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Neotropical flowering epiphyte diversity: local composition and geographic affinities

Alfredo Cascante-Marín · Angela Nivia-Ruíz

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Abstract Worldwide, the highest diversity of vascular epiphytic plants resides in the Neotropics. The general pattern of taxonomic composition of the neotropical epiphytic flora has been described, but information regarding the magnitude and geographic distribution of species richness is lacking. In this paper, we carried out a regional scale analysis in order to provide an overview of the richness, composition and geographic affinities among several neotropical epiphyte floras. Our database comprised 7,524 flowering epiphyte species (48 % of the estimated total of neotropical epiphytes) from eight representative localities with politically-defined boundaries. The epiphyte quotient (e.g., percentage of epiphyte species in the total flora) per locality ranged from 5.2–27.7 % (mean: 17.5 %) of the flowering plants. Ecuador represented the most species diverse locality (4,247 spp.), followed by Costa Rica (2,611 spp.). At the family level, the epiphyte composition among localities was roughly homogeneous and dominated by emblematic epiphytic groups: Orchidaceae, Bromeliaceae, and Araceae. However, the generic composition of the epiphytic floras was more heterogeneous. Ecuador and Cuba showed the highest epiphyte endemism (37 and 26 %, respectively), and in some cases vascular epiphytes represented 30 % or more of the total endemic flowering plants at a particular locality. From the available information, four main regional epiphyte floras were identified: the northwestern Andean region, the northern and southern Mesoamerican regions; Cuba as a representative of the Caribbean region remained as a separated group, though weakly related to the Mesoamerican groups. This study identified important geographic localities as targets for the conservation of neotropical epiphyte diversity.

Keywords Diversity · Epiphyte richness · Neotropical epiphytes · Epiphyte quotient

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Introduction

Worldwide, the diversity of epiphytic plants is estimated to be nearly 10 % of all vascular plant species; including gymnosperms, angiosperms, and ferns. This figure represents between 23,500 and 29,500 epiphyte species in the “broad sense”, namely, holo-epiphytes, hemi-epiphytes, and facultative epiphytes (Madison 1977; Kress 1986; Gentry and Dodson 1987a). The neotropical region stands out as the most diverse, possessing about six times more epiphytes than the epiphyte impoverished African continent, and almost 1.5 times the diversity of epiphytes of southeast Asia and the Australasian region (Madison 1977; Gentry and Dodson 1987a).

In their seminal paper on neotropical epiphytes, Gentry and Dodson (1987a) described the general pattern of taxonomic composition and reported an estimate of 15,540 species distributed over 42 plant families. Monocot species dominated the epiphytic life form, though distributed in fewer families when compared to neotropical dicots which are more diverse in epiphytic families. At the family level, Orchidaceae was the most speciose group, possessing almost ten times more species than Bromeliaceae and Araceae, the next most diverse neotropical epiphytic families (Gentry and Dodson 1987a). These authors also suggested a general trend in the geographical distribution of neotropical epiphytes; they proposed that epiphytes were particularly concentrated on the lower slopes of the northern Andes and to a lesser extent in southern Central America. However, no quantitative information exists about the species richness and degree of complementarity between these potential “hotspots” for neotropical epiphytes.

In an attempt to answer the question of how diverse neotropical epiphytes are, Ibsch et al. (1996) used data from Peru and Mexico (Aguirre-León 1992), two megadiverse neotropical countries characterized by their huge area (nearly 1.2×10^6 km²) and diversity of ecosystems, and estimated a neotropical epiphyte quotient (e.g., percentage of epiphyte species in the total flora) of about 10 %. This figure, comparable to the world estimate of Madison (1977) and Kress (1986), led Ibsch et al. (1996) to question the magnitude of the global epiphyte quotient, if considering the highest diversity of neotropical areas. However, these two localities alone may not be good representatives of the neotropical region.

Currently, the described patterns of neotropical epiphyte diversity and composition are based on data from local epiphyte inventories or florulas (e.g., Gentry and Dodson 1987b; Ibsch et al. 1996; Nieder et al. 1999; Küper et al. 2004), and relate species richness to climatic conditions and elevation. For instance, in dry habitats the number of species and individuals decreases dramatically compared to wetter habitats (Gentry and Dodson 1987b; Ibsch et al. 1996). On the other hand, there is a tendency toward a better representation of epiphytes in montane forests of intermediate elevation, particularly in cloud forests, compared to lowland and montane forests at high elevations (Gentry and Dodson 1987a; Ibsch et al. 1996; Küper et al. 2004; Cardelús et al. 2006). A further assessment using regional scale data will provide information about the magnitude and geographic distribution of neotropical epiphyte diversity to complement the existing information.

In the present study, we provide an overview of the taxonomic contribution and geographic affinities of epiphytic vascular plants within the neotropical region. We carried out the analysis based on published floristic data from eight localities, mainly defined by country-based political boundaries. We specifically addressed the following questions: (1) what is the contribution of epiphytes to plant diversity and endemism among localities within the Neotropics?, (2) how different is the composition at the familial and generic level of the epiphytic flora among localities?, and (3) what are the floristic relationships of the epiphytic flora among neotropical localities?

Methods

Epiphyte database

We compiled a database from the most recently published floristic information, which included plant manuals, catalogues, and papers representing eight neotropical localities: the Catalogue of the Flowering Plants and Gymnosperms of Peru (Brako and Zarucchi 1993), The Catalogue of Vascular Plants of Ecuador (Jørgensen and León-Yáñez 1999), the Checklist of the Vascular Plants of Belize (Balick et al. 2000), the Flora of Nicaragua (Stevens et al. 2001a, b, c), the Epiphytic Angiosperms of Cuba (Hechavarría Schwesinger et al. 2002), the vascular epiphytes from the State of Chiapas in Mexico (Wolf and Flamenco 2003), the Catalogue of Vascular Plants of Panama (Correa et al. 2004), and the Plant Manual of Costa Rica (Hammel et al. 2003a, b, 2007). Detailed data on epiphytic fern species were not available, except for global figures of diversity mentioned in the respective sources. Therefore, ferns were not considered in the analyses of composition and floristic affinities among localities.

The information entered in the database for each locality contained the following variables: (1) taxonomic group (i.e., monocots or dicots), (2) botanical family, (3) scientific name, (4) endemism within political localities, and (5) the epiphytic life form. By “epiphytic life form” we refer to: *holo-epiphytes* or plants that complete their entire life cycle without contacting the forest floor, *hemi-epiphytes* or plants that partially spend their life on other plants, and *facultative epiphytes*, or plant species in which some individuals may grow as terrestrial (sensu Kress 1986). Hemi-parasitic epiphytes (i.e., members of Loranthaceae, Viscaceae, and Eremolepidaceae) were not included. The epiphytic life form indicated by the literature source was generally accepted, and when missing or incomplete (i.e., epiphyte—sensu lato) we assigned a category based on related publications and the tendency displayed by the specific taxonomic group. However, the lack of complete information on epiphyte life form is likely a source of bias.

In order to reduce taxonomic synonymy or redundancy of species names in the database, we used as reference the latest published work, e.g., The Plant Manual of Costa Rica (Hammel et al. 2003a, b, 2007), and additionally consulted the TROPICOS Database of the Missouri Botanical Garden (<http://www.tropicos.org>). Thus, some discrepancies between the number of species here reported and the respective publications may occur.

Data analysis

The contribution of epiphytic plants was described as the “epiphyte quotient” (Hosokawa 1950) which expresses the contribution of epiphytes as a percentage with respect to the total flora for each locality. Here, we included the data on flowering plants (monocots and dicots) and the reported global figures on epiphytic ferns. In order to appropriately compare the pattern of epiphyte richness (only flowering plants) among localities, it was necessary to account for area size. The relation between the size of an area (A) and the number of species present (S) is conventionally expressed by the model $S = cA^z$, where c and z are constants, usually interpreted as the intercept and the slope of the relationship on a double-logarithmic plot, respectively (Rosenzweig 1995). Following Brummitt (2005), area needs to be scaled to a suitable exponent value (z), the chosen value $z = 0.14$ is within the range of empirical values for mainland areas and non-isolated island (0.12–0.17, sensu MacArthur and Wilson 1967). Then, the relative values of c for areas of different size

are calculated as S/A^z and interpreted as scores of relative diversity, where the most species rich locality has the highest c -values and is assigned the value 1.0.

The overall composition of the neotropical epiphytic flora was described by estimating the contribution (in percentage) of the ten most diverse, in terms of species richness, angiosperm families and genera from the pooled data of the eight examined localities. Hereafter, also the term “important” is equal to most diverse, either families or genera. The degree of heterogeneity in the composition of local epiphyte floras was determined by comparing separately the local composition (top ten families and genera) to the overall neotropical pattern by means of Chi squared tests. Expected values were based on the percent contribution relative to the total number of species of the top ten families or genera from the overall composition.

We estimated the total number of endemic epiphytes for each locality and calculated their contribution to total plant endemism as the ratio of epiphytic endemics to total endemic angiosperm plants (terrestrial and epiphytes). The contribution of families and genera to the endemic epiphytic flora was analyzed among the studied localities.

The floristic affinities among the study localities were examined by estimating the pairwise similarity between epiphytic floras (angiosperms only) using the Sørensen Index, $C_s = 2j/(a + b)$, where j : number of shared epiphytic species, a : total of epiphytic species in locality A, b : total of epiphytic species in locality B (Magurran 1988). Using the latter data, we assembled a dissimilarity matrix ($1 - C_s$) and used the Weighted Pair-Group Average Method or WPGMA (Legendre and Legendre 1998) to calculate the modified similarity values in order to construct a dendrogram showing the affinities among the study localities. This method employs a sequential grouping algorithm that calculates the arithmetic mean of similarities or distances between objects, differences in sample size among groups are considered as a weighting variable (Legendre and Legendre 1998).

Results

Epiphyte diversity

Our database comprised 7,524 flowering epiphyte species, representing nearly half of all the flowering epiphytic plants that have been reported for the entire neotropical region. The average epiphyte quotient from the examined neotropical localities was 17.5 % and ranged from 5.2 % in the Caribbean island of Cuba to 27.7 % in Ecuador at the northwestern Andes. Our species richness estimates, based on the c -values, placed Ecuador as the most epiphyte-diverse neotropical locality, followed by Costa Rica, and Panama (Table 1).

Monocotyledonous epiphytes represented from two-thirds to nearly three quarters of all species at each locality, and ferns usually contributed more epiphytic species than dicots (mean: 18.0 vs. 14.8 %, respectively) (Fig. 1). At the family level, there were more dicot families with at least one epiphytic species reported in the literature sources than monocots (60 vs. 12, respectively).

Epiphyte composition

The overall composition of the neotropical epiphytic flora as described by the ten most species rich plant families included around 93 % of all species (Table 2). A single monocot family, Orchidaceae, accounted for nearly two-thirds of all the flowering epiphyte species

Table 1 Diversity and endemism of vascular epiphytic plants from selected localities of the Neotropical region

Locality	Area (km ²)	Epiphyte species	Epiphyte quotient	Relative number of species ^a	Endemic epiphytes (%)	Contribution to Endemism (%) ^b
Ecuador	283,000	4,247	27.7	1.00	1,575 (37 %)	38.0
Costa Rica	51,100	2,611	27.4	0.78	502 (19 %)	47.8
Panama	78,200	1,993	22.7	0.56	305 (15 %)	30.3
Peru	1,285,000	1,784	10.6	0.34	315 (18 %)	5.9
Chiapas	75,000	1,163	13.8	0.33	nd	nd
Nicaragua	129,794	1,057	20.1	0.28	9 (1 %)	17.0
Belize	22,963	414	12.1	0.14	0	0.0
Cuba ^c	110,922	317	5.2	0.08	82 (26 %)	2.4

Data from flowering plants and ferns

nd no data available

^a Represents the relative *c*-values in the relationship $S = cA^z$

^b Contribution of epiphytes to total plant endemism

^c Ferns not included

with almost seven times more species than the second and third more important epiphyte families, Bromeliaceae, and Araceae.

The dominance of the abovementioned epiphyte families was similar among the studied localities, except for Cuba, where the dicotyledonous family Piperaceae replaced Araceae (Fig. 2a). Nonetheless, when including the contribution of other epiphytic families, there existed significant deviations of all localities with respect to the general neotropical pattern (all χ^2 tests: $P < 0.001$).

For instance, Panama and Costa Rica showed the highest χ^2 -values, meaning highly significant departures from the general composition. In the case of Panama, epiphytic aroids (family Araceae), melastomes (family Melastomataceae) and Ericaceae had a higher contribution in species than expected (Fig. 2b). In Costa Rica, there were higher numbers of epiphytic melastomes, gesneriads (Gesneriaceae), and representatives of the fig family (Moraceae) than expected. Cuba is interesting as its epiphytic flora lacked some important epiphytic neotropical families such as Ericaceae and Melastomataceae or was reduced as in Gesneriaceae (Fig. 2a).

At the generic level, the ten most diverse neotropical epiphytic genera comprised 45 % of all the species from our database and were mostly represented by orchid genera: *Pleurothallis*, *Epidendrum*, *Lepanthes*, *Maxillaria*, *Masdevallia*, *Oncidium*, and *Stelis* (Table 2). The degree of heterogeneity among localities at the genera level was higher than at the family level, judging by the higher χ^2 -values obtained (all tests: $P < 0.001$).

For instance, Peru and Chiapas showed the highest deviations (highest χ^2 -values) from the expected neotropical pattern. In Peru, *Maxillaria* exhibited nearly twice the expected values and replaced *Pleurothallis* as the most diverse genus; while *Lepanthes* had four times fewer species than expected and positioned farther from the top-ten most diverse genera locally (Fig. 2b). In Chiapas, the number of *Epidendrum* and *Tillandsia* (Bromeliaceae) species was higher than expected, being the first and second most diverse genera, respectively. Also, there were fewer *Masdevallia* species than expected and this genus was not among the most important genera (Fig. 2b). In Cuba, *Masdevallia* was absent and

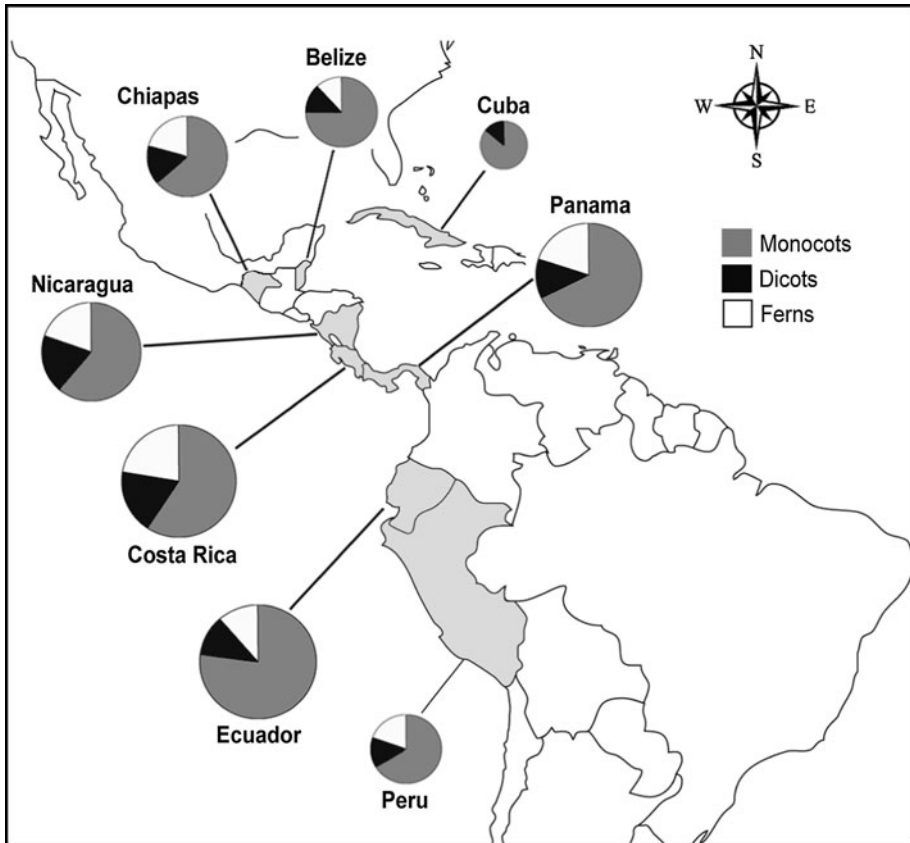


Fig. 1 Distribution of vascular epiphyte species among major taxonomic groups in the flora of several neotropical localities. The size of each pie chart is proportional to the respective epiphyte quotient value (see Table 1)

Anthurium species amounted to less than half the expected number, while *Tillandsia* showed three times more species than expected (Fig. 2b).

Epiphyte endemism

The exclusivity (i.e., degree of endemism) of the epiphytic flora at the studied neotropical localities greatly varied (Table 1), from as low as none in Belize up to nearly one-third of the epiphytes in Ecuador. Epiphyte contribution to total plant endemism was high in Costa Rica, Ecuador, and Panama, where they represented one-third or more of the total endemic flowering plants including both, terrestrial and epiphytes (Table 1).

At every locality, the endemic species were mainly representatives from the most diverse epiphytic families: Orchidaceae, Bromeliaceae, and Araceae. However, in Panama the endemic melastomes (Melastomataceae) replaced Bromeliaceae. At the genus level, a similar pattern was observed, the most speciose orchid genera (i.e., *Pleurothallis*, *Lepanthes*, *Epidendrum*, *Masdevallia*, and *Maxillaria*) were among the groups with more endemic species (Table 3). Some non-orchid genera with high number of endemic species

Table 2 Composition of the neotropical epiphytic flora (flowering plants) as represented by the ten most important, in terms of species number, epiphyte families and genera

Familial composition				Generic composition		
Family		Total species	%	Genera	Total species	%
1	Orchidaceae	4,743	63.0	<i>Pleurothallis</i> (Orchidaceae)	614	8.2
2	Bromeliaceae	665	8.8	<i>Epidendrum</i> (Orchidaceae)	478	6.4
3	Araceae	655	8.7	<i>Lepanthes</i> (Orchidaceae)	451	6.0
4	Piperaceae	312	4.1	<i>Anthurium</i> (Araceae)	354	4.7
5	Gesneriaceae	182	2.4	<i>Maxillaria</i> (Orchidaceae)	313	4.2
6	Ericaceae	167	2.2	<i>Peperomia</i> (Piperaceae)	295	3.9
7	Clusiaceae	79	1.0	<i>Masdevallia</i> (Orchidaceae)	271	3.6
8	Moraceae	77	1.0	<i>Tillandsia</i> (Bromeliaceae)	222	2.9
9	Melastomataceae	73	1.0	<i>Oncidium</i> (Orchidaceae)	196	2.6
10	Cactaceae	65	0.9	<i>Stelis</i> (Orchidaceae)	194	2.6

The percentage value was calculated from the pooled data of the eight neotropical localities

were restricted to certain localities, such as *Werauhia* (Bromeliaceae) and *Columnea* (Gesneriaceae) in Costa Rica; *Philodendron* (Araceae) and *Cavendishia* (Ericaceae) in Panama; *Anthurium* (Araceae) and *Guzmania* (Bromeliaceae) in Ecuador; and *Tillandsia* (Bromeliaceae) and *Peperomia* (Piperaceae) in Peru. In the island of Cuba, the most important genera of endemic species included some otherwise less important orchid genera at the neotropical level, such as *Encyclia* and *Tolumnia* (both in Orchidaceae) (Table 3).

Epiphyte geographic affinities

The analysis of taxonomic similarities among the examined epiphytic floras revealed four distinctive geographic groups (Fig. 3). A first group was formed by the localities at the northwestern Andean region, Peru and Ecuador. A second group represented the southern Mesoamerican region, formed by Nicaragua, Costa Rica, and Panama. Both Costa Rica and Panama, showed the highest degree of similarity between their epiphytic floras. A third group is composed by localities on the northern Mesoamerican region, Chiapas and Belize, with a closer affinity with southern Mesoamerican. The island of Cuba constitutes in itself an additional group, relatively isolated and which epiphytic flora only showed a low floristic affinity with the Mesoamerican localities.

Discussion

Information on flowering epiphyte richness based on ecologically defined regions and at the spatial scale of our analysis is not available at present; however, our analysis based on politically delimited localities provides a meaningful insight into the pattern of neotropical epiphyte diversity distribution from which interpretations derived from biogeographic, ecological or climatic factors can be drawn. The major outcomes of the present work showed a significant heterogeneity in species richness and composition among epiphyte floras and a clear geographic partitioning of different subsets of epiphytes within the neotropical region.

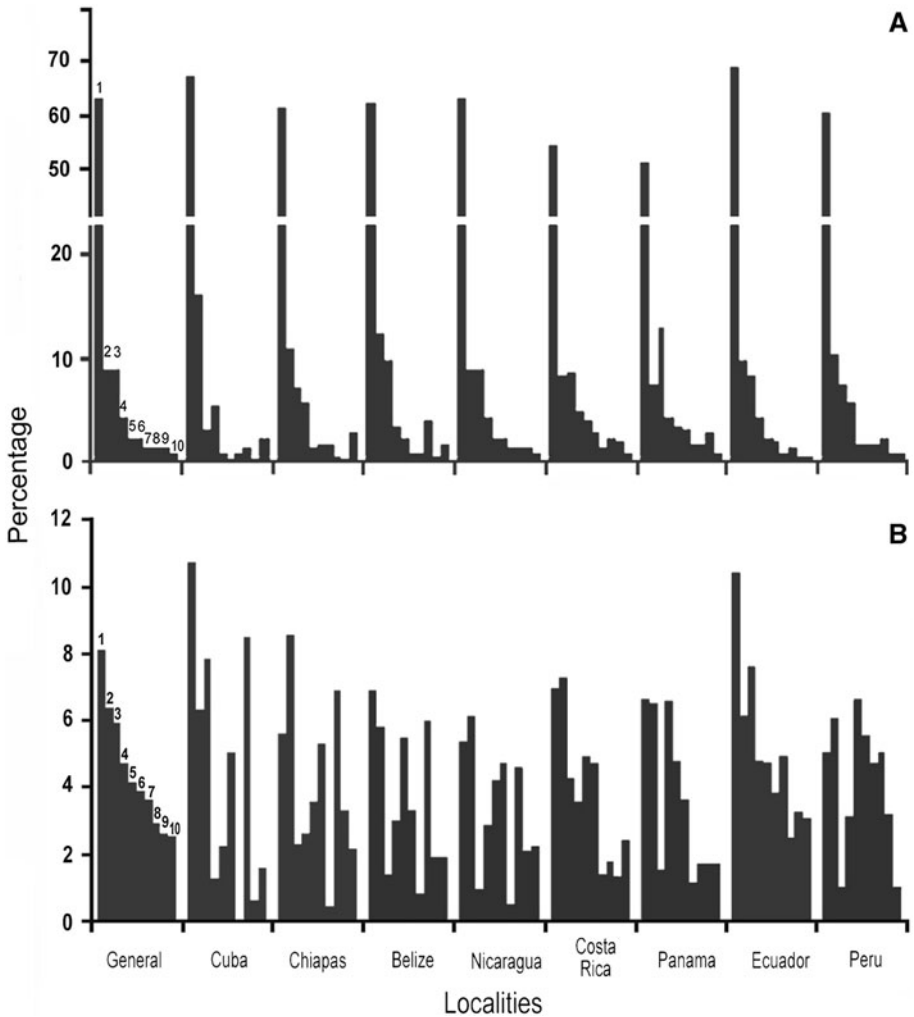


Fig. 2 Familial (a) and generic (b) composition of the epiphytic flora (flowering plants) of several neotropical localities. Data from the ten most important families and genera at each of the examined localities. Data are percentages and general composition refers to the pooled data. Bars are arranged in the following order: (families) 1. Orchidaceae, 2. Bromeliaceae, 3. Araceae, 4. Piperaceae, 5. Gesneriaceae, 6. Ericaceae, 7. Clusiaceae, 8. Moraceae, 9. Melastomataceae, 10. Cactaceae; (genera) 1. *Pleurothallis*, 2. *Epidendrum*, 3. *Lepanthes*, 4. *Anthurium*, 5. *Maxillaria*, 6. *Peperomia*, 7. *Masdevallia*, 8. *Tillandsia*, 9. *Oncidium*, 10. *Stelis*

Our database is reasonably representative of the neotropical diversity of epiphyte flowering plants consisting of nearly half (48 % or 7,524 spp.) of the estimated species by Gentry and Dodson (1987a). The average neotropical epiphyte quotient of 17.5 % is still above the world estimate of 10 % (Madison 1977; Kress 1986) and the previous assessment of Ibisch et al. (1996) for the neotropical area. A source of bias in our study is the lack of information from eastern South America which includes the Amazonian flora that covers an extensive lowland forest area of the Neotropics. However, according to Gentry (1982, 1990), the Amazonian-centered taxa are more diverse in trees and lianas while

Table 3 Epiphytic plant genera with the highest number of endemic species in the angiosperm flora of some neotropical localities¹

Costa Rica		Panama		Ecuador		Peru		Cuba	
Genera	Spp.	Genera	Spp.	Genera	Spp.	Genera	Spp.	Genera	Spp.
<i>Lepanthes</i> ²	64	<i>Anthurium</i> ⁴	42	<i>Pleurothallis</i> ²	216	<i>Masdevallia</i> ²	48	<i>Lepanthes</i> ²	23
<i>Pleurothallis</i> ²	43	<i>Pleurothallis</i> ²	27	<i>Lepanthes</i> ²	215	<i>Tillandsia</i> ³	22	<i>Pleurothallis</i> ²	15
<i>Epidendrum</i> ²	40	<i>Philodendron</i> ⁴	24	<i>Masdevallia</i> ²	119	<i>Maxillaria</i> ²	17	<i>Encyclia</i> ²	7
<i>Werauhia</i> ³	26	<i>Epidendrum</i> ²	20	<i>Anthurium</i> ⁴	112	<i>Telipogon</i> ²	15	<i>Tolumnia</i> ²	5
<i>Telipogon</i> ²	18	<i>Lepanthes</i> ²	15	<i>Epidendrum</i> ²	79	<i>Peperomia</i> ⁸	14	<i>Epidendrum</i> ²	3
<i>Maxillaria</i> ²	15	<i>Cavendishia</i> ⁶	11	<i>Maxillaria</i> ²	40	<i>Pleurothallis</i> ²	12	<i>Stelis</i> ²	3
<i>Stelis</i> ²	15	<i>Maxillaria</i> ²	9	<i>Guzmania</i> ³	40	<i>Anthurium</i> ⁴	12		
<i>Masdevallia</i> ²	11	<i>Stelis</i> ²	7	<i>Stelis</i> ²	38	<i>Epidendrum</i> ²	10		
<i>Anthurium</i> ⁴	10	<i>Guzmania</i> ³	6	<i>Dracula</i> ²	33	<i>Scelochilus</i> ²	9		
<i>Columnnea</i> ⁵	10	<i>Blakea</i> ⁷	6	<i>Peperomia</i> ⁸	32	<i>Catasetum</i> ²	8		
<i>Cavendishia</i> ⁶	10	<i>Topobea</i> ⁷	6	<i>Oncidium</i> ²	32				
		<i>Monolena</i> ⁷	6						

¹ Belize had no endemic epiphytes; the available information from Chiapas did not specify endemic species and Nicaragua's epiphytes only contained nine endemic species distributed in a similar number of genera. ² Orchidaceae, ³ Bromeliaceae, ⁴ Araceae, ⁵ Gesneriaceae, ⁶ Ericaceae, ⁷ Melastomataceae, ⁸ Piperaceae

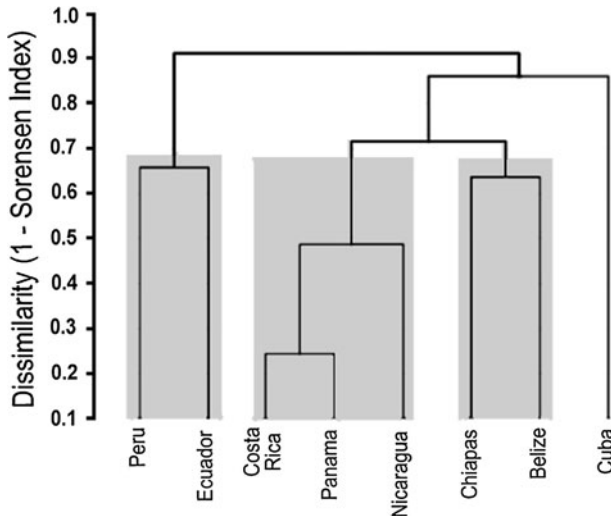


Fig. 3 Floristic affinities among epiphytic floras (flowering plants) of several neotropical localities. Clustering based on the WPGMA algorithm

plants of the epiphytic habit had a lower species radiation there. Thus, the inclusion of data from Amazonian epiphytes is likely to reduce our neotropical epiphyte quotient estimate but it is expected to remain above the world estimate.

The heterogeneous composition of the epiphytic neotropical flora is more evident at the generic than at the familial level and is possibly related to local speciation of particular groups. For example, in southern Central America some important endemic groups (with

10 or more endemics) belonged to speciose and widespread neotropical orchid genera, such as *Epidendrum*, *Lepanthes*, *Pleurothallis*, and *Telipogon*. Other non-orchid groups have radiated there too, for example the bromeliad genus *Werauhia* shows a marked center of diversity at the Talamanca Mountain Range that extends from Costa Rica to northwestern Panama with nearly 80 % (58) of the known species (Morales 2003). The aroid genus *Anthurium* also shows an important center of diversification in Costa Rica and Panama (Croat and Baker 1979). Similarly, the localities at the northern part of Central America (Belize and Chiapas) that formed a distinctive group, had a few groups that experienced diversification, such as the hemi-epiphytic shrubs and trees of *Oreopanax* (Araliaceae), the epiphytic herbs of *Begonia* (Begoniaceae), the bromeliads *Catopsis* and *Tillandsia* (Bromeliaceae), the crassulacean herbs of *Echeverria* (Crassulaceae), and the *Encyclia* orchids (Orchidaceae). The distinctiveness of the epiphytic flora of northern Central America is also characterized by the absence or scarcity of some typical southern montane non-orchid taxa, such as *Blakea* in Melastomataceae (Renner 1986), *Cavendishia* in Ericaceae (Luteyn 2002), *Columnea* and *Drymonia* in Gesneriaceae (Wiehler 1983).

There is a clear pattern in the concentration of flowering epiphytes at some particular localities of the Neotropics. Our results showed the highest concentration of epiphytes per area in Costa Rica with 5.1 species per 100 km² which contrasts with that of Ecuador with 1.5 species per 100 km², the locality with the highest absolute epiphyte richness (4,247 spp.) but distributed in an area 5.5 times the size of Costa Rica. However, simply dividing species number by area to obtain an un-scaled species-area ratio is misleading (Connor and McCoy 1979). Consequently, the estimation of rescaled richness using the *c*-values which accounted for area size (sensu Brummitt 2005) positioned Ecuador as the most-diverse neotropical locality, followed by Costa Rica with 78 % of the epiphyte diversity present in Ecuador. The low (10.6 %) epiphyte quotient and low relative diversity (*c* = 0.34) of Peru's epiphytes is remarkable considering its proximity to Ecuador, nonetheless the political boundaries of Peru comprise significant areas of Amazonian lowland forest, high elevation Andean areas and a dry coastal region where epiphyte diversity is relatively low (Ibisch et al. 1996).

The documented high epiphyte richness found at the abovementioned localities constitutes evidence in favor of the geographic pattern proposed by Gentry and Dodson (1987a) of higher species concentration on the lower slopes of the northern Andes (e.g., Ecuador) and to a lesser extent in southern Central America (e.g., Costa Rica). Both geographic regions have been major evolutionary centers for epiphytic plants (Gentry 1982), and our results indicated that endemic epiphytes represent an important component (30–48 %) of all endemic flowering plants at each locality. This pattern of endemism coincides with important geological events: the rising of the Andean mountains about 5 Ma in northwestern South America and the Talamanca mountain range in southern Central America during the Pliocene around the same period (Denyer and Kussmaul 2000). In addition, the glaciation events during the Quaternary period about 1.8 Ma (Horn 1990) promoted the northward movement of several, predominantly mountain taxa from the Andean region (sensu Gentry 1982). When glaciers retreated (the last event occurring about 10,000 years ago, sensu Horn 1990) and temperature increased, several epiphytic groups may have remained isolated in mountain areas and experienced further speciation, creating particular species assemblages which, at the present time, distinguishes the epiphytic flora of southern Central America from that of the northern Andean region. Furthermore, the differences between the epiphytic floras of northern and southern Central America can be interpreted as a result of the discontinuity of the isthmus' mountain range. Benzing (1990) has suggested that the absence of evidence from ancient fossil records, the

concentration of epiphytes in a few large advanced families, as well as their concentration in geologically young montane habitats indicates a recent (Pliocene/Pleistocene) species radiation of angiosperm epiphytes. For the Ericaceae family, a group exhibiting a specialized pollination system associated with hummingbirds, Luteyn (2002) has proposed that speciation of this group in the Neotropics occurred during the last 2 millions years.

An additional subset of the neotropical epiphyte flora identified in this study was in Cuba, a representative locality of the Caribbean islands. The epiphytic flora of Cuba significantly differed in composition from the continental localities, both at familial and generic level. Orchid taxa mainly contributed to its diversity and endemism (e.g., *Encyclia*, *Lepanthes*, *Pleurothallis*, and *Tolumnia*). A remarkable pattern in the epiphytic flora of Cuba is the relatively high endemism (26 %), which is a recurrent feature of island vegetations (Kier et al. 2009). The low diversity of Cuban epiphytes (5.2 %) is likely to increase when information on epiphytic ferns becomes available, but probably will remain low compared to other neotropical localities. According to the pattern described by Gentry and Dodson (1987a), the lower epiphyte richness of Cuba is probably related to its subtropical condition at its higher latitude. Additionally, the occurrence of hurricanes that cause frequent population disturbances by dislodging epiphytes from their host-trees has been proposed as a regulator of epiphyte diversity in islands (Migenis and Ackerman 1993; Hsu and Wolf 2009) and that is a common climatic phenomenon in the Caribbean region (Bellingham 1991; Walker et al. 1991).

The distribution of the neotropical epiphyte richness among discrete geographic groups representing the northern and southern Central American region, the northwestern Andes and the Caribbean islands is consistent with diversity patterns of flowering plants at a global (Brummitt 2005) and regional scale (Distler et al. 2009). Thus, our findings indicate that epiphytes are an important component of the angiosperm flora of these neotropical areas, which are also known for their high overall vascular plant diversity (Myers et al. 2000; Barthlott et al. 2005). Particularly, Ecuador and Costa Rica seem to represent important geographic “hotspots” for flowering epiphytes, and we recommend that this plant habit should become a conservation target for future regional programs of plant conservation.

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