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# Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes

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**Abstract**

Species diversity of vascular epiphyte plant communities was studied in La Carbonera, a montane rain forest dominated by Podocarpaceae in the Venezuelan Andes. We compared the epiphyte communities of the primary, disturbed, and secondary forest areas of La Carbonera in order to augment the scarce knowledge on the effects of anthropogenic disturbance on these important elements of tropical vegetation. Diversity of vascular epiphytes (191 species in the whole forest area) was low in the disturbed and secondary areas (81 spp.) compared to adjacent primary forest (178 spp.). Four types of disturbed forest and secondary vegetation supported different numbers of epiphyte species, showing a decline with increasing degrees of disturbance (65 spp. along a road transect, 42 spp. on relict trees in disturbed forest, 13 spp. in a tree plantation and 7 spp. in a former clearing, both secondary vegetation units). Epiphytic species composition in primary and disturbed or secondary forest areas differed markedly: disturbed habitats harboured fewer fern and orchid species but more bromeliad species than the primary forest. Probably the families occurring only in primary forest sites of our study may be useful as bioindicators to determine the degree of disturbance in other habitats of mountain rain forests as well. Epiphyte abundance was also lower in disturbed habitats: a remnant emergent tree supported only about half as many epiphyte individuals as a member of the same species of similar size in the primary forest. The decrease in species numbers and abundance as well as the differences in species composition are mainly due to the less diverse phorophyte structure and less differentiated microclimate in the disturbed and secondary vegetation compared to the primary forest.

## Introduction

Epiphytes, a characteristic and distinctive component of tropical rain forests, have attracted scientific attention since A.F.W. Schimper's (1888) extensive monograph on neotropical epiphytes. Classical studies on epiphyte distribution enclose those of Went (1940) and Johansson (1974).

Montane rain forests are especially rich in epiphytes, which contribute significantly to total biomass (Nadkarni 1985, 1992), species diversity (Gentry & Dodson 1987a, b; Ibisch 1996; Ibisch et al. 1996), and nutrient cycling (Edwards & Grubb 1977; Nadkarni 1985, 1992) in these ecosystems. They also provide habitat and food for a variety of insects and birds (Benzing 1984, 1990; Lugo & Scatena 1992; Nadkarni 1992). Epiphytes have also been used extensively by man for medical, agricultural and horticultural purposes (Bennett 1992; Nadkarni 1992; Rauh 1992). It has been suggested that epiphytes can be used as bioindicators of climatic changes, pollution, and ecological damage (Richter 1991; Lugo & Scatena 1992; Engwald 1999). The importance of epiphyte studies for biodiversity research has been emphasised recently by Porembski & Barthlott (2000).

Today tropical rain forests, and montane rain forests in particular, are subject to logging and land use with serious consequences for resident epiphytes. Epiphyte abundance, species numbers and community composition were shown to be significantly lower in secondary than in primary forest (Turner et al. 1994). However, documentation is scanty (e.g. Olmsted &

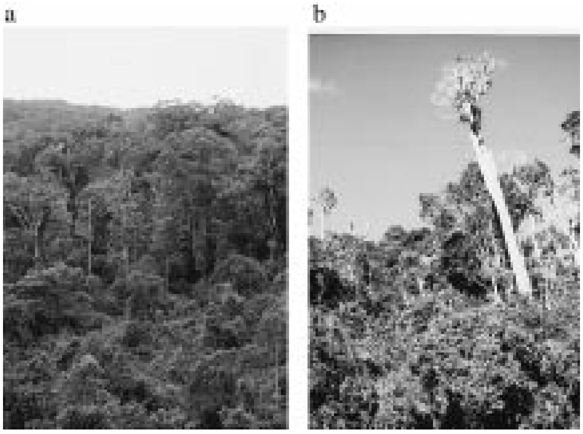

*Figure 1.* La Carbonera mountain rain forest: (a) the former clearing in the foreground and primary forest in background; (b) disturbed forest seen from the dirt road.

Gómez Juárez 1995; Hietz-Seifert et al. 1996), although the increasing importance of secondary forests has been widely recognised (Chazdon 1994). The present study compares for the first time ever epiphyte diversity and species composition in primary, disturbed and secondary forest plots in a montane rain forest in the Venezuelan Andes.

## Study site and methods

### *Study area*

The study area 'El Bosque La Carbonera – San Eusebio' is a montane cloud forest in the Venezuelan Andes, approximately 30 km north-west of Mérida, located at 8°37′ N and 71°21′ W between 2200 and 2700 m. A 360 ha part of the 4000 ha forest area 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.

Mean annual temperature is 12.6 °C (absolute min. 5 °C, absolute max. 20 °C). Rainfall is 1460 mm annually (7 year average) with a slightly drier period between December and February (Hetsch & Hoheisel 1976). Slight cloud cover and fog occurs normally on a daily basis.

In this study, we distinguished disturbed vegetation, where after logging events remnants of primary vegetation remained, and secondary vegetation, where primary vegetation had been removed completely. The entire university forest area (approximately 360 ha) contains primary, disturbed and secondary vegetation (tree plantations and a former clearing). Primary forest (background vegetation in Figure 1a), comprising approximately 240 ha, is dominated by the emergent tree *Decussocarpus rospigliosii* (Pilg.) de Laub. (Podocarpaceae). It is clearly stratified into shrub layer (0–2 m), understorey (2–7 m), and middle (7–25 m) and upper canopy (25–50 m).

In the approximately 120 ha of disturbed forest, three types of vegetation can be distinguished according to the degree of human impact: firstly, disturbed vegetation: relics of primary forest area (Figure 1b), where the last selective logging events took place some 50 years ago. The shrub layer is well developed, the subcanopy is composed by climbing bamboo, Melastomataceae, Lauraceae and others, whereas a midcanopy is completely lacking. The upper canopy harbours solitary remnant trees (e.g., *Decussocarpus*). Secondly, two types of secondary vegetation, where primary vegetation had been removed completely: tree plantations of, e.g., *Cedrela* and *Pinus* species with a very uniform structure due to plantation method and the absence of an understorey. Most of the approximately 35 year old plantations border to either primary forest or the only dirt road leading through the forest. Furthermore, there is a 50 × 50 m area of a former clearing, which was completely cleared for biomass determination 23 years ago (Brun 1979) and left untouched ever since (foreground vegetation in Figure 1a). Here, the vegetation is not stratified and dominated by weedy fast-growing plants such as ferns (e.g., Gleicheniaceae), some Melastomataceae and bamboo reaching up to 5 m. Epiphytes grow either on the ground (!) and, occasionally, on lianas (Melastomataceae) or on remnant trunks left behind after biomass determination.

A dirt road constructed some 30 years ago leads through the secondary and the disturbed forest and is bordered by each of the types of disturbed and secondary vegetation described above. Therefore, its accompanying vegetation is neither uniform in structure nor species composition. Plantation trees of different ages as well as units of primary vegetation relics with Lauraceae, Meliaceae, Podocarpaceae of different ages form the vegetation in this part of the forest.

### *Data collection*

Field work was carried out during three main sampling periods in January–March 1996, July 1996–January 1997 and April–May 1997.

In the primary forest described above, a plot was chosen, which formed an approximately 0.1 ha triangle containing a total of 71 examined trees with three emergent *Decussocarpus* and various midcanopy-trees like *Prunus sphaerocarpa* Sw. (Rosaceae), *Ficus velutina* Humb. & Bonpl. ex Willd. (Moraceae) as well as some Lauraceae and Myrtaceae. The area of primary forest around this plot was searched systematically for additional epiphyte species in order to complete the inventory. Crown openness was 8.21%; average daily amount of photosynthetically active radiation (PAR) was 0.6 mol $m^{-2}$; in a one week period (30 April–6 May 1997), the maximum temperature reached 18 °C, and minimal relative humidity was 61% (own measurements at 2 m above ground level).

In the disturbed and secondary vegetation we chose four typical locations according to the degree of human impact:

1. A 114 $m^2$ plot was embedded in the disturbed forest described above, harbouring one emergent tree (*Decussocarpus*, 28 m high, DBH 80 cm) and two other phorophytes (*Graffenrieda latifolia* (Naudin) Triana, Melastomataceae, 17 m high, DBH 40 cm, and one undetermined specimen, 22 m high, DBH 44 cm). Crown openness was 24.76%, average daily amount of PAR in 2 m above ground level was 4.05 mol $m^{-2}$, which was remarkably similar to the outer crown third in primary forest (4.71 mol $m^{-2}$); in a one week period (30 April–6 May 1997), maximum temperature was 21 °C, and minimal relative humidity 38.5% (own data taken at 2 m above ground level).
2. A 32 year-old plantation of *Cedrela montana* Moritz ex Turcz. (Meliaceae), comprised approximately 400 trees (mean DBH about 15 cm, height 8 m) forming a 0.25 ha rectangle (25 × 100 m). It is bordered by primary forest on the one side and the dirt road mentioned above on the other. As the plantation was established on marshy ground, the trees did not develop well in the past. Due to both the uniform plantation structure and the poor development of plantation tree crowns, which almost completely lack foliage (crown openness more than 50%), sun exposure and therefore drought stress of epiphytes is exceptionally high in this plot.
3. A sector of 30 $m^2$ (2 m × 15 m) in the 23 year old clearing described above, was examined. Due to the extraordinary dense structure of re-growing vegetation, the microclimatic conditions for epiphytes in this location are comparable with those at the 2 m above ground level of the primary forest described above.
4. A 3 km transect was established along the 30 year old road through the disturbed forest section. Only the sun-exposed, high-radiation understorey stretching 5 m from the road margin into the forest on each side of the road was examined.

Epiphytes were sampled using two ascenders in a climbing rope following the technique of mountaineering climbing (Perry 1978). If possible, specimens were collected from the ground, using pruning-shears. Plants were identified and vouchers deposited at the Herbarium of the Centro Jardín Botánico, Facultad de Ciencias, Universidad de los Andes, Mérida (MERC), with duplicates at the Herbario Nacional de Venezuela (VEN).

Epiphyte individuals on trunks and branches were counted during climbing, if necessary by means of binoculars. Species occurring in dense stands (sensu Sanford 1968) like most of the ferns, some orchid species (e.g., *Epidendrum moritzii* Rchb. f., *Encyclia* spp.) and Piperaceae were counted as stands, one stand meaning one ‘individual’.

Only in the *Cedrela* tree plantation, the abundance of bromeliad individuals was estimated rather than determined by counting: Individuals of Bromeliaceae on 7 plantation trees randomly chosen were counted. Since an ANOVA did not show significant differences in frequency or abundance of bromeliad species between those phorophytes, we estimated the total number of bromeliads for the 400 plantation trees. For every other epiphytic family on the plantation, the individuals were counted separately.

In order to directly compare epiphyte vegetation of primary and disturbed vegetation despite of the different study area sizes, we chose one phorophyte (*Decussocarpus*) each in primary forest and disturbed vegetation (relics of primary forest), respectively, with almost the same height (35 m, 32 m), diameter at breast height (1.21 m, 1.05 m), trunk height at first ramification (22 m, 20 m) and crown diameter (12 m, 14 m).

### *Data analysis*

The Shannon-Weaver-Index H′ of alpha-diversity and the Sørensen-Index $CC_S$ of beta-diversity were used to describe epiphyte diversity (Magurran 1988). For statistic analyses we used Statistica 5.1 by StatSoft, Inc.

*Table 1.* Species list of epiphytes in the primary and the secondary forest; + species present; - species absent; a – species present in disturbed forest plot; b – species present in dirt road transect; c – species present in tree plantation; d – species present in former clearing

| No. | Family | Genus | Species | Author | Primary forest | Secondary vegetation |
|---|---|---|---|---|---|---|
| 1 | Araceae | *Anthurium* | cf.*humboldtianum* | Kunth | + | b |
| 2 | A. | *A.* | *julianii* | G.S.Bunting | + | d |
| 3 | A. | *A.* | *nymphaefolium* | C. Koch & Bouché | + | a b |
| 4 | A. | *A.* | *scandens* | (Aubl.) Engl. | + | a b |
| 5 | A. | *A.* | *smithii* | Croat & R. Baker | + | b |
| 6 | A. | *A.* | cf. *subsagittatum* | (Kunth) Kunth | + | – |
| 7 | A. | A. | sp. | | + | b |
| 8 | Araliaceae | *Oreopanax* | *capitatum* | (Jacq.) Decne. & Planch. | + | – |
| 9 | Aspleniaceae | *Asplenium* | *auritum* | Sw. | + | b |
| 10 | A. | *A.* | *cirrhatum* | Rich. ex Willd. | + | – |
| 11 | A. | *A.* | *cuspidatum* | Lam. | + | – |
| 12 | A. | *A.* | *harpeodes* | Kunze | + | b |
| 13 | A. | *A.* | *hastatum* | Klotzsch ex Kunze | + | b |
| 14 | A. | *A.* | *rutaceum* | (Willd.) Mett. | + | – |
| 15 | Asteraceae | *Pentacalia* | *scortifolia* | (Greenm.) Cuatrec. | + | – |
| 16 | Blechnaceae | *Blechnum* | *meridense* | Klotzsch | + | b |
| 17 | Bromeliaceae | *Guzmania* | *mitis* | L.B.Sm. | + | a b d |
| 18 | B. | *G.* | cf. *squarrosa* | (Mez & Sodiro) L.B.Sm. & Pittendr. | – | b |
| 19 | B. | *Racinaea* | *spiculosa* | (Griseb.) Spencer & L.B.Sm. | – | b |
| 20 | B. | *R.* | *tetrantha* var. *aurantiaca* | (Ruiz & Pav.) Spencer & L.B.Sm. | + | a b c |
| 21 | B. | *Tillandsia* | *biflora* | Ruiz & Pav. | + | a b c |
| 22 | B. | *T.* | *complanata* | Benth. | + | b c |
| 23 | B. | *T.* | *fendleri* | Griseb. | – | b |
| 24 | B. | *T.* | *longifolia* | Baker | + | a b c |
| 25 | B. | *T.* | *tovarensis* | Mez | + | a b c |
| 26 | B. | *Vriesea* | *tequendamae* | (L.E. André) L.B. Sm. | + | a b c |
| 27 | Clusiaceae | *Clusia* | *multiflora* | Kunth | + | a b |
| 28 | Cyclanthaceae | *Asplundia* | *moritziana* | (Klotzsch) Harling | + | b |
| 29 | Dryopteridaceae | *Elaphoglossum* | *andicola* | (Fée) T.Moore | + | a b |
| 30 | D. | *E.* | *bellermannianum* | (Klotzsch) T.Moore | + | a |
| 31 | D. | *E.* | cf. *cuspidatum* | (Willd.) T.Moore | + | a |
| 32 | D. | *E.* | *herminierii* | (Bory & Fée) T.Moore | + | – |
| 33 | D. | *E.* | *latifolium* | (Sw.) J.Sm. | + | a d |
| 34 | D. | *E.* | *meridense* | (Klotzsch) T.Moore | + | – |
| 35 | D. | *E.* | *minutum* | (Pohl ex Fée) T.Moore | + | – |
| 36 | D. | *E.* | *plumosum* | (Fée) T.Moore | + | – |
| 37 | D. | *E.* | *rigidum* | (Aubl.) Urb. | – | a b |
| 38 | D. | *E.* | *scolopendrifolium* | (Raddi) J.Sm. | + | – |
| 39 | D. | *E.* | *spathulatum* | (Bory) T.Moore | + | – |
| 40 | D. | *E.* | *strictum* | (Raddi) T.Moore | + | a b |
| 41 | Ericaceae | *Sphyrospermum* | *buxifolium* | Poepp. & Endl. | + | – |
| 42 | E. | *S.* | *cordifolium* | Benth. | + | b |
| 43 | Gesneriaceae | cf. *Columnea* | sp. | | + | – |
| 44 | G. | *Campanea* | *grandiflora* | (Kunth) Decne. ex Planchon | + | – |
| 45 | Grammitidaceae | *Ceradenia* | *spixiana* | (Mart. ex Mett.) L.E.Bishop | + | – |
| 46 | G. | *Enterosora* | *parietina* | (Klotzsch) L.E.Bishop | + | – |
| 47 | G. | *Grammitis* | *anfractuosa* | (Kunze ex Klotzsch) Proctor | + | – |
| 48 | G. | *G.* | *asplenifolia* | (L.) Proctor | + | – |
| 49 | G. | *G.* | *bryophila* | (Maxon) F. Seym. | + | – |

*Table 1 continued.*

| No. | Family | Genus | Species | Author | Primary forest | Secondary vegetation |
|---|---|---|---|---|---|---|
| 50 | Grammitidaceae | *Grammitis* | cf. *cultrata* | (Bory ex Willd.) Proctor | + | – |
| 51 | G. | *G.* | *intricata* | C.V.Morton | + | – |
| 52 | G. | *G.* | *pilosissima* | (Mart. & Galeotti) C.V.Morton | + | – |
| 53 | G. | *G.* | *subsessilis* | (Baker) C.V.Morton | + | – |
| 54 | G. | *G.* | *taenifolia* | (Jenman) Proctor | + | – |
| 55 | G. | *G.* | *taxifolia* | (L.) Proctor | + | – |
| 56 | G. | *G.* | *truncicola* | (Klotzsch) C.V.Morton | + | – |
| 57 | G. | *G.* | *xiphopteroides* | (Liebm.) A.R.Sm. | – | a b |
| 58 | Hymenophyllaceae | *Hymenophyllum* | *crassipetiolatum* | Stolze | + | b |
| 59 | H. | *H.* | *crispum* | Kunth | + | – |
| 60 | H. | *H.* | *fucoides* | (Sw.) Sw. | + | a b d |
| 61 | H. | *H.* | *microcarpum* | Desv. | + | – |
| 62 | H. | *H.* | *polyanthos* | (Sw.) Sw. | + | – |
| 63 | H. | *Trichomanes* | *capillaceum* | L. | + | – |
| 64 | H. | *T.* | *diaphanum* | Kunth | + | – |
| 65 | H. | *T.* | *reptans* | (Sw.) Sw. | + | – |
| 66 | L. | *H.* | *callitrichifolia* | (Mett.) Holub | + | – |
| 67 | L. | *H.* | *cuneifolia* | (Hieron.) Holub | + | – |
| 68 | L. | *H.* | *linifolia* | (L.) Trevis. | + | – |
| 69 | L. | *H.* | *taxifolia* | (Sw.) Trevis. | + | – |
| 70 | Melastomataceae | *Blakea* | *schlimii* | (Naud.) Triana | + | – |
| 71 | Orchidaceae | *Altensteinia* | *paleacea* | (Kunth) Kunth | + | – |
| 72 | O. | *Brachtia* | *glumacea* | Rchb.f. | + | – |
| 73 | O. | *B.* | *sulphurea* | Rchb.f | + | – |
| 74 | O. | *Comparettia* | *falcata* | Poepp. & Endl. | + | – |
| 75 | O. | *Elleanthus* | *columnaris* | (Lindl.) Rchb.f. | + | – |
| 76 | O. | *E.* | *furfuraceaus* | (Lindl.) Rchb.f. | + | b |
| 77 | O. | *Encyclia* | *hartwegii* | (Lindl.) R.Vásquez & Dodson | + | a |
| 78 | O. | *E.* | *lindenii* | (Lindl.) Carnevali & Ramírez | – | a b |
| 79 | O. | *Epidendrum* | *alpicolum* | Rchb.f. | + | – |
| 80 | O. | *E.* | *bifarium* | Sw. | + | – |
| 81 | O. | *E.* | *difforme* | Jacq. | + | – |
| 82 | O. | *E.* | *klotzscheanum* | Rchb.f. | + | – |
| 83 | O. | *E.* | *lilijae* | Foldats | + | – |
| 84 | O. | *E.* | *moritzii* | Rchb.f. | + | a b c |
| 85 | O. | *E.* | *paniculatum* | Ruiz & Pav. | + | – |
| 86 | O. | *E.* | *renzii* | Garay & Dunst. | + | – |
| 87 | O. | *E.* | *repens* | Cogn. | + | – |
| 88 | O. | *E.* | *sceptrum* | Lindl. | + | – |
| 89 | O. | *E.* | *scutella* | Lindl. | + | – |
| 90 | O. | *E.* | *secundum* | Jacq. | + | – |
| 91 | O. | *Gomphichis* | *foliosa* | R.N. Ames | + | – |
| 92 | O. | *G.* | cf. *steyermarkii* | Foldats | + | – |
| 93 | O. | *Lepanthes* | *capitana* | Rchb.f. | + | – |
| 94 | O. | *L.* | *lasiopetala* | Garay & Dunst. | + | – |
| 95 | O. | *L.* | *lindleyana* | Oerst. ex Rchb.f. | + | a |
| 96 | O. | *L.* | cf. *norae* | Foldats | + | – |
| 97 | O. | *L.* | *ruscifolia* | Rchb.f. | + | a |
| 98 | O. | *L.* | *samacensis* | R.N. Ames | – | b c |
| 99 | O. | *L.* | *steyermarkii* | Foldats | – | a |

*Table 1 continued.*

| No. | Family | Genus | species | Author | Primary forest | Secondary vegetation |
|---|---|---|---|---|---|---|
| 100 | Orchidaceae | *Lepanthes* | *wageneri* | Rchb.f. | + | – |
| 101 | O. | *Masdevallia* | cf. *civilis* | Rchb.f. & Warsz. | + | – |
| 102 | O. | *Maxillaria* | *albata* | Lindl. | + | – |
| 103 | O. | *M.* | *anatomorum* | Rchb.f. | + | – |
| 104 | O. | *M.* | *arachnites* | Rchb.f. | + | – |
| 105 | O. | *M.* | *lawrenceana* | (Rolfe) Garay & Dunst. | + | – |
| 106 | O. | *M.* | *longibracteata* var. *luteorubra* | (Lindl.) C.Schweinf. | + | b |
| 107 | O. | *M.* | *luteo–alba* | Lindl. | + | – |
| 108 | O. | *M.* | *macrura* | Rchb.f. | + | – |
| 109 | O. | *M.* | *nivea* | (Lindl.) L.O.Williams | + | a b |
| 110 | O. | *M.* | *sanguinolenta* | (Lindl.) C.Schweinf. | + | a |
| 111 | O. | *Myoxanthus* | *hystrix* | (Rchb.f.) Luer | + | – |
| 112 | O. | *M.* | *reymondii* | (P. Karst.) Luer | + | a b |
| 113 | O. | *Odontoglossum* | × *andersonianum* | Rchb.f. | + | b |
| 114 | O. | *O.* | *odoratum* | Lindl. | + | b |
| 115 | O. | *Oncidium* | *cimiciferum* | (Rchb.f.) Rchb.f. ex Lindl. | + | – |
| 116 | O. | *O.* | *falcipetalum* | Lindl. | + | b |
| 117 | O. | *Otoglossum* | *chiriquense* | (Rchb.f.) Garay & Dunst. | + | – |
| 118 | O. | *Platystele* | *lancilabris* | (Rchb.f.) Schltr. | + | – |
| 119 | O. | *Pleurothallis* | *archidiaconi* | R.N. Ames | + | – |
| 120 | O. | *P.* | *breviscapa* | C.Schweinf. | + | b |
| 121 | O. | *P.* | *cardiantha* | Rchb.f. | + | – |
| 122 | O. | *P.* | *elegans* | (Kunth) Lindl. | + | – |
| 123 | O. | *P.* | *galeata* | Lindl. | + | b |
| 124 | O. | *P.* | *grandiflora* | Lindl. | + | – |
| 125 | O. | *P.* | *lanceolata* | Lindl. | + | a |
| 126 | O. | *P.* | *linguifera* | Lindl. | + | – |
| 127 | O. | *P.* | *magnispatha* | Foldats | + | – |
| 128 | O. | *P.* | *meridana* | Rchb.f. | + | – |
| 129 | O. | *P.* | cf. *orbicularis* | Lindl. | + | – |
| 130 | O. | *P.* | *peduncularis* | J.M. Hook. | + | a b |
| 131 | O. | *P.* | *phalangifera* | (C. Presl) Schltr. | + | – |
| 132 | O. | *P.* | *quadrifida* | (La Llave & Lex.) Lindl. | + | – |
| 133 | O. | *P.* | *sclerophylla* | Lindl. | + | a |
| 134 | O. | *P.* | *secunda* | Poepp. & Endl. | + | – |
| 135 | O. | *P.* | *setigera* | Lindl. | + | – |
| 136 | O. | *P.* | *subtilis* | C.Schweinf. | + | a b |
| 137 | O. | *P.* | *talpinaria* | Rchb.f. | + | a |
| 138 | O. | *P.* | *velaticaulis* | Rchb.f. | + | – |
| 139 | O. | *P.* | sp. | | + | – |
| 140 | O. | *Restrepia* | *antennifera* | Kunth | + | b |
| 141 | O. | *R.* | *elegans* | P. Karst. | + | b |
| 142 | O. | *R.* | *erythroxantha* | Rchb.f. | + | – |
| 143 | O. | *Restrepiopsis* | *tubulosa* | (Lindl.) Luer | + | – |
| 144 | O. | *Scelochilus* | *ottonis* | Klotzsch | + | – |
| 145 | O. | *S.* | *stenochilus* | (Lindl.) Rchb.f. | + | – |
| 146 | O. | *Spiranthes* | *reichenbachiana* | Garay & Dunst. | + | – |
| 147 | O. | *Stelis* | *biserrula* | Lindl. | + | b |
| 148 | O. | *S.* | *dispar* | C.Schweinf. | + | – |
| 149 | O. | *S.* | *eublepharis* | Rchb.f. | + | a |

*Table 1 continued.*

| No. | Family | Genus | Species | Author | Primary forest | Secondary vegetation |
|---|---|---|---|---|---|---|
| 150 | Orechidaceae | *Stelis* | *fendleri* | Lindl. | + | b c |
| 151 | O. | *S.* | cf. *humilis* | Lindl. | + | – |
| 152 | O. | *S.* | cf. *lanceolata* | (Ruiz & Pav.) Willd. | + | b |
| 153 | O. | *S.* | *lindenii* | Lindl. | + | a |
| 154 | O. | *S.* | cf. *nitens* | Rchb.f. | + | a b |
| 155 | O. | *S.* | sp. 1 | | + | – |
| 156 | O. | *S.* | sp. 2 | | – | a b |
| 157 | O. | *S.* | sp. 3 | | – | a |
| 158 | O. | *S.* | sp. 4 | | – | a |
| 159 | O. | *S.* | *striolata* | Lindl. | + | b |
| 160 | O. | *S.* | *tenuilabris* | Lindl. | + | – |
| 161 | O. | *Telipogon* | *bruchmuelleri* | Rchb.f. | + | – |
| 162 | O. | *T.* | *klotzscheanus* | Rchb.f. | + | – |
| 163 | O. | *Trichocentrum* | *pulchrum* | Poepp. & Endl. | + | – |
| 164 | O. | *Gen. 1* | sp. | | – | a |
| 165 | O. | *Gen. 2* | sp. | | – | a b c |
| 166 | Piperaceae | *Peperomia* | *adscendens* | C. DC. | + | b |
| 167 | P. | *P.* | *alata* | Ruiz & Pav. | + | b |
| 168 | P. | *P.* | *berryi* | Steyerm. | + | – |
| 169 | P. | *P.* | *blanda* var. *poriginifera* | (Trel. & Yunck.) Steyerm. | + | – |
| 170 | P. | *P.* | *galioides* | Kunth | + | – |
| 171 | P. | *P.* | *omnicola* var. *omnicola* | C. DC. | + | c |
| 172 | P. | *P.* | *peltoidea* | Kunth | + | – |
| 173 | P. | *P.* | *pennellii* | Trel. & Yunck. | + | – |
| 174 | P. | *P.* | *rhexiifolia* | C. DC. | + | – |
| 175 | P. | *P.* | *rotundata* var. *trinervula* | (C. DC.) Steyerm. | + | – |
| 176 | P. | *P.* | *tetraphylla* | (G. Forst.) Hook. & Arn. | + | a b d |
| 177 | P. | *P.* | cf. *turboensis* | Yunck. | + | – |
| 178 | Polypodiaceae | *Campyloneuron* | *angustifolium* | (Sw.) Fée | + | b |
| 179 | P. | *C.* | *repens* | (Aubl.) C.Presl | + | b |
| 180 | P. | *Niphidium* | *crassifolium* | (L.) Lellinger | + | – |
| 181 | P. | *Pecluma* | *eurybasis* | (C. Chr.) M.G. Price | + | – |
| 182 | P. | *P.* | *hygrometrica* | (Splitg.) M.G. Price | + | – |
| 183 | P. | *Pleopeltis* | *macrocarpa* | (Bory ex Willd.) Kaulf. | + | a b c |
| 184 | P. | *Polypodium* | *fraxinifolium* | Jacq. | + | a b c d |
| 185 | P. | *P.* | *funckii* | Mett. | + | a b d |
| 186 | P. | *P.* | *leucosporum* | Klotzsch | + | b |
| 187 | P. | *P.* | *sessilifolium* | Desv. | + | – |
| 188 | Solanaceae | *Trianaea* | *spectabilis* | Cuatrec. | + | – |
| 189 | Vittariaceae | *Antrophyum* | *lineatum* | (Sw.) Kaulf. | + | b |
| 190 | V. | *Vittaria* | *graminifolia* | Kaulf. | + | a b |
| 191 | V. | *V.* | *moritziana* | Mett. | + | b |

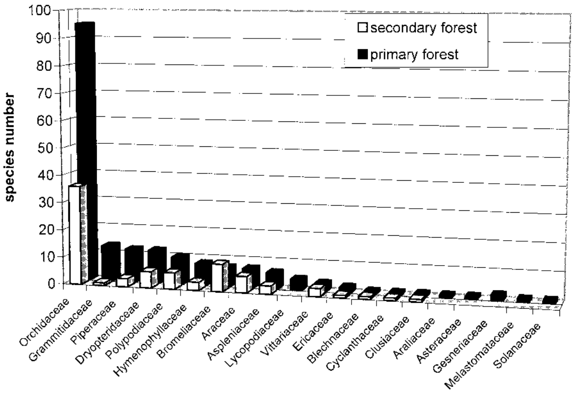


*Figure 2.* Epiphyte species numbers of families in the primary and secondary forest of La Carbonera forest in comparison.

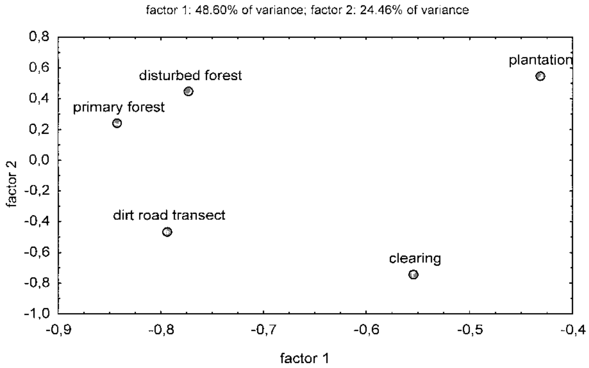


*Figure 3.* Factor analysis of floristic similarities of the epiphyte communities at the primary, secondary, and disturbed forest study sites in La Carbonera forest.

## Results

### *Alpha diversity*

In total, 191 vascular epiphyte species from 20 families were found in the entire forest area comprising all types of vegetation (primary, disturbed and secondary vegetation) (Tables 1 and 2).

In the secondary and disturbed forest plots, 81 epiphytic species from 14 families were collected (Table 1). The most species rich families were Orchidaceae (34 spp.), Bromeliaceae (10 spp.), Araceae, Dryopteridaceae, Polypodiaceae (6 spp. each), and Piperaceae (5 spp.) (Figure 2). Bromeliads and one orchid species, *E. moritzii*, had the highest number of individuals. The different types of vegetation in secondary and disturbed forest contained varying numbers of epiphytes: 42 epiphytic species were found in the relict forest plot, whereas the tree plantation supported only 13 species of epiphytes despite of the relatively large study area (Table 2).

Within the primary forest, 178 epiphytic species from 20 families were documented. Orchidaceae, like in the secondary forest, were the most species-rich family (86 spp.), followed by Grammitidaceae (12 spp.), Piperaceae (11 spp.), Polypodiaceae and Dryopteridaceae (each 9 species), Hymenophyllaceae (8 spp.), Araceae and Bromeliaceae (each 7 spp.) (Figure 2). Epiphytic alpha-diversity in primary forest was extremely high, with 119 epiphyte species in the 0.1 ha plot.

Compared to the secondary and disturbed forest, the low diversity in Bromeliaceae in the primary forest (only 7 spp. versus 10 spp. in secondary and disturbed forest) was striking (Figure 2). Seven out of 81 (= 8.6%) epiphyte species were restricted to the secondary or disturbed vegetation. On the other hand, 110 species out of the total of 178 (= 61.8%) and here especially epiphytic Araliaceae, Asteraceae, Gesneriaceae, Lycopodiaceae, Melastomataceae and Solanaceae occurred in the primary forest only (Table 1, Figure 2).

The secondary habitats (tree plantation and former clear-cutting) had only 17 species of epiphytes, 9% of the primary forest epiphytes. The disturbed habitats (relict forest plot and road transect) on the other hand had 42 and 65 species respectively, i.e., up to 39% of the primary forest epiphyte flora (Table 2).

The epiphyte community in the primary forest plot showed an alpha-diversity of $H' = 3.15$. In the disturbed and especially the secondary vegetation, alpha-diversity was distinctively lower: 2.84 in the relict forest plot, 1.61 and 1.70 in the tree plantation and the former clearing, respectively (Table 2).

### *Beta diversity*

Epiphyte communities in the primary and the secondary forest (all four locations) showed a mean similarity of $CC_S = 0.56$. The epiphyte community of the road transect and the relict forest plot with one emergent *Decussocarpus* showed the highest similarity to the primary forest plot epiphytes ($CC_S = 0.45$ and 0.32 respectively), followed by the epiphyte community of the tree plantation ($CC_S = 0.11$) and the former clearing ($CC_S = 0.08$). A list of $CC_S$ and the absolute numbers of shared species for the different plots is given in Table 3.

A factor analysis of the study sites based on the presence or absence of species in the communities (Figure 3) revealed a distinct similarity between plots

*Table 2.* Numbers of epiphytic genera and species in primary, disturbed and secondary forest plots in La Carbonera forest.

| Family | Primary forest | | Disturbed forest plot | | Road transect | | Tree plantation | | Former clearing | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Genera | Species | Genera | Species | Genera | Species | Genera | Species | Genera | Species |
| Dryopteridaceae | 1 | 11 | 1 | 6 | 1 | 3 | – | – | 11 | |
| Grammitidaceae | 3 | 12 | 1 | 1 | 1 | 1 | – | – | – | – |
| Hymenophyllaceae | 2 | 8 | 1 | 1 | 1 | 2 | – | – | 11 | |
| Polypodiaceae | 5 | 10 | 2 | 3 | 3 | 6 | 2 | 2 | 1 | 2 |
| other ferns | 5 | 14 | 1 | 1 | 4 | 7 | – | – | – | – |
| Araceae | 1 | 7 | 1 | 2 | 1 | 5 | – | – | 11 | |
| Bromeliaceae | 4 | 7 | 4 | 6 | 4 | 10 | 3 | 6 | 11 | |
| Orchidaceae | 23 | 87 | 9 | 22 | 12 | 23 | 44 | – | – | |
| other angiosperms | 10 | 22 | 2 | 2 | 4 | 6 | 1 | 1 | 1 | 1 |
| Total | 54 | 178 | 22 | 44 | 31 | 63 | 10 | 13 | 6 | 7 |
| H′ | | 3.15 | | 2.4 | | 3.06 | | 1.61 | | 1.70 |

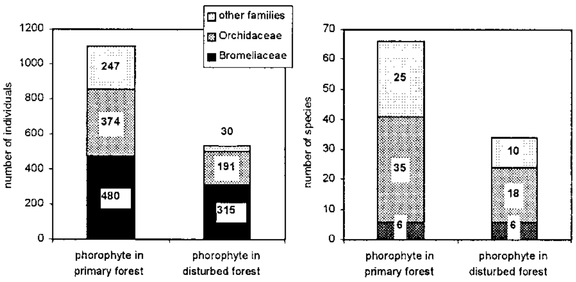


*Figure 4.* Abundance and species richness of epiphyte families on two phorophyte individuals in the primary and the disturbed forest at La Carbonera forest.

in primary and disturbed forest. The other study plots were isolated.

Data from the solitary emergent *Decussocarpus* specimen in the relict forest plot and another of similar height and structure embedded in the primary forest illustrate the effects of disturbance on epiphyte abundance and species richness in detail (Figure 4). In general, we observed a decrease in both species richness and abundance by 50%. Bromeliaceae were the most important family on the disturbed forest phorophyte: they made up 58.8% of the individuals compared to 43.6% on the primary forest phorophyte. Species richness remained the same, which meant an increase in relative species numbers from 9.1% to 17.6%. Orchidaceae continued to make up approximately 35% of individual number and approximately 53% of species number on the disturbed forest phorophyte. The decline of individual and species numbers of all other epiphyte families is marked sharply: whereas on the primary forest phorophyte 22.4% of the individuals and 37.9% of the species did not belong to bromeliads or orchids, these percentages declined to 5.6% for individual numbers and 29.4% for species numbers on the disturbed forest tree. The most abundant species on both phorophytes was *Tillandsia longifolia* Baker (226 = 21% individuals on the primary versus 183 = 34% on the disturbed forest tree). Next in abundance on the primary forest tree was *T. tovarensis* Mez (221 individuals versus 2 individuals on the disturbed forest tree). On the disturbed forest tree, *Vriesea tequendamae* (André) L.B. Sm. (103 = 19% versus 5 individuals on the primary tree) and *E. moritzii* (102 versus 51 individuals) were the most abundant species after *T. longifolia*.

## Discussion

Both epiphyte abundance and diversity are considerably reduced in disturbed and especially secondary study sites, which are more or less similar in age, compared to the old adjacent primary forest. This is consistent with the patterns of forest vegetation in other habitats (Whitmore 1990; Turner et al. 1994; Hietz et al. 1996). Hall (1978) reported that a secondary forest in Ghana harboured only 109 species of vascular plants, compared to 504 in closed canopy primary forest. Of the 43 epiphytes in the latter, only one species occurred in the secondary forest.

Looking at the varying degrees of disturbance in the present study, we observe on the one hand a

*Table 3.* Sørensen indices and absolute numbers of shared epiphyte species of the different study sites in La Carbonera forest.

| | Disturbed forest plot | Tree plantation | Former clearing | Secondary/disturbed forest (total) | Primary forest |
|---|---|---|---|---|---|
| Sørensen | | | | | |
| Road transect | 0.52 | 0.32 | 0.14 | 0.84 | 0.45 |
| Disturbed forest plot | – | 0.31 | 0.24 | 0.67 | 0.32 |
| Tree plantation | | – | 0.10 | 0.26 | 0.11 |
| Former clearing | | | – | 0.15 | 0.08 |
| Secondary/disturbed forest (total) | | | | – | 0.56 |
| Species shared (absolute numbers) | | | | | |
| Road transect | 28 | 12 | 5 | 63 | 54 |
| Disturbed forest plot | 44 | 9 | 6 | 44 | 35 |
| Tree plantation | 9 | 13 | 1 | 13 | 11 |
| Former clearing | 6 | 1 | 7 | 7 | 7 |
| Secondary/disturbed forest (total) | 44 | 13 | 7 | 87 | 74 |

progressive decrease of epiphyte diversity along a gradient of increasing disturbance: from the road transect, relict trees, tree plantation to the former clearing (Table 2). On the other hand, there is a sharp difference in species richness between primary and disturbed forest (relict forest plot and dirt road) and secondary vegetation (plantation and clearing). Tree species growing along the road and in disturbed forest also occur in the primary forest, and offer a similarly complex and diverse habitat, a 'physical mosaic' after Benzing (1995), for epiphytes. Remnant phorophytes continue to support diverse arboricole flora. One isolated *Decussocarpus* had 34 species of epiphytes compared to a maximum of 66 species in the primary forest (Figure 4). Since disturbed habitats are generally drier and more sun exposed (though not to such a degree as the plantation described below) the general adaptation of epiphytes to temporary water stress and the fact that many epiphyte species grow slowly and reach considerable ages (Zotz 1995), may explain the resilience of the epiphyte community in the disturbed forest. Especially the only partially drought tolerant Grammitidaceae and Hymenophyllaceae were affected by disturbance, whereas succulent orchids like *E. moritzii* and *Pleurothallis sclerophylla* Lindl. and the drought tolerant bromeliads (all species of the primary forest, except *Guzmania mitis* L.B. Sm.) remained abundant in the disturbed forest (Table 1, Figure 2). Nevertheless, some moist and shady habitats have been preserved in the disturbed forest and in the clearing, to which shade tolerant species like *G. mitis* and the Vittariaceae are adapted.

The decrease in epiphyte abundance at disturbed sites as shown in Figure 4 was driven mainly by a decrease in ferns and other epiphytes growing in large stands and mats, which tend to accumulate litter and substrate, building up a reservoir of nutrients and water exploitable by many other epiphytes. On the disturbed forest tree, however, epiphytes mostly grew on the bare bark. Substrate was accumulated only in the rosettes of bromeliads.

On the disturbed forest phorophyte, insolation was much higher than on the primary forest phorophyte, which not only could be measured but was also shown in the colour of Bromeliad leaves: on primary forest trees, bromeliads showed red coloured leaves only in the outermost part of the tree crown, whereas on secondary and disturbed forest trees even *G. mitis* specimens growing on the lower parts of trunks also showed red coloured leaves. Litter and substrate accumulating epiphytes might have been absent on the disturbed tree due to higher insolation to which they are not as well adapted as bromeliads and some of the orchids.

Three bromeliad and five orchid species of La Carbonera, among them *E. moritzii*, the third most abundant epiphyte on the disturbed forest phorophyte in Figure 4, by far the most abundant orchid in the disturbed forest, are suspected to be $C_3$/CAM-intermediate plants with a $\delta^{13}$C-value between $-26$ and $-23$ (Engwald 1999). Due to this feature and to special adaptations, e.g., foliar trichomes or tank like growth forms in Bromeliaceae and succulence in some Orchidaceae, they are particularly well adapted to the drier and more sun exposed habitats of the upper canopy (Smith et al. 1985; Smith 1986) in primary or disturbed forest and the plantation, consequently dominating its epiphytic community. Interestingly enough, the secondary habitats had even three more bromeliad species than the primary forest. One of them, *Tillandsia fendleri* Griseb., could be found frequently outside the La Carbonera forest where insolation was high, e.g., on isolated trees on pastures. After further and more detailed studies, some of the taxa restricted to primary habitats could probably be used as bioindicators for a determination of degree of disturbance and afterwards the choice of measures to protect epiphyte diversity in other montane rain forests as well.

The tree plantation was much poorer in epiphyte species, although the investigated area was the largest one. Species richness on only one *Decussocarpus* tree in the primary forest (example used for Figure 4) was five times higher than in the whole *Cedrela* tree plantation, and even the isolated *Decussocarpus* phorophyte in the disturbed forest (Figure 4) harboured more than twice as many species as the approximately 400 plantation trees. In the plantation, the uniform tree structure and the deteriorated state of the trees with a crown openness of more than 50% reduced the number of suitable micro-habitats for epiphytes, compared to primary and disturbed forest. Sun exposure of epiphytes there was much higher than in most habitats of primary and secondary forest, except the outer canopy third (Johansson zone 5, tree zonation following Johansson 1974). Interestingly enough, this layer in the primary and secondary forest was mainly occupied by bromeliads except for one species: *G. mitis,* preferring shady conditions and being completely absent in the plantation, grew well in the lower levels of primary and secondary forest and in the clearing. Because of high light exposure, bromeliads in the plantation showed red coloured leaves, a reaction that has been described among others by Pittendrigh (1948), in the case of bromeliads in a sun exposed cacao plantation in Trinidad.

The clearing supported the lowest numbers of both epiphyte species and individuals. Although the area sampled was very small, the data reflect conditions in the entire clearing. Its dense undergrowth and little developed and very uniform phorophyte structures did not favour epiphyte establishment except for ferns because they tolerate shade and require high humidity (Andrade & Nobel 1997). *G. mitis* represented the single exception and it also heavily exploits dark micro-sites in the primary forest. Furthermore, there appears to be an ongoing process of re-colonisation by epiphytes. When suitable phorophytes will have re-grown, epiphytes adapted to less damp and shady conditions may enter this habitat as well. However, epiphytes tend to establish slowly, which could be shown by removal experiments of epiphyte growth on tree branches (Nadkarni pers. comm.; Ibisch 1996), so it may take a long time to receive a more diverse epiphytic species community in the clearing.

In the factor analysis (Figure 3), primary forest plot and the plantation are separated widely by factor 1. We presume that the degree of disturbance is reflected by this factor: the dirt road transect and the disturbed forest plot, both compounds of the disturbed forest, are put together according to this factor and placed near the primary forest plot. The two plots, where primary vegetation had been removed completely or replaced in the case of tree plantation, show the widest distance to the primary forest plot.

Factor 2 may reflect the degree of insolation: the clearing was by far the most shady habitat with shade tolerant epiphyte species, whereas the plantation was characterised by the highest degree of insolation. Consequently epiphyte species of the plantation were those growing in the outer canopy layers of the disturbed and primary forest. They were absent in the clearing.

We suppose that the position of the dirt road transect in the PCA is an artefact. On the one hand insolation of this study site was very high. But the consequent water stress was mitigated by an abundant offer of substrate matter on the forest floor which functioned as a water storage.

We conclude that disturbance significantly reduces epiphyte diversity. Epiphytes depend on substrates the basis of which only structurally complex phorophytes (i.e., generally old trees) can provide: In the primary forest of our study substrate was accumulated mostly by stand forming epiphytes such as ferns. Probably in the disturbed habitats these epiphytes were not able to cope with the high insolation. In a highly insolated secondary habitat like the plantation, they were not even able to establish as seedlings. Due to the lack of accumulated substrate, other not stand forming epiphyte species were not able to grow, e.g. many solitary orchids.

Consequently, the persistence of a relatively diverse community of epiphytes on relict trees suggests that even small remnants of primary tropical forest in the tropics might help to preserve an important component of these systems.

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## References

Andrade, J. L. & Nobel, P. S. 1997. Microhabitats and water relations of epiphytic cacti and ferns in lowland neotropical forest. Biotropica 29: 261–270.

Bennett, B. C. 1992. Uses of epiphytes, lianas, and parasites by the Shuae People of Amazonian Ecuador. Selbyana 13: 99–114.

Benzing, D. H. 1984. Epiphytic vegetation: A profile and suggestions for future inquiries. Pp. 155–171. In: Medina, E., Mooney, H. A. & Vásquez-Yánes, C. (eds), Physiological ecology of plants in the wet tropics. Dr. W. Junk Publishers, The Hague.

Benzing, D. H. 1990. Vascular epiphytes. Cambridge University Press, Cambridge.

Benzing, D. H. 1995. The physical mosaic and plant variety in forest canopies. Selbyana 16: 159–168.

Brun, R. 1979. Methods and results of biomass determination in a cloud forest ecosystem in the Venezuelan Andes. Plant Res. Devel. 9: 61–70.

Chazdon, R. L. 1994. The primary importance of secondary forests in the tropics. Tropinet 5: 1.

Edwards, P. J. & Grubb, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. J. Ecol. 65: 943–969.

Engwald, S. 1999. Diversität und Ökologie der vaskulären Epiphyten in einem Berg- und einem Tieflandregenwald in Venezuela. Libri – Books on Demand, Hamburg.

Gentry, A. H. & Dodson, C. H. 1987a. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Garden 74: 205–233.

Gentry, A. H. & Dodson, C. H. 1987b: Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19 (2): 149–156.

Hall, J. B. 1978. Check-list of the vascular plants of Bia National Park and Bia Game Production Reserve. In: Martin, C. (ed.), Management plan for the Bia Wildlife Conservation Areas, Part I. Wildlife and National Parks Division, Ghana Forestry Commission. Final Report IUCN/WWF Project 1251.

Hetsch, W. & Hoheisel, H. 1976. Standorts- und Vegetationstypengliederung in einem tropischen Nebelwald. Allgemeine Forst- und Jagdzeitung 147: 10–11.

Hietz-Seifert, U., Hietz, P. & Guevara, S. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz. Biol. Cons. 75: 103–111.

Ibisch, P. 1996. Neotropische Epiphytendiversität – das Beispiel Bolivien. Archiv naturwissenschaftlicher Dissertationen. Martina Galunder-Verlag, Wiehl.

Ibisch, P. I., Boegner, A., Nieder, J. & Barthlott, W. 1996. How diverse are neotropical epiphytes? An analysis based on the 'Catalogue of the Flowering Plants and Gymnosperms of Peru'. Ecotropica 2: 13–28.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica 59: 1–136.

Lugo, A. E. & Scatena, F. N. 1992. Epiphytes and climate change research in the Caribbean: a proposal. Selbyana 13: 123–130.

Magurran, A. E. 1988. Ecological diversity and its measurement. Chapman and Hall, London, New York, Tokyo, Melbourne, Madras.

Nadkarni, N. M. 1985. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16(4): 249–256.

Nadkarni, N. M. 1992. The conservation of epiphytes and their habitats: Summary of a discussion at the international symposium on the biology and conservation of epiphytes. Selbyana 13: 140–142.

Olmsted, I. & Gómez Juárez, M. 1995. Distribution and conservation of epiphytes on the Yucatán Peninsula. Selbyana 17: 58–70.

Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.

Pittendrigh, C. S. 1948. The bromeliad-*Anopheles*-malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58–89.

Porembski, S. & Barthlott, W. 2000. Biodiversity research in Botany. Prog. Bot. 21: 335–362.

Rauh, W. 1992. Are Tillandsias endangered plants? Selbyana 13: 138–139.

Richter, M. 1991. Methoden der Klimaindikation durch pflanzenmorphologische Merkmale in den Kordilleren der Neotropis. Die Erde 122 (4): 267–289.

Sanford, W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. J. Ecol. 56: 697–705.

Schimper, A. F. W. 1888. Die epiphytische Vegetation Amerikas. G.Fischer, Jena.

Smith, J. A. C. 1986. Comparative ecophysiology of crassulacean acid metabolism and 3-carbon pathway bromeliads. 4. Plant water relations. Plant, Cell Environ. 9: 395–410.

Smith, J. A. C., Griffiths, H., Bassett, M. & Griffiths, N. M. 1985. Day-night changes in the leaf water relations of epiphytic bromeliads in the rain forests of Trinidad. Oecologia 67: 475–485.

Turner, I. M., Tan, H. T. W., Wee, Y. C., Ibrahim, A. B., Chew, P. T. & Corlett, R. T. 1994. A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. Cons. Biol. 8(3): 705–712.

Went, F. W. 1940. Soziologie der Epiphyten eines tropischen Urwaldes. Ann. Jardin Botanique de Buitenzorg 50: 1–98 .

Whitmore, T. C. 1990. An introduction to tropical rain forests. Oxford University Press, Oxford.

Zotz, G. 1995. How fast does an epiphyte grow? Selbyana 16: 150–154.