 Rev. Bol. Ecol. y Cons. Amb. 23: 27-38, 2008

Patrones de diversidad y distribución vertical en epífitas vasculares en la Cordillera Mosetenes, Cochabamba, Bolivia

Diversity and vertical distribution patterns of vascular epiphytes in the Cordillera Mosetenes, Cochabamba, Bolivia

Thorsten Krömer[1], Ivan Jimenez[2], and Michael Kessler[3]

RESUMEN

La diversidad de epífitas vasculares fue estudiada en nueve árboles maduros de dosel y sus parcelas circundantes de sotobosque de 400 m^2 cada una a 1200-1600 m en la botánicamente inexplorada Cordillera Mosetenes, Cochabamba, Bolivia. Registramos un total de aproximadamente 207 especies de epífitas vasculares, distribuidas en 23 familias y 70 géneros, mientras que el muestreo adicional en 11 parcelas donde nosotros no trepamos árboles resultó en un total de aproximadamente 268 especie. La Cordillera Mosetenes está situada entre las localidades con mayor riqueza de especies en el Neotrópico y confirma el patrón altitudinal de curva en forma de campana propuesta para la riqueza de epifitas vasculares. Un total de 83 especies de epifitas vasculares encontradas en un solo árbol es el valor máximo que ha sido registrado en Bolivia. El número más alto de especies fue encontrado en el interior del dosel, donde prevalecen condiciones especialmente favorables de crecimiento. Sin embargo, el sotobosque tuvo más especies de epifitas que algunas zonas individuales del dosel, lo cual indica que ambos, tanto el sotobosque sombreado como los árboles grandes del dosel deben ser inventariados para un muestreo completo de epifitas.

Palabras Claves: Andes, Bolivia, bosque montano tropical, riqueza de especies, Araceae, Bromeliaceae, Orchidaceae, *Peperomia*, Pteridophyta

ABSTRACT

Vascular epiphyte diversity was studied on nine mature canopy trees and their surrounding understory plots of 400 m^2 each at 1200-1600 m in the botanically previously unexplored Cordillera Mosetenes, Cochabamba, Bolivia. We recorded a total of about 207 species of vascular epiphytes, distributed over 23 families and 70 genera, whereas additional sampling in 11 plots where we did not climb trees resulted in a total of about 268 species. The Cordillera Mosetenes ranks among the most species-rich localities in the Neotropics and confirms the proposed hump-shaped elevational pattern of vascular epiphyte richness. The 83 vascular epiphyte species found on a single tree is the maximum value that has ever been recorded in Bolivia. The highest number of species was found in the inner crown, where especially favorable growth conditions prevail. However, the understory had more epiphyte species than any individual zone in the canopy, which indicates that both the shady understory and large canopy trees must be inventoried for complete epiphyte sampling.

Key words: Andes, Bolivia, tropical montane forest, species richness, Araceae, Bromeliaceae, Orchidaceae, *Peperomia*, Pteridophyta

[1] Centro de Investigaciones Tropicales, Universidad Veracruzana, Interior de la Ex-hacienda Lucas Martín, Privada de Araucarias s/n, Col. 21 de Marzo, C.P. 91019 Xalapa, Veracruz, México; E-mail: tkroemer@gmx.de
[2] Herbario Nacional de Bolivia, Casilla 10077, La Paz, Bolivia; E-mail: suniruna@hotmail.com
[3] Systematic Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland; E-mail: michael.kessler@systbot.uzh.ch

INTRODUCTION

The enormous diversity of epiphytes is one of the most striking characteristics of humid tropical montane forests. Vascular epiphytes, which include orchids, ferns, bromeliads, aroids, and numerous other, less species-rich families, are a key component of these forests, both in terms of species richness (Gentry & Dodson, 1987; Nieder *et al*., 1999; Küper *et al*., 2004; Krömer *et al*., 2005) and their roles in water-balance and nutrient cycles (Nadkarni, 1984; Coxson & Nadkarni, 1995; Hölscher *et al*., 2004; Köhler *et al*., 2007). They are an important source of food and habitat for birds, bats, amphibians, and reptiles, as well as for a great variety of invertebrates and micro-organisms (Nadkarni & Matelson, 1989; Benzing, 1990).

The aim of this study was to assess the species diversity, composition, and vertical distribution of the epiphyte communities in the Cordillera Mosetenes, Cochabamba, Bolivia, and its comparison with similar studies in Bolivia and other Neotropical countries. Here, the number of epiphyte studies has greatly increased since the landmark study by Gentry & Dodson (1987). Most fieldwork in this field has been done in Costa Rica, Ecuador, the Guianas, Mexico, Panama, and Venezuela (e.g., ter Steege & Cornelissen, 1989; Hietz & Hietz-Seifert, 1995; Ingram *et al*., 1996; Freiberg, 1996, 1999; Engwald, 1999; Nieder & Barthlott, 2001; Wolf & Flamenco, 2003; Kelly *et al*., 2004; Werner *et al*., 2005; Cardelús *et al*., 2006; Zotz & Schultz, 2008). For Bolivia, Ibisch (1996) provided a preliminary checklist of vascular epiphytes, which has been extended especially for ferns, aroids, and bromeliads by studies of Kessler (2000, 2001a, b) and Kessler *et al*. (1999, 2001). Moreover, Acebey & Krömer (2001) and Krömer & Gradstein (2003) added complete epiphyte inventories for three sites along an elevational gradient in the montane forests of the department of La Paz.

MATERIALS AND METHODS

The Cordillera Mosetenes in the department of Cochabamba, Bolivia, is a semi-isolated mountain range about 130 km long, 20-25 km wide, and up to about 2050 m high. The present study was conducted in the immediate vicinity of a small lagoon, which we called Laguna Carachupa, located at an elevation of 1310 m at the following geographical coordinates: 16°13’58”S, 66°24’54”E (UTM 0776352, 8203586). Studies were mainly conducted in a radius of 1 km around the lagoon, with several trails reaching from stream valleys at about 1200 m elevation to a mountain ridge at 1600 m. A detailed description of the study area is provided by Macía & Fuertes (2008).

Field work was conducted from 27 August to 17 September 2003. Vascular epiphyte diversity was studied in nine plots of 20 x 20 m^2 each following the epiphyte sampling protocol developed by Gradstein *et al*. (2003). In every plot, one mature canopy tree (phorophyte) was selected and sampled from the base to the outer portion of the tree crown by recording all vascular epiphyte species within the five vertical zones according to Johansson (1974), using the single rope technique (Perry, 1978). This technique allows a nearly complete inventory of epiphyte diversity of the forest canopy (Flores-Palacios & García-Franco, 2001). In tall, mature forest (tree plot 2 of Macía & Fuertes, 2008) at 1250 m four *Ficus* spp. (Moraceae) with a height of 25-35 m and a diameter at breast hight (dbh) of 0.73-0.86 m were inventoried. In stunted ridge forest (tree plot 4 of Macía & Fuertes, 2008) at 1550 m two *Podocarpus* sp. (Podocarpaceae) and two unknown tree species (MK 13274, MK 13277) with a height of 10-15 m and a dbh of 0.38-0.86 m were climbed. Additionally, one *Ficus* sp. (25-28m, dbh 0.76 m) was studied in tree plot 1 of Macía & Fuertes (2008) at 1350 m. Because the epiphyte flora in the forest understory is usually different from that on the large canopy trees, epiphytes on shrubs and treelets were sampled within the 20 x 20 m^2 plot around each sampled canopy tree, using collecting poles and binoculars (Shaw & Bergstrom, 1997; Gradstein *et al*., 2003; Krömer *et al*., 2007). Additionally, epiphytic species of Araceae, Bromeliaceae, Cactaceae, and Pteridophyta were recorded in 11 plots of 400 m^2 each in which we did not climb the trees (see Kessler *et al*., 2008).

All species encountered in the survey area (but not in every single plot) were collected in triplicate and have been deposited at the Herbario Nacional de Bolivia (including all unicates), at the Herbarium Göttingen, Germany, and with the respective specialists: T.B. Croat (St. Louis, Missouri; Araceae), H. Luther (Sarasota, Florida; Bromeliaceae), R. Vásquez (Santa Cruz; Orchidaceae), J.T. Mickel and R.C. Moran (New York; *Elaphoglossum*), and A.R. Smith (Berkeley, California; most pteridophyta).

For data analysis, we differentiated between the dominant Neotropical epiphytic families Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Pteridophyta (treated here as a ‘family’), as well as all eight other families

(Araliaceae, Cactaceae, Clusiaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Marcgraviaceae, Melastomataceae) combined as 'others'.

RESULTS AND DISCUSSION

Diversity

We recorded about 207 species of vascular epiphytes, distributed over 23 families and 70 genera, within nine complete epiphyte inventory plots: orchids were the most important family in terms of species number (ca. 99), followed by ferns (52), aroids (24), piperoids (11), bromeliads (8), and all other families combined (13) (Appendix 1). Furthermore, in the 11 additional plots (see Appendix 1 in Kessler *et al.*, 2008), we recorded one additional family, 13 genera, and 61 species of vascular epiphytes, resulting in a total of about 268 species, distributed in 24 families and 83 genera.

In the following, vascular epiphyte diversity of the Cordillera Mosetenes is compared with data from complete epiphyte inventories obtained by Acebey & Krömer (2001) and Krömer & Gradstein (2003) in three study sites in the foothill and montane forests of Parque Nacional Madidi (300-350 masl; 14°25'S, 67°55'W), Sapecho (600-1200 masl; 15°27-32'S, 67°18-23'W), and Parque Nacional Cotapata (1600-2200 masl; 16°11-13'S, 67°51-54'W) in the Bolivian department of La Paz using the same sampling method (Table 1, Fig. 1).

Table 1. General information about the four study sites Madidi, Sapecho, Mosetenes, and Cotapata.

	Madidi	Sapecho	Mosetenes	Cotapata
Elevation (m)	300-350	600-1200	1200-1600	1600-2200
Montane forest belt	Andean foothill	Submontane	Intermediate	Lower montane
Precipitation (mm)	2000	1500-2000	5000 ?	2500
Number of plots	8	40	9 (+11 plots without climbed trees)	24
Species/genera/families	89/43/14	255/87/23	ca. 207/70/23	292/76/24
			(ca. 268/83/24)	

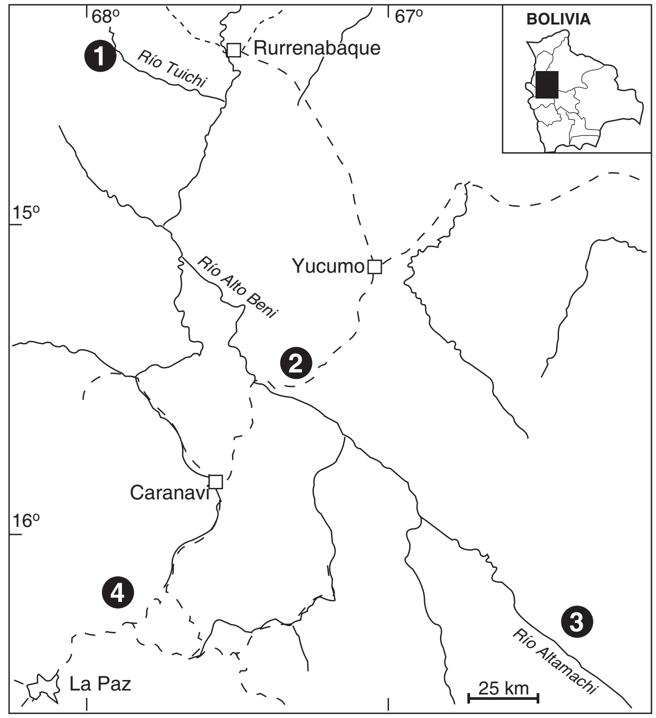

Figura 1. Map of central Bolivia showing the location of the study sites (1:Madidi, 2:Sapecho, 3:Mosetenes, 4:Cotapata). Continuous lines show main rivers, dashed lines main roads.

The different number of plots per study area (Table 1) indicates that the sampling intensity varies strongly between study areas, which must be taken into account when comparing the total species numbers. Nevertheless, it is apparent that Mosetenes, with a preliminary species number of ca. 268 vascular epiphytes, is very species-rich in comparison to the foothill and submontane forests of Madidi and Sapecho (Table 1). The species number corresponds to that of Cotapata, but in Mosetenes fewer trees were sampled. The values for the genera and families are less dependent on the number of plots and appear quite constant.

Species number per phorophyte

Maximum, minimum, and mean species number per phorophyte vary considerably within and between areas (Table 2): In Madidi, the range of values is 12-34, in Sapecho 20-59, in Cotapata 30-75, and in Mosetenes 27-83. The maximum value of 83 vascular epipyhte species on a single *Ficus* sp. tree at 1250 m in Mosetenes is especially striking. This tree had the highest species number of epiphytes that has ever been recorded in Bolivia. It surpasses the maximum value of 75 species found at 2100 m in Cotapata (Krömer, 2003). Comparable values in the lite-rature are given only by Kreft *et al*. (2004), who found 81 species on a single tree in Ecuador, Freiberg (1996, 1999), who recorded 65 and 74 epiphytes in French-Guyana, and Engwald (1999), who found 66 species in Venezuela. However, even higher values of 98 and 126 species were found by Werner *et al*. (2005) in Ecuador and by Schuettpelz & Trapnell (2006) in Costa Rica, respectively. Three plots located in stunted ridge forests differed consistently from plots on slopes by their number of species per tree (Table 2), as a consequence of the lower stature of individual trees which provided less surface for epiphyte growth.

Table 2. Maximum, mean and minimum species number per phorophyte within the corresponding elevation for the four study sites.*ridge forests.

	Madidi		Sapecho		Mosetenes			Cotapata			
Elev. (m)	350	600	650	700	900	1200*	1250	1550*	1650	1850*	2100
Max	34	44	59	46	51	42	83	37	64	48	75
Mean	22.3	31.1	42.5	34.3	37.9	32.4	63.6	33.5	52.6	35.6	53.1
Min	12	20	26	23	28	29	53	27	38	30	41

Species number per plot

Regarding species numbers for the 20 x 20 m^2-plots including the understory (Table 3), values for the ridge forests tended towards values of the zonal forests, presumably because of the better light conditions in the understorey on ridges. This was especially important for bromeliads, which had a higher contribution to epiphyte richness on ridges than on slopes. For the mean species number per plot (= point diversity), the highest value (89.8) of epiphyte species per 400 m^2 was found again in the zonal forest of Mosetenes. Here, the maximum species number per plot is 111 species. Species numbers of epiphytes increase along the elevational gradient, reaching a clear maximum in the zonal forest of Mosetenes before decreasing gradually with increasing elevation in Cotapata (Table 3).

Our study thus confirms the hump-shaped elevational pattern of vascular epiphyte richness proposed by Gentry & Dodson (1987), but the causes of this pattern are still poorly understood. However, four main factors have mostly been invoked: air humidity, rainfall, the topographical complexity and young orogeny of the Andes. Schimper (1888) already considered air humidity to be the most important factor determining epiphytic plant diversity, a suggestion confirmed by, e.g., Gentry & Dodson (1987), Kessler (2001b), Kreft *et al*. (2004), and Küper *et al*. (2004). Ecophysiologically, this relationship appears to be well founded, because water availability is of critical importance to epiphytes (Benzing, 1990; Zotz & Hietz, 2001).

Table 3. Maximum, mean and minimum species number per plot (including phorophyte) within the corresponding altitude for the four study sites.*ridge forests

	Madidi		Sapecho		Mosetenes			Cotapata			
Elev. (m)	350	600	650	700	900	1200*	1250	1550*	1650	1850*	2100
Max	51	57	71	63	59	66	111	76	94	71	83
Mean	34.8	47	62.1	48.6	53.8	55.4	89.8	62.6	76	62.1	68.5
Min	25	34	55	34	44	49	77	48	54	55	57

Diversity of the four most important epiphyte groups

Surprisingly, many more species of aroids were found in Mosetenes than in Madidi and Sapecho (Table 4), although aroids in South America usually have their highest richness below 1000 m (Ibisch *et al*., 1996; Kessler, 2002). A striking feature was the extremely high number of species of *Anthurium* in Mosetenes. However, this genus has also more species in Cotapata than in Sapecho and seems to have its maximum diversity, at least in Bolivia, at mid-elevations. In Venezuelan Guyana, *Anthurium* as well as *Philodendron* show a strongly negative correlation with elevation (Engwald, 1999). In the four study sites in Bolivia, the large genus *Philodendron* also shows a richness peak in the Andean foothill forest of Madidi and a clear decrease of richness with increasing elevation.

The high aroid diversity in Mosetenes (Table 4) is also caused by the intermediate elevation, where genera from the submontane (*Rhodospatha*, *Syngonium*) as well as from the montane belt (*Stenospermation*) co-occur. In addition, the heterogeneous structure of the forest, caused by disturbances due to either landslides or tree falls, offers optimal growth conditions for aroids, which often show a high diversity and abundance in young successional stages (Krömer & Gradstein, 2003).

Table 4. Number of species, genera, and families within the four most important epiphyte groups (Araceae, Bromeliaceae, Orchidaceae and Pteriodophyta) of the four study sites.

	Madidi	Sapecho	Mosetenes	Cotapata
Species/Genera/Fam.	89/43/14	255/87/23	ca. 68/83/24	292/76/24
Araceae	19/5	24/5	37/8	17/3
Anthurium	3	6	16	11
Philodendron	12	11	7	5
Bromeliaceae	7/5	20/9	14/6	21/5
Guzmania	2	5	7	5
Tillandsia	1	4	1	9
Orchidaceae	27/13	111/34	ca. 99/27	114/29
Epidendrum	3	12	11	12
Maxillaria	8	19	30	26
Pleurothallis	4	19	13	17
Pteridophyta	21/14/6	74/28/11	ca. 92/29/12	105/24/11
Grammitidaceae	0	5	12	14
Hymenophyllaceae	1	12	16	17
Lomariopsidaceae	3	12	20	29
Polypodiaceae	9	21	17	21

Bromeliads were rather species-poor in Mosetenes in comparison to Sapecho and Cotapata. While there was a high total species number (7) in *Guzmania*, reflecting the preference of this genus for mid-elevations, the genera *Aechmea*, *Billbergia*, *Catopsis*, and *Werauhia*, which occur in Madidi and Sapecho, were completely absent in Mosetenes. Another striking fact was the low number of *Tillandsia* species in comparison to Cotapata, where this genus amounts to almost half of all bromeliad species.

The number of orchid species was mostly determined on the basis of morphospecies because most species were not found in flower. Overall, orchid diversity in Mosetenes was comparable with that of Sapecho and Cotapata, although the number of sampled trees was lower. The genus *Maxillaria* showed the highest species number in all four study sites, but was especially species-rich in Mosetenes and seems to reach its maximum at mid-elevations. The values of *Epidendrum* and *Pleurothallis* are quite similar. These genera also have their highest diversity in the montane forests and not in the lowlands.

The total species number of ferns in Mosetenes more or less equaled the value in Cotapata, but was clearly higher than in Sapecho. The high species numbers of epiphytic ferns in Mosetenes and Cotapata reflects their diversity maximum at mid-elevations in Bolivia. A similar hump-shaped curve with a peak at 1200 m and a strong decrease of species numbers above 2000 m was observed by Kessler (2001a) in Carrasco National Park.

The increase of species numbers with (increasing) elevation is pronounced in Grammitidaceae, Hymenophyllaceae, and *Elaphoglossum* (Lomariopsidaceae), which have fewer species in Madidi and Sapecho than in Mosetenes and Cotapata. The taxon-specific patterns suggest that some taxa have a phylogenetically determined propensity for survival under extreme conditions (low temperatures, low humidity, and low light levels in the forest interior).

Vertical distribution of vascular epiphytes

We studied the vertical distribution of epiphyte groups within the different growth zones based on the data of the aforementioned *Ficus* sp. with 83 species, including 35 orchids and 28 ferns (Table 5). Overall, zones Z3-5 of the canopy had many more species than the trunk zones Z1-2b. The highest number of species was found on major limbs in the inner crown (Z3), in accordance with previous studies (ter Steege & Cornelissen, 1989; Ek *et al*., 1997; Freiberg, 1999; Krömer *et al*., 2007). Here, especially favorable growth conditions prevail in the area of large horizontal branches, presumably because light levels are reasonably high while the abundance of organic substrate and moss mats, which serve as water and nutrient suppliers of vascular epiphytes, provides optimal rooting conditions. In contrast to the other studies mentioned above and described in more detailed in Krömer *et al*. (2007), in Mosetenes ferns and not orchids were the most species-rich taxon in zone Z3. However, in the middle and outer crown (Z4-5) orchids were by far the most species-rich in Mosetenes in accordance with other studies. In the lower trunk area (Z1-2a), aroids together with ferns were most important, while orchids only appear in zone Z2b.

Interestingly, the understory with a surface of 20 x 20 m^2 had more epiphyte species (48) than any individual zone in the canopy (Table 5). This shows that small trees and shrubs in the understory of zonal forests, in contrast to young secondary forests, are well-suited for the establishment of epiphytes. Here, ferns were clearly the richest in species and even aroids outnumbered orchids (Table 5). Of the epiphyte species found in the understory, 28 were not recorded on the phorophyte; the majority of these species were ferns. This is another indication that the shady understory must also be inventoried for a complete sampling, whereas large trees must be sampled in order to consider all orchids, because many of these only grow in the canopy (Gradstein *et al*., 2003; Krömer *et al*., 2007).

Table 5. Species numbers of different epiphyte groups in the understorey (U) and within the vertical zones (Z1-5) of a sin-gle *Ficus* sp. tree at Cordillera Mosetenes.

	U	Z1	Z2a	Z2b	Z3	Z4	Z5
Location	Understory	Trunk base	Lower trunk	Upper trunk	Major limbs	Intermed. branches	Twigs
Araceae	12	4	4	3	6	3	2
Bromeliaceae	1	1	1	0	2	2	1
Orchidaceae	8	0	0	3	13	19	18
Pteridophyta	23	3	4	4	16	10	10
Other	4	0	1	1	5	2	3
Total	48	8	10	11	42	36	34

Conclusions and conservation implications

The high species richness of the vascular epiphyte communities at Mosetenes, including the highest values per 400 m^2 plot ever reported in Bolivia, show that mid-elevation forests are particularly important for the conservation of epiphytic plants. With ca. 207 species in 0.36 ha, the humid montane forest at Mosetenes is as species-rich as lower montane areas inventoried elsewhere in Bolivia (Ibisch, 1996) and Ecuador (Nieder *et al*., 1999; Werner *et al*., 2005), and richer than lower and upper montane cloud forests in Venezuela (Engwald, 1999; Kelly *et al*., 2004). In general, epiphyte richness in the Bolivian Andes shows a typical mid-elevation bulge that peaks around 1500-2000 m (Krömer *et al*., 2005), similar to other neotropical study sites in Ecuador (Küper *et al*., 2004), Peru (van der Werff & Consiglio, 2004), Costa Rica (Cardelús *et al*., 2006), and Chiapas, Mexico (Wolf & Flamenco, 2003). High epiphyte diversity is mainly correlated with the existence of old canopy trees and mature humid montane forests, emphasizing the importance of preserving natural forests of this kind. Fortunately, the natural protection of the Cordillera Mosetenes, in combination with the low density of valuable timber trees (Macía & Fuerte, 2008) inhibits a major logging activity in this area. This implies that for vascular epiphytes conservation of at least this site of the Cordillera Mosetenes is of low priority in Bolivia.

ACKNOWLEDGMENTS

We thank the National Geographic Society, the Weeden Foundation, the Deutsche Forschungsgemeinschaft, BIOPAT, the Deutsche Bromeliengesellschaft, and the A.F.W. Schimper-Stiftung for funding the field work, the official Bolivian institutions (Dirección Nacional para la Conservación de la Biodiversidad; Herbario Nacional) for permits and collaboration, T.B. Croat, H. Luther, G. Mathieu, J.T. Mickel, R.C. Moran, A.R. Smith, and R. Vásquez for species identifications, and F. Werner for reviewing the manuscript.

BIBLIOGRAPHY

Acebey, A., and T. Krömer. 2001. Diversidad y distribución vertical de epífitas en los alrededores del campamento río Eslabón y de la laguna Chalalán, Parque Nacional Madidi, Dpto. La Paz, Bolivia. Revista de la Sociedad Boliviana de Botánica. 3: 104-123.

Benzing, D.H. 1990. The biology of vascular epiphytes. Cambridge University Press. Cambridge, UK.

Cardelús, C.L., R.K. Colwell, and J.E. Watkins. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. Journal of Ecology 94: 144-156.

Coxson, D., and N.M. Nadkarni. 1995. Ecological roles of epiphtyes in nutrient cycles of forest ecosystems. In: Lowman, M. and N.M. Nadkarni (Eds.). Forest canopies. Academic Press. San Diego, California, USA. Pp. 495-546.

Ek, R.C., H. ter Steege, and K.C. Biesmeijer. 1997. Vertical distribution and associations of vascular epiphytes in four different forest types in the Guianas. In: TROPENBOS (Ed.). Botanical diversity in the tropical rain forest of Guyana. TROPENBOS. Utrecht, The Netherlands. Pp. 65-89.

Engwald, S. 1999. Diversität und Ökologie der vaskulären Epiphyten eines Berg- und eines Tieflandregenwaldes in Venezuela. Libri - Books on Demand. Hamburg, Germany.

Flores-Palacios, A., and J.G. García-Franco. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 22: 181-191.

Freiberg, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. Biotropica 28: 345-355.

Freiberg, M. 1999. The vascular epiphytes on a *Virola michelii* tree (Myristicaceae) in French Guiana. Ecotropica 5: 75-81.

Gentry, A.H., and C.H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. Annals of the Missouri Botanical Garden 74: 205-233.

Gradstein, S.R., N.M. Nadkarni, T. Krömer, I. Holz, and N. Nöske. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana 24: 105-111.

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

Hölscher, D., L. Köhler, A.I.J.M. Van Dijk, and L.A. Bruijnzeel. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. Journal of Hydrology 292: 308-322.

Ibisch, P.L. 1996. Neotropische Epiphytendiversität - das Beispiel Bolivien. Martina Galunder-Verlag. Wiehl, Germany.

Ibisch, P.L., A. Boegner, J. Nieder, and W. Barthlott. 1996. How diverse are neotropical epiphytes? An analysis based on the „Catalogue of flowering plants and gymnosperms of Peru“. Ecotropica 2: 13-28.

Ingram, A.U., S.W. Ferrell, K. Ingram, and N.M. Nadkarni. 1996. Floristic composition of vascular epiphytes in a Neotropical cloud forest, Monteverde, Costa Rica. Selbyana.17: 88-103.

Johansson, D.R. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica 59: 1-136.

Kelly D.L., G. O'Donovan, J. Feehan, S. Murphy, S.O. Drangeid, and L. Marcano-Berti. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. Journal of Tropical Ecology 20: 643-666.

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. 2001a. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. Biodiversity and Conservation 10: 1897-1921.

Kessler, M. 2001b. Pteridophyte species richness in Andean forests in Bolivia. Biodiversity and Conservation 10: 1473-1495.

Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. Journal of Biogeography 29: 1159-1165.

Kessler, M., A.R Smith., A. Acebey, and J. Gonzales. 2001. Registros adicionales de pteridófitos del Parque Nacional Carrasco, en el departamento de

Cochabamaba, Bolivia. Revista de la Sociedad Boliviana de Botanica 3: 146-150.

Kessler, M., A.R. Smith, and J. Gonzales. 1999. Inventarios de pteridófitos en una transecta altitudinal en el Parque Nacional Carrasco, dpto. Cochabamba, Bolivia. Revista de la Sociedad Boliviana de Botanica 2: 227-250.

Kessler, M., I. Jimenez, and T. Krömer. 2008. Diversity and endemism of six plant groups in the Cordillera Mosetenes, Cochabamba, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 23:15-25.

Köhler, L., C. Tobón, K.F.A. Frumau, and L.A. Bruijnzeel. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. Plant Ecology 193: 171-184.

Kreft, H., N. Köster, W. Küper, J. Nieder, and W. Barthlott. 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. Cuvillier Verlag. Göttingen, Germany.

Krömer, T., and S.R Gradstein. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. Selbyana 24: 190-195.

Krömer, T., M. Kessler, S.R. Gradstein, and A. Acebey. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. Journal of Biogeography 32: 1799-1809.

Krömer, T., M. Kessler, and S.R. Gradstein. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecology 189: 261-278.

Küper, W., H. Kreft, J. Nieder, N. Köster, and W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. Journal of Biogeography 31: 1477-1487.

Macía, M.J., and J. Fuertes. 2008. Composición florística y estructura de los árboles en un bosque tropical montano de la Cordillera Mosetenes, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 23: 1-14.

Nadkarni, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16: 249-256.

Nadkarni, N.M., and T. Matelson. 1989. Bird use of epiphyte resources in neotropical trees. Condor 69: 891-907.

Nieder, J., and W. Barthlott (Eds.). 2001. 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). Bonn, Germany.

Nieder, J., S. Engwald, and W. Barthlott. 1999. Patterns of neotropical epiphyte diversity. Selbyana 20: 66-75.

Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155-157.

Schimper, A.F.W. 1888. Die epiphytische Vegetation Amerikas. G. Fischer. Jena, Germany.

Schuettpelz, E., and D.W. Trapnell. 2006. Exceptional epiphyte diversity on a single tree in Costa Rica. Selbyana 27: 65-71.

Shaw, J.D., and D.M. Bergstrom. 1997. A rapid assessment technique of vascular epiphyte diversity at forest and regional levels. Selbyana 18: 195-199.

ter Steege, H., and J.H.C. Cornelissen. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21: 331-339.

van der Werff, H., and T. Consiglio. 2004. Distribution and conservation significance of endemic species of flowering plants in Peru. Biodiversity and Conservation 13: 1699-1713.

Werner, F., J. Homeier, and S.R. Gradstein. 2005. Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. Ecotropica 11: 21-40.

Wolf, J.H.D., and A. Flamenco. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. Journal of Biogeography 30: 1689-1707.

Zotz, G., and P. Hietz. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. Journal of Experimental Botany 52: 2067-2078.

Zotz, G., and S. Schultz. 2008. The vascular epiphytes of a lowland forest in Panama - species composition and spatial structure. Plant Ecology 195:131-141.

Appendix 1. Species of epiphytes recorded at the Laguna Carachupa study site in the Cordillera Mosetenes, distinguishing zonal forest habitats at 1250-1400 m, and ridge forest at 1500-1600 m.

	1250-1400	1500-1600	voucher
ARACEAE			
Anthurium ernestii Engler	x		MK 13027
Anthurium gracile (Rudge) Schott	x		MK 13084
Anthurium macleanii Schott	x	x	MK 12962
Anthurium scandens (Aubl.) Engl. s.l. sp. 1	x	x	MK 13026
Anthurium scandens (Aubl.) Engl. s.l. sp. 2	x	x	MK 13104
Anthurium scandens (Aubl.) Engl. s.l. sp. 3	x	x	MK 13153
Anthurium scandens (Aubl.) Engl. s.l. sp. 4	x		MK 13398
Anthurium versicolor Sodiro	x	x	MK 12966
Anthurium sp. 2	x		MK 13083
Monstera lechleriana Schott	x		MK 12963
Philodendron kroemerii Croat & Acebey	x	x	MK 13031
Philodendron lechlerianum Schott	x		MK 12972
Philodendron ornatum Schott	x	x	MK 13105
Philodendron cf. *palacioanum* Croat & Grayum	x		MK 12967
Philodendron sp. 1	x	x	MK 12971
Rhodospatha sp. 1	x		MK 12964
Rhodospatha sp. 2	x		MK 13017
Stenospermation reticulinervium Croat & Acebey	x	x	MK 13140
Stenospermation cf. *reticulinervium* Croat & Acebey	x		MK 13332
Stenospermation sp. 1	x	x	MK 13025
Stenospermation sp. 2		x	MK 13189
Stenospermation sp. 3		x	MK 13214
Xanthosoma sp.	x		MK 13298
Gen. sp.		x	MK 13281
ARALIACEAE			
Schefflera sp.	x	x	s.n.
BROMELIACEAE			
Guzmania killipiana L.B. Sm.	x	x	MK 13402
Guzmania melinonis Regel	x		MK 13093
Guzmania sphaeroidea (André) André ex Mez	x	x	MK 13132
Guzmania squarrosa (Mez & Sodiro) L.B. Sm. & Pittendr.		x	MK 13155
Racinaea schumanniana (Wittm.) J.R. Grant	x	x	MK 13126
Racinaea spiculosa (Ruiz & Pav.) M.A. Spencer & L.B. Sm.	x	x	MK 13399
Tillandsia asplundii L.B. Sm.		x	MK 13156
Vriesea heterandra (André) L.B. Sm.	x	x	MK 13401
CACTACEAE			
Rhipsalis cuneata Britt. & Rose	x		MK 13024
CLUSICEAE			
Clusia sp.	x	x	s.n.
CYCLANTHACEAE			
Gen. sp.	x	x	MK 13366
ERICACEAE			
Sphyrospermum cordifolium Bentham	x	x	MK 13030
Thibaudia sp.		x	MK 13464
Gen. sp. 1		x	MK 13203
Gen. sp. 2	x		MK 13345
Gen. sp. 3	x		MK 13346
Gen. sp. 4	x		MK 13360
GESNERIACEAE			
Gen. sp.	x		MK 12878
MARCGRAVIACEAE			
Noranthea cf. *anomala* Kunth	x		MK 13374

Cont. Appendix 1.

	1250-1400	1500-1600	voucher
MELASTOMATACEAE			
Blakea sp.	x	x	MK 13276
ORCHIDACEAE			
Cranichis sp.	x		MK 13085
Cranichis cf. sp.	x		MK 13357
Crossoglossa dodsonii Vásquez	x		MK 13086
Cyclopogon cf. sp.		x	MK 13247
Dichaea morrisii Fawc. & Rendl.	x		MK 13310
Dichaea muricata (Sw.) Lindl.	x	x	MK 13039
Dichaea sp. 1		x	MK 13202
Dichaea sp. 2		x	MK 13209
Dichaea trulla Rchb. F.		x	MK 13259
Elleanthus capitatus (Poepp. & Endl.) Rchb. F.	x		MK 13335
Elleanthus graminifolius (Barb. Rodr.) Lojmant	x	x	MK 13046
Elleanthus sp. 1	x		MK 13037
Elleanthus sp. 2	x	x	MK 13089
Elleanthus sp. 3		x	MK 13194
Epidendrum amplum D.E. Benn. & Christenson	x		MK 13088
Epidendrum armeniacum Lindl.	x		MK 13128
Epidendrum gr. *paniculatum* R. & Pav.	x		MK 13228
Epidendrum ramosum Jacq.	x		MK 13081
Epidendrum sp. 1	x		MK 13034
Epidendrum sp. 2		x	MK 13248
Epidendrum sp. 3	x		MK 13311
Epidendrum sp. 4	x		MK 13333
Epidendrum sp. 5	x		MK 13419
Epidendrum sp. 6	x		MK 13446
Epidendrum ?	x		MK 13425
Frondaria caulescens (Lindl.) Luer	x	x	MK 13182
Gongora sp. 1	x		MK 13033
Gongora sp. 2	x		MK 13434
Kefersteinia sp. 1	x		MK 13433
Kefersteinia sp. 2	x		MK 13450
Masdevallia sp.	x		MK 13370
Maxillaria aggregata (Kunth.) Lindl.		x	MK 13180
Maxillaria alpestris Lindl.		x	MK 13159
Maxillaria cf. *guareimensis* Rchb. F.	x	x	MK 13080
Maxillaria conferta (Griseb.) C. Schweinf.	x		MK 13348
Maxillaria juergensii Schltr.	x		MK 13440
Maxillaria longicaulis Schltr.		x	MK 13179
Maxillaria mapiriensis (Kraenz.) L.O. Williams	x	x	MK 13036
Maxillaria maria-isabelae J.T. Adwood		x	MK 13185
Maxillaria polyphylla Rchb. F.	x	x	MK 13197
Maxillaria reichenheimiana Endres & Rchb. F.	x		MK 13082
Maxillaria sp. 1	x		MK 13035
Maxillaria sp. 2	x		MK 13043
Maxillaria sp. 3	x		MK 13044
Maxillaria sp. 4	x		MK 13127
Maxillaria sp. 5		x	MK 13158
Maxillaria sp. 6	x	x	MK 13191
Maxillaria sp. 7	x	x	MK 13192
Maxillaria sp. 8	x	x	MK 13195
Maxillaria sp. 9		x	MK 13256
Maxillaria sp. 10	x		MK 13312
Maxillaria sp. 11	x		MK 13334
Maxillaria sp. 12	x		MK 13339
Maxillaria sp. 13	x		MK 13342
Maxillaria sp. 14	x		MK 13347
Maxillaria sp. 15	x		MK 13368
Maxillaria sp. 16	x		MK 13421
Maxillaria sp. 17	x		MK 13427
Maxillaria sp. 18	x		MK 13441

Cont. Appendix 1.

	1250-1400	1500-1600	voucher
Maxillaria sp. 19	x		MK 13442
Maxillaria sp. 20	x		MK 13445
Myoxanthus sp. 1		x	MK 13200
Myoxanthus sp. 2	x		MK 13341
Octomeria sp.	x		MK 13340
Odontoglossum sp.	x		MK 13424
Oncidium scansor Rchb. F.	x	x	MK 13160
Paphinia cristata Lindl.		x	MK 13210
Pityphyllum sp.	x	x	MK 13428
Pleurothallis ancora Luer & Vásquez	x		MK 13365
Pleurothallis discoidea Lindl.	x		MK 13363
Pleurothallis sp. 1	x		MK 13040
Pleurothallis sp. 2	x	x	MK 13207
Pleurothallis sp. 3		x	MK 13208
Pleurothallis sp. 4	x		MK 13217
Pleurothallis sp. 5		x	MK 13258
Pleurothallis sp. 6		x	MK 13283
Pleurothallis sp. 7	x		MK 13336
Pleurothallis sp. 8	x		MK 13337
Pleurothallis sp. 9	x		MK 13422
Pleurothallis sp. 10	x		MK 13423
Pleurothallis sp. 11	x		MK 13439
Prosthechea vasquezii Christenson	x	x	MK 13042
Rusbyella caespitosa Rolfe	x		MK 13426
Scaphyglottis lindeniana (A. Rich. & Gal.) L.O. Williams	x		MK 13367
Scaphyglottis sp.	x	x	MK 13190
Scelochilus sp.	x		MK 13313
Sobralia sp.	x		MK 13418
Stelis sp. 1	x	x	MK 13041
Stelis sp. 2	x	x	MK 13193
Stelis sp. 3		x	MK 13199
Stelis sp. 4		x	MK 13201
Stelis sp. 5		x	MK 13249
Stelis sp. 6		x	MK 13253
Telipogon sp.		x	MK 13255
Trichosalpinx cedralensis (Ames) Luer		x	MK 13220
Trichosalpinx sp.		x	MK 13211
Xylobium sp. 1	x		MK 13032
Xylobium sp. 2	x		MK 13338
Xylobium sp. 3	x		MK 13449
PIPERACEAE			
Peperomia alata Ruiz & Pav.	x		MK 12973
Peperomia aff. alata Ruiz & Pav.	x		MK 13435
Peperomia bangii C. DC.	x		MK 12977
Peperomia buchtienii Yunck.	x		MK 13023
Peperomia aff. *curruciformis* Trel.	x		MK 12975
Peperomia divaricata Yunck.	x		MK 13431
Peperomia lorentzii C. DC.	x		MK 12974
Peperomia quadrifolia (L.) Kunth	x		MK 13430
Peperomia tetraphylla Hook. & Arn.	x		MK 13448
Peperomia williamsii C. DC.	x	x	MK 13216
Peperomia sp. 1	x		MK 13361
PTERIDOPHYTA			
Asplenium auriculatum Sw.	x		MK 12944
Asplenium cuspidatum Lam.	x	x	MK 12996
Asplenium repens Hook.	x		MK 12953
Asplenium rutaceum (Willd.) Mett.	x		MK 12987
Blechnum acutum (Desv.) Mett.	x		MK 12928
Blechnum fragile (Liebm.) C.V. Morton & Lellinger	x		MK 13005
Campyloneurum asplundii (C. Chr.) Ching	x		MK 13010
Campyloneurum ophiocaulon (Klotzsch) Fée	x		MK 12931

Cont. Appendix 1.

	1250-1400	1500-1600	voucher
Ceradenia jungermannioides (Klotzsch) L.E. Bishop	x		MK 13326
Ceradenia pilipecten L.E. Bishop ex M. Kessler & A.R. Sm.		x	MK 13146
Ceradenia spixiana (Mart. ex Mett.) L. E. Bishop	x		MK 13324
Elaphoglossum andicola (Fée) T. Moore		x	MK 13173
Elaphoglossum angustius Mickel	x		MK 13013
Elaphoglossum ballivianii Rosenst.	x	x	MK 12997
Elaphoglossum blandum Rosenst.	x	x	MK 13152
Elaphoglossum buchtienii Rosenst.	x	x	MK 13020
Elaphoglossum eatonianum (E. Britton) C. Chr.	x	x	MK 13019
Elaphoglossum erinaceum (Fée) T. Moore	x		MK 12929
Elaphoglossum guentheri Rosenst.	x	x	MK 13170
Elaphoglossum inaequalifolium (Jenm.) C. Chr.		x	MK 13273
Elaphoglossum lloense (Hook.) T. Moore	x		MK 12947
Elaphoglossum nigrescens (Hook.) T. Moore ex Diels	x	x	MK 12941
Elaphoglossum orbignyanum (Fée) T. Moore	x	x	MK 12932
Elaphoglossum puberulentum M. Kessler & Mickel	x		MK 13007
Elaphoglossum smithii (Baker) H. Christ	x		MK 12998
Huperzia taxifolia (Sw.) Trevis. vel aff.	x		MK 13325
Hymenophyllum elegans Sprengel	x	x	MK 13175
Hymenophyllum fendlerianum J.W. Sturm	x		MK 13327pp
Hymenophyllum interruptum Kunze	x	x	MK 13053
Hymenophyllum microcarpum Desv.	x	x	MK 12984
Hymenophyllum polyanthos (Sw.) Sw.	x	x	MK 13278
Hymenophyllum cf. *trichomanoides* Bosch	x	x	MK 13327pp
Hymenophyllum undulatum (Sw.) Sw.		x	MK 13171
Melpomene xiphopteroides (Liebm.) A.R. Sm. & R.C. Moran	x	x	MK 13149
Microgramma fuscopunctata (Hook.) Vareschi	x		MK 12937
Microgramma percussa (Cav.) de la Sota	x	x	MK 12943
Nephrolepis pendula (Raddi) J. Sm.	x	x	MK 12994
Niphidium crassifolium (L.) Lellinger	x		MK 13011
Pleopeltis ballivianii (Rosenst.)	x		MK 12946
Polybotrya fractiserialis (Baker) J. Sm.	x		MK 13002
Polybotrya hickeyi R.C. Moran cf.	x		MK 12933
Polytaenium brasilianum (Desv.) Benedict	x		MK 12940
Pteris podophylla Sw.	x		MK 12990
Radiovittaria stipitata (Kunze) E.H. Crane	x	x	MK 13144
Salpichlaena volubilis (Kaulf.) Hook.	x	x	MK 12927
Serpocaulon latipes (Langsd. & Fisch.) A.R. Sm.	x	x	MK 12951
Serpocaulon latissimum (R.C. Moran & B. Øllg.) A.R. Sm.	x		MK 12938
Serpocaulon polystichum (Link) A.R. Sm.	x		MK 12989
Serpocaulon sessilifolium (Desv.) A.R. Sm.	x	x	MK 13174
Terpsichore mollissima (Fée) Proctor	x		MK 13021
Trichomanes herzogii Rosenst.	x		MK 12952
Vittaria graminifolia Kaulf.	x	x	MK 13008