# Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest line

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## Abstract

**Questions:** Do local plant–plant interactions and facilitation play an important role in vegetation dynamics after disturbance in the high tropical Andes? In particular, does the dominant shrub *Baccharis prunifolia* have an effect on microclimate and local vegetation structure within old-fields at the upper forest line? Does distance from the border of the surrounding forests also influence community structure within fallow plots? Is there an interaction between facilitation and edge effects on vegetation regeneration?

**Location:** Gavidia Valley, Sierra Nevada de Mérida, Venezuela.

**Methods:** Plant cover, species richness and community structure were compared in circular micro-plots placed under the canopy of *B. prunifolia* shrubs and in open areas (12 micro-plots in each case) both near and far from the forest border within two 10–12 yr successional plots at 3400 m a.s.l. (a total of 96 micro-plots). Additionally, topsoil temperature was monitored for 1 mo in the four situations under study.

**Results:** Average and maximum temperature and temperature amplitudes were lower under the canopy of *B. prunifolia* shrubs than in open areas; this effect being more marked far from the forest edge. Species richness, vegetation cover and the density of dominant forest trees were higher under the shrubs' canopy than in the inter-shrub spaces. The proximity to the edge of the surrounding forest also had a positive effect on species richness, with no significant interaction with the local sampling situation (under shrub vs outside).

**Conclusions:** Our results suggest that both facilitation and edge effects influence the effectiveness of vegetation regeneration within old-fields in the high tropical Andes. Consequently, these processes should be considered for interpreting vegetation dynamics in environmental change scenarios at the tropical mountain tree line and for the design of ecological restoration strategies in these high-diversity ecotones, which have been subjected to large-scale anthropogenic transformations in recent decades.

## Introduction

Secondary succession is a key aspect of vegetation dynamics after human disturbance, with a direct impact on the regeneration of biodiversity and ecosystem functioning (Myster 2004a). The outcome of the successional process is determined by the interaction of several factors, both biotic (e.g. regional species pool, soil seed bank and propagule sources, species interactions) and abiotic (e.g. nutrient availability, temperature regimes, radiation intensity; Guariguata & Ostertag 2001). Disturbance from agricultural activities, one of the main factors causing the loss of forested areas in the tropics, has been shown to influence these factors to varied extents, creating barriers for the reestablishment of forest species in old-fields (Cramer et al. 2008; Baeten et al. 2010). The clearance of vegetation results in an increase of incident radiation and temperature (Duncan & Duncan 2000), while agricultural practices can have lasting effects on soil nutrient content and the soil seed bank (Cubina & Aide 2001; Guariguata & Ostertag

2001). The degree of landscape fragmentation can also influence variables that change with the distance to the edge of surrounding woodlands, including microclimate and propagule pressure (Duncan & Duncan 2000; Myster 2004b).

Another set of key processes determining the speed and direction of the successional process are facilitative/nurse plant interactions (Myster 2004a; Padilla & Pugnaire 2006; Callaway 2007). The main mechanism behind facilitation is the modification of micro-environmental conditions under the canopy of the facilitator species, which can result in an enhancement of the physiological performance of the plants growing under their influence (Pugnaire et al. 1996; Holmgren et al. 1997; Ramírez et al. 2015). Plants may also exert a facilitation effect through other processes, such as litter accumulation (Facelli & Pickett 1991) or by attracting seed dispersing animals, reducing the effect that the distance to the forest edge has on dispersal (Duncan & Chapman 1999).

The results of these positive interactions can be useful when designing ecological restoration practices (Padilla & Pugnaire 2006), and there are an increasing number of examples of the application of facilitation in this regard (Gómez-Aparicio 2009; Gómez-Ruiz et al. 2013). Shrubs have been suggested as a promising tool to accelerate secondary succession and tree establishment, because of the combination of the beneficial effects they exert on abiotic conditions under their canopy and their reduced detrimental effects due to competition: they are not as strong competitors as herbaceous species for underground resources, and not as strong competitors as trees for above-ground resources (Padilla & Pugnaire 2006; López et al. 2007; Gómez-Aparicio 2009).

Most studies that document an important role of facilitation by shrubs and other life forms in mature or successional communities, come from high alpine and arid/mediterranean environments (e.g. Holzapfel & Mahall 1999; Castro et al. 2004; Larrea-Alcázar et al. 2005; Padilla & Pugnaire 2006; Cuevas et al. 2013; Cáceres et al. 2015). However, in the more mesic conditions of tropical mountain forests this issue remains largely unexplored. Even though in these humid forests water availability could be less limiting for plant growth, agricultural activities result in an increase in incident radiation, temperature amplitudes and a reduction in soil moisture (Duncan & Duncan 2000), affecting the regeneration of tree species adapted to conditions within closed forests (Holmgren & Scheffer 2010). This effect could be particularly important at the tree-line ecotone, given the high radiation levels and daily temperature amplitudes that characterize high tropical mountains, which have been shown to hinder tree colonization in open alpine ecosystems just above continuous forests (Bader et al. 2007). Upper forest-line species have

also been found to establish preferentially under the canopy of small sclerophyllous shrubs above the tree line (Llambí et al. 2013).

In the case of the high tropical Andes, the diverse ecosystems at the tree-line ecotone are subjected to widespread anthropogenic transformations, including the opening of the forest canopy for cultivation or the creation of secondary pastures, resulting in severe limitations for tree regeneration, even after several decades (Kok et al. 1995; Velasco-Linares & Vargas-Ríos 2008; González et al. 2011). Therefore, studies that contribute to understanding the mechanisms behind forest regeneration are critical for the design of ecological restoration efforts. Here, we explore the importance of facilitation by shrubs and the effects of the distance to the forest border in old-fields at the upper forest line in the Venezuelan Andes, as a contribution to understanding the processes that influence vegetation dynamics in tropical mountain forests.

Given that the upper vegetation stratum of fallow plots in our study area is strongly dominated by the sclerophyllous shrub *Baccharis prunifolia* and that agricultural disturbance creates a landscape mosaic in which old-fields are still surrounded by dense forest relicts, we evaluated the following hypothesis: (1) within the fallow plots, the areas under the shrub's canopy will present a different community structure compared to areas outside, showing higher plant cover, species richness and abundance of seedlings/saplings of dominant woody species from the adjacent mature forests; (2) the shrub's canopy will generate more favourable microclimatic conditions, inducing lower maximum temperatures and temperature amplitudes; and (3) these positive effects of shrubs should be more evident in areas within old-fields adjacent to the forest border.

## Methods

### Study area

The study area is located in Las Piñuelas valley, one of the two main valleys of Gavidia, Sierra Nevada National Park, in Mérida, Venezuela (8°35'–8°45' N, 70°52'–70°57' W). Altitude in the area ranges from 3200 m a.s.l. to 4300 m a.s.l. Climate is characterized by a unimodal precipitation pattern with a distinct dry season between December and March (7% of total precipitation). Mean annual precipitation is 1300 mm and mean temperature is 8 °C (Sarmiento et al. 2003). During the dry season soil water content within fallow fields can fall below the permanent wilting point, and solar radiation is very high, with maximum daily values of 28 MJ·m$^{-2}$·d$^{-1}$ (Sarmiento 2000). Soils are sandy loam, with low pH and low mineral nutrient content and high organic matter content (Abreu et al. 2009).

Traditional long fallow agriculture was practiced in the area for more than 70 yr, and is now being abandoned.

Periods of 1 to 4 yr of commercial potato production in small plots were followed by a period during which the plots were left under succession-regeneration (between 4 and >10 yr). These old-fields were and are still used for extensive cattle grazing (grazing loads below 0.1 animal unit·ha$^{-1}$). The system has resulted in a mosaic landscape of plots in different successional stages surrounded by relictual high Andean forest (also known as 'subpáramos' or 'páramo' forests; Monasterio 1980) and páramos along the upper forest line (Sarmiento et al. 1993, 2002).

Previous studies have shown that secondary succession is characterized by the initial colonization of the exotic herb *Rumex acetosella*, followed by forbs which dominate the intermediate stages (e.g. *Lupinus meridanus*), and finally a shrub-rosette community, dominated by shrubs such as *Baccharis prunifolia* and *Hypericum laricifolium* and the stem rosette *Espeletia schultzii*, with very limited colonization of the dominant forest tree species (Sarmiento et al. 2003). The dominant woody species in the forests include *Berberis discolor*, *Vaccinium floribundum*, *Chaetolepis lindeniana*, *Vallea stipularis* and *Myrsine dependens,* forming dense vegetation with canopy heights between 4–10 m.

### Study sites

Sampling took place during the wet season, between May and Jul 2013. Using a detailed database established in 1990 with information on the location and use history of all plots in the area (Smith 1995; updated to 2012), two fallow fields were chosen according to several criteria: (a) fallow times of 10–12 yr; (b) a mid-position on the valley slopes to ensure that plots were surrounded by forest and not by the open vegetation found at higher elevations, and to avoid the stronger anthropogenic pressure at lower elevations (Sarmiento et al. 2003); and (c) plot size (>0.25 ha) large enough to allow for a clear distinction between border and 'far from the border' areas. Both sites were separated by ca. 400 m, had a SW orientation and were located at 3400–3450 m a.s.l. In Gavidia, 10–12-yr fallow plots are dominated by shrubs (42% of relative cover). The species with highest cover in these seral stages are the shrubs *B. prunifolia* (reaching an average of 23.5% of relative cover in 12-yr fallow plots) and *H. laricifolium* (7.6%), as well as the small rosette herb *Noticastrum marginatum* (14.3%) and the stem rosette *E. schultzii* (9.3%; Sarmiento et al. 2003).

### Vegetation sampling

In each site, the sampling design consisted of two fixed, orthogonal treatments, with two levels each, and 12 replicates in each level. The two levels of the *Facilitation*

treatment were 'canopy' (C), under the canopy of *B. prunifolia*, and 'open' (O), outside of the canopy. The two levels of the *Border* treatment were: (a) 'near' the border (N), 1–2 m from the border of the remnant forest surrounding the plots; and (b) 'far' (F), further into the fallow field, as far from the border as the plot shape permitted (typically between 5–20 m from the edge).

For both the canopy-near and canopy-far situations, 12 individuals of *B. prunifolia* were randomly chosen and marked, among those meeting the minimum size requirements of 1-m height and at least 40-cm radius. A 1-m diameter circular sampling micro-plot was placed on the ground, centred on each replicate individual. In the case of the open-near and open-far situations, the micro-plots were placed on the ground randomly, always outside the influence of the shrub's canopy. Within the micro-plots, the presence of all vascular plant species and the density of seedlings/saplings of all woody species were recorded. To measure the cover of each species, as well as litter, bare ground and bare rock (superficial scree), the point-quadrat method was employed (Greig-Smith 1983), and 30 pin hits were made within each micro-plot.

### Temperature recording

Temperature was recorded at Site 1 in each of the four situations. Four HOBO Onset Tidbit v 2 (Onset Computer Corp., Bourne, MA, US) temperature loggers were employed, located under the canopy of *B. prunifolia* and in open areas, both far from and near to the border. Loggers were buried in the soil at a depth of 3 cm, within the A horizon. Temperature was recorded every 15 min during a period of 1 mo (Jul 2013).

### Data analysis

All analyses were performed using PERMANOVA + for PRIMER 6.0 (Anderson et al. 2008), a robust technique which makes no explicit assumption about the distribution of the original variables (e.g. normality), something important when analysing factorial designs. The pseudo-*F* statistic was calculated based on 9999 permutations of the Bray-Curtis distance matrix between samples, and a probability of type-I error of 5% was used. Figures were prepared with SigmaPlot (v 13.0; Systat Software, San Jose, CA, US) except for Fig. 2, which was prepared with PRIMER.

For each site, species richness was estimated both for the entire site and for each situation. Rank abundance diagrams were prepared based on the mean percentage cover of each species. To evaluate whether there was a significant difference among situations in terms of species richness and the cover of different substrate types (bare

ground, bare rock and litter), two-way PERMANOVA were performed, using *Facilitation* and *Border* as fixed factors.

Principal coordinates analysis (PCO) ordinations were constructed from a dissimilarity matrix based on the Bray-Curtis index, and using square root-transformed data. A two-way PERMANOVA was performed on this matrix (Anderson et al. 2008) to evaluate differences in the community structure among situations (Facilitation and Border effects). When the interaction term was found to be significant, further pair-wise tests were performed (adjusting the probability of type-I error to 1%).

## Results

### Species richness and plant abundance patterns

A total of 75 species, belonging to 31 families, were recorded in the two fallow plots studied. At Site 1, 53 species were recorded, 12 of which were only found in this site. At Site 2, 63 species were recorded, 22 unique to this site. The best represented families were Asteraceae (27% of all species) and Poaceae (13%).

At both sites, species richness and vegetation cover were highest near the border and under the canopy, and lowest far from the border in the open area (Table 1).

The patterns for species richness were confirmed when PERMANOVA tests were performed. At both sites, the interaction between the two factors (local situation and distance to the forest edge) was not significant, and the average species richness under the canopy of *B. prunifolia* was significantly higher than that in open areas (Site 1: Pperm = 0.0161; Site 2: Pperm = 0.0323). Similarly, there was a significant difference in richness between the micro-plots near and far from the border (Site 1: Pperm = 0.0351; Site 2: 0.0133).

With respect to total vegetation cover, at Site 1 there was a significant difference between the area under the canopy of *B. prunifolia* and the open areas (Pperm = 0.0001), but no significant difference between near and far from the border (Pperm = 0.1053). At Site 2,

the interaction between factors was significant (Pperm = 0.0209), and pair-wise tests show a significant difference in total vegetation cover between the area under the canopy of *B. prunifolia* and the open areas only near the border to the forest (Pperm = 0.0001).

Rank abundance diagrams are presented for each situation under study, at both sites (Fig. 1). At Site 1, in general, far from the border the differences in abundance between the open areas and under the canopy of *B. prunifolia* tended to be larger for many species than the differences near the border of the forest, while the opposite pattern was found at Site 2. These patterns are consistent with the multivariate analyses (see Fig. 2).

Near the border of the forest, some species were more abundant under the canopy than in the open areas (e.g. *Bromus carinatus*, *Acaena elongata* and *Galium hypocarpium*), while others were more abundant in the open areas than under the canopy of the shrub (e.g. *H. laricifolium* and *Agrostis trichoides*). On the other hand, species such as *R. acetosella*, *Gaultheria myrsinoides* and mosses displayed opposite patterns of abundance between sites, i.e. they were more abundant under the canopy at one site, but more abundant in the open areas at the other site (Fig. 1).

Far from the border, at both sites, species such as *A. elongata*, *G. chamaense*, *A. trichoides* and *Orthrosanthus chimboracensis* had higher cover values under the canopy than in the open areas, while *T. irazuense* and *N. marginatum* showed the opposite pattern. Finally, other species, such as *R. acetosella* and *S. elatior* showed differences in abundance between the situations under the canopy and open area at one site, but no differences at the other site (Fig. 1).

### Multivariate analysis of community structure

At Site 1, a significant interaction between canopy and distance to the border was detected (Pperm = 0.0189), confirming the patterns seen in the PCO ordination of the micro-plots (Fig. 2a). Far from the border, the communities

**Table 1.** Total and mean species richness, and mean total cover, recorded in circular micro-plots (0.78 m$^2$) placed under the canopy of *B. prunifolia* and in the open area, and near and far from the border of two fallow plots in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela). For each situation, replicates number is 12. Total richness was calculated considering all replicates for a given situation. Mean values are presented with SE.

| | Site 1 | | | Site 2 | | |
|---|---|---|---|---|---|---|
| | Total Richness | Mean Richness | Mean total Cover | Total Richness | Mean Richness | Mean total Cover |
| Near Border | | | | | | |
| Under Canopy | 40 | 11.3 ± 0.5 | 108.8 ± 9.9 | 50 | 11.8 ± 0.7 | 127.1 ± 9.1 |
| Open Area | 35 | 9.5 ± 0.5 | 84.4 ± 8.1 | 37 | 8.6 ± 0.6 | 71.8 ± 5.9 |
| Far From Border | | | | | | |
| Under Canopy | 30 | 9.5 ± 0.3 | 108.1 ± 6.9 | 29 | 8.4 ± 0.4 | 103.6 ± 5.9 |
| Open Area | 27 | 8.3 ± 0.5 | 59.1 ± 4.4 | 21 | 8.3 ± 0.3 | 91.8 ± 13.8 |
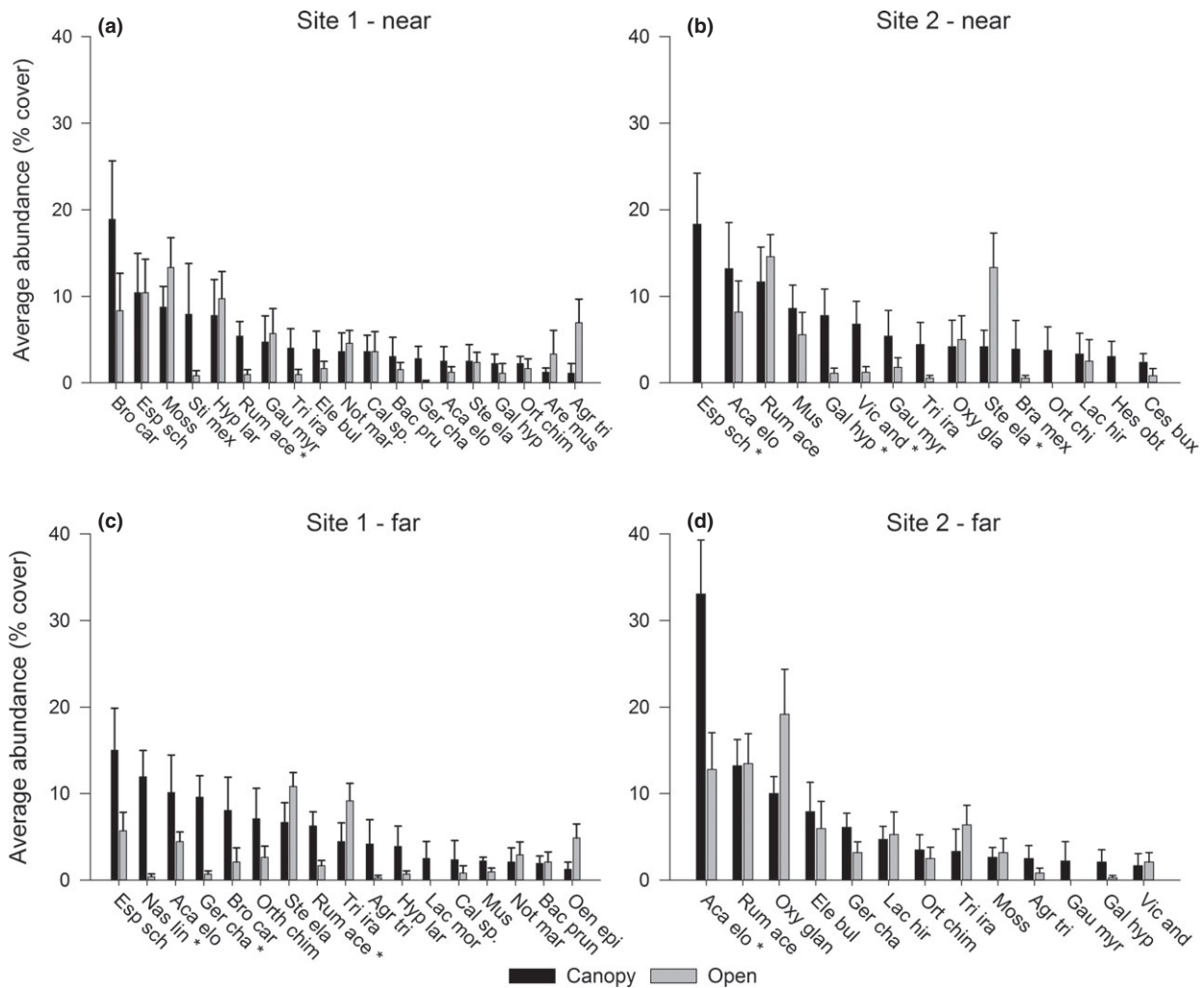
**Fig. 1.** Rank abundance diagrams of average species cover for each species in circular micro-plots (0.78 m$^2$) placed near and far from the border of two fallow plots in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela). Species with average cover <2% are not shown. Asterisks mark species with significant differences in percentage cover ($P < 0.05$). Error bars show SE.

under *B. prunifolia* and outside of its canopy differed significantly (Pperm = 0.0006), while near the border there was no significant difference (Pperm = 0.0900).

At Site 2, an interaction between the factors was also detected (Pperm = 0.0056). However, contrary to the results obtained at Site 1, the community under the canopy of *B. prunifolia* and the community of the open area did not differ far from the border (Pperm = 0.0971), but significant differences were detected near the border of the forest (Pperm = 0.0009).

At both sites, under the canopy of *B. prunifolia* the community far from the border was significantly different from that near the border (Pperm = 0.0067 and Pperm = 0.0001, respectively, for Site 1 and 2), and the same pattern was found in the open areas (Pperm = 0.0002 and Pperm = 0.0001, respectively).

## Patterns of woody species density

A total of six woody species typically found in the adjacent forest were recorded in the sampling micro-plots as seedlings and/or saplings. Density of woody species was low at both sites, with Site 1 displaying higher values than Site 2. The highest density was reached by *H. laricifolium* in the open area near the border at Site 1 (2.24 individuals·m$^{-2}$). When considering the tree/shrub species that are abundant in the surrounding forest, the highest density value was 0.53 individuals·m$^{-2}$, recorded at Site 1 for *B. discolor* present under the canopy of *B. prunifolia*, near the border. In the open area of the fallow plots, this species reached densities of 0.11 individuals·m$^{-2}$. At Site 2 it was recorded solely under the canopy of the shrub (0.43 and 0.21 individuals·m$^{-2}$,
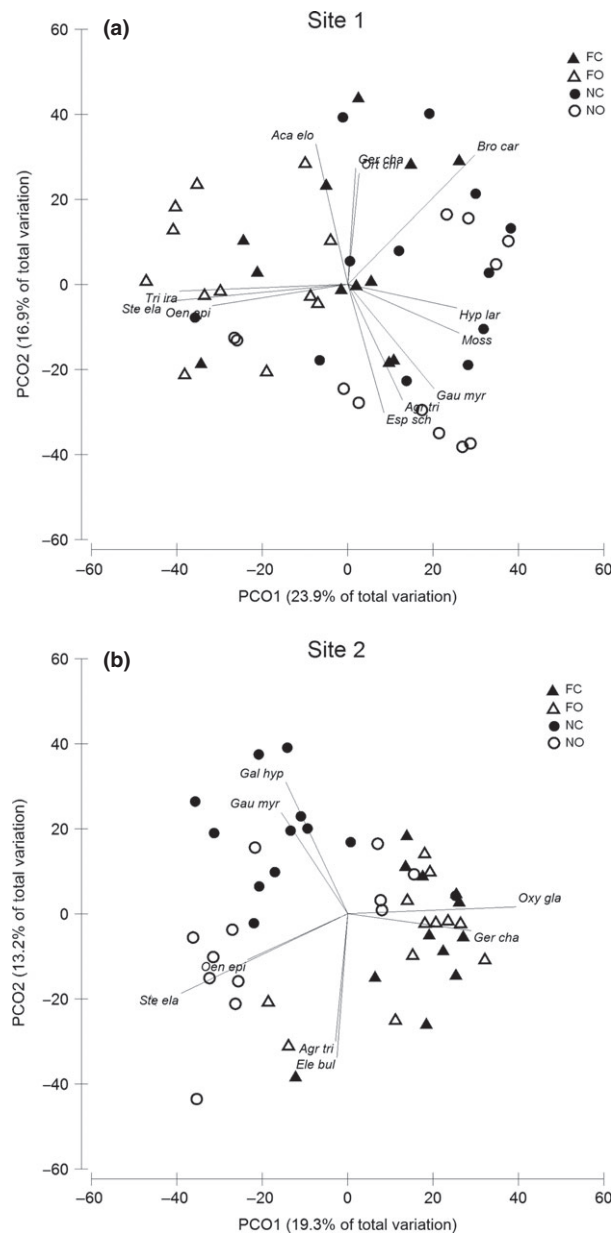
Fig. 2. Principal coordinates analysis ordination (PCO) of plant species cover in circular micro-plots (0.78 m²) placed under the canopy of *B. prunifolia* and in the open area, and near and far from the border of two fallow plots in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela). Vectors show species with a Pearson correlation with the ordination axes >0.5. FC, far from border, under canopy; FO, far from the border, open area; NC, near the border, under canopy; NO, near the border, open area.

near and far from the border, respectively). Another tree species from the forest, *Vallea stipularis*, was found at Site 1 only under the canopy of *B. prunifolia*, with a density of 0.43 individuals·m⁻² near the border of the forest, and 0.1 individuals·m⁻² far from the border. At Site 2 it
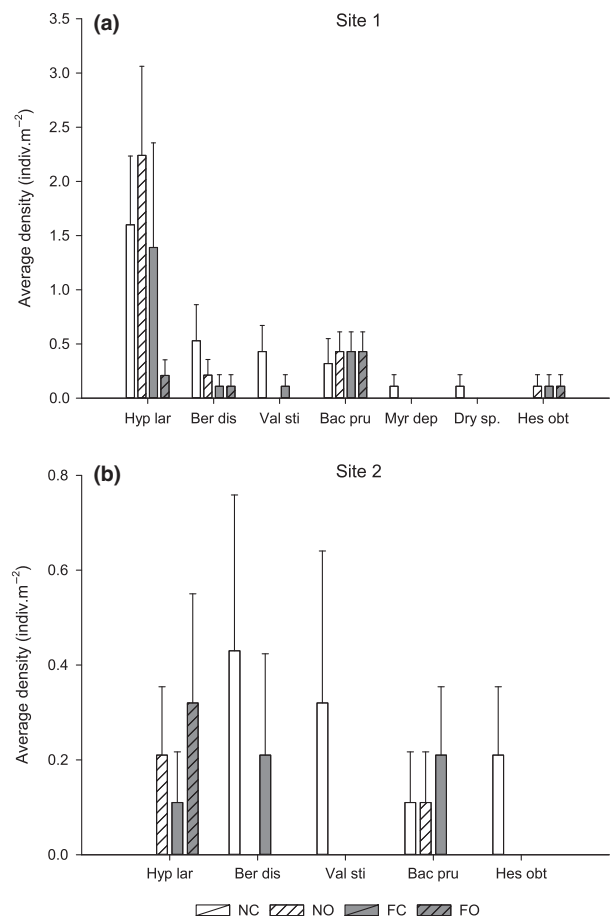
Fig. 3. Average density of woody species recorded in circular micro-plots (0.78 m²) placed under the canopy of *B. prunifolia* and in the open area, and near and far from the border of two fallow plots in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela). NC, near the border, under canopy; NO, near the border, open area; FC, far from border, under canopy; FO, far from the border, open area. Error bars show SE. Note the difference in the scale of the y-axis.

was recorded solely under the canopy near the border (0.32 individuals·m⁻²; Fig. 3).

## Abiotic variables

### Temperature

Average temperature and absolute maxima over the entire measurement period were lowest under the canopy of *B. prunifolia*, close to the border from the woodland, and highest in the open space. The thermal amplitude (difference between absolute minimum and maximum temperature) was lowest under the canopy and near the border, and highest in the open space far from the border. The other two situations under study had intermediate values (Table 2).

**Table 2.** Summary of temperature values (°C) recorded over a 1-mo period under the canopy of *B. prunifolia* and in the open area, near and far from the border of the forest, in a fallow plot in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela).

|  | Mean Temperature | Mean Minimum Temperature | Lowest Temperature | Mean Maximum Temperature | Highest Temperature |
|---|---|---|---|---|---|
| **Near Border** |  |  |  |  |  |
| Under Canopy | 11.5 | 7.6 | 3.8 | 20.2 | 29.9 |
| Open Area | 13.6 | 7.9 | 5.2 | 28.2 | 47.3 |
| **Far From Border** |  |  |  |  |  |
| Under Canopy | 12.0 | 7.3 | 3.9 | 23.3 | 36.7 |
| Open Area | 13.4 | 6.2 | 2.3 | 31.8 | 49.6 |

### Bare ground, bare rock and litter

Bare ground and rock cover was significantly higher in the open area of the fallow field compared to under the canopy of *B. prunifolia* (Pperm bare ground = 0.001 at both sites; Pperm bare rock = 0.0455 at Site 1 and 0.0041 at Site 2). Furthermore, at Site 1 there was no significant difference between near and far from the border, but at Site 2 their cover was significantly higher near to the border compared to far from the border (Pperm bare ground = 0.0371; Pperm bare rock = 0.0482; Fig. 4).

Regarding litter cover, there were no significant differences either between the area under the canopy of *B. prunifolia* and the open area of the fallow field, or between near and far from the border to the forest. This result was consistent at both sites.

## Discussion

The results of this study suggest that in old-fields at the tropical forest line, both facilitation by dominant shrubs and edge effects can influence vegetation regeneration, ameliorating micro-environmental conditions, increasing plant cover and richness and favouring the establishment of seedlings/samplings of woody species from adjacent mature forests. Thus, the interplay of these processes should be explicitly incorporated into the design of ecological restoration strategies in these diverse ecosystems facing increasing pressure from anthropogenic transformation (Young & León 2007; Velasco-Linares & Vargas-Ríos 2008).

### Patterns of species richness and abundance

Total species richness and average richness and cover were higher under the canopy of the shrub than in open areas of the fallow plots, and this pattern was found consistently at both study sites. Moreover, 12 species were only found under the shrub canopy (although because of their relatively low cover this pattern should be interpreted with caution, as they could have been missed in open areas due to insufficient replication). These findings are in agreement with those reported by other studies evaluating facilitation processes by shrubs in alpine and arid communities (Castro et al. 2004; Gómez-Aparicio et al. 2004; Larrea-Alcázar et al. 2005; Gómez-Aparicio 2009; Cáceres et al. 2015), as well as research exploring the potential of some species to act as nurses in old-fields where forests are reestablishing (Holl et al. 2000).

These results could be due to several mechanisms that might be acting simultaneously, such as microclimate amelioration, protection from herbivores and soil modifications induced by the nurse plant. Furthermore, the shrub could attract seed-dispersing animals (Duncan & Chapman 1999; Holl 2002) or act as a trap for wind-dispersed seeds (López et al. 2007; Cuevas et al. 2013). This last hypothesis is supported by the tendency for a higher total density of many forest woody species (e.g. *V. stipularis*, *B. discolor*) found here under the shrub canopy near the forest border in both studied plots. Nevertheless, all of these processes would result in a higher richness and cover under the shrub canopy, which can be important from an ecological restoration perspective. Interestingly, the most abundant exotic species, *R. acetosella*, showed positive association with *B. prunifolia* at one site, but negative at the second site. Positive effects of species of *Baccharis* on the performance and establishment of exotic species have been reported in other systems, where protection from herbivory has been the suggested mechanism (Cushman et al. 2011; Ganade et al. 2011).

Total species richness was higher near the border of the fallow field than far from it, and this pattern was consistent at both sites. Several studies have documented how the density and diversity of species in the seed rain and seed bank decrease as distance from the edge of the forest increases (e.g. Cubina & Aide 2001; Vargas-Ríos 2007b). This could also be linked with the milder environmental conditions found close to the forest than far from it.

The resulting pattern of species establishment could then be the outcome of the interaction between propagule availability and micro-environmental conditions influenced by the presence or absence of the facilitating shrub, as suggested by Meiners et al. (2002). On the other hand, studies conducted in the Bolivian Andes that also
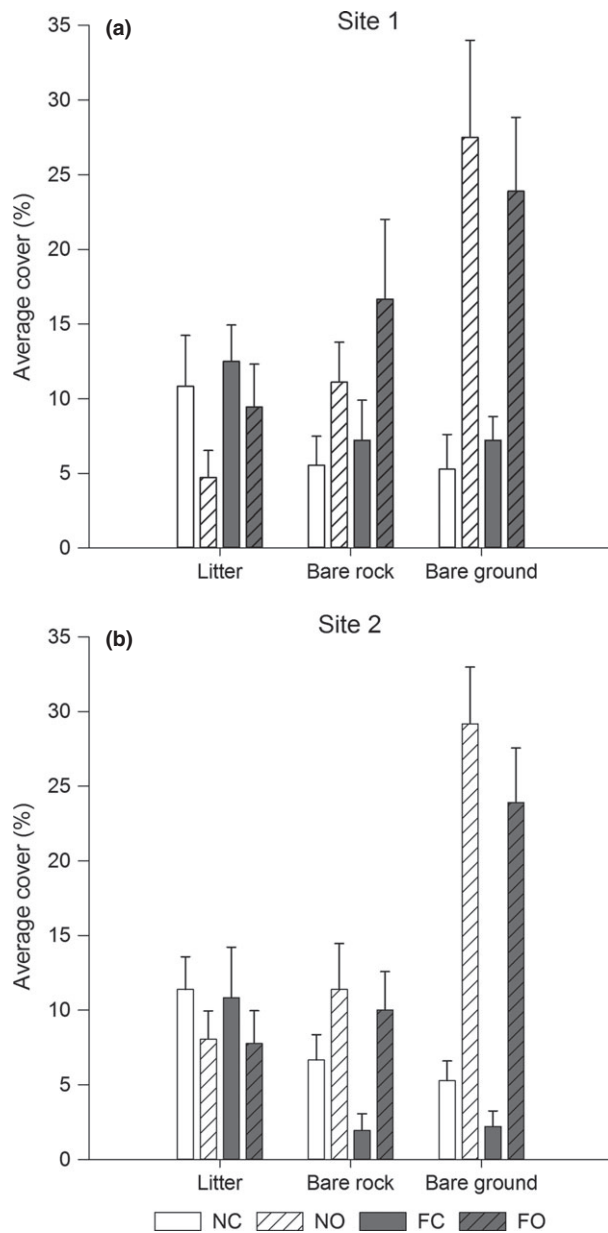
**Fig. 4.** Average cover of litter, bare rock and bare ground under the canopy of *B. prunifolia* and in the open area, and near and far from the border of two fallow plots in the Gavidia Valley, Sierra Nevada de Mérida (Venezuela). NC: near the border, under canopy. NO, near the border, open area; FC, far from border, under canopy; FO, far from the border, open area. Error bars show SE.

evaluated the effect of the distance to the forest on secondary plant communities, found higher basal area and species richness away from the edge (Lippok et al. 2013a).

At Site 1, there is a difference in community structure between the area under *B. prunifolia* and the open area of the fallow plots, and this difference is larger far from the border than close to it, as shown by the

ordination plots. This suggests that the facilitation process becomes more important as the distance to the forest increases.

However, at Site 2 differences between the community under the canopy of *B. prunifolia* and in the open area of the fallow plot were larger near the forest border than far from it, and a similar pattern was detected in terms of total vegetation cover. This may be due to the relatively high cover of the shrub *A. elongata* and the forb *Oxylobus glanduliferus* at this site. These two species could have had a homogenizing effect on the micro-environmental conditions across the plot, possibly overriding the potential facilitation effect of our focal shrub. The presence of *A. elongata* could also be an indicator of a stronger effect of grazing, as this species was effectively dispersed through cattle in the area (Molinillo & Farji-Brener 1993). Nevertheless, this supports the idea that species dispersal patterns and spatial heterogeneity at a landscape scale can not only affect the particular pathways of succession (Sarmiento et al. 2003; Sarmiento & Llambí 2004), but also the net outcome of plant–plant interactions at a site scale (Cáceres et al. 2015).

### Forest woody species density

Woody species from the forest were found at low densities in the fallow plots, offering support to the idea that there are important barriers for woody plant establishment in disturbed areas of high Andean forests (e.g. Kok et al. 1995; Velasco-Linares & Vargas-Ríos 2008), and in accordance with previous work performed in the region (González et al. 2011). This could be due to the hindering effects of extensive cattle grazing, which has been suggested to influence the succession process in high Andean forests (Sarmiento 2006; Vargas-Ríos 2007b; González et al. 2011). Other potential barriers to the establishment of woody species could be related to limitations of water or nutrient availability within the fallow plots (as reported by Jiménez et al. 2011 in our study area) or to dispersal strategies and seed bank formation processes (Cubina & Aide 2001; Khurana & Singh 2001; Vargas-Ríos 2007b; Lippok et al. 2013b).

Even at these low densities, establishment of saplings of forest woody species seems to be favoured by the presence of *B. prunifolia*. In fact, *V. stipularis* was exclusively found under the shrub canopy in both studied plots; this was also the case for *B. discolor* in one of the two plots, while in the other it showed the highest densities under the shrub. Vargas-Ríos (2007a) also found positive spatial associations between individuals of *B. discolor* and the shrub *B. prunifolia* at 3300 m a.s.l. (within secondary pastures at the Cordillera Oriental, Colombia), while Jiménez et al. (2011), evaluating the regeneration niche of *B. discolor* in fallow

plots in our study site, found that the cover of the shrub *H. laricifolium* was higher in the vicinity of the saplings. The same pattern of local spatial association between the saplings of another forest species (*Diplostephium venezuelense*) and *H. laricifolium* was reported in Llambí et al. (2013), in this case in non-cultivated páramos just above the continuous forest-line in the Venezuelan Andes.

### Abiotic variables

Maximum temperatures were attenuated under the canopy of *B. prunifolia* in comparison to the open areas, while the thermal amplitude was smaller, indicating that *B. prunifolia* buffers the relatively high temperatures that can be found in open areas of the fallow plots. The effect of nurse shrubs on temperature is generally accepted as one of the main mechanisms behind facilitation (Gómez-Aparicio et al. 2004). Furthermore, maximum temperatures were lower near the forest edge than far from it, which suggests that microclimate can also be ameliorated in fallow areas adjacent to the surrounding woodland (Duncan & Duncan 2000; Wright et al. 2010).

On the other hand, there is higher cover of bare ground and small superficial rocks (scree) in the open areas compared to under the canopy of *B. prunifolia*. Higher vegetation cover could provide benefits such as protection of slopes from rainfall run-off and soil erosion (Harden 1996). Previous studies in the area have shown that soil loss decreases as vegetation cover increases with the development of the successional process (Sarmiento 2000).

Several additional approaches can be suggested to improve our understanding of the patterns found in this study. It would be important to study areas with longer fallow times, to evaluate whether the relative importance of facilitation by our focal species decreases as the canopies are no longer isolated (and thus abiotic conditions are less heterogeneous in the fallow plots). The inclusion of more sampling sites would be useful to check for the generality of our results, given that landscape heterogeneity is a characteristic feature of high tropical mountain environments (Sarmiento & Llambí 2004). Diverging succession pathways have been reported in the study area before (see Sarmiento et al. 2003), and this has important implications for the design of management strategies that rely on the natural recovery of vegetation (Baeten et al. 2010). Furthermore, potential facilitation effects might be more evident during the dry season when conditions are less favourable for seedling establishment (Gómez-Aparicio et al. 2004), especially in areas with marked rainfall seasonality such as those found in intermountain valleys in the high Venezuelan Andes. Additionally, to further understand the role that seed availability plays in the recovery of vegetation in the fallow plots, the species composition and abundance of the seed rain and seed bank need to be evaluated.

Nevertheless, in our view, the approach utilized here can provide key insights into the role played by plant–plant interactions and facilitation in the regeneration process, which are increasingly being recognized as fundamental drivers shaping plant community organization. Given that these diverse forests have been affected by agricultural activities across the region, the understanding of the underlying processes influencing their regeneration in old-fields is of fundamental importance for the design of restoration and management strategies, and for the interpretation of treeline dynamics in climate change scenarios.

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