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A COMPARISON OF SIX METHODS TO DETECT ALTITUDINAL BELTS OF VEGETATION IN TROPICAL MOUNTAINS

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Abstract. We explore the question of whether clear-cut elevational vegetation limits can be recognized in species-rich humid tropical mountains to serve as a basis for an altitudinal zonation scheme. To this purpose all species of ferns, aroids, bromeliads, melastomes, palms, and cacti along an elevational transect between 1700 to 3400 m in the Andes of Bolivia were sampled in 400-m² plots at 50 m elevational intervals. Plot analysis was conducted using phytosociological analysis, ordination, cluster analysis, parsimony analysis, structure-based classification, and species turnover. Phytosociological analysis, cluster analysis, and parsimony analysis failed to resolve significant elevational limits, whereas vegetation structure and ordination revealed a major discontinuity between plots at *ca.* 3000/3050 m elevation. Species turnover analysis resolved significant elevational limits at *ca.* 2000 m for ferns, and at *ca.* 2000 m and *ca.* 3050 m for all taxa. The 2000-m limit corresponded with the lower level of the condensation belt as expressed by hypsometric changes in soil parameters; the 3000-m limit with the transition from high forest to dwarf forest. We conclude that discrete limits to vegetation belts in tropical mountains are usually lacking. Discrete boundaries may be observed where sudden shifts in abiotic conditions occur. Statistical analysis of species turnover was the most effective method for detecting elevational vegetation limits in the studied species-rich tropical mountains of Bolivia. *Accepted 29 December 2010.*

Keywords: Altitudinal zonation, Andes, Bolivia, cluster analysis, DCA, ordination, parsimony analysis, phytosociology, species turnover, vegetation structure.

INTRODUCTION

Altitudinal belts on tropical mountains have been of interest since the pioneering work of Alexander von Humboldt in Ecuador (Humboldt 1807). Many different zonation schemes, reflecting abiotic and biotic hypsometric changes, have been proposed, e.g., thermohygric criteria (*tierra caliente – tierra templada – tierra fria – tierra helada*, Troll 1959), vegetation structure (*planar – collin – montan – oreal – alpin – nival*, Ellenberg 1975), and abiotic factors, vegetation structure, and floristics (*lowland – submontane – lower montane – upper montane – subalpine – alpine*, Grubb 1974, Frahm & Gradstein 1991, Bruijnzeel & Hamilton 2000). The elevational limits of the altitudinal belts vary depending on local humidity conditions (cloud condensation levels, distance to ocean), substrate, relief (inclination, rain shadow), latitude (trade wind inversion effect), and mountain mass elevation (*Massenerhebung* effect) (Grubb 1974, Frahm & Gradstein 1991).

Several studies, however, failed to identify discrete altitudinal belts (e.g. Lieberman *et al.* 1996, Vázquez & Givnish 1998, Kessler 2000a). Elevational changes in vegetation belts normally occurred gradually,

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not abruptly, and coincided with the gradual hypsometric change in air temperature along the gradient. Sharp limits in vegetation were deemed local phenomena occurring because of sudden shifts in abiotic factors such as soils, cloud condensation layers, or micro relief. The argument is reminiscent of the classic debate on continuum and discontinuum concepts in vegetation science (Gleason 1926, Braun-Blanquet 1964).

We investigated altitudinal vegetation belts in the Andes using six methods of analysis: phytosociological classification, detrended correspondence analysis (DCA), cluster analysis, parsimony analysis, structure-based classification, and species turnover (= β-diversity; Whittaker 1960). We applied these to a large dataset from the humid mountain forests of the Andes of Bolivia. Several schemes of elevational zonation using different classification methods have been proposed for this area. Beck *et al.* (1993) and Ribera (1995) recognized two, Paniagua *et al.* (2003) three elevational belts. In contrast, Navarro and Maldonado (2002) presented several narrow belts. The main purpose of this study was to 1) describe the vegetational changes along an elevational gradient in the Andes of Bolivia using different methods of analysis, and 2) explore the suitability of the chosen methods for identifying discrete elevational vegetation limits in these species-rich humid tropical mountains that may serve as the basis for an altitudinal zonation scheme.

METHODS

Study area. The field study was carried out in Cotapata National Park (16°15'S, 68°55'W), ca. 80 km NE of La Paz, Bolivia, between 1700 and 3400 m. Very steep slopes (up to 55°) and frequent landslides and tree-falls are characteristic of the area. The geological substrate consists of ordovicial metasilts and metasandstones (Morales 1995). The vegetation of the area has been well described (Beck *et al.* 1993, Ribera 1995, Navarro & Maldonado 2002, Paniagua *et al.* 2003), and consists of humid montane forest and *páramo*. The flora is very rich, with over 1500 species of vascular plants (Moraes & Beck 1992), including more than 300 epiphyte species (Krömer & Gradstein 2003).

We analysed a 5.2 km-long transect (1700-3400 m a.s.l.) on the south-eastern slope of Mt. Hornuni (3650 m). Soils and climate along the transect have been investigated (Schawe 2005) and correlations of soil parameters with species turnover rates were calculated. Average air temperature along the gradient decreased with elevation from *ca.* 17°C to 10°C; annual precipitation increased from 2300 mm to > 5000 mm (Schawe *et al.* 2007, Gerold 2008). A permanent cloud belt occurred from *ca.* 2200 m upward. Soils were very acid (pH < 4.5) with very low effective CEC, high Al^{3+} saturation, and high C/N ratio. Thickness of organic layer, podzolization, and soil humidity increased with elevation (Schawe *et al.* 2007, Gerold 2008). The forest vegetation along the transect was undisturbed except for traces of mining activities at 2600-2700 m. The summit area of Mt. Hornuni (above 3400 m) was covered by *páramo* (Beck *et al.* 1993), whereas drought-deciduous forest fragments occurred along with cultivated areas near the valley bottom at *ca.* 1600 m.

Sampling. Vegetation analysis along the transect was done by sampling all species of Pteridophyta, Araceae, Bromeliaceae, Melastomataceae, Arecaceae, and Cactaceae in 105 20 x 20 m^2 plots positioned at 50 m elevational intervals. We included at least two horizontal replicates per interval, generally exposed to the south-east. At 1850 m, 2550 m, and 3000 m horizontal trails with different exposures were investigated. Landslides and gaps were avoided. Selection of our six plant groups followed Kessler & Bach (1999). The chosen plant groups have been used by Kessler and his research associates in elevational gradient studies in the Bolivian Andes (Kessler 2000b, Kessler 2001, Kessler *et al.* 2001) and have been shown to work well as a surrogate for a whole vegetation. They represent about 15% of total plant species richness along an elevational transect through Andean forests of Colombia (Rangel 1995), and are representative of about 81% of vegetation composition (see Kessler & Bach 1999). While ferns and melastomes are commonly distributed in montane cloud forests up to the altiplano, the other groups are indicators for humidity (especially cacti, aroids) and temperature (palms). Gray bromeliads are characteristic for dry forests; they are replaced by green bromeliads in cloud forests. In each plot, vegetation structure (height of herbs, shrubs, forest understory, forest canopy, and of emergent trees) was estimated and species cover and abundance were sampled using the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974). Epiphytic taxa were determined by climbing small trees, sampling fallen trees and branches, and with binoculars. Species identification was done by the first author and by specialists; vouchers were deposited in the National Herbarium of

Bolivia (LPB). Nomenclature follows specialist identifications for aroids, bromeliads, melastomes, palms, and cacti, and Kramer & Green (1990) for ferns except for Grammitidaceae (Smith 1993), Hymenophyllaceae (Morton 1968), and Vittariaceae (Crane 1997). Juvenile or sterile material of *Sphaeroconium* and *Mecodium* (Hymenophyllaceae), and of selected melastomes, was excluded from the analysis.

Data analysis. Plot analysis was conducted using phytosociological classification, detrended correspondence analysis (DCA), cluster analysis, parsimony analysis, structure-based classification, and species turnover. Phytosociological analysis included identification of species groups and diagnostic taxa by calculating fidelity to particular vegetation units using the phi coefficient of association (Φ). Standardization of the plot group size follows Chytrý *et al.* (2002); target group size was 33.33% of the total dataset. The range of Φ was between -1 and 1, where 1 indicates that the taxon is present in all plots of the target vegetation unit and absent outside. Phytosociological arrangement was carried out for all species having an abundance ≥ 10% with JUICE 6.5 (Tichý 2002).

Before running further multivariate analysis, Beals smoothing was applied to the data to minimize noisiness in vegetation community matrixes. Clusters recovered in the Ward cluster analysis were tested for significance following Pillar (1999). DCA was conducted with default program parameters (rescaled axes, rescaling threshold 0, and 26 segments, downweighting of rare species). For both analyses PC-ORD software was used (McCune & Mefford 1999).

For parsimony analysis, plots were grouped based on the presence or absence of species (coded as 0 or 1) and rooted with an artificial area coded all zeros using PAUP (Luna *et al.* 1999, Swofford 2001). Most parsimonious groupings were combined in a strict consensus tree. Statistical support of plot groups ("clades") was calculated using bootstrapping.

For the structure-based classification and the species turnover analysis, sample plots were aggregated at elevational intervals of 100 and/or 200 m for ecological reasons: narrower belts are more strongly influenced by local heterogeneity, e.g. landslides and treefalls. Vegetation structure was calculated at 200-m elevational intervals based on mean stratum heights of all sample plots within an interval. Species turnover was determined by counting the number of species having either their upper or lower distribution limits in a distinct interval and by calculating the Wilson-Shmida index (Wilson & Shmida 1984) between adjacent steps. Intervals were arranged in 100 and 200-m elevational steps, respectively. Turnover analysis was conducted separately for four of the six plant groups (ferns, aroids, bromeliads, melastomes), for epiphytic and terrestrial species (excluding hemiepiphytic aroids), and for the fern families Lomariopsidaceae and Hymenophyllaceae. To determine whether observed variation in species turnover was due to stochastic variations of species elevational distributions, we applied Monte Carlo simulations (Bach *et al.* 2007).

RESULTS

We recorded a total of 342 plant species (228 ferns, 64 melastomes, 22 aroids, 21 bromeliads, 5 palms, 2 cacti). Cacti occurred only in 4 sample plots at the lower end of the transect, whereas palms were distributed up to 2800 m. Species richness was highest between 1900 m and 2000 m.

Phytosociological analysis (see Supplementary material Appendix S1 for the complete table), conducted with 133 species, resulted in an elevational arrangement of sample plots without discrete limits. About 20 species groups were resolved (2-9 species each), all of them showing elevational overlap. Diagnostic species were detected for each species group (Table 1), but because of the overlap no clear-cut elevational plot units could be distinguished. Nevertheless, clear differences in floristic composition were observed at opposite ends of the transect. At the lower end species characteristic of dry forests occurred: *Anthurium paraguayense, Asplenium bangii, Microgramma percussa and Epiphyllum phyllanthus.* At the upper end, *Miconia mandonii, Elaphoglossum mathewsii, Lellingeria pseudocapillaris, Melpomene pilosissima* (all of them members of species group 20) occurred exclusively in plots located in dwarf forest remnants.

DCA revealed four groups (Fig. 1), one made up of plots in the open shrubby dwarf forest remnants (subalpine forest s_3; 3050-3400 m), a second set of plots (subalpine forest s_2) at 2900-3075 m (thus slightly overlapping the first group), a third set of plots at different exposures along the horizontal trail at *ca.* 3000 m (subalpine forest s_1), and a fourth group (montane cloud forest mo; 1700-2850 m) containing all remaining plots. The latter were ordered in a straight line with a slightly wider distance at the upper end of the transect and a weak discontinuity at about 2300 m. This extension (axis 1) is highly correlated with elevation (post-correlation of

TABLE 1. Diagnostic species of the species groups resolved in the phytosociological table (see Supplementary material Appendix S1). Average phi coefficient (Av. Φ) refers to the fidelity values of all species occurring in the same plots of that group.

No.	Diagnostic species (Φ)	Constant species (Frequency %)	Elevation (m) min.	max.	Av. Φ	No. of plots
1	*Asplenium cirrhatum* (0.847), *Miconia spennerostachya* (0.804)	*Asplenium cirrhatum* (89), *Philodendron ornatum* (100)	1700	2000	0.541	18
2	*Philodendron ornatum* (0.861), *Pecluma divaricata* (0.771)	*Anthurium yungasense* (89), *Philodendron ornatum* (100)	1700	2050	0.511	28
3	*Stenospermation rusbyi* (0.807), *Cyathea delgadii* (0.795)	*Cyathea delgadii* (100), *Stenospermation rusbyi* (100), *Polypodium fraxinifolium* (89)	1750	2200	0.490	19
4	*Polypodium fraxinifolium* (0.813)	*Polypodium fraxinifolium* (88)	1700	2620	0.447	60
5	*Asplenium cirrhatum* (0.895), *Miconia spennerostachya* (0.833), *Asplenium auritum* (0.817)	*Philodendron ornatum* (100), *Asplenium cirrhatum* (100), *Polypodium fraxinifolium* (92), *Miconia staphidioides* (92), *Miconia spennerostachya* (92)	1700	2000	0.605	13
6	*Hymenophyllum microcarpum* (0.794), *Anthurium stephanii* (0.787), *Miconia bangii* (0.779), *Miconia staphidioides* (0.766)	*Polypodium latipes* (91), *Miconia staphidioides* (91), *Elaphoglossum papillosum* (87)	1750	2125	0.536	23
7	*Terpsichore chrysleri* (0.896), *Anthurium triphyllum* (0.799)	*Terpsichore chrysleri* (96), *Polypodium latipes* (87)	1750	2175	0.522	23
8	*Melastomataceae* sp. KB1424 (0.840), *Hymenophyllum interruptum* (0.823), *Elaphoglossum buchtienii* (0.779)	*Hymenophyllum interruptum* (88), *Elaphoglossum lechlerianum* (88)	1700	2350	0.512	32
9	*Guzmania marantoidea* (0.819)	*Guzmania marantoidea* (94), *Melpomene firma* (91)	2000	2575	0.475	32
10	*Miconia micropetala* (0.929)	*Miconia micropetala* (100), *Hymenophyllum plumieri* (100)	2150	3100	0.468	45
11	*Miconia plumifera* (0.808), *Elaphoglossum lingua* (0.791)	*Hymenophyllum plumieri* (94), *Anthurium weberbaueri* (92), *Miconia plumifera* (86), *Melpomene firma* (86)	2100	2725	0.519	36

No.	Diagnostic species (Φ)	Constant species (Frequency %)	Elevation (m) min.	max.	Av. Φ	No. of plots
12	*Hymenophyllum speciosum* (0.854), *Zygophlebia mathewsii* (0.784), *Cyathea delgadii* vel aff. (0.757)	*Hymenophyllum speciosum* (94), *Hymenophyllum plumieri* (94), *Blechnum lechleri* (90), *Zygophlebia mathewsii* (87), *Micropolypodium blepharideum* (87), *Anthurium weberbaueri* (87)	2150	2900	0.521	31
13	*Miconia setulosa* (0.834), *Miconia* cf. *cyanocarpa* (0.786)	*Hymenophyllum plumieri* (100), *Micropolypodium blepharideum* (95), *Blechnum lechleri* (95), *Anthurium weberbaueri* (95), *Miconia setulosa* (89)	2350	2700	0.567	19
14	*Melpomene anfractuosa* (0.955), *Niphidium crassifolium* (0.927)	all 100%: *Terpsichore laxa, Polypodium fraxinifolium, Niphidium crassifolium, Miconia plumifera, Melpomene anfractuosa, Hymenophyllum plumieri, Elaphoglossum setigerum, Elaphoglossum cuspidatum, Blechnum lechleri*	2350	2500	0.696	8
15	*Melpomene flabelliformis* (0.854), *Hymenophyllum ruizianum* (0.812), *Miconia aff. hirta* (0.775)	*Melpomene flabelliformis* (95), *Hymenophyllum plumieri* (95), *Hymenophyllum ruizianum* (90)	2400	3200	0.549	39
16	*Lellingeria apiculata* (0.821)	*Hymenophyllum plumieri* (100), *Miconia micropetala* (94), *Melpomene flabelliformis* (94)	2600	3050	0.546	16
17	*Terpsichore semihirsuta* (0.806), *Culcita coniifolia* (0.796)	*Miconia micropetala* (100), *Melpomene flabelliformis* (100), *Hymenophyllum plumieri* (100), *Hymenophyllum ruizianum* (94), *Hymenophyllum axillare* (94)	2725	3075	0.576	16
18	*Melastomataceae* sp. KB1058 (0.953), *Lellingeria flagellipinnata* (0.909), *Greigia kessleri* (0.851)	all 100%: *Racinaea seemannii, Miconia micropetala, Melpomene flabelliformis, Melastomataceae* sp. KB1058, *Hymenophyllum ruizianum, Hymenophyllum plumieri*	2900	3075	0.668	13
19	*Miconia* sp. KB1059 (0.945), *Elaphoglossum unduaviense* (0.889), *Lellingeria flagellipinnata* (0.780), *Blechnum lima* (0.780), *Zygophlebia dudleyi* (0.758)	*Melpomene flabelliformis* (100), *Miconia* sp. KB1059 (95), *Hymenophyllum ruizianum* (95), *Racinaea seemannii* (90), *Elaphoglossum unduaviense* (90)	2820	3300	0.595	20
20	*Elaphoglossum mathewsii* (1), *Terpsichore longisetosa* (0.957)	all 100%: *Terpsichore longisetosa, Melpomene flabelliformis, Hymenophyllum axillare, Elaphoglossum mathewsii*	3200	3400	0.979	4

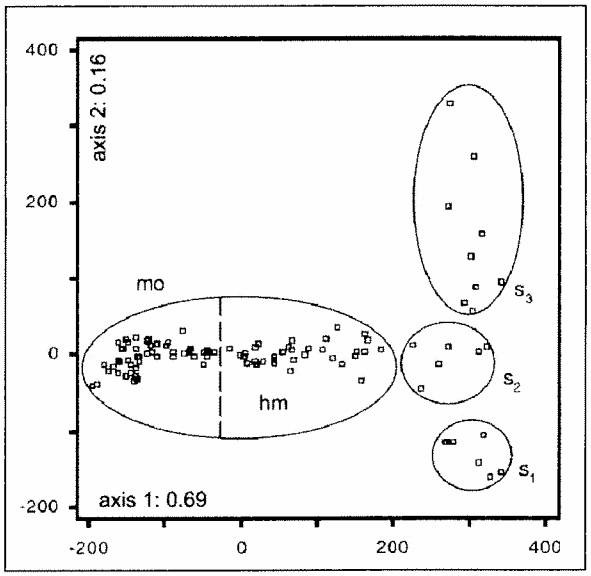

FIG. 1. Classification of plots by detrended correspondence analysis (DCA). Four groups of plots are recognizable, as indicated by graphically added circles: montane cloud forest mo (1700 – 2850 m), and subalpine forest s_1 (2820 – 3015 m), s_2 (2900 – 3075 m), and s_3 (3050 – 3400 m). Plots of group s1 are located mostly along a horizontal trail at 3000 m, those of group s_3 in shrubby dwarf forest remnants. Group mo revealed a weak discontinuity at *ca.* 2300 m, separating lower from upper montane (hm) cloud forest. Post-correlation of axis 1 (eigenvalue = 0.69) with elevation was highly significant (r = 0.98) and gradient length was 0.5771, indicating a complete species turnover.

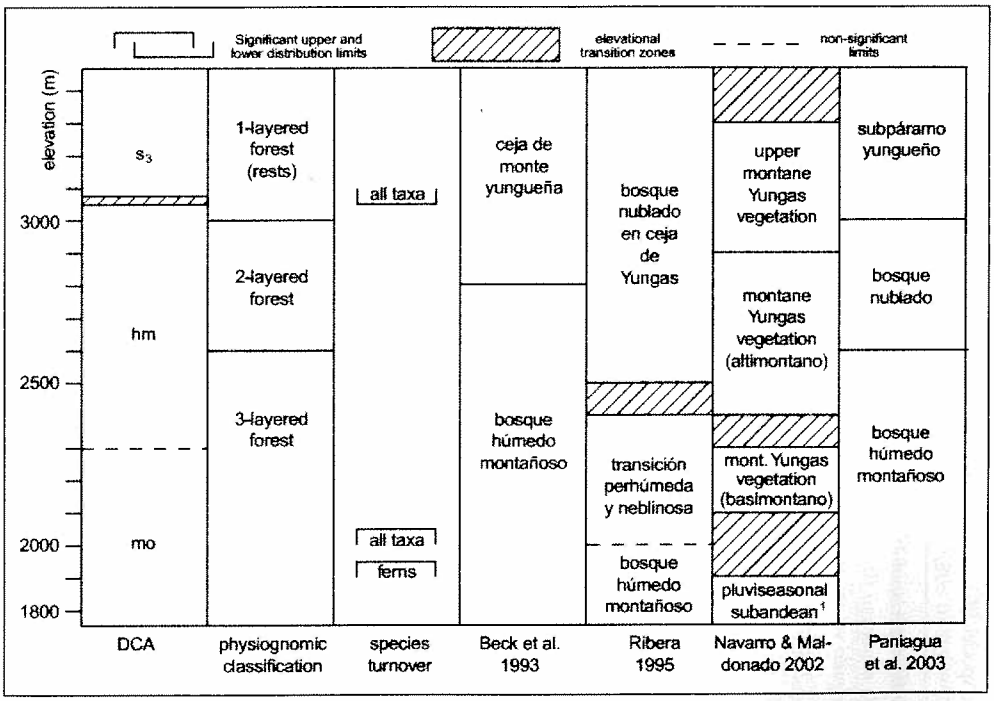

FIG. 2. Elevational limits in vegetation composition along the transect, as resolved by DCA, analysis of forest structure and species turnover, and by other authors. Significant upper and lower distribution limits of all taxa and ferns are detected using species turnover analysis and Monte Carlo simulations (see Figures 2 and 3). Simulation follows Bach *et al.* (2007). Abbreviations of DCA groups as in Fig. 1.

[1] Pluviseasonal subandean vegetation of the Yungas.

scores, r = 0.98). In contrast, axis 2, which clearly separates s_2 from s_3, reflects differences in species composition due to light intensity, i.e. exposure (s_1) and canopy closing (s_3).

Cluster analysis (Supplementary material Appendix S2) revealed three elevational plot groups with little elevational overlap at the 20% threshold line (1700-2400 m; 2350-2850 m; 2800-3400 m). The grouping of plots revealed in this analysis was not significant ($p = 0.092$).

Parsimony analysis (Supplementary material Appendix S3) resulted in 189 most parsimonious cladograms of 1956 steps, revealing two small clades made up of two adjacent plots each (2200-2250 m; 2675-2725 m) with bootstrap support (BS) > 70%. Other clades had BS < 50% and were of little use in terms of plot grouping.

Canopy height data revealed the occurrence of three structural types of vegetation along the transect: a) *ca.* 15-20-m high, 3-layered forest up to 2600 m, b) *ca.* 10-15-m high, 2-layered forest between 2600 and 3000 m, and c) *ca.* 5-m high, one-layered dwarf forest above 3000 m (Fig. 2).

Species turnover along 100-m elevational intervals lacked clear peak values in most of the plant taxa we analyzed. More informative patterns were resolved when lower and upper distribution limits were analyzed separately and subjected to simulation. Significant peak values occurred at 1950 m for upper limits of all ferns ($p < 0.05$), at 2050 m for upper limits of all species ($p < 0.001$), and at 3050 m for lower limits of all species ($p < 0.001$). In general, the number of lower limits was highest below 2400 m and gradually decreased towards higher elevations, whereas upper limits oscillated along the transect (Fig. 3). Applying these limits to the phytosociological table revealed diagnostic species with fidelity values as follows: *Philodendron ornatum* (0.902) and *Anthurium yungasense* (0.752) for forest up to 2000 m, *Micropolypodium blepharideum* (0.752) for forest between 2000 and 3050 m, and *Miconia* sp. KB 1059 (0.875) and *Zygophlebia dudleyi* (0.81) for dwarf forest above 3050 m.

Species turnover along 200-m elevational intervals yielded higher Wilson-Shmida index values and fewer peaks. Terrestrial taxa and epiphytic bromeliads had maximum turnover rates at 2700 m, other epiphytic groups lacked maximum rates. We detected significant accumulations for upper elevational limits of all species (1950 m; $p < 0.05$) and all epiphytic species (2000 m; $p < 0.05$).

DISCUSSION

The proposed schemes of elevational zonation differ clearly in the number of belts and concrete altitudinal limits (Fig. 2). Paniagua *et al.* (2003) recognized three elevational belts: humid montane forest (*bosque húmedo montano*) at 1500 – 2600 m; upper montane cloud forest (*bosque nublado*) at 2600 – 3000 m, and subalpine forest (*ceja de monte*) above 3000 m. Beck *et al.* (1993) and Ribera (1995) recognized only two elevational belts, with upper montane cloud forest and subalpine forest being combined into a single belt (*ceja de monte yungeño, bosque nublado en ceja de Yungas*, respectively). Navarro & Maldonado (2002) presented in their study a more elaborate subdivision into narrow belts of only a few hundred meters each (Fig. 2). The differences in zonation schemes are probably due to the different methodologies and data sets used by the various authors. Beck *et al.* (1993) and Ribera (1995) used vegetation structure and dominant species, Navarro & Maldonado (2002) vegetation classification and bioclimate, and Paniagua *et al.* (2003) general floristic composition and remote sensing. None of these authors applied ordination, cluster analysis, parsimony, or species turnover analysis.

In our study, phytosociological analysis of the plot data (Table 1) showed a large overlap among species groups along the transect. This method only permits subjective recognition of elevational belts. Dividing the transect into three plot groups with limits positioned below species groups 10 and 11 (comprising plots up to 2200 m), and below species groups 18 and 19 (comprising plots above 2200 m and below 2900 m), reveals the following diagnostic species with high fidelity values: *Miconia staphidioides* (0.835) and *Philodendron ornatum* (0.813) for the first plot group, *Miconia plumifera* (0.761) and *Micropolypodium blepharideum* (0.858) for the second, and *Elaphoglossum unduaviense* (0.852) and *Miconia* sp. KB 1059 (0.904) for the third. Moving the limits towards higher or lower elevation, however, yields other diagnostic species with high fidelity values. It thus appears that phytosociological analysis of our data does not allow for recognition of elevational belts, contrary to previous phytosociological investigations in the study area.

DCA differentiates between the plots at different exposures at ca. 3000 m (plot group s_1) and between those from 2900-3075 m (s_2) and 3050-3400 m (s_3), with a slight overlap between 3050 and 3075 m. In Table 1, however, these latter two plot groups are not

clearly discriminated. Thus the s_1-s_2 plots are mixed and situated beyond species groups 12 and 16, sharing exclusively species of group 18. The s_3 plots are positioned beyond species group 18, with the exception of two plots associated with species groups 17 and 18. When these two plots are excluded from the analysis, however, the lower limit of group s_3 shifts from 3050 to 3080 m, and groups s_2 and s_3 no longer overlap. Diagnostic for group s_3 is the filmy fern *Hymenophyllum undulatum* (Φ = 0.806), which also occurs at lower elevations. For the remaining groups revealed by DCA, no diagnostic species can be assigned by fidelity measurements. This clearly demonstrates the gradual nature of floristic changes along the study transect.

The failure of cluster analysis to detect significant elevational borders is not surprising since this method defines groups regardless of the presence of limits (Pillar 1999). The trends revealed by the cluster approach, however, show interesting correlations with the results of DCA and phytosociology. Thus the weak border detected by cluster analysis at 2800/2850 m coincides with the 2900 m borders detected by DCA, and is also reflected by the upper limit of species groups 12 and 16 in the phytosociological table. Fidelity analysis of the results obtained by cluster analysis revealed two diagnostic species for the dwarf forest, *Elaphoglossum unduaviense*, (Φ = 0.844) and *Miconia* sp. KB 1059 (Φ = 0.904). The two are also diagnostic elements of species group 19 in the phytosociological table, but with higher fidelity values due to the lower number of plots used in phytosociological analysis. Hence phytosociology allows a more detailed description of the vegetation units than DCA or cluster analysis.

Parsimony analysis, as a further clustering method with significance testing (bootstrapping), was also unable to assign significance to any cluster containing more than two plots. The result suggests that the method is only appropriate where discrete groups exist (Cavieres *et al.* 2002, Aguilar *et al.* 2003). In contrast to cluster analysis, which always suggests sharply limited units, parsimony analysis applies significance tests to identified exclusive species combinations. Because of the persistent species overlap along the gradient, however, parsimony analysis failed to detect significant floristic groups. Our analysis casts doubt on the suitability of this approach to detect patterns in species-rich vegetation systems.

The structure-based classification revealed a similar shift of vegetation types at 3000 m as recovered with DCA (s_1 and s_3) and by a significant accumulation of lower distribution limits of all species. This underlines the suggestion that axis 2 (eigenvalue: 0.16) of the DCA represents light conditions along the transect. The shift in vegetation structure at 2600 m was not recovered by the other methods applied but coincided with the classification of Paniagua *et al.* (2003) based on remote sensing. This shift possibly does not reflect altitudinal changes but rather human influence or relief heterogeneity, as described from a species-rich Andean forest of southern Ecuador (Paulsch *et al.* 2008).

Species turnover revealed clear elevational limits, with significant borders resolved at *ca.* 2000 m (upper limit of all taxa at 2050 m; ferns at 1950 m) and 3050 m (lower limit of all taxa analyzed together). The border at 3050 m was also detected by DCA and phytosociology, but the 2000-m limit was not detected by any other method. The concordance of all taxa and ferns may be due to the preponderance of fern species, which included about two-thirds of all taxa. The slight elevational difference in the peak values of the two groups may reflect variation in group-specific responses to ecological constraints. Fern distribution, for example, is strongly determined by air humidity (Kluge *et al.* 2006) while that of melastomes is more strongly influenced by edaphic conditions (Tuomisto & Ruokolainen 1994). Fidelity analysis of the phytosociological table, taking account of detected species turnover borders, shows the diagnostic value of some taxa (e.g. *Zygophlebia dudleyi*), which was not demonstrated with other methods applied in this study. This reinforces the observation that different results may be obtained by different methods of analysis.

Shipley and Keddy (1987) have argued that, in general, distinct floristic limits occur when significant upper and lower turnovers coincide. Several authors, however, have suggested that the prevalent parameters determining upper and lower distribution limits of species are not the same (Dobzhansky 1950, MacArthur 1972, Grubb 1977, Kaufman 1995, Stohlgren & Bachand 1997, Liancourt & Tielbörger 2009), with abiotic constraints primarily influencing upper levels (temperature, humidity, soils) and biotic ones (competition, herbivory, pathogens) influencing lower levels. The notion that upper distribution limits are constraint by abiotic factors is confirmed by our study. The statistically significant upper elevational limit of many plant species at about 2000 m along the transect appears to correlate with pro-

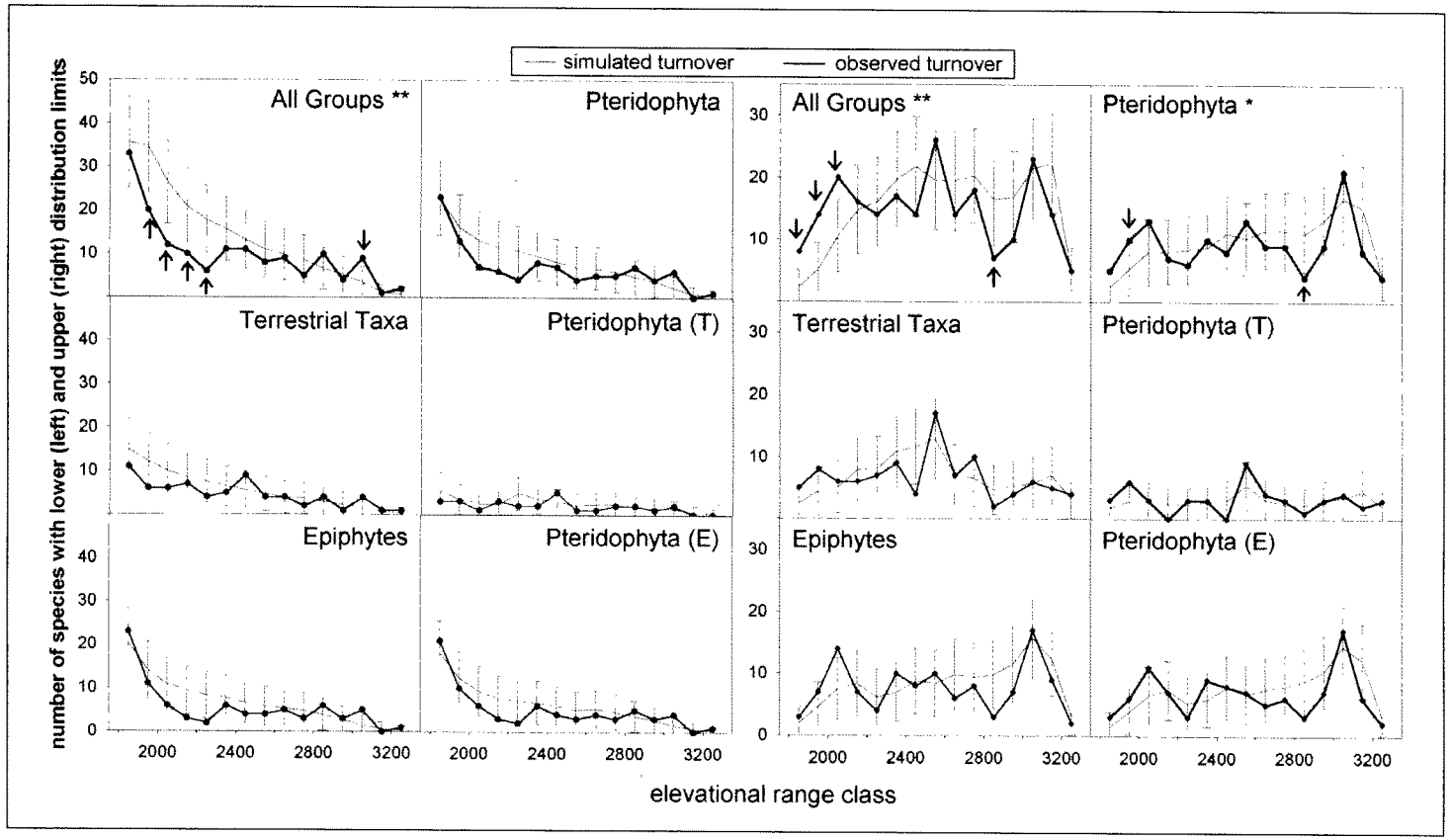

FIG. 3. Observed number of lower (left) and upper (right) elevational distribution limits of species along the transect (black line), and simulated number (gray line). Simulation as described in Bach *et al.* (2007): Error bars indicate double standard deviation of 1000 simulated numbers of limits (95.4% acceptance region). Because of alpha inflation under repeated tests (at each elevation), significance was additionaly calculated by χ^2 test. Arrows mark significant outliers (**: P<0.001, *: P<0.05, E = epiphytes, T = terrestrial taxa).

nounced hypsometric changes in soil and climate parameters (Schawe *et al.* 2007, Gerold 2008). Above 2000 m, strong soil acidification was observed as indicated by significant changes in base saturation and exchangeable H^+-ions of the A_h soil layer. Species turnover of all studied plant groups showed a strong correlation with the base saturation ($r = 0.93$; $P < 0.05$ Bonferroni corrected) and to exchangeable H^+-ions of the A_h horizon ($r = 0.94$; $P < 0.05$ Bonferroni corrected), respectively. Significant correlations with exchangeable cations (K, Mg) and total N-content of the A_h horizon ($P < 0.05$) were found for the species turnover of all terrestrial taxa and of epiphytic bromeliads. The later results certainly do not indicate a direct relationship. In fact, Hietz *et al.* (1999) showed that the litterfall of the supporting trees serves as a nutrient source for epiphytes, particularly for bromeliads with funnels. Because no changes occurred in the underlying geological substrate at this elevation, the increased soil acidification above 2000 m is apparently due to the increased wetness caused by the occurrence of persistent clouds above 2000 m (Schawe *et al.* 2007, Gerold 2008). Thus we conclude that the significant species turnover at *ca.* 2000 m may have been induced by the lower level of the cloud bank in the area.

Cloud bank elevations may vary considerably with season, El Niño Southern Oscillation events, solar radiation, and evapotranspiration. These fluctuations in abiotic conditions may lead to incidental species range extensions in "good" years, beyond the limits of vegetation belts (Levin 1974). The dispersal of species in the ecotone between adjacent vegetation belts, in turn, may act as a homogenizing force, blurring sharp vegetations borders. These dispersal events may eventually lead to the absence of discrete elevational limits in humid tropical montane forests (Loreau 2000), such as our study area.

At 3050 m the significant species turnover is due to the high accumulation of lower distribution limits of all taxa, indicating biotic constraints (see above). At this part of the transect, cloud banks are still persistent, while other abiotic changes occur gradually: vegetation structure changes gradually from dense forest to open páramo and species distributions are less driven by competition for light. At 3000 m the 2-layered forest is replaced by a one-layered dwarf forest (Fig. 2). The majority of species contributing to the accumulation of lower elevational limits at this elevation are terrestrial páramo species that do not occur inside dense forests (e.g. *Blechnum auratum, Ceradenia ayopayae, Ceradenia bishopii, Elaphoglossum paleaceum* vel aff., *Hymenophyllum trichophyllum, Miconia* aff. *setulosa*).

CONCLUSION

Our study supports the viewpoint that there is a lack of clear-cut limits of vegetation belts in humid, species-rich tropical mountains (Lieberman *et al.* 1996, Vázquez & Givnish 1998, Kessler 2000a). Discrete vegetation borders can be observed where sudden shifts in abiotic conditions occur, e.g., due to the occurrence of stable condensation belts or marked topographic or pedological changes (Frahm & Gradstein 1991), and in species-poor ecosystems where prominent key species induce distribution limits (e.g. the Alps). Otherwise, broad transition zones between elevational belts occur, reflecting the individual species ranges which, in turn, depend on autecological constraints and mass effects.

When accepting the existence of broad transition zones, the vegetation of Cotapata National Park may be classified into three elevational belts according to the UNESCO classification (Bruijnzeel & Hamilton 2000): *lower montane cloud forest* (mo) - *upper montane cloud forest* (hm) - *subalpine forest* (s). The limits of these units are not sharp and elevations valid for all methodological approaches cannot be given. The transition between lower and upper montane cloud forest in the area is between about 1900 and 2400 m and is apparently determined by the variation of the lower cloud condensation level. The transition was only detected by species turnover analysis. The transition from upper montane to subalpine dwarf forest lies at 2900-3050 m and was detected by all approaches except parsimony analysis.

For local purposes, cluster analysis and structure-based vegetation analysis appear to be suitable preliminary approaches to detecting elevational belts. Correlations between vegetation belts and abiotic conditions are best explored using principal component analysis (e.g. DCA). Whether phytosociological classification is a suitable method for detecting elevational vegetation belts in species-rich tropical mountain areas remains unclear. In our study, phytosociology alone was not informative on the questions posed. However, it allowed for a better understanding of the zonation scheme and a more detailed description of vegetation units. Parsimony analysis combined with bootstrapping was unsuitable due to the lack of sharp vegetation borders. We conclude that statistical analysis of species turnover based on counts

of upper and lower distribution limits is the most effective method for detecting elevational vegetation limits in species-rich tropical mountain forests.

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SUPPLEMENTARY MATERIAL ON ECOTROPICA WEBSITE

Appendix S1: Ordered phytosociological table of Mt. Hornuni, Cotapata National Park, Bolivia.
Appendix S2: Result of the cluster analysis. Three clusters are recognizable at the 20% similarity threshold.
Appendix S3: Result of the parsimony analysis. Numbers at the terminal dichotomies correspond to the plot number. Numbers at the axes display the bootstrap confidence values of the parsimony analysis.
Appendix S4: Complete list of species found along the investigated transect.

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