



## Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes

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### Abstract

I analyzed the distribution of Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Melastomataceae, and Pteridophyta in 62 vegetation plots of 400 m<sup>2</sup> along an elevational transect between 500 m and 2450 m, and at a nearby lowland site in western Santa Cruz department, Bolivia. These groups were selected because they are physiognomically distinctive, have high species numbers, are comparatively easy to identify, adequately reflect overall floristic relationships, include a wide range of life forms, and are small. The transect was located in the Tucumano-Boliviano biogeographic zone and included drought-deciduous (<850–1000 m), mixed evergreen (850–1000 m to 1800 m), and evergreen *Podocarpus*-dominated (>1800 m) forests. Elevational patterns of species richness were group-specific and probably related to the ecophysiological properties of each group. Species richness in Pteridophyta and Melastomataceae was correlated with moss cover (i.e., humidity), with elevation (i.e., temperatures) in Acanthaceae and epiphytic Bromeliaceae, with potential evapotranspiration (i.e., ecosystem productivity) in Araceae, and with light availability at ground level in terrestrial Bromeliaceae and Cactaceae. Community endemism generally increased with elevation, but showed a maximum at 1700 m for terrestrial Pteridophyta, and a nonsignificant decline for epiphytic Bromeliaceae and Cactaceae. Endemism was higher for terrestrial than for epiphytic taxa, and was lower among Pteridophyta compared to all other groups, reflecting different dispersal ability among taxonomic and ecological groups. Elevational zonation, tested against a null-model of random distribution of elevational limits, revealed a significant accumulation of upper and lower elevational range boundaries at 900–1050 m and at 1500–1850 m, corresponding to the elevational limits of the main physiognomic vegetation types.

### Introduction

The tropical Andes are among the botanically most diverse regions worldwide (Barthlott et al. 1996). However, due to the difficulty of adequately sampling and identifying species-rich tropical plant communities, our knowledge of the magnitude and distribution of this diversity remains fragmentary (Gentry 1995). Perhaps the most conspicuous changes of community composition and richness in tropical mountains are related to differences in elevation, but few studies have covered entire elevational gradients in enough detail to describe with precision the way in which tropical forest characteristics change with altitude (Lieber-

man et al. 1996). The majority of elevational studies have focussed on species richness (e.g., Gentry 1995; Lieberman et al. 1996; Vásquez & Givnish 1998) and elevational zonation of vegetation types (see Frahm & Gradstein 1991) and have been based on woody plants (e.g., Gentry 1988, 1995; Kitayama 1992; Lieberman et al. 1996) even though the majority of plant species in humid tropical forests belong to non-tree life forms (Gentry & Dodson 1987; Ibisch 1996; Balslev et al. 1998). As a result, it is not yet known whether a general relationship exists between species richness and elevation, or even whether an universal explanation or model can be given (Colwell & Hurtt 1994; Rahbek 1995, 1997). The hump-shaped relation of species-

richness to elevation, which may be the most prevalent pattern (Rahbek 1997), has been linked to a variety of factors, including (i) the random elevational association between the extent and the position of elevational ranges of species along bounded geographical ranges (Colwell & Hurtt 1994), (ii) highest humidity at mid-elevations (Rahbek 1995), and (iii) a hump-shaped regional pattern of species-richness with respect to productivity (Rosenzweig 1995).

In the present study, I analyzed patterns of species richness and endemism of Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Melastomataceae, and Pteridophyta along an elevational transect between 500 m and 2450 m, and at a nearby lowland site in western depto. Santa Cruz, Bolivia (Figure 1). The study region is located just south of the 'Andean knee' where the general direction of the Andean chain switches from NW-SE to N-S, marking the northern boundary of the climatically and floristically distinct Tucumano-Boliviano biogeographic region (Ribera et al. 1992). The forests of this zone have been relatively well-studied in northwestern Argentina (e.g., Cabrera 1976; Brown et al. 1985; Moyano & Movia 1989; Grau & Brown 1995) but only two Bolivian sites have received any attention so far (Gerold 1987; Beck et al. 1992; Schulenberg & Awbrey 1997). All studies on diversity and altitudinal zonation in this biogeographic region so far have been based on trees.

In addition to species richness and altitudinal zonation, I also considered range-size distribution, here called community endemism. Endemism has mostly received attention at larger geographical scales, e.g., for defining areas of endemism (Myers 1988) and for conservation purposes, where endemic plant species are frequently given high priority (Terborgh & Winter 1983; Davis et al. 1997). Andean mountain regions are well known to harbour more endemic plant species than adjacent lowland areas (Balslev 1988), but little is known about the exact elevational distribution of endemism and differences of endemism between plant groups and life forms.

## Methods

### *Study areas and the environment*

The study transect was located in the Masicurí valley from the confluence of the rivers Masicurí and Río Grande at 500 m (19°02' S, 63°42' W) to the highest accessible peaks at 2500 m at San Lorenzo (18°41' S,

63°55' W) on the west side of the valley along the road from Vallegrande to Masicurí in western Santa Cruz Department, Bolivia (Figure 1). Geologically, the entire area consists of red sandstones of Ordovician age (Pareja et al. 1978), often forming vertical rock faces at higher elevations. The bottom of the Masicurí valley is covered by broad Tertiary and Quaternary alluvial plains. Mean annual precipitation at the village of Masicurí (800 m) is 1792 mm, with a year-to-year variation from about 1100 mm to 2600 mm. Precipitation declines towards lower elevations, with values between 1000 mm and 1200 mm reported from various climatic stations along the Andean foothill base to the east of the study area. At higher elevations, precipitation and fog intensity increase noticeably (see Bianchi 1981, for data from Argentina), especially at about 1000–1200 m elevation (pers. obs.), but no quantitative measurements are available (Figure 2). Mean annual temperatures are about 25 °C at 500 m and decline by about 0.6 °C per 100 m elevational increase (Eriksen 1986; Gerold 1987). Climate is seasonal, with about 80% of the precipitation falling in summer (November to May), and a lowering of the frost limit by over 2000 m in winter down to 800 m (Eriksen 1986). Of particular importance is the regular influx of cold polar fronts along the Andean base in winter, locally known as *surazos*, that reduce temperatures considerably for several days and represent the main source of precipitation in this season (Fjeldså et al. 1999).

In accordance with climatic changes, three main elevational vegetation zones were discernible (Figure 2) that are typical for the biogeographic region as a whole (Cabrera 1976; Ribera et al. 1992; Navarro 1997; Schulenberg & Awbrey 1997). Up to 850–1000 m, forests are deciduous to semi-deciduous and composed primarily of Leguminosae such as *Anadenanthera macrocarpa*, *Enterolobium contortisiliquum*, and *Parapiptadenia excelsa*. Between 850–1000 m and about 1800 m, forests are evergreen and contain *Cedrela lilloi* (Meliaceae), *Chrysophyllum gonocarpum* (Sapotaceae), *Crinodendron tucumanum* (Elaeocarpaceae), *Ficus* spp. (Moraceae), *Miconia* spp. (Melastomataceae), as well as numerous naturalized orange trees (*Citrus aurantium*, Rutaceae). Above 1800 m, the evergreen forest is dominated by *Podocarpus parlatorei* (Podocarpaceae) and numerous Myrtaceae such as *Blepharocalyx salicifolius*, *Myrcianthes callicoma*, *M. pseudomato*, and *Siphoneugenia occidentalis*.

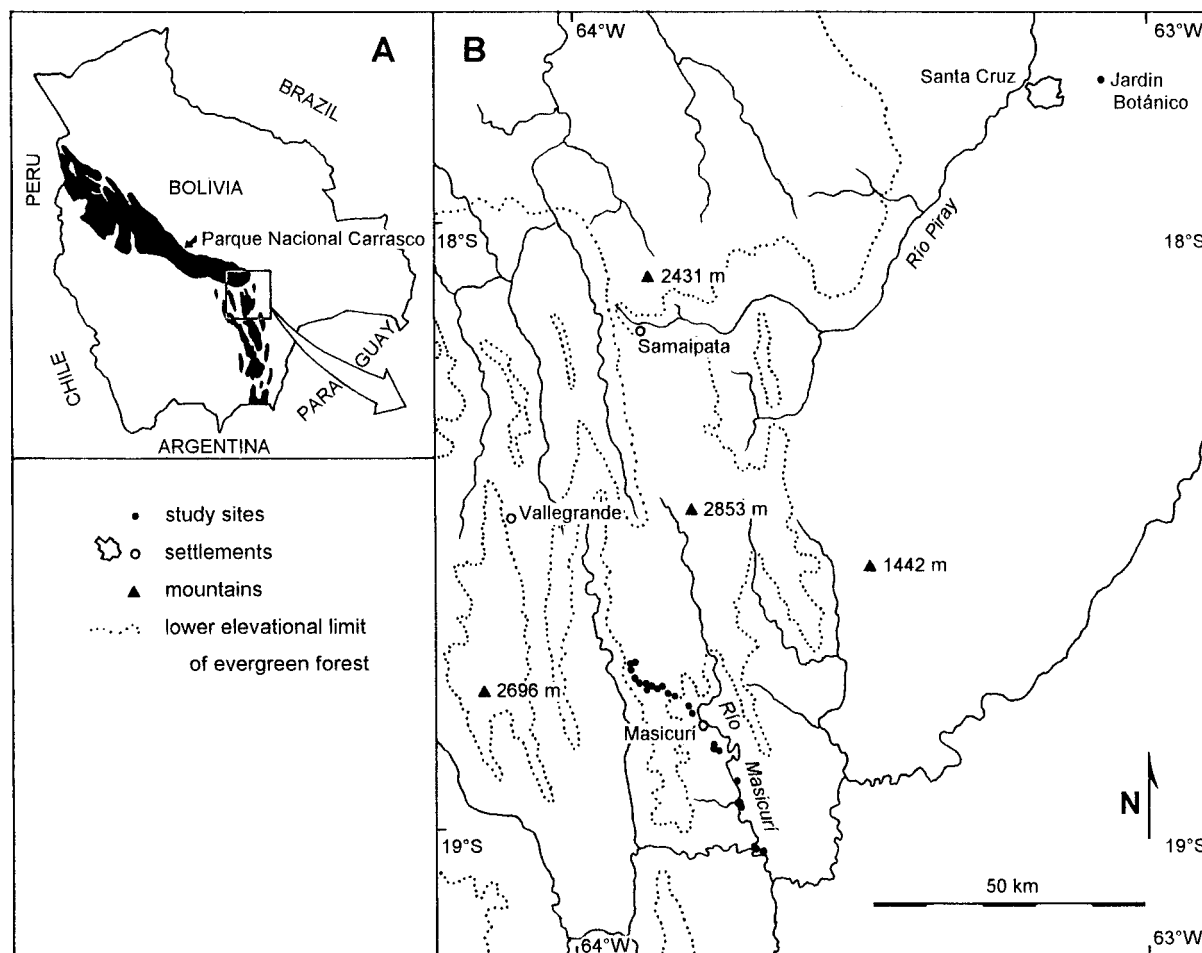


Figure 1. Location of the study region and of humid montane forests in Bolivia (A) and of the study sites in the region (B).

Human activity varied according to climatic and topographic conditions (Figure 2). The alluvial plain of the Masicurí valley was completely deforested and used for intensive agriculture. Agricultural areas on slopes were located primarily at 900–1200 m and at 1700–2000 m, corresponding to the elevations with the most benign climate and least steeply inclined slopes. Forests on hillsides and slopes throughout the entire transect experienced selective timber extraction (especially *Cedrela*, *Podocarpus*, *Tabebuia*, depending on vegetation zone) and extensive cattle grazing. Many higher mountain areas had been burnt to establish cattle pastures.

In order to extend the study transect into the lowlands, the Santa Cruz Botanical Garden (440 m, 17°47' S, 63°04' W) was selected because of its relative proximity to the Masicurí area and because it contains fairly well-preserved forest that has been

subject to several previous botanical studies (Saldias 1991; Parker et al. 1993; M. Nee & G. Coimbra S. 1991, unpubl. manuscript). Mean annual precipitation at nearby Santa Cruz city is 1171 mm, mean annual temperature is 24.4 °C (Morales 1990).

#### Field work and data analysis

Field work was carried out from 9 to 15 July 1995 and from 20 May to 14 June 1996. Due to high species richness, the difficulty of identification of many taxa, and logistic limitations of visiting in the dry season when roads are open, botanical sampling was restricted to Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Melastomataceae, and Pteridophyta. These groups were selected because they are physiognomically distinctive (enabling efficient sampling), have high species numbers (allowing for quantitative analyses), are comparatively easy to identify, adequately

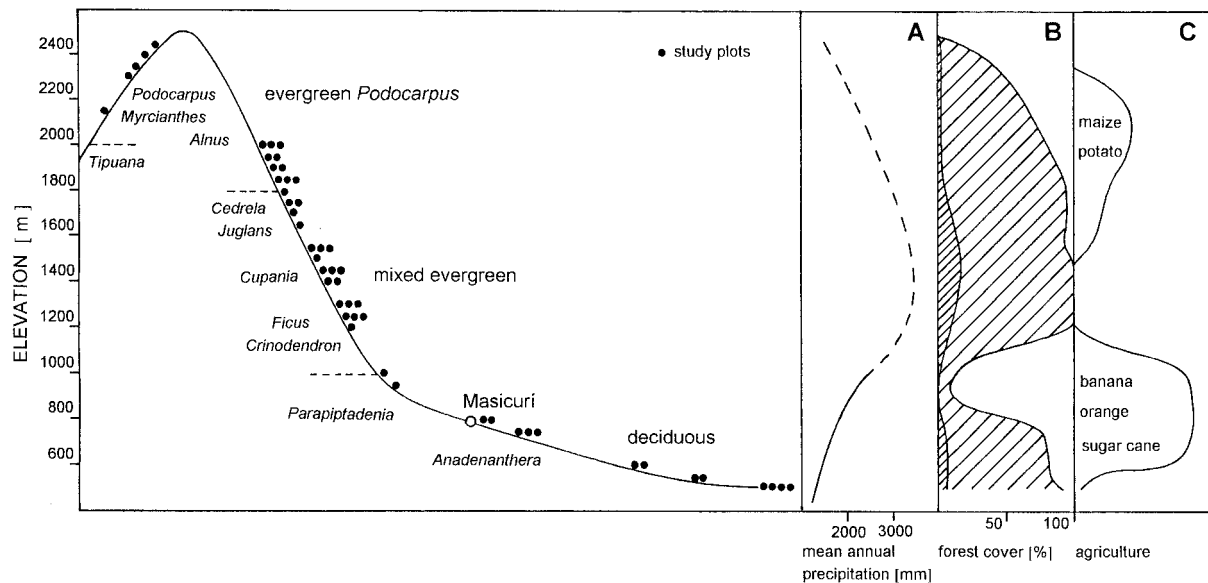


Figure 2. Schematic cross section of the study area, showing the general vegetation zonation and the location of study plots (black dots) as well as (A) mean annual precipitation values (above 1000 m estimated after Bianchi (1981) and by comparison to other areas with reliable climatic stations), (B) remaining forest cover within about 1 km of the study road (dense hatching = mature forest; light hatching = degraded forest), (C) and relative intensity and type of agricultural activity.

reflect overall floristic relationships, include a wide range of life forms, and are small (allowing for high species richness on fairly small plots). For details on the method, see Kessler & Bach (1999).

Forest vegetation was studied on 62 non-permanent 400 m<sup>2</sup> plots, mostly of square shape but occasionally in other shapes to minimize habitat heterogeneity. This size corresponds to the minimum area required for representative surveys of the study groups in the vegetation types sampled and is small enough to keep environmental factors more or less uniform throughout the plot (Kessler & Bach 1999). Plot location was chosen so as to include ecologically homogeneous and physiognomically representative forest samples, excluding ravines, rock faces, and secondary vegetation. Difficult terrain and human influence limited the number of plots at 900–1200 m and above 2000 m (Figure 2). Elevation was measured with a handheld Eschenbach altimeter to the nearest 50 m, correcting for weather-related inaccuracies by repeated measures and through reference to 1:250 000 topographic maps. Average canopy height and bryophyte cover on tree branches were estimated in each plot to the closest 3 m and 10%, respectively. Presence of all species was registered in each plot, treating terrestrial and epiphytic plants separately. All species encountered in the survey area

(but not in every single plot) were collected in triplicate and were deposited at the Herbario Nacional de Bolivia (LPB, including all unicates), with the respective specialists and at the Herbarium Göttingen (GOET). Specimen identification was undertaken by T. B. Croat (St. Louis; Araceae), H. Luther (Sarasota; Bromeliaceae), J. T. Mickel (New York; *Elaphoglossum*), R. C. Moran (New York; Pteridophyta), G. Navarro (Cochabamba; Cactaceae), B. Øllgaard (Aarhus; Lycopodiaceae), S. S. Renner (St. Louis; Melastomataceae), A. R. Smith (Berkeley; Pteridophyta), D. Wasshausen (Washington, D.C.; Acanthaceae), and by myself (Cactaceae and Melastomataceae). Distinct morphospecies were included in the species counts, but were only used for the endemism analysis if considered to represent undescribed species whose known range in most cases is limited to the study region. A list of all species encountered at Masicuri is presented in Kessler et al. (in press).

All study groups were analyzed individually. In Bromeliaceae, Cactaceae, and Pteridophyta separate calculations were conducted for epiphytically and terrestrially growing species. Among Araceae, overall species number was too low and overlap between terrestrially and epiphytically growing taxa was too high, to warrant treating epiphytes and terrestrial species

separately. Plots were combined into elevational steps of 200 m (500–650 m, 700–850 m, etc.).

Total species numbers for the whole transect were calculated with the Chao 1 species richness estimator (Chao 1984; Colwell & Coddington 1995) based on the number of species recorded only in one or two plots, excluding the Santa Cruz site.

Species richness was calculated as the mean number of species per plot for all plots of an elevational step. Because plots are considered to have been sampled exhaustively (1–4 hours with 2–4 persons), and since plot area was kept constant, this measure of species richness controls for both sampling effort and area (Rahbek 1997). Total species numbers recorded per elevational step were not analyzed because of unequal sampling intensity per elevational step and because this diversity measure would have included aspects of both  $\alpha$ - and  $\beta$ -diversity (within- and between-habitat diversity sensu Cody 1986).

I correlated species richness with the following variables: (a) elevation, (b) expected richness according to null model 2 with bounded random geographical ranges of Colwell & Hurtt (1994), (c) mean percent cover of canopy tree branches by bryophytes, (d) potential evapotranspiration (PET) calculated after Thornthwaite & Mather (1957), and (e) mean canopy height of trees in mature forest plots (Figure 2). In the null model,  $r_{\max}$  was set at 1800 m, corresponding to largest individual elevational species range recorded along the transect (*Microgramma squamulosa* (Kaulf.) de la Sota), and the uppermost elevation was set at 3000 m, corresponding to the highest elevation (2989 m) within a 100-km radius of the study site. In the absence of more precise data, bryophyte cover was used as a measure of humidity (Frahm & Gradstein 1991; Wolf 1993), and PET and canopy height as measures of ecosystem productivity (Rosenzweig 1968; Lieth 1975). Limited sample size prevented the use of multivariate statistics.

Community endemism  $E$  was calculated as

$$E = \left( \sum_{i=1}^n A_i^{-1} \right) n^{-1},$$

where  $A$  is the range size of species  $i$  measured as the number of  $1^\circ$ -cells covered by the species' presumed range, and  $n$  is the number of species in the community (Williams & Humphries 1994; Fjelds & Rahbek 1997). The global ranges of all species encountered were mapped in a  $1^\circ$ -grid-map based primarily on the following sources: Acanthaceae: D. Wasshausen, pers. comm., collections at the United

States National Herbarium, Washington, D.C. (US); Araceae: T. Croat, pers. comm., collections at the Missouri Botanical Garden, St. Louis (MO), various generic treatments; Bromeliaceae: H. Luther pers. comm., Smith & Downs (1974–1979), Kromer et al. (1999); Cactaceae: Backeberg (1979), Ritter (1980), Navarro (1996); Palmae: Henderson et al. (1995); Pteridophytes: A. R. Smith, pers. commun., R. Moran, pers. commun., J. T. Mickel, pers. commun., collections at The New York Botanical Garden (NY), the Univ. Herbarium, Berkeley (UC), MO, US, de la Sota (1977), Tryon & Stolze (1989–1994), Davidse et al. (1995), Steyermark et al. (1995) and numerous generic treatments. The resulting dot maps were interpolated on the basis of the species' ecological requirements and the distribution of main vegetation types (Hueck & Seibert 1981; Dinerstein et al. 1995) to obtain maps of the presumed natural range of the species. No endemism indices were calculated for Melastomataceae because of the high number of unidentified species. Endemism values were correlated with (a) elevation, (b) mean percent cover of canopy tree branches by bryophytes, (c) PET, and (d) mean canopy height.

Altitudinal zonation was tested with an analysis of deviance (Karson 1982; McCullogh & Nelder 1983; Austin 1985) following the method proposed by Shipley & Keddy (1987). This test can be used to evaluate whether variation of elevational turn-over of community composition corresponds to stochastic variation when the species' are distributed independently of each other or whether the elevational limits of different species are coupled (see Kessler 2000, for details). To obtain a large enough sample size, all study groups were combined in this analysis. Independent calculations were made for upper and elevational limits. To control for type I error, significance levels were subjected to a Bonferroni correction following the Dunn-Šidak method (Sokal & Rohlf 1995). The Santa Cruz area was excluded because it is geographically too remote and floristically distinct. The upper- and lowermost elevational steps of the Masicur transect were likewise excluded because it was impossible to discern real elevational limits from sampling artifacts.

Statistics were carried out with SYSTAT version 7.0 for Windows (SYSTAT 1997). Curves in Figures 3–5 were fitted by distance-weighted least-square smoothing with tension 0.4. Because of unequal sample size between elevational steps and corresponding stochastic variability, data interpretation focused on general patterns of species richness and endemism

Table 1. Correlations between the null model of Colwell & Hurr (1994) and variables used as indicators of environmental conditions.

	Null Model	PET	Tree height
PET	0.78**		
Tree height	0.75**	0.35	
Moss cover	0.67*	0.11	0.85***

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

as shown by the smoothed curves, rather than on differences between adjacent elevational steps.

## Results

In total, 134 species of Pteridophyta, 29 of Bromeliaceae, 23 of Cactaceae, 20 of Melastomataceae, 17 of Acanthaceae, and 8 of Araceae were recorded in the 51 forest plots along the Masicurí transect (Kessler et al. in press). Using the Chao 1 species richness estimator, actual species numbers were estimated to be around 170 for Pteridophyta, 40 for Bromeliaceae, 27 for Cactaceae, 26 for Melastomataceae, 23 for Acanthaceae, and 8 for Araceae. Consequently, the study may have included about 73–100% of the total number of species in the study groups.

The null model of Colwell & Hurr (1994), potential evapotranspiration, tree height, and moss cover all showed hump-shaped curves, but with different maxima and slopes (Figure 3). Many of these factors were highly significantly intercorrelated (Table 1).

Species richness showed three main elevational patterns: a roughly monotonic decline with increasing elevation in Acanthaceae, inverse hump-shaped curves with minima at intermediate elevations in terrestrial Bromeliaceae and Cactaceae, and hump-shaped curves with maxima at intermediate elevations in all remaining study groups (Figure 4). The highest correlations between species richness and environmental variables or the null model (Table 2) were to tree height in Acanthaceae, to elevation in Araceae (negative) and epiphytic Bromeliaceae, to moss cover in terrestrial Bromeliaceae (negative), Melastomataceae and Pteridophyta, to PET in epiphytic Cactaceae, and to the null model in terrestrial Cactaceae (negative).

Endemism increased more or less monotonically in epiphytic Pteridophyta and all terrestrial groups, except Pteridophyta, which showed a maximum at 1700 m (Figure 5). Epiphytic Bromeliaceae and Cactaceae showed a nonsignificant decline of endemism

with increasing elevation. The highest correlations between endemism and environmental variables were to tree height in Acanthaceae and epiphytic Pteridophyta, to elevation in Araceae, terrestrial Bromeliaceae, and terrestrial Cactaceae, and to moss cover in terrestrial Cactaceae (Table 2). Values of endemism were roughly similar among most terrestrial groups, excepting Pteridophyta which had considerably lower values. Endemism values of terrestrial taxa generally tended to be higher than those of epiphytic taxa, especially at higher elevations.

The test of elevational zonation revealed significantly high numbers of upper elevational limits at 900–1050 m and 1500–1650 m, and of lower elevational limits at 1700–1850 m (Figure 6). Conversely, there were significantly low numbers of upper elevational limits at 1300–1450 m and 1900–2050 m, and of lower elevational limits at 1300–1450 m and 2100–2250 m (Figure 6). Consequently, the analysis revealed three floristically distinct elevational zones, with boundaries located at about 1000 m and 1700 m.

## Discussion

### Species richness

The species numbers registered along the transect were considerably lower than those recorded in the northern Bolivian Andes. For example, in Parque Nacional Carrasco, about 300 km northwest of Masicurí (Figure 1), 347 species of Pteridophyta, 140 of Melastomataceae, 55 of Araceae, and 49 of Bromeliaceae have been recorded between 220 m and 3950 m in a comparable transect study (M. Kessler, unpubl. data). Only Cactaceae were more species rich at Masicurí than in more northerly zones. These trends presumably reflect the more arid and colder climate of the Tucumano-Boliviano zone. On the other hand, the number of fern species at Masicurí (134 species in forest habitats, 168 in all habitats, Kessler et al. in press) is almost identical to that of the whole Jujuy Province, northwestern Argentina, with 169 species (de la Sota 1977). Since the latter area is considerably larger than the present study area, has been subject to more intensive studies, and includes a wider elevational range, species richness appears to be higher at Masicurí, suggesting a southward decrease of species richness within the Tucumano-Boliviano region. A comparable latitudinal decline of species richness in the Tucumano-Boliviano region has been noted among

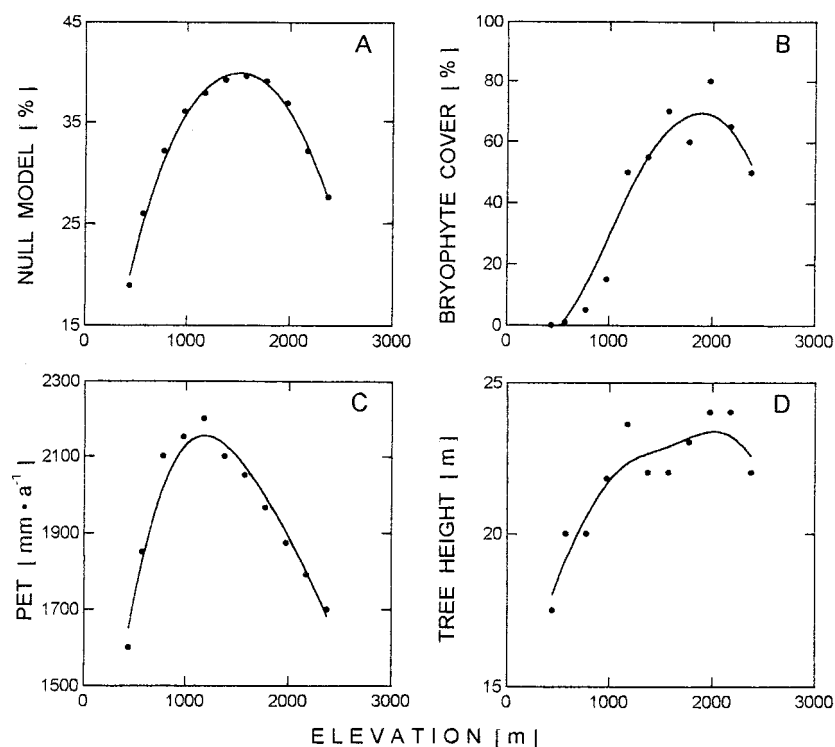


Figure 3. Null model 2 of Colwell & Hurr (A), mean bryophyte cover (B), estimated potential evapotranspiration (C), and mean canopy tree height (D) along the Masicuri study transect.

Table 2. Correlations of plant species richness and community endemism indices to elevation, the null model of Colwell & Hurr (1994), and environmental indicators. The null model is only applicable to species richness.

Elevation	Null	PET	Tree height	Moss cover	
<i>Species richness</i>					
Acanthaceae	-0.77**	-0.48	-0.08	-0.80**	-0.76**
Araceae	-0.70*	0.09	0.63*	-0.30	-0.59
Epiphytic bromeliaceae	-0.72*	0.03	0.51	0.39	0.58
Terrestrial bromeliaceae	-0.47	-0.71*	-0.42	-0.64*	-0.73*
Epiphytic cactaceae	-0.58	0.24	0.60*	-0.21	-0.32
Terrestrial cactaceae	-0.67*	-0.84***	-0.56	-0.81**	-0.73
Melastomataceae	0.73*	0.64*	0.12	0.71*	0.91***
Epiphytic pteridophyta	0.70*	0.70*	0.23	0.78**	0.92***
Terrestrial pteridophyta	0.77**	0.62*	0.11	0.68*	0.78**
<i>Endemism</i>					
Acanthaceae	0.50		0.60	0.78*	0.37
Araceae	0.93***		0.53	0.67*	0.80**
Epiphytic bromeliaceae	-0.15		-0.09	0.26	0.37
Terrestrial bromeliaceae	0.80**		-0.35	0.40	0.47
Epiphytic cactaceae	-0.27		-0.54	-0.47	-0.11
Terrestrial cactaceae	0.98*		-0.21	0.75	0.98*
Epiphytic pteridophyta	0.68*		0.40	0.83**	0.65*
Terrestrial pteridophyta	0.50		-0.01	0.41	0.59

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

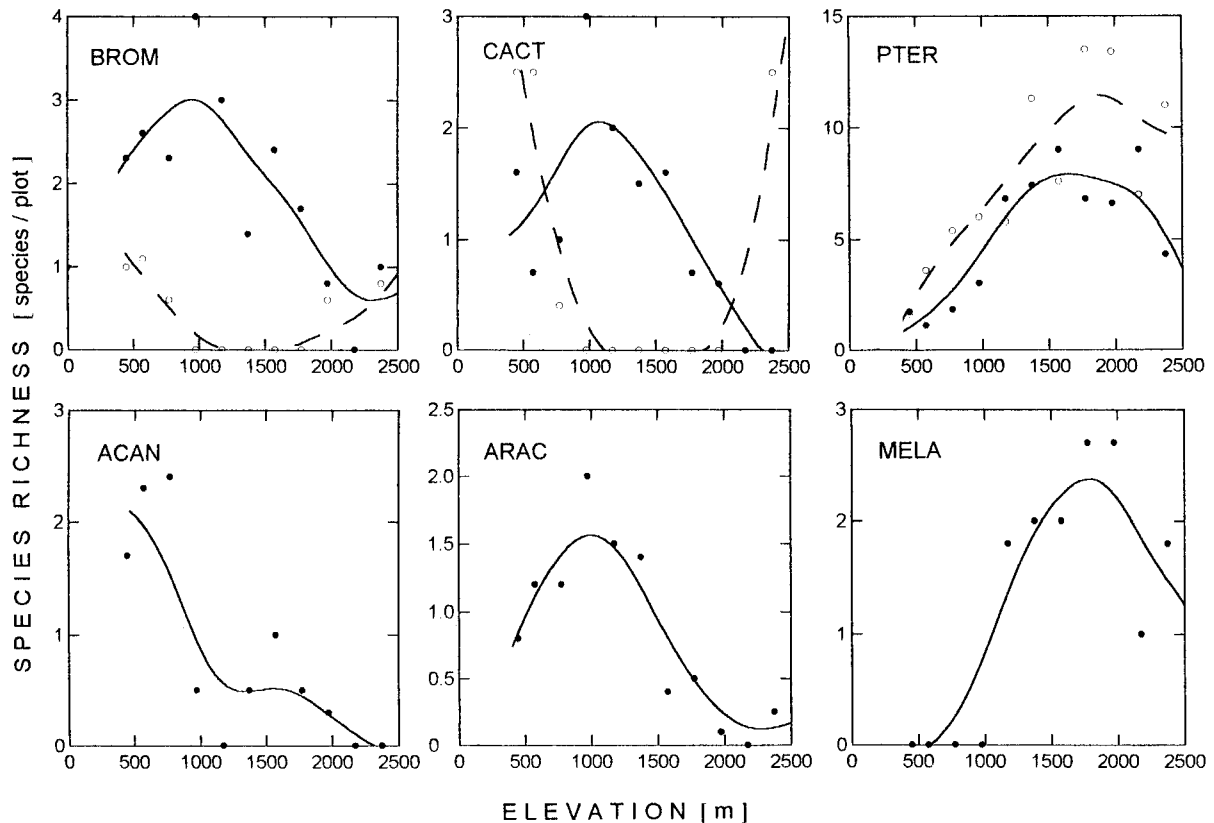


Figure 4. Mean number of species per vegetation plot of Acanthaceae (ACAN), Araceae (ARAC), Bromeliaceae (BROM), Cactaceae (CACT), Melastomataceae (MELA), and Pteridophyta (PTER) along the elevational study transect. Among Bromeliaceae, Cactaceae, and Pteridophyta open circles and broken lines correspond to epiphytic taxa, filled circles and continuous lines to terrestrial taxa.

trees in northwestern Argentina (Grau & Brown 1995) and among birds from central Bolivia southwards (Fjeldså & Mayer 1996).

Among the environmental parameters analyzed in relation to species richness, the low correlation between PET and tree height is surprising, given that both are assumed to reflect ecosystem productivity (Rosenzweig 1968; Lieth 1975). This difference could be due to unreliable climatic data for calculating PET, but this is unlikely, because the estimated elevation of highest PET corresponds to the region of most intensive agricultural activity (Figure 2), a typical pattern in tropical mountain regions (Holdridge et al. 1971). Alternatively, *Podocarpus* trees may grow taller than expected at comparatively low ecosystem productivity. In fact, the tree-height graph (Figure 3d) shows a slightly bimodal distribution of tree height with a first hump at about 1100 m that closely corresponds to the maximum value of PET and a second hump above 1800 m due to the presence of *Podocarpus*. Thus, the

PET estimates are believed to more closely correspond to ecosystem productivity than tree height.

The variety of patterns of species richness with increasing elevation shown by the study groups renders it impossible to derive a general pattern of plant species richness along the study transect. This variability is not surprising and presumably reflects the ecophysiological adaptations of the different study groups. Pteridophytes and Melastomataceae, for example, are well known to require humid conditions (Gurung 1985; Richter & Lauer 1987; van der Werff 1990). In Masicurí, this was shown by their close correlation to moss cover, here used as an indicator of air humidity. The higher correlation values of epiphytic Pteridophytes compared to terrestrial species likely reflects the higher dependence of epiphytic taxa on humidity (Frahm & Gradstein 1991; Wolf 1993). The higher elevation of the maximum species richness of terrestrial Pteridophytes compared to epiphytic species has also been found at two other elevational transects in different biogeographic settings farther



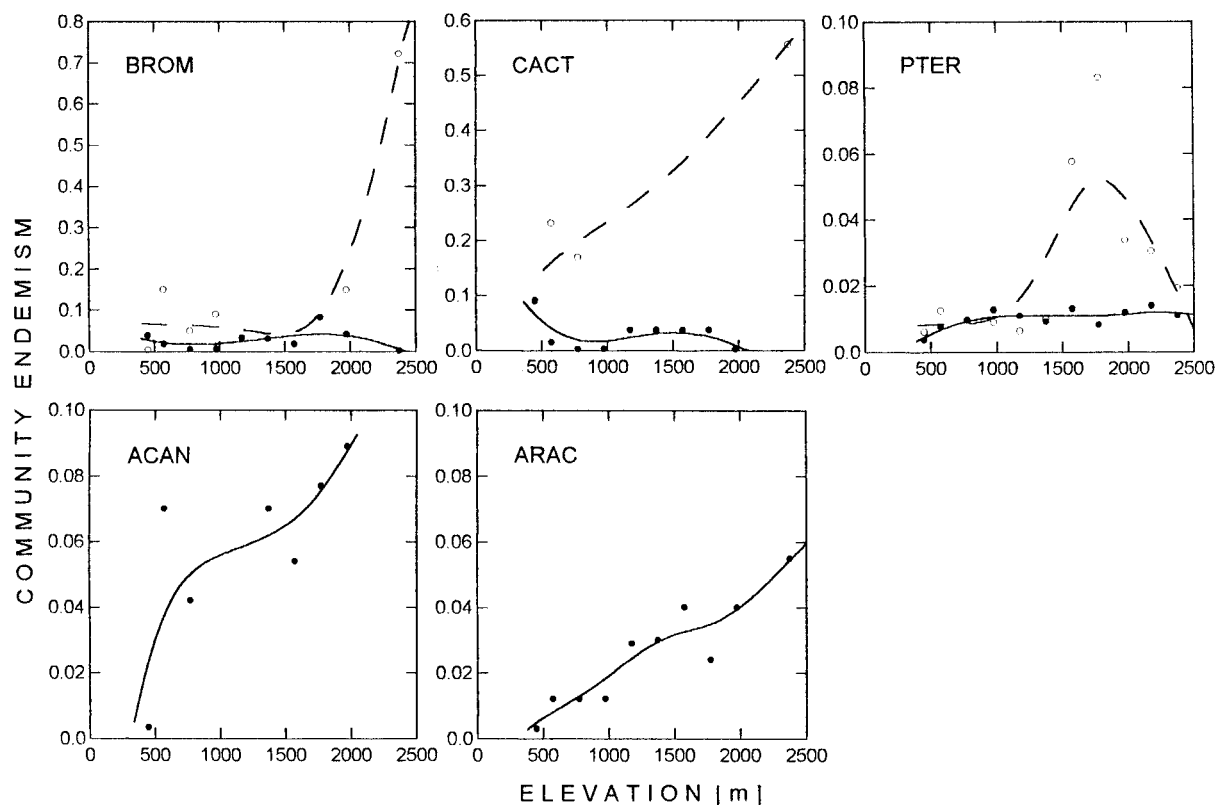


Figure 5. Community endemism per 200 m elevational belt of Acanthaceae (ACAN), Araceae (ARAC), Bromeliaceae (BROM), Cactaceae (CACT), Melastomataceae (MELA), and Pteridophyta (PTER) along the elevational study transect. Among Bromeliaceae, Cactaceae, and Pteridophyta open circles and broken lines correspond to epiphytic taxa, filled circles and continuous lines to terrestrial taxa.

north in Bolivia (Fjeldså et al. 1999; M. Kessler unpubl. data) and thus appears to represent a general pattern of fern species richness in the Bolivian Andes. Possibly, epiphytic taxa are more susceptible to lower temperatures at higher elevations. Alternatively, decreasing canopy height with increasing elevation allows more light to reach the understory of higher-elevation forests, thus favouring terrestrial taxa. These hypotheses could be subjected to experimental testing.

The inverse hump-shaped species richness patterns of terrestrial Bromeliaceae and Cactaceae probably relate to the dependence of these groups on high light conditions in the forest understory. Along the study transect, such conditions are available in the deciduous forests at low elevations and in the steep, rocky *Podocarpus* forests at highest elevations. In fact, all species of terrestrial Bromeliaceae and Cactaceae recorded above 1000 m in Masicurí grew mainly in open scrub vegetation or on rock faces, and were only locally recorded on boulders inside forest habitats (pers. obs.).

The species richness patterns of epiphytic Bromeliaceae and Cactaceae differed strikingly from those of the terrestrial species. The strong decline of epiphytic Bromeliaceae with increasing elevation is intriguing, considering that this plant group could be expected to respond positively to increasing humidity and hence show a pattern resembling that of epiphytic Pteridophytes. Along an elevational transect in a perhumid evergreen montane forest in Parque Nacional Carrasco, species richness of epiphytic Bromeliaceae in fact peaked at about 2000 m (M. Kessler, unpubl. data). Possibly, the strong impact of cold southern air influxes, which can lead to nocturnal frost events down to elevations of 800 m in the study area (Eriksen 1986) and whose effect is greatly ameliorated farther north (Fjeldså et al. 1999) may limit the occurrence of epiphytic Bromeliaceae at Masicurí, especially of species with water-holding leaf bases that may be damaged by frost. Finally, the species richness patterns of Acanthaceae may be linked to a sensitivity to low temperatures, whereas Araceae are known to

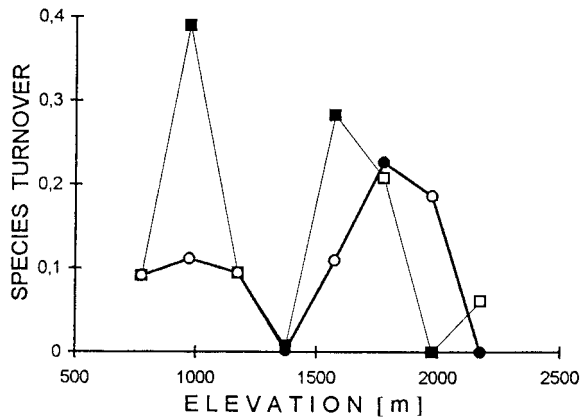


Figure 6. Turnover of species composition of all study groups combined along the Masicuri transect, expressed as the proportion of species reaching their upper (squares, thin line) or lower (circles, bold line) elevational limits at each 200 m elevational belt. Black signs differ significantly (at  $P < 0.05$ ) from a null model of random distribution of elevational range boundaries.

depend on both high temperatures and high humidity (Croat 1995), leading to the good correlation with potential evapotranspiration observed here.

Many of these interpretations of the observed patterns of species richness appear highly plausible, given our knowledge of the ecophysiological requirements of the study groups. However, the present study does not allow to establish direct causal relationships (Levins & Lewontin 1982). Thus, the above explanations are presented as hypotheses, whose mechanistic component should be tested by experimental manipulation.

#### Community endemism

The increase of endemism with increasing elevation shown by most study groups is a well-documented pattern among Andean plants (Balslev 1988; Fjelds  et al. 1999; Kessler 2000) and birds (Graves 1985; Fjelds  1994). This pattern is probably related to the more limited surface area of elevational steps with increasing elevation, and to the rugged topography and the small-scale habitat differentiation in mountain regions, leading to isolated populations and hence local speciation (Graves 1985). Interestingly, the maximum endemism of terrestrial Pteridophyta at 1700 m closely corresponds to the elevational maximum in Parque Nacional Carrasco (1800 m) and as such may represent a general characteristic of this study group in the Bolivian Andes. The most striking deviation from the pattern of increasing endemism with elevation was found among epiphytic Bromeliaceae and Cactaceae,

that showed a slight nonsignificant decline. Too little is known about the ecological correlates of endemism to interpret this pattern.

The differences of endemism values among the study groups presumably reflect their different dispersal abilities. Pteridophytes, which had the lowest values of endemism, are well known for their wide-ranging spore dispersal (Smith 1972; Tryon 1985). The lower endemism values of epiphytic vs terrestrial taxa in Bromeliaceae, Cactaceae, and Pteridophyta is consistent with previously documented patterns and may relate to the need for higher dispersal ability among epiphytic taxa and the more localized habitat distribution experienced by terrestrial species, e.g., saxicolous taxa (Ibisch 1996; Ibisch et al. 1996).

#### Altitudinal zonation

The floristic altitudinal zonation found along the study transect corresponds to the three main physiognomic vegetation zones discernable in the field, i.e., deciduous forest, mixed evergreen forest, and *Podocarpus* forest. Thus, the present study confirms the elevational zonation of the Tucumano-Boliviano region documented in previous studies (Cabrera 1976; Ribera et al. 1992; Navarro 1997; Schulenberg & Awbrey 1997).

Interestingly, methodologically identical studies along an elevational transect in a more diverse perhumid evergreen montane forest in Parque Nacional Carrasco, farther north in the Bolivian Andes, revealed no zonation, except at timberline and at the transition from the foothills to the flat lowland terrain (Kessler 2000). Lieberman et al. (1996) and V squez & Givnish (1998) likewise found no altitudinal vegetation zonation along transects in Costa Rica and western Mexico, respectively. Kitayama (1992) detected a floristic zonation on Mount Kinabalu, Borneo, but this result could have been biased by small sample size (Lieberman et al. 1996) and the use of TWINSpan as analysis method which tends to develop a grouping of plots based on even minimal and possibly random differences among plots. Conceivably, in very species-rich plant communities, no single plant species dominates the ecosystem in such a way as to influence the occurrence of other species. In such situations, species are distributed independently along environmental gradients (Shipley & Keddy 1987). Along the present study transect, however, the transition from deciduous to evergreen and from mixed evergreen to *Podocarpus*-dominated forests is dominated by one or a few tree species.

These transitions are also related to changes in nutrient cycling, soil development, and light conditions (Gerold 1987), and thus determine changes of overall plant community composition. The boundary between the deciduous and evergreen forests, in particular, is extremely sharp at Masicurí, as shown by the abrupt increases of moss cover and Melastomataceae species richness (Figures 3 and 4). This may be due to the remarkably stable location of the lower limit of cloud banks on the mountain slopes on the west side of the Masicurí valley, which is determined by the mountain ridges farther east, that intercepts cloud layers at lower elevations (pers. obs.) (Figure 1). Elsewhere in the Bolivian Andes, diurnal and seasonal variations of the elevation of cloud condensation layers leads to more diffuse transition zones between deciduous and evergreen forests (Fjeldsá et al. 1999).

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