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Epiphytes in rain forests of Venezuela – diversity and dynamics of a biocenosis*

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Synopsis:

This paper gives an overview about the activities and first results of the epiphyte research projects of the Botanical Institute of the University of Bonn in Venezuela. Since 1995 the epiphytic vegetation of an Andean cloud forest (La Carbonera) at 2300 m a. s. l. and Amazonian lowland forest (Surumoni crane project) at about 100 m a. s. l. in Venezuela have been investigated. Both studies were carried out in co-operation with the Centro Jardín Botánico of the University of Mérida, Venezuela. Epiphyte diversity, spatial distribution and dynamic processes of the vascular epiphytic vegetation were analysed comparatively in different forest types. In the 1.5 ha plot in the lowland rain forest species number is relatively low (53 species including hemiepiphytes), whereas in the Andean cloud forest alpha-diversity of epiphytes is much higher (191 spp.). In both areas Orchidaceae are the dominant family, followed by ferns in the cloud forest and by Araceae (mostly hemiepiphytes) in the lowland rain forest. Abundance of epiphyte species shows another order: in the cloud forest most individuals belong to the Bromeliaceae, mainly the genus *Tillandsia*, and at the Surumoni study site the Araceae are the most abundant family. In secondary vegetation and disturbed areas of the cloud forest a dramatic loss of species was recorded (55 %). Disturbances seem to have a great influence on the floristic composition and abundance of epiphytes, as some families are lacking completely (Lycopodiaceae, Gesneriaceae a.o.) and the number of individuals of e.g. Orchidaceae shows a significant decrease. Dynamic processes in natural habitats at the Surumoni study site are most recognisable in the presence of ant garden epiphytes, which amount to 51 % of all individuals in the plot. The occurrence of the four epiphyte species specialised in growing in ant nests were mainly restricted to the two years old gap areas of the crane plot.

Key words: **Epiphytes, lowland rain forest, cloud forest, Venezuela, biodiversity, primary forest, secondary forest, Surumoni crane project, spatial distribution**

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* Dedicated to Dr. Loki Schmidt on the occasion of her 80th birthday for her tireless efforts on the German-Venezuelan co-operations.

1. Introduction

"Die Physiognomie des tropischen Urwalds ist in erster Linie durch den Kampf um das Licht bedingt (...). Während der Boden zwischen den Baumstämmen, den Lianen und Luftwurzeln oft beinahe keine Pflanzen trägt, prangt über dem Laubdache eine üppige und artenreiche Vegetation, die sich der Bäume als Stütze bedient hat, um an das Licht zu gelangen."

A. F. W. Schimper (1888)

Epiphytes are important structural elements of tropical rain forests. In some montane rain forests they amount up to 50 % of all plant species (KELLY & al. 1994) and 35,5 % of living foliage biomass (BRUN 1979). SCHIMPER (1888) presented the first comprehensive monograph on the ecology of neotropical epiphytes. Many of his early observations have been confirmed today and remain still valid. He was followed later on by the classical works of WENT (1940), JOHANSSON (1974), LÜTTGE (1989) and BENZING (1990). In the past two decades the literature on ecology of epiphytes has increased considerably (see NADKARNI & FERRELL-INGRAM 1992), but so far an synchronous analysis of spatial distribution and changes of epiphytic vegetation in time has not been carried out, mostly due to the missing of suitable methods of canopy access with the guarantee of non-destructive and reiterated sampling of epiphytes over a long period (e.g. with cranes or permanent installations of rope systems). There is also a lack of comparative studies between lowland and montane rain forest applying the same sampling parameters, as the here presented investigation intends.

2. The Surumoni crane project – lowland rain forest

2.1. Study site and methods

The project was carried out within the context of an interdisciplinary research project of the Austrian Academy of Science and the Venezuelan government, the "Surumoni crane project" (MORAWETZ 1998, NIEDER & al. accepted). The study plot is situated on the banks of the black water river Surumoni, a tributary of the upper Orinoco river. Fig. 1 shows the geographical position of the study area, which lies within the Guayana region, one of the main phytogeographic regions of northern South America (STEYERMARK & al. 1995). Basic geographical information is summarised in Tab.1. (see also NIEDER & al. accepted).

Tab. 1:
Basic geographical data of the two investigation sites

	La Carbonera Venezuelan Andes	**Surumoni Crane project** banks of the upper Orinoco-tributary Río Surumoni
Geographical location	8°37' N, 71°21' W	3°10' N, 65°40' W
Height above sea level	2200–2500 m	100 m
Mean annual temperature	12.6 °C	27.5 °C
Mean annual precipitation	1460 mm, with daily cloud and mist entry	2700 mm

The forest is between 25 and 30 meters high, on poor lateritic sand soils and with an irregular crown closure. The surroundings of the study plot are covered by a vast ombrophilous lowland rain forest which has remained largely untouched by human influence.

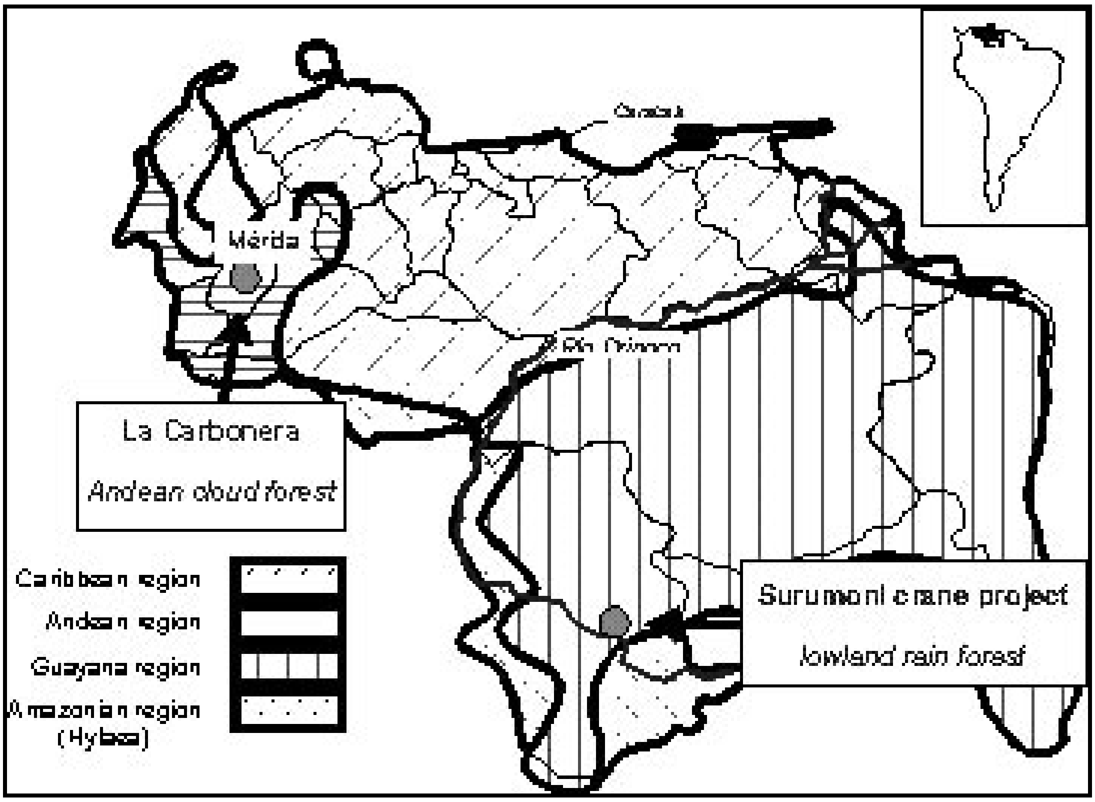

Fig. 1
Geographical position of the both study sites within the main phytogeographical regions of Venezuela.

A crane was used as observation platform and working tool. This crane is 40 m high, its boom is 40 m long and it runs on rails along a length of 120 m. This technique allowed for the first time ever a complete survey of epiphytes in the 1.5 ha plot (see Fig. 2). We examined 1085 trees and treelets (DBH more than 5 cm), counting and measuring all vascular epiphyte individuals larger than 1 cm plant height growing in the canopy. Generally the authors used the term "epiphytes" in this paper including hemiepiphytes (epiphytic plants with a terrestrial life stage); hemiepiphytes normally have been distinguished from "true epiphytes" which complete their life-cycles on their host trees (BENZING 1990). The term "phorophyte" used in this context is another designation for host trees, stressing the non-parasitic relationship between epiphytes and the trees they use for mechanical support (BENZING 1990).

2.2. Results

A total of 778 individual plants of 53 species of epiphytes were found on only 138 trees in the 1.5 ha plot. The exact three dimensional distribution of all epiphyte individuals (important families are marked in different shapes) is indicated in Fig. 2. With 19 species out of 12 genera, Orchidaceae were the most diverse family (but with 80 individuals not very abundant), followed by the Araceae with 14 species, but 337 individuals. 12 orchid species with less than 3 individuals were found in the plot.

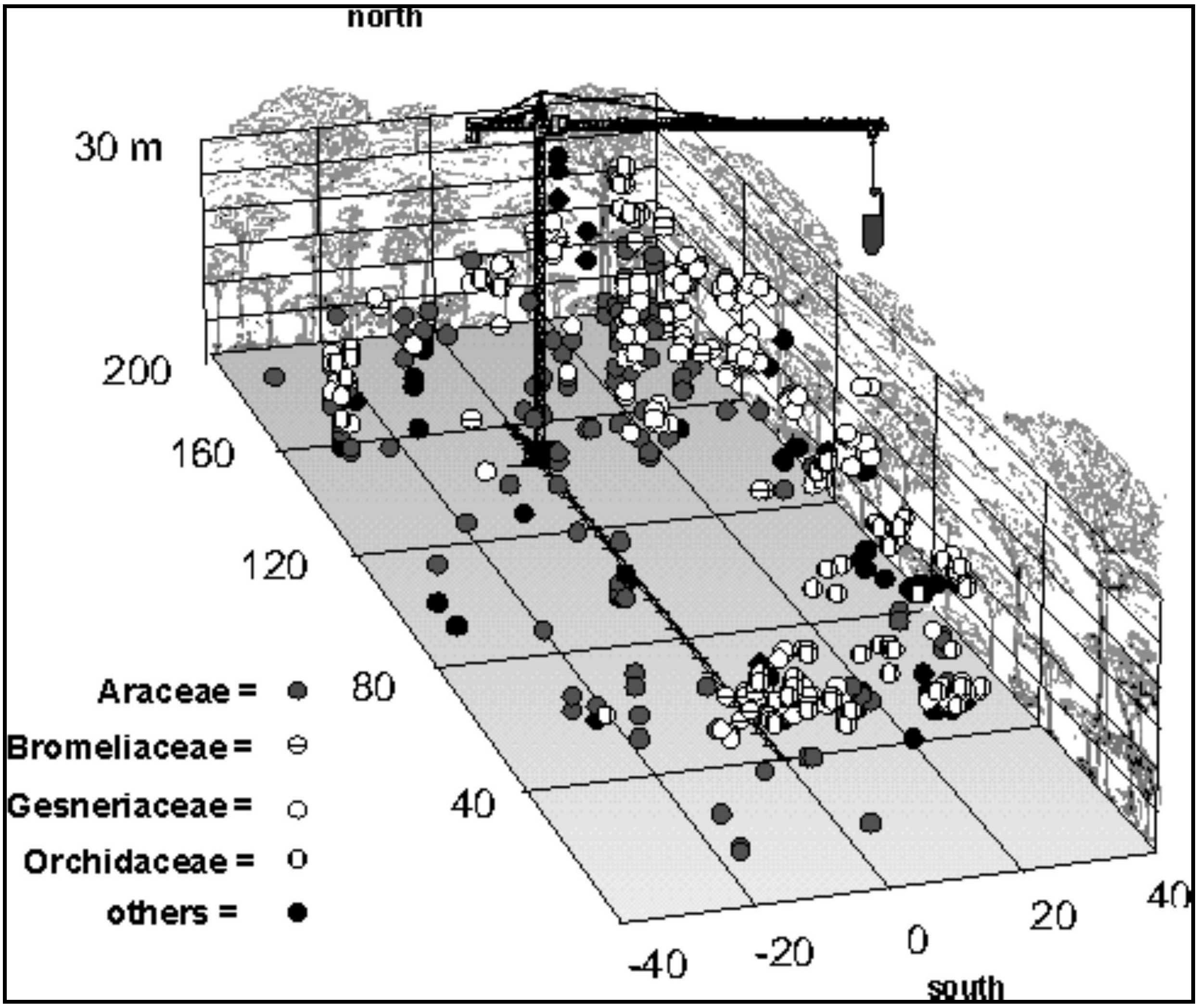

Fig. 2
Schematic presentation of the three dimensional distribution of epiphytes in the Surumoni crane plot. Most abundant families are marked by different shadings and patterns. Each dot represents one epiphyte individual; many individuals are not visible due to mutual overlap.

The two gesneriad species contributed with 130 individuals to the floristic composition and bromeliads with two species and 111 individuals. Next in importance were ferns (12 species and 106 ind.), Clusiaceae (2 spp., 3 ind.), Piperaceae (1 sp., 7 ind.) and only one individual of the Cactaceae was registered. Approximately 70 % of all species had less than 10 individuals in the plot, only five species had more than 50 individuals, four of them can be designated as obligate ant garden epiphytes (epiphytes that are specialised in growing in ant nests (ULE 1905)). These ant garden epiphytes *Anthurium gracile* (Rudge) Schott, *Philodendron deflexum* Poepp. ex. Schott (both Araceae), *Aechmea tillandsioides* (Mart. ex Schult.) Baker (Bromeliaceae) and *Codonanthe calcarata* Miqu. (Gesneriaceae) were a remarkable element of the epiphyte community. With 51 % of all individuals (397 out of 778) they were frequent in the ant nests of the drier and lighter gap areas of the plot, whose age could be determined to almost two years.
The high percentage (28 %) of hemiepiphytes within the epiphytic plot flora is important. All species of epiphytes showed a highly clumped and not random horizontal distribution. Table 2 specifies the vertical distribution of selected epiphyte taxa, which showed significant differences based on data of an ANOVA/ Tukey HSD test ($p<0.05$). In all other species, numbers of individuals were not sufficient for statistical analysis.

By sampling epiphytes in the surrounding of the crane plot within a circuit of 10 km we could add 63 more species, which were not present in the plot.
Our further investigations will be concentrated on observations of dynamic processes. By repeating complete registrations of epiphytes in the study plot with the same methodology, species turnover will be documented. Fluctuations of individual numbers particularly of ant depending epiphyte species have already been observed. During the recent registrations in summer 1998 two new species were found in the plot.

Tab. 2
Analysis of vertical epiphyte distribution in the Surumoni plot. The listed taxa in each row can be seperated from the other ones with statistically distinct occurrences in height based on a factor analysis (ANOVA/Tukey HSD test: p<0.05).

Taxa with the same height occurrence grouped by a factor analysis	Mean height of the enclosed taxa within standard deviation
Philodendron spp. (Araceae)	2 – 8 m
Aechmea tillandsioides (Bromeliaceae)	8 – 25 m
Anthurium spp. (Araceae), *Microgramma* spp. (Polypodiaceae), *Codonanthe calcarata* (Gesne-riaceae)	10 – 18 m
Cattleya violacea (Orchidaceae), *Codonanthe crassifolia* (Gesneriaceae)	19 – 22 m
Tillandsia paraënsis (Bromeliaceae)	23 – 27 m

3. La Carbonera – Andean cloud forest

3.1. Study site and methods

The study area El Bosque La Carbonera – San Eusebio is a montane cloud forest in the Venezuelan Andes, approximately 60 km air distance north-west of Mérida (Fig. 1). Tab. 1 contains the basic geographical data (for site description see also LAMPRECHT & VEILLON 1957 and VARESCHI 1980). The forest has been in possession of the University of the Andes (ULA), Instituto de Silvicultura de la Facultad de Ciencias Forestales, for the last 50 years. The 370 ha forest consists mainly of primary vegetation, but includes an area of about 120 ha secondary vegetation: relics of primary forest where some selective logging has taken place and some abandoned tree plantations of *Cedrela montana* Moritz ex Turcz. (Meliaceae) are situated. In the primary forest the emergent tree *Decussocarpus rospigliosii* (Pilger) de Laub. (Podocarpaceae) is dominant. The plots were established in primary forest (a triangle of approximately 0.1 ha with four emergent *D. rospigliosii* and 66 subcanopy and understory trees), and in secondary and disturbed vegetation at four representatively selected locations: a) A plot in a relic forest with one emergent tree (*D. rospigliosii*). b) A transect along the dirt road through secondary and disturbed forest. c) A tree plantation of *Cedrela montana* comprising approximately 400 trees. d) A sector of a former clear cutting, which was completely cleared for a biomass determination 26 years ago (BRUN 1979) and left undisturbed since then.
Epiphytes were sampled following the single rope technique of mountaineering climbing (PERRY 1978). In primary forest reiterated access to the canopy was provided by installing a permanent rope system, connecting three emerging phorophytes in a triangle with transversal ropes. Reaching all the tree crowns within the triangle was possible by lowering down from the transversal ropes (ENGWALD 1999). Here epiphyte individuals of 60 trees (DBH > 5 cm) were completely registered and measured (in total 4121 individuals).

3.2. Results

The total of 191 epiphyte species documented for the forest belonged to 21 families (Fig. 3). Including terrestrial vascular plants the forest hosts about 430 spp., that means an epiphyte quotient (definition after HOSOKAWA 1950) of 45 %, which makes La Carbonera to one of the epiphyte richest habitat in a world-wide comparison (NIEDER & al. submitted). With 96 species Orchidaceae represent the taxa with highest species richness, followed by the ferns (56 spp.). Next in importance were the Piperaceae (12 spp.), the Bromeliaceae with 10 spp. and the Araceae comprising 7 spp. 177 species occurred in the primary forest (even the permanent plot yielded 120 spp.) and in all investigated secondary vegetation plots we found 81 species from 14 families, which means a species loss of 55 % (Fig. 3). 110 out of the 177 primary forest species seemed to be restricted to undisturbed vegetation, whereas only 14 species were sampled exclusively in secondary vegetation. The loss of species is most marked in taxa which includes some relatively few epiphytic representatives. A complete disappearing of families in secondary vegetation can be recognised in Ericaceae, Gesneriaceae, Solanaceae, Melastomataceae and Lycopodiaceae. It is a striking aspect that Bromeliaceae were the only family with more species represented in secondary vegetation (10 spp.) than in primary forest (7 spp.).

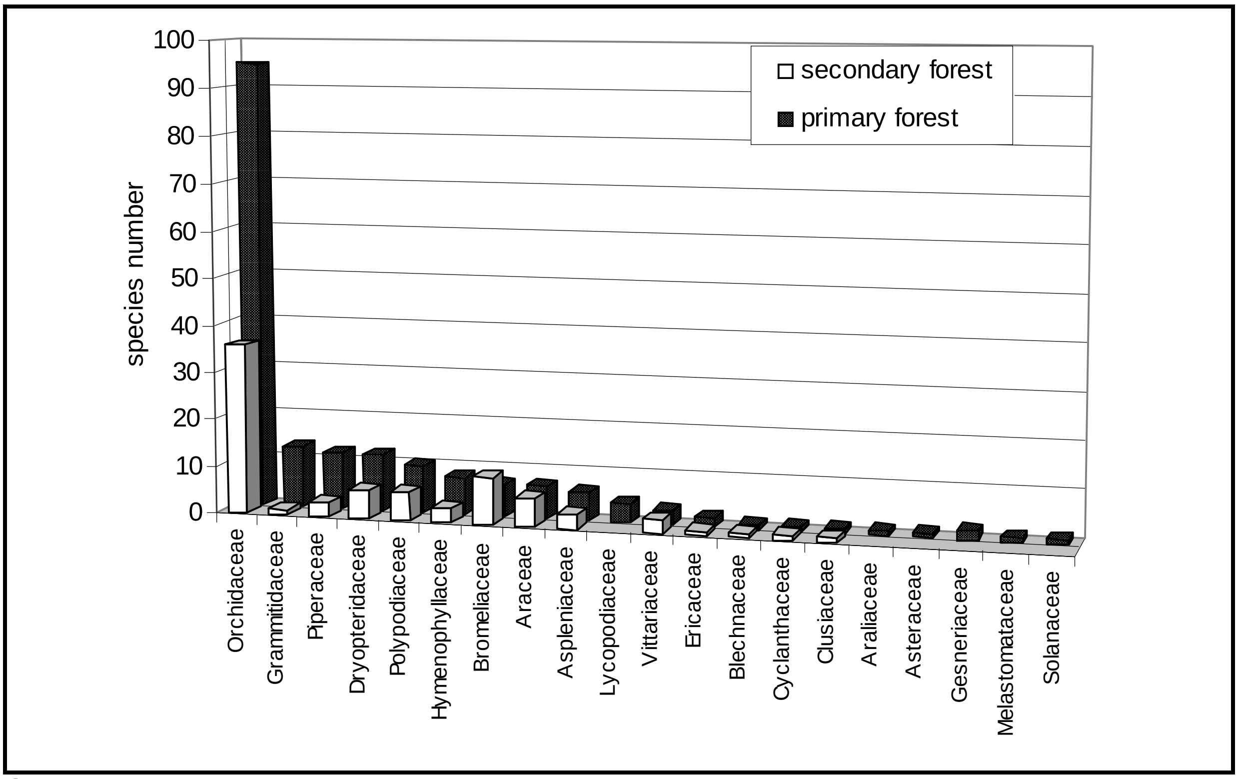

Fig. 3
Species number of epiphytes per family in primary forest and secondary vegetation at La Carbonera. Stars indicate families not occurring in secondary vegetation.

Not only species numbers but also abundance of epiphytes decreased intensely in disturbed areas. Fig. 4 illustrates changes in individual numbers, considering a direct comparison between a phorophyte in primary forest and in secondary forest. Both phorophytes were emergent *D. rospigliosii* – trees with nearly the same height and crown diameter. Bromeliads were the most abundant epiphytes, in both primary forest as well as secondary vegetation. In the permanent plot in dense primary forest they reached a number of 2327 out of 4121 registered plant individuals and in secondary vegetation 1000 out of 1469 individuals were Bromeliads.

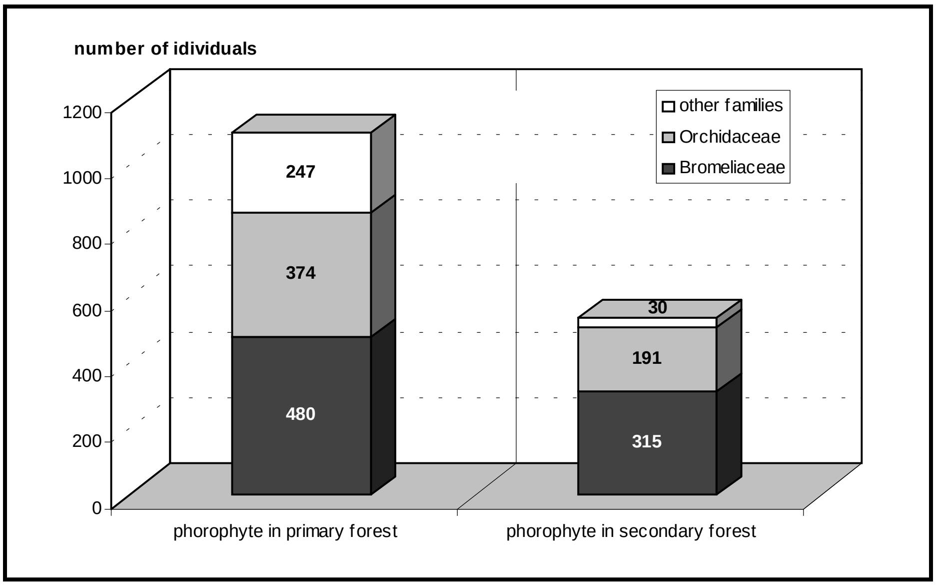

Fig. 4
Comparison of the number of epiphyte individuals on one phorophyte in primary forest and another in secondary forest (both *Decussocarpus rospigliosii*).

4. Concluding remarks

Regarding the species composition of the Surumoni crane plot the high species numbers of orchids (37 % of all species found) and low percentage of fern species (14 %) are similar to the forest studied by TER STEEGE & CORNELISSEN (1989) and the epiphyte flora of lowland forest canopy trees (FREIBERG 1996), both in Guyana. High number of species and high abundance of Araceae is likewise typical of lowland forests (IBISCH 1996). Our results also match those of EK & al. (1997) in the comparison of four different forest types in Guyana and French Guiana, especially the percentages of orchids and ferns of the most common forest type, called "mixed forest". La Carbonera also shows the typical floristic composition for montane rain forest (IBISCH 1996, RUDOLPH & al. 1998), perhaps with the exception of the high percentage of epiphytic ferns (41 %).

This studies generally confirm former works which showed the relatively poorness of epiphytes regarding to species number as well as abundance in lowland rain forests in contrast to montane rain forests (GOTTSBERGER & MORAWETZ 1993, TER STEEGE & CORNELISSEN 1989, FREIBERG 1996, IBISCH 1996). Extreme climatic conditions and the missing of pronounced canopy substrate could be held responsible for this observations (ENGWALD 1999, NIEDER & al. accepted). Our investigations could show the great importance of ant garden epiphytes in natural habitats in an Amazonian lowland forest, where ants provide the only considerable amount of substrate for epiphytes. In the epiphytic biocenosis of the cloud forest ants can be neglected. Another hint for the prominent role of canopy substrate is the high percentage of hemiepiphytes at the Surumoni site (28 %), whereas at La Carbonera, where substrate is not a limiting factor, only 5 % of the canopy flora is hemiepiphytic.

Especially in montane rain forests epiphytes seem to be particularly sensible to habitat changes (see also TURNER & al. 1994), presumably because they depend more on the regrowth of structurally complex old trees. This is obvious for species number and abundance. In lowland forest, where treelets of gap areas were occupied in a relatively short time by ant garden epiphytes, there could be ascertained the highest abundance of epiphytes in the whole crane plot, but species richness was very low.

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