Lowland Vegetation of Tropical South America -- An Overview

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[modified from this reference:]
Daly, D. C. & J. D. Mitchell 2000. Lowland vegetation of tropical South America -- an overview. Pages 391-454. In: D. Lentz, ed. *Imperfect Balance: Landscape Transformations in the pre-Columbian Americas.* Columbia University Press, New York.

Contents

Introduction

Tropical lowland South America boasts a diversity of vegetation cover as impressive -- and often as bewildering -- as its diversity of plant species. In this chapter, we attempt to describe the major types of vegetation cover in this vast region as they occurred in pre-Columbian times and outline the conditions that support them. Examining the large-scale phytogeographic regions characterized by each major cover type (see Fig. I), we provide basic information on geology, geological history, topography, and climate; describe variants of physiognomy (vegetation structure) and geography; discuss transitions; and examine some floristic patterns and affinities within and among these regions. We mention some of the better-known useful plant species native to each region.

Preceding the primarily descriptive body of the text are brief discussions on vegetation classification and on folk classifications of vegetation. For humid forests, we briefly explore trends and patterns of floristic diversity. Throughout the chapter, we cite relevant references from both classical and recent literature.

The map in Fig. I reflects the classification of vegetation cover on a broad scale as an integration of floristics and physiognomy; one vegetation cover type (or a particular mosaic) predominates in each region. The figure is modified from Prance (e.g., 1989), who classified the American tropical forests using the "phytochorion," a concept widely used in studies of African vegetation, that emphasizes species distributions rather than vegetation types while stressing the correlation between the two; White (1979, see applications in White 1983) considered phytochoria to have 50% endemism or more than 1000 endemic species. Historically, the integration of floristics and physiognomy was dealt with by Beard (e.g., 1955) in a hierarchical fashion: the "formations" he defined were physiognomic reduction series, while floristics characterized the next level, "associations."

In some regions, it is difficult to reconstruct the nature of the original vegetation because human disturbance has been so intense over such a long period of time. The Magdalena Valley of Colombia shows complex patterns of such parameters as soil, topography, and drainage, but most of the region the vegetation was converted before it could be investigated. The forests dominated by the "babassu" palm (*Attalea speciosa [Orbignya phalerata]*) in western Maranhão and south-central Pará, Brazil are clearly secondary formations, but what is not clear is the nature of the vegetation prior to intensive human disturbance there. The extent of arboreal caatinga (as opposed to scrubby types) in Northeastern Brazil was probably far greater prior to the grazing, clearing, and charcoal-making the region has suffered since European contact.

Observations on vegetation classification

Continental-scale vegetation maps of South America published to date are largely unsatisfactory (see compilation of Küchler 1980). The UNESCO (1981) map includes only a half-dozen cover types for all of Amazonia. Veloso's (1966) first classification of vegetation in Brazil relied on very broad physiognomic types with no regional specificity, although the accompanying text contains floristic information. Hueck and Seibert's (1972) map is much more detailed, as is the accompanying text (Hueck 1972), but it still fails to do justice to the diversity of cover types, and ultimately to the beta-diversity -- essentially the habitat diversity -- of the continent.

The question to be posed is whether it is possible to classify vegetation cover adequately on a continental scale. Recent work in Peruvian Amazonia has identified numerous floristic consociations and vegetation cover types even on a rather local scale, based on multiple sampling using two taxonomic groups of plants (Tuomisto and Ruokolainen 1994) and on satellite images (Tuomisto et al. 1994, 1995), respectively. Indeed, the use of pixel (i.e., spectral) diversity on satellite images as a tool for measuring beta-diversity and for sampling biodiversity shows great promise (e.g., Podolsky 1992, 1994).

One major challenge to understanding the vegetation cover of northern South America is the staggering diversity of terminology utilized in various regions and in the literature. An extremely useful guide (in the form of a glossary) to the terms used in Spanish-speaking South America -- and an important step toward eventual standardization -- was prepared by Huber and Riina (1997).

Such characterization can work on a local up to a landscape or sometimes regional scale but runs into trouble toward the continental scale. One fundamental quality of the lowland vegetation of South America (and the tropics in general) is that similar climatic and edaphic conditions in geographically distant regions can give rise to strikingly similar vegetation physiognomies. In some instances the floristic connections are minor, such as the classical "campo rupestre" of the Serra do Espinhaço in southeastern Brazil (e.g., Giulietti and Pirani 1988) versus the so-called campos rupestres of the Serra do Cachimbo in southwestern Pará and of the Rio Cururu in the Rio Tapajós basin (see Pires and Prance 1985 and discussion below).

In other cases, there are floristic as well as physiognomic affinities that signal former physical connections and therefore genetic exchange, such as the now-interrupted areas of dry forest that form an arc around the southern periphery of Amazonia. Numerous species show distributions around part or all of this arc from Ceará in northeastern Brazil around and up to Acre in Brazil and even to Tarapoto in Peru (Prado and Gibbs 1993).

In general, however, the floristic component of a given physiognomy must be painted with very broad brush strokes between regions of humid tropical forests, at least. For example, Condit (results cited in Cook 1998) examined the composition of moist forests at a number of sites in Costa Rica with comparable climates and topographies and found that the only reliable predictor of community similarity between sites was proximity. Indeed, as Condit (1996) has noted elsewhere, it is unclear how well climatic and structural classifications correlate with species distributions.

This was borne out in a study by Terborgh and Andresen (1998): seeking to address the lack of composition-based vegetation classification systems in Amazonia, they examined the relative densities of tree taxa in 48 forest inventories in several portions of the region. They found that ordinations based on species and genera were essentially unusable because site similarity diverged so much over distance. Ultimately they used relative densities of families, and based on this criterion, at least, they concluded that floodplain and terra firme forests in a given area are more similar to each other than to the same forest type in another part of Amazonia. Again, history must play a key role, but this time in the form of historic barriers rather than connections; one must also consider that on a regional scale, floodplain taxa may have given rise to terra firme taxa (as suggested by Goulding 1993) or vice versa.

The poorly defined alliance between physiognomy and floristics continues. The combination used depends on scale and on objectives, and whether the focus is more on mapping the distribution of habitats, on explaining plant distributions, or perhaps on knowing the distributions of particular species or plant products.

Folk classifications

Local classifications, reflecting cultural perceptions of the surroundings, may be based on physiognomy or topography/drainage; a sort of folk Braun-Blanquet plant-sociology system is applied to some formations in which a species or set of confamilials is dominant. The "varillales" (from the word for "pole") on white sand in Peruvian Amazonia are characterized by the densely packed slender trees implicated by the name. "Caatinga" is derived from the Tupi for "white forest," referring to the blanched trunks so common in arid northeastern Brazil. "Mata de cipó," or liana forest, is self-explanatory. The various popular terms for formations in the Cerrado, (e.g., "campo limpo," "campo cerrado," "cerradão") describe the relative density of woody plant cover.

Local names for humid forest formations tend to be oriented toward terrain, as are many of those in the scientific literature. Such terms as "várzea," "baixio" ("bajio" in Spanish), "terraço (alto and baixo)," and "barranco" involve the elevation of the terrain relative to river levels and to flooding regimes.

Popular names referring to particular taxa when those taxa are locally dominant in some way. In Peruvian Amazonia, the "irapayales," relatively tall forests on sandy soils whose understory is dominated by the palm *Lepidocaryum tenue* (see Whitney and Alvarez 1998), and "moenales," forests on young terraces dominated by several Lauraceae. In southwestern Brazilian Amazonia and contiguous Peru, the "tabocais" or "pacales" are forests dominated by arborescent bamboos in the genus *Guadua*. The "wallaba" forests of Guyana are dominated by *Eperua* spp.

This phenomenon is more frequent in drier formations, where dominance by one or a few taxa is more common. The "quebrachales" of the Chaco are dominated by *Schinopsis* spp. or *Aspidosperma quebracho-blanco*. Also in the Chaco, "palo-santales" are dominated by *Bulnesia sarmientoi*, and "algarrobales" are dominated by *Prosopis* spp.

Some terms are not used consistently, or the same term may have different meanings among regions. The "caatinga" of northeastern Brazil has nothing to do with the Amazonian caatingas of the upper Rio Negro described below except perhaps the sun-bleached barks of some of their trees. "Igapó" as used by Prance (e.g., 1979) applies to forests seasonally inundated by black-water rivers, whereas most Brazilian botanists (e.g., Pires, 1973) **have used** the term to describe permanently flooded forests.

Humid Forests

Introduction

Lowland moist to wet forests dominate the landscape of northern South America, although not to the extent often assumed (Mares 1992). The largest single area of these mostly humid forests, the Amazonian hylaea, covers approximately six million km^2, and the remaining areas cover perhaps an additional 500,000 km^2, but the assemblage of drier lowland formations totals nearly that much: the "caatinga" vegetation of northeastern Brazil covers 600,000-900,000 km^2 (Andrade-Lima 1981; Sampaio 1995), the Chaco of Paraguay and Bolivia another 800,000-1 million km^2 (Hueck 1972; Galera & Ramela 1997), the Cerrado of central Brazil approximately 1.8 million km^2 (Ab'Sáber 1971; Coutinho 1990), the Llanos of Venezuela and Colombia 500,000 km^2 (Sarmiento 1984), the Llanos de Moxos savannas 150,000 km^2 (Beck & Moraes-R.

1997), the Pantanal 150,000-170,000 km^2 (Prance and Schaller 1982; Dubs 1992a), and the Roraima-Rupununi savannas 54,000 km^2 (Pires and Prance 1972; Eden and McGregor 1992).

The humid forests comprise a complex array of formations; only an exceedingly small portion of these forests correspond to the cathedral-like rainforests usually associated with Amazonia and other parts of northern South America. Many of the formations have canopies that are discontinuous and far from towering, and many have an understory congested with coarse herbs or lianas or slender trees. Similarly, most of the Neotropical lowland forests occur in climates that are markedly or at least somewhat seasonal (see Walsh 1996).

The largest and floristically most significant regions of lowland humid forests in northern South America are the Amazonian hylaea, largely continuous floristically with the Guianas (Fig. 1a); Brazil's Atlantic coastal forests (Fig. 2b), extending from Rio Grande do Norte around the horn of Brazil and south to Paraná state; and the Chocó biogeographic region (Fig. 2a), west of the Andes and extending from southern Panama south to central Ecuador. The precise area originally occupied by each of these is obscured by unclear transitions to dry and/or montane formations, and increasingly to anthropically modified or degraded regions. The limits of Amazonia have been variously defined (see review in Daly and Prance 1989); the rivers Amazon drain an area of some 7,050,000 km^2 (Sioli 1984), but the hydrological basin extends farther than the Amazonian vegetation, whose extent in Brazil has been estimated at between 4 million (Nelson 1994) and 6 million km^2 (Pires 1973).

Structure of moist forests

Lowland humid tropical forests can be characterized by a disparate set of factors. The canopy is generally high (to 40 m) but often discontinuous, and emergent trees may reach 65 m in height. It is usually not possible to distinguish strata. Palms and lianas occur in varying densities. Cauliflory and buttresses are common. Compared to dry or lower montane forests, the lowland humid forests have greater stand height, height to the first branch, trunk volume, buttress height, and buttress area (see Table 295 in Holdridge 1971). Many tree species have trunks that are not cylindric but rather have trunks that are sulcate, fluted, or fenestrate (Pires 1973; see definitions in Mori et al. 1997). Unlike many trees in dry forests and particularly savannas (Pinard and Huffman 1997), few show adaptations to fire such as very thick bark or underground trunks, and some even have highly combustible sap, such as the resin of many Burseraceae. Hepatics are high in both density and diversity, and epiphytic mosses are common but not so much as in montane forests. Also compared to montane forests, the lowland humid forests are poorer in epiphytes in general, and particularly in epiphytic monocots (e.g., Ducke and Black 1953), epiphytic shrubs, and tree ferns (Holdridge 1971). The understory is occupied more by tree regeneration and less by herbs and shrubs than in montane forests. A number of tree and epiphyte species have various morphological adaptations that make them hosts to biting or stinging ants (Ducke and Black 1953). A number of species are monocarpic (Pires 1973).

The diversity of these lowland forests is derived more from trees as well. In an inventory of all plants >0.5 m height in 1.8 ha each of upland and floodplain forests near Araracuara in Colombian Amazonia, in both formations trees contributed 65% of the diversity, followed by climbers (24%), shrubs (8%), and terrestrial herbs (3%) (Londoño-Vega **and Álvarez-Dávila** 1997). On 100 x 100 m (1 ha) terra firme forest plots at Cuyabeno, Amazonian Ecuador, Valencia et al. (1994) found 307 species of trees 10 cm or greater DBH, but Poulsen and Balslev (1991) found only 96 species of terrestrial (vascular) herbs; the most important taxonomic groups of herbs in terms of both species and cover were Araceae, pteridophytes, Marantaceae, Poaceae, and Rubiaceae, less so Cyperaceae, Heliconiaceae, Costaceae, Zingiberaceae, Bromeliaceae, and Gesneriaceae.

Conditions that suppport moist forests

Humid lowland forests occur in a remarkable range of climatic regimes and substrates. Mean temperatures do not vary much within the lowland tropics; in this context, the principal climatic factor determining vegetation is the equilibrium between precipitation and evapotranspiration and, above certain minima, the limiting factor is seasonality of rainfall. Schimper (1903) was among the first to note the importance of this factor in the tropics. A key parameter for the tropics in the classical climatic classification of Köppen (1901) is the number of months with less than 60 mm of precipitation.

Annual precipitation exceeds 9000 mm in some northern parts of the Chocó region (Herrera-MacBryde et al. 1997), and in most regions of northern South America the lower limit for humid forests is approximately 1300 mm where there is no dry season (Köppen 1901), but where there is a pronounced dry season, semi-deciduous forests may occur with 1700 mm or more (e.g., Pires-O'Brien 1997). The importance of seasonality is underscored, however, in the southern Bahian portion of Brazil's Atlantic forest complex, where species-rich evergreen moist forest thrives under 1850 mm of precipitation that is evenly distributed throughout the year (Mori et al. 1982).

Rainfall patterns, particularly in large regions such as Amazonia, are far from uniform. The spectrum of modified Walter/Lieth climate diagrams presented by Walsh (1996) show at least three degrees of seasonality in the region, ranging from super-wet to wet to seasonal. It is significant to note that four of the phytogeographic divisions of Amazonia proposed by Ducke and Black (1953) correspond to "eco-climate" subdivisions of Aubréville, which were defined by the timing and number of dry months with under 30 mm rainfall (see Daly and Prance 1989). Annual precipitation often exceeds 3000 mm in the eastern Andean piedmont, while further east there is a large swath cutting NW-SE across the Rio Trombetas and the lower Rio Xingu that receives only 1,750 mm of rain. This is known as the "transverse dry belt" (Pires-O'Brien 1997) or "Aw belt," referring to a category in Köppen's (1901) climate system in which the driest month has less than 60-65 mm rainfall and results in seasonal formations and savannas. Although consideration of the length and severity of the dry season is a more appropriate measure of climate (see Walsh 1996), in this region Köppen's system accurately predicts the vegetation.

Formations and how to define them

Formations are defined on a purely physiognomic basis. A given phytogeographic subdivision is often characterized by the predominance of a given formation or formation-series, while each formation in that region may be characterized by taxa of various ranks. Formations within the broader category of moist and wet forests have been defined using canopy height; canopy continuity, presence and number of strata; stand density; dominance; species richness, presence and density of lianas as well as epiphytes, palms, and herbs; biomass (often expressed in relative terms using basal area); number of deciduous species; leaf type; density of mosses; bark types; and other characters.

The formations or vegetation types of Amazonia account for much of the physiognomic spectrum of humid forests in northern South America, and were summarized by Pires (1973) and revised by Pires and Prance (1985), Prance and Brown (1987), and Prance (1989):

Dense forest or "mata pesada" (literally, "heavy forest") show a basal area of 40 m^2 or more. The canopy is high and often continuous, the understory relatively open. There are relatively few grasses and sedges, shrubs, herbs, and vines. Prance and Brown (1987) recognized a distinct forest type on undulating terrain, "dense and open hill forest on richer soils."

Open forests have a basal area of 18-24 m^2. In these forests, there are more shrubs and lianas, but fewer epiphytes. Open forests may be associated with a low water table, impermeable soils, poor drainage, poor root penetration, a longer dry season, and/or low relative humidity. Some open forests lack palms almost entirely, while others show a strong presence of palms; in Amazonia some of the more prevalent palms in open forests are *Oenocarpus bacaba* and *O. mapora* ("bacaba"), *Oenocarpus [Jessenia] bataua* ("patauá"), *Euterpe* spp. ("açaí"), and *Attalea (Maximilliana) maripa* ("inajá").

Both types of open forest were considered transitional by Prance (1989) even though they are not confined to the periphery of Amazonia. Forests displaying this type of physiognomy occur in many hilly regions where the trees are subject to unstable slopes and especially winds.

Moist forests on latosols (red, porous clays) occur in the Rio Negro region, but the most characteristic vegetation of the region is the "Amazon caatingas" or "campina" forests (also called "campinaranas;" see Fig. 1b; Anderson 1981; Coomes and Grubb 1996), particularly in the upper Rio Negro, which drains much of northern Brazil, part of southern Amazonas state in Venezuela, and part of Vaupés and Guainía departments in Colombia. They are edaphic formations not separated climatically from the rest of Amazonia. These forests on extremely nutrient-poor podzols (white-sand soils) are still inadequately studied. The most developed of them consist of closely packed slender trees with an often closed canopy to approximately 20 m high, with occasional large emergents. The understory has a thick layer of poorly decomposed litter. Epiphytes are common, but not lianas.

There is actually a continuum from campina forest to open, shrubby campina (called "bana" in Venezuela); this is function of the elevation above the water table (Jordan 1985). The area covered by the Amazon caatingas in Brazil has been estimated at 30,000 km^2 and a similar figure for "low campina" (Pires and Prance 1985), but these have yet to be confirmed by ground-truthing and interpretation of satellite images.

Above the Rio Negro's confluence with the Rio Branco, there is a complex mosaic of soil types and correlated moist forests, Amazon caatingas, and shrub communities (Projeto RADAMBRASIL 1975-1981). The great paradox of the upper Rio Negro is the occurrence of high species diversity in a region characterized by poor soils (podzols predominant) and often perched water tables (Goulding et al. 1988). There is considerable endemism at the generic level (e.g., Ducke and Black 1953; Pires and Prance 1985), which is not surprising considering most of the white-sand soils of Amazonia are concentrated here. Some of the typical genera of the Rio Negro are *Clusia, Tovomita, Lissocarpa, Pagamea, Campnosperma, Retiniphyllum, Barcella, Platycarpus*, and *Henriquezia*. In the Venezuelan part of the Rio Negro basin, some taller forests little affected by inundation are dominated by *Eperua purpurea* and others by *Monopteryx uacu*, while true Amazon caatingas (forests) there may be dominated by *Eperua leucantha* or *Micrandra sprucei* (Huber 1995). Other tree species characteristic of that region are *Lissocarpa benthamii, Hevea pauciflora, Pradosia schomburgkiana, Pagamea coriacea,* **[genus cut]** and *Sclerolobium dwyeri* (Huber 1995).

Formations of varying extents that are disjunct but physiognomically similar to the Rio Negro vegetation occur elsewhere in Amazonia. Areas containing campina forest include the upper Rio Solimões near São Paulo de Olivença, the lower Rio Tonantins, and the "varillales" of Amazonian Peru. Shrubby and open campinas (discussed further in the following section) occur sporadically through much of Amazonia; large areas of campina occur south of the upper Rio Madeira. Räsänen (1993) interpreted many of the white-sand soils in Amazonia as being derived from the Guiana Shield, from which they were transported to western South America prior to the Andean orogeny when continental drainage flowed east-west.

Arborescent bamboos are the dominant element of a vegetation type covering more than 180,000 km^2 in the southwest Brazilian Amazon and neighboring Peru and Bolivia (B. W. Nelson, unpublished data, expanded from Nelson 1994). This unusual and until recently unstudied vegetation type was remarked upon by early travelers to the region (e.g., Chandless 1866, Huber 1906) but the first rough estimate of its extent in Brazil was not made until 1976 (Projeto RADAMBRASIL 1976), and only recently has it been mapped to any extent.

Physiognomically, bamboo forests resemble liana forests, and like that formation they were considered transitional by Prance (1989) although they are not transitional to extra-Amazonian vegetation. Adult culms (stems) of these species average 8 cm in diameter and 15 m in height but may reach a height of 30 m, approximately equivalent to the top of the forest canopy. As culms grow towards the canopy, their habit often changes from erect to sarmentose, i.e., neighboring trees serve as props to support upward growth for the strong but flexible culms of bamboo. Amazonian *Guadua* are notorious for their well-developed stem spines that are present on both culms and branches. These spines, actually morphologically modified branches, facilitate the climbing habit by acting as hooks. A frequent result of this opportunistic growth is a dense spread of bamboo culms filling gaps between individual trees and covering their canopy. In the forest understory, young erect culms and fallen branches can produce an almost impenetrable tangle of spiny vegetation.

These so-called bamboo forests dominate the lower portions of terra firme landscapes in parts of southwest Amazonia, including valleys and relict river terraces, but not usually on plateaus. In dissected hill-and-slope terrains, there are frequently abrupt transitions between bamboo forest and mixed-species forest, often independent of obvious topographic features.

Two aspects of the bamboos' basic ecology have a profound impact on the forest dynamics of the region. One is its ability to spread aggressively by means of rhizomes. There is evidence that the already enormous area covered by this formation is expanding; bamboo forests may be favored by large-scale natural and/or anthropogenic disturbance. The other conspicuous aspect of their ecology is the synchronous flowering and subsequent die-back that characterize many species of bamboo worldwide, and this appears to involve numerous populations on at least a regional scale. By their cycles of expansion and collapse, to a large degree these forests mediate the rather tumultuous forest dynamics of the region.

Inclusions and archipelagos

The extent of humid lowland forests is in places vast but not unbroken. There may be continuous mosaics of edaphic conditions, defining the beta-diversity of a region. Large regions of humid forests may also contain anomalous formations either covering considerable areas or occurring as irregular islands. The most significant of these are the Amazonian savannas, which may cover 100,000-150,000 km^2 or about 3-4% of Brazilian Amazonia (Pires and Prance 1985).

These include a number of non-flooded formations such as the subcoastal savannas in Amapá (Sanaiotti et al. 1996; see Fig. 6b), the upland savannas of Marajó Island at the mouth of the Rio Amazonas (Bastos 1984), the campos de Ariramba of the upper Rio Trombetas in northern Pará (Egler 1960), and those near Santarém in western Pará (Miranda 1993). They also include riverine flooded savannas. Although the upland savannas share some species with the Cerrado, there are important physiognomic differences indicating non-adaptation to fire: the root systems are more superficial, the relative humidity is higher, and fewer woody species are capable of sprouting from roots or stumps. Some of the Amazonian savannas are species-poor, such as those in Amapá, while others like those of the upper Rio Trombetas are relatively biodiverse (Pires and Prance 1985).

Shrubby campinas on partly exposed white sands (discussed in previous section) occur sporadically throughout much of Amazonia as islands on the scale of hectares or of square kilometers. The campinas have little in common floristically with the surrounding tall forests on clay soils (Guillaumet 1987), and they function as islands, with numerous adaptations to relatively long-distance dispersal (Anderson 1981; Macedo 1977; Macedo and Prance 1978). They show a high degree of endemism, even including some endemic genera (e.g., Struwe et al. 1997).

Another archipelago of inclusions occurs in the southern part of Venezuela's Guayana Highland (Fig. I), where isolated plateaus -- the tepuis -- are all that remain of an ancient sandstone tableland. The (pre-)montane forests on the upper slopes of the tepuis and the vegetation of the bogs and rock outcrops on their summits contrasts greatly with the surrounding Amazonian forests (Huber 1995). Smaller and lower sandstone plateau outcrops with related floras extend into the Caquetá-Araracuara-Cahuinarí region of Colombia (Sánchez-S. et al. 1997).

Inselbergs are isolated granitic mountains up to 700 meters in elevation (Sarthou and Villiers 1998). The inselbergs are restricted to the Guiana and Brazilian shields, principally in French Guiana, Surinam, and Brazil and including the Serra do Mar in the latter. The summit vegetation consists mostly of mats of monocots, characterized by Velloziaceae but also including Bromeliaceae and Orchidaceae, plus some dicots, including *Clusia* and (in Brazil) principally Cactaceae. The inselbergs include Nouragues and Mitaraka in French Guiana (de Granville and Sastre 1974; Barthlott et al. 1993) and the Pão de Açucar in Rio de Janeiro, Brazil. On the inselbergs in French Guiana, Cactaceae are scarce and Velloziaceae lacking (Sarthou and Villiers 1998).

In some regions it is the humid forests that occur as islands. In most of the northeastern Brazilian states, isolated patches of moist forest occur (or occurred) on the "brejos." These are granitic plateaus of up to 1000 m elevation, found 30-90 km from the coast. Humid microclimates occur at higher elevations on the southern and eastern slopes, which are exposed to coastal winds. These islands of forest have affinities with Amazonia and with the Atlantic coastal forests further south (e.g., Andrade-Lima 1982; Mayo and Fevereiro 1982).

"Campo rupestre" is a term that has been applied to several open formations on stony soils that are geographically distant and floristically rather distinct. The classical "campo rupestre" is that occurring on the quartzite Serra do Espinhaço in southeastern Brazil, where that vegetation occurs between (700)1000-2000+ m. This vegetation consists of a more or less continuous herbaceous stratum with evergreen small shrubs and subshrubs. Characteristic taxa include Velloziaceae, Eriocaulaceae, Xyridaceae, Poaceae, Melastomataceae, and Bromeliaceae.

(e.g., Giulietti and Pirani 1988, 1997; see discussion below under Savannas).

Two other major areas of campo rupestre in the broader sense occur toward the southern periphery of the Amazon basin; the one on part of the Serra do Cachimbo in SW Pará covers some 16,000 km^2 (Pires and Prance 1985), while a smaller extent is found near the Rio Cururu in the upper Rio Tapajós. Despite their physiognomy, some typical cerrado species do not occur in these formations, such as *Curatella americana, Hancornia speciosa, Salvertia convallariodora,* and *Qualea grandiflora*. Certain plant groups important in the Serra do Espinhaço are also prominent there, such as *Vellozia*, Eriocaulaceae, *Byrsonima*, and several genera of terrestrial Bromeliaceae (see Pires and Prance 1985), but otherwise their floras, which are still poorly known, appear to be rather distinct.

Trends and patterns of diversity in humid forests

The plant diversity of moist and wet tropical forests of northern South America is accounted for primarily by trees. Forests strongly dominated by one or a few species (monodominant and oligarchic forests, respectively) do occur -- usually but not always under relatively extreme environmental conditions --, but the majority of humid forests show marked dominance only by a changing consortium of multiple species. Conversely, often half the tree species are rare on a scale of 1-50 hectares or more (see Condit et al. 1996). Among moist forest regions, there are recognizable trends in relative alpha-diversity (species richness per site) related to soil nutrients, total rainfall, seasonality, and latitude. Major changes over distance in composition and often physiognomy usually correspond to existing barriers and/or transitions of soil or climate, but in some cases they coincide with non-obvious historical geological features. On a landscape scale, species richness and composition correlate with topography and soils, but only up to a point.

One of the hallmarks of humid lowlands is the rapidity with which the forests change over distance, be it from one vegetation type or even one spot to the next (e.g., Campbell et al. 1986). For example, near the confluence of the Rio Negro and Rio Uaupés in northern Amazonian Brazil, Takeuchi (1962) found remarkable differences between two sites within a high campina formation in terms of humus depth, soil moisture, relative humidity, canopy height, canopy tree species composition, the number of strata, the density and composition of understory, dominance, and the occurrence of palms and epiphytes.

Compared to montane forests and dry forests, trees are a far more important source of diversity in the lowland humid forests. In the Río Caquetá of Colombia, for example, most species-rich families and genera tend to be tree groups, although in contrast to other regions much of the diversity is represented by small trees <=2.5 cm DBH (diameter at breast height, ca. 1.3 m), and those less than 10 cm DBH were the most species-rich habit group (Duivenvoorden 1994).

Considering margins of error and variability, forests that are "mega-diverse" in trees have been documented in Amazonian Ecuador, Amazonian Peru, the Chocó region of Colombia, and the vicinity of Manaus in Brazil (Valencia et al. 1994, also Balslev and Renner 1993; Gentry 1988; Gentry 1986; and Oliveira and Mori [in press], respectively), all with approximately 300 species of trees and lianas >/= 10 cm DBH per hectare.

Monodominant and oligarchic forests are not rare. For example, "mora" forests dominated by *Mora excelsa* are frequent in low-lying areas of Guyana and contiguous Delta Amacuro, Venezuela (e.g., David and Richards 1934; Connell and Lowman 1989; ter Steege et al. 1993; Huber 1995), and "tabocais" or "pacales" dominated by *Guadua weberbaueri* cover large areas of southwestern Amazonia (e.g., Nelson 1994).

Many monodominant and oligarchic forests are associated with extremes of drainage or poor soils. Floodplains and other relative edaphic extremes tend to support forests with relatively lower alpha diversity and higher dominance, some of them dominated by well-known economic species (cf. Peters 1992); examples are the palm forests of the Orinoco delta and Rio Amazonas that are often dominated by "buriti" or "moriche" *(Mauritia flexuosa)* and "açaí" (*Euterpe oleracea)* palms (Huber 1995; Pires and Prance 1985). It has been estimated that almost 10,000 km^2 of pure stands of the former occur in Peru alone, and the same estimate has been made for pure stands of the latter in the Amazon estuary (reported in Peters 1992).

On the other hand, some monodominant forests may show low relative density of many species while maintaining alpha diversity comparable to surrounding mixed-dominant forests; an example is the bamboo-dominated forests of southwestern Amazonia (M. J. Stern, unpublished results).

At one site at Yanamono in Peru, there were only twice as many individuals as species of trees (Gentry 1988). Salomão and Lisboa (1988) reviewed 13 published Amazonian forest inventories of 1-3.5 ha, most with a 9.5-10 cm DBH cutoff, and found that in most cases between 36-53% of the trees censused were singletons, i.e., represented by only one individual per hectare or more.

In the Neotropics overall, there are fairly consistent trends in alpha diversity across several gradients. In general, humid lowland forests are more alpha-diverse in areas with higher total rainfall; this is often correlated with poorer soils, higher productivity, higher stem density, somewhat smaller stature (Huston 1994); higher diversity also tends to be found in areas with more aseasonal climates, and in more alluvial and less sandy soils (Gentry 1988). Within Amazonia, forests tend to be more alpha-diverse along an east-west gradient.

There are notable exceptions to these trends. For example, one of the highest levels of alpha-diversity in the world for trees >/= 10 cm DBH has been found in the region of Manaus (Oliveira and Mori, in press), but it is centrally located in Amazonia at a low latitude, and the rainfall is relatively low and markedly seasonal. One possible explanation for this is the status of Manaus as a biotic crossroads where the distributional limits of numerous taxa of plants and animals coincide; this may be a region of re-convergence for distributions disrupted by one or another factor during glacial periods (Oliveira and Daly, in press).

The features and factors that separate one phytogeographically distinct area of humid forest from another are usually evident, but some are more subtle, others appear to be historic, and still others are invisible. Barriers such as the Andes separating the Chocó from western Amazonia, the cordilleras that flank the Magdalena Valley in Colombia, and the Serra do Mar that sets apart the Mata Atlântica of Brazil help to circumscribe phytochoria. Major rivers such as the Rio Solimões-Amazonas function as barriers to dispersal and can create and help define biogeographic subdivisions, (see Wallace, 1849; Ayres and Clutton-Brock 1992).

Other major changes in vegetation observable on satellite images coincide with historical geological features such as paleoarches, long zones of ancient uplift barely perceptible except on satellite images; an example occurs on either side of the Fitzcarrald Arch in southwestern Amazonia (R. Kalliola, pers. comm., and pers. obs.). It is interesting to note that another paleoarch in western and southwestern Amazonia, the Iquitos Arch, runs perpendicular to the Rio Juruá and coincides with a sharp line of genetic divergence between in several genera of arboreal rodents between the upper and lower Juruá (Patton et al. 1997). The role of these paleoarches in vicariant events much older than the Pleistocene has been explored only superficially (see Rasanen 1993; Daly and Prance 1989; Patton et al. 1997).

Still other major changes observable on satellite images do not coincide with any known barrier, past or present. Many of these unpredictable differences may be due to natural disturbances (Nelson 1994), pest outbreaks, or chaotic fluctuations (Condit 1996); given the slow turnover rate in some tropical forests (e.g., Hartshorn, 1978) and the limited dispersal capacity of many humid forest tree species, such changes could persist for centuries (cf. Condit 1996).

Up to a point, differences in soils and topography correlate with changes in species diversity, species composition, and forest structure; indeed, they often determine distinct forest types. In the mosaic of habitats one often encounters in regions of lowland humid forests, particularly in western Amazonia, there are generalists in each component, but there are also edaphic specialists (e.g., Young and León 1989), and the compositional differences are often statistically rather clear-cut except when it comes to comparing sites with different clay soils. Guillaumet (1987) compared sites of terra firme (upland) forest, swamp forest, campinarana, and campina in central Amazonia, and found that the latter two were closely linked floristically with each other but not to the terra firme or swamp forest. Not one tree species was found in common to all four formations.

The work of Tuomisto et al. (1995) in Peruvian Amazonia confirmed and expanded on these results. They found that plant communities were sharply differentiated on white sand vs. clay soils, ridge tops versus valleys, and white-sand formations (campinarana analogs) versus swamp forests, but among different clay soils they found only weak evidence that tree communities correlate with soil nutrients (data cited in Condit 1996). In an area of clay soils in French Guiana, Lescure and Boulet (1985) mapped trees >20 cm diam. onto drainage types (which affected soil structure) and found that most trees could occur in more than one drainage type. In a central French Guianan forest, Mitchell and Mori (1987a) found that some species of Lecythidaceae preferred ridgetops while others were associated either with hill slopes or low-lying areas.

Similarly, on the middle río Caquetá in Colombian Amazonia, Duivenvoorden (1995) found meaningful patterns of tree species composition related to drainage, flooding, humus forms, and soil nutrients. On well-drained upland sites, species composition depended significantly on soil properties, but it was basically a dichotomous pattern and not the super-high beta pattern that might have been expected. Comparing swamp forest and formations on sandy (podzolized) soils on one hand versus forests on well-drained soils on the other, in the former he found more dominance in general and greater importance of palms, Clusiaeae, Bombacaceae, and Apocynaceae, and in the latter greater importance of Lauraceae, Chrysobalanaceae, Moraceae, and Lecythidaceae (Duivenvoorden 1995).

Working with Amazonian palms, Clark et al. (1995) found there was species sorting by soils and topography, e.g., between infertile upland areas adjacent to young alluvial terraces. In Ecuadorean Amazonia, Poulsen and Balslev (1991) found that spatial distribution of understory herbs may be correlated with topography.

Transitions

The shifts from lowland humid forests to other formations may be abrupt, such as the transition from gallery forests to grassy campos in subcoastal Amapá, but much more often they are gradual or patchy and occur along gradients of elevation, soils, and/or rainfall; Prance (1985) observed that transitions tend to occur in areas with moderate (2000 mm/year) and highly seasonal rainfall. Moreover, humid forests grade into markedly different formations in different regions.

In Amazonia, each portion of the periphery may show a different kind of transition to the extra-Amazonian floras (see review in Daly and Prance 1989). In general, the northern perimeter is characterized by rather abrupt transitions to savannas, while the southern perimeter usually shows mosaic-like transitions involving semi-deciduous and/or liana forests. An exception in the north is the mosaic of campina, low caatinga (or campina forest), and high caatinga in the Upper Rio Negro region. In northwestern Amapá and northern Pará, the middle and upper reaches of the rios Trombetas and Paru show extensive savannas that reach up to the Serra do Tumucumaque and the borders of French Guiana and Surinam. The transitions to the Roraima savannas are often abrupt, but there also some patches of poorly studied semi-deciduous forests.

Semi-deciduous forests comprise the principal type of transition in Amazonia. These forests, essentially Amazonian but with some endemics and Cerrado elements, frequently occur in patches along the southern periphery of Amazonia, as well as in Roraima, where their floristic composition is different. A number of tree species show largely peri-Amazonian distributions, especially around the southern periphery in what could be considered transition zones; these include the Balsam of Peru, *Myroxylon balsamum* (see de Granville 1992; Prado and Gibbs 1993).

Brazil borders on a part of the Guayana Highland (Fig. I) of sandstone plateaus (tepuis), and in places along the Venezuelan border in northwestern Roraima and northeastern Amazonas the sandy Amazonian campos or caatingas give way to tall forests on the lower slopes of the tepuis, which in turn may grade into montane forests on the upper slopes.

The upper Rio Negro basin is characterized by the Amazonian caatingas, which extend beyond into southwestern Venezuela and southeastern Colombia, where a drier climate, slightly higher elevation, and other edaphic factors mark the transition to the savannas of the Llanos region.

The southern Amazonia transition zone was mapped as a distinct transition-type phytochorion by Prance (1989; see also Fig. I) and is discussed in a separate section at the end of this chapter. There are diverse transitions to cerrado vegetation, mostly semi-deciduous forests but also including liana forests and campo rupestre.

Floodplain forests

The periodically flooded forests that flank the rivers Amazon and other river systems of northern South America are significant features of the landscape in many parts of the region. Although a given parcel of floodplain forest will show lower alpha-diversity than its upland counterpart, these forests contribute greatly to overall floristic diversity because both species composition and physiognomy change not only between regions but also locally as a function of small changes in topography (and therefore flooding regimes). The resulting mosaic of habitats is most complex and most finely divided in western Amazonia. The floodplains have ecological importance way out of proportion to their area because of their roles in capturing and cycling nutrients, harboring (and feeding) incomparably rich freshwater fish life and great invertebrate diversity, stabilizing flooded soils and landscapes, and requiring remarkable physiological adaptations.

Moreover, over many millennia they may have constituted a source of new taxa that colonize surrounding terra firme. Ducke (1948) noted the presence in Amazonia of a large number of tree genera within which one species or group of species occurs in floodplains and floats, i.e., is adapted for dispersal by water, while the other occurs in upland soils and is adapted for dispersal by wind or animals. Species with winged fruits and others with unwinged fruits are found in *Machaerium, Dalbergia, Pterocarpus, Vatairea*, and *Hymenolobium. Aspidosperma* has species with winged seeds and others with unwinged seeds. In the legumes *Swartzia, Ormosia*, and *Parkia* and the Proteaceae *Panopsis*, most species are dehiscent, but each genus has one or more species with indehiscent fruits that float. The fruits of most *Inga, Caryocar*, and *Saccoglottis* contain a pulp or mesocarp sought by land animals, but each has at least one floodplain species in which the food reward is absent, reduced, or chemically modified (e.g., highly acidic).

The greatest extent of floodplain forests occurs in Amazonia, where Goulding (1993) estimated that they cover some 150,000 km^2. The principal areas of várzea or white-water floodplains are the Rio Solimões-Amazonas and large areas along the Madeira and Purus rivers (Fig. 4a); on the lower Rio Branco there is a large region of igapó or blackwater floodplain forest (Fig. 3b).

In Amazonia, the river levels can fluctuate 7-13 m/year (Goulding 1993), and several meters more in extreme years. Still, the floodplains are mostly evergreen, even in lower-lying areas where many of the trees are completely under water during annual flooding. Most floodplain trees have no visible adaptations to having at least their root systems submerged for part of the year, although in the Amazon estuary it is more common to find trees with aerial roots or pneumatophores, as in mangroves (Pires 1973).

It appears that plant species in floodplain habitats have different "preferences" (i.e., tolerances and competitive abilities) depending on the depth and duration of the annual floods, consequently slight topographic differences yield dramatic changes in species composition. On the lower Rio Negro, Keel and Prance (1979) found distinct zonation of species along the flooding gradient, although the boundaries were not clear. Downstream from Manaus in a white-water várzea, Junk (1989) found clear zonation along a flood level gradient of different depths and durations of inundation: 1) a low-lying shrub community at 20.5 m above average sea-level, including *Coccoloba ovata, Eugenia inundata, Ruprechtia ternifolia*, and *Symmeria paniculata*; 2) a mid-level tree community at 22+ m, including *Acosmium nitens, Buchenavia macrophylla, Cecropia latiloba, Crataeva benthamii, Ficus anthelminthica (= F. insipida), Machaerium leiophyllum, Macrolobium angustifolium, Piranhea trifoliata, Pseudobombax munguba*, and *Tabebuia barbata*; and 3) a higher-ground tree community at 25+ m, including *Calycophyllum spruceanum, Ceiba pentandra, Couroupita guianensis, Genipa americana, Hevea brasiliensis, Lecointea amazonica, Sterculia elata*, and *Rheedia brasiliensis*. Vegetation zones and their boundaries are often very clear in the successional bands found in the white-water floodplains of western Amazonia, where river courses are continually changing (e.g., Foster, 1990; Gentry and Terborgh 1990; Puhakka et al. 1993; Fig. 3a).

Floodplain forests in Amazonia do show lower alpha-diversity than adjacent terra firme (Balslev et al. 1987; Campbell et al. 1986; Duivenvoorden 1994), but their distinct composition adds significantly even to local floristic diversity. At Araracuara in Colombian Amazonia, an inventory of all plants >0.5 m height in 1.8 ha of terra firme and floodplain found the floristic similarity to be high (67%) at the family level and moderate (36%) at the generic level, but only 5% at the species level (Londoño-Vega and Álvarez-Dávila 1997).

River types

The chemical and optical properties of rivers reflect the soil properties of the regions they drain. Different conditions of parent material, topography, age, and weathering result in rivers with different pH, transparency, sediment and nutrient load, and even temperature (Sioli 1984). These provide a basis for drawing inferences about the floodplain vegetation.

Alfred Russel Wallace (1853) was the first to classify the Amazon and its tributaries into white-, clear-, and black-water rivers. The white-water rivers drain the Andes and Andean forelands; these are still weathering and often steep. The waters are rather opaque and neutral or slightly basic, and carry a nutrient-rich sediment load, so the floodplains are essentially fertilized each year. The white-water rivers cut through soft sediments and many are continually changing course; this and river-level fluctuations over geological time result in a tremendously complex mosaic of habitats including levees and the back-slopes behind them, seasonal lakes, oxbow lakes, recent and older forested terraces, canals, curves with successional bands on new waves of depositions, and various stages of succession in places where sedimentation has progressed. Peanuts, native in southwestern Amazonia, are cultivated on recently exposed silty beaches. The character of the white waters dominates the main course of the Rio Solimões-Amazonas. The floodplain forests of these rivers are called várzea forests, while those of the clear- and black-water rivers are usually referred to as igapó forests (Prance 1979).

The clear-water rivers of Amazonia drain the ancient, highly weathered Brazilian and Guianan crystalline shields that flank the Amazon Valley. The river beds are rocky and the courses are stable. The waters are transparent and nutrient-poor, and have a very low sediment load. Their floodplains are not broad and their floodplain forests are relatively species-poor.

One of three explanations for the black waters of the Rio Negro proposed by the great Amazon explorer Alexandre Rodrigues Ferreira in the diaries on his two years on that river during 1785-1787 was that they are derived from plant extracts. This was echoed several years later by Alexander von Humboldt (see Goulding et al. 1988). The Rio Negro drains the usually nutrient-poor, acidic, sandy lowlands of the northwestern Amazon basin. Litter decomposition is slow and incomplete, and there is no clay to filter the humic acids. The result is tea-colored, cool, acidic, nutrient-poor waters with a low sediment load.

The igapó forests have lower within-site diversity than the várzeas, and a lower diversity of habitats as well. Without a rich sediment load, there are no levees. Some of the more common tree species in the Rio Negro igapós are *Eugenia inundata, Alchornea castaneifolia, Allantoma lineata, Copaifera martii, Couepia paraensis, Licania apetala, Piranhea trifoliata, Tabebuia barbata*, and *Triplaris surinamensis* (Pires and Prance 1985; Prance 1989)

Largely as a consequence of the river types, three sectors can be distinguished on the main course of the Amazon: the estuary, the lower Amazonas, and the upper Amazonas. The estuary is a labyrinth of islands and canals formed of sediments from slowing rivers. The influence of the tides penetrates far in from the mouth, and this, like the estuaries of the río Orinoco and of rivers draining western Colombia, is a zone of tidal várzeas that are flooded twice daily by a freshwater backup. A colonizing species on freshly exposed muds is *Montrichardia arborescens* (Fig. 4b). There is a strong presence of palms, in Amazonia including *Euterpe oleracea, Manicaria saccifera, Socratea exorrhiza, Astrocaryum murumuru,* *Mauritia flexuosa, Raphia taedigera, Oenocarpus bacaba*, and *O. pataua*. In addition to palms, characteristic trees are *Calophyllum brasiliense, Ficus spp., Macrolobium acaciifolium, Pachira aquatica, Symphonia globulifera*, and *Triplaris surinamensis* (Pires 1973; Prance 1989).

In contrast, the lower Amazonas várzeas have few palms. In this region there are many grassy meadows and seasonal lakes behind forested levees, the latter being especially large near Monte Alegre in Pará (Pires and Prance 1985). Some of the most common trees of the várzea forests of the lower Amazonas are *Hura crepitans, Triplaris surinamensis, Calycophyllum spruceanum, Pseudobombax (Bombax) munguba*, and *Ceiba pentandra* (Pires 1973).

There are few grassy meadows in the upper Amazonas. Here, the várzea forests show the greatest complexity, diversity, and extent. The area flooded is very large between the Japurá and Içá rivers (e.g., Pires and Prance 1985). Above Parintins one begins to see the tall grass "canarana" ("caña brava" in Spanish), *Gynerium sagittatum*, which is a prominent species in the early successional bands on recent sediments. In western and southwestern Amazonia, other species associated with the early successional bands are *Alchornea castaneifolia, Salix humboldtiana*, and *Tessaria integrifolia*.

The understory of shallowly inundated várzeas in this region is rich in *Heliconia* spp., Cyclanthaceae, Marantaceae, and Zingiberaceae; characteristic trees include *Carapa guianaensis, Caryocar microcarpum, Hevea brasiliensis*, and *Eschweilera* spp. (Prance 1989).

Other inundated forests

Swamp forests on gleyed soils (deeply buried clayey soils in water-logged conditions) occur sporadically in the northern South American lowlands. One formation that covers large areas in western Amazonia is the often monodominant "aguajales" or *Mauritia flexuosa* stands on poorly drained sands.

The mangroves of northern South America are extremely depauperate in species compared to many of their Old World counterparts. This is particularly true on the Caribbean and Atlantic coasts, where the mangroves tend to be more discontinuous, and where the dominant trees are mostly *Rhizophora mangle, Avicennia tomentosa* and *A. germinans* further inland, and *Laguncularia racemosa* in brackish, sandy areas. On the Pacific side, the mangroves are relatively more continuous and species-rich down to San Lorenzo, Ecuador, and in the Tumbes Delta in Peru (Prance 1989).

Phytochoria

Each of the following sections corresponds to one of the phytochoria mapped in Figure I, and while each contains a range of vegetation types, humid forests predominate in all, with two exceptions: the Magdalena/NW Caribbean coastal region, which is rather evenly divided between dry and humid formations; and the Southern Amazonia transitions to various drier formations.

Chocó (Fig. 2a)

The Chocó *sensu lato* extends along the Pacific coast of South America from southern Panama south to inland from Guayaquil in central-west Ecuador, where the desiccating Humboldt current from the south is deflected westward into the Pacific. A thin strip of mesic forest inland from the coastal plain extends into southern Ecuador. This topographically diverse region of mostly lowland tropical pluvial to moist forests originally covered approximately

180,000 km^2 (Herrera-MacBryde et al. 1997; Neill 1997). It is flanked by Andean montane forests to the east, tropical dry forests to the south, and gradually drier conditions to the northwest in Panama. Along the Colombian coast it is interrupted by mangroves, while southward from the Ecuadorean border the progressively drier climate supports coastal dry forests and the western edge of the original mesic forests shifts inland. The Chocó flora was once continuous with that of Amazonia but has been isolated from it since the uplift of the Andes in the Tertiary, resulting in a level of endemism above twenty percent, including many species whose closest relatives are in Amazonia (Gentry 1989).

The northern (mostly Colombian) part of the Chocó experiences aseasonal climate and extremely high rainfall (often 4000-9000 mm/year and averaging 11,770 in one locality; Herrera-MacBryde et al. 1997) and in places supports pluvial forests that are physiognomically distinct from those with lower and particularly with more seasonal rainfall. There is a high density of small and medium-sized trees; there are fewer lianas and more hemi-epiphytic climbers; and a large number of species with remarkably large fruits and/or large leaves (Gentry 1986).

Some Chocó forests show less dominance of Fabaceae (Leguminosae) *sensu lato* than do most Neotropical forests. There is a prevalence of Clusiaceae, Arecaceae, Myrtaceae, and Melastomataceae, also Rubiaceae, Annonaceae, Sapotaceae, and (on good soils) Moraceae. Gentry (1986) reported that on white clays at Bajo Calima and two sites in the Ecuadorean Chocó with richer soils, the Fabaceae was not among the most species-rich families; at Bajo Calima there were more species of Rubiaceae, while on the Ecuadorean sites there were more Moraceae, and the two sites were also strong in Sapotaceae, Annonaceae, Lecythidaceae, and Chrysobalanaceae. The Clusiaceae, Marcgraviaceae, and Melastomataceae are represented by numerous hemi-epiphytic climbers and have centers of diversity in the region.

Well-known useful plants of this region include the prized endemic fruit/medicinal tree "borojó" (*Borojoa patinoi*, cf. Ricker et al. 1997), vegetable ivory ("tágua," *Palandra [Phytelephas] aequatorialis*), and one of the early sources of rubber, *Castilla elastica*.

Magdalena and NW Caribbean coast

This complex region is bordered to the north by the Caribbean, to the east by the Coastal Cordillera of Venezuela, to the southeast by the Sierra Nevada de Mérida, and to the west by the Chocó region, with whose flora it shares poorly investigated affinities. The natural vegetation is mangroves along parts of the coast, dry forests in broad bands flanking Lake Maracaibo and across to near the Gulf of Urabá (cf. Hueck and Seibert 1972), humid forests in parts of the Magdalena valley and near Lake Maracaibo and the Gulf of Urabá and, on the mountainous Guajira peninsula, an elevational series ranging from thorn scrub to dry forest to montane cloud forest (Forero 1988).

The Magdalena Valley of northern Colombia formerly contained extensive humid forests, with large swampy areas in the northern part (Gentry 1989; Prance 1989); the flora is difficult to reconstruct because it was largely destroyed before it could be adequately inventoried. It is possible to say that the region's forests were a mix principally of Central American and Amazonian elements that reached their southeastern and northwestern limits there, respectively, plus some Chocó elements and a number of endemics. The latter are mostly woody taxa and include the endemic genera *Tetralocularia, Romeroa*, and *Brachycyclix* (Gentry 1989). *Caryocar amygdaliferum* is an example of a Magdalena Valley endemic, while *Cariniana pyriformis* occurs there and in the northern Chocó (Prance 1989).

Also formerly covered by tall humid forests, but even more often overlooked and more poorly known, are the lowland regions proximal to the mangroves around the Golfo de Urabá in Colombia (extending into part of Darién in Panama) and around Lake Maracaibo flanking the Colombia-Venezuela border. One species endemic to that region is *Bursera inversa* (Daly 1993). The map in Prance (1989) includes this region in his Magdalena phytochorion.

Venezuelan Guayana/Guayana Highlands

The widely scattered table mountains or steep-walled "tepuis" that characterize Venezuelan Guayana are ancient sandstones and quartzites overlying the even more ancient and mostly granitic Guiana Shield. More than 90% of these table mountains are in Venezuela (Amazonas and Bolívar states); the rest are in northernmost Brazil, northwestern Guyana, and Colombia. Most of the region is drained by the Orinoco River, while the remainder is drained by the Cuyuni and Mazaruni rivers of Guyana and by the Rio Branco and Rio Negro, which drain into the Amazon (Huber 1995).

The circumscription of the region containing the tepuis embraces a vast area of mostly forested lowlands and piedmont areas. The numerous isolated montane and summit regions above 1300 m, collectively referred to as Pantepui or the Guayana Highlands, comprise a straightforward example of an archipelago-type phytochorion (*sensu* White 1979). They cover only about 6000-7000 km^2, although the area under their influence due to runoff (of both water and nutrients) and wind patterns is far larger and results in an expanded interpretation of the piedmont (see Huber 1995).

The broader Venezuelan Guayana region, which includes Delta Amacuro state and so the Orinoco delta, is about 83% forest. The vegetation map prepared by Huber (1995) distinguishes 54 forest "units" -- 18 of them in the lowlands -- that are both physiognomically and floristically defined, reflecting the extensive if incomplete ecological and botanical surveys of the region. Some of them can be summarized as follows (see Huber 1995):

* On the lower Orinoco there are coastal mangroves and three Delta zones distinguished by flooding regimes and species composition. The Middle Delta forests reach 25 m; they are seasonally flooded and include a number of species characteristic of the Amazon estuarine region, including *Euterpe oleracea, Manicaria saccifera, Mauritia flexuosa, Pachira aquatica*, and *Symphonia globulifera*.

* The riverine forests flanking the middle and lower Orinoco are similar in both physiognomy and composition to the "várzeas" of Amazonia.

* Much of southeastern Delta Amacuro and northern Bolívar experiences a drier and more seasonal climate than areas further south. On the gently rolling hills between the Cuyuní and Caroní rivers, tall forests alternate with scrub savannas. Farther north and west one finds semi-deciduous forests 15-25 m tall. The sandy or rocky hilltops south of the middle and lower Orinoco are covered by low deciduous forests; dominants include *Bursera simaruba, Copaifera pubiflora, Tabebuia capitata*, and *Bourreria cumanensis*. The northwestern piedmont, between the Orinoco and the western highlands, is mostly a mosaic of savannas (disjunct with those of NE Bolívar) and semi-deciduous, medium to low forests dominated in places by *Swartzia laevicarpa, Anadenanthera peregrina, Cassia moschata,* and *Copaifera pubiflora*.

* The most extensive continuous lowland humid forests of the region (and of Venezuela) occur on the undulating terrain of the lower and middle Caura and Paragua river basins; some of the tallest trees belong to the genera *Anacardium, Calophyllum, Protium, Parkia, Copaifera*, and

Erythrina, and well-known economic species include tonka beans (*Dipteryx* spp.) and balata (e.g., *Manilkara bidentata* and *Pradosia surinamensis*).

* Most of the southwestern lowlands (essentially Amazonas state) experience an average annual temperature of more than 24°C and rainfall rather evenly distributed throughout the year and in excess of 2000 mm, increasing along north-south and east-west gradients. This region displays a complex mosaic of forest types and associations determined by the climatic gradients plus differences in underlying parent rock and geomorphological processes (alluvial, depositional, and erosional) that have produced a variety of soil conditions.

Hilly central and southeastern Amazonas state is characterized by tall, dense forests; common trees are *Lecointea amazonica*, *Clathrotropis glaucophylla, Peltogyne venosa, Erisma uncinatum*, and various species in the genera *Ocotea, Nectandra, Licania, Trichilia, Guarea*, and *Toulicia*, and a high density of tall palms in the genera *Oenocarpus, Socratea, Leopoldinia*, and *Bactris*.

Much of southwestern Amazonas state is a continuation of the upper Rio Negro vegetation and flora, mostly on podzolized white-sand soils (discussed above), with a reduction-series from relatively tall forest to open scrub depending largely on elevation above the perched water table and the duration of periods of flooding alternating with water stress.

Numerous types of scrub formations are found at elevations under 1000 m, including those on level to inclined sandstone in the Caroní-Paragua drainage, the rocky sandstones and deep sands of the Gran Sabana (up to 1500 m), the plinthic and bauxite substrates on dry hilltops in drier NW Bolívar, and the dune-islands of the often flooded Sipapo, Atabapo, and Guainía lowlands (Huber 1995).

The highlands themselves are constantly humid; they receive approx. 2000-4000 mm of rain per year and experience no true dry season. The mean annual temperatures range between 8°-20°C, depending on elevation, with an absolute minimum of near 0°C on the highest summits above 2800 m.

The vegetation of the Pantepui region is physiognomically diverse -- no fewer than 14 vegetation types have been recognized in the zones above 1300 m -- but it can be broken down into four broad categories: forests, scrub, high mountain fields, and what some call "pioneer" formations on rock outcrops and walls. Most of the highland forests occur on the upper slopes of the tepui bases. These include cloud forests and some extremely tall (to 60 m) forests; the most frequent families are Lauraceae, Magnoliaceae, Elaeocarpaceae, Rubiaceae, and Myrtaceae. Some summit areas also support dense, low forests (8-12 m high); some of the typical summit tree genera are *Bonnetia, Schefflera*, and *Stenopadus* (Huber 1995).

The scrub formations are the most diverse, both physiognomically and floristically. Taxa frequently found in the summit scrub include *Tepuianthus, Gongylolepis* (and other Asteraceae), *Clusia, Bonnetia, Maguireothamnus, Tyleria, Ilex*, and *Blepharandra*. On the higher summits one finds páramo-like formations with colonies of stem-rosette Asteraceae as well as thick-stemmed *Bonnetia* spp. The high-mountain fields are rich in Rapateaceae, Xyridaceae, Cyperaceae, and Eriocaulaceae. The pioneer formations are characterized most by terrestrial rosettes of several genera of Bromeliaceae (Huber 1995). Overall, Pantepui shows a remarkably high degree of endemism, including 23 endemic genera (Berry et al., 1995).

Guianas-Eastern Amazonia

East of the transverse dry belt discussed above, the region including Amapá, eastern Pará, and northwestern Maranhão states and extending through the Guianas has been treated in several ways by phytogeographers (much of the following review is taken from Daly and Prance [1989]). It has strong floristic affinities with Brazil's Atlantic forests and probably was connected to them via the coast during past interglacials (e.g., Mori et al. 1981; Andrade-Lima 1982). [sentence moved up] Ducke and Black (1953) considered the region under the influence of the tides, i.e., the estuary of the Rio Amazonas and the lower Rio Tocantins ("Atlantic Sector"), to be a separate region strongly characterized by tidal várzeas; Marajó, at the mouth of the Rio Amazonas is a still poorly-known island the size of Switzerland with vast floodplain forests and flooded "campos" but also large areas of humid terra firme forest (Huber, 1898).

Ducke and Black (1953) subdivided the eastern region into the Northeastern and Southeastern Hylaea on opposite sides of the main river. Hueck's (1972) homolog of the latter excluded the basin of the Rio Xingu, and he used the low mountains separating Brazil from the Guianas to divide northeastern Amazonia into the Northeast Sector and the Guianas.

Prance (1989) eventually considered the entire eastern region (minus a homolog of Hueck's Northeast Sector) to be a phytochorion distinct from the rest of Amazonia, even though it does not meet White's (1979) criteria of 50% endemism or 1000 endemic species. Mori (1991) considered the Guianas and parts of adjacent Brazil and Venezuela to comprise a distinct floristic province. In contrast, Huber (1994) proposed a more restricted Eastern Guayana Province consisting essentially of the Guianas plus the Orinoco delta, and so excluding the northeastern Amazon Valley. He argued that this represents a more homogeneous geomorphologic unit, i.e., alluvial coastal plains alternating with hilly terrain on the eastern Guiana Shield, while maintaining high endemism, including the genera *Potarophytum* and *Windsorina* (Rapateaceae), *Elephantomene* (Menispermaceae), and *Lembocarpus* (Gesneriaceae). Clearly, the delimitation of this region is still under debate.

The region as defined by Prance (see map) is more diverse than western Amazonia in climates and topography, if not biologically. The southern Guianas are bordered by modest east-west oriented mountain ranges plus some high inselbergs, and southeastern Amazonia by a number of lower north-south oriented ranges. In the northeastern portion of the region there is the "hill country" (Ducke and Black 1953) of the middle and upper courses of the Atlantic-draining rivers between the Amazon and Essequibo. Many of the sediments of the region are old and derived from the Barreira formation; one finds mostly nutrient-poor kaolinic soils on level ground and sandy podzols on slopes.

Rainfall is moderate to relatively high, and seasonal to markedly so in most places; Mazaruni Station in Guyana has ca. 2570 mm of rain and no month with less than 100 mm; on the other hand, Belém receives more rain (ca. 2730 mm) but experiences a brief dry season, and Sipaliwini, Surinam receives ca. 2070 mm of rain but experiences a five-month dry season and hydrologic stress for about two months (cf. climate diagrams in Walsh 1996).

It is a region mostly of clear-water rivers draining the ancient, weathered crystalline Guiana and Brazilian shields. The rivers have well-defined, often rocky beds, and stable banks, so the terra firme and floodplains are better defined than in western Amazonia; the upper reaches of many have rapids, which are difficult for transport but make excellent habitats for Podostemaceae and some other aquatics adapted to fast-flowing clear waters. The lower reaches of many have broad mouth-bays.

The vegetation in the northeastern part of this region is heterogeneous; it is dominated by humid forests but there is also a strong presence of seasonal forests. There are also edaphic monodominant and oligarchic forests, notably the aforementioned "wallaba" (*Eperua* spp.) forests on white-sand soils and the "mora" (*Mora excelsa*) forests in low-lying and some poorly drained areas, both in Guyana (ter Steege 1993). A species characteristic of dry hills from Monte Alegre to Macapá is *Peltogyne paradoxa* (Ducke and Black 1953).

The southeastern portion is more homogeneous and more thoroughly dominated by humid forests. Prominent elements here are the Brazil nut (*Bertholletia excelsa*), *Cenostigma tocantina, Bombax tocantinum*, and *Bauhinia bombaciflora* (Ducke and Black 1953).

Dominant families in much of eastern Amazonia and the Guianas include the Lecythidaceae, Chrysobalanaceae, Burseraceae, Fabaceae s.l., Lauraceae, and Sapotaceae. One of many species restricted to the eastern region as a whole is the important leguminous timber tree "acapú," *Vouacapoua americana*, **replaced in central Guyana by *V. macropetala*. Other endemic taxa are *Protium demerarense, P. plagiocarpium, Corythophora amapaensis,* and *Lecythis persistens*. There are more narrow endemics in French Guiana and Guyana than elsewhere in this phytochorion.**

Amazonia (remainder)

Except for the vicinity of Manaus, the flora of the remainder of Amazonia is considerably more poorly known than that of eastern Amazonia and the Guianas. While this vast region is mapped here as a single unit, further research on the subdivisions of Amazonia discussed below will permit better definition of their boundaries and will likely reveal that they are as distinct from each other as they are from the eastern phytochorion and therefore deserving of equal status. Although several phytogeographic subdivions of Amazonia have been proposed since that presented by Ducke and Black in 1953 (see comparison in Daly and Prance 1989), all have been based on that seminal work (as is much of the discussion below), and the more than 500 species distributions analyzed therein have yet to be re-examined.

The Northern Hylaea consists of the Rio Negro basin, the lower and middle Japurá, and the western Trombetas basin. Excluded is the upper Rio Branco, which has a 6-8 month dry season and large areas of dry forest and savanna vegetation. Prance's (1977) northern sector included only the lower Negro basin. Particularly in the upper Rio Negro, the rainfall is greater than south of the Solimões-Amazonas and is displaced later in the year; Taraquá receives almost 3500 mm/year, and the months of highest rainfall are in the middle of the year versus the end of the year in extreme southern Amazonia (Nimer 1977). The river drains ancient sandstone and quartzite formations, consequently the region is characterized by blackwater rivers and much (but by no means all) of its vegetation grows on white-sand soils. Much of the topography is relatively flat and low, but farther north there are isolated low granitic mountain ranges to 800 m elevation whose summits shelter species of *Clusia* and terrestrial Bromeliaceae and Orchidaceae. Still farther north, the Northern Hylaea lowlands overlap geographically with the isolated sandstone plateaus of southern (principally Venezuelan) Guayana, discussed above.

Soils are diverse (Projeto RADAMBRASIL 1975-1981); tall humid forests on clayey soils are particularly frequent in the lower Rio Negro basin, but the most characteristic formations are the Amazonian caatingas and their transitions to campina (described above). Dominant families in the Northern Hylaea are the Fabaceae s.l. (especially Caesalpiniaceae), Vochysiaceae, Sapotaceae, Chrysobalanaceae (outside the caatingas), Euphorbiaceae, Clusiaceae, and Linaceae. There is higher diversity and density of Orchidaceae, Proteaceae, Linaceae, and arborescent Malpighiaceae than elsewhere in Amazonia. The Rapateaceae have one center of diversity here; the other is in the Guayana Highland.

The Northern Hylaea is higher in endemism than most of Amazonia, especially at the generic level; examples are the monotypic genera *Asteranthos* (Lecythidaceae) and *Lorostemon* (Clusiaceae), the immense *Aguiaria* (Bombacaceae), and *Barcella* (Arecaceae). There are many endemic species in the legume genera *Dimorphandra, Peltogyne, Eperua, Heterostemon,* and *Elizabetha;* among the many other northern endemics are *Protium reticulatum, P. carolense, Campnosperma gummiferum*, and *Eschweilera rionegrense*.

One of the more significant economic species that is (probably) endemic to the Northern Hylaea is guaraná, *Paullinia cupana* var. *sorbilis*, now known only in cultivation.

The Northwestern Hylaea of Ducke and Black lies entirely within Colombia; in addition to the Colombian upper Rio Negro (upper Uaupés and Içana) it includes the Guainía, Guaviare, Vichada, Apaporis, and upper Caquetá rivers. Although the latter are not tributaries of the upper Rio Negro, they are linked by the high rainfall and relatively aseasonal climate; the frequency of sandy soils and therefore blackwater rivers; the isolated plateaus of quartzite and sandstone, and their proximity.

Prance's (1977) northwestern sector was more broadly -- and probably more satisfactorily -- defined and includes this region plus all of the upper Rio Negro, which better unites the areas of Amazonian caatingas and campinas/banas on very poor white-sand soils (see above) and outlying sandstone plateaus. The Western Guayana Province of Huber (1994) is similarly defined, but he ascribed its affinities to the greater Guayana Region. Indeed, most of the region lies on the Guayana Shield, most of the soils are derived from granitic parent rock or weathering of quartzite or sandstone mountains, and several of the typical Guayanan families are well represented there (Rapateaceae, Tepuianthaceae, Theaceae, Humiriaceae, Xyridaceae). In addition, more recent analyses have indicated closer relationships between the Guayana Highland flora and the surrounding lowlands (e.g., Berry et al., 1995).

The lowland forests of the Northwestern Hylaea display a modest range of physiognomies correlated with soil type and drainage. Some existing floodplains have somewhat fertile soils, while the remaining soils tend to be strongly leached and nutrient-poor. Most of the forest species diversity is accounted for by slender trees. In the middle Caquetá, the predominant families in well-drained soils are the Fabaceae s.l., Sapotaceae, Lauraceae, Chrysobalanaceae, Moraceae, and Lecythidaceae; typical species are *Goupia glabra, Clathrotropis macrocarpa*, and *Swartzia schomburgkii*. The affinities are mostly Amazonian, especially with the Rio Negro (Duivenvoorden 1994, 1995).

The sandstone plateaus and associated lowlands, notably the Sierra de Chiribiquete and the Mesa de Araracuara, are characterized more by species-poor low forests and especially by open and shrubby formations in which shrubs and herbs dominate in number, diversity, and endemics. The affinities of these formations is definitely with the Guayana region, evidenced by *Tepuianthus, Vellozia, Bonnetia, Abolboda, Graffenrieda, Navia*, and other typical Guayanan genera (Estrada and Fuertes 1993). The most species-rich families are Rubiaceae, Melastomataceae, Orchidaceae, Bromeliaceae, and Cyperaceae. Species apparently endemic to Chiribiquete include *Cuphea chiribiquetea, Hibiscus sebastianii, Ouratea chiribiquetensis, Croton chiribiquetensis*, and *Apodandra corniculata* (Cortés-B. et al. 1998); other taxa endemic to the plateaus of this region include *Clusia chiribiquetensis, Styrax rigidifolius, Navia garcia-barrigae, Schoenocephalium martianum, Xyris araracuarae* (Duivenvoorden and Lips 1995), and the monotypic genus *Pseudomonotes*.

The Western Hylaea is essentially an immense alluvial plain, with flat or usually gently undulating terain, on both sides of the Rio Solimões/Marañon. It is a region of great beta-diversity (habitat diversity) characterized by instability: the white-water rivers are meandering and often braided, and their courses are continually changing; as a consequence, one quarter of the lowland forests in this region show characteristics of recent erosional or depositional activity, and 12% of these forests in Peru are currently in successional stages along rivers (Salo et al. 1986).

In this region, the distinction between terra firme and the often broad várzeas (floodplains) is blurred. The floodplain forests are richer and floristically distinct from those of eastern Amazonia; species unknown in the floodplains of the Eastern Hylaea are *Piptadenia pteroclada, Parkia inundabilis*, and *Manilkara inundata*.

Compared with the eastern portion of the hylaea, there are more species and individuals of epiphytes in general and of palms. The non-flooded forests are rich in Meliaceae, Moraceae, and Cecropiaceae (including high densities of *Ficus* and *Cecropia*) and species of *Strychnos* and *Theobroma*; the understory is rich in *Heliconia*, Zingiberaceae, and Marantaceae. The northern part of the region is relatively poorer in Fabaceae and Lecythidaceae, which dominate more in more nutrient-poor soils.

Numerous species are endemic to the Western Hylaea in the broader sense (including part of the northwestern and southwestern Hylaea); among them are the monotypic Rubiaceae genus *Striolaria*, as well as *Matisia cordata, Pradosia atroviolacea*, *Fittonia albivenis*, *Encephalosphaera lasiandra, Schoenobiblus peruvianus*, *Zamia amazonum, Platymiscium stipulare, Tapirira retusa, Thyrsodium herrerense, Anacardium parvifolium*, and various species of *Strychnos*.

Several areas of white-sand soils occur along the upper Solimões/Marañon, such as those near São Paulo de Olivença, the mouth of the rio Tonantins, and Iquitos, Peru. These areas are notably lacking in Rapateaceae, but other species otherwise characteristic of the upper Rio Negro are *Ladenbergia amazonensis*, *Lissocarpa benthamii*, and *Iryanthera obovata*.

The Southern Hylaea includes the basins of the Rio Tapajós, the Rio Madeira except for the latter's extreme southern and southwestern portions, and possibly the lower Purus; Prance (1977) included part of the Xingu basin. Much of this region is on the Brazilian Shield, so most of the rivers are clear-water and have stable courses. Like western Pará north of the Amazonas (from which the great river serves as a barrier for many species), much of this region receives only moderate rainfall and experiences a pronounced dry season.

Most of the vegetation is humid non-flooded forest, but there are some areas of semi-deciduous forest (notably near Belterra in the Tapajós basin), and there are large areas of white-sand campinas on the upper Tapajós and particularly the upper Madeira, whence the monotypic genus *Aripuana* (Gentianaceae) was described in 1997 (Struwe et al. 1997). The Tapajós is home to a number of endemics, including *Lophanthera lactescens* (Malpighiaceae). Other species endemic to the Southern Hylaea include *Goniodiscus elaeospermus.* Still, this region is not as distinctive as the Northern Hylaea, with which it shares many species, especially those whose distributions straddle the middle Amazonas; many others reach their eastern or western limits in the Southern Hylaea.

The Southwestern Hylaea of Ducke and Black consisted of the state of Acre in Brazil, and they indicated its flora as being essentially hylaean but including some southern (extra-Amazonian) elements. More recent research shows that this region is larger, that its floristic affinities are rather more complex, and that it can be divided into two rather distinct sectors based on geomorphology, climate, and floristic composition. The mix of affinities in southwestern Amazonia makes it the basin's center of diversity for palms; some 75 species occur in Acre alone (E. Ferreira, unpublished data).

The phytogeographic significance in Amazonia of ancient zones of uplift is only gradually being recognized (cf. Daly and Prance 1989, Patton et al. 1994, 1997); one of these, the Fitzcarrald Arch, separates the upper Rio Juruá of Acre and contiguous Peru on the one hand from the upper Purus and upper Madeira of the southeastern half of Acre plus parts of Rondônia, Pando in Bolivia, and Madre de Dios in Peru (see map in Rasanen 1993).

In the latter sector of the Southwestern Hylaea, precipitation is lower and more seasonal; the high concentration of ground sloth fossils points to a long history of relatively dry conditions (Oren 1993). Indeed, a number of species represent northern extensions of Cerrado or Paraguayan elements (e.g., *Casearia gossypiosperma, Cariniana estrellensis, Couepia uiti, Samanea tubulosa, Aspidosperma ramiflorum*), while others make up part of circum-Amazonian or southern peri-Amazonian distributions (e.g., *Amburana cearensis, Poeppigia procera, Myroxylon balsamum, Rhamnidium elaeocarpum*; cf. also Prado and Gibbs 1993). Species restricted to this sector include *Thyrsodium bolivianum, Protium carnosum, Inga pulchriflora, and Byttneria pescapraeifolia*. This sector is also the geographic center of the bamboo-dominated forests of southwestern Amazonia, discussed above (see section on definition of formations).

The upper Juruá receives more rainfall and experiences less of a dry season. Few data are available on soils, but those of the Tarauacá are highly fertile and are famous for producing large fruits. The Brazil nut, *Bertholletia excelsa*, is not known from the upper Juruá. Among the endemics in this sector are *Aristolochia dalyi, Attalea tessmannii, Guapira uleana, Psittacanthus amazonicus, Erythrochiton trichanthus, Eugenia acrensis, Malvaviscus palmatus*. This sector includes outlying Andean foothills such as the Serra do Divisor, which harbors characteristic sub-Andean taxa such the tree fern *Cyathea bipinnatifida,* the cycad *Zamia poeppigiana,* and the palm genera *Aiphanes, Aphandra, Chamaedorea, Chelyocarpus*, and *Dictyocaryum*.

The sub-Andean belt is an ill-defined zone with mixed floristic affinities, many of whose species show rather broad altitudinal ranges. A portion of this flora follows a band of relatively rich soils from southern Central America along the Andean piedmont down to Bolivia; Barro Colorado Island in Panama shares some 22% of its flora with Cocha Cashu in Peru, including *Tabebuia chrysantha*, *Celtis schippii,* and *Mansoa parvifolia* (Gentry and Ortiz 1993). The latter two occur in Acre, Brazil, as do other Central American elements such as *Euphorbia elata* and *Phyllocarpus riedelii*. There are islands of relatively fertile soils and/or higher elevations more distant from the piedmont, such as parts of northwestern Acre and northeast of Iquitos around Yanamono (Gentry and Ortiz 1993). Sub-Andean species occurring in some of these islands include *Solanum grandiflorum, Brunfelsia grandiflorum, Cuatresia fosteriana, Monolena primuliflora, Centropogon cornutus, Wettinia augusta*, and *Dicranopygium rheithrophilum*.

A number of small plant families are endemic to Amazonia or Amazonia plus the Guianas, although few of them are widespread in the region. They include the Dialypetalanthaceae, Peridiscaceae, Duckeodendraceae, Rhabdodendraceae, Lissocarpaceae, and Polygonanthaceae. [no paragraph] Well-known plant resources native to at least part of Amazonia include guaraná (*Paullinia cupana*), manioc (*Manihot esculentum* cvs.), rubber (*Hevea brasiliensis*, etc.), ipecac (*Psychotria [Cephaelis] ipecacuanha*), cocoa (*Theobroma* *cacao*), several types of curare (e.g., *Chondodendron tomentosum*), rosewood (*Aniba duckei*, etc.), Brazil nut (*Bertholletia excelsa*), and vegetable ivory (*Phytelephas* spp.).

Southern Amazonia transitions

Semi-deciduous forests comprise the principal type of transition in southern Amazonia. These forests, essentially Amazonian but with some endemics and Cerrado elements (see section below on the Cerrado), frequently occur in patches along the southern periphery of Amazonia.

Moving from west to east, near the border with northeastern Bolivia the Serra dos Parecis and the Serra dos Pacaás Novos in Rondônia are long narrow strips of high ground running NW-SE which include often rocky campos of uncertain affinities; they probably should not be classified under "campo rupestre," a term that carries strong geological and floristic connotations with the Serra do Espinhaço in Minas Gerais and southern Bahia (discussed below under Savannas).

In Mato Grosso, the Amazon forest reaches south and up into many of the river's southern tributaries, gradually narrowing to gallery forests as they penetrate into the Cerrado (Ackerly et al. 1989).

The limits of Amazonia in Maranhão are confused by the dissected terrain and the roles of additional vegetation types. The moister northwestern part of the state is already markedly seasonal and a significant minority of the trees is deciduous. The center is at present a large, highly disturbed area of mostly secondary forests and anthropic savannas, both dominated by the "babassu" (*Attalea speciosa [Orbignya phalerata]*) palm. To the east, babassu formations, seasonally flooded grasslands and hardpan savannas intergrade irregularly not into Cerrado but into the xerophytic "caatinga" vegetation of northeastern Brazil, with some Cerrado elements present. In the rolling hills and small plateaus toward the southern periphery, semi-deciduous forests and liana forests (including babassu forests) form a mosaic with patches of Cerrado vegetation.

In southeastern Pará, the boundary of Amazonia angles northeastward, following but not including the Rio Araguaia basin, crossing it and cutting across the northern tip of Goiás just south of the confluence with the Rio Tocantins. This region shows the greatest extent of liana forests.

The babassu forests and liana forests are not easily distinguished and indeed have been treated either together (e.g., Pires and Prance 1985) or separately (Prance and Brown 1987). Here the former is considered an anthropic version of the latter, and judgment is reserved on the origin of liana forests.

Liana forests display moderate biomass, a highly irregular and generally lower canopy, few large trees, and a rather impenetrable understory of climbing, fallen, and winding lianas. The woody species appear to flower and fruit only briefly and probably supra-annually, so their floras are poorly documented, but they contain Amazonian elements plus some Cerrado elements and some endemics. In Amazonia, the principal liana families are the Fabaceae s.l., Bignoniaceae, Malpighiaceae, Dilleniaceae, and Menispermaceae; the babassu palm is of course often common; and tall trees include *Hymenaea parvifolia, Bagassa guianensis, Tetragastris altissima, Astronium graveolens* (syn: *A. gracile*), *Apuleia leiocarpa var. molaris, Sapium marmieri, Castilla ulei, Myrocarpus frondosus, Acacia polyphylla*, and two important economic trees: Brazil nut (*Bertholletia excelsa*) and, on more humid sites, mahogany (Pires and Prance 1985; Prance 1989). Pires (1973) estimated that liana forests occupy as much as 100,000 km^2 in southern Pará state between Cametá on the Rio Tocantins and Altamira on the Rio Xingu (later, Pires and Prance [1985] wrote wrote that the boundaries are between Santarém and Marabá and south to the Cerrado).

Liana forests have been the object of more discussion than research. There are serious disagreements as to whether they are natural or anthropic formations. There is no dispute that they occur in climatic and vegetational transitions between moist forests and cerrado or other savanna/savanna woodland vegetation, including other large areas in the Rio Jari basin and in Roraima (Prance 1989), as well as a long inland belt in Brazil's Atlantic forest complex (e.g., Thomas et al. 1997). Pires (1973) observed that many are rich in mineral deposits. Nelson (1994) observed that post-burn sites tend to have high density of lianas, and stressed the need to compare the species of burn survivors with those of liana forest. He proposed that larger patches of liana forest could be a result of larger natural fires such as El Niño fires, and small ones could be due to indigenous swidden fires, as proposed by Balée and Campbell (1990).

Atlantic forest complex (Fig. 2b)

Brazil's "Complexo Mata Atlântica" or Atlantic forest complex comprised a relatively narrow and essentially continuous fringe of moist vegetation between the coast and drier uplands of the Brazilian Shield. In southern Bahia the width of the fringe was 100-200 km (references in Thomas et al. 1997). The vegetation cover consisted principally of humid forests but included relatively small areas of floodplain forests, species-poor mangroves, transitional liana forests (inland in southern Bahia), piedmont slope forests of the Serra do Mar, and edaphic grassy or thicket-type savannas (e.g., Mori 1989). The coastal plain supports a complex continuum of vegetation types on sandy soils referred to collectively as "restinga," which ranges from sparse coastal scrub (including dune vegetation) to forest (e.g., Lacerda et al. 1993, Araújo 1997; Mamede et al. 1997; Peixoto and Silva 1997; Thomas et al. 1997). The restinga forests include *Allagoptera*, *Bonnetia* and, in coastal Bahia, the economically important palm "paxiúba," *Attalea funifera.*

From southern Bahia south to Rio de Janeiro state, most of the lowlands do not receive more than 1500 mm of rain annually, but in many places it is well-distributed throughout the year and the relative humidity is high; in these areas the region can support well-developed humid forests with higher densities of epiphytes than in most Amazonian forests. Southward from São Paulo, most of the lowland forests are semi-deciduous.

In stark contrast with Amazonia, the Atlantic forest complex is the land of Myrtaceae. This family and the legumes are usually the two dominant tree families in the humid forests of southern Bahia, the "tabuleiro" forests on low flat tablelands in Espírito Santo, and the piedmont slope forests of the Serra da Juréia in São Paulo. At one site in southern Bahia, the Myrtaceae comprised 20-25% of the trees >10 cm diam. (Mori et al. 1983). Other important tree families include the Sapotaceae and Euphorbiaceae in southern Bahia; Sapotaceae, Lauraceae, and Rubiaceae in Espírito Santo, and Melastomataceae and Annonaceae in Juréia (Thomas et al. 1997; Peixoto and Silva 1997; Mámede et al. 1997, respectively).

The flora of the Atlantic forest complex is ancient. Climatic cycles not only affected the width of the fringe, they apparently caused cyclical interruptions (e.g., Daly 1992, and references cited therein) as well. The region shows strong affinities with Amazonia (Rizzini 1963, 1979), with which it shares a number of species; clearly the two floras were linked during more humid interglacials via the coast and/or gallery forests (e.g., Mori et al. 1981). Mixtures of Amazonian and Atlantic complex elements are found on the (aforementioned) isolated moist inland granitic plateaus or "brejos" of northeastern Brazil (e.g., Andrade-Lima 1982; Mayo and Fevereiro 1982).

For a continental flora, however ancient, the endemism in the Atlantic forest complex is remarkable and has been estimated from various study sites at approximately 41.6-44.1% overall (Thomas et al. 1998), 53% for trees (Mori et al. 1983), 74% for Bromeliaceae, and 64% for palms, plus a stunning 40.9% of the genera of bambusoid grasses occurring in the region (see Mamede et al. 1997). The latter include *Alvimia, Criciuma,* and *Eremocaulon* (Soderstrom et al. 1988; Judziewicz et al. 1999).

Brazil's Atlantic coastal range forms an interrupted chain 0-25 km inland from the coastal plain in Rio de Janeiro, São Paulo, and eastern Minas Gerais states. The Serra da Mantiqueira parallels and is separated from the Serra do Mar by the valley of the Rio Paraíba do Sul near the vertex of the three states.

The topography of the mountain ranges is irregular and highly dissected. Several peaks near Teresópolis exceed 2200 m, and those of Itatiaia in the Serra da Mantiqueira reach nearly 2800 m. Rainfall varies greatly by location, ranging from ca. 1000 mm in the lowlands to 2000-2500 mm in montane forests (Guedes-Bruni and Lima 1997).

The rounded and dissected hillsides of the piedmont zones have not only topographies but also soils very different from the sandy "restingas" of the coastal plains, and they support a distinct flora. Trees characteristic of the up to 35 m canopy include *Cariniana estrellensis, Hyeronima alchorneoides, Virola oleifera, Jacaratia spinosa, Eugenia spp., Pseudopiptadenia inaequalis, Moldenhawera floribunda, Chrysophyllum imperiale*, and *Aspidosperma parvifolium*. The montane zones above 800 m support dense, humid forests rich in epiphytes and lianas. Canopy species include numerous *Lauraceae, Eugenia, Tibouchina, Solanum swartzianum, Vernonia arborea, Cabralea canjerana*, and *Symplocos variabilis*, while typical understory taxa are *Hedyosmum brasiliensis, Myrcia* spp., *Psychotria velloziana, Guatteria nigrescens*, and large numbers of *Euterpe edulis* (a source of hearts of palm) and the tree fern *Cyathea delgadii*.

Between 1400-1800 m are lower and more open forests on shallow soils and large rock outcrops. Tree species include *Miconia* spp., *Rapanea* spp., *Lamanonia speciosa, Weinmannia* spp., and *Drimys brasiliensis*. Finally, in similar substrates at the highest elevations are the "campos de altitude" ("high fields"), which support an open formation of herbs and shrubs, the former rich in Bromeliaceae, Cyperaceae, Xyridaceae, Eriocaulaceae, and Orchidaceae, and the latter in Melastomataceae, *Fuchsia* spp., Asteraceae, Ericaceae, and the bamboo *Chusquea pinnifolia* (Guedes-Bruni and Lima 1997).

The more important useful plants of this region include an important source of hearts of palm, *Euterpe edulis*, the timber tree "caxeta" (*Tabebuia cassinoides*), Brazilian rosewood (*Dalbergia nigra*), one of the "piassava" palms, *Attalea funifera*, and Brazil-wood (*Caesalpinia echinata*), whose wood is used as a dyestuff and fine woodwork, and for which the country of Brazil was named (e.g., Mamede et al. 1997; Thomas et al. 1997).

Tropical Dry Forests

Introduction

Tropical dry forests are the dominant type of vegetation cover in a significant portion of the Neotropics, including large areas of Mexico, the Greater Antilles, northern Colombia, northern Venezuela, Brazil south of the Amazon basin, the western Ecuador-Peru frontier region (Young 1997; Centro de Datos para la Conservación [CDC]-Peru et al. 1997), southeastern Bolivia (Killeen 1997), Paraguay, and northern Argentina. They support a significant percentage of the Neotropics' biodiversity (Mares et al. 1992; see Fig. 9a, 9b).

These forests generally have an annual preciptation of less than 1600 mm, whereas tropical moist forests generally receive more than 2000 mm/year. Some areas in the Neotropics receiving 1400-1800 mm are covered with tropical moist forest, such as the Atlantic coastal forests ("Mata Atlântica") of southern Bahia, Brazil (Mori et al. 1983). This is due to the equable distribution of rainfall throughout the year and consequent lack of a dry season. Some tropical dry forests have two dry seasons per year.

Tropical dry forests are often similar physiognomically to tropical humid forests. The major differences are that most of the woody plants are deciduous during the dry season, they are generally shorter in stature and lower in biomass, diversity, density of epiphytes, and density of lianas (but more vines, see Gentry 1995). Toward the more arid extreme, however, as in most of the Guajira Peninsula in Colombia and in most of Lara and Falcón states in northwestern Venezuela, tropical dry forest formations generally become much lower in stature, more open tropical arid scrub formation with an abundance of cacti.

Tropical dry forests are generally much less rich in plant species than tropical humid forests, typically ca. 50-70 species >7.5 cm dbh in 0.1 ha sample plots (Gentry 1995). In some of the most arid tropical dry forest formations, monospecific stands can occur, such as *Loxopterygium huasango* or *Prosopis* sp. woodlands in the region of Tumbes in southwestern Ecuador/northwestern Peru. On the other hand, tropical dry forests are often higher in endemism than adjacent humid forests (Gentry 1995). The most diverse tropical dry forests known in the Neotropics occur at higher latitudes; examples are found in Chamela and Jalisco in Mexico (Gentry 1995) and Chiquitanía in eastern Bolivia; in the latter, trees contributed 124 species in a 400 ha plot, while there were 101 species of herbs and 85 species of lianas (Killeen et al. 1998).

An interesting structural feature of the transition between tropical humid forests and tropical dry forests or other seasonal formations such as savannas is the frequent occurrence of a belt of liana forest, i.e., forest with a greater than usual abundance of lianas. Examples of liana forest occur in the transition between the Mata Atlântica and caatinga, and that between the southern Amazonian forests and the Cerrado. The occurrence also has been noted in the Old World, e.g., liana forests in eastern Australia (e.g., Webb. & Tracey 1994).

A significant difference between tropical dry and humid forests is the greater importance of seed dispersal by wind in the former (Gentry 1982; Wikander 1984; Armesto 1987). In some dry forests, the canopy is made up almost entirely of wind-dispersed tree species (Killeen et al. 1998). In contrast, in the moist forests of central French Guiana only 9.8% of dicotyledonous plants are wind-dispersed (Mori and Brown 1994), and in the wettest of the tropical forests, e.g., the Chocó of the Pacific coast of Colombia, more than 90% of the trees are animal-dispersed (Gentry 1982, 1991).

The flowering plant family composition of tropical dry forests is similar to that of humid forests, with a few exceptions, such as the greater richness and abundance in the former of the Capparidaceae, Cactaceae, Erythroxylaceae, Zygophyllaceae, Anacardiaceae, Asteraceae, Malvaceae, and Lamiaceae. An example of this pattern is illustrated by the Anacardiaceae. In tropical humid forest plots of 0.1-1+ ha, this family is usually represented by only a few individuals, but it is dominant or co-dominant in some dry forests, e.g., *Schinopsis*-dominated forests in the Chaco.

Tropical dry forests occur in many of the phytochoria covered by this chapter (Fig. 9b). The following discussion emphasizes the two most significant regions dominated by dry forest, the caatinga of northeastern Brazil and the Chaco of south-central South America. For an enlightening discussion of the disjunct patches of tropical dry forest that arch across south-central South America, we refer to the reader to Prado and Gibbs (1992).

Additional important areas of tropical dry forests occur in the following areas: the Tucavaca Valley and adjacent parts of eastern Bolivia (Parker et al., 1993), the Tumbes region the western Ecuador-Peru frontier; northern Colombia-Venezuela (Catatumbo-Magdalena): the fringes of the Llanos region of Venezuela and Colombia; parts of northern Venezuelan Guayana; parts of Roraima, Brazil; the Tarapoto region of central Peru; some dry inter-Andean valleys; the transition zone between Amazonia and the Cerrado; the Cerrado region; the Pantanal; and the those occurring in the diagonal dry belt crossing through Santarém in eastern Amazonia.

Coastal Cordillera of Venezuela

Venezuela's Coastal Cordillera is an ancient complex of approximately 45,000 km^2. The uplift in this region took place in the lower Tertiary some 60 million BP, making it almost twice as old as the Andes, with whose northeastern branch it is in contact. The western portion of the Coastal Cordillera consists of two parallel, essentially east-west oriented mountain chains, the Serranía del Litoral and behind it the Serranía del Interior. The eastern portion, separated by the Depression of Unare, is the Turumiquire massif (2590 m) and the lower cerros Humo and Patao and continuing on to Trinidad as the Northern Range (Huber 1997).

The topography ranges from sea level to a number of peaks over 2000 m, reaching 2765 m on Pico Naiguatá. The climate varies greatly as a function of elevation and orientation. Those of the lower elevations tend to be highly seasonal and arid: Barcelona (7 m elev.) experiences hydrological stress seven months of the year (climate diagram in UNESCO 1981), and in places the average annual temperature is over 24°C (Huber 1997), whereas above 800 m on the windward slopes and 1000 on the leeward slopes there are frequent mists and cooler temperatures (10-20°C).

Forests predominate, but the vegetation types range from coastal mangroves to coastal thorn scrub, hill savanna, deciduous forest, montane forests that are semi-deciduous to evergreen, montane cloud forest, upper montane elfin forest, and upper montane scrub ("subpáramo"). The cloud forests are the most complex in structure, most species-rich, and highest in number of endemics. The floristic affinities of the Coastal Cordillera are with Mesoamerica, the Caribbean and, to a lesser degree, the Andes (Huber 1997).

Caatinga

The semi-arid region of northeastern Brazil commonly known as the caatinga was probably covered to a large extent in early Holocene times by tropical dry forest or woodland. However, much of the caatinga vegetation is a shrub steppe, with extensive patches of bare soil or rock. The dominant plant cover today reflects the long history of human occupation of northeastern Brazil. Prado and Gibbs (1993) have postulated that the caatinga is the northeastern extension of a formerly much broader arc of tropical dry forest that covered a large portion of south-central South America, particularly during the period 18,000-12,000 b.p. and probably earlier dry periods as well.

There are two published opinions as to the origin of the Tupi word caatinga. The most commonly cited etymology is "white forest" (Andrade-Lima 1954), which probably refers to the whitish bark of many of the trees, most apparent during the dry season. Another interpretation is "open forest" or "open vegetation" (Andrade-Lima 1981). This vegetation should not be confused with the caatinga or campinarana of the upper Rio Negro region of Brazil and Venezuela.

The caatinga phytogeographical region extends from about 2^{o}54' - 17 ^{o}21' S, and covers an area between 600,000-900,000 km2 (Andrade-Lima 1981; Sampaio 1995). Caatinga vegetation covers part or all of the Brazilian states of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, and smaller parts of Minas Gerais and Maranhão. Rainfall varies from 300-1,000 mm/year and is concentrated in a 3-5 month period. The rainfall pattern is extremely erratic, characterized by years of extreme drought, followed by an occasional year of torrential rains. The rainy season occurs during the Southern Hemisphere summer and autumn (January-June). The climate is consistently hot, the average temperature ranging between 23-27 ^{o}C. The average relative humidity is about 50%, and the rate of evapotranspiration is very high.

The caatinga is underlain by severely eroded crystalline bedrock of the pre-Cambrian Brazilian Shield and Paleozoic and Mesozoic sedimentary basins. The generally level terrain, which lies at approximately 400-500 m elevation, is broken by occasional mesas and isolated mountain ranges which reach 1,000 m elevation. The soils of the caatinga are highly variable, ranging from shallow and rich in clay to rocky, deep, and sandy. In the southern extension of the caatinga into southern and northern Minas Gerais, soils derived from the Bambuí Group limestone are calcareous. In general, the soils of the caatinga are poor in organic material but richer in nutrients than the soils that support cerrado vegetation (Andrade-Lima 1981).

The boundaries of the caatinga are not always clear-cut. The caatinga grades into cerrado toward the south and west. In many cases the change from caatinga to cerrado follows the topographic gradient. The basins support caatinga vegetation and the plateaus suppport cerrado. To the east, particularly in Bahia, the caatinga grades into a transitional sequence of tropical dry forest, tropical semi-deciduous forest, liana forest, and tropical humid forests (Mata Atlântica; Mori 1989). In parts of Rio Grande do Norte, caatinga extends virtually to the coast.

The caatinga is essentially a mosaic of vegetation types. The core caatinga vegetation is characterized by trees and shrubs that are often spiny, mostly deciduous during the dry season, sometimes with small leaves with a waxy cuticle. Only a few woody species retain their leaves during the dry season, for example *Ziziphus joazeiro* and *Maytenus rigida*. Several of the woody plants store water in their swollen trunks, e.g., *Cavanillesia arborea* and *Chorisia glaziovii*. Others, such as *Spondias tuberosa, Sterculia striata,* and *Thiloa glaucocarpa*, store water and/or food in tuberous roots. Succulents such as cacti, bromeliads, and *Euphorbia phosphorea*, are components of typical caatinga vegetation.

This mosaic also includes gallery forest along the Rio São Francisco and its tributaries; cerrado (Castro et al. 1998); humid submontane forest ("brejo de altitude"); and grasslands that may or may not be floristically be part of the Cerrado phytogeographical region.

The core caatinga is divided by some authors into two types based on a moisture gradient: an eastern band of more humid vegetation called "agreste" and a drier inland type called "sertão." This division is somewhat arbitrary. Andrade-Lima (1981) classified the vegetation into six units with 12 subunits, and Eiten (1983) divided it into eight physiognomic categories. A thorough review of these classification schemes is beyond the scope of this summary; a few characteristic types will be mentioned.

- Arboreal caatinga (Fig. 7b. Height 8-10 m, on soils deeper and moister relative to other caatinga units; canopy coverage over 60%. Characteristic taxa include *Cavanillesia arborea, Tabebuia* spp., *Myracrodruon urundeuva* ("aroeira"), *Schinopsis brasiliensis* ("brauna"), *Aspidosperma spp., Pterogyne nitens, Cereus jamacaru*.
- "Carrasco." Arboreal to shrubby caatinga with tree cover ranging from 10-60% (Eiten 1983).
- "Seridó." A short-grass savanna with deciduous scrub (Eiten 1983).
- Caatinga proper. The most common form of caatinga is a closed-canopy thorn scrub 3-5 m in height with an occasional tree 6-8 m tall.

Species richness in caatinga vegetation varies markedly. In a survey of quantitative inventories cited by Sampaio et al. (1993), there were 38-195 species of woody plants >3 cm diameter at 50 cm above the ground on sites 3-5 hectares in area. Empéraire (1989) catalogued 615 species of vascular plants in the Serra da Capivara National Park, Piauí.

The most speciose flowering plant families are the Fabaceae *sensu lato*, Euphorbiaceae, and Cactaceae. Among the species with the broadest distributions in the caatinga vegetation are *Commiphora leptophloeos, Myracrodruon urundeuva*, and *Anadenanthera colubrina* var. *cebil* ("angico"; *A. macrocarpa* in much of the caatinga literature).

In addition to the core caatinga vegetation of tropical dry forest, woodland, or shrub steppe, there are a few other discrete vegetation units to be mentioned. On the summits of hills and isolated mountain ranges, often occur patches of humid submontane forest called "brejos" or "brejos de altitude." These mostly broad-leaved evergreen forests with trees up to 30-35 m tall have floristic affinities with both the Amazonian and the Atlantic humid forests. Some of the characteristic species of this type of brejo are *Cedrela odorata, Schefflera morototoni, Pilocarpus jaborandi, Dalbergia variabilis, Machaerium amplum, Hymenaea courbaril, Manilkara rufula*, and *Symphonia globulifera* (Andrade-Lima 1981; Lleras 1997).

One distinctive plant community of the caatinga is the sparsely vegetated rocky outcrops dominated by cacti and bromeliads. A plant community often associated with alluvial soils is *Copernicia prunifera, Licania rigida, Geoffroea spinosa* association (Andradade-Lima 1981). Stands dominated by palms are found in various parts of the caatinga, including stands of carnaúba (*Copernicia prunifera*), babassu (*Attalea speciosa [Orbignya phalerata]*), tucum (*Astrocaryum aculeatissimum*), and macaúba (*Acrocomia aculeata*).

The caatinga is recognized by both botanists and zoologists as a biogeographic region and center of endemism (Cabrera and Willink 1973; Andrade-Lima 1981; Cracraft 1985; Prado and Gibbs 1993; Sampaio 1995; Lleras 1997). Its status as a center of endemism for plants is supported by the presence of several endemic genera, such as *Apterokarpos* (Anacardiaceae), *Auxemma* (Boraginaceae), *Neoglaziovia* (Bromeliaceae), and *Fraunhofera* (Celastraceae). Approximately 180 woody plant species are endemic to the caatinga; examples include *Cereus jamacaru*, *Pilosocereus gounellei*, *Cyrtocarpa caatingae*, *Spondias tuberosa, Balfourodendron molle*, and *Patagonula bahiana* (Mitchell and Daly 1991; Lleras 1997; Pirani 1998; see Fig. 8a). It should be noted that floristic inventory of this region is still rather incomplete, and modern taxonomic treatments for many of the key genera are not available.

Contrary to the opinion of some authors (e.g., Andrade-Lima 1981; Bucher 1982), the floristic link between the Chaco and the caatinga is negligible (Prado and Gibbs 1993).

Chaco

The vast region called the Gran Chaco is one of the few places in the world where the transition between the tropics and the temperate zone is not a desert but a transition of landscapes dominated by dry forests and woodlands. A shortened version of the etymology of "Chaco" is "hunting land," from the Quechua word "chaku" (Prado 1993b). The Chaco phytogeographical region falls between about 17-33 S and 57-67 W and covers an area estimated at between 800,000 km2 (Hueck, 1972) and 1,010,000 km2 (Galera and Ramela 1997).

Prado (1993a) indicated that previous authors have confused the Chaco phytochorion (phytogeographical region) with the Chaco geographical region. His phytogeographical concept of the Chaco is narrower than that of previous authors (see Fig. 4 in Prado 1993a). Chaco *sensu stricto* covers parts of northwestern Paraguay, southeastern Bolivia, northern Argentina, and a few square kilometers around Porto Murtinho of Mato Grosso do Sul, Brazil (Prado et al. 1992).

Precipitation varies along an east-west gradient from 1,267 mm/yr in Formosa City to about 350 mm/yr in the southwestern Chaco, both in Argentina. The rainy season occurs in the months of October-April, followed by a harsh dry season in the remaining months of the year. This is the general pattern for the Chaco, however, there is a strong east-west gradient in the duration of the dry season, varying from no dry month in Formosa City to a six-month dry season in Rivadavia, Salta, Argentina.

The climate of the Chaco is strongly continental, with temperature maxima as high as 48^{o}C, and lows to -7.2 ^{o}C. During the austral winter, no point in the Chaco is free from frost except for a narrow band paralleling the major rivers in the eastern Chaco. The mean annual temperature follows a north-south latitudinal gradient varying from about 26 ^{o}C in northern Paraguay to 17 C or less in the Sierra Chaco. There is an east-west gradient in lowest absolute temperatures varying from -1.1^{o}C in Corrientes to -7.2^{o}C in Santiago de Estero, both in Argentina.

The Chaco is a vast, virtually unbroken plain 100-500 m above sea level, which is tilted at a very slight angle to the west. It is underlain by a massive accumulation of Quaternary, Tertiary, Mesozoic, and Paleozoic sediments. The unconsolidated aeolian (i.e., formed by wind) and fluvial Quaternary sediments originated from erosion of the Andes. This approximately 3000 m-thick layer of sediments presses down on the deeply sunken pre-Cambrian Brazilian Shield. The Chaco plains are interrupted by the emergence of hills and mountains such as the Sierra Pampeanas, Argentina, Cerro León, Paraguay, and the Sierra Chiquitos, Bolivia, which range in elevation from 400-2400 m above the plain.

The soils of the Gran Chaco are derived from parent materials consisting of aeolian, fluvial, lacustrine, or marine sediments. In general, the size of the soil particles remains the same along an east-west gradient in the Chaco. The soils are generally fertile, but the main limitations of Chaco soils are poor drainage, high salinity or alkalinity, occasional severe flooding, and some areas of hard-pan (Prado 1993a).

The Chaco s.s. vegetation is bounded by several by several different vegetation types, some of which are transitional in floristic composition, particularly along the eastern Chaco boundary. The Chaco grades into the Monte in its southern limit in Argentina (Cabrera 1976). The westernmost type of Chaco, the Sierra Chaco, is bordered by transition forests (e.g., "Tipa-

Pacará" and "Palo Blanco" forest, which will be discussed later), which in some parts separate the Chaco from the Yungas and the Tucumán-Bolivian montane forests (Cabrera 1976; Prado 1993b).

Chaquenian vegetation. The dominant form of Chaco vegetation is characterized by a forest of trees and shrubs that are often spiny and mostly deciduous in the dry season. The understory is often shrubby, with a variety of herbs and grasses growing in association with bromeliads and cacti, some of which are arborescent. As is the case with the caatinga, the Chaco is a mosaic of vegetation types. This mosaic includes annually flooded gallery forests, the adjacent "selva de ribera," wetlands, palm savannas, grasslands, halophytic shrubby steppes, cactus stands, and communities dominated by *Prosopis* spp. (e.g., algarrobales).

A unique aspect of Chaquenian vegetation is the dominance of the genus *Schinopsis* (Anacardiaceae). In the more humid, frequently waterlogged woodlands of the eastern Chaco, the dominant species is the simple-leaved *Schinopsis balansae*. In the semi-arid, central and western Chaco, the dominant species is the multifoliolate *S. quebracho-colorado*. And on the lower slopes of the western sierras, the dominant species is another multifoliolate species, *S. haenkeana.*

The vernacular name for *Schinopsis* species in the Chaco is "quebracho" (from "quebra hacha," or "break axe"), which refers to the very hard, tannin-rich wood (Prado 1993a). The "quebrachal" of *Schinopsis balansae* is a forest with the canopy dominated by *Schinopsis balansae* in association with *Aspidosperma quebracho-blanco* and *Caesalpinia paraguariensis*. This semi-open forest grows in seasonally waterlogged, saline soils. Its understory often includes thickets of *Schinus fasciculata*, various Cactaceae, *Capparis* spp., and *Celtis* spp. The branches are often festooned with lichens and *Tillandsia* spp.

The central Chaco forests are somewhat transitional between the eastern and the western Chaco, and they are characterized by two different vegetation types with similar floristic composition. The "quebrachal of three quebrachos" is more xerophytic in aspect than the eastern Chaco, and is dominated by *Schinopsis quebracho-colorado, S. balansae*, and *Aspidosperma quebracho-blanco* ("white quebracho"). The "quebrachal of white quebracho" is dominated by *Aspidosperma quebracho-bla*nco, and is characterized by the absence of *Schinopsis* spp.

The Western Chaco forests and the driest and most continental in climate, i.e., with the highest and lowest temperatures. Lianas and epiphytes are rare, and arborescent cacti are abundant. A few of the prominent cacti present include *Stetsonia coryne, Opuntia quimilo*, *Cereus validus, Quiabentia pflanzii*, and *Pereskia sacharosa.*

The most widespread forest in the Western Chaco is the "quebrachal of two quebrachos," which has shared dominance by *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco*. Forests of *Bulnesia sarmientoi* ("palosantales") are also characteristic of the Western Chaco. *Schinopsis quebracho-colorado* is sometimes a subdominant, and some of the characteristic species of this community include *S. triternatum, Tabebuia nodosa, Ruprechtia triflora, Capparis* spp., and the columnar cactus *Stetsonia coryne*.

The third principal formation in the Western Chaco, called arid Chaco woodland, is dominated by *Aspidosperma quebracho-blanco* in association with *Geoffroea decorticans, Prosopsis nigra*, *Cercidium praecox*, etc., along with some characteristic Argentinian Monte species such as *Prosopis torquata, Larrea* spp., *Bulnesia retama*, etc. In some ways the Western Chaco forests resemble the Sonoran deserts of North America, in the dominance by columnar cacti in association with a variety of trees and shrubs. A few genera such as *Cercidium,* *Prosopsis, Acacia*, and *Larrea*, are characteristic of the deserts of North America and the semi-arid regions of south-central South America.

The Sierra Chaco is the upland portion of the Chaco s.s. Three of the Sierra Chaco types are the piedmont sierra forest, which is rich in *Prosopis* spp., the "quebrachal of *Schinopsis haenckiana*," (the western counterpart of *Schinopsis quebracho-colorado*), and the "Mollar" of *Lithrea ternifolia*, which generally occurs on sierran slopes above the belt dominated by *S. haenckiana* and below the floristically Andean belt of *Flourensia* spp. or *Heterothalamus* spp. shrublands.

In addition to the dry forests and woodlands previously described, the Chaco s.s. includes several other vegetation types, such as extensive stands of *Prosopis* spp. and the palm stands and palm savannas of *Copernicia alba*, halophytic grasslands dominated by *Spartina argentinensis* (with or without trees; this is the same grass that dominates north-temperate salt marshes).

Non-chaquenian vegetation. The Chaco s.s. is intruded upon by a few non-Chaquenian vegetation types as defined by Prado (1993a, 1993b). These vegetation types are 1) gallery forests bordering the rivers Paraguay, Paraná, and their western tributaries; 2) the "selva de ribera", which is a non-flooded semi-deciduous forest that borders the outer margins of the gallery forest; and 3) patches of tropical dry forest on calcareous or other mineral-rich soils that are floristically related to the band of dry forests that extends across south-central South America (sense Prado & Gibbs, 1993). The austro-Brazilian transition forests and several different vegetation types which are part of the Pantanal mosaic mostly border the Chaco s.s. on its eastern boundary.

The gallery forests which grow along the rivers Paraná, Paraguai, and its western tributaries, is characterized by tree species such as *Albizia polyantha, Crataeva tapia, Peschiera australis, Croton urucurana, Arecastrum romansoffianum, Nectandra falcifolia, Banara arguta,* etc. It is floristically an attenuation of the southern Brazilian ("paranaense") forest.

The "selva de ribera" (river margin forest) grows on non-flooded soils adjacent to the gallery forest. It is taller than the Chaco, up to 30 m. It is a semi-deciduous subtropical forest represented by some of the following species, e.g., *Holocalyx balansae, Ficus luschnathiana*, *Patagonula americana, Pouteria gardneriana, Ruprechtia laxiflora, Phytolacca dioica* (a tree-sized pokeweed), *Enterolobium contortisiliquum*, etc. This forest also is a relatively impoverished extension of the southern Brazilian forest with a few dry tropical forest elements included.

Patches of tropical dry forest which are floristically similar to arboreal caatinga occur on some of the Paraguayan uplands, surrounded by a matrix of quebrachales. Cerrados also occupy some of the uplands with shallow soils surrounded by Chaco plains in parts of Paraguay and southeastern Bolivia.

Transitional vegetation. Occupying a narrow belt between the Chaco and the more humid submontane forests known as the Yungas and the Tucumán-Bolivian forests are the transition forests (Prado, 1993b; Cabrera A., 1976). The two major forest types in this category are the "palo blanco" forests dominated by *Calycophyllum multiflorum*, which are taller than Chaco, reaching 30 m in height, and the "tipa-pacará" forest of the legumes *Tipuana tipu* and *Enterolobium contortisiliquum*. The transition forests have virtually disappeared due to human activity; they are floristically related to the arc of tropical dry forest which extends from the caatinga in the northeast of Brazil to the foothills of the Andes (Prado and Gibbs 1993; Prado 1993b).

One of the transitional vegetation types which is briefly mentioned here is the austro-Brazilian transitional forest. Its well-developed to intermediate soils support an association of woody plants such as *Myracrodruon balansae, Myrcianthes pungens, Eugenia uniflora*, *Tabebuia impetiginosa,* and a weird Sapindaceae, *Diplokeleba floribunda*. Sometimes *Schinopsis balansae* is present. Additional transitional vegetation types are discussed in great detail in Prado (1992) and Dubs (1992).

Some of the most important plant families of the Chaco s.s. are the Fabaceae s.l. (e.g., *Acacia, Prosopis, Caesalpinia, Cercidium*, and *Geoffroea*), the Anacardiaceae (*Schinopsis*, *Lithrea, Schinus*), Apocynaceae (*Aspidosperma*), Arecaceae (*Copernicia, Trithrinax*), Zygophyllaceae (*Bulnesia*), Rhamnaceae (*Ziziphus*), Cactaceae (*Opuntia, Cereus, Stetsonia*, *Pereskia*, *Quiabentia*), Bromeliaceae (*Dyckia, Bromelia, Puya, Ananas*), and Poaceae (*Eleoneuris*, *Paspalum, Chloris, Spartina*) (Galera and Ramela, 1997). The Chaco has several endemic genera such as *Lophocarpinia, Mimozyganthus*, and *Stenodrepanum*. The Chaco is the domain of a few wild relatives of the pineapple (*Ananas* spp.; Galera and Ramela 1997).

Southern Brazilian region

The southern Brazilian region (Paranaense province of Cabrera & Willink, 1973) lies in Brazil south of the Cerrado and west of the Atlantic forests; it also includes northeastern Argentina (Missiones) and eastern Paraguay. The original vegetation consisted primarily of a mosaic of forests dominated by *Araucaria angustifolia*, semi-deciduous forests, temperate grasslands (particularly in Rio Grande do Sul), and small outliers of cerrado in São Paulo and Paraná. Some taxa typical of this region include *Podocarpus lambertii, Dicksonia sellowiana, Holocalyx balansae, Tabebuia ipe, Myrocarpus frondosus, Balfourodendron riedelianum, Syagrus romansoffiana, Myracrodruon balansae. Cedrela fissilis, Cariniana estrellensis*, and "yerba mate", *Ilex paraguariensis* (Smith 1962; Takhtajan 1986; Keel 1997; Leitão-Filho 1997; Hueck & Seibert 1972; Spichiger et al. 1995; Reitz 1965).

Savannas

Introduction

In South America, savannas cover an area of approximately 2 million sq. km. (Sarmiento 1983; see Fig. I). They comprise the second most extensive vegetation type in tropical South America after tropical humid forests. The largest expanse of savanna in South America is the Cerrado phytogeographic province (Eiten 1978) of central Brazil and adjacent areas of Paraguay and Bolivia. The second largest savanna-dominated region is the Llanos of eastern Venezuela and Colombia. Smaller areas of savanna include the Llanos de Moxos of northern Bolivia, islands of savanna surrounded by humid forest in the Amazon basin, the Gran Sabana of Venezuelan Guayana, the Roraima-Rupununi savannas, the Guianan savannas, and disjunct areas of "campo rupestre." The Pantanal region of Brazil and contiguous Bolivia also includes extensive areas of hyperseasonal savanna and cerrado vegetation; this is discussed in a separate section.

The area of savanna in South America has apparently expanded and contracted during cool-dry and warm-wet intervals during the Quaternary. It has been postulated that two or more recent episodes of savanna and other dry vegetation type expansion and concomitant tropical humid forest contraction occurred during glacial periods in the Northern Hemisphere. The most severe episode of cooling and drying probably occurred during the Northern Hemisphere Würm-Wisconsin ice age (Brown and Ab'Saber 1979; van der Hammen 1982; Dickinson and Virji 1987; Absy et al. 1991).

Savannas are tropical grasslands varying from treeless areas dominated by grasses, sedges, and other herbs to dense woodlands with grass-dominated understories. Sarmiento (1983) divided Neotropical savannas into three basic types. The most widespread type of savanna is the seasonal savannas, which is maintained by a severe dry season and frequent fires (e.g., central Brazilian savannas and the Llanos of western Veneuzuela and contiguous Colombia). The second type of savanna, the hyper-seasonal savanna, is a product of excessive drought and fires with severe flooding during the wet seaon. These savannas are particularly prominent in the poorly drained bottomlands of the Grão Pantanal, the Llanos de Moxos, Bolivia, the Roraima-Rupununi savannas, and the Llanos of Colombia/Venezuela. Hyperseasonal savannas often have large numbers of monocots, represented by the Commelinaceae, Costaceae, Eriocaulaceae, Iridaceae, Rapateaceae, Xyridaceae, etc. They are also characterized by palm stands, especially of *Mauritia flexuosa* Mart. The third type of savanna is the semi-seasonal savanna, which occurs as disjunct patches surrounded by tropical humid forest. These occur in a more humid climate with one or two short dry seasons and less frequent fires (e.g., some of the Amazonian and Guianan savannas).

The savanna flora contains a suite of species that are widespread throughout the Neotropics, such as the woody plants *Byrsonima coccolobifolia*, *B. crassifolia*, *B. verbascifolia*, *Bowdichia virgilioides*, *Anacardium occidentale* (includes *A. microcarpum*), *Curatella americana*, *Hancornia speciosa*, and *Salvertia convallariodora*. (Fig. 5b). Local floristic richness in Neotropical savannas varies considerably, from core central Brazilian cerrado communities with more than 100 species of trees and shrubs (not including perennial herbs and subshrubs with woody underground structures) to plots in some Amazonian savannas with only seven. A comparison of inventory data from 98 savanna sites of various sizes from the Cerrado and Amazonia, which totaled 534 species of trees and large shrubs, concluded that the Amazonian savannas are depauperate, disjunct islands of cerrado vegetation (Ratter et al. 1996). In contrast, Pires and Prance (1985) stated that savannas of the upper Rio Trombetas (Ariramba and Tiriós) and of Roraima-Rupununi are species-rich, and that the latter show considerable endemism while lacking *Hancornia* and *Salvertia*. Both studies agree that the savannas of Amapá were found to be particularly species-poor.

Cerrado

The Cerrado phytochorion covers an area of about 1.8 million sq. km. (Ab'Sáber 1971; Coutinho 1990; Fig. I) . It covers most of central Brazil, from southern Maranhão and Tocantins in the north to southern cerrado outliers in São Paulo and Paraná, and extends west to include parts of Paraguay and eastern Bolivia. Rainfall is generally higher than in the caatinga region to the northeast and less than that of the humid forests to the southeast and northwest. Annual precipitation averages about 1500 mm, and varies from 750 mm at the caatinga ecotone to more than 2,000 at the Amazonian transition zone. The dry season lasts about 3-5 months (May-September) during the austral winter. At its southern limit, cerrado vegetation is occasionally affected by frosts, which can severely damage woody plants. Occasional severe frost may be a factor that sets the southern limits of cerrado vegetation (Sarmiento 1983).

The Cerrado is essentially a landscape of savanna-covered plateaus and tablelands ("chapadas", Fig. 7a) that are remnants of a vast mid-Tertiary peneplain separated by broad river valleys with gallery forests. The deep bedrocks underlying most of the Cerrado are of the pre-Cambrian Brazilian Shield. Much of the Cerrado in central Brazil occupies terrain ranging from 1000-1500 m elevation. Cerrado outliers in southern Brazil and the Pantanal of southwestern Brazil and Paraguay occur at much lower elevations (Sarmiento 1983).

Soil fertility and drainage play preeminent roles in determining the large-scale vegetation patterns in the Cerrado. Soils supporting the dominant savanna vegetation are dystrophic (i.e., very poor in nitrogen, phosphorus, calcium, etc., and high in aluminum; Ratter et al. 1995, 1996; Oliveira-Filho and Ratter 1995; Coutinho 1990; Goodland 1971; Filgueiras 1997). Mesotrophic soils which are much richer in Ca and other essential nutrients support tropical dry forests (deciduous or semi-deciduous) and sclerophyllous woodlands (e.g., mesotrophic cerradão) under relatively undisturbed conditions. These woodlands and forests are usually in valleys where erosion of the tablelands has cut into nutrient-rich underlying rock (e.g., silts and mudstones) or they are growing on limestone-derived soils (Oliveira-Filho and Ratter 1995; Prado and Gibbs 1993). Seasonally waterlogged soils are the substrate for hyperseasonal savannas and "esteros" (sedge- and grass-dominated, often permanently wet campos). Moist soils adjacent to rivers support a dendritic network of gallery forests. Cerrado is frequently separated from gallery forest by a narrow band of estero (Sarmiento 1983; see Fig. 5a).

In Brazil, the core vegetation of cerrado is a complex savanna continuum varying from treeless grassland to dense woodland. This continuum is often broken down into five physiognomic units (e.g., Eiten 1972; Sarmiento 1983; see Ratter et al. 1973 for classification of woody vegetation types).

- campo limpo ("clear field"). A treeless grassland with herbs, a few small shrubs, and suffrutices (subshrubs)
- campo sujo ("dirty field"). A grassland with less than 2% woody plant cover
- campo cerrado. A grassland with 2-15% woody plant cover
- cerrado. An open woodland with 15-40% woody plant cover
- cerradão. A sclerophyllous woodland with more than 40% woody plant cover and 3000-4000 trees per hectare.

The tortuous and often grotesque habit and thick bark of most cerrado trees and shrubs belies the essential role of fire in the ecology of the cerrado (Coutinho 1990). Cerrado differs from many other types of dry tropical vegetation in that many of its woody plants have mesophyllous, thickly coriaceous leaves that are retained during the dry season.

The more open forms of cerrado vegetation depend on fire for their maintenance. In the past, humans have undoubtedly played an important role in the management and possibly expansion of cerrado vegetation. The numerous and complex adaptations of cerrado plants to fire, however, in addition to the high degree of endemism in the region, suggest a long history of fire ecology predating man by millions of years. Many woody plants escape destruction from fire by having most of their biomass beneath the soil surface. Frequently, these species have woody underground structures called xylopodia or lignotubers. These structures are large and have dormant buds at or below the ground surface that are capable of re-sprouting shortly after a fire has scorched the ground surface (Coutinho 1990). Sometimes these xylopodia appear to be underground tree trunks; two notable examples of "underground trees" are *Andira humilis* and the dwarf cashew, *Anacardium humile* (López Naranjo 1977; Mitchell and Mori 1987b; Rawitscher and Rachid 1946). In the case of *Anacardium humile* and many other suffrutices with large xylopodia, the only structure that emerge above the ground are the inflorescences and a few orthotropic leafy shoots. These suffrutices often have arborescent relatives in the Cerrado and sister taxa that may be giant trees in the Amazon basin; the counterpart of *Anacardium humile* in Amazonia is *A. spruceanum* (Mitchell and Mori 1987b*).*

It has been assumed that some xylopodia function as water storage organs. A study of the xylopodia of *Isostigma peucedanifolium* and *Lantana montevidensis* revealed that the water content of the xylopodia remained relatively constant during both dry and wet seasons. This study found that after a fire the xylopodia absorbed minerals and other nutrients released into the soil by the burning of vegetation (Coutinho 1990). The diversity and abundance of suffrutices with xylopodia or similar adaptations for resistance to and re-sprouting after fires comprise one attribute of the Cerrado phytogeographic that sets it apart from the Amazonian and other savanna regions of the Neotropics (Pires and Prance 1985). The only other region of the world with a similarly rich flora of "underground trees" is the Zambesian region of Africa (White 1976).

Even though the dominant vegetation of the cerrado is a savanna continuum, a major portion of the region was originally covered by woodlands and forests. There may have been times in the past several thousand years when dry forests were the dominant type of vegetation (Prado and Gibbs 1993; Oliveira Filho and Ratter 1995). It is very difficult to reconstruct the vegetation history of the cerrado due to the paucity of palynological studies. A recent palynological study by Ledru (1993) carried out at Salitre, western Minas Gerais suggests that between 33,000-25,000 BP, that region was cooler and moister than today and was covered by semi-deciduous forests that included southern Brazilian elements such *as Araucaria, Podocarpus, Symplocos,* and *Drimys.*

Remnants of these formerly extensive forests can still be seen today. The type of forest present is determined by the edaphic gradient. Cerrado grades into two different types of cerradão (sclerophyllous woodland), depending on whether or not the soils are dystrophic or mesotrophic. In the transition zone between the Amazon forest and the cerrado, dystrophic cerradão is prevalent. Characteristic species of dystrophic cerradão include *Hirtella glandulosa*, *Emmotum nitens, Aspidosperma macrocarpon, Vochysia haenkiana*, and *Xylopia sericea*. Two indicator species for mesotrophic cerradão which is common in central Brazil and the fringes of the Pantanal are *Magonia pubescens* and *Callisthene fasciculata*. The vegetation types dystrophic cerradão and mesotrophic cerradão are based on Oliveira Filho and Ratter's (1995) modification of the Brazilian government vegetation classification scheme (Veloso et al. 1991). Tropical dry forests (including deciduous and semi-deciduous forests) are widespread and grow in mesotrophic soils. They are floristically linked to the caatinga, the sub-Andean dry forests and, in the southern areas of the cerrado province, they are floristically linked to the southern Brazilian (paranaense) forests. Some characteristic species are *Anadenanthera colubrina, Tabebuia impetiginosa, Myracrodruon urundeuva, Dilodendron bipinnatum, Sterculia striata*, and *Enterolobium contortisiliquum*. The extensive network of gallery forests in the river valleys of the Cerrado comprise a corridor linking the Amazonian forests to the Atlantic coastal forests of Brazil. Many of the woody species in the gallery forests are habitat generalists, e.g., *Tapirira guianensis*, *T. obtusa, Protium heptaphyllum, Hymenaea courbaril*, and *Virola sebifera*. Some species are endemic to the gallery forests of the Cerrado, including *Virola malmei, V. urbaniana*, and *Hirtella hoehnei* (Oliveira-Filho and Ratter 1995). The central and southern gallery forests are floristically linked with the southern Brazilian semi-deciduous forests. In Mato Grosso, some Amazonian tree genera reach their southern limit in gallery forests, e.g., *Hevea*, a genus considered Guianan-Amazonian.

The cerrado is recognized by both botanists and zoologists as a major center of biodiversity. For example, Dias (1992) estimated that 160,000 species of plants, animals, and fungi occupy the cerrado biome; Ratter (1986) provided a key to the genera of the region's rich woody plant flora. It is also an important center of endemism for plants and animals (Cracraft 1985; Heringer et al. 1977; Cabrera and Willink 1973; Filgueiras 1997; Ratter et al. 1996). It is very heterogeneous in floristic composition. In a comparative study of 98 areas of cerrado and Amazonian savannas, 158 (30%) of 534 species of trees and shrubs occurred at a single site only. Only 28 species were present at 50% or more of the study sites. Local areas of cerrado can be extremely rich in plant species, for example, Heringer (1971) found more than 300 species in one hectare of protected cerrado near Brasília, D.F.

Some of the most important plant families in the cerrado are the Fabaceae s.l., Poaceae, Asteraceae, Orchidaceae, Rubiaceae, Myrtaceae, Melastomataceae, and Apocynaceae. Among the more species-rich genera are *Paspalum, Panicum, Habenaria (including Platanthera), Vernonia s.l., Chamaecrista, Senna,* and *Hyptis*. Some of the most widespread species of trees and shrubs, occurring on at least 50% of 98 sites sampled throughout the cerrado, include *Qualea grandiflora, Annona crassiflora, Astronium fraxinifolium, Bowdichia virgilioides, Lafoensia pacari, Kielmeyera coriacea, Hymenaea stigonocarpa, Copaifera langsdorffii, Caryocar brasiliense, Machaerium acutifolium, Tocoyena formosa, Tabebuia aurea,* and *Byrsonima coccolobifolia* (Ratter et al., 1996). Some of the characteristic suffrutices include *Anacardium humile, A. nanum, Andira humilis, Annona pygmaea, Parinari obtusifolia,* and *Stryphnodendron confertum*. Grass genera include *Andropogon, Aristida, Axonopus, Elionurus, Paspalum*, and Trachypogon, which are widespread in most Neotropical savannas (Sarmiento 1983). Some of the characteristic palms include *Butia leiospatha, Syagrus acaulus, S. campestris, Attalea exigua, Astrocaryum campestre*, and *Acanthococos emensis* (Sarmiento 1983; Coutinho 1990).

The cerrado is the domain of the important fruit piquí (*Caryocar brasiliensis*; Araújo 1995; Filgueiras 1997) and wild relatives of the cashew of commerce (*Anacardium* spp.; Mitchell and Mori 1987b).

Llanos of Venezuela and Colombia

The Llanos, covering some 500,000 km^2 (Sarmiento 1984), is the second most extensive region dominated by savanna in South America after the Cerrado. The vegetation of the Llanos and its relationship to the regional physiography were comprehensively reviewed by Sarmiento (1983). This region is a huge plain drained by the Orinoco River and its tributaries, enclosed to the west and north by the Andes and the Coastal Cordillera, respectively. The Guaviare River in central Colombia forms the southern boundary with Amazonia. It is bordered to the east by the Orinoco Delta and the Guayana Highlands. Most of the Llanos is underlain by Quaternary alluvial and aeolian sediments. The major area of tropical dry forests in the Llanos occupies terrain underlain by Tertiary clays and shales which extends south from the coastal cordillera. Annual rainfall varies from 1,000 mm in parts of the eastern Llanos to 2,200 mm in the southwest corner at the Guaviare River. The dry season becomes less pronounced across a northeast-southwest gradient, decreasing from 5-6 months to 1-2 months.

The Llanos can be divided into four regions:

The piedmont. This is a narrow strip bordering the Andes and the western portion of the coastal cordillera. It is a mosaic of semi-deciduous forests, savannas, and gallery forests, growing on a complex of alluvial terraces and fans. Savanna woodland usually occupies the oldest Quaternary deposits, and the youngest and lowest alluvial terraces are usually occupied by gallery forests. Hyperseasonal savannas in the piedmont are fairly local in their distribution.

The woody plants of the piedmont are mostly widespread species typical of most Neotropical savannas, such as *Bowdichia virgilioides, Byrsonima coccolobifolia*, *B. crassifolia, Cochlospermum vitifolium, Curatella americana, Genipa americana*, and *Xylopia aromatica*.

The high plains. Mesas are the dominant land form of much of the eastern and southern Llanos (a large portion of the Colombian Llanos). They are the eroded remnants of a vast tableland of late Pleiocene or early Pleistocene age. The predominant vegetation on the mesas, which are often 200-300 m above sea level, is an open savanna to savanna woodland with widespread tree species such as *Bowdichia virgilioides, Byrsonima crassifolia*, and *Curatella americana.*. Treeless, seasonal, and hyperseasonal savannas dominate the wide valleys separating the mesas. Hyperseasonal savannas, with the locally abundant palm *Copernicia tectorum*, being the only woody plant present, are common in the valleys of the high plains region. Savanna parkland, consisting of groves of tropical dry forest (including species such as *Copaifera officinalis* and *Vochysia venezuelana*) surrounded by treeless hyperseasonal savanna, is another common vegetation type in this region.

The alluvial overflow plains. A huge depression in the central part of the Llanos, bounded by the piedmont to the west and north, and by the high plains to the south and east, is covered by the alluvial overflow plains. Its vegetation varies tremendously along an extremely slight elevational gradient of 1-2 meters. It is reminiscent of the well-known wetland ecosystems, the Everglades of Florida, and the Okavango Delta of Botswana. It is the northern South American counterpart of the hyperseasonal savannas and wetlands of the Pantanal. Both the alluvial overflow plains and the Pantanal are characterized by enormous flocks of waterfowl, ibises, and storks, and large herds of capybaras, the world's largest rodent.

During the rainy season, most of the region is flooded for periods of a few weeks to several months. The flooding is not caused by streams overflowing their banks, but rather by the accumulation of rainwater which drains very slowly due to the remarkably flat terrain. The upper portions of the elevational gradient support savannas with scattered trees, savanna woodlands, or groves of trees ("matas") in a hyperseasonal savanna parkland landscape. These groves of trees typically include tree species such as *Spondias mombin L., Annona jahnii, Platymiscium pinnatum, Vochysia venezuelana,* and *Pterocarpus podocarpus*. The lowest areas in the elevational gradient are characterized by species-poor "esteros", commonly dominated by grasses such as *Paspalum fasciculatum* or *Leersia hexandra*, and *Hymenachne crassicaulis*, or sometimes extensive herbaceous wetlands. The riverbanks support either savanna or gallery forest, depending on the height of the water table.

The aeolian plains. A continuous belt characterized by extensive dune fields extends from the upper Meta River in central Colombia to the Cinaruco River in southern Venezuela. These plains are apparently the remnants of an arid landscape whose origin dates back to the Würm Wisconsin glacial period (Tricart, 1974). A seasonal savanna with a very depauperate tree flora (often *Byrsonima crassifolia* is the only tree species present) grows on these dunes. The ground layer is dominated by *Trachypogon ligularis* and *Paspalum carinatum*.

Hyperseasonal savannas and esteros occupy depressions between the dunes and the plains. The hyperseasonal savannas are often dominated by grasses of the genus *Mesosetum*, and the estero often include "morichales" (stands of *Mauritia* sp.).

The Llanos flora includes many of the widespread woody plants of the Cerrado and widespread Amazonian savannas. Its woody plant flora is depauperate in comparison with the Cerrado. Some of the widespread grass and sedge genera that dominate the ground layer of the Llanos include Andropogon, Aristida, Axonopus, Panicum, Paspalum, Mesosetum, Elionurus, Sporobolus, Trachypogon, Bulbostylis, and Rhynchospora, and Scleria.

As is the case in the Cerrado, fire plays an extremely important role in maintaining the savanna landscape of the Llanos. According to Sarmiento (1983), the Llanos flora is perhaps one of the best-known savanna floras in the Neotropics.

Roraima-Rupununi savannas

The savannas of Roraima, Brazil are continuous with the Rupununi savannas of Guyana, and together they cover some 54,000 km^2 (Pires and Prance 1985; Eden and McGregor 1992). Although they are situated in the Amazon basin, they are not Amazonian climatically or floristically: the region is the northern end of the roughly NW-SE transverse dry belt that crosses the Amazon east of Manaus (see map in Pires-O'Brien 1997), and it experiences a long dry season and relatively low rainfall (Walsh 1996). The southern part of the region is flatter, while the terrain of the northern portion is more undulating and the savannas lie between hills (Pires and Prance 1985).

These are mostly well-drained savannas with few trees. As in parts of Amazonia, there are many swampy areas of sands underlain by an impermeable hardpan that are dominated by *Mauritia flexuosa*. Some of the swamps have *Xyris*, Eriocaulaceae, *Cephalostemon, Abolboda, Rapatea*, and some *Drosera* spp. The well-drained savannas share many tree species characteristic of the Cerrado except for *Hancornia speciosa* and *Salvertia convallariodora*, but there is also appreciable endemism (Pires and Prance 1985). Overall, the floristic affinities of this region are strongest with the eastern Llanos of Venezuela and Colombia (Berry et al., 1995).

Llanos de Moxos

The Llanos de Moxos (Mojos in some references) region is a mosaic of forests (ca. 120,000 km^2) and savannas (ca. 150,000 km^2) and various associated wetlands in northeastern Bolivia. It is the third largest complex of savannas in South America after the Cerrado and the Llanos of Venezuela and Colombia. This region is primarily in Beni Department and extends into other adjacent departments, 11-16^{o}S, 64-69^{o}W. The brief description of the region and its vegetation which follows is based on the relatively scant literature available (Beck and Moraes-R. 1997; Beck 1984; Haase 1990; Haase and Beck 1989).

It is a flat plain, between 130-235 m elevation, in the lowlands northeast of the Andes. The three main rivers that drain the Llanos de Moxos are the Beni, Mamoré, and Guaporé (or Iteñez), which unite in the north to form the major southwestern tributary of the Amazon, the Rio Madeira. This huge plain is bounded to the east by the Serra dos Pacaás Novos and Chapada dos Parecis, Brazil (Rondônia and Mato Grosso states). Mean annual rainfall increases along and east-west gradient from 1300 mm/yr in Magdalena to over 2000 mm/yr in Rurrenabaque. The austral summer is characterized by heavy rainfall and a 2-3 month dry season that usually lasts from June to August. The mean annual temperature is ca. 26^{o}C, but during the austral winter, cold fronts ("surazos") frequently chill the air. The lowest temperature recorded in the Llanos de Moxos was 6^{o}C at Santa Ana de Yacuma.

The Llanos de Moxos are underlain by extensive Andean-derived alluvial sediments dating from the late Pleistocene to the Quaternary. Because of its low relief, the vegetation of the region varies tremendously along an extremely slight elevational gradient. This particularly true for the central portion of the region between the Beni and Mamoré rivers, which is reminiscent of the alluvial overflow plains of the Pantanal and the Llanos of Venezuela and Colombia.

This central portion is dominated by "esteros" and hyperseasonal savannas, with an abundance of associated wetlands, some of which are dominated by sedges and *Thalia geniculata*, others by *Cyperus giganteus*, and palm stands of *Coperinicia alba* are common in some area. Beck (1984) classified more than 30 plant communities with more than 400 species of vascular plants within a small portion of the central Llanos de Moxos. The savannas of the northwestern Llanos de Moxos, in the vicinity of the río Beni, occupy acidic soils, are depauperate in woody plant diversity; and show termite mounds as a characteristic feature. One type of mostly treeless savanna is characterized by *Leptocoryphium lanatum-Trachypogon plumosus* association; another type is characterized by the melastomataceous shrub *Macairea scabra* with a ground layer mostly of *Mesosetum penicillatum* and *Bulbostylis juncoides*. Palm stands of *Mauritia flexuosa* or sometimes of *Mauritiella aculeata* are common. Gallery forests line both black-water and white-water rivers in this region. A detailed study of savanna in an area of ca. 2,000 km^{2} just west of the río Beni identified ca. 600 species of vascular plants and classified several vegetation types (Haase and Beck 1989). The northwestern savannas are floristically and physiognomically similar to portions of the Llanos of Venezuela and Colombia and other northern South American savannas. The savannas of the northern portion, between the Beni and Iteñez/Guaporé or Mamoré rivers are predominintly seasonal savannas that are floristically and physiognomically similar to the Cerrado.

The northern portion of the Llanos de Moxos is the southernmost extension of the Amazon forest. Two of the typical Amazonian species are the Pará rubber tree (*Hevea brasiliensis*) and the Brazil nut (*Bertholletia excelsa*). A more humid forest covers the foothills of the Andes bordering the Llanos de Moxos to the west. Gallery forests and parkland savannas (i.e., with forest islands) are widespread in the savanna-dominated portions of this region. The southern portion of the Llanos de Moxos is supported by a mostly evergreen forest with a strongly seasonal climate.

The vascular flora of the Llanos de Moxos is estimated to consist of more than 5,000 species, of which ca. 1500 are found in the savannas. The flora includes widespread Neotropical savanna, Cerrado, and Amazonian species, primarily. The number of endemic species is probably low (Beck and Moraes-R. 1997). The flora includes wild relatives of the pineapple (*Ananas comosus*) and numerous cultivars of the peanut (*Arachis hypogaea*).

The Pantanal

The Pantanal is treated as a regional mosaic or transition in Prance's (1989) description of South American phytochoria. Is not a center of endemism but rather a blending of floristic elements that lies at the vertex of the Cerrado, Amazonia, the Gran Chaco, and the southern Brazilian flora. Based on the additional floristic elements it contains, it must also lie in current or historic migration routes of the caatinga of northeastern Brazil (Prado and Gibbs 1993).

The Pantanal is considered by many to be one of the most extensive and significant wetland-savanna complexes in the world. It is an alluvial plain of between 150,000-170,000 km^2 in the upper Paraguay River basin. The Pantanal is situated between 16-22 °S and 55-58 °W. It is bordered by the Cerrado to the north and east, the Serra de Bodoquena to the south, and the Paraguay River to the west. Most of the Pantanal is in Brazil (Mato Grosso and Mato Grosso do Sul), but a small portion crosses the Paraguay River into southeastern Bolivia. It is a relatively flat plain that lies mostly at 100 m elevation, tilted very slightly in a northeast-to-southwest direction. This very level terrain is broken in a few places by a few emergent pre-Cambrian uplands, such as the Serra de Amolar along the Paraguay River. Annual rainfall of 1,000-1,400 mm falls mostly during the rainy season from November to April. The harsh dry season lasts 3-4 months during the austral winter. This brief review is based primarily on Dubs (1992a, 1992b), Prance and Schaller (1982), Frey (1995), Sarmiento, (1983), and Ratter et al. (1988).

The Pantanal is underlain by a sediment-filled subsidence zone extending from the Llanos of Venezuela and Colombia south to the Gran Chaco. This subsidence zone was formed at the time of the Andean orogeny. The Pantanal's complex mosaic of wetlands, savannas, and forests is a product of annual flooding and its dynamic effects on a landscape of alluvial and aeolian forms shaped by Quaternary climatic fluctuations. The contemporary landscape and vegetation of this region is very similar to that of the Llanos of Venezuela and Colombia and Bolivia's Llanos de Moxos.

Cerrado vegetation, including the whole continuum from campo limpo to cerradão, dominates in the eastern and northern frontiers, and is common on uplands and on sandy interfluves with deep water tables (Dubs 1992b; Sarmiento 1983; Prance and Schaller 1982). Typical cerrado and widespread Neotropical savanna taxa such as *Bowdichia virgilioides, Caryocar brasiliense, Curatella americana, Qualea parviflora,* and *Anacardium humile* occur in the cerrados of the Pantanal.

Mesotrophic cerradão is also widespread in areas unaffected by flooding. The cerradão of the Pantanal often contains a mixture of typical central Brazilian mesotrophic cerradão species such as *Magonia pubescens, Luehea paniculata, Buchenavia tomentosa, Astronium fraxinifolium*, and some calcicolous species typical of deciduous forests, such as *Myracrodruon urundeuva, Vitex cymosa, Sterculia striata, Dipteryx alata,* and *Platypodium grandiflorum*. Its canopy is generally 10-14 m high, and the ground layer often contains numerous terrestrial bromeliads (Dubs 1992a).

Tropical dry forests (deciduous and semi-deciduous) are particularly common in the uplands and areas bordering the Pantanal. In the southern Pantanal, semi-deciduous forests with a canopy 18-21 m high often contains a dense understory of "acurí" palms (Attalea phalerata). Typical trees of these forests are *Myracrodruon urundeuva*, *Astronium fraxinifolia, Talisia esculenta, Hymenaea courbaril, Tabebuia ochracea, T. impetiginosa, T. roseo-alba, Acacia paniculata, Caesalpinia floribunda, Dilodendron bipinnatum, Casearia gossypiosperma*, and *Combretum leprosum* (Dubs 1992a; Ratter et al. 1988; Prance and Schaller 1982). Some species of the Chaco or Chaco transitions occupy dry uplands, but these are a minor component of the vegetation. Some of these transitional or chaquenian species *include Bulnesia sarmientoi, Pereskia saccharosa,* and *Schinopsis balansae* (see later section on the Chaco), and transitional forest species such as *Calycophyllum multiflorum* and *Enterolobium contortisiliquum*.

Gallery forests and some upland forests, particularly in the northern frontier of the Pantanal, are evergreen. These evergreen forests include some Amazonian species such as

Guarea macrophylla, Abuta grandifolia, Mouriri guianensis, and *Rudgea cornifolia*.

The floodplains are a mosaic of narrow to broad rivers, oxbow lakes, ponds, permanent swamps, and hyperseasonal savannas. The wetlands are characterized by mostly pantropical and Neotropical floating and rooted aquatic plants, e.g., *Eichornia crassipes, Salvinia auriculata, Pistia stratiodes, Ludwigia* spp., *Isoetes* spp., *Utricularia* spp., *Victoria amazonica* (Dubs 1992a; Prance and Shaller 1982; Frey 1995). Dense marshes dominated by *Cyperus giganteus* or *Typha dominguensis* are also characteristic. Hyperseasonal savannas flooded up to several months during the rainy season include treeless grasslands to lightly wooded savannas with *Curatella americana, Byrsonima orbignyana, Bactris glaucescens*, and *Licania parvifolia; Copernicia alba* palm savannas; and savannas with small forest islands associated with termite or ant colonies (sometimes called "campos de murundus"; Oliveira-Filho 1992a). *Tabebuia aurea* is a characteristic tree of decayed termite mounds. The term "capão" is sometimes used to refer to the kind of larger forest islands in the hyperseasonal savannas of the Pantanal. These "capões" should not be confused with those of the campo rupestre, which have completely different floras.

Campo rupestre

The complex of montane vegetation commonly referred to as campo rupestre is primarily associated with the discontinuous range of rocky summits called the Serra do Espinhaço. This narrow range, 50-100 km wide, extends about 1,000 km from northern Bahia south to Minas Gerais (a short distance south of Belo Horizonte), 10-20°35'S. The northern portion of the campo rupestre is nested within the caatinga phytochorion. The southern portion penetrates the Cerrado region. The area covered by campo rupestre is 6,000-7,000 km2. The numerous low mountains range in elevation from 900-2,107 m. Outliers of campo rupestre vegetation are found in some of the low mountains ("serras") in Goiás, Mato Grosso, and southeastern Bolivia (Parker et al. 1993; see Fig. 6a). A few areas of Amazonian Brazil have vegetation that has been called campo rupestre, such as part of the Serra do Cachimbo in southwestern Pará, and at Ariramba on the Rio Trombetas in northern Pará (Pires and Prance 1985). The application of the term campo rupestre to these areas needs further study, as these are rather different from the core area of campo rupestre associated with the Serra do Espinhaço.

The climate of the Serra do Espinhaço is characterized by a mild summer (average temperature varies between 17.4-19.8° C and below 22°C even at the hottest time of the year). The dry season lasts 3-4 months during the austral winter, but the higher elevation areas remain fairly moist due to dew and rain, especially on the eastern slopes. Pre-Cambrian rocks of the Brazilian Shield underwent extensive folding and subsequent erosion from the Paleozoic up until the Tertiary. The rocky substrate for the unique campo rupestre vegetation consists mostly of metamorphosed sedimentary rocks and includes sandstones, quartzites, schists, filites, and dolomites. The soils derived from these rocks are frequently shallow, sandy or stony, and highly acidic. Forests occur in areas of deeper soil accumulation (Giulietti and Pirani 1988, 1997; Harley 1995).

Most of the vegetation is open, with many plants possessing special adaptations to growing on rocks. Some of these adaptations include specialized roots, dense vestiture and, in some families, persistent leaf bases (e.g., Velloziaceae, Bromeliaceae, and Orchidaceae). Sandy soils are generally covered by diverse grassland dominated by Poaceae, Cyperaceae, Eriocaulaceae, and Xyridaceae. Poorly drained areas often have bogs characterized by Xyridaceae, Eriocaulaceae, Cyperaceae, Gentianaceae, Lentibulariaceae, Droseraceae, and

Burmanniaceae (Giulietti and Pirani 1997). Woody plants in the open campo rupestre are represented by scattered small trees, shrubs, or suffrutices, which are usually sclerophyllous and evergreen. As mentioned, campo rupestre is not a homogeneous vegetation type, but rather consists of a mosaic of additional plant formations, such as oligotrophic marshes, cerrados, gallery forests, deciduous forests, and "capões," which are isolated islands of forest occurring in grasslands at higher elevations.

It has been suggested that the campo rupestre has the highest degree of endemism of any Brazilian vegetation type. More than 70% of the world's ca. 250 spp. of Velloziaceae and more than 60% of the world's Eriocaulaceae and Xyridaceae are endemic to the Serra do Espinhaço (Giulietti and Pirani 1988, 1997). Examples of endemic genera include *Burlemarxia* (Velloziaceae), *Pseudotrimezia* (Iridaceae), *Cipocereus* (Cactaceae), *Raylea* (Sterculiaceae), *Morithamnus* (Asteraceae), and *Bishopiella* (Asteraceae).

The core area of campo rupestre is amazingly rich in species; for example, 1,590 species of vascular plants are estimated to occur in ca. 200 km^2 of the Serra do Cipó. The flora of the core area is estimated to exceed 4,000 species of vascular plants (Giulietti and Pirani 1997). The largest dicot families in the campo rupestre are the Asteraceae, Melastomataceae, Rubiaceae, Fabaceae s.l., Myrtaceae, Malpighiaceae, and Euphorbiaceae; the largest monocot families are the Poaceae, Eriocaulaceae, Orchidaceae, Velloziaceae, Xyridaceae, Bromeliaceae, and Cyperaceae (Giulietti and Pirani 1997).

In Minas Gerais, the campos rupestres are surounded by lower-lying areas dominated by cerrado. In fact, the cerrado flora shares many species and genera with the campo rupestre. Some genera occurring in both floras include *Eremanthus, Qualea, Campomanesia, Hyptis, Kielmeyera, Jacaranda, Diplusodon,* and *Aristida*. In central Bahia, campo rupestre is often separated by lower-lying areas dominated by caatinga vegetation. In contrast with the Cerrado, the campo rupestre and caatinga floras have very little in common floristically (Giulietti and Pirani 1997).

The campo rupestre has floristic connections with the tepuis of Venezuelan Guayana and the restinga vegetation of Atlantic coastal Brazil. Both the tepuis and campos rupestres are humid, higher elevation islands formed in part from pre-Cambrian shields; the tepui summits contain rocky outcrops and bogs, and are rich in Eriocaulaceae and Xyridaceae. There are even a few species shared by and restricted to these two regions.

Conclusions

A continental-scale introduction to the late Holocene vegetation of tropical South America must of necessity paint the landscape in broad strokes. Behind the simplicity implied by the unifying name for each phytogeographic region or phytochorion is a riot of heterogeneity, of changes across often independently varying gradients and shifts in key environmental factors. Transitions to other phytochoria may occur abruptly or gradually, as continuums or as mosaics of vegetation cover derived from two or three surrounding regions. In addition to transitions, there may be inclusions, often totaling large areas and in some cases occurring as archipelagos, of vegetation cover that is either unique or has analogs or homologs elsewhere.

The vegetation types themselves include numerous variations on themes, and even where large areas are under the influence of relatively uniform conditions, non-obvious changes in such factors as drainage can yield dramatically different physiognomies and species compositions. An example is the alluvial overflow plains of the Llanos and the Pantanal.

Still, there are patterns. Each phytochorion is characterized by prevailing climates, geology, topography, vegetation types, principal life forms, adaptations, dominant plant groups, floristic affinities, diversity patterns, and species distribution patterns. Each has a set of endemic taxa.

We noted that similar climatic and edaphic conditions in geographically distant regions can give rise to strikingly similar vegetation physiognomies. In lowland northern South America, some of the same taxa can be found in comparable vegetation types hundreds or thousands of kilometers distant, particularly in savannas, floodplain forests, and swampy palm forests; particularly interesting examples occur between true campo rupestre in east-central Brazil and the tepuis of Venezuelan Guayana. Given similar vegetation cover any pair of distant localities, however, most of the species and some of the genera differ, as do family dominance patterns.

It is essential to expand on the measures that have been taken toward a standardized analysis of vegetation cover -- including both physiognomic and floristic information -- on a finer scale across the continent. There is a bewildering array of vegetation cover terminology, much of it derived from local or regional folk classifications. The compilation of definitions for Spanish South America developed by Huber and Riina (1997) lays a partial foundation for making comparisons. In addition to thorough descriptions of physiognomies and the edaphic conditions that give rise to them, these comparisons depend on adequate and accurate floristic surveys, which ultimately depend on updated monographs and revisions, i.e., modern taxonomic classification. There is an urgent need for more analyses of floristic affinities, such as those carried out for the Venezuelan Guayana (Berry et al., 1995) and for the Serranía de Chiribiquete (Cortés-B. and P. Franco-R. 1997; Cortés-B. et al. 1998) in Colombia. There is also a need for the application of more statistical methods in floristics. Mechanisms are needed for gathering and mapping information from disparate sources on plant distributions. With massive amounts of fieldwork, vastly increased efforts in systematic studies, and improved bioinformatics, the vegetation cover of tropical South America can be understood and mapped.

Acknowledgments

We thank Scott Mori and Hans ter Steege for their comments on the manuscript and for assistance with the literature survey; Marina Tereza Campos for information on the "capão" vegetation and the "campos rupestres"; Marlene Bellengi for preparing the map; and Muriel Weinerman for preparing the photographs from color slides.

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Figure Legends

1 Generalized map of the major phytochoria of northern South America (modified from Prance 1989).

1a. Profile of tropical moist forest on terra firme. Road construction near EMBRAPA reserve, Camaipi, Amapá, Amazonian Brazil, September 1983. Photo by D. Daly.

1b. Profile of disjunct "campinarana" ("Amazonian caatinga"). São Paulo de Olivença, upper Rio Solimões, Amazonas, Brazil, November 1986. Photo by D. Daly.

2a. Wet tropical forest near base of Cerro Torrá, Chocó, Colombia, February 1977. Photo by D. Daly.

2b. Atlantic coastal forest, Estação Ecológica de Juréia, São Paulo, Brazil, January 1994. Photo by D. Daly

3a. Early successional bands on inner (convex) curve of meandering tributary in southwestern Amazonia, Rio Acre, Acre, Brazil, October 1997. The lower shrubs are *Alchornea castaneifolia*, backed by *Tessaria integrifolia*, then *Gynerium sagittatum*, then *Cecropia* sp. Photo by D. Daly.

3b. Igapó (Amazonian black-water floodplain forest) at high water, Rio Cueiras, Amazonas, Brazil, June 1989. Photo by J. D. Mitchell.

4a. Várzea (Amazonian white-water floodplain forest), river receding, Riozinho do Andirá (basin of Rio Purus), Acre, Brazil, April 1995. Photo by D. Daly.

4b. Tidal várzea, Amazon estuary near Mocambo, Pará, December 1985. The broad-leaved aroid in the foreground is *Montrichardia arborescens*, a pioneer species of mud flats. Photo by B. Nelson.

5a. Cerrado landscape with "estero" (permanently wet meadow; right foreground) between gallery forest (right background) and cerrado (left foreground), near Gama, Distrito Federal, Brazil, July 1984. Photo by J. D. Mitchell.

5b. Cerrado landscape with the widespread Neotropical savanna species *Salvertia convallariodora* (Vochysiaceae) in foreground, São Gonçalo, Minas Gerais, Brazil, July 1984. Photo by J. D. Mitchell.

6a. "Campo rupestre" *sensu lato*, summit of Serranía de Santiago, Santa Cruz, Bolivia, August, 1983. Photo by D. Daly.

6b. Abrupt savanna-gallery forest transition, between Macapá and Porto Grande, Amapá, Amazonian Brazil, November 1986. Photo by D. Daly.

7a. Cerrado landscape on Chapada dos Guimarães, with patch of gallery forest at "Véu da Noiva" waterfall, , Mato Grosso, Brazil, January 1989. Photo by D. Daly.

7b. Arboreal "caatinga" with *Commiphora leptophloeos* (Burseraceae) and *Cereus jamacaru* (Cactaceae), near Santa Quitéria, Ceará, northeastern Brazil, January 1990. Photo by D. Daly.

8a. Open "caatinga" with *Pilosocereus* cf. *gounellii* (Cactaceae), west of Fortaleza, Ceará, northeastern Brazil, January 1990. Photo by D. Daly.

9a. Disturbed tropical deciduous forest, João Pinheiro, Minas Gerais, July 1984. Photo by J. D. Mitchell.

9b. Tropical dry forest, Tucavaca Valley, Santa Cruz, Bolivia, July 1983. Photo by D. Daly.