Journal of Biogeography (*J. Biogeogr.*) (2004) **31**, 1477–1487

ORIGINAL ARTICLE

Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests

W. Küper*, H. Kreft, J. Nieder, N. Köster and W. Barthlott

Nees-Institute for the Biodiversity of Plants, University of Bonn, Germany

*Correspondence: Wolfgang Küper, Nees-Institute for the Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany.
E-mail: wk@uni-bonn.de

ABSTRACT

Aim Epiphytes contribute up to 30% to the number of vascular plant species in certain global biodiversity hotspots, e.g. the Ecuadorian Andes. However, their large scale diversity patterns are still discussed on the base of results from a few, local epiphyte inventories. Consequently, explanatory models on epiphyte diversity concentrate on the impact of local climate on small scale epiphyte species richness. Our aim was to analyse large scale elevational patterns of epiphyte diversity integrating data from different geographic scales.

Location Tropical America, with special emphasis on the Ecuadorian Andes.

Methods Our study is based on two data sources. First, we analysed the elevational patterns of epiphyte diversity based on the Catalogue of the Vascular Plants of Ecuador and the Libro Rojo de las Plantas Endèmicas del Ecuador. Secondly, the floristic turnover between the epiphyte inventories of seven montane and four lowland study sites in the Neotropics was analysed.

Results The floristic turnover between Neotropical montane epiphyte floras is higher than the one between lowland epiphyte floras. Montane study sites located only a few kilometres apart from each other show considerable differences in their epiphyte species inventories. Irrespectively of their similar dispersal mode, the floristic turnover is much higher for orchids than for Pteridophyta. The Orchidaceae are the species richest group in all of the examined 11 Neotropical epiphyte floras. At the larger scale of the Ecuadorian Flora, *c.* 50% of the species in the elevational zone with maximum epiphyte diversity (between 1000 and 1500 m) are orchids. Elevational patterns of epiphyte diversity strongly reflect patterns of Orchidaceae.

Main conclusions Our results support the observation of a 'mid-elevation bulge' of epiphyte diversity by Gentry and Dodson. It has been frequently shown that the high humidity in mid-elevations is suitable to maintan a high epiphyte species richness. Our findings show that in addition, large scale epiphyte diversity in montane rain forest is increased by the high floristic turnover at local and regional scale. Based on the importance of Orchidaceae for epiphyte diversity, we discuss that speciation processes corresponding to the highly diverse environment are a driving force for endemism, floristic heterogeneity and consequently for large scale epiphyte species richness in montane forests.

Keywords

Neotropics, Ecuador, cloud forest, Andes, epiphyte, diversity, hot spots, Orchidaceae, pteridophytes, floristic turnover.

RESUMEN

Objetivo Epífitas contribuyen hasta un 30% al número de especies de plantas vasculares en ciertos centros de biodiversidad de importancia global, por ejemplo los Andes ecuatorianos. A pesar de esto, sus patrones de diversidad a escala grande se discuten todavía a base de resultados de pocos inventarios locales. En consequencia, modelos explicatorios de la diversidad de epífitas se concentran en el impacto del clima al número de especies epífitas a escala local. Por eso, nuestro objetivo era un análisis de los patrones altitudinales de la diversidad y del endemismo de epífitas, integrando datos de diferentes escalas geográficas.

Lugar America tropical, especialmente los Andes ecuatorianos.

Métodos Nuestro estudio está basado en dos fuentes de datos. Por un lado analizamos los patrones altitudinales de la diversidad de epífitas basado en el Catálogo de las Plantas Vasculares del Ecuador y el Libro Rojo de las Plantas Endémicas del Ecuador. Por otro lado analizamos el turnover florístico entre los inventarios de epífitas de once sitios de investigación neotropicales, siete de bosques montanos y cuatro de bosques de tierras bajas.

Resultados El turnover florístico entre inventarios neotropicales de epífitas es mayor en bosques montanos que en bosques de tierras bajas. Sitios de investigación montanos con una distancia de unos pocos kilómetros entre si demuestran diferencias considerables en sus inventarios de especies epífitas. A pesar de su modo de dispersión similar, el turnover florístico es mucho más alto en la familia de las orquídeas que en el grupo de las pteridofitas. Orchidaceae representan el grupo más rico en especies en todas las floras epífitas examinadas. A escala de la flora del Ecuador, un 50% de las especies en la zona altitudinal de mayor diversidad de epífitas (entre 1000m y 1500m) son orquídeas. Por consiguiente, los patrones altitudinales de la diversidad de epífitas en general reflejan los de las orquídeas en alto grado.

Conclusiones principales Nuestros resultados apoyan la observación de un ‘mid elevation bulge’ de la diversidad de epífitas, propuesto por Gentry & Dodson. Se ha mostrado frecuentemente que la humedad en bosques montanos favorece el mantenimiento de una elevada diversidad de epífitas. Nuestros resultados demuestran además que en bosques montanos el alto turnover florístico a escala regional y local aumenta la diversidad de epífitas a escala grande. Basado en la importancia de las orquídeas para la diversidad de epífitas discutimos que los procesos de especiación correspondientes al medio ambiente altamente diverso son una fuerza motriz para el endemismo, la heterogeneidad florística y, a consecuencia, para la riqueza en especies epífitas a escala grande en bosques montanos.

INTRODUCTION

The Ecuadorian Andes are one of the global biodiversity hotspots. Their extraordinary diversity (Olsen & Dinerstein, 1998, Barthlott *et al.*, 1999) is threatened by a rapid loss of habitat and high extinction rates (Myers *et al.*, 2000). More than a third of the plant species in the submontane and montane rain forests of Ecuador (located at intermediate elevations between 1000 and 2000 m) belong to the epiphytic or hemi-epiphytic life form (Jørgensen & León-Yánez, 1999). For the whole Ecuadorian territory, epiphytes represent more than 25% of the species richness of vascular plants. Furthermore, 35% of the Ecuadorian endemics belong to this life form (calculated on the basis of Valencia *et al.*, 2001).

Epiphytes are comparatively poorly studied, probably due to their hardly accessible habitat. We estimate that less than 120 epiphyte inventories exist for the Neotropics, including sites ranging from several 1000 ha down to plots of less than 1 ha. Only a small proportion of the inventories covers montane sites (Grubb & Whitmore, 1963, Gentry & Dodson, 1987, Catling & Lefkovitch, 1989, Bøgh, 1992, Kelly *et al.*, 1994, Ibisch, 1996, Acebey & Krömer, 2001), including a few elevational transects (Sudgen & Robins, 1979, Cleef *et al.*, 1984, Wolf, 1994, Hietz & Hietz-Seifert, 1995, Bussmann, 2001, Kessler, 2001, 2002a, Muñoz & Küper, 2001).

Gentry & Dodson (1987) discussed patterns of neotropical epiphyte species richness. Their 'mid-elevation bulge' model of epiphyte diversity became widely accepted, but the authors had themselves stated that the data on which their study was based were 'too incomplete to draw definite conclusions', especially for the elevational trends of epiphyte diversity on a large scale. Their hypotheses were, however, supported by the few more recent studies addressing large scale diversity patterns of epiphytes (Kelly *et al.*, 1994, Ibisch *et al.*, 1996, Nieder *et al.*, 1999). Kessler (2002b) has shown that elevational patterns of species richness in certain Ecuadorian taxa correspond to family-specific character traits, but did not evaluate life form specific patterns in this context. For Ecuador, the latter has been partly done by Jørgensen & León-Yánez (1999) and Braun *et al.* (2002), but not with a specific focus on epiphyte biology.

In this study, we analyse the checklist of Ecuador (Jørgensen & León-Yánez, 1999) and the Red List of Ecuador (Valencia *et al.*, 2001) in respect to the elevational trends of epiphyte species richness, especially of endemic epiphytes in Ecuador. In addition, we analyse the floristic turnover between seven montane and four lowland epiphyte inventories (Table 1, Fig. 1). Special emphasis is placed on the role that the Orchidaceae play for the species richness and endemism of epiphytes as well as the floristic turnover between epiphyte inventories.

METHODS

Analyses based on the Checklist and the Red List of Ecuador

The analysis of the elevational patterns of (endemic) epiphytes in Ecuador is based on data from the Checklist of Ecuador (Jørgensen & León-Yánez, 1999) and the Red List of Ecuador (Valencia *et al.*, 2001). We counted the total number of epiphyte species and endemic epiphyte species occurring in each elevational band (intervals of 500 m) in Ecuador. For 205 of the 4231 epiphyte species in Ecuador, no information is available concerning their elevational ocurrence. They were not considered in our analyses. While the definition of being 'endemic' to Ecuador is of limited biogeographic significance, it is nevertheless consistent within the analysis and therefore suitable to compare patterns.

Due to the structure of the plant data, the varying area size of the elevational bands could not be included into the analyses. Area size has to be considered if one wants to quantitatively compare the species richness of the different elevational bands or correlate species richness and environmental parameters (Barthlott *et al.*, 1999). Unfortunately, the calculation of species richnesss–area ratios requires more comprehensive and more detailed information than available from the aforementioned sources, especially to consider the floristic heterogeneity of an area when standardizing its species richness with area size (Arrhenius 1921). For a better overview, Fig. 2a shows the area size of the elevational zones in Ecuador based on data from Jørgensen & León-Yánez (1999) and Picker & Jørgensen (2001).

Analyses based on Neotropical epiphyte inventories

Six of the 11 epiphyte inventories of Neotropical study sites compared in this study (Table 1) are based on field work of members of our own working group. This study includes three new Ecuadorian epiphyte inventories, the submontane forests Reserva Otonga and Reserva Río Guajalito, and the lowland forest site Tiputini. Other data were taken from literature or have been provided by the respective authors (see Acknowledgements). We only included 11 inventories covering the whole area of a reserve or research station, being representative for the respective locality due to size and sampling effort indicated by the authors.

Species lists were fully adopted from the original publications, assuming that the high intensity of sampling diminishes determination errors to a level which does not cause considerable errors in the comparative analyses. The classification of life forms was also taken from the original sources, if available. In problematic cases, we compared the data with the checklists

Table 1 Locality, elevation, size, precipitation and species number of Neotropical epiphyte inventories (compare also Fig. 1)

Author	Country	Study site	Elevation (m a.s.l.)	Size (ha)	Number spp.	Precipitation (mm)
Küper *et al.* (this study)	Ecuador	Otonga	1400–2200	1000	456	2600
Küper *et al.* (this study)	Ecuador	Guajalito	1800–2200	400	256	2700
Ingram *et al.* (1996)	Costa Rica	Monteverde	1525	20	333	2500
Nieder *et al.* (2000)	Venezuela	La Carbonera	2100–2300	368	191	1460
Webster & Rhode (2001)	Ecuador	Maquipucuna	1100–2800	22,000	453	–
Bussmann (2001)	Ecuador	Podocarpus	1800–3150	–	644	3900
H. Kreft *et al.* (2004)	Ecuador	Tiputini	220	650	313	3700
Schmit-Neuerburg (2002)	Venezuela	Surumoni	100	–	148	2700
Missouri Botanical Garden (2002)	Ecuador	Jatun Sacha	450	2000	393	4000
Ibisch (1996)	Bolivia	Sehuencas	2100–2300	–	230	5000
N.A. Zamora et al. (pers. comm.)	Costa Rica	La Selva	30–200	1500	391	4000

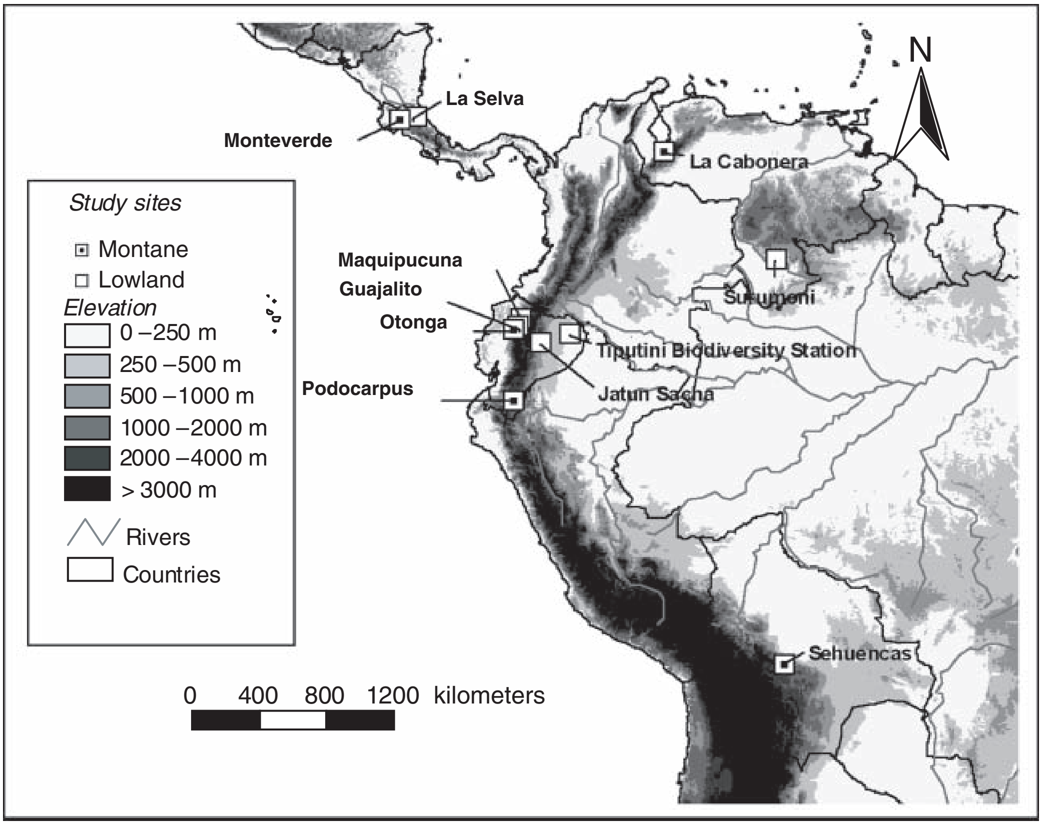

Figure 1 Location of the Neotropical epiphyte inventories compared in this study (compare Table 1).

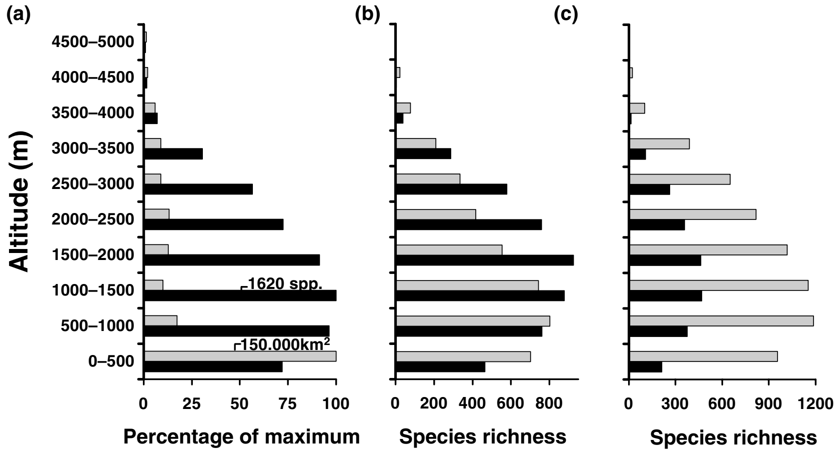

Figure 2 Species richness and number of endemics per elevational zone (500 m intervals on *y*-axis) in Ecuador. (a) In order to compare patterns of area size and species richness, values on *x*-axis were rescaled, expressing the maximum of each individual graph as 100%. This maximum is indicated for the respective maximum class. Black bars: species richness of Ecuadorian epiphytes; grey bars: area size of each elevational zone. (b) Epiphyte species richness: orchids (black bars) vs. all other taxa (grey bars). (c) Richness of epiphytes: endemics (black bars) vs. non-endemics (grey bars). Analyzes based on data from Jørgensen & León-Yánez (1999) and Valencia *et al.* (2001).

for the respective national flora [for Ecuador: Jørgensen & León-Yánez (1999), for Peru: Brako & Zarrucchi (1993), for Costa Rica: data provided by Zamora & Hammel (1996–2002)]. In conflicting cases, we assigned life forms based on own field experiences.

Analogous to Tuomisto *et al.* (2003), the complement of the Søerensen-Index (1 − Søerensen-Index) was used as measure for floristic turnover. The values for floristic turnover where then plotted against distance (in km) between the respective sites.

RESULTS

Elevational patterns of epiphyte species richness and endemism in Ecuador

In Ecuador, the elevational zone of 1000–1500 m hosts the largest number of epiphyte species (Fig. 2a). The next most species rich zones are those between 500 and 1000 m and between 1500 and 2000 m. At higher elevations, species richness decreases continuously. The upper elevational limit of epiphyte occurrence is set by the forest line at *c.* 3500–4000 m, with very few species occurring at elevations higher than 4000 m.

A comparison of epiphytic orchids with those of all other taxa (Fig. 2b) shows that the elevational patterns of species richness are strongly influenced by the Orchidaceae. Orchid species richness shows a hump shape with a maximum between 1500 and 2000 m. A 53% of the epiphyte species in the most diverse elevational zone are orchids. The elevational distribution of the richness of all other taxa has a similar shape but is at a maximum at 500–1000 m.

Endemic species contribute considerably to epiphyte species richness. According to the Red List of Ecuador (Valencia *et al.*, 2001), 1470 (35%) of the 4231 Ecuadorian epiphyte and hemiepiphyte species are national endemics. The maximum number of endemic epiphytes occurs at elevations between 1000 and 1500 m, followed by the zone between 1500 and 2000 m (compare Fig. 2c).

The proportion of endemic species among the epiphytes rises from 18% in the lowland to more than 30% at 1500–2000 m and then declines again (data not graphically represented here). Between 1000 and 1500 m, more than a third of the epiphyte species are Ecuadorian endemics. Again, the elevational patterns of the species richness of epiphytic endemics is clearly formed by that of epiphytic orchids. This is due to the fact that more than 70% of the Ecuadorian endemic epiphytes are Orchidaceae. In general, the contribution of epiphytic orchids to Ecuadorian plant diversity is very high: more than a quarter of all plant species endemic to Ecuador are epiphytic orchids.

Floristic turnover between Neotropical epiphyte inventories

Figure 4a shows the Søerensen-Index as a function of the geographical distances between the epiphyte inventories of Neotropical study sites. The floristic turnover between any pair of montane epiphyte inventories is very high. Even the lowest floristic turnover between the epiphyte inventories of sites located not more than a few kilometres apart from each other (e.g. Río Guajalito, Reserva Otonga and Maquipucuna) is at 0.7 or even higher, which means that 70% of the species occurring at one site does not occur at the other site.

The floristic turnover between pairs of montane epiphyte inventories is clearly higher than the turnover between pairs of lowland epiphyte inventories. This difference is most pronounced at distances of *c.* 1–1000 km. For example, the turnover between the epiphyte inventories of the montane sites Reserva Otonga and the Podocarpus site (less than 400 km distance) is higher than that between the lowland sites Tiputini and Surumoni, although the latter sites are located more than 1200 km apart. Hence, floristic turnover is strongly correlated with geographic distance, but this effect varies depending on the elevation of the sites compared.

This is also underlined by the comparison of pairs of one montane and one lowland epiphyte inventory, respectively (Fig. 4a). Even in the cases where two of these sites are relatively close to each other, they are floristically very distinct. For example, the floristic similarity between the Reserva Otonga (or Río Guajalito) and Jatun Sacha (distance: *c.* 170 km), or even between La Selva and Monteverde (distance: *c.* 90 km) is extremely low. The elevational difference between the sites obviously predominates the effect of their geographic distance.

The role of different taxa for epiphyte diversity

Species richness

Epiphyte species richness is – on any spatial scale and in nearly all habitat types – made up by a few families. At the majority of sites, more than 75% of the species belong to the 'top four' taxa Orchidaceae, Pteridophyta, Araceae and Bromeliaceae (Fig. 3).

The contribution of Orchidaceae to epiphyte species richness is highest compared to all other systematic groups. Values from montane sites frequently exceed 30% and reach maxima of 50%, e.g. in Sehuencas and Podocarpus (Fig. 3). Characteristic of montane study sites is the comparatively high proportion of epiphytic Ericaceae. Between 5% and 14% of the (hemi-) epiphyte species in montane rain forests are Araceae, which is typically a bit lower than the average at lowland forests.

Floristic turnover

The contribution of taxa to the floristic turnover between epiphyte inventory differs considerably. In nearly all cases, the floristic turnover of Orchidaceae from one site to another is drastically higher than that of any other taxon, especially the Pteridophyta (Fig. 4b–d). This holds true as well if comparing either lowland epiphyte inventories, montane epiphyte inventories or inventories from both. The largest differences between the floristic turnover of Orchidaceae and Pteridophyta is observed if comparing montane epiphyte inventories.

A remaining 'minimum' floristic overlap of montane sites (Fig. 4a) is due to a small set of widespread and often comparatively abundant species. The majority of them belongs to few genera, e.g. *Polypodium* L., *Asplenium* L., *Anthurium* Schott, *Peperomia* Ruiz & Pav. and *Elaphoglossum* Schott ex J. Sm. The proportion of these extremely widespread species rarely exceeds 5% of the inventories.

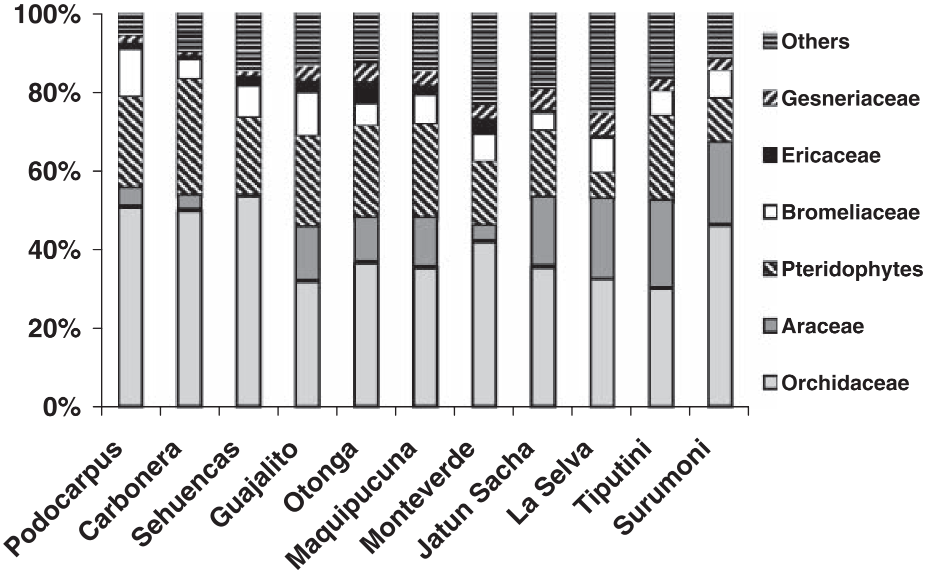

Figure 3 Proportion of families among species richness of Neotropical epiphyte inventories. All fern families summarized under 'Pteridophyta'.

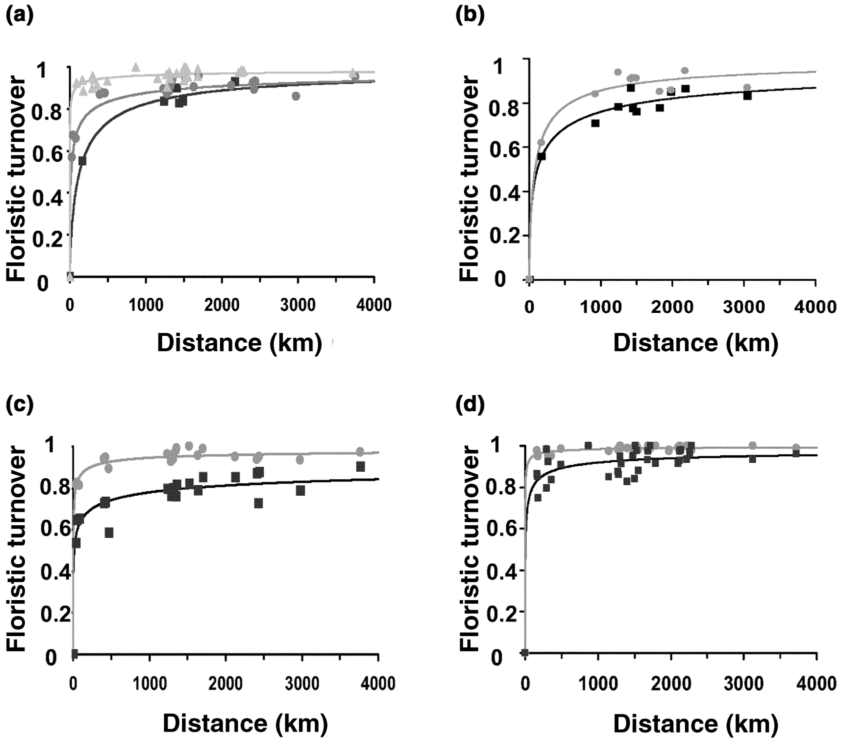

Figure 4 Floristic turnover (complement of Søerensen-Index) as a function of distance between Neotropical epiphyte inventories. Each symbol represents a pair of two compared sites. (a) Black boxes (and line): lowland vs. lowland inventories: $n = 7$, $r^2 = 0.72$, dark grey circles (and line): Montane vs. montane inventories ($n = 22$, $r^2 = 0.79$), hatched bright grey triangles (and uppermost line): lowland vs. montane inventories ($n = 28$, $r^2 = 0.79$). All $P < 0.01$. (b–d) For the same patterns, the floristic turnover in Orchidaceae (grey lines and circles) and Pteridophyta (black lines and boxes) are compared. (b) Lowland inventories vs. lowland inventories; (c) Montane vs. montane inventories; (d) lowland vs. montane inventories. Regression lines: best fit nonlinear regressions. N as in graph A, all $r^2 > 0.64$, all $P < 0.01$.

DISCUSSION

Factors promoting a high local species richness in montane rain forest

Already Schimper (1888) observed that epiphyte species richness in montane habitats is made possible by high air humidity. This is confirmed by numerous local studies, some of them referring to study sites included in the present study (Ingram *et al.*, 1996, Nieder *et al.*, 1999, Schmit-Neuerburg, 2002, Kreft *et al.*, 2004). One main difference between lowland and montane forests is that regular dry periods but also periodically occurring events such as El Niño reduce the abundance and diversity of epiphytes in Amazonian lowland forests drastically, e.g. at the Surumoni site (Schmit-Neuerburg, 2002). In contrast, in montane rain forests, the impact of dry periods is mitigated by the 'horizontal precipitation' (Vogelmann, 1973), which in cloud forests frequently contributes 20% or more to total water input (Juvik & Ekern, 1978, Stadtmüller, 1987). Unfortunately, suitable quantitative climate data (e.g. on water input by cloud condensation) are still not available for larger scale (Kessler, 2000, R. Rollenbeck, pers. comm.). However, the zones of maximum epiphyte species richness in Ecuador coincide well with the elevational zones with maximum precipitation and cloud formation shown for the East Andean slope in Ecuador (Lauer & Rafiqpoor, 2002).

A quantitative correlation of species richness with environmental parameters would have to be based on species richness per area (Arrhenius 1921, Barthlott *et al.*, 1999), which we could not calculate with the available plant data set. In which way would a consideration of area size per elevational band affect our results? The area size of the lowland band is so large in comparison to the mid-elevations that the hump shape of the curves would probably be more pronounced. In addition, floristic heterogeneity tends to be lower in the lowland, as shown by our own analyses based on the floristic turnover between Neotropical epiphyte floras. The more pronounced hump shape would result in an even better fit to patterns of available climate data (Lauer & Rafiqpoor, 2002) for eastern Ecuador, which shows low annual precipitation in the lowlands compared with the Andean slopes. An additional effect of correcting for area could be a reduction of the general differences in the elevational patterns of the species richness of epiphytic orchids and non-orchids.

The montane epiphyte flora is not only characterized by a high species richness, but also a pronounced endemism, in which orchids play a significant part. So the mid-elevation bulge of Gentry and Dodson is in part a result of a strong presence of endemic (orchid) species, which cannot be comprehensively explained by favourable climate conditions.

Floristic turnover and large scale species richness

Obviously, large scale 'species richness' (e.g. in entire elevational zones) is not just the sum of a large number of species evenly distributed in the entire area. Since species are not distributed evenly, large scale species richness results from the intensity of the floristic turnover at local and regional level. This is underlined by two observations based on literature data:

First, differences between the species richness of montane and lowland sites are scale dependent. Our analysis of large scale differences in species richness (comparing entire elevational zones) show that the montane epiphyte flora is much richer in species than the lowland epiphyte flora. However, epiphyte richness of small samples (plots of 0.01–2 ha size) in lowland forests with a high and comparatively continuous rainfall (Freiberg, 1996, Galeano *et al.*, 1998, H. Kreft *et al.*, 2004) frequently host an equal or sometimes even higher amount of epiphyte species and individuals than montane plots of comparable size and climate (Catling & Lefkovitch, 1989, Kelly *et al.*, 1994, Hietz & Hietz-Seifert, 1995, Muñoz & Küper, 2001, Nowicki, 2001). This pattern is not exclusive (see, e.g. Krömer, 2003) and may well depend on microhabitat characteristics. The number of large phorophytes included per plot for example has a strong effect on its epiphyte abundance and diversity. However, the differences between lowland and montane epiphyte inventories clearly increase with scale.

Second, it is frequently observed that with increasing plot size, the proportion of Orchidaceae rises steeply and continuously – at the expense of all other groups (compare Bøgh, 1992, Engwald, 1999, Muñoz & Küper, 2001, Nowicki, 2001). At the sites analysed in this study, orchids already contribute at least 26% to overall species richness (compare Fig. 3). For the Ecuadorian provinces and elevational zones, the contribution of orchids to epiphyte species finally reaches values of 62%, e.g. for the Andean region between 1000 and 2000 m (Jørgensen & León-Yánez, 1999). At this spatial scale, the proportion of orchids among epiphyte species richness is without exception clearly higher in montane than in lowland forests.

Obviously, the higher species richness and the higher proportion of orchids in the montane epiphyte flora both result from the higher floristic turnover in montane habitats (in particular of orchids). More and more species accumulate with increasing area. On national scale, orchids finally dominate the patterns in epiphyte diversity, not only in Ecuador but also in Peru (Ibisch *et al.*, 1996) and Bolivia (P. Ibisch, pers. comm.).

Which factors cause the high floristic turnover and endemism?

Abundance structure and sampling effort

Epiphytes (especially Orchids) often show a scattered and patchy distribution and population sizes tend to be small (Engwald, 1999, Nieder *et al.*, 2000, Muñoz & Küper, 2001, Schmit-Neuerburg, 2002). Even in areas which have been surveyed intensively and repeatedly for years (as done, e.g. in our own study sites Río Guajalito, Otonga, Surumoni, La Carbonera), frequently more than 25% of the species are present with less than five individuals (Rudolph *et al.*, 1998, Nieder *et al.*, 2000, Schmit-Neuerburg, 2002, C. Cardelus, pers. comm.). Absences due either to incomplete sampling or too small sampling areas are difficult to separate from beta or gamma diversity (Pitman *et al.*, 1999, Kessler, 2001). However, we do not think that the floristic turnover between our sites is artificially inflated by the potential sampling artefacts mentioned above because of three reasons:

First, at two of our own study sites, the Reserva Otonga and Río Guajalito, further sampling in the years 2000 and 2001 slightly enlarged the previous species list (compare Jaramillo, 2001). But the 'discovery' of additional species did even decrease the proportion of species shared among both sites. We suppose that the situation is similar for other sites, since they all share a comparable, high level of exploration. Secondly, among the species absent in Guajalito or Maquipucuna, several are quite abundant in the Otonga forest (and vice versa). It is very unlikely that these species have so varying abundance structures just a few kilometres apart, that they were overseen in the intensive and repeated sampling activities and in areas of several hundred hectare. Thirdly, the consistency of the patterns of floristic turnover and in particular the differences between lowland and montane sites indicate that our observations base on biogeographic mechanisms rather than sampling artefacts.

Ecological dissimilarity

A classic explanation for the floristic differences between two sites is their ecological dissimilarity. Even if both sites were located within the distributional range of the species populations, differing ecological conditions at the sites can exclude a species at one of them.

One might conclude that the role that elevation plays for the floristic turnover between epiphyte inventories reflects their ecological differences. At local level, the diversity of montane habitats along the steep climatic gradients and the pronounced orography is known as a promoting factor for species richness (Sudgen & Robins, 1979, Gentry & Dodson, 1987, Kelly *et al.*, 1994, Hietz & Hietz-Seifert, 1995). Trejo-Torres & Ackermann (2001) have shown that the overlap in the Orchid inventories of distanced Caribbean islands was high, when the physiographic and ecological conditions allowed the species presence. In contrast, even neighbouring islands had a small floristic overlap if their physiognomy was different.

However, the larger and generally more similar two sites are, the less likely it is that climatic differences explain the absence of species in one of them. Three of the montane sites compared in this study, Maquipucuna, Río Guajalito and the Reserva Otonga are located very close to each other and cover several hundred hectare each. The latter two sites lie just 30 km apart and have a very similar climate. In addition, both sites cover several hundred hectare of area and a large variety of habitats. It is unlikely that for *c.* 70% of the species which were found at these sites, one of the sites does not provide a suitable habitat.

Spatial distance

Floristic differences between the compared epiphyte inventories were much larger between montane forests than between lowland forests. Braun *et al.* (2002) show that geodiversity, including diversity of climate and variances of the relief, is very high at intermediate elevations in Ecuador. As it has been pointed out in earlier studies (Gentry, 1986, Balslev, 1988), high numbers of endemic species are often observed at elevations with a pronounced relief. Reduced area size of the montane zones has been considered as an approximation of 'fragmentation and narrowness' by Kessler (2002b) and was positively correlated with endemism and species richness. The importance of geographic isolation for the diversity in montane habitats has been underlined by studies on *Anthurium* in isolated cloud forests in Panama (Croat, 1986) and the Pleurothallidinae in Bolivia (Vasquez & Ibisch, 2000).

In this context, it is instructive that Orchids are the pacemakers of the endemism, the floristic turnover and the species richness of epiphytes on all spatial scales. It has been suggested that their diversity is due to their exceptional evolutionary plasticity (Benzing, 1990, Ackerman & Ward, 1999) and the high velocity of their adaptive radiation in combination with the Andean orogenesis and geodiversity. The latter favours the genetic isolation of populations through geographical separation (Gentry & Dodson, 1987), especially in the case of the small and scattered populations of Orchidaceae. The geographical isolation of orchid populations during processes of the Andean orogenesis and during paleoclimatic fluctuations is one potential explanation for their pronounced endemism.

But how can montane habitats contribute to such a high degree of endemism and floristic turnover in the montane epiphyte flora? Dispersal limitation is a classical explanation for the floristic turnover at regional and larger scale. Low endemism of certain taxa, especially pteridophytes, has been interpreted as a consequence of their high spore vagility (Kessler, 2000, Tuomisto *et al.*, 2003). But the contributions of pteridophytes and orchids to endemism within the montane epiphyte flora are opposed despite the fact that orchids seeds can be dispersed over several hundred kilometres (Trejo-Torres & Ackermann, 2001), even in the Andes (Gentry & Dodson, 1987). This is an indication for the significance which the highly specialized pollination mode of orchids and several other epiphytic taxa (Ackerman, 1986, Benzing, 1998, Borba & Semir, 2001) could have for the pronounced endemism in the Orchidaceae. We think that the pollination of plant individuals in so called 'founder populations' (Gentry & Dodson, 1987) is the process when geographic distance and topodiversity come into effect. The presence of specific pollinators becomes less probable with increasing distance to the point of origin of a seed and the geodiversity of the area. The effect is that individuals of an orchid species can establish at a considerable distance to the parental population. But then, preference of phenotypes by new and different pollinators leads to a rapid speciation of the plant species. Hence, the difference between the dispersal radius of seeds and the range of pollinators could be a key to understand the impact of geographical barriers on the distribution of epiphyte species, as suggested by Ibisch (1996).

Interestingly, the character traits of orchids discussed in the context of their high endemicity are taxon-specific rather than life form-specific, which supports findings on the Ecuadorian flora by Kessler (2002b) and on Peruvian Orchidaceae (Ibisch *et al.*, 1996). Future studies therefore should compare life form-specific diversity patterns with taxon-specific diversity patterns. We do not only urgently need suitable data on the abiotic factors most relevant for epiphytes (in particular water input by air humidity) and comprehensive information on their distribution areas. The explanation of large scale epiphyte diversity requires models going beyond the mechanism of species richness promoted by environmental favourableness. If we want to understand and conserve epiphyte diversity, our recent focus on the mechanisms which maintain their species richness should be complemented by an intensive investigation of those evolutionary processes which lead to speciation and therefore are causal for epiphyte diversity.

ACKNOWLEDGMENTS

This research was supported by the Deutsche Forschungsgemeinschaft (DFG), grant Ba 605/10-1. Several authors generously provided data on the epiphyte inventories of their study sites and from checklists, among those Renato Valencia and Hugo Navarrete (Pontifícia Universidad Católica del Ecuador, Quito), Peter Jørgensen (Missouri Botanical Garden, St Louis), Nelson Zamora, Barry Hammel and collaborators (Inbio, San José and Missouri Botanical Garden, St Louis), and Rainer Bussmann (University of Bayreuth). The Missouri Botanical Garden is acknowledged for making accessible research results and raw data via Internet, as in the case of the Checklist of Jatun Sacha. Laura Arcos, Jaime Jaramillo and Giovanni Onore are acknowledged for their emphatic administrative and personal support during our studies in Ecuador. Discussions with the following persons have contributed in a substantial way to the manuscript: Andrea Muñoz (University of Göttingen, Germany), Henning Sommer, Daud Rafigpoor (University of Bonn, Germany), Pierre Ibisch (FAN, Bolivia), Catherine Cardelus (University of Connecticut, USA), Rüttger Rollenbeck (University of Mannheim, Germany) and Michael Kessler (University of Göttingen, Germany). We thank them very much. An anonymous referee provided valuable comments on the manuscript. The paper is dedicated to Don César and his son Élicio Tapia, tireless curators of the Otonga Reserve in Ecuador. This research was supported by the Deutsche Forschungsgemeinschaft (DFG), grant Ba 605/10-1.

REFERENCES

Acebey, A. & Krömer, T. (2001) Diversidad y distribución vertical de epífitas en los alrededores del campamento río Eslabón y de la laguna Chalalán, Parque Nacionál Madidi, Dpto. La Paz, Bolivia. *Revista de la Sociedad Boliviana de Botánica*, **3,** 104–123.

Ackerman, J.D. (1986) Coping with the epiphytic existence: pollination strategies. *Selbyana*, **9,** 52–60.

Ackerman, J.D. & Ward, S. (1999) Genetic variation in a widespread, epiphytic orchid: where is the evolutionary potential? *Systematic Botany*, **24,** 282–291.

Arrhenius, O. (1921) Species and area. *J. Ecol.*, **9,** 95–99.

Balslev, H. (1988) Distribution patterns of Ecuadorian Plant species. *Taxon*, **37,** 567–577.

Barthlott, W., Biedinger, N., Braun, G., Feig, F., Kier, G. & Mutke, J. (1999) Terminological and methodological aspects of the mapping and analysis of global biodiversity. *Acta Botanica Fennica*, **162,** 103–110.

Benzing, D.H. (1990) *Vascular epiphytes: general biology and related biota*. Cambridge University Press, Cambridge.

Benzing, D.H. (1998) Vulnerabilities of tropical forest to climate change: the significance of resident epiphytes. *Climate Change*, **39,** 519–540.

Brako, L. & Zarrucchi, J.L. (1993) *Catalogue of the flowering plants and Gymnosperms of Peru. Monographs in Systematic Botany from the Missouri Botanical Garden 45*. Missouri Botanical Garden, St Louis.

Braun, G., Mutke, J., Reeder, A. & Barthlott, W. (2002) Biotope patterns, phytodiversity and forestline in the Andes, based on GIS and remote sensing data. In: *Mountain biodiversity: a global assessment* (ed. by Ch. Körner and E.M. Spehn), pp. 75–89. Parthenon Publishing, London.

Borba, E.L. & Semir, J. (2001) Pollinator specificity and convergence in fly-pollinated *Pleurothallis* (Orchidaceae) species: a multiple population approach. *Annals of Botany*, **88,** 75–88.

Bøgh, A. (1992) The composition and distribution of the vascular epiphyte flora of an Ecuadorian mountain rain forest. *Selbyana*, **13,** 25–34.

Bussmann, R.W. (2001) Epiphyte diversity in a tropical Andean forest-Reserva Biológica San Francisco, Zamora-Chinchipe, Ecuador. *Ecotropica*, **7,** 43–59.

Catling & Lefkovitch (1989) Associations of vascular epiphytes in a Guatemalan cloud forest. *Biotropica*, **21,** 35–40.

Cleef, A.M., Rangel, Ch., van der Hammen, T. & Jaramillo, R.M. (1984) La Vegetación de las selvas del Transecto Buritaca. *La Sierra Nevada de Santa Marta (Colombia) – Transecto Buritaca – La cumbre* (ed. by T. van der Hammen and P.M. Ruiz), pp. 203–266. Cramer-Verlag, Berlin.

Croat, T. (1986) The distribution of *Anthurium* (Araceae) in Mexico, Middle America and Panama. *Selbyana*, **9,** 94–99.

Engwald, S. (1999) *Diversität und Ökologie der Epiphyten eines Berg- und eines Tieflandregenwaldes in Venezuela – Eine vergleichende Analyse*. Books on demand (http://www.bod.de), Norderstedt.

Freiberg, M. (1996) Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guyana. *Biotropica*, **28,** 345–355.

Galeano, G., Suárez, S. & Balslev, H. (1998) Vascular plant species count in a wet forest in the Chocó area on the pacific coast of Colombia. *Biodiversity and Conservation*, **7,** 1563–1675.

Gentry, A.H. (1986) Endemism in tropical vs. temperate plant communities. Conservation biology. *The science of scarcity and diversity* (ed. by M. Soulé), pp. 153–181. Sinauer Press, Sunderland, MA.

Gentry, A.H. & Dodson, C. (1987) Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, **74,** 205–233.

Grubb, P.J. & Whitmore, C.T. (1963) A comparison of mountain and lowland rain forest in Ecuador II. The climate and its effects on the distribution and physiognomy of the forests. *Journal of Ecology*, **54,** 303–333.

Hietz, P. & Hietz-Seifert, U. (1995) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science*, **6,** 487–498.

Ibisch, P. (1996) Neotropische Epiphytendiversität – das Beispiel Bolivien. Martina Galunder-Verlag, Wiehl.

Ibisch, P., 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.

Ingram, A.U., Ferrell, S.W., Ingram, K. & Nadkarni, N.M. (1996) Floristic composition of vascular epiphytes in a Neotropical cloud forest, Monteverde, Costa Rica. *Selbyana*, **17,** 88–103.

Jaramillo, J. (2001) Flora de Río Guajalito. The Flora of the Río Guajalito Mountain Rain Forest (Ecuador). *Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation*, Vol. 1 of 2 (ed. by J. Nieder & W. Barthlott), pp. 47–322. Books on Demand (http://www.bod.de), Norderstedt.

Jørgensen P.M. & León-Yánez S. (eds) (1999) *Catalogue of the vascular plants of Ecuador*. Monographs in systematic botany of the Missouri Botanical Garden, 75. Missouri Botanical Garden, St Louis.

Juvik, J.O. & Ekern, P.C. (1978) A climatology of mountain fog on Mauna Lona, Hawaii Island. Water Resources Research Center, University of Hawaii, Hawaii, Technical report No. 118.

Kelly, D.L., Tanner, V.J., NicLughada, E.M. & Kapos, V. (1994) Floristics and Biogeography of a rain forest in the Venezuelan Andes. *Journal of Biogeography*, **21,** 421–440.

Kessler, M. (2000) Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology*, **149,** 181–193.

Kessler, M. (2001) Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and Conservation*, **10,** 1473–1495.

Kessler, M. (2002a) Plant species richness and endemism of upper Montane forests and timberline habitats in the Bolivian Andes. In: *Mountain biodiversity: a global assessment* (ed. by Ch. Körner & E.M. Spehn), pp. 59–74. Parthenon Publishing, London.

Kessler, M. (2002b) The elevational gradient of Andean plant endemism: varying influences of taxon specific traits and topography at different taxonomic levels. *Journal of Biogeography*, **29,** 1–7.

Kreft, H., Köster, N., Küper, W., Nieder, J. & Barthlott, W. (2004) Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. *Journal of Biogeography*, **31,** 1463–1476.

Krömer, T. (2003) *Diversität und Ökologie der vaskulären Epiphyten in primären und sekundären Bergwäldern Boliviens*. Cuviller Verlag, Göttingen.

Lauer, W. & Rafiqpoor, D. (2002) *Die Klimate der Erde. Eine Klassifikation auf der Grundlage der ökophysiologischen Merkmale der realen Vegetation*. Erdwissenschaftliche Forschung, Bd. 40. Franz Steiner Verlag, Stuttgart.

Missouri Botanical Garden (2002) (download 01.06.2002): *Checklist of the Flora of Jatun Sacha., Ecuador*. Downloaded at: http://mobot.mobot.org/W3T/Search/Ecuador/projsjs.html.

Muñoz, A. & Küper, W. (2001) Diversity and distribution of vascular epiphytes along an altitudinal gradient in an Andean cloud forest (Reserva Otonga, Ecuador). *Epiphytes and canopy fauna of the Otonga rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation*, Vol. 2 of 2 (ed. by J. Nieder & W. Barthlott), pp. 189–216. Books on Demand (http://www.bod.de), Norderstedt.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403,** 853–858.

Nieder, J., Engwald, S. & Barthlott, W. (1999) Patterns of neotropical epiphyte diversity. *Selbyana*, **20,** 66–75.

Nieder, J., Engwald, S., Klawun, M. & Barthlott, W. (2000) Spatial distribution of vascular epiphytes (inclusive hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) in southern Venezuela. *Biotropica*, **32,** 385–396.

Nowicki, C. (2001) Epífitas vasculares de la Reserva Otonga. *Epiphytes and canopy fauna of the Otonga rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation*, Vol. 2 of 2 (ed. by J. Nieder & W. Barthlott), pp. 115–160. Books on Demand (http://www.bod.de), Norderstedt.

Olsen, D.M. & Dinerstein, E. (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, **12,** 502–515.

Picker, T. & Jørgensen, P.M. (2001) Epiphyte diversity in Ecuador – a geographical information system (GIS) Project. *Epiphytes and canopy fauna of the Otonga rain forest (Ecuador). Results of the Bonn – Quito epiphyte project, funded by the Volkswagen Foundation*, Vol. 2 of 2 (ed. by

J. Nieder & W. Barthlott), pp. 115–160. Books on Demand (http://www.bod.de), Norderstedt.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñoz, P, Neill, D.A., Cerón, C.E., Palacios, W.A. & Aulestia, M. (1999) Dominance and distribution of tree species in upper Amazonian Terra Firme Forests. *Ecology*, **82,** 2101–2117.

Rudolph, D., Rauer, G., Nieder, J. & Barthlott, W. (1998) Distributional patterns of epiphytes in the canopy and phorophyte characteristics in a western Andean rain forest in Ecuador. *Selbyana*, **19,** 27–33.

Schimper, A.F.W. (1888) *Die epiphytische Vegetation Amerikas*. Gustav Fischer Verlag, Jena.

Schmit-Neuerburg (2002) *Dynamics of vascular epiphyte vegetation in the Venezuelan lowland rain forest of the Surumoni Crane Project*. Dissertation, Botanical Institute of the University of Bonn, Bonn, Germany.

Stadtmüller, T. (1987) *Cloud forests in the humid tropics. A bibliographic review*. The United Nations University Press, Tokyo.

Sudgen, A.M. & Robins, J. (1979) Aspects of the Ecology of vascular epiphytes in Colombian cloud forests, I. The distribution of the epiphytic flora. *Biotropica*, **11,** 173–188.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, Environment, and Floristic Variation of Western Amazonian Forests. *Science*, **299,** 241–244.

Trejo-Torres, C.J. & Ackermann, J.D. (2001) Biogeography of the Antilles based on a parsimony analysis of orchid distributions. *Journal of Biogeography*, **28,** 775–794.

Valencia, R., Pitman, N., León-Yánez, S. & Jørgensen, P.M.(eds) (2001) *Libro rojo de las plantas endémicas del Ecuador*. Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito.

Vasquez, R. & Ibisch, P. (2000) *Orchids of Bolivia. Diversity and conservation status. Vol. I: Subtribu Pleurothallidinae*. Editorial FAN, Santa Cruz de la Sierra.

Vogelmann, H.W. (1973) Fog precipitation in the cloud forests of eastern Mexico. *Bioscience*, **23,** 96–100.

Webster, G.L. & Rhode, R.M. (2001) *Plant diversity of an Andean cloud forest: inventory of the vascular plants of Maquipucuna, Ecuador*. University of California Publications in Botany 82, Berkeley.

Wolf, J.H.D. (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, **112,** 15–28.

Zamora, N.A., Hammel, B.E. & collaborators (1996–2002) *Lista plantas: database of species characteristics from the Costa Rican Vascular Flora*. INBio, San Jose.

BIOSKETCHES

Since 1995, the epiphyte working group of the Nees Institute for the Biodiversity of Plants, University of Bonn, has been carrying out field research on epiphyte diversity. The group participated in the Surumoni Crane Project (Venezuela) and contributed to the botanical inventory of mountain forests in Venezuela (La Carbonera), Ecuador (Otonga, Río Guajalito), Bolivia (Sehuencas), and most recently at the Tiputini lowland site (eastern Ecuador).

Wolfgang Küper has conducted fieldwork at several of the mentioned sites in Venezuela and Ecuador. He is particularly interested in the evolution of large scale patterns of plant diversity and distributions.

Holger Kreft and **Nils Köster** have studied large and small scale epiphyte diversity patterns at Tiputini.

Jürgen Nieder started working on epiphyte diversity in 1993, and – together with his co-workers – published a number of publications on the subject.

Wilhelm Barthlott is the head of the institute and has for 30 years done research on epiphytes.