TAXON 37(3): 578–594. AUGUST 1988

PHYTOGEOGRAPHICAL CHARACTERISTICS OF THE GUIANAN FORESTS

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Summary

In a brief introduction to the Guianan area (location, geomorphology and climate), the author gives a short description of the main forest types occurring in the Guianas: upland moist forest, montane and lower montane forest, inundated forests, transition forests, and forests on white sand soils. Then, the distribution patterns of selected plant groups represented in the Guianan lowland forest region (Meliaceae, Caryocaraceae, Tabernaemontanoideae, Musaceae, Zingiberaceae, Arecaceae, Passifloraceae, *Lindsaea,* Ochnaceae) are analyzed. The endemism and floristic affinities of the Guianan forests are briefly discussed in relation to the theory of the South American forest refugia.

Résumé

Après une présentation de la région des Guyanes (situation, géomorphologie et climat), l'auteur donne une brève description de chacun des types de forêt existant dans les Guyanes: forêt humide tropicale sempervirente de l'intérieur, forêt de montagne et de basse montagne, forêts inondées, forêts de transition et forêts sur sables blancs. Dans un second chapitre, il analyse quelques modèles de répartition de différents taxons présents en forêt guyanaise (Meliaceae, Caryocaraceae, Tabernaemontanoideae, Musaceae, Zingiberaceae, Arecaceae, Passifloraceae, *Lindsaea,* Ochnaceae). L'endémisme de la région des hauts plateaux gréseux guyanais fait l'objet d'une courte discussion et les affinités floristiques des Guyanes sont données en relation avec la théorie des refuges forestiers en Amérique du Sud.

Introduction

The geographical unity of the three Guianas is derived from the presence of the Guiana Shield, a Precambrian eroded base, sweeping from the Orinoco Delta in Venezuela to the Amazon Delta, beyond Amapá, in Brazil. The political boundaries of the Guianas, however, limit the region, from east to west, to French Guiana (which is a French department), Suriname (formerly Dutch Guiana) and Guyana (formerly British Guiana). The latter two are now independent countries. The Guianas are situated between 1°15′ and 8°N, 57°10′ and 66°28′W (Map 1).

In the coastal zone, the Precambrian base is overlain by Quaternary marine silts forming the alluvial coastal plain or *lowlands.* This coastal plain, very narrow in French Guiana, is much wider in Guyana and Suriname. It has many vegetation types (mangrove, swamps, savannas, forests) but, as we will see elsewhere, the flora includes few endemics. Everywhere else in the interior zone or *uplands* or *inlands,* it is the bedrock of the Guiana Shield that gives the landscape its physiognomy, depending on the nature of the rocks: more or less undulating terrain or a multitude of hills isolated by the meshes of the hydrographic network. The soils are red, clayey and ferrallitic. In some places, the bedrock is overlain by continental, detritic, leached white sands where dry forests and savannas are found. Elsewhere, fragments of residual lateritic crusts overlying the Guiana Shield form tabular mountains which are remains of former peneplains. Their altitudes vary from 300 to 1200 m. The highest reliefs consist of old sandstones, the Roraima Formation or Guayana Highlands, which are superimposed on the Guiana Shield and are principally developed in Venezuela (tepuis), reaching 2800 m in Guyana (Mt. Roraima) and 3000 m in Venezuela

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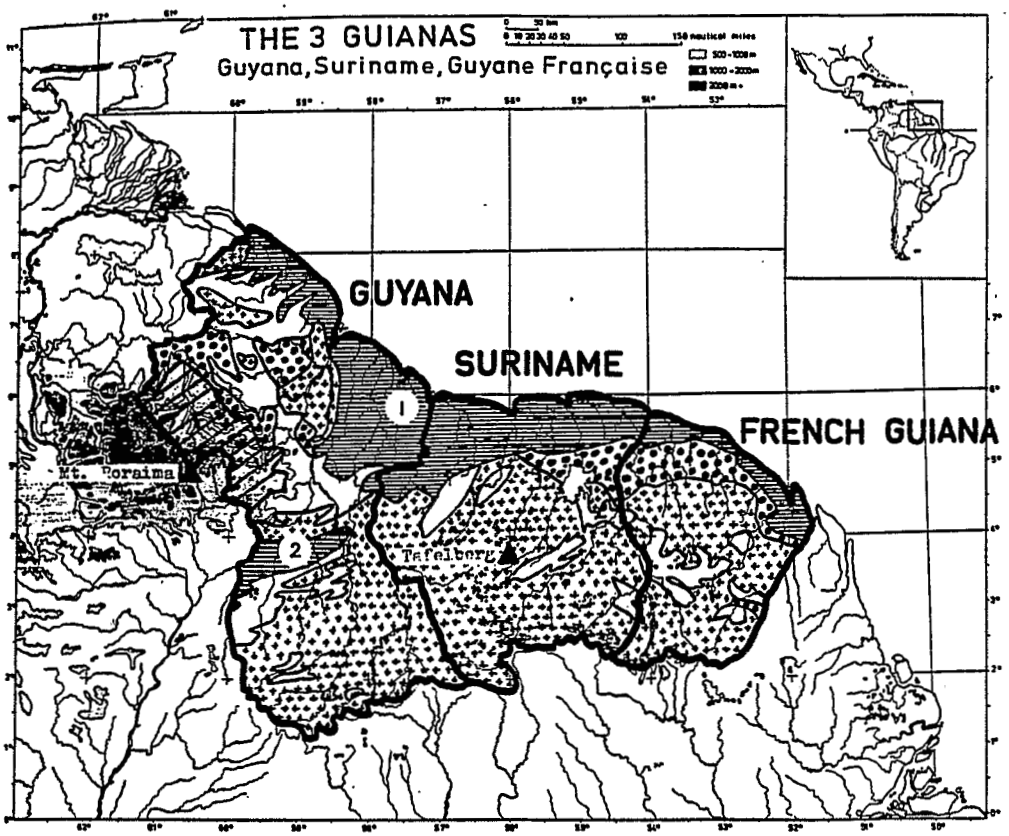

Map 1. Geologic formations and vegetation types in the Guianas. Lowlands: Horizontal hatching (1)—Alluvial coastal plain: mangrove, savannas, herbaceous swamps, marsh and swamp forests, transition forests. Horizontal hatching (2)—Roraima-Rupununi savannas. Uplands (or Inlands): Stippled—Schist, conglomerate, and quartzite of the Orapu-Bonidoro series: low rain forest on impoverished soils. Unshaded—Geosynclines of the Paramaca series: high rain forest on deep soils, submontane forest, forest on lateritic crusts. Crosses—Southern peneplain on crystalline base: medium-sized rain forest. Diagonal hatching—Guayana Highland: forests, scrubby vegetation, and savannas on sandstone table mountains.

(Cerro de la Neblina). Like the lateritic crusts, these mountains are relicts of more extensive mountain areas degraded by erosion after the Oligocene–Miocene uplift.

The climate of the Guianas is equatorial, hot and wet with a short dry season in March and a longer one from September to November. The average annual rainfall varies, depending on the locality, from 1500 to more than 4000 mm. The trade winds, which prevail all year long, blow from the southeast in the major dry season and from the northeast in the rainy season. The average annual air temperature is between 25° and 30°C at low altitudes. Temperatures may drop to 5°C at night on the tepuis.

The natural vegetation of the Guianas consists principally of tropical forests. In addition, there are savannas, both coastal and inland types (e.g., Donselaar, 1965; Hoock, 1971), the herbaceous swamps of the coastal plain (Lindeman, 1953) and herbaceous and shrubby vegetations of rocks (rocky shores, rock outcrops, stream boulders, etc.). The present paper focuses on the classification and phytogeography of the forests. The classification presented here is based on original observations and on previously published descriptions, in particular the recent papers by Prance (1979, in press) on the American tropical forests. We


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have also consulted the earlier works on forests of the region by Davis and Richards (1933, 1934), Beard (1944), Fanshawe (1952), Richards (1952) and Lindeman (1953).

The Classification of the Guianan Forests

The upland moist forest.—The upland moist forest is found in the interior of the region on the hilly Precambrian base, in contrast to the periodically or permanently flooded forests of the alluvial coastal plain. The upland moist forests of the Guianas are the equivalent of the "lowland tropical moist forest" of Prance (1979), the "lowland rain forest" of Richards (1952) and the "rain forest" of Fanshawe (1952).

Upland moist forest on ferrallitic soil: This evergreen forest type occurs from sea level up to 400–600 m. It is the most common and floristically richest forest formation of the Guianas, found everywhere on undulating terrain, on well drained soils, in areas with a rather uniform climate and an annual rainfall of more than 2000 mm. General characteristics of the upland moist forest are the presence of a high and dense canopy at 20–45 m and emergent trees up to 50–60 m. Species diversity is enormous (according to different authors, the tropical American lowland moist forests have between 100 and 300 tree species per hectare) and there is a correlation between higher rainfall and increasing diversity. The forest inventories carried out by ORSTOM, Cayenne, show a diversity of 746 trees over 15 cm in diameter for the whole of French Guiana (D. Sabatier, pers. comm.). In the uplands of Guyana, Davis and Richards (1953) recognized three different moist forest types and Fanshawe two associations, all based on species dominance (Table 1). The "mixed forest consociation" was considered the climatic climax of the lower Essequibo region of Guyana. We think, however, that a forest classification based on ecological features is more applicable to the entire region of the Guianas than a classification based on floristic data, because the Guianan flora varies from east to west, even under the same ecological conditions. Thus, we found that in French Guiana the upland forests on the basic lavas and gabbros of the Paramaca series are higher and richer in species than those occurring on conglomerates, quartzites or crystalline bedrock (see Table 1, Figs. 2, 3).

Upland moist forest on lateritic crusts: Occurring mainly on the top of the hills on basic rocks, this forest type is less species rich than the previous types, has a lower canopy, many lianas, and a scrubby understory (Fig. 1). Most of the forests on laterite are found at medium altitudes and resemble the lower montane forests.

Montane and lower montane moist forests.—Lower montane moist forest: The lower montane forests occur in the Guianas from approximately 400–600 m up to 1000–1300 m. Prance (in press) notices that "small changes in altitude can have extremely important changes in vegetation type, physiognomy, species composition and climate" and "there are many small patches of typically montane or cloud forests on small outcrops throughout the lowland region. Also the altitudinal limits of the different forest types vary considerably depending on local climate effects, soil, latitude etc. . . . ." These forests are scattered throughout the Guianas on the highest hills, often overlain by a lateritic crust (see above), reaching 860 m in French Guiana (Montagnes de l'Inini, Sommet Tabulaire) and 1200 m in Suriname (Juliana Top). They are wrapped in fog during the rainy season and also in the morning during the dry season. Mosses, liverworts and vascular epiphytes are abundant. Some species of trees seem to be dominant, especially trees with latex, depending on the

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Figs. 1–4. *1.* Liana forest, on lateritic crust. Mont Atachi Bacca, French Guiana, 1971. *2.* Evergreen moist forest with open canopy and understory dominated by *Astrocaryum paramaca* Mart. (Arecaceae). Saül, French Guiana, 1972. *3.* High evergreen moist forest on deep soil associated to the Paramaca series (basic lavas), with a closed canopy and an enormous *Terminalia amazonia* (J. F. Gmel.) Exell (Combretaceae). Saül, French Guiana, 1971. *4.* Swamp forest dominated by *Euterpe oleracea* Mart. (Arecaceae). Sommet Tabulaire, French Guiana, 1980.

Table 1. The upland moist forest types in the Guianas according to different authors.

Davis and Richards, 1933, 1934	Fanshawe, 1952	J.-J. de Granville, msc.
1. Mixed forest consociation	1. *Eschweilera-Licania* association	1. High rain forest on deep soils associated to the Paramaca series (gabbros, basic lavas)
2. Green heart consociation	2. *Eschweilera-Dicymbe* association	2. Low rain forest on impoverished soils, conglomerate and quartzite, associated to the Orapu and Bonidoro series
3. Morabukea consociation		3. Rain forest on soils associated with the crystalline base

localities: each tabular summit has its own characteristics (Figs. 5, 6). Prance points out that, in the montane formations, the tendency towards dominance accompanies the loss of species diversity in angiosperms.

Montane moist forest: The montane moist forest occurs in the Guianas only on the slopes of the higher tepuis of the Guayana Highlands in western Guyana, e.g., on the north slope of Mt. Roraima at altitudes of 1200–1600 m (Gradstein, 1986) (Fig. 8). The forest is very rich in ferns and bryophytes and holds phytogeographic ties with the montane forests of the northern Andes. The vegetation of the tepuis of western Guyana is still poorly known (see also the contributions by Huber and Prance and Campbell, this symposium). Some tepuis are covered with dense, high forests, others have more open and scrubby vegetation except for the gallery forests along the streams. On the summit plateaus the forest vegetation is usually replaced by open savanna and swamp formations.

Inundated forest.—The various classifications of inundated forests proposed by the botanists show how difficult it is to divide these forests into well defined types. Although all these classifications are based on the duration of the flood, the limits between the permanently and the periodically flooded forest types seem unclear (Table 2).

Permanent swamp forest: The "permanent swamp forest" of Prance corresponds roughly to the "swamp forest" of Beard (1944), Fanshawe (1952) and Lindeman (1953). However, the permanent swamp forests are said to be dominated by palms when, according to the others, true permanent swamp forests have only a few palms, the latter occurring principally in periodically flooded forests. We consider that palms can be found in both types but only a few species, including *Euterpe oleracea* and *Mauritia flexuosa,* tolerate permanently flooded soils (Fig. 4). Trees commonly found in these forest types are *Triplaris surinamensis* and, in Guyana, *Mora excelsa.* The permanent swamp forests occur generally on recent coastal and subcoastal marine alluvia, on low ground behind natural levees.

Periodically flooded forest: The "periodically flooded forest" of Prance (1979, in press) corresponds to the "marsh forest" of Lindeman (1953) and includes mangrove forests, flooded daily by the tide, and some other forest types (Table 2). The mangrove forest can be divided into two types: 1) the "coastal mangrove," very poor in species and consisting of *Avicennia nitida.* It is a pioneer and unstable vegetation linked to the moving of the silt banks from the east to the west; 2) the "estuary mangrove," where *Rhizophora racemosa*

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Figs. 5–8. *5.* Montane forest with high trees, on ferrallitic soil. Mont Galbao, French Guiana, 1986. *6.* Montane forest with *Borreria alata* (Aubl.) DC. (Rubiaceae) layer in the understory. Mont Galbao, French Guiana, 1986. *7.* Low transition forest on crystalline base with Myrtaceae cover and *Calathea propinqua* (Poepp. & Endl.) Koern. (Marantaceae) layer in the understory. Mitaraka, Tumuc-Humac, French Guiana, 1972. *8.* The Guayana Highlands: northern side of Mount Roraima, Guyana, 1985 (photograph by R. Gradstein).


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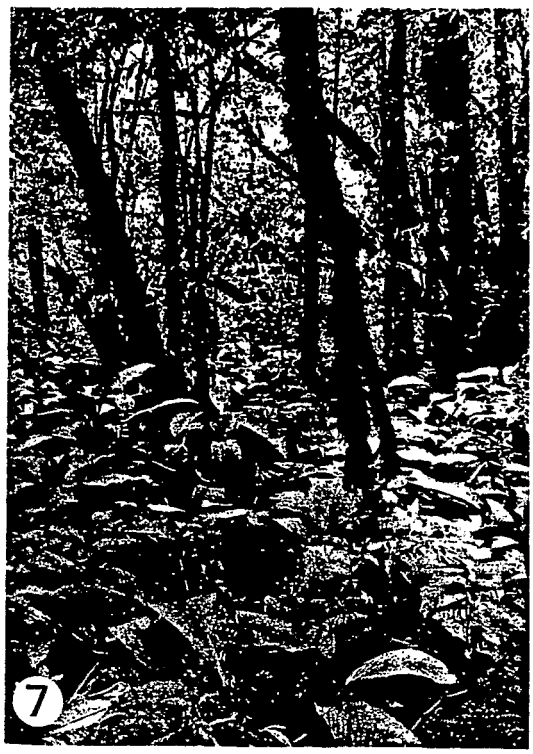
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Table 2. The inundated forest types in the Guianas according to different authors.

Beard, 1944; Fanshawe, 1952	Lindeman, 1953	Prance, in press
A. Marsh forest	A. Marsh forest	A. Periodically flooded forests
1. Palm marsh forest	1. *Triplaris surinamensis-Bonafousia tetrastachya* type	1. Mangrove forests
2. Marsh forest	2. *Symphonia globulifera* type	2. Tidal swamp forest (tidal varzea)
3. Marsh woodland	3. *Hura crepitans* forest	3. Seasonal swamp forest (seasonal varzea)
4. Palm marsh	4. *Mauritia-Chrysobalanus* association	4. Flood plain forest
B. Swamp forest	B. Swamp forest	B. Permanent swamp forests
1. *Mora* forest	1. Mixed swamp wood	C. Gallery forests
2. Swamp forest	2. *Machaerium lunatum* scrub	
3. Swamp woodland		
4. Mangrove forest		

Table 3. The evergreen seasonal forest types in the Guianas according to different authors.

Lindeman, 1953	Prance, in press
1. *Cereus* ridge wood	1. Open forest
2. Intermediate ridge forest	2. Liana forest
3. Typical evergreen seasonal forest	
4. Parinari ridge forest	
5. Forest on the ridges near Coronie	

is dominant. The other periodically flooded forests are divided by Prance into "tidal swamp forest" near the coast and "seasonal swamp forest" along the muddy water rivers, whereas Lindeman distinguishes four types based on floristic composition. *Virola surinamensis* and *Symphonia globulifera* are, with the palms, the most characteristic species. Lastly, Prance (1979, in press) mentions the "flood plain forest," commonly found along the creeks and flooded by quickly draining flash floods. In spite of a lower species diversity, it is rather similar to the rain forest on well drained soils.

Gallery forests: The gallery forests are found along water courses in the Roraima-Rupununi savannas. *Mauritia flexuosa* is frequent in this forest type.

Transition forests.—According to Prance (1979, in press), transition forests are intermediate between the tall rain forests and the open areas. They may correspond to the "seasonal forests" of Beard (1944) and Fanshawe (1952), which occur on well drained soils in areas with a more pronounced dry season, generally on subcoastal and coastal sandy alluvia (Table 3).

Evergreen seasonal forest: From the beach to the interior in Suriname, the forests increase in species diversity and the canopy becomes progressively higher. Lindeman (1953) distinguishes four types of evergreen seasonal forest in the coastal plain of Suriname (Table 3). The "typical evergreen seasonal forest" is the most common one. Some upland areas have transition forests as well, like the scrub forests of the granitic outcrops (Fig. 7), the open forests at the margins of the Gran Sabana and the liana forests found especially near Mt. Roraima.

Semi-evergreen seasonal forest: The "semi-evergreen seasonal forest" of Fanshawe (1952) corresponds to the "dry forest" of Prance (1979, in press) with high deciduous trees and evergreen treelets in the understory. This forest type is found only in the western region of the Guianas with a more seasonal and much drier climate.

Forests on white sand soils.—The "forests on white sand soils" (Prance, 1979, in press) or "dry evergreen forests" (Beard, 1944; Fanshawe, 1952) or "savanna forests" (Lindeman, 1953) are generally found on former sea beaches, near the coast. They occur also on leached continental sands and sandstones and include: 1) *the wallaba forest,* an important facies with dominance of *Eperua falcata* and *Eperua rubiginosa,* occurring mostly in Guyana and western Suriname on leached continental white sands, and 2) *the "xeromorphic rain forest, woodland and scrub,"* which are progressively more open and lower formations, the latter two included by Lindeman (1953) in the "savanna forest." All are characterized by the presence of more or less tortuose trees with coriaceous small leaves. *Humiria balsamifera* is often dominant, as well as *Humiria floribunda, Clusia nemorosa,* and *Clusia fockeana.*

The Forest Flora: Some Distribution Patterns and Floristic Affinities

In his study on the American tropical forests and their phytogeography, Prance (in press) discerns 18 "phytochoria." A phytochorion is an area with 50% or more of the species confined to it and with a total of more than 1000 endemic species (White, 1979). The phytochoria, based on the distribution of the species, are more or less equivalent to the "regions" in the sense of Engler (1964). Two of the eighteen tropical American forest phytochoria concern the Guianas: 1) the "Guiana-Eastern Amazonian Regional Center,"

which includes the Amazon delta plus parts of Pará, Amapá, French Guiana, Suriname and Guyana except its western border; and 2) the "Guayana Highland Region," particularly well represented in Venezuela south of the Orinoco, but including also the western part of Guyana. As it is impossible to give a good account of the entire flora of such complex formations in just a few pages, we will limit ourselves to some remarks about the floristic affinities, based on an analysis of selected plant groups.

The Guiana-Eastern Amazonian Regional Center.—This is essentially a lowland region, covered by many vegetation types but mostly by tropical moist forest. The coastal areas (marine alluvia) have a rather poor flora, comprised mainly of widespread species able to colonize new and highly dynamic habitats such as mangroves, beaches, subcoastal herbaceous swamps, swamp and marsh forest, coastal savannas, and seasonal ridge forests. Endemic species are infrequent. The interior uplands have a much more diversified flora in terms of phytogeographic affinities and distribution types.

In what follows, we will examine the distribution of the Guianan species of eight plant groups occurring particularly in forests: two families of trees of the canopy (Meliaceae, Caryocaraceae), one group of shrubs of the understory (Apocynaceae subfamily Tabernaemontanoideae), the palms (Arecaceae), two families of herbs (Musaceae, Zingiberaceae), one family of lianas (Passifloraceae) and one genus of ferns (*Lindsaea*). These data are summarized in Map 4.

Meliaceae (data from Pennington, 1981)

Thirty-one of the 120 American species (26%) occur in the Guianas. Their distribution can be linked to the following groups:

Eleven species (35%) are widespread in South and Central America or in northern South America.

Eleven (35%) are confined to the Guianas and the Amazon Basin.

Two are "periamazonian": *Guarea macrophylla* subsp. *pachycarpa* in the Guianas, Peru, Bolivia and Atlantic coast of Brazil and *Trichilia martiana* in the Guianas, northern Venezuela, West Indies, Colombia and the Atlantic coast of Brazil.

One is found in Central America, northern Venezuela and Colombia and in the Guianas: *Carapa guianensis.*

Three occur in the Guianas and in the central (*Carapa procera*) or lower Amazon Valley (*Trichilia lecointei* and *Trichilia surinamensis*).

Three species are endemic to the Guianas: *Guarea costata, Trichilia lepidota* subsp. *leucastera* and *T. surumuensis.* Only the latter seems to be confined to the Guayana Highlands.

Caryocaraceae (data from Prance and da Silva, 1973)

Seven of the 23 species occurring in tropical America (30%) grow in the Guianas:

None of them is a widespread species.

Three are found in the Guianas and the Amazon Basin.

Four are endemic to the Guianas: *Anthodiscus trifoliatus, Caryocar nuciferum,* and, exclusively on the Roraima sandstones, *Anthodiscus mazarunensis* and *Caryocar montanum.*

Apocynaceae subfamily Tabernaemontanoideae (data from Allorge, 1985)

Fifteen of the 89 tropical American species (17%) occur in the Guianas:

Four (27%) are widespread species.

One occurs in Central America and in an area from northern Venezuela and Colombia to the Guianas: *Stemmadenia galeottiana.*

Two are periamazonian species: *Anartia meyeri* in Pará (Brazil), the Guianas, Venezuela,

Trinidad and Amazonian Colombia. *Anartia olivacea* has a typical periamazonian distribution, from Pará to Peru through the Guianas and Venezuela. It grows also on the Atlantic coast of Brazil.

One is found in the Guianas and eastern Amazonia: *Bonafousia rupicola.*

Seven (46%) are endemic to the Guianas. Six of them belong to the genus *Bonafousia*: *B. albiflora, B. angulata, B. disticha, B. lorifera* (also once found near Manaus), *B. macrocalyx,* and *B. morettii. Anartia cerea* is confined to the Guayana Highlands.

Musaceae (data from Maas, 1985a)

Sixteen of the 100 species growing in tropical America (16%) occur in the Guianas:

Six (30%) are widespread tropical American species. Four of them are rain forest species and the three others are found in open places and secondary forest.

Two species occur in northwestern South America: *Heliconia bihai* and *H. stricta.*

One grows in the Guianas, Amazonian Brazil, Venezuela, Colombia, Ecuador, and Peru: *H. chartacea.*

Two species are more or less periamazonian: *H. densiflora* is distributed in northern South America and the southwestern Amazon Basin to Peru and Bolivia and *H. lourteigiae* occurs in Peru, Colombia, northern Amazon Basin and the Guianas.

Three species are confined to the Guianas and the eastern Amazon Basin: *H. acuminata, H. pendula,* and *H. richardiana.*

Two species only are endemic to the Guianas: *H. dasyantha* and *H. nickeriensis.*

Zingiberaceae (data from Maas, 1985b)

Twenty-one of the 125 tropical American species (16%) are found in the Guianas:

Six of them (30%) are widespread species.

Five (25%) are northwestern South American species.

Two occur in Central America, northern Venezuela and Colombia: *Costus guanaiensis* and *C. villosissimus.*

Three are found in the Guianas and eastern Amazon Basin: *Costus congestiflorus, C. lanceolatus,* and *Renealmia guianensis.*

One grows in northern South America from Venezuela to French Guiana: *Renealmia orinocensis.*

Four (20%) are endemic to the Guianas: *Costus claviger, C. curcumoides* (restricted to French Guiana), *C.* aff. *erythrothyrsus,* and *Renealmia thyrsoidea* subsp. *chrysantha.*

Arecaceae

Eighty-nine of the 1160 American species (8%) occur in the Guianas. Among 80 Guianan species of which we could study the distribution:

Twenty-five (31%) are widespread in northern South America. Six of them grow in open places (mangrove, savannas, secondary vegetation), the others are primarily forest species.

Twenty are confined to the Guianas and the Amazon Basin.

Four are periamazonian: *Bactris* cf. *cuspidata, Geonoma euspatha, G. interrupta,* and *G. triglochin.*

Thirty-one (39%) are endemic to the Guianas: *Acrocomia lasiospatha, Asterogyne* sp. nov., *Astrocaryum* sp. nov., *Bactris* sp. nov. 1 aff. *B. acanthocarpoides, B. aubletiana, B. rhaphidacantha, B.* sp. nov. 2, *B.* sp. nov. 3, *Euterpe stenophylla, Geonoma bartlettii, G. oldemanii, G. poiteauana, G. stricta, G.* "*stricta* × *pycnostachys,*" *G.* sp. nov., *Jessenia bataua* subsp. *oligocarpa, Lepidocaryum guianense, Maximiliana macropetala, Scheelea camopiensis, S. degranvillei, S. guianensis, S. maripensis, S. passargeri,* and *Syagrus stratincola.* Seven species are found only in the Guayana Highlands: *Bactris ptariana, B. ulei, Euterpe aurantiaca, E. roraimae, E. tenuiramosa, Geonoma appuniana,* and *G. fusca.*

Passifloraceae (data from Feuillet, 1986)

Fifty-four of the 400 American species (13%) occur in the Guianas:

Ten (18%) are widespread species.

Six (11%) are found in the Guianas and the Amazon Basin.

One is confined to the coastal area of the Guianas, Venezuela and Colombia: *Passiflora foetida* var. *moritziana.*

Two species occur in the Guianas and northeastern Brazil: *Passiflora glandulosa* and *P. nitida.*

Three can be linked to the "periamazonian" group: *Mitostemma glaziovii* occurs both in the Guianas and on the Atlantic coast of Brazil, *Passiflora riparia* in the Guianas and eastern Peru, and *P. costata* in the Guianas, Amazonian Peru and Brazilian Atlantic coast.

Thirty-two species (59%!) are endemic to the Guianas: *Dilkea magnifica, Mitostemma jenmanii, Passiflora acuminata, P. amicorum, P. bomareifolia, P. candida, P. capparidifolia, P. cardonae, P. ceratocarpa, P. cirrhiflora, P. citrifolia, P. crenata, P. deficiens, P. fanchonae, P. fuchsiiflora, P. garckei, P. gleasoni, P holtii, P. laurifolia, P. leptopoda, P. lonchophora, P. longiracemosa, P. maguirei, P. nuriensis, P. ovata, P. pachyantha, P. phaeocaula, P. picturata, P. plumosa, P. quelchii, P. retipetala, P. rufostipulata, P. sclerophylla, P. securidata, P. stipulata,* and *P. stoupyana.*

Dennstaedtiaceae, genus Lindsaea (data from Cremers, pers. comm. and Kramer, 1957)

Twenty-seven of the tropical American species and subspecies (60%) of the genus *Lindsaea* occur in the Guianas:

Four are widespread in South and Central America and generally also in the Caribbean Islands.

Two are found in northwestern South America.

Two are more or less periamazonian: *L. coarctata* from Guyana, eastern Colombia and coastal Brazil, *L. ulei* from Guyana, Venezuela and southwestern Amazon Basin.

Eight species (30%) have an area limited to the north of the Amazon Basin (Guianas, southern Venezuela and Colombia, northern Brazil). They could also have been classified as periamazonian but they have a more restricted area. These are: *L. cyclophylla, L. dubia, L. javitensis, L. lancea* var. *elatior* and var. *leprieurii, L. pendula, L. semilunata, L. sphenomeridopsis,* and *L. surinamensis.*

Two are found both in the Guianas and the Amazon Basin.

Two species are confined to the Guianas and the eastern Amazon Basin: *L. schomburgkii,* and *L. lancea* var. *remota.*

Two species grow in the Guianas and the Caribbean Islands: *L. quadrangularis* subsp. *antillensis* and *L. stricta* var. *jamesoniiformis.*

Five (19%) are endemic to the Guianas: *L. parkeri, L. reniformis, L. sagittata, L. pleioptera,* and *L. tenuis.* Only the latter two are exclusively confined to the Guayana Highlands.

Discussion

Our study of the distribution patterns of 251 Guianan species in eight plant groups (Table 4) shows that the three most important phytogeographic elements are respectively the *endemic species* (35%), the *widespread species* (26.3%) and the *Guianas-Amazonian Basin species* (17.1%). The endemism varies depending on the taxa, from 12.5% (Musaceae) to 59.2% (Passifloraceae). Although it would be dangerous to generalize without studying more taxa, the rather high endemism seems to confirm the hypothesis of the existence of one or several centers of endemism in the Guianas. Furthermore, it appears that the forest flora of the Guianas has more affinities with the adjacent Amazonian Basin than with other regions. This is not surprising taking into account the absence of geographical barriers between the two regions.

Table 4. Distribution patterns of the Guianan species for eight groups of vascular plants occurring mostly in forests.

Types of distribution patterns											Endemic to the Guianas 	TOTAL
MELIACEAE	11		1			2		11		3	3 (9.7 %)	31
CARYOCARACEAE								3			4 (57.1 %)	7
Tabernaemont.	4		1			2				1	7 (46.7 %)	15
ARECACEAE	25					4		20			31 (38.7 %)	80
MUSACEAE	6	2				2		1	3		2 (12.5 %)	16
ZINGIBERACEAE	6	5	2				1		3		4 (19.0 %)	21
PASSIFLORACEAE	10			1		3		6	2		32 (59.2 %)	54
Lindsaea	4	2			2	2	8	2	2		5 (18.5 %)	27
TOTAL	66	9	4	1	2	15	9	43	10	4	88	251
%	26.3 %	3.6 %	1.6 %	0.4 %	0.8 %	6.0 %	3.6 %	17.1 %	4.0 %	1.6 %	35.0 %	

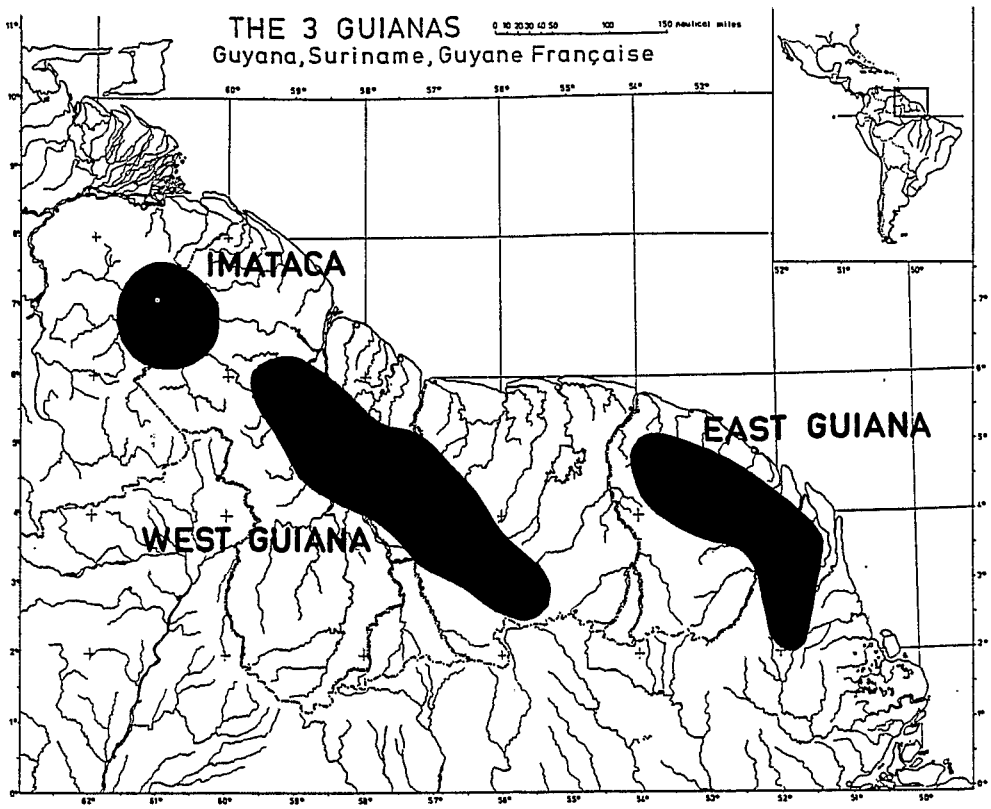
A fourth group of interest are the *periamazonian species* (6%), which occur in the Guianas, southern Venezuela, Colombia, eastern Peru and sometimes Bolivia. Some of them occur also on the Atlantic coast of Brazil. In the Guianas, these plants are generally found on the highest hills, in low montane forest or in cloud forest rather than in the valleys. Examples we can mention are: *Hyptis pachycephala* (Lamiaceae), *Anomospermum chloranthum* subsp. *confusum* (Menispermaceae), *Dichorisandra* sp. nov. (Commelinaceae), *Mouriri oligantha* (Melastomaceae), *Tassadia guianensis* (Asclepiadaceae), all occurring both in the Guianas and eastern Peru; *Costus* aff. *erythrothyrsus* (Guianas) is closely related (may be conspecific) to *C. erythrothyrsus* (Peru); *Couepia parillo* (Chrysobalanaceae) is present in Amapá, the Guianas, eastern Colombia and Peru; *Geonoma triglochin* (Arecaceae) occurs in the Guianas but also in Venezuela, Colombia, Peru, and Brazil except in the Amazon Basin; *Geonoma euspatha* is found in the Guianas, Venezuela and Colombia; and *Cyathea lasiosora* (Cyatheaceae) grows in the Guianas and from Venezuela to northern Bolivia.

The Guayana Highland Region.—The Guayana Highland Region is first of all characterized by a very rich and highly endemic flora. According to Maguire (1970), the total vascular flora would be "in magnitude of 8000 species of which considerably more than 50% are endemic." Recent studies by Steyermark (1982) indicate that the proportion of endemism in the Guayana Highlands was much overestimated and that species endemism varies, depending on the tepuis, from 5.3% to 63%. At the generic level, 39 genera (8.5%) appear to be strictly endemic to the summits of the sandstone table mountains and 40 additional genera are endemic to the surrounding area (bluffs, slopes, and the Gran Sabana), totalling 17.2%.

The families well represented in the Guayana Highland Region are not generally the same as the predominant ones in the Guianas-Eastern Amazonian Regional Center. The Leguminosae, for instance, are better represented in the lowland forests whereas certain herbaceous and shrubby groups are more diversified in the Highlands. Only one family seems to be endemic to the Highlands region, the monogeneric Tepuianthaceae (Maguire and Steyermark, 1981).

The relationships between the Guayana Highlands flora and the flora of the lower altitude forests, principally of the Guianas and Amazonia, has been discussed by Steyermark (1982). He distinguishes between constituents of autochthonous origin and those, more recently evolved, originating from Amazonian centers.

One example of plant groups well represented on the tepuis and also found in the Guianas



Map 2. Proposed forest refuges (black) in the Guianas, as based on distribution of woody angiosperm families (Prance, 1982).

is discussed below. For further details concerning plant groups of the tepuis we may refer to Huber's contribution to this Symposium.

Ochnaceae (data from Maguire, 1970)

The family is represented in the Guayana Highland Region by 10 of the 16 known genera. Five genera are endemic to the summits of the tepuis: *Adenanthe, Adenarake, Leitgebia, Philacra,* and *Poecilandra.* Three genera are found in the Guianas: *Elvasia, Ouratea,* and *Sauvagesia.*

The distributions of the 15 species of *Sauvagesia* (data from Sastre, 1971, 1984) occurring in the Guianas indicate that:

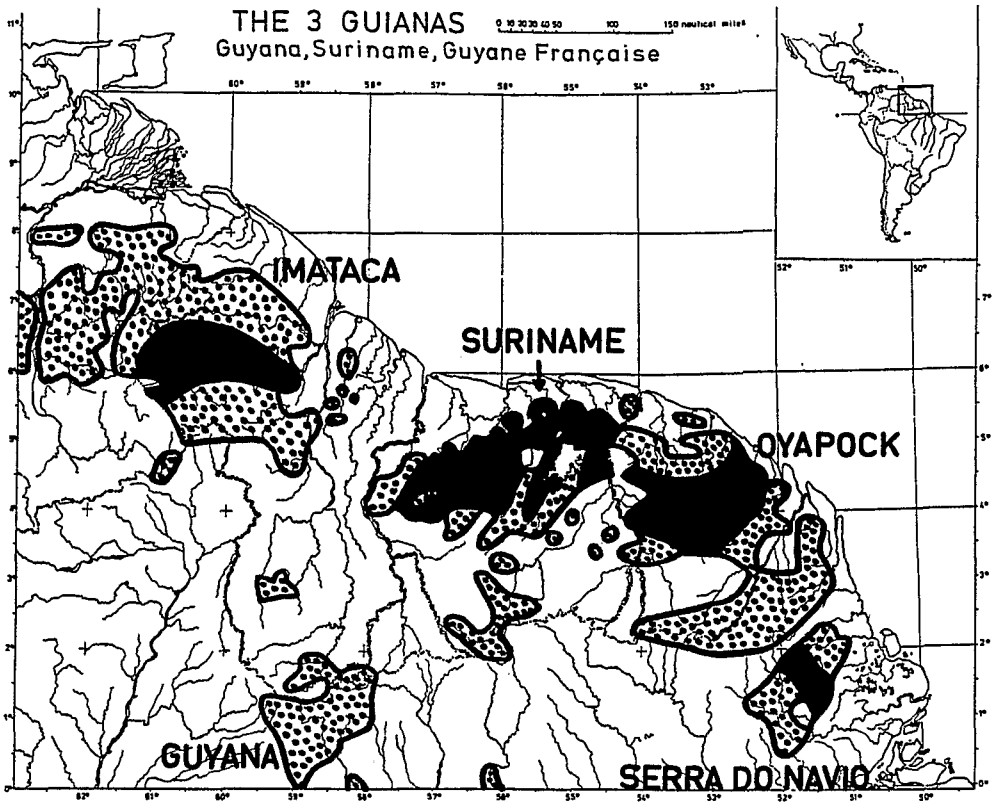
Fifty percent of the 30 American species are found in the Guianas.

Only three (20%) are widespread species growing in wet sandy savannas of northern South America, often Central America and Caribbean Islands.

One species occurs in Colombia, Venezuela, the Guianas and in northern Amazon Basin: *S. ramosissima.*

Four species (26%) are found in the Guianas and in the northeastern Amazon Basin: *S. elata* and *S. longifolia* are species of forest clearings, *S. rubiginosa* and *S. sprengelii* are savanna species. The latter is found also along the Brazilian coast.

Seven species (46%) are endemic to the Guianas. *S. guianensis, S. imthurniana, S. roraimensis* and *S. longipes* are endemic to the Guayana Highland Region, at altitudes higher than 1000–1500 m. *S. tafelbergensis* occurs at lower altitudes both on Roraima sandstone and on granitic outcrops in Suriname and French Guiana. *S. aliciae* subsp.



Map 3. Proposed forest refuges in the Guianas (areas of high probability for stability of tropical forest over the last 20,000 years), as determined by summation of data from geomorphology, paleoclimate, soils and vegetation types. Dotted areas: 60% probability; black areas: 80–100% probability (Brown, 1982).

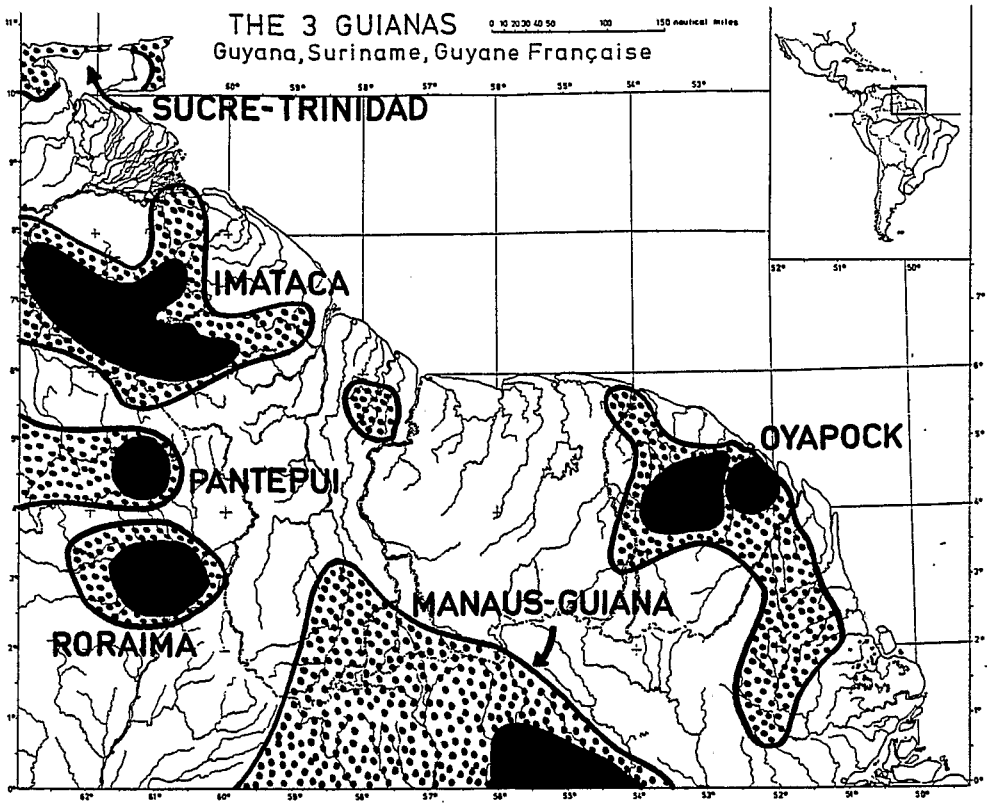
aratayensis grows on granitic outcrops of French Guiana and *S. angustifolia* is a species of the Gran Sabana, between 500 and 1500 m.

The widespread species of *Sauvagesia* grow in savannas and in open places at low altitudes while the endemic species occur in montane or submontane areas. Moreover, according to Sastre (1971, 1984), the endemic species are generally shrubs whereas the widespread ones are always annual herbs. Most of the Guianan species supposedly evolved during the Oligocene with the uplift of the Guiana Shield, which has been the main center of differentiation of the genus.

Conclusions

The vegetation of the Guianas is constituted primarily of tropical forests differentiated into many types, depending on the nature of the bedrock, the soils, the drainage conditions, the local climate and also on the paleohistory of the region. The forest types may furthermore be characterized by their floristic composition, but in relatively limited areas only, not throughout the Guianas. Analysis of species distributions on a continental scale provides useful information, especially on general endemism in the Guianas, which is rather high.

Analyses of species distributions within the Guianas might be particularly rewarding for tracing centers of endemism in the region, but are still hazardous because of the very



Map 4. Centers of endemism in the Guianan forests, as based on subspecific differentiation in Heliconiini and Ithomiinae (aposematic butterflies). Dotted areas: ⅓ of maximum isoline; black areas: ⅔ of maximum isoline (Brown, 1982).

incomplete floristic inventory. As a consequence, centers of species diversity and endemism may simply coincide with well prospected regions (usually the easily reached areas!).

Nevertheless, some areas seem to be really more species-diverse and to harbor more endemic species than others. These areas are presumed to coincide with the forest refuges that existed during the dry periods of the late Pleistocene and the Holocene. Patterns of forest refuges in South America have been proposed by several scientists, especially Haffer (1969), Vanzolini and Williams (1970), Morley (1975), Prance (1973, 1982a, b), and Brown (1979). The results of the last two authors, whose investigations are more recent and detailed, agree with the hypothesis of at least three centers of endemism in the Guianas (Maps 2, 3, 4), correlated with past forest refuges. Though the proposed sizes and shapes of these refuges vary according to author, their distribution is rather similar and in agreement with the one we proposed for French Guiana (Granville, 1982). Moreover, the periamazonian disjunct species distributed in isolated populations, especially in the Guianas and in eastern Peru (and also, in a lower proportion, along the Atlantic coast of Brazil), fit rather well with the other proposed forest refuges and seem to be remnants of former continuous populations in tropical South America, which became dissected by the forest recessions. However that may be, the floristic inventory has to be continued intensively, especially in the southern part of Guyana, in order to confirm or to modify these hypotheses and to arrive at a better estimation of the endemism and interrelationships of the Guianan forest refuges.

Acknowledgments

The author is much indebted to Dr. S. Rob Gradstein for correcting and improving the English text.

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