



# Diversity patterns of vascular epiphytes along an elevational gradient in the Andes

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## ABSTRACT

**Aim** To document the elevational pattern of epiphyte species richness at the local scale in the tropical Andes with a consistent methodology.

**Location** The northern Bolivian Andes at 350–4000 m above sea level.

**Methods** We surveyed epiphytic vascular plant assemblages in humid forests in (a) single trees located in (b) 90 subplots of 400 m<sup>2</sup> each located in (c) 14 plots of 1 ha each. The plots were separated by 100–800 m along the elevational gradient.

**Results** We recorded about 800 epiphyte species in total, with up to 83 species found on a single tree. Species richness peaked at *c.* 1500 m and declined by *c.* 65% to 350 m and by *c.* 99% to 4000 m, while forests on mountain ridges had richness values lowered by *c.* 30% relative to slope forests at the same elevations. The hump-shaped richness pattern differed from a null-model of random species distribution within a bounded domain (the mid-domain effect) as well as from the pattern of mean annual precipitation by a shift of the diversity peak to lower elevations and by a more pronounced decline of species richness at higher elevations. With the exception of Araceae, which declined almost monotonically, all epiphyte taxa showed hump-shaped curves, albeit with slightly differing shapes. Orchids and pteridophytes were the most species-rich epiphytic taxa, but their relative contributions shifted with elevation from a predominance of orchids at low elevations to purely fern-dominated epiphyte assemblages at 4000 m. Within the pteridophytes, the polygrammoid clade was conspicuously overrepresented in dry or cold environments. Orchids, various small groups (Cyclanthaceae, Ericaceae, Melastomataceae, etc.), and Bromeliaceae (below 1000 m) were mostly restricted to the forest canopy, while Araceae and Pteridophyta were well represented in the forest understorey.

**Main conclusions** Our study confirms the hump-shaped elevational pattern of vascular epiphyte richness, but the causes of this are still poorly understood. We hypothesize that the decline of richness at high elevations is a result of low temperatures, but the mechanism involved is unknown. 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). The three spatial sampling scales show some different patterns, highlighting the influence of the sampling methodology.

## Keywords

Andes, aroids, Bolivia, bromeliads, diversity, elevational gradient, ferns, orchids, tropical montane forest, vascular epiphytes.

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## INTRODUCTION

Vascular epiphytes, including orchids, bromeliads, aroids, and pteridophytes, are an important component of the vegetation of tropical montane forests, in terms both of species richness and of their role in forest water-balance and nutrient cycles (Nadkarni, 1984; Gentry & Dodson, 1987; Coxson & Nadkarni, 1995; Nieder *et al.*, 1999). Owing to the difficulty of quantitatively sampling and of identifying tropical epiphytes, the number of epiphyte inventories in lowland and montane forests is still rather small (Wolf & Flamenco-S, 2003; Küper *et al.*, 2004). For example, there are only about 20 local inventories in montane forests in the Americas and only 12 studies dealing with the elevational distribution of neotropical epiphytes (Sugden & Robins, 1979; Cleef *et al.*, 1984; Gentry & Dodson, 1987; Wolf, 1994; Hietz & Hietz-Seifert, 1995; Ibisch *et al.*, 1996; Kessler, 2000, 2001b, 2002b; Bussmann, 2001; Muñoz & Küper, 2001; Krömer, 2003; Wolf & Flamenco-S, 2003; Küper *et al.*, 2004). Taken together, these studies indicate that epiphyte diversity peaks at mid-elevations at around 1000–1500 m. However, none of the studies covers an entire elevational transect from the lowlands to timberline, and only one (Krömer, 2003) presents a quantitative survey in the elevational zone between 450 m and 1400 m, where diversity is assumed to be highest. Data from this elevation are generally based on unstandardized sampling at the regional or country level (e.g. Ibisch *et al.*, 1996; Küper *et al.*, 2004) or from interpolation. Furthermore, there are methodological inconsistencies within some and among most of the studies listed above, with different sampling methods employed (e.g. varying plot size, varying plot number at different elevations, sampling only from the ground, inclusion/exclusion of the forest understorey), and different spatial scales (from 1 ha to 10,000 ha) covered. For this reason, a combined analysis of the individual data sets is problematic.

The present study was designed to overcome these shortcomings by application of a consistent sampling method at three local scales (single tree, 400 m<sup>2</sup> and 1 ha) from 350 m to 4000 m. Sampling was most intensive at elevations of 600–2200 m, specifically addressing the survey gap outlined above. These data are of interest both to ecologists seeking to understand the distribution and generation of patterns of plant diversity, and to conservationists faced with establishing conservation priorities in view of the ever-increasing deforestation in the Andes.

## METHODS

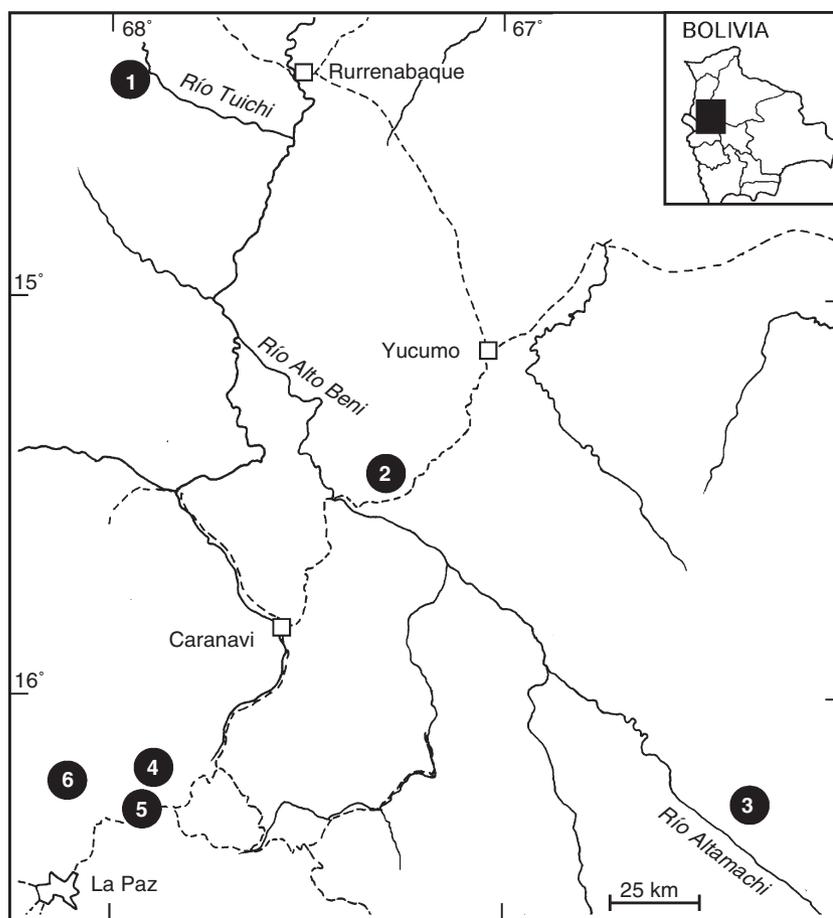
The study was conducted at six sites on the eastern slopes of the Andes, the so-called ‘Yungas’, in the Department of La Paz and Cochabamba, Bolivia (Fig. 1). The location of the study plots at different elevations was determined by the presence of intact forests and accessibility. The lowermost study site was located at 350 m in the surroundings of the Río Eslabón (14°27′ S, 67°56′ W) in Parque Nacional y Área Natural-de Manejo Integrado (PN-ANMI) Madidi (Acebey & Krömer,

2001). Annual precipitation is about 2000 mm and air temperature averages 24–26° C (Ribera, 1992). The forest of this area has over 150 tree species > 10 cm d.b.h. per ha (M. Macía, pers. comm.), with a canopy averaging about 30 m and emergent trees frequently surpassing 40 m. Among the most common tree species are *Cedrela odorata* L., *Ficus* spp., *Spondias mombin* L., *Ceiba pentandra* (L.) P. Gaert., *Hura crepitans* L., and *Poulsenia armata* (Miq.) Standl. Palms are of great importance in the forest structure, characterizing the dense intermediate stratum. Among the most important species are *Attalea phalerata* Mart. ex Spreng., *Astrocaryum* spp., *Iriartea deltoidea* Ruiz & Pav., and *Socratea exorrhiza* (Mart.) Wendl. In certain parts, various species of the genus *Geonoma* form dense ‘jatatales’.

The second study site was located above the village of Sapecho (450 m), where plots were established from 600 m along the Alto Beni river to 1200 m on the nearby Serranía Marimonos (15°27′–32′ S, 67°18′–23′ W). Mean annual rainfall varies from c. 1500 mm in the valley to over 2000 mm on the higher slopes, while temperatures average c. 24–25° C (Elbers, 1995). The natural forest on the slopes of the Serranía Marimonos is an evergreen or semi-evergreen submontane forest comprising trees 30–40 m tall and a well-developed shrub layer. Tree diversity averages c. 120 species per ha (Seidel, 1995). The most common tree species are *Poulsenia armata* (Miq.) Standl., *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr., *Clarisia racemosa* Ruiz & Pav., *Brosium lactescens* (S. Moore) C.C. Berg, *Otoba parviflora* (Markgr.) Gentry, *Leonia racemosa* Mart., *Tetragastris altissima* (Aubl.) Sw., and *Iriartea deltoidea* Ruiz & Pav.

The next-highest study site was located at 1300–1600 m on the isolated Serranía de Mosetenes in PN-ANMI Isiboro Sécure. No climatic stations exist in the vicinity of the study area, but rough estimates can be made based on comparisons with sites of physiognomically similar vegetation. Thus, mean annual precipitation is estimated at 3000–6000 mm, while mean annual temperatures are around 16° C at 1500 m. Forest structure in this steep and notably rocky terrain is lower than that of the previous sites, with the closed canopy at 20–25 m and emergent trees 30–35 m in height. On mountain ridges, forests are stunted and only 5–15 m tall. In slope forests, the most important tree families are Rubiaceae, Euphorbiaceae, Melastomataceae, Cyatheaceae, and Poaceae (bamboos), while the ridges were dominated by *Podocarpus* sp., *Chinchona* sp., *Miconia* spp., and *Clethra* sp. (M. Macía, pers. comm.).

The fourth study site was located at 1650–2200 m in the surroundings of Tunquini Biological Station in PN-ANMI Cotapata (16°11′–13′ S, 67°51′–54′ W). Mean annual rainfall is about 2500 mm and the mean annual temperature averages about 18° C at 1600 m (Bach *et al.*, 2003; M. Schawe, pers. comm.). The evergreen forest is 15–25 m tall and has dense shrub and herb layers. Tree diversity is unknown but probably lower than at Sapecho. The dominant tree families are Burseraceae, Lauraceae, Melastomataceae, Moraceae, and Rubiaceae (Gentry, 1995).



**Figure 1** Map of central Bolivia showing the locations of the study sites (1: Madidi, 2: Sapecho, 3: Mosestenes, 4: Cotapata, 5: Coscapa, 6: Zongo). Continuous lines show the main rivers; dashed lines show the main roads.

The fifth site was located in the upper Coscapa valley (3000–3500 m) in PN-ANMI Cotapata, accessible from the La Paz–Caranavi road. Mean annual precipitation probably exceeds 4000 mm, while the mean annual temperature is about 7° C at 3500 m (M. Schawe, pers. comm.). The forests are about 5–10 m tall and are dominated by the genera *Weinmannia*, *Miconia*, and *Clusia*.

The uppermost site was found at a 1–2 m tall relict stand of *Polylepis pepeii* Simpson at 4000 m in Zongo Valley. Precipitation is unknown but probably around 1000 mm, while the mean annual temperature is 4–5° C (Kessler & Hohnwald, 1998).

Vascular epiphytes, including all hemi- but no accidental epiphytes *sensu* Ibsch (1996), were sampled according to the protocols described in detail in Gradstein *et al.* (2003) and Krömer (2003). At each site, one to five plots of c. 1 ha each were established at different elevations. One plot was sampled at Madidi (350 m), five at Sapecho (600, 650, 700, 900, 1200 m), two at Mosestenes (1300, 1600 m), three at Tunquini (1650, 1850, 2200 m), two at Coscapa (3000, 3500 m), and one in Zongo (4000 m). In each of the plots, four or eight (two at Zongo) subplots of 20 × 20 m were selected for the actual sampling. The number of subplots was limited in some plots because of time constraints, and in Zongo by the extremely low diversity (with two vascular epiphytes found in the entire

forest patch). In each subplot, except those at 3000 m and higher, a single mature canopy tree was selected and fully sampled from the base to the outer portion of the tree crown, using the single-rope technique (Perry, 1978). This technique allows for a nearly complete inventory of epiphyte diversity of the forest canopy (Flores-Palacios & García-Franco, 2001). Because the epiphyte flora on shrubs and small trees in the forest understorey is usually different from that on the large canopy trees, epiphytes on shrubs and small trees were sampled within the subplots, using collecting poles and binoculars (Shaw & Bergstrom, 1997; Gradstein *et al.*, 2003; Krömer, 2003). Presence–absence was recorded for all species. Voucher specimens were deposited in the Herbario Nacional de Bolivia (LPB), with duplicates in the Herbarium of the University of Göttingen (GOET), Marie Selby Botanical Gardens (SEL), Missouri Botanical Garden, St Louis (MO), and the Jepson Herbarium, University of California, Berkeley (UC).

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 15 other families (Araliaceae, Cactaceae, Clusiaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Lentibulariaceae, Marcgraviaceae, Melastomataceae, Moraceae, Onagraceae, Oxalidaceae, Rubiaceae, Saxifragaceae, Urticaceae)

combined as 'others'. We use the term 'pteridophytes' to refer to all ferns and other seed-free vascular plants, and the term 'ferns' to refer to the monilophytes, i.e. ferns excluding the lycophytes (Pryer *et al.*, 2004). We further analysed the fern families Polypodiaceae and Grammitidaceae separately, because field experience and an analysis of secondary forests (Krömer, 2003; Krömer & Gradstein, 2003) suggested that these might show distinct patterns. Species richness for each group and for all groups combined were calculated separately for each climbed canopy tree, for each subplot (canopy tree + surrounding understorey within 20 × 20 m), and for the sum of four subplots within a plot. In plots with eight subplots, we calculated rarefaction curves based on all eight subplots to obtain average values after four plots. At Zongo, where only two subplots were established, a search of the remaining forest area showed that no other epiphyte species were present. The plot is thus considered comparable in its completeness to the plots with more subplots.

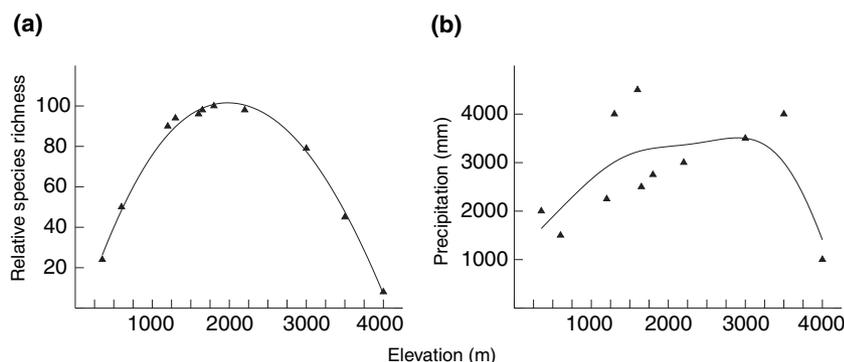
As explanatory variables for the observed richness patterns, we considered elevation, estimated mean annual precipitation, and an area-corrected model of the mid-domain effect (Fig. 2). The latter is a statistical null-model assuming a random distribution of species in a bounded domain, leading to an accumulation of species in the middle of the domain (Colwell & Hurtt, 1994; Colwell *et al.*, 2004). Because the transect data had irregular gaps, the mid-domain model could not be calculated by a randomization of the actual survey data as recommended by Colwell *et al.* (2004), but was based on the theoretical model 2 of Colwell & Hurtt (1994) using sea level and timberline (4100 m) as domain limits. This was further corrected for area-effects because land surface area decreases steadily with increasing elevation (Graves, 1988; Rahbek, 1997). The effect of the area of elevational belts on species richness at the regional scale was illustrated by Rahbek (1997) for birds. As a proxy for area we measured the horizontal width of 250-m belts (250–500, 500–750 m, etc.) in central Bolivia on topographic maps (scale 1 : 50,000) issued by the Instituto Geográfico Militar, La Paz, Bolivia (for details see Herzog *et al.*, 2005). As species richness does not increase linearly with area, we multiplied the mean horizontal width of each belt by an area-dependent factor, assuming a slope of  $z = 0.15$  in a double-log species–area plot, which corresponds to the

typical  $z$ -value obtained for pteridophytes in tropical mountains (J. Kluge and M. Kessler, unpubl. data). We did not calculate regression values between the observed richness patterns and the explanatory variables because the latter are partly based on rough estimates, and a quantitative analysis based on such data would suggest analytical precision simply not possible with the data at hand. Other potential explanatory variables such as temperature, ecosystem productivity, air humidity, or regional species pool were not considered either because they are closely correlated with elevation (especially temperature) or because no reliable data were available. Trend curves in Figs 2–5 were calculated with distance-weighted least-squares smoothing at tension 0.5 in SYSTAT 7.0 (SYSTAT, 1997).

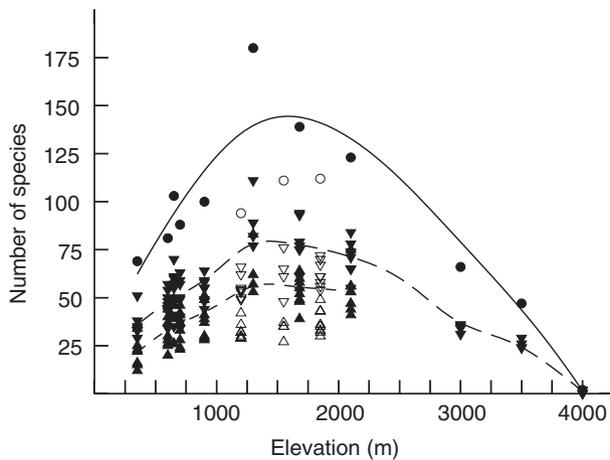
## RESULTS

In the 90 subplots (of 400 m<sup>2</sup> each) a total of about 800 species of vascular epiphytes, in 30 families and 131 genera, were recorded: 89 in Madidi (14 families, 42 genera) (Acebey & Krömer, 2001), 255 in Sapecho (23 families, 87 genera) (Krömer, 2003), 243 in Mosetenes (21 families, 70 genera), 292 in Cotapata (24 families, 76 genera) (Krömer, 2003), 98 in Coscapa (18 families, 45 genera), and two in Zongo (two families, two genera). Orchids were the most species-rich family, with about 314 species recorded, followed by Pteridophyta (264), aroids (59), piperoids (57), bromeliads (48), and all other families (together 58). 470 species (59%) of all species were identified to species level, with the remaining 330 (41%) separated at the level of morphospecies, especially among the 'others' (76%), Piperaceae (65%), Orchidaceae (52%, especially in the genera *Maxillaria*, *Pleurothallis*, and *Stelis*), and Pteridophyta (30%, especially in *Elaphoglossum*).

Epiphyte richness, in terms of number of species per tree, peaked at 1300 m, with up to 83 vascular plant species recorded on a single *Ficus* sp. tree (Fig. 3). Richness per tree decreased slightly up to 2200 m and more strongly so to lower elevations, with only 12–34 species found on single trees at 350 m. Conspicuously low species numbers were recorded at 1200, 1600, and 1850 m. Plots at these three elevation were all located on or near ridges, where trees were smaller in stature than on slopes.



**Figure 2** Elevational distribution (a) of expected species richness according to the area-corrected mid-domain null model 2 of Colwell & Hurtt (1994), and (b) of estimated mean annual precipitation at the elevations of the 11 zonal forest sites along the study transect, i.e. excluding plots on ridges. Temperature is not shown graphically because it shows a simple linear relationship with elevation.



**Figure 3** Elevational distribution of vascular epiphytic plant species richness on single trees (upright triangles), subplots of 400 m<sup>2</sup> each (inverted triangles), and plots combining four subplots in an area of c. 1 ha (circles) along an elevational gradient in Bolivia. Plots in stunted ridge forests at 1200, 1600, and 1850 m are indicated by open symbols and were not included in the calculation of the trend curves.

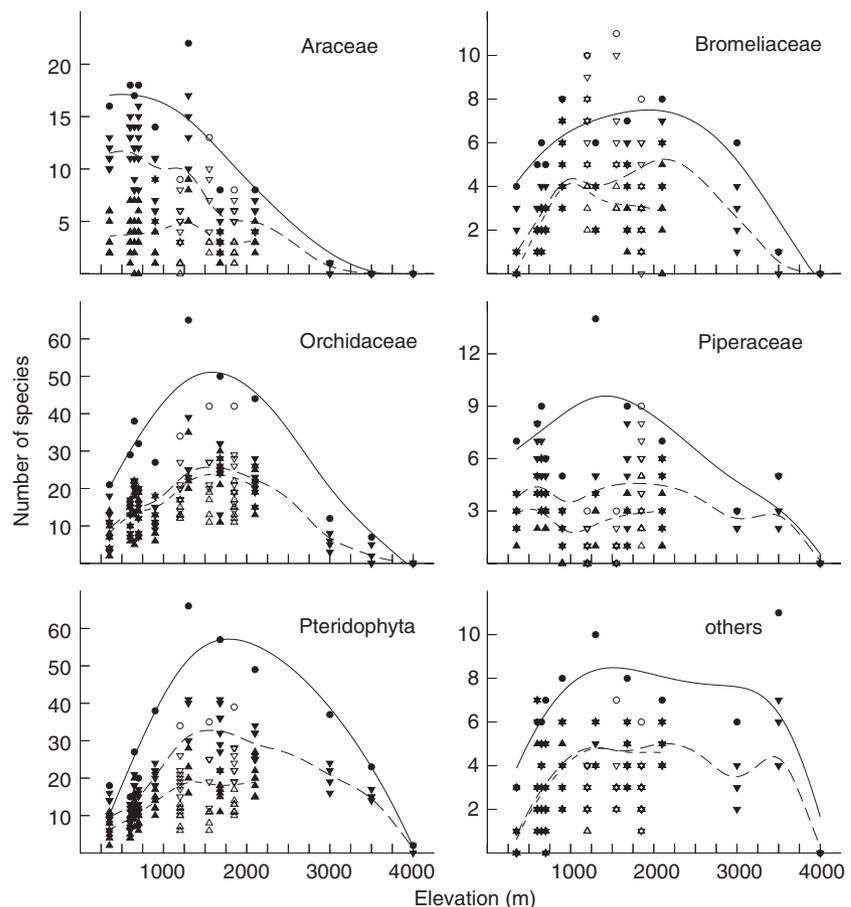
The distribution pattern of species numbers per subplot was hump-shaped with a maximum at 1300 m of up to 111 species per 400 m<sup>2</sup> (Fig. 3). Richness decreased roughly linearly to

timberline at 4000 m, and less markedly to the Amazonian lowlands, where 25–51 species were recorded per subplot. The ridge plots at 1200, 1600, and 1850 m had lower species richness.

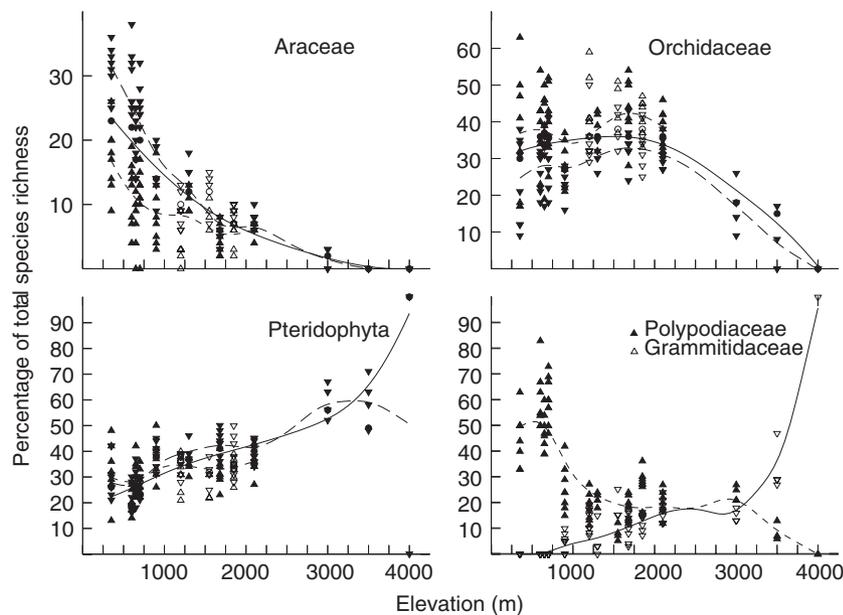
The distribution of species richness per plot was also hump-shaped, with a maximum at about 1500 m. Again, the three ridge plots showed considerably lower richness values. Overall, the shapes of the species richness curves at all three spatial scales were very similar to each other.

In the analysis of species richness of individual families by elevation, Bromeliaceae, Orchidaceae, Piperaceae, and Pteridophyta roughly paralleled the overall bulging pattern of epiphyte species richness (Fig. 4). However, elevations of highest diversity varied slightly among taxa, and in the trend curves were c. 2000 m for Bromeliaceae, 1500 m for Orchidaceae, 1300 m for Piperaceae, and 1700 m for Pteridophyta (with highest richness at a given site at 1300 m). Likewise, the decrease of diversity with elevations varied between groups. Araceae values were constant up to about 1000 m and then linearly decreased, while the remaining taxa ('others') showed a plateau of richness at higher elevations.

In a comparison of group-specific richness curves at the three sampling scales, conspicuous differences emerged between the study groups. In Orchidaceae, 'others', and in Bromeliaceae below 1000 m, single-tree and subplot values were almost identical, showing that most epiphytic species of



**Figure 4** Elevational distribution of the species richness of vascular epiphytes for six study groups along an elevational gradient in Bolivia. Symbols as in Fig. 3.



**Figure 5** Elevational distribution of the relative contribution of five plant groups along an elevational gradient in Bolivia. Relative values of Araceae, Orchidaceae, and Pteridophyta are relative to overall vascular epiphytic plant diversity; those of Polyypodiaceae and Grammitidaceae are relative to total Pteridophyta species richness. Symbols as in Fig. 3, except for the polygrammoid ferns.

these taxa were represented on the large canopy trees. In contrast, Araceae, Piperaceae, and Pteridophyta all had much higher richness values in subplots than on single trees, showing that a considerable proportion of the species occurred exclusively in the understory and on small subcanopy trees.

An analysis of the relative contributions of the various taxa to overall epiphyte diversity showed marked elevational differences (Fig. 5). Araceae contributed up to 40% of all epiphytes in the lowlands, but their contribution decreased linearly with elevation. Bromeliaceae and 'others' showed plateaus at about 500–3000 m, with values between 5% and 10%, the highest values of 'others' being at 3500 m. Orchidaceae had slightly increasing values from the lowlands (20–40% on average) to about 1750 m (25–45%), followed by a steep decline to high elevations. Piperaceae had relatively high values below 750 m (10–15%) and roughly constant values at 750–3500 m (5–10%). Pteridophyta, finally, had roughly linearly increasing values from the lowlands (20–30%) to timberline (100%). In a comparison of the relative contributions of the study taxa at the three spatial sampling scales, most groups showed very similar values. Exceptions were the Orchidaceae, which had considerably higher values on single trees and in plots than in subplots, and Araceae, which had higher values in subplots and plots than on trees, reflecting the stronger representation of these taxa on canopy trees and in the understory, respectively.

Finally, we analysed the contribution of two important fern families, Polyypodiaceae and Grammitidaceae, to total pteridophyte diversity within the plots. Species richness of Polyypodiaceae remained roughly constant from lowlands to 3000 m, and decreased at higher elevations, while Grammitidaceae species numbers increased from the lowlands to about 2000 m, remained high to 3500 m, and only decreased around timberline. On a relative level, the contributions of the two families to overall pteridophyte richness showed opposite patterns,

decreasing constantly from the lowlands to timberline in Polyypodiaceae, and increasing in Grammitidaceae (Fig. 5).

Of the explanatory variables, the area-corrected mid-domain model showed a hump-shaped pattern with a maximum at around 2000 m and a more pronounced decrease to higher elevations than towards the lowlands, while rainfall showed an irregular elevational pattern, with estimated maxima at 1300–1600 m and 3000–3500 m (Fig. 2).

## DISCUSSION

This is the first study to document the elevational gradient of vascular epiphyte diversity at the local level from the Amazonian lowlands to timberline in the Andes. It confirms the assertion of Gentry & Dodson (1987) and Küper *et al.* (2004) that vascular epiphytes show a distinct mid-elevation bulge in species richness. In our study, this bulge was located at about 1500 m. Previous local-scale studies found richness peaks at 1430 m in Mexico (Hietz & Hietz-Seifert, 1995), at 2350–2600 m (Sugden & Robins, 1979) and at about 1700 m (Cleef *et al.*, 1984; Wolf, 1994) in Colombia, and at 1600 m in western Ecuador (Muñoz & Küper, 2001). At the regional level, peaks of epiphyte richness between 1000 and 1500 m were found in Chiapas, Mexico (Wolf & Flamenco-S, 2003), in Ecuador (Küper *et al.*, 2004), and at 1500–2000 m in Peru (van der Werff & Consiglio, 2004). The total species number recorded in this study is unusually high and suggests that the number of vascular epiphytes for the whole of Bolivia exceeds the 1500 species estimated by Ibisch (1996).

The causes determining the hump-shaped diversity curve of vascular epiphytes are still little-known, but four main factors have mostly been invoked: air humidity; rainfall; the topographical complexity and young orogeny of the Andes; and hard boundaries, such as the lack of tree-habitats above timberline. Schimper (1888) already considered air humidity

to be the most important factor determining epiphytic plant diversity, a suggestion followed by van Reenen & Gradstein (1983); Gentry & Dodson (1987); Kessler (2001b); Kreft *et al.* (2004), and Küper *et al.* (2004), among many others. Eco-physiologically, this relationship appears to be well founded, since water availability is of critical importance to epiphytes (Benzing, 1990; Zotz & Hietz, 2001). In the region of our study transect, at 450 m Krömer (2003) measured an annual average relative air humidity of around 85%, while Bach *et al.* (2003) reported values of 90% at 1820 m and 97% at 3010 m over the course of several months, i.e. actually showing an increase of humidity at an elevation where epiphyte diversity declines. Recent measurements at four elevations (40, 650, 1900, 2900 m) over the course of a year in Braulio Carrillo National Park, Costa Rica, have documented a maximum of air humidity at mid-elevations (1900 m), with a strong decline to the lowlands and only a moderate decline to higher elevations (J. Kluge and M. Kessler, unpubl. data). If these patterns hold true elsewhere in the Neotropics [which is likely based on our field observations; see also Richter (2003) for Ecuador], then the decline of vascular epiphyte richness at low elevations may well be explained by the low air humidity there, while the decline at high elevations cannot be related directly to a decline of air humidity. As previously suggested by Gentry & Dodson (1987); Kessler (2001a,b); Bhattarai *et al.* (2004), and Kreft *et al.* (2004), among others, it is likely that low temperatures, in particular the regular occurrence of frost, are limiting to epiphyte diversity in the highlands. In the lowlands, however, it is probable that air humidity is limiting to epiphyte diversity, because high temperatures cause high evapotranspiration and hence induce water stress (Benzing, 1990; Zotz & Hietz, 2001). The role of high fog incidence on epiphyte diversity has been shown in the lowland rainforests of Guyana and French Guiana (Ek, 1997; Freiberg, 1999), where high air humidity is maintained due to frequent occurrences of morning fog (Gradstein, 2003, in press).

The relationship of epiphyte diversity to rainfall follows the same reasoning as that for air humidity. On a regional scale, Kessler (2001b) and Kreft *et al.* (2004) have documented the increase of epiphyte species richness with increasing rainfall, even though Wolf & Flamenco-S (2003) found a decrease of epiphyte richness in the most humid habitats in Chiapas, Mexico. Along our study transect, the increase of rainfall from the lowlands to mid-elevations thus corresponds to an increase of epiphyte diversity and to the general elevational pattern described above. However, as for air humidity, the decline of epiphyte richness at high elevations contradicts the high precipitation levels at least at 3000–3500 m.

Stochastic null-models are currently often invoked for the interpretation of hump-shaped diversity curves (e.g. Colwell & Hurtt, 1994; Colwell & Lees, 2000; Jetz & Rahbek, 2001; Grytnes, 2003; Colwell *et al.*, 2004). Our area-corrected mid-domain model (Fig. 2a) indeed predicts that, if the individual species were randomly distributed along the elevational gradient, epiphyte diversity would peak at mid-elevations. While we refrained from a quantitative analysis of the

correspondence of observed data and explanatory variables owing to the poor quality of the environmental data (see Methods), visual comparison shows that the modelled diversity curve resembles the observed pattern much better than either precipitation (Fig. 2b) or temperature (with a linear decrease) alone. However, the predicted peak at about 2000 m is located at higher elevations than the observed peak (1500 m), and the observed decline towards high elevations is more pronounced than predicted by the model.

Kreft *et al.* (2004) and Küper *et al.* (2004) have proposed that the complex Andean topography has enhanced the potential for allopatric speciation and ecological specialization in epiphytes. Kessler (2002a,b) also found a relationship of topography to plant endemism in Bolivia and Ecuador, but the peaks of relative endemism, corresponding to the elevation of the steepest slopes at 2500–3000 m, were located at a higher elevation than the peak of epiphyte diversity documented here. Again, it appears that at high elevations epiphyte richness is lower than would be expected if topographical complexity alone were the main determining factor.

Clearly, one of the challenges in explaining patterns of epiphyte diversity is to elucidate the massive decline at high elevations. This could be a result either of the stunting of the forest vegetation near timberline and the corresponding limitation of the number of growth sites and niches, and/or of the limiting role of low temperatures. While there is no doubt that epiphyte growth is physiologically limited at low temperatures (Benzing, 1990; Zotz, 2005), the actual mechanisms limiting species richness as such are still unknown. This problem is analogous to explaining the factors limiting overall biotic diversity in temperate and boreal regions along the latitudinal gradient (Willig *et al.*, 2003), and is beyond the scope of this study.

Within the overall hump-shaped richness pattern, it is evident that plots from a given site were relatively similar to each other. The relative similarity of plots within a site suggests that some regional effect influences observed local richness. Whether this involves regional species pool or climate, nutrient availability, or environmental history at the regional scale cannot be answered with the data at hand, and calls for comparative studies of different sites at a constant elevation.

Considering single trees, the maximum value of 83 epiphyte species on a single *Ficus* sp. at 1250 m in Mosetenes represents the highest species number of epiphytes that has ever been sampled in Bolivia, surpassing the maximum value of 75 species found at 2100 m in Cotapata by Krömer (2003). Comparable values are given only by Kreft *et al.* (2004), who found 81 species on a single tree in Ecuador at 230 m, Freiberg (1996, 1999, who registered 65 and 74 epiphytes in French Guiana (200 and 45 m), and Engwald (1999), who found 66 species in Venezuela (2300 m).

The three plots located in stunted ridge forests differed consistently from plots on slopes by their lower overall species numbers, especially with respect to the number of species per tree (see, for example, pteridophytes in Fig. 4), as a consequence of the lower stature of individual trees in stunted ridge

forests. However, species richness of subplots in ridge forests tended to be similar to that in 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.

As in all previous neotropical epiphyte studies, orchids were the most species-rich family, followed by pteridophytes. Both groups showed hump-shaped diversity patterns essentially identical to the overall pattern. The relative contribution of both groups to overall epiphyte diversity showed interesting differences, however. While the contribution of orchids remained roughly constant at about 30–40% from the lowlands to about 2000 m and then declined precipitously, that of pteridophytes increased continuously, starting in the lowlands at lower levels than orchids but reaching 100% at 4000 m (Fig. 5). Interestingly, these values deviate from numbers obtained elsewhere in the Neotropics, where orchids often contribute over 50% to epiphyte diversity while pteridophytes generally have values below 30%, and often as low as 20% (e.g. Bussmann, 2001; Muñoz & Küper, 2001; Wolf & Flamenco-S, 2003). This may partly be a result of the scale of sampling. Orchid species typically occur at low densities and often have small ranges (Nieder *et al.*, 1999), leading to high relative values at a regional level, e.g. 62% for all of Peru (Ibisch *et al.*, 1996), and lower values at local scales, e.g. 45% at single sites in Ecuador (Kreft *et al.*, 2004). However, the tendency for relatively lower orchid numbers in Bolivia is also evident at the country level. In Ecuador, species richness of epiphytic orchids is at least five times higher than that of epiphytic pteridophytes (data from Jørgensen & León-Yáñez, 1999), whereas in Bolivia it is only three times as high (Ibisch, 1996). We suggest that this is a biogeographical pattern determined by the location of Bolivia on the transition from the tropics to the subtropics, i.e. revealing a large-scale trend of a concentration of orchid diversity in the inner tropics and a relative increase of pteridophytes as epiphytes away from the tropics.

The important contribution of pteridophytes to epiphytic plant diversity under less benign environmental conditions (high elevations, subtropics) appears to be a general pattern. In humid temperate regions, ferns are the most common vascular epiphytes (Zotz, 2005), while in dry tropical regions ferns, along with drought-tolerant bromeliads, reach furthest into arid habitats (Ibisch, 1996). Interestingly, in all these cases, the ferns reaching the most extreme habitats belong mostly to the polygrammoid clade, which has about 750 species worldwide in the families Polypodiaceae and Grammitidaceae (Schneider *et al.*, 2004b). In temperate regions epiphytic ferns often belong to the genus *Polypodium* (Zotz, 2005), in tropical mountains at highest elevations to Grammitidaceae (this study; Fig. 5), and in arid tropical regions mainly to the Polypodiaceae genera *Pleopeltis* and *Microgramma* (M. Kessler, unpubl. data). Indeed, in our study, the family Polypodiaceae is by far the dominant pteridophyte family at elevations below 1000 m, where relatively low precipitation and high temperatures create

the least humid conditions along the transect (but still humid enough for evergreen rain forest). A similar trend was also evident in a comparison of primary and secondary forests at 550 m near Sapecho, where secondary forests had much lower values of air humidity owing to the open forest structure, and whose fern assemblages were dominated by species of the families Polypodiaceae and Aspleniaceae (Krömer & Gradstein, 2003; Krömer, 2003). In contrast, Grammitidaceae, Hymenophyllaceae, and Lomariopsidaceae, each represented by high numbers of species in the primary forests, were virtually lacking in the secondary forests. A similar trend is also evident in a study by Barthlott *et al.* (2001) from Venezuela, where the fraction of Polypodiaceae and Aspleniaceae relative to overall pteridophyte richness increased from 0.2 in natural forests to 0.3 in disturbed forests, 0.5 in secondary forests, and 1.0 in timber plantations. This raises the possibility of using the richness ratio of specific fern families as indicators of environmental stress in tropical forests. The ecophysiological traits enabling polygrammoid ferns to cope with these extreme environmental conditions, both with regard to humidity and temperature, being among the most extreme ones experienced by any vascular epiphytes, are unknown and would be well worth studying.

The patterns of species richness across the three sampling scales (tree, subplot, plot) showed some interesting trends, especially with regard to individual trees and subplots (= tree + surrounding understorey). The richness of orchids and 'others' was almost similar on trees and in subplots, showing that these study groups were almost exclusively restricted to the canopy of large trees. Bromeliads showed the same pattern to about 1000 m elevation, where the two diversity curves diverged (Fig. 4). This implies that in lowland forests bromeliads are essentially restricted to the forest canopy, while in montane forests numerous species can also be found in the forest understorey. This is in accordance with height zonation of bromeliads within the forest (Krömer, 2003) and can be explained by the growth of bromeliads at fairly high light levels (Benzing, 1990, 2000; Zotz & Hietz, 2001). In montane forests, the open canopy on slopes enables much more light to reach the forest interior than in lowland forests with their dense, closed, canopy. Araceae and pteridophytes had large numbers of species in the forest understorey all along the elevational gradient. At least in the case of the latter group, this may be explained by the presence of a particularly sensitive photoreceptor that enables ferns to thrive under low light conditions (Schneider *et al.*, 2004a). It is unknown whether Araceae have a comparable photosynthetic mechanism, but different genera and subgenera within this family preferentially occupy different height strata in the forest (Jácome *et al.*, 2004), suggesting that phylogenetically determined adaptive features determine the height distribution of Araceae. Regardless of the underlying ecological causes, our study shows that sampling methodology (inclusion or exclusion of the forest understorey) will have a significant influence on the observed epiphyte richness patterns, especially on the relative richness of different taxa.

In conclusion, our study confirms the expected mid-elevation bulge of epiphyte richness in the Andes and raises important questions for future research, including, for example, the mechanisms limiting epiphyte diversity under low temperature conditions and the adaptive features enabling polygrammoid ferns to live in the most inhospitable habitats colonized by vascular epiphytic plants.

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