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A STUDY OF THE ORIGIN OF CENTRAL BRAZILIAN FORESTS BY THE ANALYSIS OF PLANT SPECIES DISTRIBUTION PATTERNS

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The floristic nature of central Brazilian forests, as well as their links to other main forest formations of eastern tropical South America, is assessed by means of multivariate analyses of 106 existing floristic checklists and by the analysis of a series of dot-maps showing the distribution of 55 woody species. Most species of central Brazilian forests seem to conform to two main distribution patterns: (1) species of deciduous and semideciduous forests are dependent essentially on the occurrence of patches of soils of intermediate to high fertility within the cerrado domain and tend to be distributed mostly along a northeast-southwest arch connecting the caatingas to the chaco boundaries; (2) considerable numbers of gallery forest species are dependent on high soil moisture and many appear to link the Amazonian and Atlantic rainforests by crossing the cerrado region in a northwest-southeast route via the dendritic net of gallery forests. Many gallery forest species are habitat generalists, some even occurring in the cerrado vegetation. Nevertheless, significant numbers of gallery endemics are also present. Galleries of the west and north of the Cerrado Province show stronger floristic links to the Amazonian rainforests, while those of the centre and south show stronger affinity with the montane semideciduous forests of southeastern Brazil. Present-day distribution patterns are discussed in the light of the current knowledge of palaeoenvironmental changes in the Neotropics.

A natureza florística das florestas do Brasil Central bem como seus laços com outras grandes formações florestais da América do Sul trópico-oriental é avaliada por meio de análises multivariadas de 106 listagens florísticas existentes e pela análise de uma série de mapas de distribuição geográfica de 55 espécies lenhosas. A maioria das espécies das florestas do Brasil Central parece ajustar-se a dois grandes padrões de distribuição: (1) espécies de florestas decíduas e semidecíduas dependem essencialmente da ocorrência de manchas de solos de média a alta fertilidade dentro do domínio dos cerrados e tendem a se distribuir principalmente ao longo de um arco nordeste-sudoeste que conecta as caatingas às fronteiras do chaco; (2) um considerável número de espécies de florestas de galeria depende basicamente de alta umidade no solo e muitas delas parecem distribuir-se das florestas pluviais da Amazônia até as Atlânticas, cruzando a região do cerrado numa rota noroeste-sudeste através da rede dendrítica de florestas de galeria. Muitas espécies de floresta de galeria são generalistas quanto ao habitat, sendo inclusive compartilhadas com os cerrados. Um significativo número,

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entretanto, é endêmico das florestas de galeria. As galerias do oeste e norte da Província do Cerrado mostram uma ligação florística mais forte com as florestas pluviais da Amazônia, ao passo que as do centro e sul mostram uma estreita afinidade com as florestas semidecíduas montanas do sudeste brasileiro. Os padrões de distribuição geográfica atuais que emergiram das análises são discutidos sob a luz do presente conhecimento sobre as mudanças paleoambientais nos Neotrópicos.

INTRODUCTION

The Cerrado Biogeographic Province of tropical South America covers an area of about 2 million km^2 in Brazil, corresponding to one quarter of the land surface of the country, plus small areas in northwestern Paraguay and eastern Bolivia; it is surpassed in area only by the Amazonian Province (Cabrera & Willink, 1973). The predominant vegetation prior to the main human disturbances of this century was of a woody savanna with a physiognomy varying from closed woodland to open grassland. The Cerrado Province extends mainly over the plateaux of central Brazil and is part of the so-called 'diagonal of open formations' (Vanzolini, 1963) or 'corridor of xeric vegetation' (Bucher, 1982), that includes the much drier Caatinga Province, in northeastern Brazil, and Chaco Province, in Argentina-Paraguay-Bolivia. This dry corridor runs between the two main regions of moist forest of tropical South America, the Amazonian Province, in the northwest, and the Atlantic-Paranense Provinces, in the east and southeast (Fig. 1).

Most of the recent and controversial discussion on the palaeoenvironmental changes of tropical South America addresses the waxing and waning of both the open seasonal formations and humid forests during the late Quaternary climatic fluctuations. Geoecological data derived from soils, landforms and palynology, plus present-day distribution patterns of plants and animals, have given substantial evidence for the expansion of open vegetation formations and accompanying forest contraction during the glacial maxima as a result of drier, cooler macroclimates (Brown & Ab'Sáber, 1979; Van der Hammen, 1982; Dickinson & Virji, 1987). Most studies indicate two main dry, cool periods of forest contraction, the first and more severe during the Pleistocene, coinciding with the Northern Hemisphere Würm-Wisconsin glaciation, and the second during the Holocene (Ab'Sáber, 1979, 1980, 1982; Bigarella & Andrade-Lima, 1982). Although most authors now agree that major glacial cycle-related climatic and vegetation shifts did occur, a great deal of controversy still focuses on the role that possible fragmentation of forest into isolated refugia played in speciation and on present-day distribution patterns (Haffer, 1969, 1982; Prance, 1973; Brown & Ab'Sáber, 1979; Benson, 1982; Endler, 1982; Forero & Gentry, 1987; Beven et al., 1984). The postulated geographical location of some refugia has also been seriously challenged (Liu & Colinvaux, 1985; Colinvaux, 1989).

One of the most concrete sources of evidence for palaeoenvironmental changes at any latitude is the pollen record. However, palaeopalynological data for the Neotropics are very scarce and most of the studies relating pollen record to palaeoclimatic changes are centred in the Andean and Amazonian regions or in Central America (Van der Hammen, 1974; Absy & Van der Hammen, 1976; Absy, 1982; Liu

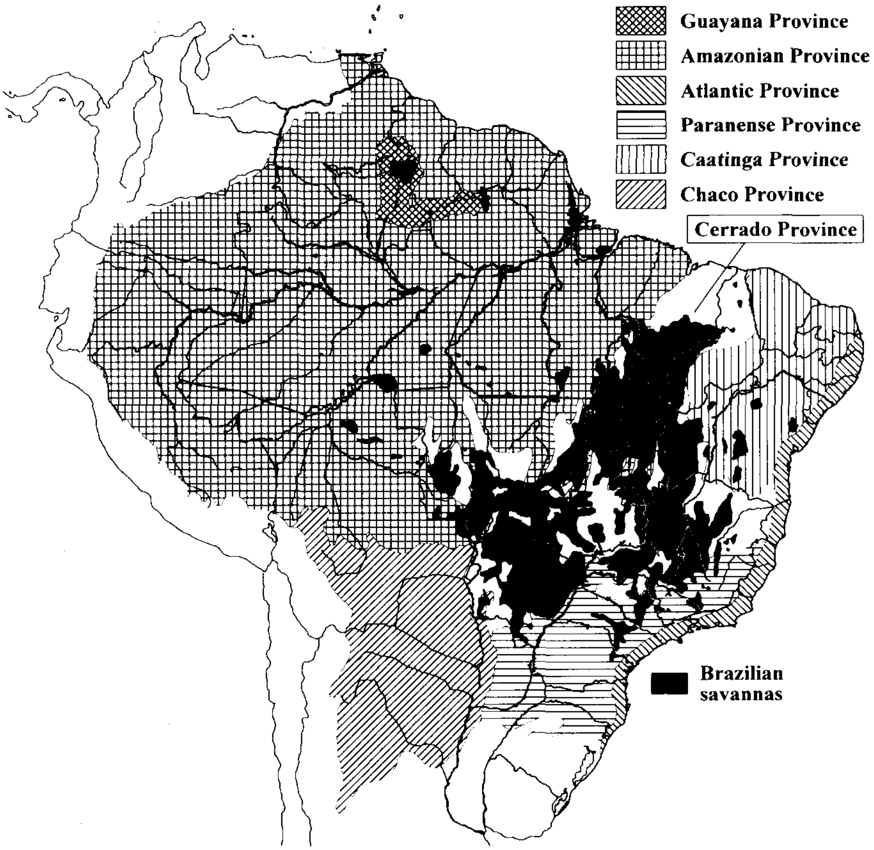


FIG. 1. Map showing the distribution of Brazilian savannas (cerrados), according to IBGE (1993), superimposed on the seven phytogeographic provinces of eastern tropical South America, according to Cabrera & Willink (1973).

& Colinvaux, 1985; Colinvaux, 1989; Markgraf, 1989; Busch & Colinvaux, 1990; Busch et al., 1990; Absy et al., 1991). It was only recently that Ledru (1991, 1993) contributed the first palaeopalynological study for the Cerrado Province of central Brazil, carried out at Salitre in western Minas Gerais. She concluded from the analysis of pollen distribution and modern vegetation and climate that between 33,000 and 25,000 BP the region was moister than today and was covered by rainforests (Ledru, 1993). During the Pleistocene glacial maximum, from 17,000 to 13,000 BP, a drier climate predominated and the proportion of trees in the vegetation declined, although only in the final term did arboreal cover reduce to the extent of a forest retreat. In another recent study, based on the analysis of plant species distribution, Prado & Gibbs (1993) proposed that during the Pleistocene glacial maximum the present-day corridor of xeric vegetation was covered mostly by an extensive seasonal woodland formation. This agrees with the findings of Ledru (1993) at Salitre (right in the middle of the corridor) who suggested the predominance of a seasonal arboreal vegetation during most of the Pleistocene, when the climate would be drier than now but not severely arid as previously thought (Brown & Ab'Sáber, 1979; Bigarella & Andrade-Lima, 1982).

According to Ledru (1993), the period following the last Pleistocene glacial maximum was characterized by the expansion of the *Araucaria* forest, indicating the predominance of a cooler and moister climate until 8500 BP. This period suffered a sudden and short-term interruption between 11,000 and 10,000 BP, corresponding to a dry interval accompanied by forest retreat. After 8500 BP the *Araucaria* forest was replaced by mesophytic forest, indicating an episode of moist climate with higher temperatures lasting until 5500 BP. The mid-Holocene dry interval which ensued at about 5000 BP caused a severe reduction in the forest area; since then forest expansion has once more occurred but not enough to recover the whole extent of the previous mesophytic forest period. Some authors believe that disturbances, both anthropogenic and natural (fire in particular), helped retard forest expansion within the Cerrado Province during the late Holocene, despite the fact that climate and soils certainly favour the establishment of forests in most of the region (Reis, 1971; Klein, 1975). The isolated areas of cerrado (savanna) that are found enclosed by the Amazonian forest (see Fig. 1) provide evidence both of the forest expansion through a previously cerrado-dominated landscape and of the maintenance of cerrado vegetation in areas where the climatic conditions could support forest vegetation (Bigarella et al., 1975).

It is now clear that the effects of the late Quaternary climatic fluctuations on the open vegetation formations of central Brazil were not restricted to a simple expansion and contraction of cerrado vs. rainforest, but also included complex changes within the dry corridor region itself. Cerrados, seasonal forests, rainforests, and even *Araucaria* forests appear to have thrived in various epochs at least in certain areas of the region. In addition to climatic variation, other factors such as soils, biotic pressure and disturbance could also have had profound palaeoenvironmental effects, and further data are necessary to provide a reliable description of the past history of the vegetation cover of central Brazil.

The dry corridor of open formations has been considered by many authors as an important impediment to species migration between the two main South American forest regions, thus explaining many of the differences in floristic composition between them. On the other hand, the disjunct distribution patterns of a considerable number of species in the coastal Atlantic and Amazonian rainforests suggest the possibility of past forest links (Rambo, 1961; Rizzini, 1963; Andrade-Lima, 1966). Andrade-Lima (1964) and Rizzini (1963) refer to a possible migration route through a postulated mesophytic forest corridor that would have traversed the present-day Caatinga Province of northeastern Brazil at certain periods since the late Tertiary. Andrade-Lima (1982) suggested that the montane forests ('brejos') that presently exist isolated within the semi-arid region are relics of an ancient and wider forest cover. Bigarella et al. (1975) argued that, in addition to this Northeast Bridge, the floristic similarity between the eastern Amazonian and southeastern Atlantic rainforests demonstrates that there must have been a second migration route, which they called the Southeast-Northwest Bridge.

Although Bigarella et al. (1975) did not themselves suggest how the Southeast-Northwest Bridge connected the two forest regions, one could postulate that such a connection could have run through central Brazil, either as a continuous forest corridor or as a series of forest patches between which 'island-hopping' occurred. The idea of the Cerrado Province acting as an effective obstacle to the migration of forest species seems rather doubtful when a detailed map of present-day vegetation is examined. The map of Brazilian savannas (cerrados) (Fig. 1), extracted from IBGE (1993), clearly shows that the distribution of cerrados in central Brazil is far from continuous. When this is superimposed on the Cerrado Province of Cabrera & Willink (1973) a great proportion of gaps is shown (Fig. 1). These correspond essentially to patches of semideciduous forests, deciduous forests and to the transitional mosaics between these forests and the cerrado, called 'areas of ecological tension' by IBGE (1993). In addition to this, the savanna (cerrado) vegetation formation in the IBGE's classification system includes gallery forests, which are ubiquitous throughout the cerrado region. Therefore, forests are a far from negligible component of central Brazilian vegetation and their role as migration routes for forest species cannot be neglected, especially when evidence exists of a wider forest cover during a number of episodes in the late Quaternary. In fact, even now, the occurrence of mesophytic forest (deciduous and semideciduous forests) within the cerrado biome is very extensive and generally underestimated; during a recent journey by road from the Distrito Federal to Estreito in Maranhão, crossing c.1400km of the states of Goiás and Tocantins, one of us (J.A.R.) estimated that probably nearly 50% of the vegetation traversed was degraded mesophytic forest or the closely related mesotrophic cerradão. The deciduous forests that occur within the Cerrado Province on patches of calcium-rich soils have already been regarded by Prado & Gibbs (1993) as an important 'island-hopping' migration route connecting the semi-arid caatingas to the semideciduous forests of the Paraná basin and of the Andean flanks. If such a NE-SW route existed in central Brazil for deciduous calciphilous species, the existence of a NW-SE route for species associated with higher soil moisture is also conceivable through gallery forests.

A number of authors have already suggested that the central Brazilian gallery forests represent floristic intrusions of the Amazonian and/or Atlantic forests into the cerrado domain. Cabrera & Willink (1973) mentioned that the galleries are actually a net connecting the forests of the Amazonian and Paranense Provinces. Based on floristic similarities, Rizzini (1979) stated that the galleries, together with other hinterland forests, are 'mediterranean extensions of the great Atlantic forest'. He also added that in Mato Grosso the continuous link to the Hylaea would give the galleries an Amazonian floristic nature. In fact, a considerable number of Amazonian species are known to penetrate the cerrados via gallery forests in that state, including species of rubber-tree (*Hevea*), a genus which is often reported to define the borders of the Amazonian forests (Veloso, 1966; Pires & Prance, 1977; Daly & Prance, 1989). Pires (1984) argued that if forest refuges did exist in the Amazon during the glacial ages they would not have had the postulated island configuration, but a dendritic pattern following river drainage. This author also suggested that present-day galleries within the cerrado region constitute hodiernal forest refuges.

In the present contribution we investigate the floristic nature of central Brazilian forests by the analysis of present-day distribution patterns. Our work was based essentially on multivariate analyses of existing floristic checklists and on the analysis of a series of dot-maps showing the distribution of woody species. The links to other main forest formations were assessed, with special attention to the connections to the Amazonian and Atlantic forests. Although we are aware of the many risks of drawing conclusions from the still poor floristic record, we believe that major patterns did emerge from our analyses and that these added an important contribution to the discussion of the past evolution of central Brazilian ecological spaces. In addition, we believe that the results contribute valuable information on the pattern of biodiversity in the region and that this type of information is essential in the planning of conservation areas.

MATERIALS AND METHODS

Selection of floristic checklists

One of the main purposes of this study was to assess the patterns of floristic differentiation of central Brazilian forests, both among the many forest types of the region and in relation to the forests of neighbouring vegetation provinces. To that end, a total of 106 floristic checklists were obtained from literature and other sources available in the Royal Botanic Gardens of Edinburgh and Kew in 1992–94. These were selected from floristic surveys of the woody flora of forests of eastern tropical South America, with special emphasis on central Brazilian forests. To ensure accuracy, only surveys with at least 85% of the taxa identified to species level were used. Unfortunately, standardization by area size proved impossible as this varied widely. However, 'regional lists' (those for areas of thousands of hectares) were included only for non-central Brazilian forests, which were incorporated in the dataset as paradigms. The 106 floristic checklists comprised only areas which could be classified physiognomically as forests or dense woodlands, i.e. predominantly arboreal, although sometimes with an incomplete canopy. Therefore, the array of vegetation types ranged from dense Amazonian rainforests to cerradões (forested savannas). The 106 forest areas chosen extended from the state of Roraima, in northern Brazil, to Chaco and Santa Fe Provinces, in northeastern Argentina, and from the state of Pernambuco, in eastern Brazil, to Pando Province, in northern Bolivia. Their location is shown in Fig. 2 while Table 1 gives summarized information for each area.

Classification of the vegetation types

The environmental information available for the 106 forest areas was either very poor or hardly comparable due to the miscellaneous methods used (especially for

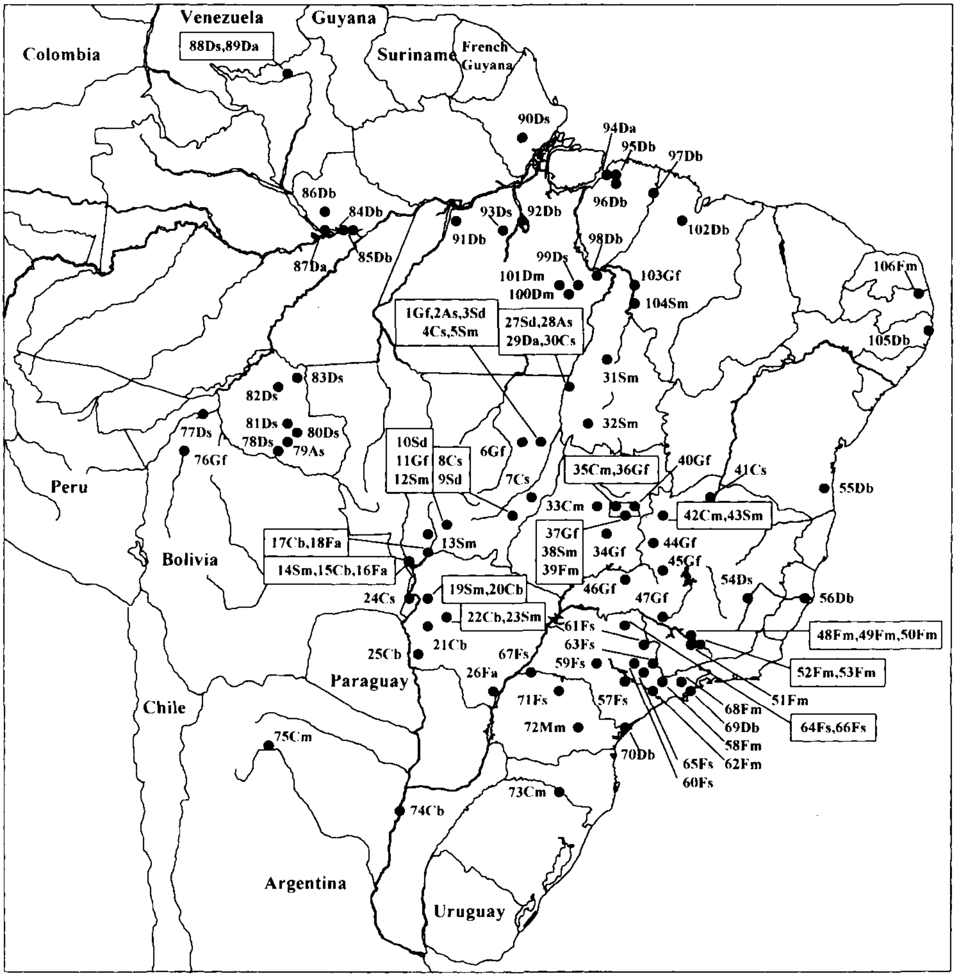


FIG. 2. Map of Brazil and neighbouring countries showing the location of the 106 forest areas used in the analyses. The forest areas are identified by their number in Table 1, followed by the two-letter code corresponding to their classification according to the modified IBGE's classification system for Brazilian vegetation (see text, pp. 154–5).

soil data). However, an environmental background was necessary to make sense of the results emerging from the multivariate analyses. So, we decided to apply to the forest areas a vegetation classification system highly dependent on both physiognomy and environmental conditions and to assess the classification categories in the multivariate analyses. The choice of a single well-defined classification system which suited our needs also allowed skirting the byzantine discussion about the best nomenclature for Brazilian vegetation.

We chose the IBGE classification system for Brazilian vegetation (Veloso et al.,

TABLE 1. Vegetation formation, locality, geographical coordinates, altitude, climatic type and source for each of the 106 forest areas used in the analyses. The two-letter codes after the identification numbers correspond to the classification of the forest areas according to the modified IBGE classification system for Brazilian vegetation (see text, pp. 154–5), which is also given in full in the following column. The double capitals after the localities are the official abbreviations of Brazilian states. Latitudes are South unless indicated. Altitudes are medians where a range was given in the source. An HS after the reference indicates that herbarium specimens were also used in the preparation of the checklist.

Ident. no.	Vegetation formation (modified IBGE system)	Locality
1 Gf	Gallery forest	Serra do Roncador (MT)
2 As	Submontane open rainforest	Serra do Roncador (MT)
3 Sd	Dystrophic cerradão	Serra do Roncador (MT)
4 Cs	Submontane deciduous forest	Serra do Roncador (MT)
5 Sm	Mesotrophic cerradão	Serra do Roncador (MT)
6 Gf	Gallery forest	Rio Suiá-Missu (MT)
7 Cs	Submontane deciduous forest	Vale dos Sonhos (MT)
8 Cs	Submontane deciduous forest	Torixoréu (MT)
9 Sm	Mesotrophic cerradão	Torixoréu (MT)
10 Sd	Dystrophic cerradão	Chapada dos Guimarães (MT)
11 Gf	Gallery forest	Chapada dos Guimarães (MT)
12 Sm	Mesotrophic cerradão	Rio Claro, Cuiabá (MT)
13 Sm	Mesotrophic cerradão	Poconé, Pantanal (MT)
14 Sm	Mesotrophic cerradão	Faz. Acurizal, Pantanal (MT)
15 Cb	Lowland deciduous forest	Faz. Acurizal, Pantanal (MT)
16 Fa	Alluvial semideciduous forest	Faz. Acurizal, Pantanal (MT)
17 Cb	Lowland deciduous forest	Poconé, Pantanal (MT)
18 Fa	Alluvial semideciduous forest	Poconé, Pantanal (MT)
19 Sm	Mesotrophic cerradão	Faz. Nhumirim, Pantanal (MS)
20 Cb	Lowland deciduous forest	Faz. Nhumirim, Pantanal (MS)
21 Cb	Lowland deciduous forest	Rio Abobral, Pantanal (MS)
22 Cb	Lowland deciduous forest	Faz. Salina, Pantanal (MS)
23 Sm	Mesotrophic cerradão	Faz. Salina, Pantanal (MS)
24 Cs	Submontane deciduous forest	Corumbá (MS)
25 Cb	Lowland deciduous forest	Porto Murtinho (MS)
26 Fa	Alluvial semideciduous forest	Rio Ivinheima (MS)
27 Sd	Dystrophic cerradão	Ilha do Bananal (TO)
28 As	Submontane open rainforest	Ilha do Bananal (TO)
29 Da	Alluvial dense rainforest	Ilha do Bananal (TO)
30 Cs	Submontane deciduous forest	Ilha do Bananal (TO)
31 Sm	Mesotrophic cerradão	Barrolândia (TO)
32 Sm	Mesotrophic cerradão	Figueirópolis (TO)
33 Cm	Montane deciduous forest	Padre Bernardo (GO)
34 Gf	Gallery forest	Silvânia (GO)
35 Cm	Montane deciduous forest	FERCAL (DF)

TABLE 1. *(cont.)*

Lat. S*	Long. W	Alt. (m)	Climate (Köppen)	Source
12°49′	51°46′	380	Aw/Am	Ratter et al. 1973, HS
12°49′	51°46′	400	Aw/Am	Ratter et al. 1973, HS
12°49′	51°46′	400	Aw/Am	Ratter et al. 1973
12°49′	51°46′	400	Aw/Am	Ratter et al. 1973, 1977, 1978b
12°49′	51°46′	400	Aw/Am	Ratter et al. 1973, 1977
12°46′	52°03′	350	Aw/Am	Ratter et al. 1978a, HS
15°00′	54°30′	450	Aw	Ratter et al. 1977, 1978b
15°53′	52°15′	490	Aw	Furley et al. 1988, Ratter et al. 1978b
15°53′	52°15′	490	Aw	Furley et al. 1988
15°21′	55°49′	350	Aw	Oliveira-Filho & Martins 1986, Oliveira-Filho et al. 1990
15°21′	55°49′	350	Aw	Oliveira-Filho 1989, Oliveira-Filho et al. 1990
15°20′	55°51′	270	Aw	Oliveira-Filho & Martins 1986, 1991
16°25′	56°50′	95	Aw	Cunha 1990, Ratter et al. 1988
17°45′	57°37′	85	Aw	Prance & Schaller 1982
17°45′	57°37′	85	Aw	Prance & Schaller 1982
17°45′	57°37′	85	Aw	Prance & Schaller 1982
17°05′	56°57′	85	Aw	Cunha 1990
17°10′	56°57′	85	Aw	Cunha 1990
18°59′	56°39′	89	Aw	Ratter et al. 1988
18°59′	56°39′	89	Aw	Ratter et al. 1988
19°45′	56°45′	95	Aw	Cunha et al. 1986, Ratter et al. 1988, HS
19°30′	56°10′	95	Aw	Dubs 1992
19°30′	56°10′	95	Aw	Dubs 1992
19°01′	57°39′	120	Aw/Bs	Ratter et al. 1988, Prado et al. 1992, HS
21°15′	57°40′	100	Aw/Bs	Prado et al. 1992
22°47′	53°32′	250	Cw	Assis 1991
10°25′	50°20′	240	Aw/Am	Ratter 1987
10°25′	50°20′	240	Aw/Am	Ratter 1987
10°25′	50°20′	240	Aw/Am	Ratter 1987
10°25′	50°20′	240	Aw/Am	Ratter 1987
10°05′	48°55′	250	Aw	Ratter et al., unpubl. data
12°04′	49°10′	400	Aw	Ratter et al., unpubl. data
15°15′	48°30′	650	Aw	Ratter et al. 1977, 1978b
16°40′	48°37′	1050	Aw	Felfili 1990, 1993b, HS
15°40′	47°56′	1100	Aw	Ramos 1989

TABLE 1. (*cont.*)

Ident. no.	Vegetation formation (modified IBGE system)	Locality
36 Gf	Gallery forest	PN Brasília (DF)
37 Gf	Gallery forest	APA Gama-C. do Veado (DF)
38 Sd	Dystrophic cerradão	Faz. Água Limpa (DF)
39 Fm	Montane semideciduous forest	Brasília Botanic Garden (DF)
40 Gf	Gallery forest	APA Rio S. Bartolomeu (DF)
41 Cs	Submontane deciduous forest	Pandeiros, Januária (MG)
42 Cm	Montane deciduous forest	Sagarana (MG)
43 Sm	Mesotrophic cerradão	Sagarana (MG)
44 Gf	Gallery forest	Paracatu (MG)
45 Gf	Gallery forest	Patrocínio (MG)
46 Gf	Gallery forest	EE Panga, Uberlândia (MG)
47 Gf	Gallery forest	PN Serra da Canastra (MG)
48 Fm	Montane semideciduous forest	ESAL, Lavras (MG)
49 Fm	Montane semideciduous forest	RB Poço Bonito, Lavras (MG)
50 Fm	Montane semideciduous forest	Bom Sucesso (MG)
51 Fm	Montane semideciduous forest	Camargos, Itutinga (MG)
52 Fm	Montane semideciduous forest	Madre de Deus de Minas (MG)
53 Fm	Montane semideciduous forest	Serra S. José, Tiradentes (MG)
54 Ds	Submontane dense rainforest	RF Rio Doce (MG)
55 Db	Lowland dense rainforest	Southern Bahia (BA)
56 Db	Lowland dense rainforest	RF CVRD, Linhares (ES)
57 Fs	Submontane semideciduous forest	Anhembi (SP)
58 Fm	Montane semideciduous forest	PM Grota Funda, Atibaia (SP)
59 Fs	Submontane semideciduous forest	RE Bauru (SP)
60 Fs	Submontane semideciduous forest	APA Corumbataí, Ipeúna (SP)
61 Fs	Submontane semideciduous forest	UNESP, Jaboticabal (SP)
62 Fm	Montane semideciduous forest	Serra do Japi, Jundiaí (SP)
63 Fs	Submontane semideciduous forest	RB Mogi Guaçu (SP)
64 Fs	Submontane semideciduous forest	RE Porto Ferreira (SP)
65 Fs	Submontane semideciduous forest	Rio Claro (SP)
66 Fs	Submontane semideciduous forest	PE S. Rita Passa Quatro (SP)
67 Fs	Submontane semideciduous forest	PE Teodoro Sampaio (SP)
68 Fm	Montane semideciduous forest	FR S. José dos Campos (SP)
69 Db	Lowland dense rainforest	EE Ubatuba (SP)
70 Db	Lowland dense rainforest	PE Ilha do Cardoso (SP)

TABLE 1. (*cont.*)

Lat. S*	Long. W	Alt. (m)	Climate (Köppen)	Source
15°40′	47°56′	1100	Aw	Felfili 1990, 1993b, Ramos 1994
15°55′	47°54′	1100	Aw	Ratter 1980, 1991, Felfili & Silva Jr 1992, Felfili 1993a
15°57′	47°56′	1100	Aw	Ratter 1980, 1991, Felfili & Silva Jr 1992
15°53′	47°51′	1100	Aw	Azevedo et al. 1990
15°40′	47°56′	1100	Aw	Pereira et al. 1985
15°28′	44°23′	350	Aw/Bs	Ratter et al. 1977, 1978b
16°00′	47°00′	550	Aw/Bs	Ratter et al., unpubl. data
16°00′	47°00′	550	Aw/Bs	Ratter et al., unpubl. data
17°10′	46°57′	900	Aw	Felfili 1990, 1993b, HS
19°20′	46°47′	950	Aw	Felfili 1990, 1993b, HS
19°10′	48°24′	800	Aw	Schiavini 1992
20°30′	46°30′	950	Aw/Cw	Mota 1984, HS
21°13′	45°00′	925	Cw	Oliveira-Filho et al. 1994b
21°20′	45°00′	1150	Cw	Gavilanes et al. 1992a, Oliveira-Filho et al. 1994a
21°09′	44°54′	825	Cw	Carvalho et al. 1992, Oliveira-Filho et al. 1994c
21°22′	44°37′	917	Cw	Vilela et al. 1995, Oliveira-Filho et al. 1994c
21°29′	44°22′	925	Cw	Gavilanes et al. 1992b, Oliveira-Filho et al. 1994d
21°01′	44°14′	900	Cw	Oliveira-Filho & Machado 1993
19°40′	42°35′	450	Aw/Cw	CETEC 1982, Silva Jr et al. 1994, HS
15°20′	39°10′	50	Af	Harley & Mayo 1980, Mori et al. 1983
19°18′	40°04′	50	Am	Peixoto & Gentry 1990, HS
22°40′	48°10′	500	Cw	Cesar & Leitão-Filho 1990a, 1990b
23°10′	46°25′	1200	Cf	Meira Neto et al. 1989, Grombone et al. 1990
22°19′	49°04′	570	Cw	Cavassan et al. 1984
22°25′	48°45′	600	Cw	Mantovani et al. 1986, Rodrigues 1991
21°15′	48°20′	560	Cw	Pinto 1989, Marchiori et al. 1992
23°11′	46°52′	1020	Cf	Rodrigues 1986, Rodrigues et al. 1989
22°16′	47°10′	595	Cw	Gibbs & Leitão Filho 1978, Mantovani et al. 1989
21°49′	47°25′	580	Cw	Bertoni et al. 1982, Bertoni & Martins 1987
22°22′	47°28′	630	Cw	Pagano & Leitão Filho 1987, Pagano et al. 1987
21°40′	47°38′	630	Cw	Bertoni et al. 1988, Martins 1991
22°30′	52°20′	300	Cw	Campos & Heinsdijk 1970, Baitello et al. 1988
23°05′	45°55′	840	Cf	Silva 1989
23°27′	45°04′	105	Af	Silva & Leitão Filho 1982
25°10′	48°00′	100	Af	Barros et al. 1991

TABLE 1. *(cont.)*

Ident. no.	Vegetation formation (modified IBGE system)	Locality
71 Fs	Submontane semideciduous forest	PE Mata Godoy, Londrina (PR)
72 Mm	Montane mixed forest	FN Irati, Teixeira Soares (PR)
73 Cm	Montane deciduous forest	Alto Rio Uruguai (SC/RS)
74 Cb	Lowland deciduous forest	Eastern Chaco (Argentina)
75 Cm	Montane deciduous forest	Western Chaco (Argentina)
76 Gf	Gallery forest	Rio Beni savannas (Bolivia)
77 Ds	Submontane dense rainforest	Rio Ivon (Bolivia)
78 Ds	Submontane dense rainforest	Alvorada D'Oeste (RO)
79 As	Submontane open rainforest	Presidente Médici (RO)
80 Ds	Submontane dense rainforest	Jiparaná (RO)
81 Ds	Submontane dense rainforest	Presidente Médici (RO)
82 Ds	Submontane dense rainforest	Jaru (RO)
83 Ds	Submontane dense rainforest	Ariquemes (RO)
84 Db	Lowland dense rainforest	Manaus-Itacoatiara (AM)
85 Db	Lowland dense rainforest	Reserva Ducke, Manaus (AM)
86 Db	Lowland dense rainforest	EE INPA (AM)
87 Da	Alluvial dense rainforest	Rio Solimões, Manaus (AM)
88 Ds	Submontane dense rainforest	EE Ilha de Maracá (RR)
89 Da	Alluvial dense rainforest	EE Ilha de Maracá (RR)
90 Ds	Submontane dense rainforest	Serra do Navio (AP)
91 Db	Lowland dense rainforest	Belterra, Santarém (PA)
92 Db	Lowland dense rainforest	O Deserto, Altamira (PA)
93 Ds	Submontane dense rainforest	Transamazonica, Altamira (PA)
94 Da	Alluvial dense rainforest	Rio Amazonas, Belém (PA)
95 Db	Lowland dense rainforest	Mucambo, Belém (PA)
96 Db	Lowland dense rainforest	Capitão Poço (PA)
97 Db	Lowland dense rainforest	Rio Gurupi (PA)
98 Db	Lowland dense rainforest	Marabá (PA)
99 Ds	Submontane dense rainforest	Rio Gelado, Carajás (PA)
100 Dm	Montane dense rainforest	Iron ore, Carajás (PA)
101 Dm	Montane dense rainforest	Copper ore, Carajás (PA)
102 Db	Lowland dense rainforest	Aldeia Urutawy (MA)
103 Gf	Gallery forest	Carolina (MA)
104 Sm	Mesotrophic cerradão	Rio Lajes (MA)
105 Db	Lowland dense rainforest	Coastal Pernambuco (PE)
106 Fm	Montane semideciduous forest	Mata de Pau Ferro, Areias (PB)

* Unless otherwise indicated

TABLE 1. *(cont.)*

Lat. S*	Long. W	Alt. (m)	Climate (Köppen)	Source
23°27′	51°15′	700	Cf	Soares-Silva & Barroso 1992
25°26′	50°24′	870	Cf	Galvão et al. 1989
28°00′	52°00′	c.500	Cf	Klein 1972, Rambo 1980
28°30′	59°30′	80	Cw/Bs	Prado 1991, Prado et al. 1989, Franceschi & Lewis 1979
24°45′	64°40′	1050	Cw/Bs	Brown et al. 1985, Prado 1991, Lewis & Pire 1981
13°10′	67°30′	180	Am/Cw	Haase & Beck 1989
11°45′	66°02′	200	Am	Boom 1986, 1987
11°25′	63°30′	180	Am	Lisboa 1990, Lisboa & Lisboa 1990
11°10′	62°20′	200	Am/Aw	Lisboa 1990
11°00′	61°57′	230	Am/Aw	Salomão & Lisboa 1988, Lisboa 1989, 1990
11°10′	62°15′	230	Am/Aw	Maciel & Lisboa 1989, Lisboa 1990
09°35′	61°57′	200	Am	Absy et al. 1986/87
09°20′	62°00′	200	Am	Absy et al. 1986/87
02°55′	59°45′	50	Am/Af	Prance et al. 1976
02°55′	59°35′	50	Am/Af	Higuchi et al. unpubl. data, Ribeiro & Hopkins (HS)
02°30′	60°05′	100	Am/Af	Porto et al. 1976
03°20′	60°20′	24	Am/Af	Worbes et al. 1992
03°22′N	61°26′	180	Am	Milliken & Ratter 1989
03°22′N	61°26′	180	Am	Milliken & Ratter 1989
00°55′N	52°01′	280	Am/Af	Rodrigues 1963
02°40′	54°45′	60	Am	Carvalho et al. 1986a, 1986b
03°29′	51°40′	30	Am/Aw	Campbell et al. 1986
03°35′	53°10′	200	Am	Dantas & Muller 1979
01°40′	48°30′	3	Am	Cain et al. 1956, Pires & Koury 1958
01°35′	48°30′	25	Am	Cain et al. 1956
01°44′	47°09′	65	Am	Dantas et al. 1980
02°20′	46°30′	65	Aw	Ballé 1987
05°43′	49°00′	90	Aw	Salomão 1991
06°10′	50°20′	550	Aw	Silva et al. 1987
06°17′	50°23′	700	Aw	Salomão et al. 1988, Salomão & Rosa 1989, Morellato & Rosa 1991
06°10′	50°50′	650	Aw	Silva & Rosa 1989
03°10′	45°06′	75	Aw	Ballé 1986
07°11′	47°25′	150	Aw/Am	Ratter et al., unpubl. data
07°21′	47°26′	170	Aw/Am	Ratter et al., unpubl. data
08°30′	35°00′	30	As	Andrade-Lima 1960, HS
06°58′	35°42′	550	Bs/As	Mayo & Fevereiro 1982, HS

1991), which met nearly all our requirements. However, a few modifications were necessary:

(a) Gallery forests, which are part of the cerrado (savanna) formation in the IBGE system, were separated as a distinct category. However, this was applied only to the galleries occurring within the Cerrado Province, as defined by Cabrera & Willink (1973), and riverine forests of other provinces fell into other IBGE categories.

(b) The altitudinal limit between the submontane and montane formations for latitudes between 16°S and 24°S was changed from 500 to 750m, as this latter figure was more effective in distinguishing the montane forests of the states of São Paulo (Torres et al., 1995) and Minas Gerais (Oliveira-Filho et al ., 1994c).

(c) The IBGE category 'forested savanna' (cerradão) was split into two, the 'mesotrophic cerradão' and the 'dystrophic cerradão', since an important ecological distinction has been found between the two formations (Ratter, 1971; Ratter et al., 1973, 1977; Ratter & Dargie, 1992).

The map of Brazilian vegetation produced by the IBGE (1993) helped in classifying the forest areas. Information from the literature was also used, especially in dubious situations such as those of transitional areas, and when extending the classification system to the four areas in Argentina and Bolivia. The resulting classification of the 106 forest areas is given both in Table 1 and Fig. 2. A brief description of the 15 categories used follows:

(a) **Gallery forest (Gf)**: riverine forests occurring within the cerrado domain as more or less narrow strips along the valley bottoms and as rather larger areas around headwaters ('cabeceiras') often showing sharp boundaries with the neighbouring open formations. Number of areas: 13.

(b) **Dystrophic cerradão (Sd)**: dense savanna woodlands associated with base-poor, often sandy, soils; particularly common in the transition to the Hylaea and in association with galleries. Number of areas: 4.

(c) **Mesotrophic cerradão (Sm)**: dense savanna woodlands associated with base-rich soils, often derived from calcareous material; frequently found in association with deciduous forests. Number of areas: 11.

(d) **Lowland deciduous forest (Cb)**: seasonal forests occurring at low altitudes (< 100m) on base-rich soils, especially in the Mato Grosso Pantanal and in the Chaco fringes. Number of areas: 7.

(e) **Submontane deciduous forest (Cs)**: seasonal calciphilous forests occurring on patches of base-rich soils at intermediate altitudes (100–750m) within the cerrado domain or in the transitional areas to the caatinga domain. Number of areas: 6.

(f) **Montane deciduous forest (Cm)**: seasonal calciphilous forests occurring on patches of base-rich soils at higher altitudes (> 750m) within the cerrado domain or in the transitional area to the caatinga domain. This category also included the piedmont forests of central-western Argentina. Number of areas: 5.

(g) **Alluvial semideciduous forest (Fa)**: seasonal but moderately deciduous forests occurring on the floodplains of the major rivers of the Paraná-Paraguay basin. These were the only riverine forests of central Brazil not classified as gallery forest since they are distinguished by their flood regime. Number of areas: 3.

(h) **Submontane semideciduous forest (Fs)**: seasonal subtropical forests occurring mainly in the mid-altitude hinterlands of southeastern and southern Brazil (100–750m), also appearing on soils of intermediate fertility in central Brazil. Number of areas: 10.

(i) **Montane semideciduous forest (Fm)**: seasonal but moderately deciduous forests, occurring in the high-altitude hinterlands of southeastern and central Brazil (>750m), often associated with soils of intermediate fertility. This category also includes the 'brejo' forests that cover the hinterland plateaux of northeastern Brazil. Number of areas: 11.

(j) **Montane mixed rainforest (Mm)**: subtropical *Araucaria* forests, occurring on the highlands of southern and southeastern Brazil. Number of areas: 1.

(k) **Submontane open rainforest (As)**: transitional forests found mainly in the southern fringes of the Hylaea, often on base-poor and sandy soils. A confused nomenclature has been applied to this physiognomy, e.g. evergreen seasonal forest, monsoon forest, and dry forest ('mata seca'). Number of areas: 3.

(l) **Alluvial dense rainforest (Da)**: evergreen rainforests occurring on the floodplains of the Amazonian rivers; also called 'várzea forests'. Number of areas: 4.

(m) **Lowland dense rainforest (Db)**: evergreen rainforests occurring at low altitudes both in the Amazonian ('terra firme' forests) and Atlantic coastal regions. Number of areas: 11 Amazonian and 4 Atlantic.

(n) **Submontane dense rainforest (Ds)**: evergreen rainforests occurring at mid-altitudes both in the Amazonian ('terra firme' forests) and Atlantic coastal regions. Number of areas: 10 Amazonian and 1 Atlantic.

(o) **Montane dense rainforest (Dm)**: evergreen Amazonian rainforests ('terra firme' forests) occurring at higher altitudes in the Carajás mountains system. Number of areas: 2.

Preparation and revision of the database

The floristic information contained in the 106 checklists was organized in a database using Microsoft Excel 4. The first part of this database consisted of basic information about each area: geographical coordinates, altitude, climatic type, topographic position, soil type, vegetation formation and sources of information. Most of these are given in Table 1. The second part of the database was essentially a presence/absence matrix for woody species registered in the 106 forest areas. This is not reproduced here because of space limitations. However, the printed version is available from the libraries of the Royal Botanic Garden Edinburgh and Universidade Federal de Lavras (Oliveira-Filho & Ratter, 1994).

Before reaching its final form, the information contained in the database went through a detailed revision to check the 3528 species names cited in the checklists for synonymy and growth form. A minimum potential height of 3m was established as the criterion for inclusion and climbers were excluded. Checking synonymy was no trivial task: no less than 332 monographs and revisions were consulted, and we were also helped by specialists from the Royal Botanic Gardens Kew, New York Botanical Garden, Missouri Botanical Garden and University of São Paulo. After eliminating 312 synonyms and 101 non-arboreal taxa, the number of species fell to 3114 (11.7% reduction). Another 118 synonyms were replaced by their presently accepted names without reducing the number of species. A total of 13.8% of synonyms was found in the original list of 3427 names for arboreal species. These figures demonstrate the level of caution necessary when dealing with vegetation survey data for this part of the world, and the risks of performing floristic analyses without a careful verification of all names. Details of literature used in the revision of the database as well as the list of synonyms eliminated are available from the first author.

In addition to the records obtained from the literature, the database was amplified by examination and revision of the extensive collections from central Brazilian forests lodged in the herbarium of the Royal Botanic Garden Edinburgh (E).

Multivariate analyses

The floristic information (presence records) contained in the database was simplified by techniques of multivariate analyses in order to seek main patterns of data structure that could be associated with geographic/environmental variables. Special attention was given to the vegetation classification categories described above, which were treated here as synthetic geographic/environmental parameters. It is important to stress at this point that the whole procedure was an exploratory data analysis carried out with a hypothesis-generating purpose (Kent & Coker, 1992; Ratter & Dargie, 1992).

Three techniques of multivariate analysis, corresponding to different methodological approaches, were used. The purpose was to seek patterns that could be accentuated in common by different analytical procedures. The techniques were: (1) an ordination by Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980), (2) a divisive hierarchical classification by Two-Way INdicator SPecies ANalysis (TWINSPAN) (Hill, 1979), and (3) an agglomerative hierarchical classification by UPGMA (Unweighted Pair-Groups Method using Arithmetic averages) using the Sørensen Coefficient of Community (CC) as a measure of similarity (Kent & Coker, 1992).

For DCA and TWINSPAN, we used the versions contained in the package VESPAN II (Malloch, 1988). The floristic matrix analysed by both methods had 1423 species and 106 forest areas as a result of the elimination of 1691 species occurring in only one area, following the procedures described in Ratter & Dargie (1992). However, the full matrix with 3114 species and 106 areas was analysed by UPGMA. The CCs were calculated by database management in Microsoft Excel 4 and processed by the package NTSYS (Rohlf, 1992) in order to produce the clustering dendrogram.

The floristic information contained in the database was eventually condensed by clustering the presence records within each of 12 groups of forest areas corresponding to the main floristic patterns indicated by the multivariate analyses. The results were used to allow a direct quantitative assessment of the floristic links between the groups by both the number of species in common and the calculation of a similarity index: the Sørensen Coefficient of Community (CC). A consecutive clustering operation was carried out with the 12 groups and these were agglomerated into five wider groups: gallery forests, Amazonian and Atlantic forests, cerradões and deciduous forests. These were compared in terms of number of species in common.

Maps of geographical distribution

A series of 52 maps of the geographical distribution of 55 tree species was produced to illustrate the distribution patterns of characteristic species of central Brazilian forest species. These concentrated on gallery forest species since the assessment of their floristic links to the Amazonian and Atlantic forests was one of the primary aims of this study. Besides, the distribution patterns of South American deciduous forest species, which represent another important component of central Brazilian forests, has already been investigated in a series of maps produced by Prado & Gibbs (1993).

The selection of the 55 species for mapping followed two criteria: (1) the 13 most frequent species in the 13 gallery forests of the database were chosen regardless of their geographical or ecological distribution; (2) the remaining 42 species were deliberately chosen in order to illustrate patterns of geographical and ecological distribution of typical species of central Brazilian gallery forests. This choice was based both on the authors' field experience and on the 'indicator species' given by TWINSPAN. Unless we had valuable additional information, we also avoided producing maps of species already available in the recent literature (e.g. for *Anadenathera colubrina*, *Sterculia striata* and *Astronium fraxinifolium* given by Prado & Gibbs (1993)).

The maps were produced using two sources of information: (1) herbarium specimens lodged at the herbaria of Kew (K) and Edinburgh (E), or cited in taxonomic literature, and (2) citations in reliable floristic checklists, always followed by verification in the literature for correspondence with the geographical distribution given by specialists. Following Prado & Gibbs (1993), different symbols are used in the maps to distinguish the two sources of information.

MULTIVARIATE ANALYSES

The multivariate analyses of the floristic data show a great deal of coincidence in the patterns arising from the three techniques used (Figs 3–5). Most of the vegetation classification categories we used appear as cohesive groups, demonstrating that the geographical and ecological variables underlying the classification system probably have a strong correlation with the main floristic patterns detected. A detailed description and discussion of these results are given below.

Ordination (DCA)

The ordination of the 106 areas in the first two DCA axes is given by Fig. 3. The distribution of the forest areas in the ordination space conforms basically to the shape of a triangle whose vertices are made up of: (a) Amazonian 'terra firme' rainforests (right vertex), the most distinct group in the whole array of forest areas, (b) semideciduous and mixed forests of southeastern Brazil (bottom left vertex), and (c) central Brazilian cerradões and deciduous forests (top left vertex). These three groups also correspond, respectively, to the main vegetation formations of the Amazonian, Paranense and Cerrado Provinces of Cabrera & Willink (1973).

In the space defined by the three vertices lie other important vegetation formations. The Atlantic rainforests (**D) appear between the Amazonian rainforests and

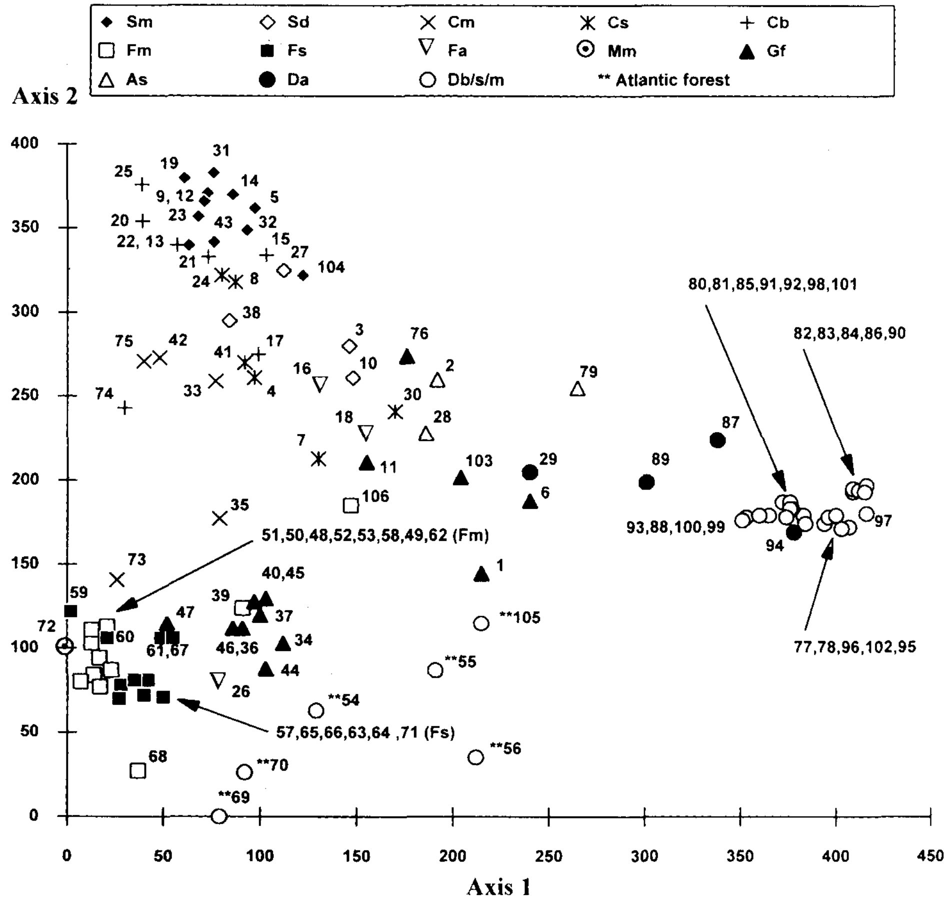


FIG. 3. Ordination of the 106 forest areas on the first two DCA axes. The forest areas are identified by their number in Table 1 while the symbols indicate their classification according to the modified IBGE classification system for Brazilian vegetation (see text, pp. 154–5). Lowland, submontane and montane dense rainforests are indicated by the same symbol for clarity.

Paranense semideciduous forests (Fs, Fm), though closer to the latter. They also follow an interesting north-south sequence that suggests a decrease of Amazonian floristic influence with increasing latitude. The area containing all rainforests (D) in the ordination diagram can also be seen as that of tropical rain climates with lower seasonality (Köppen's Af and Am types), while marked seasonal climates, both tropical and subtropical (Köppen's Aw, Cw and Cf types), occupy the remaining space.

Most lowland and submontane deciduous forests (Cb, Cs) appear in close association with mesotrophic cerradões (Sm), while the dystrophic cerradões (Sd) seem to link the former group to the transitional open rainforests (As). As mesotrophic cerradões and deciduous forests are known to appear on soils of higher fertility, the top left vertex can be regarded as an area that corresponds to seasonal climate plus high soil fertility, while the space extending to the right would correspond to a transition to Amazonian forests on soils of lower fertility.

Montane deciduous forests (Cm) appear in the space extending from the top vertex down to the Paranense semideciduous forests (Fs, Fm), so that this area of the diagram could be associated with cooler climates, either subtropical or montane (Köppen's Cw and Cf types). Nevertheless, DCA indicates little differentiation between submontane and montane semideciduous forests (Fm and Fs). In addition to this, two Fm areas, one in the Distrito Federal (39) and the other in Paraíba (106), are placed well apart from other semideciduous forests. However, this could be associated with geographical variables as they were rather isolated and distant from the others of their category. Area 68 is somewhat displaced towards the Atlantic rainforests, probably as a result of its geographical proximity to the coast.

Gallery forests (Gf) are clearly the most widespread category in the ordination space. Nevertheless, two main groups can be detected. The first and more cohesive one (34, 36, 37, 40, and 44 to 47) is that of the centre and south of the Cerrado Province (Distrito Federal and states of Goiás and Minas Gerais), which appears in a closer association with the Paranense semideciduous forests. The second and more widespread group (1, 6, 11, 76 and 103) is that of the north and west of the Cerrado Province (states of Mato Grosso and Tocantins), which appears amongst dystrophic cerradões (Sm), transitional open rainforests (As) and alluvial forests (Da, Fa). The basic factor that appears to underline this differentiation is geographic, since the first group is basically on the Paraná and São Francisco river basins, while the second lies on the Amazon and Paraguay river basins. The influence of rivers also seems to be important in the floristic links between the galleries and Amazonian forests, since most 'várzea' forests (Da) appear on the space between galleries and 'terra firme' forests (Db, Ds, Dm). On the other hand, the alluvial semideciduous forests (Fa) appear to connect the galleries to the Paranense forests.

As an overall analysis of the patterns arising from the DCA ordination diagram we can say that the first ordination component has a strong latitudinal influence, especially discriminating the equatorial space, while the second is highly influenced by rainfall seasonality. Riverine forests (galleries and alluvial), together with hinterland montane forests and transitional open rainforests, appear to provide the floristic connections between rainforests, seasonal forests and cerradões.

Divisive hierarchical classification (TWINSPAN)

The first level of division in the cladogram yielded by TWINSPAN (Fig. 4) separates the Amazonian forests (group 3) from the others (group 2), coinciding with the high floristic distinctness indicated for these forests by the first DCA axis. However, TWINSPAN indicates a high level of internal heterogeneity for the Amazonian forests which DCA fails to show in the first two ordination axes. This heterogeneity appears in the subsequent divisions of group 3, the first of which separates the two várzea (alluvial) forests from central and northern Amazonia (group 7) from the remainder (group 6). However, the other divisions make little sense in terms of topographic range (lowland, submontane and montane). In addition to this, none of the floristic divisions of the Amazonian forest into geographical sectors cited by Prance (1977) coincides clearly with the classification groups. This is probably a consequence of the very high level of floristic and environmental heterogeneity of the Amazonian forests, which cannot be analysed properly from the small number of existing surveys. Nevertheless, in spite of this heterogeneity, the Amazonian forests certainly form a well-defined floristic province and this is without doubt helped by a number of widespread and typically Amazonian species, such as *Minquartia guianensis*, *Eschweilera coriacea*, *Brosimum guianense*, *Socratea exorrhiza* and *Jacaranda copaia* (TWINSPAN's main indicator species for group 3).

The division of group 2 indicates two important main groups. Group 4 includes essentially central Brazilian cerradões (Sm, Sd), deciduous (Cs/Cb/Cm) and semideciduous forests (Fa/Fm) together with transitional open rainforests (As) and the western and northern gallery forests (Gf). Group 5 includes the Atlantic rainforests (Db/Ds), Paranense semideciduous forests (Fs/Fm), the mixed rainforest (Mm) and the central and southern gallery forests (Gf). This division has a clear influence of coastal-interior and vegetation seasonality factors, and a high correspondence to the main patterns indicated by the second DCA axis. It also places at a high level the same division between the two groups of gallery forests indicated by DCA. So, the same pattern arises for the galleries, indicating a mainly Atlantic/Paranense floristic link to the central-southern and a mainly Amazonian floristic link to the northern-western groups.

The divisions within group 4 show some interesting patterns. Most mesotrophic cerradões (Sm) and deciduous forests (Cs/Cb/Cm) fall into group 8, confirming the importance of the edaphic factor to those formations. The main indicator species given by TWINSPAN for this group were *Sterculia striata*, *Anadenanthera colubrina*, *Tabebuia impetiginosa*, *Myracrodruon urundeuva*, *Dilodendron bipinnatum*, *Maclura tinctoria*, *Cordia glabrata*, *Enterolobium contortisiliquum* and *Combretum leprosum*, all of which have also been cited by Ratter (Ratter, 1971; Ratter et al., 1977, 1978a, b) as indicators of mesotrophic soils in central Brazil. Group 16 discriminates mainly

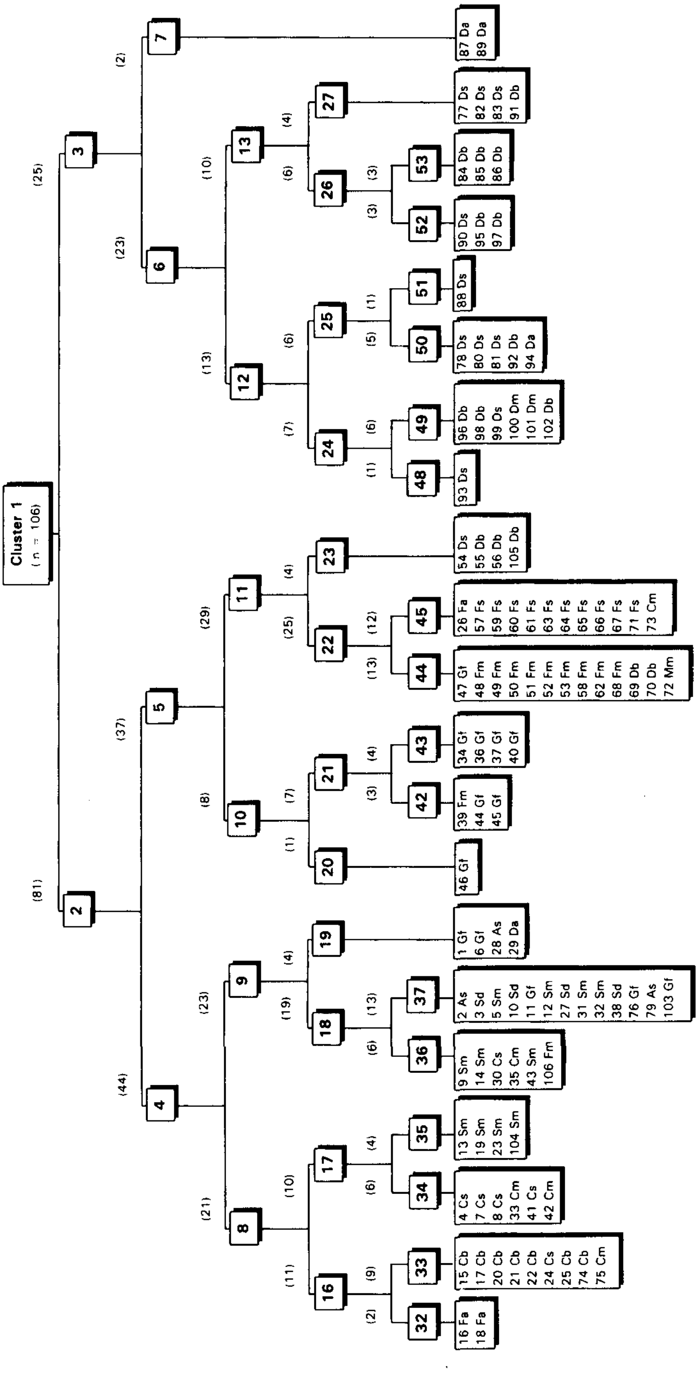


FIG. 4. Cladogram yielded by TWINSPAN showing the hierarchical classification of the 106 forest areas after five levels of division. The forest areas are shown in the bottom boxes and identified by their number in Table 1, followed by the two-letter code corresponding to their classification according to the modified IBGE classification system for Brazilian vegetation (see text, pp. 154–5). The upper boxes contain the numbers that identify the groups and divisions following the standard TWINSPAN numbering. Numbers in parentheses indicate the number of areas in each group.

the forests of the Mato Grosso Pantanal (including the seasonally flooded ones (Fa) in subgroup 32) and of the fringing Chaco, while group 17 contains some central Brazilian deciduous forests (group 34) together with the Pantanal cerradões (group 35). The subdivisions of group 9 are rather confusing, since northern-western galleries appear mixed with cerradões (of both types), transitional open rainforests and some deciduous forests. Most of these areas appear in the same ordination space of the DCA dendrogram that links the central Brazilian seasonal formations to the Amazonian forest. A possible explanation is that the five western-northern gallery forests are in transitional regions where a considerable number of forest formations meet each other, as happens in the forests of the Ilha do Bananal (Ratter, 1987). This certainly increases the number of species shared by different forests surveyed in those regions and causes them to be clustered within the same groups.

The divisions within group 5 are the most clearly organized of the whole cladogram. Most central and southern gallery forests are included in group 10 together with the only central Brazilian montane semideciduous forest (39), while group 11 contains essentially the Atlantic rainforests (Db/Ds) and Paranense semideciduous (Fs/Fm) and mixed forests (Mm). The only gallery to appear in group 11 is the southernmost (47), for which a strong floristic similarity with the Paranense forests could be expected. The main indicator species given by TWINSPAN for the central-southern galleries are *Cheiloclinium cognatum*, *Virola sebifera*, *Sclerolobium paniculatum*, *Hirtella glandulosa*, *Ocotea spixiana*, *Xylopia emarginata* and *Mauritia flexuosa.* The division of group 11 discriminates the northern Atlantic rainforests (group 23) from the remainder (group 22). The southern Atlantic rainforests are included with the montane semideciduous forests (Fm) and mixed rainforest (Mm) in group 44. Group 45 is composed mostly of submontane semideciduous forests (Fs). One important pattern arising from these is the notable floristic diversity of the Atlantic rainforests and their strong floristic links to the Paranense semideciduous forests, especially in the southern sector where the transition occurs via montane forests. Leitão-Filho (1987) has already pointed out that the Atlantic rainforests shelter a bewildering north-south floristic variation. In actual fact, there seem to be stronger floristic links between adjacent tracts of rainforests and semideciduous forests than between different sectors of the Atlantic rainforest along the Brazilian coast.

Agglomerative hierarchical classification (UPGMA)

Most patterns already indicated by both DCA and TWINSPAN also appear in the UPGMA dendrogram (Fig. 5). This is of particular methodological importance as UPGMA analysed the whole dataset, indicating that the elimination of the unicates had little or no effect on the main patterns arising via TWINSPAN or DCA. However, some important additional patterns arose. These are dealt with below and brief descriptions of the main groups are given:

Group a: this includes all Amazonian 'terra firme' forests (Db/s/m) plus a tran-

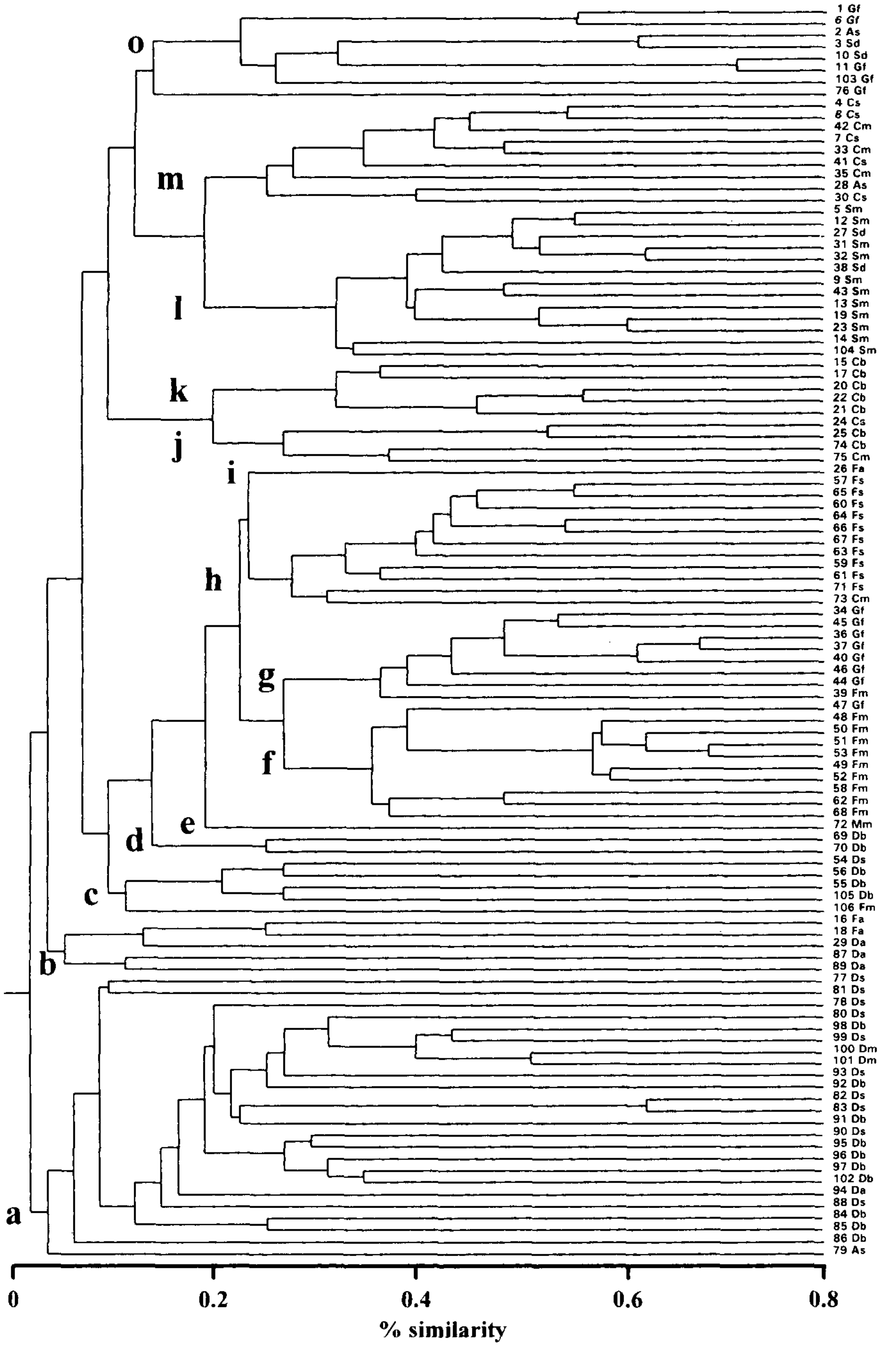


FIG. 5. Similarity dendrogram yielded by UPGMA, using Sørensen Coefficients of Community, showing the hierarchical classification of the 106 forest areas. The areas are identified by their number in Table 1, followed by the two-letter code corresponding to the modified IBGE classification system for Brazilian vegetation (see text, pp. 154–5). Other letters marking branches of the dendrogram identify groups discussed in the text.

sitional open rainforest (79As) and a 'várzea' forest (94Da). The heterogeneity of Amazonian forests is reflected by the high level of most clusterings.

Group b: this is made up of highly heterogeneous riverine forests, all liable to seasonal floods, including 'várzea' forests of the Amazon basin (Da) and floodplain forests of the Mato Grosso Pantanal (Fa). This pattern only appeared with UPGMA.

Group c: this contains the four northern Atlantic rainforests (Db/s) and the hinterland 'brejo' forest (54Ds). High floristic heterogeneity is also detected.

Group d: this includes the two southern Atlantic rainforests (Db).

Group e: this consists of the single area of montane mixed rainforest (72Mm), its distinctness being indicated only by UPGMA.

Group f: this contains the montane semideciduous forests of the (Fm) Paranense Province plus the southernmost area of gallery forest (47Gf).

Group g: this comprises the central and southern gallery forests (Gf) plus the montane semideciduous forest of the Distrito Federal (39Fm). The close floristic links between those galleries and the Paranense montane forests are shown by the low clustering level of groups f and g.

Group h: this consists of 10 areas of submontane semideciduous forests of the Paranense Province (Fs) plus the southern Brazilian deciduous forest (Cm).

Group i: this includes only a single area of alluvial semideciduous forest of the Paraná river (26Fa). Groups e to i contain all deciduous and semideciduous forests, and the mixed rainforest that constitutes the Paranense Province, according to Cabrera & Willink (1973). These patterns indicate that the gallery forests of the central and southern part of the Cerrado Province are actually floristic expansions of the forests of the Paranense Province.

Group j: this includes the deciduous forests occurring in the transition to the Chaco in the Mato Grosso Pantanal (24Cs, 25Cb), the Paraná river valley (74Cb), and the piedmont forests (75Cm). A clearer discrimination of this group was made only by UPGMA.

Group k: this consists of the five areas of lowland deciduous forests of the Mato Grosso Pantanal (Cb). The deciduous forests of the Pantanal and transitional Chaco (groups j and k) appear quite distinct from the other deciduous forests of central Brazil (group m), a pattern shown more clearly than by the other two analytical methods.

Group l: this contains areas of mesotrophic cerradão (Sm), although it also includes the dystrophic cerradões of the Ilha do Bananal (27Sd) and the Distrito Federal (38Sd).

Group m: this comprises the central Brazilian deciduous forests (Cs and Cm) and the transitional open rainforest of the Ilha do Bananal (28As).

Group n: this consists of all five northern and western gallery forests (Gf) plus a transitional open rainforest (2As) and two dystrophic cerradões (Sd). This group, which was entangled amidst other formations in the two previous methods, emerged quite clearly by UPGMA. The stronger floristic links of the northern-western galleries to the dystrophic cerradões and transitional open rainforests were once again demonstrated. The transition from Sd and As on dystrophic soils has already been described by Ratter et al. (1973) in the state of Mato Grosso, while the connections between Sd on the headwaters of gallery forests were referred to by Oliveira-Filho et al. (1990).

Condensed floristic information

As they were extracted from floristic checklists for particular forest areas, the condensed information given in Table 2 must be regarded as a means of quantitative assessment of the floristic links between the main vegetation groups and not as their actual figures for number of species, either total or in common.

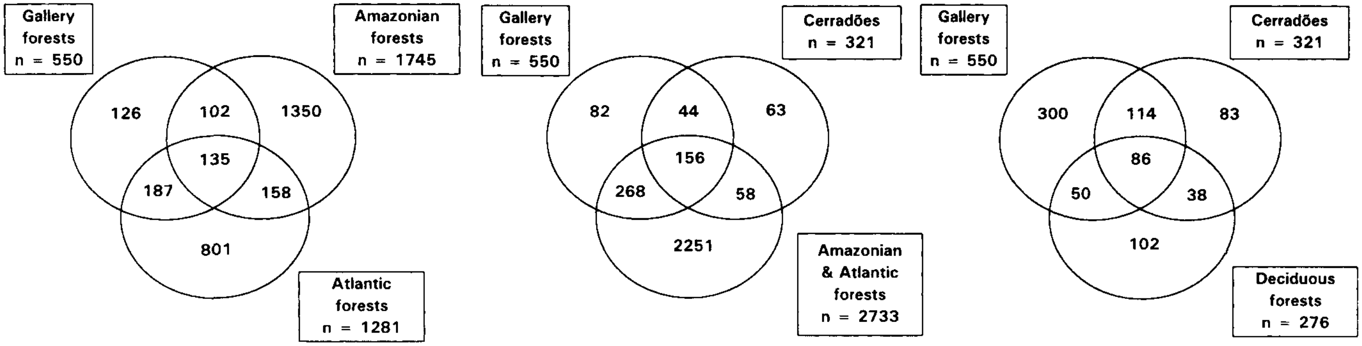
The western-northern gallery forests showed highest floristic similarity, measured by the Sørensen Coefficient of Community (CC), in the comparisons with the dystrophic cerradões, followed by the transitional open rainforests (dry forests) and the central-southern galleries. This confirms their strong links to the transitional formations that occur on base-poor soils in the southern fringe of the Amazonian Province. The central-southern gallery forests showed the highest CC values in the comparisons with the montane semideciduous forests, followed by those for the submontane semideciduous forests. Then follow those for the cerradões (of both types), deciduous forests and the other galleries, all at a more or less similar level. This confirms that their stronger floristic links are with the Paranense semideciduous forests. Curiously enough, the comparisons with the southern Amazonian forests yielded similar figures for both groups of galleries. However, stronger floristic links were shown between the western-northern galleries, the central Amazonian rainforests, and the central-southern galleries and the Atlantic coastal rainforests.

The transitional nature of the Amazonian open rainforests (dry forests) is clear from the figures obtained in the comparisons with central Brazilian forests (cerradões, galleries and deciduous forests) which were significantly higher than those obtained in the comparisons with the other Amazonian rainforests. The riverine connection between Amazonian 'várzea' forests and the western-northern galleries is probably shown by the fact that although the CC value for this comparison is in itself not particularly high it is nevertheless higher than those with the Amazonian 'terra firme' forests. The floristic links between Amazonian and Atlantic rainforests appeared weaker than those between the latter and the semideciduous forests. The high affinity between dystrophic and mesotrophic cerradões only confirms that they have much of the cerrado arboreal flora in common. However, the high CC value found for the comparison between deciduous forests and mesotrophic cerradões indicates the well-known affinity of these two communities.

The Venn diagrams at the bottom of Table 2 give an assessment of the composition of the arboreal flora of gallery forests in relation to that of other main forest groups. The first Venn diagram makes clear that a high percentage (77%) of gallery species is made up of those shared with the main Amazonian rainforests and Atlantic forests *sensu lato* (including Paranense semideciduous forests). The proportion of non-

TABLE 2. Synthetic figures for the main forest types represented by the 106 checklists of the original database. Top: similarity matrix showing the Sørensen Coefficients of Community (CC) (lower left diagonal) and number of species in common (upper right diagonal). Bottom: Venn diagrams showing number of species shared by gallery forests and other main forest types.

Groups:	Gf/WN	Gf/CS	As	Da	D/Am/S	D/Am/C	D/Atl	Sd	Sm	C/C	Fs	Fm
Description:	Gallery forests, west and north	Gallery forests, centre and south	Transitional open forests, southern Amazonia	Amazonian várzea forests	Amazonian terra firme forests, south	Amazonian terra firme forests, centre	Atlantic coastal forests	Dystrophic cerradões	Mesotrophic cerradões	Deciduous forests, Central Brazil	Submontane semi-deciduous forests	Montane semi-deciduous forest
Gf/WN		113	83	50	95	99	81	109	76	71	65	69
Gf/CS	0.341		70	30	91	69	178	109	103	112	167	229
As	0.365	0.242		31	78	79	56	90	64	55	41	44
Da	0.172	0.085	0.124		145	152	59	20	19	38	23	23
D/Am/S	0.167	0.145	0.149	0.246		496	173	48	50	66	77	72
D/Am/C	0.137	0.088	0.116	0.205	0.487		141	48	33	51	53	48
D/Atl	0.143	0.284	0.107	0.101	0.200	0.139		55	57	94	216	260
Sd	0.445	0.356	0.444	0.075	0.088	0.069	0.102		124	68	59	73
Sm	0.307	0.333	0.312	0.071	0.092	0.047	0.105	0.557		105	69	77
C/C	0.260	0.335	0.239	0.129	0.116	0.070	0.165	0.274	0.419		104	108
Fs	0.180	0.395	0.129	0.060	0.117	0.065	0.329	0.176	0.204	0.286		83
Fm	0.165	0.479	0.117	0.052	0.101	0.055	0.365	0.186	0.195	0.257	0.163	
N. of species	270	393	185	313	865	1173	861	220	225	276	452	564



shared species in galleries was only 22.9%, a figure that falls to 14.9% when the cerradão flora is included in the second diagram. The interface with seasonal formations is assessed in the third diagram, where a relatively weaker floristic link occurs. The stronger floristic links between galleries and moist forests is certainly explained by the similarity of their habitats depending on higher soil moisture in the valley bottoms within the Cerrado Province. This compensates to a large extent the seasonal droughts, allowing moist forest species to penetrate the cerrado region via gallery forests. However, soil moisture on the margins of galleries is not so high and this is where a dry transition to cerradões occurs—thus explaining the floristic links between gallery forests and cerradões, particularly of the dystrophic type. A link to deciduous forests is also present and this is probably related to transitions from gallery to upland forests on soils of higher fertility. The weaker overall floristic link between galleries and communities of mesotrophic as opposed to dystrophic soils undoubtedly derives from the simple fact that base-poor soils predominate in the Cerrado Province.

DISTRIBUTION MAPS

The species distribution maps given in Figs 6–18 were organized in a sequence starting with the most widespread distribution patterns and ending with the most restricted. Unless otherwise indicated, the ecological discussion of the species distribution is based mostly on the authors' field experience and previous publications. Important synonyms found in the checklists are given in the text, while footnotes explain some taxonomic complications. The 13 species with highest frequency ($\geqslant 9$) in the 13 gallery forest areas were: *Siparuna guianensis* (13), *Copaifera langsdorffii* (12), *Tapirira guianensis* (11), *Calophyllum brasiliense* (11), *Protium spruceanum* (10), *Endlicheria paniculata* (10), *Virola sebifera* (10), *Eugenia florida* (10), *Xylopia aromatica* (9), *Protium heptaphyllum* (9), *Maprounea guianensis* (9), *Cheiloclinium cognatum* (9), and *Emmotum nitens* (9). Most of these are very widespread species and many are generalists in terms of habitat preference.

Four examples of extremely widespread species are given in Fig. 6. Their geographical range extends virtually through the whole of the Neotropics, although *Calophyllum brasiliense* (but see footnote 2, p. 168) and *Hieronyma alchorneoides* are not found in the Caribbean islands. *Maclura tinctoria* (L.) Don (= *Chlorophora tinctoria* (L.) Benth.) is one of only two mesotrophic soil indicator species represented in the maps.[1] It occurs in a wide range of habitats from the arid semi-deserts of northern Mexico and northeastern Brazil to the humid Amazon valley and the seasonally flooded forests of the Mato Grosso Pantanal, only requiring soils of intermediate to high fertility. Its occurrence in gallery forests is thus probably dependent on higher soil fertility and not soil moisture. On the other hand, *Margaritaria nobilis*

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[1] However, the recent publication of Prado & Gibbs (1993) maps the distribution of a number of species of mesotrophic soils, such as *Anadenanthera colubrina*, *Myracrodruon urundeuva*, *Combretum leprosum*, *Enterolobium contortisiliquum*, *Sterculia striata* and *Tabebuia impetiginosa*.

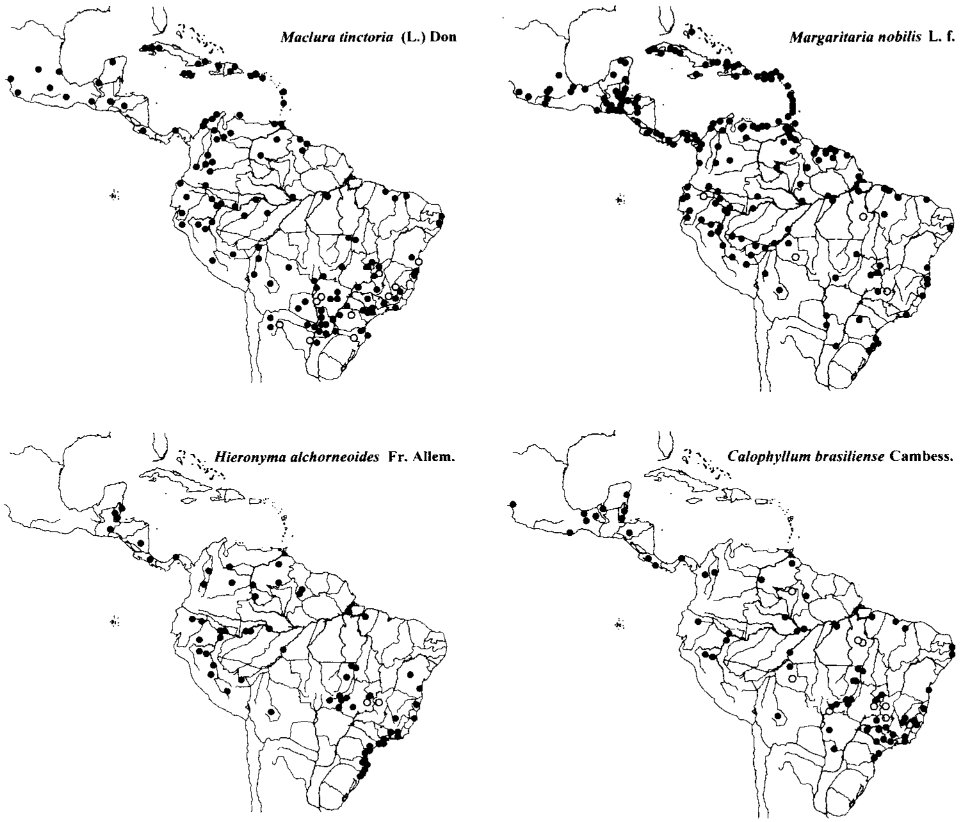

FIG. 6. Distribution of *Maclura tinctoria*, *Margaritaria nobilis*, *Hieronyma alchorneoides* and *Calophyllum brasiliense*. Solid symbols represent information from herbarium specimens or references in monographs, while open symbols represent citations in floristic checklists.

L.f. (= *Phyllanthus nobilis* (L.f.) Müll. Arg.) and *Hieronyma alchorneoides* Fr. Allem., although very widespread, require higher humidity, either through soil moisture or through rainfall. This explains why they normally appear on the valley bottoms within the galleries. *Calophyllum brasiliense* Cambess.[2] is even more dependent on high soil moisture and tends to appear in the dampest sites within galleries. It also tolerates floods, so that it is a common species in the Amazonian 'várzea' forests and on the fringes of mangrove forests.

Richeria grandis Vahl (Fig. 7) is also a widespread species associated with high soil moisture, often growing on river margins in tropical South America and the Caribbean. It is very characteristic of central Brazilian gallery forests, especially on the sandy headwaters of hinterland plateaux. *Cespedesia spathulata* (Ruiz & Pavon) Planchon (Fig. 7) also appears as a riverside species in the gallery forests of the

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[2] *C. antillanum* Britton (= *C. caloba* Jacq.), of Caribbean distribution, is not included in the map, although Standley (pers. letter lodged at K) believes that it is conspecific with *C. brasiliense* Cambess.

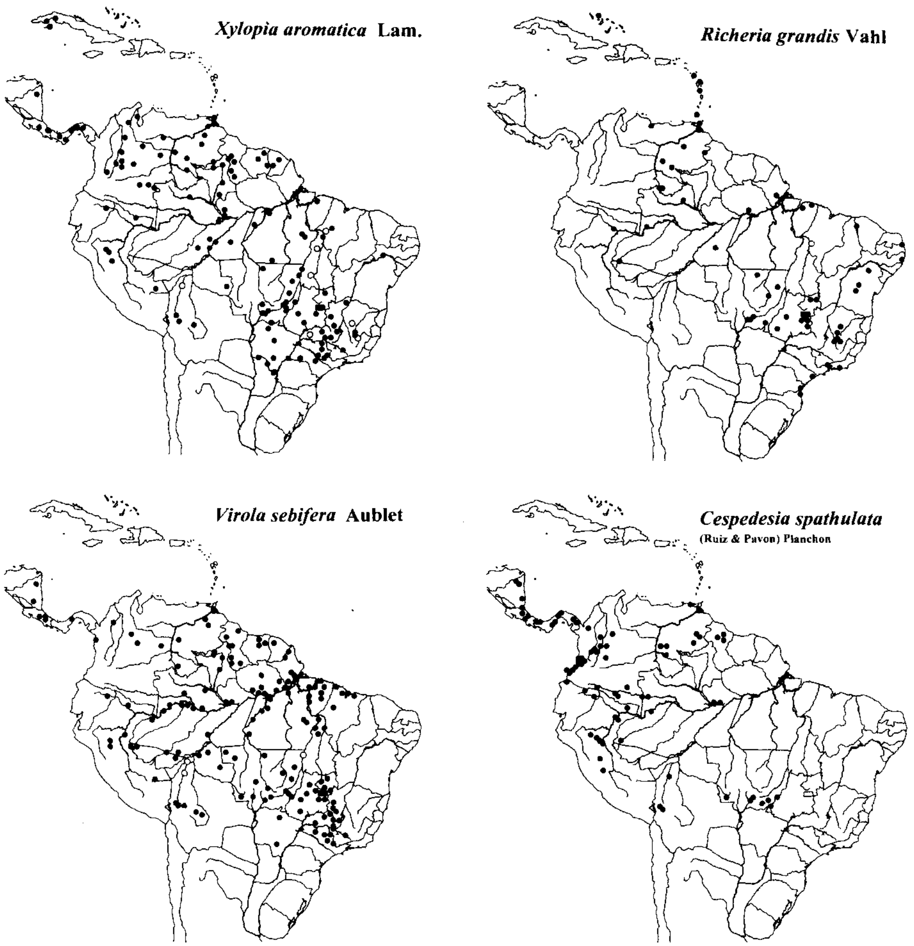

FIG. 7. Distribution of *Xylopia aromatica*, *Richeria grandis*, *Virola sebifera* and *Cespedesia spathulata*. For explanation of symbols see Fig. 6.

sandstone plateaux of southern Mato Grosso. However, the species is not a river margin preferential in the rainforest parts of its distribution range (Sastre, 1975), suggesting that it requires higher water availability throughout the year, a condition provided essentially by galleries within the cerrado region. *Xylopia aromatica* Lam. and *Virola sebifera* Aublet (Fig. 7) are also widespread species distributed from Central America to central Brazil, being particularly common in the latter region. They are light-demanding species which grow mostly in more or less open habitats, either colonizing tree-fall gaps in the rainforest or as common trees in cerrado vegetation. *X. aromatica* is also a common species of disturbed habitats and the hummocks of 'campos de murundus'.

Tree ferns are normally dependent on high moisture, being particularly abundant in the rainy (and often cloudy) mountain flanks in both the Andes and eastern

Brazilian mountains, as well as along turbulent streams and creeks. The scarcity of tree ferns along larger rivers, especially in the Amazon basin, is probably due to low tolerance of floods and heavy shade. Some species penetrating the Cerrado Province follow the gallery forests associated with the narrower rivers. They are probably a successional feature of such forests, as we have often seen areas in northeastern Mato Grosso where they have all died because of excessive shade from the closing canopy. Figure 8 gives three examples within the Cyatheaceae. *Trichipteris procera* (Willd.) Tryon seems to have a north Andean origin spreading to the central Brazilian highlands, and to the Caribbean. *Cyathea delgadii* Sternb. is distributed from Central America to eastern Brazil, including the Andes and the Guyana and central Brazilian highlands. The distribution of *Trichipteris phalerata* (Mart.) Barr. is centred in the eastern Brazilian mountains, spreading to central Brazil via the hinterland plateaux.

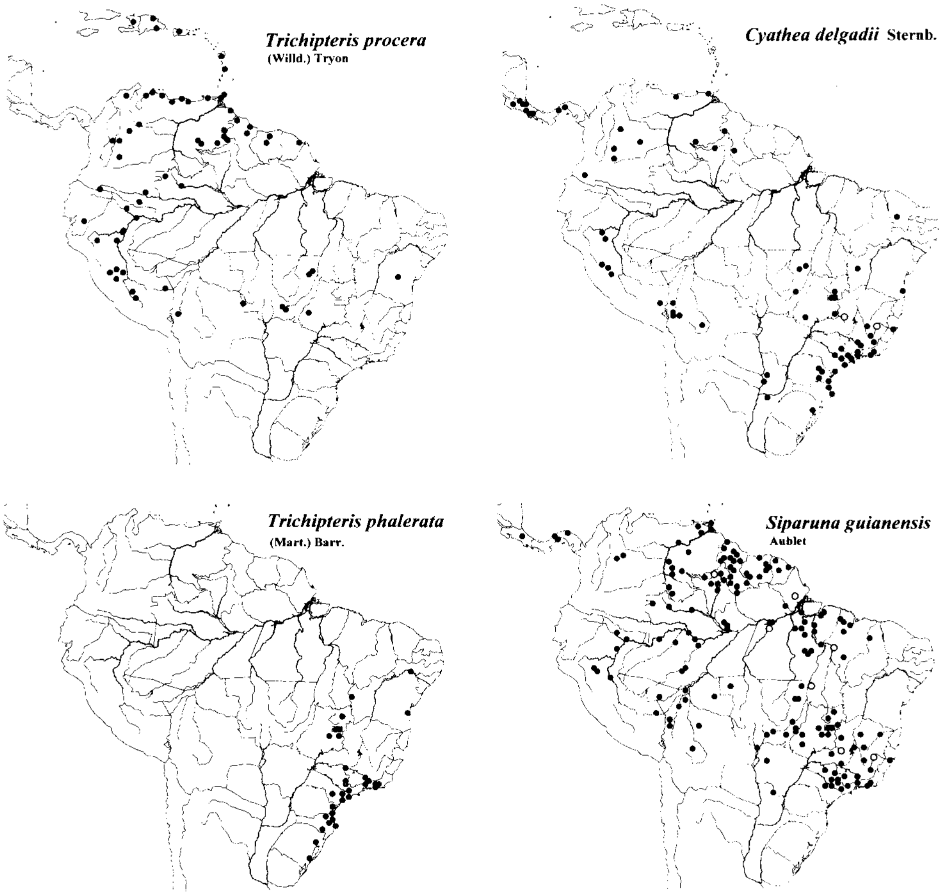

FIG. 8. Distribution of *Trichipteris procera*, *Cyathea delgadii*, *Trichipteris phalerata* and *Siparuna guianensis*. For explanation of symbols see Fig. 6.

The following nine species (last species in Fig. 8, and Figs 9–10) are all very widespread with a distribution pattern extending from the Amazonian to the Atlantic forests through central Brazil, some of them also crossing the semi-arid Caatinga Province via the 'brejo' forests. Although they are all frequent species in central Brazilian galleries, they differ in terms of habitat preference. Some are notable generalists in terms of habitat. *Siparuna guianensis* Aublet (Fig. 8), for instance, is a slender treelet that can be found in the shady forest understorey as well as less frequently on the open cerrado. *Tapirira guianensis* Aublet and *Protium heptaphyllum* (Aublet) Marchand (Fig. 9) are two jack-of-all-trades that are found in most cerradões and forests of tropical South America, although they seem to have a slight preference for sandy sites and to avoid the patches of very dry terrain. *Tapirira obtusa* (Benth.) Mitchell (= *T. marchandii* Engler) and *Protium spruceanum* (Benth.)

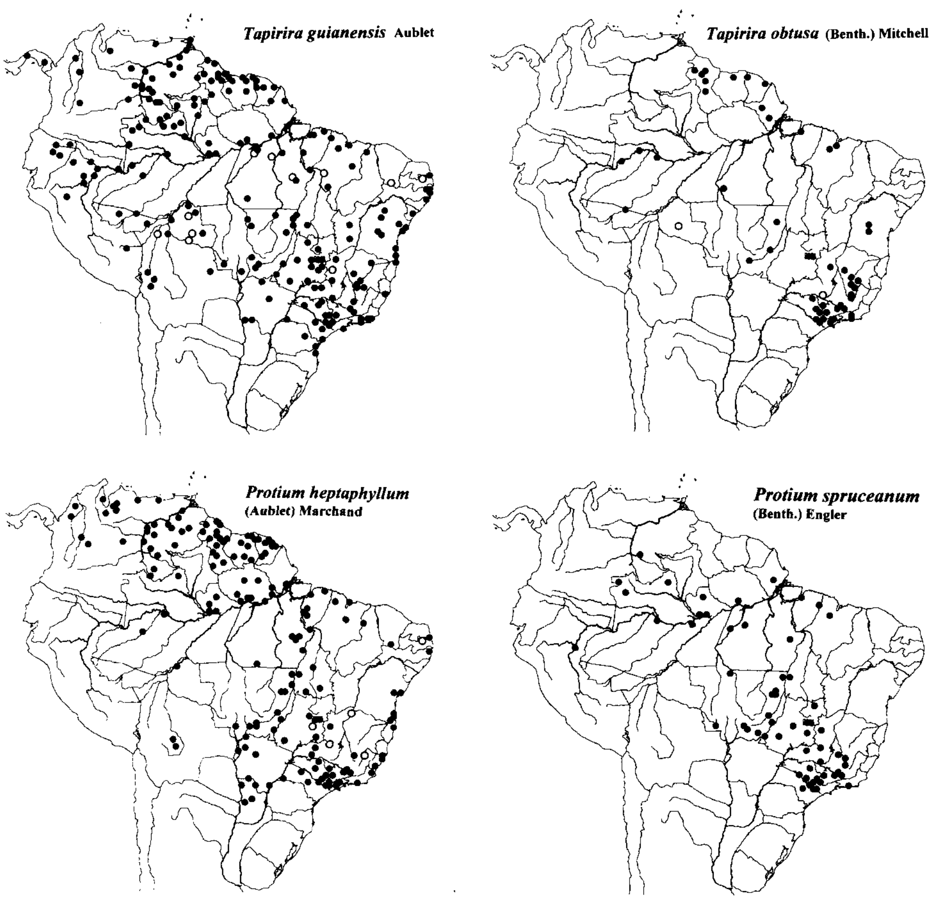

FIG. 9. Distribution of *Tapirira guianensis*, *Tapirira obtusa*, *Protium heptaphyllum* and *Protium spruceanum*. For explanation of symbols see Fig. 6.

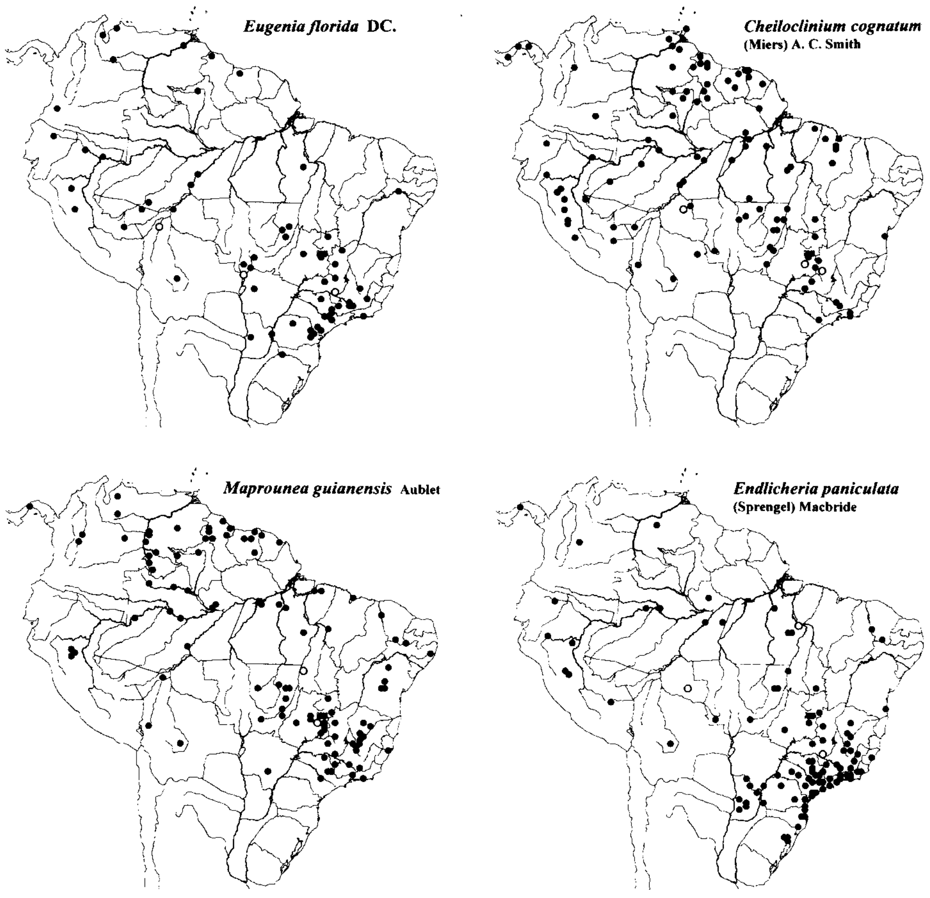

FIG. 10. Distribution of *Eugenia florida*, *Cheiloclinium cognatum*, *Maprounea guianensis* and *Endlicheria paniculata*. For explanation of symbols see Fig. 6.

Engler[3] have a more restricted ecological distribution than their congeneric relatives in Fig. 9 as they clearly prefer forest habitats, thus avoiding the cerrado. *P. spruceanum*, in particular, is highly dependent on high soil moisture and is a typical riverside and valley bottom species in forests extending from southeastern Brazil to the Amazon basin. *Eugenia florida* DC. (= *E. gardneriana* Berg) (Fig. 10) is very often found on sites of high soil moisture and under direct sunlight, so that it is particularly common on the margins of large rivers, as well as in very narrow gallery forests. On the other hand, *Cheiloclinium cognatum* (Miers) A. C. Smith is a shade-tolerant slender tree that grows abundantly in the understorey of both rain-

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[3] This species appears as *Protium brasiliense* Engler in most checklists published for central Brazilian galleries. Although the herbarium specimens at E and K have already been transferred to *P. almecega* Marchand, this will also become a synonym of *P. spruceanum* (Benth.) Engler in the forthcoming revision of the genus by D. Daly (pers. comm.).

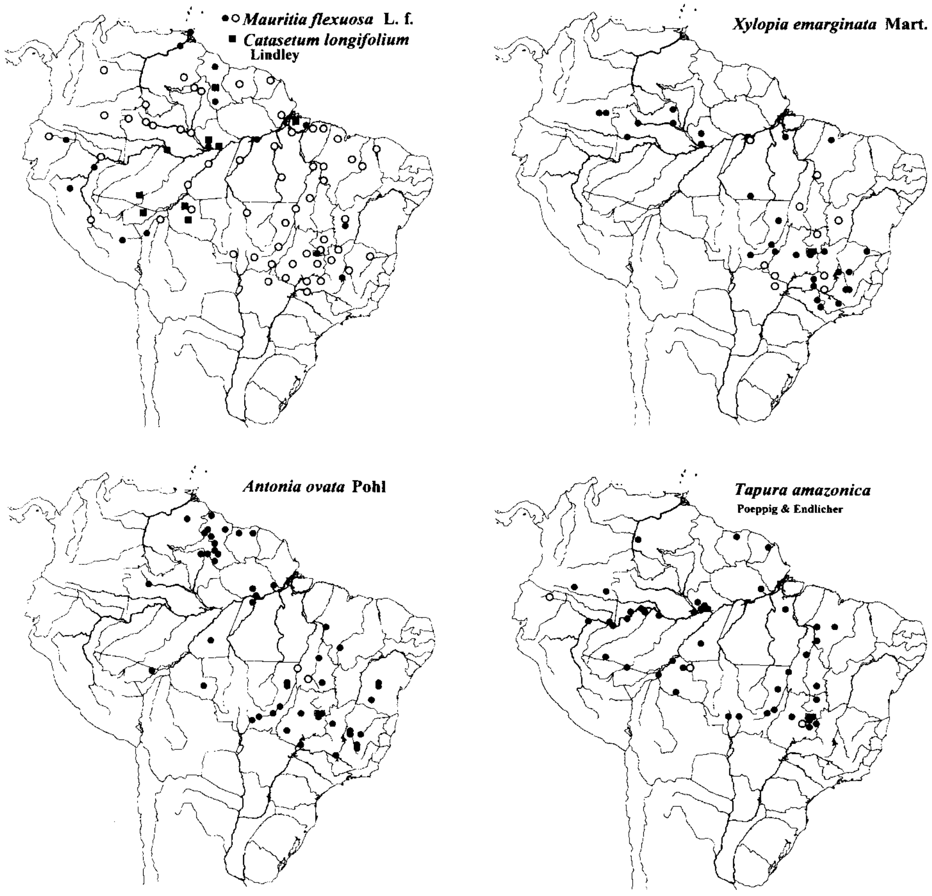

FIG. 11. Distribution of *Mauritia flexuosa* and *Catasetum longifolium*, *Xylopia emarginata*, *Antonia ovata* and *Tapura amazonica*. For explanation of symbols see Fig. 6.

forests and galleries. *Maprounea guianensis* Aublet (= *M. brasiliensis* A. St.-Hil.) is another example of a light-demanding species shared by cerrado and by the forest, where it is a typical pioneer species.[4] *Endlicheria paniculata* (Sprengel) Macbride (= *E. hirsuta* (Schott.) Nees, *Nectandra lucida* Nees) shows high preference for damp sites, following rivercourses from the Atlantic to the Amazonian provinces.

The next four maps represent species shared by the Amazonian and Cerrado Provinces (Fig. 11). The 'buriti' palm, *Mauritia flexuosa* L.f. (= *M. vinifera* Mart.), and the 'pindaíba', *Xylopia emarginata* Mart., (Fig. 11) are certainly amongst the most characteristic species of central Brazilian gallery forests. They are confined to very wet sites, especially when these are formed on sandy soils, occurring mostly on the swampy stretches of galleries and Amazonian riverine forests. Unlike

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[4] Previously *M. guianensis* Aublet and *M. brasiliensis* A. St.-Hil. were distinguished as separate forest and cerrado species respectively. However, Allem (1976) has demonstrated that they are conspecific.

X. emarginata, which is a forest species, *M. flexuosa* is also found in open and pure stands on the valley-side marshy campos that often flank the galleries, frequently producing elegant palmeries, known as 'veredas', in such places. The distribution map of this poorly collected, although abundant, species was based mostly on literature and field-trip records. It was also helped by noting the distribution of the orchid *Catasetum longifolium* L.f., which grows exclusively on the crowns of *M. flexuosa* (J. B. Silva, pers. comm., and specimens). *Antonia ovata* Pohl and *Tapura amazonica* Poeppig & Endlicher are mostly forest species shared by galleries and Amazonian 'terra firme' forests, the former extending its distribution farther south than the latter. Both are also widespread in cerradão vegetation.

The species represented in Fig. 12 illustrate the connection between galleries, cerradões and transitional open rainforests of southern Amazonia. *Hirtella glandulosa* Sprengel, *Emmotum nitens* (Benth.) Miers and *Vochysia haenkeana* Mart. have all

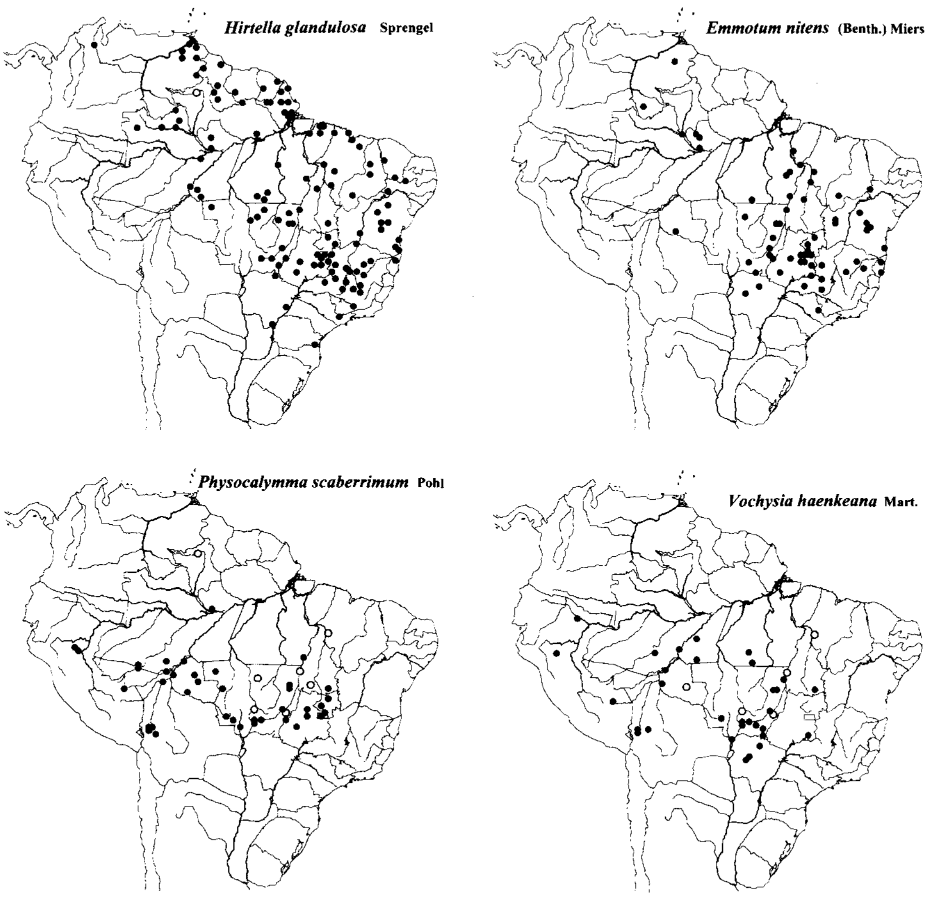
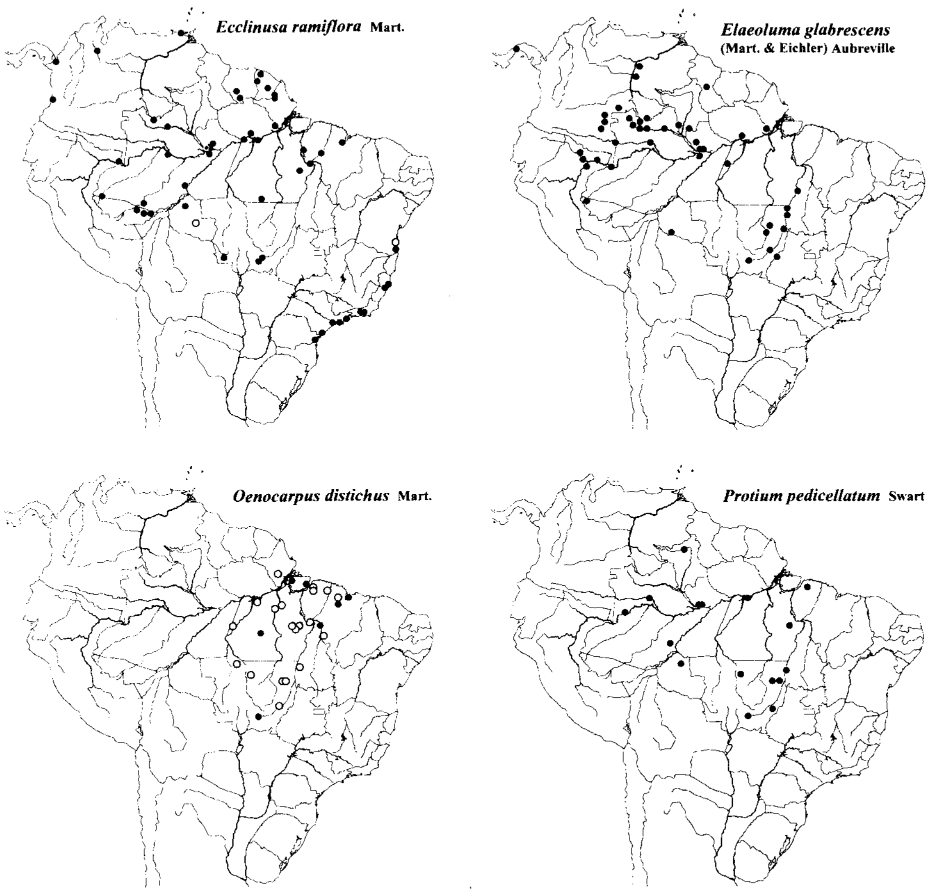


FIG. 12. Distribution of *Hirtella glandulosa*, *Emmotum nitens*, *Physocalymma scaberrimum* and *Vochysia haenkeana*. For explanation of symbols see Fig. 6.

been referred by Ratter et al. (1973) as indicators of the dystrophic cerradão that occurs in the transition to the Amazonian forests on sandy soils. Unlike the other species, *Physocalymma scaberrimum* Pohl tends to prefer soils of intermediate to high fertility. The distribution of these species is predominantly central Brazilian although permeating the Amazonian forests. *H. glandulosa* is the most widespread, while *E. nitens* appears to concentrate in central Brazil, both species also reaching the Atlantic forests. *V. haenkeana* and *P. scaberrimum* have a more restricted distribution, extending from the central and western part of the cerrado region to the southern fringes of the Amazonian forest. All four species are common in galleries, transitional rainforests and cerradões, sporadically appearing in open cerrado.

Examples of typical Amazonian species extending their distribution to the cerrado region through the western-northern gallery forests are given in Fig. 13. The sapotaceous *Ecclinusa ramiflora* Mart. and *Elaeoluma glabrescens* (Mart. & Eichler)


Ecclinusa ramiflora Mart.

Elaeoluma glabrescens (Mart. & Eichler) Aubreville

Oenocarpus distichus Mart.

Protium pedicellatum Swart

FIG. 13. Distribution of *Ecclinusa ramiflora*, *Elaeoluma glabrescens*, *Oenocarpus distichus* and *Protium pedicellatum*. For explanation of symbols see Fig. 6.

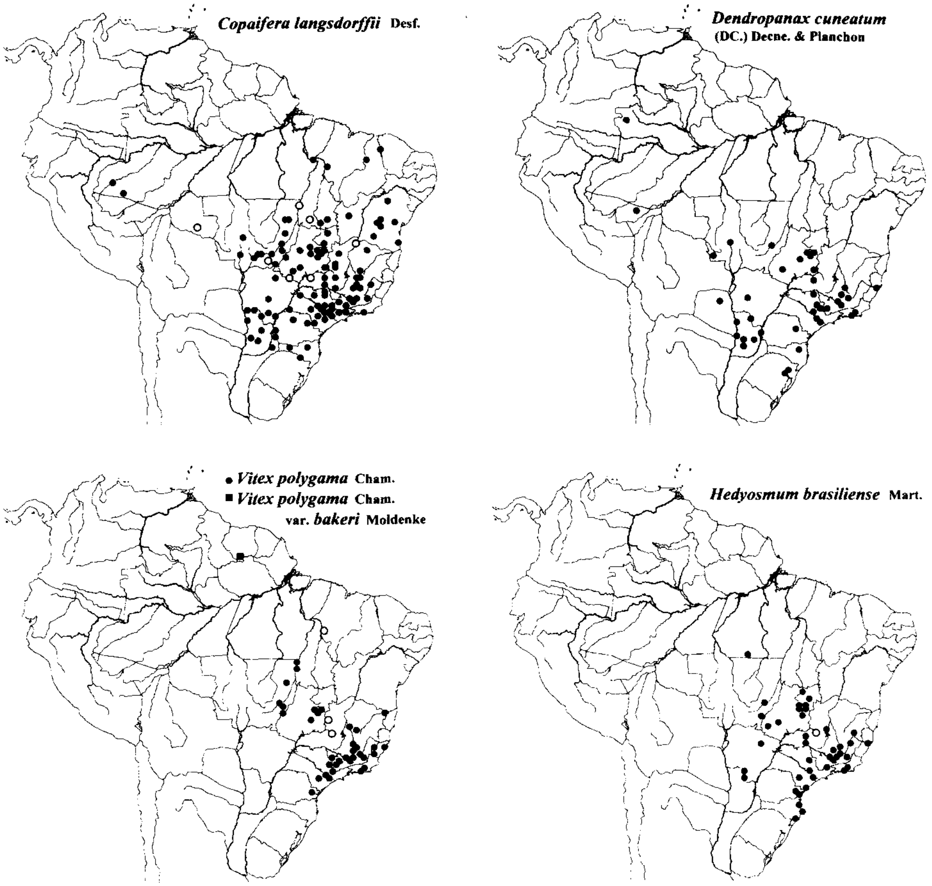


FIG. 14. Distribution of *Copaifera langsdorffii*, *Dendropanax cuneatum*, *Vitex polygama* and *Hedyosmum brasiliense*. For explanation of symbols see Fig. 6.

Aubrev. were found in galleries as far south as the Chapada dos Guimarães, in Mato Grosso. The former shows a disjunct distribution, also appearing in the Atlantic forest, suggesting that an ancient connection must have existed. The distribution of the bizarre distichous palm *Oenocarpus distichus* Mart., also found in the galleries of the Chapada dos Guimarães, suggests a connection through the Araguaia, Xingu and Tapajós river basins. *Protium pedicellatum* Swart[5] also seems to conform to such a pattern although it has a wider distribution range within the Amazon basin.

The four species in Fig. 14 represent a distribution pattern which is centred basically in the Paranense semideciduous forests and extends to the Cerrado Province, reaching a few areas of the Amazonian and Atlantic Provinces. *Copaifera langsdorffii* Desf. is the most widespread of them, also reaching the hinterland plateaux within

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[5] This species appears as *Protium elegans* Engler and *Protium krukoffii* Swart in the checklists for north-eastern Mato Grosso and Chapada dos Guimarães, respectively.

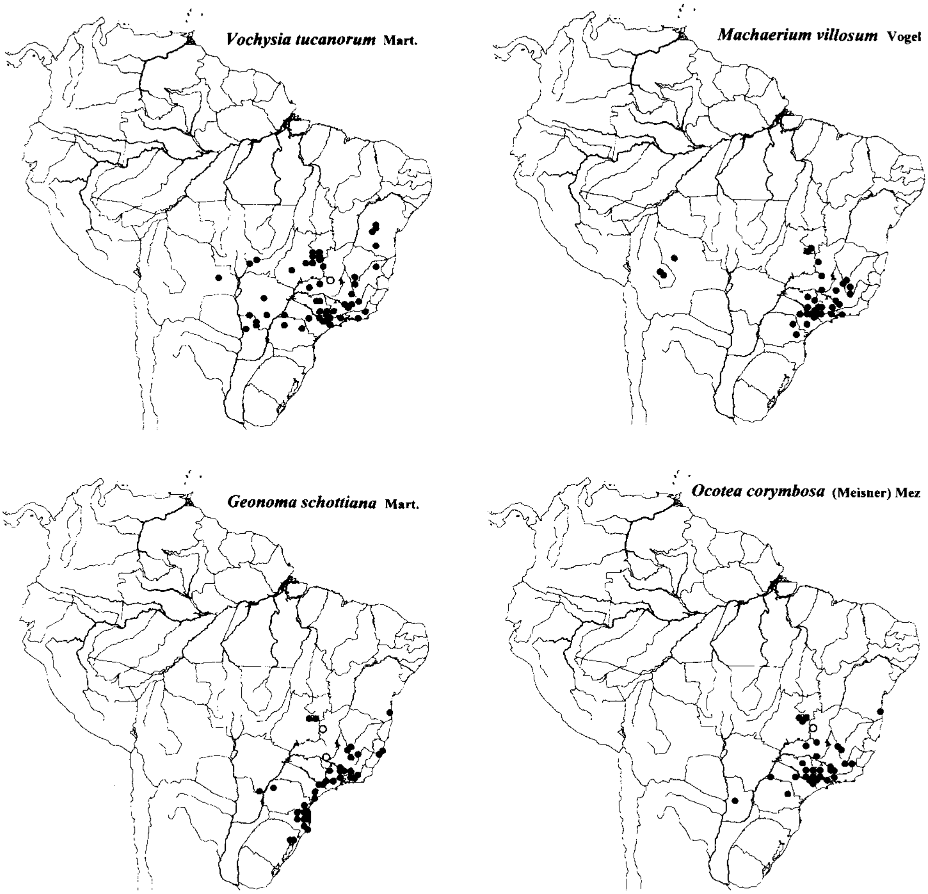

FIG. 15. Distribution of *Vochysia tucanorum*, *Machaerium villosum*, *Geonoma schottiana* and *Ocotea corymbosa*. For explanation of symbols see Fig. 6.

the Caatinga Province. Its distribution appears to follow Aw and Cw climate types. The species is also a great habitat generalist, appearing on a wide array of soil types, in both cerrado and forest. *Dendropanax cuneatum* (DC.) Decne. & Planchon and *Vitex polygama* Cham. are also distributed from the southern semideciduous forests to central Brazil, although these species only occasionally appear in cerrado vegetation. The latter is associated with mesotrophic soils of higher pH and calcium content. *Hedyosmum brasiliense* Mart. is a strict forest species and its distribution differs from the previous species in its higher frequency in the Atlantic rainforests and its preference for the high altitude forests in the hinterlands, reaching the Amazonian region in the Serra do Cachimbo highlands. It is very abundant on the margin of damp gallery forests in the Distrito Federal, as a small, prop-rooted tree, rarely more than 5m tall.

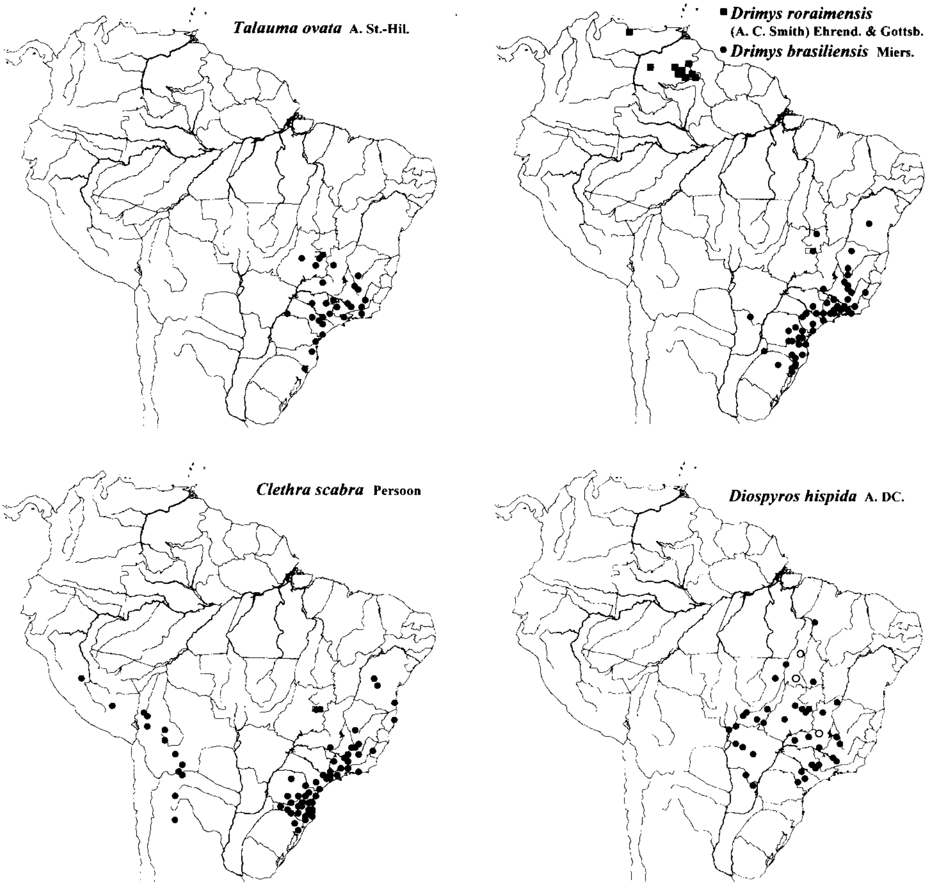

FIG. 16. Distribution of *Talauma ovata*, *Drimys roraimensis* and *D. brasiliensis*, *Clethra scabra* and *Diospyros hispida*. For explanation of symbols see Fig. 6.

The species in Fig. 15 also represent distribution patterns centred in the southern forests with extensions into the Cerrado Province mostly via gallery forests. Some interesting ecological and geographical differences can be enumerated. Although *Vochysia tucanorum* Mart. is mainly a forest-margin species, it is sometimes found in cerrado vegetation. It has a wider distribution than the other three species which only reach the central-southern gallery forests of the Distrito Federal. *Machaerium villosum* Vogel and *Ocotea corymbosa* (Meisner) Mez are semideciduous forest species, occasionally appearing in the cerrado. They seem to prefer better-drained soils as they commonly appear on the most elevated sites within the galleries. *M. villosum* has a curious disjunct pattern, appearing in the semideciduous and gallery forests of southeastern Brazil and on the semideciduous forests of the Andes foothills in Bolivia. The distribution of the low palm *Geonoma schottiana* Mart.,

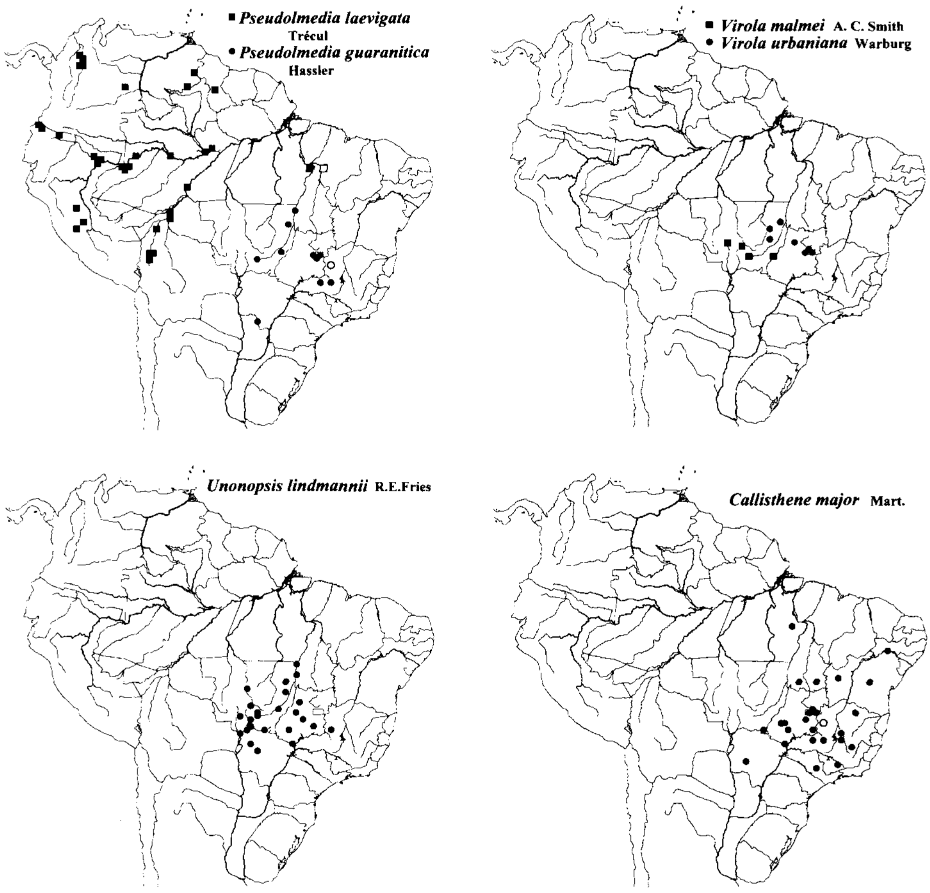

FIG. 17. Distribution of *Pseudolmedia laevigata* and *P. guaranitica, Virola malmei* and *Virola urbaniana, Unonopsis lindmannii* and *Callisthene major*. For explanation of symbols see Fig. 6.

associated with damp soils, extends from the Atlantic rainforests to the Planalto Central via the interior of gallery forests.

The first three species in Fig. 16 illustrate the links between Atlantic rainforests, montane semideciduous forests and the central-southern gallery forests. *Talauma ovata* A. St.-Hil. is found exclusively on highly anoxic waterlogged sites, so that its distribution typically follows these habitats from the Atlantic rainforests to the Planalto Central highlands. *Drimys brasiliensis* Miers and *Clethra scabra* Persoon are strongly associated with high altitudes (> 1000m) and their distribution follows the Atlantic coastal ridge and the hinterland mountains through the Espinhaço range and the Planalto Central. Both species show interesting disjunctions associated with high altitude. *C. scabra* also appears along the high Andean foothills while *Drimys*

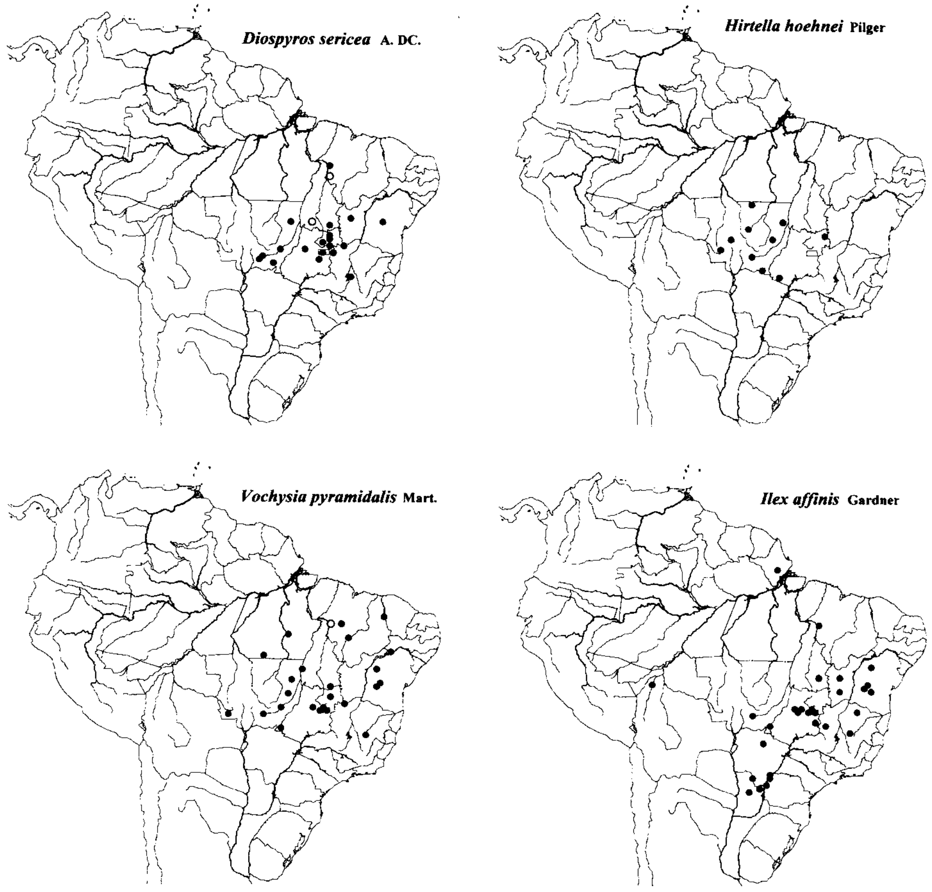

FIG. 18. Distribution of *Diospyros sericea*, *Hirtella hoehnei*, *Vochysia pyramidalis* and *Ilex affinis*. For explanation of symbols see Fig. 6.

roraimensis (A. C. Smith) Ehrend. & Gottsb., which was formerly recognized as a subspecies of *D. brasiliensis*, appears in the Guyana highlands. In addition to these two, other gallery species known to follow an upper montane distribution pattern along hinterland mountain ranges are *Weinmannia discolor* Gardner and *W. paullinifolia* Pohl, *Podocarpus lambertii* Klotz., *P. sellowii* Klotz. and the already mentioned *Hedyosmum brasiliense* (Giulietti & Pirani, 1988).

The remaining nine maps (Figs 16–18) represent gallery forest species with a distribution pattern concentrated in central Brazil. The first species, *Diospyros hispida* A. DC. (Fig. 16), is common in galleries with soils of intermediate fertility and is also found in cerradão and cerrado. Hence its distribution map conforms to that of the cerrado vegetation. *Unonopsis lindmannii* R. E. Fries and *Callisthene major* Mart. (Fig. 17) also appear occasionally in cerrado vegetation, but their typical habitat is the margin of galleries where they receive full sunlight. *Pseudolmedia guaranitica* Hassler,[6] *Virola malmei* A. C. Smith, and *Virola urbaniana* Warburg are strict gallery species, with high preference for moist soils. Other typical riverside species found in central Brazilian galleries are given in Fig. 18. These are *Diospyros sericea* A. DC., *Hirtella hoehnei* Pilger, *Vochysia pyramidalis* Mart. and *Ilex affinis* Gardner. Of these *D. sericea* is also common in cerradão.

CONCLUSIONS

A long-lasting controversy has been associated with the factors determining the distribution of cerrado vegetation but in general the following are considered important: seasonal rainfall, soil fertility and drainage, fire (especially man-made), and the climatic fluctuations of the Quaternary. These are, in fact, the same factors identified as important in maintaining the savanna biome worldwide, although in other areas, such as Africa, grazing also plays an important role (see papers in Werner (1991) and in Furley et al. (1992)). As pointed out by a number of authors, climatic seasonality by itself cannot explain the predominance of cerrado vegetation within its distribution range as the present climatic conditions would favour the establishment of forests in most of the Cerrado Province (e.g. Rizzini & Pinto, 1964; Reis, 1971; Klein, 1975; Van der Hammen, 1983). This is true, and actually forests are an extremely important constituent of the Cerrado Province in central Brazil and probably occur in all habitats where environmental factors allow their establishment and growth.

Where more fertile mesotrophic soils occur in the Cerrado Province the climax vegetation is deciduous or semideciduous (mesophytic) forest. Such forests are seen in valleys where the topography has cut into more mineral-rich underlying rocks (e.g. silts and mudstones) or as great extensions in more fertile areas. One of the largest of the latter, the 'Mato Grosso de Goiás', is estimated to have had an area of 40,000km^2 (see in Fig. 1 the great gap in the distribution of cerrados in the state of Goiás) while the anecdotal evidence of our road journey from the Distrito Federal to Maranhão (p. 145) demonstrates how much of the Cerrado Province was previously covered by this type of forest. The soils of these forests are particularly good for agriculture and because of this the vegetation has been devastated to such an extent that in many areas it is difficult to realize that forest was once an important, or even dominant, land cover. In our experience it is rare to encounter cerrado regions where at least some of this forest does not occur: even the most dystrophic chapadas have small fertile forested valleys! Such mesophytic forests are particularly common on the base-rich soils of the peripheral areas that connect the Cerrado to the Caatinga Province, in the East, and to the Chaco Province, in the western bound-

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[6] This species appears as *Pseudolmedia laevigata* Trécul in all checklists published for central Brazilian galleries and this is why both species were mapped. Berg (1972) in his revision of the genus regarded the two species as very similar. It would be no surprise if in the future they are united as a single species, thus completely changing the distribution pattern illustrated.

aries of the Mato Grosso Pantanal. They also appear on calcareous outcrops throughout the region, forming the so-called 'mata calcárea'. These have already been regarded by Prado & Gibbs (1993) as relics of a once even more extensive deciduous forest that during the glacial maxima would have connected the caatingas, in northeastern Brazil, to the semideciduous forests, in southeastern Brazil and southern Paraguay, and to the piedmont forests, in central-western Argentina. Palynological evidence is given by Ledru (1993) for the existence of such a forest during the Würm-Wisconsin glacial period in present-day cerrado areas. It is reasonable to think that an intense process of soil-leaching and acidification following the return of more humid climates to the cerrado region would have favoured the establishment of cerrado in most places and the isolation of deciduous forests on the present-day areas of mesotrophic and calcareous soils (Ratter et al., 1988). Although these forests have been almost entirely devastated by man, their original distribution given by the IBGE (1993) seems to indicate that they represent expansions of the Paranense semideciduous forests penetrating into the Cerrado Province via the basalt-derived fertile soils of western Minas Gerais and southern Goiás.

There seem to be no clear-cut ecological and floristic differences between deciduous and semideciduous forests. The level of deciduousness probably depends on the conjunction of soil moisture and chemical properties and the increasing role of a cool winter with increasing altitude and latitude. Often there are quite local differences in deciduousness: for instance, at Vale dos Sonhos, Mato Grosso, the same forest community is deciduous on the well-drained valley sides but semideciduous in the moister valley bottom (Ratter et al., 1978b). Transitional vegetation at the cerrado interface is interesting and widespread. The mesotrophic cerradão represents an intermediate community between mesophytic forest and cerrado associated with soils of intermediate fertility (Ratter 1971, 1992; Ratter et al., 1977; Furley et al., 1988). It usually occurs at the mesophytic forest/cerrado interface but also covers very large extensions of the Cerrado Province where such intermediate soils occur.

Thus the mesophytic forests are an important element of central Brazilian vegetation associated with soil fertility and following a northeast-southwest geographical pattern (Prado & Gibbs, 1993). A second element is the dendritic net of gallery forests, highly dependent on soil moisture, extending in a northwest-southeast direction to connect the Amazonian and Atlantic forests. A considerable number of species shared by these two great forest provinces cross central Brazil via the gallery forests. Others extend their range into the Cerrado Province along the galleries but do not complete the crossing, while the majority of species remain strictly confined to their own rainforest region. Thus the movement of individual species along the Northwest-Southeast Bridge migration route seems to be very variable. Many of the species established throughout the galleries are habitat generalists (e.g. *Schefflera morototoni*, *Casearia sylvestris*, *Protium heptaphyllum*, *Tapirira guianensis*, *Virola sebifera*, *Copaifera langsdorffii* and *Hymenaea courbaril*) and probably environmental conditions are not suitable for more specialized forest species. One could suggest a number of such limiting factors of which climate, with decrease of average temperature and increasing seasonality of rainfall, is probably the most important.

Palynological evidence indicates that the levels of aridity in the central Brazilian region during most of the Würm-Wisconsin glaciation were not as high as previously thought (Ledru, 1993). This could suggest that gallery forests remained in the region during this period, and other observations tend to support this. High plateaux predominate in central Brazil and these are known to concentrate rainfall and preserve humidity: for example, even within the present-day semi-arid Caatinga Province, the hinterland highlands have abundant water sources and both upland and gallery forests ('brejo' forests). In addition, the considerable number of endemic gallery species illustrated in the distribution maps also provide evidence of the survival of these forests during the glaciations. Nevertheless, there must have been a notable reduction in the extent of gallery forests during more arid periods, and where close observations are made it can be seen that they are at present in a phase of expansion (see Ratter, 1980, 1991). Probably this expansion has been accompanied by species-enrichment with immigrants from the Amazon basin and southern mesophytic forests, which in turn has produced a strong floristic differentiation between the central-southern and western-northern galleries considered in the next paragraphs.

The stronger floristic link between the central-southern galleries and the Paranense semideciduous forests, and especially its montane formations, gives evidence that lower temperatures were an important factor in the differentiation of those forests. Another source of evidence is given by the pollen record which indicates the establishment of the *Araucaria* forest in this region at the beginning of the last humid period (Ledru, 1993). The high altitude species found in the flora of galleries of the Espinhaço range and Planalto Central are probably the relics of the expansion of the *Araucaria* forest through central Brazil during the early Holocene. The pollen record also indicates the expansion of the mesophytic forests (deciduous and semideciduous) in the region following the retreat of the *Araucaria* forest. However, these forests were replaced by cerrado during the brief Holocenic dry episode and have not regained their area although rainfall apparently returned to previous levels. This failure of forest to re-establish may be man-induced, since certainly man and his fires were important elements in the region at least after the mid-Holocene. The occurrence of semideciduous forests on dry soils of very low fertility in the cerrado region of southern Minas Gerais (Oliveira-Filho et al., 1994b, c) demonstrates that the present-day environmental conditions favour the establishment of forests in much of the region and that factors unrelated to the physical environment are preventing the expansion of forest into cerrado.

The western-northern galleries are set in a wide region where the complex transition between the central Brazilian cerrados and the Amazonian Hylaea takes place (Ratter et al., 1973, 1978a; Ackerly et al., 1989). All rivers of this part of the cerrado region flow northwards to the Amazon basin, so it is easy to understand the strong floristic links of the galleries to the Amazonian flora. An interesting floristic pattern that emerged from the analysis is that connecting galleries, dystrophic cerradões and transitional open rainforests ('mata seca', or dry forest). This floristic pattern apparently unites species related to very infertile, often sandy, soils of quite high moisture content. Palynological records for Carajás, in eastern Amazonia (Absy et al., 1991) give evidence of forest retreat during the Würm-Wisconsin glaciation period, while the work of Ratter et al. (1973, 1978a) demonstrates a surprisingly rapid present-day expansion of Amazonian forest in eastern Mato Grosso. As is known, the situation has been extremely dynamic and at times the galleries of Amazonia probably constituted important forest refuges (Pires, 1984).

An important aspect of gallery forests is that they have interfaces with so many other types of vegetation, including rainforests, mesophytic forests and the cerrado itself. They are thus subjected to enormously different floristic influences resulting in great heterogeneity: the gallery forests undoubtedly harbour a remarkably diverse flora. In addition to this, they are an extremely important habitat for the cerrado fauna and act as migration corridors. Thus any policy aimed at conservation of biodiversity in Brazil must give high priority to protection of galleries and riparian forests.

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