

# Diversity of vegetation types in the Guayana Region: An overview

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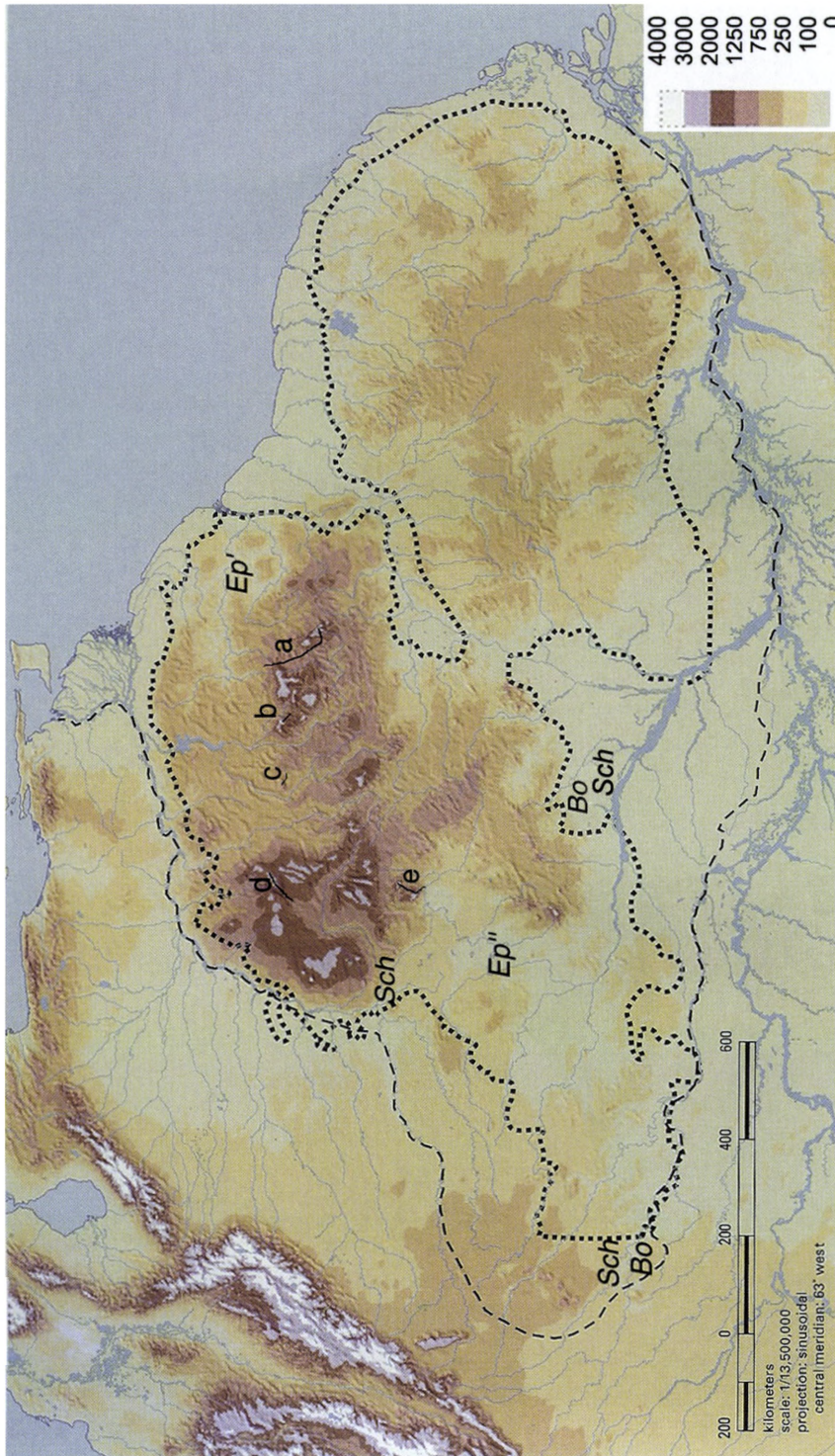
As a result of more than 200 years of botanical explorations in the area of the Guayana Shield in northeastern South America, the floristic knowledge about this still relatively remote and inaccessible land is rapidly increasing. Based on the presence of numerous families and genera with high levels of endemism and unusual patterns of plant distribution especially on the peculiar tabular mountains ("tepui"), a separate phytogeographical Guayana Region has been recognized for a long time. This was confirmed recently through the evidence of more complete and accurate data on its flora and other geographic characteristics. In this paper an attempt is made to provide further evidence for an autochthonous origin and evolution of plant life in the Guayana Region analyzing the nature and geographical distribution of the most important vegetation types and some of their characteristic plant communities. Using a series of ecological transects along different Guayanan mountain systems, as well as descriptions of local plant communities adapted to typically Guayanan ecological site conditions (such as oligotrophy or nature of substrate), it is shown that the diversity of vegetation types of the Guayana Region is very pronounced and remarkably different compared to that of the adjacent phytogeographic regions. The reasons for such a high concentration of floristic and vegetational properties in this relatively small portion of the Neotropics are strongly related to its long geologic stability allowing uninterrupted speciation processes since late Gondwanic times, the continuously increasing diversification of landscapes and site conditions, and a progressive increase of oligotrophic site conditions leading to more effective ecological adaptation processes at local scales. At the same time, such a stable land mass as the Guayana Shield must also be seen as an important refuge area for immigration and subsequent differentiation processes from the surrounding areas which were much more exposed to drastic changes in their life conditions during the process of their geologic evolution.

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## Introduction

Since the publication of "*Versuch einer Flora und Fauna von Britisch Guiana*" (Essay of a Flora and Fauna of British Guiana) by Schomburgk (1848), the scientific world became aware that the land between the Amazonas and the Orinoco rivers with its strange, flat topped

mountains was home to a rare and curious assemblage of plants and animals. During these last 150 years a large amount of biological collections and other scientific activities has been made in the area of the Guayana Shield, yielding an increasingly more detailed knowledge on the main characteristics of this rich and unique biota. Although some biogeo-



**Fig. 1.** Location and extension of the Guayana Region between the Amazonas and Orinoco rivers in northeastern South America (outer broken line) and of the geologic Guayana Shield (dotted line, *vide* Gibbs & Barron 1993). Base map taken from Huber and Foster (2003). Key to elevations in meters in lower right corner. Letters **a** through **e** correspond to the location of the altitudinal transects indicated in Fig. 3. **Ep'** = Guyanan *Eperua* forests; **Ep''** = Upper Rio Negro *Eperua* forests. **Bo** = *Bonnetia martiana* shrublands; **Sch** = *Schoenocaphalum* lowland meadows.



graphic classifications of the Neotropics recognize the Guayana region as a distinct phyto-, zoo- or biogeographic unit (but under several different names and even more different geographic locations), other publications consider this region still to be nothing other than a northward extension of the Amazonian region (*e.g.* Cabrera & Willink 1973).

In this paper an attempt will be made to present a more comprehensive overview of the main characteristics of the varied Guayanan biota, in order to demonstrate its autochthonous character derived from a unique evolutionary history and documented today not only by a high alpha (taxonomic) diversity, but also by a similarly and no less interesting diversity of plant communities and landscape types. For this purpose, the results of an interdisciplinary workshop on Guayanan biota held at Paramaribo (Suriname) in April 2002 (Huber & Foster 2003), as well as the author's personal field experience accumulated over approximately 30 years mainly in the Venezuelan Guayana will be taken into account. Since southern Venezuelan has the most numerous and most diverse of the Guayanan montane environments, a bias towards this area is unavoidable. However, it must also be mentioned that the Venezuela Guayana region is presently one of the ecologically and biologically better known sections of the biogeographic

region of Guayana, which extends more or less widely in six neotropical equatorial countries (Guyana, Suriname, French Guiana, northern Brazil, southeastern Colombia, and southern Venezuela).

Some of the following geological and geomorphological considerations referring to the Guayanan landscape evolution since late Mesozoic times (approx. 150 million years ago to present), are based on Gibbs and Barron (1993), Mendoza (1977), Gosh (1985), and Sidder and Mendoza (1999); furthermore, many on-site discussions during numerous field trips with colleagues of Earth Sciences, such as Alfred Zinck, Carlos Schubert(†), Henry Briceño and Franco Urbani have also contributed to obtain valuable insights into Guayanan geological history. For detailed and updated floristic and phytogeographic data on the Guayana Region, and especially of its highlands (*Pantepui*), the reader is also referred to the paper of Berry and Riina (this volume).

## Short overview of the Guayana Region and its main vegetation types

### *Geographical characteristics*

The Guayana Region in its widest sense occupies roughly an area of 2-2.5 million km<sup>2</sup> (Huber & Foster 2003), corresponding to the consolidated basement area of the Guayana Shield

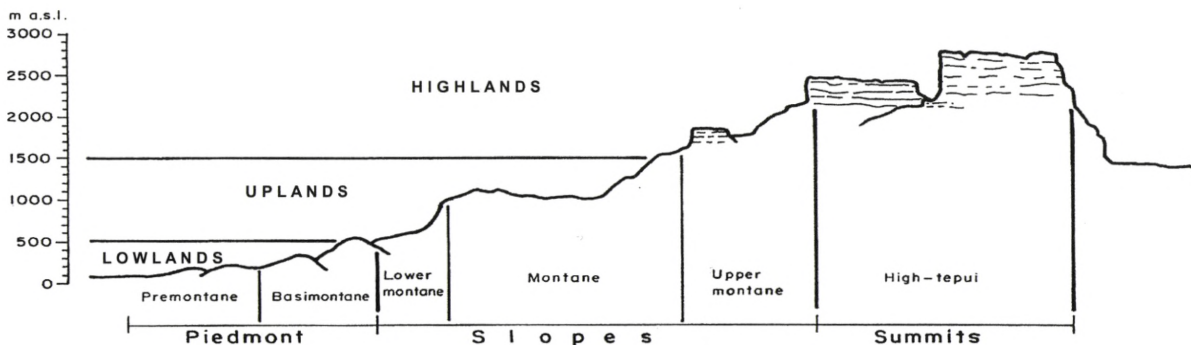


Fig. 2. Altitudinal zonation in the Guayana Region (from Huber 1995a).

and its surrounding forelands (Fig. 1). The Guayana Shield, together with a few other similar nuclei located in various parts of the Earth, is considered to be one of the oldest cratons that had initially solidified in the Earth's mantle, approx. 3-4,000 million years ago. This huge Proterozoic landmass was later subject to intermittent phases of intensive sedimentation processes, which eventually buried wide parts of it under a cover several thousand meters thick and formed by innumerable layers of sandy and quartzitic material of predominantly siliceous geochemical composition, classified today as the Precambrian quartzites and sandstones of the Roraima Group (Mendoza 1977). A series of large tectonic events, which included repeated Palaeo- and Mesozoic volcanic intrusions of ultramafic lava flows among the strata, and successive intense and prolonged periods of erosional processes have subsequently substantially modified the originally undulating highland plateau of this western section of the ancient Gondwana supercontinent.

Since no convincing fossil records have so far been found from the entire Guayana Shield area, the Palaeo- and Mesozoic history of its geological and biological evolution is still unknown. However, there are no reasons to assume that such an ancient, permanently emerged landmass located mostly at tropical latitudes at least since Mesozoic times and composed of a variety of geological substrates, should not have been colonized by plants like in the rest of the world. The widespread presence of so called Gondwanan families (*e.g.* Annonaceae, Bombacaceae, Chrysobalanaceae, Ebenaceae, Sapotaceae, etc.) in the modern flora of the Guayana Region strongly suggests that it was covered by a succession of archaic, Gondwana related proto-floras. Their members aggregated into continuously evolving and differentiating series of vegetation types which were forced permanently to adapt to the progressively expanding oligotrophic

site conditions produced by the intense weathering processes of the predominantly quartzitic substrate.

But especially after the breakup of the Gondwana continent during the Cretaceous Period (starting approx. 145 million years ago), the erosional and weathering processes acting upon the landscapes of its western segment, of which the Guayana Shield made part, must have suffered important changes in intensity and direction. The appearance of a steadily expanding oceanic watermass along the eastern border of that new continent during the Tertiary, surely created entirely different regional climatic cycles in that area. It is probable that since that time the Guayanan biota must have been heavily conditioned by a monsoon-type of climatic regime with its characteristically alternating wet and dry phases during the year.

As a consequence, the relatively uniform topography of the original Precambrian Roraima sandstone cover was soon interrupted by the formation of numerous creeks and valleys eroding downwards along the intricate pattern of fault lines, diachases, and contact zones extending between the differential rock types. These intensive erosion processes were probably reinforced by vertical tectonic movements of the Shield induced by the Andean orogenesis which since the middle of the Tertiary (approx. 30 million years ago) was operating in the adjacent western periphery of the Guayana Shield. As a result, the once continuous strata of the Roraima Group broke up creating an increasing number of progressively isolated mountain blocks; at the same time, the characteristic Guayanan step-like landscape originated, with its alternating horizontal levels and steep slopes, testifying to the sequence of different erosion cycles which had succeeded one another during the various geological epochs of the Tertiary and Quaternary (Briceño & Schubert 1990, 1992).



While this long lasting erosional process of the Roraima quartzite and sandstones is still ongoing, an altitudinal zonation of life zones can easily be recognized in most Guayanan mountain systems ranging from near sea level up to average elevations between 2000 and 3000 m a.s.l. This zonation (see Huber 1995a) consists of a *lowland zone*, usually between 0 and 500 m a.s.l. with an equatorial macrothermic temperature regime, followed upwards by the *upland zone* or belt, usually between 500 and 1500 m a.s.l. with a cooler submeso- to mesothermic temperature regime, which in turn is topped in most cases by a *highland zone*, between 1500 and 3000 m a.s.l. and subject to a cool or cold meso- to submicrothermic temperature regime (Fig. 2). The climatic, geologic, edaphic and ecologic parameters prevailing in each of these altitudinal sections have been described elsewhere (*e.g.*, in Huber 1995a).

The recognition of these altitudinal belts in the Guayana mountains is a basic tool for the better understanding of the present distribution of plants and vegetation types in the Guayana Shield region. For the same purpose, it is useful to summarize the following landscape characteristics, which distinguish the Guayana region markedly from the surrounding Amazonian and Andean landscapes:

(1) an unparalleled long, uninterrupted continental geologic and evolutionary history since Precambrian times;

(2) the upper orographic levels (highlands) are geomorphologically older than the more recently formed lower upland and lowland levels;

(3) the landscape possesses an essentially horizontal structure alternating with slopes or vertical walls; therefore, the totality of these microlevels at each orographic level (low-, up- and highland) offers a wider spectrum of local ecosystems and niches than would be possible on a continuously ascending mountain slope;

(4) the principal erosional processes govern-

ing the Guayana Shield are chemical and physical weathering, erosion and outwash in the highlands, transient accumulation, erosion and outwash in the uplands, and accumulation and erosion in the lowlands; therefore, soil forming processes attain minimum rates in the highlands and maximal rates in the lowlands, where extensive volumes of sediments deriving from the surrounding uplands and highlands are accumulated in the form of wide glacis (slightly inclined piedmont slopes);

(5) both the underlying igneous-metamorphic as well as the sedimentary rock types of the Guayana Shield are extremely poor in minerals and their decomposition yields generally extremely nutrient poor soils with acidic quartz as its main mineral component; therefore, in the Guayana Shield and its peripheral forelands oligotrophic soil conditions predominate.

All these mainly physical circumstances have contributed to the outstanding characteristics of the biota developed in and around the Guayana Shield, and which are particularly evident in its plant life, both in the floristic and in the ecologic, vegetational aspect. The present-day rich and diverse flora of the Guayana Region contains a number of elements at the family and genus level, which point strongly towards the recognition of an autochthonous plant evolution center (speciation center?) in this area since early geological times, in spite of the absence of concrete fossil records. Such Guayana centered taxa like Rapateaceae, Bonnetiaceae, *Tepuianthus*, *Saccifolium*, *Euphronia*, tribe Mutisieae of the Asteraceae, Ochnaceae, Bromeliaceae, and Rubiaceae, as well as nearly 150 endemic genera and more than 4000 endemic species (Berry *et al.* 1995) give sufficient evidence of the existence of an authentic Guayana-rooted biota. This can be observed not only through their taxonomic position, but especially through their consistently noticeable ecological and physiognomical structures and



processes, developed in response to the particular Guayanan environmental conditions. Particularly the latter, however, can only be seen in the field and requires, therefore, considerable field work and direct knowledge of the plants themselves, as well as the plant communities in which they occur. Ironically, it is becoming increasingly more difficult to accumulate this kind of field knowledge due to logistical and permit concerns.

### *Main vegetation types*

An examination of recent vegetation maps of the Guayana region (e.g. Eva *et al.* 1999, 2002) reveals that the equatorial and tropical *forest zonobiome* (*sensu* Walter & Breckle 1984) is by far the most widespread, covering probably more than 80% of the entire area. A still largely undetermined diversity of forest types covers the extensive lowlands, as well as most of the intermediate upland plateaus and lower and mid elevation slopes of the many mountain systems up to approximately 1000-1500 m a.s.l. Ter Steege (2000) has presented a good overview of the presently known forest types studied in numerous sites located in the Guianas, and is preparing a wider paper on this subject to include southern Venezuela, northern Brazil and southeastern Colombia.

The array of forest types found in the Guayanan lowlands includes *Mora* and Greenheart (*Chlorocardium*) forests, *Eperua* forests, Lecythidaceae forests, *Hevea* forests, *Erismia* forests, *Clathrotropis* forests, *Micrandra* forests, *Dipteryx* forests, to mention just a few well known examples from current literature (see ter Steege 2000). A short flight at low elevation above any forested lowland in the upper Orinoco drainage of Venezuela, or in the Essequibo basin of Guyana, or in the Rio Negro watershed of Brazil gives evidence of the existence of a highly diversified mosaic of numerous forest communities on the ground. On the other hand, the submontane and montane

slope forests of the tepuis as well as of the other larger mountain ranges and upland plateaus (such as Pakaraima, Parima, Sierra de Unturán) are still largely unknown in both their latitudinal extension and their altitudinal zonation; only a few point studies have been published so far, such as the ones made on the upper slopes of Ptari-tepui, where interesting montane forests with *Platycarpum* and *Moronobea* were described (Steyermark 1966), or in the Duida-Marahuaka massif with its extensive *Dimorphandra* and *Perissocarpa* forests (Dezzeo & Huber 1995). Perhaps one of the best studied forest ecosystems of the higher Guayana region are the little forest islands growing on the flat topped summits of many tepuis, where these ecosystems occupy low depressions or creeks (Vareschi 1992a). Invariably, the dominant tree above 1500-1800 m belongs to the genus *Bonnetia* of the Bonnetiaceae (formerly included in the Theaceae), but at the species level significant variations are found not only at the different altitudinal levels, but also from mountain to mountain. The only exception to this *Bonnetia* predominance has been found in the summit forests of the granitic Sierra Maigualida, where the most frequent tree species are *Cyrilla racemiflora*, *Clusia* spp., *Ecclinusa ulei* (Sapotaceae), *Weinmannia* spp. (Cunoniaceae) and *Schefflera* sp. (Araliaceae) (see Huber *et al.* 1997).

In general, one can notice in the Guayana mountains a steep decline in both alpha and beta-diversity of forest ecosystems along a lowland-upland-highland gradient. Unfortunately, there are insufficient quantitative data to allow statistically significant comparisons, but average numbers of tree species per hectare with DBH  $\geq 10$  cm range between 150-280 in neotropical lowland forests (Phillips *et al.* 1994) and probably less than 10 in the tepui highland forests (personal estimation). Also the physiognomic diversity of the forest types tends to become much more uniform with



increasing elevation, a phenomenon already observed in the Andes and other tropical American mountains (Vareschi 1992a; 1992b).

In spite of their relatively small extension, the *shrublands* and the *herbaceous vegetation types* of the Guayana region show an enormous degree of diversity, to the extent that one might consider them to be the true characteristic and, at the same time, differential vegetational features of this phytogeographic region. In most cases these two formations belong to the class pedo-biomes in the sense of Walter and Breckle (1984), since they are invariably associated with particular edaphic conditions. They include litho-biomes, psammo-biomes, histo-biomes, and peino-biomes and are easily recognized in the field as characteristic Guayanan vegetation types by their floristic and physiognomic properties.

The *shrubland ecosystems* found at the various altitudinal levels of the Venezuelan Guayana were presented in a comprehensive overview by Huber (1989, 1995b, 1995c). Previously, Heyligers (1963) in Suriname, Cooper (1979) in Guyana, Anderson (1981) and Prance and Schubart (1978) in northern Brazil described some of these peculiar ecosystems growing principally on lowland white sands. Again the scanty published data on the Guayana shrublands do not allow a more detailed analysis of their floristic composition and physiognomic variability; however, it seems as if the scrub types growing at intermediate elevational levels (uplands, between 800 and 1500 m a.s.l.) show the highest rates of alpha- and beta diversity, although in the high tepui shrublands (on summits above 1800 m a.s.l.) some of the most unusual habits have developed including the caulirosette growth form, predominant elsewhere only in the high Andean páramos and the upper vegetation belts of some African volcanoes.

The *herbaceous formation* is well represented in many landscapes of the Guayana region;

tropical, grass-dominated savannas are found predominantly in the central-eastern Guayana lowlands and uplands, ranging from the Guianas in the east to the Rio Branco savannas in northern Brazil, the Gran Sabana in south-eastern Venezuela and some transitional savannas in the southwestern border area of the Orinoco Llanos with the Guayana region. Almost all of these grass savannas belong to the large phytosociological Class Trachypogonetalia (van Donselaar 1968), in which *Trachypogon spicatus* is the dominant and at the same time ecologically characteristic grass element.

The numerous savanna ecosystems scattered over the Guayana Shield area and ranging there from near sea level in the coastal savannas of the Guianas to approx. 1400-1600 m a.s.l. in the Venezuelan Gran Sabana region, are therefore true members of the neotropical savanna biome, a zono-biome (*sensu* Walter & Breckle 1984) which is widespread from central-southern Brazil and northern Paraguay to southern Mexico. This formation, probably of ancient (Gondwanic?) origin (*Trachypogon* is also an important grass component of the African paleotropical savannas), includes a large number of more or less species-rich ecosystems and plant communities with their highest diversification in the central Brazilian uplands, where they form a wide array of physiognomically distinct and floristically diverse communities grouped under the term "*cerrado*". The ancient, rolling open landscape type of the *cerrado*, characteristic of the *Planalto Brasileiro* and its numerous peripheral mountain systems, have originated on the Brazilian or Guaporé Shield, considered to be the sister-shield of the Guayana Shield, from which it is separated today by the valley of the Amazon River. Most likely, ancestral savanna communities initially spread from the Brazilian core area to the adjacent continental uplands located to the north and west. During later expansion phases, concurrent with the climatic oscilla-



tions which occurred during the late Tertiary and Quaternary, some of these grass communities began to occupy the large basins created after the Andean uplift around the continental masses of the Guayana and Brazilian Shield, such as the Orinoco Llanos in Colombia and Venezuela and the Beni plains in northeastern Bolivia. Interestingly, in spite of an evident and well marked floristic differentiation in all major regional savanna fragments of the neotropics, a common "basic floristic matrix" of grasses and accompanying shrubs can still be found today throughout the entire area (see Huber 1987).

In contrast to these tropical grasslands (savannas), the Guayana Shield harbors another herbaceous biome, which is restricted exclusively to that biogeographic region: it consists of mainly broadleaved herbaceous meadows, whose dominant species and genera belong to highly specialized, but non-gramineous families, such as the Rapateaceae, Bromeliaceae, Xyridaceae, Eriocaulaceae and Cyperaceae. A few genera of Rapateaceae, like *Stegolepis*, *Marahuacaea* and *Kunhardtia* in the uplands and highlands, as well as *Schoenocephalum*, *Monotrema* and *Cephalostemon* in the lowlands, form extensive communities and may well be considered as the true "flagship species" of Guayanian herbaceous biota (see Huber 1988). Although sometimes they may resemble each other superficially, these Guayanian broadleaved meadows have little in common with a traditional neotropical savanna, either from the physiognomic or the floristic points of view. For that reason, and because of their distribution strictly limited to the Guayana region, they should be regarded as a separate herbaceous pedo-biome (psammo-biome in the lowlands, histo-biome in the uplands and highlands).

Guayanian broadleaved meadows grow in the uplands and highlands from 800 to 2500 m a.s.l., usually on water-saturated organic soils

(histosols or peat), or rarely on open sandstone surfaces, where they compete with other, nongramineous herbaceous communities formed mainly by terrestrial bromeliads of the genera *Brocchinia*, *Lindmania* and *Navia*. In the lowlands (below 500 m a.s.l.), they are found characteristically on alternating dry/wet, alluvial white-sand soils, which represent extremely acidic and oligotrophic habitats (peino-psammobiome *sensu* Walter & Breckle 1984). As will be seen in the following chapter, it is mainly this biome of the Guayana region, that shows a marked differentiation in both the vertical (altitudinal) sense as well as in the horizontal (geographical) sense. Furthermore, these herbaceous communities also contain a great variety of peculiar growth forms (*e.g.*, dense rosettes in Eriocaulaceae or Cyperaceae, sigmoid leaf arrangement in Rapateaceae, tubular leaf arrangement in Bromeliaceae), as is the case with the shrublands.

Finally, the last large habitat type present in the Guayana region is represented by the *rock surfaces*, which are very extensive in the Guayana mountains, especially along their upper walls and cliffs, as well as on their mostly flat-topped summit plateaus. The saxicolous plants and plant communities adapted to grow in this harsh biome extending from near sea level to the summit of the highest mountain peak of Cerro de la Neblina on the southernmost Brazilian/Venezuela frontier at 3014 m a.s.l., belong to epilithic cyanobacteria, algae and lichens, or to Bromeliaceae, Cyperaceae and Xyridaceae, and to a characteristic and highly endemic assemblage of herbaceous and/or woody species belonging to various families. Each of these plant associations can also be interpreted as a particular seral phase in the process of colonization proceeding from the open, exposed rock to shallow depressions, cracks and crevices, and finally into more extended depressions with low arborescent vegetation.



	Transect a	Transect b	Transect c	Transect d	Transect e
3000	Cuyuní - Gran Sabana - Roraima 100-2700 m	Kamarata - Guayaraca - Auyántepeui 400-2450 m	Río Aro - Río Trueno - Guaiquinima 50-1650 m	Lower Caño Iguana - Upper Caño Iguana - Cerro Yudi 100-2400 m	La Esmeralda - Duida - Marahuaka 100-2800 m
-	Open rock veg. High tepui forest w. <i>Bonnetia roraimae</i>	Open rock veg. Tepui meadow & scrub High tepui forest w. <i>Bonnetia roraimae</i>			Open rock veg. High tepui meadow & scrub (Marahuaka)
2500					
-					
-					
2000	WALLS	WALLS		Open rock veg. Tepui meadow & scrub	WALLS (Marahuaka) Tepui meadow & scrub (Duida)
-					
-	Montane forest	Montane forest w. <i>Bonnetia steyermarkii</i>		Montane forest w. <i>Dugandiodendron</i>	Montane forest w. <i>Perissocarpa</i>
1500	w. <i>Bonnetia tepuiensis</i>	Montane forest		Montane scrub	
-					
-	Upland meadow & scrub	Submontane forest	Tepui meadow	Montane forest	Submontane forest w. <i>Dimorphandra</i>
-					
1000	Palm savanna (morichal) Open savanna	Upland scrub Open savanna	Submontane forest		WALLS (Duida)
-					
-					
500	Submontane forest	Submontane forest	WALLS	Submontane forest	Submontane forest
-		Shrub savanna	Shrubland		
-					
-	Lowland forest		Lowland forest Tree savanna	Lowland forest	Savanna Lowland forest
0					

Fig. 3. Five altitudinal transects (a through e) along selected mountains ("tepuis") of the Venezuelan Guayana. The lowland (0-500 m), upland (500-1500 m) and highland (1500-3000 m) zones are indicated with horizontal lines.

## Beta-diversity in the Guayana Region

Although a large part of the Guayana Region still lacks detailed inventories of its alpha- and beta-diversity (see Huber & Foster 2003), an attempt will be made here to illustrate the diversity of habitats already found in places which have been visited during ecological explorations in the past 50 years. For this purpose, three different approaches will be used: altitudinal transects, horizontal wide-scale comparisons within the four recognised provinces of the Guayana Region, and geo-ecological parameters.

### *Vertical (altitudinal) differentiation:*

Figure 3 shows the altitudinal sequence of the main vegetation types observed by the author from the basal lowlands to the summits of five important mountain systems selected in the Venezuelan Guayana (see Fig. 1 for location of transects a-e).

(a). *Transect Cuyuní River-Gran Sabana-Mt. Roraima.* – This NW-SE oriented transect is located along the border of eastern Estado Bolívar in Venezuela and the Pakaraima region in Guyana, stretching approx. over 125 km and 2600 m of elevation. It starts in the north with dense evergreen lowland forests in the Cuyuní river basin, ascending quickly through lush submontane and cloud forests along the northern slopes of Sierra de Lema up to 1400 m a.s.l. and then enters the Gran Sabana uplands, which are covered mostly by treeless *Trachypogon* and *Axonopus* dominated grass savannas. In this wide, gently rolling landscape large areas of the broadleaved *Stegolepis* meadows with an interesting shrubby flora are present in the upper section, whereas in the lower southern section (between 900 and 1200 m a.s.l. approx.) extensive *Mauritia flexuosa* palm savannas, on partly flooded terrain, are predominant. These are the highest *Mauritia* palm savannas known in Venezuela. The base of Mt.

Roraima is located in the southeastern corner of the Gran Sabana at approx. 1300 m a.s.l. and is covered in its western and northern base by dense submontane forest; this forest soon changes into a lower montane *Bonnetia tepuiensis* forest, which covers the upper part of the talus slope up to the base of the wall at approx. 2000 m a.s.l. Once the summit is reached at approx. 2700 m a.s.l., the predominant vegetation is open rock pioneer vegetation formed by cyanobacteria, algae and lichens, alternating with small pools containing herbaceous or low shrubby high-tepui vegetation dominated by Rapateaceae, Xyridaceae, Eriocaulaceae among the herbs and Rubiaceae, Clusiaceae, Bonnetiaceae, and Araliaceae among the low shrubs. In larger depressions almost monospecific low forest islands formed by *Bonnetia roraimae* are found scattered over the wide, flat, wind swept rocky plateau.

(b). *Transect Kamarata-Guayaraca-Auyántepui.* – Less than hundred kilometers to the west of the former transect, this short, but steep transect starts at 400 m a.s.l. in the alluvial plains of the valley of Kamarata, where dense *Humiria balsamifera* and *Platycarpum rhododactylum* shrublands on white sands alternate with neotropical *Trachypogon* grass savannas, surrounded by evergreen lowland forests. On the next altitudinal step, the Guayaraca plateau at approx. 1000 m a.s.l., *Clusia*, *Euphronia* and *Dicymbe* shrublands with a dense grass cover of *Trachypogon* and *Axonopus* give way to other types of dense, still largely unexplored submontane forests on the slopes leading to the following plateau at 1500 m elevation; there, part of the original forest cover has been destroyed by fire, but above 1600 m a dense, although lower montane forest can be recognized, followed by a narrow belt of *Bonnetia steyermarkii* forests at the base of the walls (approx. 1900 m a.s.l.) of the southern Auyántepui massif. After traversing the upper walls, the southernmost and at the same time highest elevation of Auyántepui (2450 m a.s.l.)



is reached. Typical high-tepui scrub dominated by *Chimantaea similis*, *Tepuianthus auyantepuiensis*, *Clusia* sp. and *Blepharandra hypoleuca* covers large extensions of the otherwise almost bare sandstone surface, where a few saxicolous plant communities of the bromeliads *Ayensua uaipaiensis* or of the showy *Connellia varadarajanii* can be found. The huge summit plateau of Auyántepeui is covered mostly by a great variety of vegetation types, including dense *Bonnetia ro-raimae* forests, species rich shrublands and extensive, swampy meadows.

(c). *Transect Río Aro-Río Trueno-Guaiquinima S-N.* – This transect starts in the northeastern piedmont slopes of the large but relatively low tepui Guaiquinima massif in the Paragua River drainage, where interesting tree savannas of *Caraipa* and *Bonyunia* growing with *Bulbostylis lanata* and *Mesosetum rottboellioides* in the herbaceous layer form a unique mosaic with tall semideciduous and evergreen lowland forests. From this approx. 100 m level one climbs to the following level at approx. 400 m a.s.l., consisting of wide, concentrically inclined rocky slopes covered by extraordinarily rich and diversified shrublands dominated by *Platycarpum rhododactylum*, *Terminalia* spp., *Euphronia guianensis*, and *Pakaraimaea dipterocarpacea*, to mention just a few outstanding members. The following step of the transect brings us to the southeastern rim of Cerro Guaiquinima, at approx. 750-850 m a.s.l., covered by low, submontane forest alternating with open scrub with *Clusia* spp., *Marlierea pudica* and many melastomes on open sandstone layers. Only above 1200 m a.s.l. and mostly in the northern summit plateau, large herbaceous meadows appear on peat, dominated by the endemic rapateaceous *Stegolepis squarrosa* mixed with low sprawling shrubs of *Blepharandra fimbriata* and *Bonnetia lanceifolia*. This unique, open low-tepui vegetation extends up to the northern summit of Guaiquinima-tepui at 1600 m a.s.l.

(d). *Transect Lower Caño Iguana-Upper Caño*

*Iguana-Cerro Yudi.* – Contrary to the former transects, this one runs along the continuous southwest-facing slopes of Sierra Maigualida, the largest igneous-metamorphic, granitic mountain system in the Guayana Shield; it covers a length of approx. 80 km, whereas the difference in altitude is 2300 m, from 100 to more than 2400 m a.s.l. According to Zent & López (pers. comm.) the forests of the lower Caño Iguana are tall lowland forests dominated by Lauraceae, Sapotaceae and legumes, some of them semideciduous. These lowland forests give way to even taller and apparently diversified submontane forests around 600 m a.s.l. until elevations of approx. 1500 m a.s.l.; unfortunately, no studies are yet available from this belt. Higher up, between 1600 and 1800/2000 m a.s.l., montane forests with typically dense and flattened crowns are common; one forest type visited by us in this belt seemed to be dominated by almost pure stands of the genus *Perisocarpha* (Ochnaceae) and the ground cover was formed by dense fern communities, mixed with numerous terrestrial aroid colonies. Towards the summit of Cerro Yudi, between 2100 and 2400 m a.s.l., low high-tepui forest dominated by *Cyrilla racemiflora* (the same species dominating elfin forests in Puerto Rico!) mixed with *Magnolia* sp., *Clusia* sp. and *Gongylolepis jauaensis* grows in protected depressions (Huber *et al.* 1997), whereas the mostly flat valley bottoms are filled with deep, water saturated peat covered by dense meadows of *Kunhardtia rhodantha*, *Orectanthe sceptrum* and a still undescribed species of a densely pubescent *Axonopus*. On the numerous granitic rock outcrops strange open shrublands formed by mostly endemic taxa of *Spathelia* (Rutaceae), *Coccochondra* (Rubiaceae), *Huberopappus* (Asteraceae), *Cuphea* (Lythraceae) and *Phyllanthus* (Euphorbiaceae) characterize this outstanding high mountain landscape of Sierra Maigualida that was explored for the first time less than two decades ago.



(e). *Transect La Esmeralda-Cerro Duida Plateau-Cerro Marahuaka.* – The last transect treated here is also the highest, spanning from 150 m to 2800 m a.s.l., but it includes two mountains which, although close to each other, are remarkably different in their physiographic and vegetational aspects. The transect starts at the southern tip of Cerro Duida, in the savanna of La Esmeralda stretching along the northern shore of the upper Orinoco River (150 m a.s.l.). This typical dense *Trachypogon* grass savanna including palm swamps of *Mauritia flexuosa* is considered by Eden (1974) to be a relictual savanna from Pleistocenic climatic oscillations. The Esmeralda savannas are embedded in a mosaic of evergreen lowland forests, ranging from typical tall terra firme forests with *Ceiba*, *Goupia*, Moraceae, etc. to lower and more open caatinga forests dominated by *Eperua obtusata* (Coomes & Grubb 1996). The next belt is formed by submontane forests which cover the lower slopes of Cerro Duida up to the base of the cliffs at approx. 1000 m a.s.l.; the southern summit of Duida is reached at almost 2400 m a.s.l., where a wide variety of tepui meadows dominated by *Amphiphyllum rigidum* and *Stegolepis pungens* alternate with diverse shrublands of Rubiaceae, Melastomataceae and especially Ochnaceae of the genus *Tyleria*. The huge plateau of Cerro Duida (>1000 km<sup>2</sup>!) slowly descends northwards to about 800 m a.s.l. Below approx. 1500 m a.s.l., the mosaic of tepui meadows and shrublands is replaced by dense submontane forests mostly dominated by *Dimorphandra*, which extend to the steep base of the majestic Cerro Marahuaka rising abruptly from the northeastern border of the Duida plateau up to 2800 m a.s.l., making this the second highest mountain of the Guayana Shield. On its slopes, a series of altitudinally distinct forest types can readily be recognized, but they have not yet been ecologically characterized. Interestingly, the two summits of

Marahuaka, although only separated from each other by a shallow valley, have very different biota, the northern one covered by dense meadows on peat dominated by *Stegolepis terramaris*, *Brewcaria* and *Steyerbromelia*, whereas on the slightly lower southern summit mainly shrublands and small forests grow on the extensive rocky plateau, and the northern *Stegolepis* is almost exclusively replaced by the endemic Rapateaceae genus and species *Marahuaca schomburgkii* (Steyermark & Maguire 1984).

Even from such a short description of five altitudinal transects made on just a few of the more than 50 tepuis and mountains recognized in the central Guayana Shield, the following conclusions can be drawn:

(1). There exists a general altitudinal zonation in the distribution of vegetation types which corresponds roughly to the climatic belts of *macrothermic lowlands* (0-500 m a.s.l., mean annual temperature >24° C), *submesothermic uplands* (500-1500 m a.s.l., mean annual temperature 18-24° C), and *meso- and submicrothermic highlands* (1500-3000 m a.s.l., mean annual temperature 8-18° C), regardless of the geology and of the principal orographic features of the mountains (*e.g.*: steplike *vs.* continuous slopes).

(2). The extent and course of each altitudinal zone may vary from one mountain to another, depending on the mountain's size or mass ("*Massenerhebungseffekt*") and its overall elevation, as well as of the local (meso)climatic exposure of the slopes considered; furthermore, local edaphic, geomorphologic or physiographic features may also influence the nature and extension of the vegetational belt. Therefore, the above mentioned numeric altitudinal values are only indicative and must be corroborated in the field on each single mountain and on each exposure.

(3). Thus far, no two equal transects have been reported from any Guayanan tepui or



mountain in any of the three altitudinal belts, showing significant differences either in the physiognomic, or the floristic components, or both of the vegetation types analyzed. This indicates that the long emphasized floristic (alpha) diversity found on each tepui summit is actually also well represented through a similarly highly diversified assemblage of vegetation types (beta diversity) progressing from the base to the summit of these mountains. It seems unlikely that the factor "isolation", usually invoked for explanation of the high speciation rates on the tepui summits, could also be responsible for the high beta diversity found on the slopes and in the surrounding lowlands. It must be admitted, however, that at this moment the available amount of comparable and verifiable field data is still too scanty and does not allow definite conclusions on this subject.

#### ***Horizontal (geographical) differentiation***

Examining the large area occupied by the geologic Guayana Shield on an elevational physiographic map (see Fig. 1), one notices that it includes a central, rather concentrated mountainous area, surrounded by more or less wide forelands in all four directions; it is furthermore bounded by two large valleys, one in the north (Orinoco) and the other in the south (Amazonas), whereas in the east it is limited by the Atlantic Ocean and in the west by the Andean piedmont slopes (glacis).

As mentioned before, the age of formation of the various erosion surfaces of the sedimentary mountain systems of the Guayana Shield decreases from top to bottom (*i.e.*, from Precambrian to Quaternary), contrary to what may happen in other mountain systems of mainly tectonical orogenesis (*e.g.*, the Andes), where the uppermost zones have often originated most recently. The enormous, slightly inclined piedmont slopes (glacis) surrounding the core Guayanian mountains in the east,

south and west were mainly built up of acidic quartzitic sand grains originally washed down from the tepui summits, then deposited at their base and then relocated at progressively increasing distances according to their decreasing particle weight. This cyclic erosion-sedimentation-erosion process, has taken place at the base of the Guayana mountains for many millions of years (*e.g.*, in the Casiquiare and the Rio Negro peneplains). The product consists of a peculiar environment, characterized by thick layers of relatively homogeneous sandy substrate with two well pronounced features: an extremely low content of mineral nutrients (edaphic oligotrophy) and a very low water and cation retention capacity. Elsewhere such permeable soils (psammets, or, in this specific case: quartzipsammets), paired with critical rainfall amounts, are considered to be among the most adverse substrates for a vigorous plant life and in many places on earth they only allow the growth of simple plant communities consisting of a few rachitic, though often highly endemic plant species ("peinobiomes" of Walter & Breckle 1984).

Surprisingly, however, the entire Guayana lowlands, including most of these white sand ecosystems, exhibit an extraordinary richness of vegetation types resulting from the establishment there of a very diversified mosaic of plant communities obviously well adapted to the prevailing adverse edaphic and hydrologic conditions. Also the floristic richness is not negligible, although far from other tropical "hotspot" values (see, for example, Clark *et al.* 2000). One main reason for such a successful colonization must certainly be a sufficient and relatively continuous rainfall supply over longer evolutionary periods (at least during the Tertiary), providing not only the edaphic water resources necessary for plant growth, but also the sustained input of significant amounts of nutrients over the region in form of suspended dust particles (aerosols).



Although white sand soils are widespread in the Tropics, some examples of Guayanan ecosystems on such a substrate in the lowlands give evidence of interesting geographical differentiation processes. It should be noted here that such psammic ecosystems are virtually absent from the upland and highland levels of the Guayana Shield, where the prevailing substrate consists either of peat or of open sandstone or quartzite surfaces.

*Eperua forests in NE Guyana and in SW Venezuela.* – The small (15 spp.) caesalpinoid genus *Eperua* shows a remarkable differentiation in the Guayana region: large areas of the lowlands of Guyana including white sand soils are covered by peculiar forests dominated by *Eperua falcata* and *E. jenmanii* (“wallaba” forests) (**Ep**’ on Fig. 1); at the opposite corner of the Guayana Shield, *i.e.* in the upper Río Negro basin, other *Eperua* forests, but there dominated by *E. purpurea* and *E. leucantha*, characterize the “caatinga” landscape with their showy purple crowns (**Ep**” on Fig. 1). In addition, the Guyanese nucleus of *Eperua* also shows a discrete altitudinal differentiation into the Pakaraima uplands, where *E. jenmanii* subsp. *sandwithii* and *E. schomburgkiana* form open forests from the lowlands up to 1200 m a.s.l.

*Bonnetia shrublands along the southwestern Guayana Shield.* – The genus *Bonnetia* of the Theaceae represents one of the key floristic elements of most Guayanan mountain biota. In the lowlands, however, it is found in only two species, *B. martiana* and *B. crassa*; of these, the former is the main component of extensive and very dense shrublands on water logged white sands stretching in a wide arc from the western Rio Branco Basin in northern Brazil to the middle Caquetá river (near Araracuara) in southern Colombia (**Bo** on Fig. 1). *Bonnetia crassa* instead barely descends from its preferred habitat, the rocky uplands and highlands of the tepuis in the Venezuelan state of

Amazonas, to a few open shrublands in the Casiquiare and Atabapo drainages, always associated with white sand soil. In this case we observe that only one species (*B. martiana*), out of 30+ species otherwise widely distributed over virtually all mountains of the Guayana Shield, has succeeded in establishing such a wide and apparently continuous population along the southwestern Guayanan lowland piedmont slopes (glacis).

*Schoenocephalium meadows in the Guayana lowlands.* – Herbaceous ecosystems are certainly not rare in and around the Guayana Shield: extensive grass savannas with or without woody elements grow abundantly in the lowlands and uplands (*e.g.*, the Colombian-Venezuelan Llanos savannas, the Venezuelan-Guyanese Gran Sabana, the Brazilian-Guyanese Rio Branco/Rupununi savannas, to mention a few); herbaceous coastal swamps with *Typha*, *Montrichardia* and Cyperaceae are common along the entire Atlantic Coast; and the typical Guayanan broadleaved meadows of the rapateaceous genera *Stegolepis* or *Kunhardtia* are well known examples of autochthonous ecosystems of the tepui up- and highlands. There is, however, one small genus of that remarkable family Rapateaceae, which illustrates, like *Bonnetia* among the shrubs, a peculiar evolutionary pattern linked to the white sand habitat of the peripheral Guayana lowlands. This is the genus *Schoenocephalium*, originally discovered by Martius along the Caquetá river in Colombia (*S. martianum*), but later found much more abundantly in the upper Río Negro and Orinoco drainages (**Sch** on Fig. 1), with two additional species presently recognized (*S. cucullatum* and *S. teretifolium*); a fourth, but doubtful species (*S. schultesii*) has been described from Cerro Isibukuri near Araracuara in Colombia. Of these, according to Steyermark (1988) and Berry (pers. comm.), the first two (*S. martianum* and *S. cucullatum*) are hardly distinguishable from



each other taxonomically, whereas the remaining species (*S. teretifolium*) is morphologically well distinct due to its needle-like, long leaves and more delicate flower heads. This genus then represents another case of ongoing geographical and probably ecological differentiation within a huge, roughly triangular area of distribution whose vertices are the middle Ventuari basin in the northern state of Amazonas in Venezuela, Sierra de Chiribiquete in Colombia and the lower Demini river in the Brazilian Rio Negro basin.

Again, these three examples only serve to show that the beta diversity found on the ground even in the contiguous Guayana lowland areas is more pronounced than could be expected by a mere extrapolation from general environmental or even floristic data. Of course, more examples could be cited here, but this argument will be treated with more detail in a forthcoming publication. Again, it must be repeated that large areas of this fascinating phytogeographic region are still unexplored and the final degree of diversity may well result in being considerably higher than assumed today.

### ***Geo-ecological differentiation***

In addition to the large-scale differentiation patterns described above, it is also important to consider more locally acting processes, such as geo-ecological factors. For example, oligotrophy is an extremely powerful cause of stress on virtually any living community, but the response to this limiting factor can be (and almost invariably is) very different, depending on a wide array of mostly unpredictable spatial and temporal site conditions.

Examples of such geo-ecological differentiations within Guayanan vegetation types can be seen in the following situations:

*Quartzite and sandstone habitats (acidic).* – There exists a set of epilithic life communities including cyanobacteria, algae, and lichens

that are found on virtually any rocky substrate in the Guayana mountains, from the lowlands to the highlands. In addition to this “basic epilithic colonization matrix”, one also finds many different, post-colonizing higher plant communities growing on various rock types, exposure and altitude. Such diversification, particularly abundant in certain terrestrial genera of the bromeliad family (*e.g.*, *Navia*, *Brocchinia*, *Steyerbromelia*, and *Lindmannia*), is more pronounced towards the saxicolous highland biota (above 1500 m a.s.l.) and could only be explained tentatively by invoking historical (vicariance) distribution processes and micro-ecological adaptation processes.

*Granite and gneissic habitats (acidic).* – In general, a “basic epilithic colonization matrix” can also be recognized which is perhaps largely identical to the one found on sandstone or quartzite. The post-colonizing plant communities, however, differ considerably from the ones seen in the former group, although many belong to the same family, Bromeliaceae. The granitic outcrop flora and vegetation of the lowlands has recently been studied intensively by de Granville in French Guiana (Granville & Sastre 1973) and Gröger (2000) in Venezuela, which have demonstrated several interesting systematic, chorologic and ecologic convergence phenomena. In the highlands, the differences with the sandstone substrate are more evident: apparently, *Bonnetia*, present on all typical sandstone tepuis with numerous endemic species, is absent from granitic substrate, where it may locally be replaced by the widespread neotropical *Cyrilla racemiflora*. On the other hand, in the herbaceous meadows growing on granitic substrate, the otherwise ubiquitous tepui herb *Stegolepis* is almost entirely substituted by *Kunhardtia rhodantha*, another genus of Rapateaceae. This intensely red flowered, broadleaved herb, however, grows on all the tepuis in northern Amazonas state (*i.e.*, from Autana and Cuao-Sipapo in the



west to Sierra Maigualida and Sierra Uasadi in the east at approx. 1000 to 2300 m a.s.l.), forming large and dense communities on peat, but independently of their sandstone or granitic geology.

*Diabase intrusions (mafic and ultra-mafic).* – Soils derived from Paleozoic volcanic intrusions in the earlier sandstone layers, are usually richer in mineral nutrients and also have better cation exchange capacities than soils derived from sandstone substrate, where clay particles are largely absent. Therefore, such diabase intrusions are usually recognizable by two characteristics: first, through their generally more rounded terrain forms, contrasting with the more angular, steplike terrain forms of the surrounding sedimentary landscape; and secondly, by a generally much denser vegetation cover, consisting often of forests in the middle of a wide, open savanna landscape (*e.g.*, in the Gran Sabana uplands, see Dezzeo (1994) and Hernández (1999)) or in a mostly rocky, open high-tepui landscape (see Huber 1992). Although no plant species seem to be exclusively associated with mafic or ultra-mafic substrate, differences in species composition (*e.g.*, higher species diversity) and in the physiognomy of the corresponding vegetation types are always recognizable (*e.g.*, taller tree growth).

*Peat habitats (acidic and sulphurous).* – Organic substrates (histosols) occur in the Guayana region in two opposite landscape types: either in coastal swampy areas influenced to some degree by marine water and often with sulphuric components, or on mountain summits above 1200 m a.s.l., but mostly between 1500 and 2500 m a.s.l. The vegetation associated with this substrate consists in both cases of open, either herbaceous or mixed shrubby/herbaceous plant communities. In the case of the coastal swamps, dominant genera are *Typha*, *Montrichardia*, Cyperaceae, and some floating grasses; this relatively poor and

monotonous vegetation type is widely distributed along most tropical and subtropical coasts, but is particularly widespread in the Orinoco delta floodplains. The montane bogs, on the other hand, are very common on the flat or little inclined plateaus of the Guayanan tepuis, occurring occasionally as low as 800–1000 m a.s.l., but generally above 1500/1800 m a.s.l. on any tepui, regardless of its geologic constitution. These peat layers are up to 2 m thick and often several square kilometers wide. They harbor a wide variety of plant communities and contain much of the endemic vascular Pantepui flora; bryophytes, however, are not conspicuous and only represented by a few species (Ahti 1992). By far the predominant vegetation types are broadleaved herbaceous meadows dominated by one or a few of the more than 30 species of *Stegolepis* known so far from these mountains; but these meadows can also consist of large colonies of terrestrial bromeliads (especially *Brocchinia*, *Navia*, etc.), Cyperaceae, *Heliamphora*, Xyridaceae, Eriocaulaceae, together with a variable degree of shrubby or low woody elements. Many of these bogs are also covered by dense shrublands, the most outstanding of which is the paramoid scrub formed by various species of *Chimantaea*. This remarkable genus, consisting of 8 or 9, mostly caulirosette species in the Chimantá massif, represents the only case in the Guayana Highlands of convergent high-mountain growth form with the characteristic Andean counterpart *Espeletia* s.l. from the páramo landscape. Recent research on the palynology and paleoecology of some tepui bogs seems to indicate that these communities were subject to more or less pronounced climatic oscillations in the Quaternary, similar to the Andean high mountain ecosystems (Rull 1996).

*Psammic (white-sand) habitats (acidic, dry-flooded).* – Due to the wide regional distribution of this habitat type, some aspects of the vegetational diversity associated with this substrate



have already been indicated above. Kubitzki (1990) dealt with the floristic aspects of these ecosystems. Nevertheless, it may be interesting to add here, that in the area around Cerro Yapacana, near the confluence of the Orinoco and Ventuari rivers in central Amazonas state of Venezuela, a unusually high concentration of plant communities with endemic species or genera has been found. In relatively small but numerous patches of white sand fields, characterized by a most peculiar superficial labyrinthic drainage pattern and surrounded either by terra firme or by gallery forests, a surprising diversity of herbaceous and shrubby plant communities occurs, which still has to be described in greater detail (Huber 1982). This particular region has received considerable attention since the first explorations of Bassett Maguire and collaborators in the early 1950s and may be considered as botanically (though not ecologically) relatively well explored; but also the wide glacia (piedmont slopes) made up mainly of white sands, which stretch almost continuously across the northern part of the State of Amazonas of Brazil from the Rio Negro in the west to the Rio Branco in the east, may be shown to harbor a similarly high diversity of plant communities, once it is better explored ecologically.

## Discussion and conclusion

From the above descriptions it is evident that the phytogeographical Guayana Region, formally established by Maguire (1970, 1979) and recently redefined by Huber (1994) and Berry *et al.* (1995) contains a well known, significant set of floristic qualities (*e.g.*, an estimated number of 15,000 -20,000 vascular plant species, high degree of endemicity at the generic and specific level), and also a remarkable and highly autochthonous beta-diversity (plant communities) and, very likely, a similar pronounced gamma-diversity at the landscape

level. Unfortunately, more than half of the entire area of the geological Guayana Shield area is essentially unexplored (Huber & Foster 2003): although this finding should not be applied equally to all parts and landscapes of the region, any attempt to produce definitive conclusions under such circumstances should be made with caution.

However, the existing knowledge allows us to begin verifying the set of criteria proposed by Huber (1994) for the establishment of more scientifically sound and corroborated phytogeographic categories. As a result we can start to define the main intrinsic characteristics of the so-called *Guayanan Biota Complex*, together with the parameters which differentiate it from the adjacent phytogeographic entities.

(1). The Guayanan Biota Complex (GBC) consists of a core area occupied by essentially montane biota with a clearly recognizable altitudinal floristic and ecological differentiation.

(2). The montane core area of the GBC is surrounded by forelands in all four directions, consisting mainly of well developed piedmont slopes (glacia) which originated principally from the core area (through erosion and downslope sedimentation) or from *in situ* weathering processes (through bedrock alteration).

(3). According to all available results of past and present research in the area, there is no evidence suggesting that the continental area of the GBC has suffered, at least since Paleozoic times, marine transgressions with the consequent temporal elimination of all its terrestrial biomes.

(4). On the contrary, due to the extraordinary age of the Guayana Shield and its relative geological stability, at least the montane core area must be assumed to have offered continuous and uninterrupted opportunities for the evolution of terrestrial biota at least since Paleozoic (Gondwanic) times.

(5). Such a stable landmass as the Guayana

Shield, however, must also be seen as an important target destination for immigration and subsequent differentiation processes from the surrounding areas which reportedly were much more exposed to drastic changes in their life conditions during their geologic evolution processes.

Such past and present geologic and physiographic conditions are unique in northern South America and justify a clear historic and evolutionary differentiation of the Guayana Region from all adjacent (bio-) phytogeographic entities, which are:

(1). The Amazon Region to the south and southwest, an essentially lowland region consisting of the large Amazonas/Solimões valley up to approx. 500 m a.s.l., mainly filled up with recent sediments from the adjacent mountain systems.

(2). The Andean Region to the west, an essentially montane region with entirely different historical dimensions and orogenetic processes (rapid tectonic uplifting, pronounced volcanism);

(3). The Llanos Province with the adjacent Coastal Cordillera to the north and northwest, both belonging to the Caribbean Region; the Llanos depression consisting of a large geosyncline extending between the Guayana Shield to the south and the Coastal Cordillera to the north, and which only recently has been filled up with sediments from the surrounding mountain systems, but mainly from the Andes.

Together with the forthcoming conclusion of the *Flora of the Guianas* (Görts-van Rijn 1985-), the *Flora of the Venezuelan Guayana* (Steyermark *et al.* 1995-), and the publication of an increasing number of local floras and checklists (such as Boggan *et al.* 1997; Mori *et al.* 1997, 2002; Clark *et al.* 2000), our floristic knowledge of the region is becoming more and more detailed, although still far from being complete. The same cannot be said about the Guayanan plant communities and vegetation

types, the study of which is still in a very initial stage. Despite several earlier, more or less successful attempts in Brazil (Projeto RADAM), Colombia (ProRADAR) and Venezuela (CODESUR, PIRNRG), a realistic description and cartography of the natural vegetation pattern of this region is still very difficult to obtain. This is due not only to the complex and largely unaccessible topography, but also to the use of incompatible classification schemes in the various countries of the region; hopefully, these problems can be resolved with the aid of the modern remote sensing techniques.

For this reason, it is my belief that the production of scientifically sound and reliable data on the vegetation of the Guayana Region requires, probably more than any other area of the Neotropics, a high proportion of solid field work, during which the scientists are enabled to acquire the taxonomic, ecologic and geographic expertise needed for such a difficult but extremely stimulating task. This could be achieved by carrying out concurrent medium term research programmes (*e.g.*, 5-10 years), in each country possessing Guayanan biota. These should consist of:

(1) numerous, short term but wide range explorations for vegetation analysis (including [phytosociological] relevés, collection of botanical specimens and of information on relevant environmental parameters (geology, soils, climate, hydrology, etc.);

(2) longer, in-depth studies at selected localities;

(3) staff of professionals for the coordinated elaboration of the products (*i.e.* a classification of vegetation types, their physiognomic and floristic description and their cartographic representation in GIS format).

This is the only way to produce a coherent and reliable inventory of the Guayanan beta- and gamma- (phyto)diversity in due time, in order to provide every country with a serious basis for the rational and hopefully successful



management of such an extraordinary concentration of natural treasures and biological diversity.

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