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Spatial relations and population structure of a dominant tree along a treeline ecotone in the Tropical Andes: interactions at gradient and plant-neighbourhood scales

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Abstract

Background: Studies in temperate mountains suggest that plant-plant interactions modulate tree establishment above the forest line. In tropical mountains worldwide this issue remains largely unexplored.

Aims: To analyse the population structure and local spatial relationships of a dominant tree at a species-rich tropical Andean forest line.

Methods: We determined changes in the population structure of *Diplostephium venezuelense* along an elevation gradient between continuous forest and open páramo and analysed plant community structure and superficial rock cover in the neighbourhood of saplings and adults at the upper forest line.

Results: Sapling and adult densities were highest in low-altitude páramos adjacent to the forest line and at the borders of small forest islands. Saplings showed local spatial aggregation, were positively associated with small boulders and low shrubs and negatively associated with mosses and lichens. However, no spatial association was found between scattered adults in the páramo and saplings of other forest trees.

Conclusions: Complex species-specific local spatial interactions, suggesting both facilitative and antagonistic effects, seem to modulate the establishment of the dominant tree *D. venezuelense* at and above the upper forest line. Nevertheless, the establishment of other tree species above continuous forests does not appear to be facilitated by the canopy cover offered by the isolated *D. venezuelense* individuals established in open páramo environments.

Key words: elevation gradient, facilitation, local spatial structure, plant-plant interactions, safe-sites, treeline dynamics.

Introduction

The study of the size-age structure and spatial patterns of plant populations along environmental gradients can provide key insights for understanding the processes that control population dynamics, reflecting past and present opportunities for establishment, survival and growth (Hutchings 1997; Wiegand et al. 2006). In particular, the factors that affect the establishment phase can be critical for both the persistence and range expansion of a species (Smith et al. 2009). Establishment not only depends on seed production and dispersal but also on the availability of safe-sites (*sensu* Harper 1977). These safe-sites can be characterised by studying the abiotic and biotic conditions within the local neighbourhood of seedlings and saplings. Given that survival and growth of plants are mainly determined by abiotic and biotic interactions in their immediate neighbourhood, this approach reflects what Turkington and Harper (1979) called the 'plant's eye-view'. In fact, it is increasingly recognised that the interplay between local spatial structure and plant-plant interactions (e.g. competition, facilitation) can have large effects on population and community dynamics (Law and Dieckmann 2000; Stoll and Prati 2001; Llambi et al. 2004). However, remarkably few studies in the highland tropics have explicitly analysed the role of plant-plant interactions on vegetation structure and dynamics (see review by Anthelme and Dangles 2012).

In the context of understanding the processes that influence the dynamics of the mountain treeline, the available evidence suggests that its altitudinal position at a global scale is mainly associated with thermal limitations for tree growth (Körner and Paulsen 2004; Körner 2012). Even so, studies in temperate treelines suggest that autogenic, plant-plant interactions can be important in modulating the spatio-temporal patterns of tree establishment above the treeline in response to changes in climate and/or land use (Smith et al. 2009; Bansal et al. 2011; Oriol et al. 2013); Some of these studies have pointed to a net competitive effect of the alpine vegetation on tree colonisation (e.g. Wardle and Coleman 1992; Castro et al. 2002; Dullinger et al. 2003). However, other studies have suggested that plant cover above the treeline could have a facilitation effect (Smith et al. 2003). For example, in the Colorado Rocky Mountains, studies on colonisation of conifer tree seedlings above the treeline reported that tree and grass cover reduced mortality and photoinhibition of photosynthesis of sheltered seedlings (Germino and Smith 1999, 2002; Germino et al. 2002; Maher et al. 2005).

In the northern tropical Andes, the treeline ecotone (sensu Bader et al. 2007a) corresponds to a transition zone between continuous mountane forests (locally known as *subpáramo* or *bosque paramero*) and open alpine grasslands (known as *páramo*). Along this zone, there is a complex juxtaposition of both ecosystems, with forest tongues and islands that penetrate into the open páramo matrix.

In contrast with the situation in many temperate mountains, the tropical treeline ecotone is characterised by very high species richness, with tree abundance and diversity decreasing abruptly above continuous forests (Young 1993; Keating 1999; Wille et al. 2002; Bader et al. 2007a; Ramirez et al. 2009; Moscol-Olivera and Cleef 2009). Paleocological studies have shown a dynamic response of the Andean forest-line during the glacial-interglacial cycles of the Pleistocene and the more recent climate changes after the last glacial maximum (van der Hammen 1974; Salgado-Labouriau 1991; Wille et al. 2002; Bakker et al. 2008).

In the only detailed study analysing the importance of the local páramo vegetation on tree establishment, Bader et al. (2007b) transplanted seedlings of several upper forest-line species in Ecuador above continuous forests under different conditions: artificial shading, placement under natural grass cover, full exposure to incident radiation. A tree species of the genus *Diplostephium*, which occurs naturally in the low páramos just above the treeline, was the only species which showed high survival, even in treatments in which all plant cover was removed around seedlings. This suggests *Diplostephium* sp. could potentially act as a colonising species in scenarios of forest expansion induced by current climate change (with an expected increase in temperatures for northern South America of 2-4 °C for the end of this century, see review in Rull et al. 2007).

However, we lack a detailed understanding on the patterns of distribution and the conditions that modulate the establishment of tree species which have the ability to colonise open environments above the treeline in the highland tropics. How are these species distributed along the complex forest-páramo transition zone? Are there differences in the distribution of different size classes? Is seedling establishment spatially random or is it associated with particular biotic and abiotic conditions in their immediate neighbourhood? Is the local community structure around seedlings/saplings different from the average community? Do these trees facilitate the colonisation of other woody species above the treeline?

These were the main questions explored in the present paper. To do this, we established a transect along the forest-páramo transition zone in the Sierra Nevada de

Mérida (Venezuela), where *Diplostegium venezuelense* Cuatrec. is the most abundant tree species in forest borders and in the scattered tree cover of the low páramo (Ramirez et al. 2009; Rodriguez et al. 2011). We determined changes in density of *D. venezuelense* along the gradient between forests and open páramo and analysed community structure and the cover of superficial rocks (small boulders) in the neighbourhood of saplings and adults. In our view, this kind of explicit analysis of spatial patterns of distribution of dominant upper forest line trees integrating different spatial scales can provide key insights on the role played by local plant-plant interactions on vegetation dynamics in the treeline ecotone.

Materials and methods

Study area

The study was carried out on the northern slopes of the Sierra Nevada de Mérida, Venezuela, along a transect in the forest-páramo transition belt (3250 m to 3550 m a.s.l.), which probably corresponds to the altitude span of the potential climatic treeline. The study site was located near *La Fría* Lagoon, 1.6 km of *La Aguada* Station of the Mérida Cable Car system (8° 35' N, 71° 09' W). The climate has been classified by Andresen and Ponte (1973) as 'very humid páramo climate' with an average annual precipitation of 1811 mm (*La Aguada*, 3452 m). Rainfall has a bimodal pattern, with maxima in June and October and the driest months are between December and February. There are small variations in average temperature between different months (no thermal seasonality) but daily temperatures show very large amplitudes (which can exceed 20 °C), a pattern typical of the highland tropics. Hence, in contrast with temperate mountains, the growing season last the whole year and snow is rare at treeline elevations, although temperatures can occasionally fall below freezing, especially during the dry season. Ataroff and Soto (unpublished results) recorded during > 1 year of monitoring (2008-2009) average annual temperatures ranging between 7.0 °C and 7.9 °C (at 1.5 m above the ground) in forest and páramo at the treeline ecotone in our study area. During this period absolute minimum temperatures reached -3.4 °C while the maximum reached 21.2 °C.

Soils in the study area are young (Inceptisols and Entisols), with a loam to sandy-loam texture, low pH (4.1 to 4.7), low cation exchange capacity and base saturation, but high total nitrogen (0.6% to 0.9%) and total organic carbon contents (11.0% to 16.2%). Soils

within forests tend to show significantly higher base contents than adjacent páramo soils (L. Sarmiento and D. Acevedo, unpublished results).

Vegetation structure along our study transect was characterised by Ramirez et al. (2009). In the forest, emergent trees can reach > 10 m. There is a dense intermediate stratum with trees and shrubs between 1 and 5 m high, while on the forest floor herbs, ferns and mosses dominate. Tree species abundances differ markedly between continuous forests (dominated by *Psammisia penduliflora* (Dunal) Klotzsch, *Miconia tinifolia* Naudin and *Libanothamnus neriifolius* Ernst), forest tongues (dominated by *Cybianthus marginatus* (Benth.) Pipoly) and the small forest islands (where *D. venezuelense* and *Vaccinium meridionale* Sw. show the highest abundances). The edges of forest tongues and islands are dominated by *D. venezuelense*.

Páramo vegetation has a dense upper stratum (50 cm - 1 m high) with plant cover from 80 to 100%. This upper stratum is strongly dominated by the tussock grass *Calamagrostis effusa* (Kunth) Steud. Within the grass matrix there are sparse small trees, sclerophyllous shrubs and caulescent rosettes. The lower stratum (0-50 cm) is dominated by herbaceous plants with the presence of occasional prostrate shrubs. Woody species richness decreases sharply from the low páramo adjacent to continuous forests (with eight tree and shrub species, *D. venezuelense* being the most abundant) to the high páramo (with only one shrub species, *Chaetolepis lindeniana* (Naudin) Triana). Land use is restricted to a very extensive cattle grazing. Contrary to the situation in Colombia and Ecuador, in Venezuela fires are not a practice associated with forage management in the páramo. A study on vegetation cover changes in the region based on the interpretation of 1952 and 1998 aerial photographs, showed no direct evidence of land clearing (i.e. agriculture, abandoned fields, secondary pastures) near the study transect and indicated a densification of the woody component around the forest-line (Santaella 2007). Hence, although it is possible that vegetation dynamics could have been influenced by a decrease in grazing pressure after the creation of the Sierra Nevada National Park in 1952, we can be fairly confident that there have not been drastic changes in vegetation cover due to forest clearing in the last five decades.

Sampling at landscape scale

An elevation transect of 250 m width with a north-west orientation was established along the forest-páramo transition belt (3260 m to 3550 m). All sampling sites had the same

aspect and slopes ranged between 15° and 30°. The transect avoided areas with azonal vegetation such as large rocky outcrops, deep ravines or flat areas dominated by small bogs.

At ca. 3260 m we randomly located four replicate sampling plots (15 m x 2 m) inside the upper limit of continuous forest. At ca. 3350 m we located four plots inside a forest tongue, four along the border with paramo and four in adjacent páramo areas. At ca. 3440 m, we established four plots inside a small forest island of ca. 0.25 ha), four along the border of this island and four in the adjacent páramo. Finally, at 3550 m, we established four plots in an open páramo area (no more forest islands were present at this altitude). Each 15 m x 2 m plot was oriented perpendicular to the main slope. Inside each plot we quantified the total density of *D. venezuelense* individuals, classifying them in three size classes defined in terms of stem length: (a) < 5 cm; (b) 5 – 30 cm; (c) > 30 cm. All sampling was carried out during the first three months of the wet season (March to May 2008).

Sampling at the plant-neighbourhood scale

To characterise some of the abiotic and biotic conditions associated with the establishment of *D. venezuelense* seedlings/saplings (stem length <5.0 cm), we randomly selected 20 individuals, 10 located on the border of a forest island and 10 in the adjacent páramo at 3440 m (within the same transect studied at the gradient scale). Around each individual we established circular micro-plots with a 10 cm radius. The small size used for analysis at this scale was meant to characterise the local conditions in the immediate neighbourhood that could influence the growth and survival of individual seedlings and saplings. Within each circular plot we determined the density of all conspecific individuals and estimated the cover of all plant species present and of small superficial boulders using the point-quadrat method (Greig-Smith 1983) with 20 pin hits within each circular plot. Mosses and lichens were recorded as a single group (non-vascular species). To obtain a comparative reference we selected 20 random points at the border of the forest islands and the páramo (10 in each case) and placed a circular 10 cm radius plot around each random point. As before, we estimated rock and plant cover and determined *D. venezuelense* densities. The same procedure was repeated to record the local neighbourhood of adults (stem length larger than ≥ 50 cm) using circular plots of larger radius (25 cm). This radius was chosen so that the circular plots lay directly under the influence of the small round crowns of adult *D. venezuelense* trees

(which typically had crowns of about 50 – 100 cm diameter) present in the forest borders and open páramos. Plant names were verified in the Catalogue for the Vascular Flora of Venezuela (Hokche et al. 2008) and The Plant List (2013).

Data analysis

No individuals of *D. venezuelense* were recorded in the two extremes of the studied transect (forest plots at 3260 m and páramo plots at 3550 m). To compare the densities of individuals in each size class between the two intermediate altitudes (3350 and 3440 m) and between vegetation types (forest, forest border, páramo) we used a permutational two-way analysis of variance (permanova), defining both elevation and physiognomic situation as fixed factors. Given that our data was not normally distributed, we decided to use permanova, a robust technique which removes the assumption of normality required by fully parametric anova procedures. We also evaluated the homogeneity of variances in each case. Since our data was not homocedastic in the case of the densities of seedlings and adults, we used a square root transformation before carrying out the analysis (Permanova+ for Primer 6, Anderson et al. 2008).

To obtain an integrated view of the differences between local community structure in the neighbourhood of saplings and adults and the average community structure in the forest island borders and páramos we constructed a matrix with the cover of all species found in all plots sampled (with separate matrixes for the 10-cm radius plots used for saplings and the 25-cm radius plots used for adults). These matrices were analysed by using non-metric multidimensional scaling ordination (MDS), with the Bray-Curtis measure as a dissimilarity metric. We present the two dimensional ordination diagrams for sites (micro-plots), and the Pearson's correlations between species abundances and plot scores on these two axes (Primer 6, Clarke and Gorley 2006; see also Clarke 1993). We tested for differences in community structure in micro-plots in different physiognomic situations and local sampling situations (neighbourhoods of saplings or adults vs. random centred) using two-way permanova. The sums of squares for the permanova analysis were calculated from the plot distances between and within the different sampling situations on the Bray-Curtis dissimilarity matrix (see Anderson 2001 and Anderson et al. 2008 for details).

We also compared the cover of each individual species within the circular plots centred around saplings and adults with the cover found in the circular plots centred around

randomly located points in both the island borders and páramo. We used a two-way permanova with the local situation (sapling centred vs. random centred plots) and vegetation (forest border vs. páramo) as fixed factors. The same was done for comparison of rock cover and densities of *D. venezuelense* conspecifics. In all cases, the probability of Type I error was set to 95% ($\alpha=0.05$).

Results

Distribution of Diplostegium venezuelense along the forest-páramo ecotone

For the density of the smallest (< 5 cm) and largest (>30 cm) diameter individuals, there was a significant interaction between altitude and vegetation type ($P<0.05$). Hence, the patterns of density between vegetation types differed at the two altitudes studied, both for saplings and adults. At 3350 the pair-wise tests showed a significantly higher density of saplings in the páramo than in the forest border, while for adults density was higher in the páramo than inside the forests (Figure 1). In the forest islands at 3440 m, the highest sapling densities were recorded in the borders, while the adults showed higher densities both in the páramo and borders than inside the islands. The densities in the intermediate size class showed no statistically significant differences between physiognomic situations or altitudes at $\alpha=0.05$.

Characterisation of sapling and adult neighbourhood conditions

Average rock cover and conspecific densities were significantly higher ($P<0.001$) around saplings of *D. venezuelense* than in randomly located plots; there was no significant effect of vegetation type and no significant interaction between factors. For adults, there was no significant difference between rock cover and conspecific densities between random plots and plots centred on adults, no significant effect of physiognomy and no significant interaction (Table1). In plant-centred micro-plots (for 10 cm and 25 cm radius), we observed that conspecific individuals corresponded in their large majority to seedlings and saplings (although we did not separate conspecifics within micro-plots in size classes during sampling).

In general, the plots centred on *D. venezuelense* saplings showed a different relative position in the ordination diagram than those placed randomly, reflecting differences in

community composition. The position on the MDS diagram for sapling-centred micro-

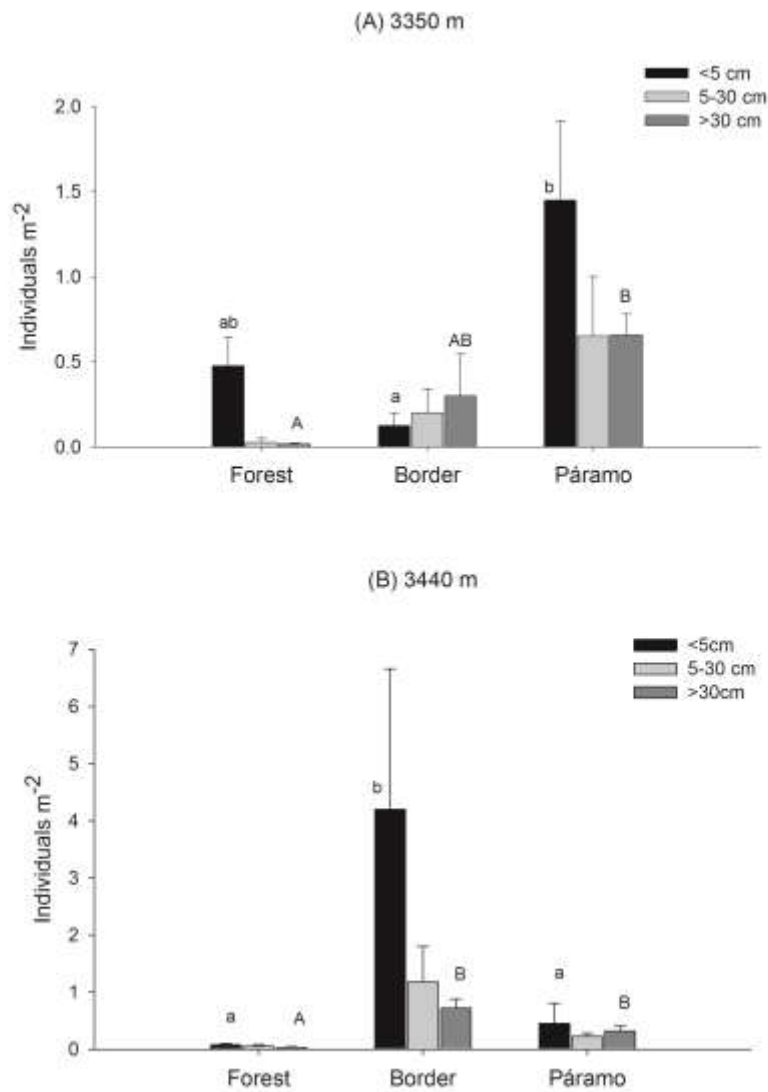


Figure 1. Average densities of *Diplostephium venezuelense* individuals classified into three size classes in terms of stem length (<5 cm; 5 – 30 cm; > 30 cm) inside forests, at the border of forests and in adjacent open páramos at 3350 m and 3440 m (error bars indicate standard error), La Aguada, Sierra Nevada de Merida, Venezuela. At 3350 m the forest corresponds to a forest tongue, while at 3440 m it corresponds to a small forest island within the páramo matrix. Letters indicate statistically significant differences based on permanova (n=4, α=0.05; small case letters for < 5 cm individuals; large case letters for individuals > 30 cm). No statistically significant differences in densities were found for the intermediate size class.

plots was positively correlated with higher abundances of *Lycopodium clavatum* L., *Disterigma empetrifolium* (Kunth) Nied, *Hypericum laricifolium* Juss. and *Calamagrostis*

effusa, and negatively correlated with the abundance of non-vascular species (mosses and lichens) and *Chaetolepis lindeniana* (Figure 2).

Table 1. Average (\pm standard error) density of all conspecifics (individuals m^{-2}) and boulder cover (%) within circular plots placed around *D. venezuelense* saplings (<5 cm in stem length) and adults (<50 cm in stem length) and in random locations (average conditions) at the border of a forest island and the adjacent open páramo at 3440 m, La Aguada, Sierra Nevada de Merida, Venezuela. We used 10-cm-radius plots for seedlings and 25-cm plots for adults. Significant differences (Permanova pair-wise comparisons, $\alpha=0.05$) are indicated with small case letters.

Vegetation type	Locale	Density (ind. m^{-2})	Boulder cover (%)
Forest island border	Around saplings	92.3 \pm 26.7(a)	25.0 \pm 12.9 (a)
	Random plots	6.4 \pm 4.3 (b)	7.0 \pm 5.9 (b)
	Around adults	8.7 \pm 6.6	7.0 \pm 6.2
	Random plots	7.13 \pm 2.4	3.5 \pm 2.5
Open páramo	Around sapling	47.7 \pm 10.9 (a)	58.5 \pm 14.0 (a)
	Random plots	0.0 \pm 0.0 (b)	1.5 \pm 1.1 (b)
	Around adults	0.51 \pm 0.5	8.5 \pm 4.2
	Random plots	0.51 \pm 0.5	0.5 \pm 0.5

The permanova on the dissimilarity matrix confirmed that there was a statistically significant difference in community structure between plots centred on saplings and those centred on random points ($P=0.0015$); no significant effect of vegetation type or significant interaction were detected.

In the case of the adults, the MDS ordination of micro-plots showed a clear separation between those around random points and those centred on adults in the forest borders. However, in the case of the páramo, there was no clear separation between them in the ordination diagram. The separation in the MDS diagram between adult-centred and random plots at the borders seem to reflect higher abundance of non-vascular species in random plots and higher abundance of *D. empetrifolium*, *L. clavatum* and *Jamesonia imbricata* (Sw.) Hook. & Grev., in adult-centred plots (Figure 3).

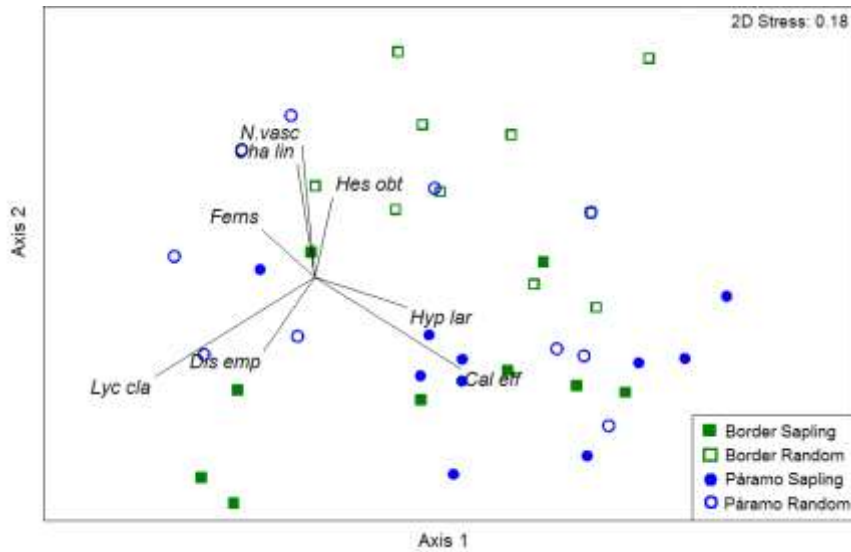


Figure 2. Non-metric multidimensional scaling ordination (MDS) of the 40 sampling micro-plots (10 cm radius) based on their dissimilarity (Bray-Curtis) in plant species cover in La Aguada, Sierra Nevada de Merida, Venezuela. Micro-plots were classified in terms of two factors: vegetation type (forest island borders vs. páramos) and location (circular plots centred on *D. venezuelense* saplings and random plots). Vectors represent the Pearson's correlation coefficient of the abundance of each species with the scores of each microplot on the two MDS axes (only species with $p > 0.3$ are included). *Cal eff*, *Calamagrostis effusa*; *N. vasc*, mosses and lichens; *Cha lin*, *Chaetolepis lindeniana*; *Lyc cla*, *Lycopodium clavatum*; *Hes obt*, *Hesperomeles obtusifolia*; *Hyp lar*, *Hypericum laricifolium*; *Dis emp*, *Disterigma empetrifolium*.

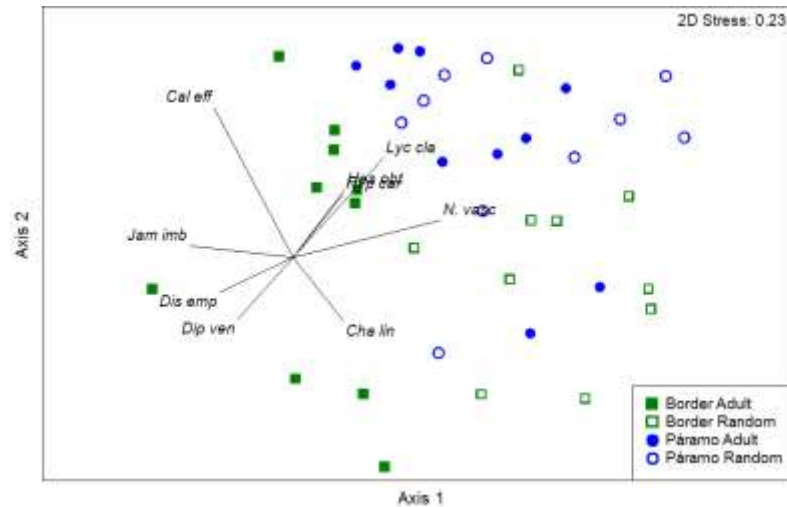


Figure 3. Non-metric multidimensional scaling ordination (MDS) of the 40 sampling micro-plots (25 cm radius) based on their dissimilarity (Bray-Curtis) in La Aguada, Sierra Nevada de Merida, Venezuela. Micro-plots were classified in terms of two factors: vegetation type (forest island borders vs. páramos) and location (circular plots centred on *Diplostegium venezuelense* adults and random plots). Vectors represent the Pearson's correlation coefficient of the abundance of each species with the scores of each microplot on the two MDS axes (only species with $p > 0.3$ are included). *Cal eff*, *Calamagrostis effusa*; *N. vasc*, mosses and lichens; *Cha lin*, *Chaetolepis lindeniana*; *Lyc cla*, *Lycopodium clavatum*; *Hes obt*, *Hesperomeles obtusifolia*; *Dis emp*, *Disterigma empetrifolium*; *Hyp car*, *Hypericum caracasenum*; *Jam imb*, *Jamesonia imbricata*; *Dip ven*, *D. venezuelense*.

The permanova on the dissimilarity matrix showed a significant interaction between the two factors ($P=0.038$). As expected from what was observed in the MDS diagram, the pair-wise test showed a significant difference in community dissimilarity between plots centred on adults and random plots ($P=0.0001$) in forest island borders but no significant difference in the páramo ($P=0.417$).

The dominant tussock grass *Calamagrostis effusa*, showed a higher average cover around samplings than in random plots (Figure 4), but the difference in cover was not statistically significant. *L. clavatum*, *D. empetrifolium* and *H. laricifolium* showed significantly higher cover around saplings than their environmental average ($P<0.05$), while mosses and lichens showed significantly lower cover in the neighbourhood of saplings than in randomly located plots ($P=0.005$). In all of these cases there was no effect of vegetation type and no significant interaction term. Interestingly, for the adults (Figure 5) there were changes in the patterns of local spatial relations: *L. clavatum* showed a significantly lower cover in the neighbourhood of adults ($P=0.0075$) irrespective of the physiognomic situation, while *J. imbricata* showed a significant interaction between both factors ($P=0.043$), with significantly higher cover only in the forest borders ($P=0.0031$). For non-vascular species there was also a significant interaction between vegetation type and local situation (random vs. sapling centred, $P=0.044$), with a significantly lower cover in the neighbourhood of adults at the forest borders. There were many rare species which were only found in some of the random plots, but were not detected in the plant-centred plots (Figures 4 and 5). In the case of the 10 cm radius micro-plots these corresponded to *Pernettya prostrata* (Cav.) DC., *Hesperomeles obtusifolia* (Pers.) Lindl., *Ruilopezia atropurpurea* Cuatrec., *Hypericum caracasenum* Willd. and *Jamesonia imbricata*. In the case of the 25 cm micro-plots they were *H. obtusifolia*, *Vaccinium meridionale*, *Arcytophyllum nitidum* (Kunth) Schldl., *Hypericum juniperinum* Kunth and *Luzula racemosa* Desv.

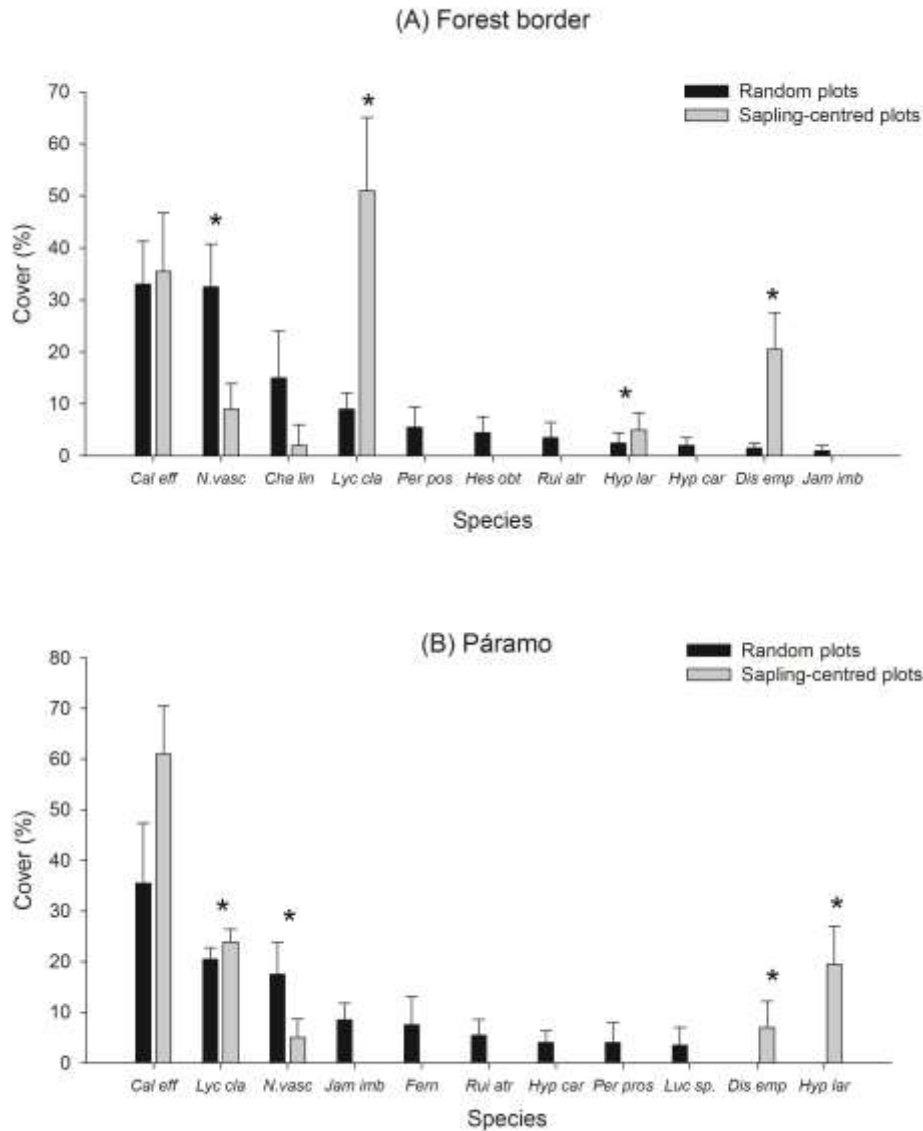
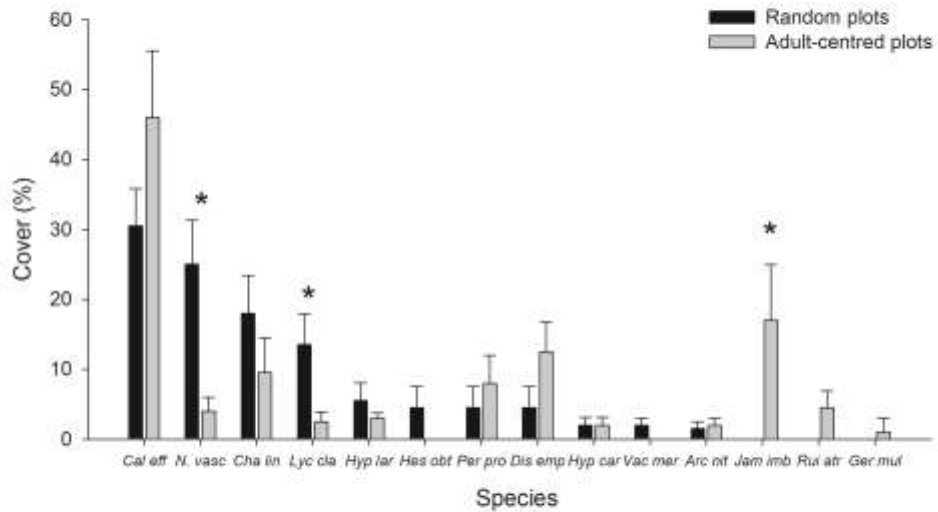


Figure 4. Average plant species cover inside circular plots (10 cm radius) centred on saplings of *Diplostegium venezuelense* (black bars) and on random points (grey bars) in forest island borders (A) and adjacent páramos (B) at 3440 m, La Aguada, Sierra Nevada de Merida, Venezuela. Error bars indicate standard error. Species were ordered in terms of their cover in the random plots. Significant differences (permanova, $n=10$, $\alpha=0.05$) in the cover of each species between seedling-centred plots and random centred plots are indicated by asterisk. Cal eff, *Calamagrostis effusa*; N. vasc, mosses and lichens; Cha lin, *Chaetolepis lindeniana*; Lyc cla, *Lycopodium clavatum*; Per pros, *Pernettya prostrata*; Hes obt, *Hesperomeles obtusifolia*; Rui atr, *Ruilopezia atropurpurea*; Hyp lar, *Hypericum laricifolium*; Hyp car, *Hypericum caracasenum*; Dis emp, *Disterigma empetrifolium*; Jam imb, *Jamesonia imbricata*; Luc sp., *Lucilia* sp.

(A) Forest Border



(B) Páramo

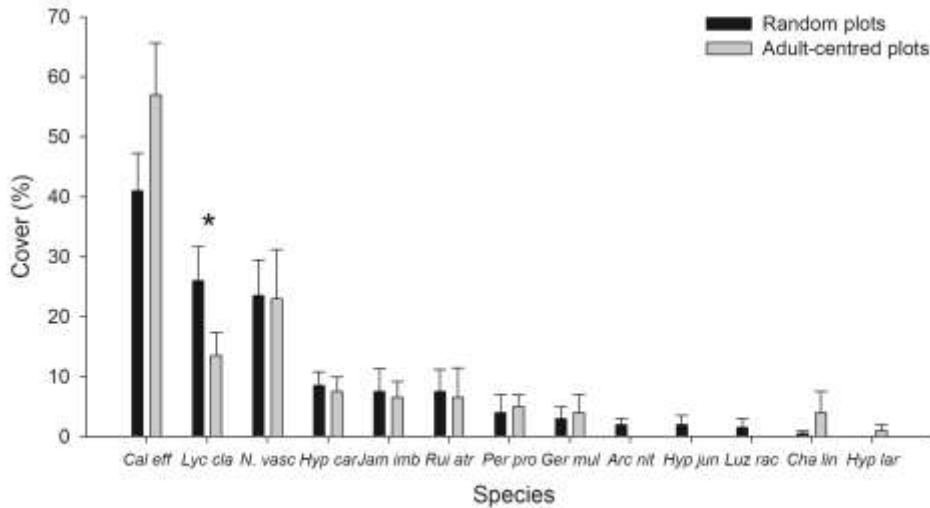


Figure 5. Average plant species cover inside circular plots (25 cm radius) centred on adults of *Diplostephium venezuelense* (black bars) and on random points (grey bars) in forest island borders (A) and adjacent páramos (B) at 3440 m, La Aguada, Sierra Nevada de Merida, Venezuela. Error bars indicate standard error. Species were ordered in terms of their cover in the random plots. Significant differences (permanova, $n=10$, $\alpha=0.05$) in the cover of each species between adult centred and random centred plots are indicated by asterisk. Cal eff, *Calamagrostis effusa*; N.vasc, mosses and lichens; Cha lin: *Chaetolepis lindeniana*; Lyc cla: *Lycopodium clavatum*; Hyp lar, *Hypericum laricifolium*; Hes obt, *Hesperomeles obtusifolia*; Per pros, *Pernettya prostrata*; Dis emp, *Disterigma empetrifolium*; Hyp car, *Hypericum caracasenum*; Vac mer, *Vaccinium meridionale*; Arc nit, *Arcytophyllum nitidum*; Jam imb, *Jamesonia imbricata*; Rui atr, *Ruilopezia atropurpurea*; Ger mul, *Geranium multiceps*; Hyp jun, *Hypericum juniperinum*; Luz rac, *Luzula racemosa*.

Discussion

More than 50 tree and shrub species coexist along the forest-páramo transition zone in the Venezuelan Andes, but very few tree species can grow above the limit of continuous forest (González et al. 2011; Ramirez et al. 2009). Of these, *Diplostephium venezuelense* has been reported as the most abundant tree in forest borders and adjacent páramo in several sites in the Sierra Nevada de Mérida (Ramirez et al. 2009; Rodriguez et al. 2011).

Our results in this study indicate that *D. venezuelense* has the ability to establish and reach adult sizes in the lower páramo adjacent to the forest line. At higher elevations it is more abundant along the edge of forest islands, being still able to establish in adjacent páramo, but with lower densities. Research in our study site (Puentes 2010) and in Ecuador (Bader et al. 2007) suggests that the ability of *Diplostephium* to establish above the treeline could be in part associated with the marked resistance of its saplings to freezing temperatures (through super-cooling mechanisms) and to the high radiation levels found in the open páramo. Hence, its adaptive characteristics, distribution patterns and dominance in the upper treeline suggest that this species could play an important role in scenarios of upward displacement of the forest line as a response to climate change.

At a plant neighbourhood scale, our results indicate that the establishment patterns of *D. venezuelense* in forest borders and open páramo are not spatially random. We found evidence of strong local spatial aggregation of saplings, with significantly higher conspecific densities when comparing their neighbourhood with average densities in these environments. However, we found no evidence of conspecific aggregation under adults growing in the páramo. This suggests that *D. venezuelense* adults in the páramo do not act as nurse plants for their own seedlings. To explore this hypothesis, it would be interesting to establish spatial distribution maps of individuals of different size classes at intermediate spatial scales (beyond the local neighbourhood of saplings and adults), quantifying their spatial relations through spatial covariance or autocorrelation functions (e.g. see Llambí et al. 2004).

Moreover, we found a significant spatial association between saplings and the cover of small rocks at the surface (Table 1), a phenomenon that has also been reported by other authors at temperate treelines (e.g. Wardle and Coleman 1992; Germino and Smith

2002; Mellmann-Brown 2005). The presence of boulders / stones could induce more favourable micro-climatic conditions by increasing minimum temperatures in their neighbourhood (see evidence from the high Andean páramo in Smith 1977 and Pfitsh 1988) or could be associated with higher soil organic matter or soil moisture under them (e.g. Wardle and Coleman 1992). Interestingly, although average rock cover was also higher in the neighbourhood of adults than the environmental average, the difference in cover was not statistically significant in this case. This probably indicates that saplings were mainly associated with rocks at a very local scale, the association being less evident in the larger sampling plots used for adults. However, we cannot rule out the alternative hypothesis that these microsites favour seedling establishment but are not so favourable once the plants attain larger sizes.

Local plant community structure around saplings in forest borders and adjacent páramo was significantly different from the plant community in random locations. The fern *L. clavatum* and two common sclerophyllous páramo shrubs (*D. empetrifolium* and *H. laricifolium*) were significantly overrepresented around saplings. This spatial association could be the result of these species sharing local habitat requirements with the saplings of *D. venezuelense*, but could also be linked with a facilitation effect on their establishment. While *L. clavatum* occurred in very dense patches, *D. empetrifolium* occurred as a low and compact prostrate shrub with profuse ramification, resembling a cushion. Hence, they could act as seed traps and/or could contribute to create more favourable microhabitats, protecting saplings from water stress, excess radiation or herbivores (see Grau et al. 2012). The widely distributed *H. laricifolium* has also been found to be spatially associated with saplings of one of the few tree species (*Berberis discolor* Turcz.) that is able to colonise old fields in advanced seral stages within forests at the upper treeline in another locality in the Sierra Nevada de Mérida (Jimenez et al. 2011). At higher elevations, in the super-páramo, Cáceres (2011) found that *H. laricifolium* could induce more favourable environmental conditions under its low and compact crown, reducing incident radiation and damping oscillations in air temperature and relative humidity and showing higher soil organic matter and soil water contents in its neighbourhood than adjacent open areas.

We also found clear evidence of a negative spatial relation between *D. venezuelense* saplings and the local cover of mosses and lichens. Interestingly, research on a dominant treeline species in central Argentina (*Polylepis australis* Bitt.) also showed a

negative association between seedlings and moss cover, which the authors attributed to the production of allelopathic substances by mosses (Enrico et al. 2004).

In the case of adult *D. venezuelense* individuals, while the negative spatial relationship found between saplings and non-vascular species was maintained, the positive association found between saplings and *L. clavatum* turned into a negative spatial relationship with adults (Figure 5). This reversal in spatial relationships with a change in the relative size of interacting plants could reflect a shift in the net balance of the interaction from facilitation (favouring sapling establishment) to competition (reducing fern growth under the canopy of the adult tree, see Callaway 2007).

In addition, there were several species with relatively low abundances which were only sampled in random micro-plots, but were not found in the local neighbourhood of *D. venezuelense* individuals. This suggests that *D. venezuelense* individuals interact with a sub-set of the overall plant community in their immediate neighbourhood; however, a larger sampling effort would be required to establish with more certainty the local spatial relationships of *D. venezuelense* with rare species in particular, and with conspecifics and heterospecifics in general.

Interestingly, we found no spatial association between adults established in the páramo and other forest tree species. Hence, our results indicate that individuals of this dominant species do not facilitate the colonisation of other trees above the forest-line, contrary to what has been reported for tree species in temperate treelines (e.g. Camarero et al. 2000; Germino et al. 2002; Maher et al. 2005; Becker 2005). We can hypothesise that the relatively open crown of *D. venezuelense* individuals does not offer enough cover to modify the local microenvironment as much as the lower and more compact crown of páramo shrubs like *Hypericum laricifolium* or *krummholz* trees in many temperate treelines.

Summing up, the distribution of *D. venezuelense* at a landscape scale (across the treeline ecotone) suggests that this species could have the potential to act as a pivotal species in forest expansion scenarios. However, our results at the plant-neighbourhood scale do not support the hypothesis that *D. venezuelense* adults established in the páramo, in turn, promote the establishment above the forest line of other trees. This suggests that forest expansion in climate change scenarios could require the consolidation of colonisation fronts along the edge of continuous forests. Such advance of the treeline could allow for the expansion of the more favourable environmental conditions associated with a continuous canopy cover, including lower incident radiation,

higher air and soil humidity and lower temperature amplitudes (see Bader et al. 2007a; Cierjacks et al. 2007; Rada et al. 2011). Finally, our results indicate that the establishment of *D. venezuelense* above the treeline can be modulated by complex local interactions with other species (both positive and negative). This supports the idea that autogenic plant-plant interactions need to be considered for interpreting the processes that control treeline dynamics (Smith et al. 2009; Grau et al. 2012).

Even so, the results presented here constitute a snap-shot at a single site of processes operating over large spatio-temporal scales. For a more mechanistic understanding of the processes controlling the dynamics of the tropical forest-line further research is needed on role played by environmental drivers and plant-plant interactions at different scales. Spatial pattern analyses need to be complemented by long-term studies across several localities in the highland tropics (Young and Leon 2007), including information on tree age-size relationships. In our view, this research should place particular emphasis on the processes affecting the critical stages of seedling establishment (Holtmeier and Broll 2007; Smith et al. 2009; Bansal et al. 2011; Grau et al. 2012), integrating different approaches in the analysis (e.g. ecophysiology, manipulative experiments, modelling).

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