



Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador

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ABSTRACT

Aim Although vascular epiphytes are important components of species richness and complexity of Neotropical forests, vascular epiphytes are under-represented in large scale biogeographical analyses. We studied the diversity, biogeography and floristic relationships of the epiphytic flora of the Yasuní region (Western Amazonia) in a Neotropical context, with special emphasis on the influence of the Andean flora on floristic composition and diversity of surrounding lowland forests.

Location Western Amazonian lowland rainforest, Tiputini Biodiversity Station (0°38' S 76°09' W, 230 m a.s.l., 650 ha), Yasuní National Park, Ecuador.

Methods We compared the vascular epiphyte flora of Yasuní with 16 published Neotropical epiphyte inventories. Secondly, based on a floristic database with records of more than 70,000 specimens of vascular epiphytes from the Neotropics the elevational composition of eight selected inventories was analysed in detail.

Results The vascular epiphyte flora of Yasuní is characterized by a very high species richness (313 spp.). A moderate portion of species is endemic to the Upper Napo region (*c.* 10%). However, this figure is much higher than previous analyses primarily based on woody species suggested. Geographical ranges of these species match with a proposed Pleistocene forest refuge. Compared with Northern and Central Amazonian sites, Western Amazonian epiphyte communities are characterized by a higher portion of montane and submontane species. Species richness of vascular epiphytes at the sites was correlated with the amount of rainfall, which is negatively correlated with the number of dry months.

Main conclusion Recent and historic patterns of rainfall are the driving forces behind diversity and floristic composition of vascular epiphytes in Western Amazonia: high annual rainfall in combination with low seasonality provides suitable conditions to harbour high species richness. The proximity to the Andes, the most important centre of speciation for most Neotropical epiphytic taxa, in combination with the climatic setting has allowed a continuous supply of species richness to the region. At least for epiphytes, the borderline between the Andean and Amazonian flora is much hazier than previously thought. Moreover, the comparatively moist climate in Western Amazonia during the Pleistocene has probably led to fewer extinctions and/or more speciation than in more affected surrounding lowlands.

Keywords

Amazon basin, Andes, floristic composition, Pleistocene refugia, rainfall–diversity relationship, seasonality, species richness, Tiputini Biodiversity Station, Upper Napo.

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INTRODUCTION

Our present knowledge on structure, diversity and phyto-geography of Neotropical forests is mainly based on studies of woody plants (e.g. Prance, 1982; Gentry, 1995, 1988; de Oliveira & Daly, 1999; Pitman *et al.*, 2001, 2002; Condit *et al.*, 2002; ter Steege *et al.*, 2003), although non-woody life-forms are largely responsible for the high species richness and ecological complexity of these ecosystems (Gentry & Dodson, 1987a; Nieder *et al.*, 1999). In a mega-diverse tropical country such as Ecuador, epiphytes contribute up to 27% to the total flora (Jørgensen & León-Yáñez, 1999), and on a local scale they may even outnumber all other life-forms (Kelly *et al.*, 1994; Ibisch, 1996; Schneider, 2001). However, studies explicitly addressing biogeographical aspects of epiphytes (e.g. Gentry & Dodson, 1987a; Benzing, 1989; Kelly *et al.*, 1994; Nieder *et al.*, 1999; Kessler, 2001a; Wolf & Flamenco-S, 2003) are scarce, often based on data from only a very few study sites or restricted to a narrowly defined region. This under-exploration of vascular epiphytes is probably because of the inaccessibility of the epiphytic habitat and – in contrast to woody plants – a lack of standardized sampling methods (compare Nieder & Zotz, 1998). Furthermore, because of a lack of monographic treatments of many epiphytic taxa, epiphytes are largely under-represented in data sets of large-scale biogeographical and diversity analyses (e.g. Balslev, 1988; Borchsenius, 1997). However, understanding of biogeographical patterns and underlying causes is urgently needed to develop scientific concepts for conservation planning.

The westernmost part of the Amazon basin is one of the richest regions of the world in terms of plant diversity (Barthlott *et al.*, 1996, 1999; Gentry, 1988). Alpha-diversity of trees (Korning & Balslev, 1994; Valencia *et al.*, 1994; Gentry, 1988) and lianas (Nabe-Nielsen, 2001) is the highest ever recorded. Although the flora of the Yasuní region can be

considered relatively well collected compared with other parts of Amazonia (Herrera-MacBryde & Neill, 1997; Pitman, 2000), biogeographical origin and floristic relationships on a larger scale have not been studied in detail. We therefore conducted the first analysis of the diversity and biogeography of vascular epiphytes in Western Amazonia in a Neotropical context. In this paper, we attempt to quantify different phyto-geographical influences exemplarily for a regional epiphyte flora in Western Amazonia and analyse local to regional diversity patterns.

METHODS

Study area

Fieldwork was carried out from November 2001 to March 2002 at the Tiputini Biodiversity Station (TBS). The TBS (0°38' S 76°09' W, 230 m a.s.l., 650 ha) is situated in the province of Orellana, Ecuador, at the Río Tiputini, a tributary of the Río Napo (Fig. 1). The Río Tiputini represents the border to Yasuní National Park (982,000 ha) which – together with the Waorani Ethnic Reserve (610,000 ha) – is Ecuador's largest protected area (Herrera-MacBryde & Neill, 1997). In general, the topography of the region is flat at about 230 m a.s.l. and only interrupted by minor streams and ravines.

Because there are no long-term climate data available, Pitman (2000) interpolated mean monthly precipitations and temperatures for Yasuní from suitable records of surrounding climate stations (Fig. 2). The climate is characterized by relatively high and largely non-seasonal rainfall. Mean annual precipitation is about 3200 mm with all months exceeding 200 mm on average. Precipitation in Yasuní is directly influenced by the proximity of the Andes, with a steep gradient of annual rainfall increasing towards the Andean foothills which receive more than 4000 mm year⁻¹. Mean

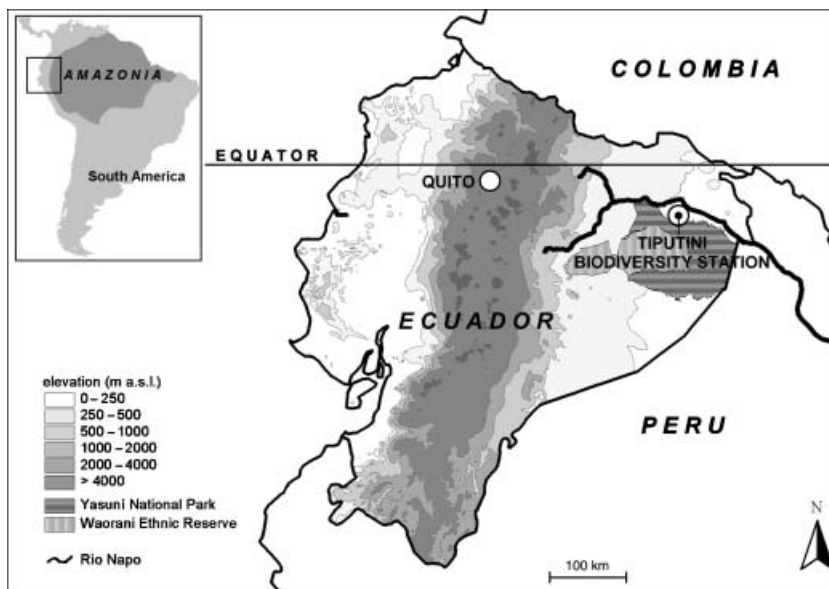


Figure 1 Position of the Tiputini Biodiversity Station, Yasuní National Park, and Waorani Ethnic Reserve.

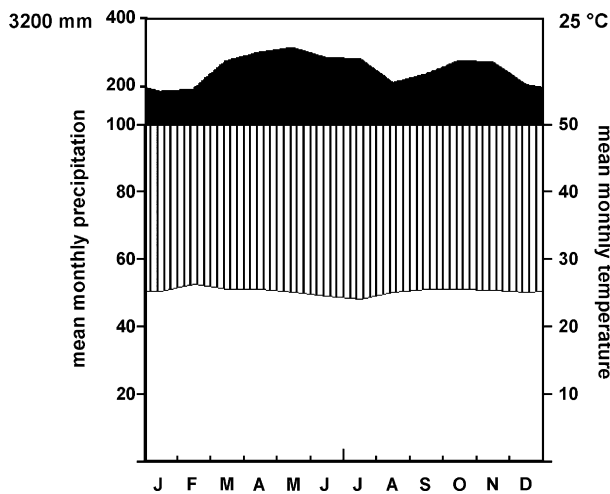


Figure 2 Climate diagram according to Walter & Lieth (1967) for the Yasuní region after data from Pitman (2000).

annual temperature in Yasuní is about 25 °C without seasonal changes.

Yasuní belongs to a big block of still intact Amazonian lowland rainforest named either 'Napo Moist Forest' (Olson *et al.*, 2001) or 'Napo Piedmont' (Pitman, 2000). The whole region of the Upper Napo falls into the category of 'Tropical Moist Forest' after Holdridge's (1967) classification scheme. Most of the Yasuní region is covered with primary terra firme forests and the canopy normally reaches a height of 30 m. Common tree species of the upper canopy are *Iriartea deltoidea* Ruiz & Pav., *Eschweilera coriacea* (DC.) S.A. Mori, *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr. and *Otoba glycyarpa* (Ducke) W.A. Rodriguez & T.S. Jaramillo (Pitman, 2000). Typical trees of the middle and lower canopy are *Rinorea apiculata* Hekking, *Matisia malacocalyx* (A. Robyns & S. Nilsson) W.S. Alverson, *Brownea grandiceps* Jacq. and *Grias neubertii* J.F. Macbr. Emergent tree species, commonly exceeding 40 m, are e.g. *Ceiba pentandra* (L.) Gaertn., *Parkia multijuga* Benth. and *Cedrelinga cateniformis* (Ducke) Ducke. Terra firme formations in the region are characterized by an extraordinarily high density of old emergent trees. Various authors explain this observation with the high maturity and integrity of these forests (Korning & Balslev, 1994; Pitman, 2000). Along the Tiputini river terra firme formations are replaced by narrow strips of frequently inundated floodplain forests. Furthermore, small patches of palm swamps dominated by *Mauritia flexuosa* L.f. occur locally.

The tree species richness in the Yasuní region is among the highest of the world. Pitman (2000) found a mean of 248 tree species (d.b.h. ≥ 10 cm) in a series of 1-ha plots. Romoleroux *et al.* (1997) even recorded 825 species of woody plants (≥ 1 cm) on 2 ha and Nabe-Nielsen (2001) 96 liana species in a 0.2-ha plot, the highest number so far reported. Leimbeck & Balslev's (2001) survey of (hemi-)epiphytic Araceae in adjacent floodplain and terra firme forests is the only study addressing explicitly the epiphytic vegetation of Yasuní. They found a

generally high species richness and higher abundance and diversity in flooded forests. Freiberg & Freiberg (2000) studied differences in biomass and diversity of vascular epiphytes on single trees between two lowland rainforests within the Yasuní region and two Ecuadorian montane forests.

Field sampling and identification

The definition of the term 'epiphyte' is here used in a broad sense sensu Barkman (1958), including holo-epiphytes, which grow exclusively epiphytic throughout their life, as well as hemi-epiphytes, which have one epiphytic phase during their life cycle. We did not include (hemi-) parasitic plants (i.e. Loranthaceae) as proposed by Benzing (1990), as they draw water and nutrients from their host and for this reason are ecologically unlike.

The total area of the TBS (650 ha) was representatively sampled including all habitat types. Collections were conducted on selected phorophytes using alpine climbing techniques (Perry, 1978), in tree fall gaps, along trails, and along the Tiputini river and an adjacent black-water system. Additionally, the epiphytic vegetation of an 0.1-ha plot was surveyed in detail. In this plot, the three-dimensional position of every epiphytic plant of a size of ≥ 1 cm on trees with d.b.h. ≥ 10 cm was determined. A detailed analysis of the micro-spatial distribution patterns within the plot will be published elsewhere.

Specimens were identified with the aid of herbarium material at QCA and QCNE. Identifications were kindly checked by T.B. Croat (MO, Araceae), C.H. Dodson (MO, Orchidaceae in part), J.M. Manzanares (Quito, Bromeliaceae in part), J. Mickel (NYBG, Elaphoglossum) and H. Navarrete (QCA, Pteridophyta). Voucher specimens (leg. numbers: Köster & Kreft #1-1219) are deposited at QCA, QCNE, QUSF, and a set of aroid duplicates at MO. For a complete species list see Appendix S1 in Supplementary Material.

Biogeographical data base and analysis

In order to analyse the diversity and biogeography of the vascular epiphyte flora of Yasuní we applied a comparative approach. All analyses are based on two independent data sets: first, we collected checklists of 16 other Neotropical study sites of comparable size and state of exploration (see Table 1) based on our own former study sites and published florulas and checklists. Additionally, some species richness figures were taken from the literature for some study sites. This data set was used to compare species richness and systematic composition of the vascular epiphytes at different study sites with special emphasis on the effect of altitude, rainfall and seasonality. Floristic similarities between all sites were measured with Sørensen's Index.

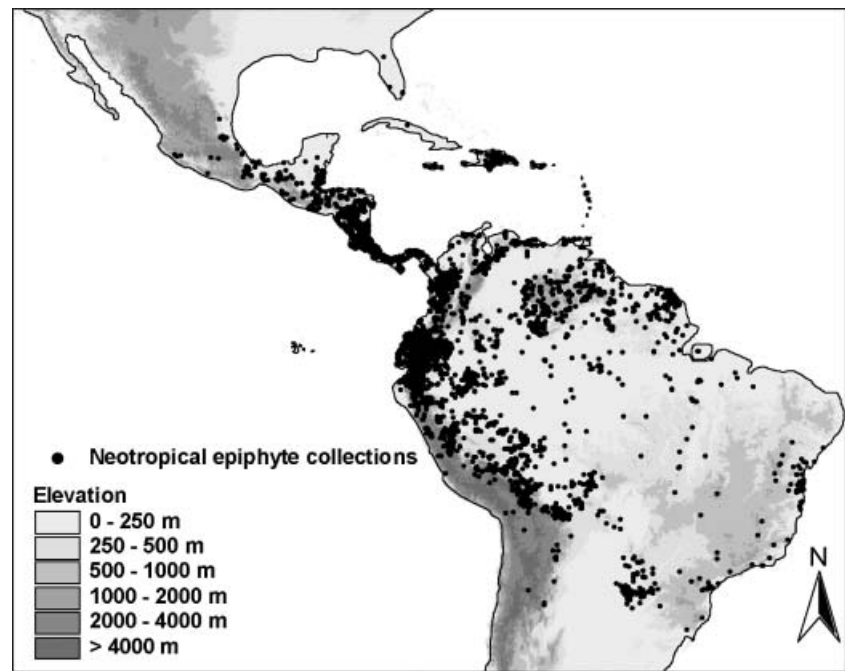
Secondly, for each reliably determined species from Yasuní distribution data were collected based on label data from herbarium specimens (QCA, QCNE, AAU, MO, NYBG; see *Acknowledgments*). Specimen label data including locality

Table 1 Summarized data of the analysed Neotropical epiphyte floras. Species, genus, and family numbers and relative contribution of different families (ORCH-Orchidaceae, PTER - pteridophytes, BROM - Bromeliaceae, ERIC - Ericaceae, GESN - Gesneriaceae, PIP - Piperaceae) to species richness in percentage

No.	Country	Study site	Location	Elevation (m a.s.l.)	No. spp.	No. gen.	No. fam.	ORCH%	PTER%	ARAC%	BROM%	ERIC%	GESN%	PIP%	Others%
Lowland															
1	Ecuador	Tiputini Biodiversity Station ¹	0°64' S 76°9' W	220	313	100	25	29.8	21.9	22.2	6.7	0.0	2.5	3.5	13.4
2	Ecuador	Jatun Sacha ²	1°7' S 77°36' W	450	393	118	25	35.4	17.3	17.6	4.6	1.0	4.8	3.1	16.2
3	Ecuador	Rio Palenque ³	1°43' S 79°44' W	220	297	129	29	34.0	12.0	15.0	7.5	1.0	5.0	2.4	23.1
4	Costa Rica	La Selva ⁴	10°42' N 84°0' W	115	391	122	32	32.4	6.6	20.4	9.1	0.6	5.7	5.1	20.1
5	Bolivia	Madidi ⁵	14°45' S 67°55' W	250–500	152	72	19	35.5	28.3	15.8	6.6	0.0	0.7	8.6	4.5
6	Venezuela	Surumoni Crane Project ⁶	3°17' N 65°40' W	100	148	62	23	45.9	11.5	20.9	7.4	0.0	2.7	5.4	6.2
7	Brazil	Reserva Ducke; Manaus ⁷	2°87' S 59°57' W	80	248	100	29	33.9	14.9	17.8	6.2	0.4	2.5	0.4	23.9
8	Guayana	Iwokrama ⁸	4°50' N 58°50' W	120	178	84	29	34.2	26.7	17.4	3.1	0.0	2.5	3.5	12.6
9	Guayana	Kaieeteur ⁹	5°17' N 59°29' W	750	202	84	33	31.1	26.0	10.7	15.3	1.7	1.7	2.6	10.9
Montane															
10	Venezuela	La Montana ¹⁰	8°37' N 71°03' W	2600	128	35	13	53.9	24.3	5.2	11.3	2.6	0.0	1.7	1.0
11	Venezuela	La Carbonera ^{11,12}	8°62' N 71°21' W	2200–2700	191	55	20	49.7	29.8	3.7	5.2	1.0	0.5	6.3	3.8
12	Bolivia	Sehuencas ¹³	17°50' S 65°16' W	2100–2300	230	77	30	53.5	19.1	0.9	8.3	2.6	0.9	6.9	7.8
13	Costa Rica	Monteverde ¹⁴	10°30' N 84°48' W	1500–1550	333	105	37	41.7	16.5	3.9	7.2	3.9	3.3	4.2	19.3
14	Ecuador	Podocarpus National Park ¹⁵	4°1' S 79°1' W	1800–3400	644	121	24	50.6	23.4	4.7	12.4	1.7	1.4	4.3	1.5
15	Ecuador	Guajalito ¹⁶	0°22' S 78°48' W	1800–2200	256	70	29	31.6	23.4	13.7	11.3	3.1	3.5	4.3	9.1
16	Ecuador	Otonga ¹⁶	0°42' S 79°0' W	1400–2200	456	93	30	36.4	23.7	11.2	5.9	5.7	4.2	3.7	9.2
17	Ecuador	Maquipucuma ¹⁷	0°17' N 78°38' W	1100–2800	453	123	32	35.2	24.2	12.4	7.5	2.6	3.3	7.0	7.8

Sources: ¹this study, ²Missouri Botanical Garden (2002), ³Gentry & Dodson (1987a), ⁴Hammel (unpublished), ⁵Acebey & Krömer (2001), ⁶Schmit-Neuerburg (2002), ⁷Ribeiro et al. (1999), ⁸Clarke et al. (2001), ⁹Kelloff & Funk (1998), ¹⁰Kelly et al. (1994), ¹¹Engwald (1999), ¹²Barthlott et al. (2001), ¹³Ibisch (1996), ¹⁴Ingram et al. (1996), ¹⁵Bussmann (2001), ¹⁶Küper et al. (2004), ¹⁷Webster & Rhode (2001).

Figure 3 Distribution of more than 70,000 Neotropical epiphyte collections of the species from Yasuní and seven other study sites in the floristic data base (list in text).



names, elevation and geographical coordinates of the plant collection locality were checked and – if necessary – georeferenced. Collection records with obviously inaccurate or doubtful data were excluded from the analyses. All collection data were entered in a database and a GIS (ArcView 3.2). In order to compare our results from Yasuní, we compiled distribution data for all species of another seven Neotropical epiphyte inventories in the same way (Jatun Sacha, Reserva Ducke, Surumoni, Otonga, Guajalito, La Carbonera, La Montana; see Table 1). In all, the database consists of more than 70,000 individual plant collections (Fig. 3).

We attempted to quantify the influence of the Andes and the different elevational belts upon species composition in Yasuní and the seven other inventories. Species are not uniformly distributed within their geographical range (Hengeveld, 1990; Brown, 1995; Brown & Lomolino, 1998). Along large-scale environmental gradients (e.g. latitude or elevation), the abundance of a species rather tends to decrease from the centre of the range towards its margins (Hengeveld & Haeck, 1982). This frequently observed pattern is considered to reflect a complex response of the geographic range to the niche requirements of a species (Brown, 1984). The variability in the abundance of populations along large-scale gradients can also be observed in the density of collections made of a certain species (Fig. 4, compare Hengeveld & Haeck, 1982). It is self-evident that altitude can only be regarded as a proxy for the change of a variety of major abiotic determinants of plant distributions that change with altitude (i.e. rainfall, humidity, temperature, frequency of frost etc.).

For each species the centre of its elevational distribution was derived from all collection records included in the floristic data base:

$$C_e = \frac{[(E_{\max} + E_{\min})/2] + (\sum_{i=1}^n E_{CL})/n}{2}$$

Derivation of the centre of elevational distribution (C_e) of a single species: E_{\max} , highest recorded elevation; E_{\min} , lowest recorded elevation; E_{CL} , elevation of collection locality; n , number of collections.

We have chosen this approximation to weigh the observed absolute elevational range as well as the density of collection of each species per altitude class. Thereby we attempt to minimize possible bias of poorly collected species and consider empirical observations that density is not an equal distribution (Hengeveld & Haeck, 1982, compare Fig. 4). The elevational composition of the whole epiphytic flora of a study site was summarized by adding up centres of all species in classes of 500 m width. All statistics were performed with STATISTICA (StatSoft, 1999).

RESULTS

Species richness and systematic composition of the vascular epiphyte flora of Yasuní

Three hundred and thirteen epiphytic taxa were recorded for the area of the TBS (a complete species list is given in Appendix 1). Of these, 256 could be identified to species level. Compared with other Neotropical lowland sites, species richness is remarkably high (see Table 1 and Fig. 7). Higher species numbers are solely achieved by the Costa Rican site La Selva and by the Ecuadorian sites Jatun Sacha and Centinela. In our 0.1-ha plot at Tiputini we recorded 8762 epiphytic individuals from 146 species, to our knowledge the highest

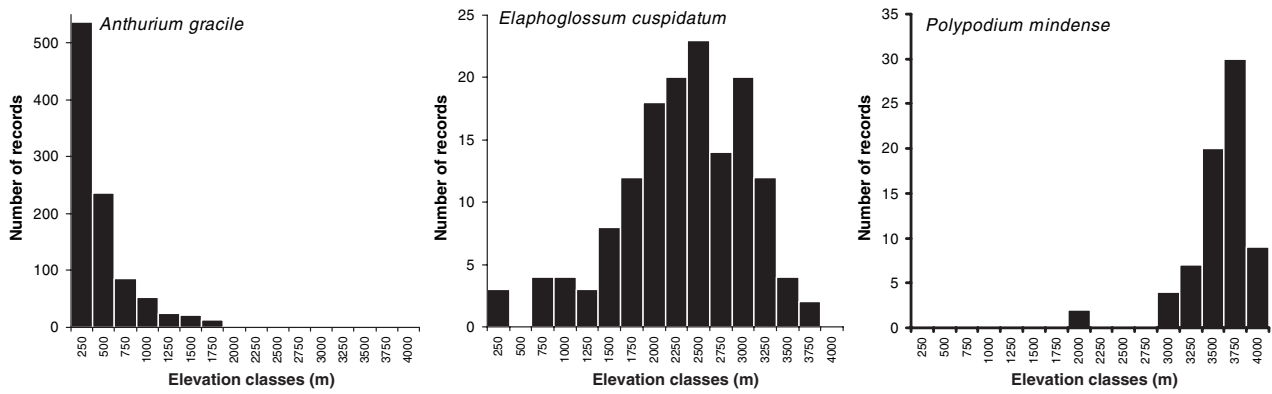


Figure 4 Distribution of collections along the elevational gradient from the floristic data base for three exemplary species. Number of records per 250-m-elevation-class.

numbers ever recorded for a lowland plot of that size. Eighty-one epiphyte species were recorded on a single emergent *Ceiba pentandra* (Bombacaceae) in immediate vicinity of the plot. This high alpha-diversity goes along with comparatively low beta-diversity (sensu Whittaker, 1977), as nearly half of the regional species pool is present in the study plot. Highest relative contribution to species richness was found for Orchidaceae (30%), followed by Araceae and pteridophytes (both 22%). The familial composition is similar to other Neotropical lowland epiphyte inventories (compare Table 1). In general, the systematic composition of Neotropical epiphyte communities is highly predictable at the family level (Fig. 5, Table 1). At all compared sites Orchidaceae are the most species rich family followed by either Araceae or Pteridophytes.

Floristic similarities to other Neotropical study sites and geographical distribution patterns

The floristic relationship of the vascular epiphytes of Tiputini to 16 other Neotropical study sites is shown in Fig. 6 as a result of a principal co-ordinate analysis (PCoA). Montane sites are well separated from lowland sites. Each main cluster group consists of two distinct subgroups. All study sites that fall into the group of Tiputini are situated in proximity to the Andes and characterized by high and largely non-seasonal annual rainfalls. The Northern and Central Amazonian sites are floristically distinct from these sites and form a different group of closely related sites.

The epiphyte species of Yasuni belong to mainly four distinct geographic distribution patterns (Fig. 7): a large

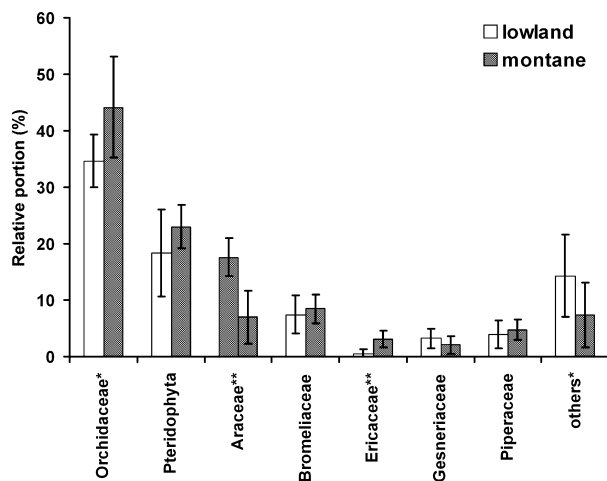


Figure 5 Mean proportion of the most important families at various Neotropical lowland and montane study sites (compare Table 1). Statistically significant differences between montane and lowland sites are marked with asterisks (* $P < 0.05$; ** $P < 0.001$; t -tests). Error bars indicate standard deviations.

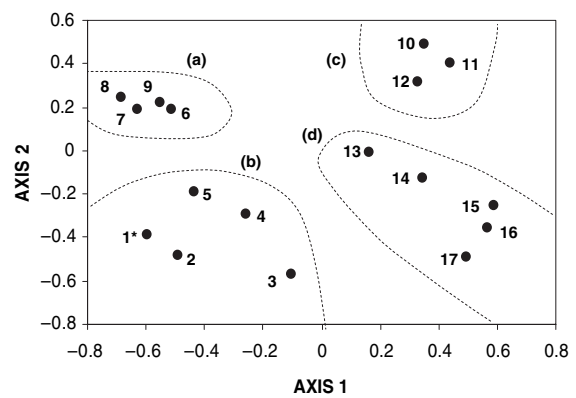
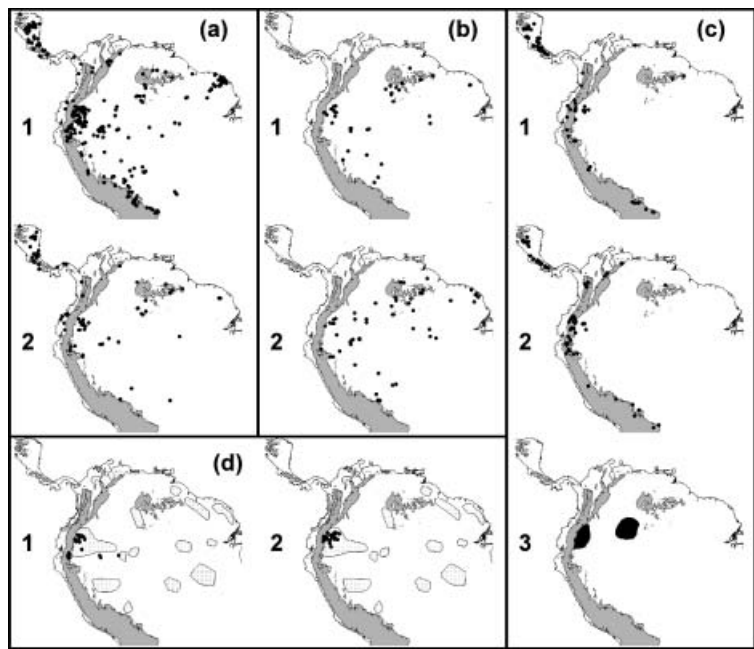


Figure 6 Floristic relationship of the epiphyte flora of Tiputini (1*) and of 16 other Neotropical study sites. Principal co-ordinate analysis (PCoA) based on a similarity matrix (Sørensen's Index). Montane sites (dashed line) are well separated from lowland sites (continuous line). Four sub-groups are revealed: (a) Northern and Central Amazonia, (b) Western Amazonia and other peri-Andean lowlands, (c) Lower montane, (d) Upper montane. Numbering of study sites corresponds to Table 1.

Figure 7 Typical geographical ranges for exemplary species from Yasuní. (a) Species widespread in Neotropical lowlands (1, *Anthurium gracile*; 2, *Codonanthe crassifolia*). (b) Amazonian species (1, *Aechmea mertensii*; 2, *Philodendron hylaeae*); (c) Species with a principal montane distribution which also occur in the Western Amazonian lowlands [1, *Pleopeltis macrocarpa*; 2, *Polypodium loriceum*; 3. dark-shaded areas mark regions within Amazonia with mean annual precipitation > 3000 mm and all months > 100 mm (data after New *et al.* (2002) and ter Steege *et al.* (2003))]. (d) Endemic species of the Upper Napo region [1, *Aechmea hoppii*; 2, *Rhodospatha neillii*; 3, dark-shaded areas show Pleistocene forest refugia after Prance (1982)].



number of species has a wide geographical range – many of them occurring in virtually all Neotropical humid lowlands (Fig. 7a). Species restricted to Amazonia (Fig. 7b) form another important group of species in Yasuní. At least 10% of the species are endemics of a comparatively small region of the westernmost part of Amazonia known as the Napo region (Fig. 7d). A considerable high number of species (about 15%) shows a principal Andean distribution but also occur in the high rainfall/low seasonality regions of Western Amazonian lowlands (Fig. 7c).

Elevational composition

Each floristic group identified in the PCoA is also distinguished by a characteristic elevational composition (Fig. 8). The Northern and Central Amazonian sites Reserva Ducke and Surumoni are characterized by a high portion of true lowland species (i.e. centre of altitudinal distribution < 500 m; 50% and 54%, respectively). There is only minor presence of species with a broad elevational range. As expected, most species have the centre of their elevational distribution within the class where the site itself is situated. In this regard, the floristic composition of the Western Amazonian Tiputini and Jatun Sacha differs markedly from all other Neotropical sites. The elevational composition is significantly shifted towards a higher percentage of (sub-) montane species within the flora (18–22%). Lowland species are merely the second largest group (28%). Most of the species do not have the centre of their elevational distribution within the particular elevational class of the site. The four study sites belonging to the two montane clusters have their maximum in the respective class where the study site is situated. In the upper montane group there is stronger influence from lower elevations, whereas the

spectrum of the lower montane sites resembles a bell-shaped curve with approximately intermediate influence from higher as well as from lower elevations.

Rainfall and seasonality as determinants of large-scale patterns of species richness

The comparison of Neotropical epiphyte inventories indicates two climatic parameters as strong predictors for epiphyte diversity: annual rainfall and its distribution throughout the year (here we measured seasonality as the number of months with < 100 mm precipitation, Fig. 9). Species richness of epiphytes on the examined spatial scale increases in an S-shaped mode with increasing precipitation (Fig. 9a), whereas it decreases with increasing number of dry months (Fig. 9b) ($r^2 = 0.86$ and 0.88 , respectively; all $P < 0.0001$, best-fit nonlinear regression). Both parameters are highly correlated (Pearson $r = -0.93$, $P < 0.0001$).

DISCUSSION

Determinants of epiphyte diversity on regional and continental scale

The epiphyte flora of Yasuní belongs to the most speciose Neotropical lowland sites. The comparison of species numbers of epiphytes at different Neotropical lowland sites reveals a sigmoid increase of species richness with increasing annual precipitation and a strong decrease with increasing seasonality (Fig. 9). Both climatic parameters show a high correlation and explain most of the variation in epiphyte diversity on the examined geographical scale. We attribute low species richness and relatively slow increase in low rainfall regions to the

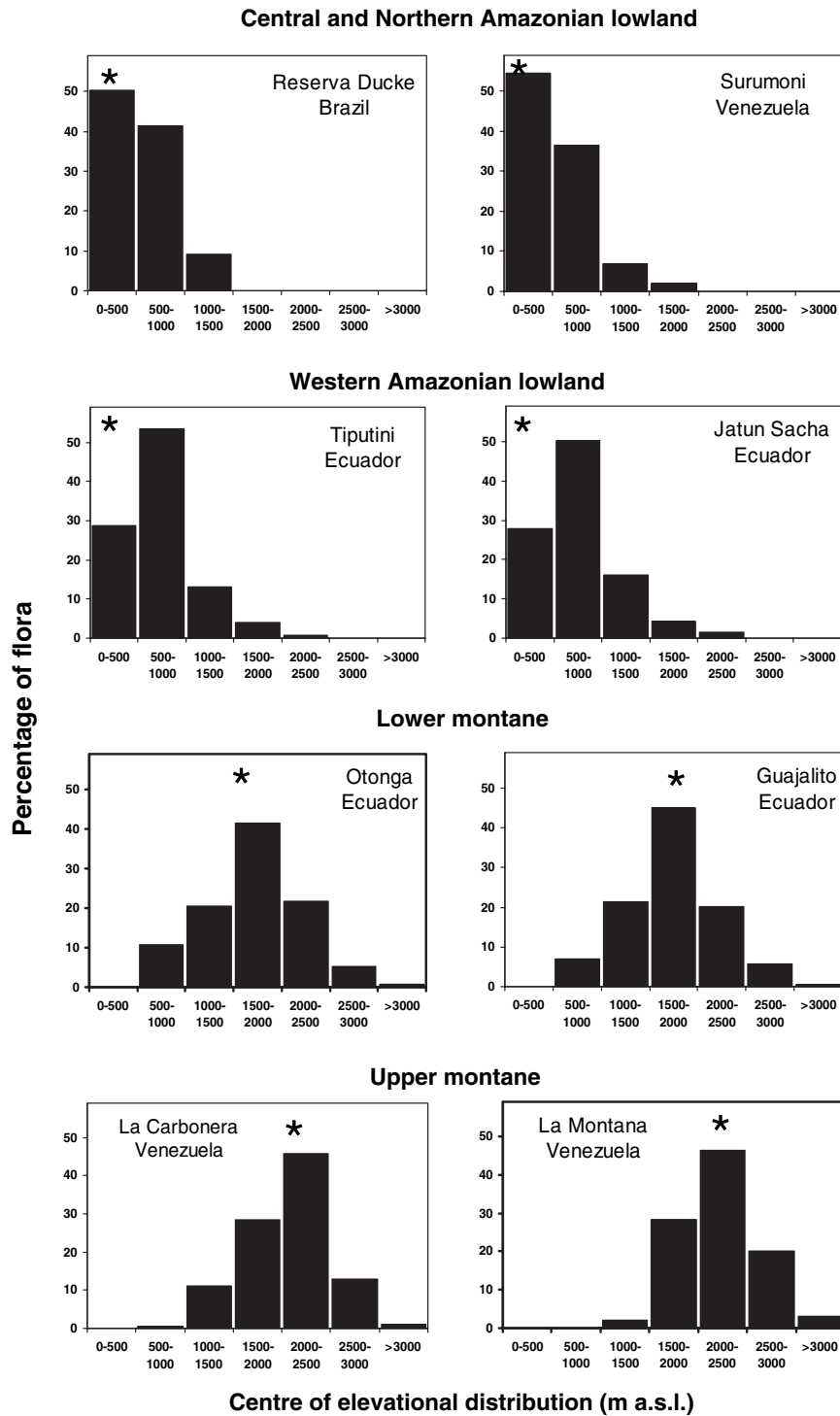


Figure 8 Elevational composition of the epiphytic flora of Yasuni and seven other Neotropical study sites. Asterisks indicate the respective altitude class where the site itself is located in.

presence of only very few, highly specialized species which have to resist long periods of harsh climatic conditions. Highest species richness is reached at wet forest sites with about 4000 mm rainfall and little seasonality. At the upper end of the rainfall range epiphyte diversity seems to tend towards a

maximum. Contradicting data are reported by Wolf & Flanenco-S (2003) for Chiapas where maximum species richness was found in regions between 2000 and 2500 mm annual rainfall because of a decrease in wind dispersed taxa. However, predictions about species richness at the wettest

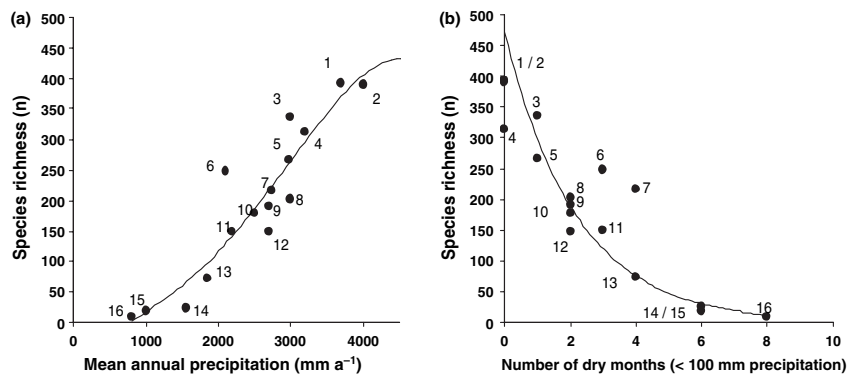


Figure 9 Relationship between mean annual precipitation (a, $r^2 = 0.86$; $P < 0.0001$) and length of dry season (b, $r^2 = 0.88$; $P < 0.0001$) to species richness of vascular epiphytes at various Neotropical lowland sites. 1, Jatun Sacha, Ecuador (Missouri Botanical Garden, 2002); 2, La Selva, Costa Rica (Hammel unpublished); 3, Centinela, Ecuador (Gentry & Dodson, 1987a); 4, Tiputini, Ecuador (this study); 5, Palenque, Ecuador (Gentry & Dodson, 1987a); 6, Reserva Ducke, Brazil (Ribeiro *et al.*, 1999); 7, BCI, Panama (Croat, 1978); 8, Kaieteur, Guyana (Kelloff & Funk, 1998); 9, Mabura Hill, Guyana (Ek, 1997); 10, Iwokrama, Guyana (Clarke *et al.*, 2001); 11, Manu, Peru (Foster, 1990); 12, Surumoni, Venezuela (Schmit-Neuerburg, 2002); 13, Jauneche, Ecuador (Gentry & Dodson, 1987a); 14, Santa Rosa, Costa Rica (Gentry & Dodson, 1987a); 15, Pico das Almas, Brazil (Stannard, 1995); 16, Capeira, Ecuador (Gentry & Dodson, 1987a). If not given in the original sources, values for mean annual precipitation and length of dry season were estimated from New *et al.* (2002) and ter Steege *et al.* (2003).

Neotropical sites (i.e. > 4000 mm) remain elusive because of the few available data from very wet sites.

Correlations between parameters of rainfall and species richness of vascular epiphytes are much stronger than reported, for example, for trees (Givnish, 1999). The analysis of Amazonian and Guianan tree data from ter Steege *et al.* (2000) even implies that mean annual precipitation is a weak predictor for alpha-diversity of Amazonian tree communities. Epiphytes, on the other hand, occupy an 'unusually climate-defined ecospace' (Benzing, 1998). In fact, recent ecophysiological studies show that epiphytic growth is more water- than nutrient-limited (Laube & Zotz, 2003). Seasonality and interannual changes of rainfall like, e.g. El Niño years are also very likely to affect growth and mortality of epiphytes (Schmit-Neuerburg, 2002; Laube & Zotz, 2003), thus affecting overall patterns of species richness. Especially during the juvenile phase many epiphytic species are very sensitive towards drought (Zotz, 1998; Zotz & Hietz, 2001). As rainfall and seasonality are far from being homogenously distributed across Amazonia (compare ter Steege *et al.*, 2003), earlier hypotheses claiming that diversity of Amazonian epiphyte communities is evenly low (Nieder *et al.*, 1999) have to be revised. On the contrary, there are considerable differences in epiphyte diversity within Amazonia associated with gradients of annual rainfall and number of dry months ranging from about 150 epiphyte species at the Southern Venezuelan site Surumoni (Schmit-Neuerburg, 2002) to roughly 400 epiphyte species at the Western Amazonian Jatun Sacha (Missouri Botanical Garden, 2002).

Western Amazonian endemics: the Pleistocene refugia debate

According to the *Catalogue of the Vascular Plants of Ecuador* (Jørgensen & León-Yáñez, 1999) 2% of the epiphytes

recorded in this study for Yasuní are endemic to Ecuador. Compared with the Ecuadorian mid-elevation forest site Otonga, where at least 15% of the epiphyte species are endemic to Ecuador (Küper *et al.*, in press), endemism in Western Amazonia seems to be negligibly low. However, as the Napo region comprises parts of Ecuador, Colombia, and Peru, endemism of epiphytes in this region is probably much higher than previously estimated by national accounts for Ecuador (compare also Balslev, 1988; Borchsenius, 1997). In a recent evaluation for Western Amazonian tree communities, Pitman *et al.* (1999) estimate that endemism in the Yasuní region does not exceed 2%. Based on our data (compare Fig. 7d) we estimate that at least 10% of the epiphyte species of Yasuní are endemic to the region of the Upper Napo – a relatively small portion of Western Amazonia comprising about 100,000 km². This notable difference between epiphytic and terrestrial plants is somewhat conflicting to the prevalent hypothesis that epiphytes tend to have larger ranges than terrestrial plants (e.g. Nieder *et al.*, 1999; Kessler, 2000, 2001a). In fact, most species in Yasuní have a very wide distribution (compare Fig. 7a and b). On the contrary, there is a stereotypical distribution pattern (Fig. 7d) that strikingly corresponds with the Upper Napo refugia – the largest of the rain forest refugia proposed by Prance (1982) and other authors and a region characterized by high rainfall and low seasonality present climate. We do not attribute the observed patterns to sampling bias, because Yasuní is surrounded by comparatively well collected areas (Herrera-MacBryde & Neill, 1997; Pitman, 2000).

How Amazonian vegetation and its biota were affected by drier periods during the Pleistocene and what consequences this had on speciation and extinction in the Neotropics has been a controversial and heavily discussed issue since the proposition of the refugia theory more than 30 years ago (Haffer, 1969). Advocates of the refugia theory state that a

reduction of rainfall in Amazonia has led to significant changes in vegetation structure and species composition (Haffer & Prance, 2001), whereas its opponents reject significant vegetation changes (Colinvaux *et al.*, 2001). In a recent, comprehensive review, van der Hammen & Hooghiemstra (2000) point out that both views are not necessarily conflicting. They stress the consensus in the debate that some areas within Amazonia were less affected by drier and cooler Pleistocene climate than others. There is also little doubt that Western Amazonia was one of the least affected regions within Amazonia. Furthermore, there is good evidence that even slight changes in temperature, rainfall, and CO₂ levels in Amazonia during the Pleistocene could have had strong impacts on canopy structure (e.g. canopy density, leaf area index) and canopy humidity (Cowling *et al.*, 2001). As epiphytes dwell in the canopy acting as interface to the abiotic world, they are directly exposed to changing climatic conditions and thus much more sensitive than other life-forms. Studies on the community level document that even slight microclimatic differences in humidity have effects on the floristic composition of epiphyte communities (Sugden & Robins, 1979; Barthlott *et al.*, 2001; Leimbeck & Balslev, 2001; Krömer, 2003). The impacts of forest structure and humidity on vascular epiphytes are inseparably intermingled, indicating that epiphytes might have been more directly affected by a drier Pleistocene climate than other life-forms. Insights also come from the present-day relationship between rainfall and species richness (Fig. 9). A conservative estimate of a 20% decrease in rainfall during the last glacial maximum could have easily led to corresponding regional species loss. However, it remains uncertain, whether the observed present-day endemism in the Upper Napo region is rather a consequence of lower extinction or higher speciation rates compared to the more heavily affected surrounding areas of Amazonia. This can only be tested by detailed phylogeographical investigations.

Influence of Andean taxa on diversity and floristic composition of Western Amazonia

Andean species contribute substantially to the high epiphyte diversity in Yasuní. Up to 15% of the epiphyte species in this region have a primarily montane distribution, but also occur in the very western lowlands of the Amazon basin. In this regard Central and Western Amazonian forests differ tremendously (compare Fig. 8). The Northern Andes are the most important centre of evolution for Neotropical epiphytes (Gentry, 1982; Gentry & Dodson, 1987b). A hump-shaped relationship between altitude and species richness with a peak at mid-elevations in Andean forests has been frequently reported (Gentry & Dodson, 1987b; Kessler, 2000; Küper *et al.*, 2004). High species richness in the altitudinal belt between 1000 and 2000 m seems to be associated with a relation between rainfall and temperature which provides favourable conditions for the epiphytic life-form (Gentry & Dodson, 1987b; Kessler, 2001b; Küper *et al.*, 2004). On the contrary, the recent Andean uplift and the complex topogra-

phy foster speciation by geographical isolation in this altitudinal belt (Gentry, 1982; Ibisch *et al.*, 1996). Küper *et al.* (2004) point out that it is important to distinguish between climatic factors maintaining high epiphyte diversity and high levels of geographic isolation fostering speciation processes in this altitudinal belt. Although floristic differences in the familial composition between montane and lowland epiphyte floras are not as pronounced as for terrestrial plants (compare e.g. Gentry, 1995), there is a recognizable differentiation. Especially epiphytic orchids have undergone an extensive radiation in Andean forests, resulting in an increase of their importance in montane floras (Fig. 5). This also applies to the epiphytic Ericaceae (Gentry, 1982; Luteyn, 1989, 2002). Araceae and smaller, mainly hemi-epiphytic families like Moraceae, Clusiaceae and Cyclanthaceae on the contrary have higher relative importance in the lowlands. Seventy epiphytic aroids found in Yasuní are contrasted by the very wide-spread *Anthurium scandens* (Aubl.) Engl. as the only epiphytic aroid at the Bolivian cloud forest site Sehuencas at an altitude of 2200 m above sea level (Ibisch, 1996). This pattern has also been reported in studies on a larger scale for the floras of Peru and Ecuador (Ibisch *et al.*, 1996; Kessler, 2002). The higher relative importance of hemi-epiphytic species in lowland forests might be due to a benefit from ground water during their terrestrial phase. Thus, they are less affected by periodical droughts which are much more common in lowland forests than in montane altitudinal belts.

The occurrence of many primarily Andean species in Western Amazonia (Fig. 7c) is of particular biogeographical interest. On the one hand, it is a further indication for the significance of humidity on large-scale distribution and diversity patterns of epiphytes, as occurrence of these species in the lowland coincides with highest rainfall and low seasonality. On the other hand, it contradicts earlier assumptions that the altitudinal belt between 600 and 900 m demarcates the natural transition zone between the Andean and Amazonian flora (Balslev & Renner, 1990). The results of this study rather suggest a more continual transition between Andean and Amazonian elements that extends much farther east than previously thought. The floristic composition of Western Amazonian epiphyte communities is thus affected by the hyper-diverse Andean flora. Although these montane species are most likely at their ecological limits in Western Amazonia, the extraordinarily high and evenly distributed rainfall and the lack of a pronounced dry season resemble to a certain extent the perhumid bioclimatic conditions of mid-elevation forests. These conditions are only found in a very restricted part of Amazonia. Kessler (2001b) found similar distribution patterns for terrestrial ferns and relates them to high rainfall and low seasonality. Gentry & Dodson (1987a) explain the occurrence of epiphytic Ericaceae – a primarily Andean-centred group – at the Western Ecuadorian lowland site Río Palenque by high rainfall and proximity to the Andes. However, Pitman *et al.* (2002) do not attribute higher alpha and regional diversity of trees in the Yasuní area to an Andean influence. A possible explanation for this noteworthy differ-

ence between trees and epiphytes might be the high dispersal ability of epiphytes. Relatively low species richness from the Colombian Amazon (Benavides *et al.*, in press) might suggest that despite ecological conditions, proximity to the Andes and dispersal are important factors.

CONCLUSIONS

Three factors are mainly responsible of high epiphyte diversity in Yasuní: (1) The equably humid climate provides suitable present-day conditions for the epiphytic life-form. Our results support the rainfall-diversity hypothesis from Gentry & Dodson (1987a), indicating that high species richness of epiphytes is achieved in regions with high annual rainfall, but dry season length is an equably important explanatory factor. (2) The comparatively moist climate in Western Amazonia during the Pleistocene has probably led to fewer extinctions and/or more speciation than in the more affected surrounding lowlands. (3) Because of the humid climate and the proximity to the Andes, species richness in Yasuní profits from the extraordinary rich Andean species pool in terms of epiphyte diversity.

Our result indicate that the borderline between the Andean and Amazonian flora is much more hazy than previously thought. Because of this particular biogeographical position and the unique combination of Andean and Amazonian floristic elements, the pre-Andean lowlands are areas of top-rate interest for conservation within Amazonia. Particularly considering anthropogenic climate change by either global climatic change or large scale deforestation, Western Amazonian forests could provide stable forest refugia in the near future.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1083/JBI1083sm.htm>

Appendix S1 Species list of vascular epiphytes from the Tiputini Biodiversity Station

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