

CANOPY STRUCTURE AND WOODY SPECIES DISTRIBUTION AT THE UPPER TREELINE IN THE VENEZUELAN ANDES

ESTRUCTURA DEL DOSEL Y DISTRIBUCION DE ESPECIES LEÑOSAS EN EL LÍMITE SUPERIOR DEL BOSQUE EN LOS ANDES VENEZOLANOS

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ABSTRACT

At the treeline in the Venezuelan Andes forest tongues and islands intermingle into the herbaceous páramo vegetation. The transition between both ecosystems is abrupt. Previous studies in the tropical Andes suggest radiation and grazing as key factors limiting the advance of woody species into the páramo. We analyzed juvenile and adult woody species composition along basal and apical transects from the páramo to the interior of three forest tongues. Canopy structure was determined along these transects. Our results show a higher species diversity in the basal transects. Most species seemed to be restricted to the interior and borders of forest tongues and associated with higher LAI (leaf area index), while *Diplostephium venezuelense*, previously suggested as a pioneer tree, was the only species able to colonize the low LAI environments of the open páramo. Our results also suggest that aspect plays an important role in the establishment patterns of treeline species, as a result of differential shading in the N and S facing borders of tongues and adjacent páramos. Hence, our results support the idea that radiation could be an important limiting factor in scenarios of forest expansion into the páramo matrix and that the abrupt nature of the treeline is independent of fire and grazing, since these factors were absent in our study site.

Key words: basal area, páramo, bosque preparamero, canopy structure, leaf area index, species diversity, trees, vegetation dynamics

RESUMEN

En el ecotono del límite superior del bosque en los Andes Venezolanos se presentan lenguas e islas de bosque preparamero interdigitadas con el páramo, cuya transición es abrupta. Estudios sobre este ecotono en zonas tropicales andinas sugieren que la radiación y el pastoreo son los principales factores que limitan la colonización del páramo por especies leñosas. En este estudio analizamos la composición de juveniles y adultos de las especies leñosas en transectas desde el páramo hacia el interior de tres lenguas de bosque. Se establecieron transectas apicales y basales en tres lenguas de bosque. Sobre dichas transectas se determinó la estructura del dosel. Las transectas basales presentaron mayor diversidad. La mayoría de las especies parecen estar restringidas al interior y borde de las lenguas y están asociadas a valores más elevados de LAI (índice de área foliar), mientras *Diplostephium venezuelense* fue la única especie capaz de colonizar el páramo abierto. Las especies que tienen óptimos de LAI superiores se presentan fundamentalmente en los bordes y en las transectas apicales. Se encontró que la exposición juega un papel importante en la distribución de estas especies, como consecuencia del sombreado diferencial, lo que sugiere que un factor limitante del avance del bosque hacia el páramo es la radiación y que la naturaleza abrupta del límite no es el resultado del fuego y el pastoreo, los cuales estaban ausentes en la zona de estudio.

Palabras clave: árboles, área basal, bosque preparamero, dinámica de la vegetación, diversidad de especies, estructura del dosel, índice de área foliar, páramo

INTRODUCCIÓN

The treeline in the Venezuelan Andes is a transition zone between elfin forests (locally known as “bosque preparamero”) and the continuous alpine vegetation, known as “páramo”. This ecotone is a dynamic zone where species spatial patterns may indicate responses to local and global climate change (Camarero *et al.* 2000; Kimball and Weihrauch 2000).

The causes and mechanisms controlling the altitudinal position of the treeline at a global scale are still unclear, although in most situations temperature seem to play a major role (Körner 1998). However, different combinations of biotic, abiotic and antropogenic factors may be responsible for regional patterns not explained by temperature alone. These factors may impact woody species reproduction and establishment at the treeline (Autio 2006; Holtmeier 2003; Körner 1998; Körner and Paulsen 2004).

Treelines in the tropical Andes have been described as fairly abrupt. Wille *et al.* (2002) describe the ecotone between the upper forest and the open páramo in Ecuador as a zone of forest patches and tongues advancing into the páramo vegetation between 3800 and 3900 m. Bader *et al.* (2007a) report abrupt transitions at the treeline as a result of high radiation and fire producing positive feedbacks induced by forest cover which tend to stabilize the ecotone. Also in Ecuador, Keating (1999) studied the structure and composition of the páramo vegetation at the treeline on an elevation gradient from 3250 to 3385 m and found that most herbaceous species occupy a wide range of habitats, while the patterns of woody species change with altitude.

The treeline in the Venezuelan Andes is generally abrupt, with tongue shaped forest intrusions, forest islands and a sharp decrease of woody species abundance, richness and diversity with elevation, as has been found at the Sierra Nevada de Mérida (Ramirez *et al.* 2009). In the same area, Yanez (1998) studied the changes in floristic composition on an elevation gradient in the transition zone between the cloud forest and the páramo. He found that the floristic composition in the ecotone is a mix of higher and lower elevation species as well as species found only in the ecotone. Arzac *et al.* (2011), looking at the spatial distribution of life forms along an

elevation gradient at the treeline ecotone, found that trees decrease in abundance abruptly above 3450 m. Ramirez *et al.* (2009) observed that the borders between páramo and forest vegetation have a distinct composition and that woody species composition in the islands differs from that in the forest tongues and continuous forests at lower altitudes.

Information on the factor(s) controlling the dynamics of the tropical treeline is scarce. Research on Andean treelines suggest high radiation together with low temperatures as limiting factors to the altitudinal advance of the treeline (Bader *et al.* 2007b; Dulhoste 2010; Puentes 2010). The establishment of woody juveniles above the treeline was studied by Bader *et al.* (2007a) in Northern Ecuador. They found that most species do not regenerate naturally in the more open vegetation and suggested that high radiation is limiting the advance of woody species above the treeline. They also suggest that this phenomenon contributes to the stability of the treeline. Puentes (2010) studied the responses of two dominant tree species' seedlings to low temperature and high radiation at the treeline in the Venezuelan Andes. Her results suggest that the ability of the species to colonize open páramo vegetation could depend on their sensitivity to higher radiation levels as a result of chronic photoinhibition of photosynthesis.

High radiation (Puentes 2010; Dulhoste 2010) or both, radiation and fire, (Bader *et al.* 2007a) have been suggested to play a major role limiting woody species establishment in the nearby open páramo. However, spontaneous and human induced fire is very unusual in the high Venezuelan Andes. This provides a unique opportunity to single out the impact of these two factors. We studied the abundance and composition of woody species along a gradient from the páramo to the interior of the forest tongues, which may reveal patterns of differential advance and sensitivity of the woody species to changes in canopy openness. We analyze the woody species abundance at juvenile and adult stages, as well as the canopy structure, along páramo-forest gradients of forest tongues at the treeline in the Sierra Nevada de Mérida. The following questions are addressed: 1. Is composition and diversity the same at the base and at the apical part of the forest tongue? If forest tongues are the result of the advance

of the forest towards the páramo, it is expected that the apical zone of the tongues should show a different species composition than its base; 2. How is the distribution of woody species along the interior-exterior gradient? 3. Is this distribution different among juveniles and large individuals of the same species? 4. Are juveniles of different species associated with different ranges of canopy openness?

STUDY AREA

The study was performed at the Páramo de San José in the Andean Cordillera, Mérida State, Venezuela (08° 30' N 71° 40' W) at an elevation of 3150 m. The site is located near a ridge, on north-west facing slopes, which are influenced by a drier climate than the south-east facing slopes. Nearest average precipitation data indicates ca. 900 mm at the dry slopes at 2400 m a.s.l. and 1300 mm at the wetter side at 1630 m a.s.l. According to Andressen and Ponte (1973), mean annual temperature at the lower limit of the páramo vegetation in the Venezuelan Andes (the upper limit of the treeline) ranges between 10 and 12 °C, although freezing temperatures may occasionally occur, especially during the dry season. The area is located at the contact of two geological formations: the Formación Mucuchachí, composed of black silty slates and the Formación Sierra Nevada, dominated by shales and granitic rocks PDVSA-INTEVEP, 2007). The soil has been described as acid, stony and clayey (Durán, 1992).

Körner and Paulsen (2004) suggest three zones along the altitudinal gradient at the treeline: a continuous forest at the bottom, a zone of forest patches and a zone of isolated trees. Sampling was carried out in the second zone, where forest and páramo vegetation occur in form of patches. This transition zone is a complex mosaic of forest islands and tongues, which gradually decrease in height with elevation. According to Ramirez *et al.* (2009), who studied the vegetation at the treeline in the Sierra Nevada in the Venezuelan Andes, the vegetation corresponds to the "bosque preparamero", which is below the páramo and above the upper mountain cloud forest, between 2500 and 3500 m a.s.l. Its woody component is dominated by small trees and shrubs, including cloud forest and open páramo species.

MATERIALS AND METHODS

Sampling was carried out between July and September 2009. Three nearby forest tongues, connected with the continuous forest were chosen. All three were located at the same slope, oriented towards the west; therefore, each tongue had one N and one S facing border. Perpendicularly to each tongue two parallel transects were established, as shown in Fig. 1. The upper transects were called apical and were placed at ca. 10 m below the tip of the tongues. The lower transects were called basal, and were situated 15 m above the continuous forest. Each of the six transects (2 m wide) crossed the forest tongues and extended 10 m into the open páramo. Transects were divided into 2x2 m plots, in which all woody species were recorded according to two categories: large individuals with DBH > 2.5 cm and small individuals with DBH < 2.5 cm. Those belonging to the first category were identified to species level and its DBH was recorded. When stem branching started below 1.3 m, each branch was measured and recorded separately. Individuals of the second category were only identified and counted. At each plot two hemispherical photographs were taken with a 10 megapixel Nikon Coolpix camera with a Nikon FC-E8 Fisheye converter. Pictures were taken after camera was leveled at 1 m above the soil surface under overcast sky to guarantee uniform light. North position was registered at each picture. Slope was determined with a digital hypsometer (Vertex III, Haglof), and geographic position was recorded with a handheld GPS (GPSMAP 60CSx, Garmin). Total basal area per plot was calculated for large individuals (DBH>2.5 cm). Species density per plot was calculated for large and small individuals (DBH<2.5 cm). Diversity of both groups were used to compare basal and apical transects by means of a t test for Shannon diversity index (Zar 1984). The test was performed with the same number of apical and basal plots to avoid biases due to different sampling area size. The same test was carried out to compare diversity between tongues.

Digital hemispherical photographs were displayed, processed, and analyzed using the Gap Light Analyzer (GLA) software (<http://www.ecostudies.org/gla/>). Geographic position,

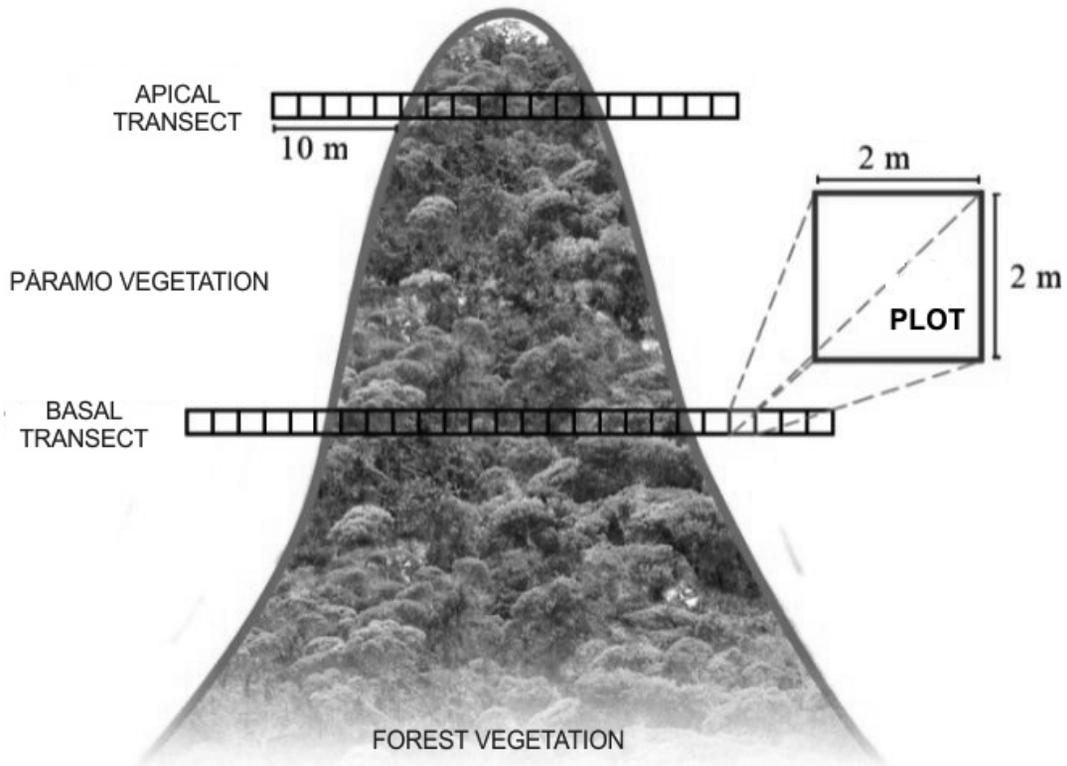


Figure 1. Schematic representation of the position of transects and plots on a forest tongue and on the matrix of páramo vegetation.

slope and declination angle were provided. For each plot the best quality picture was selected to calculate leaf area index (LAI) and % direct light transmission. The relationships between these canopy structure variables and the abundance of individuals in the smaller size category of the most common species was analyzed through the weighted average method to determine the species' indicator value (Gauch 1982). The optimum, defined as the species' indicator value; the amplitude, defined as the 95% probability interval around the optimum; and the range between maximum and minimum values measured for each species, were graphically represented. At the data analysis stage, percent direct light transmission was also used to determine the position of the forest borders on each transect. The border was defined as the plots where a sharp decrease in light transmission was observed.

RESULTS

A total of 30 woody species, including shrubs, were found in the sampled area. They belonged to 18 families, the most abundant being the Asteraceae (20% of the species), Ericaceae (13%), Melastomataceae (10%) and Hypericaceae (7%) (Table 1). Shannon diversity index was significantly higher in basal transects compared to apical transects ($p < 0.05$) (Table 2). Significant differences in diversity were also found between forest tongues.

Between 17 and 11 species were recorded among large individuals at the three forest tongues. Figure 2 shows a decrease in basal area from the interior to the exterior on both basal and apical transects. It is remarkable that no large individuals were found at the South-border and South-exterior sections of the apical transects. The rank abundance diagrams by species for total

Table 1. List of species found in the study.

Family	Species
Araliaceae	<i>Oreopanax reticulatus</i> (Willd. ex Schult.) Decne. & Planch.
Asteraceae	<i>Diplostephium venezuelense</i> Cuatrec.
Asteraceae	<i>Gynoxys meridana</i> Cuatrec.
Asteraceae	<i>Paragynoxys magnifolia</i> Cuatrec.
Asteraceae	<i>Pentacalia pachypus</i> (Greenm.) Cuatrec.
Asteraceae	<i>Pentacalia</i> sp.
Asteraceae	<i>Stevia ovata</i> Willd.
Clethraceae	<i>Clethra</i> sp.
Clusiaceae	<i>Clusia multiflora</i> Kunth
Cunoniaceae	<i>Weinmannia fagaroides</i> Kunth
Elaeocarpaceae	<i>Vallea stipularis</i> L.f.
Ericaceae	<i>Gaultheria buxifolia</i> Willd.
Ericaceae	<i>Macleania rupestris</i> (Kunth) A.C.Sm.
Ericaceae	<i>Themistoclesia dependens</i> (Benth.) A.C.Sm.
Ericaceae	<i>Vaccinium meridionale</i> Sw.
Escalloniaceae	<i>Escallonia</i> sp.
Hypericaceae	<i>Hypericum marahuacanum</i> N. Robson
Hypericaceae	<i>Hypericum cardonae</i> Cuatrec.
Loranthaceae	<i>Gaiadendron punctatum</i> (Ruiz & Pav.) G.Don
Gentianaceae	<i>Macrocarpaea</i> sp.
Melastomataceae	<i>Chaetolepis lindeniana</i> (Naudin) Triana
Melastomataceae	<i>Miconia jahnii</i> Pittier
Melastomataceae	<i>Miconia minutiflora</i> (Bonpl.) DC.
Primulaceae	<i>Cybianthus marginatus</i> (Benth.) Pipoly
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.
Podocarpaceae	<i>Podocarpus oleifolius</i> D. Don
Polygalaceae	<i>Monnina meridensis</i> Planch. & Linden ex Wedd.
Rosaceae	<i>Rubus coriaceous</i> Poir.
Rubiaceae	<i>Arcytophillum nitidum</i> (Kunth) Schtdl.
Winteraceae	<i>Drimys winterii</i> J.R.Forst. & G.Forst.

large individuals (Fig. 3) show that *Cybianthus marginatus* is clearly the dominant species in basal and apical transects and that its dominance is stronger in apical transects.

Total species richness in the small size category was 11 at two forest tongues and 10 at one forest

tongue. Dominant species differ between basal and apical transects. *Clusia multiflora* dominates in apical transects, while *C. marginatus* dominates in basal transects (Fig. 4). In this size category species dominance is also stronger in apical transects.

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Table 2. Average and standard deviation of Shannon diversity index and species richness for apical and basal transects. (*) Statistically different ($p < 0.05$).

Position	APICAL			BASAL		
	Adult	Juvenile	Total	Adult	Juvenile	Total
Diversity Index	0,86 ± 0,00229	1,07 ± 0,00017	1,09 (*) ± 0,00016	0,97 ± 0,00013	1,16 ± 0,00014	1,16 (*) ± 0,00014
Species richness	15	21	25	20	26	29

Three species were chosen (*Diplostegium venezuelense*, *C. multiflora* and *C. marginatus*) to display their abundances along the six transects divided by sections from N to S and from the exterior to the interior. The selected species were among the most abundant species. The first species has a unique distribution, while the other two species illustrate the diverse patterns of the remaining species. Average densities per plot of small and large individuals of these species are shown in Figure 5. Clearly, *D. venezuelense* is more abundant outside and at the edge of the forest, while the other two species are more abundant in the forest interior. These two species also have the tendency of being less abundant at the South-border and South-exterior situations. Regarding canopy structure, Figure 6 depicts the LAI and percent direct light transmission at

the plots along each of the six transects. Since length of transects is variable, large plateaus in the middle of the transects are not shown for clarity. Exterior plots show lower LAI, which increases towards the forest interior, and the opposite is observed for the percent direct light transmission. Interestingly, transitions between interior and exterior are fairly abrupt, taking only a few meters.

Figure 7 shows optimum, amplitude, maximum and minimum values of the distribution range of the most abundant species with respect to LAI. *D. venezuelense* has the lowest optimum (0,91) and is among the species with a wider distribution range. The remaining species tend all to have higher optimum LAI. The amplitude of their ranges are between 1 and 1.5, except for *Miconia jahnii*, which is below 1. Among the

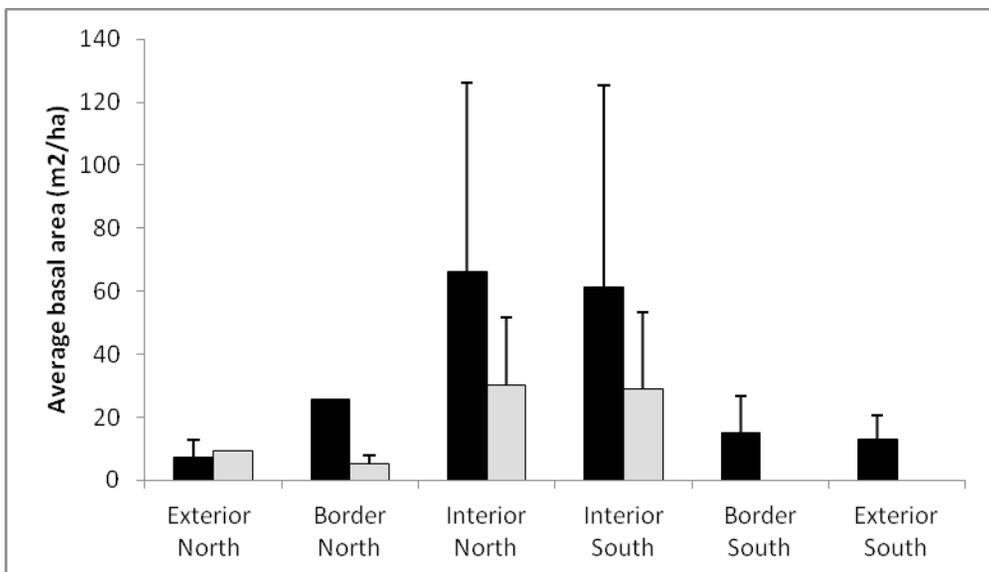


Figure 2. Basal area on basal (■) and apical (□) transects, by transect section (exterior, border and interior) and orientation, averaged over the three tongues.

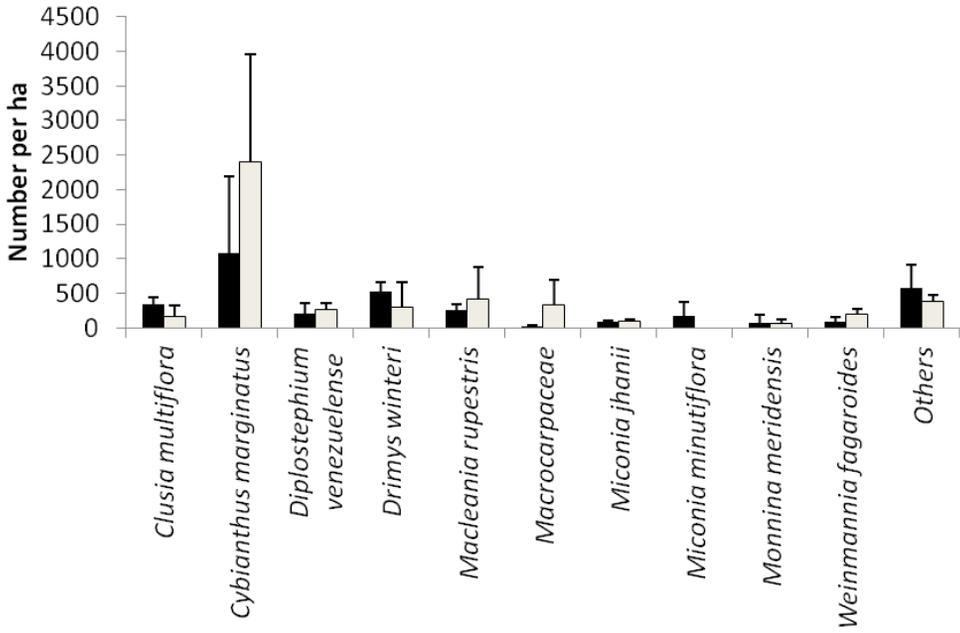


Figure 3. Average density of individuals by species with DBH>2.5 cm on basal and apical transects across the three forest tongues.

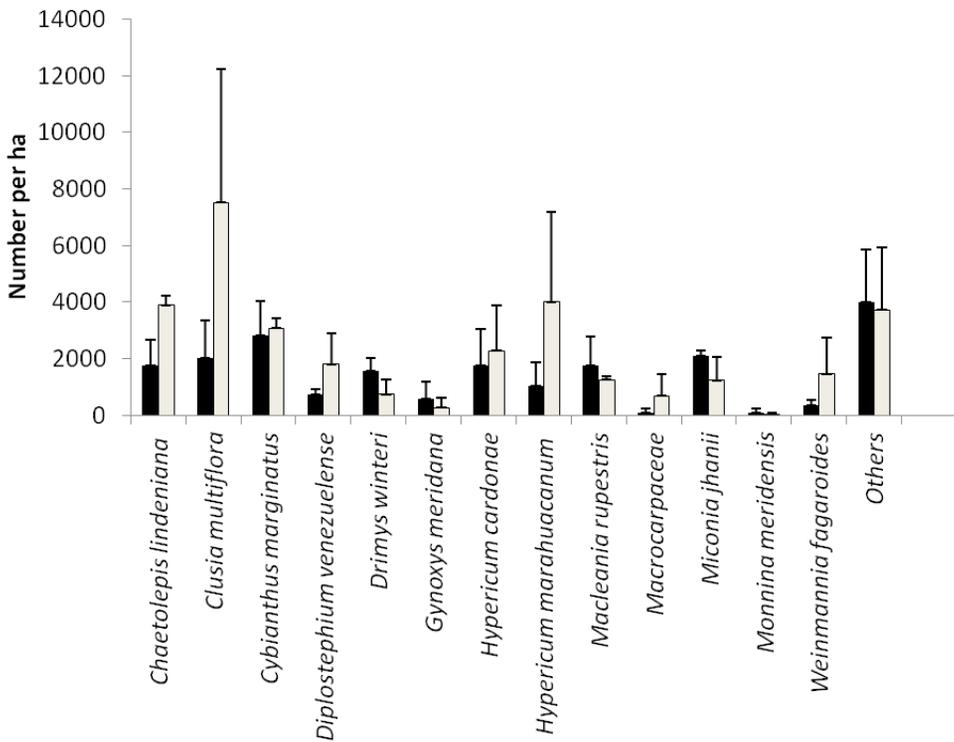


Figure 4. Average density of woody species with DBH<2.5 cm on basal and apical transects across the three forest tongues.

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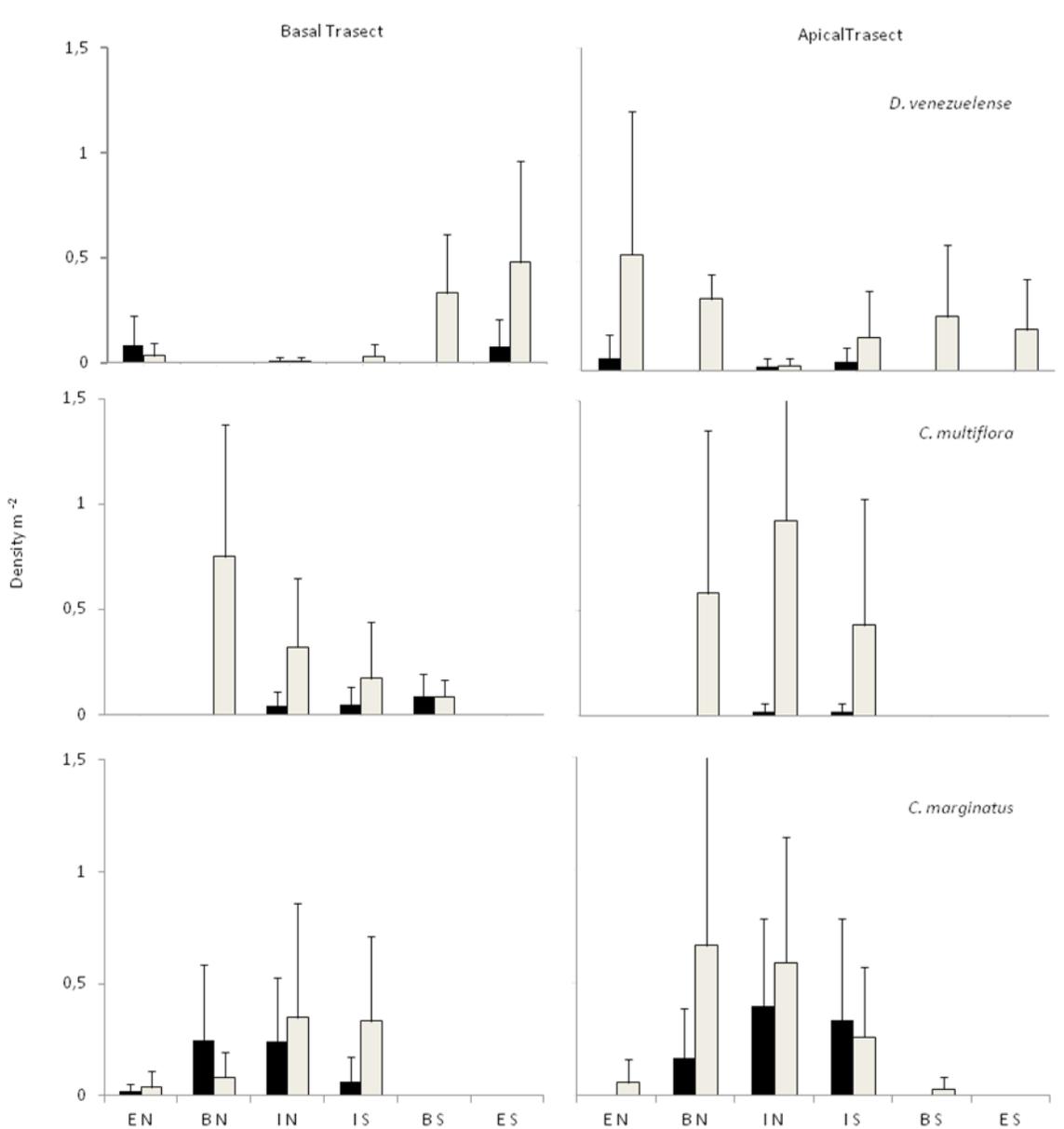


Figure 5. Comparison of basal and apical transects in terms of the densities (individuals per m^2) of *Diplostephium venezuelense*, *Clusia multiflora*, and *Cybianthus marginatus*. From the North facing side to the South facing side of the tongue: Exterior North (EN), Border North (BN), Interior North (IN), Interior South (IS), Border South (BS), Exterior South (ES). ■ Individuals with $DBH > 2.5$ cm and □ individuals with $DBH < 2.5$ cm.

species analyzed, *Myrsine coriacea* is the less tolerant to open canopies.

DISCUSSION

Forest structure, diversity and floristic composition

Basal area values along transects are larger

towards the center, which suggests that forest tongues are in expansion, since the larger values in the middle of the tongues are the result of trees with much larger diameter. The smaller basal areas found in the apical transects support this hypothesis. The consistent lack of trees in the apical South border and exterior situations is discussed later.

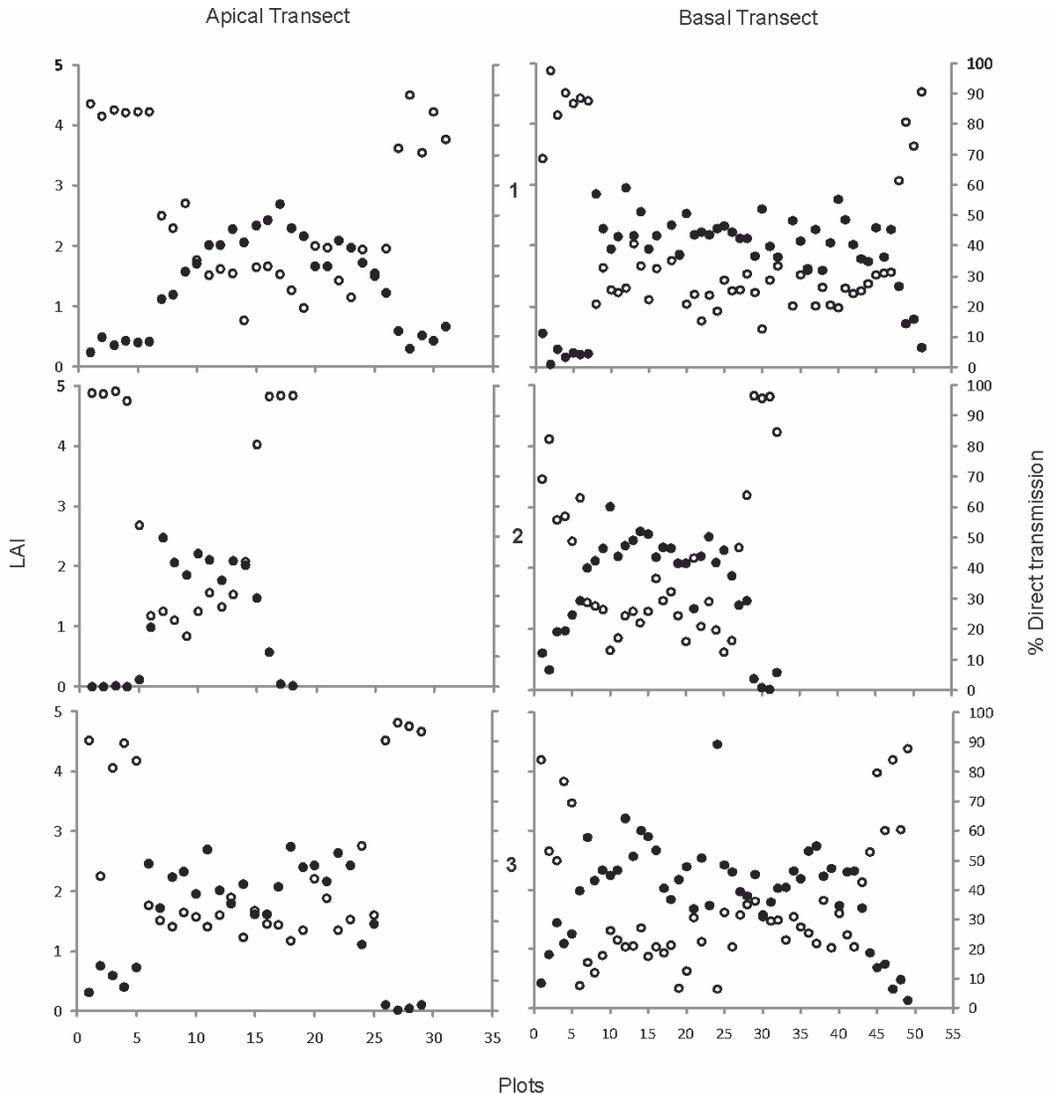


Figure 6. Leaf area index (LAI) (●) and percent direct light transmission (○) per plot along each transect (1,2,3).

The floristic composition at the treeline in the Páramo de San José is remarkably similar to those reported in other treelines in tropical Andes. At the family level, our study indicates Asteraceae, Ericaceae, and Melastomataceae as the most abundant, which coincides with other studies in the Sierra Nevada de Mérida, (Abele 2000; Ramirez *et al.* 2009; Sodja 2001) and in Ecuador (Bader *et al.* 2007a; Keating 1999). At the genus level, *Myrsine*, *Gaiadendron*, *Oreopanax*, *Diplosthepium*, *Gynoxis*, *Weinmannia*, *Miconia* and *Monnina* were found in both countries' treelines (Bader *et al.* 2007a; Ramirez *et al.* 2009; Young and León 2007).

Ramirez *et al.* (2009) suggest that the forest islands could constitute advance nuclei of trees into the páramos near the treeline, since their species composition is very different to the continuous forests, being dominated by species that are also very abundant in the contact borders between forests and páramos. Our results indicate a higher diversity in basal than in apical transects, as a result of a higher species richness in the former and a higher species dominance in the latter. This would be compatible with a hypothetical process of gradual ascent of tree species from the basal to the apical zones along these tongues. Moreover, the apical transects

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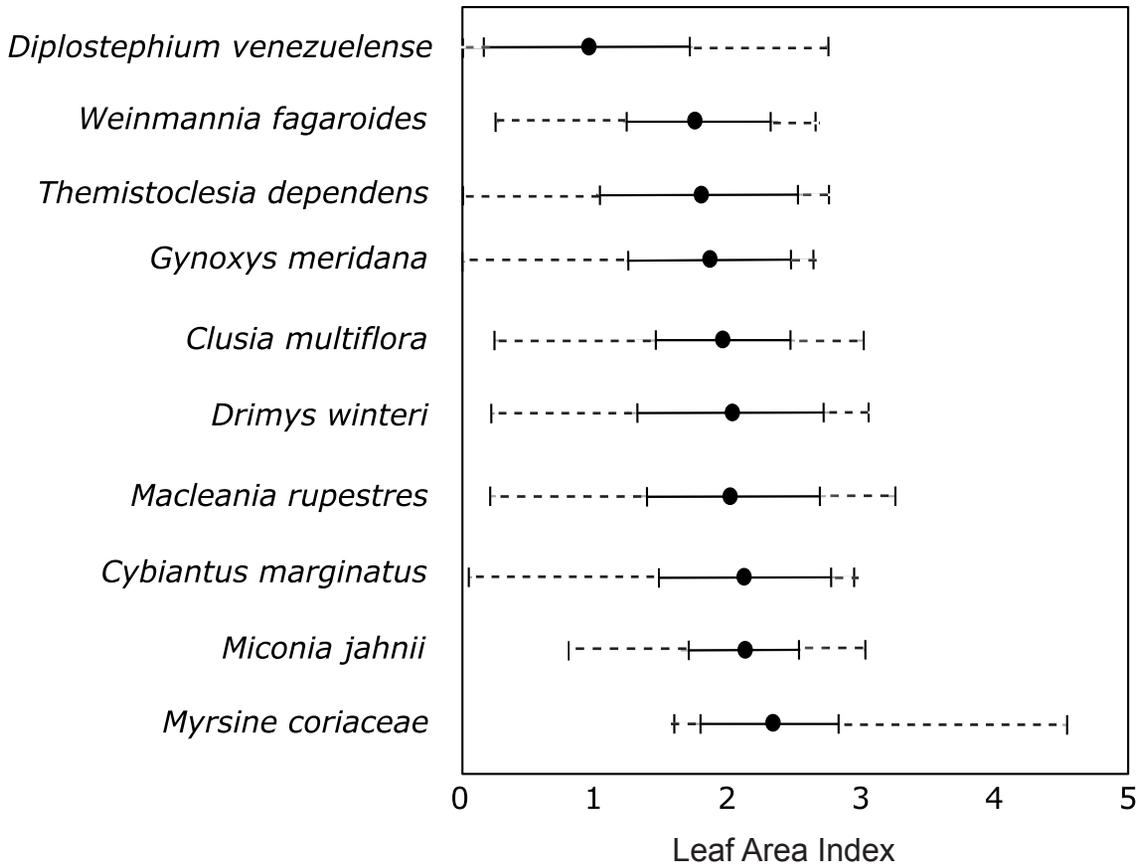


Figure 7. Optimum (species indicator value) ●, amplitude (95% confidence interval) - - - - and maximum to minimum values — of LAI for the most abundant species, based on the weighted averages method.

were dominated by tree species regarded by Ramirez *et al.* (2009) and Puentes (2010) as possible pioneer open páramo and border species (e.g. *C. marginatus*).

Canopy structure relationships with species distribution

Leaf area index and percent direct light transmission show clear trends of change around the forest edges revealing an abrupt limit usually no more than 2 m wide. This rather common pattern in tropical treelines has been attributed to stabilizing dynamics at the edges as a result of positive feedbacks driven by high radiation sensitivity of the tree species and/or fire (Bader *et al.* 2007a). Since there is neither evidence nor recent known history of fire at our study site, we suggest a positive feedback mechanism induced mainly by radiation as an important determinant

of the dynamics and abruptness of this tropical treeline.

Leaf area index values found in this study (roughly 0-3), are similar to those found for cloud forests immediately below the treeline in the same mountain range (Schwarzkopf *et al.* 2011). However, at lower elevations in the cloud forest, Dulhoste (2002) measured LAI values up to 6 during the rainy season. Although cloud forests are close to the treeline, these comparisons may not be informative, since cloudiness and topography seem to impact their LAI (Schwarzkopf *et al.* 2011), which is unlikely to be the case at the treeline where cloudiness should be lower. The values of LAI found in this study are similar to those found in temperate treelines, reaching up to 5 during the summer in deciduous forests (Korner 2003), and up to 2.7 calculated from satellite images

(Heiskanen 2006). Nevertheless, local LAI measurements may be useful to compare levels of radiation exposure which seem crucial for tree species establishment at the treeline (Hogan and Machado 2002; Bader *et al.* 2007b).

D. venezuelense shows the lowest LAI optimum in this study, which could be explained by its tolerance to the radiation levels common in the open páramo (Puentes 2010). We also found a clear preference of small and large individuals of the species for border and exterior (open páramo) situations, as reported by Puentes (2010; see also Ramirez *et al.* 2009). The species has been reported to grow in the páramo of the Sierra Nevada de Mérida up to 3600 m elevation (Yanez 1998). In Ecuador Bader *et al.* (2007b) found another species of the genus *Diplostephium* with similar spatial distribution. Interestingly, these authors reported that this species showed the highest sapling survival rates in transplant experiments immediately above the treeline, even in plots in which local páramo vegetation cover was removed.

Large and small individuals of *C. multiflora* were found only at the interior and borders of the forest tongues. Its LAI optimum is higher than the optimum of the previous species. In fact, *C. multiflora* has been reported in the study area as a species typically growing in the forest interior (Abele 2000; Sodja 2001). However, it is the dominant species in apical transects.

Both size categories of *C. marginatus* are fairly abundant in the forest interior, although it is also found at the borders and even open páramo situations next to N facing borders. Puentes (2010) characterized *C. marginatus* as a species of the border and interior of the forest, while Ramirez *et al.* (2009) describe the species as a forest species with the ability to colonize the open páramo at lower elevations (closer to the continuous forest). However, Puentes (2010) suggests that the species may be limited to establish in the open páramo, where transplanted saplings showed chronic photoinhibition of photosynthesis.

The role of topography

The bias of the distribution of the total basal area and abundance of certain species towards the N side of the transects is likely to be the result of differential shading, since the study site is in the northern hemisphere (8.5°). The larger shade

casted by the forest on the N side may favor the establishment and development of species more sensitive to radiation. The more shaded microsites may not only receive less radiation but may also have lower evaporative demands and less temperature fluctuations. Although higher levels of radiation seem to limit the advance of forest species into the páramo in tropical treelines (Bader *et al.* 2007b), topography may change environmental conditions even in subtle quantities close to threshold levels for some species. This seems to be the case of *C. marginatus*, which is able to establish in the open páramos and N borders of the tongues, where micro-environmental conditions could be less extreme. The effect of topography on the treeline in Ecuador was studied by Bader and Ruijten (2008) who found that on E facing slopes the treeline is at lower elevations than on W facing slopes. The authors suggest that the difference is due to the fact that E slopes receive a higher radiation load. Our results, as well as those reported by Bader *et al.* (2007b), Puentes (2010), and González *et al.* (this volume) suggest that reduced radiation loads, like those resulting from topographic effects interacting with the cover provided by the forest canopy, could be important for the establishment of woody species. The impact of slope orientation on vegetation in the area has also been reported for cloud forests in the Venezuelan Andes, a light limited ecosystem, where LAI at S facing slopes was higher than at N facing slopes, probably as a result of a higher radiation load on the former (Schwarzkopf *et al.* 2011). Therefore, our results support the idea that topography is an important modulating factor for radiation, probably a key environmental driver limiting treeline advance in the tropical Andes.

Concluding remarks

The higher species diversity and higher abundance of trees considered as border and open páramo species (see above) at the tip of the forest tongues and the contrasting optima and distribution ranges of species along the LAI gradient are compatible with a scenario of forest expansion towards the páramo and suggest that this process could operate in two phases. The first phase could be driven by species with lower LAI optima (e.g. *D. venezuelense*), followed by a second phase dominated by species less

tolerant to the high radiation levels of the open páramo, benefiting from the shade of the colonizing species. In this scenario, species like *D. venezuelense* could favor the successful establishment of the less radiation tolerant species in forest borders and open páramos. However, according to our observations in the field and to quantitative data by Puentes (2010), adults of this species do not seem to be spatially associated with other woody species in the open páramo. This suggests that either the species locally excludes other species through competitive effects, or it provides insufficient shade when growing in isolation, or the other species are limited by dispersal. Consequently, the advance of the forest could be rather slow and limited to its border where species like *C. multiflora* and *C. marginatus* are dominant.

The available evidence in the tropical Andes suggests that the dynamics of the treeline could be limited by a high sensitivity of tree species to the high radiation loads characteristic of the páramo environment, modulated by topographic effects. Moreover, we conclude that the abruptness of the treeline in the tropical Andes does not seem to be the result of the contribution of anthropogenic factors, as has been suggested by Bader *et al.* (2007a), since fire and grazing are absent in the study area (although they could have been important at some point in the past). The impact and interactions of low temperature, high daily temperature oscillations and water stress on the woody species' tolerance to radiation thresholds needs to be addressed for a better understanding and prediction of the future dynamics of the tropical alpine treeline.

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