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ARTICLE



Modelling the effect of temperature changes on plant life-form distribution across a treeline ecotone in the tropical Andes

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ABSTRACT

Background: Classifying plant species from the high tropical Andes into distinct plant life forms (PLF) can provide a more functional understanding of tropical treeline dynamics. However, little is known about the potential response of different PLFs to climate warming.

Aims: The objective of this work was to evaluate the response of PLFs to environmental conditions above the upper montane forest in the Venezuelan Andes and forecast their potential distribution under warming scenarios based on habitat suitability models.

Methods: We classified the plant species present above the forest line into nine PLFs including trees, shrubs, tussock grasses and caulescent rosettes, analysed and modelled their current distribution using Canonical Correspondence Analysis and non-linear multiple regressions and forecasted their potential distribution under warming scenarios (RCP4.5, RCP6.0, and RCP8.5). We used anatomical leaf traits for shrubs and caulescent rosettes to refine their potential responses to climate change.

Results: Tree cover sharply decreased with increasing elevation, while the distribution of shrubs and caulescent rosettes at higher elevations differed depending on their leaf traits. Projections suggested an upslope shift of all PLFs as a response to warming and an increase in tree cover.

Conclusions: The analysis of the distribution of PLFs, by linking different plant adaptive strategies to topography/climate, allowed projecting changes in vegetation physiognomy in response to warming. Projections of a moderate increase in tree cover in the grassland páramo did not indicate the formation of closed forests above the current upper forest line.

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Introduction

The tropical Andes constitute the largest tropical mountain region worldwide, harbouring more than 20,000 endemic plant species (Myers et al. 2000; Young et al. 2002; Swenson et al. 2012) and providing critical ecosystem services such as carbon storage and water regulation (Price 2003; Harden et al. 2013; Molina et al. 2015; Hribljan et al. 2016, 2017). However, the dynamics and structure of the ecosystems are being increasingly affected by land use (Young 2009; Feeley and Silman 2010; Mathez-Stiefel et al. 2017) and climate (Young and León 2007; Anderson et al. 2011; Tovar et al. 2013). Moreover, future climate projections suggest potential species loss in the tropical Andes (Ramirez-Villegas et al. 2014; Báez et al. 2016).

In the tropical Andes, the transition between the upper montane forest and grassland páramo (treeline ecotone) is a zone of particular interest due its outstanding species and functional diversity (Bader et al.

2007a; Ramírez et al. 2009; Hofstede et al. 2014; Peters et al. 2014; Llambí 2015). The treeline is characterised by clear physiognomic changes with elevation, where tussock grasses, small sclerophyllous shrubs and caulescent rosettes replace trees and tall shrubs (Sklenář and Jørgensen 1999; Arzac et al. 2011; Sarmiento Pinzón and León Moya 2015). Reported temperature increases of up to 0.4–0.5°C per decade above 3000 m a.s.l. in the tropical Andes (Vuille and Bradley 2000; Vuille et al. 2018) demand a better understanding on how changes in environmental conditions along topographic gradients influence vegetation distribution at the Andean treeline. However, to date there is little information on this topic, as most treeline studies globally have concentrated on extra-tropical regions (Holtmeier and Broll 2005; Holtmeier 2009; Körner 2012).

Evidence from permanent plots established in the 1990s indicates an upward migration and thermophilisation of tree communities in Andean upper

70 montane forests (Duque et al. 2015; Fadrique et al.
2018). The displacement of the main vegetation
types because of climate warming has also been
forecasted by models based on topographic/climatic
75 variables (Bader and Ruijten 2008; Tovar et al.
2013). However, it is species, and not whole plant
communities, that respond to climate change on the
bases of their adaptive strategies, inducing the
assembly of novel non-analogue communities
(Williams and Jackson 2007). Hence, given the out-
80 standing species and functional diversity character-
istic of tropical treeline vegetation, an approach
based on functional traits would be useful to
model the patterns of change in plant community
structure in response to climate.

85 High Andean plant species have been classified
into architectural types or plant life forms (PLFs)
using readily identifiable morphological traits
(Hedberg 1964; Hedberg and Hedberg 1979; Wolfe
1979; Ramsay and Oxley 1997). The use of PLFs is as
90 a functionally meaningful strategy to represent spa-
tial and temporal changes in the distribution of
plant species, linking the adaptive characteristics
expressed in a PLF with environmental gradients
(Furze et al. 2013). Analysing the current distribu-
95 tion of PLFs at a landscape scale, and potential
changes in it, may be used to assess and compare
treeline dynamics under warming scenarios
between regions with widely contrasting floristic
composition but similarities in vegetation structure
100 (e.g. Scherrer and Körner 2011). Some previous
studies have analysed the distribution of PLFs
along elevation gradients in the tropical Andes
(e.g. Balslev and de Vries 1989; Ramsay and Oxley
1997; Arzac et al. 2011). However, the potential
105 response of vegetation and life-form structure to
climate change scenarios remains unexplored.

In this work, we analysed the spatial distribution
of dominant PLFs in a relatively undisturbed land-
scape above the continuous limit between upper
110 montane forest and grassland páramos and
assessed their potential response to climate warm-
ing. We expanded the basic PLF classification sys-
tem of Hedberg (1964) by including trees and
forbs, which are important components structuring
115 vegetation across the treeline. Moreover, we
explored the effect of adaptive traits that can influ-
ence leaf thermal/radiation balance (i.e. pubescence
and leaf size, see Cuatrecasas 1968; Vareschi 1992),
in modulating the spatial distribution of caulescent
120 rosettes and sclerophyllous shrubs, which consti-
tute dominant PLFs above the treeline (Arzac et al.
2011; Sarmiento Pinzón and León Moya 2015).

We characterised the current distribution of PLFs
in relation to local topographic variables (slope orien-
tation and inclination) along an elevation/thermal
125 gradient with low anthropogenic impact and hypothe-
sised that: (1) anatomical leaf attributes would be an
important factor in the distribution of PLFs along the
elevation/thermal gradient; and (2) warming scenarios
would have a differential impact on the potential dis-
130 tribution of PLFs, expressed as elevational shifts linked
to slope orientation, modifying landscape vegetation
physiognomy above the treeline.

Materials and methods

Study area

135 We sampled six transects along an elevation gra-
dient of 250 m ranging from 3300 to 3550 m a.s.l.
(Figure 1(a)), above the upper montane forest in
the Sierra Nevada mountain range, Mérida,
Venezuela, near La Aguada station of the Mérida
140 cable car system (8° 33' 54.56" N, 71° 5' 22.65" W).
The area is within the limits of the Sierra Nevada
National Park, created in 1952, where land-use has
been restricted in the last decades to very low-
density livestock grazing (density below 0.1 ani-
145 mals ha⁻¹) without the use of fires. A diachronic
analysis of land-cover in the area, comparing aerial
photographs from 1952 and 1998, has shown no
evidence of vegetation cover changes related to
agriculture or the creation of secondary pastures
150 (Santaella 2007), indicating the current treeline
position in the region has not been directly altered
by land-use change, at least in the last 60 years.

The climate in the region is characterised by two
155 periods of high rainfall (April–June and October–
November). A dry period occurs between January
and March; during this time night frosts may occur
(reaching minima of −3°C). Mean annual tempera-
ture at the upper forest line is 7.1°C and the mean
total annual precipitation is 1811 mm (data from
160 La Aguada meteorological station, 3452 m a.s.l.).

The vegetation of the upper montane forest
(3200–3300 m) is dominated by *Psammisia penduli-
165 flora* (Dunal) Klotzsch, *Miconia tinifolia* Naudin and
Libanothamnus neriifolius Ernst. A grassland páramo
appears above (over 3300 m asl), dominated by the
tussock grass *Calamagrostis effusa* (Kunth) Steud.
and scattered woody species (small trees and tall
shrubs such as *Cybianthus marginatus* (Benth.)
170 Pipoly, *Hesperomeles ferruginea* (Pers.) Benth.,
Diplostephium venezuelense Cuatrec., and *Senecio
pachypus* Greenm Trans. Vegetation at higher

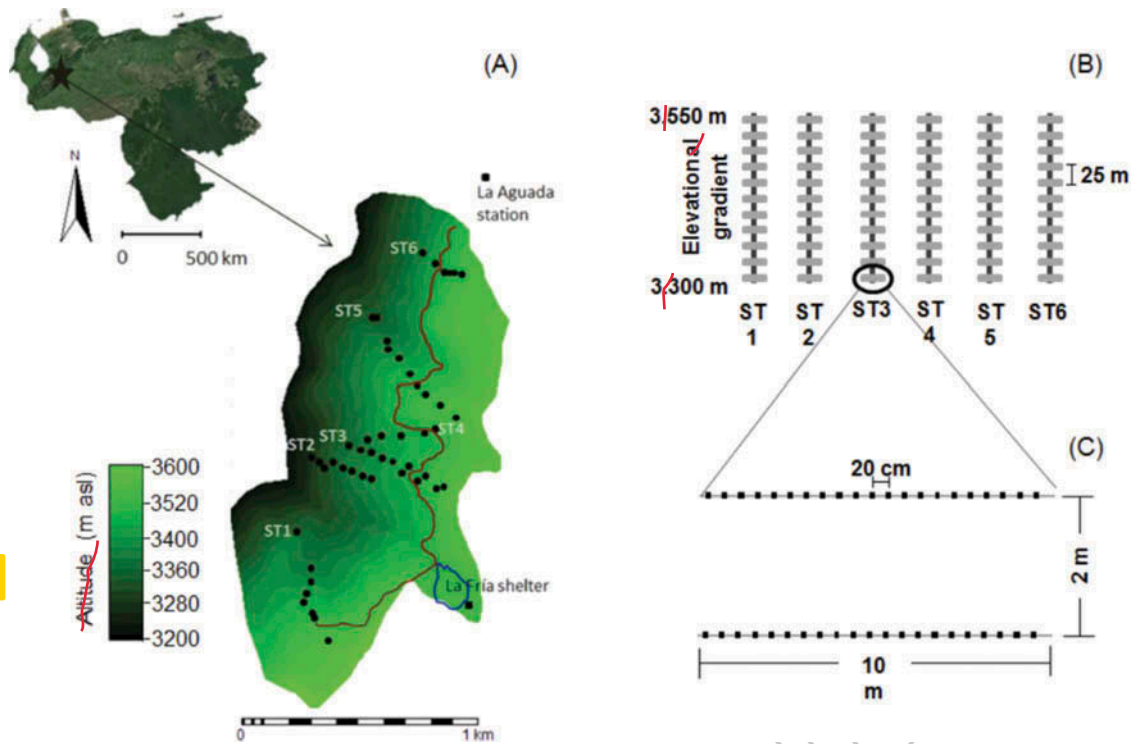


Figure 1. Location of the study area in the Sierra Nevada mountain range, Venezuelan Andes. (a) Digital elevation model of the sampling site showing the distribution of sampling transects (ST1-ST6). (b) Schematic distribution of sampling units along the sampling transects; grey rectangles represent the position of sampling units. (c) Schematic design of sampling units; each black square indicates a sampling point.

elevations is dominated by caulescent rosettes (mainly *Espeletia shultzei* Wedd. and *Ruilopezia atropurpurea* (A.C.Sm.) Cuatrec.), and smaller sclerophyllous shrubs (e.g. *Hypericum laricifolium* Juss.); see Ramírez et al. (2009) and Llambí et al. (2014) for further details.

Plant life-form (PLF) selection and field sampling

We complemented the life forms system of tropical alpine vegetation (caulescent rosettes, sclerophyllous shrubs, cushion plants, tussock grasses and acaulescent rosettes) of Hedberg (1964) by including trees and forbs as additional growth forms. Based on morphological characteristics that could influence the leaf energy balance, we subdivided caulescent rosettes into pubescent and non-pubescent and sclerophyllous shrubs into leptophyllous and nanophyllous types (Rada et al. 1985; Meinzer et al. 1994; Azócar and Rada 2006). In total, nine PLFs were identified: acaulescent rosettes (AR), caulescent pubescent rosettes (CPR), caulescent non-pubescent rosettes (CNR), leptophyllous sclerophyllous shrubs (LSS, leaf size 0.2 cm^2), nanophyllous sclerophyllous shrubs (NSS, $0.2\text{--}2\text{ cm}^2</math>), microphyllous sclerophyllous shrubs (MSS, $2\text{--}20\text{ cm}^2</math>), tussock grasses (TG), forbs (F) and trees (T).$$

During July and August 2007 six transects were established over an elevation gradient from the upper natural limit of montane forest (3300 m a.s.l.) to the grassland páramo (3550 m a.s.l.). The upper limit of the transects was established at the elevation at which no forest trees were observed within the páramo matrix (isolated or in clumps). Each replicate transect was separated from the other by 100 to 500 m in the direction perpendicular to the slope (to increase independence between replicate transects). Two transects were located on the dominant slope orientations within the area (north, north-west, and west). In each transect, 10 sampling units (consisting of two 10-m-long parallel lines separated by 2 m) were placed, separated by 25 m in elevation (Figure 1(b)). The cover of selected PLFs was measured using the point quadrat method (Greig-Smith 1983), using 50 sampling points per line, each separated by 20 cm (Figure 1(c)). For each sampling unit geographical position, elevation, slope orientation and slope inclination were recorded.

PLF distribution along the elevation gradient

The relationship between the abundance (cover) of PLFs and environmental factors (elevation, slope orientation and slope inclination) was evaluated by canonical correspondence analysis (CCA). The

225 elevation distribution optimum for the studied
 PLFs along the gradient was determined by the
 weighted arithmetic mean and the amplitude of
 distribution by the weighted standard deviation
 (or tolerance), combining the data for the six trans-
 230 ects (see Legendre and Legendre 2012 for details).
 Finally, regression models based on sigmoidal and
 Gaussian response curves or a combination of both
 were used to analyse the response of PLF cover-
 abundance to the environmental factors. Here, we
 235 used as replicates each of the six transects sampled
 (more than 100 m of separation), which were dis-
 tributed along the study area to attempt to obtain
 an adequate representation of the distribution of
 PLFs across the treeline in this sector (with an
 240 observation window of ca. 3 km²).

PLF distribution models and warming scenarios

We modelled the spatial distribution of PLF's under
 current climate conditions by producing habitat suit-
 ability models (Dirnböck et al. 2003), in response to
 245 elevation/temperature and slope orientation and
 their interaction. An environmental predictor was
 obtained through non-linear multiple regression
 models (Guisan and Zimmermann 2000) analysing
 the cover of each PLF (dependent variable) as
 250 a function of environmental factors (independent
 variables). This approach allowed a smooth integra-
 tion of the obtained environmental predictor vari-
 ables into a geographical information system
 (Chacón-Moreno 2007; Chacón-Moreno et al.
 255 2007). Whereas the CCA was used to analyse the
 relation between environmental variables and
 changes in vegetation community structure when
 all nine PLF are considered together, non-linear mul-
 tiple regression regressions evaluated them one by
 260 one, allowing the modelling of PLF spatial distribu-
 tion and their potential changes in temperature
 warming scenarios.

The geographical information used for the spa-
 tial models (elevation and slope orientation) was
 265 obtained from a digital elevation model (DEM)
 produced by digitalising the 5941-I-SE contour
 line map of the area (Venezuelan National
 Cartography; scale 1:25,000). Habitat suitability
 models were built with the ITC-ILWIS 3.8 software
 270 (ITC-ILWIS 2001). Models were developed for the
 most abundant PLFs (CPR, CNR, LSS, TG and T).
 Each pixel of the distribution maps represents
 a probabilistic cover value for a particular PLF.

To forecast potential PLF distribution patterns
 275 under warming scenarios, we used as starting point

the habitat suitability models for current distribu-
 tion (including elevation and slope orientation) in
 which elevation was replaced by temperature
 values, using the linear regression model:
 280 temperature = 27.98–0.006 x elevation (Suárez del
 Moral and Chacón-Moreno 2011). This equation
 was produced from linear interpolations of 89
 meteorological stations in Mérida state, monitored
 by the Ministry of Environment and Natural
 Resources (MARN) and the Universidad de Los
 285 Andes (see Suárez del Moral and Chacón-Moreno
 2011 for further details).

The selection of future warming scenarios was
 based on projections from climate change models
 used in the Fifth Assessment Report of the
 290 Intergovernmental Panel on Climate Change
 (AR5) (IPCC 2013). Thus, three Representative
 Concentration Pathways (RCP) scenarios were
 selected, identified by the twenty-first century
 peak or stabilisation value of the Radiative
 295 Forcing: RCP4.5, RCP6.0, and RCP8.5 (IPCC
 2013). We used the projections for temperature
 expressed as anomalies over the mean temperature
 values for the reference period 1986–2005, ana-
 lysed in two periods of 30 years (period 2025 to
 300 2055, focused on the year 2040, and period 2045 to
 2075, centred on the year 2060; Table 1).

Results

PLF distribution along the gradient and habitat suitability models

PLF distribution was structured along the elevation
 gradient (Figure 2), with each PLF occupying
 a different elevation (and temperature optimum),
 although with some overlapping in their distribu-
 310 tion amplitude (± 60 m on average), with CPR and
 NSS showing the lowest and highest amplitude
 values (± 36 m and ± 80 m respectively). Trees
 occupied the lowest elevation at the bottom of the
 gradient (3300 ± 69 m a.s.l.; corresponding to
 315 a mean temperature of 8.2°C), while LSS and AR
 were found at the highest elevation at the top

Table 1. Temperature increments for the different Representative Concentration Pathway (RCP) scenarios for 2040 and 2060 at the Sierra Nevada de Mérida, Venezuelan Andes.

| | | Temperature difference in relation to the period 1986–2005 (K) | |
|-----|--------|---|------|
| | | 2040 | 2060 |
| RCP | RCP4.5 | 0.7 | 0.9 |
| | RCP6.0 | 1.3 | 1.9 |
| | RCP8.5 | 1.8 | 2.6 |

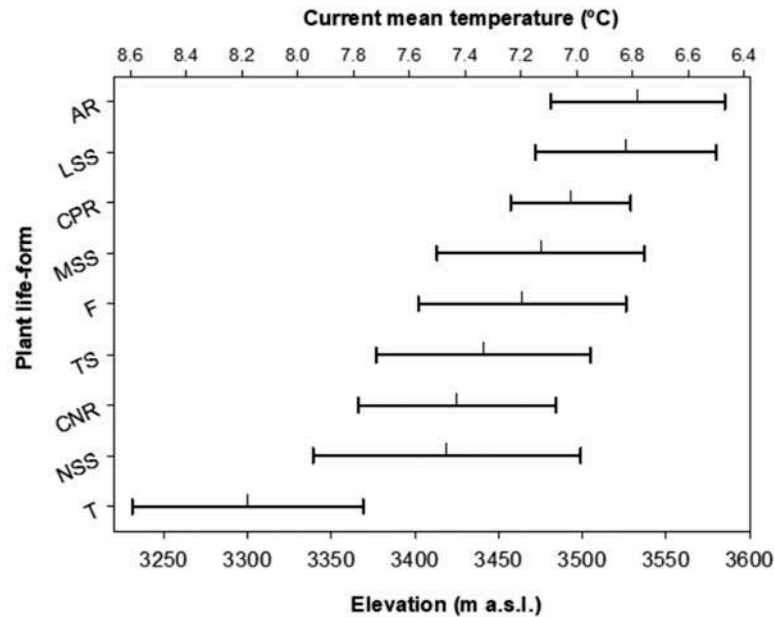


Figure 2. The distribution of PLFs along the elevation – temperature gradient, indicating the elevation optimum, amplitude of distribution and thermal gradient. Vertical lines indicate the elevation optimum and horizontal lines show the amplitude of distribution. T, trees; NSS, nanophyllous shrubs; CNR, caulescent non-pubescent rosettes; TG, tussock grasses; F, forbs; MSS, microphyllous shrubs; CPR, caulescent pubescent rosettes; LSS, leptophyllous shrubs and AR, acaulescent rosettes.

(3526 ± 54 m a.s.l. and 3533 ± 52 m a.s.l. respectively; 6.8°C). The thermal amplitude of the gradient ranged from 8.2 to 6.7°C (Figure 2), NSS, CNR, TG, F, MSS and CPR occupied successive positions along the elevation/thermal gradient (Figure 2).

Leaf morphological characteristics in caulescent rosettes and sclerophyllous shrubs appeared to be related with their spatial distribution in the landscape. Thus, CPR, LSS and MSS showed elevation optima higher than CNR (rosettes without leaf pubescence) and NSS. At their optimum elevation distribution, TG reached the highest cover values (84%), while other PLFs showed maximum cover values of less than 30% at their optimum distribution.

Canonical correspondence analysis (CCA) showed that slope orientation and elevation were the most significant factors evaluated related to the distribution of PLFs (Figure S1). The CCA ordination (over the two main axes comprising 60.0% and 29.9% of overall variance) suggested that CPR and AR were associated with the highest elevations whereas trees occupied the opposite extreme of the ordination diagram. Slope orientation appeared to be related with the distribution of caulescent rosettes and shrubs, with CNR being associated with north-facing slopes, while CPR, AR, NSS and LSS showed higher cover in north-west- and west-facing slopes (see Figure S1 for further details); local slope inclination was not a statistically significant factor related to the distribution of PLFs.

Regression models indicated a significant effect of both elevation and slope orientation on the cover of all PLFs, with R^2 values ranging between 0.38 and 0.77 ($P < 0.001$), with the lowest explained variance for non-pubescent rosettes ($R^2 = 0.28$; $P < 0.01$; Table S1).

Habitat suitability models under current climate conditions for the selected PLFs (i.e. CPR, CNR, LSS, NSS, TG and T) showed differences in the spatial distribution of cover values for each of them within the study site (Figure 3(a-e)). Trees exhibited higher relative cover values (8–25%) at lower elevations, on north-west-facing slopes (Figure 2(a)). Tussock grasses had the highest cover values (60–90%) and a wide elevation distribution across the gradient, with a slightly higher cover on north-facing slopes (Figure 3(b)). Habitat suitability models predicted a higher abundance of LSS towards the top of the gradient on west-facing slopes (Figure 3(c)), with cover values between 8–15%, in comparison with NSS with a lower elevation range (data not shown). The presence/absence of pubescence in studied species of caulescent rosettes also appeared to be related to their distribution. Caulescent rosettes with pubescent leaves (CPR) showed cover values (between 10 and 20%) at higher elevations, mostly in west-facing slopes (Figure 3(d)), while those without pubescence (CNR) showed their higher cover values (between 4 and 16%) at mid-elevations on north-facing slopes (Figure 3(e)).

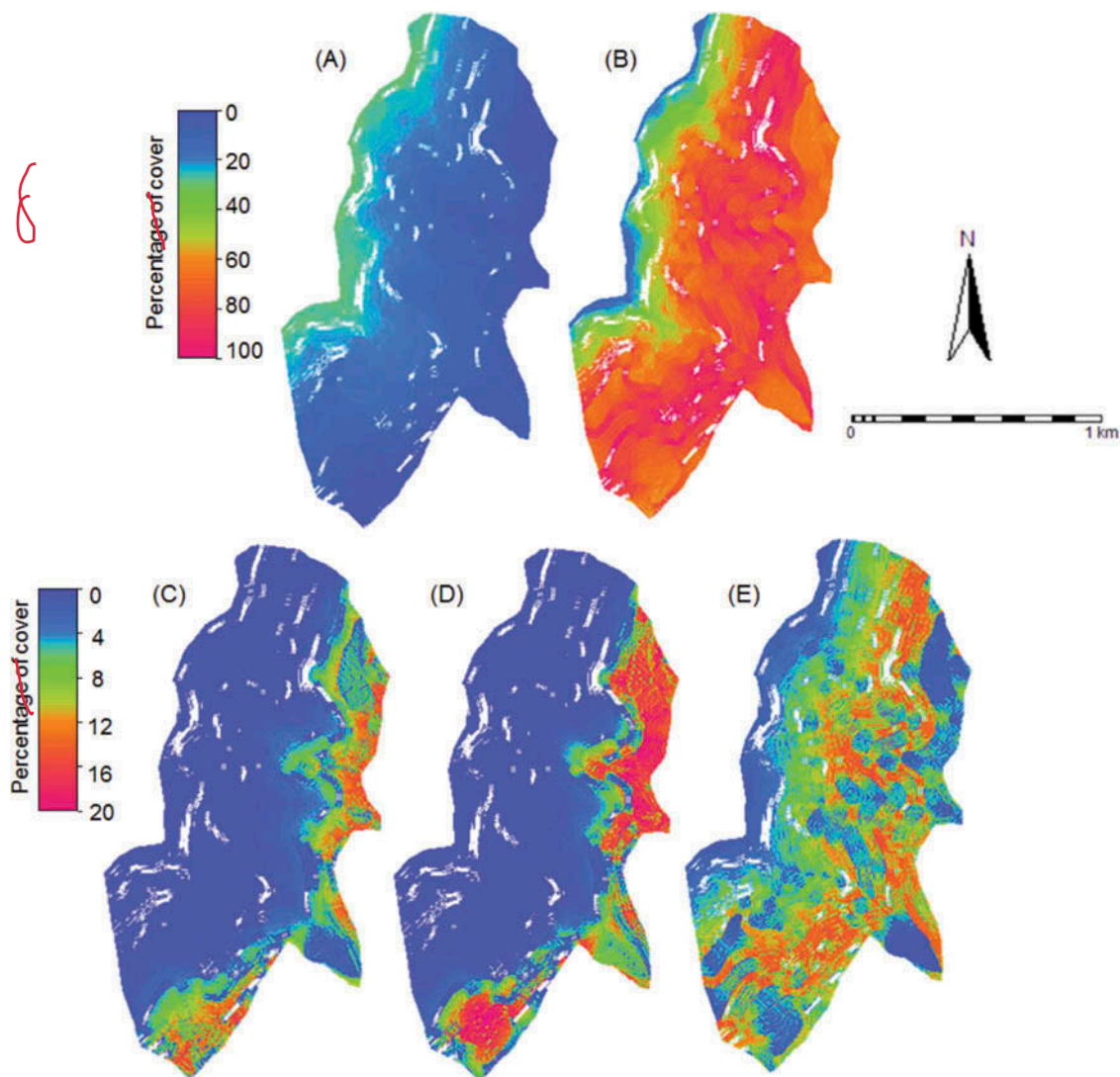


Figure 3. Spatial distribution models showing the percentage of surface cover for the selected plant life-forms at the sampling site, Sierra Nevada mountain range, Venezuela, under current climate conditions. (a) Trees, (b) tussock grasses, (c) nanophyllous sclerophyllous shrubs, (d) leptophyllous sclerophyllous shrubs, (e) Caulescent pubescent rosettes and (f) caulescent non-pubescent rosettes. Pixels in the habitat suitability models represent a probabilistic cover value for a particular PLF. Colours represent the cover percentage from blue (low cover) to red (high cover).

Habitat suitability models under warming scenarios

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Projections based on elevation and slope orientation considering the increments of mean annual temperature under different warming scenarios, suggested an upslope migration for all PLFs analysed, with consequent changes in the configuration and structure of vegetation above the upper montane forest by the years 2040 and 2060, independently of the scenario considered (RCP4.5, RCP6.0 and RCP8.5). Projections suggested an elevational advance of trees (Figure 4(a–f)), expanding their current distribution limit and increasing their cover above the current forest line. The rate of expansion was related to the magnitude of the temperature increase, reaching cover values of 30–40% in the middle of the gradient (3450 m a.s.l.) for the scenario RCP6.0 by

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the year 2040 (Figure 4(c)) and close to 40% at the top of the gradient (3550 m a.s.l.) for the warmest scenario RCP8.5 by the year 2060 (Figure 4(f)). Projections for tussock grasses (Figure 4(g–l)) suggested a marked decrease in their cover and relative importance above the forest line. Under the scenario RCP4.5, TG cover would be reduced in the lower elevations to 20–40% by the years 2040 and 2060, respectively (Figure 3(g and h)). This trend was more pronounced for the scenario RCP6.0, for which the cover could reach values around 40% at the top of the gradient (3400–3550 m a.s.l.) by the year 2060 (Figure 4(j)). In the scenario RCP8.0, projections suggest that by the year 2060 TG cover could be lower than 20% in the whole area, implying an important change in vegetation physiognomy, currently dominated by TG.

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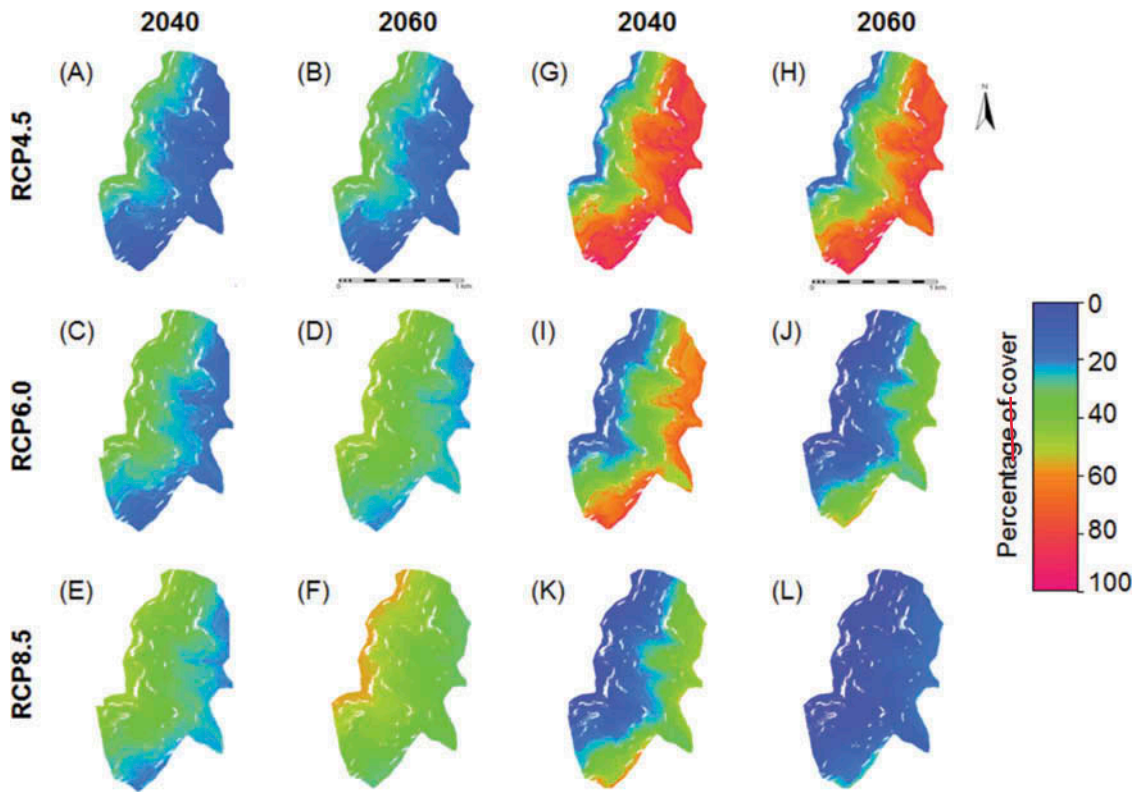


Figure 4. Cover distribution models for tress (a–f) and tussock grasses (g–l) under climate change scenarios for the study site in the Sierra Nevada de Mérida, Venezuela. The Representative Concentration Pathway (RCP) and the future time periods are indicated. Pixels in the habitat suitability models represent a probabilistic cover value for a particular PLF. Colours represent the percent cover from blue (low cover) to red (high cover).

Caulescent non-pubescent rosettes, currently occupying lower elevations close to the upper montane forest limit, may shift upslope with a significant decrease in their coverage by the year 2060 under the scenario RCP4.5 (Figure 5(b)). By the year 2040 and the scenario RCP6.0, CNR would only occur at the top of the gradient with cover values below 8% (Figure 5(c)). On the other hand, caulescent pubescent rosettes (Figure 5(g)) currently occupying a highest elevation, could reduce their cover to values lower than 4% by the years 2040 in the scenario RCP4.5 (Figure 5(g)) and absent thereafter. In the rest of the scenarios considered, pubescent rosettes could be absent from the study site, thus moving to elevations above the current Andean treeline ecotone. Scenario RCP8.5 could imply the disappearance of both rosette life-forms within the 300 m above the current Andean treeline within the study area. Habitat suitability models under future warming scenarios for sclerophyllous shrubs suggested the displacement to higher elevations of LSS above the study area by the year 2040 even in the scenario RCP4.5, with a cover value below 9% (Figure S2).

Discussion

Plant life form (PLF) distribution was associated with changes in elevation/mean temperature, with tussock grasses, caulescent rosettes and sclerophyllous shrubs replacing trees as the dominant PLF above the current forest limit. The distribution of shrubs and caulescent rosettes in relation to elevation and slope orientation was related to their leaf traits. Using habitat suitability models, we found that changes in temperature could modify the elevation distribution range of the dominant PLFs and the position of the Andean treeline under future warming scenarios, with a moderate increase in tree cover in the grassland páramo over the next decades without the formation of closed forests above the current upper montane forest line.

Plant life-form distribution along the elevation/thermal gradient

Our results suggest that within an area with very low anthropogenic pressure at least during the last 70 years, the distribution of PLFs was strongly

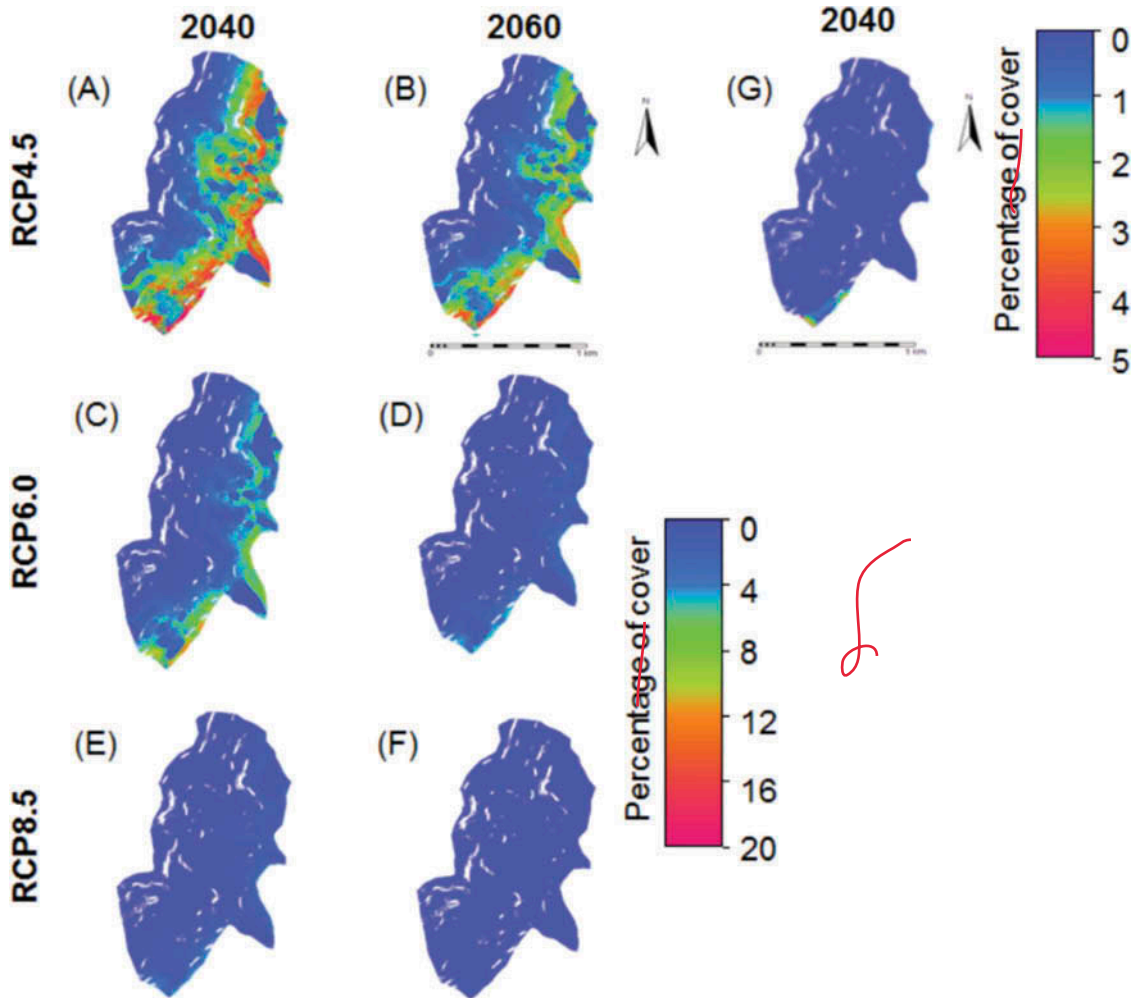


Figure 5. Cover distribution models of caulescent non-pubescent rosettes (a–f) and caulescent pubescent rosettes (only RCP4.5 by the year 2040 is shown, G) under climate change scenarios for the study site at the Cordillera de Mérida, Venezuelan Andean, Mérida State. The Representative Concentration Pathway (RCP) and the future time periods are indicated. Pixels in the habitat suitability models represent a probabilistic cover value for a particular PLF. Colours represent the percent cover from blue (low cover) to red (high cover).

related to topographic variables (elevation and slope orientation). Both factors interact to determine incident radiation and temperature regimes at the local scale. These results are supported by previous studies within the same study area (Ramírez et al. 2009; Llambí et al. 2014) and the Ecuadorian Andes (Keating 1999; Wille et al. 2002; Bader et al. 2008; Bader and Ruijten 2008; Hofstede et al. 2014), documenting the relationship of species abundance and forest cover patterns across the tropical treeline. The thermal amplitude of the studied gradient (where trees are replaced by characteristic páramo PLF), ranged from 8.2 to 6.7°C, corresponding with the mean growing season temperature range that defines the treeline globally (Körner 2012).

However, at local spatial scales PLFs distribution patterns may be more complex, since other parameters associated with local topographic heterogeneity in mountain areas could also have an impact

on plant distribution ranges through their effect on microhabitat conditions (Scherrer and Körner 2011; Frankin et al. 2013). This is indicated by the coefficient of determination of PLF response models to elevation and slope orientation (R^2 values ranged from 0.76 for trees to 0.28 for caulescent non-pubescent rosettes), which suggest the existence of unaccounted variation being associated with the distribution of PLFs. Although, slope inclination was not found to be a significantly related to the distribution of PLFs, a more detailed understanding of how changes in topography and vegetation cover modify local temperature regimes would be a key step for improving our capacity to model the spatial responses of vegetation to warming across the Andean treeline. Other local features such as the presence of rocky outcrops or biogenic microclimatic changes attributable to local plant cover could be important in influencing patterns of tree establishment above upper montane forest (see

Llambí et al. 2013; Bueno and Llambí 2015). In addition, establishing a higher number of replicate transects, distributed over a wider region could be important to obtain a more representative set of independent samples and to allow the validation of the exploratory models presented here against an independent data set.

A sharp decrease in the abundance of trees in the grassland páramo and a non-linear decrease in maximum tree sizes (Arzac 2008) with increasing elevation, appears to be linked to an increase in the abundance of small sclerophyllous shrubs and caulescent rosettes (which are common elements of the grassland páramo). On the other hand, the fact that the highest tree cover-abundance values were found on north-west facing slopes (Figure 3(a)) might be related to lower incident radiation, which could decrease tree mortalities (e.g. by decreasing either photoinhibition or water stress). According to modelling results from Bader and Ruijten (2008), variability in Andean treeline elevation can be associated with slope orientation in Central Ecuador, which influences solar radiation loads.

Plant species inhabiting grassland páramos have developed adaptive mechanisms that allow them to tolerate high incident radiation and daily temperature amplitude (Squeo et al. 1991; Azócar and Rada 2006). Modifications in leaf structure (size and pubescence) might help to explain the contrasting distribution pattern observed within sclerophyllous shrubs (with larger leaf sizes being associated with a lower elevation optimum) and caulescent rosettes (species with non-pubescent leaves showing a lower elevation optimum). The decrease in leaf area of sclerophyllous shrubs with elevation has been proposed as a drought resistance mechanism (Vareschi 1992; Ely and Torres 2003). In fact, the shrubs with the smallest leaf size (LSS) showed their optimum abundance at higher elevations on west-facing slopes, which had the highest incident radiation in our study site (Arzac 2008).

Leaf pubescence in caulescent rosettes can strongly influence the leaf energy balance, reducing the absorption of solar radiation (Rada et al. 1985; Vareschi 1992; Meinzer et al. 1994; Azócar and Rada 2006). This mechanism might explain the higher abundance observed for pubescent rosettes (CPR) values towards the upper extreme of the gradient, on the west-facing slopes, which tend to show lower minimum temperatures but higher solar irradiance in the study area (Figure 3(e)), whereas non-pubescent rosettes (CNR) peaked at lower elevations on north-facing slopes (with lower

radiation loads, see Arzac 2008). In addition, CPR's show freezing avoidance strategies through the protection of organs by insulating structures (e.g. marcescent leaves) and supercooling (Rada et al. 1985; García-Varela and Rada 2003), allowing them to resist low minimum air temperatures.

Forecasting PLF distribution under warming scenarios

Our projections suggest an expansion of woody plants over the páramos just above the current treeline, increasing the density of trees and their elevation range, while tussock grasses and caulescent rosettes would decrease in abundance (Figures 4(g–l) and 5). The upslope extension projected for all life-forms as a response to warming is in accordance with observed upslope migrations of plants and animals in the Andes (e.g. Deutsch et al. 2008; Chen et al. 2009; Feeley et al. 2011; Feeley 2012; Morueta-Holme et al. 2015). However, there is a paucity of studies in the tropical Andes documenting tree species and vegetation shifts specifically at the treeline ecotone; and those available, indicate an upward response of the treeline in the last decades only in sites within protected areas with limited human impacts (Lutz et al. 2013; Rehm and Feeley 2015), as is the case in our study region (Santaella 2007).

The elevation shift might not necessarily be linear as parameters other than temperature can lead to azonal vegetation patterns, such as the presence of nearby water sources which provide a heterogeneous mosaic of micro-climatic conditions or water availability for tree growth (see Bush et al. 2010 results from the Central Andes and Arzac et al. 2016; Arzac et al. 2018 for soil moisture in Mediterranean environments). Albeit the high annual precipitation in our study area (1,811 mm), low mean temperatures and a very short dry season might suggest that soil water availability is not a limiting factor, water availability could explain the higher elevations reached by forests in azonal areas associated with ravines and watercourses (which were excluded from our sampling transects).

Interestingly, even under the warmest scenario (RCP8.5), the simple modelling exercise carried out here indicates that tree cover would reach values of ca. 40–50% in the study area in the next decades (extending 300 m of elevation above the present continuous forest), but without the formation of a closed forest canopy. This agrees with an analysis of changes in vegetation cover in the same

region between 1952 and 1998, which indicated an increase in tree densities at and above the treeline, rather than a clear elevation advance of closed forests over the páramo (Santaella 2007).

Previous studies in the Venezuelan and Ecuadorian Andes have shown that only some small tree and tall shrub species that dominate the upper montane forest edge (e.g. *Cybianthus*, *Diplostegium*, *Hesperomeles*) can establish and reach adult sizes in the páramos outside upper montane forests (Bader et al. 2007b; Ramírez et al. 2009; Llambí et al. 2013). Some of these species (e.g. *Diplostegium* spp.) have a higher tolerance to the high radiation characteristic of open páramo environments than species dominating continuous forests (Bader et al. 2007b).

The limitations faced by forest trees to establish in open environments outside the forest canopy may support the existence of positive feedback mechanisms which could stabilise the dynamics of the upper forest line in the tropical Andes (Bader et al. 2008). Facilitation by shrubs might play a role in seedling establishment outside of the forest by providing the necessary micro-climatic conditions (García-Cervigón et al. 2012; Cáceres et al. 2015; Ramírez et al. 2015). Different pieces of evidence suggest that this phenomenon may be important at the tropical treeline ecotone (González et al. 2011; Llambí et al. 2013; Rehm and Feeley 2013; Bueno and Llambí 2015).

All of this would agree with scenarios (as the one suggested by our modelling exercise) in which the elevation advance of forest over the páramos is initiated by the establishment of individual pioneer trees outside the treeline border, prior to the formation of a closed canopy, facilitating the subsequent colonisation of other tree species dependent on the more favourable conditions within closed forests (Rehm and Feeley 2013; Rehm et al. 2015). However, incorporating biotic interactions into treeline dynamics models would be necessary to evaluate how much of the variance can be explained by biotic vs abiotic drivers and their interactions.

Limitations of the approach and challenges for further research

Our approach is an exercise to evaluate changes in treeline structure and spatial dynamics using a non-taxonomic classification based on PLF, morphological traits and simple habitat suitability models as a prospective tool. Further research is needed to widen the spatial extent of field sampling

and validate the model with an independent data set and at wider spatial scales. However, the use of PLFs seems a promising approach to synthesise the response of individual species to environmental factors in highly diverse environments.

There is also a need to develop a more mechanistic understanding of treeline dynamics in climate change scenarios, considering variations in both, temperature and precipitation, as well as the effects of changes in soil properties and micro-topographic heterogeneity across tropical Andean treelines (Frankin et al. 2013). In addition, a further refinement would consider developing mechanistic spatial models by incorporating information on the: (a) the ecophysiological and demographic responses of woody species to abiotic drivers (e.g. soil water and nutrients, solar radiation, minimum and maximum temperatures); (b) the role of biological interactions such as competition/facilitation; and (c) differences in dispersal abilities between species and life-forms (Bader et al. 2007b; Llambí et al. 2013; Ramirez-Villegas et al. 2014; Rehm and Feeley 2015).

Conclusions

The analysis of plant life-form distribution patterns was used in this work to link changes in vegetation physiognomy with climatic drivers influenced by topography, facilitating comparative analyses across regions with marked differences in floristic composition. Our analysis contribute novel information showing that leaf traits can play an important role in the distribution of caulescent rosettes and shrubs, improving our understanding of the underlying causes of PLF distribution patterns above the treeline. In addition, our results highlighted that the distribution of PLF in the treeline ecotone could be described by simple habitat suitability models combining the effects of elevation and slope orientation, which could, in turn, be linked with changes in temperature and incident radiation. Our habitat suitability models predicted an elevation advance of trees and a concomitant decrease in the cover of tussock grasses, caulescent rosettes and small-leaved sclerophyllous shrubs, but without the formation of closed forests above the current forest line during the next decades.

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