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VEGETATION STRUCTURE ALONG THE FOREST – PÁRAMO TRANSITION BELT IN THE SIERRA NEVADA DE MÉRIDA: IMPLICATIONS FOR UNDERSTANDING TREELINE DYNAMICS

ESTRUCTURA DE LA VEGETACIÓN EN LA ZONA DE TRANSICIÓN BOSQUE - PÁRAMO EN LA SIERRA NEVADA DE MÉRIDA: IMPLICACIONES PARA ANALIZAR LA DINÁMICA DEL LÍMITE FORESTAL

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ABSTRACT

The mountain treeline in the northern Andes is a complex transition zone between mountain forests (*subpáramo*) and open *páramo* grasslands, and is considered a key environment for monitoring the effects of global climate change. We analyzed the vegetation structure in the upper limit of continuous forests, in small forest islands and in open páramos along an altitudinal transect from 3260 to 3550 m a.s.l. in the NW facing flank of the Sierra Nevada de Mérida. We also included plots in the contact borders or ecotones between forests and páramos along the gradient. Diversity of the upper stratum (woody species) decreased with altitude, while in the lower stratum the opposite trend was detected. We found a clear change in species composition and abundance along the altitudinal gradient. In continuous forests bellow 3300 m cloud forest and subpáramo species were dominant (*Psammisia penduliflora, Libanothamnus nerifolius*), while they were completely absent in forest islands and open páramos at higher altitudes. In the forest islands and páramo-forest borders the dominant woody species were *Diplostephium venezuelense* and *Cybianthus marginatus*. Even though *D. venezuelense* was absent in the páramos above 3500 m it was the dominant species of the sparse tree layer of the open páramos at lower altitudes. This suggests it could act as pioneer species in scenarios of altitudinal advance of the treeline induced by climate change.

Key words: altitudinal gradient, climate change, diversity, ecotone, forest islands, pioneer species, treeline

RESUMEN

El límite altitudinal del bosque continuo corresponde en los Andes del Norte a una compleja zona de transición entre el bosque paramero y el páramo, y es considerado un ambiente clave para el monitoreo de los efectos del cambio climático global. Se analizó comparativamente la estructura de la vegetación en el límite superior del bosque continuo, en pequeñas islas de bosque y en páramos abiertos en una transecta altitudinal desde 3260 hasta 3550 m s.n.m. en la vertiente noroeste de la Sierra Nevada de Mérida. Se incluyeron también parcelas ubicadas en el ecotono bosque-páramo a lo largo del gradiente. La diversidad del estrato superior leñoso disminuyó con el aumento de altitud mientras que en el estrato inferior sucedió lo contrario. Se observó un claro patrón de cambio en la composición y abundancia de las plantas leñosas en el gradiente altitudinal. En los bosques continuos por debajo de 3300 m predominaron elementos propios de la selva nublada montana alta y del bosque paramero (ej. *Psammisia penduliflora, Libanothamnus nerifolius*), los cuales estuvieron ausentes en las islas de bosque y los páramos más altos. En las islas de bosque y en los bordes bosque-páramo dominaron las plantas leñosas *Diplostephium venezuelense* y *Cybianthus marginatus*. Aún cuando *D. venezuelense* estuvo ausente en los páramos a mayor altitud, fue predomiante en el componente leñoso del páramo a menor altitud. Esto la señala como una posible especie pionera en escenarios de ascenso altitudinal del límite del bosque por efecto del calentamiento global.

Palabras clave: cambio climático, diversidad, ecotono, especies pioneras, gradiente altitudinal, islas de bosque, límite arbóreo

INTRODUCTION

The altitudinal limit of continuous forests corresponds in the northern Andes to the transition between open *páramo* grasslands and mountain elfin forests (known locally as *subpáramo, bosque paramero* or *ceja andina*). There are several definitions of the treeline available in the literature. Körner (1998) refers to it as the line that connects the highest forest patches, while Grace *et al.* (2002) define it as the limit of tree growth in mountain forests. In the present paper we adopt Bader's *et al.* (2007a) interpretation, defining the treeline as a transition zone, of variable amplitude, located between the continuous upper limit of mountain forests and open alpine vegetation.

The treeline is a dynamic zone. The available evidence indicates there have been several events of altitudinal ascent and descent of this limit during the Pleistocene glacial-interglacial cycles (van der Hammen 1974; Graf 1996; Grace *et al.* 2002; Wille *et al.* 2002; Solomina 2005). This sensibility to past climate change has led to consider the mountain treeline as a key environment for monitoring the effects of current anthropogenic climate change (Camarero *et al*. 2000).

The causes and mechanisms of treeline formation have been widely discussed. The available evidence suggest that its altitudinal position at a global scale is determined by thermal limitations for tree establishment modulated by a series of other abiotic and biotic factors (e.g. rainfall patterns, radiation levels, herbivores, fires). These other modulating factors vary in importance depending of the planet's region (Körner 1998). The altitudinal-thermal limit of forests has been linked with the position of a mean air isotherm during the growing season of 8-10ºC for extratropical regions and 3-6ºC for tropical regions (Grace *et al*. 2002).

There are few available studies with the explicit objective of analyzing changes in vegetation structure along the tropical treeline ecotone, complicating the interpretation of the mechanisms that influence its dynamics. Regarding its spatial configuration, Bader *et al*. (2007a) described relatively abrupt transitions between forests and páramos in Venezuela and Bolivia. They also report a high similarity at a continental scale in vegetation physiognomy and vertical structure in forest and páramos in the transition zone, as well as a high floristic affinity down to the genus level. Analyzing the relation between temperature and the altitudinal position of the limit in the Tropical Andes, Bader *et al*. (2007a) suggest that it appears to be located below its climatic potential and suggest as a possible cause the burning of páramo grasslands associated with cattle grazing (particularly in Ecuador). In another study in Ecuador, Wille *et al*. (2002) report that the forests in the transition zone consist of: a) continuous forest tongues prolonging into open páramos along protected valleys; b) isolated forest patches which were probably connected with continuous forests in the past (between 3800-3900 m); and c) isolated patches above 4000 m, which probably were never linked with continuous forests. On the other hand, Keating (1999) studied vegetation structure in the páramo-forest limit (3250 – 3385 m) in the *Podocarpus* National Park (southern Ecuador). He found that although the majority of herbaceous species occurred in a wide variety of habitats, there was a clear pattern of change in woody species composition along the short elevation gradient.

In Venezuela, the available studies on the mountain treeline have concentrated in the NW facing slopes of the Sierra Nevada de Mérida. As in Ecuador, Yánez (1998) described a complex juxtaposition of forests and páramos in the same transition belt, as forest tongues and islands that penetrate into open páramos, with relatively abrupt local contact zones (see Fig. 1). In the upper forests in this transition zone, Tirado (1997) and Yánez (1998) described a clear vertical stratification with a first vegetation layer or understory formed by herbaceous plants; a second layer formed by shrubs and trees up to 2 m high; and a third canopy layer with trees between 2 and 10 m high. Arzac (2008), analyzing the spatial distribution of life forms in open páramos just above the treeline, reports an abrupt decline in tree abundance with altitude and a gradual increase in the abundance of sclerophylous shrubs (with small leaved species dominating the highest portion of the gradient). He also found an important effect of slope orientation on the distribution patterns of sclerophylous shrubs and caulescent rosettes.

However, none of the previous studies (at least in Venezuela) explicitly compare vegetation structure and composition between the lower continuous forests and the forest tongues and islands at higher altitudes. Moreover, we do not know if there is a characteristic vegetation of the local contact borders or forest-páramo ecotones at different altitudes along the transition zone. We also ignore if there are clear altitudinal differences in the identity and abundance of the tree species that are able to establish populations in open páramo areas. These are the main questions explored in the present paper.

The study was undertaken in an area south of *La Aguada* station of the Mérida Cable Car (Sierra Nevada de Mérida), along an altitudinal gradient between 3260 and 3550 m. We compared the composition, species richness, diversity and abundance of plants of the shrub-grass and tree canopy strata in plots located in the upper limit of continuous forests, in forest tongues and islands, and in open páramos (Fig. 1). We also included plots along the contact borders of these forest and páramo areas. In our view, this kind of explicit analysis of vegetation structure in the different physiognomic situations along this complex transition zone is an essential step for interpreting the factors that influence treeline dynamics in the tropics.

METHODS

Study area

Research was undertaken near *La Fría* Lagoon, located at 1.6 km of *La Aguada* station (8º35`N, 71º09`W) of the Mérida Cable Car, Sierra Nevada de Mérida, Venezuela. The average annual precipitation reported for *La Aguada* (3452 m) is 1811 mm while the average annual temperature is 7.1ºC. The climate has been classified by Andressen and Ponte (1973) as "very humid páramo climate". The rainfall pattern is bimodal with maxima in June and October. The driest months correspond to December, January and February. During this period there are occasional days in which temperatures fall below freezing at dawn. Soils in the area are generally young (Inceptisols and Entisols) with a loam to sandy-loam texture, low pH, low cation exchange capacity and base-saturation but high total nitrogen and total organic carbon contents (Acevedo and Sarmiento, unpublished results). The most important types of open páramo communities are grassland-rosette páramos (*pajonal rosetal*) and grassland-shurb páramos (*pajonal arbustal*), both dominated by *Calamagrostis sp*.

Because the study area is located within the Sierra Nevada National Park, created in 1952, land use is restricted to very extensive cattle grazing. Contrary to the situation in many páramos in Colombia and Ecuador, in Venezuela, fires are not a practice associated with forage management. Recently, Santaella (2007) analyzed changes in land cover along the treeline in the area, based on the interpretation of 1952 and 1998 aerial

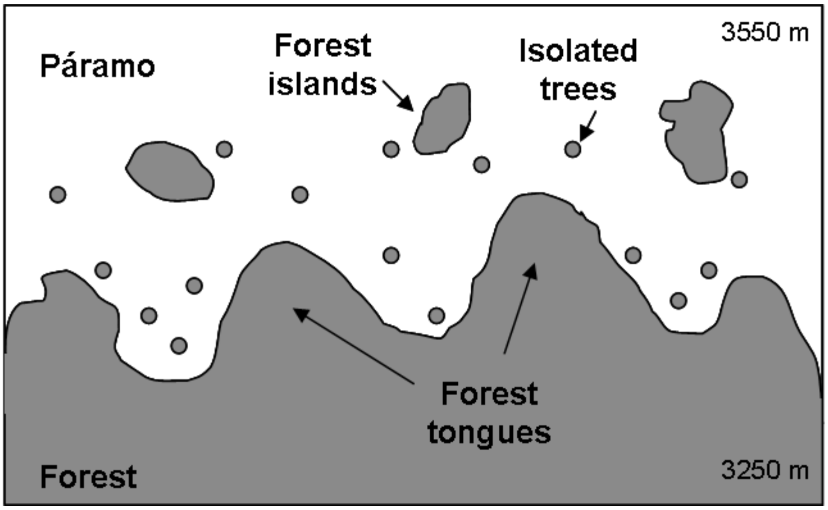

Figure 1. Schematic representation of the spatial configuration of vegetation in the study area. Modified from Körner and Paulsen (2004).

photographs. He reports less than 2% cover for landscape units with direct evidence of human intervention (agriculture, intensive grazing and areas in secondary succession). Moreover, the cleared forest plots identified by Santaella (2007) where all located much closer to *La Aguada* station than our study transect. Hence, we can be fairly confident that vegetation structure in our study area has not been influenced, at least in the last five decades, by drastic changes in vegetation cover due to forest clearing for agriculture or the establishment of secondary pastures.

Sampling design

Vegetation sampling took place between November 2007 and April 2008. Plots were established along an altitudinal transect 290 m long at four altitudes: 3260, 3330, 3420, and 3550 m. The studied transect was located on a slope with a northwest orientation and slope inclinations varying between 20 and 40°. Areas along ravines or near water courses were avoided for sampling purposes. At 3260 m, we randomly located four replicate plots near the upper limit of continuous forest in the area. At 3330 m we randomly located four replicate plots inside forest tongues, four plots in the outer edge of these tongues and four plots in adjacent open páramo areas. At 3420 m, we established four more replicates inside isolated forest patches, four plots on the edge of these patches and four plots in adjacent open páramos. Finally, at 3550 m, we established four replicate plots in open páramo areas (no more forest islands could be found at this altitude).

Vegetation in each plot was divided into an upper and a lower sampling stratum. The upper stratum was defined as the woody elements inside the plot with basal diameters larger than 2 cm (determined at 30 cm aboveground). For this sampling stratum we quantified tree and shrub densities for all the species present in areas of 2 × 15 m oriented parallel to the main slope. The sampling areas on the forest borders were oriented along the edge (so that the whole plot was located on the páramo-forest ecotone).

The lower stratum was dominated by grasses and shrubs but also included other herbaceous species, caulescent and acaulescent rosettes, cushion plants and trees. We did not include non-vascular plants or epiphytes in our study. The cover of each species was estimated using the point-quadrate method (Greig-Smith 1983). We randomly located 100 sampling points inside a 2 × 5 m area and recorded contacts between all species and a thin metal rod 1.5 m tall. These areas were nested inside the 2 × 15 m areas used for estimating woody plant densities in the upper stratum.

Data analysis

For each plot, we calculated species richness and the Shannon diversity index ($H` = -\sum p_i * \log_{10} p_i$), where pi corresponds to the relative abundance of each species. In all cases, we analyzed separately

Physiognomic situation	Altitude (m a.s.l.)	High Stratum (Number of species)	Low Stratum (Number of species)
Forest	3260	15	21
	3330	15	17
	3420	9	35
Border	3330	9	22
	3420	11	26
Páramo	3330	8	26
	3420	3	14
	3550	1	21

Table 1. Total species richness for the different sampling situations along the altitudinal gradient studied (Sierra Nevada de Mérida, Venezuela).

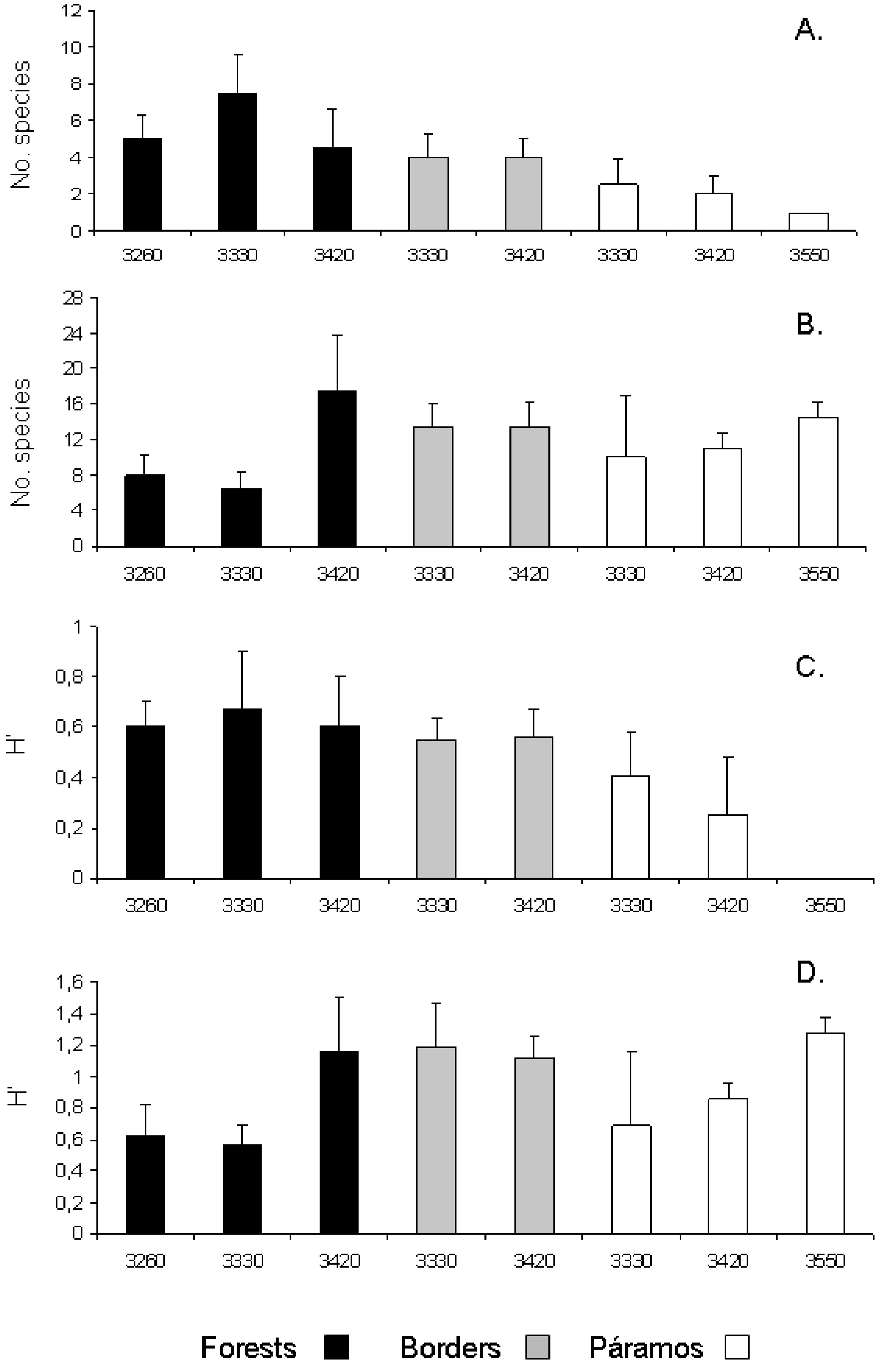

Figure 2. Average species richness and Shannon species diversity (H') in each plot along the altitudinal transect studied in the Sierra Nevada de Mérida in different physiognomic situations. Sampling altitude is specified in each case in m. a.s.l. A. Richness (high stratum); B. Richness (low stratum); C. Diversity (high stratum); D. Diversity (low stratum). Error bars: standard deviation.

the upper and lower sampling strata. We used one-way Analysis of Variance (ANOVA) for comparing the species richness and diversity of the forests in the different sampling altitudes. The same was true for the páramos. In the two intermediate altitudes (3330 and 3420 m), we used a two-way ANOVA to compare species richness and diversity between altitudes and physiognomic situations (forests, forests edges, open páramos).

We also calculated the Pearson's correlation coefficient between altitude and total tree density in each plot. Finally, to analyze changes in vegetation structure and composition along the altitudinal and physiognomic gradients we used a Detrended Correspondence Analysis (DCA). For the upper stratum we used as input data the matrix of tree densities in each plot. For the lower stratum we used the species cover data for each plot as input matrix. In both cases, detrending was done by segments. For all statistical analysis we used SPSS 12.0 and CANOCO 4.02 (ter Braak and Smilauer 1999).

RESULTS

Species richness and diversity

A total of 74 vascular plant species, distributed in 32 families, were identified in the 32 plots studied. The families with more species were: Asteraceae (16% of the species), Ericaceae (11%), Poaceae and Rosaceae (8%), Cyperaceae, Caryophyllaceae, Geraniaceae, Gentianaceae, Myrsinaceae, Orchidaceae (7%) and Melastomataceae (6%).

In table 1 the results for the total number of species recorded in each physiognomic situation and altitude are presented. For the high stratum a trend for a decrease in the number of woody species with altitude is evident in both forest and páramos. It is also apparent that the number of woody species is higher in the closed forests, followed by the borders and then the páramos, with only 1 tree species recorded at 3550 m. However, for the low stratum, the patterns for total species richness are less clear.

In figure 2 changes in the average species richness and diversity per plot are presented. In the high stratum a trend for a decrease in richness and diversity with increasing altitude was evident. This was largely the result of the significant decrease in the number of tree species able to establish in the páramos as altitude increases. We did not find significant differences in the species richness or diversity of trees within the forests located at different altitudes. A two-way ANOVA indicated that there were no significant differences in species richness and diversity between the two intermediate altitudes ($p = 0.191$), while the physiognomic situation had a significant effect, with higher richness and diversity in the forests compared to open páramo areas (there was no significant interaction between both factors).

In the case of the low stratum, both species richness and diversity were higher in the forest islands at 3420 m than in the forests at lower altitudes. While there were no differences in species richness in the páramos at different altitudes ($p = 0.398$), Shannon diversity was significantly higher in the páramos at higher altitudes ($p = 0.016$), probably as a result of a more even distribution of relative abundance of species (in the lower páramos there is a stronger dominance of *Calamagrostis sp.*). For the intermediate altitudes, in the case of species richness there was a significant interaction between altitude and physiognomic situation (two-way ANOVA, $p=0.014$). Hence, while at 3300 m there were no significant differences in richness between physiognomic situations, at 3420 m richness was higher in forests than in páramos. In the case of species diversity, physiognomic situation was the only significant factor (there were no differences in altitude and no significant interaction term). As with species richness, diversity was significantly higher in forests than in the páramos.

Tree density

We found a significant negative correlation between altitude and total tree density along the altitudinal gradient ($r = -0.44$, $p = 0.011$). However, when tree density were analyzed separately for the forests and páramos, we could not find a significant correlation between altitude and tree density. Hence, the decrease in tree density with altitude can be mainly attributed to the decrease in forest cover.

Patterns of species abundance

In figure 3, the changes in the relative abundance of the dominant species in the upper stratum are presented. In the case of the continuous forests at 3260 m there were three dominant species: *Psammisia penduliflora* (Dunal) Klotzsch, *Libanothamnus neriifolius* (Sch. Bip.) Ernst and

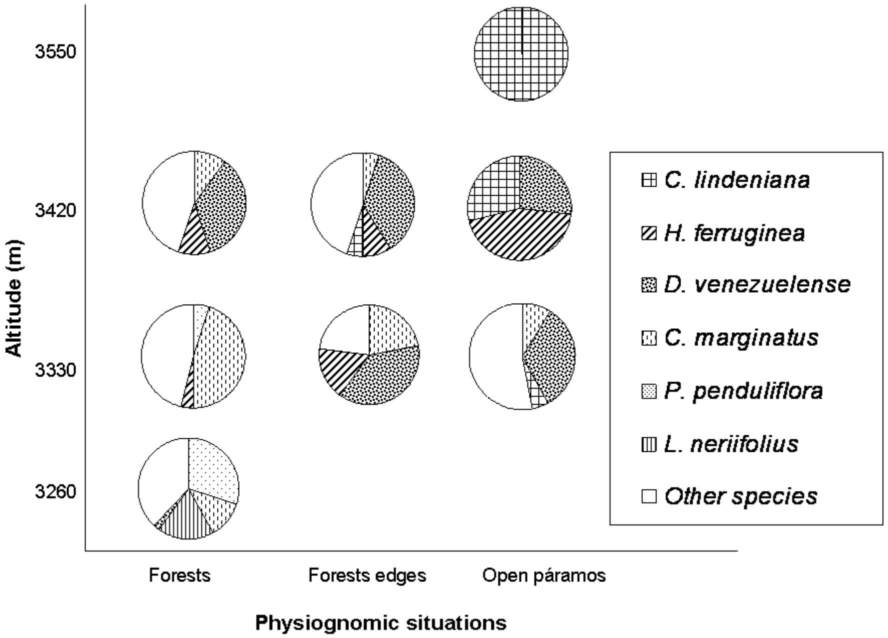

Figure 3. Relative abundance (%) of the dominant species in the high stratum along the altitudinal transect studied in the Sierra Nevada de Mérida at the different physiognomic situations.

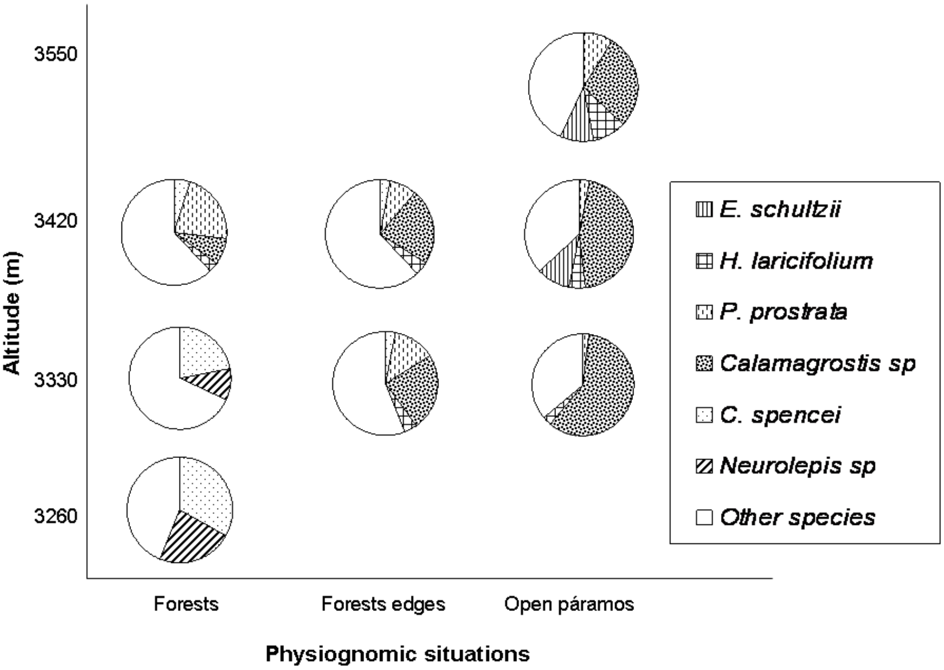

Figure 4. Relative abundance (%) of the dominant species in the low stratum along the altitudinal transect studied in the Sierra Nevada de Mérida, at the different physiognomic situations.

Cybianthus marginatus (Benth.) Pipoly. In the forest corridors at 3330 m, *C. marginatus* was the dominant species (with 5 to 10% of relative abundance). In these forests *P. penduliflora* was also abundant. In the forest islands at 3420 m, *Diplostephium venezuelense* Cuatrec showed the highest densities, followed by *C. marginatus* and *Hesperomeles ferruginea* (Pers.) Benth.

In the edges of forest corridors and islands *D. venezuelense* was the dominant species. Other abundant species in these páramo-forest borders were *C. marginatus, H. ferruginea* and *Chaetolepis lindeniana* Naud. Triana (a tall shrub characteristic of open páramos). The forests edges had a relatively similar species composition to the interior of the small forest islands.

Low altitude páramos adjacent to continuous forests (3330 m) had a sparse tree layer dominated by *D. venezuelense. C. marginatus* was also present, but in lower densities. The dominance of *D. venezuelense* in the low páramos near continuous forests is interesting, given its high abundance in forest islands and forest edges at higher altitudes.

In the páramos at 3420 m three woody species were present in this sampling stratum: *D. venezuelense, H. ferruginea* and *C. lindeniana* (common shrub species in open páramo areas). In the páramos at 3550 m, only *C. lindeniana* was present in this sampling stratum.

In figure 4 we present the distribution of relative abundances for the dominant species in the low stratum along the altitudinal gradient. In the continuous forests at 3260 m two large poaceae species dominated: *Chusquea spencei* Ernst and *Neurolepis sp.*, with cover values between 10 and 35%. In the forest corridors higher up in the gradient, *C. spencei* and *Neurolepis sp*. retained high cover values but *C. marginatus* was the dominant species. In forest islands at 3420 m the dominant species were two páramo shrubs (*Pernettya prostrata* (Cav.) DC. and *Hypericum laricifolium* Juss), while the poaceae *C. spencei* and *Calamagrostis sp*. were also abundant.

In the forest edges, *Calamagrostis sp.* was the dominant species in this stratum, accompanied by *P. prostrata, H. laricifolium* and *C. spencei.* In all the open páramos sampled *Calamagrostis sp.* was by far the dominant species with covers between 65 and 35%. The identity of subdominant species varied with altitude and included the sclerophylous shrubs *H. laricifolium, P. prostrata* and *C. lindeniana*, and the common caulescent rosette *Espeletia schultzii* Wedd.

Multivariate analyses

In figures 5 and 6 we present the ordination diagrams (DCA) for the analysis of changes in species abundances in the high and low strata. For both sampling strata, it is obvious that the 1st ordination axis is strongly associated with altitude. For the high stratum data (figure 5a) the forest plots at 3260 and 3330 m are located in the extreme right of the diagram, while the high páramo plots (3550 m) are located in the extreme left. The lower páramos, forest edges and forest island plots are located in intermediate positions along the 1st axis, reflecting a more similar community structure between these physiognomic situations. The continuous forest plots show higher dispersion along the 2nd ordination axis than the páramos, reflecting a higher dissimilarity and heterogeneity between replicates in the forest communities, while in the páramos a single species was present in the woody stratum (*C. lindeniana*). In Figure 5b the ordination of the species along the first two axes is presented. It is possible to define three groups of species on the basis of their position along the 1st axis: a) páramo shrubs (left); b) cloud and prepáramo forest trees (right); c) transitional tree and shrub species, including *D. venezuelense* and *C. marginatus* (center).

In the case of the low stratum (fig. 6a,b), the position of the plots along the 1st axis is inverted: continuous forest plots and species to the left and high páramo plots and species to the right. The forest edges and forest islands form a group in the center of the diagram. However, in this case, the low páramos are more clearly separated from the forest. The páramos show a high similarity in community structure (with a strong dominance of *Calamagrostis sp.*), while in the forest plots there is more dispersion along the 2nd axis, reflecting higher heterogeneity in species composition and abundance.

DISCUSSION

The mountain treeline in the tropical Andes of Venezuela is structured as a complex mosaic of continuous forests, forest islands and open páramos that co-occur along a an altitudinal

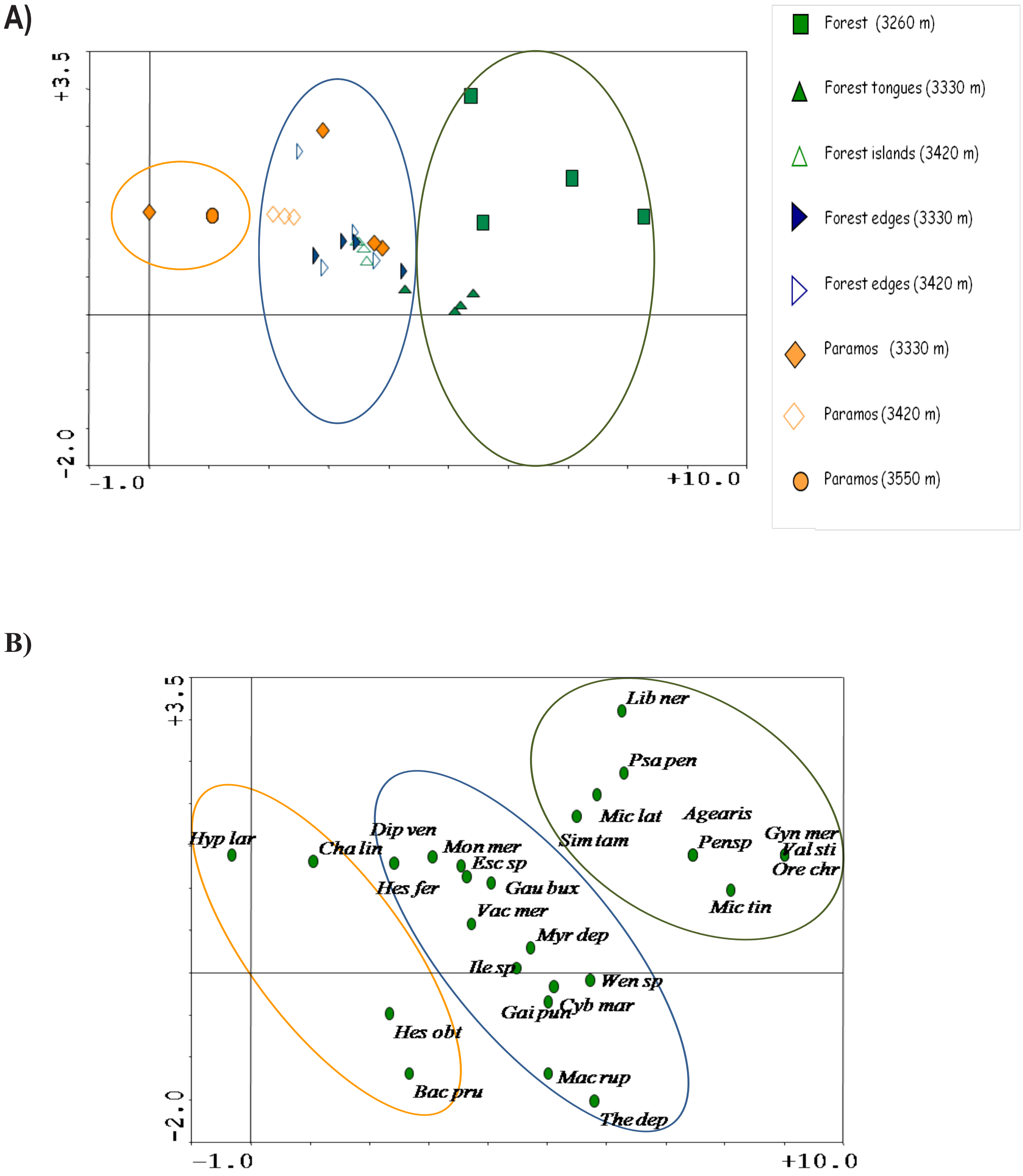

Figure 5. Detrended Correspondence Analysis of vegetation structure in the high stratum, based on the density of each species in the different plots. The 1st and 2nd ordination axes are presented, which absorb 20.6% and 8.1% of total variance each. A) Ordination diagram for the sampling plots; B) Ordination diagram for the tree species. Species names can be found in the Appendix 1.

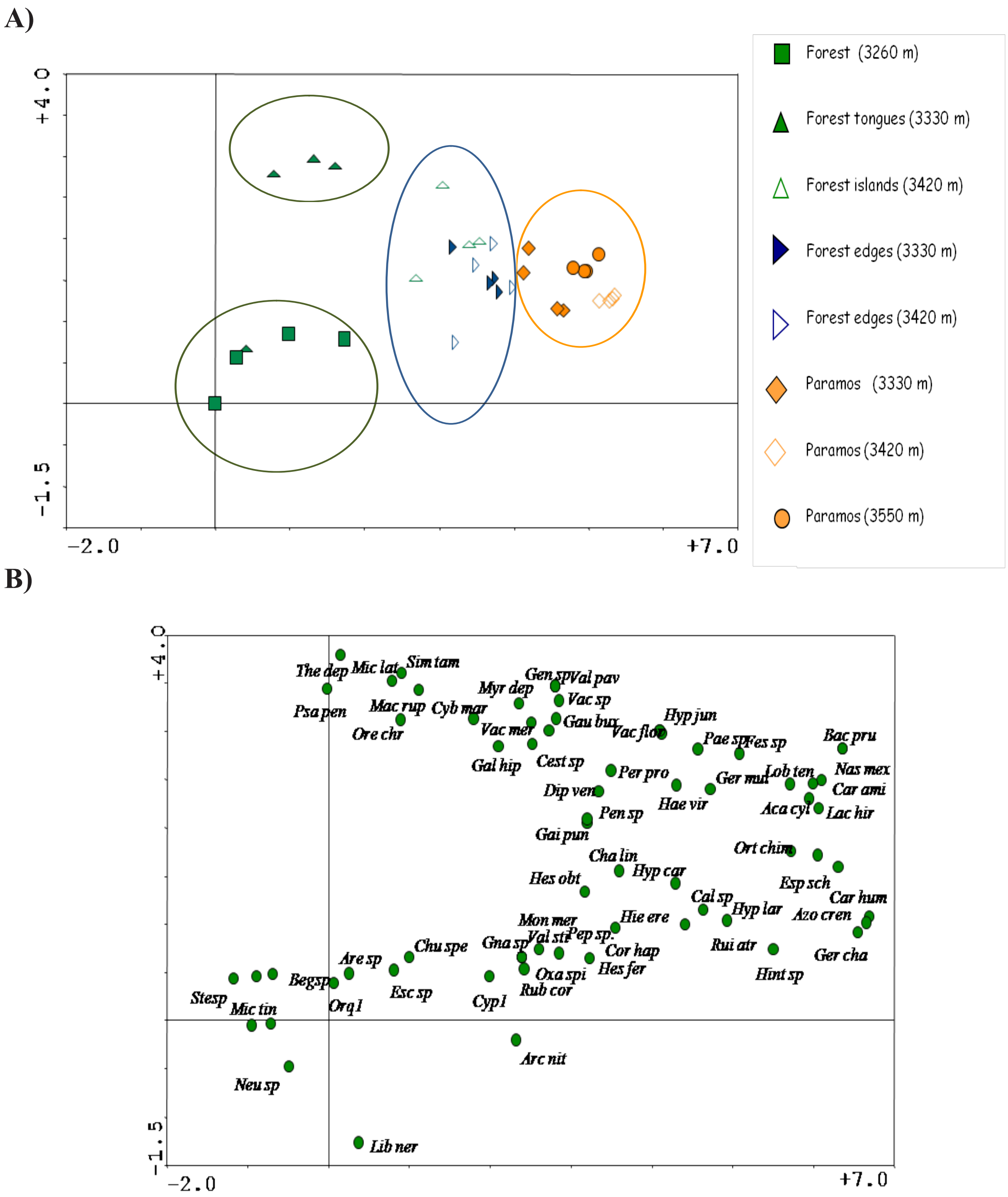

Figure 6. Detrended Correspondence Analysis of vegetation structure in the low stratum, based on the percent cover of each species in the different plots. The 1st and 2nd ordination axes are presented, which absorb 18.7% and 6.4% of total variance each. A) Ordination diagram for the sampling plots; B) Ordination diagram for the species. Species names can be found in the Appendix 2.

gradient of approximately 300 m (from ca. 3250 to ca. 3550 m in our study area). Our results indicate that there are clear differences in community structure between the forest islands in the upper extreme of the transition zone and the continuous forests in the lower extreme. The same is true of the páramos located at different altitudes along this zone. Below, we discuss in more detail these results as well as their implications for analyzing the dynamics of the tropical mountain treeline.

Species richness and diversity

There is a high floristic similarity at a genus and family level between our results and those of other studies in the tropical treeline in the tropical Andes (Yánez 1998, Keating 1999, Berg and Suchi 2002, Young and León 2006, Bader *et al.* 2007a). Obviously, given the relatively small total area sampled in this study, our data of total species richness (78 vascular plant species) is an underrepresentation of the total richness present in the study area, especially in the heterogeneous continuous forests. However, our sampling strategy was not designed to obtain a complete species inventory, but as a comparative study of changes in vegetation structure along the treeline transition zone.

We found a decrease in tree species richness and diversity along the altitudinal gradient. This trend has also been reported in the treeline in Ecuador (Keating 1999; Wille *et al.* 2002, Bader *et al.* 2007b). Interestingly, the opposite trend was detected in the low vegetation stratum (dominated by herbs, low shrubs and rosettes). This suggests that altitude exerts different effects on the diversity of the different life forms and adaptive strategies that dominate different vertical strata along the treeline. The fact that the understory within forest islands has more richness and diversity than the understory of the forests at lower altitudes could be the result of the mixture of páramo and forest species in these relatively small islands. On the other hand, the increase in temperature as we descend in the gradient and the increase in dominance of *Calamagrostis sp.* could act as filters for the establishment of páramo herbs, rosettes and shrubs, contributing to lower species diversity in the low altitude páramo areas compared with the high páramos.

Patterns of species abundance: implications for interpreting treeline dynamics

Our results show that there are clear differences in the identity of dominant species in the different forests studied, with the largest differences occurring between the forest islands in the upper part of the gradient and the continuous forests below. This suggests that these islands are not relicts of continuous forests with a wider distribution in the past (although this would need to be supported by paleoecological studies). In scenarios of altitudinal ascent of forests induced by global warming, these patches could constitute advance nuclei for pioneer trees within the open páramo matrix. Hence, they could function as dispersal foci for these species and facilitate the subsequent establishment of other trees. The fact that these islands are generally associated with rocky outcrops that break the continuity of the slopes, also suggest that their development could be favored by areas with particular environmental conditions in terms of soils, hydrology and microclimate. The similarities in vegetation structure between them and the forest-páramo ecotones sampled (sharing *D. venezuelense* as the dominant species) suggest that these small forests experiment edge effects throughout a large part of their extension. This is also suggested by the presence in the understory of these forest islands of characteristic páramo species such as *Calamagrostis sp.* and *H. laricifolium,* which is not the case in the forests at lower elevations.

It is important to note that the forest patches discussed here are a different community to the high Andean forests dominated by the tree *Polylepis sericea*, which tend to occur at higher altitudes in the Venezuelan Andes, generally associated with areas of intense glacial and periglacial influence (Goldstein *et al.* 1994).

D. venezuelense reached its maximum abundances in forest borders and was the dominant tree species present in the lowest páramos in the gradient. Moreover, Puentes (2010) found in the same area that the highest seedling densities of this species occur precisely in low open páramos and in the edges of the forest islands. Given the light coloration and abundant pubescence of its leaves, it could be that this species is more resistant to the high radiation levels of open páramo environments than other tree species restricted to closed prepáramo forest. The study by Puentes (2010) offers evidence to support this hypothesis. *D. venezuelense* seedlings showed high survival rates and did not experience chronic photoinhibition (quantified using chlorophyll fluorescence techniques) after being exposed to direct radiation in open páramo areas by experimentally removing all vegetation cover around seedlings.

The effect of radiation on the establishment of woody species above the treeline was also studied in Ecuador by Bader *et al.* (2007b). They found that the large majority of tree species transplanted from the forest into the páramo died unless they were artificially shaded. Moreover, the few species that survived without shading were trees that already had naturally occurring populations in the lower limit of the páramo. Among them was a species from the *Diplostephium* genus with pubescent leaves. Based on these results, Bader *et al.* (2007b) hypothesized that the high radiation levels characteristic of the highland tropics could be an important factor limiting the establishment of trees above the treeline, making it more stable.

It is important to emphasize that the three dominant tree species present in open páramos in our study area (*D. venezuelense*, *H. ferruginea* and *C. marginatus*) were absent from the highest páramos in the gradient. This suggests that high radiation could interact with other factors such as low minimum temperatures and water availability to establish an altitudinal limit to their distribution. Photoinhibition processes induced by low temperatures have been proposed as key factors limiting tree establishment in the alpine treeline in Europe (Germino and Smith 1999).

Contrary to the results of Keating (1999), we found clear changes in the species composition of the low herbaceous stratus along the altitudinal gradient. Interestingly, the woody bamboo *C. spencei* and *Neurolepis sp.*, are replaced as dominant species within the low continuous forest by *P. prostrata* and *Calamagrostis sp.*, which dominate within the forest islands. In the open páramos, *Calamagrostis sp.* is also the dominant species.

The multivariate analysis carried out provide us with an integrated view of the changes in community structure in the treeline, confirming that altitude is clearly associated with the main axis of variation in vegetation composition (1st axis of the DCA). The continuous forests at 3260 and 3330 m showed more similarity in vegetation structure, while the forests islands appeared more associated with the forest edges and the lowest páramos.

Summing up, we believe that explicitly analyzing the community structure of continuous forests, forests edges and páramos at different altitudes along the treeline, is a key step to appropriately interpret vegetation dynamics in these environments. This kind of information is essential for generating hypotheses about the responses of species and communities under scenarios of altitudinal displacement of the treeline induced by climate change.

Under scenarios of significant temperature increase, tree species with a higher capacity to establish in open páramo areas could be able to attain higher elevations. Our results suggest that *D. venezuelense* and to a lesser extent *C. marginatus* and *H. ferruginea* belong to this kind of pioneer species, given their dominance in forest edges and their presence in low open páramos. If we hypothesize that they are restricted to low páramo areas because of processes linked with thermal limitations (e.g. photoinhibition induced by low temperatures), under warmer climate scenarios they could act as pioneers in the altitudinal advance of the treeline. In the case of studies in temperate mountain treelines in Europe, woody species such as *Pinus mugo* and *Pinus sylvestris* have been reported as advancing from the upper forests into alpine areas (French *et al.* 1997, Camarero and Guitiérrez 1999). However, in these cases, the decrease in grazing pressure associated with the abandonment of cattle ranching complicates the interpretation of the causes of the altitudinal displacement of trees. In any case, possible pioneer tree species (such as *D. venezuelense*) could improve local microclimatic conditions and provide shading in open páramo areas, facilitating the establishment of other woody species that require cover for their survival as seedlings. In the high Andean forests of the Cordillera Oriental of Colombia the Restoration Ecology Group has shown the importance of woody species as nurse plants for the establishment of tree seedlings in open environments (Vargas 2008).

To evaluate the hypotheses suggested here, it is now necessary to analyze the relationship between vegetation structure and environmental heterogeneity in the treeline (particularly in soils and climate) and to establish monitoring programs to study this interaction over time and space. Moreover, the integration of ecophysiological, experimental and modeling strategies constitutes an exiting open challenge for furthering our understanding of the factors that influence the dynamics of the tropical mountain treeline.

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APPENDIX 1

Average of the relative abundance (% of total stem density represented by each species) in the four replicate plots for the species found in the high stratum at all altitudes and physiognomic situations. The abbreviations used to identify each species in the multivariate analysis are presented (Figure 5)

	3260 m	3330 m			3420 m			3550 m
Species	**Forest**	**Forest**	**Border**	**Páramo**	**Forest**	**Border**	**Páramo**	**Páramo**
Arcytophyllum nitidum	5,83	0	0	0	0	0	0	0
Ageratina aristiguietii	2	0	0	0	0	0	0	0
Baccharis prunifolia	0	0	2,23	0	0	0	0	0
Chaetolepis lindeniana	0	0	0	7,69	0	6,77	18,27	100,00
Cybianthus marginatus	9,04	48,84	21,79	10,47	11,04	4,17	0	0
Escalonia sp	0	0	0	0	2,24	1,79	0	0
Gaiadendron punctatum	0	2,21	1,63	0	0	1,79	0	0
Gaultheria buxifolia	0	1,15	0	16,95	4,27	1,63	0	0
Diplosthephium venezuelenze	0,90	0	36,72	29,99	34,87	37,76	18,27	0
Gynoxis aff. meridana	2,08	0	0	0	0	0	0	0
Hypericum laricifolium	0	0	0	25,641	0	0	0	0
Hesperomeles ferruginea	0	4,24	25,31	0	9,68	17,41	63,46	0
Hesperomeles obtusifolia	0	1,27	4,69	0	0,96	6,94	0	0
Libanothamnus neriifolius	18,92	0	0	0	0	0	0	0
Macleania rupestris	0	5,52	0	0	2,50	0	0	0
Miconia latifolia	3,01	1,06	0	0	0	0	0	0
Miconia tinifolia	22,92	1,15	0	0	0	0	0	0
Myrsine dependens	0,90	6,70	1,63	6,48	0	1,63	0	0
Monnina meridensis	0	0	0	0	2,24	0	0	0
Oreopanax chrysoleucum	4,86	0	0	0	0	0	0	0
Psammisia penduliflora	22,76	5,63	0	0	0	0	0	0
Pentacalia sp	2,08	0	0	0	0	0	0	0
Symplocos tamana	2,5	4,89	0	0	0	0	0	0
Ilex sp	0	1,27	0	0	0	0	0	0
Themistoclesia dependens	0	5	0	0	0	0	0	0
Vaccinium meridionale	0	7,44	6,01	2,78	32,19	20,12	0	0
Vallea stipularis	2,08	0	0	0	0	0	0	0
Weinmania sp	2,11	3,62	0	0	0	0	0	0

APPENDIX 2 **Average of the relative cover (%) in the four replicate plots for the species found in the low stratum at all altitudes and physiognomic situations. The abbreviations used to identify each species in the multivariate analysis are presented (Figure 6)**

	3260 m	3330 m			3420 m			3550 m
Species	**Forest**	**Forest**	**Border**	**Páramo**	**Forest**	**Border**	**Páramo**	**Páramo**
Acaena cylindristachya	0	0	0,5	0,25	0	0,25	1,75	9,5
Arcytophyllum nitidum	2,75	0	1,75	0,5	0	9,75	0	0,5
Arenaria sp	0,5	0	0	0	0,25	0	0	0
Azorella crenata	0	0	0	0	0	0	0,75	0
Baccharis prunifolia	0	0	0	0	0	0	0	1
Begonia sp	0,25	0	0	0	0	0	0	0
Calamagrostis sp	0	0	45,75	78,75	9,25	36,75	70,5	40
Carex amicta	0	0	0	0	0	0	0	1,5
Carex humboldtiano	0	0	0	0	0	0	0,75	0
Cestrum sp	0	0	0	0	0,75	0	0	0
Chaetolepis lindeniana	1	0	23,25	3,5	5,75	10,5	0,25	16,25
Chaptalia sp	0	0	0	0,5	4	0	0	0
Chusquea spencei	24	15,25	7,5	0	5,5	5,75	0	0
Cortaderia hapalotricha	8,5	0	25,5	4,5	8,5	16	0	0
Cybianthus marginatus	2,25	18	9,25	2,25	3,75	4	0	0
Diplosthephium venezuelense	0	0	16,75	10,75	9,75	18,5	0	0
Escalonia sp	1,25	0	0	0	1,25	0	0	0
Espeletia schultzi	0	0	0	0	0	0	15,5	14,75
Festuca sp	0	0	0,25	2,5	0	0	0	2,75
Gaiadendron punctatum	0	0	0,25	0	0,25	1	0	0
Galium hipocarpium	0,75	0,5	0	0	2,5	0	0	0
Gautheria buxifolia	0	0,5	3,5	1	8	2	0	0
Gentianella sp	0	0	0	0	0,25	0	0	0
Geranium chamaensi	0	0	0	0,25	0	0	19,5	0
Geranium multiceps	0	0	2,25	0	1	3,25	0	9,25
Gnaphalium sp	0	0	0	0	0,75	0	0	0
Halenia virides	0	0	0	1,25	0	0	0	0
Hesperomeles ferruginea	0	0	6,5	0	6,5	10	2,5	0,5
Hesperomeles obtusifolia	0	0,25	2,5	0,25	4	6,25	0	0
Hieracium erectum	0	0	0,25	0	0	0	0	0
Hinterubera sp	0	0	0	0,5	0	0	0	0
Hypericum caracasanum	0	0	1,25	5	0,75	5	1,75	5,25
Hypericum juniperinum	0	0	0	3,5	0	0	0	0
Hypericum laricifolium	0	0	6,25	5	1,5	5,5	9,25	15
Lachemilla hirta	0	0	0	0	0	0	0	0,25
Libanothamnus neriifolius	3	0	0	0	0	0	0	0
Lobelia tenera	0	0	0	0	0	0	0	0,25
Macleania rupestris	0	5,5	0	0,5	0,25	0	0	0
Miconia latifolia	0	3,75	0	0	0	0	0	0
Miconia tiniflora	2,75	1,5	0	0	0	0	0	0
Monnina meridensis	0	0	0	0	0,5	0	0	0
Myrsine dependens	0	1,5	0	0,25	1,75	1,25	0	0
Nasella mexicana	0	0	0	0	0	0	0	4,75
Neurolepis sp	16,25	7,25	0	0	0	0	0	0
Oreopanax chrysoleucus	1	0,25	0	0	0,75	0	0	0
Orthosanctus chimboracensis	0	0	0	3	1	1	7,25	13,5
Oxalis spiralis	0	0	0	0	1,25	0	0	0,25
Paepalanthus sp	0	0	0	0	0	0,25	0	0,25
Pentacalia sp	0	0	0	0	0	0,25	0	0
Peperomia sp.	0	0	0	0	1,25	0	0	0
Pernettia prostrata	0	0	24	1,25	23,5	12,75	2,5	13,5
Psammisia penduliflora	1,25	1	0	0	0	0	0	0
Rubus coriaceus	0	0	0	0	3,5	0,5	0	0
Ruilopezia atropurpurea	0	0	4,5	2,25	0	0	3,25	0
Simplocos tamana	0,25	1,75	0	0	0,5	0	0	0
Stellaria sp	0,25	0	0	0	0	0	0	0
Themistoclesia dependens	2,75	9,75	0	0	0	0	0	0
Vaccinium floribundum	0	0	0	0,75	0	0	0	0
Vaccinium meridionale	0,5	1,75	1	1	2,75	4,75	0	0
Vaccinium sp	0	0	0	0	0,5	0	0	0
Valeriana sp	0	0	0	0	0,25	0	0	0
Vallea stipularis	0	0	0	0	0,25	0	0	0