

HOW DIVERSE ARE NEOTROPICAL EPIPHYTES? AN ANALYSIS BASED ON THE “CATALOGUE OF THE FLOWERING PLANTS AND GYMNASPERMS OF PERU”

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Resumen. Usando la flora del Perú como modelo se analiza el papel cuantitativo (porcentaje) y cualitativo (porcentaje de endemismo) que juegan las epífitas en una región neotropical. Para eso se han examinado todos los datos relevantes del “Catálogo de las angiospermas y gimnospermas del Perú” (Brako & Zarucchi 1993). Un 9-11% de las 17,000 especies de angiospermas peruanas son epífitas. Los porcentajes de epifitismo de los géneros más importantes con especies epifíticas se encuentran debajo de las estimaciones recientes. Más de un 60% de las epífitas ocurre en los pisos medios y inferiores de los Andes, sin embargo en estas regiones sólo alcanzan un porcentaje modesto dentro de la fitodiversidad total (5-10%). Comparando los taxa epifíticos con los taxa exclusivamente terrestres (y ricos en especies), los primeros muestran porcentajes de endemismo muy bajos. Otro resultado importante de señalar es que (con excepción de las Orchidaceae) la ‘endemidad’ de las epífitas es significativamente más baja que la de las especies terrestres dentro de los mismos géneros (familias) (p.ej. Bromeliaceae). Las epífitas tienden a una alpha-diversidad muy alta y - en el nivel local - a un porcentaje bastante considerable de la flora; por otro lado su gamma-diversidad es muy baja y los índices de epífitas disminuyen rápidamente con la ampliación del área de inventario. Estos y otros datos (p.ej. la diversidad en los pisos altitudinales) se ilustran con diagramas y un mapa. Finalmente, se tratan de explicar los porcentajes de epifitismo y de endemismo en las familias más ricas en epífitas (Orchidaceae, Bromeliaceae, Araceae, Piperaceae). Se concluye que en el caso de las Orchidaceae (78% de las epífitas peruanas) el epifitismo en sí no es la causa de su diversidad.

Abstract. Using the flora of Peru as a model, the quantitative (percentage) and qualitative (endemism percentage) roles played by epiphytes within a neotropical region are analysed. With those aims, relevant data contained in the „Catalogue of the flowering plants and gymnosperms of Peru“ (Brako & Zarucchi 1993) are examined. Some 9-11% of the approximately 17,000 Peruvian angiosperm species are epiphytes. The epiphytism percentages of the most important genera with epiphytic species are lower than recent estimates. More than 60% of epiphyte species occur in the lower and mid-elevations of the Andes, but here they reach only a modest percentage of the total phytodiversity (5-10%). In comparison to species-rich, purely terrestrial taxa all epiphyte taxa (e.g., Orchidaceae, Bromeliaceae, Araceae) show low endemism percentages. Another remarkable result emerges: with the exception of the Orchidaceae, the endemism of epiphytes is significantly lower than the endemism of terrestrial species, even within the same genera (e.g., family Bromeliaceae). Epiphytes tend towards a very high alpha-diversity and, on local scale, to considerable percentages of the total diversity; but their gamma-diversity is low and the epiphyte-quotients decrease rapidly with increasing sample size. These and other results (e.g., diversity in different altitudinal zones) are illustrated by diagrams and a map. Finally, an explanation of the epiphyte percentages and the endemism patterns of the epiphyte-rich families is attempted (Orchidaceae, Bromeliaceae, Araceae, Piperaceae). It is concluded that in the case of the Orchidaceae (78% of all Peruvian epiphytes) epiphytism is not itself the cause of their diversity. Accepted 26 February 1996.

Key words: Epiphytes, diversity, biogeography, endemism, Peru, Neotropics.

INTRODUCTION

In many tropical forests vascular epiphytes are very conspicuous plant life-forms (Fig. 1) and contribute significantly to tropical plant diversity (Gentry & Dodson 1987a, b, Kelly 1985, Smith 1970, Schnell 1952). 10% of all vascular plants are estimated to be epiphytes (Kress 1989). Yet, significantly, patterns of epiphyte diversity and their regional importance are still poorly documented. Apart from a preliminary analysis of the epiphytes of Mexico (Aguirre-León

1992), to our knowledge no other large-scale epiphyte inventory has been realized.

With the publication of the “Catalogue of the Flowering Plants and Gymnosperms of Peru” (Brako & Zarucchi 1993), the Missouri Botanical Garden expressed its hope “that we are leaving behind the time when specialists worked in isolation” (Raven 1993). Even as a relatively incomplete “progress report” (Gentry 1993), such a checklist serves as a “powerful tool for planning future research” (Raven 1993). In our present paper, we use catalogue data

on the vascular epiphytes to analyse their species richness and biogeography. By steps, our aim will be to answer some general questions concerning epiphytes.¹ Such questions include: (1) How much do epiphytes contribute to Peruvian plant species richness and what are their spatial distribution patterns? (2) Are those patterns the result of an epiphyte-specific evolutionary development? (3) What can we learn about epiphyte evolution on the basis of endemism percentages in certain taxa?

For some tentative answers we compared terrestrial and epiphytic species within epiphyte-rich taxa.

For this kind of phytogeographic analysis Peru is ideally suited. It is the third largest country in South America, and extends from the equator to 17°20' S. Altitudinal conditions range from sea level to higher than 6,700 m. The complex tropical three-dimensional thermo-hydric conditions (Lauer 1986) contribute to an enormous biodiversity at ecosystem, species and infraspecific levels. Several authors have contributed to the characterization of the flora and vegetation of Peru; the literature includes studies of coastal, Andean and Amazonian plant communities (e.g., Weberbauer 1911, Gentry 1993).

DATA BASE

This paper chiefly seeks to analyse selected data of the "Catalogue of the Flowering Plants and Gymnosperms of Peru" (Brako & Zarucchi 1993). The Catalogue lists 17,119 plant species, indicating habit, ecology, elevational range and distribution within Peruvian departments. A potential source of error is the lack of satisfactorily complete information on possible life-forms for a given species. Distinction and identification of life-forms as indicated by the Catalogue was accepted and used for the present analysis. Undoubtedly, future collectors will find a number of species characterized as 'epiphytic' in the Catalogue on the ground. At the same time unsurveyed regional pockets are likely to harbour a number of 'terrestrial' species which grow as epiphytes. In the case of several large orchid genera we attributed species with unknown life-form to either epiphytic, facultatively epiphytic or terrestrial habit on the basis of additional information from Schlechter (1992), Schweinfurth (1958-61) and Dressler (1987), or indeed considered the 'epiphytism tendency' in un-

equivocal genera (e.g., *Pleurothallis*). The Catalogue lists a number of species as "not reconfirmed", i.e., species without known herbarium documentation. We included them in our data base.

The incidence of epiphytic species (especially among those orchids which have received scant attention, e.g., *Stelis*) will increase with future taxonomic and ecological research efforts in Peru, whereas the incidence of endemic species will decrease as a result of further research in other South American countries. Almost certainly, the known altitudinal range will be extended for a number of species. However, the results of this paper are unlikely to be affected.

THE CONCEPT OF 'EPIPHYTISM' USED IN THIS PAPER

Following the original definitions of Martius (1842) and Grisebach (1872), epiphytes are plants that use other plants as their habitat. They are distinguishable from root and canopy parasites, which draw water or nutrients from their phorophytes. Further, unlike lianas, epiphytes are not in permanent contact with the soil.

According to Benzing (1990), epiphytes can be classified according to different criteria, for example growth-habit, climatic tolerance, relationship to the host, etc., Kress (1989) applies a broad definition of 'epiphyte', which includes holo-epiphytes, casual epiphytes, hemi-epiphytes, and even semi-epiphytic climbers. However, an interpretation of their evolutionary significance and mechanisms calls for a narrower definition of epiphytes. This is necessary since the continuum from terrestrials to facultative epiphytic or hemiepiphytic plants to epiphytes covers a spectrum of "functional types" (Huston 1994) which evolved different specific adaptations in response to enormously varying qualities and quantities of resources.

The "Catalogue of angiosperms and gymnosperms of Peru" characterizes epiphytic plants as "epiphytic" or "epiphytic and terrestrial" or "hemiepiphytic". In the following we use the term "epiphyte" for obligatory holo-epiphytes. This term precludes facultative (potentially terrestrial) epiphytes and hemi-epiphytes (epiphytes in a broad sense). Generally, the classification of the checklist has been followed.

METHODS

Selection of data sets. In epiphyte-rich taxa (Orchidaceae, Bromeliaceae, Araceae, *Peperomia*) all species, epiphytic and terrestrial, listed in the Catalogue were

¹ It should be added that our theoretical work is embedded in field work undertaken in Bolivia, Ecuador, Venezuela and in Africa.



FIG. 1. Epiphytes (and especially epiphytic Bromeliaceae) are often very conspicuous, (here *Racinaea schumanniana*, *Tillandsia complanata*, *T. stenoura*, *T. biflora* on *Albus acuminata*). They frequently shape the physiognomy of neotropical forests. Despite the abundance of bromeliads their contribution to epiphyte diversity is very modest. (Photo: P.L. Ibisch)

included in our database. Of other families, only epiphytic, facultatively epiphytic and hemiepiphytic species were considered.

The data from the Catalogue entered into our database were:

- taxon (species, genus, family)
- life-form (epiphyte, hemiepiphyte, facultative epiphyte, terrestrial, unknown)
- altitudinal zone sensu Brako & Zarucchi: Amazonean, Andean I, Andean II, Andean III, Coastal
- altitudinal distribution in m above sea level in steps of 500 m
- records in *departamentos* of Peru
- endemism

Data processing. The above-mentioned data were entered into FileMaker Pro 3.0. This program was used to elaborate tables and figures which illustrate diversity and endemism patterns.

RESULTS AND DISCUSSION: DIVERSITY AND ENDEMISM PATTERNS OF PERUVIAN EPIPHYTES

Diversity

The species richness of Peruvian epiphytes in the global context

Among the 17,119 angiosperm plant species of Peru, there are between 1,550 and 1,800 epiphytes (equivalent to 10%). Additionally, of 1,000 species of Peruvian pteridophyta, 350 are recorded as epiphytes (roughly 170 of them obligatory holo-epiphytes; see Tryon & Stolze 1989 a, b; 1991; 1993). In all, there are approximately between 1,900 and 2,150 species of vascular epiphytes in Peru.

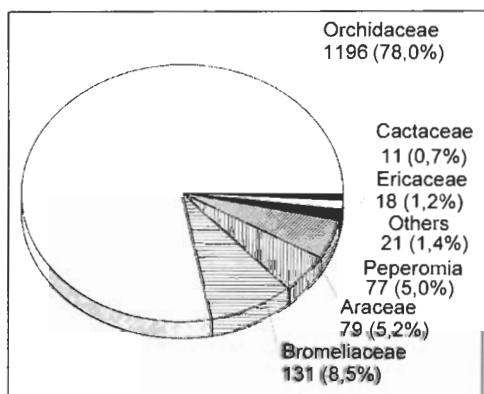


FIG. 2. The systematic distribution of Peruvian angiosperm epiphytes (obligatory holo-epiphytes).

Table 1 lists the number of epiphytic species of epiphyte-rich angiosperm taxa in Peru and allows a comparison of Peruvian and global species richness and intra-taxonomic epiphytism percentages (see Kress 1989). Fig. 2 illustrates the systematic distribution of Peruvian angiosperm epiphytes.

The epiphytic orchids represent 7% of the flora of Peru and 78% of all epiphytes (this family at the same time shows the highest epiphytism percentage: 75% to 83% of all its species are epiphytes). The physiognomically important epiphytic Bromeliaceae (Fig. 1) appear next with only 8.5% of all epiphytes. Araceae follow with 5.2% and *Peperomia* (Piperaceae) with 5.0%. Further taxa are not significantly important, an outcome which leads to a surprisingly low ratio of dicot to monocot epiphytes (1:13). Benzing (1987) predicts a global ratio of 1:5.

Between 9 and 11% of the Peruvian angiosperms are epiphytes. In tropical, epiphyte-rich Mexico, Aguirre-León (1992) found 10% (1,377 species) of the total flora to be epiphytes.

Both figures are remarkably close to Kress's estimate of 10% epiphytic species among angiosperms globally.

But percentages of epiphytic species within genera and families differ to some degree between Kress (1989) and our catalogue-based figures. For *Maxillaria* and *Epidendrum* Kress assumes epiphytism percentages of 100%: neglecting the fact that several species are never found as epiphytes. Only 90% to 95% (not 100%) of *Maxillaria* and *Epidendrum* species are epiphytic. In the case of *Pleurothallis*, *Stelis* and *Masdevallia*, epiphytism percentages of 100% are more realistic. However, the epiphytism percentages of orchids in Peru and worldwide are almost equal. Even if one takes into account that most orchids are found in tropical countries this is surprising, considering that there is a great number of terrestrial orchids in temperate and, especially, in subtropical regions. Even more marked discrepancies are shown by Bromeliaceae, Araceae and Peperomia (see Table 1). Has the global epiphyte diversity been overestimated? This question cannot be answered using the Peruvian checklist only. Preliminary data on the basis of floras of the most epiphyte-rich tropical countries (Boegner, in prep.) suggest epiphyte quotients similar or even lower than that for Peru: Sri Lanka 3.9%, Malayan peninsula 7.3%, Panama 11%. Epiphytism percentages of Central African orchids similarly indicate the diminished relative importance of epiphytes with respect to species numbers (Biedinger

TABLE 1. Number of epiphyte species in species-rich families and genera - Peruvian and global diversity.

Taxa	Number of Peruvian obligatory holo-epiphytes (of epiphytes in a broad sense)	Peruvian epiphytism percentage obligatory holo-epiphytes (epiphytes in a broad sense)	Global number of epiphytes (Kress 1989)	Global epiphytism percentage (after Kress 1989)
Angiosperms	1,533 (1,760)	9.0 %	(10.3 %)	20,863 9.4 %
Orchidaceae	1,196 (1,323)	75.4 %	(83.4 %)	13,951 72.9 %
<i>Epidendrum</i>	171 (187)	86.8 %	(94.0 %)	500 100.0 %
<i>Pleurothallis</i>	126 (129)	94.7 %	(97.0 %)	1,500 100.0 %
<i>Maxillaria</i>	114 (127)	87.0 %	(97.0 %)	600 100.0 %
<i>Masdevallia</i>	100 (101)	97.1 %	(100.0 %)	400 100.0 %
<i>Stellis</i>	89 (93)	96.7 %	(100.0 %)	300 100.0 %
<i>Oncidium</i>	70 (76)	90.9 %	(98.7 %)	430 9.5 %
Bromeliaceae	131 (175)	28.8 %	(38.5 %)	1,144 45.8 %
<i>Tillandsia</i>	69 (98)	41.1 %	(58.3 %)	400 88.9 %
Araceae	79 (98)	36.2 %	(44.9 %)	1,349 54.0 %
Piperaceae				
<i>Peperomia</i>	77 (77)	18.6 %	(18.6 %)	700 70.0 %
Ericaceae	18 (18)	13.8 %	(13.8 %)	672 19.2 %
Cactaceae	11 (12)	4.4 %	(4.8 %)	150 10.0 %

Further families with epiphytes (obligatory holo-epiphytes / epiphytes in a broad sense): Gesneriaceae (4/20), Cyclanthaceae (4/7), Solanaceae (3/6), Melastomataceae (3/4), Rubiaceae (2/5), Lentibulariaceae (1/2), Burmanniaceae (1/1), Araliaceae (1/1), Malvaceae (1/1), Euphorbiaceae (1/1), Urticaceae (0/5), Amaryllidaceae (0/1), Oxalidaceae (0/1).

1995). The tropics are home to approximately 60% of the estimated 260,000 vascular plant species on earth (Huston 1994). Vascular epiphytes are almost exclusively tropical. If the tropical regions have an epiphyte quotient of about 10%, it is highly unlikely that the global epiphyte quotient reaches the 10% proposed by Kress (1989; using the broadest possible definition of epiphytism).

The influence of altitude on epiphyte diversity

Table 2 illustrates floristic and epiphyte diversity along an altitudinal gradient from lowland Amazonia to the Andean highlands.

A maximum of epiphyte diversity can be found along the altitudinal belt of the Eastern Andean slopes between 1,500 and 3,500 metres above sea level, a tract which covers only 5% of the surface of the country (Young & Valencia 1992). Here, a maximum of angiosperm diversity is located (57% of all Peruvian angiosperms, equivalent to almost 10,000 species; cf. Gentry 1993)². About 30–40% of all epiphytes of Peru are recorded in this zone (Fig. 3a). The percentage of epiphytic species, however, is not more than 5–7% of the total angiosperm species-number.

Total epiphyte species number is highest in the lowlands and decreases with altitude when the altitudinal belts chosen by Brako & Zarucchi (1993) are divided into intervals of 500 m (Fig. 3c). Only orchids maintain a high level of diversity up to the mid-elevations. The total orchid diversity shows a mid-elevation peak (Fig. 4) which, interestingly, is caused by the peak of tetrestrial species.

Gentry & Dodson (1987a) discussed controversially whether total species diversity in mid-elevation forests was high because of the increase in epiphytes (Dodson) or whether it was lower than in the lowlands because of a decrease in species numbers of other habit

²This number includes species from humid and dry vegetation alike. If we want to analyse rain forest vegetation, the species from dry zone vegetation must be excluded. Unfortunately, the catalogue does not always allow an exact allocation of plant species to habitat types. Because of the existence of non-forest species from drier sites, especially from "Andean I" and "Andean III", epiphyte indices for rain forests should be higher than given in Table 3. However, as the maximum of species is predicted to occur in the humid forests, the estimations of Young (about 2,000 spp.; 1991) and León *et al.* (about 3,000 spp.; 1992) are certainly too low.

groups, such as lianas and trees, yielding a net loss of total species diversity at altitude, despite the increased number of epiphytes (Gentry).

Interestingly, on this matter the Catalogue supplies the basis for the insight that species richness is highest in mid-elevation forests. If epiphytes do *not* "contribute greatly to the floristic richness" (Gentry 1993) then quite obviously the diversity peak of the mid-elevations is caused by non-epiphytes.

Distribution of epiphyte diversity in different vegetational zones

Fig. 5 illustrates the geographic distribution of epiphyte diversity in Peru. Most epiphyte species are found in a small belt corresponding to the "tierra templada" (Fig. 3b). Here a minimum of seasonality, a maximum of precipitation and cloud development, and moderate temperatures are found (mean annual temperatures of about 16-12°C; absolute frost limit about 2,500 m above sea level) (Lauer & Erlenbach 1987, Young 1992) and it is here that the epiphytes reach their highest physiognomic importance. In-

deed, as early as 1888 Schimper pointed out: "(hier) zeigt sich die epiphytische Vegetation in vollster Pracht und grösstem Formenreichthum".

The majority of the epiphytic species at 0-500 m above sea level is concentrated in the sub-Andean belt (about 400-500 m above sea level.). This can be concluded from the comparison of the almost purely 'Amazonian' political departments (e.g., Loreto) with the rather 'Andean' departments which only have small portions of lowland area (<500 m) (e.g., Amazonas) in the region of the sub-Andean belt. The analysis of epiphyte species numbers shows that the latter have considerably higher epiphyte diversity.

A relatively large part of Peru, i.e. inter-Andean dry valleys, high Andes, coast and slopes of the Cordillera Occidental, is very poor in epiphytes (Table 2, Fig. 5).

Endemism

Endemism percentages in epiphytic and terrestrial taxa

31.3% of the Peruvian angiosperms are endemics. Table 3 shows the endemism percentages of the epi-

TABLE 2. Peru: angiosperm diversity and epiphyte diversity on altitudinal gradients.

Altitudinal belt – sensu Brako & Zarucchi (1993)	Angiosperms		Angiosperm epiphytes		
	Number of angiosperm species*	Percentage	Number of obligatory holo- epiphytes (of epiphytes in a broad sense)	Percentage of all epiphytes of Peru obligatory holo- epiphytes (epiphytes in a broad sense)	Epiphyte percentage of all angiosperms in the different zones (Epi. quotient) obligatory holo- epiphytes (epiphytes in a broad sense)
Total Peru	17,119	100 %	1,533 (1,760)	100 %	9.0 % (10.3%)*
Amazonian (0-500)	7,400	43 % (393)	330 (22.3 %)	21.5 % (5.3 %)	4.5 %
Andean (500–1,500)	5,800	34 % (560)	482 (31.8 %)	31.4 % (9.7 %)	8.3%
Andean II (1,500–3,500)	9,800	57 % (635)	532 (36.1 %)	34.7 % (6.5 %)	5.4 %
Andean III (3,500–4,500)	2,400	14 % (36)	28 (2.0 %)	1.8 % (1.5 %)	1.2 %
Coastal	1,200	7 % (24)	18 (1.4 %)	1.2 % (2.0 %)	1.5 %

* Calculated after percentages provided by Gentry (1993); rounded.

** The percentage of epiphytes with reference to Peru in its entirety is higher than the average of the percentages of the different altitudinal belts (for various species no information on altitudinal occurrence is available). Therefore - especially in altitudes where they are high - an increase of percentages can be expected.

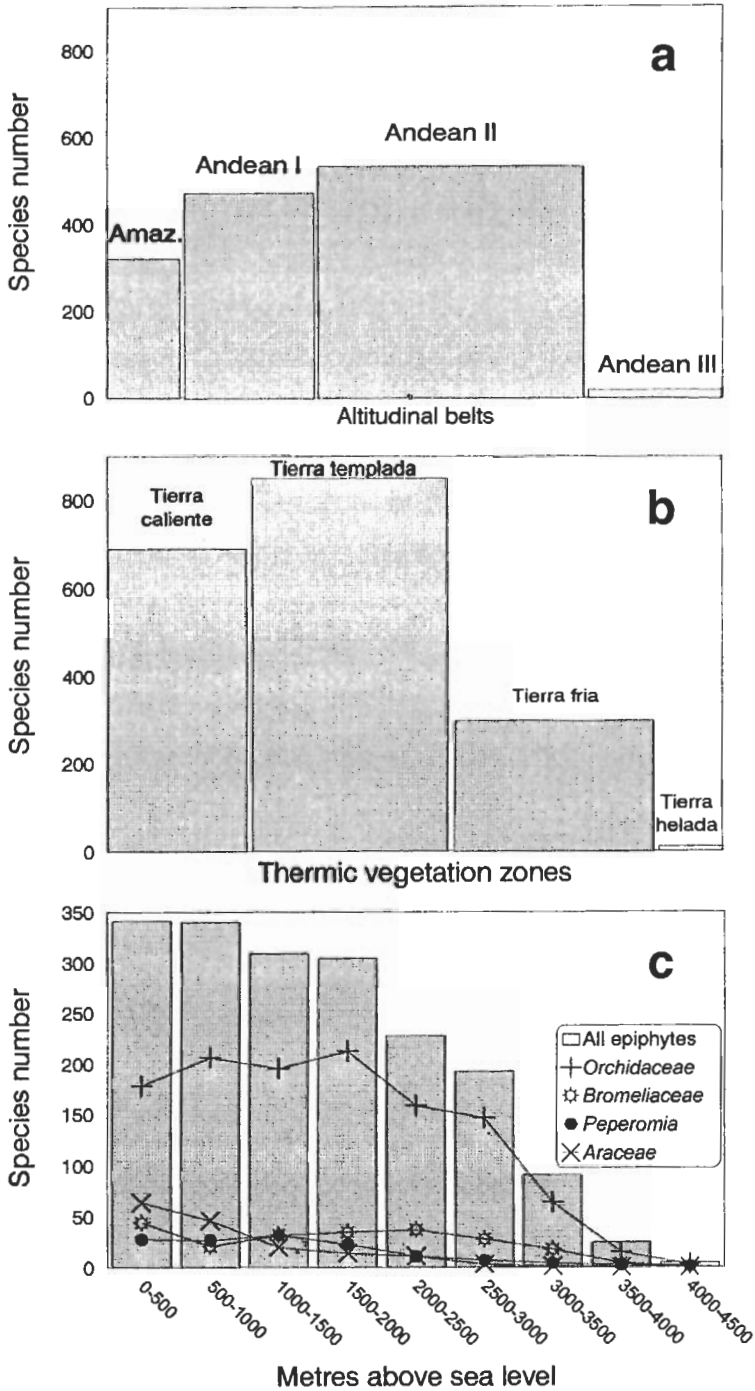


FIG. 3. Species numbers of epiphytes on the Andean altitudinal gradient. a. Altitudinal belts after Brako & Zarucchi (1993). b. Thermic altitudinal vegetation zones after Lauer & Erlenbach (1987). c. 500-metre-intervals. (Coastal species excluded).

phyte-rich taxa, including their epiphytic and their non-epiphytic species.

Orchidaceae is the only family where the percentage of endemics is higher in epiphytic species than in terrestrial species (Table 3). In contrast, the epiphytic species of Bromeliaceae, Araceae and Piperaceae show dramatically low endemism percentages.

As early as 1888 Schimper pointed out that epiphytes show wider distributions than terrestrial species, the latter tending significantly more to endemism. Indeed, endemism percentages of all epiphytic families do not reach the average endemism percentage of Peruvian angiosperms. In contrast, many species-rich terrestrial families tend to very high endemism percentages: e.g., Cactaceae (75,3%) and Asteraceae (50,9%). Even low endemism percentages of diverse 'terrestrial' families like Poaceae (15,6%), or Arecaceae (13,1%) are still higher than those of epiphytic *Peperomia*, Bromeliaceae, and Araceae.

At genus level this phenomenon is even more marked. The species-rich genera with the highest percentage of endemics (> 65%) are all terrestrial (e.g., *Puya* 73 spp./89% endemics, *Lupinus* 171/85,4%, *Genti-*

anella 82/80,5%, *Calceolaria* 120/73,3%, *Piper* 429/70,4%, *Senecio* 177/67,2%; Brako & Zarucchi 1993).

What can we learn from the comparison of endemism percentages in epiphytic and terrestrial taxa? In the Andes, which assumed their present form as late as the Miocene Epoch, most angiosperm endemics can be considered as neoendemics. They are the result of an „explosion of speciation“ (Gentry 1986). A recent evolution of the species in a taxon is manifest in the number of endemics with restricted distribution³. It

³In our case endemism is always "political endemism", a somewhat problematic concept which requires a few words of explanation. Political endemism refers to an area often (but not always) artificially limited by historical developments. Nevertheless it has for a long time been used for biogeographic analysis (see Major 1988). Using data on political endemism can be quite misleading, especially in the case of large countries. Theoretically, data on endemism density or endemism of vegetational zones should be easier to analyze. However, in the Peruvian case endemism is quite a good indicator for the tendency of plants to inhabit small restricted areas within the country.

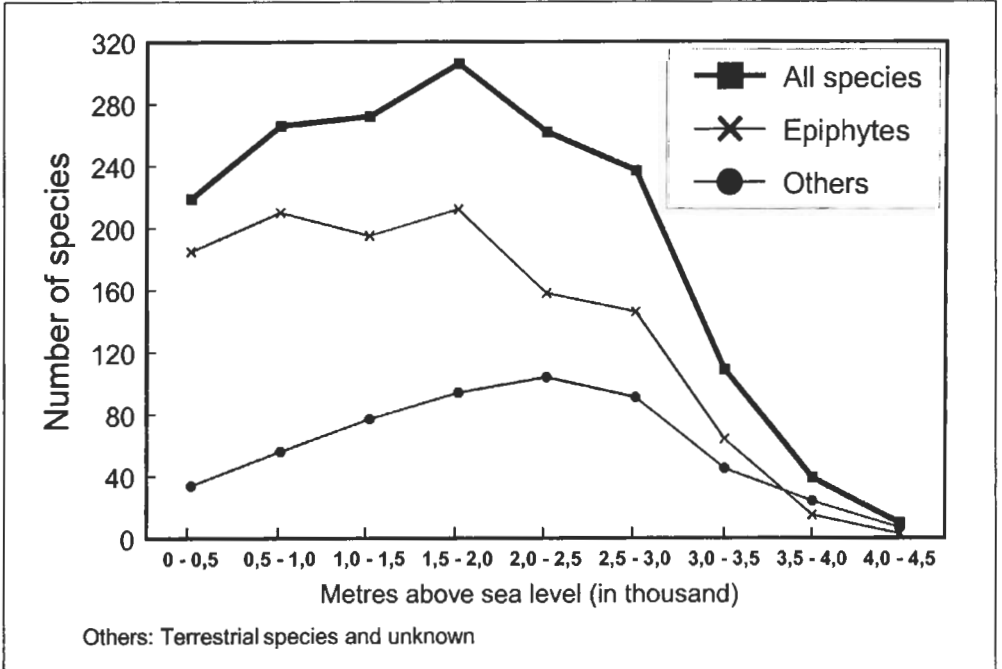


FIG. 4. Orchidaceae. Species numbers of epiphytes and non-epiphytes on the Andean altitudinal gradient (coastal species excluded). "others" are terrestrial and unknown species.

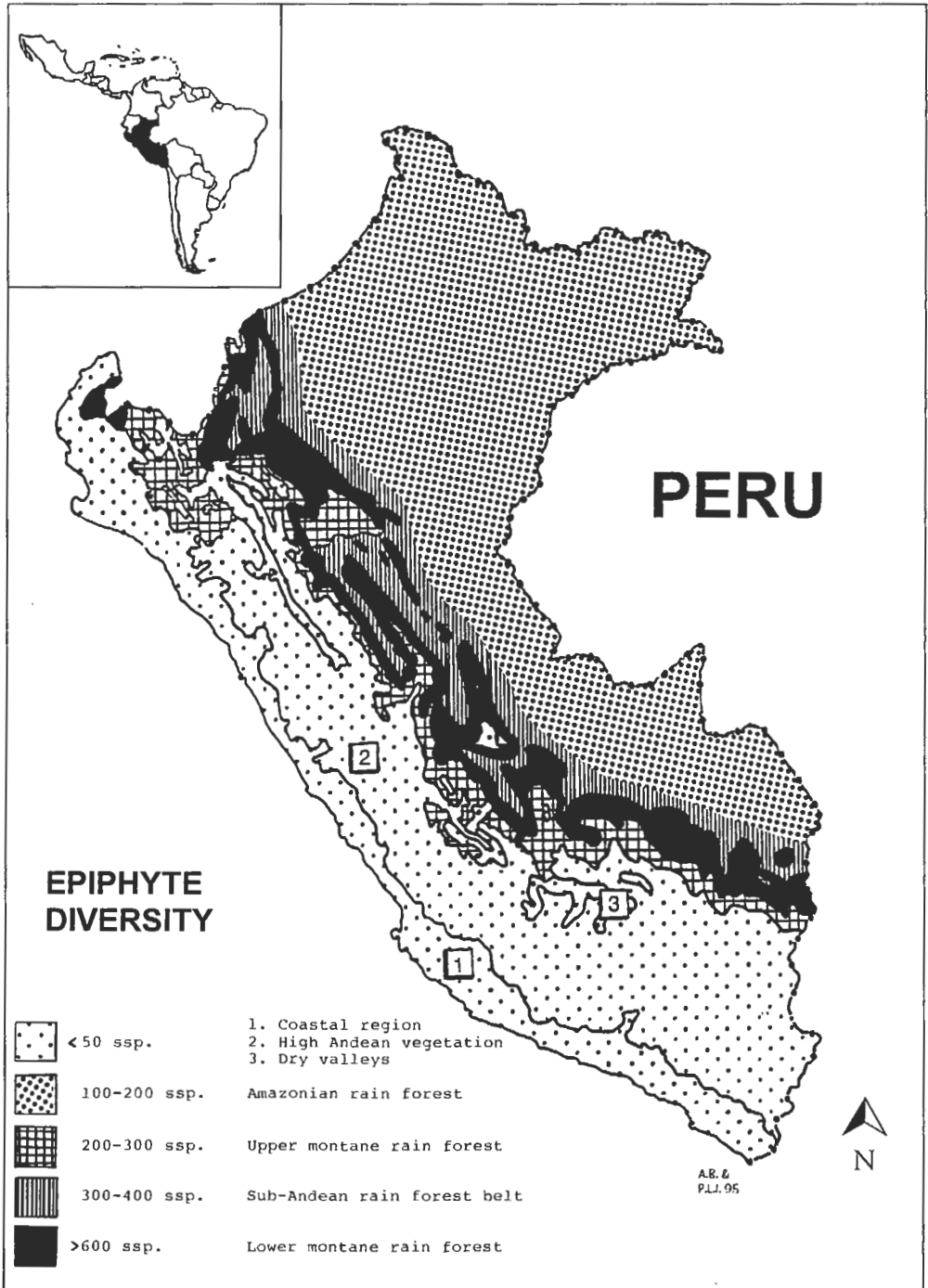


FIG. 5. Map of the absolute numbers of epiphyte species occurring in the main vegetational units of Peru (vegetation zones based on Huëck & Seibert 1981).

follows that the evolutionary activity of sufficiently large taxa may be assessed on the basis of a comparison of endemism percentages.

Gentry (1986) pointed out that local endemism is very frequent in Andean-centered groups with predominantly epiphytic, shrubby, or herbaceous taxa.

Table 3 illustrates that epiphytes are not among those life-forms that tend to abnormal evolutionary activity.

We would like to go one step further: one might expect similar grades of evolutionary activity among the species of a taxon that were subjected to the same biogeographical constraints (e.g., orogeny, climatic changes). But in most of the taxa considered (Table 3), epiphytic species show markedly lower endemism percentages (= "endemicity") than terrestrial species of the same taxon.

"Epiphyte quotients" (Hosokawa 1943, 1950) decrease drastically from small plots to regional floras (Tab 4). This is a logical consequence of the reduced endemism of epiphytic plants. On the basis of the

data in Tab. 4, the species area curves for epiphytes vs. non-epiphytes in neotropical epiphyte-rich vegetational units can be tentatively predicted (Fig. 6). It expresses the effect of reduced games-diversity (sensu Cody 1986) of epiphytes, whereas their locally very prominent alpha-diversity is one of the factors responsible for the "distinctness" (Gentry 1993) of epiphyte-rich rain forests.⁴

One point should be sufficiently clear: we should not infer regional-scale hypotheses from local observations, local and regional processes each cause different components and patterns of diversity (Huston 1994).

⁴Another effect has to be taken into account: epiphytes are concentrated in closed zonal forests, in contrast to terrestrial plants which are more frequent in open, often azonal sites (e.g., rocks, riversides). With increasing plot size, such azonal habitats are added and the number of terrestrial species rises faster than the number of epiphytes. However, even within closed forest formations on a local scale, the 'epiphyte-quotient-decrease effect' can be observed (Ibisch 1996).

TABLE 3. Percentages of endemism within epiphyte-rich taxa.

	Percentage of endemism obligatory holo-epiphytic species (%)	Percentage of endemism terrestrial species	Percentage of endemism facultative epiphytes	Percentage of endemism others (= hemiepiphytes, lianas, unknown life-form)
	(total number of obligatory holo-epiphyte endemics)	(total number of terrestrial endemics)	(total number of facultative epiphyte endemics)	(total number of other endemics)
Orchidaceae	25.9% (310)	21.0% (38)	11.8% (15)	8.6% (8)
<i>Masdevallia</i>	57.0 (57)	75.0% (3)	100 (1)	0% (0)
<i>Oncidium</i>	27.1% (19)	0% (0)	16.7% (1)	0% (0)
<i>Maxillaria</i>	24.6% (28)	25.0% (1)	0% (0)	0% (0)
<i>Epidendrum</i>	21.0% (36)	16.7% (2)	12.5% (2)	0% (0)
<i>Pleurothallis</i>	19.0% (24)	50.0% (2)	33.3% (1)	0% (0)
Bromeliaceae	10.1% (46)	76.6% (213)	13.6% (6)	0% (0)
<i>Tillandsia</i>	16.7% (28)	85.7% (60)	6.9% (2)	0% (0)
Araceae	7.4% (16)	21.4% (18)	17.6% (3)	11.4% (4)
Piperaceae				
<i>Peperomia</i>	4.6% (19)	67.7% (226)	100% (1)	0% (0)

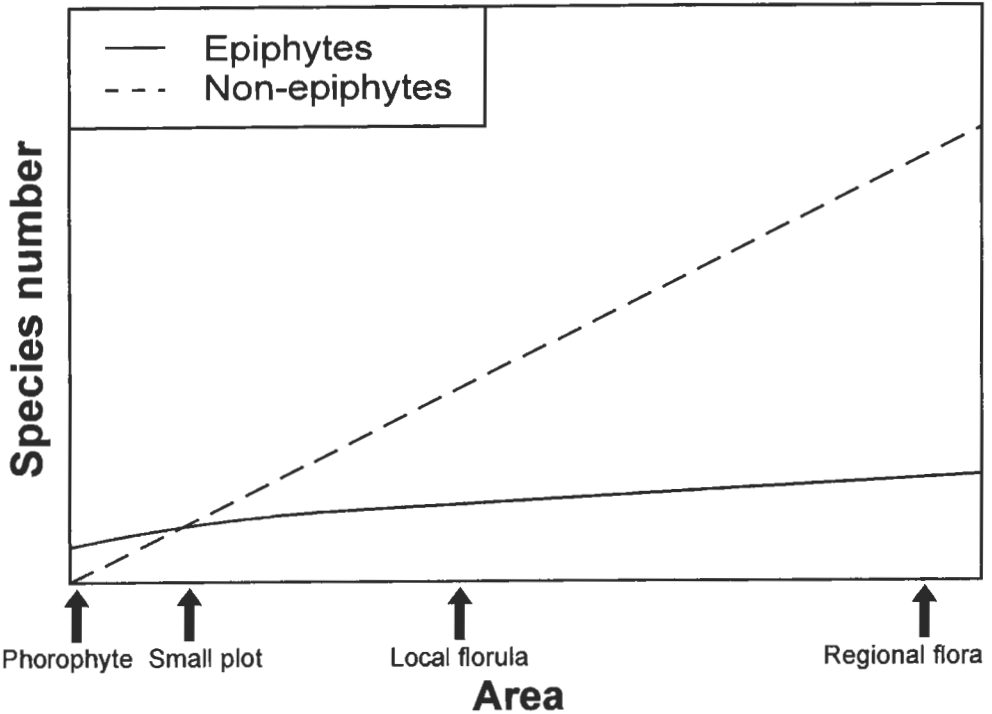


FIG. 6. Tentative scheme of species/area curves of epiphytes and terrestrial plants in epiphyte-rich forests. Epiphytes can be dominant on a local scale but lose relative importance on a large scale.

REGIONAL DIFFERENCES AND POSSIBLE CAUSES OF ENDEMICITY

While epiphyte species-richness decreases with altitude, the endemism percentage of epiphytic species increases with altitude (Fig. 7). With the exception

of the Araceae, all important epiphyte groups show similar endemism gradients.

The general Andean endemism patterns are mainly the result of orography. With increasing altitude the probability of allopatric speciation by fragmentation and isolation of populations grows (see

TABLE 4. Epiphyte-quotients of epiphyte-rich Neotropical rain forest sites in size gradient order (including ferns).

	Site	Area (km ²)	Vascular epiphyte-quotient	Source
Very small plot	Sehuencas, Bolivia	0.0001	46–61%	Ibisch 1996
Very small plot	Sehuencas, Bolivia	0.0002	44–45%	Ibisch 1996
Small plot	Sehuencas, Bolivia	0.0008	38%	Ibisch 1996
Small plot	Rio Palenque, Ecuador	0.001	35%	Gentry & Dodson 1987
Local florula	Rio Palenque, Ecuador	1.7	22%	Gentry & Dodson 1987
Flora	Peru	1,285,216	11–12%	see above

also Gentry 1986, 1982), at least up to the Altiplano where horizontal plant migration is facilitated. Similar patterns are typical for mountainous regions (see Major 1988). It is remarkable that in the Amazonian lowlands endemism percentages are strikingly low.

Most Amazonian epiphytes show a very wide distribution. Endemism in Amazonia is often associated with adaptations to specialized substrates or 'habitat islands' (Gentry 1981, 1986). Epiphytes are independent of soil types, and find in all of Amazonia suitable and similar substrates because most of the tree species do provide a substantially similar and adequate substrate for epiphytes (which was noted by Schimper, 1888). No geographical barriers restrict dispersal of diaspores. Fern distribution patterns in Amazonia support Gentry's ideas (Young & León 1989, Tryon & Conant 1975).

Another hypothesis is that the extreme and stressful conditions of the epiphytic habitat require an enhanced eco-physiological plasticity. This would sustain a greater adaptability with regard to substrate qualities. The eco-physiological plasticity in turn could

have been the precondition for pronounced gene-pool coherence during Pleistocene climatic fluctuations (with their well-known severe impacts on vegetation composition and subsequent range shifts of populations). Terrestrial species may tend to finer niche-tuning, facilitating genetic separation and subsequent speciation. Bush (1994) uses an analogous model to explain speciation in Amazonian shrub and tree taxa. He suggests that the observable centres of endemism during the Quaternary were not areas of maximal stability but of maximal disturbance. Repeated expansion and contraction of the ranges of individual species led to distinct speciation and extinction rates; the eco-physiologically plastic species were spared from speciation.

Many epiphytes probably evolved from pre-adapted forms inhabiting stressful sites (savannas, arid lands) (Lüttge *et al.* 1986, Lüttge 1985). However, the terrestrial relatives of epiphytes often are very demanding, for instance, regarding substrate quality or seasonality. The greater eco-physiological plasticity of epiphytes, among others, is well illustrated by the fact that many of them are easily cultivable house plants.

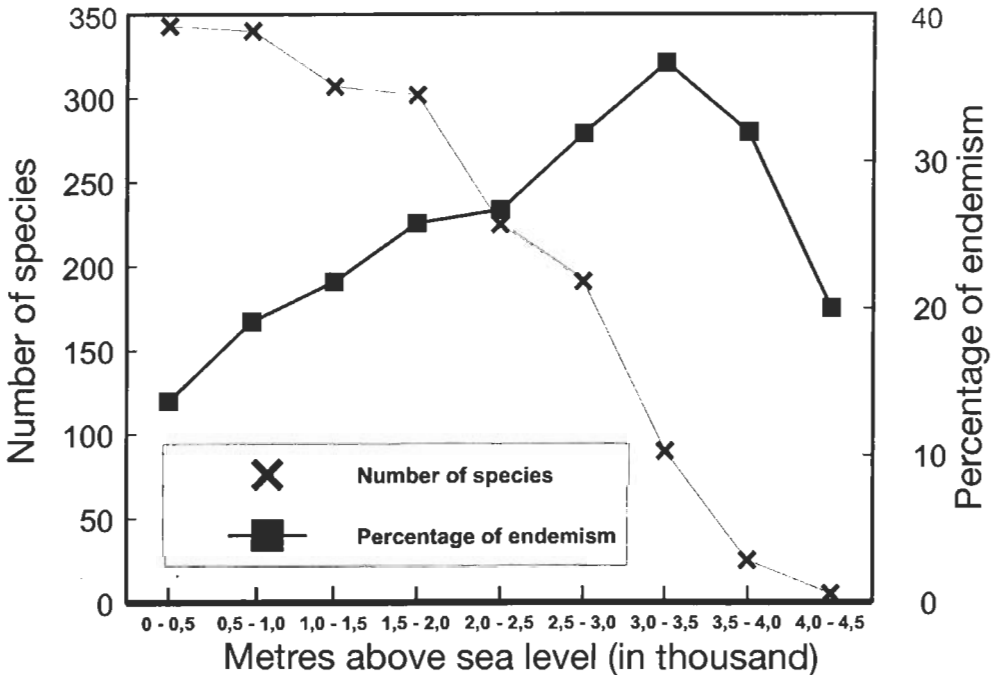


FIG. 7. Percentage endemism and species number of epiphytes on the Andean altitudinal gradient (coastal species excluded).

A PARTIAL OUTLINE OF THE EVOLUTION OF PERUVIAN EPIPHYTES: SUGGESTIONS AND OPEN QUESTIONS

In the following the observable patterns of diversity and biogeography of the four Peruvian angiosperm families with considerable numbers of epiphytic species are analysed separately. The biogeographical data presented above allow some conclusions concerning the evolutionary history of Peruvian epiphytes. Furthermore, the data prompt new questions. Epiphytism has spread from different phylogenetic bases. Separate taxonomic analyses can show how these phylogenetic origins are manifest in distinctive biogeographical patterns.

ORCHIDACEAE

Most Peruvian epiphytes are orchids and the largest taxa of orchids are almost exclusively epiphytic (Table 1). The rate of endemism in these genera can be explained by assuming a recent and possibly continuing evolutionary radiation. Orchidaceae seem to be responding strongly to the young orogeny of the Andes with active speciation (see Gentry 1982). The orchids which are found in the lowland forests are mostly epiphytes (more than 80%), whereas the light conditions in dense forests inhibit geophytes. The percentage of epiphytism within orchids decreases significantly with altitude (about 70% at 1,500-2,000 m, about 60% at 2,000-2,500 m; see Fig. 4). Consequently, terrestrial orchids are more numerous in the Andes, where open sites are more frequent. There, on steep slopes following natural erosion, terrestrial orchids (certain species of *Sobralia*, *Maxillaria*, *Epidendrum*) are typical of early successional stages. Geophytic species (for instance *Cranichis* spp., *Cyclopogon* spp.) grow in montane forests with a rather open canopy stratum.

The radiation of orchids can be attributed to different adaptive features, such as floral biology (Stebbins 1984) or physiological specialization (Benzing 1986). The Orchidaceae are marked by a degree of pollinator specialization which probably has not been attained by any other family of flowering plants. This specialization is a prerequisite for maintaining genetic exchange over distance between scattered individuals. Concentration of large amounts of pollen in pollinia ensures maximum fertilization and seed

development. Orchidaceae have developed dust-like seeds that are dispersed in huge numbers. Taking advantage of substrata enriched by fungi and lichens for germination (Pollard 1973), later incorporating fungi for mycorrhiza (Benzing & Friedman 1981, Jonsson & Nylund 1979), and development of specialized root structures (Benzing *et al.* 1983), all enhance further orchid diversity. On the other hand, extreme pollinator specialization is an adept promoter of speciation, a little genetic change (with effects, e.g., on colour or scent) can lead to ethological isolation. This ethological isolation, on the other hand, makes physiological barriers unnecessary and thus facilitates accidental hybridization of distantly related taxa. The resulting reticulate evolution opens new possibilities for evolution and diversification.

So, it is probable that pollination biology of the Orchidaceae is responsible for the predisposition to considerable evolutionary activity (see also Benzing 1986, 1989). However, the marked relative importance of epiphytism within orchids supports the concept that epiphytic life-style is a key feature contributing to the explosive radiation of this family. Is the dynamic character of the living substrate responsible for the more active speciation of epiphytes? It is possible that the dynamics of the patchy epiphyte habitat, branch growth, changing shade conditions, treefall etc., act as mild disturbances (Connell 1978) which can be 'anticipated' in an evolutionary sense, with resultant maintenance of high speciation levels. Another idea favours a finer niche partitioning by epiphytes (within community microhabitat specialization) (Gentry & Dodson 1987a).

In contrast, it could be assumed that Orchidaceae are an old, primary epiphytic family with most of the terrestrial taxa of recent derivation. This hypothesis is supported by the fact that many terrestrial orchids, which still show a velamen radicum (Schimper 1888, Porembski & Barthlott 1988), probably derived from epiphytic ancestors (the leaf surfaces of many terrestrial orchids also show features of epiphytes; unpubl. data, Barthlott). Therefore, it is reasonable to attribute the species-richness of epiphytes to the tendency of Orchidaceae, which are well equipped for life in the canopy, to intensive speciation. In this case, the epiphytic habit would not be a main cause of orchid diversity. This would correspond to the fact that other families which have evolved epiphytism are marked by their terrestrial species tending much more intensively to speciation.

BROMELIACEAE

In Peru, the relatively young neotropical family Bromeliaceae (Benzing 1994), like the orchids, has developed maximum species diversity in the Andes. However, they differ from Orchidaceae in their low relation of epiphytic vs. terrestrial species. In closed forests terrestrial bromeliads are rare, they are more adapted to open sites, like rocky slopes, for instance. Terrestrial species are more numerous than epiphytes and have higher percentages of neo-endemism. The genera of Pitcairnioideae in all habitats show higher endemism percentages than those of the more derived subfamilies Bromelioideae and Tillandsioideae. The latter two have evolved more efficient dispersal strategies: ornithochorous berries and wind-dispersed seeds respectively. They achieve wide distribution patterns more easily than Pitcairnioideae seeds, which do not attract animal dispersers and are not suitable for long-distance flights.

Surprisingly, even within Tillandsioideae, the terrestrial species of *Tillandsia* show more restricted distributions than the epiphytes (Table 3). In dry valleys the epiphytic bromeliad flora is normally quite predictable regardless of the fact that those isolated interandean valleys are known for having elevated numbers of endemic species (Gentry 1992). Many of them are terrestrial bromeliads.

In montane rain forests several epiphytic species are found which are distributed from the Caribbean Sea in the north to Bolivia in the south (e.g., *Racinaea schumanniana*, *T. complanata*, *T. fendleri*; Smith & Downs 1977) or at least are found in most parts of the eastern Andean slopes. All of the most widely spread Bromeliaceae of the Neotropics which occur in Peru are epiphytes (e.g., *Tillandsia usneoides*, *T. recurvata*, *T. tenuifolia*, *T. streptocarpa*, *T. capillaris*, *Guzmania lingulata*, *G. monostachia*; for distribution see Smith & Downs 1977).

ARACEAE

The diversity of Peruvian Araceae epiphytes is quite low when compared to their diversity, e.g., in Central America (see Croat 1986). In Peru, diversity and endemism percentages decrease with altitude. Only a few tolerant species like the widely distributed *Anthurium scandens* (which is the most widespread aroid of the New World; Croat 1986) reach the high altitude montane rain forests. In Peru, the terrestrial species tend more significantly to endemism (Table 3). Notable differences occur elsewhere, for example in Pana-

ma, where, in the case of Araceae, a maximum of diversity and maximal epiphytism percentages are found (see Croat 1986). Obviously, the biogeographical patterns of epiphytes are not uniform in all regions. What can one infer from this state of affairs in terms of understanding the origins and mechanisms of epiphyte diversity? We propose that a fruitful point of departure would be the comparative analysis of geographical centers of maximal epiphyte species diversity (combined with genera diversity) and comparison of centers of maximal intra-taxonomic epiphytism percentages. A comparative analysis of maximal epiphyte and terrestrial endemism might be a useful idea.

PIPERACEAE

Apart from one terrestrial genus (1 sp.), the large genera of Piperaceae *Peperomia* (381 spp.) and *Piper* (429 spp.) are the most diverse genera of the flora of Peru. The terrestrial species show very high endemism percentages (*Peperomia*: 68%; *Piper*: 70,4%), the epiphytic species of *Peperomia*, contrastingly, a very low one (18,6%). Perhaps the supposed high frequency of autogamy is a cause of the dynamic evolution of Piperaceae which in this case could be a consequence of the lack of sexual recombination. Yet there are no differences in reproduction biology and growth forms between terrestrial and epiphytic species of *Peperomia* (the latter with low endemism percentages; Table 3). If this is the case, why then are the terrestrials surprisingly more diverse and tend more markedly to restricted distribution? A possible answer could be the long-distance efficiency of epiornithochorous dispersal of the sticky fruits, which perhaps is facilitated in the epiphytic species (canopy visiting birds). The majority of the terrestrial *Peperomia* species are found at understory rain forest sites which are not typically visited by birds.

FINAL REMARKS

We have to acknowledge that some striking phenomena of angiosperm epiphyte diversity are phenomena of orchid diversity (compare Schimper 1888, Benzing 1987) and that the epiphytic habit does not automatically guarantee high diversity and high rates of speciation. With the exception of orchids, epiphytism in all other taxa which include epiphytes seems to signify a relatively lower evolutionary activity. The epiphytes are not the 'canopy beetles' of the plants, the arboricole animal counterparts of the epiphytes are one of the most important features of biodiversity (Erwin 1988).

However, the investigation of epiphytes promises to be an interesting model of biodiversity:

In favourable sites they show a very high alpha-diversity. As "interstitial species" (Huston 1994) they exhibit a fine niche-partitioning within a living and dynamic habitat and reach enormous percentages of local florulas.

Their regional or landscape diversity is relatively low and their biogeographical patterns contrast to those of terrestrial species of the same taxa and to those of all other plant habits. This could be a consequence of their eco-physiological plasticity.

We suggest that the new methodological concept of a comparison of the diversity and biogeography of epiphytes with related terrestrial species of the same region allows combination of three of the most important perspectives of phytodiversity research: taxonomic analysis, floristic analysis and 'life-form analysis'.

Despite the value of biodiversity models and theoretical concepts, it is evident that an elaboration and analysis of the basic floristic and biogeographical data should be the first and most important step towards the understanding of biodiversity. The "Catalogue of flowering plants and gymnosperms of Peru" has proven an extremely useful tool for diversity research.

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