PATTERNS OF NEOTROPICAL EPIPHYTE DIVERSITY

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ABSTRACT. The authors have made extensive investigations on vascular epiphytes in the last 20 years, particularly on epiphytic vegetation in four tropical montane forest sites. These are Sehuencas (Bolivia); Otonga and Río Guajalito (Ecuador); and La Carbonera and the Amazonian lowland forest crane plot at Río Surumoni (Venezuela). Based on these studies, they analyze the systematic compositions and vertical and horizontal distribution patterns of epiphytes at the sites. Orchids are the most species-rich of all local epiphyte vegetation. At lowland sites, Araceae are particularly diverse. Vertical zonation of epiphytes in the canopy is a result of different ecophysiological traits. Despite marked preference for certain strata in some taxa, overlap is considerable. The differences in epiphyte diversities of montane and lowland forests can be explained by different distribution patterns. For example, in montane forests with high alpha diversity of epiphytes, species turnover between sites separated by a small geographical distance is considerable. In contrast, alpha diversity of epiphytes in the Amazonian lowlands is low, but the number of epiphyte species increases gradually with area. Although lowland forests cover vast areas, the overall epiphyte species richness is no higher than that of the wet Andean montane forests, which occupy a far smaller land surface.

A tentative explanation of these differences in distribution patterns assumes different evolutionary scenarios. In the Andes, where geographical separation frequently has isolated gene pools, ecologically similar species occupy different areas. In the Amazonian lowlands, where considerable gene flow results from the mixing of populations by dispersal of diaspores and effective pollinators, fewer species have evolved. Dispersal and pollination tend to be highly effective in epiphytes because of their adaptation to the epiphytic habitat. The striking differences in diversity patterns have resulted from their evolution, which may have followed a specific path compared to terrestrial plants.

Key words: Neotropics, epiphyte, diversity, Bolivia, Ecuador, Venezuela

INTRODUCTION

When Christopher Columbus in 1492 reached Long Island in the Bahamas, a strange vegetation caught his attention, and he wrote: "I have never seen a more beautiful place. The . . . flowering trees . . . were covered with blossoms and fruit of the most diverse kinds . . . on one and the same trunk grew different twigs . . . one had the leaves of sugar cane, whereas another looked like the branch of a mastic tree . . . so that on one and the same tree five or six completely different species occurred" (translated from Arranz 1985). What Columbus describes here is an assemblage of different species of epiphytes on their host tree, a phorophyte. For Columbus, as for many naturalists who were to come after him, epiphytes represented the epitome of the luxuriance of tropical vegetation. The almost exclusive phenomenon of vascular epiphytism has attracted the attention of naturalists ever since. Darwin (1989) and Martius (1842) were fascinated by the epiphytes of the Atlantic rain forest of Brazil. The term "epiphyte" was introduced by Mirbel (1815, cited after Wagenitz 1996). At the end of the 19th century, Schimper first treated the epiphytes of the West Indies (1884) and later those of the neotropics and the whole world (1888). His extensive treatises already questioned the geographical distribution of epiphytes and regularities of their occurrences or "patterns" in other words.

Later classical works were less ambitious and dealt with relatively small geographic areas, such as Went (1940) in Java and Johansson (1974) in West Africa.

Since the 1980s, publications on epiphytes have increased in number and now include comprehensive works on epiphyte biology and ecology (Lüttge 1989, Benzing 1990). Gentry and Dodson's (1987) comprehensive large-scale approach to epiphyte diversity and its patterns unfortunately has not been repeated or extended. This overview of the authors' studies during the last six years may help in dealing with the unresolved question of the distribution of epiphyte diversity.

STUDY SITES, METHODS, AND SPECIES

For the last 20 years, the authors have investigated the ecology and systematics of epiphytes (in particular, orchids and cacti). Study sites have included Ecuador, Brazil, Mexico, Cote d'Ivoire, Rwanda, and Congo. The results of these studies have contributed to this paper,

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TABLE 1. Neotropical study sites of the Botanical Institute, Bonn, Germany, with basic site characteristics, number of epiphyte species (hemiepiphytes included), and epiphyte quotients. Note: * = number of epiphyte species on the crane plot plus number of species on surrounding plots.

Study site	Elevation (m above sea level)	Precipitation (mm/year)	No. of epiphyte species	Epiphyte quotient (area)
Sehuencas, Bolivia	2100–2300	5000	230	37% (0.1 ha)
Otonga, Ecuador	1700–2200	2500	196	—
Río Guajalito, Ecuador	1800–2200	2700	166	28% (400 ha)
Carbonera, Venezuela	2100–2300	1500	191	45% (360 ha)
Surumoni, Venezuela	100	2800	112 (53 + 59)*	—

which concentrates, however, on the largely unpublished data from work at four neotropical study sites. These data are the basis for more general ideas on epiphyte distribution that follow in the discussion.

Sehuencas Valley (Bolivia). A series of study plots was established in the Sehuencas Valley, Bolivia (65°16'W, 17°30'S). TABLE 1 shows elevation and precipitation (for more details, see Ibisch 1996). Five plots with a total surface area of 800 m² were sampled, and all vascular plants determined (347 species of 77 families). Of these, 204 species were epiphytes.

Río Guajalito (Ecuador). The forest reserve of Río Guajalito is on the western slopes of the Andes in the Ecuadorian province of Pichincha (78°49'W, 0°14'S). See TABLE 1 for elevations and climate data. Most of the botanical inventory of the area was made by J. Jaramillo (unpubl. data). The epiphyte vegetation has been sampled and its distribution on 22 branches of the upper canopy documented (Rauer 1995, Rudolph 1995, Rudolph et al. 1998). The forest structure was analyzed by Mutke (1996). The tentative species inventory shows a total of 597 plant species, including 122 holoepiphytes (no terrestrial contact) and 44 hemiepiphytes (terrestrial contact at some time during life cycle).

La Carbonera (Venezuela). On the northeastern slopes of the Tambor massif in the Venezuelan Andes (8°37'N, 71°21'W) is a cloud forest reserve of 368 ha at 2200–2700 m (Hetsch & Hoheisel 1976). Annual precipitation is only 1500 mm/year, but a daily cloud cover rising from Lake Maracaibo creates a high relative humidity (annual mean > 90%) and a relatively low global radiation of 296 cal/cm²/day (Hoheisel 1976). The forest is dominated by *Decussocarpus rospigliosii* (Pilg.) de Laub. (Podocarpaceae) trees (up to 47 m), bearing thick mats of epiphytes. A total of 57 trees of different sizes were sampled on 800 m². More than 5000 individuals of 191 holoepiphyte and hemiepiphyte species were identified (Engwald 1999).

Río Surumoni Crane Plot (Venezuela). The crane plot (detailed description in Morawetz 1998) is near the Surumoni River where it enters the Orinoco (3°10'N, 65°40'W) at ca. 100 m elevation. The study plot is surrounded by lowland forest that has remained largely untouched by human influence. Average annual temperature is 26.5°C, and rainfall normally does not exceed 2700 mm/year. The dry season is December to March. Field studies were carried out in a 1.5 ha rectangular plot, containing 1061 marked trees with dbh > 10 cm. A total of 80 individuals of *Goupia glabra* Aubl. (Celastraceae) form 30% of the crown coverage. Other abundant tree species are *Dialium guianense* (Aubl.) Sandw. (Caesalpiniaceae) and *Ruizterania trichanthera* (Spruce ex Warm.) Marcano-Berti (Vochysiaceae). Major phorophytes (host trees) of epiphytes are *Lecythis* species (Lecythidaceae) and *Guatteria schomburgkiana* Mart. (Annonaceae). Mean tree height is ca. 25 m; only one tree reaches 31 m. Vascular epiphytes were sampled using the mobile swing crane (40 m high, on rails of 120 m length). A total of 1085 trees > 5 cm dbh (1061 of them marked) were examined. During the first census, September 1996–April 1997, the authors recorded 778 individuals of 53 epiphyte species. Orchids were the most species-rich (19 species). The 14 species of Araceae in the plot represented the most individuals (337). In contrast, 12 orchid species had less than three individuals each. Half of all epiphytic plants grew in ant gardens.

RESULTS AND DISCUSSION

Systematic Composition

Epiphytism is a life habit that requires specialized vegetative and reproductive features. These include zoophilous pollination because of the spatial distance of individuals (Ackerman 1986) and water storage (succulence) or water acquirement (tanks and trichome scales in bromeliads; velamina in orchids, Lüttge 1985). Not surprisingly, only 19% of all vascular plant fam-

TABLE 2. Elevation, precipitation, total epiphyte species/families numbers in plot, and percentage of epiphyte species numbers in selected plant groups for different neotropical study areas.

Study site (source)	Elevation above sea level in m	Precip- itation mm/year	No. epiphyte species/ families in plot	Or- chid- aceae	Pteri- dophy- tes	Ara- ceae	Brome- liaceae	Piper- aceae	Other epi- phytes
La Selva (McDade 1994)	—	3962	380/>15	24	17	20	6	4	29
Monteverde 1 (Ingram et al. Undated)	1400	2000	332/36	42	17	4	7	4	26
Sehuencas (Ibisch 1996)	2100	3500	204/17	57	21	1	8	8	5
Otonga (Nowicki 1998)	2000	2600	196/21	25	22	18	5	4	26
Carbonera (Engwald 1999)	2200	1500	191/20	50	30	3	6	6	5
Guajalito (Rauer 1995)	2000	2700	166/18	42	21	15	8	5	9
Cajanuma (Bøgh 1992)	2900	4000	138/33	35	22	2	4	2	35
La Montaña (Kelly 1994)	2600	—	116/12	54	26	4	10	3	13
Monteverde 2 (Nadkarni 1985)	1400	2000	109/26	22	27	6	5	7	33
Guatemala (Catling 1989)	2225	—	68/12	43	29	3	6	6	13
Hog House Hill, Jamaica (Kelly 1985)	465	3800	55/?	35	44	2	9	2	7
Surumoni (Engwald 1999)	100	2700	53/10	37	14	18	4	2	25
Puerto Rico (Smith 1970)	480	2920	42/14	24	55	0	10	2	9
Veracruz (Hietz 1995)	2000	1850	39/12	26	56	0	5	5	8

ilies (84) have epiphytic plants (Kress 1986). At any given site, the number of families represented among epiphytes is much smaller than the number of other plant families present. The largest inventories in the neotropics show < 40 families of epiphytes; but even a tiny plot (175 m²) like Cajanuma in Ecuador (Bøgh 1992) has representatives of 33 families of vascular epiphytes. This is extreme epiphyte diversity at a high taxonomic level.

TABLE 2 shows the systematic composition of vascular epiphytes at different neotropical sites. The data raise the question of whether there is a "systematic pattern" in epiphytic vegetation. A striking feature is the dominance of orchids. In most cases, this is the best-represented family, reaching 57% of all species at the Sehuencas site. The obvious explanation is the large proportion of orchid species in the epiphytes in general (60% according to Kress 1986). In small samples with relatively few species, the relative importance of orchids is much lower, such as in Veracruz, Puerto Rico, and Jamaica. A possible explanation is that orchids generally have a low density; they are rarer; and the range of their species richness is less likely to be covered in a small sample. This is evident in Monteverde. When only part of the area was sampled, ferns had a higher relative importance (Nadkarni 1985); but when the whole area was well-covered (Ingram et al. undated), orchid species outnumbered other families by far. Ferns are particularly important in small samples, because they are more evenly distributed within a given area (Hietz & Hietz-Seifert 1995b).

Araceae are more species-rich in lowland forest (e.g., La Selva and Surumoni) and particularly rare in cloud forests at higher elevations (e.g., Monteverde). Even on a larger scale, the rapid decrease of aroid species at higher elevations is obvious (Ibisch et al. 1996). Epiphytic Araceae also tend to be more species-rich toward Central America. In Panama, 16% of all epiphytes are Araceae; whereas Peru has only 5% Araceae among its epiphytes (Boegner 1999). Seemingly "irregular" phenomena in systematic patterns often can be explained by similar regularities. For example, the relatively larger species richness of the Ericaceae at higher elevations is responsible for the extraordinary "others" bar at Otonga, which represents 8% of all species at the site.

Vertical Distribution Patterns

Intricately connected to the systematic pattern is the pattern of vertical stratification. A phorophyte embedded in the forest canopy represents a vertically arranged habitat, where gradients determine the growing conditions of epiphytes. For example, light decreases and humidity increases from canopy to forest floor (Parker 1995). Substrate covers on branches are usually thinner on younger branches near the upper strata of the forest.

The availability of substrate determines the abundance of epiphytes in different height zones. The Johansson scheme divides the phorophyte into five zones (Johansson 1974). Epiphytes are usually most diverse in Zones 3 and 4, where the phorophyte structure provides space and substrate. FIGURE 1 shows this for the epiphytes of Sehuencas. Relative diversity changes for different families, with orchids rel-
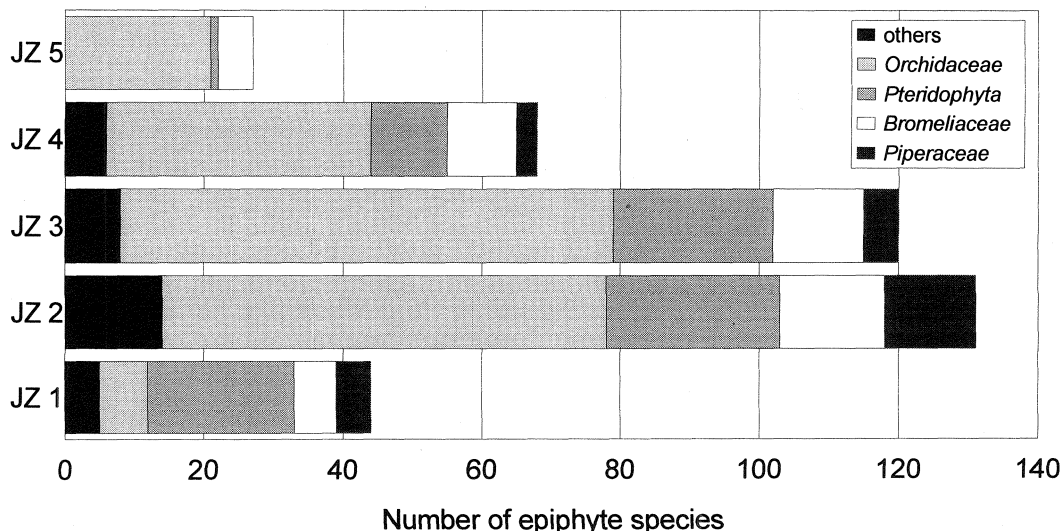
FIGURE 1. Epiphyte diversity of different phorophyte zones sensu Johansson at Sehuencas, Bolivia (after Ibisch 1996). JZ1 to JZ5 = Johansson Zone 1 to Johansson Zone 5.
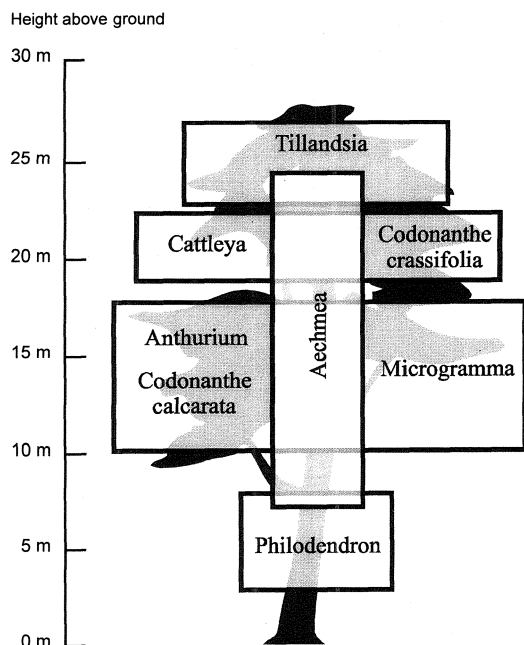

FIGURE 2. General scheme of vertical epiphyte distribution in the Surumoni plot. Blocks represent taxa with statistically distinct occurrences in height. Block width indicates mean height of enclosed taxa within standard deviation.

atively more diverse in Zones 4 and 5 and pteridophytes more diverse in Zone 1.

A similar vertical stratification, both in species numbers and family composition, was observed by ter Steege and Cornelissen (1989) in Guyana. In West Africa, Schnell (1952) distinguished between different assemblages of epiphytes in different strata of the forest (orchids and ferns are prominent examples of the top and bottom strata). Twig-orchids are even specialized on the thin branches in the outer canopy (Chase 1987).

Most species occur in more than one zone, with the exception of some ferns with inefficient water balance control, such as the Hymenophyllacae. Hietz & Hietz-Seifert (1995c) found Hymenophyllacae restricted to the bases of phorophyte stems. Otherwise, some "niche overlap" is obvious, although microhabitat preferences resulting from ecophysiological characters clearly exist.

At Surumoni, the authors were able to distinguish layers of epiphyte settlement on phorophytes by average height above ground (FIGURE 2). Each block of species could be significantly distinguished in a statistical analysis of variance. An exception was the genus *Aechmea* that occurs throughout the middle canopy. Height preferences correspond to physiological and mechanical adaptations (e.g., Crassulean Acid Metabolism in *Tillandsia*). Such preferences likely evolved from pre-adaptations typical of the families or genera, as shown for epiphytic cacti and ferns by Andrade and Nobel (1997).

TABLE 3.   Mean species numbers in five plots (2 plots of 0.01 ha, 3 of 0.02 ha) at Sehuencas, Bolivia: mean epiphyte species number; mean relative diversities = mean percentages of each life habit in the plots (Ibisch et al. 1996).

Plants	Mean epiphyte species no.	Mean relative diversity
Epiphytes	52.0	45.0
Shrubs	19.8	18.0
Herbs	18.0	16.4
Trees	15.6	15.8
Climbers	7.8	7.2

Reproductive adaptations also are reflected in the vertical stratification of epiphyte vegetation. Often epiphyte species common in the upper canopy have wind-dispersed seeds, whereas those in the lower canopy are zoochorous (Kelly 1985).

Horizontal Distribution and Alpha-Diversity

A total of 66 epiphyte species were found on a single *Decussocarpus rospigliosii* tree in the Carbonera Forest in Venezuela. Such concentrations of epiphytes on single trees have long attracted the attention of naturalists (Longman 1917, Dunsterville 1961). The sometimes extreme alpha-diversity (in the sense of "point diversity," Whittaker 1977) of the epiphytic life habit is striking, when compared to terrestrial plants. On five different plots of 0.01–0.02 ha at Sehuencas (Bolivia), epiphytes were in every case more species-rich than trees, shrubs, climb-

ers, and herbs (Ibisch 1996). TABLE 3 shows mean species numbers of life forms, with epiphyte species numbers dominant in the small plots.

At Otonga, two undergrowth plots of 0.01 ha each had 180 plant species of up to 5 cm dbh. On ten neighboring host trees, samples of tree trunks and branches yielded 159 epiphyte species (Nowicki 1998).

Species-Area Curves and Epiphyte Quotients

The average relative diversity of vascular epiphytes, i.e., their percentage contribution to the species numbers of each plot, is 45%. This "epiphyte quotient" (Hosokawa 1950) is lower for the total area sampled because the increase in epiphytic species with area is lower than that of terrestrial plant species (FIGURE 3).

Terrestrial plant species numbers tend to rise steadily with the increase of area, but epiphyte species numbers seem to reach a level of saturation relatively early. In other words, beta-diversity of epiphytes is lower than that of terrestrial plants. This explains why the high contribution of epiphytes to small-scale phytodiversity boils down to 10% epiphytism on a global scale (Kress 1986). Thus, plot size becomes a decisive factor when comparing different epiphyte quotients. Very high quotients in many cases are a consequence of a small study area. For example, Hosokawa (1954) found a 35% epiphyte quotient on a 1.8 ha plot on the Micronesian island of Kusaie. For the whole island, the epiphyte quotient was just 13.2% (Hosokawa 1943). An-
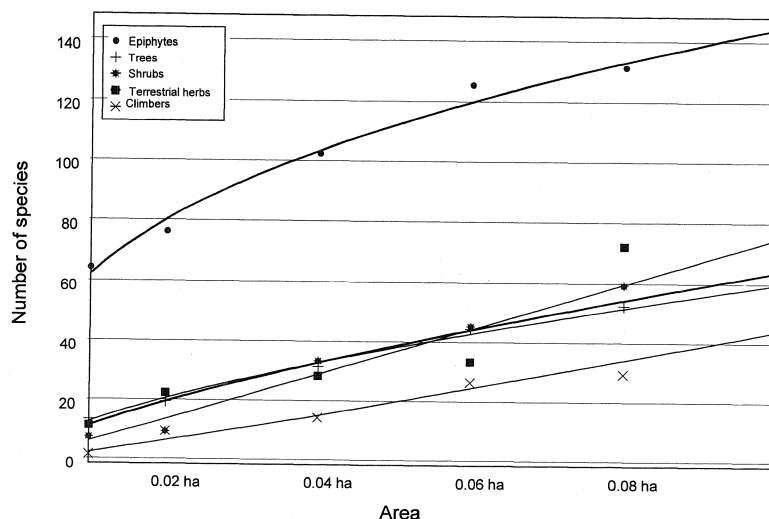

FIGURE 3.   Species-area curves for epiphytes, trees, shrubs, terrestrial herbs, and climbers at Sehuencas, Bolivia (after Ibisch 1996).
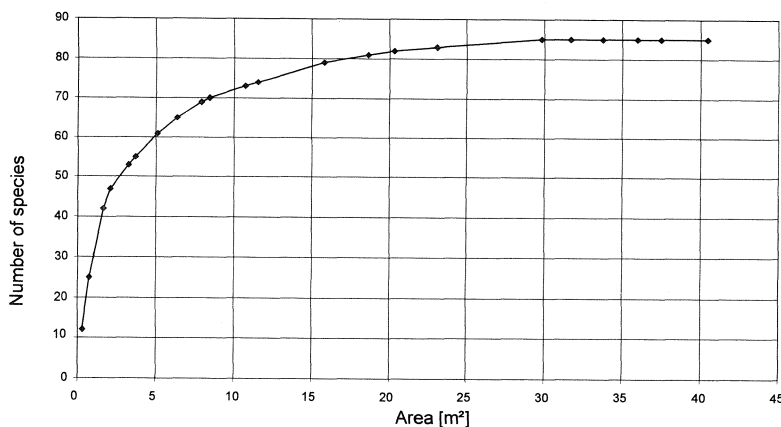
FIGURE 4. Species numbers of vascular epiphytes and branch area at Río Guajalito Reserve, Ecuador, (after Rauer 1995).

other example is the epiphyte quotient of Río Palenque (Ecuador). On 0.1 ha, it is 35%; but on 170 ha, the whole area, it is only 23% (Gentry & Dodson 1987). Interestingly, Gentry and Dodson neglected the degree of scale-dependent epiphytism. Thus, their conclusions were oversimplified concerning the relative importance of epiphytism, when they stated that "the general tendency is for epiphytes to be better represented in intermediate elevation cloud forests."

In Peru, 816 epiphyte species grow at 0–1000 m, but only 600 species at 1000–2000 m and 446 species at 2000–3000 m. The number of epiphyte species decreases continuously from the lowland and Andean foothill zone (0–500 m) to the Andean plateaus (4000–4500 m) (Ibisch et al. 1996). The same is true for Panama; and in the area between Panama and Peru, neotropical epiphytes are not likely to occur in a different pattern.

The obvious gap between small-scale (alpha-diversity) and large-scale (gamma-diversity) relative species richness is explained by different species-turnover rates within similar habitat, in other words, beta-diversity.

Beta-Diversity of Epiphytes

In comparing montane forest study plots with a lowland forest plot at Surumoni (TABLE 1), the authors found species numbers much higher in the montane forests of Otonga and Río Guajalito. Species-area curves based on increasing branch area of different phorophyte samples rise steeply and then level off (FIGURE 4).

Little information on species number-area relationships can be found in the literature. Kelly et al. (1994) felt that by sampling 12 trees they had covered ca. 90% of the epiphyte flora in a

1.5 ha montane forest. Hietz & Hietz-Seifert (1995c) found a considerable leveling of the species-area curve after just 300 m² of sampling area. In a subtropical forest of Queensland, Australia, Shaw and Bergstrom (1997) used a relatively rapid saturation of species numbers (on a low level) to illustrate the efficiency of their rapid assessment technique of epiphyte diversity.

Hietz and Hietz-Seifert (1995a) sampled only six plots with a total of 0.5 ha area over an altitudinal gradient of 1500 m in Mexico. They collected, however, 50% of all the angiosperm species of the region (4000 km²). This demonstrates the concentrated species diversity of epiphytes in montane forests.

Compared to montane forest sites, the total species number is much lower at Surumoni, and the species-area curve rises gradually. By including additional plots in the surroundings, the authors could add 59 species to the original 53 species of the plot. Alpha-diversity is low. Other data indicate that the central Amazonian epiphyte flora is relatively poor (Prance 1990). Species turnover, however, between plots in the surroundings of the Surumoni crane plot (covering a total area of ca. 400 ha) is high.

For Amazonian Ecuador up to 600 m, Renner et al. (1990) listed 116 epiphyte species (excluding orchids, whose life-forms are not indicated). If the percentage of epiphytic species within the orchids were calculated to be 80% (following Gentry & Dodson 1987), then the total number of epiphyte species in this part of Amazonia would be 420.

Peru has a similar epiphyte number (397) up to 500 m (Ibisch et al. 1996). The authors' database did not allow any further differentiation of altitudinal belts, but a comparison of "purely Amazonian" political departments with those
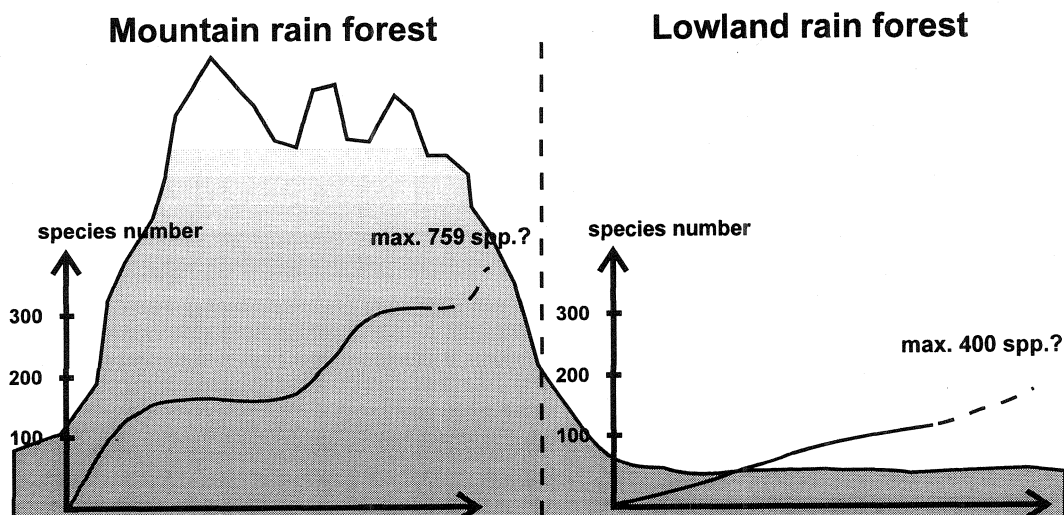
FIGURE 5. Hypothetical species-area curves for vascular epiphytes in montane rain forest and lowland forest. Maximum species numbers refer to figures from Peru (Ibisch et al. 1996).

which have "Andean" area showed the former to be much poorer in epiphyte species. Thus, most epiphytic species are likely to be concentrated in the sub-Andean belt (400–600 m). Dodson (pers. comm.) found ca.100 species of orchids with little site-to-site diversity along the Andes in Ecuador and Peru at Lago Agrio, Coca, Primavera, Cuyabeno, Sancudo, and Imuya. At 300–600 m, he found > 300 species that had little homogeneity with lower elevations.

The species numbers on small sample plots in Amazonia thus is small but tends to rise gradually with increasing area. Overall epiphyte diversity in the Amazonian lowlands is considerably less than at altitudes from the sub-Andean belt and above. On the other hand, epiphyte species richness, even in small plots in the Andean montane forests, is high (and was the starting point of the above Gentry and Dodson quote). Species-area curves for these forests rise steeply but level off on the scale of a few ha. Evidently, much of the epiphyte diversity is concentrated in montane forests. The question remains as to how these observations fit together.

A comparison of species lists for Río Guajalito and Otonga indicates that the two sites had only 35% of all epiphyte species in common, although just 30 km apart. This high figure is in part attributable to both epiphyte floras having not been sampled exhaustively. Yet, the difference is too marked to be a result of methodological imperfections. The authors suggest that

this striking species turnover indicates a pattern of epiphyte diversity perhaps typical of the epiphyte-rich Andean mountains. FIGURE 5 shows a tentative model of epiphyte species-area curves, comparing Amazonian lowland and montane forests. In comparisons of montane rain forest sites, species numbers may rise in steps, reaching ca. 600 species at 1000–2000 m and ca. 450 species at 2000–3000 m.

In contrast, the number of epiphyte species on lowland sites is much lower. In Peru, the "selva" (i.e., Amazonian forest), which covers 58% of the country (Mikus 1988), has only 30% of all epiphyte species. The concentration of epiphytes in montane forests is even more impressive, considering that this habitat represents only a small percentage of land area; 42% of Peru's surface area includes dry coastal desert, the altiplano, and the high Andes. The spatial distribution of epiphytes in the lowland forests, however, follows a completely different pattern, with epiphytes being rare and widely distributed. Species numbers rise continuously with area up to a large scale, although habitat differences along the vast stretches of Amazonian forest are small.

The explanation may be different evolutionary scenarios in montane forests than in the Amazonian lowland forest. The evolution of different species results from genetic variation and gene flow, on the one hand, and availability of ecological niches on the other. The ecological

niches that phorophytes offer do not vary much among habitats. Once the decisive abiotic preconditions (substrate, humidity, and no frost) are given, epiphytic vegetation can develop on host trees. Because of its dynamic character, this habitat is rarely saturated. Consequently, competition is of minor importance, and niche overlap is considerable (Hietz & Hietz-Seifert 1995c). The number of epiphyte species is usually positively correlated with epiphyte abundance (except in some dry valleys of the Andes, where a few *Tillandsia* species can be locally abundant). As a rule, where epiphyte abundance is low, species number is low. Over large geographical distances, however, microhabitat variability—even in "poor" conditions like those of the Amazonian lowland forest—adds up; and the overall species pool reaches a modest maximum.

The adaptations of vascular epiphytes to wide dispersal (mainly dust-like seeds and bird-dispersed seeds) and an effective gene flow over large distances (intermixing of populations by dispersal and efficient pollinators) link sub-populations and prevent genetic isolation. This could explain the relatively homogenous epiphyte vegetation in the lowlands.

For montane forests, the scenarios are completely different. The Andean orography provides valleys isolated by mountain chains overcome only by crossing various climatic zones. Such barriers are particularly impenetrable to epiphytes, which depend on favorable water regimes and temperature ranges. Under these circumstances, small populations of evolutionary active taxa, such as orchids, develop into separate species, which could explain their astonishing diversity. The result—ecologically similar but taxonomically distinguishable species—are a clear indication of evolutionary processes (Huston 1994).

CONCLUSION

The diversity patterns of epiphytes can be traced to four factors: water, phorophyte structure, gene flow barriers, and geodiversity.

Water availability increases alpha-diversity, since a reliable water supply overcomes the main physiological constraint of epiphytic existence—lack of water in the canopy. Humid habitats are generally richer in epiphytes. A second factor influencing alpha-diversity is the structural richness of phorophytes. Old, structurally diverse trees with many different micro-habitats host many different epiphyte species. Gene flow barriers in the form of mountain ranges increase beta-diversity by favoring the evolution of sub-populations into distinct species, if the reproductive biology of the epiphytes allows their survival in small populations. Lastly, geodiversity increases gamma-diversity of epiphytes but—in a big difference compared to terrestrial plants—only slightly so, because the basic parameters of the epiphytic existence are similar even in different vegetational zones.

A better understanding of these patterns will increase a basic scientific knowledge of the epiphytes and will be useful in the conservation and management of biodiversity.

ACKNOWLEDGMENTS

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