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

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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 Endémicas 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. Irrespective 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 maintain 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
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 & Kroemer, 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).

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 consecuencia, 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 turno 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 sí demuestran diferencias considerables en sus inventarios de especies epífitas. A pesar de su modo de dispersión similar, el turno 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 turno 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.
of the 4231 epiphyte species in Ecuador, no information is available concerning their elevational occurrence. 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 richness–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)

<table>
<thead>
<tr>
<th>Author</th>
<th>Country</th>
<th>Study site</th>
<th>Elevation (m a.s.l.)</th>
<th>Size (ha)</th>
<th>Number spp.</th>
<th>Precipitation (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Küper et al. (this study)</td>
<td>Ecuador</td>
<td>Otona</td>
<td>1400–2200</td>
<td>1000</td>
<td>456</td>
<td>2600</td>
</tr>
<tr>
<td>Küper et al. (this study)</td>
<td>Ecuador</td>
<td>Guajalito</td>
<td>1800–2200</td>
<td>400</td>
<td>256</td>
<td>2700</td>
</tr>
<tr>
<td>Ingram et al. (1996)</td>
<td>Costa Rica</td>
<td>Monteverde</td>
<td>1525</td>
<td>20</td>
<td>333</td>
<td>2500</td>
</tr>
<tr>
<td>Nieder et al. (2000)</td>
<td>Venezuela</td>
<td>La Carbonera</td>
<td>2100–2300</td>
<td>368</td>
<td>191</td>
<td>1460</td>
</tr>
<tr>
<td>Webster &amp; Rhode (2001)</td>
<td>Ecuador</td>
<td>Maquipucuna</td>
<td>1100–2800</td>
<td>22,000</td>
<td>453</td>
<td>–</td>
</tr>
<tr>
<td>H. Kreft et al. (2004)</td>
<td>Ecuador</td>
<td>Tiputini</td>
<td>220</td>
<td>650</td>
<td>313</td>
<td>3700</td>
</tr>
<tr>
<td>N.A. Zamora et al. (pers. comm.)</td>
<td>Costa Rica</td>
<td>La Selva</td>
<td>30–200</td>
<td>1500</td>
<td>391</td>
<td>4000</td>
</tr>
</tbody>
</table>

Analogous to Tuomisto et al. (2003), the complement of the Sørensen-Index ($1 - \text{Sørensen-Index}$) was used as measure for floristic turnover. The values for floristic turnover where then plotted against distance (in km) between the respective sites.

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). Analyses based on data from Jørgensen & León-Yánez (1999) and Valencia et al. (2001).
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 Sørensen-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-Neuernburg, 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-Neuernburg, 2002). In contrast, in montane rain forests, the impact of dry periods is mitigated by the ‘horizontal precipitation’ (Vogemann, 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-Yáñez, 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-Neuernburg, 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 physiological 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 endemity 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 (Pontificia 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 Rafiqpoor (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


**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).

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