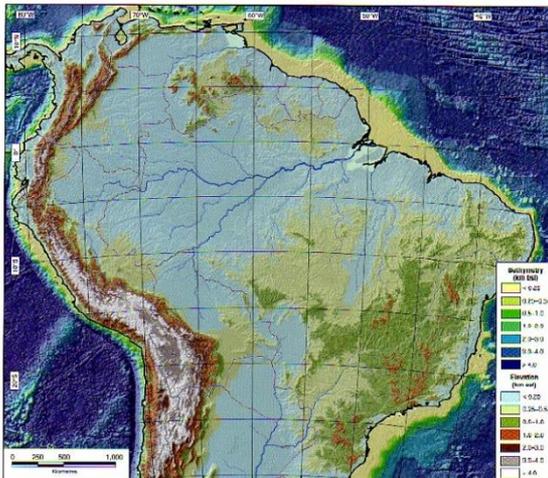


Plate 4 Shaded-relief topography and bathymetry of South America produced from ETOPO1 (Amante & Fatsis 2008, ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis, National Geophysical Data Center, NESDIS, NOAA, US Department of Commerce, Boulder, CO, August 2008). Grey lines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

Topografia e batimetria da América do Sul Tropical
Hoorn et al. 2010

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		
	TERTIARY	NEOGENE	PLIOCENE	5.2	LANDBRIDGE EXISTS
			MIOCENE	23.3	
			OLIGOCENE	34	
		PALEOGENE	EOCENE	56.5	ISOLATION
			PALEOCENE	65	
			MAESTRICHT.	74	
	MESOZOIC	CRETACEOUS	SANTONIAN	88.5	
			CONIACIAN		
TURONIAN					
CENOMANIAN					
ALBIAN					
		APTIAN	112		

Vegetação Neotropical

Florestas ombrófilas Amazônica e Atlântica

Floresta de Araucária

Campos e cerrados

Caatinga

Vegetação de altitude (ênfase em campo rupestre)

Origem das florestas Neotropicais Pluviais

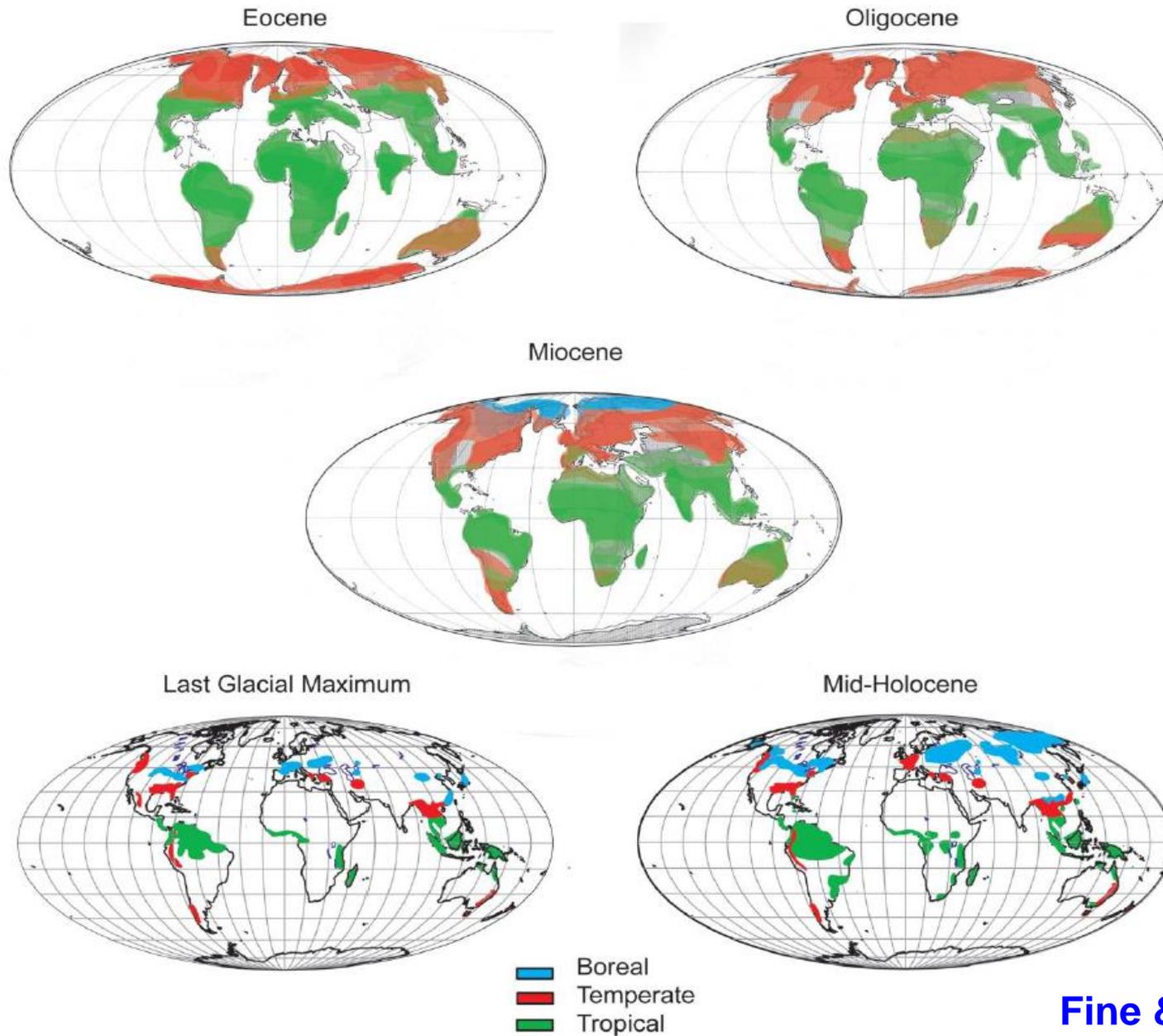
com base na paleobotânica sul-americana

Evidência de raridade no Paleoceno (60-55 m.a.)

Eoceno (55-30 m.a.):

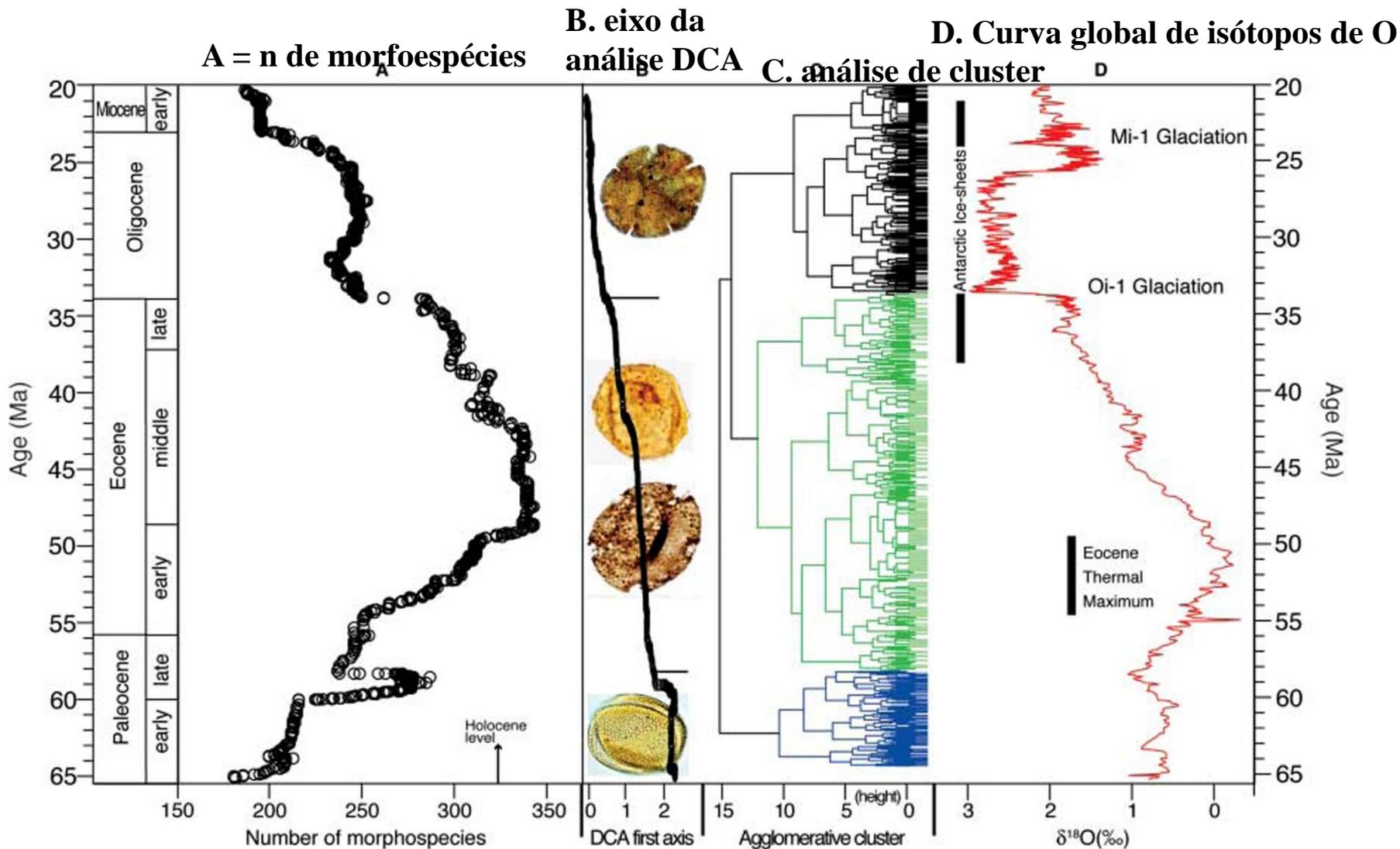
**florestas com alta diversidade,
fisionômica e taxonomicamente reconhecíveis como fl. pluviais
e taxonomicamente relacionadas às Fl. Neotr. Pluviais modernas**

Burnham & Johnson 2004



Fine & Ree 2006

Figure 2: Five interpretations of past biomes (see fig. 1), drawn on top of one another onto paleocoastlines from Smith et al. (1994) for the Eocene, Oligocene, and Miocene. The darker colors represent agreement among the sources; shades that are neither green, red, nor blue represent disagreement. Last glacial maximum and mid-Holocene reconstructions are adapted from Beerling and Woodward (2001).



Mudanças na diversidade e composição palinoflorais durante o Cenozóico Médio na Colômbia e Venezuela
Jaramillo et al. 2006

Ligações florísticas Amazônia – Floresta Atlântica

Ducke 1953 – presença de táxons amazônicos nos encraves florestais da caatinga (“brejos”)

Andrade-Lima 1954 } lista de 388 spp. florestais amazônicas,
Rizzini 1967 } sendo 277 gêneros comuns entre Amazônia e MA,
mas sem qualquer comprovação paleobotânica.

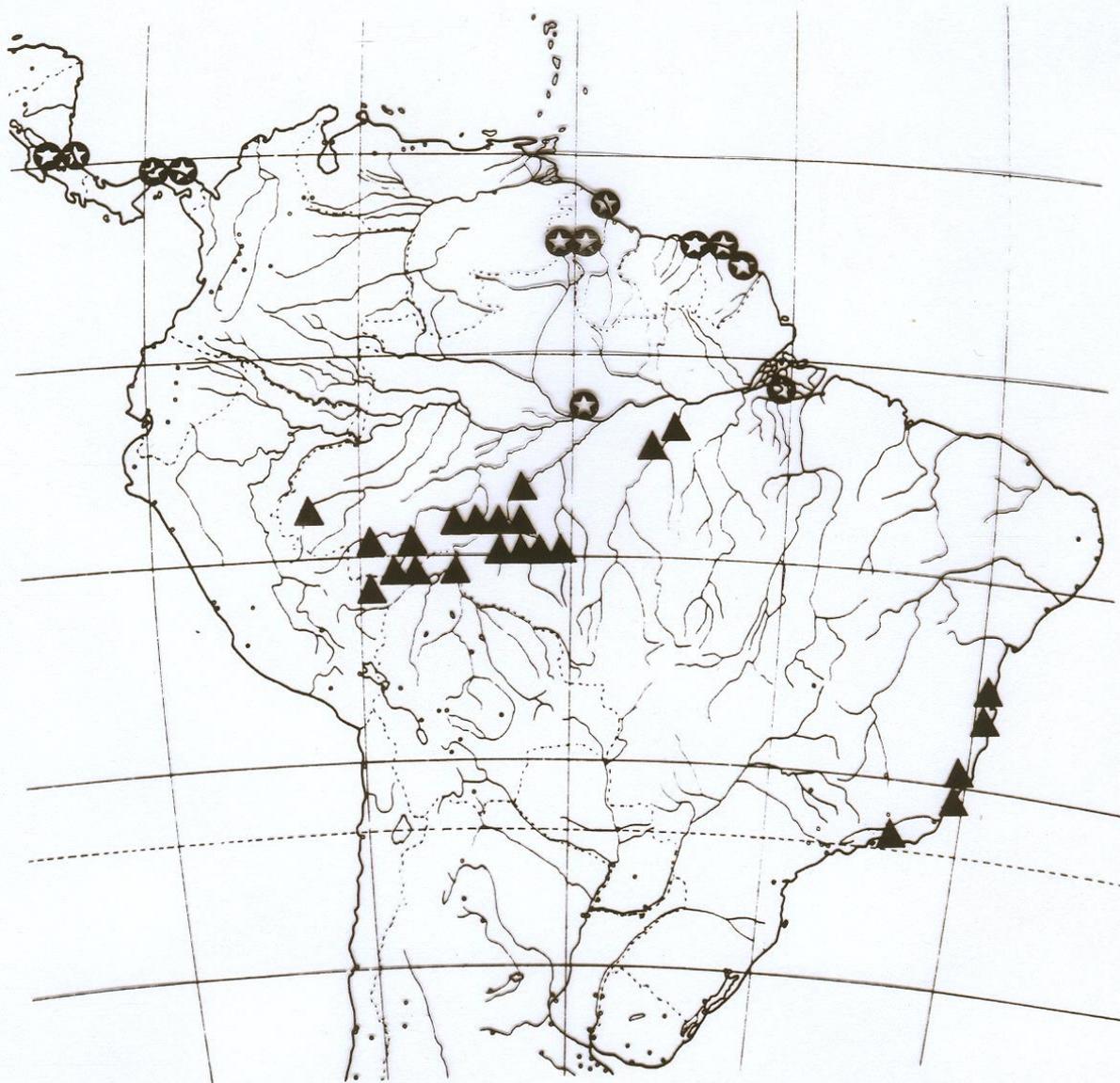
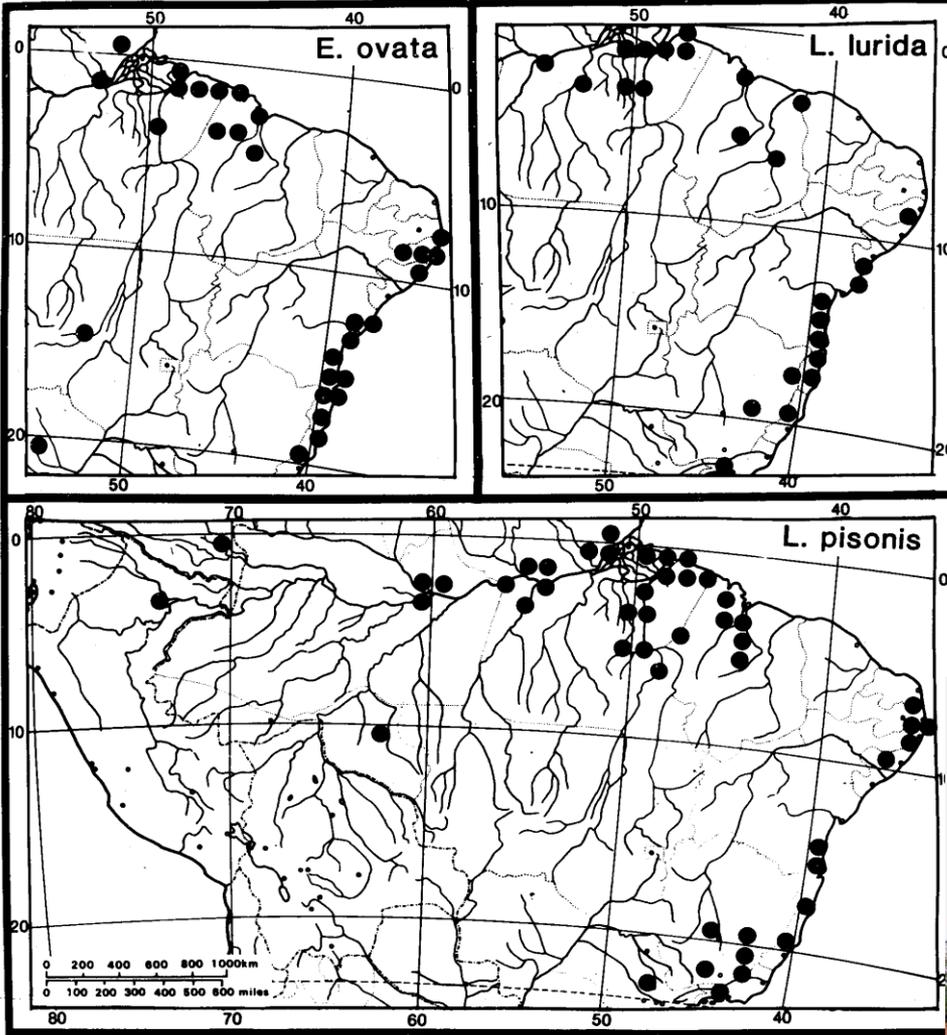


Fig. 11.3 Two examples of common patterns of species disjunction: ☆ *Licania affinis* Fritsch (Guianas-Amazonia), ▲ *Couratari macrosperma* A. C. Smith (Amazonia-Eastern Brazil).

Disjunções Amazônia - Mata Atlântica



Mori 1990

Lecythis pisonis

Eschweilera ovata, *Lecythis lurida* e
L. pisonis (LECYTHIDACEAE)



**Diagonal
seca**

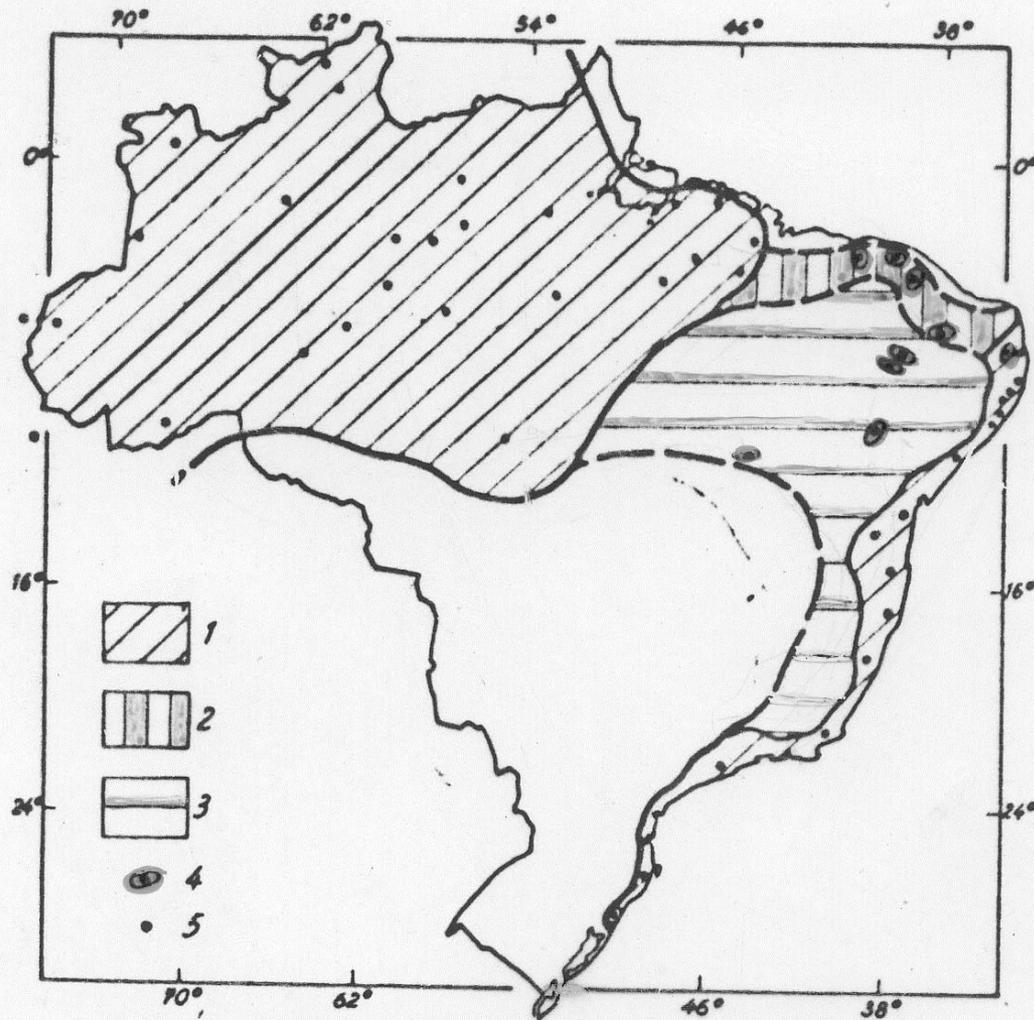


Figure 3.3 Relationship between the Atlantic and Amazonian forests. 1. present day distribution; 2. paleodistribution with many evidences; 3. paleodistribution with few evidences; 4. some of the present refuges; 5. verified occurrences.

Distribuição dos “brejos” nordestinos

Andrade-Lima
1982

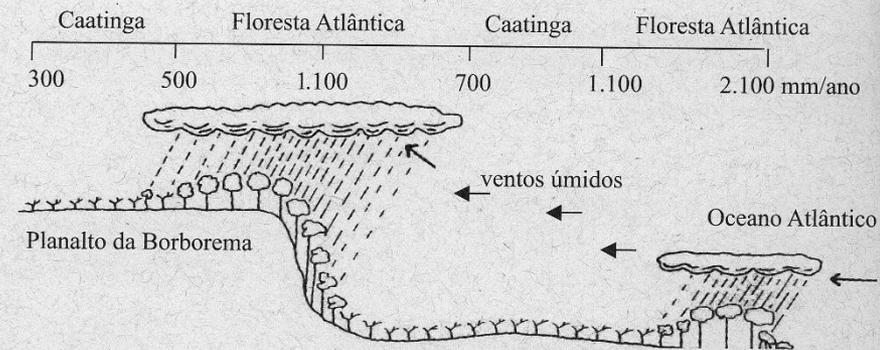
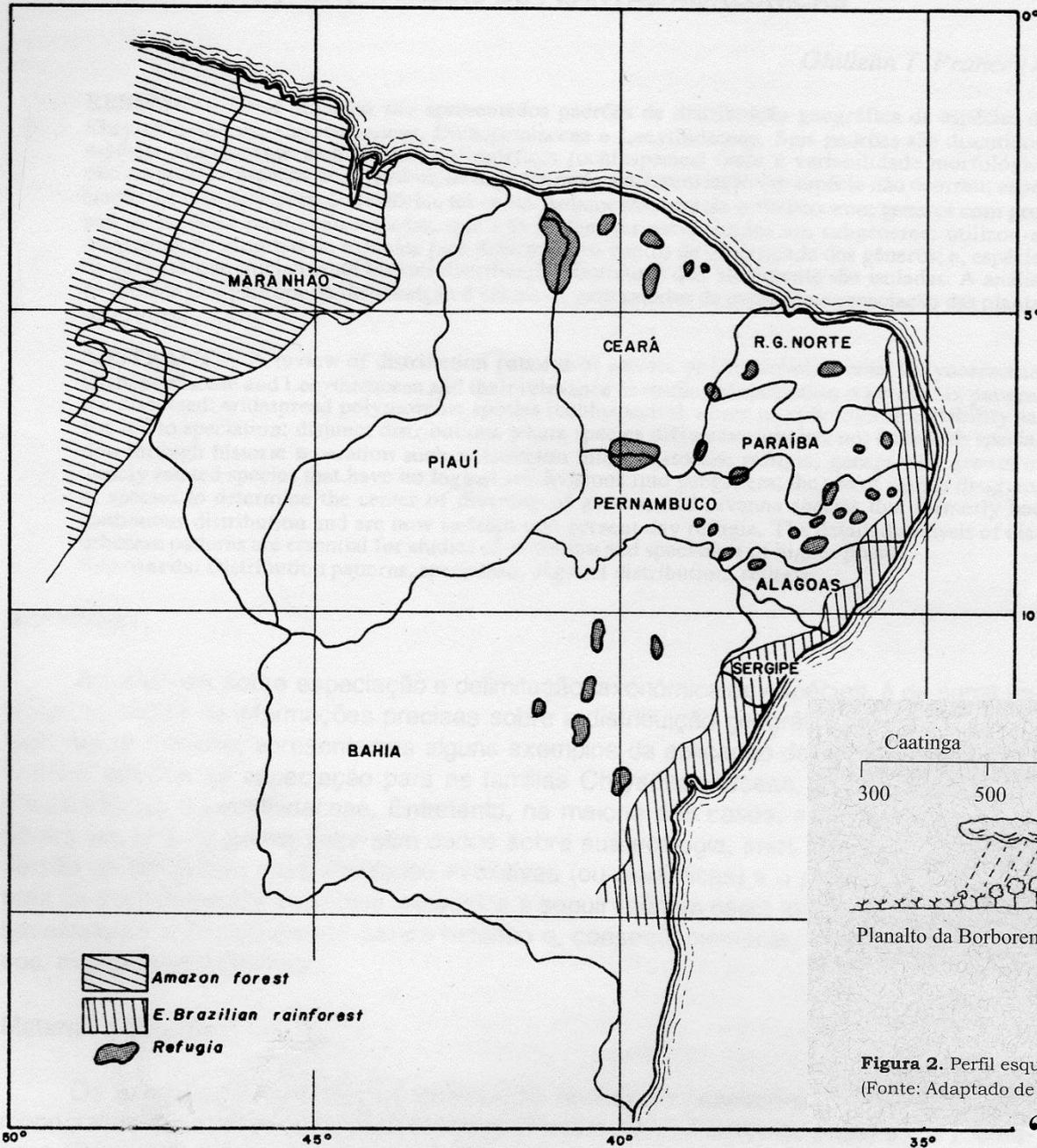


Figura 2. Perfil esquemático dos brejos de altitude no Nordeste do Brasil.
(Fonte: Adaptado de Mayo & Fevereiro 1982)

“brejos” = matas serranas

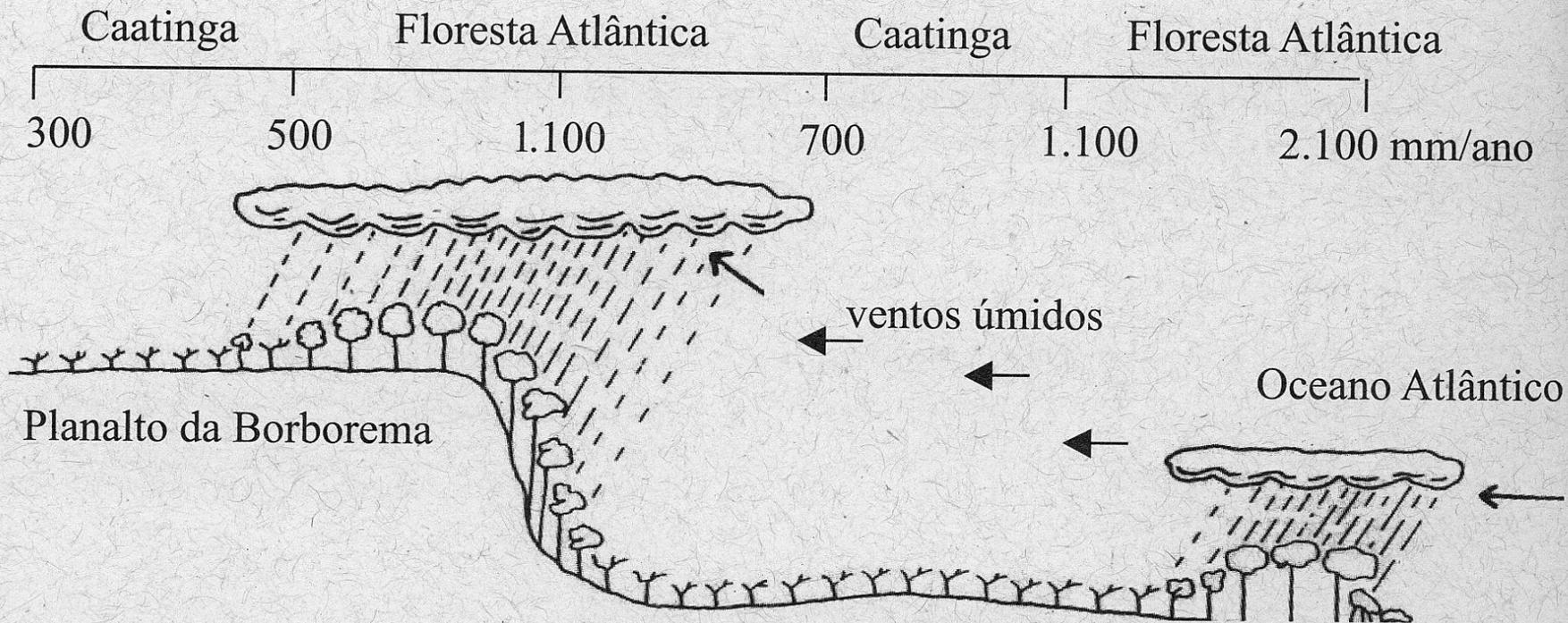


Figura 2. Perfil esquemático dos brejos de altitude no Nordeste do Brasil.
(Fonte: Adaptado de Mayo & Fevereiro 1982)

Tabarelli & Santos 2004

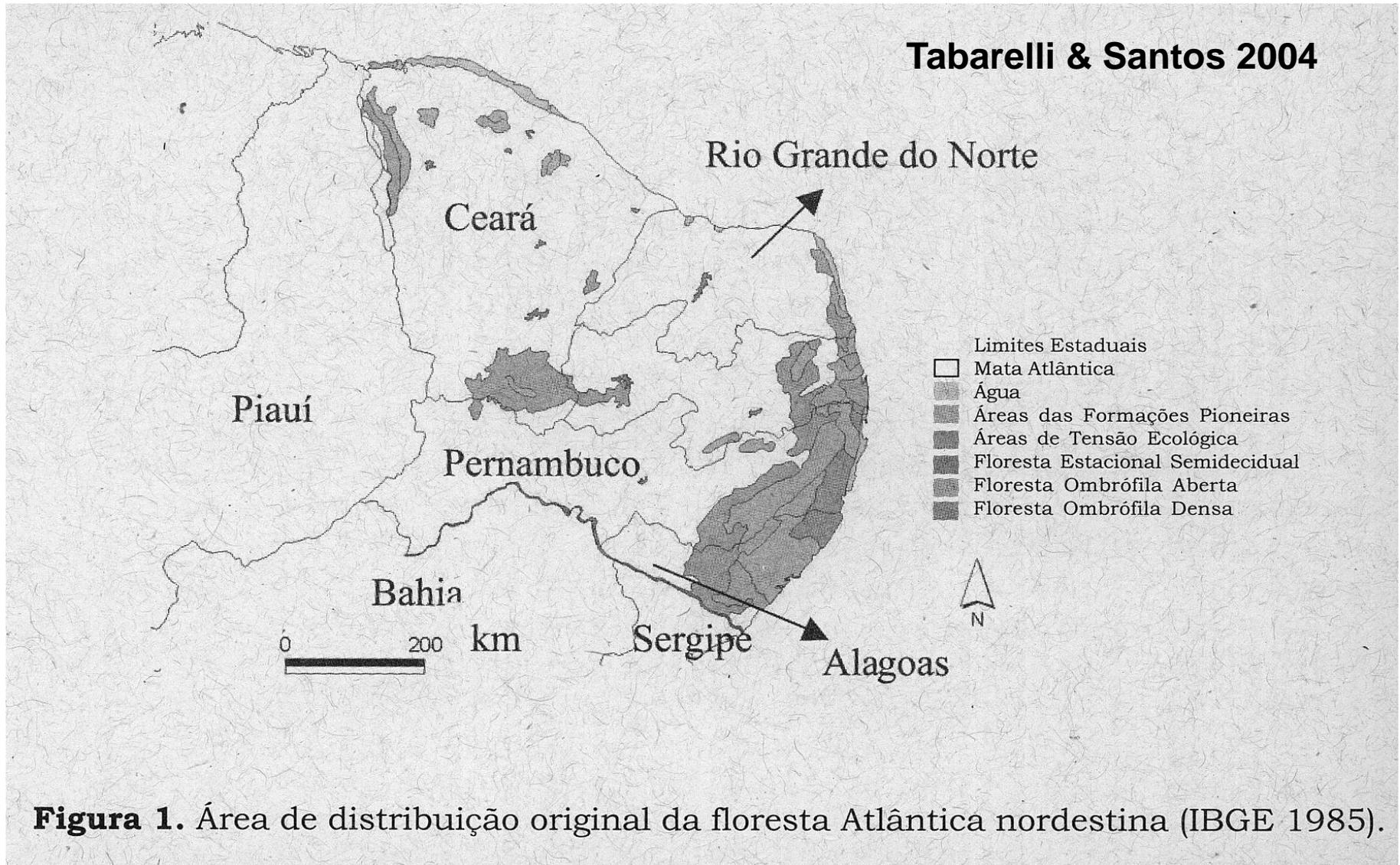


Figura 1. Área de distribuição original da floresta Atlântica nordestina (IBGE 1985).

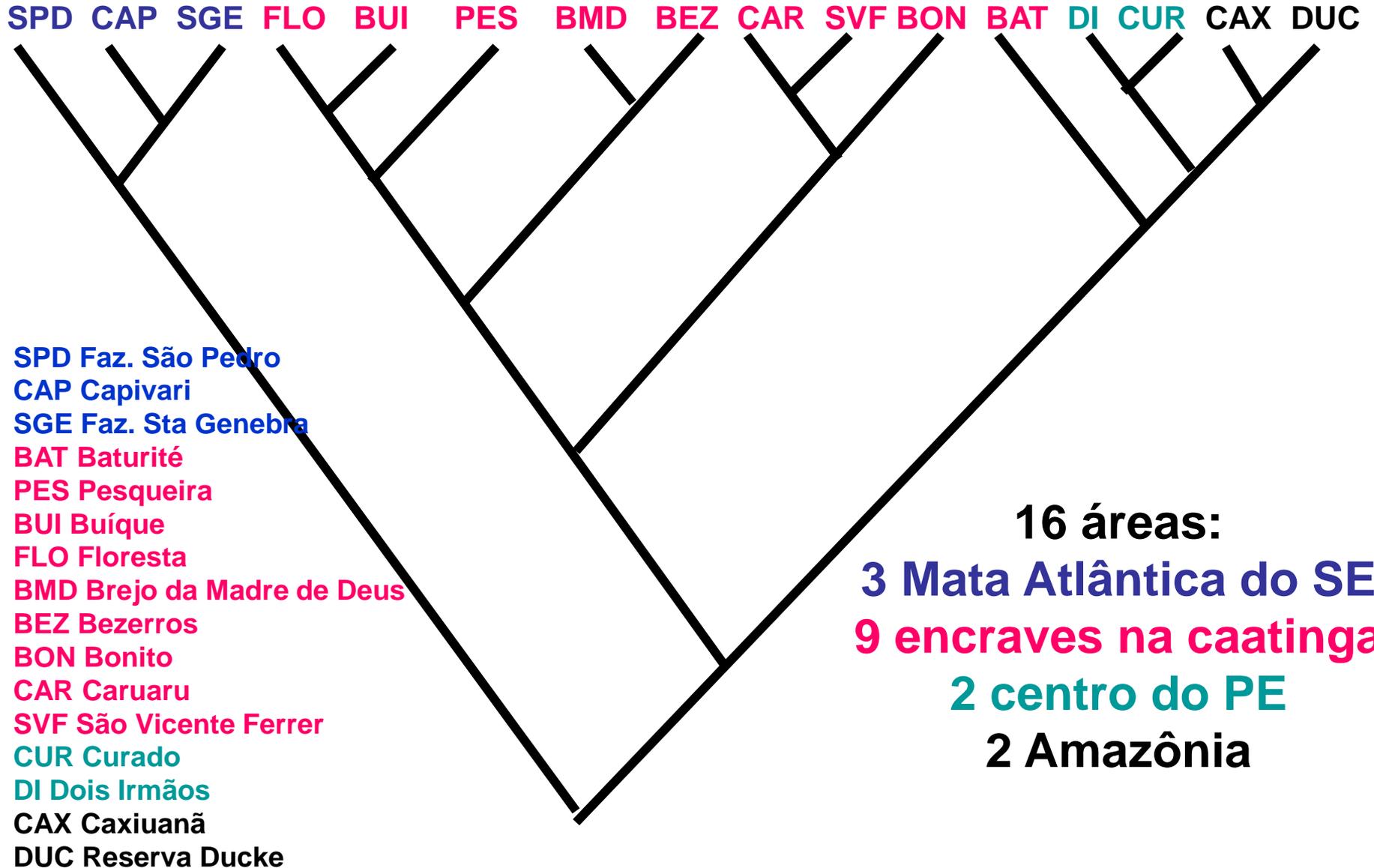
43 brejos no NE (CE, RN, PB e PE),

31 deles na PB e PE

(Vasconcelos Sobrinho 1971).

PAE de florestas do NE. Santos et al. 2007

452 spp lenhosas e
293 gên. (745 taxa)



Ligações florísticas Amazônia – Floresta Atlântica

Oliveira et al. 1999 - Vale do Rio Icatu, médio São Francisco, Bahia

P.E. De Oliveira et al. / Palaeogeography, Palaeoclimatology, Palaeoecology 152 (1999) 319–337

333

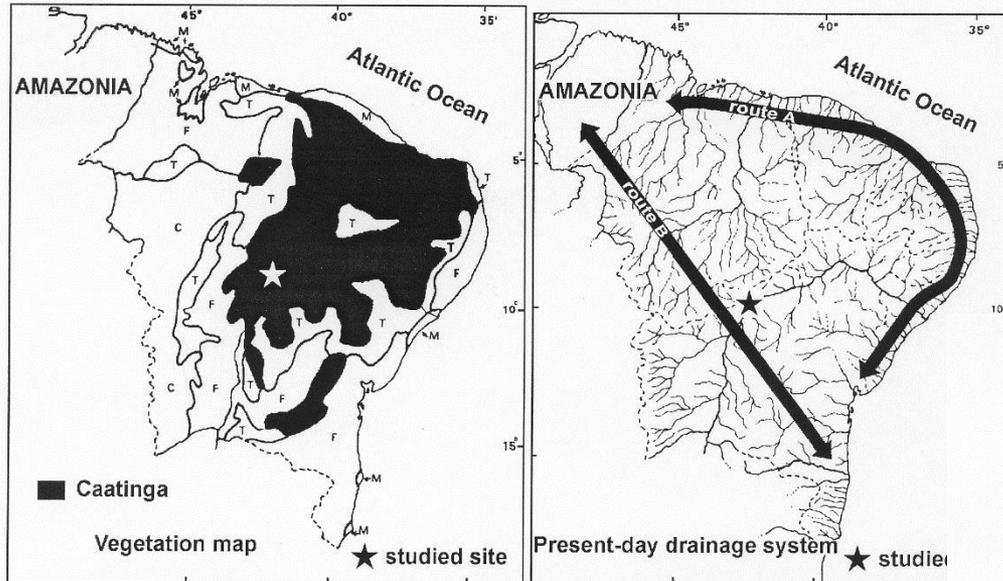


Fig. 7. Vegetation (left) and present-day drainage system maps of northeastern Brazil (right), showing possible migration routes of tropical forest taxa in the Quaternary. Modified from Coimbra-Filho and Câmara (1996). Route A is supported by botanical data (1953; Ducke and Black, 1954; De Andrade-Lima, 1966; Rizzini, 1967) whereas Route B is supported by the palynological record from the Icatu River Valley, botanical data from the Chapada da Diamantina and by paleontological data (Cartelle and Hartwig, 1996 and Cartelle, 1996). The caatinga vegetation nuclear area is represented by the black area, other vegetation types are indicated by letters: A = Atlantic Forest, M = coastal successional vegetation under marine/fluviol influence, T = transitional tropical forest (semi-deciduous) and C = cerrado.

Táxons florestais atlânticos e amazônicos ocupavam conjuntamente a região por volta de 11.000 anos atrás (Pleistoceno tardio)

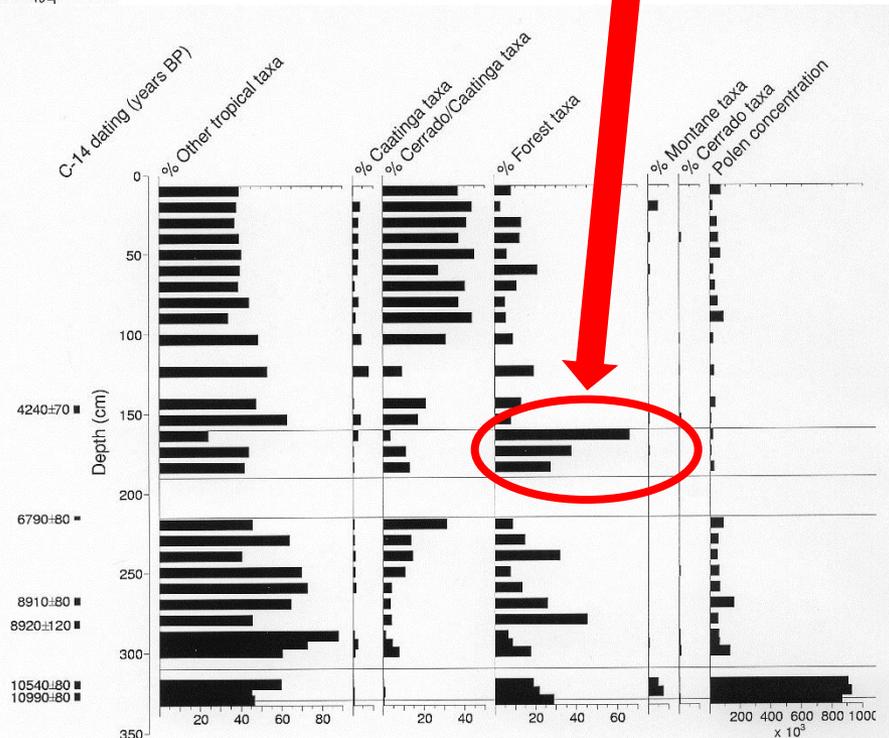
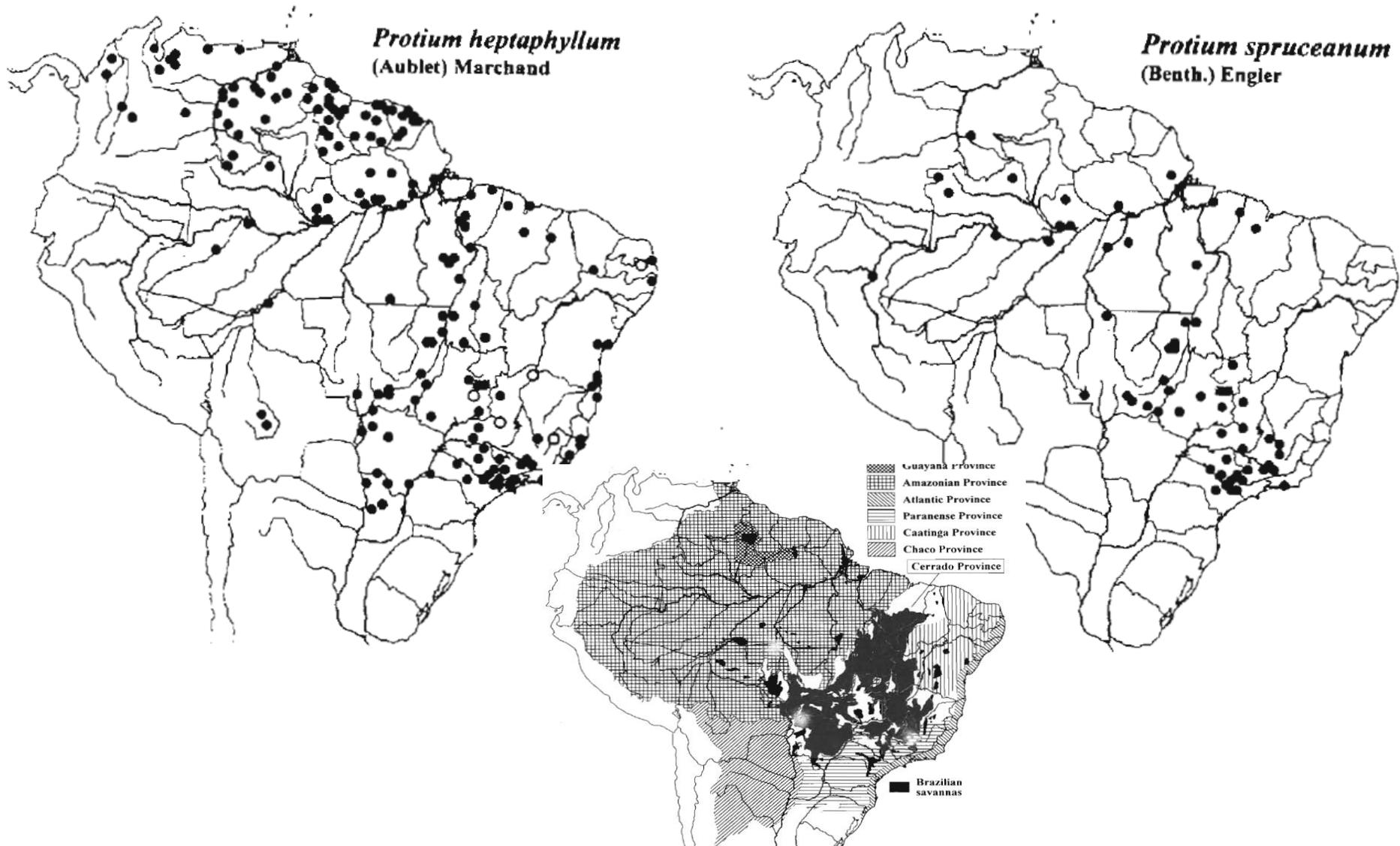


Fig. 6. Summary diagram of all caatinga, caatinga/cerrado, forest and montane taxa, pollen concentration and charcoal particles (x 10⁴)

Holoceno foi ficando árido e nos últimos 4.000 anos a caatinga estabeleceu-se permanentemente.

Ligações florísticas Amazônia – Floresta Atlântica

Rede dendrítica atual de matas ciliares = corredores (Oliveira-Filho & Ratter 1995, 2000)



Distribution and Endemism of Angiosperms in the Atlantic Forest

Werneck et al. 2011

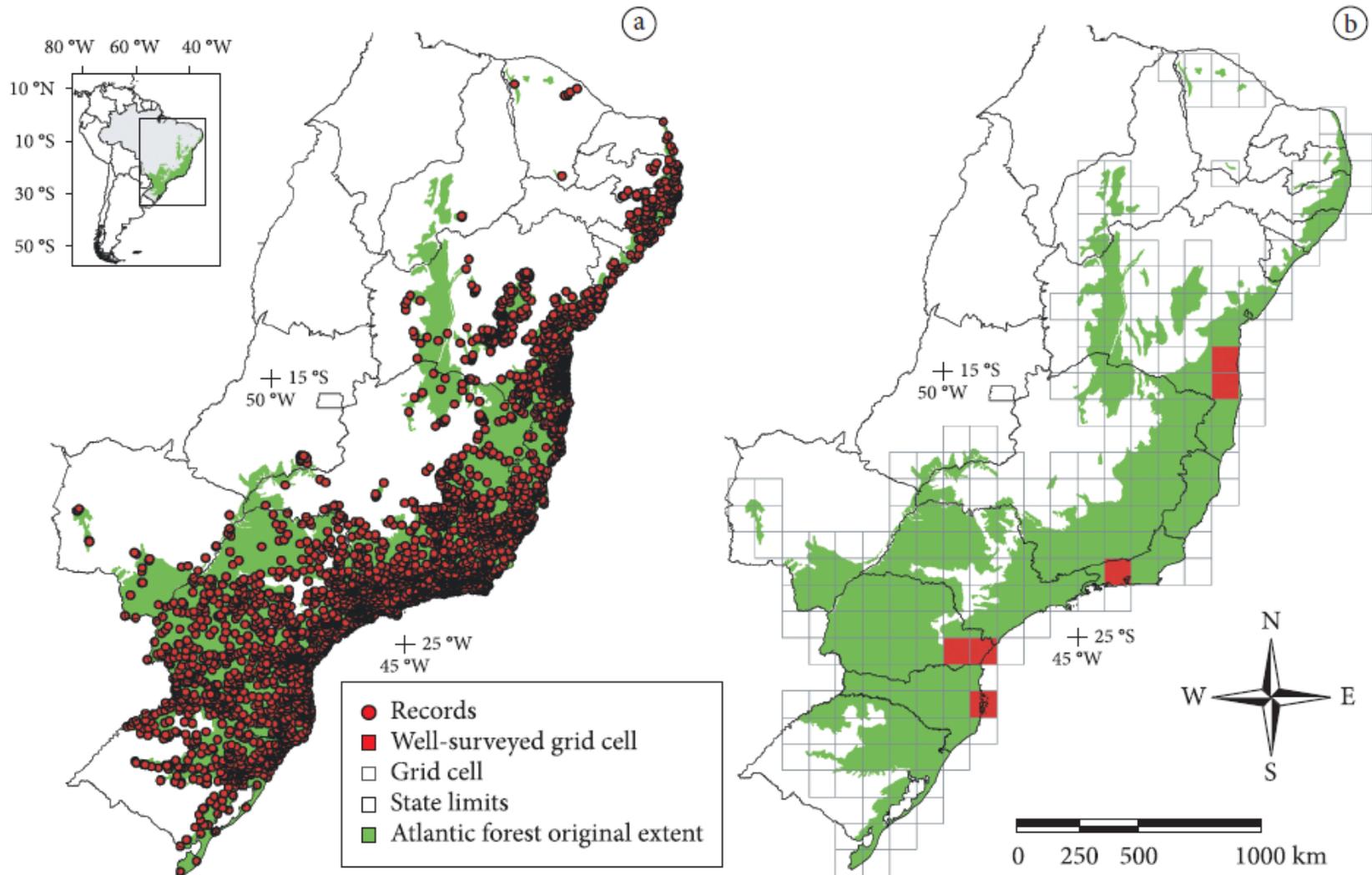
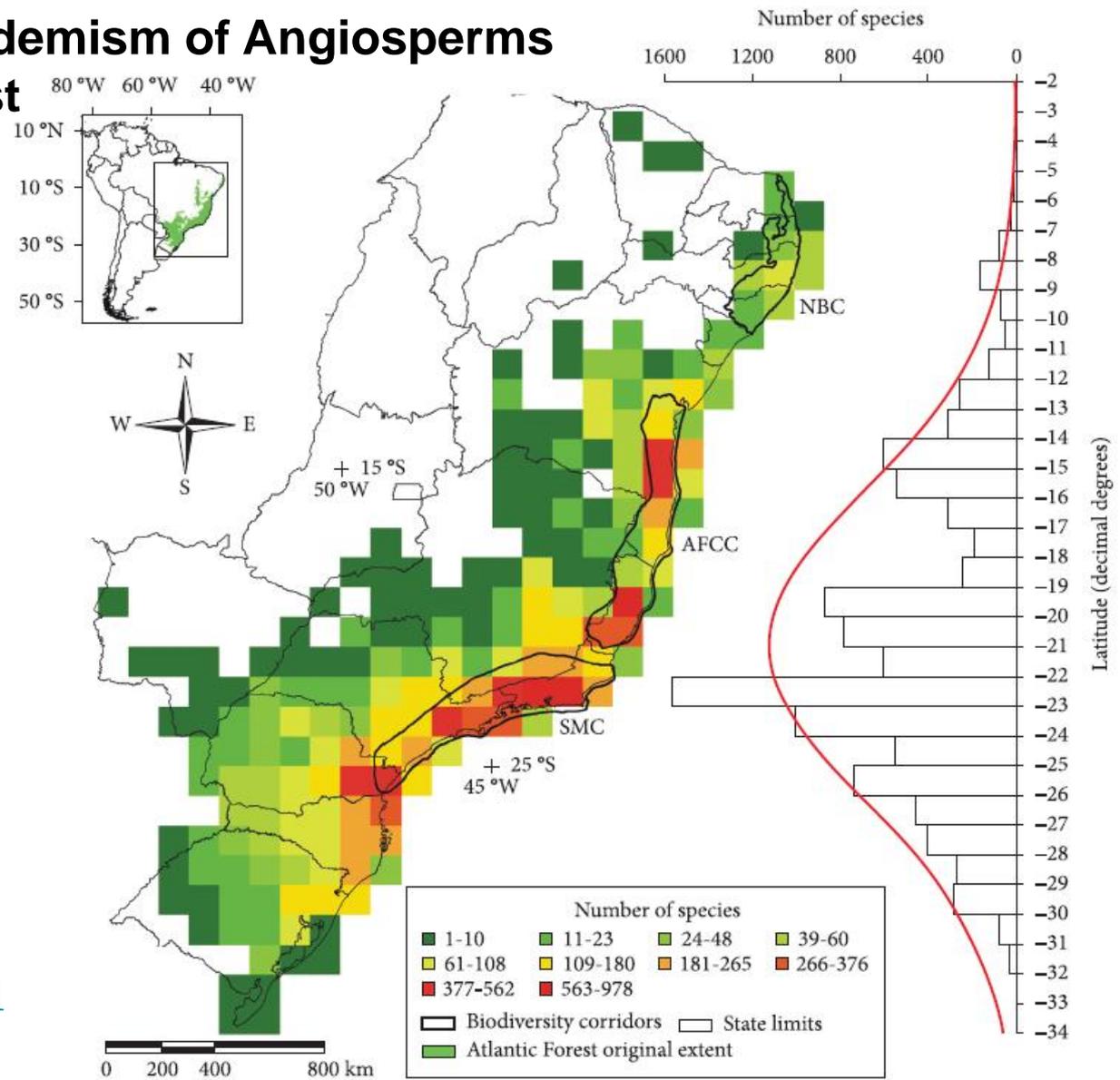


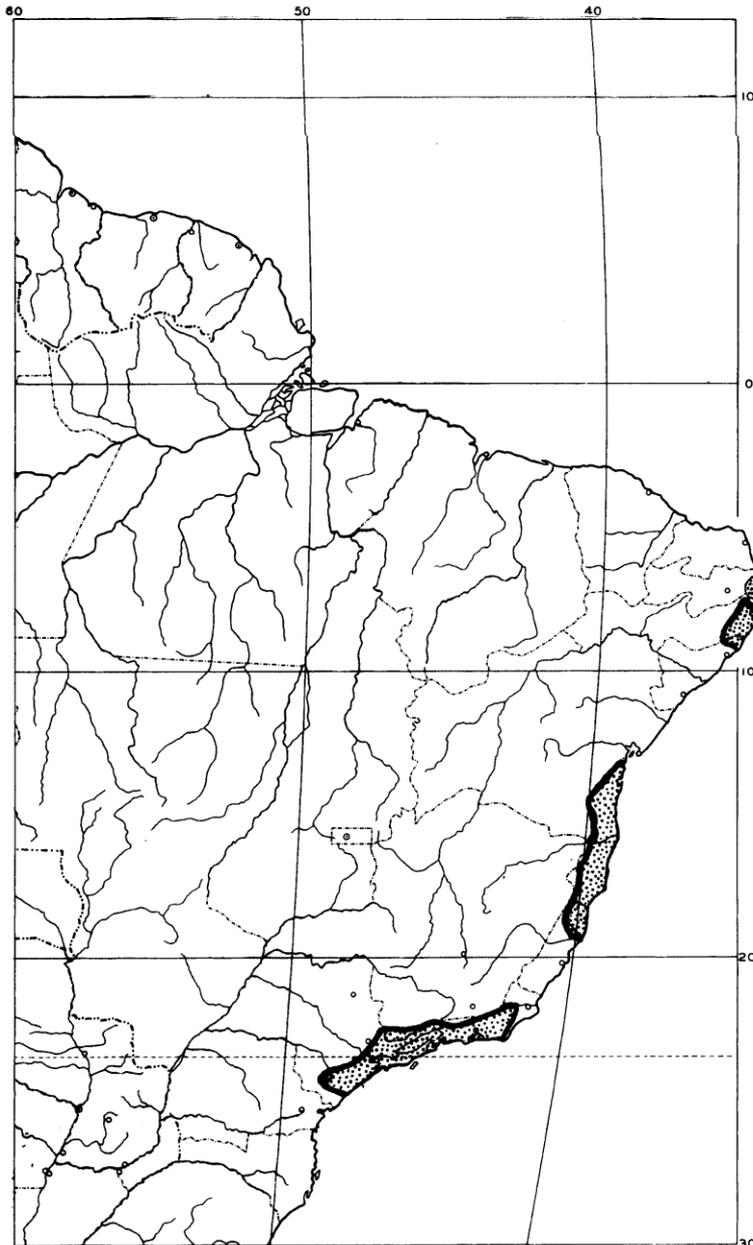
Figure 1. a) Distribution of 28,053 records of occurrence of 3,345 endemic species from Atlantic Forest. b) The grid system with 231 cells of 1° x 1° latitude/longitude overlaying the Atlantic Forest Domain original extent and distribution of the five grid cells classified as well-surveyed according to completeness results using the Jackknife1 estimator.

Distribution and Endemism of Angiosperms in the Atlantic Forest



Werneck et al. 2011

Figure 2. Species richness recorded in each 1° x 1° grid cell and frequency distribution of latitudinal extents (in decimal degrees) for the distributional range of 3,345 endemic angiosperms of Atlantic Forest. The red line is the normal distribution curve. NBC: Northeastern Biodiversity Corridor; AFCC: Atlantic Forest Central Corridor; SMC: Serra do Mar Corridor.

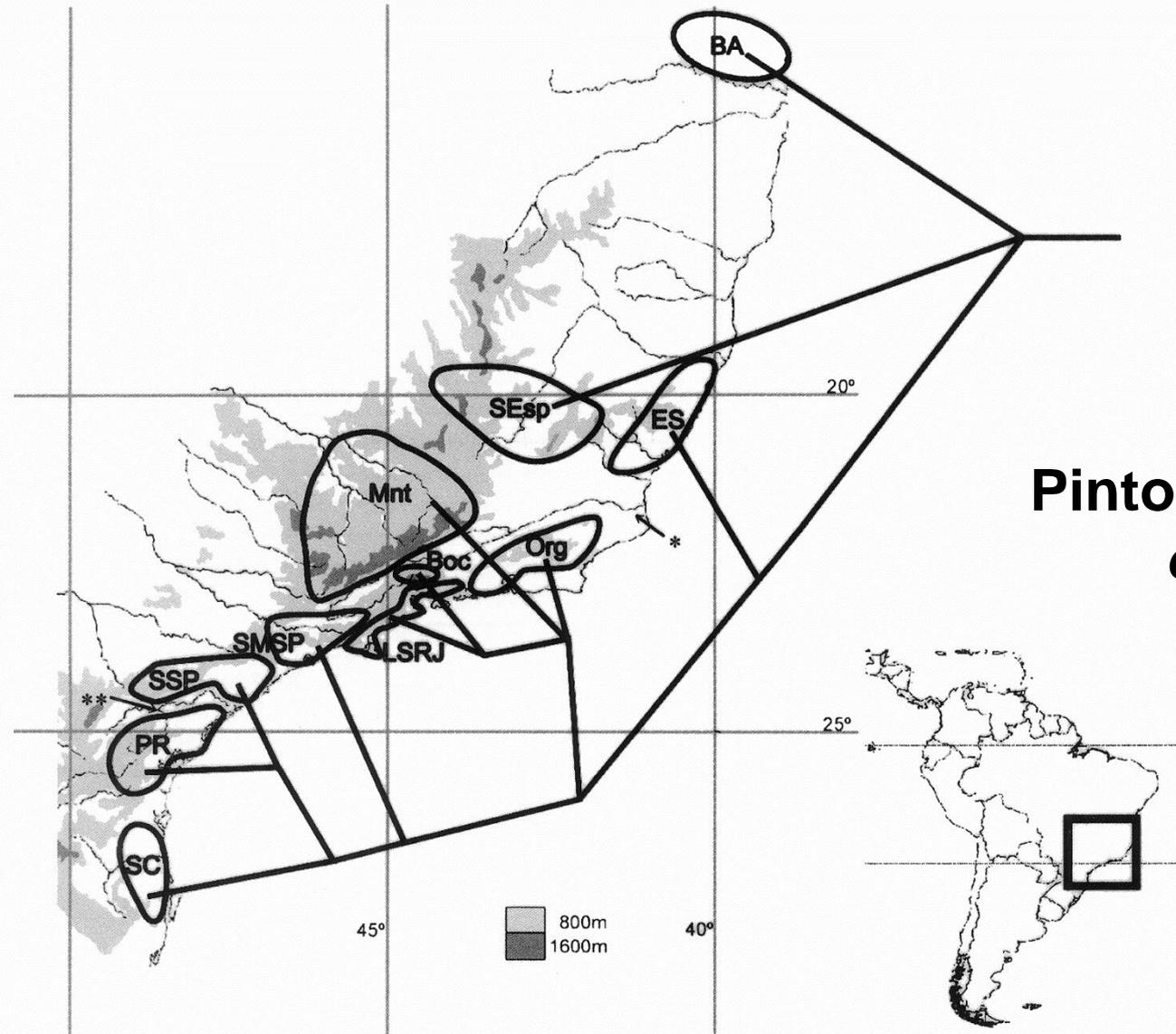


The three tropical lowland rain forest centres of endemism in coastal Brazil. From north to south these are: the Pernambuco-Alagoas centre (PE-AL), the southern Bahia-northern Espírito Santo centre (BA-ES), and the São Paulo-Rio de Janeiro centre (SP-RJ)

Thomas *et al.* 1998.

Contrações ou fragmentação da Floresta Ombrófila nos períodos secos?

Opiliões



**Pinto-da-Rocha
et al. 2006**

Figure 3.—Strict consensus area cladogram of harvestmen subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Gonyleptidae) based on three equally parsimonious trees (L = 248; CI = 0.66; RI = 0.57). Abbreviations of names in Table 1; * = Paraiba do Sul River; ** = Ribeira do Iguape River.

4 hipóteses de Áreas de Endemismo sobrepostas às fisionomias da Mata Alântica

DaSilva & Pinto-da-Rocha
2010

Teria ocorrido
fragmentação da
Floresta Ombrófila
durantes fases de
clima seco no
Neógeno?

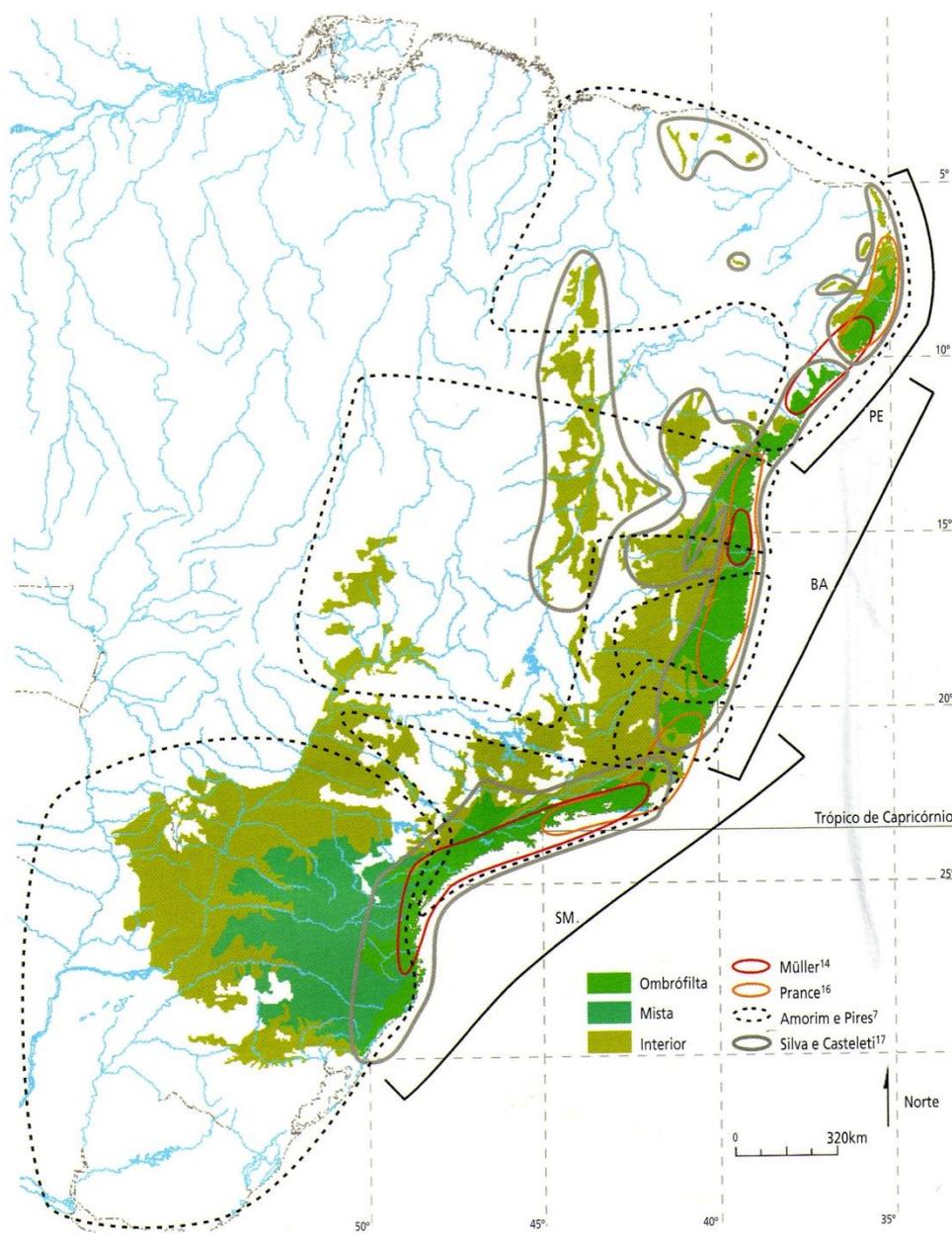


Figura 14.1 – Quatro hipóteses de áreas de endemismo sobrepostas às principais fisionomias da Mata Atlântica (Floresta Ombrófila, Mista e Estacionais, ou do Interior). As propostas indicam em geral as áreas Pernambuco (PE), Bahia (BA) e Serra do Mar (SM) com limites nunca totalmente coincidentes. As áreas de Silva e Casteleti¹⁷ têm seus limites acompanhando as linhas das fisionomias e manchas florestais. As propostas de Müller¹⁴, Prance¹⁶ e Amorim e Pires⁷ estão representadas de modo semelhante aos limites publicados originalmente.

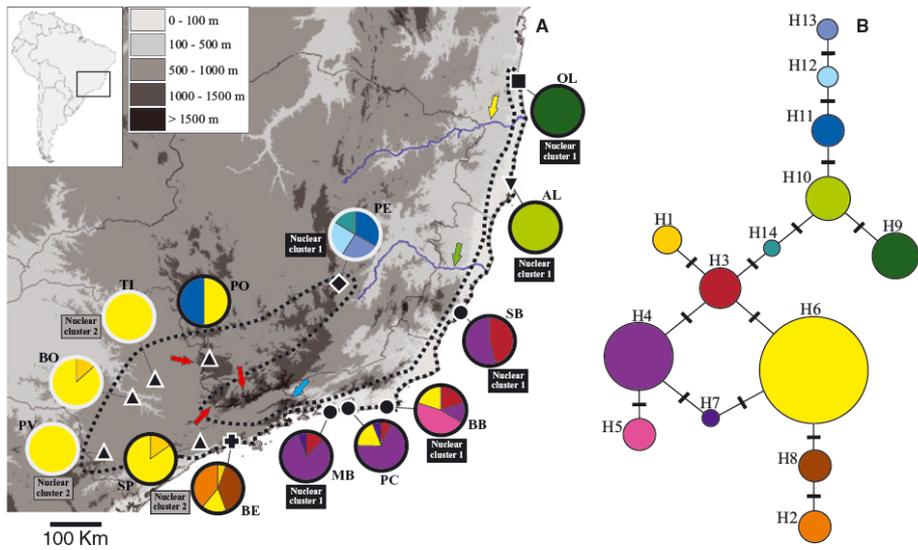


Figure 1. Map showing the current distribution of *Epidendrum denticulatum* in southeastern and northeastern Brazil, including sampled populations and genealogical relationships of the eight plastid DNA haplotypes recovered. (A) Pie charts reflect the frequency of occurrence of each haplotype in each population. Haplotype colors correspond to those shown in panel (B). Pie charts with gray and black outlines indicate the Cerrado and Brazilian Atlantic Forest populations, respectively. Nuclear genetic groups are indicated (nuclear cluster 1, black; nuclear cluster 2, gray). The dotted line delimits the geographical distribution of *Epidendrum denticulatum*. Different symbols (circles, triangles, squares, diamonds, and plus signs) indicate genetic groups identified by SAMOVA results. The Mantiqueira Range (red arrow), Bocaina Range (blue arrow), Doce River (green arrow), and Jequitinhonha River (yellow arrow) are indicated. (B) Statistical parsimony network linking the 14 haplotypes. Haplotypes are designated by numbers, and circle sizes are proportional to haplotype frequencies. The number of mutations required to explain transitions among haplotypes is indicated by cross hatches along the lines connecting the haplotypes.

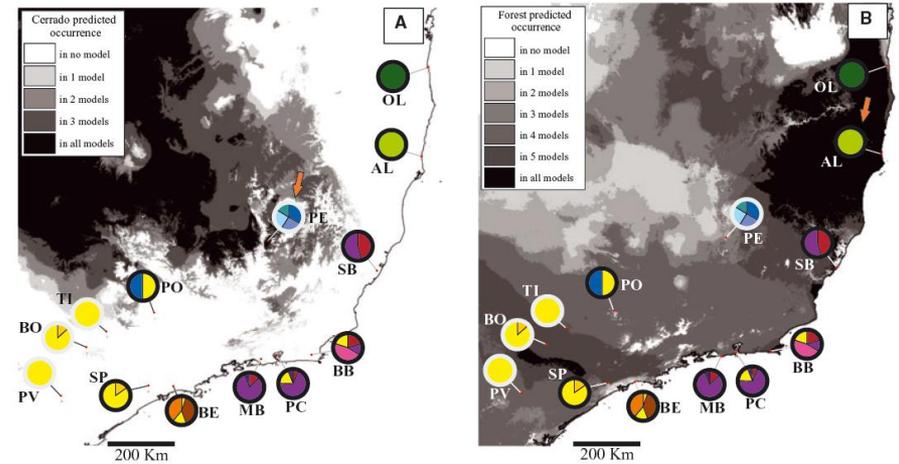


Figure 2. Summary maps of historically stable areas for the Cerrado (A, modified from Werneck et al. 2012a) and Brazilian Atlantic Forest (B, modified from Carnaval and Moritz 2008) under broader definitions. The vegetation-predicted occurrence is indicated by gray tones, and stable areas (confirmed by all models) are in black. Sample sites are represented by small red dots. Pie charts reflect the frequency of occurrence of each haplotype in each population. Haplotype colors correspond to those shown in Figure 1B. Pie charts with gray and black outlines indicate the Cerrado and Brazilian Atlantic Forest populations, respectively. Orange arrows indicate populations occurring at historically stable areas in black (refuges).

PHYLOGEOGRAPHIC STRUCTURE AND OUTBREEDING DEPRESSION REVEAL EARLY STAGES OF REPRODUCTIVE ISOLATION IN THE NEOTROPICAL ORCHID *EPIDENDRUM DENTICULATUM*

Estudo integrando filogeografia, genética de populações e biologia reprodutiva: Pinheiro et al. 2013 (com sp. herbácea de cerrado e restinga)

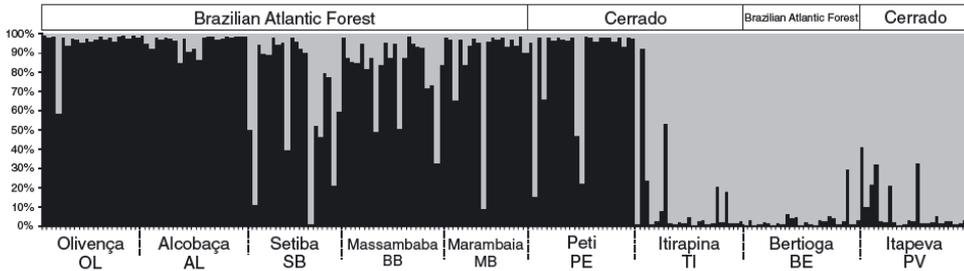


Figure 3. Summary of *Epidendrum denticulatum* population structure in southeastern and northeastern Brazil using Bayesian assignment analysis for a $K = 2$ population model. Cluster 1 (black) corresponds to coastal populations north of Bertioga, whereas specimens from the southernmost coastal population, Bertioga, and the inland populations Itirapina and Itapeva show admixture proportions strongly associated with cluster 2 (gray). Population codes and biome of origin (Brazilian Atlantic Forest and Cerrado) are indicated. See Table 1 for population details.

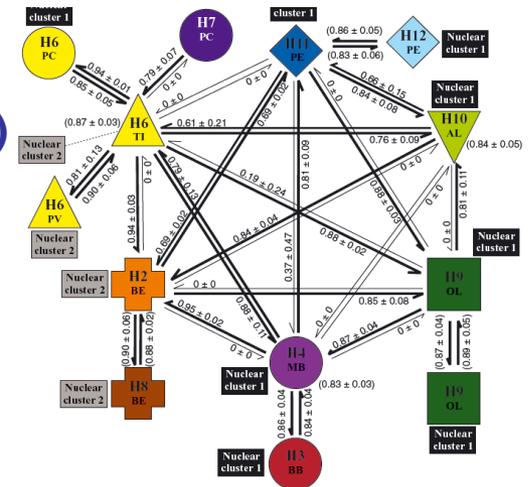


Figure 4. Reproductive compatibility among *Epidendrum denticulatum* individuals, based on seed viability following intra- and inter-population experimental crosses. Letter-number codes indicate haplotypes, and symbols (triangles, circles, squares, and diamonds) correspond to the plastid genetic groups identified by SAMOVA (see Fig. 1A). Nuclear genetic groups are indicated (nuclear cluster 1, black; nuclear cluster 2, gray). Arrows point to the maternal parents in the crossing experiments. Thickness is proportional to cross-compatibility. Numbers between parentheses indicate seed set of intrapopulation crosses (mean \pm standard deviation [SD]). Three specimens per population were used in the reciprocal crossing experiments; $H = 57.347$, $df = 21$, $P = 0.001$.

Estudo integrando filogeografia, genética de populações e biologia reprodutiva - *Epidendrum denticulatum* (Orchidaceae), herbácea de cerrado e restinga

Pinheiro et al. 2013

Reproductive barriers among divergent lineages were examined by analyzing seed viability following reciprocal crossing experiments.

Strong plastid phylogeographic structure was found, indicating that *E. denticulatum* was restricted to multiple refuges during South American forest expansion events.

In contrast, **significant phylogeographic structure was not found for nuclear markers**, suggesting higher gene flow by pollen than by seeds.

Large asymmetries in seed set were observed among different plastid genetic groups, suggesting the presence of **polymorphic genic incompatibilities** associated with cytonuclear interactions.

Results confirm the **importance of phylogeographic studies associated with reproductive isolation experiments** and suggest an important role for outbreeding depression during the early stages of lineage diversification.

Controvérsia na delimitação das classes de Florestas Tropicais

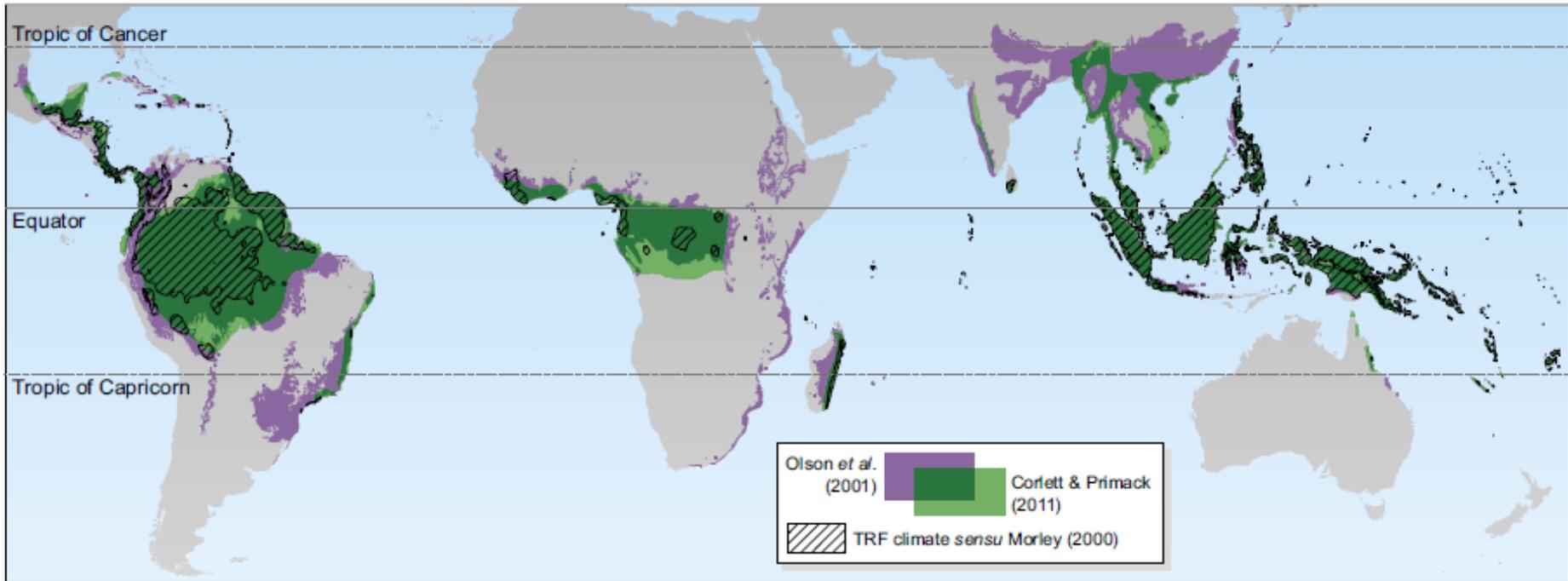


Fig. 2 Ambiguity in the definition of the tropical rainforest (TRF) biome. The 'tropical and subtropical moist broadleaf forest' biome of the World Wide Fund for Nature (Olson *et al.*, 2001) is often treated as TRF *sensu lato*, but includes nonTRF vegetation (e.g. the Madagascan high plateau). This becomes evident when compared with a recent expert-drawn map of TRF (Corlett & Primack, 2011) that reconciles biotic and climatic factors. Climatic definitions alone are insufficient; to illustrate this, we mapped a common climatic definition of TRF (annual precipitation > 2000 mm, less than four consecutive dry months (i.e. < 100 mm precipitation and mean monthly temperatures of $\geq 18^{\circ}\text{C}$); Morley, 2000) using Worldclim data (Hijmans *et al.*, 2005) at 5' resolution. This climate covers only 46% of the TRF biome as defined by Corlett & Primack (2011), and 35% of the broadly defined biome of Olson *et al.* (2001), omitting some areas that are considered classical TRF, such as the Brazilian Mata Atlântica and large parts of the Congo Basin. Considering the lack of straightforward climatic correlates (Moncrieff *et al.*, 2015), it has even been suggested that biome definitions should be based entirely on plant traits (Moncrieff *et al.*, 2016).

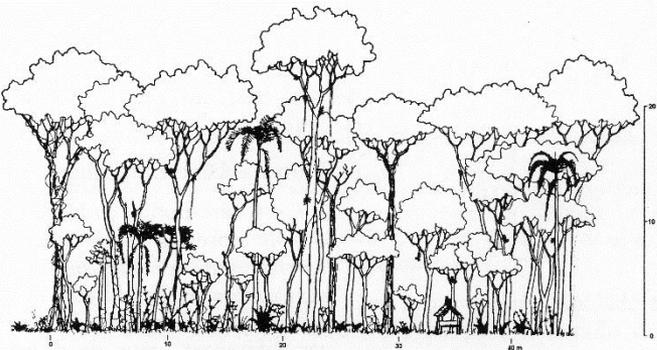


Figura 4: Perfil esquemático destacando a estrutura de um segmento de Floresta Estacional Semidecidual no município de Maringá,

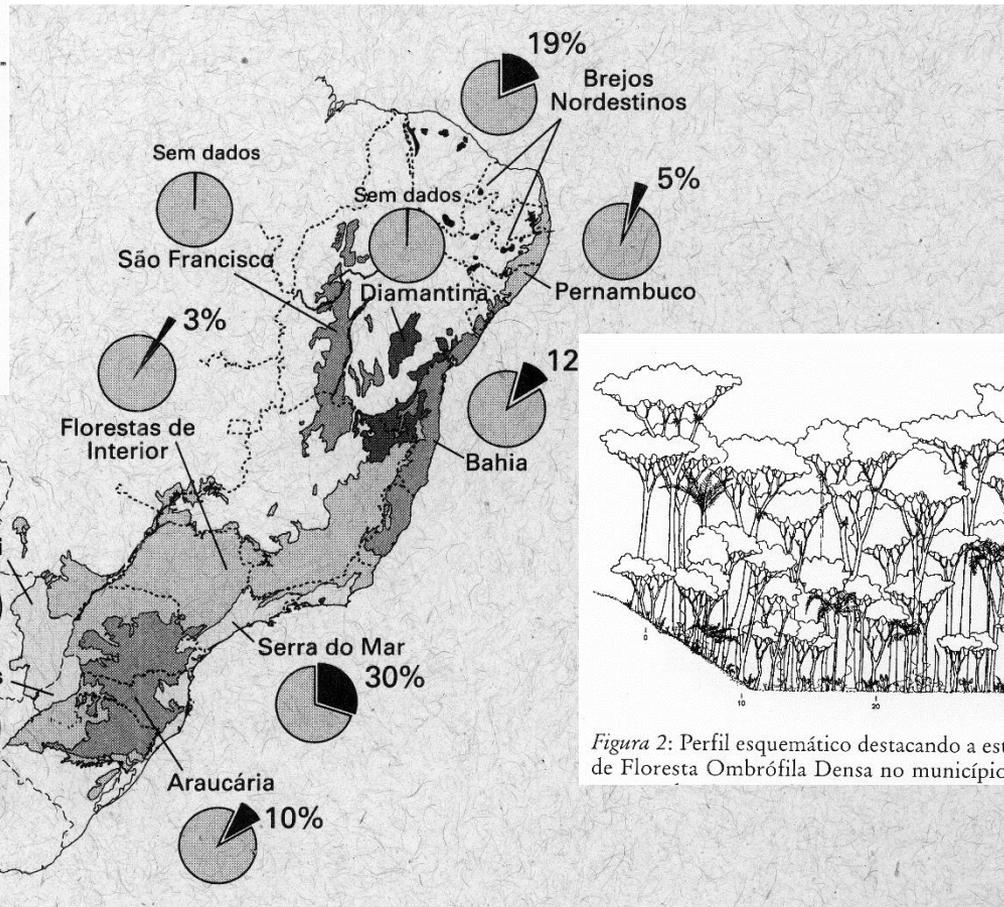


Figura 1.3. Porcentagem de remanescentes florestais (em preto) nas diferentes regiões biogeográficas do *hotspot* Mata Atlântica.

Galindo-Leal et al. 2004

Mata Atlântica

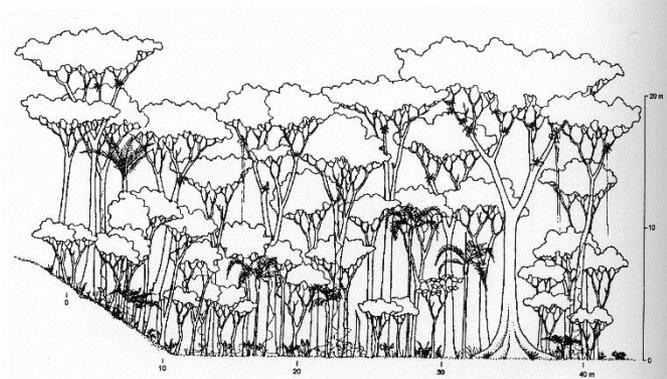


Figura 2: Perfil esquemático destacando a estrutura de um segmento de Floresta Ombrófila Densa no município de Guaratuba, Paraná,

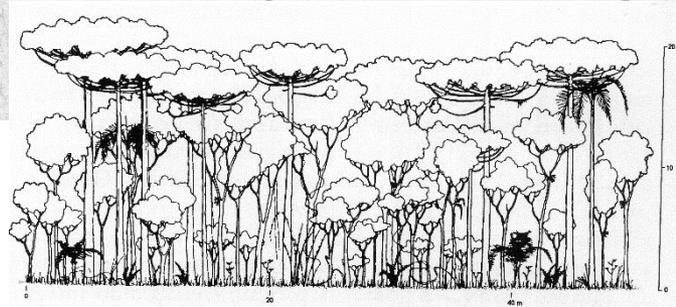
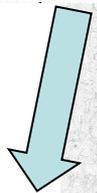


Figura 3: Perfil esquemático destacando a estrutura de um segmento de Floresta Ombrófila Mista no município de Irati, Paraná, com



Florestas estacionais no Domínio da Mata Atlântica ou compoendo o "arco de SDTFs" ?

Diagonal de formações secas

Distribuição disjunta de vegetações tropicais secas na América do Sul

(Ecorregiões de Olson et al. 2001)

Moro et al. 2016

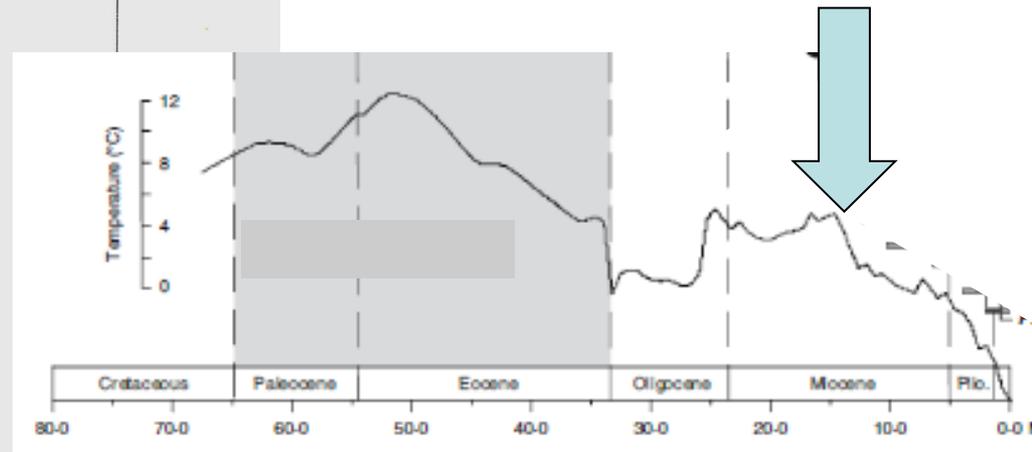


Fig. 1 Distribution of the disjunct seasonally dry tropical plant formations of South America (also called Seasonally Dry Tropical Forests - SDTF). The map shows the ecoregions of South America (as mapped by Olson et al., 2001) which are classified by Pennington et al. (2000) as SDTF. Cerrado and Chaco are also shown because enclaves of SDTF (Cerro Leon in Paraguay and “Matas Secas” in the Brazilian Cerrado) are reported to occur within their boundaries. The Bahia interior forests and Alto Paraná forests are usually considered part of the Atlantic Forest Domain, but they have more seasonal climates than the coastal, ombrophilous Atlantic forests and are considered by Pennington et al. (2000) as part of the SDTF biome. Map design: M.F. Moro

Transgressões marinhas Mioceno Médio e Tardio

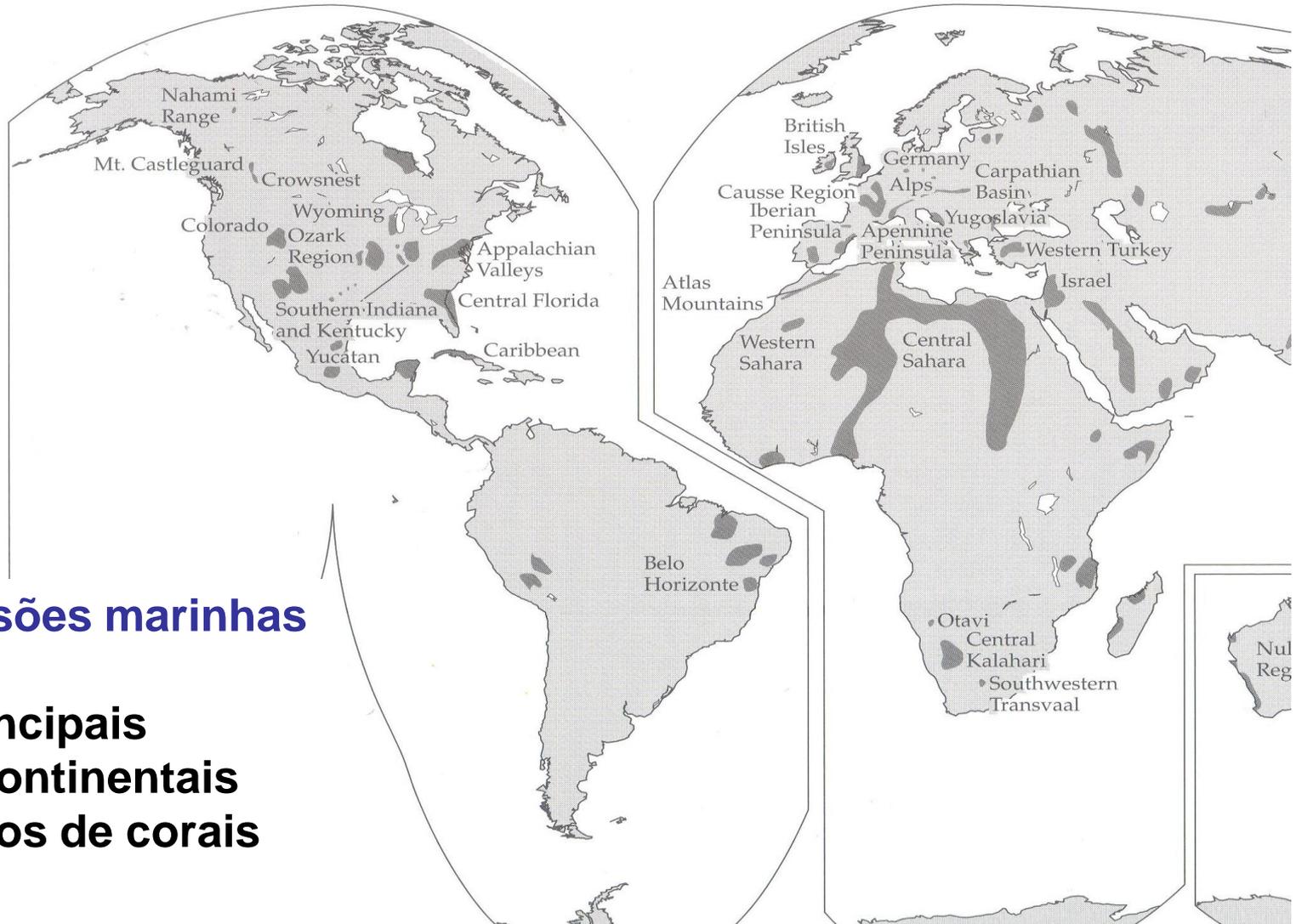
Principais áreas geográficas afetadas na América do Sul

Ortiz-Jaureguizar & Cladera
2006



Nie et al. 2013

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

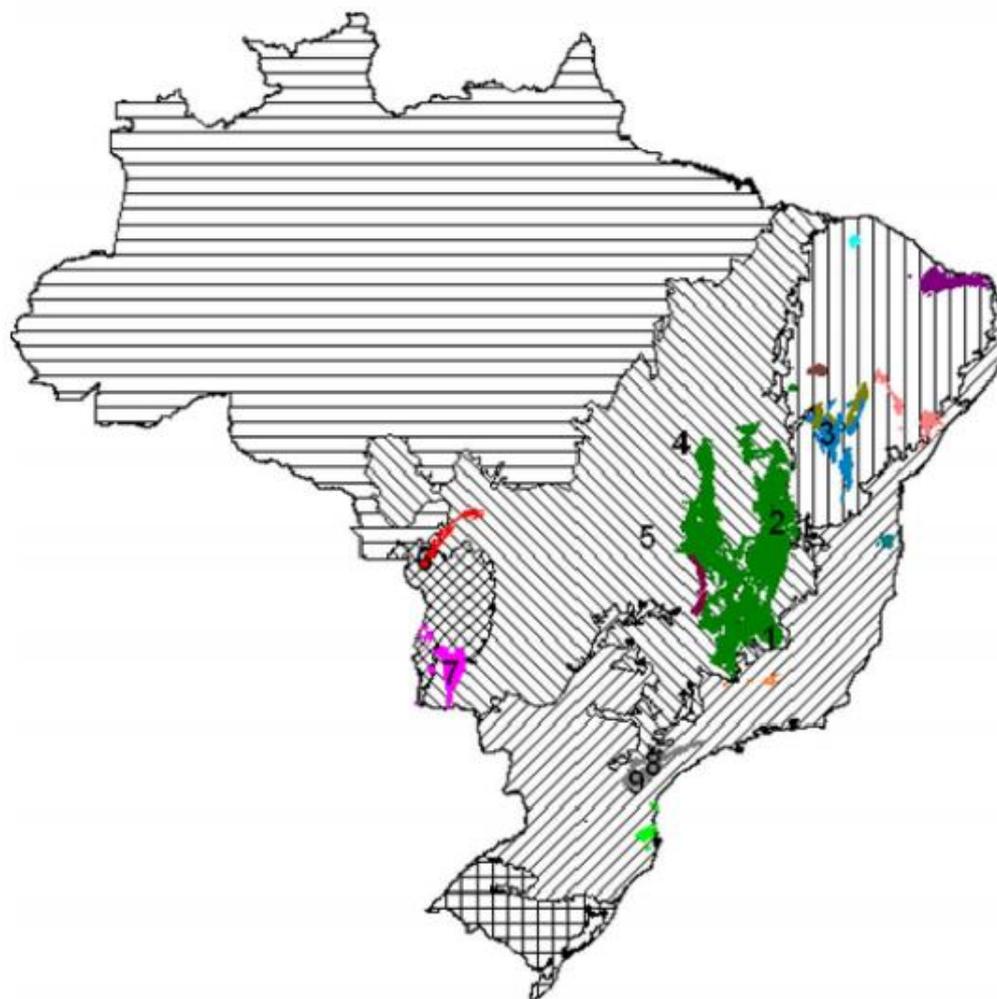


Transgressões marinhas

**Principais
áreas continentais
com restos de corais**

Lomolino et al. 2006

Regiões cársticas carbonáticas do Brasil (CECAV 2009)



Dominios Fitogeográficos

	Amazônia
	Caatinga
	Cerrado
	Mata Atlântica
	Pampa
	Pantanal

R. Cársticas Carbonáticas

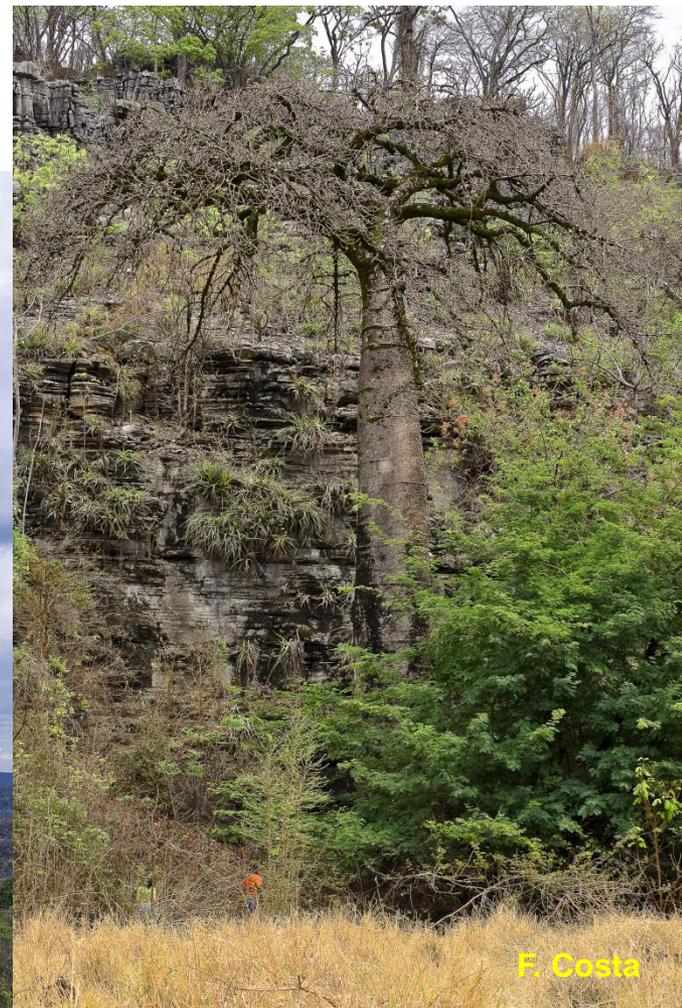
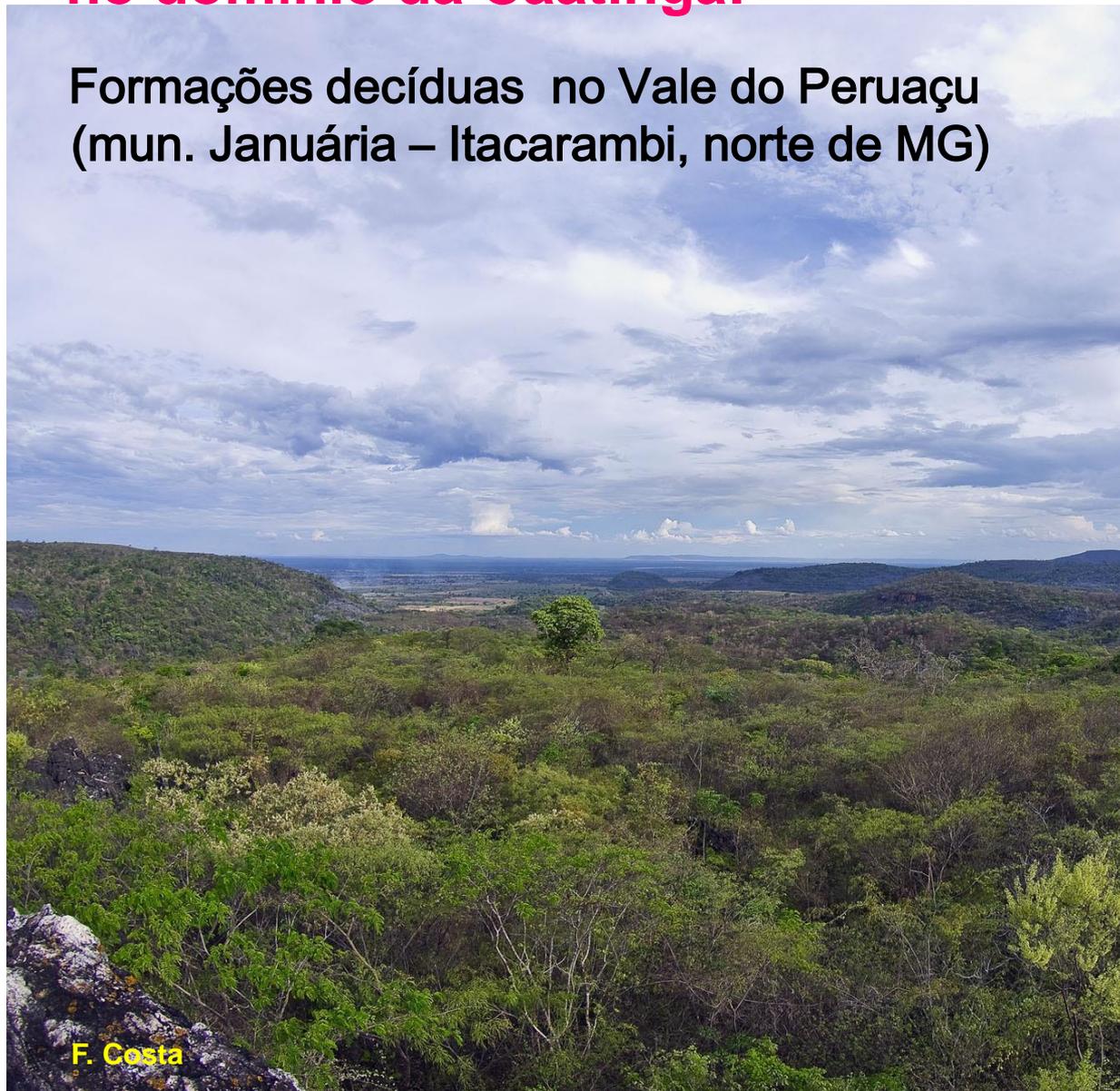
	Formação Caatinga
	Formação Vazante
	Grupo Apodi
	Grupo Araras
	Grupo Açungui
	Grupo Bambui
	Grupo Brusque
	Grupo Corumbá
	Grupo Rio Pardo
	Grupo Ubajara
	Grupo Una
	Grupo Vargem Grande
	Região Cárstica de São J
	Supergrupo Canudos

Áreas com inventários florísticos:

1. Funilândia, MG;
2. Matias Cardoso, MG;
3. Irecê, BA;
4. Natividade, GO;
5. Vila Propício;
6. Cáceres, MT;
7. Bonito, MS;
8. Apiaí, SP;
9. Rio Branco do Sul, PR.

Florestas estacionais secas da Região Neotropical: no domínio da Caatinga:

Formações decíduas no Vale do Peruaçu
(mun. Januária – Itacarambi, norte de MG)



**Florestas estacionais secas da Região
Neotropical: No domínio do Cerrado:**

**Matas decíduas sobre calcário
Santo Hipólito, MG**



**Meguro
et al. 2007**

**Florestas estacionais secas
da Região Neotropical: nos
Andes:**

**Seasonally Dry Tropical
Forests = SDTF
Loja, Equador**



Pennington *et al.* 2004

SDTF near Loja, Ecuador, showing almost complete deciduousness in the dry season.

**Florestas estacionais secas da
Região Neotropical: no México**

**Seasonally Dry Tropical
Forests = SDTF
México**



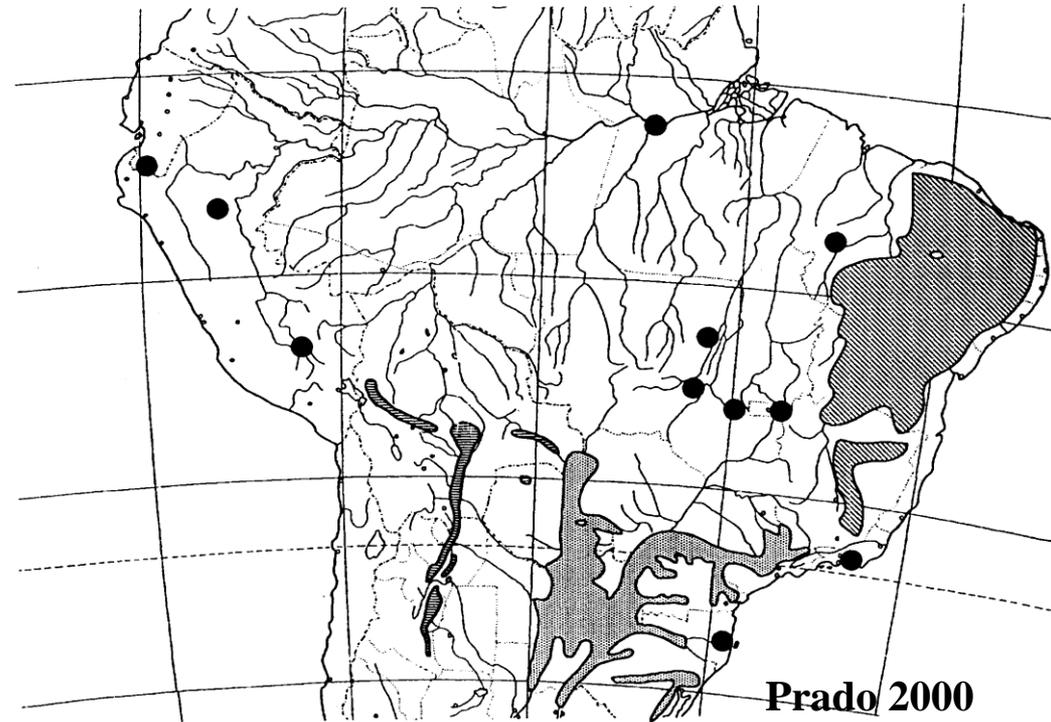
Pennington *et al.* 2004

Florestas estacionais secas da Região Neotropical

Possíveis componentes de um “*Arco Seco Pleistocênico*” ?

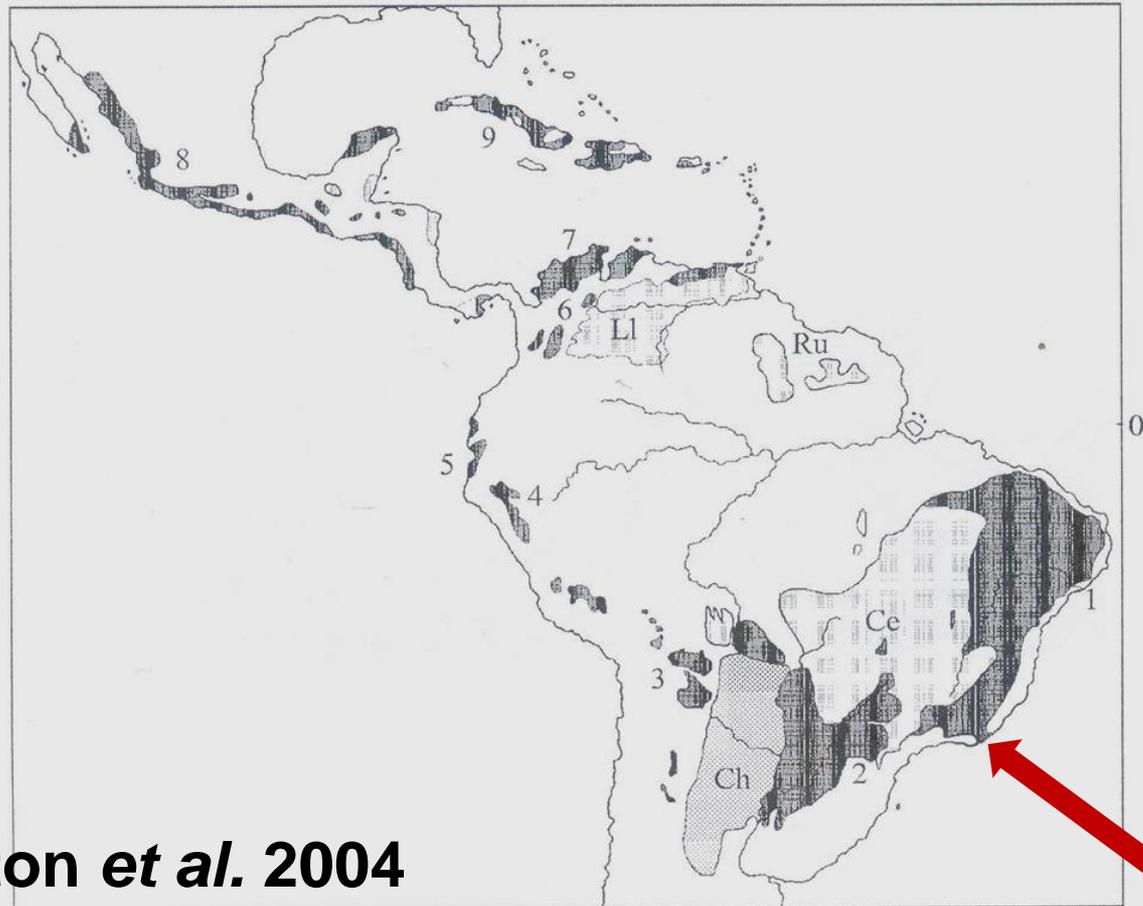
Prado & Gibbs 1993

Prado 2000



Tentative mapping of the new **Tropical Seasonal Forests Region of South America**. Oblique hatching: the Caatingas province *sensu lato*; stippled: the Paranense province *sensu auctor*; horizontal hatching: the Subandean Piedmont Forests province. □: areas with enigmatic concentration of collections that cannot be safely ascribed to the region with the present knowledge of their vegetation.

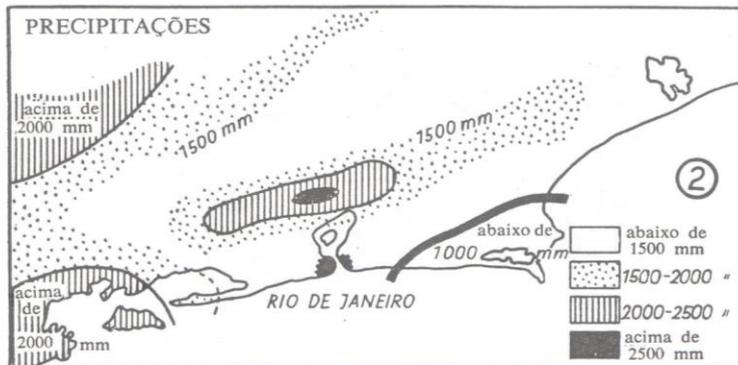
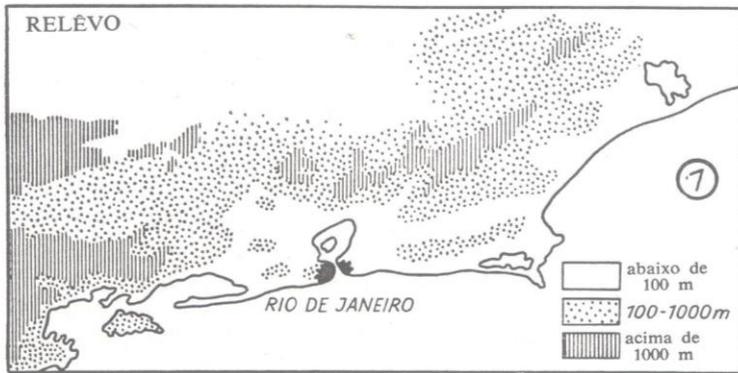
Florestas estacionais secas da Região Neotropical = SDTFs



Pennington *et al.* 2004

Figure 1. The distribution of seasonally dry vegetation in the neotropics highlighting areas of endemism. Dark grey, SDTF; white, savannah; light grey, Chaco. Seasonally dry forest: 1, Caatingas; 2, Misiones Nucleus; 3, Piedmont Nucleus (including northern Bolivian SDTF); 4, northern Peruvian inter-Andean valleys; 5, Pacific coastal Ecuador and Peru; 6, Colombian and Venezuelan inter-Andean valleys; 7, Caribbean coast of Colombia and Venezuela; 8, Mexico and Central America; 9, Caribbean Islands. Savannahs: Ce, Cerrado; Ll, Llanos; Ru, Rupununi; Ch, Chaco. Modified after Pennington *et al.* (2000).

Interrupção da Floresta Ombrófila Densa por vegetação xerófila na latitude de Cabo Frio, RJ



90. Limite leste da parte sul da mata pluvial costeira nas proximidades do Rio de Janeiro, 1, relêvo; 2, precipitação pluvial; 3, restos preservados da mata pluvial e vegetação de cactos.

Hueck 1972

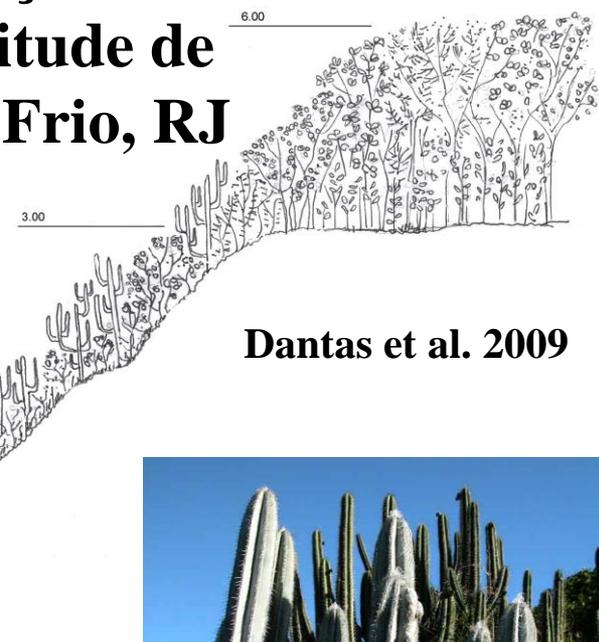


Figura 4 – Perfil nas proximidades da Ponta do Olho de Boi n (0-3), arbustiva e arbórea nos morros costeiros.

Dantas et al. 2009



Pilosocereus ulei

Chloroleucon mangense

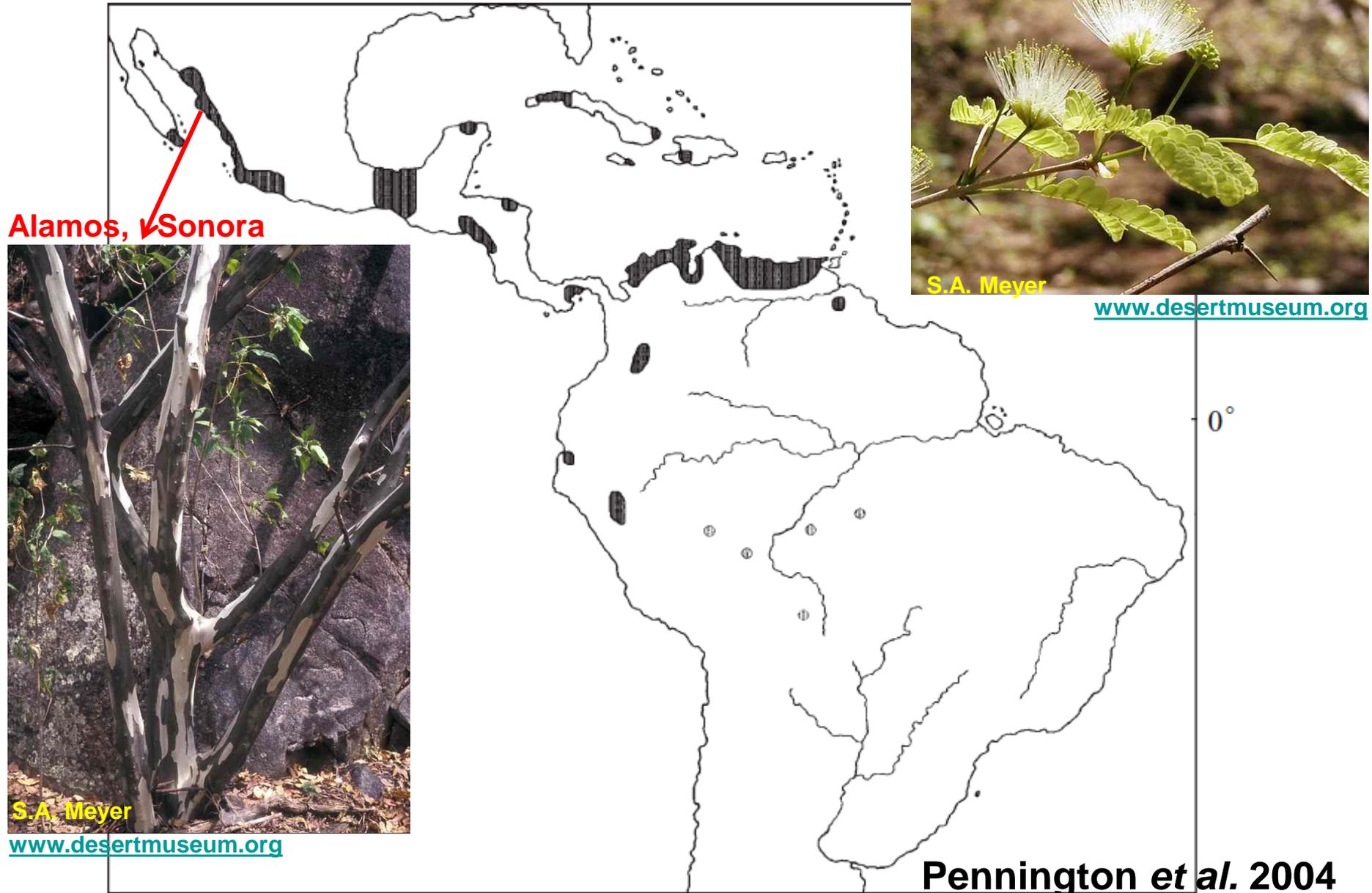
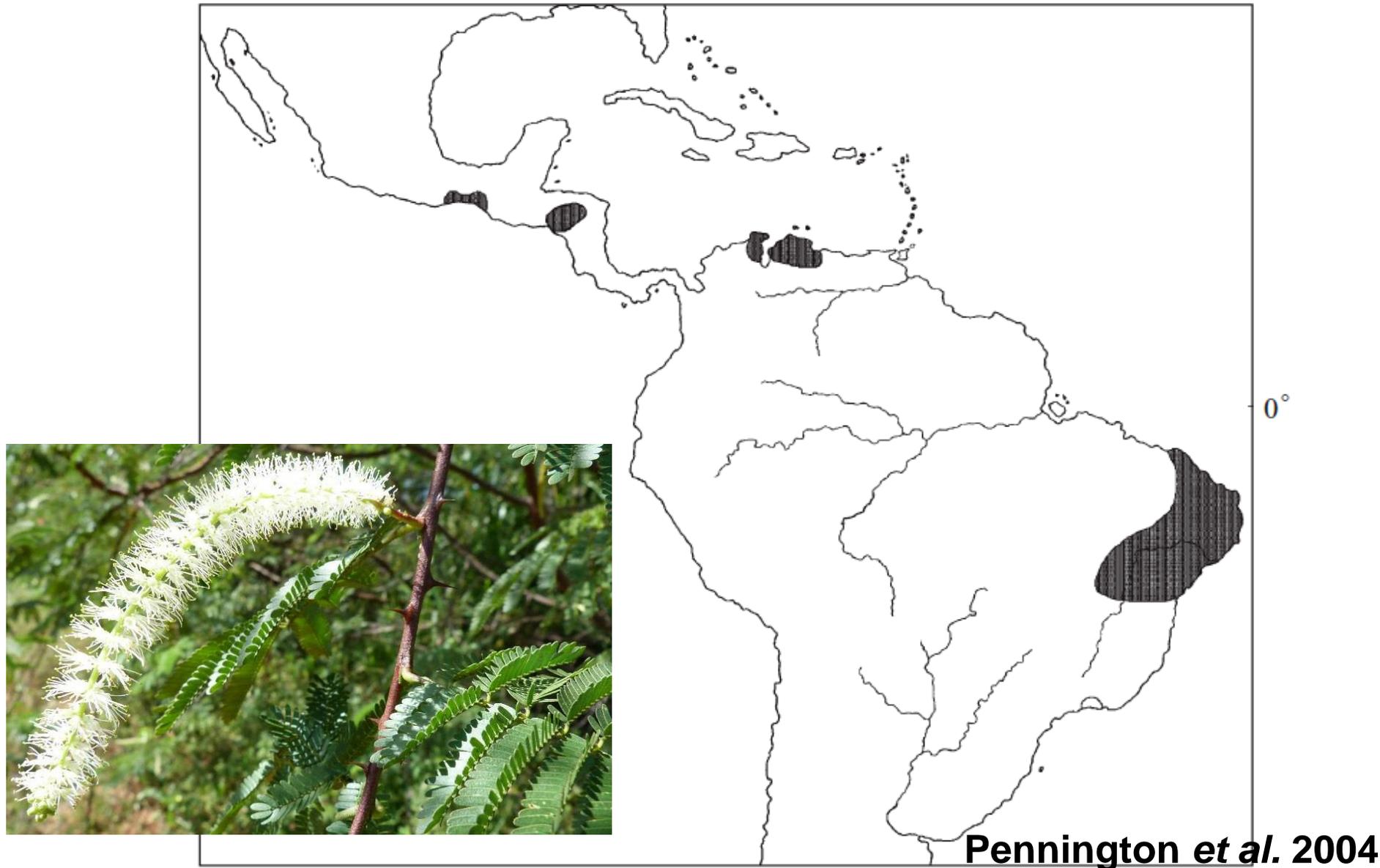


Figure 4. Distribution of *Chloroleucon mangense* (Jacquin) Britton & Rose *sensu lato* (dark-grey patches). Redrawn from Barneby & Grimes (1996) and reproduced with permission from Pennington *et al.* (2000, fig. 2; Blackwell Publishing).

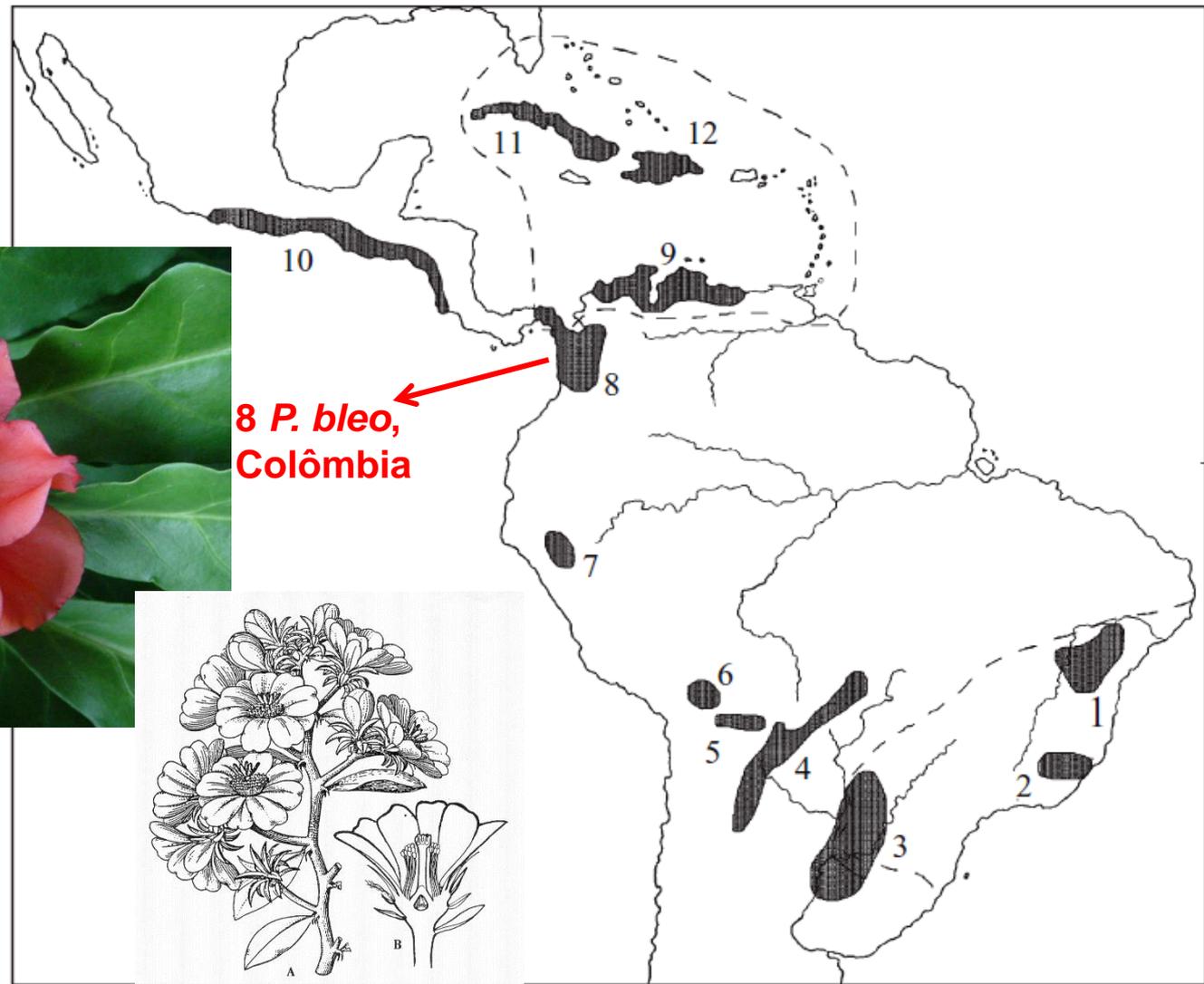
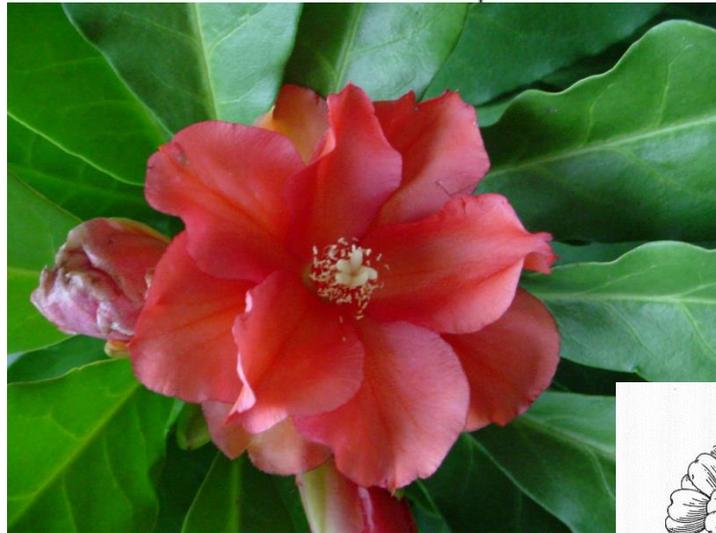
Mimosa tenuiflora (jurema-preta)



Pennington *et al.* 2004

Figure 5. Distribution of *Mimosa tenuiflora* (Willdenow) Poiret (dark-grey patches). Redrawn from Barneby & Grimes (1996) and reproduced with permission from Pennington *et al.* (2000, fig. 3; Blackwell Publishing).

Pereskia
CACTACEAE



Pennington *et al.* 2004

Figure 6. Distribution of *Pereskia*. The dashed line indicates the limits of *P. aculeata* Miller, found in the Caribbean region and eastern South America. The other species are distributed as follows: 1, *P. bahiensis* Gürke, *P. aureifolia* Ritter, *P. stenantha* Ritter; 2, *P. grandifolia* Haworth; 3, *P. nemorosa* Rojas Acosta; 4, *P. sacharosa* Griseb.; 5, *P. diaz-romeroana* Cárdenas; 6, *P. weberiana* K. Schumann; 7, *P. humboldtii* Britton & Rose; 8, *P. bleo* (Kunth) DC.; 9, *P. guamacho* F. A. C. Weber; 10, *P. lychnidiflora* DC.; 11, *P. zinniiflora* DC.; 12, *P. portulacifolia* (L.) DC., *P. quisqueyana* Liogier. Redrawn from Leuenberger (1986) and reproduced with permission from Pennington *et al.* (2000, fig. 8; Blackwell Publishing).

Pennington *et al.* 2004

1. Taxas de evolução (cronogramas):

Clado robinióide, *Chaetocalyx*,
Coursetia (Leg.)
Ruprechtia (Polygonaceae),
Pereskia (Cactaceae),
Loxopterygium (Anacardiaceae)

2. Análise cladística de vicariância; áreas de endemismo.

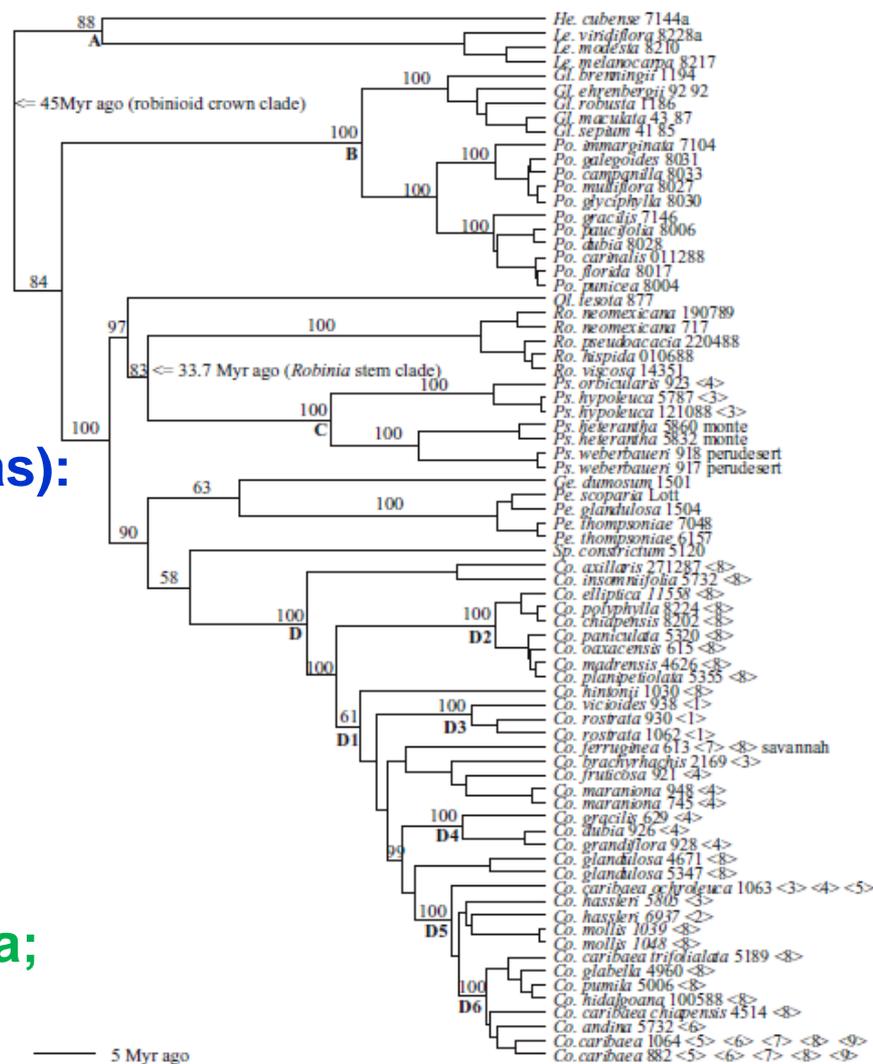


Figure 7. Chronogram for robinioid legumes derived from PL rate smoothing of a Bayesian likelihood consensus tree, which was estimated with sequences from the ITS region. Codes for crown clades (e.g. A, B, C and D) are those used in table 1 and the text. Numerical codes after terminal taxa labels are accession numbers (see Lavin *et al.* 2003). Numerical codes in angled brackets after terminal taxa labels are the SDTF areas of endemism numbered in figure 1. Non-SDTF areas are: savannah, savannah areas in Central America and northern South America; perudesert, Peruvian coastal desert; and monte, arid Andean vegetation. The 45 Myr ago maximum age constraint at the basal node is derived from an analysis of large-scale rates of all legumes (Wojciechowski 2003; M. Lavin, M. F. Wojciechowski, P. Herendeen and M. J. Sanderson, unpublished data). The 33.7 Myr ago minimum age constraint at the second lowest node is derived from the fossil wood record (see § 2). Average nucleotide substitution parameters estimated for 10 000 likelihood trees at stationarity are $r(GT) = 1.00$, $r(CT) = 6.379$, $r(CG) = 0.980$, $r(AT) = 1.758$, $r(AG) = 3.018$, $r(AC) = 1.155$, $p(A) = 0.204$, $p(C) = 0.271$, $p(G) = 0.293$, $p(T) = 0.233$, $\alpha = 1.418$, $iP = 0.216$. See table 1 for the estimated ages and rates of substitution. Numbers above branches are Bayesian posterior probabilities. *He.*, *Hebestigma*; *Le.*, *Lennea*; *Gl.*, *Gliricidia*; *Po.*, *Poitea*; *Ol.*, *Olneya*; *Ro.*, *Robinia*; *Ps.*, *Poissonia*; *Ge.*, *Genistidium*; *Pe.*, *Peteria*; *Sp.*, *Sphinctospermum*; *Co.*, *Coursetia*.

Pennington *et al.* 2004

2. Análise cladística de vicariância: (áreas de endemismo)

Análise de Componentes (consenso estrito)

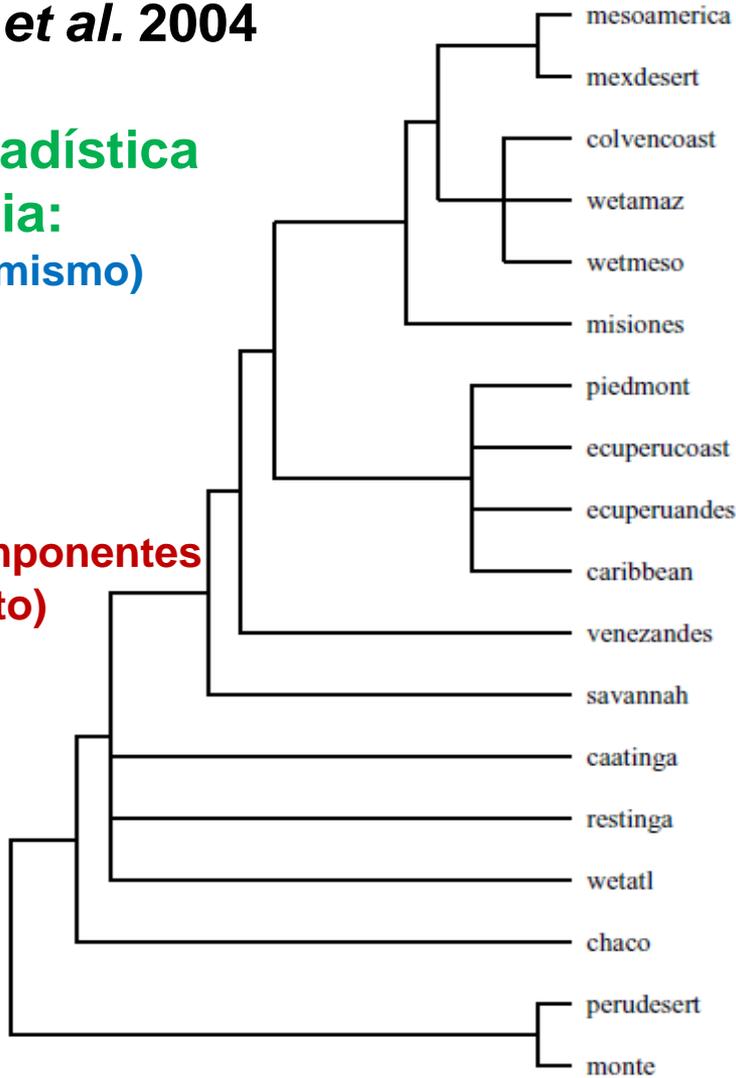


Figure 13. Strict consensus area cladogram derived from 180 trees generated by a component analysis minimizing leaves added (minimal value 461) and implementing assumption 1. For map of areas of endemism see figure 1. SDTF areas: mesoamerica, Central American SDTF; colvencoast, SDTF of Caribbean coast of Colombia and Venezuela; caribbean, SDTF of Caribbean islands; piedmont, SDTF of Piedmont Nucleus; misiones, SDTF of Misiones Nucleus (including northern Bolivian dry forests); ecuperucoast, SDTF of Pacific coastal Ecuador and Peru; venezandes, SDTF of Venezuelan inter-Andean valleys; ecuperuandes, SDTF of northern Peruvian and southern

TAS (consenso estrito)

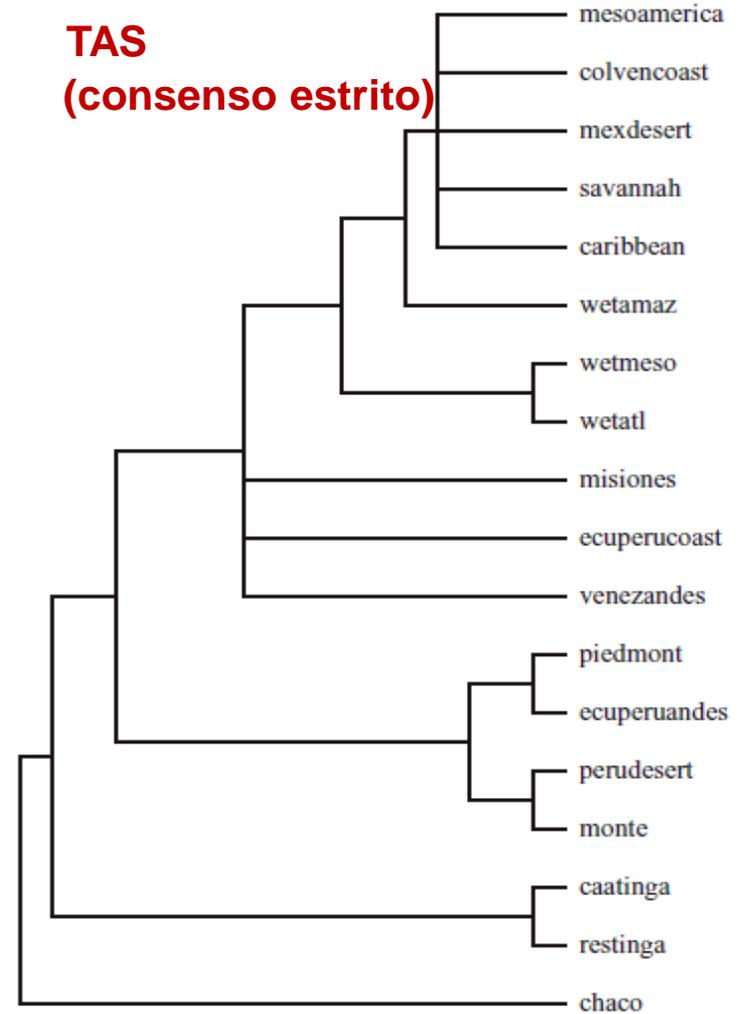
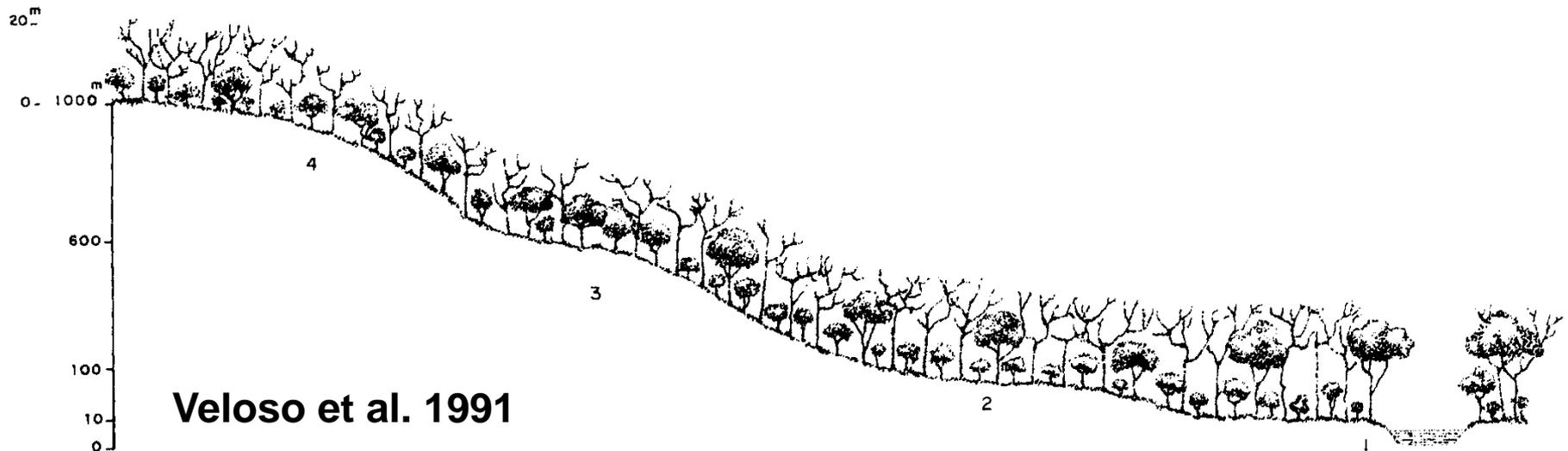


Figure 14. Strict consensus of 20 minimally resolved trees generated by a three-area statements analysis implementing Assumption 2. For map of areas of endemism see figure 1. SDTF areas: mesoamerica, Central American SDTF; colvencoast, SDTF of Caribbean coast of Colombia and Venezuela; caribbean, SDTF of Caribbean islands; piedmont, SDTF of Piedmont Nucleus; misiones, SDTF of Misiones Nucleus (including northern Bolivian dry forests); ecuperucoast, SDTF of Pacific coastal Ecuador and Peru; venezandes, SDTF of Venezuelan inter-Andean valleys; ecuperuandes, SDTF of northern Peruvian and southern

Pennington *et al.* 2004

Historical climate change and
speciation: **neotropical**
seasonally dry forest plants
show patterns of both **Tertiary**
and **Quaternary**
diversification.



Geologia da América do Sul



FIGURE 4-2. Geology of South America. R = Romeral fault zone, the boundary between accreted terranes in the west and allochthonous terranes in the east; I = Andean orogen; II = foreland basins; III = Guiana shield; IV = Brazilian shield. Paleozoic-Mesozoic basins: Amazon, Solimões, Parnaíba, São Francisco, Chaco-Paraná.

CAATINGA: limites e suas 8 ecorregiões

Ecorregiões = centros regionais de endemismo de Leguminosae (Queiroz 2006),

2 biotas distintas na Caatinga:

1. associada a solos derivados de embasamento cristalino;
2. associada aos terrenos sedimentares (com as áreas de maior endemismo da flora), porém parcialmente substituídas no Terciário Superior e Quaternário Inferior, quando pediplanação geológica expôs as superfícies cristalinas, permitindo o estabelecimento de espécies típicas de outros núcleos de SDTF.

Herpetofauna com padrão congruente:

endemismo maior nos solos arenosos (que teriam sido muito mais amplamente distribuídos no passado) – e.g. dunas do São Francisco cobrem só 0,8% da área total da Caatinga e 27% da fauna de Squamata é restrita a essa pequena região (Rodrigues 1996, 2003).

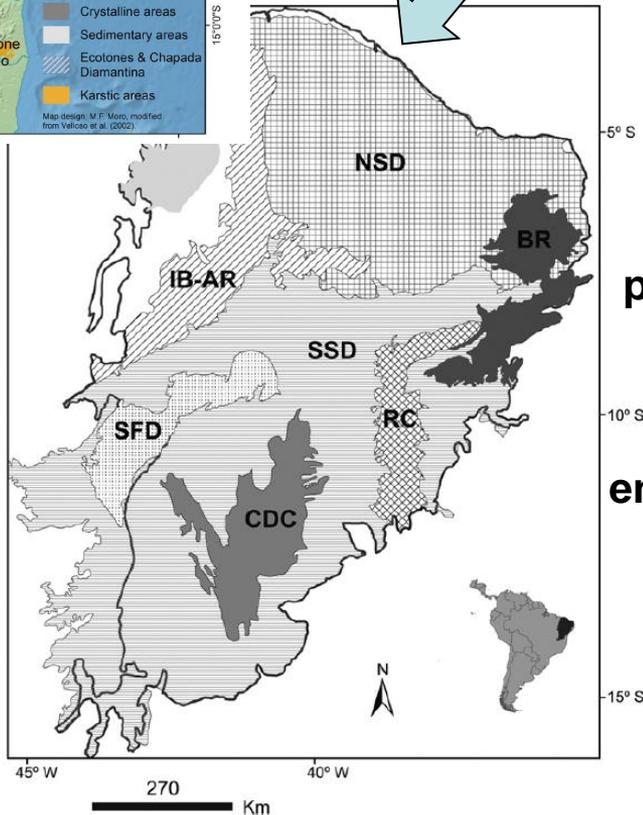
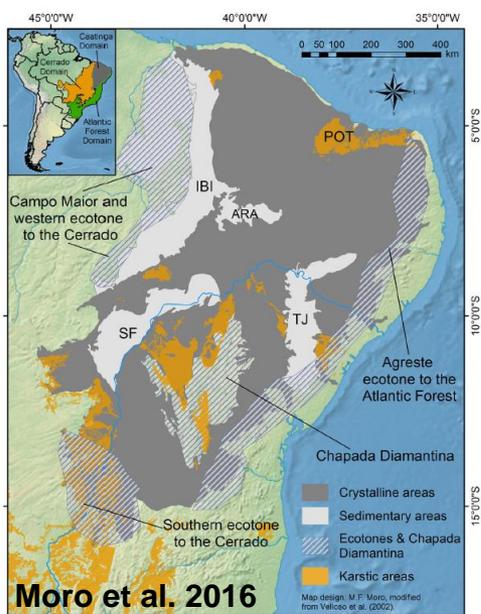


Fig. 5. Caatinga limits and major ecoregions as defined by Velloso et al. (2002). CMC, Campo Major complex; IB-AR, Ibiapaba-Araripe complex; NSD, northern Sertaneja depression; SSD, southern Sertaneja depression; BR, Borborema plateau; SFD, São Francisco sand dunes; CDC, Chapada Diamantina complex; and RC, Raso da Caatinga.

Werneck 2011

Neves *et al.* 2015

282 áreas de matas estacionais secas (SDTFs) inventariadas ao longo da *Diagonal Seca*

14 variáveis ambientais:
temperatura,
pluviosidade,
solo

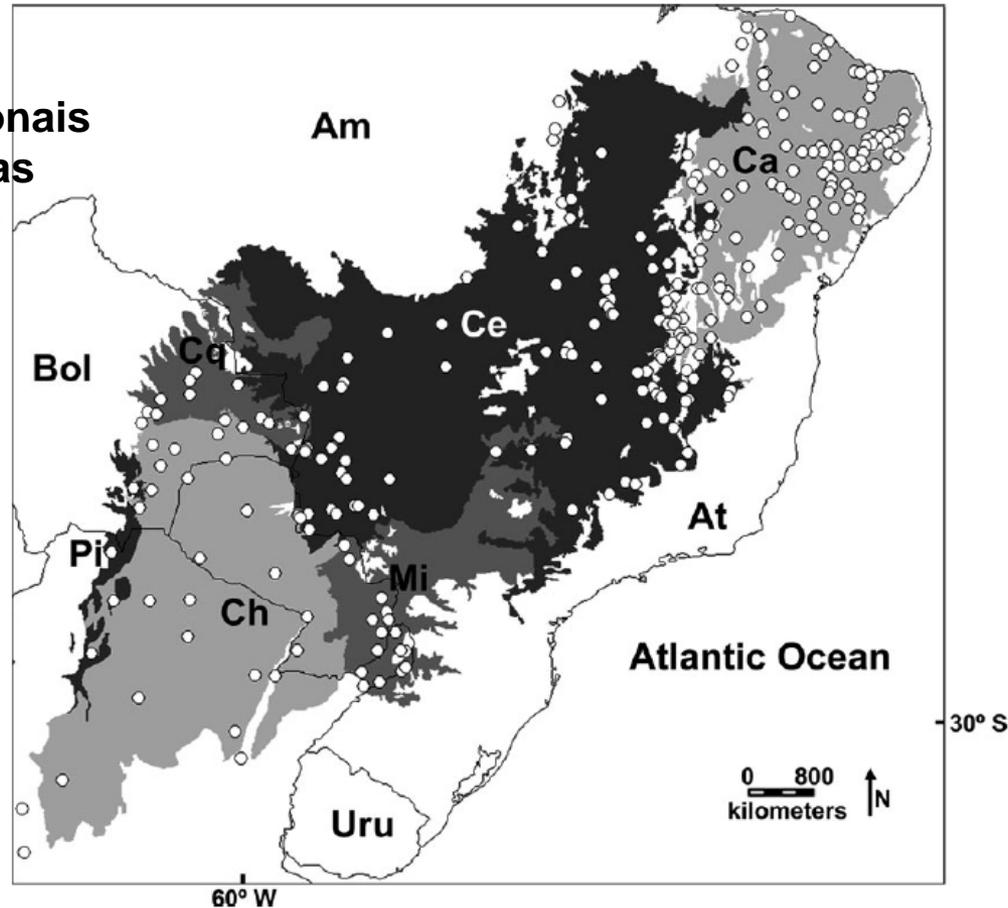


Figure 1 Map showing the location of tree species surveys and major vegetation types used for the study of environmental and historical controls of floristic composition across the South American Dry Diagonal. Circles denote the location of tree species surveys used in this study ($n = 282$). The phytogeographical domains and the seasonally dry tropical forest (SDTF) nuclei that form the South American Dry Diagonal are shaded (Ca, Caatinga; Ce, Cerrado; Ch, Chaco; Cq, Chiquitania; Pi, Piedmont; Mi, Misiones) while moist forest phytogeographical domains are white (Am, Amazon rain forest; At, Atlantic rain forest). The phytogeographical domains are named after the major vegetation type that occurs within them (e.g. chaco woodlands, caatinga woodlands and woody savannas; the latter is called cerrado woodlands in Brazil). Note that each phytogeographical domain may contain several additional vegetation types (e.g. the Cerrado phytogeographical domain contains SDTF and gallery forest in addition to the main vegetation type of savanna).

282 áreas de matas estacionais secas (SDTFs) inventariadas ao longo da *Diagonal Seca*

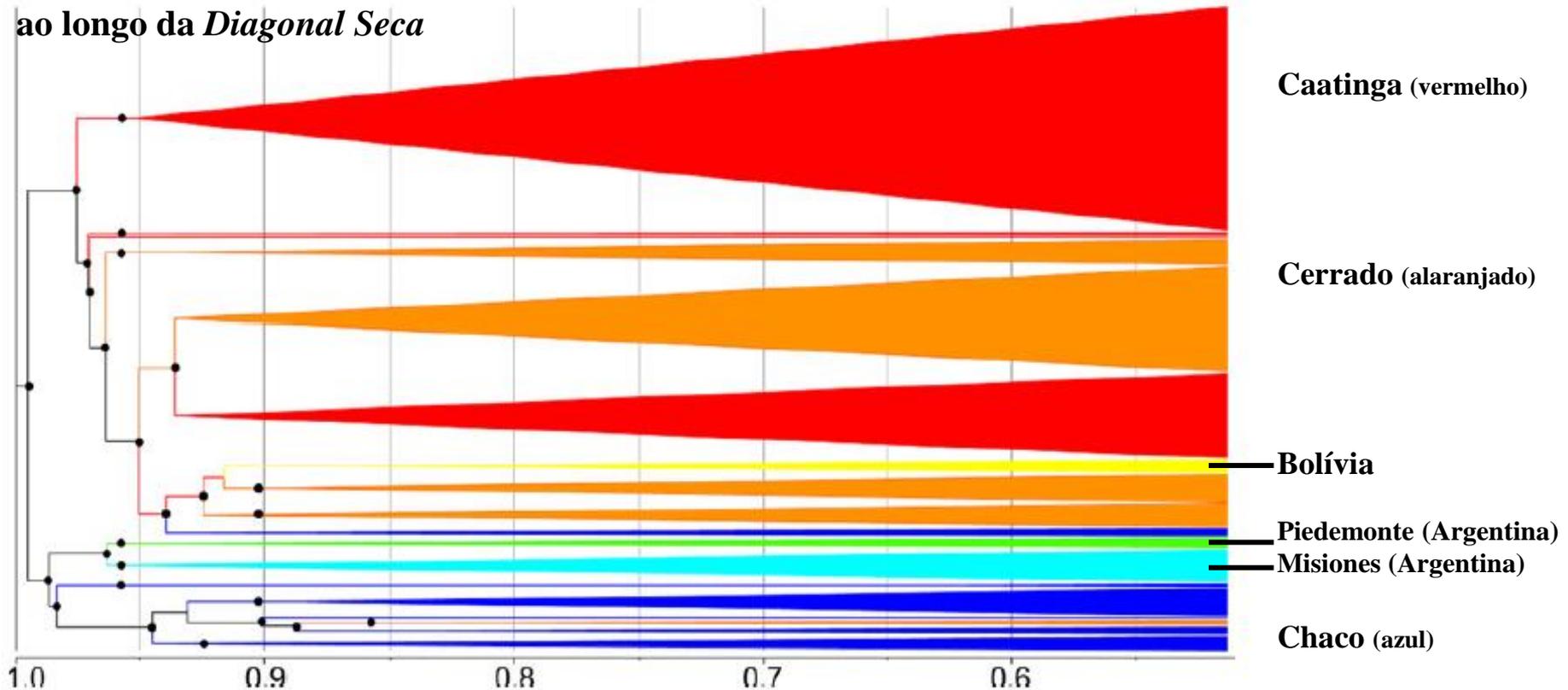


Figure 2 Hierarchical clustering of seasonally dry tropical forests (SDTFs) and chaco woodlands across the South American Dry Diagonal based on their tree species composition. The dissimilarity measure and linkage methods used were Jaccard and unweighted group average, respectively. Black bullets at the base of clusters indicate approximately unbiased bootstrap values ≥ 0.90 (Suzuki & Shimodaira, 2011). The size of the triangles is proportional to the number of sites, and the floristic nuclei are discriminated by different colours: red, 134 caatinga woodlands; orange, 91 Cerrado SDTFs; yellow, six SDTFs from Chiquitania; green, five SDTFs from Piedmont; light blue, 14 SDTFs from Misiones; dark blue, 32 chaco woodlands.

Condições ambientais (sobretudo regime térmico) são os fatores afetando a composição florística das SDTFs; fragmentação histórica e isolamento não são responsáveis pelo turnover de espécies dentro dessas florestas.

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

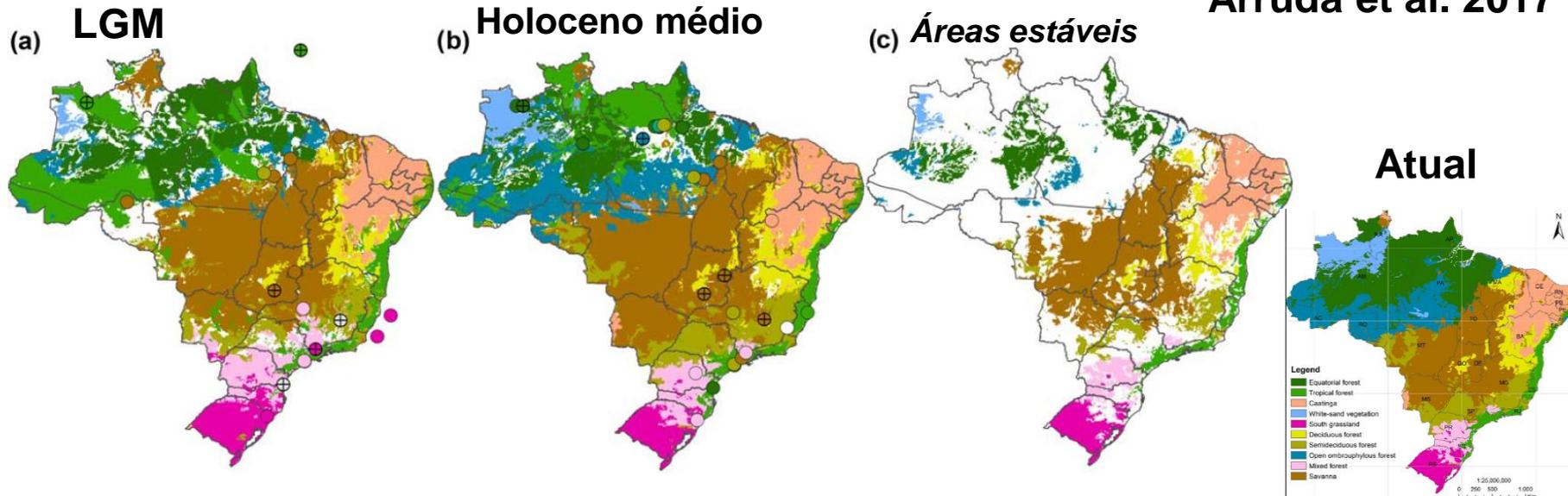


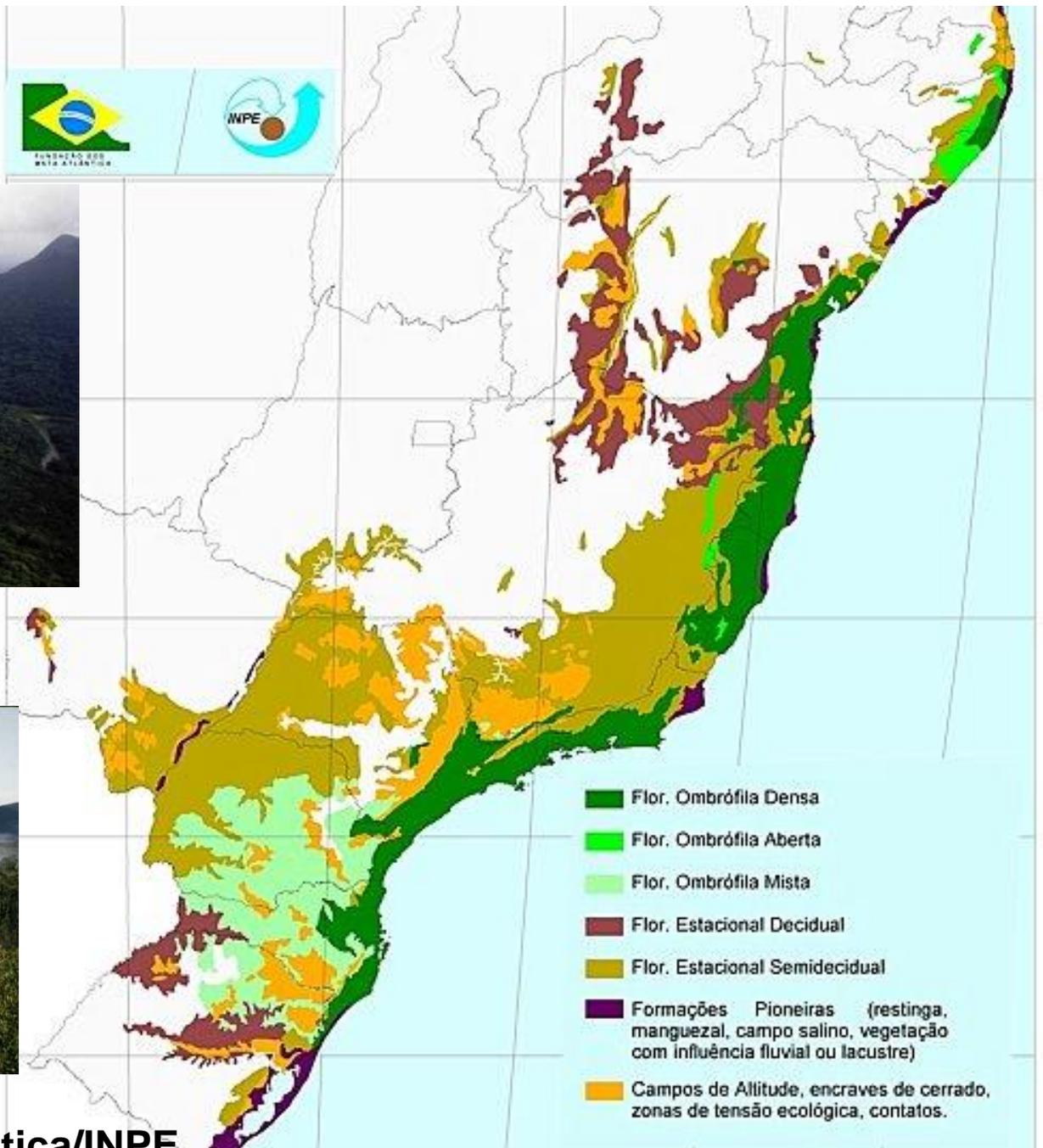
FIGURE 3 Spatial distribution of biomes at different moments in the past. Biome distribution in (a) the Last Glacial Maximum and (b) the Mid-Holocene. (c) Stability/refugia areas of the biomes based on the consensus between the two distribution scenarios and the present distribution (Figure 1). White 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



Juréia-Itatins, SP



Macaé de Cima, RJ

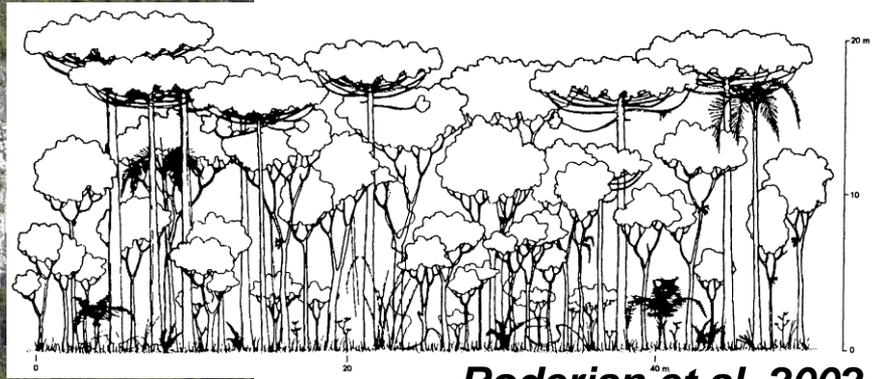


Floresta Ombrófila Mista (Mata-de-Araucária)

Itaimbezinho, RS



Fundação SOS Mata Atlântica/INPE



Roderjan et al. 2002

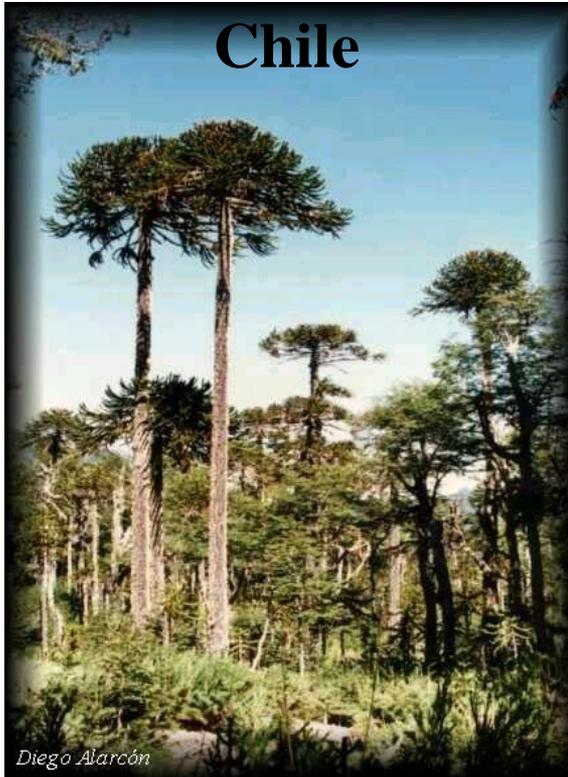
J.R. Pirani

Filogenia de Araucariaceae com mapeamento das áreas geográficas

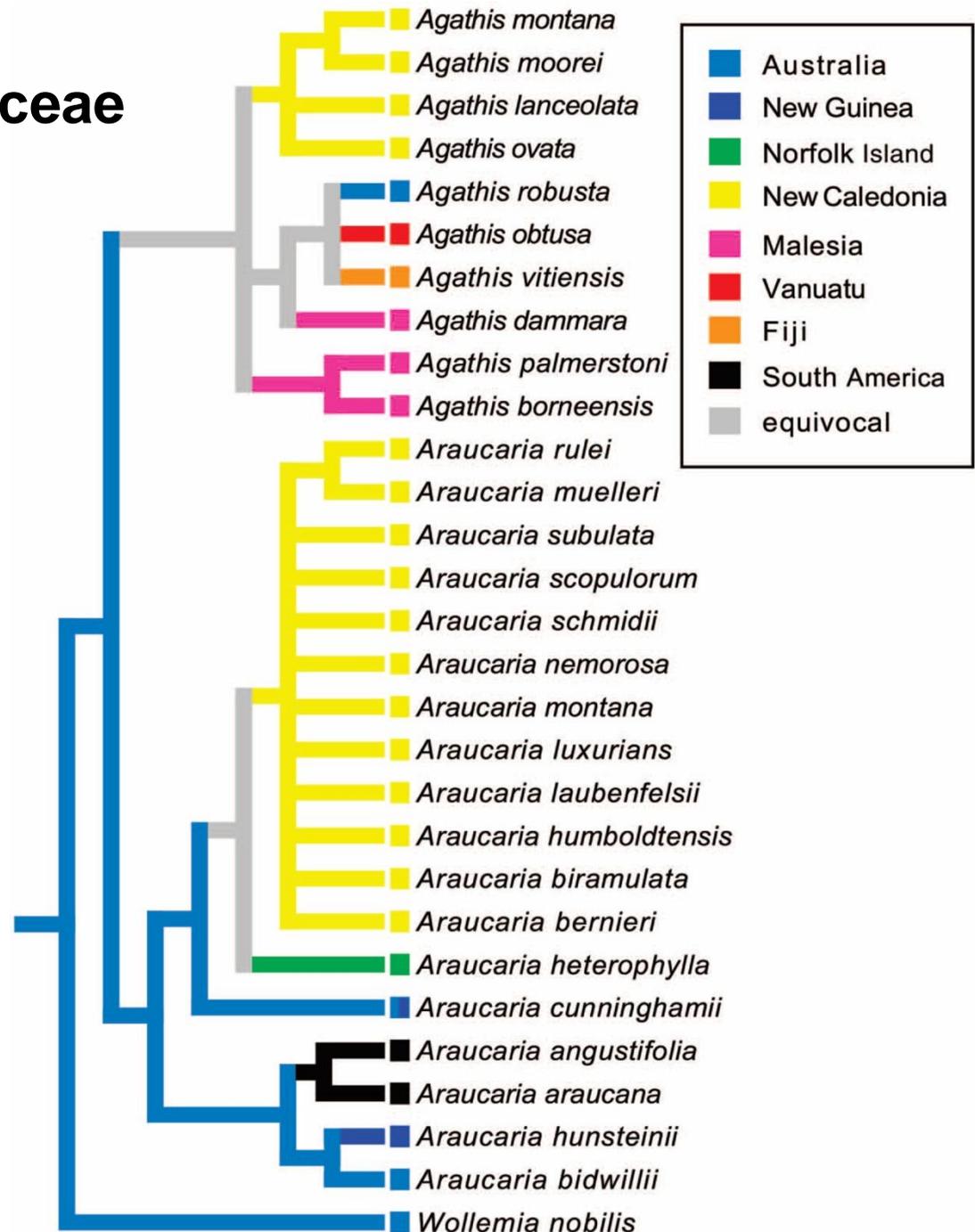
Givnish 2004

Araucaria araucana

Chile



Diego Alarcón



Araucariaceae

Distribuição atual e pretérita

Florim 1963

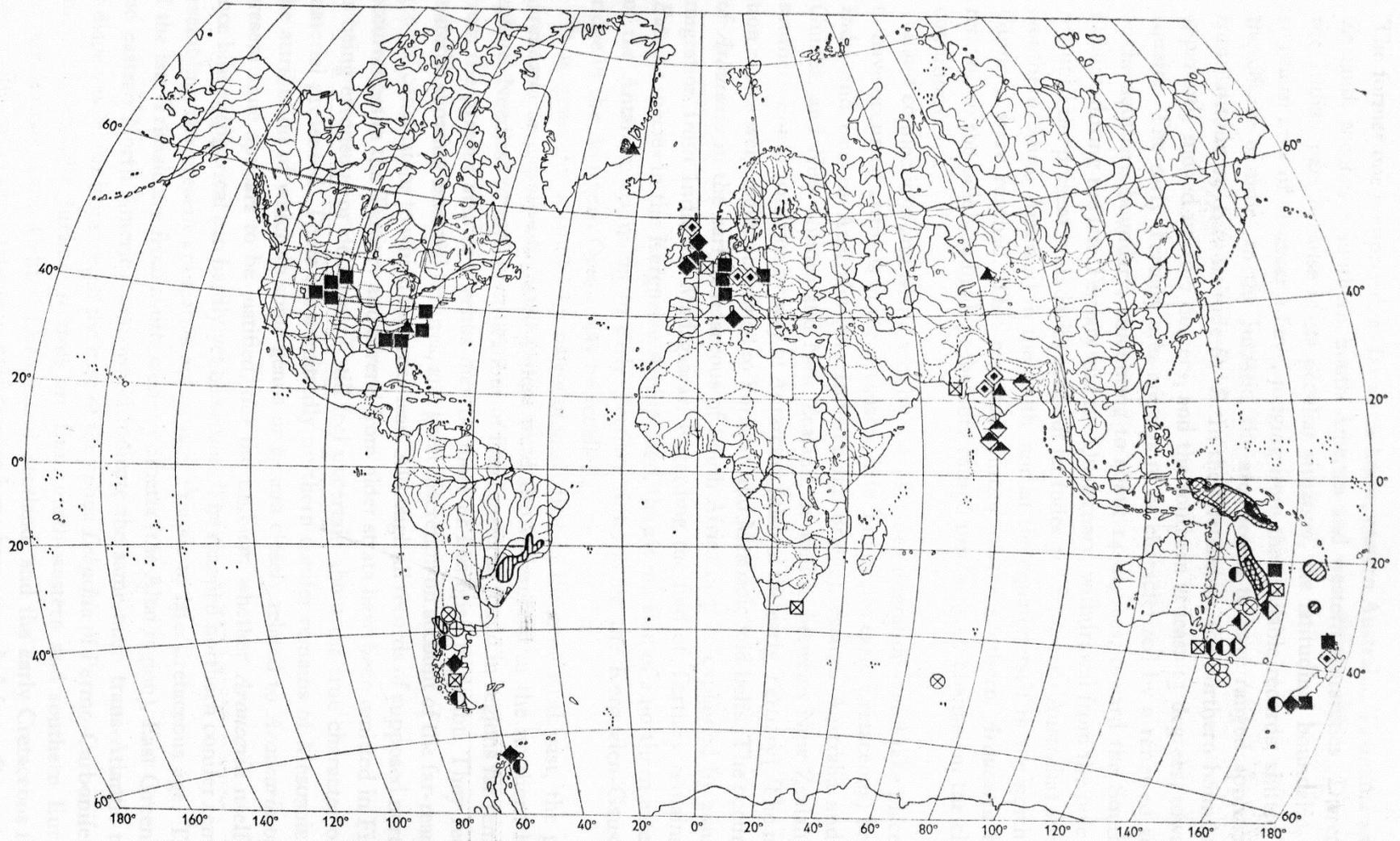


Fig. 14. *Araucaria*: Present distribution: Sect. *Bunya* ▨; Sect. *Columbea* ▩; Sect. *Eutacta* ▧ (incl. ● and ■); Sect. *Intermedia* ●. Fossil Araucarians (excl. *Agathis*). Distribution: late Triassic ▲, early Jurassic ◇, middle Jurassic ◆, late Jurassic ◇, Jurassic (indeterm.) ◇, early Cretaceous ☒, late Cretaceous ■, Eocene ⊕, Oligocene ●, Tertiary (indeterm.) ⊗.

Expansão das florestas de *Araucaria*

Ab'Saber 1982:
Há 20.000-14.000 anos,
expandiram até 19° S!
(Serra Negra)
= resfriamento de 5-6°C!
-dado confirmado por Oliveira 2000.

25°S: predomínio das
Matas de *Araucaria*
Hipótese: entre 40.000 e 20.000
anos atrás, massas polares
alcançavam limite N até
latitudes bem mais
baixas que hoje

23°S –
expansão de 8.000 até 6.000
e ca. 3.000 anos atrás

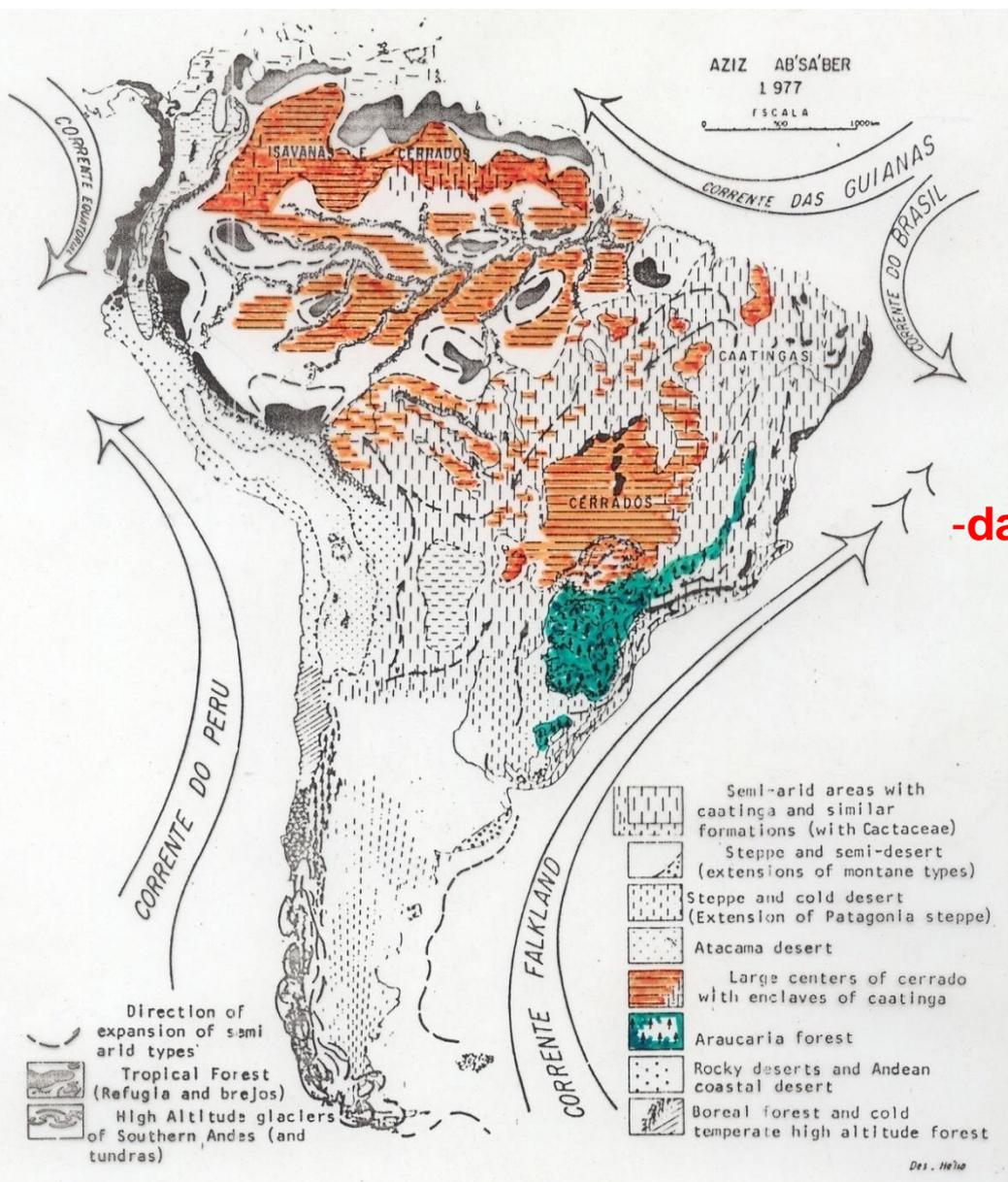


Figure 4.3 The vegetation of South America 13,000-18,000 years ago

Ledru et al. 2007: “past *Podocarpus* expansion may have been associated with an increase in moisture rates, either edaphic moisture or the length of the dry season, but **not necessarily with a decrease in temperature**”

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

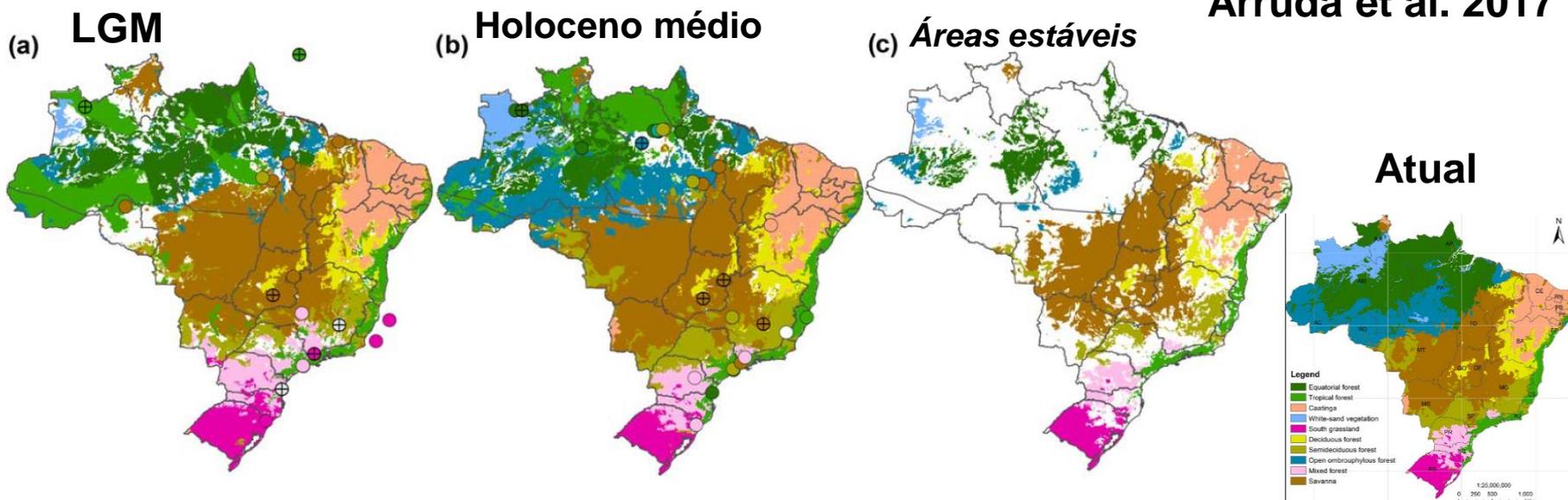


FIGURE 3 Spatial distribution of biomes at different moments in the past. Biome distribution in (a) the Last Glacial Maximum and (b) the Mid-Holocene. (c) Stability/refugia areas of the biomes based on the consensus between the two distribution scenarios and the present distribution (Figure 1). White 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

Dinâmica da *Araucaria* – campo e floresta segundo Hueck 1966

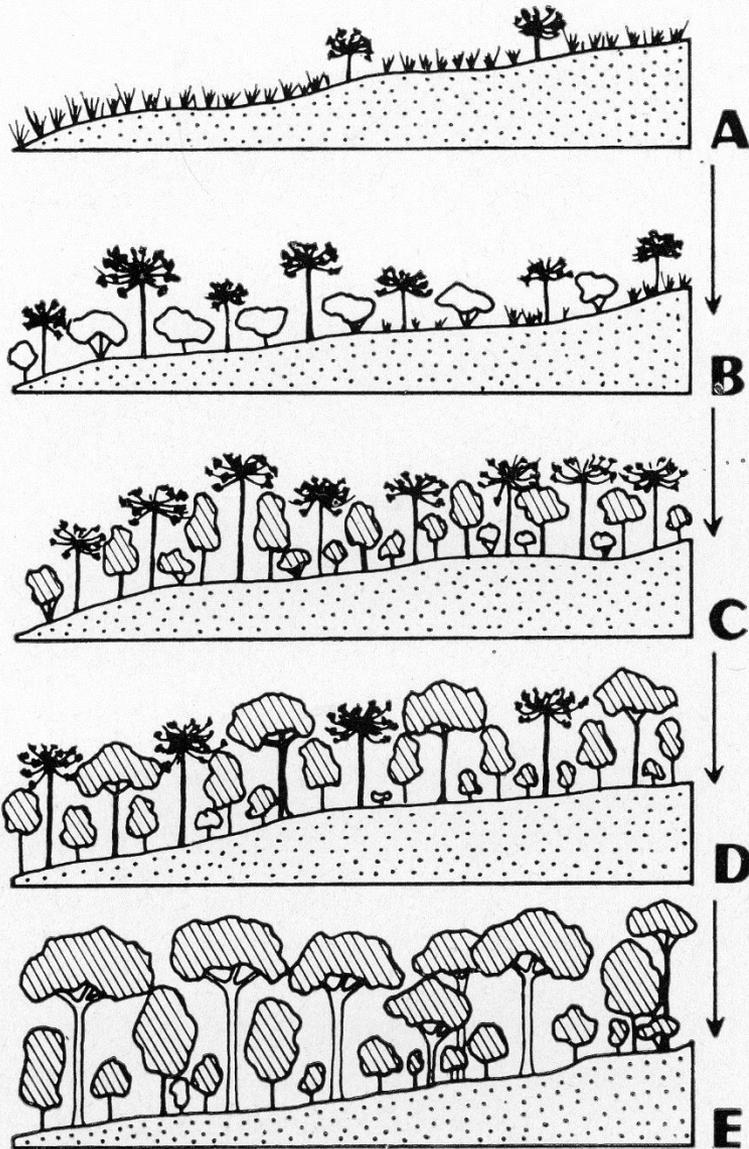


FIG. 79. — Evolution schématique de la végétation dans la région des *Araucaria* du Sud du Brésil (inspiré de HUECK, 1966). A : Campos colonisés par les jeunes *Araucaria angustifolia*, B : Jeune forêt d'*Araucaria*, avec quelques feuillus, C : Forêt d'*Araucaria* et de feuillus, D : Forêt subtropicale de feuillus, où les *Araucaria*, ne pouvant se régénérer, ont été éliminés. Cette évolution rappelle le rôle qu'ont, dans d'autres régions du globe, d'autres Gymnospermes, et illustre les relations que peuvent avoir, dans l'évolution de la végétation, les résineux et les feuillus.

Schnell 1987

Dinâmica da *Araucaria* – campo e floresta segundo Hueck 1966

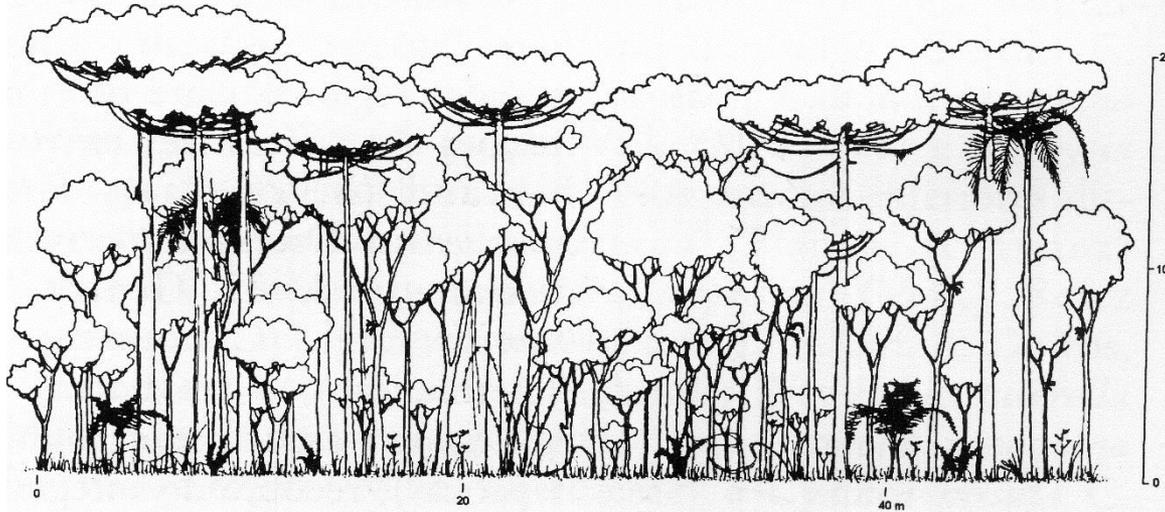
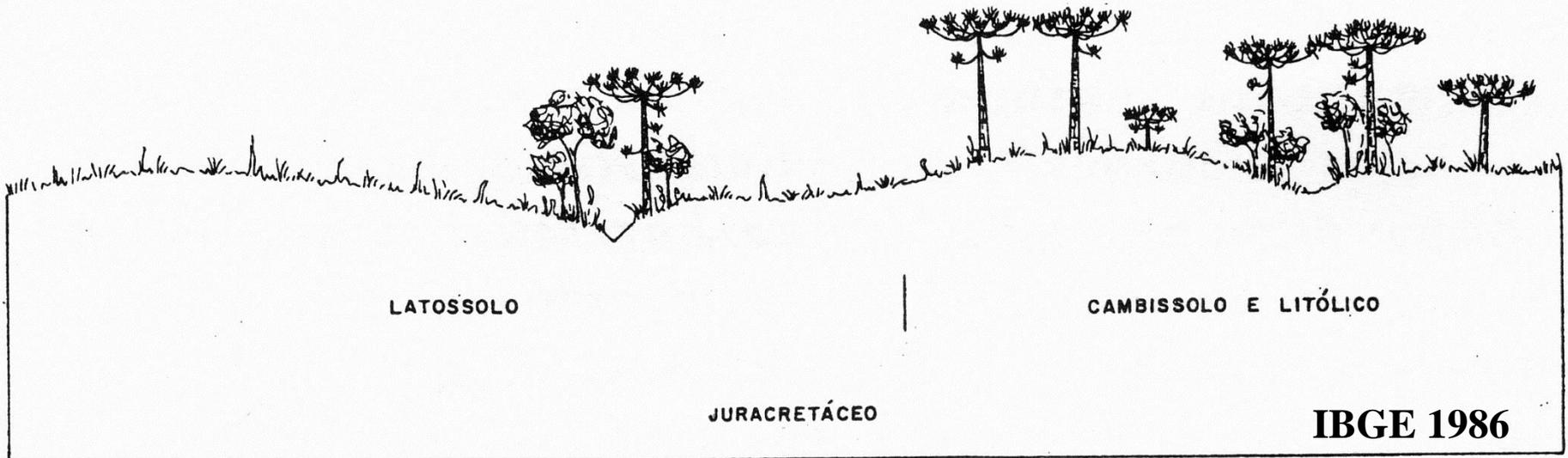
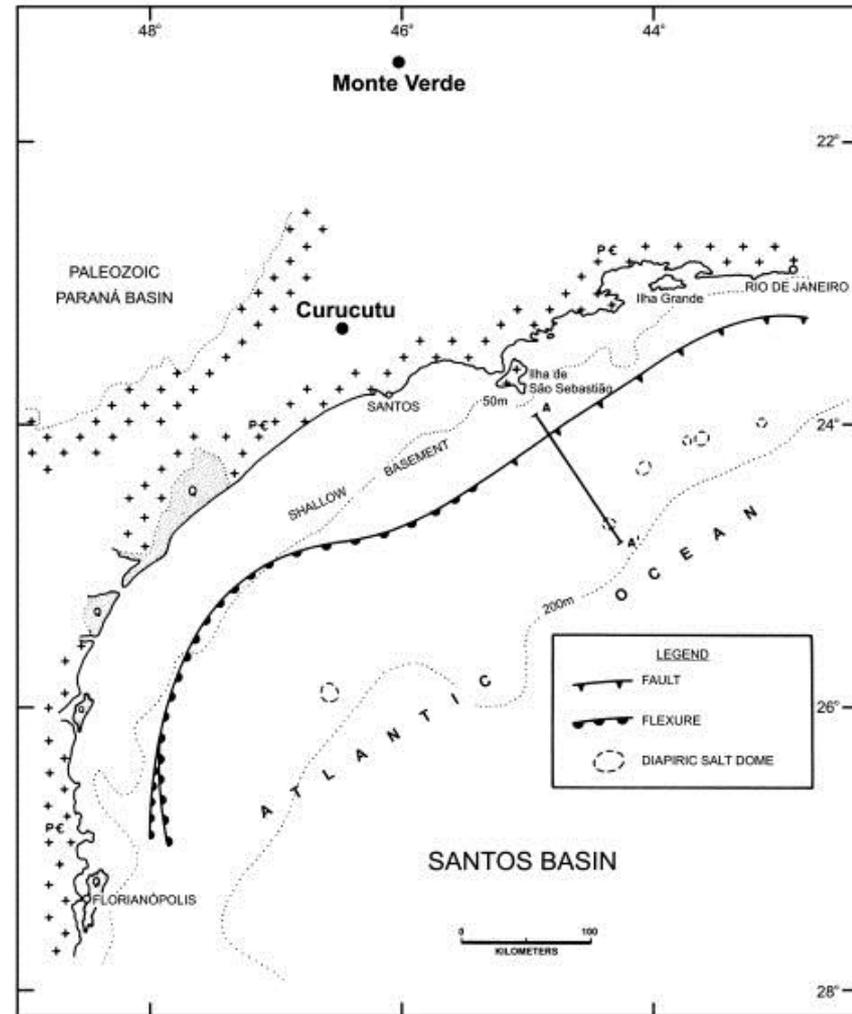


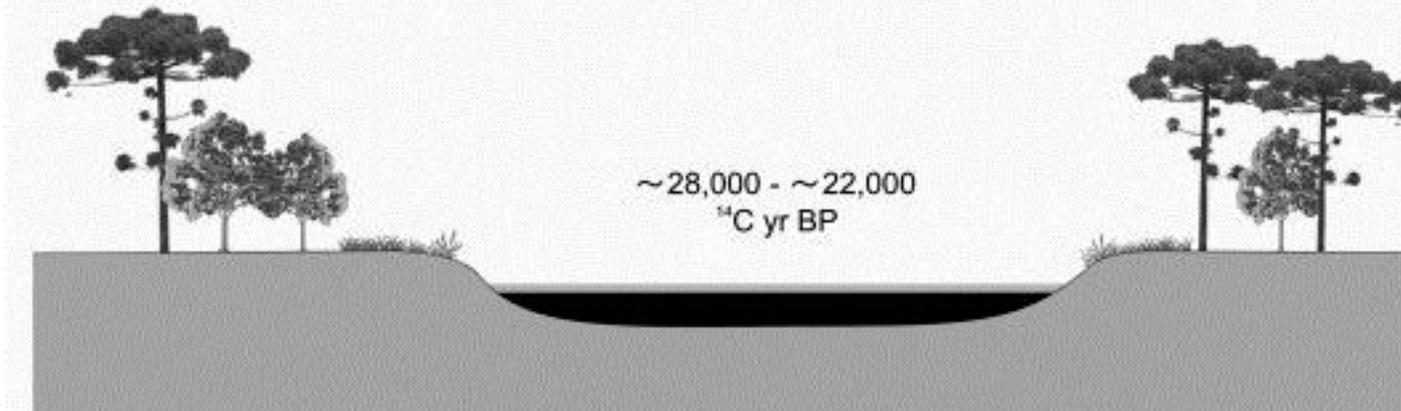
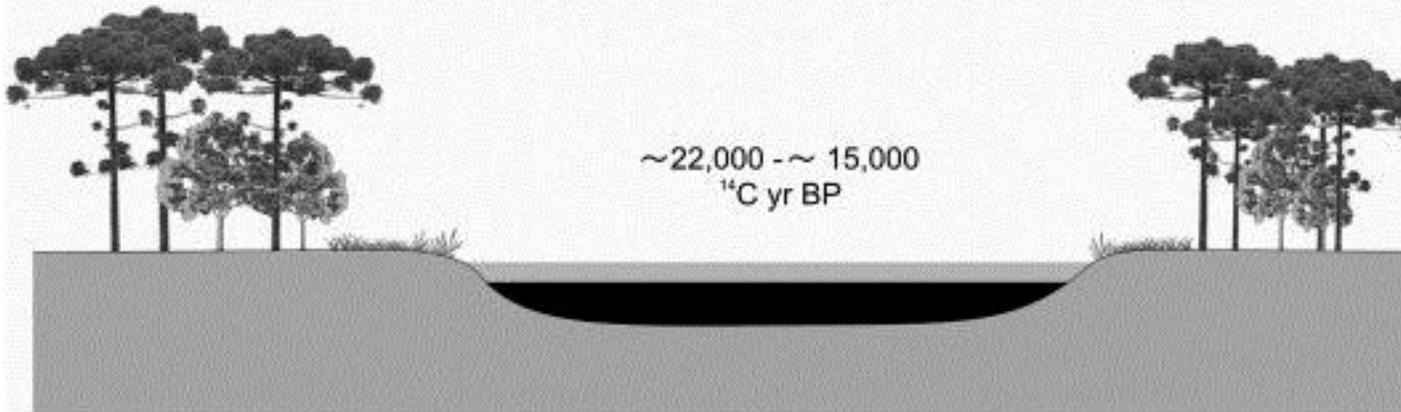
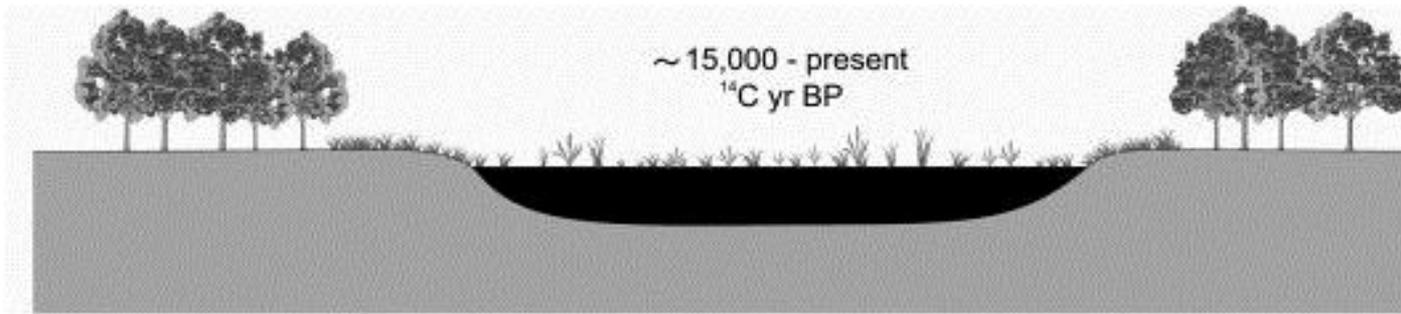
Figura 3: Perfil esquemático destacando a estrutura de um segmento de Floresta Ombrófila Mista no município de Irati, Paraná, com predominância de *Araucaria*, *Ocotea*, *Cedrela*, *Casearia*, *Sloanea*, *Podocarpus*, *Campomanesia*, *Ilex* e *Capsicodendron*.



IBGE 1986



Ruiz-Pessenda et al. 2009
Dinâmica das matas, da *Araucaria* e dos campos
na crista da Serra do Mar, SP



Ruiz-Pessenda
et al. 2009

Dinâmica das
Matas.
da *Araucaria*
e dos campos
na crista da
Serra do Mar, SP

Origem dos campos e cerrados

Jacobs *et al.* 1999



(Origin of the savanna biome

Beerling & Osborne 2006)

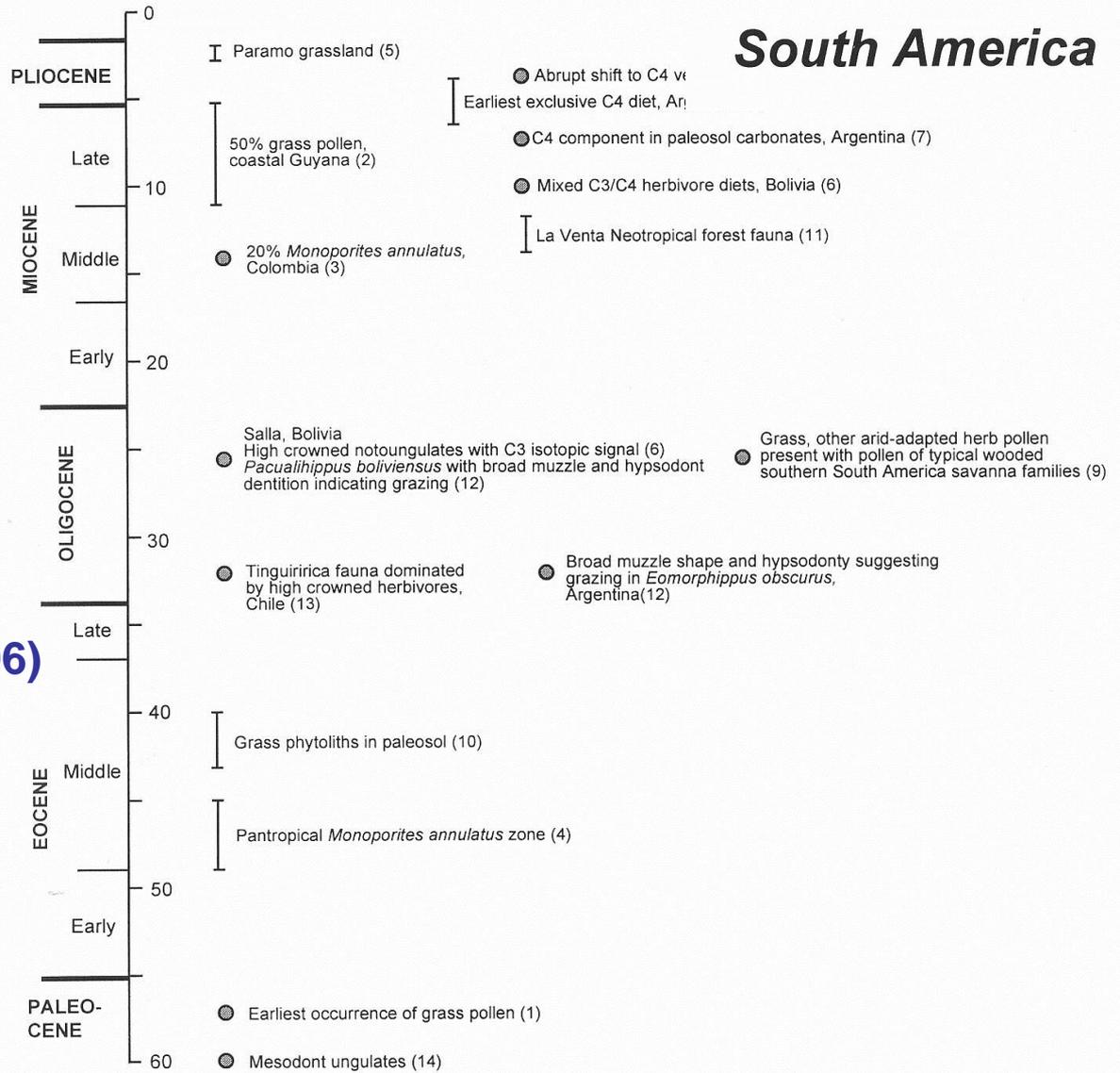
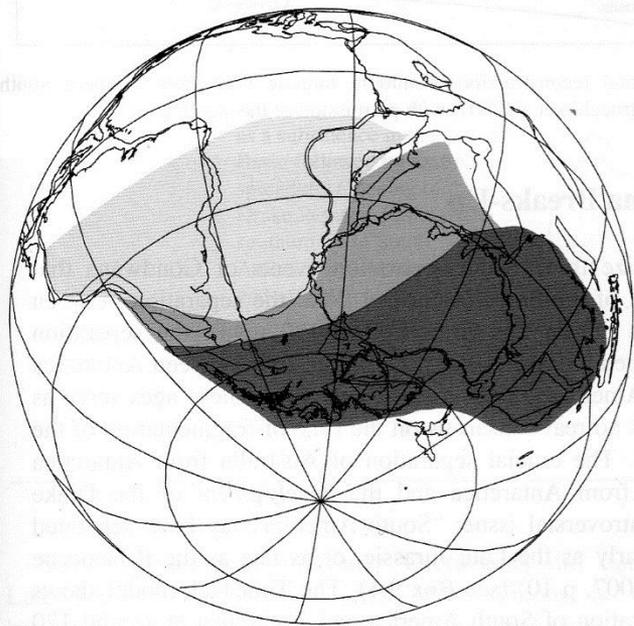


Figure 4. Summary of paleobotanical, paleofaunal, and isotopic evidence for the origin of grass-dominated ecosystems in South America. Symbols as in Figure 2. Sources: (1) Muller et al. (1987), (2) Van der Hammen & Wymstra (1964), (3) Hoorn (1993), (4) Germeraad et al. (1968), (5) Wijninga (1996), (6) MacFadden et al. (1994), (7) Latorre et al. (1997), (8) MacFadden et al. (1996), (9) Romero (1993), (10) Andreis (1972), (11) Kay et al. (1997a), (12) Shockey (1997), (13) Wyss et al. (1993), (14) Pascual & Ortiz Jaureguizar (1990).



Alterações no tipo e extensão dos climas e biomas na região austral

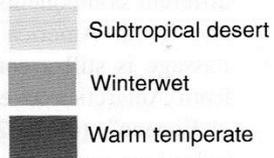


Fig. 1.11 Early Jurassic biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

Jurássico Inferior (190 m.a.)

Moreira-Muñoz 2011

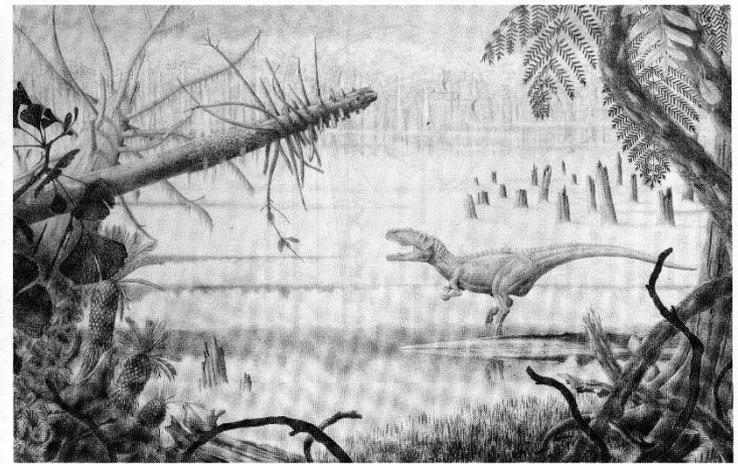
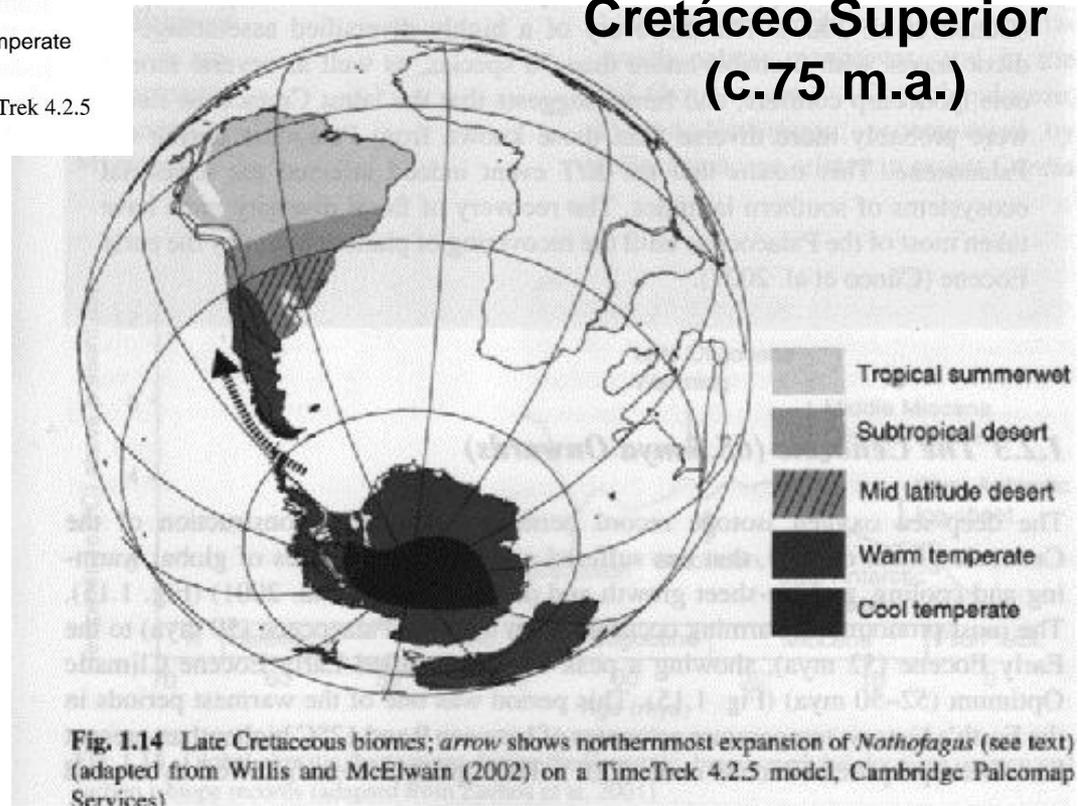


Fig. 1.13 Illustration of the biotic assemblage from the limit Jurassic/Cretaceous (145.5 mya) of the Southern Cone. Theropod dinosaur on a swamp surrounded by ginkgos, araucarias, and arboreous ferns (original illustration by Sergio Elórtégui Francioli)

Cretáceo Superior (c.75 m.a.)



Alterações no tipo e extensão dos climas e biomas na região austral

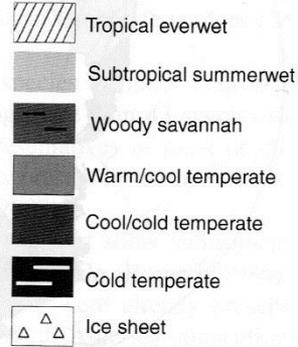
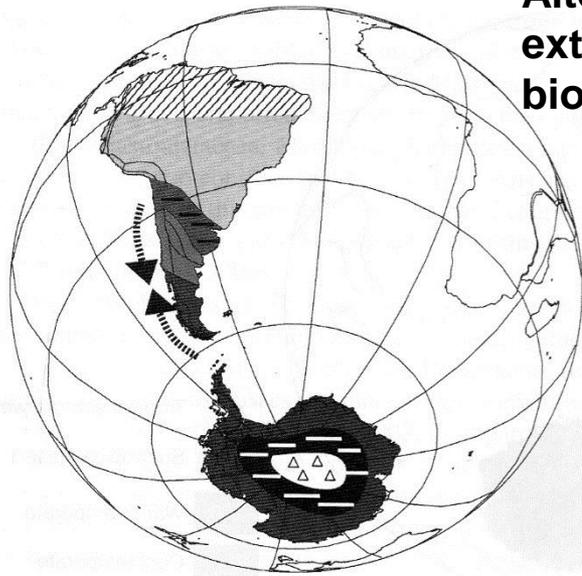


Fig. 1.17 Early Oligocene biomes; arrows show mixture of tropical and austral floras (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

Oligoceno (34 m.a.)

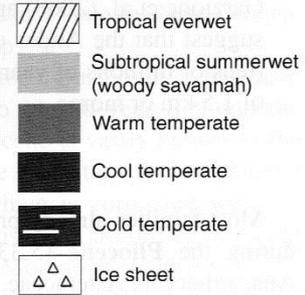
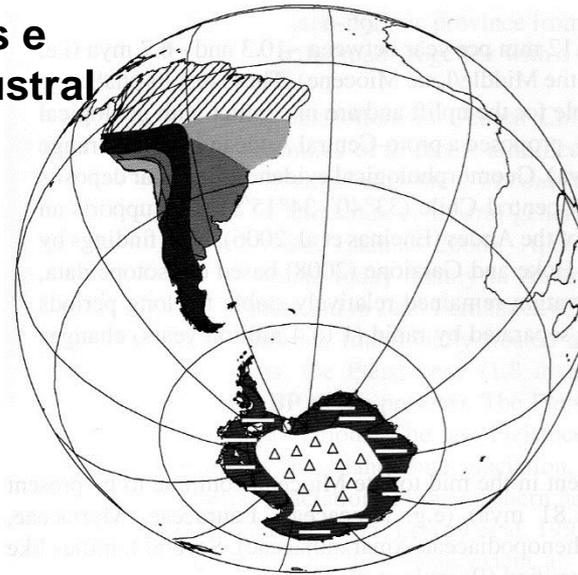
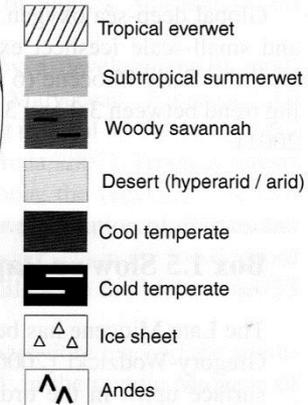
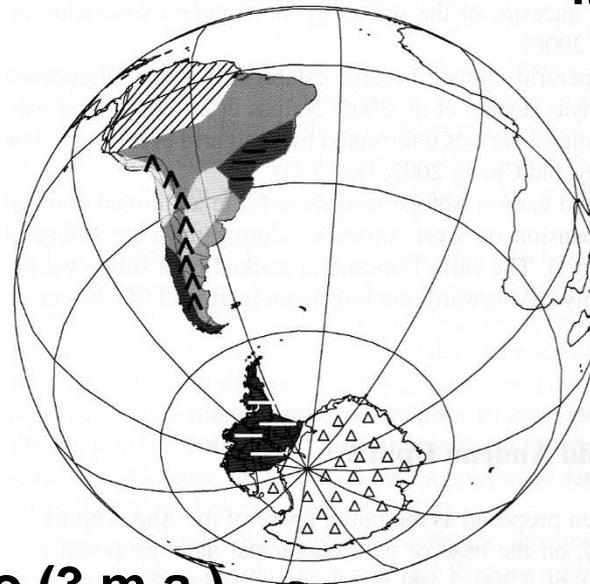


Fig. 1.18 Miocene biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

Mioceno (20-8 m.a.)

CENOZOIC		Age Ma	Modern World	
Quat.	Holocene	0.0115		
	Pleistocene	1.806		
Neogene	Pliocene	5.3		
		Upper		Messinian
				Tortonian
		Middle		Serravallian
				Langhian
		Lower		Burdigalian
				Aquitanian
		Paleogene	Oligocene	23.03
				Chatthian
			Rupelian	
Eocene	28.4			
	33.9			
Paleocene	55.8			
	65.5			

After Gradstein et al. (2004, Fig 21.1)



Plioceno (3 m.a.)

Fig. 1.19 Pliocene biomes (adapted from Dowsett et al. (1999) and Haywood et al. (2002), on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

Moreira-Muñoz 2011

de Vivo &
Carmignotto
2004

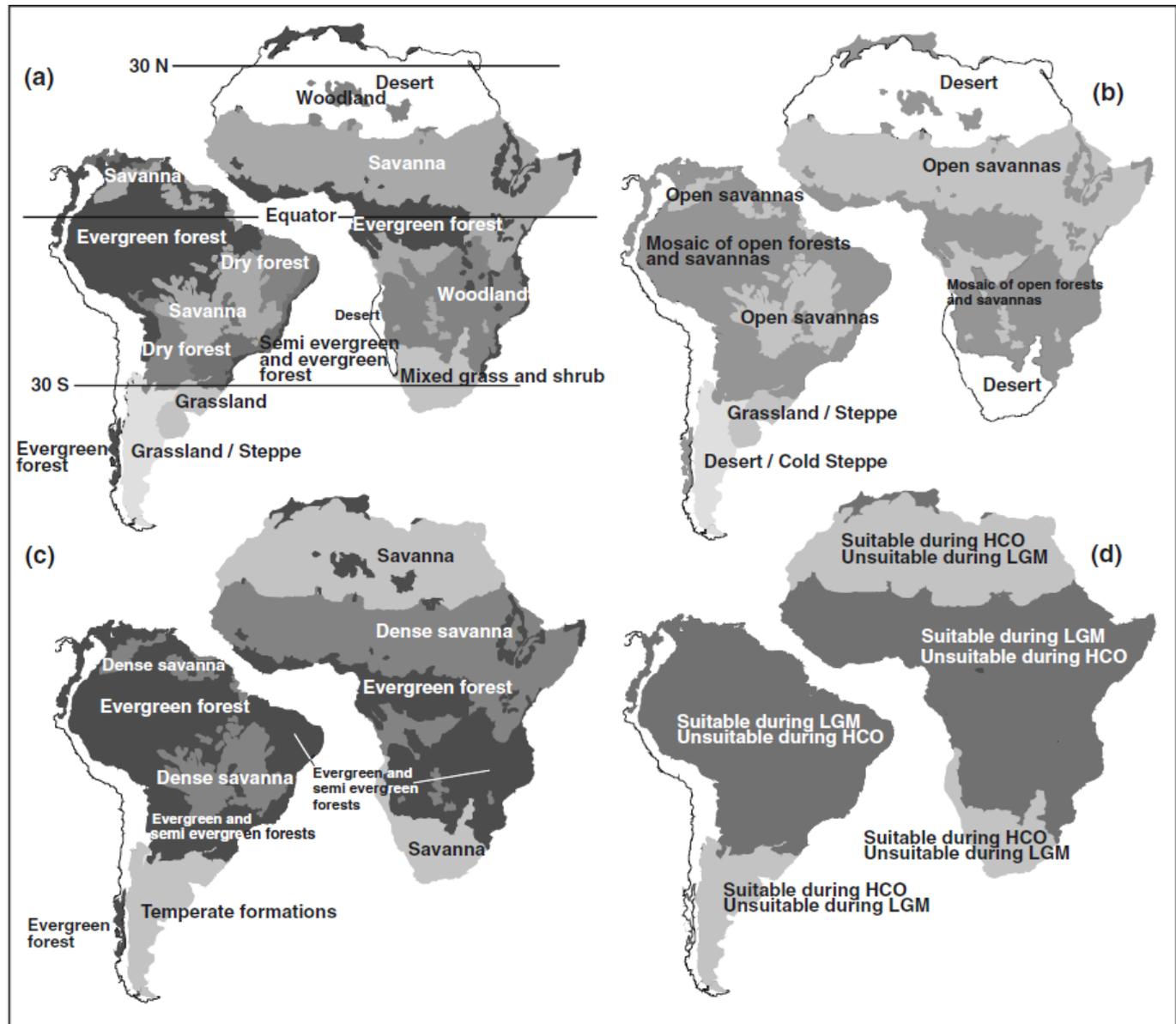


Figure 3 Present day major plant formations of South America and Africa (a) and geographical vegetation change for the two continents at the LGM (b) and the HCO (c). A summary of this change is depicted in (d), where darker grey are for areas of predominantly suitable megafauna habitat at the LGM and unsuitable habitats at the HCO; and lighter grey are for areas predominantly suitable habitats at the HCO and unsuitable at the LGM. White areas in the maps of South America mostly indicate complex Andean vegetation not considered here.

Comunidades lenhosas nas Províncias do Cerrado

Aranha & Martins
2013

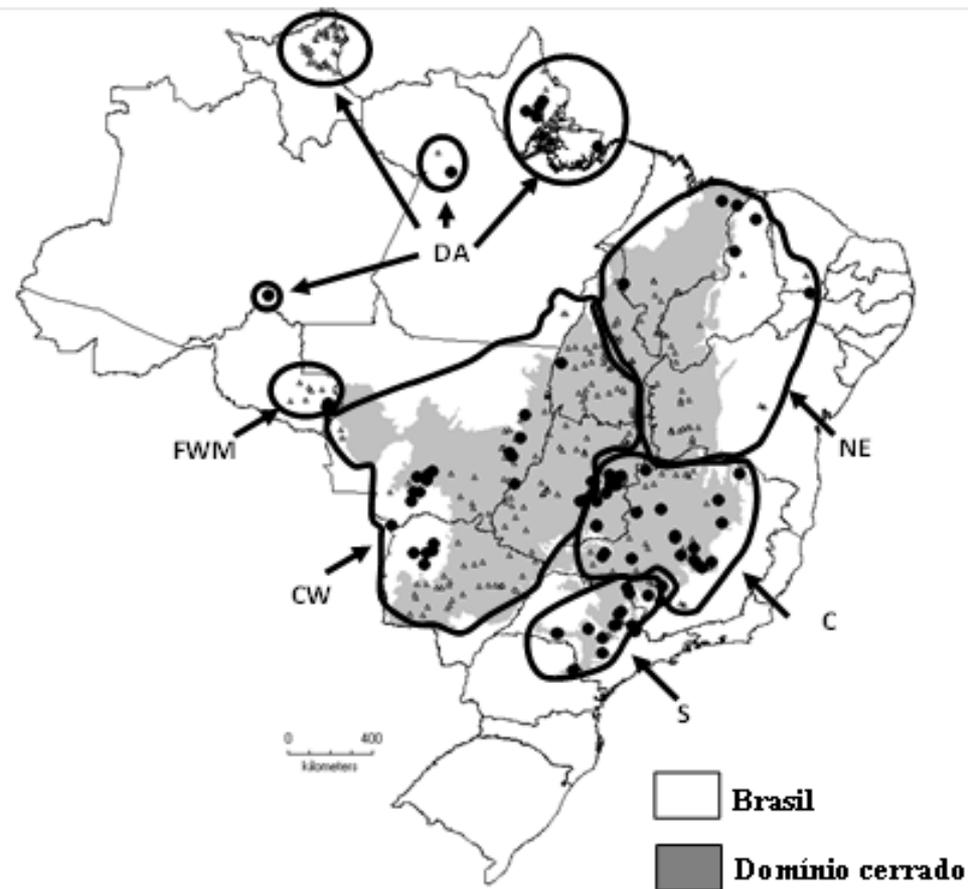
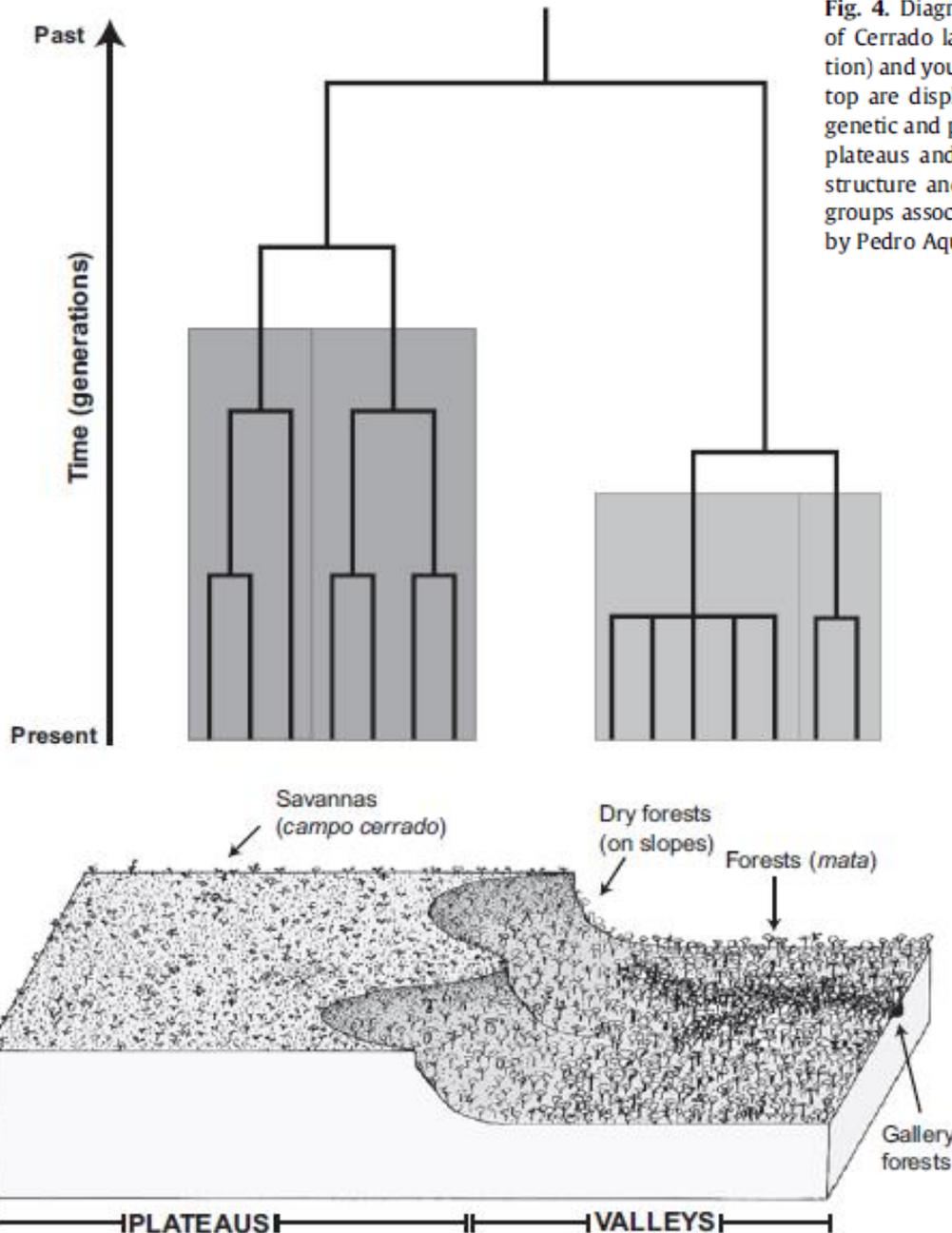


Figura 1. As 142 comunidades lenhosas do cerrado (círculos pretos) resultantes da nossa pesquisa na literatura mais os 338 levantamentos compilados por Ratter et al. (2009; triângulos brancos) distribuídos entre as províncias Centro (C), Centro Ocidental (CW), Amazônica Disjunta (DA), Ocidental Mesotrófica (FWM), Nordeste (NE) e Sudeste (S).

Fig. 4. Diagrammatic representation of the geomorphological compartmentalization of Cerrado landscape between ancient plateaus (dominated by savanna-like vegetation) and younger valleys (dominated by more heterogeneous forests assemblages). On top are displayed the corresponding diversification expectations in terms of phylogenetic and phylogeographic diversity and structure, namely: reciprocal monophyly of plateaus and valleys species groups; older diversification ages, higher genealogical structure and genetic diversity levels of plateaus species groups when compared to groups associates with valleys. Top left: a generic time axis. Geomorphology artwork by Pedro Aquino De Podestà.



Compartimentação geomorfológica da paisagem do cerrado em chapadões antigos (vegetação savânica) e vales de sedimentação mais recente (florestas) e

padrões esperados de diversidade e estrutura filogenética e filogeográfica.

Werneck 2011

Necessidade de reavaliação desse modelo!

SAVANAS do mundo: recentes (ca. 3 a 10 milhões de anos)

Diferem em fenologia, resistência ao fogo,
crescimento e arquitetura das lenhosas.

Savanas africanas: dominância de leguminosas;
megafauna expressiva.

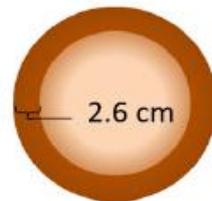
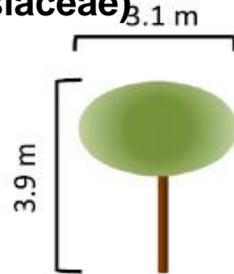
Savanas australianas: dominância de mirtáceas;
megafauna pouco expressiva.

Cerrados: flora bem mais diversificada, sem uma família dominante;
megafauna pouco expressiva.

Estação seca
muito mais pronunciada

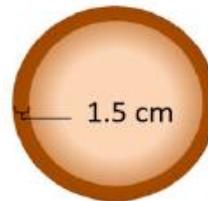
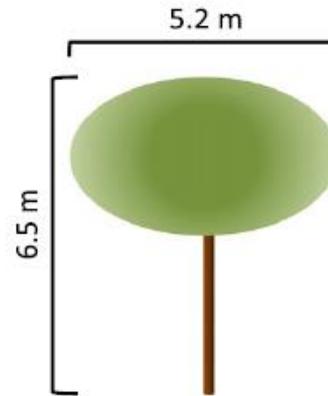


Malpighiaceae,
Melastomataceae,
Mimosoideae,
Qualea (Vochysiaceae)

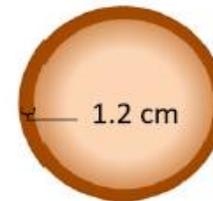
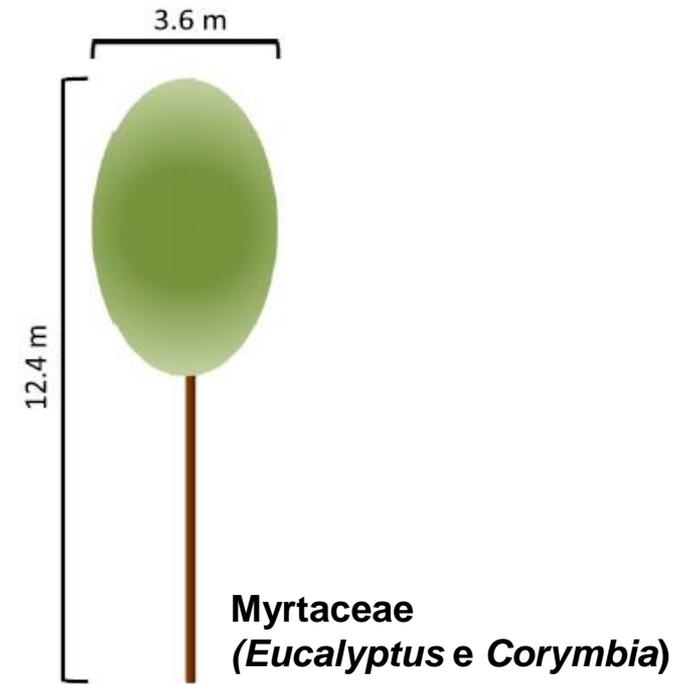


South America

Caesalpinioideae,
Mimosoideae,
Combretaceae



Africa

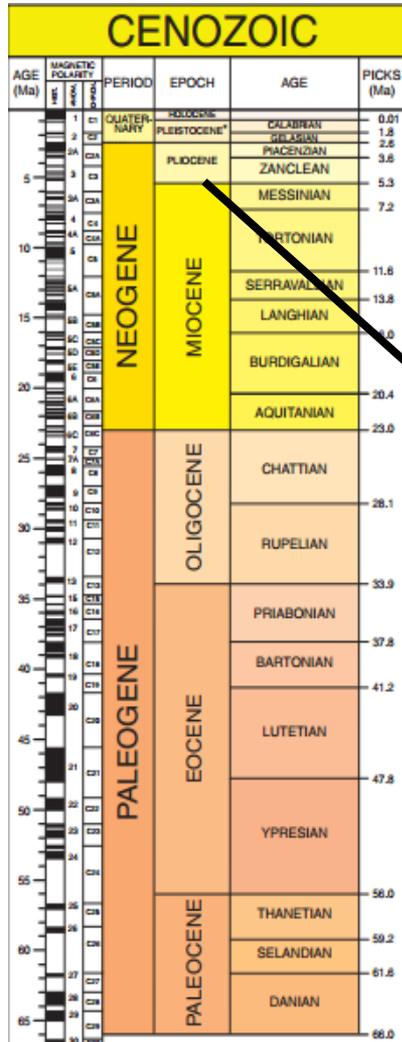


Australia

Figure 1 Comparative architecture of savanna trees from three continents. Canopy diameter, tree height and bark thickness are shown at 20 cm stem diameter summarizing data from Moncrieff *et al.* (2014a), Dantas & Pausas (2013) and Lawes *et al.* (2011). Allometries are drawn to scale except bark thickness, which is exaggerated by a factor of 2 relative to stem diameter in the diagram. The extensive savannas now found in South America, Africa and Australia evolved in the late Miocene (c. 5–8 Ma, Beerling & Osborne, 2006) long after Gondwana began to break-up; circa 184 Ma. The tree flora of each continent has thus been independently assembled. Savanna trees evolved in situ on each continent from ancestors in closed-canopy forests and sclerophyll biomes (Simon *et al.*, 2009; Bouchenak-Khelladi *et al.*, 2010; Crisp *et al.*, 2011; Maurin *et al.*, 2014). Thus, different clades characterize different continents, with Mimosoideae, Melastomataceae and Malpighiaceae and the genus *Qualea* common in South American Cerrado, Myrtaceae (particularly *Eucalyptus* and *Corymbia*) often dominant in Australian savannas and Mimosoideae, Caesalpinioideae and Combretaceae common throughout African savannas.

Formações abertas e/ou secas da América do Sul

<http://www.geosociety.org>



Origem muito recente

X

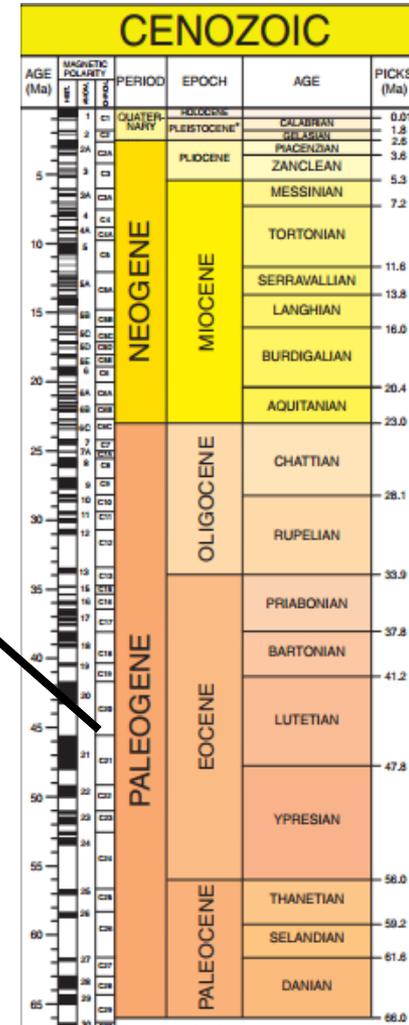
Origem bem mais antiga

Plioceno e Quaternário

Desde o início da Era Cenozoica

Lewis 1966
Raven & Axelrod 1974

Barreda & Palazzesi 2007
Roig-Juñent *et al.* 2006



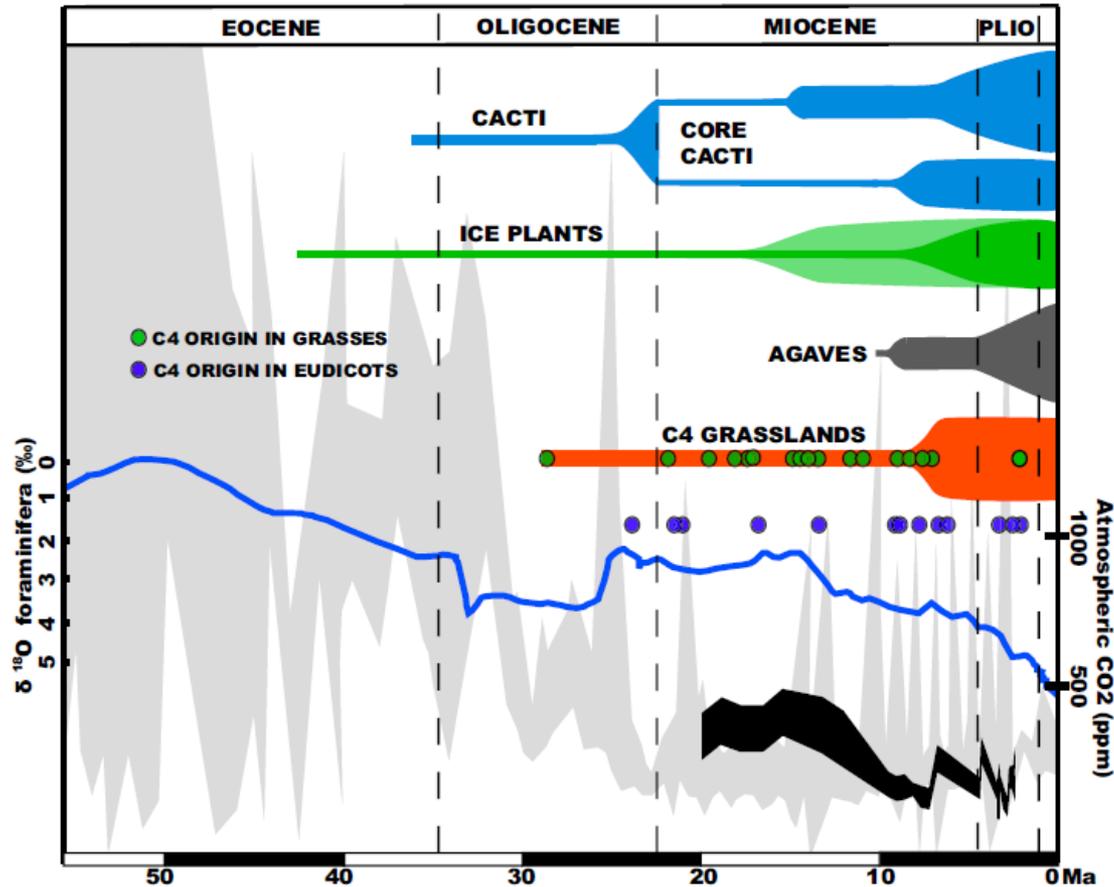


Fig. 2. CO₂, global temperature, C₄ origins, C₄ grasslands, and the diversification of succulent plants during the late Miocene/Pliocene. Lines extend back to the origin of the various succulent clades, and significant diversification events are represented by increases in line width. For the ice plants, dark green indicates timing of diversification by Klak et al. (14), and light green represents our estimated age of the same node ("core Rushioideae"; ref. 14). Blue line reflects decline in relative global temperatures, inferred from deep sea ¹⁸O, which is primarily a metric of deep sea temperature and sea-ice volume. Gray area in background represents reconstructed atmospheric CO₂ levels and their uncertainty through time, collated from multiple proxies (27). Black line is the drop in CO₂ hypothesized by Tripathi et al. (33).

Contemporaneous and recent radiations of the world's major succulent plant lineages

Arakaki et al. 2011

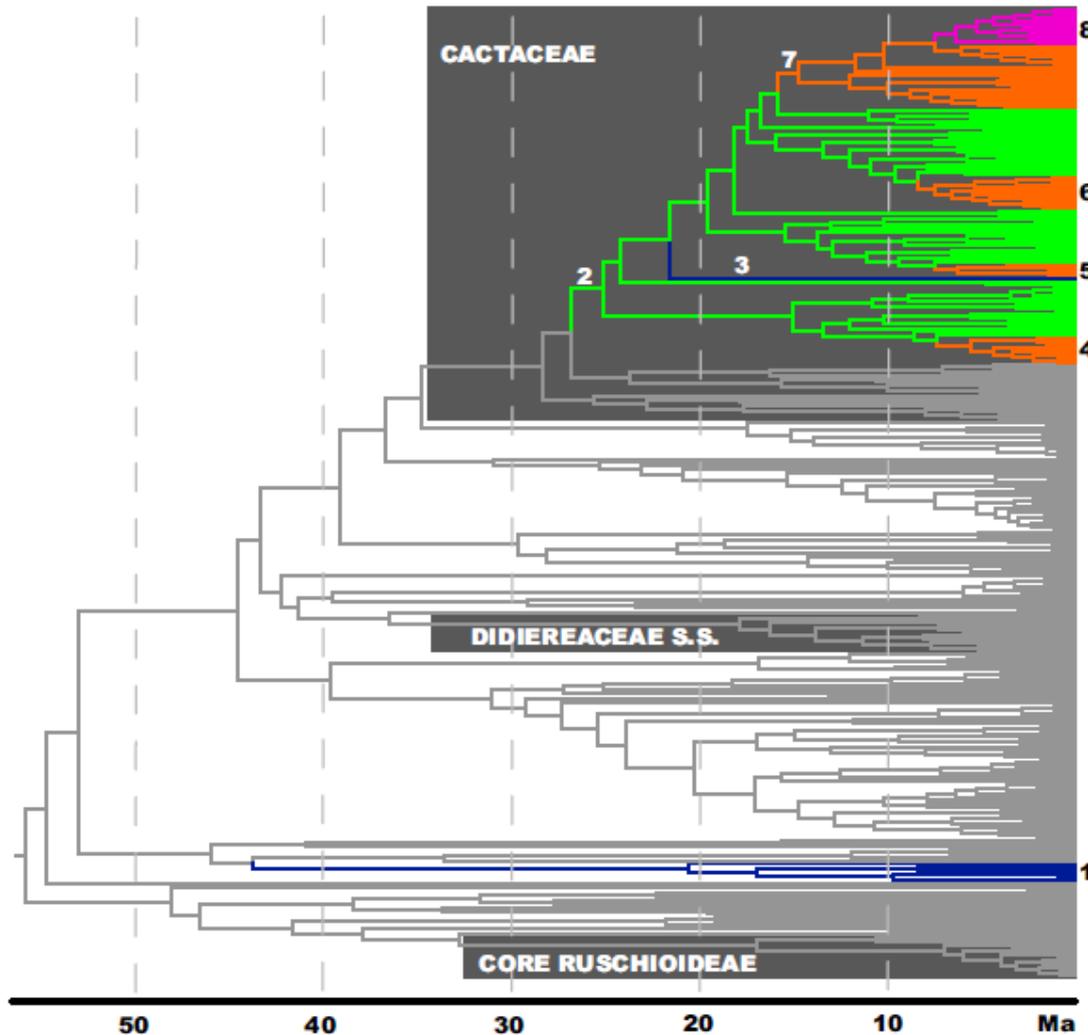
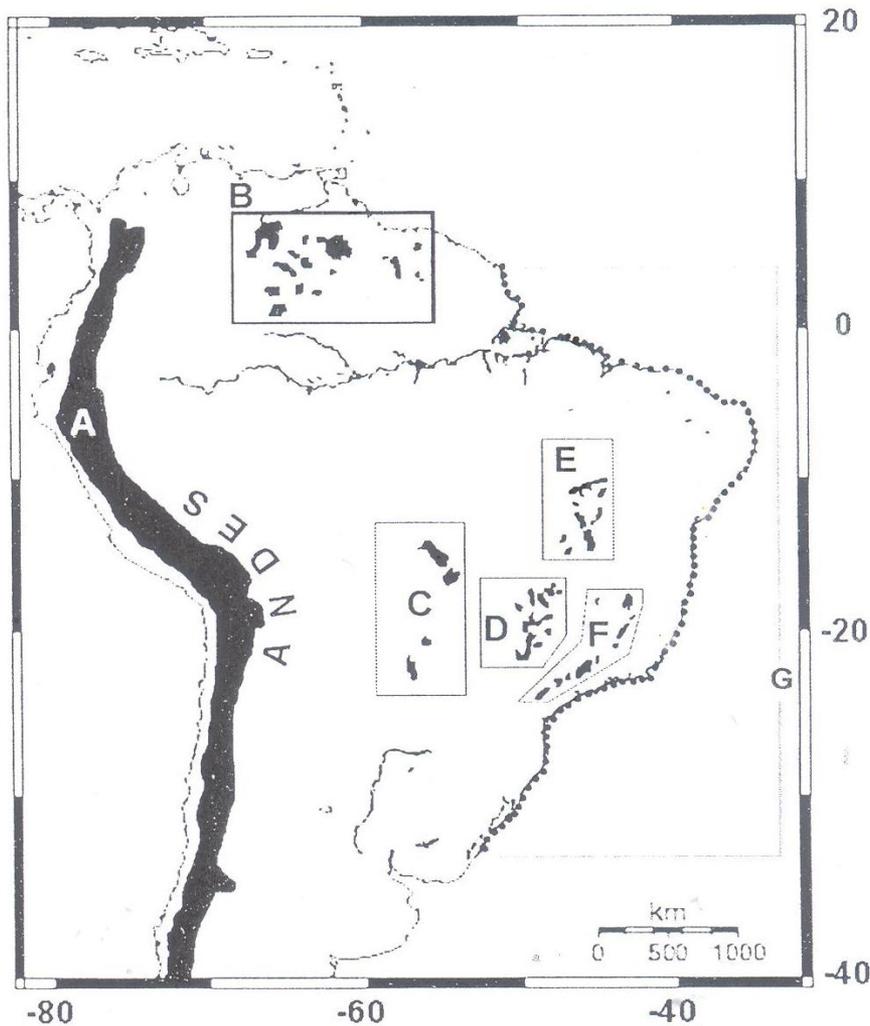


Fig. 1. Time-calibrated phylogeny of the cacti and their relatives. Colored branches indicate shifts in diversification: Blue branches represent lineages with significantly lower net diversification than the background rate; green, orange, and pink branches indicate higher diversification and/or species turnover (see Table 1 for parameter estimates and clade names). Gray boxes indicate ecologically important succulent clades: Cactaceae (New World); Malagasy Didieraceae (Madagascar); core Ruschioideae (Aizoaceae, Southern Africa).



Unidades fitogeográficas com vegetação rupícola em topos montanos na América do Sul:

A. Andes

B. Planalto das Guianas

C, D, E - Campos rupestres:

C - de GO e DF.

D - do Espinhaço - setor Mineiro

E - do Espinhaço - setor Baiano

F. Campos de altitude da Serra do Mar

Figure 1. Phytogeographic units with outcrop vegetation: A. Andes. B. *tepui*s of the Guyana shield. C. *Campos rupestres* in mountain ranges of Goiás and Distrito Federal. D. *Campos rupestres* in south of the Espinhaço chain, Minas Gerais. E. *Campos rupestres* of the Chapada Diamantina (North of the Espinhaço chain, Bahia). F. *Campos de altitude* da Serra do Mar. G. *Restingas* (Atlantic coastal strand vegetation of Brazil).

Alves et al. 2007

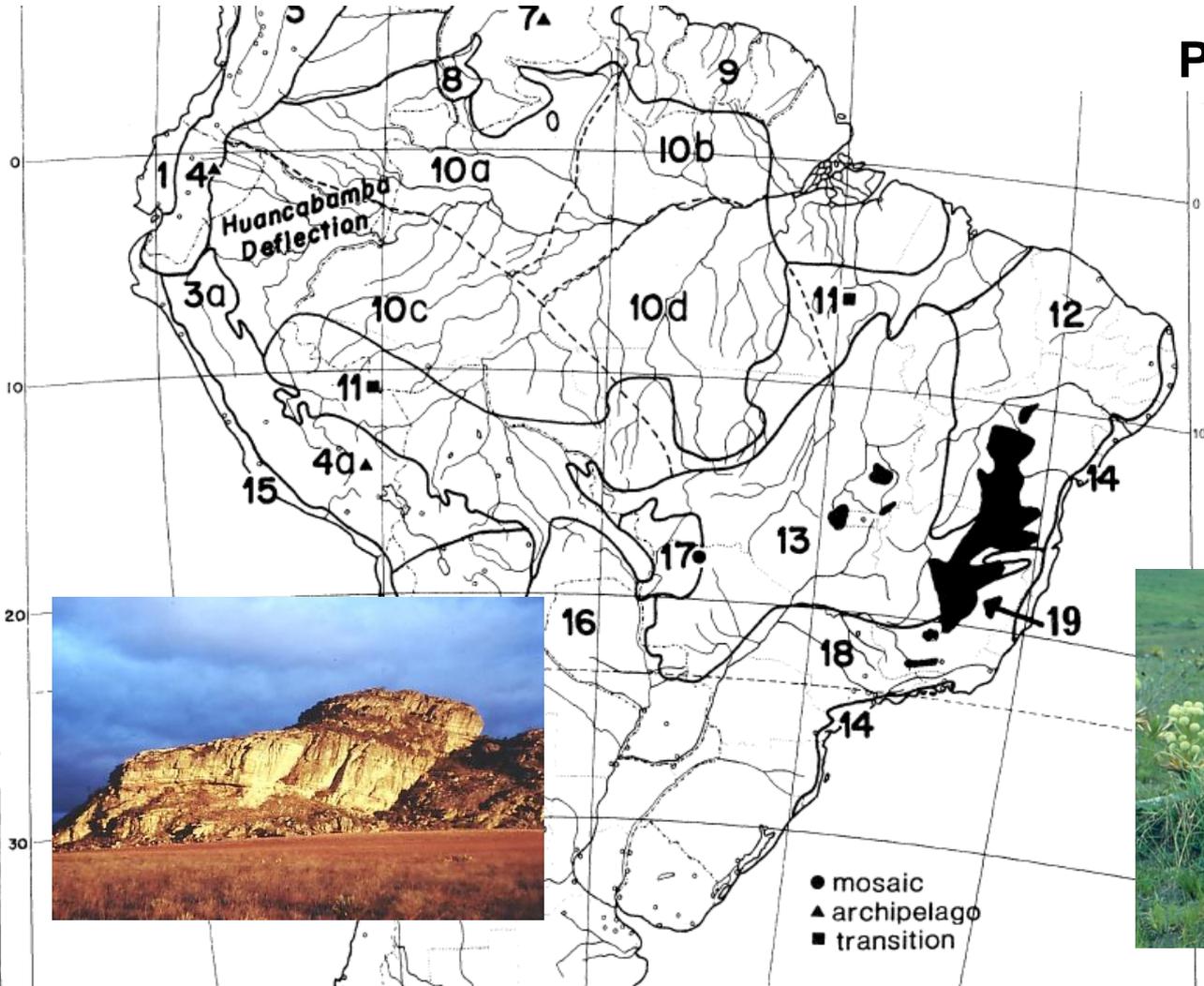
A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics

Fitocória (província florística) dos Campos rupestres

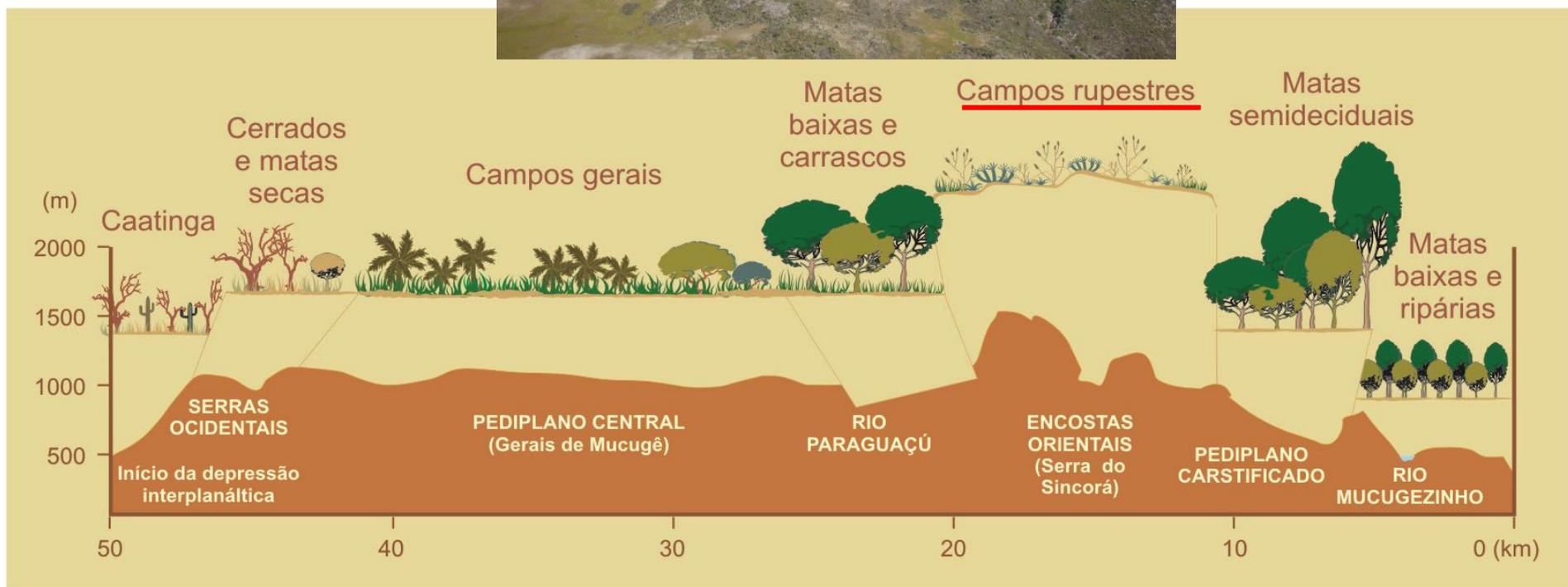
GHILLEAN T. PRANCE

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.

Prance 1994



- mosaic
- ▲ archipelago
- transition



Perfil topográfico da Chapada Diamantina, Bahia
 (modificado de Nóbrega 2003) Pirani *in* Teixeira *et al.* 2005

Vegetação dominante sobre os substratos arenosos e areno-pedregosos do Espinhaço e outras serras do Brasil Central:

campo rupestre (Magalhães 1966, Joly 1970, Eiten 1983, Giullietti *et al.* 1987, 1997, Meguro *et al.* 1994, Pirani *et al.* 1994, 2003, Harley 1995, Rapini *et al.* 2010)

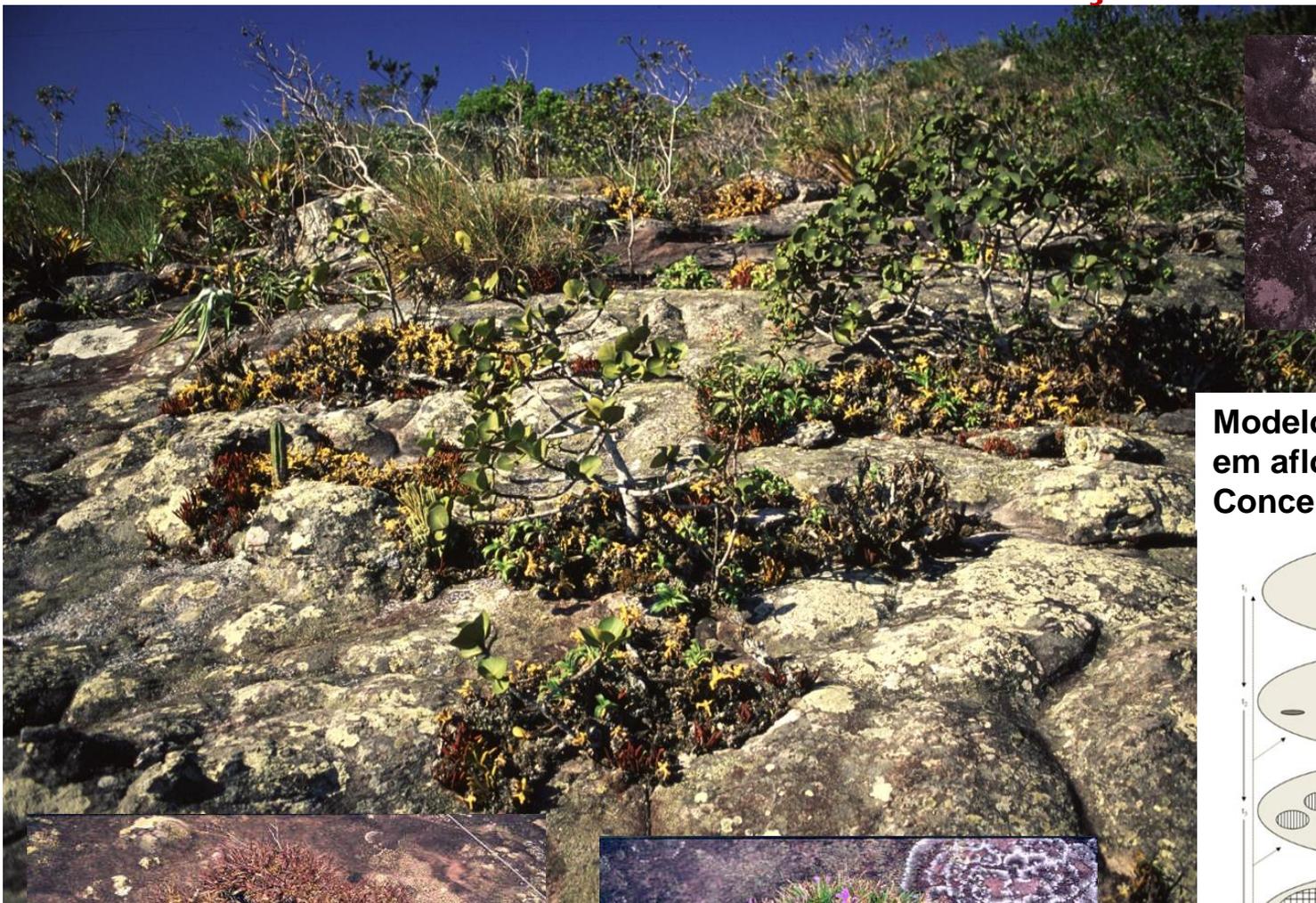
campo quartzítico (Rizzini 1979),

refúgio ecológico montano (Veloso *et al.* 1991)



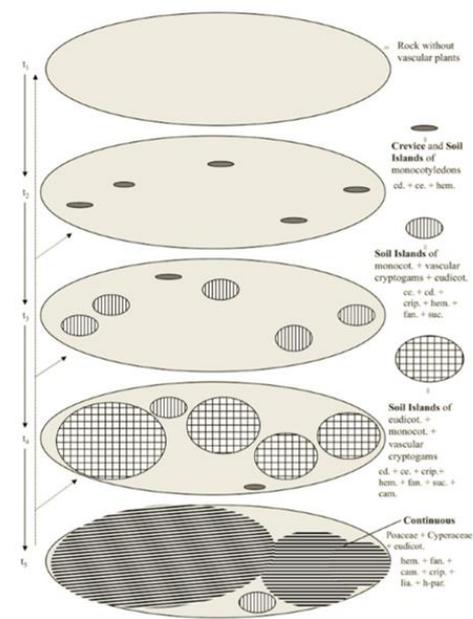
Mosaico de comunidades predominantemente herbáceo-arbustivas, esclerófilas e perenifólias, florísticamente relacionadas mas fisionômica e estruturalmente distintas, em função da topografia, substrato e clima (Giullietti *et al.* 1997).

Sucessão nos afloramentos: caméfitas epilíticas e tolerantes à dessecação



Selaginella marginata

Modelo sucessional em afloramentos rochosos Conceição & Pirani 2016



Vellozia hemisphaerica



Vellozia jolyi, *Hippeastrum puniceum*

Campo rupestre: Riqueza florística vascular alta

1590 spp - Serra do Cipó, MG (Giulietti *et al.* 1987)
- 3200 spp. (Pirani *et al.* 2015)

1044 spp - Pico das Almas, BA (Stannard 1995)

1067 spp - Grão-Mogol, MG (Pirani *et al.* 2003 - 2009)

1700 spp – Catolés, BA (Zappi *et al.* 2003)

Famílias mais ricas: Asteraceae, Leguminosae, Melastomataceae, Poaceae, Orchidaceae, Rubiaceae, Cyperaceae e Eriocaulaceae.

Abundância de Poaceae e Velloziaceae nos substratos rochosos.

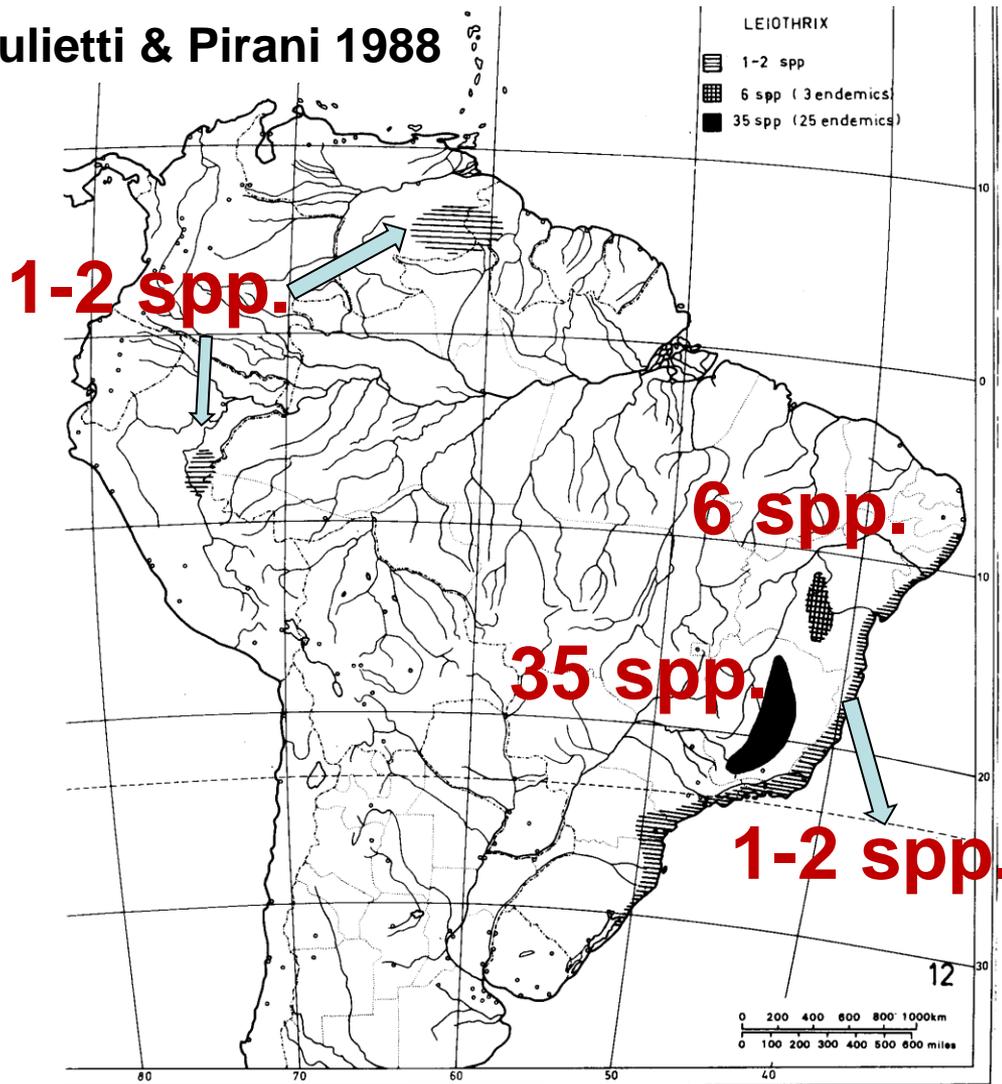
Leiothrix (Eriocaulaceae)

Densidade de espécies:

centro de diversidade no Espinhaço em Minas Gerais.



Giulietti & Pirani 1988



Padrão recorrente em:

Eriocaulaceae

Velloziaceae

Xyridaceae



Asteraceae

Ericaceae

Lamiaceae

Leguminosae

Melastomataceae

... e outras famílias



Áreas de endemismo



Flora

journal homepage: www.elsevier.de/flora

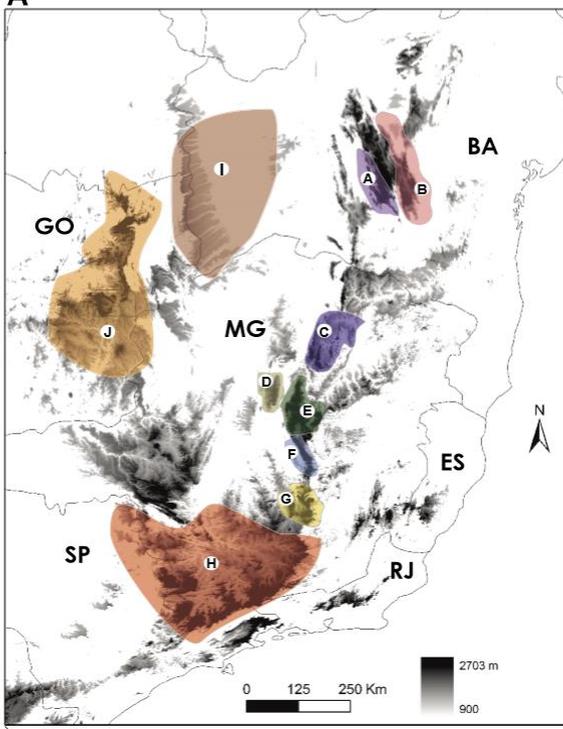
Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil
Livia Echternacht^{a,b,c,*,1}, Marcelo Trovó^{a,1}, Caetano T. Oliveira^{b,2}, José Rubens Pirani

TAXON — 3 Dec 2014: 12 pp.

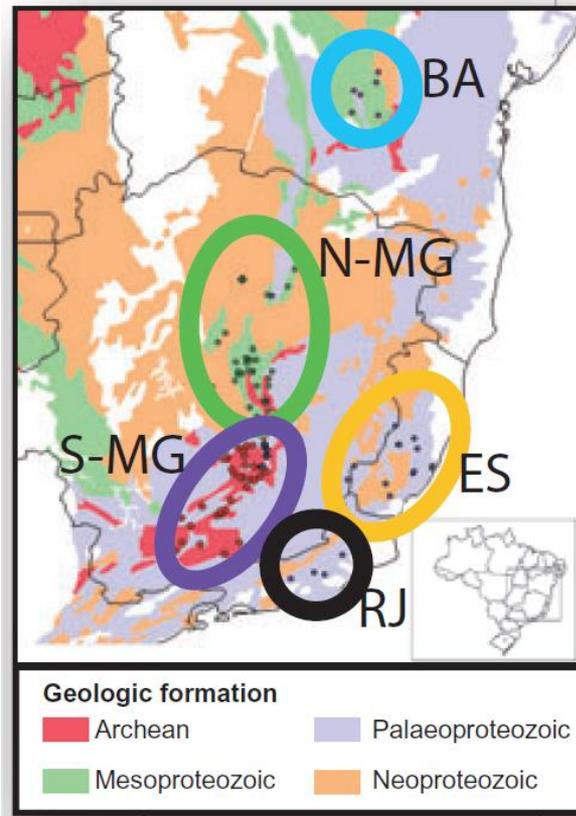
Ribeiro & al. • Plant diversification in the Espinhaço Range

Plant diversification in the Espinhaço Range: Insights from the biogeography of *Minaria* (Apocynaceae)

Patricia Luz Ribeiro,^{1,2} Alessandro Rapini,² Leilton S. Damascena² & Cássio van den Berg²

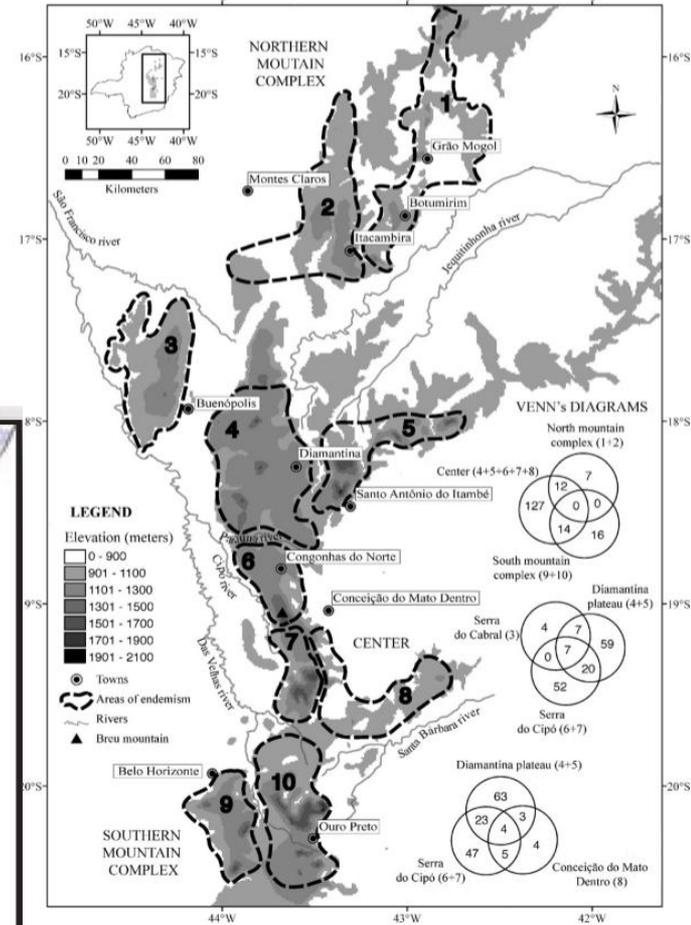


Ribeiro et al. 2014



Antonelli et al. 2010

Echternacht et al. 2011



Biological Journal of the Linnean Society, 2010, 100, 597-607. With 3 figures

Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae)

ALEXANDRE ANTONELLI^{1*}, CHRISTIANO F. VEROLA², CHRISTIAN PARISOD³ and A. LOVISA S. GUSTAFSSON³

Campos rupestres:

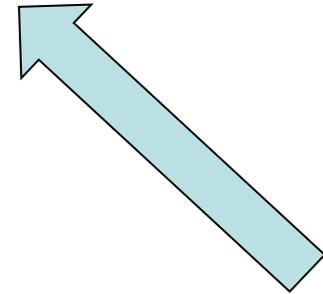
Altas taxas de **endemismo** (espécies e gêneros)
= altas taxas de especiação (época?)

Pseudotrimezia
IRIDACEAE
gênero endêmico
do Espinhaço em MG



-condições climáticas e edáficas extremas - rochas e areias expostas do alto de serras (e.g. Steyermark 1982)

- alta exposição a raios UV no topo de serras (e.g. Flenley 2011)



Why is pollen yellow? And why are there so many species in the tropical rain forest?

Flenley 2011

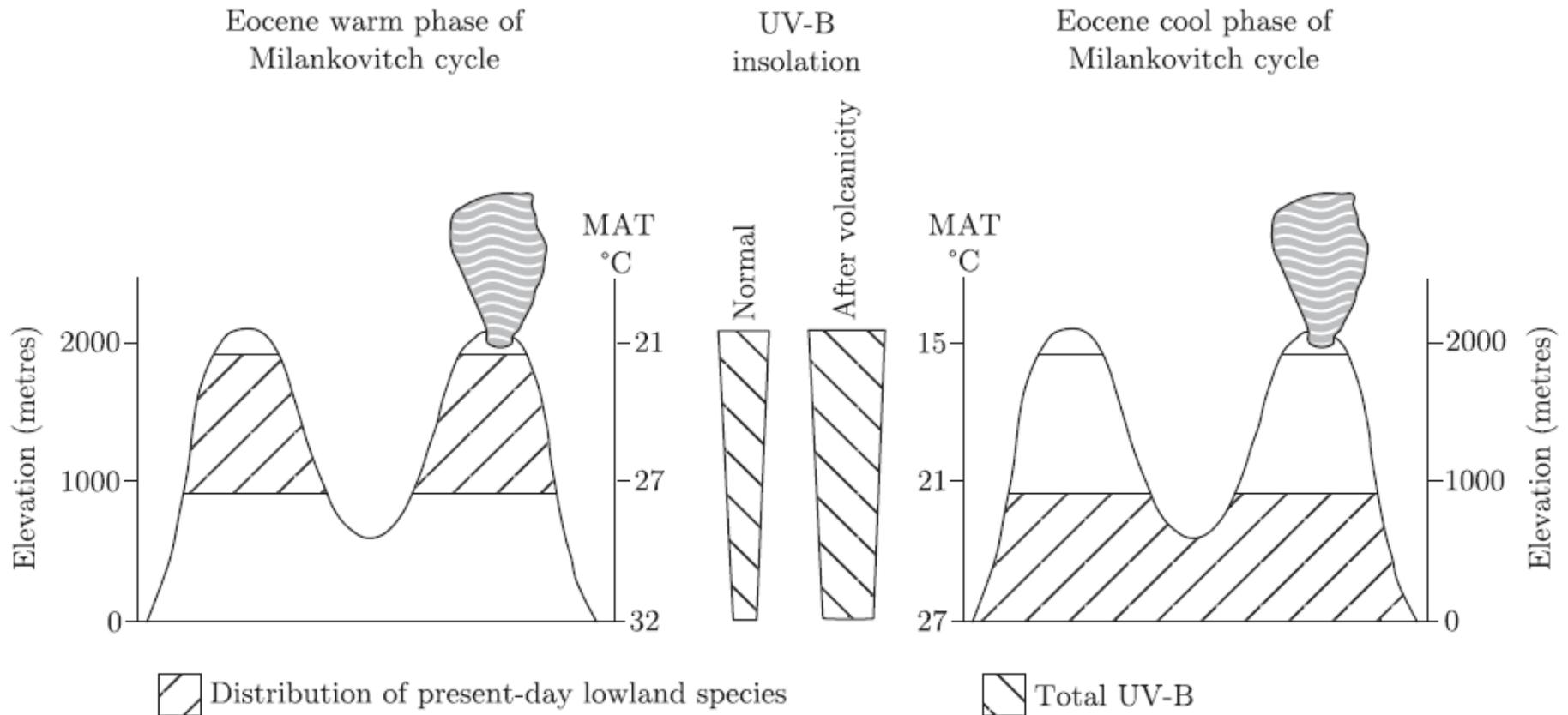


Figure 1 Diagram to show how a combination of appropriate topography, Eocene warmth, enhanced UV-B after volcanicity and Milankovitch cycling could lead to isolation, mutation, allopatric speciation, a species pump and increased biodiversity. The mountains are shown as one volcano and one resulting from uplift, as both are relevant to the Tertiary montane volcanic UV-B (TMVUVB) hypothesis. MAT, mean annual temperature.

THE TERTIARY MONTANE VOLCANIC UV-B HYPOTHESIS

It is now time to put together the following ideas expounded in the preceding pages:

1. Pollen appears to need protection from UV-B insolation.
2. UV-B insolation is mutagenic.
3. UV-B insolation increases with altitude.
4. Tropical montane vegetation experiences the highest UV-B insolation of any vegetation in the world.
5. Several tropical montane genera exhibit isolated occurrence of species on separate mountains.
6. Erupting volcanoes release SO₂ and other aerosols which destroy ozone and thus increase UV-B insolation.
7. These aerosols are active near their site of release but also spread widely.
8. Tropical regions have many volcanoes.
9. In the Permian there is evidence that strong volcanism was associated with mutagenesis, presumably by UV-B.
10. Volcanicity is associated with orogeny.
11. The last great orogeny was the Alpine, which started in the Eocene and was also active in the Early Miocene.
12. Palynological richness, used as a measure of palaeobiodiversity, shows rapid increases in the Palaeocene–Eocene and the Early Miocene.
13. The branching of DNA trees of tropical families occurs especially in the Palaeocene–Eocene and the Early Miocene.
14. Milankovitch cycles occurred throughout geological time, and would have produced vertical migrations of tropical taxa with a magnitude of *c.* 800 m.

Flenley 2011

Campos rupestres:

Altas taxas de **endemismo** (espécies e gêneros)
= altas taxas de especiação (época?)

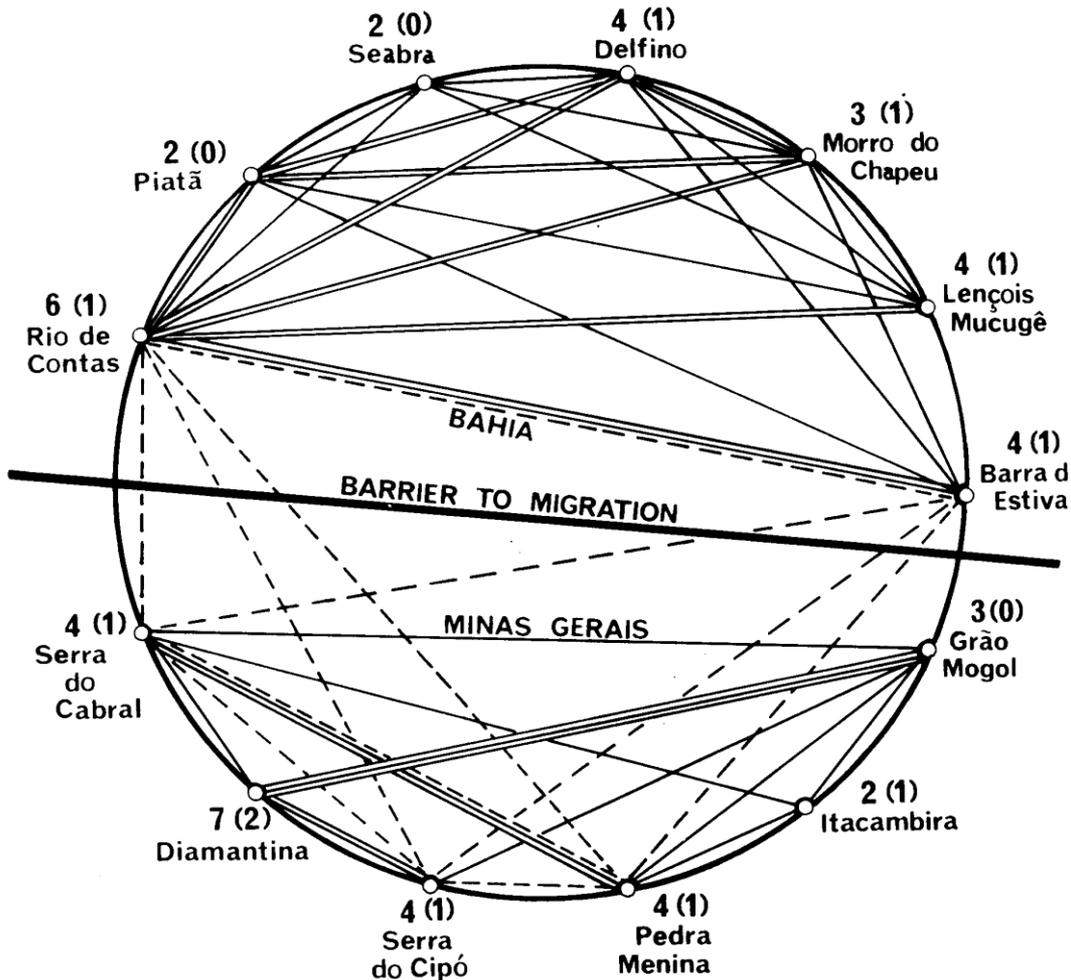
Pseudotrimezia
IRIDACEAE
gênero endêmico
do Espinhaço em MG



- condições climáticas e edáficas extremas - rochas e areias expostas do alto de serras (e.g. Steyermark 1982)
- alta exposição a raios UV no topo de serras (e.g. Flenley 2011)
- isolamento das populações aos topos de serras afastadas, flutuações paleoclimáticas (e.g. Harley 1995; Giulietti et al. 1997).

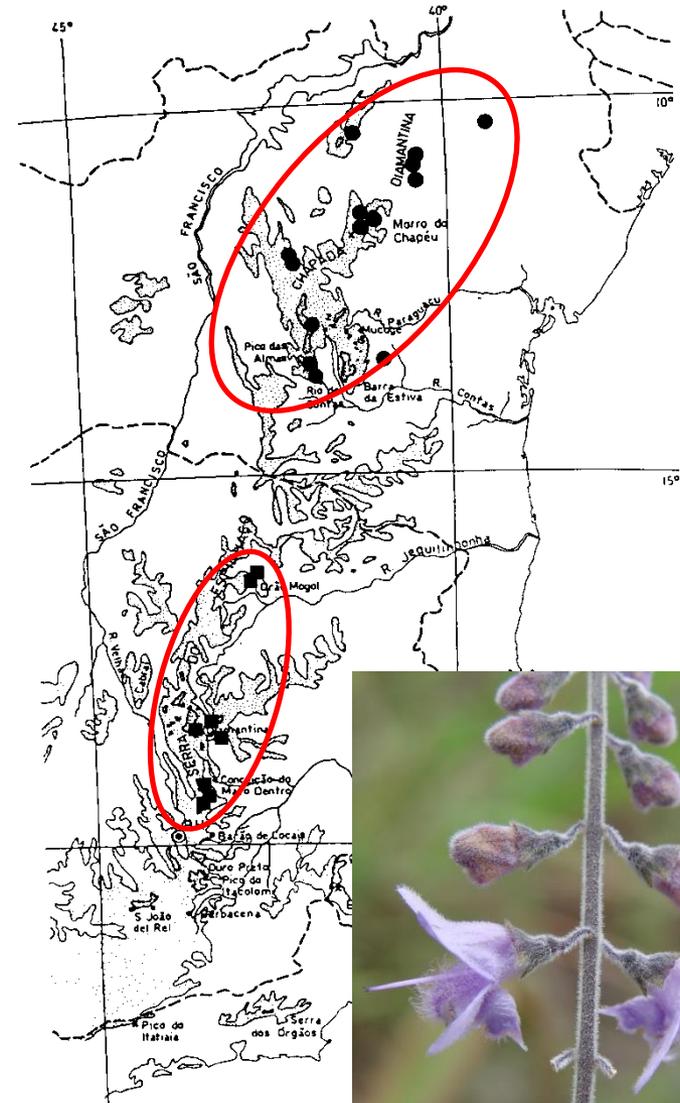
Espécies endêmicas - origem autóctone recente (**neoendemismo**) ou remanescentes de linhagens antigas (**paleoendemismo** - incluindo contração de espécies mais amplamente distribuídas no passado)
(e.g. Giulietti & Pirani 1988, Giulietti et al. 1997; Rando & Pirani 2011; Bitencourt & Rapini 2014; Conceição et al. 2016)

Isolamento das populações nos topos de serras afastadas na Cadeia do Espinhaço



Harley 1988

Distribution of *Eriope* species within campos rupestres of Minas Gerais and Bahia. Only *E. macrostachya* crosses the "barrier".



Complexo
Bulbophyllum exaltatum
Orchidaceae

Alozimas
Frequências alélicas
do locus MDH-1
(sistema enzimático malato-
dehidrogenase)
601 indivíduos, 29 pops

Ribeiro et al. 2001



www.orchidsonline.com.au

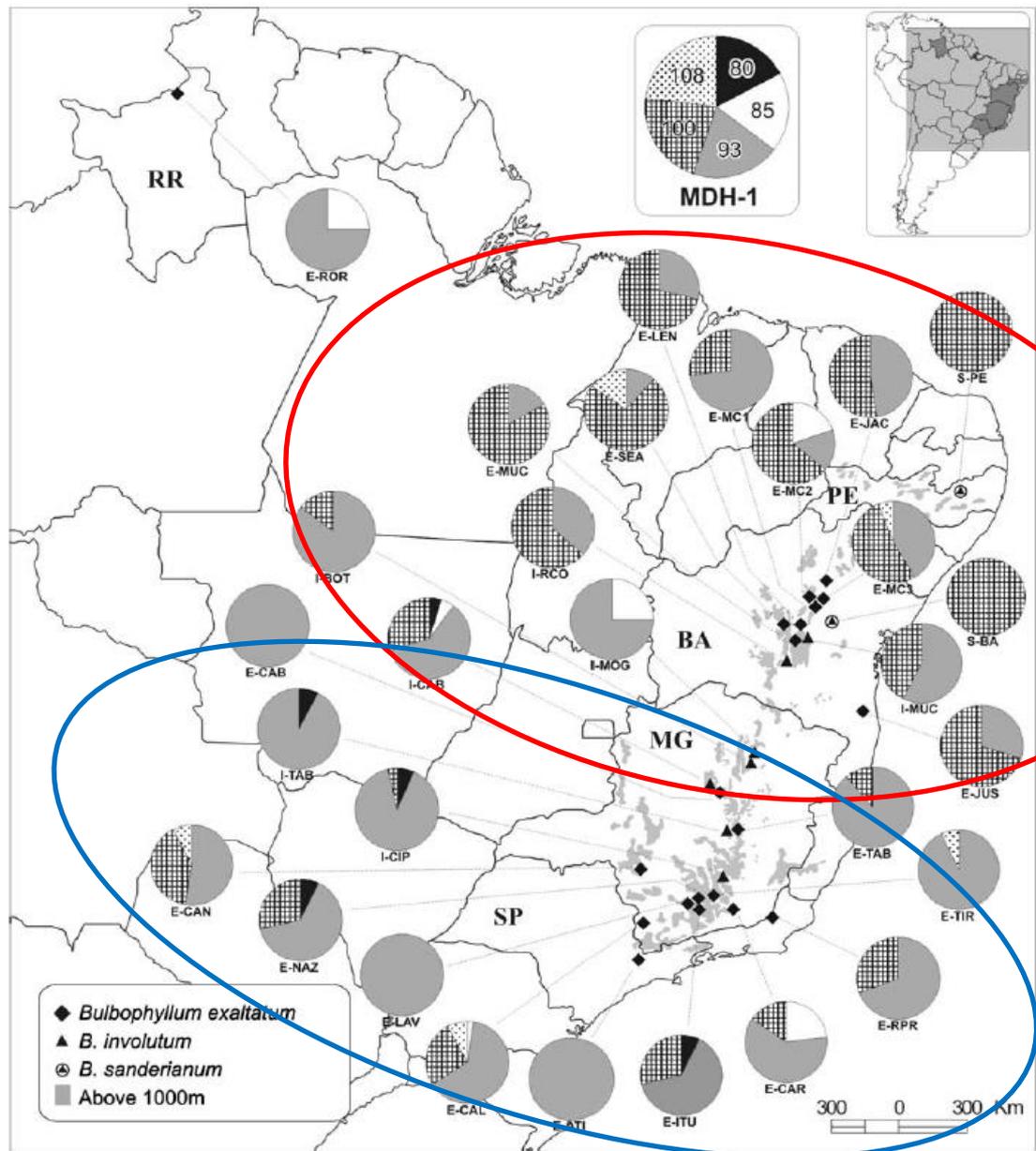


Fig. 4. Representation of the allelic frequencies of locus MDH-1 in the populations of *B. exaltatum* (E-), *B. involutum* (I-) and *B. sanderianum* (S-) studied. Notice the inversion in the relative frequency of the alleles 93 and 100 between the populations occurring in Minas Gerais and Bahia (except I-MUC and E-MC1). Acronyms for Brazilian states: BA Bahia; MG Minas Gerais; PE Pernambuco; RR Roraima; SP São Paulo. See Table 1 for the names of the populations

FILOGEOGRAFIA: processos genéticos demográficos

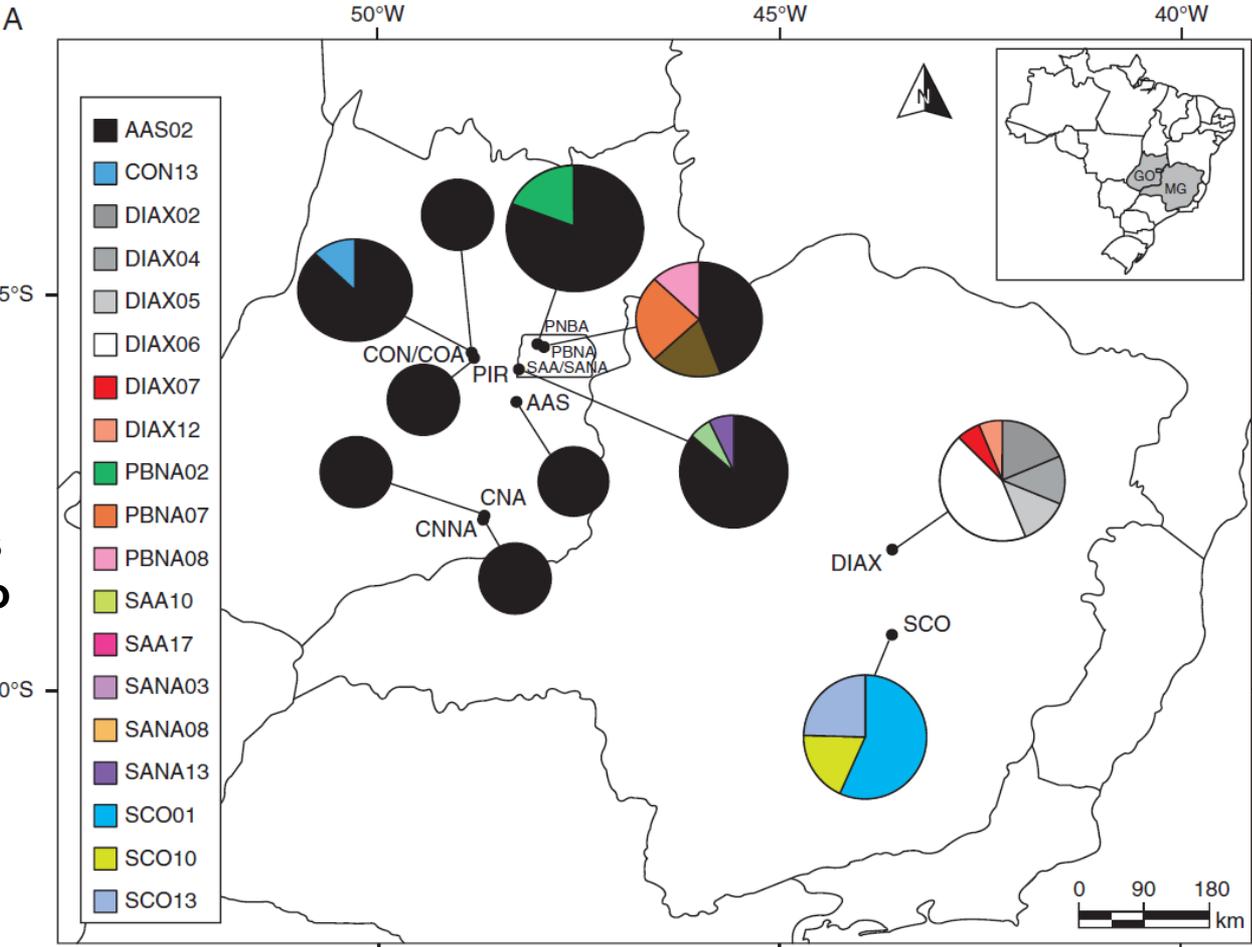
Lychnophora ericoides, Asteraceae

Collevatti et al. 2009

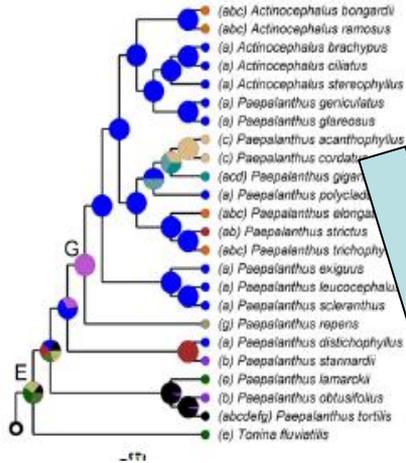


Collevatti et al. — Phylogeography and disjunct distribution of *Lychnophora*

Estruturação genética (distribuição de alelos) e distribuição espacial de populações da espécie indicam marcas de eventos Ambientais pretéritos como causadores de isolamento espacial e interrupção de fluxo gênico entre populações levando a aumento de divergência genética interpopulacional e diversificação.



Filogenias de vários grupos-chave



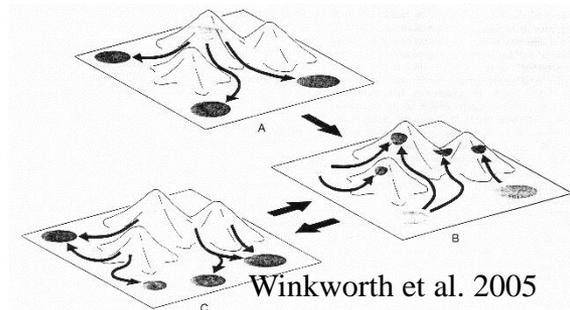
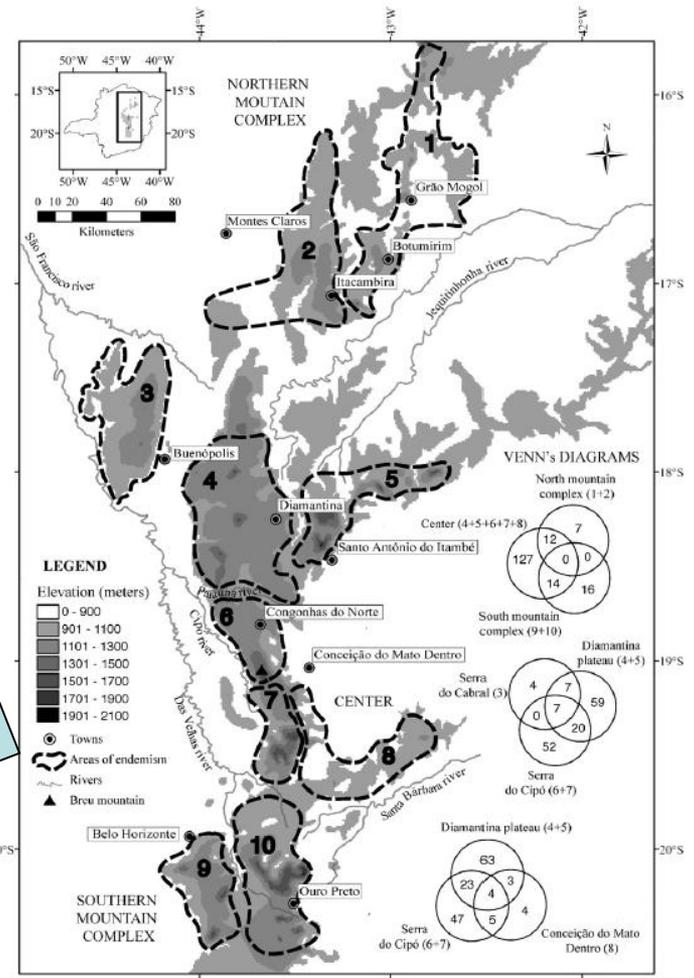
Áreas de Endemismo no Espinhaço em MG

1765 registros de 178 espécies endêmicas de plantas vasculares de 17 famílias

Echternacht et al. 2011

Avaliar modelos vigentes sobre biogeografia e diversificação em áreas montanhosas

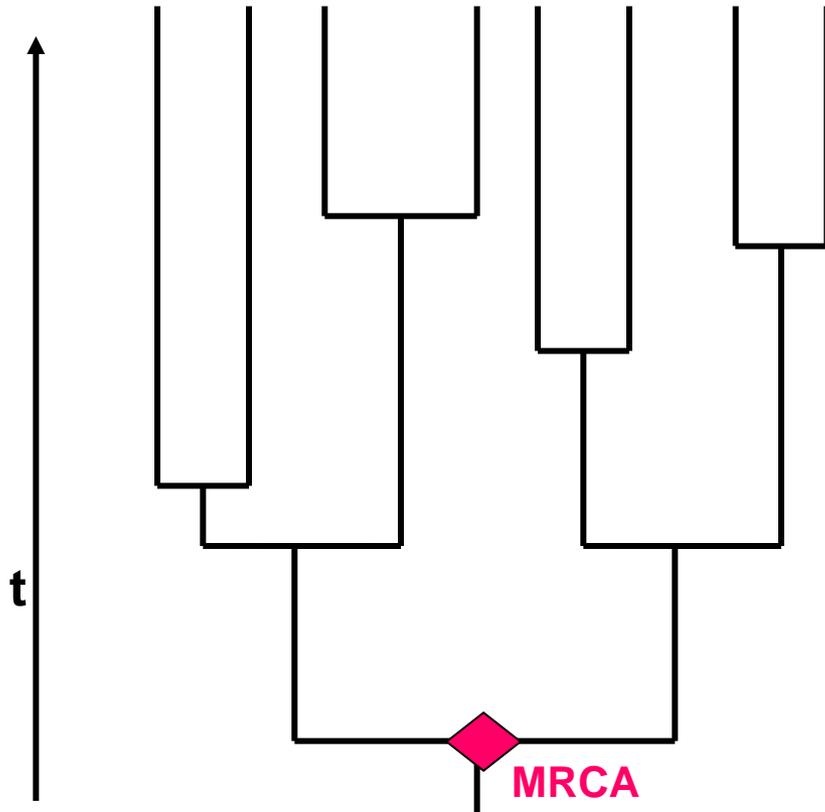
Antiguidade ou colonização recente do campo rupestre?



Winkworth et al. 2005

Modelo de MUSEU (Wallace 1878, Stebbins 1974)

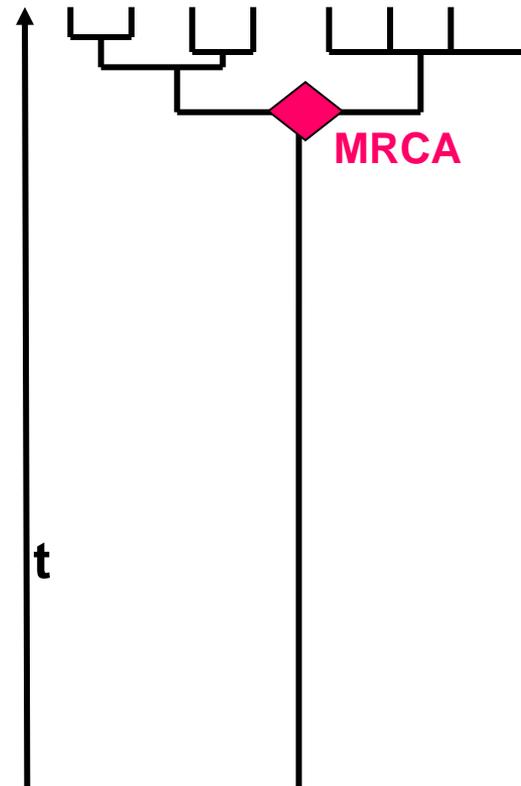
numerosas substituições de nucleotídeos
entre spp + topologia consistente com
origem das spp a partir do MRCA



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

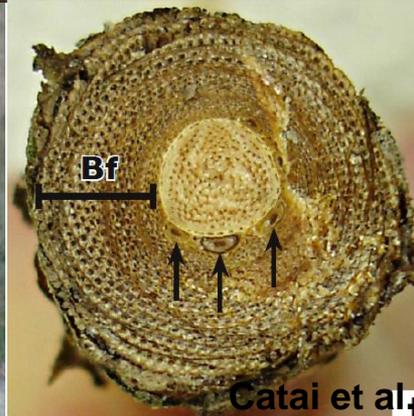
VELLOZIACEAE



Vellozia spiralis



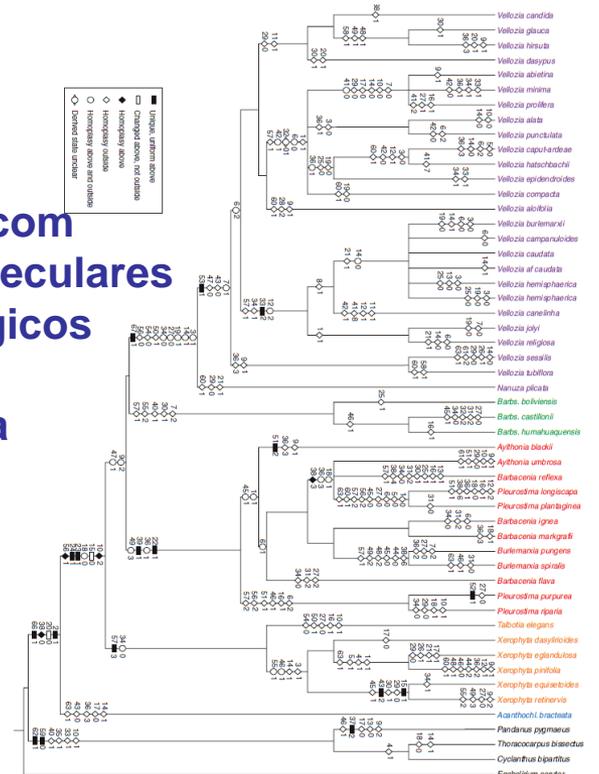
Vellozia glabra



Catai et al,

Filogenia com dados moleculares e morfológicos

Mello-Silva et al. 2011



Velloziaceae

Mello-Silva *et al.* 2011

Five vicarious genera from Gondwana: the Velloziaceae as shown by molecules and morphology

Renato Mello-Silva^{1,*}, Déborah Yara A. C. Santos¹, Maria Luiza F. Salatino¹, Lucimar B. Motta¹, Marina B. Cattai¹, Denise Sasaki¹, Juliana Lovo¹, Patrícia B. Pita¹, Cintia Rocini¹, Cristiane D. N. Rodrigues¹, Mehdi Zarrei² and Mark W. Chase²

¹Universidade de São Paulo, Departamento de Botânica, Rua do Matão 277, 05508-090 São Paulo, SP, Brazil and ²Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

*For correspondence. E-mail mellosil@usp.br

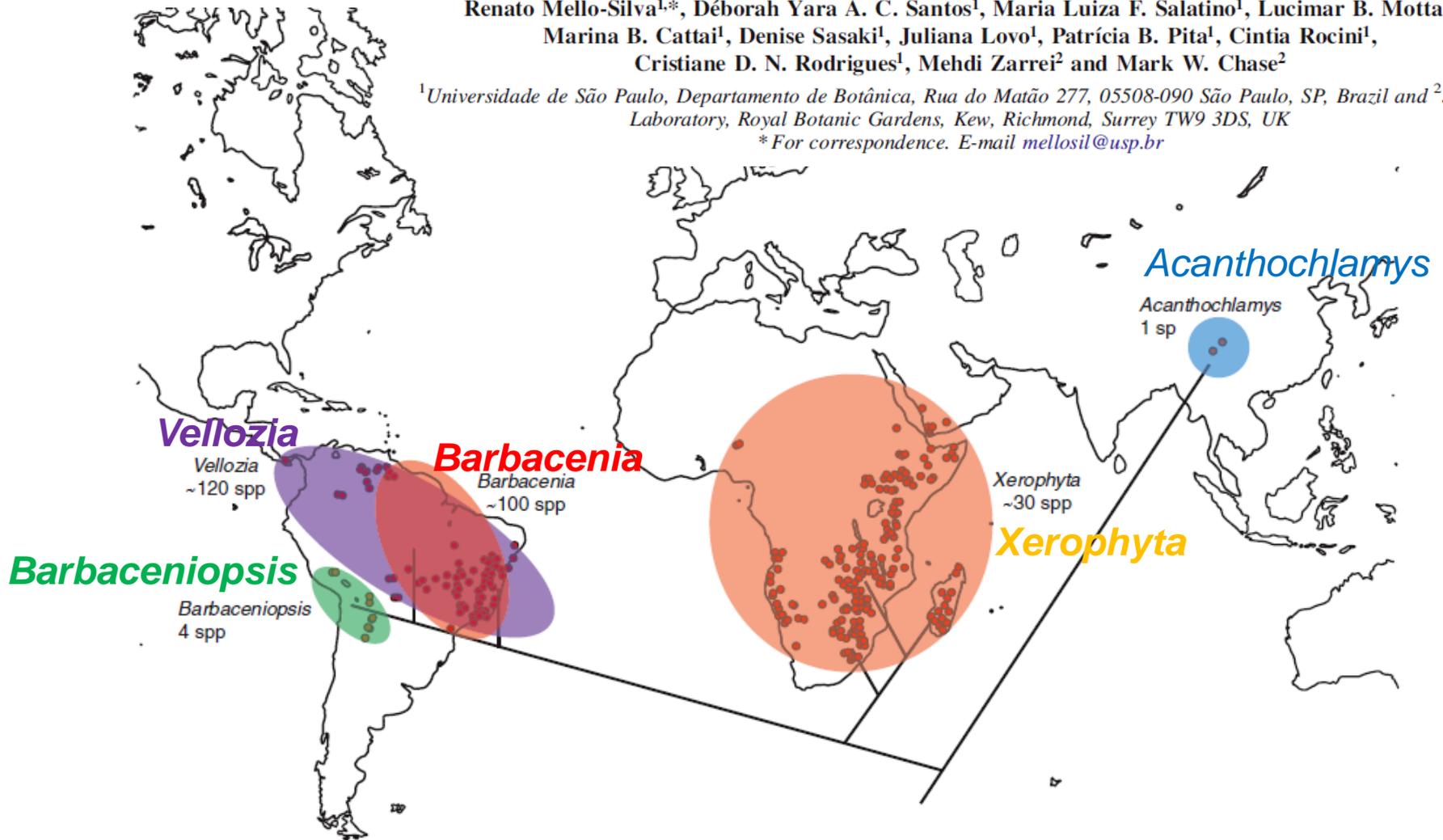


FIG. 4. Correlations between phylogenetic relationship of the five accepted genera of Velloziaceae and their geographical distribution.

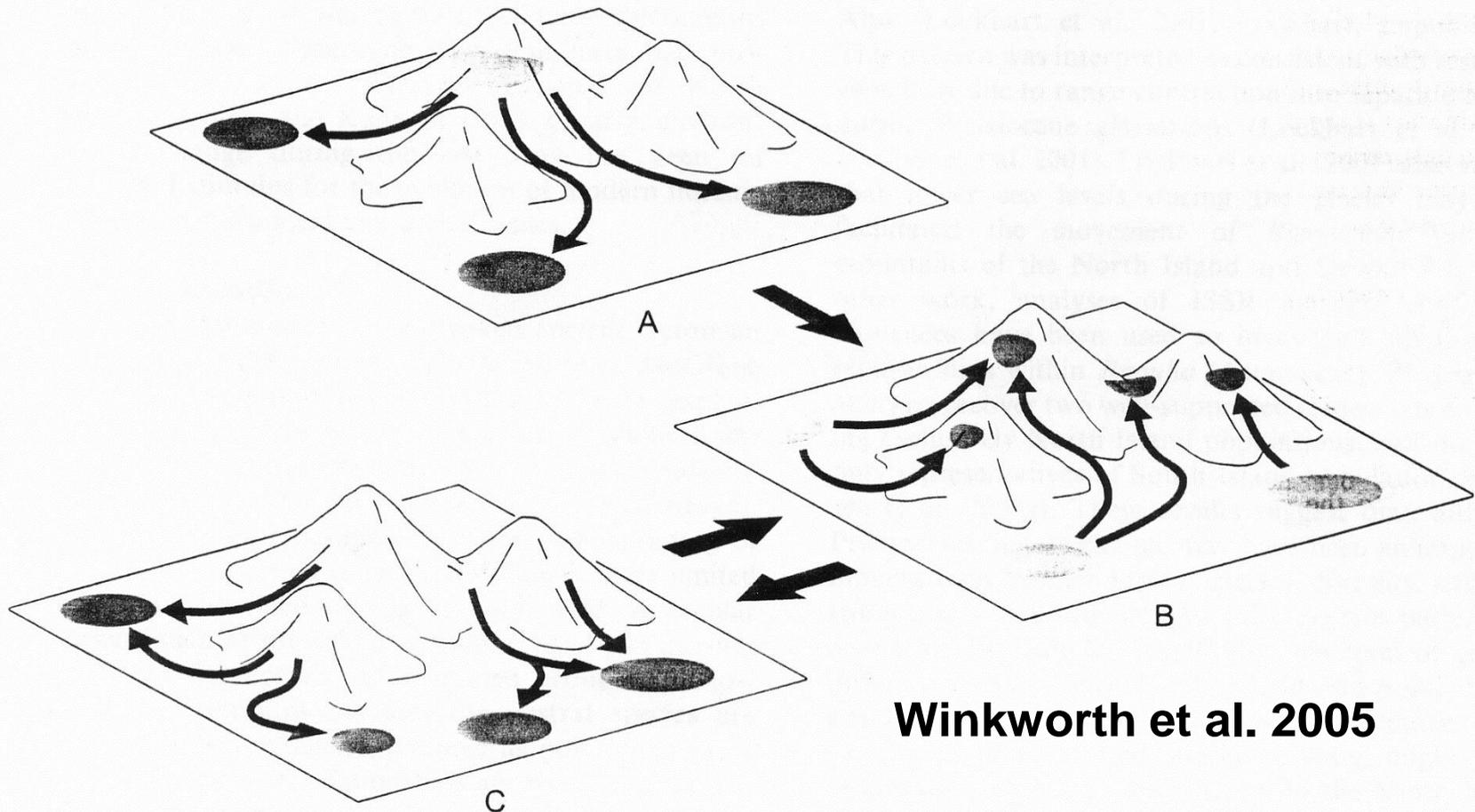
Modelo potencial para especiação rápida em linhagens montanas:

Morton 1976, Harley 1988

Diversificação provocada por ciclos alternados de contrações e expansões da área de distribuição das populações

**“bomba evolucionária”
(species pump)**

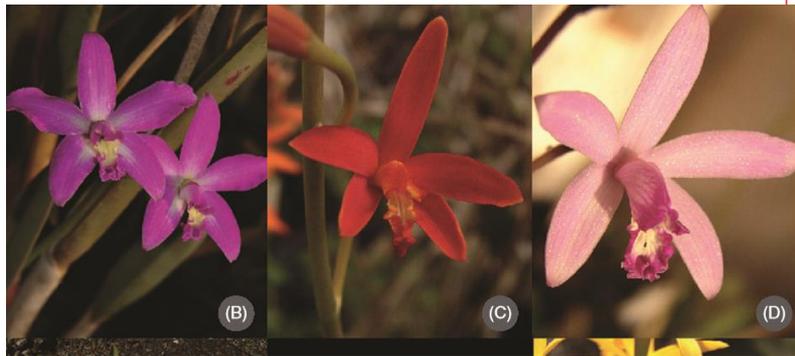
R.C. Winkworth et al. / *Organisms, Diversity & Evolution* 5 (2005) 237–247



Winkworth et al. 2005

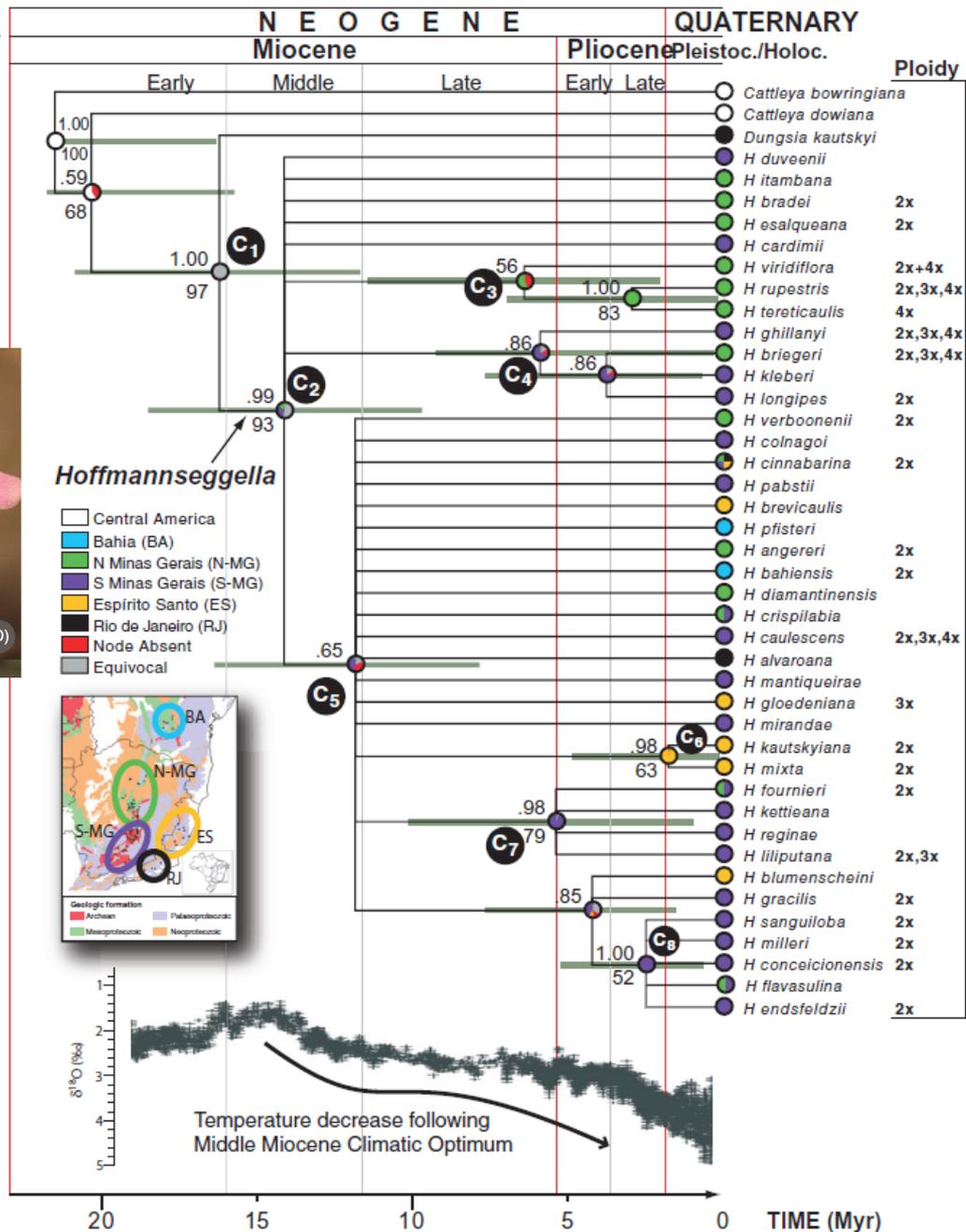
Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae)

ALEXANDRE ANTONELLI^{1*}, CHRISTIANO F. VEROLA², CHRISTIAN PARISOD³ and A. LOVISA S. GUSTAFSSON³



Hoffmannsegella Orchidaceae

Antonelli et al. 2010



Hoffmannsegella

Orchidaceae

Antonelli et al.
2010

Expansões das espécies
rupícolas por
corredores frios e secos
após o ótimo climático
do Mioceno médio

Poliploidização e
hibridação

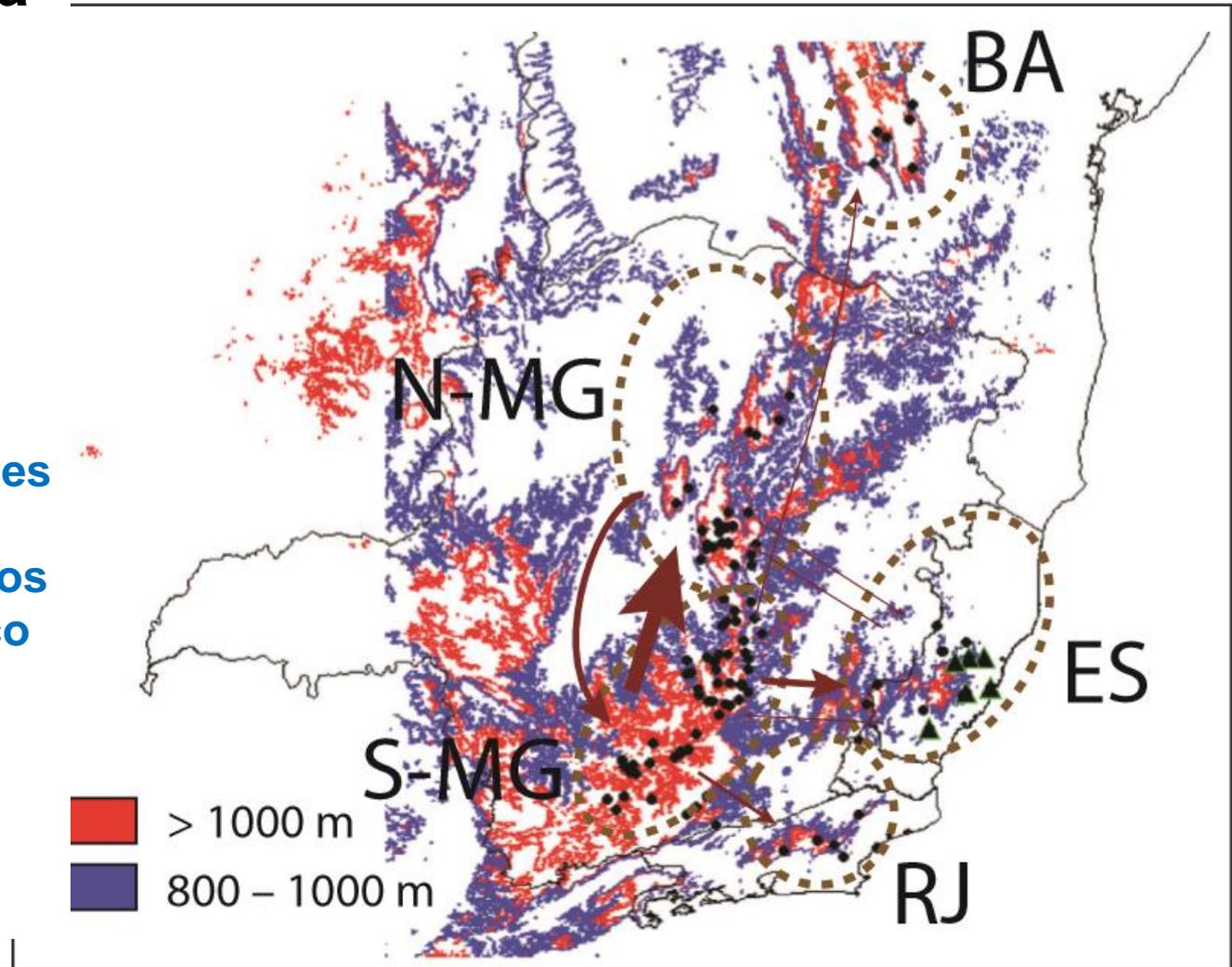


Figure 3. Range expansion of *Hoffmannsegella* in eastern Brazil. The present-day distribution of *Hoffmannsegella* (black dots) and its sister genus *Dungsia* (black triangles) are plotted. Patches in red represent areas higher than 1000 m and are equivalent to the current distribution of rocky savannas (Campos Rupestres). Patches in blue indicate areas in the range 800–1000 m, into which this vegetation type is expected to have expanded during dry (cooler) periods following the Mid-Miocene Climatic Optimum. The expansion of the Campos Rupestres appears to have created biotic corridors for the range expansion of *Hoffmannsegella*. Arrows represent the inferred directions of dispersals, with their width drawn in proportion to the relative frequency of dispersals between areas (Table 1). BA, Chapada Diamantina in the state of Bahia; N-MG, northern Minas Gerais; S-MG, southern Minas Gerais; RJ, Rio de Janeiro; ES, Espírito Santo.

**Grupos majoritariamente de formações abertas,
com clados campestres, montanos e savânicos:
(*centro de diversidade no campo rupestre*)**

Lychnophorinae - Asteraceae

Paepalanthoideae - Eriocaulaceae

***Chamaecrista* - Leguminosae**

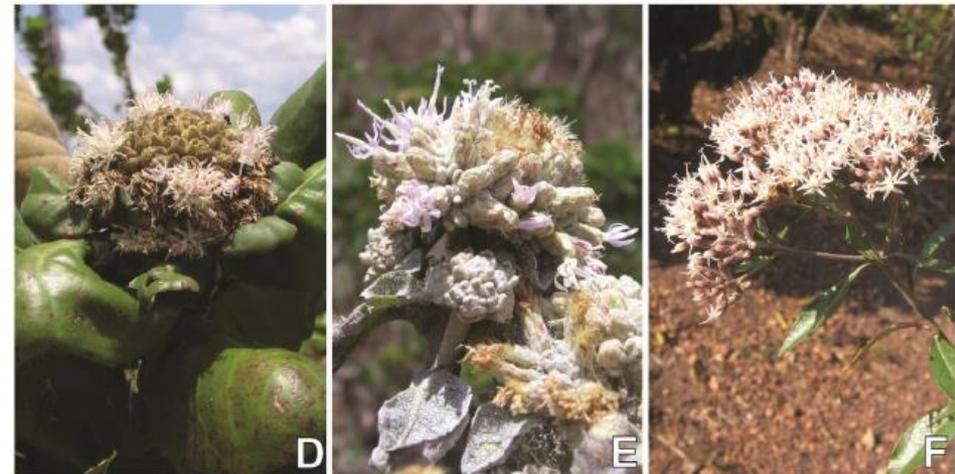
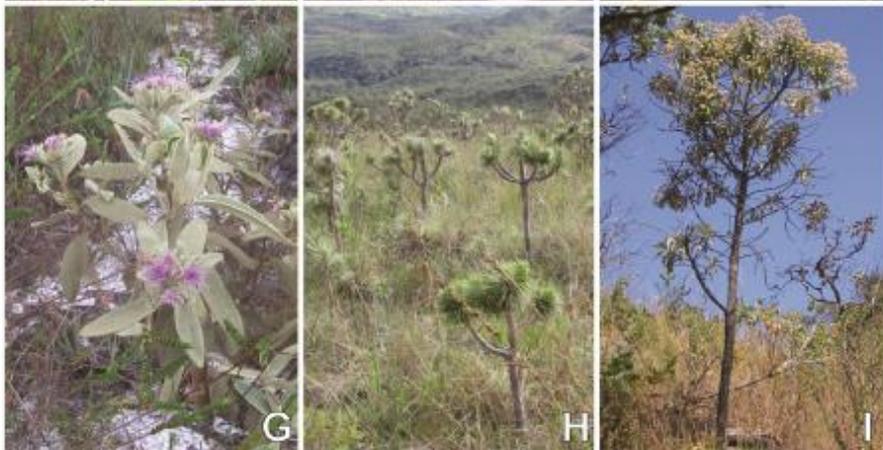
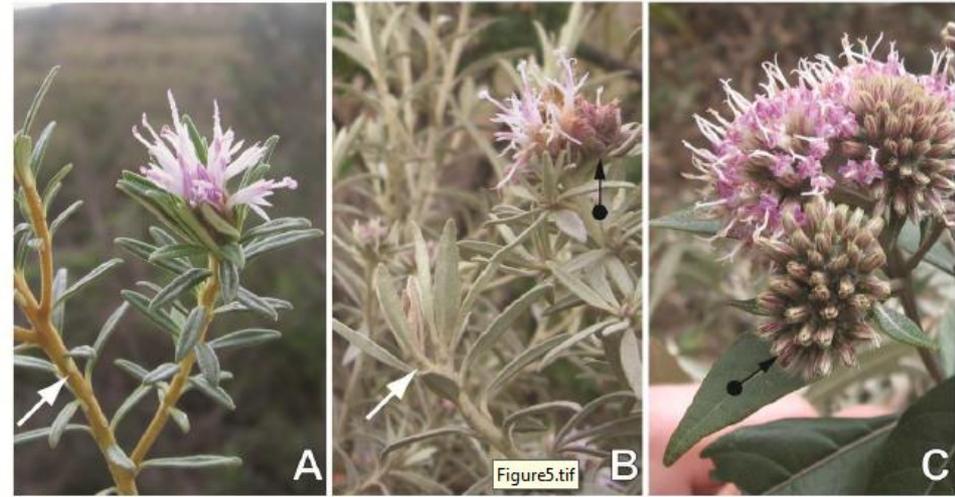
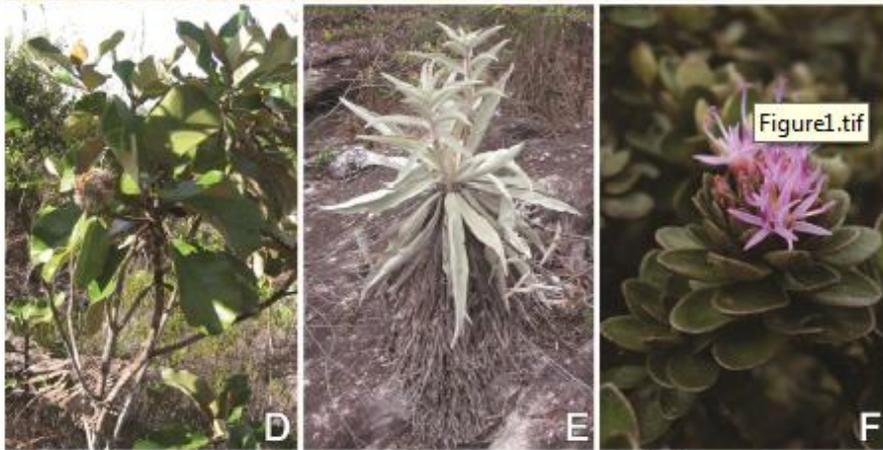
***Minaria* - Apocynaceae-Asclepiadoideae**

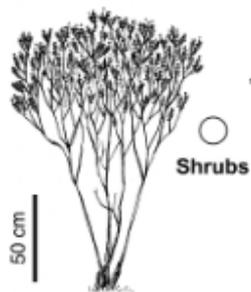
A Phylogenetic Analysis of Lychnophorinae (Asteraceae: Vernonieae) Based on Molecular and Morphological Data

Benoît Loeuille,^{1,3} João Semir,² Lúcia G. Lohmann,¹ and José R. Pirani¹

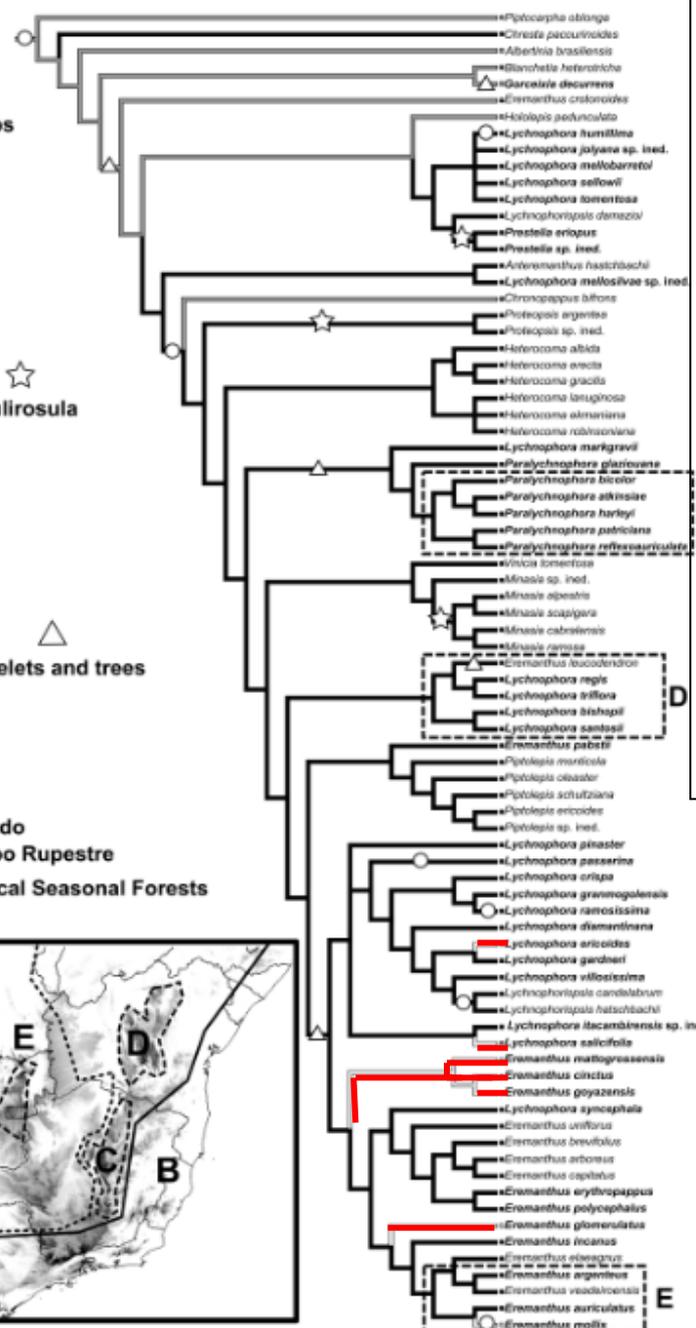
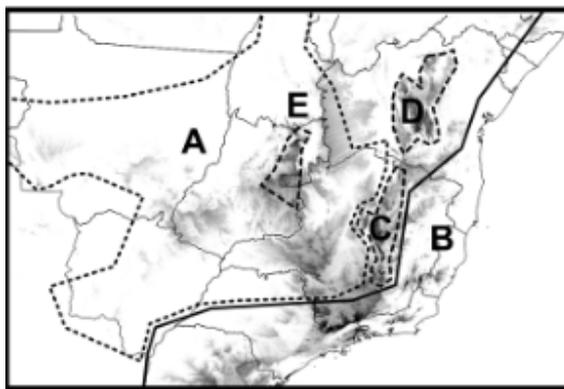
ASTERACEAE – Vernonieae Lychnophorinae

Loeuille *et al.* 2015





Cerrado
 Campo Rupestre
 Tropical Seasonal Forests



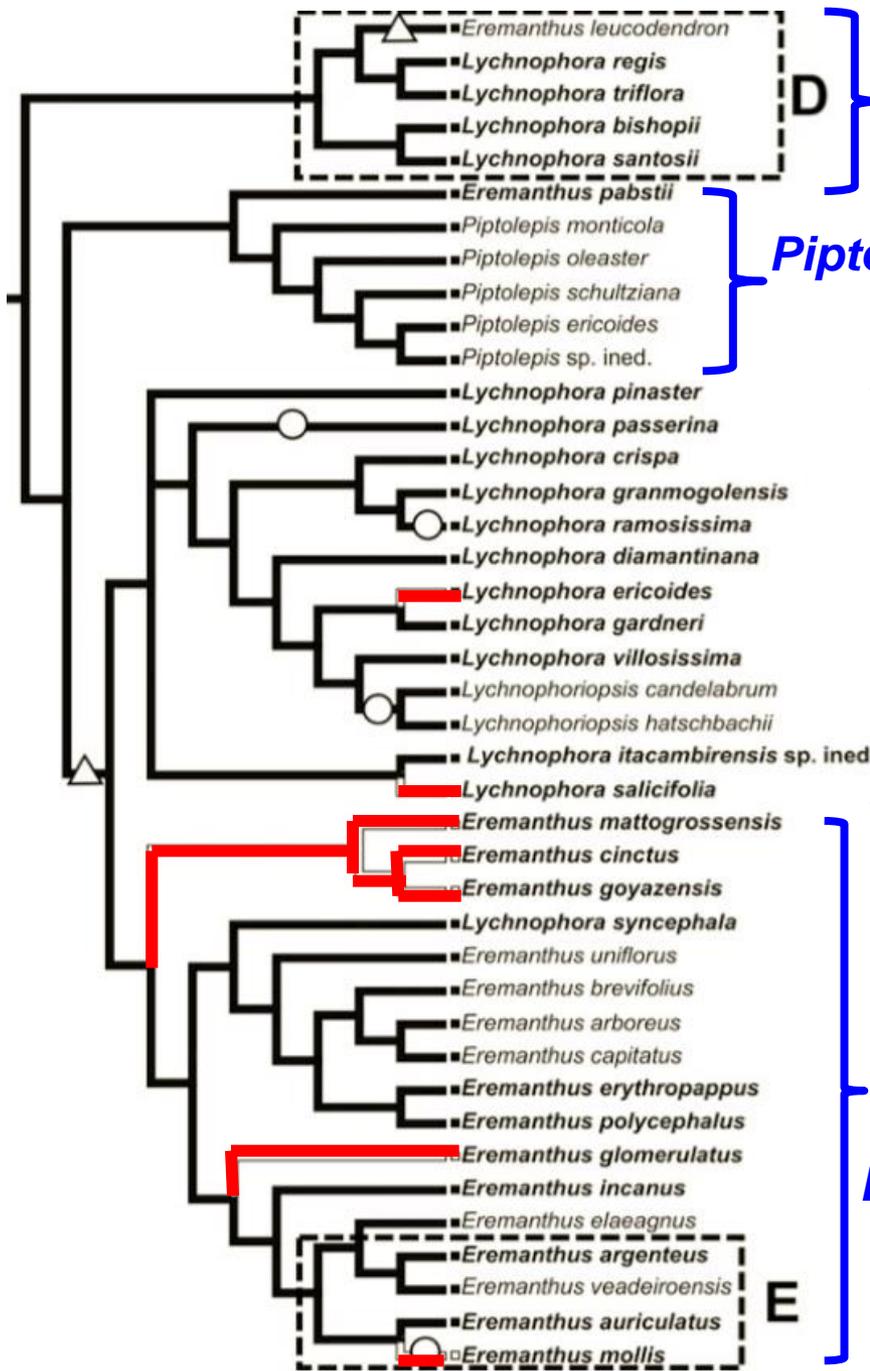
ASTERACEAE
Vernoniaeae
Lychnophorinae

100 spp - 18 genera
 mostly in the Cerrado Domain,
 higher diversity in
campo rupestre

phylogeny based on
 4 molecular regions
 (ETS, ITS, *ndhF*, *rp32-trnL*)
 + morphological dataset

Loeuille et al. 2015





Lychnophorella

ASTERACEAE
Vernoniae

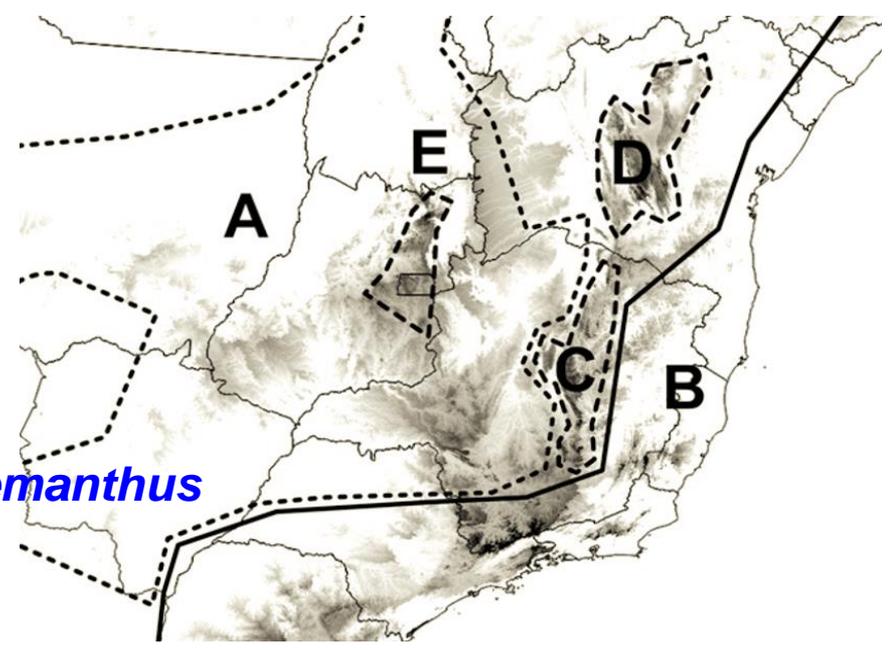
Piptolepis

Lychnophorinae

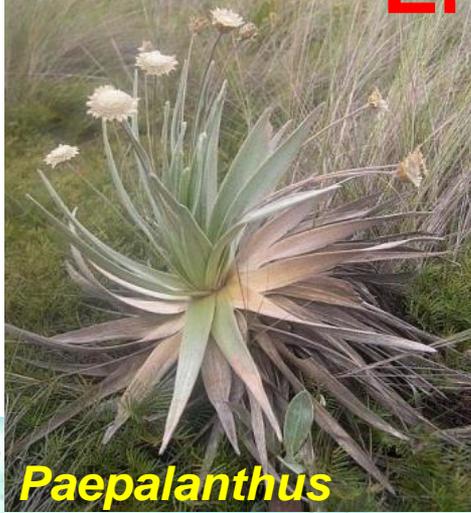
Loeulle et al. 2015

Lychnophora s.s.

Eremanthus



Eriocaulaceae



Paepalanthus

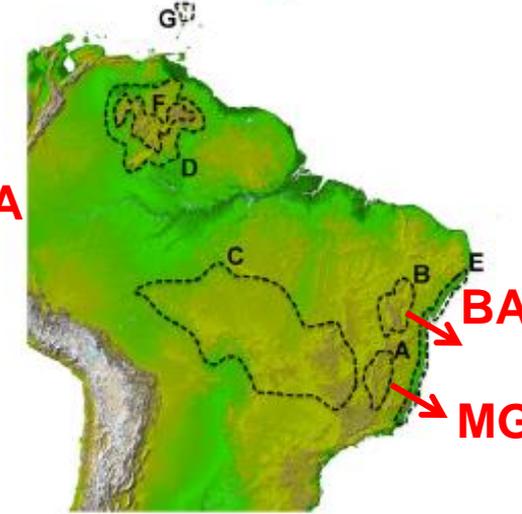
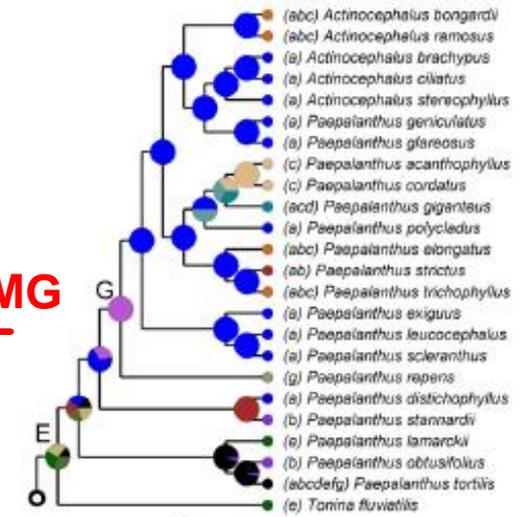
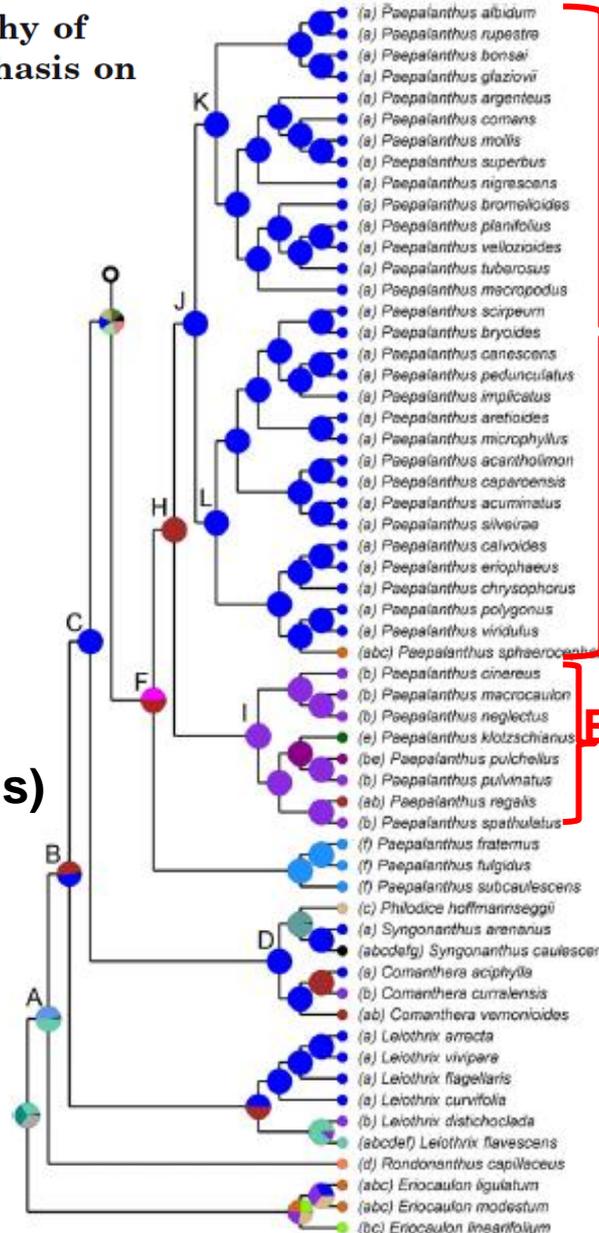


Actinocephalus



Eriocaulaceae - Paepalanthoideae

Molecular phylogenetics and biogeography of Neotropical Paepalanthoideae with emphasis on Brazilian *Paepalanthus* (Eriocaulaceae)



- (a) Espinhaço Range in Minas Gerais
- (b) Espinhaço Range in Bahia
- (c) Cerrado
- (d) Lowland Guianan Savannas
- (e) Restingas
- (f) Tepuis
- (g) Caribbean

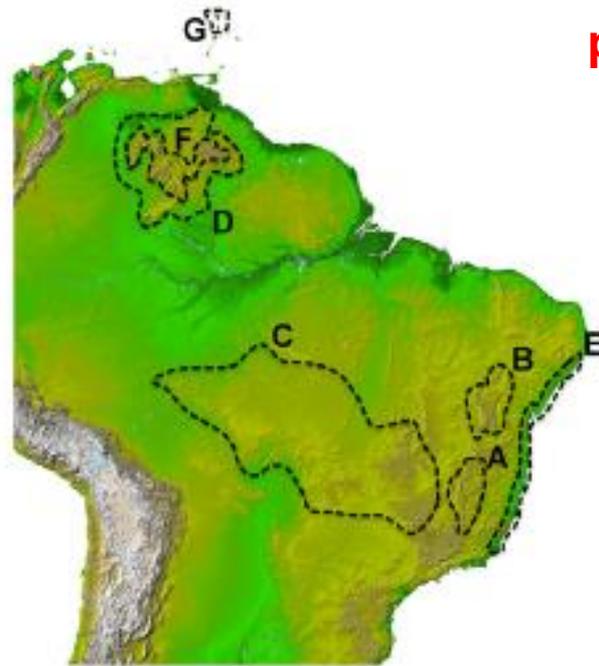
Clade H:
split between
clade I (Espinhaço Bahia)
and
Clade J (Espinhaço Minas Gerais)

Clade G:
diversification of
P. sect. Diphyomene
after difusion
to the Cerrado

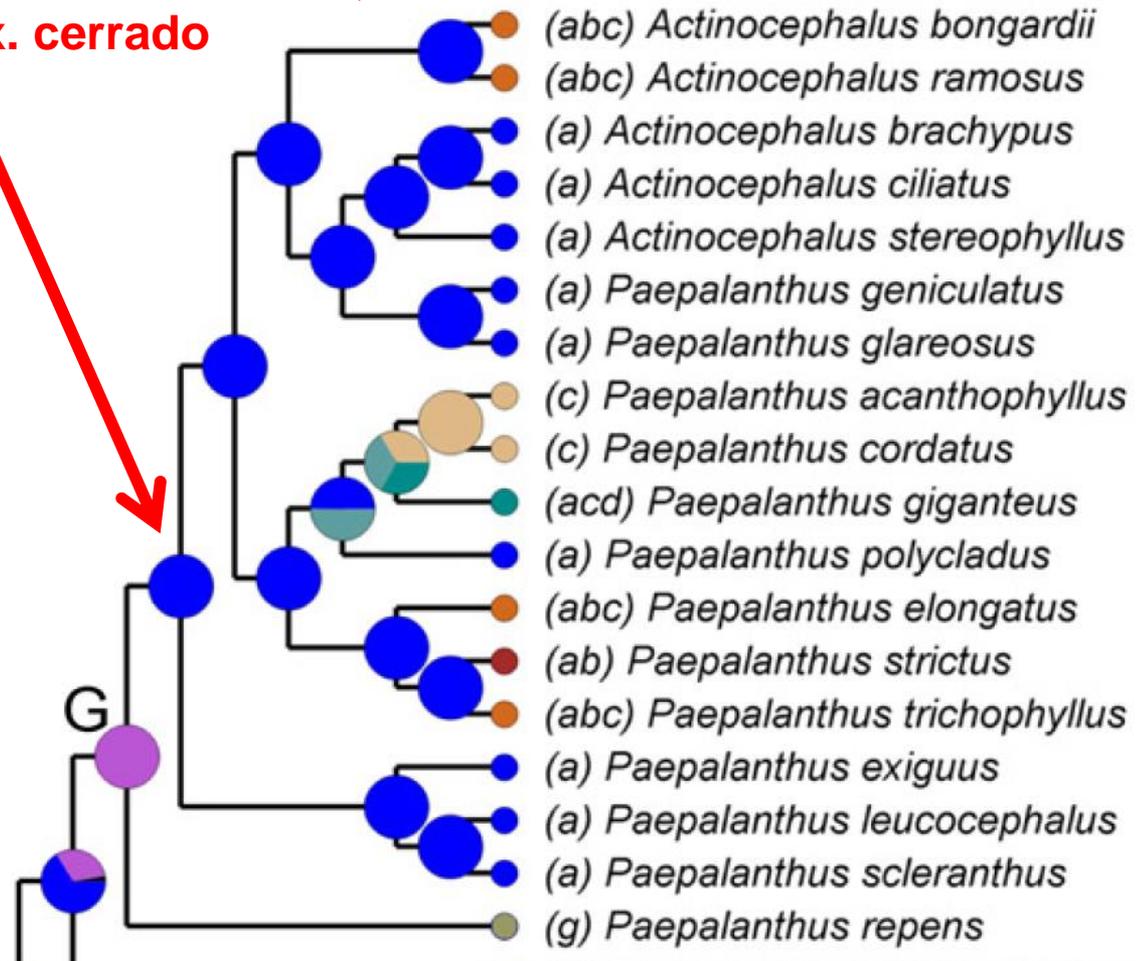
Eriocaulaceae - Paepalanthoideae



Clado predominantemente de campo rupestre com transições para outros ecossistemas, por ex. cerrado



- (a) Espinhaço Range in Minas Gerais
- (b) Espinhaço Range in Bahia
- (c) Cerrado
- (d) Lowland Guianan Savannas
- (e) Restingas
- (f) Tepuis
- (g) Caribbean





TAXON — 3 Dec 2014: 12 pp.

Ribeiro & al. • Plant diversification in the Espinhaço Range

Minaria Apocynaceae- Asclepiadoideae

Ribeiro et al. 2014

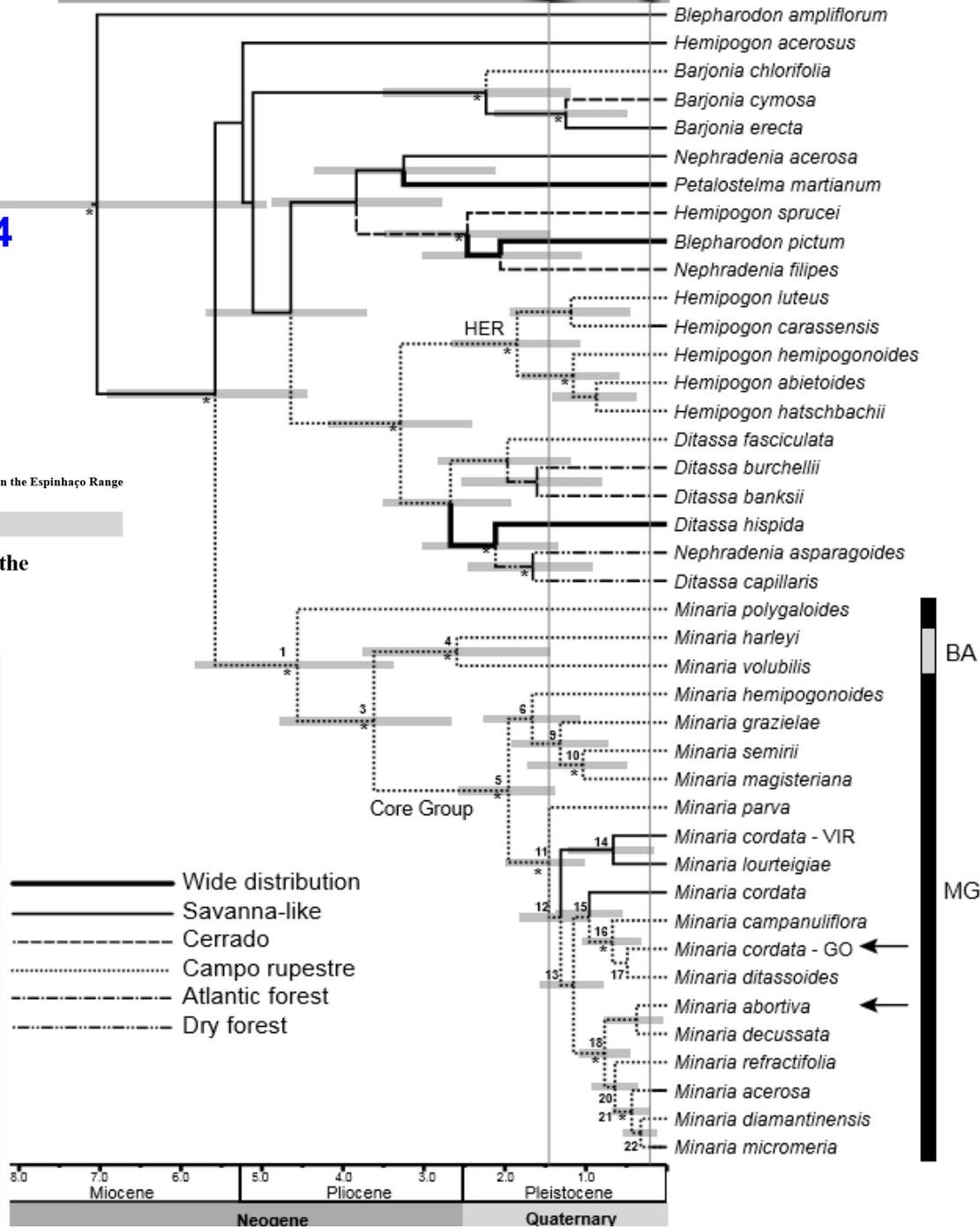
Plant diversification in the Espinhaço Range: Insights from the biogeography of *Minaria* (Apocynaceae)

Patricia Luz Ribeiro,^{1,2} Alessandro Rapini,² Leilton S. Damascena² & Cássio van den Berg²



© D. Zappi/RBG, Kew

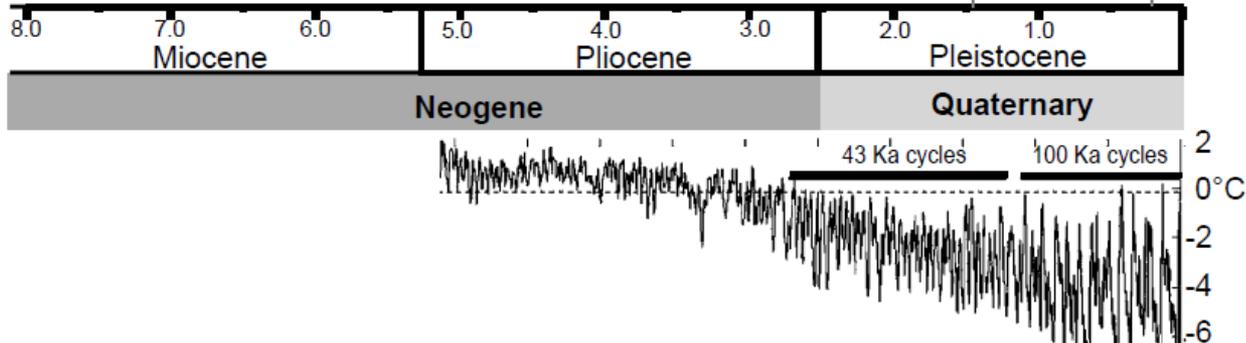
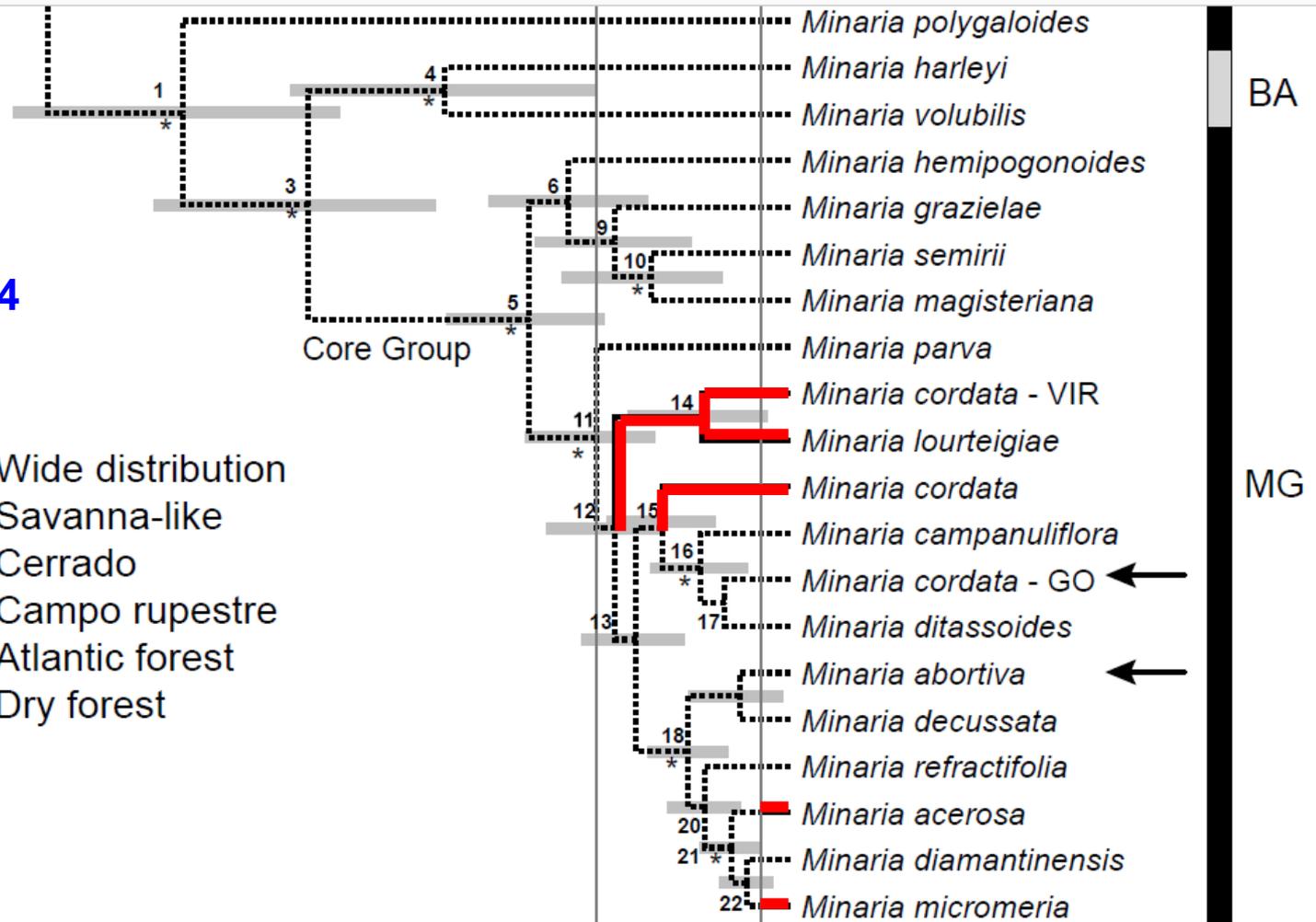
- Wide distribution
- Savanna-like
- - - - - Cerrado
- Campo rupestre
- - - - - Atlantic forest
- - - - - Dry forest



Minaria
Apocynaceae-
Asclepiadoideae

Ribeiro et al. 2014

-  Wide distribution
-  Savanna-like
-  Cerrado
-  Campo rupestre
-  Atlantic forest
-  Dry forest

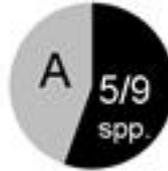


Chamaecrista LEGUMINOSAE

Rando et al. 2016
et in prep.



Amazon



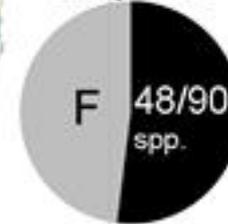
Cerrado



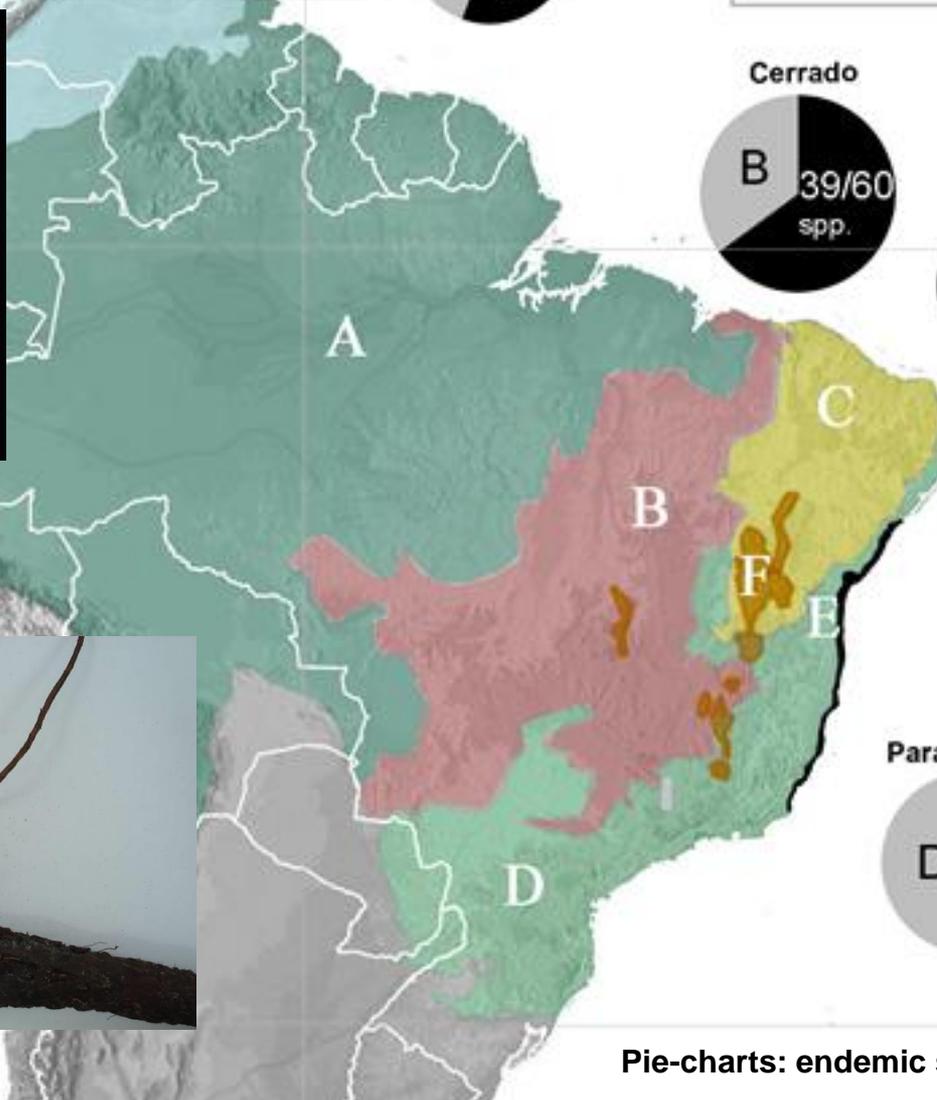
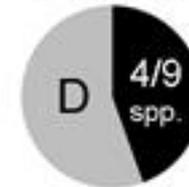
Caatinga



C. rupestris



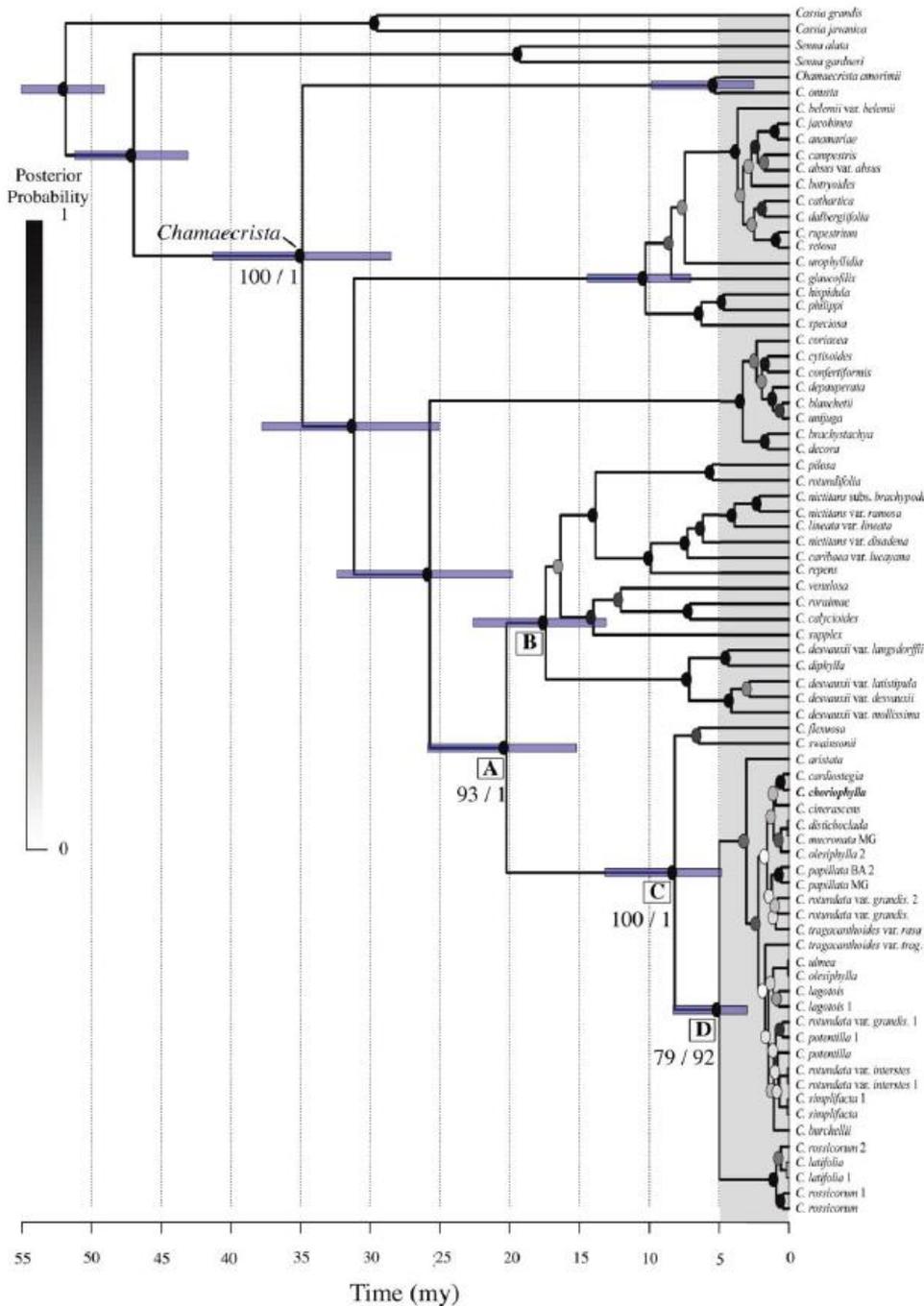
Paranaense



Pie-charts: endemic spp / total spp in each area

Chamaecrista LEGUMINOSAE

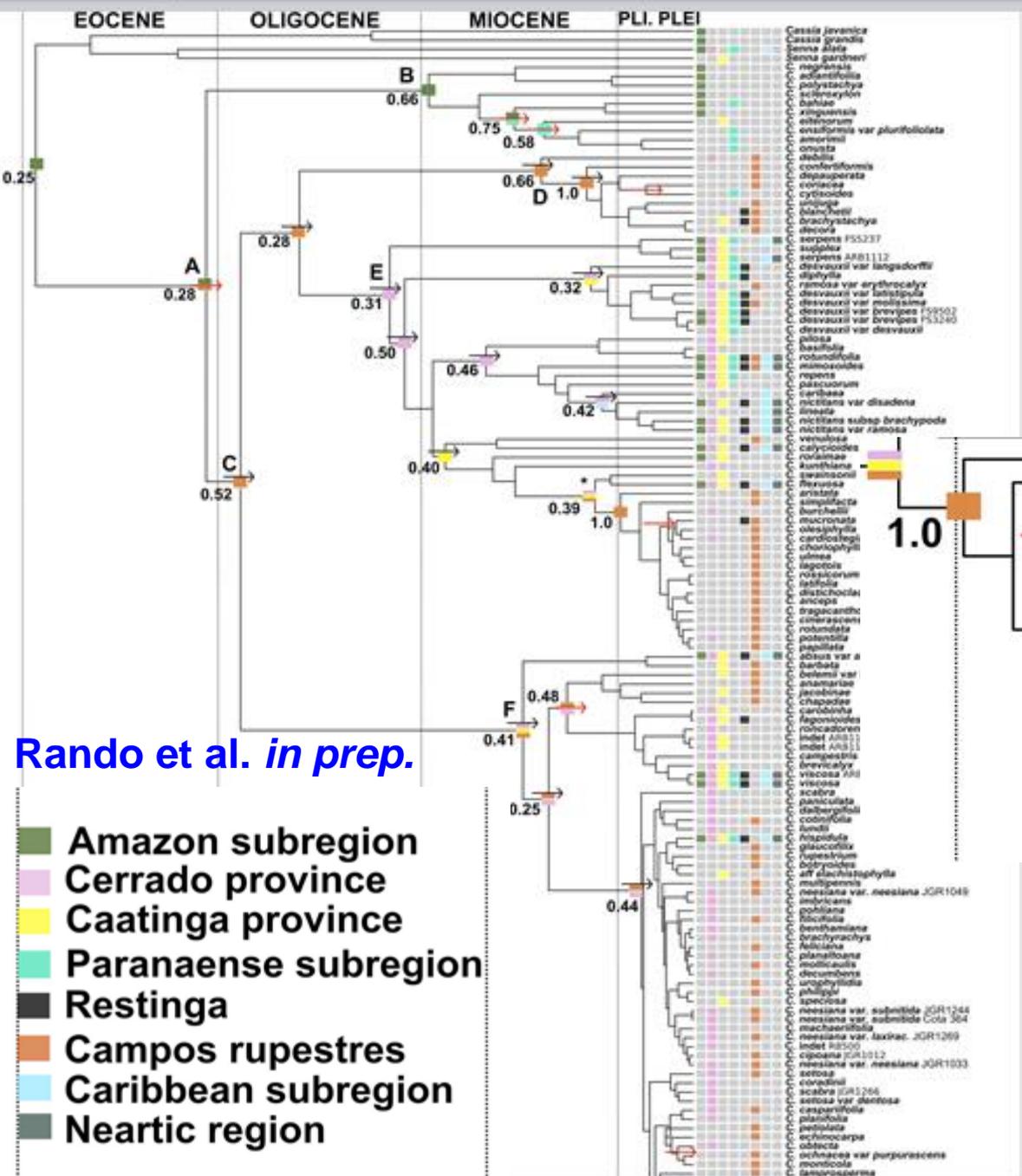
Rando et al. 2016



Clado D =
Chamaecrista
 sect. **Chamaecrista**
 ser. **Coriaceae**

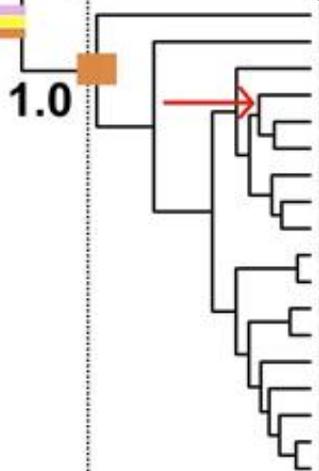
Diversificação ativa
 no campo rupestre
 nos últimos 3 M.a.

Chamaecrista LEGUMINOSAE



Rando et al. *in prep.*

- Amazon subregion
- Cerrado province
- Caatinga province
- Paranaense subregion
- Restinga
- Campos rupestres
- Caribbean subregion
- Neartic region



- *C. aristata*
- *C. simpliflora*
- *C. burchellii*
- *C. mucronata*
- *C. olesiphylla*
- *C. cardiostegia*
- *C. choriophylla*
- *C. ulmea*
- *C. lagotois*
- *C. rossicorum*
- *C. latifolia*
- *C. distichoclada*
- *C. anceps*
- *C. tragacanthoides*
- *C. cinerascens*
- *C. rotundata*
- *C. potentilla*
- *C. papillata*



2 geographic models using DEC with ML inference

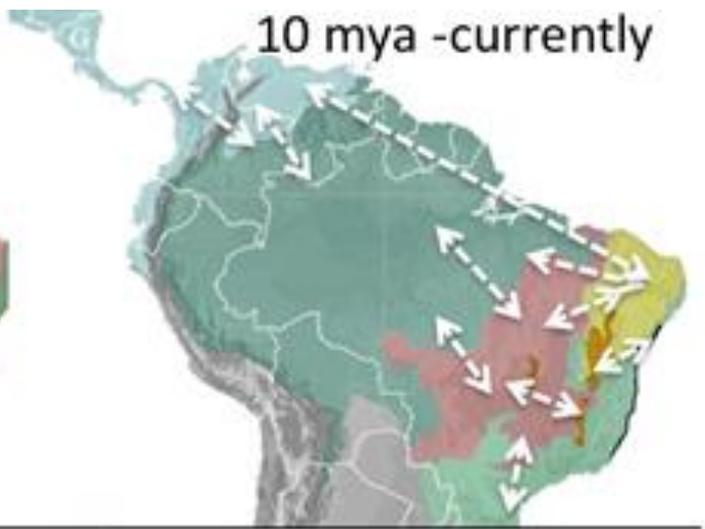
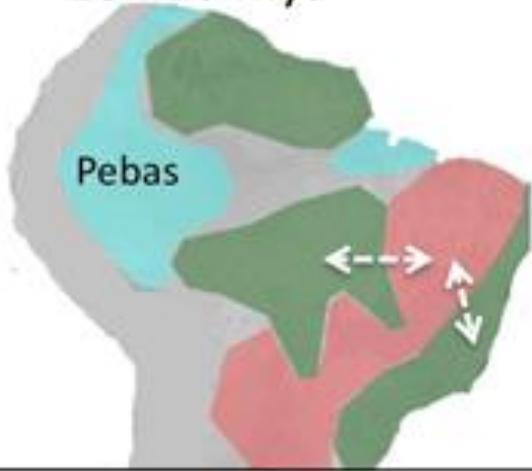
Rando et al. *in prep.*

53- 28 mya

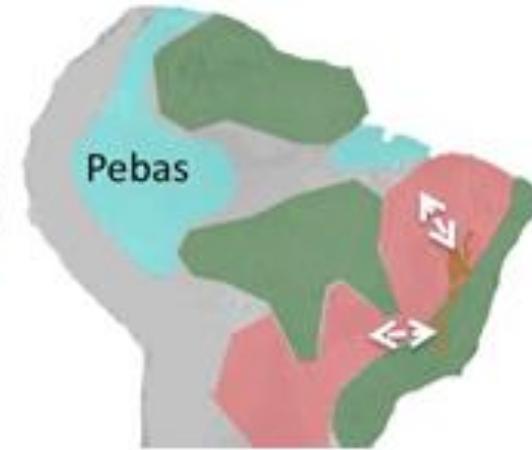
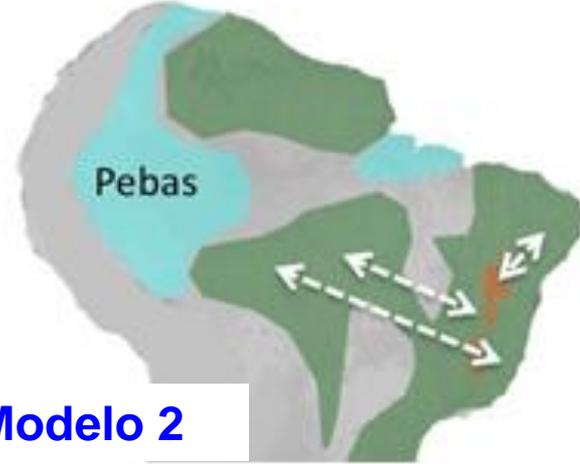
28 - 10 mya

10 mya -currently

Modelo 1



Modelo 2



Maps based on Antonelli et al. (2009) with additional data from Gottsberger & Gottsberger (2006).

Origem e diversificação da flora dos campos rupestres

1. Modelo de bomba evolucionária (*species pump*)

(e.g. Harley 1988, 1995, Rando & Pirani 2011)

Antonelli et al. 2000 – *Hoffmansegella* (Orchidaceae)

Trovó et al. 2013 – Paepalantoideae (Eriocaulaceae)

Ribeiro et al. 2014 - *Minaria* (Asclepiadoideae)

Loeuille et al. 2015 - Lychnophorinae (Asteraceae)

Rando et al. 2016 et in prep. – *Chamaecrista* (Leguminosae)

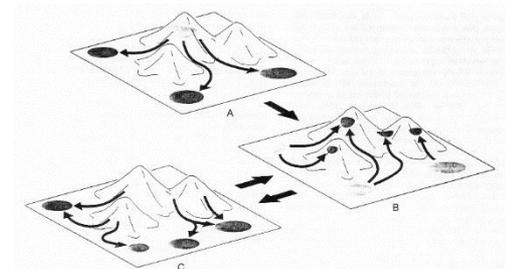
Diversificação no Neógeno Superior,

por isolamento geográfico e irradiação (*Minaria*, Paepalantoideae, Lychnophorinae),

podendo envolver hibridação (*Hoffmansegella*, algumas Lychnophorinae?);

tendência geral à retração de campos rupestres, interrompida por poucos episódios de expansão no Pleistoceno, que teriam estimulado diversificação por proverem fontes para novas retrações.

Os trabalhos sugerem que as linhagens de campos rupestres precederam a expansão das savanas regidas por fogo (cerrados)



Origem e diversificação da flora dos campos rupestres

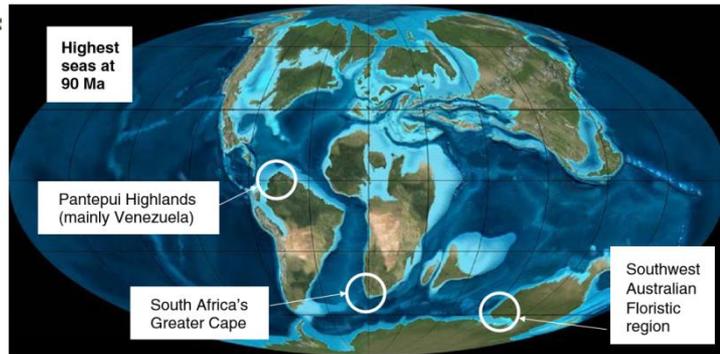
2. Modelo de Paisagens Antigas Estáveis (OLS – *Old Stable Landscapes*)

Teoria de OCBIL - Hopper 2009 - reelaborada por **Mucina & Wardell-Johnson 2011**

Plant Soil (2009) 322:49–86
DOI 10.1007/s11104-009-0068-0

REVIEW ARTICLE

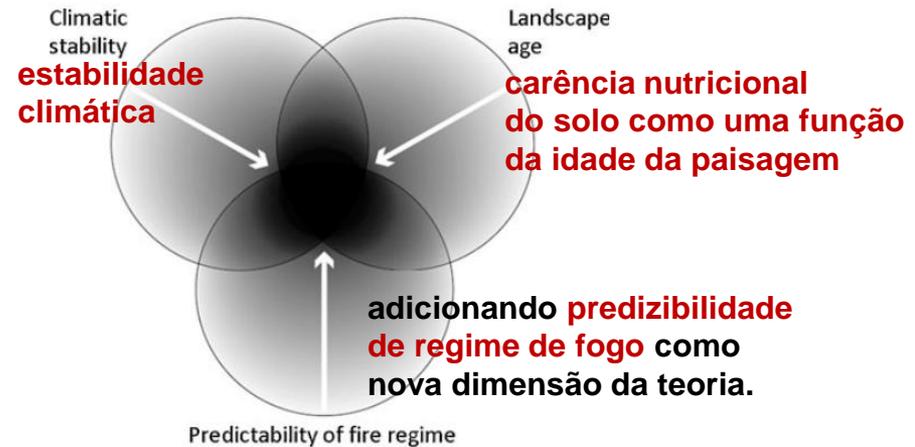
OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes



Plant Soil (2011) 341:1–23
DOI 10.1007/s11104-011-0734-x

COMMENTARY

Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework



Origem e diversificação da flora dos campos rupestres

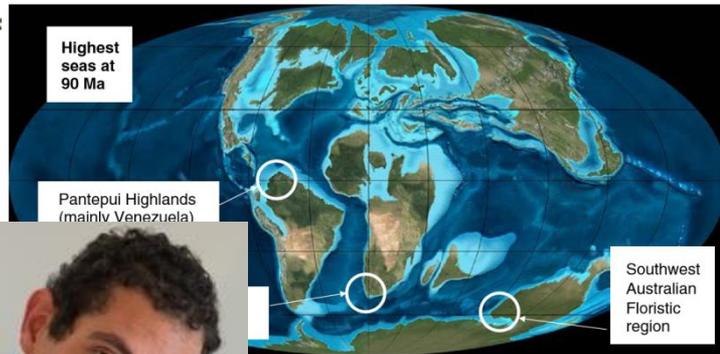
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Plant Soil (2009) 322:49–86
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REVIEW ARTICLE

OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes



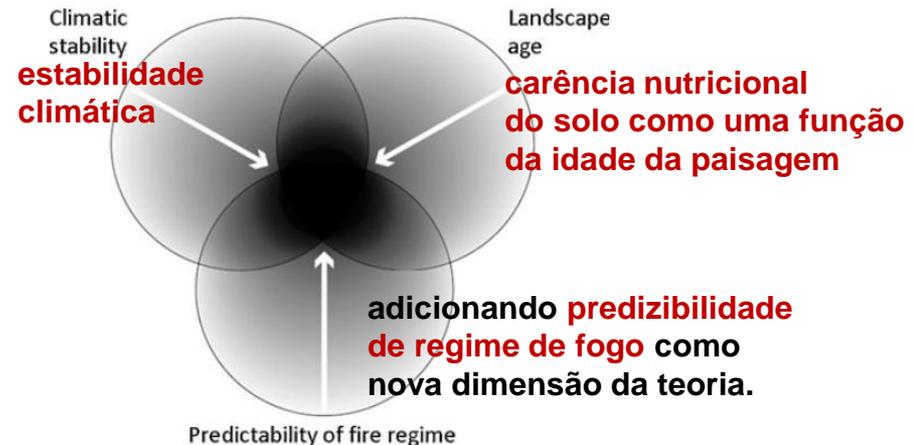
Conceição et al. 2016:

Campos rupestres ocupam terrenos antigos, geologicamente estáveis (Saadi 1995; Pedreira 1997), climaticamente mantidos por diversidade topográfica, com solos oligotróficos, severamente pobres em fósforo (Oliveira et al. 2015).

Plant Soil (2011) 341:1–23
DOI 10.1007/s11104-011-0734-x

COMMENTARY

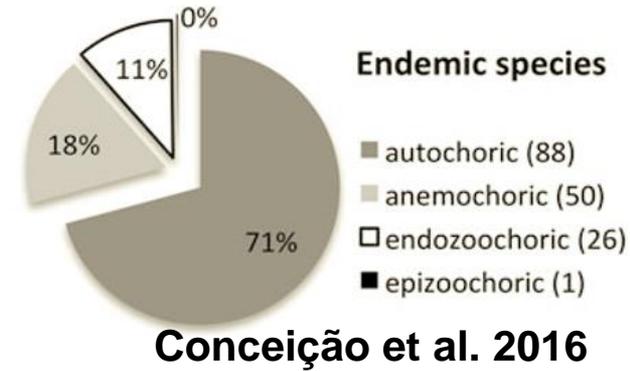
Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework



Linhagens em OSLs (Hopper 2009; Mucina and Wardell-Johnson 2011):

altamente especializadas:

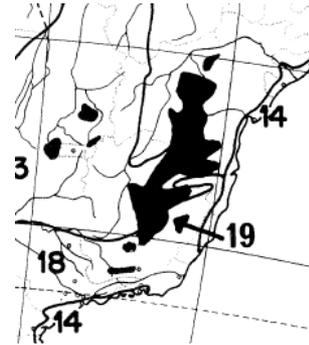
- baixa capacidade de dispersão (autocoria, anemocoria comuns);
dispersão a curta distância limita migrações entre núcleos distintos
de OSLs:



- OSLs são ricas em endemismos restritos (microendemismos) - diversidade alfa e beta são altas em OSLs, como reportado em muitas áreas de campo rupestre (e.g. Chapada Diamantina, Conceição et al. 2005; Conceição & Pirani 2016).

- longo isolamento das populações causado pela fragmentação natural:

fitocória tipo “arquipélago” (e.g. Prance 1994)



- linhagens de OSLs exibem alto **conservantismo filogenético**;

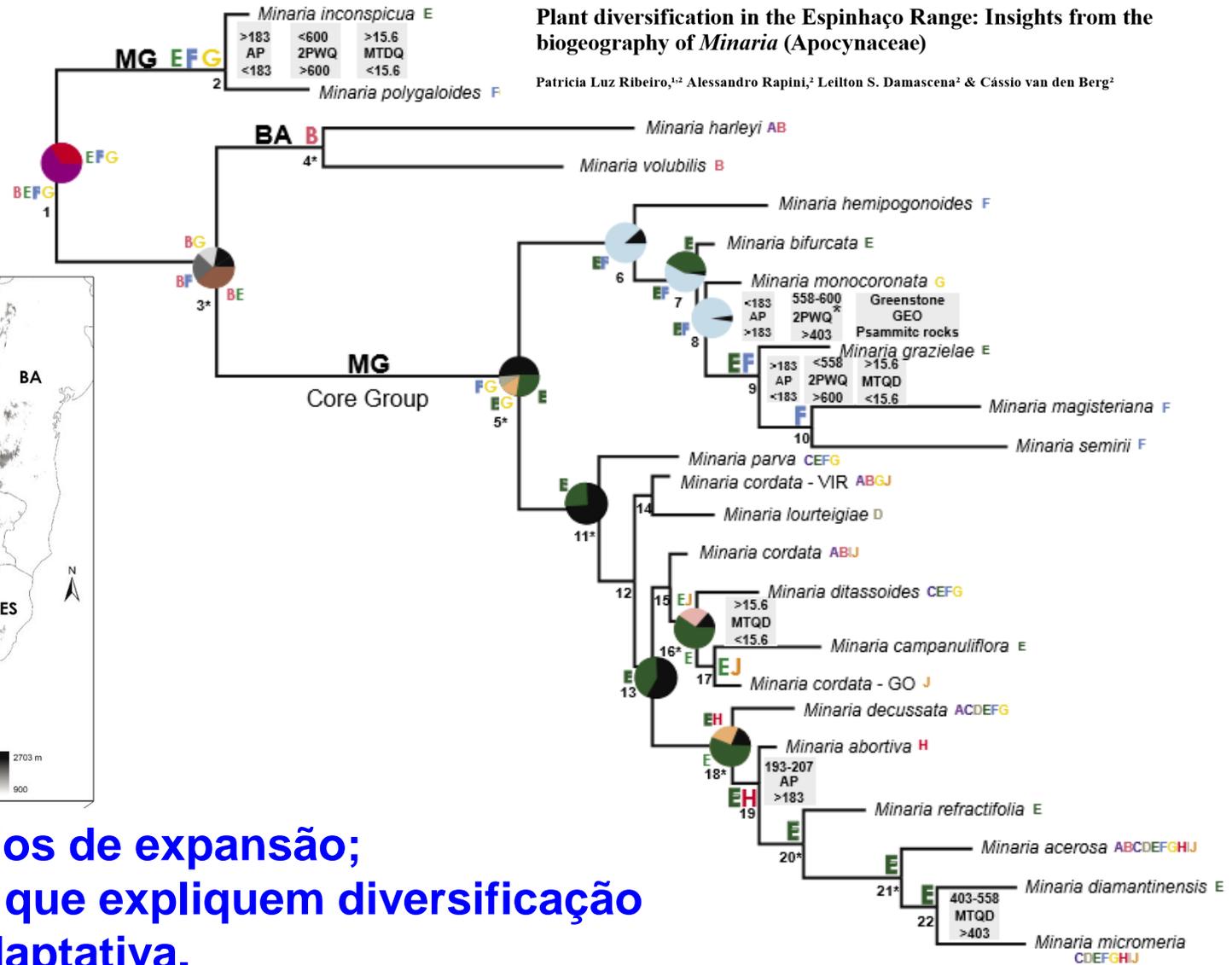
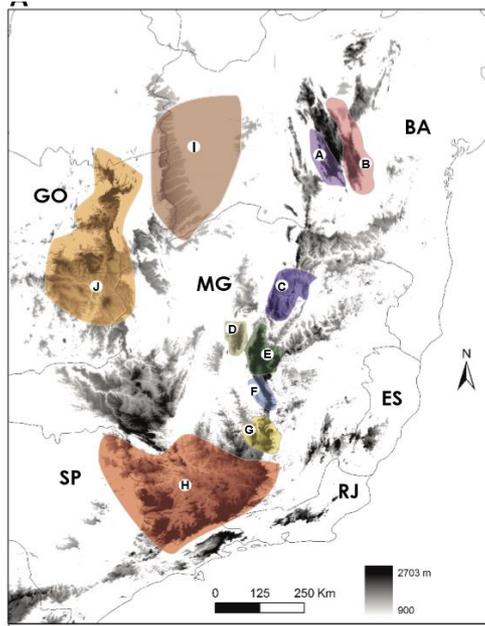
devido à estabilidade climática, elas podem persistir por longos períodos nessas paisagens, que atuam como refúgios, atuando como **berçários** ou **museus de biodiversidade**.

Minaria

Apocynaceae-

Asclepiadoideae

Ribeiro et al. 2014



Poucos episódios de expansão;
sem inovações que expliquem diversificação
por radiação adaptativa.

Campos rupestres forneceram ambientes estáveis com regimes
de fogo e estações secas menos intensos que no cerrado.

Conservantismo filogenético (poucas inovações que expliquem diversificação por radiação adaptativa) também em:

Lychnophorinae



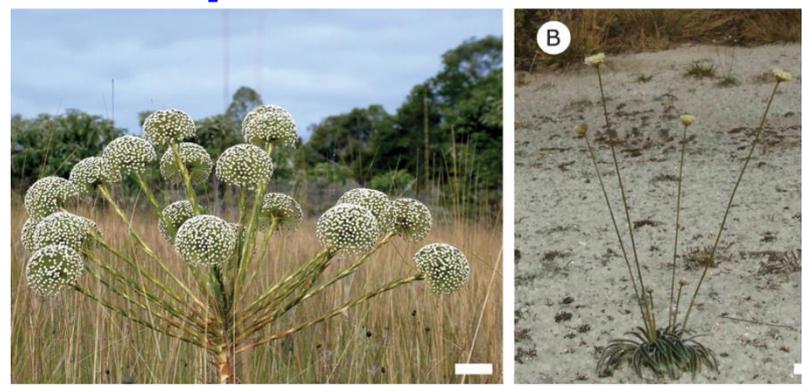
Chamaecrista



Hoffmannsegella



Paepalanthoideae



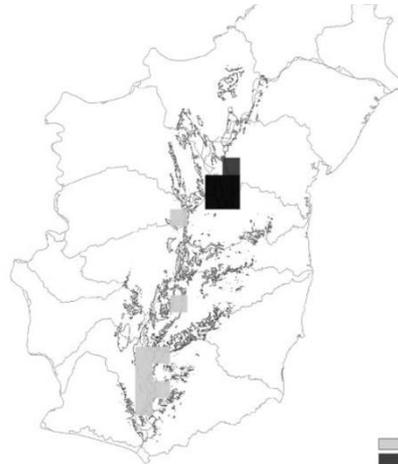
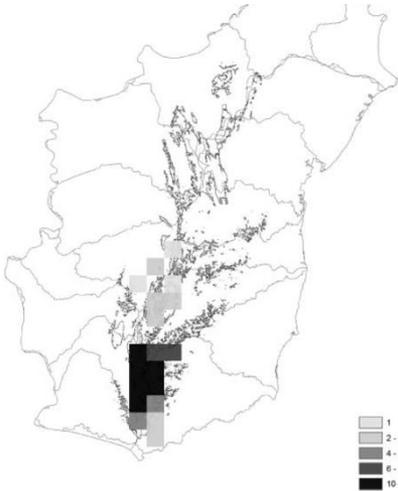
Research Article

Centres of Endemism in the Espinhaço Range: identifying cradles and museums of Asclepiadoideae (Apocynaceae)

CÁSSIA BITENCOURT & ALESSANDRO RAPINI

neoendêmicas

paleoendêmicas

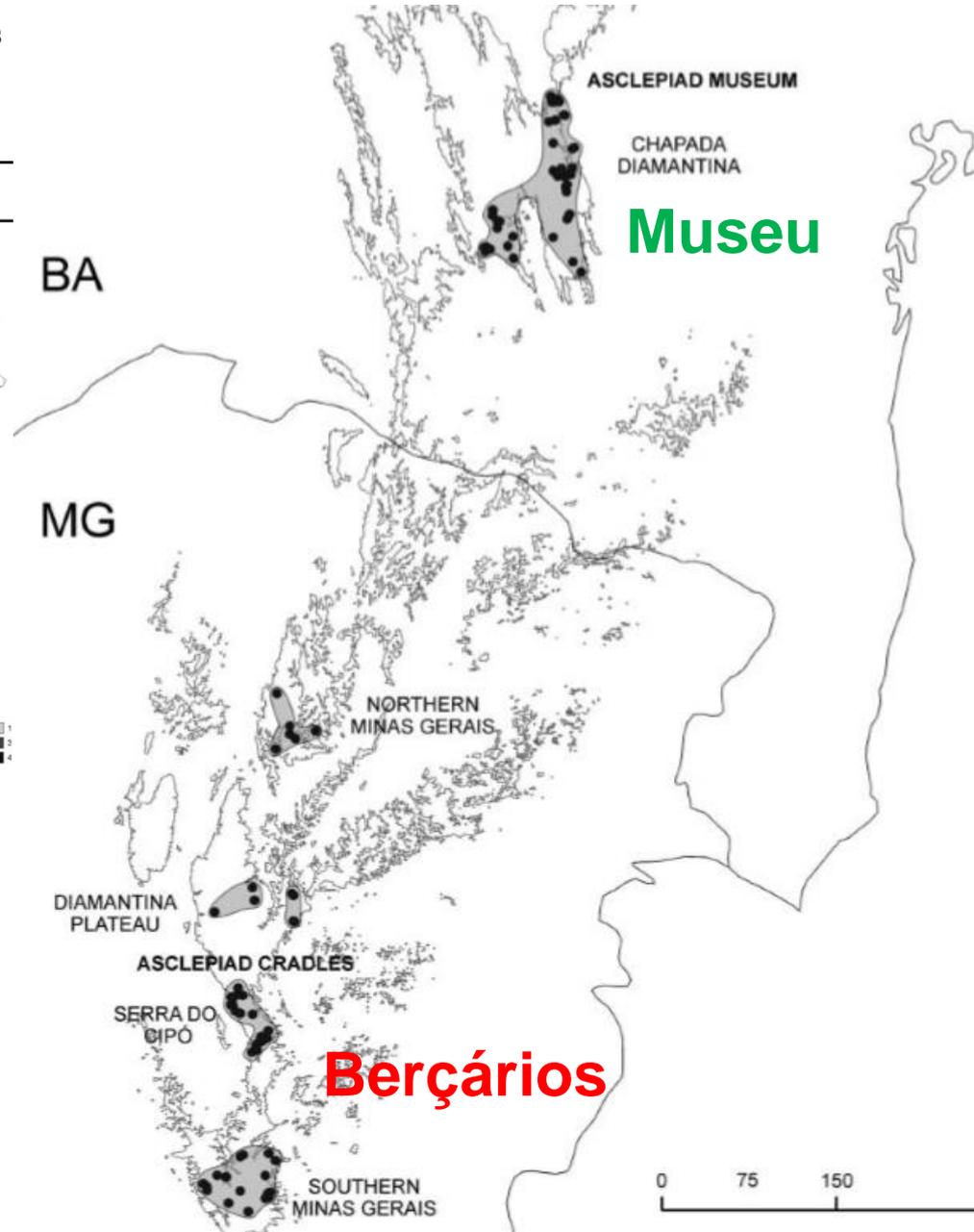


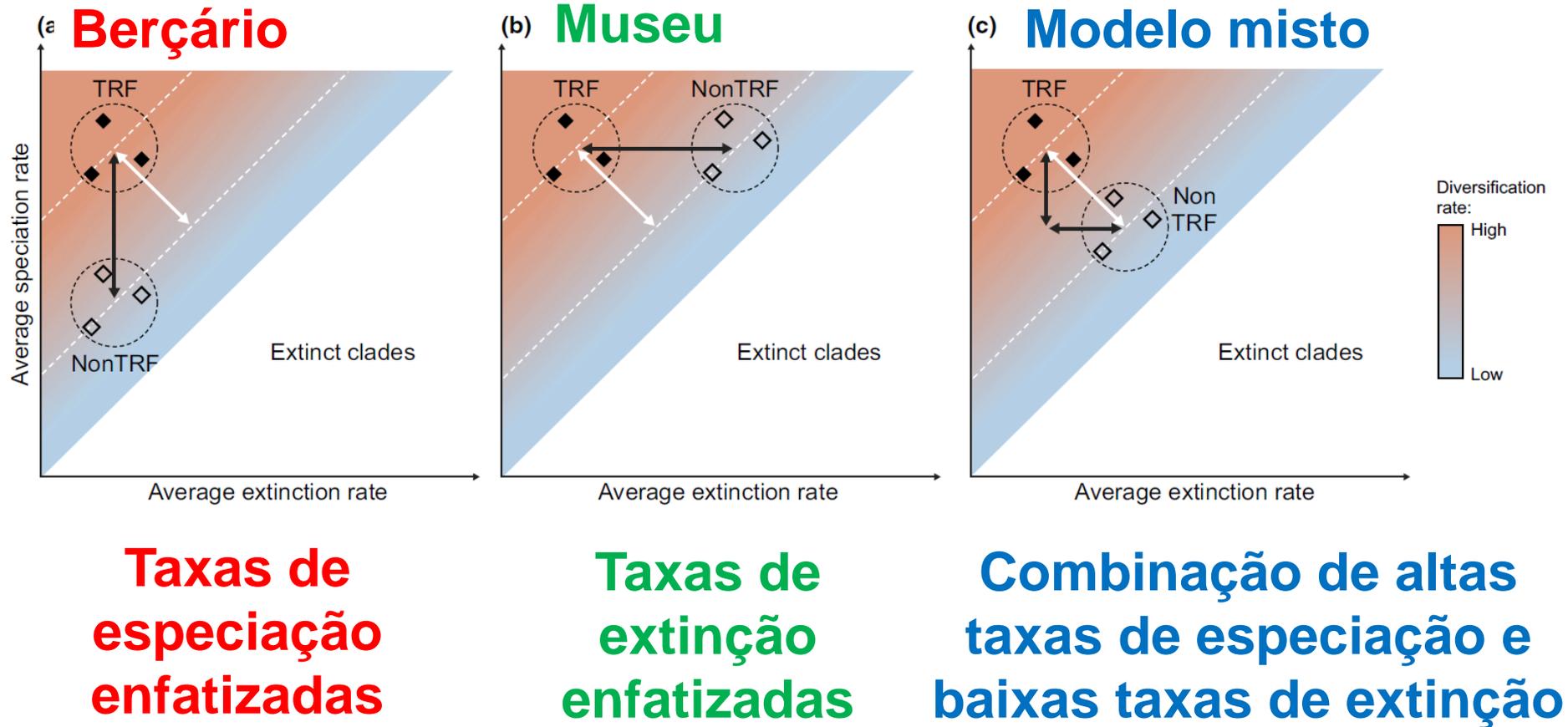
Setor Setentrional = **museu** abrigando spp.
paleoendêmicas;

Setor Meridional: muitas spp microendêmicas
(possivelmente paleoendêmicas)
e provavelmente seja um **berçário**

BA

MG

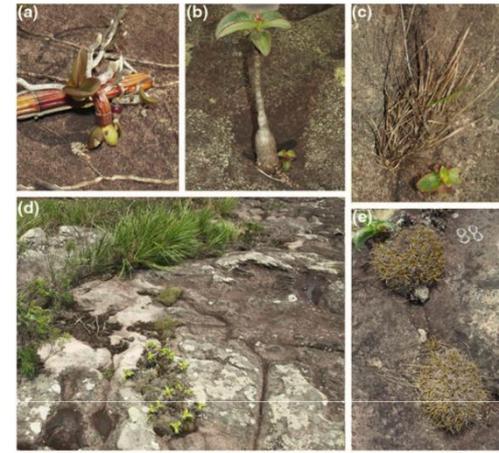




Campos rupestres podem ter atuado como refúgios para linhagens antigas sensíveis a fogo e filogeneticamente conservativas,

restritas às áreas montanas, onde frequência do fogo é menor devido a baixa proporção de gramíneas C4, alta concentração de afloramentos rochosos e clima mais ameno (sazonalidade menos marcada e umidade orográfica disponível o ano todo -neblina).

linhagens derivadas de um tipo de vegetação aberta geral que teria precedido o estabelecimento dos regimes de fogo (Ribeiro et al. 2012; Conceição et al. 2016).



Conceição & Pirani 2016



Alta diversificação pode ter sido resultado da combinação de alta taxa de especiação com baixas taxas de extinção, desde o Paleógeno, mas com maior expressividade no Neógeno superior.

Assim como em outras OSLs, plantas de campo rupestre:

- São **adaptadas a solos oligotróficos** e dotadas de estratégias de capturar e conservar nutrientes, como especializações de sistemas subterrâneos e

folhas esclerófilas

(Giulietti et al. 1987, 1997; Carmo & Jacobi 2012; Oliveira et al. 2015; Conceição et al. 2016).

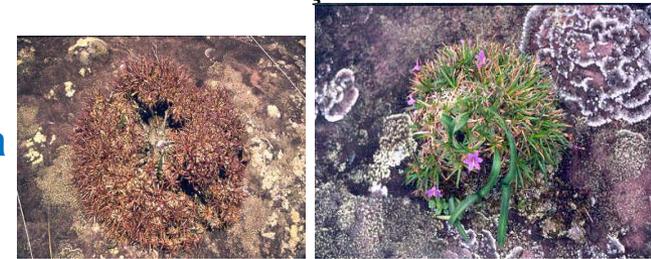


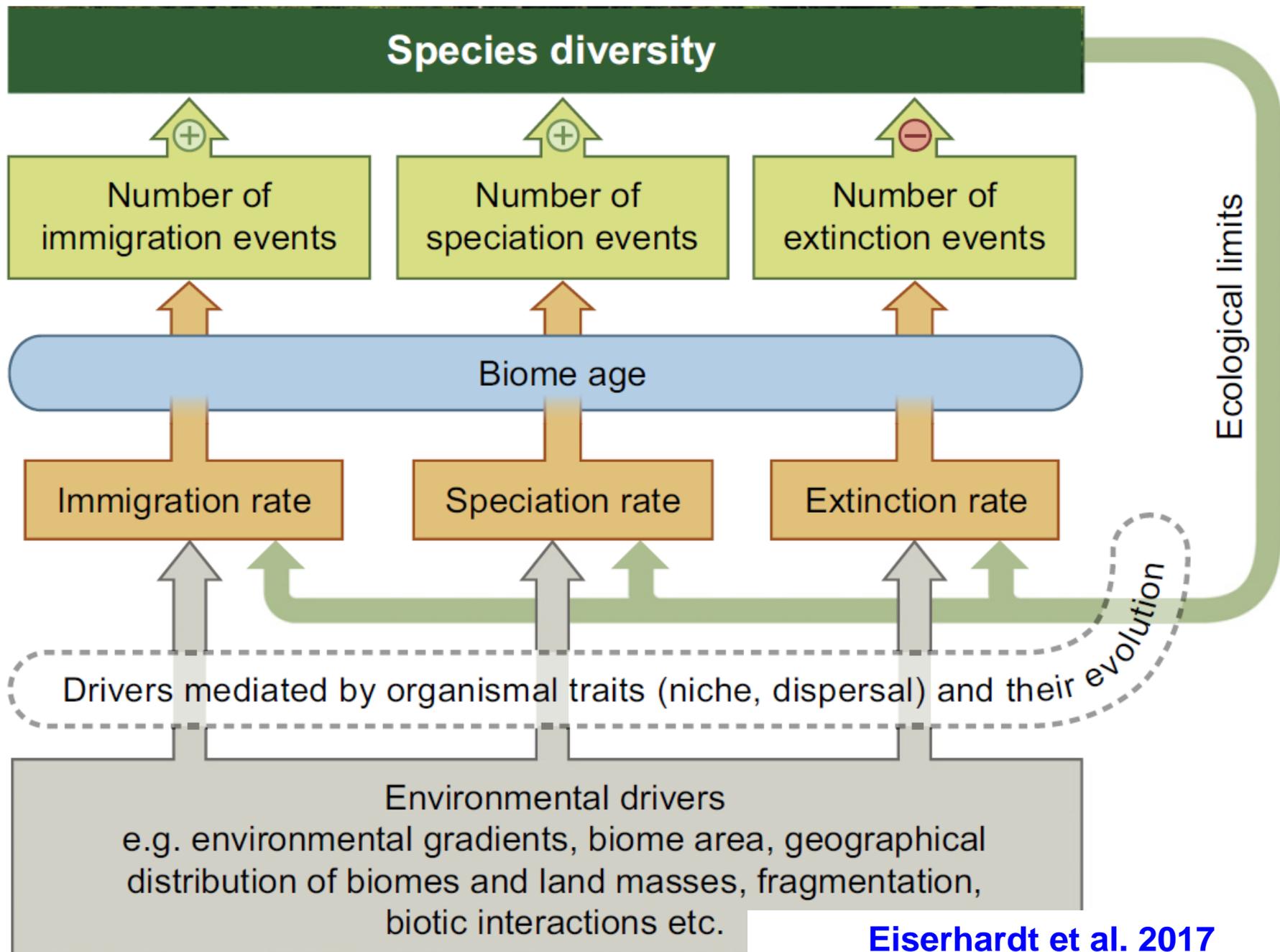
Conceição & Pirani 2016

- Têm habilidade de **rebrotamento após a seca ou queimada** pode ter evoluído em resposta a diferentes estresses e depois foi recrutada sob regimes de fogo,

constituindo **exaptação**

(Hopper 2009; Conceição et al. 2016).





Imigrantes recentes no campo rupestre

ASTERACEAE, Eupatorieae – *Mikania*

Oliveira & Pirani in prep.



Megadiverso (428 spp., apenas 9 extra-americanas)

178 spp. + 3 outgroups (ETS, ITS, *trnL*F, *psbA*).



Liana habit early acquired by the ancestor, enabling its diversification mostly at the border of American forests. Transitions to erect habits occurred several times, associated with events of colonization of open formations (**campo rupestre/cerrado**, and **pampas**), with rarer similar events on the Andes.

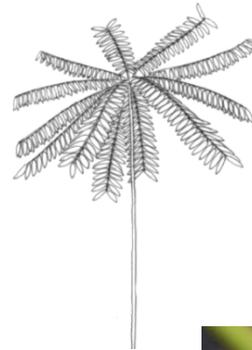


Simaroubaceae – *Simaba* - imigrantes recentes no campo rupestre

Devecchi et al. (submetido)

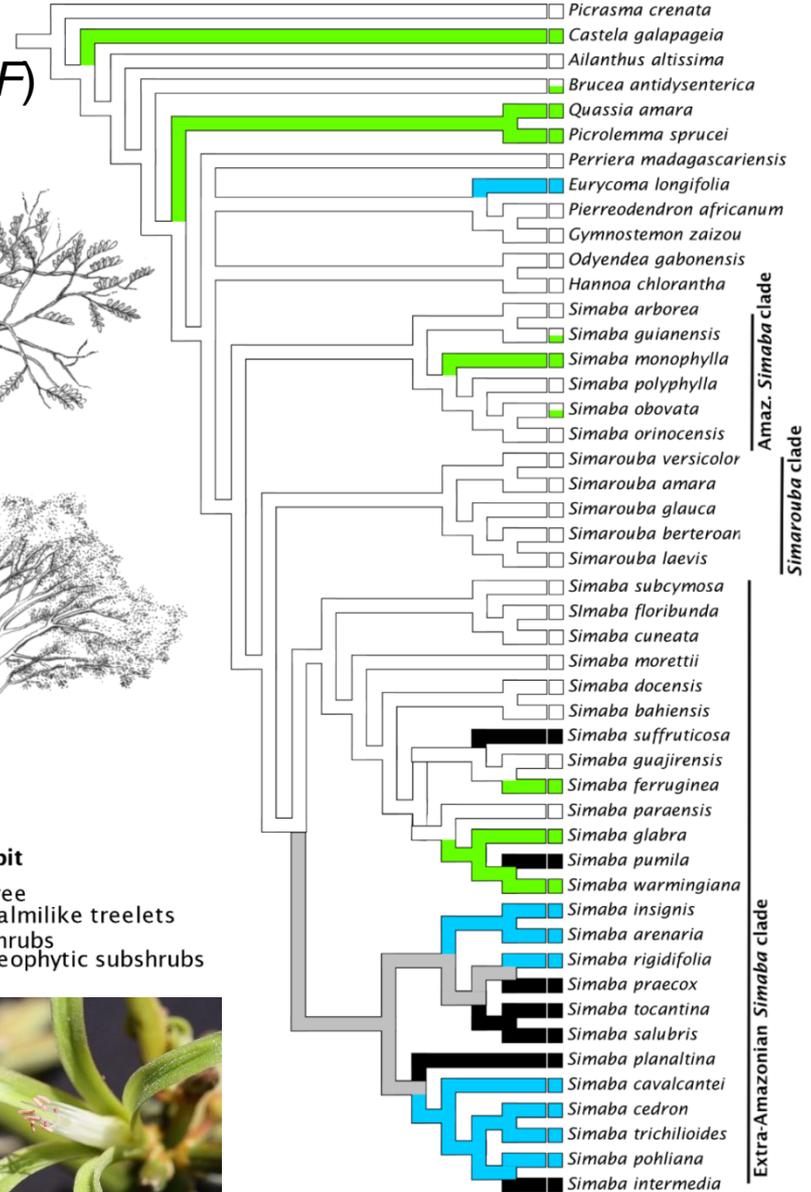
28 spp. neotropicais

5 regiões (ITS, ETS, *rps16*, *psbA-trnH*, *trnL-trnF*)



Habit

- tree
- palmilike treelets
- shrubs
- geophytic subshrubs



Evolução da flora adaptada ao fogo em 15 linhagens do Cerrado

xilopódio



paquicaule



casca espessada



Simon et al. 2009

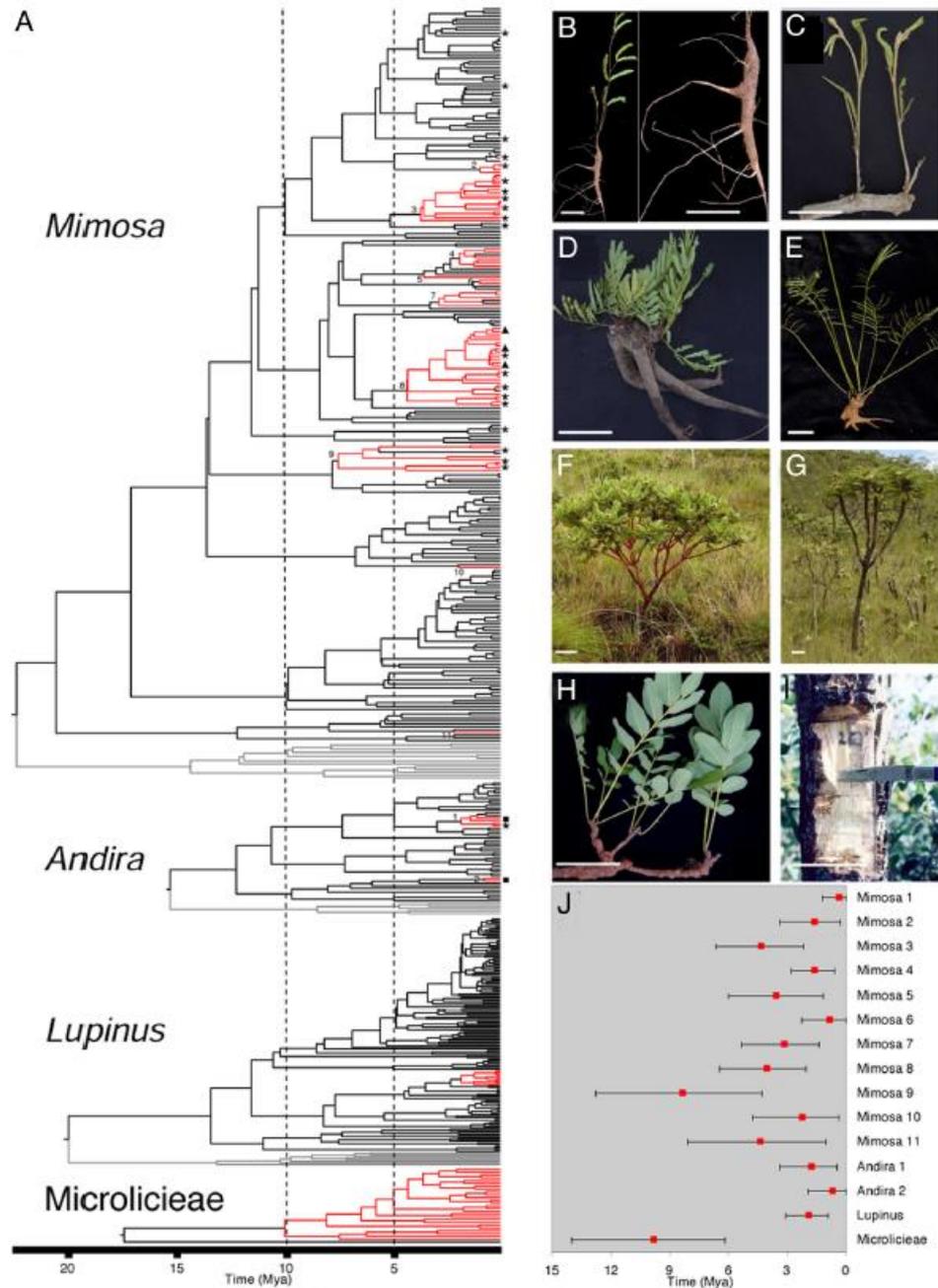


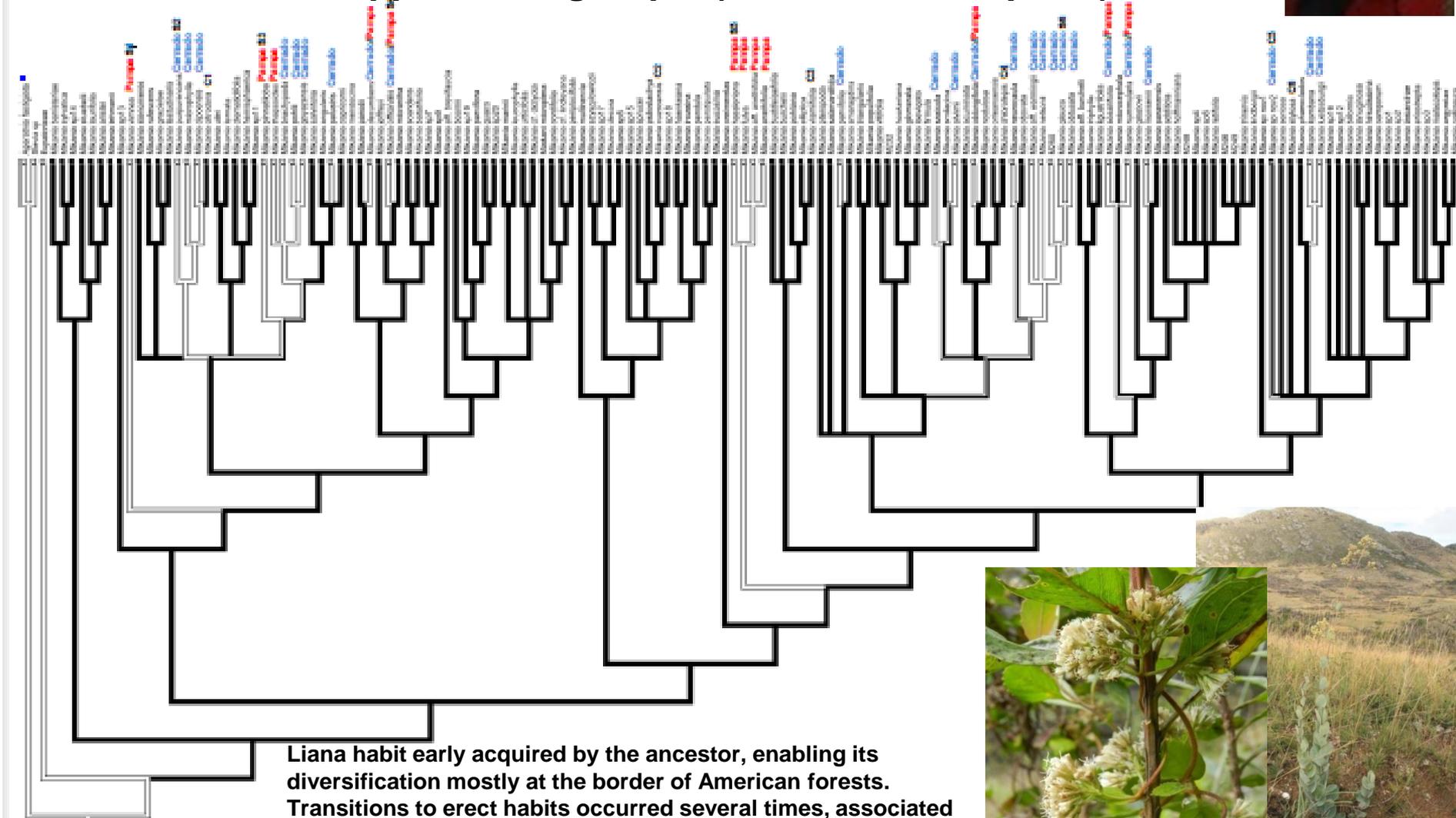
Fig. 2. Evolution of the fire-adapted Cerrado flora. (A) Chronograms for *Mimosa*, *Andira*, *Lupinus*, and *Microlicieae* showing 15 Cerrado lineages (red). Outgroups are depicted in gray. Symbols for fire adaptations: * = subshrub growing from xyllopodium; ▲ = pachycaul treelet; ■ = thick corky bark. Numbered nodes correspond to Cerrado lineages. The *Microlicieae* phylogeny has been pruned to show just the Cerrado lineage and to fit within the time scale under investigation. Expanded phylogenies, including terminal names and support values, are presented in the *SI Appendix*. (B–I) Photographs illustrate the diversity

ASTERACEAE, Eupatorieae – *Mikania*

Oliveira & Pirani in prep.

Megadiverso (428 spp., apenas 9 extra-americanas)

178 spp. + 3 outgroups (ETS, ITS, *trnL*F, *psbA*)



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**THE AGE AND DIVERSIFICATION OF TERRESTRIAL NEW WORLD
ECOSYSTEMS THROUGH CRETACEOUS AND CENOZOIC TIME¹**

ALAN GRAHAM²

Missouri Botanical Garden, P. O. Box 299, St Louis, Missouri 63166-0299 USA

March 2011]

GRAHAM—NEW WORLD ECOSYSTEMS THROUGH TIME

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TABLE 1. Estimates for time of appearance of Cretaceous and Cenozoic ecosystems in the New World.

Ecosystem	Cretaceous	Paleocene-early Eocene	Middle Eocene-Early Miocene	Middle Miocene-Pliocene
Desert	E- <i>Ephedra</i> , Welwitschiaceae (Brazil)	E	E	E-EM (Miocene-Pliocene)
Shrubland/chaparral–woodland–savanna	E- <i>Ephedra</i>	E- Poaceae, possibly some <i>Pinus/Quercus</i> sp.	EV- <i>Juniperus</i> , <i>Acacia</i> , <i>Arctostaphylos</i> , <i>Berberis</i> , <i>Bursera</i> , <i>Caesalpinia</i> , etc.	EM- grassy savanna (mid-Miocene 13 ma), <i>Artemisia</i> , <i>Sarcobatus</i>
Grassland	E (Late Cretaceous)	E	EV	EM
Mangrove	E (<i>Acrostichum</i>), <i>Nipa</i>	EV- (<i>Brevitricolpites</i>)	EM (<i>Rhizophora</i>), <i>Hibiscus</i> , <i>Pelliceria</i>	EM
Beach/strand/dune	E (preservation limited)	EV- Poaceae	EM- <i>Sabal</i> , <i>Canavalia</i>	EM
Freshwater herbaceous bog/marsh/swamp (lake margins)	E- <i>Equisetum</i> , ferns, <i>Decodon</i>	EV- Poaceae, Cyperaceae, <i>Typha</i> , <i>Sparganium</i>	EM	EM
Aquatic	EV/EM- <i>Azolla</i> , <i>Isöetes</i> , <i>Marselia</i> , <i>Salvinia</i> , <i>Ceratophyllum</i> , etc.	EM- <i>Porosia</i> , <i>Limnophyllum</i>	EM- <i>Pachria</i> , <i>Ceratopteris</i>	EM
Lowland neotropical rain forest	EV	EM (58–55 Ma, equatorial region)	EM	EM
Lower to upper montane broad-leaved forest (Latin America), deciduous forest (North America)	EV	EM	EM	EM
Coniferous forest	E (<i>Pinus</i>)	EV	EM (western montane ~45 Ma; boreal EV ~10 Ma)	EM
Tundra	—	—	EV	EM
Alpine tundra (páramo)	—	—	EV	EM

Note: E = elements; EV = early versions; EM = essentially modern versions.

Graham 2011

Eight ecosystems that were present in the Cretaceous about 100 Ma (million years ago) in the New World eventually developed into the 12 recognized for the modern Earth.

Among the **forcing mechanisms that drove biotic change** during this interval was:

a **decline in global temperatures toward the end of the Cretaceous**,

augmented by the asteroid impact at 65 Ma and drainage of seas from continental margins and interiors;

separation of South America from Africa beginning in the south at ca. 120 Ma and progressing northward until completed 90 – 100 Ma;

the **possible emission of 1500 gigatons of methane and CO₂**

attributed to explosive vents in the Norwegian Sea at ca. 55 Ma,

resulting in a temperature rise of 5 ° – 6 ° C in an already warm world;

disruption of the North Atlantic land bridge at ca. 45 Ma

at a time when temperatures were falling;

rise of the Andes Mountains beginning at ca. 40 Ma;

opening of the Drake Passage between South America and Antarctica

at ca. 32 Ma with formation of the cold Humboldt at ca. 30 Ma;

union of North and South America at ca. 3.5 Ma;

and all within the overlay of evolutionary processes.

These processes generated a sequence of elements

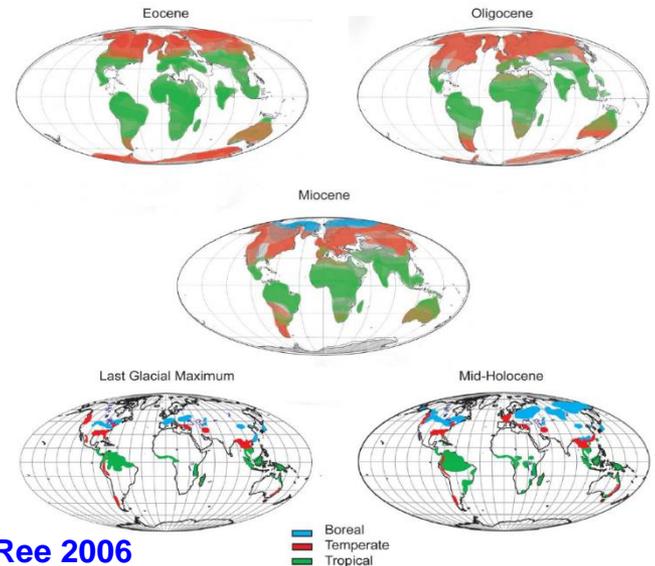
(e.g., species growing in moist habitats within an overall dry environment; gallery forests),

early versions (e.g., mangrove communities without *Rhizophora* until the middle Eocene),

and essentially modern versions of present-day New World ecosystems.

Graham 2011

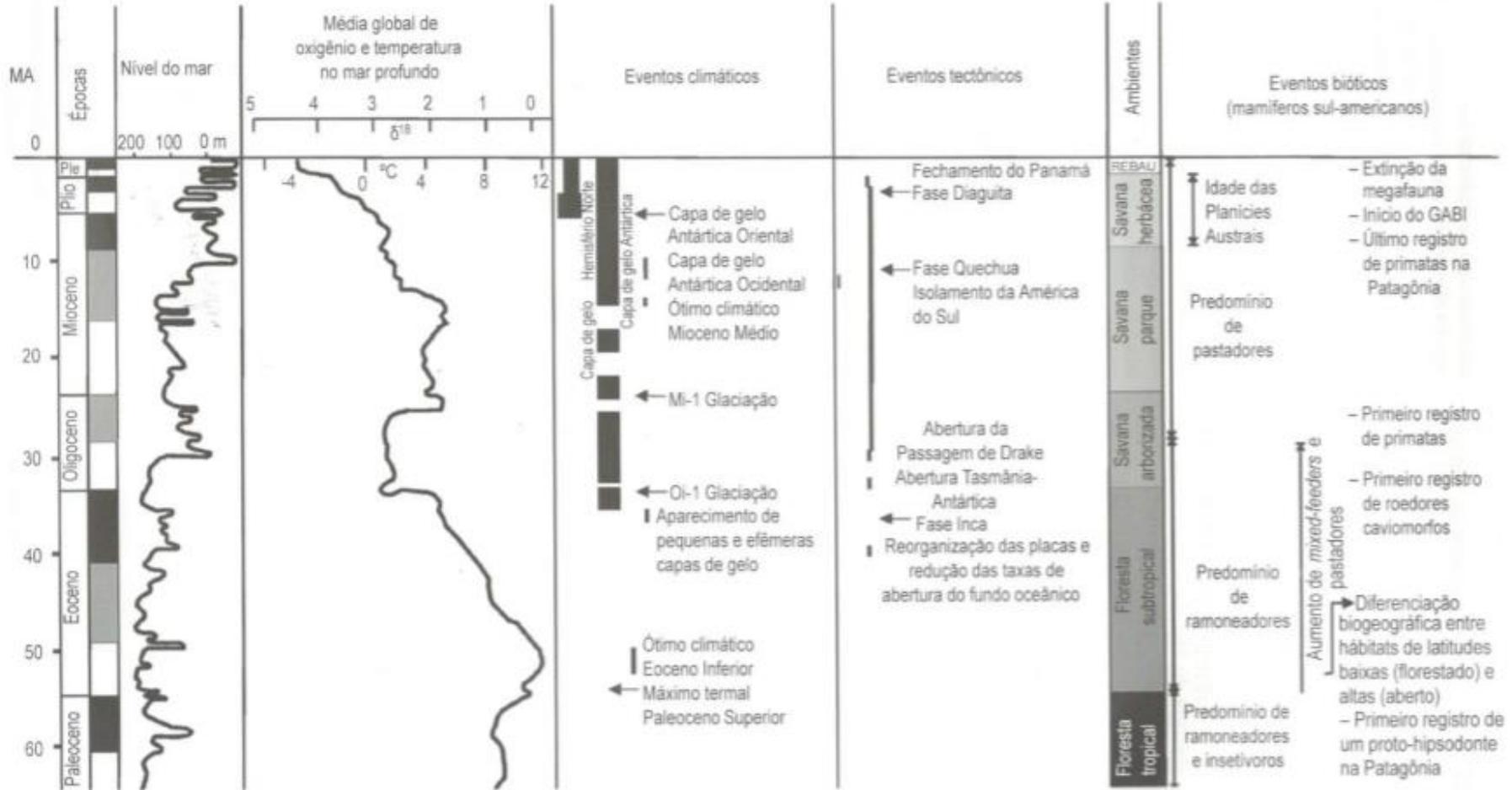
The fossil record suggests that early versions of aquatic communities (in the sense of including a prominent angiosperm component) appeared early in the Middle to Late Cretaceous, the **lowland neotropical rainforest at 64 Ma** (well developed by 58 – 55 Ma), **shrubland/chaparral – woodland – savanna and grasslands around the middle Miocene climatic optimum at ca. 15 – 13 Ma**, deserts in the middle Miocene/early Pliocene at ca. 10 Ma, significant tundra at ca. 7 – 5 Ma, and **alpine tundra (páramo)** shortly thereafter when cooling temperatures were augmented by high elevations attained, for example, in the Andes < 10 Ma and especially after 7 – 6 Ma.



CENOZÓICO

Épocas, indicadores de eventos climáticos, tectônicos e bióticos relevantes

Posadas & Ortiz-Jaureguizar 2016



CENOZÓICO

Eventos paleogeográficos e rotas florísticas na América do Sul

Fiaschi et al. 2016

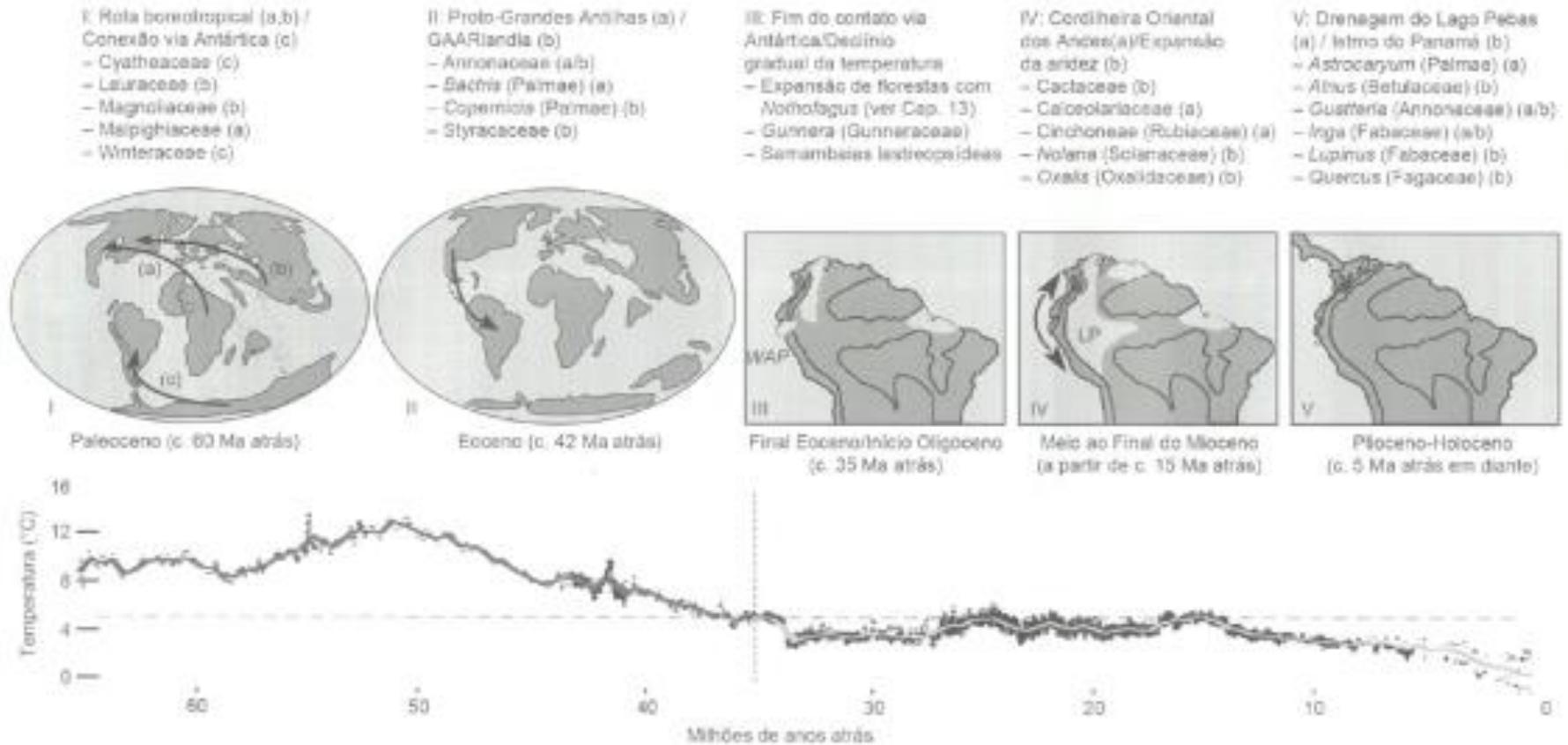


Figura 15.2 Principais rotas migratórias (I e II) e eventos paleogeográficos (III a V) relacionados com a flora da América do Sul tropical nos últimos 60 Ma (adaptado de Antonelli et al.²²). O gráfico mostra uma curva da diferença, em relação ao presente, da temperatura média global no mesmo período (Hansen et al.²³), indicando a transição de

Transição de um mundo predominantemente tropical no início do Paleógeno a um período de esfriamento, marcado pela glaciação da Antártida (35 M.a.).

Os táxons citados exemplificam como os eventos históricos afetaram a flora sul-americana de maneiras distintas em momentos distintos.

FLORA SULAMERICANA: Componente tropical + Componente temperado

Figura I.14 Mapa Biogeográfico de América del Sur (Rivas-Martínez y G. Navarro, 2000).

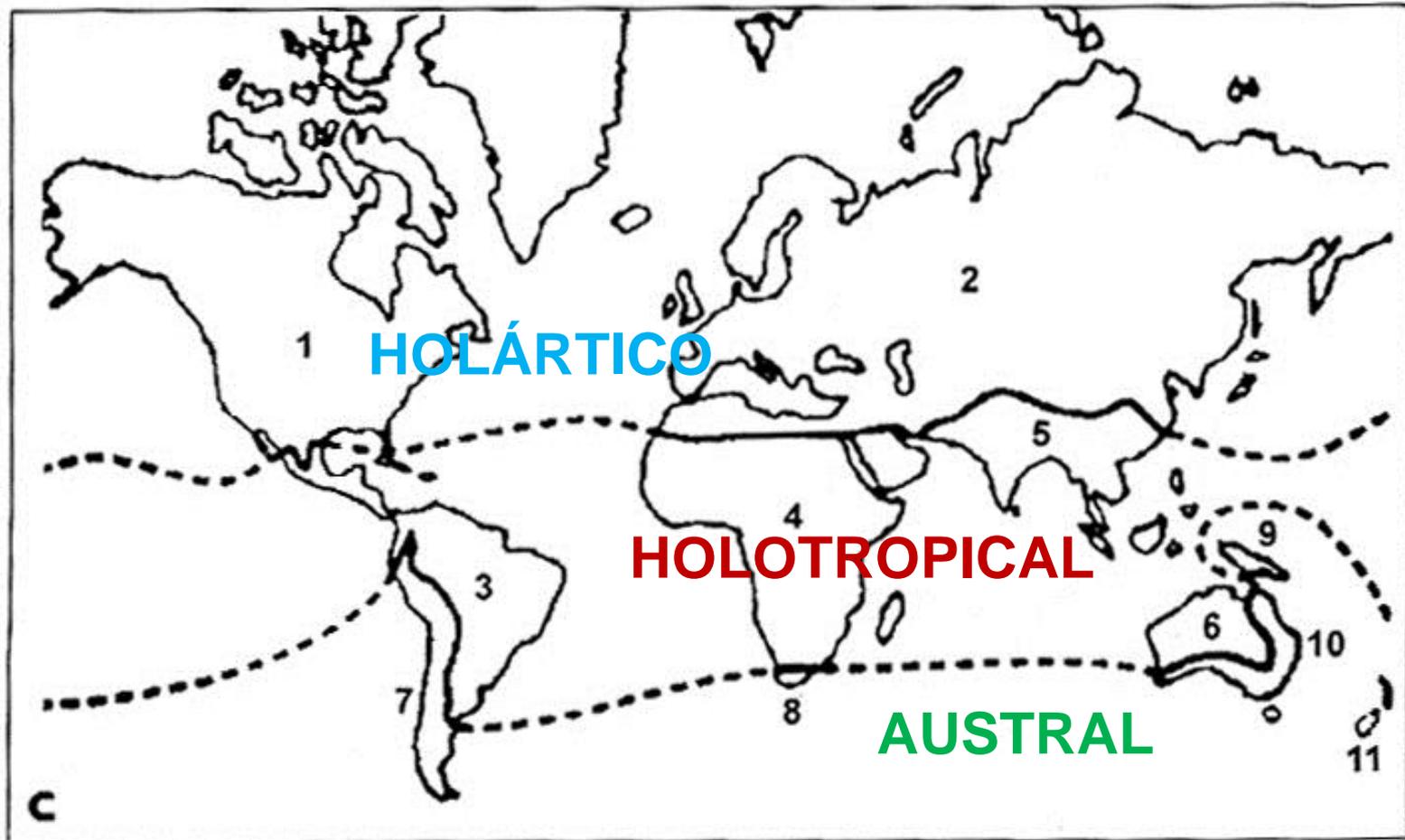


Navarro & Maldonado 2004

Reino Neotropical-Austroamericano

Sub-reino Neotropical
3 super-regiões
7 regiões

Sub-reino Austroamericano
3 regiões



Reinos biogeográficos e suas regiões, segundo Morrone (2002, 2009):

Reino HOLÁRTICO (= Laurásia) – regiões 1-Neártica e 2-Paleártica.

Reino HOLOTROPICAL (= Gondwana Oriental) – regiões 3-Neotropical, 4-Afrotropical, 5-Oriental, a 6-Australiana Tropical.

Reino AUSTRAL (= Gondwana Ocidental) – regiões 7-Andina, 8-Capense, 9-Novaguineana, 10-Australiana Temperada, 11-Neozelandesa.

Morrone (2015)

Reino AUSTRAL

REGIÃO ANDINA

e subregiões

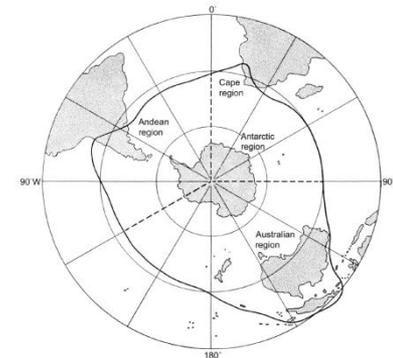
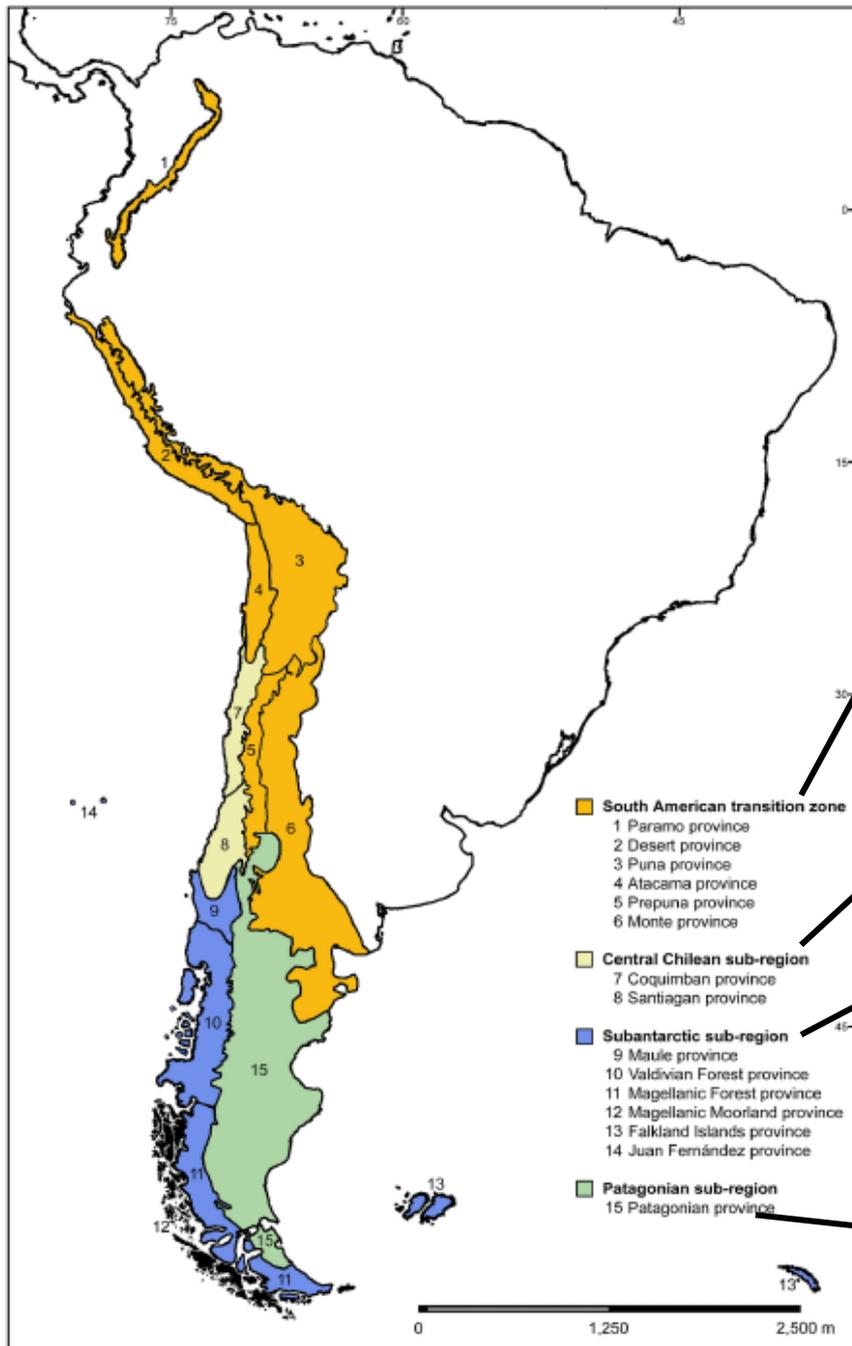


FIGURE 1. The Austral kingdom (modified from Kuschel 1964).



South American transition zone

- 1 Paramo province
- 2 Desert province
- 3 Puna province
- 4 Atacama province
- 5 Prepuna province
- 6 Monte province

Central Chilean sub-region

- 7 Coquimban province
- 8 Santiagan province

Subantarctic sub-region

- 9 Maule province
- 10 Valdivian Forest province
- 11 Magellanic Forest province
- 12 Magellanic Moorland province
- 13 Falkland Islands province
- 14 Juan Fernández province

Patagonian sub-region

- 15 Patagonian province

South American transition zone

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- 13 Falkland Islands province
- 14 Juan Fernández province

Patagonian sub-region

- 15 Patagonian province



Morrone (2014)

Reino HOLOTROPICAL

REGIÃO NEOTROPICAL

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Biogeographical regionalisation of the Neotropical region

JUAN J. MORRONE

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FIGURE 12. Biogeographic regionalisation proposed herein.

Chacoan subregion

South-eastern Amazonian dominion

40 Xingu-Tapajós province

Chacoan dominion

41 Caatinga province

42 Cerrado province

43 Chacoan province

44 Pampean province

Parana dominion

45 Atlantic province

46 Parana Forest province

47 *Araucaria* Forest province

Atlantic province Cabrera & Willink 1973

Tupí province Mello-Leitão 1937: 246; Fittkau 1969: 642.

Atlantic province Cabrera & Willink 1973: 64; Rivas-Martínez & Navarro 1994: map; Fernandes & Bezerra 1990: 99; Fernandes 2006: 67.

Serra do Mar centre Müller 1973: 125; Cracraft 1985: 72.

Serra do Mar province Udvardy 1975: 41.

Atlantic Tropical dominion Ab'Sáber 1977: map.

Southeastern Brazil area Cracraft 1988: 223.

Litoral or Coastal sub-province Fernandes & Bezerra 1990: 114; Fernandes 2006: 84.

Brazilian Atlantic Coast Restingas ecoregion Dinerstein *et al.* 1995: 106.

Brazilian Coastal Atlantic Forests ecoregion Dinerstein *et al.* 1995: 93.

Brazilian Atlantic Forest province Morrone 1999: 11, 2001e: 98, 2006: 482.

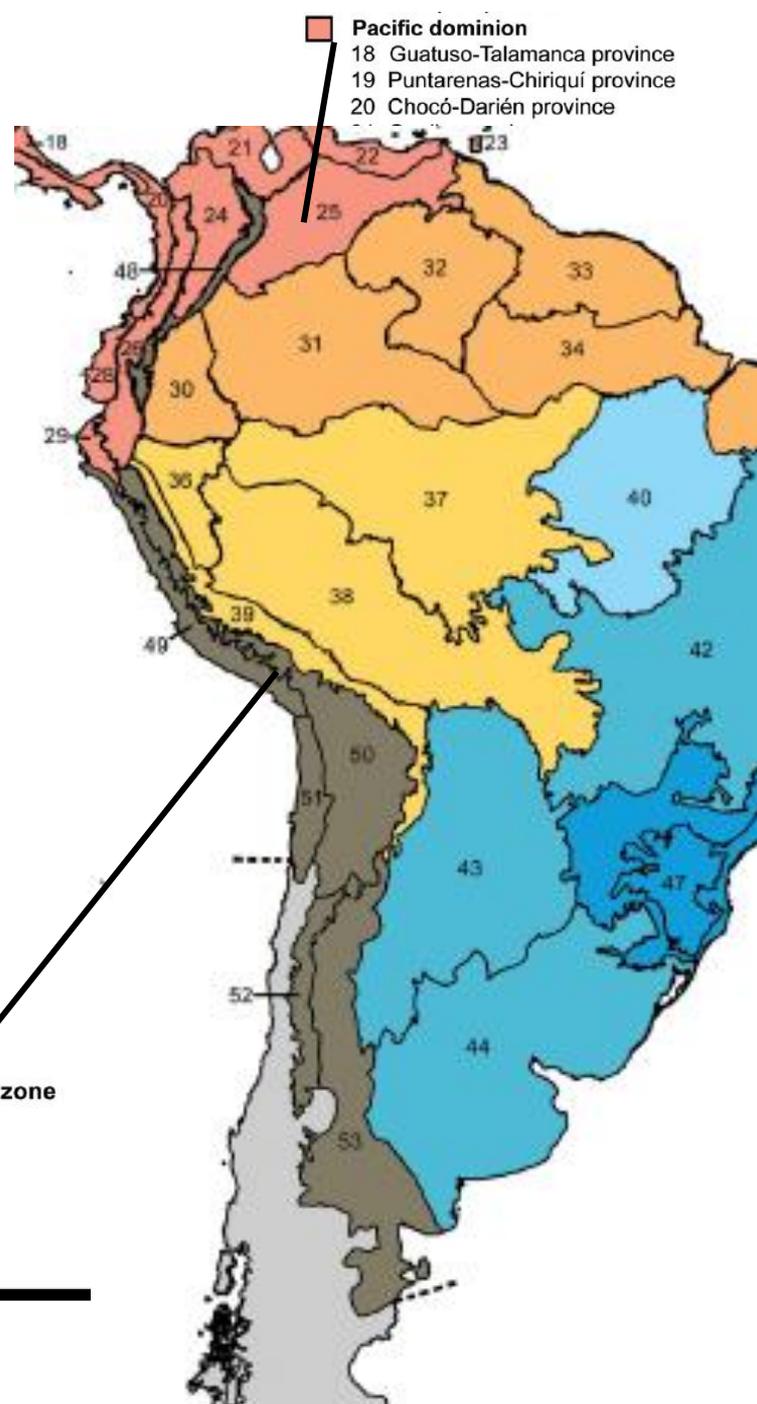
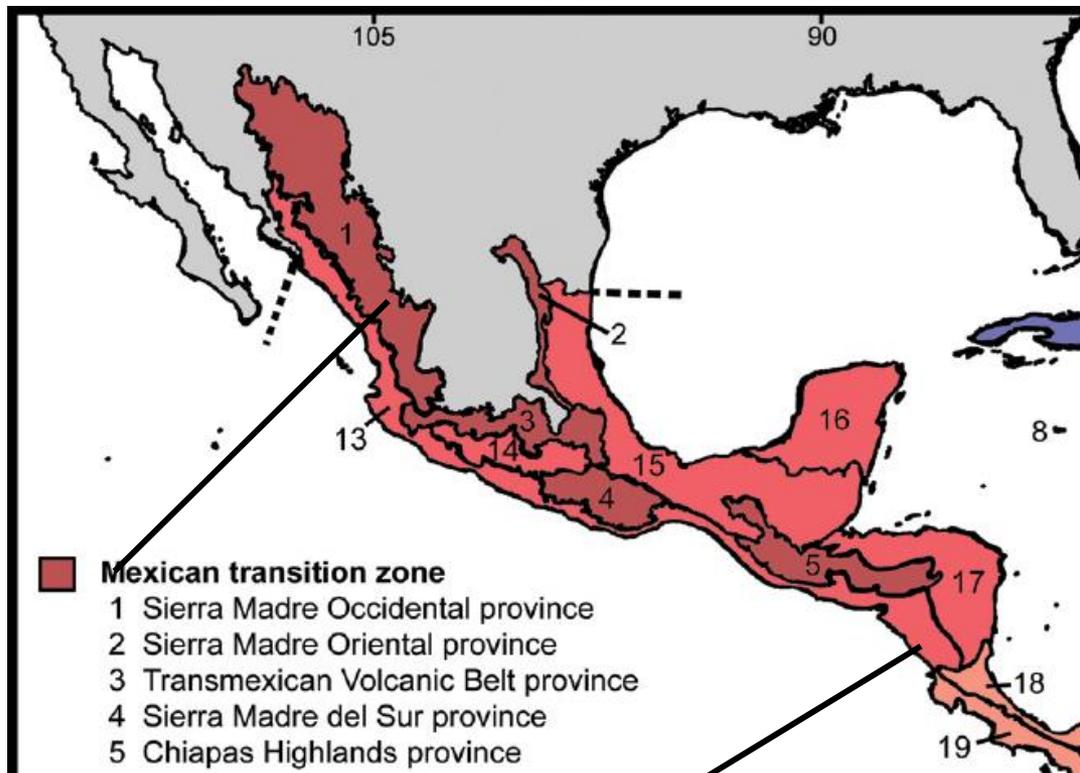
Brazilian Atlantic Coast province Morrone 2001b: 2.

Serra do Mar area Silva *et al.* 2004: 88.

Atlantic Forest area Porzecanski & Cracraft 2005: 266.

Diagnosis. Narrow strip along the Brazilian Atlantic coast east of the coastal cordillera, between 7-32 south latitude (Morrone 2001b, 2006).

Endemic taxa. MAGNOLIOPHYTA. Asteraceae: *Chionolaena capitata*, *C. isabellae*, *C. phyllicoides* and *C. wittigiana* (Freire 1993); Cecropiaceae: *Cecropia hololeuca* (Franco & Berg 1997); Elaeocarpaceae: *Crinodendron brasiliense* (Coode 1987); Onagraceae: *Fuchsia alpestris*, *F. brevilobis*, *F. glazioviana* and *F. regia* subsp. *serrae* (Berry 1989). ARTHROPODA. Carabidae: *Amblygnathus brasiliensis* (Ball & Maddison 1987); Corixidae: *Sigara denseconscripta* (Bachmann 1981); Curculionidae: *Ericydeus bahiensis*, *Erodiscus denticollis*, *E. caruaru*, *Lancearius longirostris*, *Pimelerodius ardea*, *P. birai*, *P. elongatulus*, *P. gryphus*, *P. obsoletus*, *P. pascoei*, *P. sulcatipennis*, *Prosicoderus crassipes*, *Sicoderus analis*, *S. apicalis*, *S. bondari*, *S. ciconia*, *S. distinguendus*, *S. prolatus* and *S. subcoronatus* (Vanin 1986; Lanteri 1995); Ditomyiidae: *Calliceratomyia pectinata* (Amorim & Pires 1996); Elmidae: *Stenhelmoides submaculatus* (Spangler & Perkins 1989); Membracidae: *Nicomia interrupta* and *N. monticola* (Albertson & Dietrich 2005; Sigrist & Carvalho 2009); Miridae: *Rhinaclia carvalhoi* (Schuh & Schwartz 1985); Mycetophilidae: *Cluzobra* spp. (Amorim & Oliveira 2008); Nepidae: *Curicta bilobata*, *C. lenti* and *C. longimanus* (Keffer 1996); Pholcidae: *Carapoia crasto*, *C. genitilis*, *C. ubatuba* and *C. una* (Huber 2005; Sigrist & Carvalho 2009); Reduviidae: *Rasahus grandis* and *Sirthena atra* (Morrone & Coscarón 1996); Scarabaeidae: *Coprophaneus bellicosus* (Edmonds & Zidek 2013); Schendylidae: *Schendyllops coscaroni*, *S. iguapensis*, *S. olivaceus*, *S. parahybae*, *S. perditus* and *S. luederwaldi* (Morrone & Pereira 1999); Sciaridae: *Rhynchosciara americana* (Amorim & Pires 1996); Sciomyzidae: *Sepedonea incipiens*, *S. neffi* and *S. veredae* (Freidberg *et al.* 1991); Simuliidae: Simuliidae *Simulium brachycladum* (Coscarón & Coscarón-Arias 1995); Staphylinidae: *Neolindus schubarti*, *N. unilobus* (Herman 1991); Stenomidae: *Setiostoma argyrobasis* (Duckworth



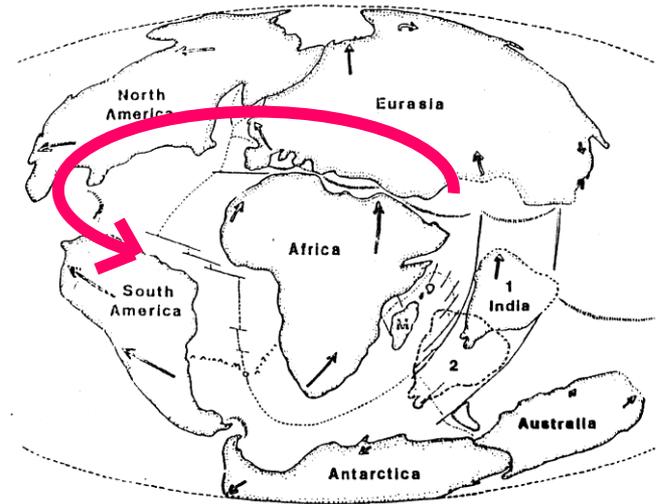
Morrone (2014 e 2015):
2 zonas de transição entre as
regiões Neotropical e Austral.
O quê as caracteriza?

FLORA SULAMERICANA:

Componente tropical:

Autóctones

+ imigrantes da América Central
(muitas linhagens chegando do
corredor boreotropical?)

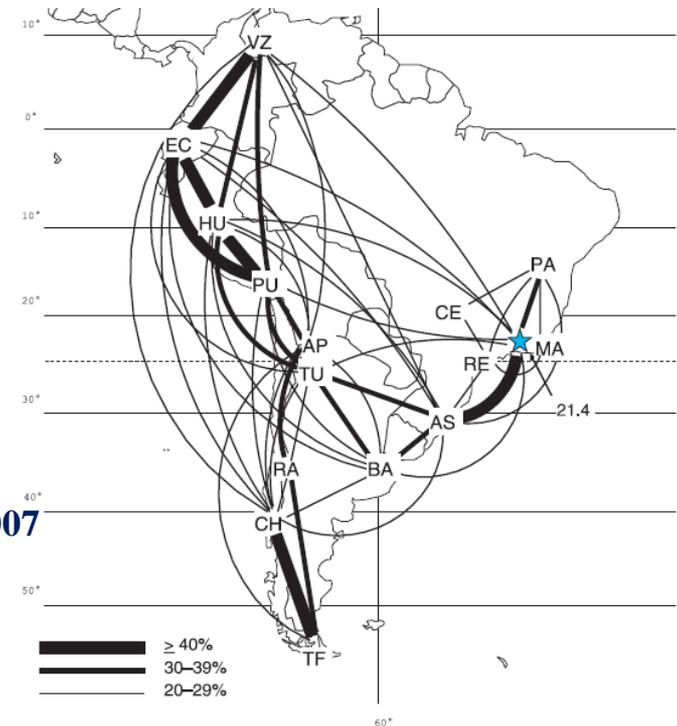


Componente temperado:

Autóctones austrais e andinos

+ imigrantes holárticos

+ imigrantes da flora australasiana



Safford 2007

Figure 4 Geographical patterns in Jaccard similarities at the level of genus for the sites treated in this paper. The campos de altitude are represented by a star. '21.4' is the Jaccard similarity between the campos de altitude and Macaé de Cima. Values from Table S2 (in Supplementary Material), site codes as in Table 1.

CONCLUSÃO

1. Avanços do conhecimento acerca das épocas de **origem e expansões/retrações dos biomas neotropicais.**

2.

3.

4.

CONCLUSÃO

1. Avanços do conhecimento acerca das épocas de **origem e expansões/retrações dos biomas neotropicais**. *Confiabilidade?*

2. Os dados filogenéticos já compilados apontam para um **mosaico complexo nos padrões biogeográficos na região Neotropical**, com algumas poucas linhagens antigas diversificando desde o fim do Cretáceo e Paleógeno, muitas outras durante o Neógeno e um número expressivo (mas bem menor do que se supunha) durante o Pleistoceno.

3.

4.

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3. **Transições entre habitats** ocorreram múltiplas vezes em muitas linhagens neotropicais (e.g. florestas - formações abertas) , frequentemente associadas a transições morfológicas-fisiológicas.
- 4.

CONCLUSÃO

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4. Necessidade de **integração de múltiplos estudos de caso** (histórias filogenéticas de vários grupos), e seguir aprimorando os variados métodos analíticos modernos = **visão multidisciplinar e integradora** para entender o papel de **fatores abióticos** (mudanças climáticas e geográficas) e de **fatores bióticos** (conservantismo/evolução de nicho, competição, adaptação e especialização) na formação histórica e diversificação da rica biota neotropical.

GEOGENÔMICA

Baker et al. 2014

Earth-Science Reviews 135 (2014) 38–47



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The emerging field of *geogenomics*: Constraining geological problems with genetic data



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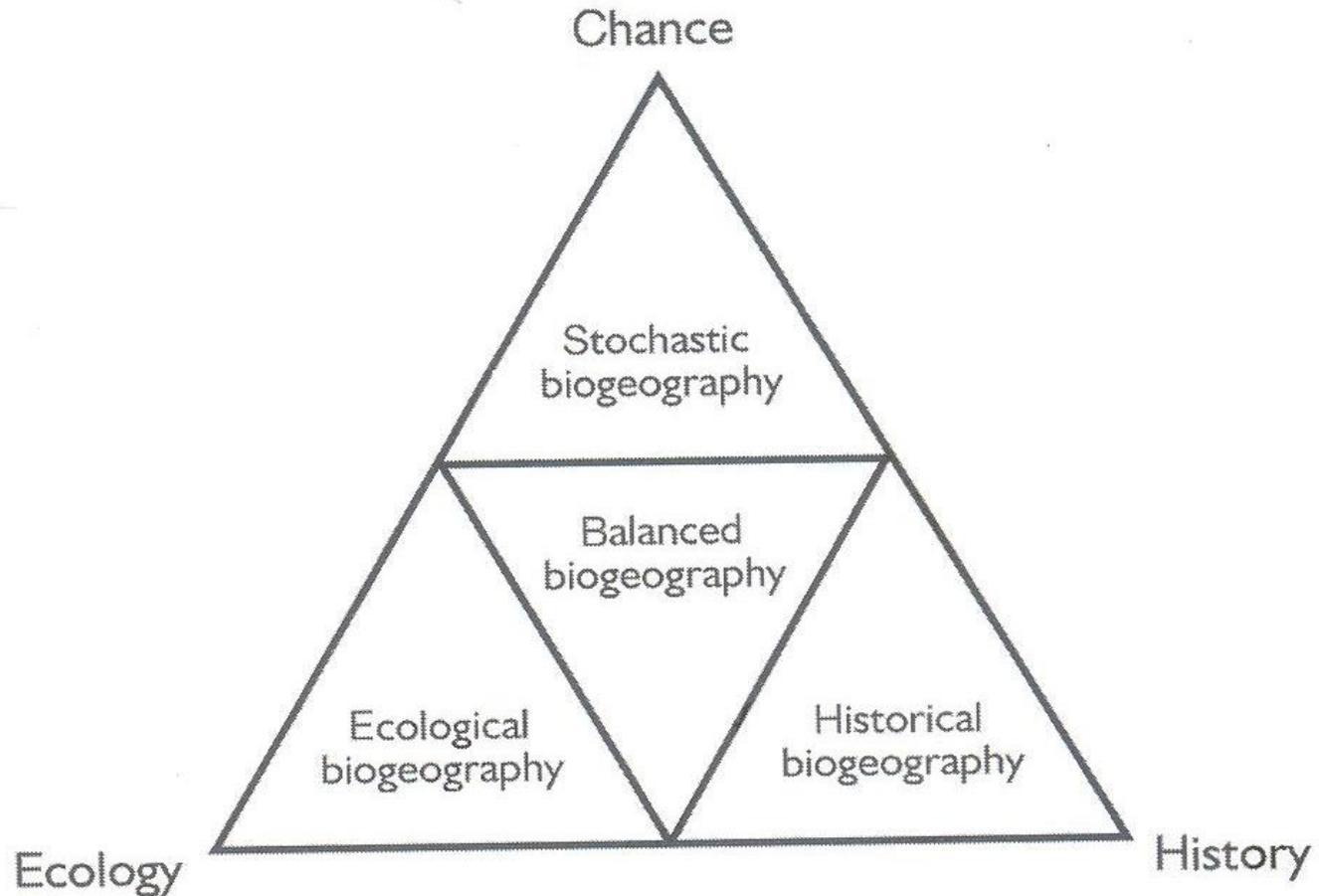
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Síntese emergente na Biogeografia



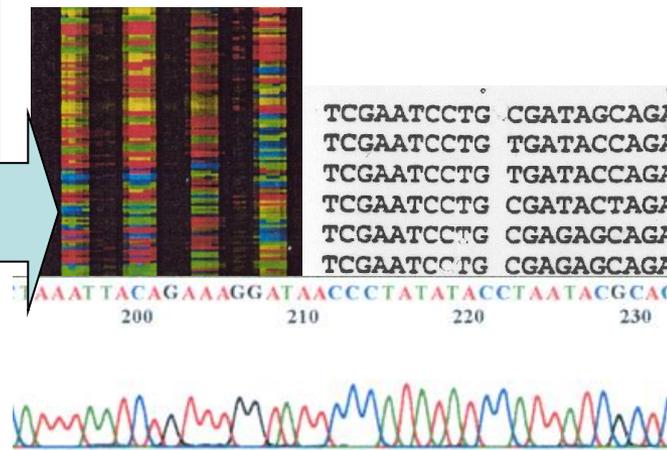
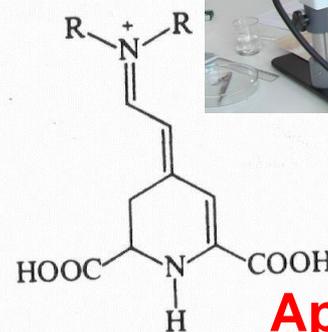
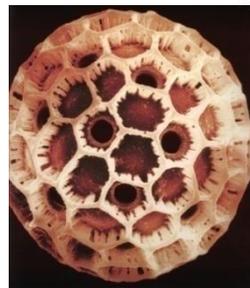
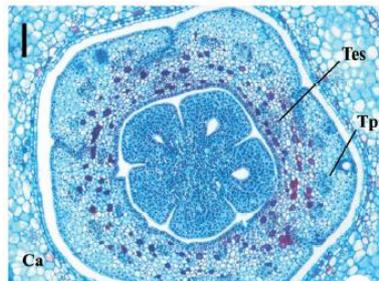
Haydon et al. 1994
Morrone 2009

Para novos progressos no estudo da biota neotropical:

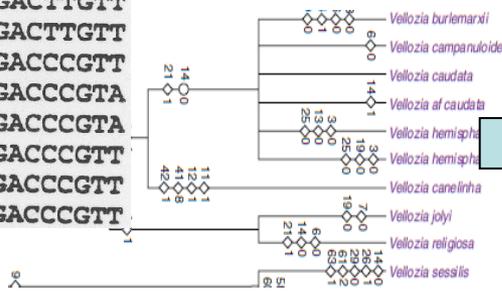
Explorações a campo, dados georreferenciados

Colaborações para obtenção e análise de dados:

- morfológicos
- anatômicos
- palinológicos
- citológicos
- micromoleculares
- macromoleculares



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ATGACCCGTT
ATGACCCGTT
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Aprofundar o conhecimento dos grupos e executar análises biogeográficas com métodos explícitos



Dimorphandra F.P. Costa



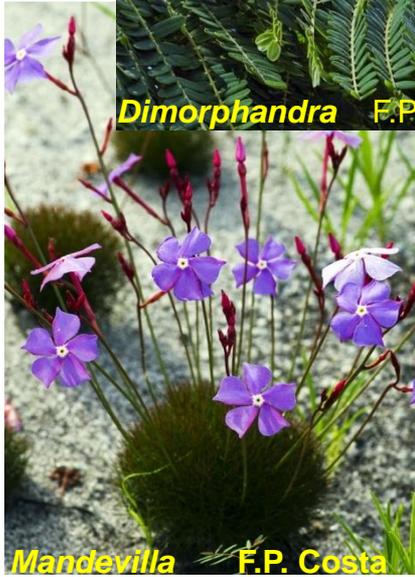
Huperzia P.R. Souza



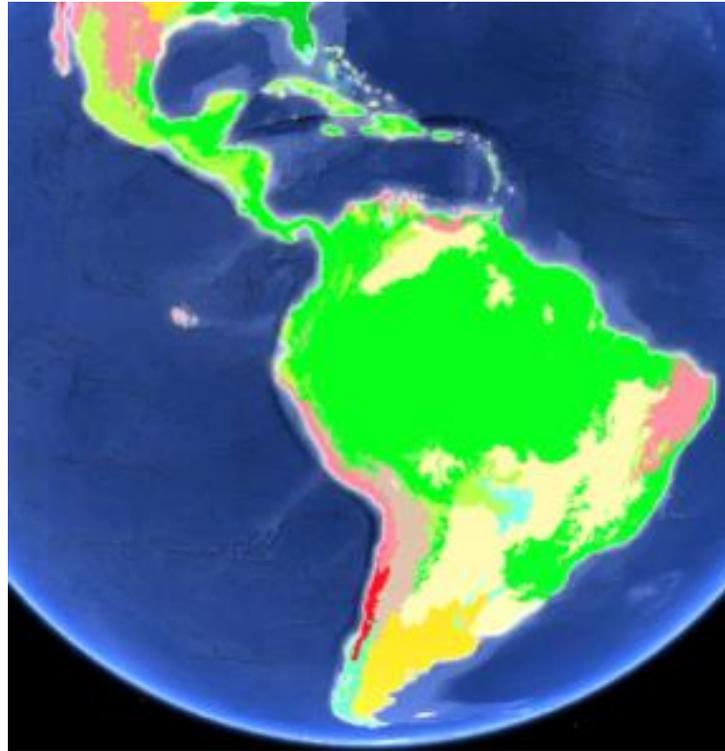
Passiflora F.P. Costa



Pavonia F.P. Costa



Mandevilla F.P. Costa



Annona F.P. Costa



Pseudotrimezia F.P. Costa



Discocactus F.P. Costa

Região Neotropical