

Islands in Amazonia

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SUMMARY

There are a number of habitats within the lowland Amazonian rainforest ecosystem that are functional islands. Those that are discussed are savannas, white sand campinas and caatingas, inselbergs and sandstone table mountains or tepuis. Each of these habitats is a series of isolated islands of vegetation and in some cases speciation has taken place between islands, especially the older tepuis, and in other cases there is still little differentiation due to more vagile diaspores and recent climatic changes. The effects of Pleistocene climatic changes that altered the balance between the distribution of savanna and rainforest is discussed.

1. INTRODUCTION

I was quite surprised to receive an invitation to speak about the Amazon Basin, a continental area *par excellence*, in a meeting about evolution on islands. There are hundreds of islands within Amazonia varying from Marajó Island in the Amazon Delta, the size of Switzerland, to tiny islands that come and go all along the principal rivers. These islands are not of particular interest in the evolution of species although recent work has shown their importance in creating a succession of many different types of flood-plain vegetation types (Tuomisto *et al.* 1995), and thereby increasing the vegetational diversity of the region. I am not, however, going to treat the actual river islands, but rather areas of vegetation that are in situations which are comparable to islands within the forested regions of Amazonia. In the lowlands there are many patches of savanna and of white sand caatinga or campina that are in effect small isolated islands surrounded by rainforest. Where higher ground exists in Amazonia, principally on the Guiana shield to the north and the Brazilian shield to the South, there are isolated granite peaks (inselbergs) and a large number of sandstone table mountains (tepuis), the tops of which are in effect isolated islands of vegetation. It is these four areas each with their own vegetation type that are treated here.

The vegetational cover of Amazonia has not been stable through the geological timescale and variations in climate have resulted in variations in the balance between the drier types of vegetation such as savanna, deciduous forest and caatinga and the wetter tropical moist forest. At times the current situation has been reversed and patches of rainforest have been islands within savanna. (Haffer 1969; Prance 1973, 1983; Van der Hammen 1974; Thomson *et al.* 1995). These changes have all had a profound effect on the evolution and distribution of plant species. This too has created islands of rainforest surrounded by savanna which

acted as refugia for the species of the more humid rainforest vegetation.

It is, therefore, worthwhile considering the vegetation of Amazonia in terms of islands as well as in terms of being the largest continental mass of rainforest.

2. AMAZONIAN SAVANNAS

The Amazon basin is bordered by the two major savanna regions of S. America the Llanos of Colombia and Venezuela to the north and the cerrado of the Planalto of Central Brazil to the South. However, within the rainforest region there are a considerable number of smaller isolated savannas and some quite large ones such as the Roraima-Rupununi savanna of Roraima Territory, Brazil and the Rupununi district of Guyana, and the Llanos de Mojos in Bolivia (figures 1 & 3).

The savanna islands within Amazonia have been known and discussed for many years (for example, Huber 1900, 1902; Ducke 1907, 1913) but only more recently have sufficient phytosociological studies been made to compare the distribution of their component species (for example, Takeuchi 1960; Medina 1969; Eiten 1972; Eden 1974; Huber 1982; Gottsberger & Morawetz 1986). Extensive work has been carried out on the cerrados of central Brazil (for example, Eiten 1972, 1982; Prance & Schaller 1982; Ratter & Dargie 1992; Guarim Neto *et al.* 1994). Although there are some species of plants common to almost all the S. American savannas from Mexico to Paraguay such as *Curatella americana* L., most workers agree that the Amazonian savanna islands are considerably different from those of the cerrado and the llanos (Eiten 1978; Kubitzki 1979, 1983). Huber (1982) divided the savannas of Amazonas Territory in Venezuela into three distinct types.

1. Savanna in seasonally flooded areas where the absence of woody vegetation is clearly due to edaphic factors. The large flooded savannas of Amapá and

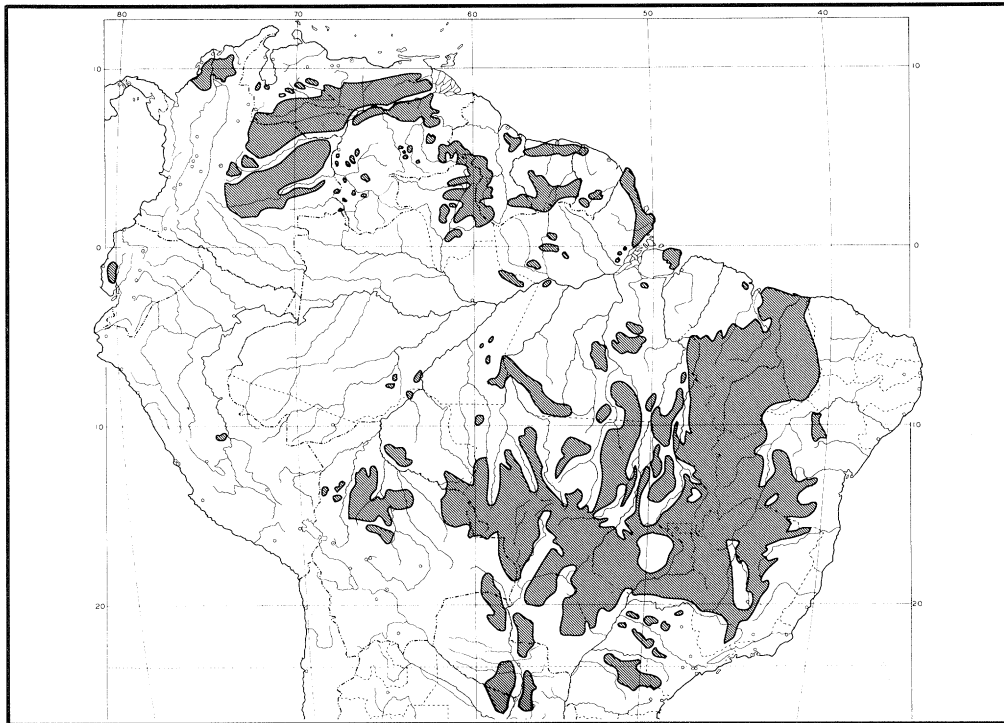


Figure 1. Map of the distribution of savanna in tropical south America (after Huber, 1974).

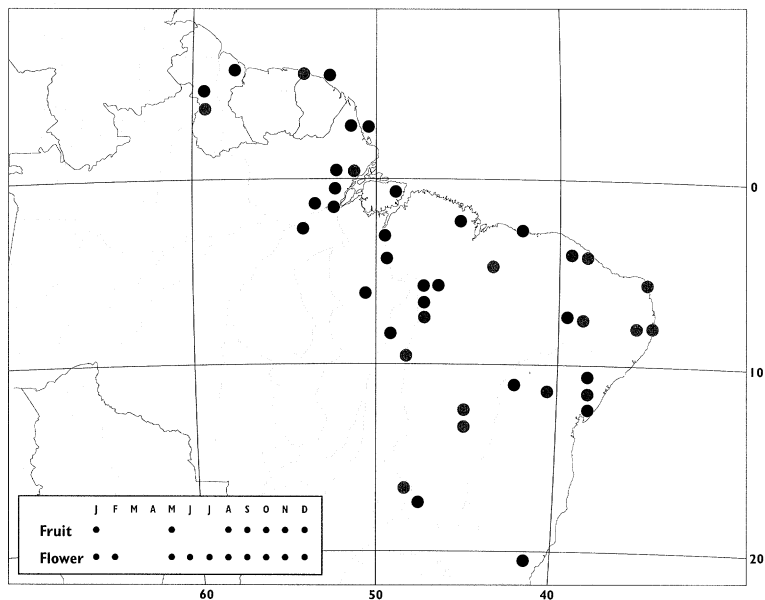


Figure 2. Distribution of *Hirtella ciliata* Mart., a savanna species.

Marajó island in Brazil also fall into this category although they are quite different in their species composition.

2. Savannas on white sand soil, with extremely poor nutrient availability and rapid drainage. In these savannas there is a considerable amount of endemism and Huber (1982) suggested that these are 'highly selected and specialised plant communities surviving best on these sites where they evolved'. These are different from the campinas and amazonian caatingas discussed below.

3. The llanos-type savanna which has a more or less continuous grass layer and a sparse covering of trees

and shrubs. Unlike the white-sand savannas, endemism is rare and fire is a common feature. Many of the smaller savanna patches within Amazonia fall into this category.

The existence of the first two categories of savanna is easy to explain, the environmental factors of flooding and of white sand control their existence. They are likely to remain savanna even during periods of the most favourable climate for rainforests. In the case of the white sand savannas it is not surprising that there is a high degree of endemism because many white-sand specialist species appear to remain on white sand even when there is more savanna surrounding them. Once



Figure 3. Top, an Amazonian savanna island at Humaitá, Amazonas; lower, general aspect of a white sand campina near to Manaus.

adapted to white sand and its specific low nutrient availability these species do not readily migrate to the richer clay soil habitats.

The non-flooded grassland savannas which occur scattered throughout Amazonia, llanos-type of Huber (1982) occur on both sandy and lateritic soils and it is notable that there is no difference between the soil under savanna vegetation and the adjacent forest areas (Eden 1974; Blancaneaux *et al.* 1977; G. T. Prance, unpublished data). These savannas are probably relicts of formerly widespread vegetation that developed during the drier climatic conditions of the late Pleistocene (Ducke & Black 1953; Prance 1973; Eden 1974; Huber 1982). That so many of these patches of savanna remain and did not return to a rainforest cover during the Holocene is probably partly due to

human intervention. Early hunter-gatherer peoples used repeated burning of natural islands of savanna to flush game and to kill small animals, thereby maintaining or even expanding the savannas (Aubréville 1961; Hills 1969; Rivière 1972; Smith 1995). The occurrence of a large number of widespread species that are in most Amazonian savannas and beyond supports the theory that these savanna patches are relicts of a more extensive savanna (table 1). As would be expected the northern Amazonian savannas show a closer link to the llanos and the southern ones a closer link to the cerrados. For example, in the Humaitá-Puciarí savannas of Amazonia, Brazil contain such cerrado species as *Orthopappus angustifolius* (Sw.) Gleason, *Cyperus diffusus* Vahl, *Axonopus aureus* Beauv., *Vochysia haenkeana* Mart., *Didymopanax distractiflorum* Harms (Gottsberger and

Table 1. *Some wide ranging neotropical savanna species*

species	family	distribution
<i>Arrabidaea corallina</i> (Jacq.) Sandw.	Bignoniaceae	Mexico to Argentina
<i>Bowdichia virgilioides</i> H.B.K.	Leguminosae	Venezuela to S. Brazil
<i>Byrsonima crassifolia</i> (L.) H.B.K.	Malpighiaceae	Cuba to S. Brazil
<i>Byrsonima verbascifolia</i> Juss.	Malpighiaceae	Cuba to S. Brazil
<i>Curatella americana</i> L.	Dilleniaceae	Mexico to Paraguay
<i>Hirtella glandulosa</i> Spreng.	Chrysobalanaceae	Venezuela to São Paulo
<i>Palicourea rigida</i> H.B.K.	Rubiaceae	Colombia to São Paulo
<i>Polystachya estrellensis</i> Rchb.f.	Orchidaceae	Trinidad to Paraguay
<i>Roupala montana</i> Aubl.	Proteaceae	Mexico to Brazil
<i>Xylopia aromatica</i> (Lam.) Mart.	Annonaceae	Panama, Cuba to Paraguay

Morawetz 1986), *Keilmeyera coriacea* Mart. (Kubitzki 1979; Janssen 1986), and *Hirtella ciliata* Mart. (Prance 1972, figure 2). Various northern species extend southwards through the savannas. For example, the savanna de Amelia on the south bank of the Rio Negro near Manas contains such species as *Ouratea spruceana* Engl. (Ochnaceae); *Ruizterrania retusa* (Spruce ex Warm.) Marcano Berti (Vochysiaceae). It is also interesting that this savanna is dominated by the ubiquitous savanna species *Antonia ovata* Pohl (Asteraceae).

There is also little morphological differentiation between populations of the common savanna species in different savanna islands which is an indication of more recent origin. In the widespread savanna species which I have studied such as *Hirtella glandulosa* Spreng. (Chrysobalanaceae) no morphological differences can be found in individuals in such isolated places as the Humaitá Savanna or the Savanna de Amelia near to Manaus. The only example of differentiation that has been published is that of Gentry in the Bignoniaceae occurring in the Savannas of Peru (Gentry 1979, 1982). (Gentry studied the species of Bignoniaceae that occur in isolated patches of dry forest along the Andes. Some species such as *Tabebuia impetiginosa* (Mart. ex DC.) Standl. showed no differentiation between isolated populations; others, for example *Tabebuia ochracea* (Cham.) Standl. was divided into taxonomic subspecies because of the variation in different patches of dry forest. Two species of *Tecoma* seem to be in an intermediate situation where the populations in adjacent Andean valleys are perceptibly different, but 'their taxonomic circumscriptions and states remain murky' (Gentry 1979). This is exactly what one might expect in more recently separated populations where evolution towards taxonomic isolation is actively progressing. This topic of contemporary refugia would make a very interesting molecular study where differences between populations might be revealed.

Many savanna species are easily dispersed (Kubitzki 1979, 1983) and this explains their ability to migrate rapidly during times of drier climate. Kubitzki showed that several cerrado species with large diaspores such as *Caryocar brasiliense* Camb. do not occur in most savannas. The only isolated savanna in which I have

found that species is at Serra do Cachimbo in Pará, which is only separated from the cerrado by about 200 km of forest and was evidently connected to the cerrado during periods of drier climate.

3. CAMPINAS AND AMAZONIAN CAATINGAS

These two Brazilian terms are applied to areas of vegetation over white sand which differ considerably in their physiognomy from the surrounding rainforest on oxisols. The Amazonian caatinga is a large area of white sand which lies between the Rio Branco and the Rio Negro in northwestern Amazonian Brazil and which extends into Venezuela. The campinas are similar patches of white sand vegetation throughout Amazonia and are equivalent to the heath forests of tropical Asia. The large area of caatinga is formed on the sand leached from the sandstone highlands of Venezuela and most of the campinas are formed from uplifted former river beaches. The effect of both is the same, a nutrient poor sandy soil (spodosol). Caatingas have been described by Spruce (1908), Takeuchi (1962), Rodrigues (1961), Ducke & Black (1953), Klinge *et al.* (1977), Klinge & Medina (1979) and campinas by Takeuchi (1961), Anderson *et al.* (1975) and Anderson (1981). The caatinga and the campinas have some species in common, (e.g. *Glycoxydon inophyllum* (Miq.) Ducke and *Humiria balsamifera* St. Hil.), but are notably different in species composition. Some of the characteristic species of the caatinga are given in table 2.

The Amazonian white sand caatingas should not be confused with the caatingas of northeastern Brazil where the same term is used for semi-arid scrubland. The Amazonian caatinga is dominated by species of Leguminosae, especially the genus *Eperua*. A similar white sand vegetation called Wallaba forest occurs in the Guianas (Richards 1952), and is dominated by *Eperua falcata* (Wallaba). Despite dominance by two or three species both the caatinga and the Wallaba forest is rich in total species and in endemic species (Ducke & Black 1953) most of which are from the common genera of the Amazonian rainforest (for example, *Caryocar gracile* Wittm. and *Couepia racemosa* Benth.).

Table 2. *Some characteristic woody species of Amazonian caatinga and Amazonian campina*

caatinga	campina
<i>Aldina discolor</i> Spruce ex Benth. (Leguminosae)	<i>Aldina heterophylla</i> Spruce ex Benth. (Leguminosae)
<i>Bactris cuspidata</i> Mart. (Arecaceae)	<i>Clusia insignis</i> Mart. (Clusiaceae)
<i>Barcela odora</i> Mart. (Arecaceae)	<i>Eperua purpurea</i> Benth. (Leguminosae)
<i>Carocar gracile</i> Wittm. (Caryocaraceae)	<i>Humiria balsamifera</i> St. Hil. (Humiriaceae)
<i>Clusia insignis</i> Mart. (Clusiaceae)	<i>Macrobium arenarium</i> Ducke (Leguminosae)
<i>Compsonera debilis</i> (A.DC.) Warb. (Myristicaceae)	<i>Pagamea duckei</i> Standl. (Rubiaceae)
<i>Eperua leucantha</i> Benth. (Leguminosae)	<i>Protium heptaphyllum</i> (Aubl.) March (Burseraeae)
<i>E. purpurea</i> Benth.	<i>Sandemania hoehnei</i> (Cogn.) Wurdack (Melastomataceae)
<i>E. rubiginosa</i> Miq.	<i>Swartzia dolichopoda</i> Cowan (Leguminosae)
<i>Hevea rigidifolia</i> (Benth.) M.Arg. (Euphorbiaceae)	
<i>Lissocarpa benthamii</i> Guerke (Ebenaceae)	
<i>Lucuma</i> sp. (Sapotaceae)	
<i>Micrandra crassipes</i> (M.Arg.) R.E. Schult. (Euphorbiaceae)	
<i>M. sprucei</i> (M.Arg.) R.E. Schult.	
<i>Peltogyne calingae</i> Ducke (Leguminosae)	
<i>Retiniphyllum chloranthum</i> Ducke (Rubiaceae)	

The poor soil and the low sclerophyllous vegetation of the caatinga is a separate formation and species have adapted to it and separated through niche specialization. The caatinga formation can be defined both by its characteristic sclerophyllous vegetation with tortuous branched trees and by the presence of an extremely large number of endemic species.

More island-like are the smaller patches of campina within the rainforest. These small areas have a physiognomy similar to that of the caatinga and vary from a continuous forest cover to open areas with scattered shrubs. As would be expected from this small area, these areas have less endemism than the large caatinga area, but many of the species which occur are those which are confined to the white sand areas. An analysis of a campina near to Manaus (Macedo & Prance 1978) showed that the majority of species (75.5%) have the capacity for long distance dispersal (59.5% birds, 13.5% wind, 2.5% bats) which accounts for the relatively low endemism in campinas. The species are mainly either those occurring in the caatingas, the sandy black water river beaches or the white sand forests of the Guianas. Their vagility has tended to reduce both endemism and the evolution of new species in each of these isolated islands of campina.

There are a large number of white sand savannas and savanna forests in the Guianas. Although termed savannas there, they are much more comparable to the white sand campinas and caatingas than to the grass

dominated savannas. A good description of an area of white sand vegetation in Suriname was given by Heyligers (1963).

4. INSELBERGS

Scattered throughout the Guianas and northern Amazonian Brazil there are a series of granitic outcrops which rise above the rainforest to a height of 300–800 m. In some cases these hills are covered by dense forest (e.g. Palunlouimémpéu and Mitraka), but most of them are characteristic inselbergs (Grabert 1976) with low scrub forest and open areas of exposed rocks (Granville & Sastre 1974; Hurault 1974; Sastre 1977). These are obviously islands of a special type of vegetation surrounded by rainforest. The top of the inselbergs are well drained and become very dry in the dry season and so the vegetation is often dominated by sclerophyllous plants or any with other adaptations to drought such as the orchid *Cyrtopodium andersonii* R. Brown with large pseudobulbs that store water or various cacti (*Epiphyllum* and *Melocactus*). The dominant shrub is usually a species of *Clusia* and other terrestrial orchids include *Epidendrum nocturnum* Jaq. and *Encyclia ionosma* (Lindl.) Schlecht. and the Bromeliad *Pitcairnia geyskesii* L.B. Smith is common. Sastre (1977) found that about 55% of the plant species on the inselbergs of the Guianas are confined to that habitat. There has been considerable speciation in adaptation to the summit of inselbergs with their arid dry season conditions and very humid rainy season conditions. However, in contrast to tepuis, there has been much less speciation between the different inselbergs.

5. TEPUIS

Tepui is the Venezuelan term for the sandstone mountains of the Guayana Highland (figure 4). They extend from the easternmost tepui Tafelberg in Suriname through Guyana and Venezuela into Amazonian Colombia and south just into Brazil. Mount Roraima is on the corner of Venezuela, Guyana and Brazil and two tepuis occur within the Brazilian Amazon, Tepequém and Araca. The highest one is Mount Neblina (3045 m) on the Brazil–Venezuela frontier. The lowland area between the tepuis is either rainforest or savanna, depending on the locality. These spectacular mountains which tower above the surrounding forest are from 800–3000 m and are islands of montane vegetation surrounded by lowland forest. The Guyana Highlands have now been well studied largely through the work of Bassett Maguire of the New York Botanical Garden (Maguire 1956, 1970, 1953–1984) Julian Steyermark (1967, 1974, 1979, 1984, 1987) and Otto Huber (1987, 1990) and the Flora of which the first two volumes have just been published (Steyermark *et al.* 1995). This work has demonstrated that there is a great deal of endemism on the tepuis and that many less vagile genera have speciated extensively through the isolation of one tepui from another. Maguire

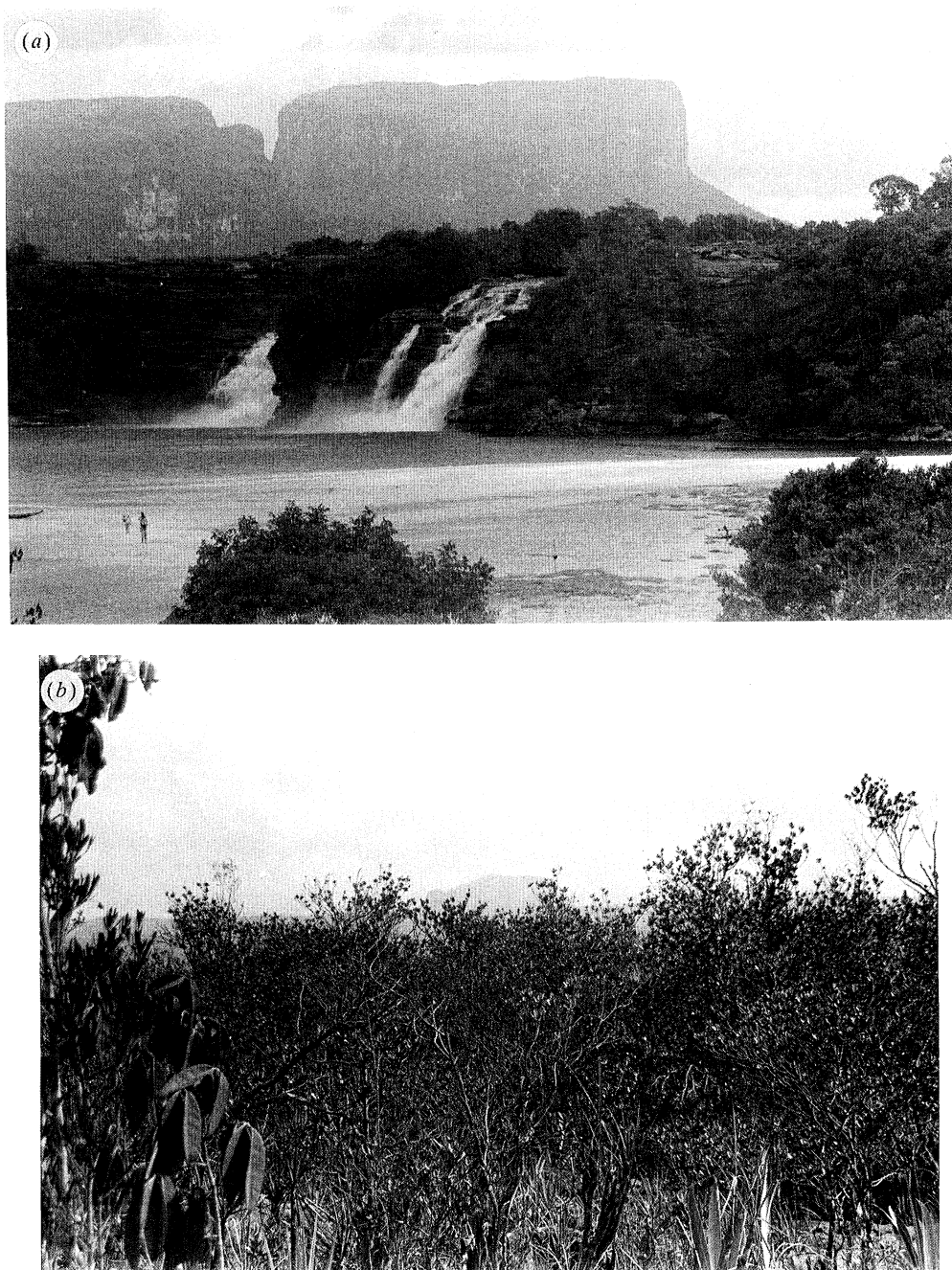


Figure 4. Top, a typical tepui, Kirun-tepui near to Canaima, Venezuela; lower, the plateau vegetation of Serra Araca a Brazilian tepui with a granitic dome in the background.

(1970) almost certainly overestimated the level of endemism on the tepuis when he estimated it as between 90–95% of the species and this was challenged by Steyermark (1979) who showed that 39 out of the 459 genera known to occur on the summits of tepuis (8.5%) were endemic to the summits. However as an additional 40 genera are found mainly on the summits but also occur on the lower talus slopes of the surrounding lower altitudes of contiguous areas, making a total of 79 or 17.2% of the genera largely confined to tepuis. That differentiation has taken place to such an extent at the generic level as well as the specific level would argue for the tepuis being ancient formations rather than recent upheavals of the Neogene or Pleistocene as argued by Kubitzki (1989). Both Steyermark (1979) and Maguire (1956) argue

from an analysis of summit species of the tepuis that dispersal was centripetal rather than centrifugal i.e. migration has taken place from the lowlands to the highlands rather than the reverse.

Table 3 confirms that there is considerable endemism on tepuis, the table lists the 16 new species that were described as a result of the author's two expeditions to Serra Araca, a rather low (1000–1400 m) outlier of Guayana Highland well into Brazil. This tepui was little explored until the expeditions of 1985 and 1986 and so the endemics were only recently described. Like other tepuis Araca also contains a large number of more widespread species characteristic of the Guayana Highland such as *Oedematopus duidae* Gleason, *Saxofridericia spongiosa* Maguire, *Retiniphyllum scabrum* Benth., *Perissocarpha steyermarkii* (Maguire) Steyermark &

Table 3. *New species and subspecies from Serra Araca, a sandstone tepui in Brazil, from two expeditions there by author*

(See Prance & Johnson 1992 for further details.)

<i>Caraipta aracaensis</i> Kubitzki (Clusiaceae)
<i>Diacidia aracaensis</i> Anderson (Malpighiaceae)
<i>Gleasonia prancei</i> Boom (Rubiaceae)
<i>Gongylolepis oblanceolata</i> Pruski (Asteraceae)
<i>Licania aracaensis</i> Prance (Chrysobalanaceae)
<i>Meriana aracaensis</i> Wurdack (Melastomataceae)
<i>Pitcairnia pranceana</i> L.B. Smith (Bromeliaceae)
<i>Podocarpus aracaensis</i> De Laubenfels & Silba (Podocarpaceae)
<i>Raveniopsis aracaensis</i> Kallunki & Steyer. (Rutaceae)
<i>Stenopadus aracaensis</i> Pruski (Asteraceae)
<i>Styrax tepuiensis</i> Steyer. & Maguire subsp. nov. (Styracaceae)
<i>Tepuianthus aracaensis</i> Steyer. (Tepuianthaceae)
<i>Ternstroemia aracaensis</i> Boom (Theaceae)
<i>Ternstroemia prancei</i> Boom (Theaceae)
<i>Tetrapterys cordifolia</i> Anderson (Malpighiaceae)
<i>Vaccinium pipolyi</i> Luteyn (Ericaceae)
<i>Xyris brachyfolia</i> Kral & Wanderley (Xyridaceae)

Maguire and *Macairea duidae* Gleason. The phyto-geographic affinities of the species that are not endemic to Araca are given in table 4 with a few selected examples. It can be seen that the affinity is strongly within the Guayana Highland with a few more widespread and lowland Amazonian species also occurring there.

There are many genera that have differentiated at the species or subspecies level from one tepui to another. Details of two such genera which also occur in the lowland savannas, *Tepuianthus* (Tepuianthaceae a Guayana endemic family) and *Heliampora* (Sarracenaceae) are given in table 4. It can be seen that in both genera there are several species confined to one tepui.

There is sufficient isolation for speciation to have taken place. The higher tepuis such as Sierra de la Neblina (over 3000 m) have a greater number of endemic species. Neblina even has an endemic family, the insectivorous Saccifoliaceae. The tepuis can certainly be treated as islands in terms of phytogeographic analysis.

Another reason for the species diversity of the tepuis is the large range of habitat which they offer. Steyermark (1979) recognized five major habitats on the summits of tepuis: Forest associations on soils; forest associations of epiphytes; shaded bluffs, ledges and crevices; savannas; exposed rocks, sands and rocky open areas. There is also a lot of scrubland on top of many tepuis and the habitats can obviously be much more finely divided. This accounts for some genera which have more than one species on a single tepui. The lower mountains have a considerable amount of forest on their summits. For example, Steyermark and Dunsterville (1980) showed that Cerro Guaiquinima, one of the largest tepuis, has 40% of the summit covered by forest. The species in this forest are generally closely related to those of the surrounding lowlands.

6. RAINFOREST ISLANDS IN THE HISTORY OF AMAZONIA

Today's Amazonian landscape is a forest with small islands of the vegetation types already discussed. There is now extensive data from pollen, charcoal and phytoliths to show that the present forest cover of the region has by no means been constant (for example, Van der Hammen 1974; Absy & Van der Hammen 1976; Absy 1979; Brown & Ab'Saber 1979; Absy *et al.* 1993; Colinvaux 1993; Thompson *et al.* 1995). Corresponding with the lower temperatures and drier climates of the periods of glaciation there was a much more widespread distribution of savanna and caatinga

Table 4. *The Phytogeographic affinities of species of Serra Araca plateau flora which are not endemic with a few examples of each category*

(From Prance & Johnson (1992), where further details are given)

	examples
widespread	<i>Cyrilla racemiflora</i> L. (Cyrillaceae) <i>Viburnum tinoides</i> L. f. (Rosaceae) <i>Burmannia bicolor</i> Mart. (Burmanniaceae)
Lowland Amazonia	<i>Pochota amazonica</i> (Robyns) (Bombacaceae) <i>Acanthera parviflora</i> W. Anderson (Malpighiaceae)
confined to Guyana Highland but widespread	<i>Cyathea demissa</i> (C. Morton) A. R. Smith ex Lel. (Cyatheaceae) <i>Ouratea roraimae</i> Engl. (Ochnaceae) <i>Schefflera duidae</i> Steyer. (Araliaceae)
restricted Guayana Highland:	
1. Neblina massif	<i>Gongylolepis oblanceolata</i> Pruski (Asteraceae) <i>Phyllanthus neblinae</i> Jabl. (Euphorbiaceae) <i>Remijia maguirei</i> Steyer. (Rubiaceae)
2. Duida complex	<i>Pagamea montana</i> Gleason & Standl. (Rubiaceae) <i>Sipaneopsis maguirei</i> Steyer. (Rubiaceae) <i>Stegolepis membranacea</i> Maguire (Rapateaceae)
3. Roraima complex	<i>Symbolanthus elisabethae</i> (Schomb.) Gilg (Gentianaceae) <i>Bactris simplicifrons</i> Mart. (Arecaceae)

Table 5. *The species of Tepuianthus (Tepuianthaceae) and Heliamphora (Sarraceniaceae) showing the distribution which is largely on summits of tepuis, in Venezuela unless otherwise indicated*

species	locality
<i>Tepuianthus auyantepuiensis</i> Mag. & Steyerl.	Auyán-tepui
<i>T. yapacanaensis</i> Mag. & Steyerl.	Cerro Yapacana
<i>T. savannensis</i> Mag. & Steyerl.	White sand savannas of SW Amazonas, Venezuela
<i>T. colombianus</i> Mag. & Steyerl.	Cerro Isibukuri (Colombia)
<i>T. sarisariñamensis</i> Mag. & Steyerl.	Sarisariñama tepui
subsp. <i>sarisariñamensis</i>	
subsp. <i>duidensis</i>	Cerro Duida
<i>T. aracaensis</i> Steyerl.	Serra Araca (Brazil)
<i>Heliamphora nutans</i> Benth.	Mount Roraima to Ilu-tepui
<i>H. minor</i> Gleason	Auyán-tepui and Chimantá-tepui
<i>H. heterodoxa</i> Steyerl.	Eastern Gran Sabana from Ptari-tepui northward
<i>H. ionasi</i> Maguire	Ilu-tepui
<i>H. tatei</i> Gleason	Cerro Duida
<i>H. neblinae</i> Maguire	Cerro Neblina

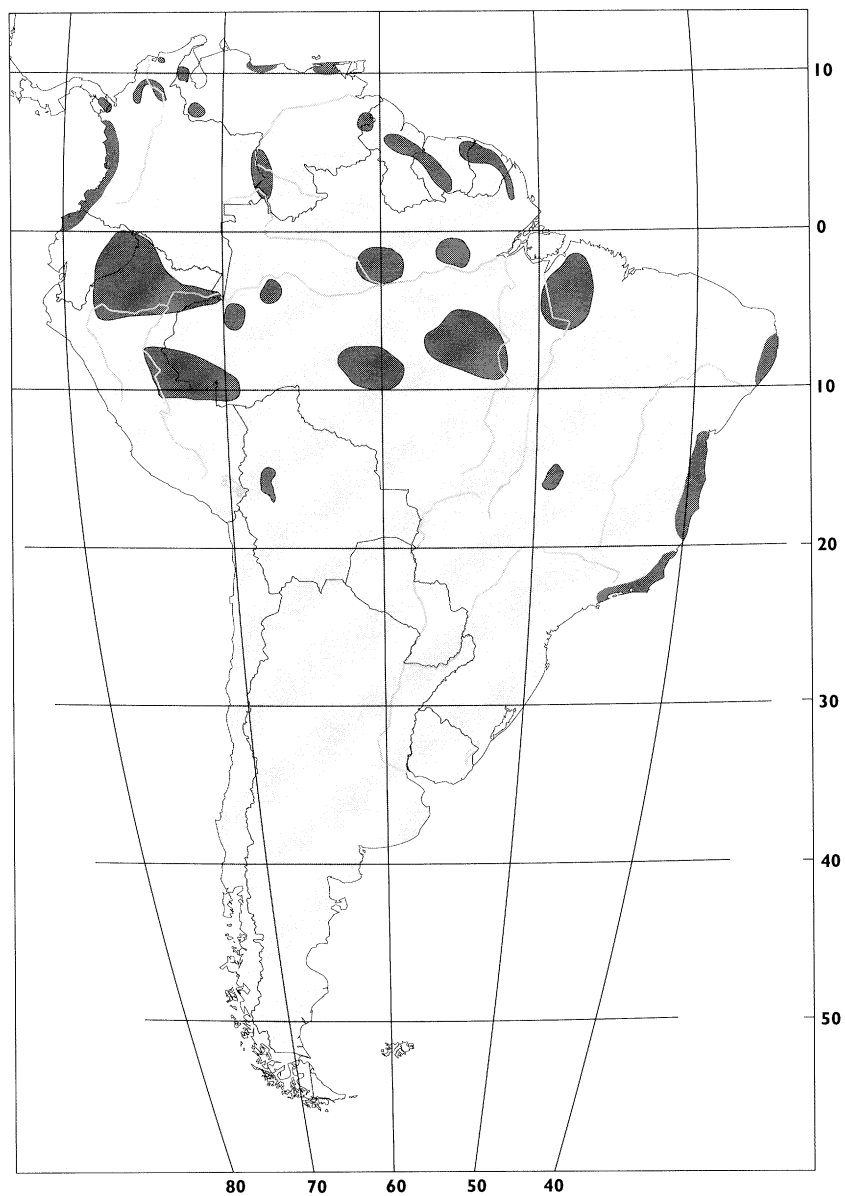


Figure 5. Centres of plant endemism in tropical south America (adapted from Prance 1982).

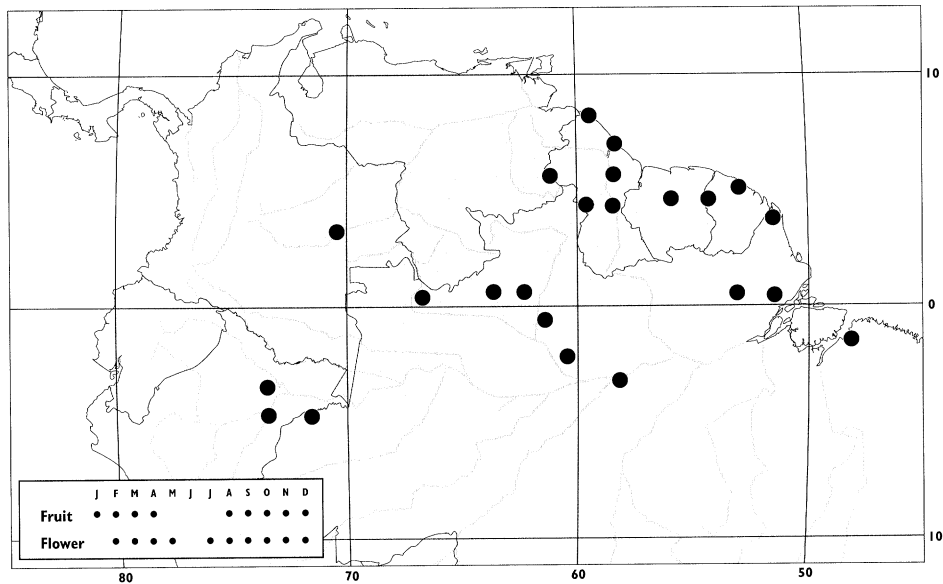


Figure 6. Distribution of *Couepia parillo* DC. with an eastern and western population probably separated by Pleistocene climate changes.

within the areas covered with rainforest (Prance 1973, 1982, 1987). These changes in vegetational cover over history have resulted in islands of rainforest which have been termed refugia. In many cases the refugia correspond with centres of endemism (figure 5) of forest organisms, for example, birds (Haffer 1969); insects (Brown 1976, 1987) and plants (Prance 1973, 1983, 1987). The reduction of the forest in this way has led to both extinctions and speciation through isolation in refugia. This expansion and contraction of forest has occurred four times over the last 60 000 years (Absy *et al.* 1991). Both the processes of isolation and of the dynamics of disturbance caused by changing vegetation have contributed to the biological diversity of lowland Amazonia. The forest, however, was certainly not reduced into neat discreet areas as depicted in many papers in refugia. It would have been much more like some of the contemporary savanna landscapes where there are also many small islands of forest and large areas of gallery forest along the waterways. In most work on refugia the importance of these corridors of gallery forest has often been ignored. The study of speciation and of the distribution of species (figure 6) in Amazonia must take into account the fact that the vegetation cover has oscillated several times between savanna and rainforest and that the rainforest has been in an island situation before its current wide distribution.

7. CONCLUSIONS

The various islands of different types of vegetation described above offer a diversity of habitats which greatly increase the total plant species diversity of Amazonia. These islands offer new niches for adaptation and many genera of plants have diversified by extending into each of the habitats. For example, in the genus *Caryocar* (Caryocaraceae) which is predominantly distributed in lowland Amazonia rainforest *C. brasiliense* Camb. is a savanna species, *C. gracile*

Wittm. is a species of Amazonian caatinga and *C. montanum* Prance occurs on the slopes of tepuis in the Guayana Highland.

Conservation planning for the region needs to focus not only on the rainforests but also on the small island habitats to preserve the maximum number of species.

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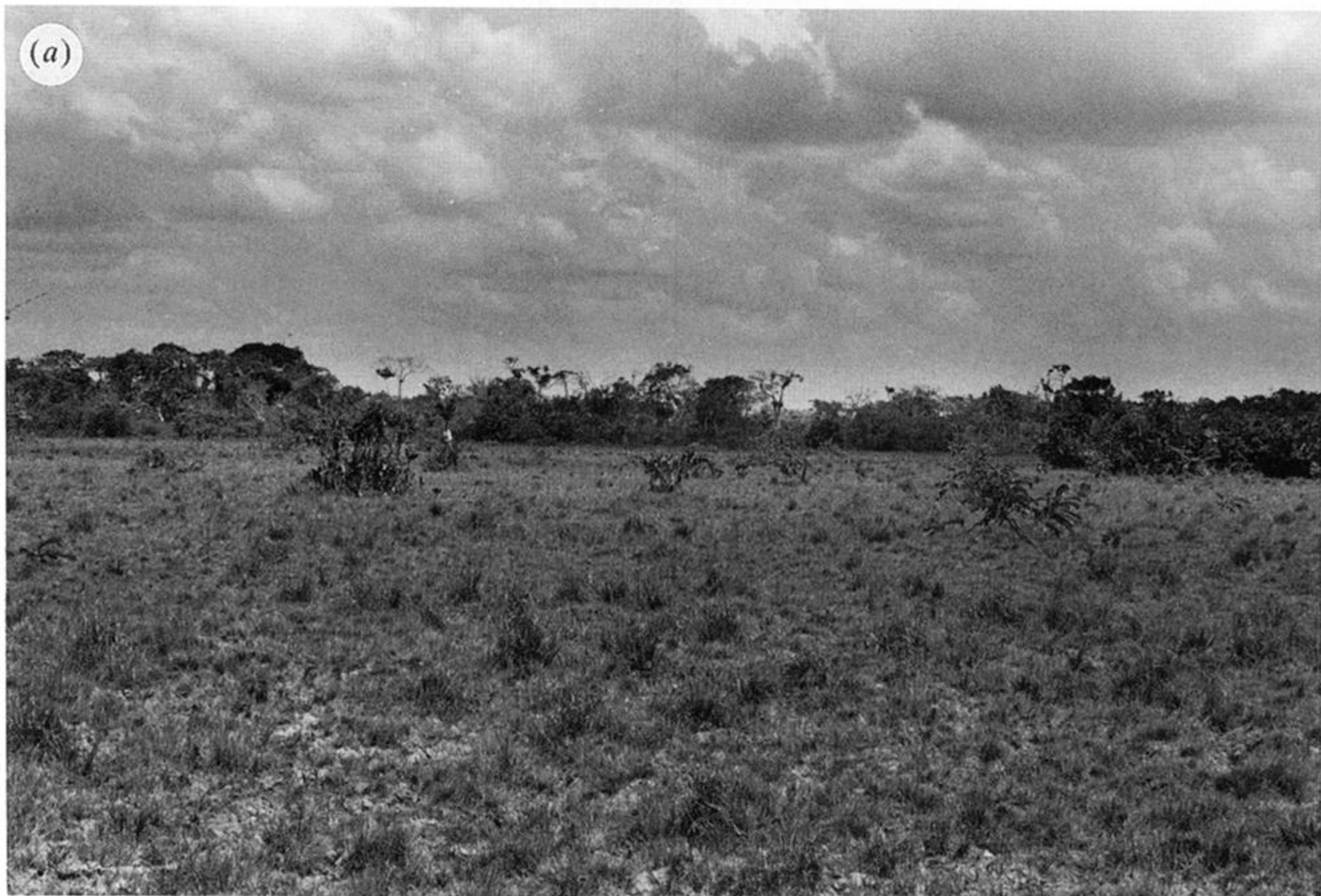


Figure 3. Top, an Amazonian savanna island at Humaitá, Amazonas; lower, general aspect of a white sand campina near to Manaus.



Figure 4. Top, a typical tepui, Kirun-tepui near to Canaima, Venezuela; lower, the plateau vegetation of Serra Araca a Brazilian tepui with a granitic dome in the background.

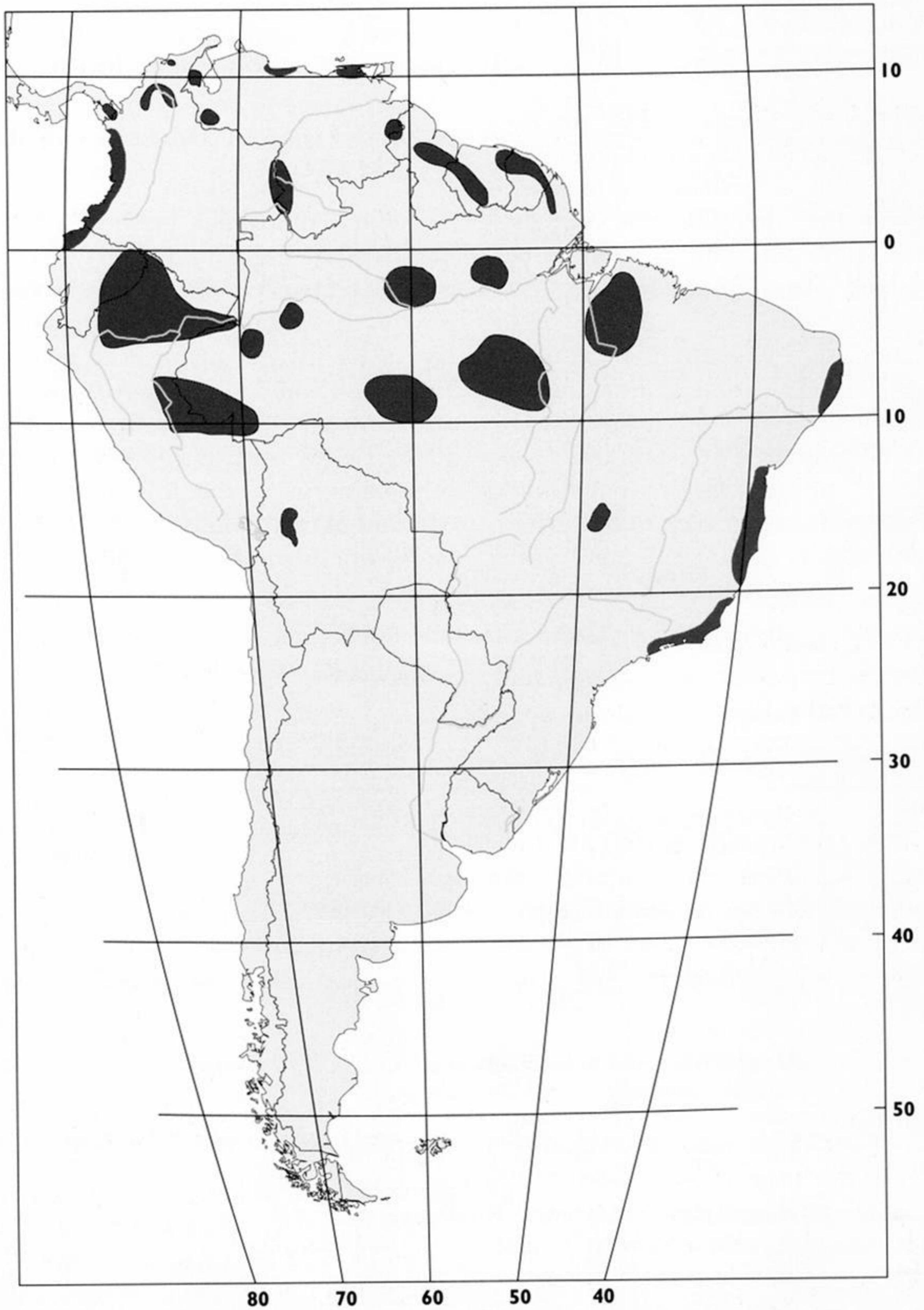


Figure 5. Centres of plant endemism in tropical south America (adapted from Prance 1982).

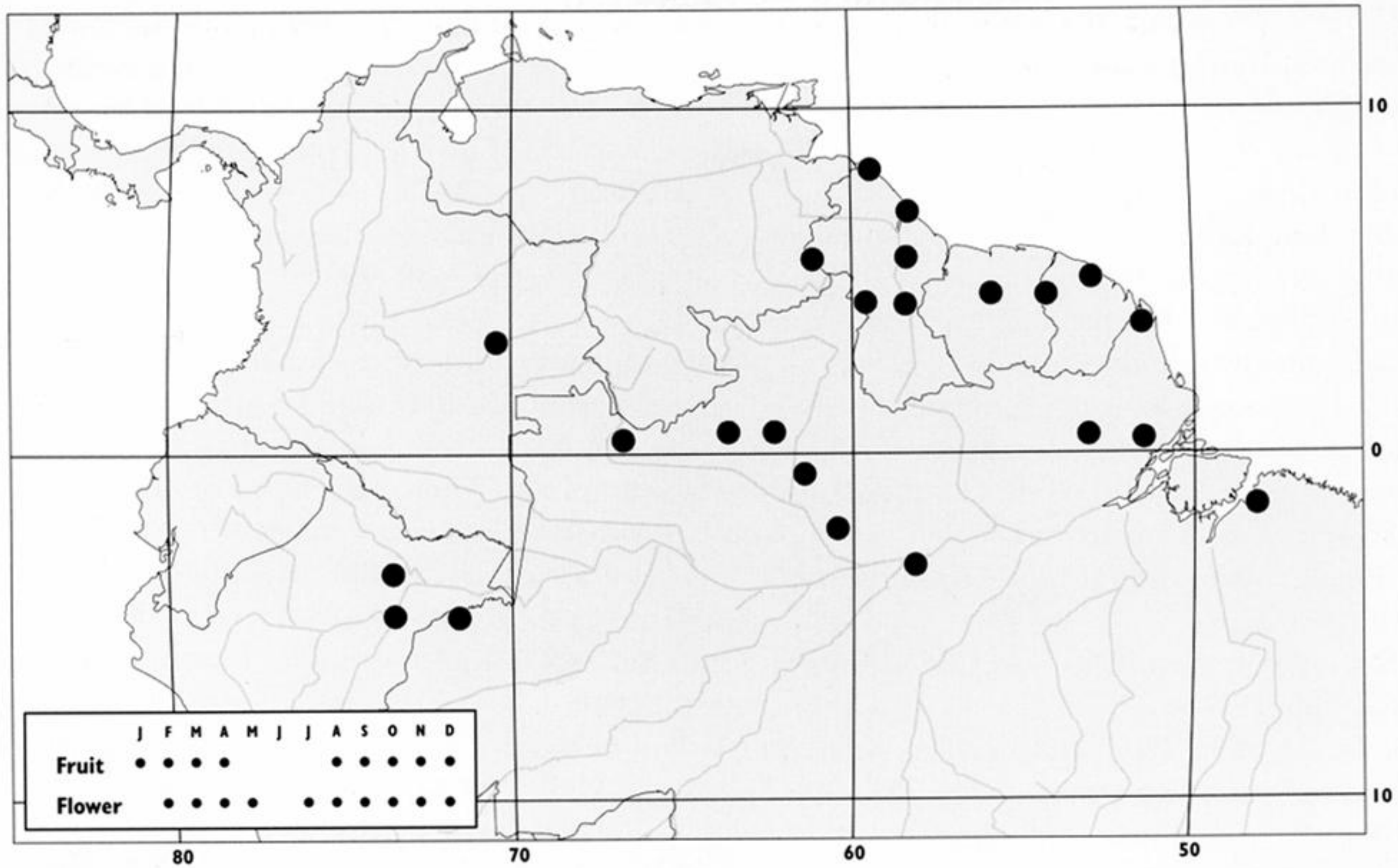


Figure 6. Distribution of *Couepia parillo* DC. with an eastern and western population probably separated by Pleistocene climate changes.