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ORIGINAL PAPER

Human impact on tropical-alpine plant diversity in the northern Andes

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Abstract Conserving páramo diversity and ecosystem services in the northern Andes is urgent, and understanding factors that control vegetation changes is therefore crucial. Although anthropogenic activities have been common in the Andean highlands for centuries, the role of human influence in shaping páramo vegetation remains unclear. To assess the relative importance of human disturbance associated with cattle farming and cultivation for plant species diversity and composition, we analyzed variables driven by both natural and human impact in the Santurbán páramo, Colombia. Canonical correspondence analysis (CCA) showed that the main gradient in plant species composition is related to the gradient of human impact. Partial CCA showed that the pure effect of the variables driven by human impact on floristic composition is twice the size of the pure effect of the variables driven by natural impact. Forward selection procedure indicated that the impact of human disturbance on floristic composition is determined by the level of accessibility. Vegetation patterns are driven by a complex set of elevation-related environmental factors, and human disturbance plays a primary role. Strict protection should be granted to remote and upper sites of the páramo. Restriction of fire and agriculture along steep slopes may counteract negative effects of human disturbance on plant species diversity.

Keywords Conservation · Floristic composition · Human disturbance · Páramo · Santurbán · Species richness

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Introduction

The vegetation of the Andes above the tree-line is fascinating and known for its diverse flora which is more species-rich than that of any other tropical-alpine ecosystem (Smith and Cleef 1988; Sklenář et al. 2011; Madriñán et al. 2013). This tropical-alpine ecosystem between the tree-line and the permanent snow-line in the northern Andes (3000–4900 m a.s.l.) is known as the páramo (Cuatrecasas 1968; van der Hammen and Cleef 1986). It has been estimated that the páramo flora comprises more than 3500 species, of which 60 % are endemic (Luteyn 1999; Sklenář et al. 2011).

Besides the value of the biodiversity per se, the páramo is important for many other ecosystem services (Troll 1968). This includes production of crops (potato, onion, carrot, etc.) and livestock farming, mainly cattle, sheep, and goat farming although in Ecuador and Peru, llama (*Lama glama*), alpaca (*Vicugna pacos*), and vicuña (*Vicugna vicugna*) breeding are common. Nevertheless, the most important ecosystem service provided by the páramo is its regulation of the hydrological cycle. Because of their high water retention capacity, páramo soils act as sponges during wet periods capturing the precipitation surplus, which is then released during dryer periods (Podwojewski and Poulenard 2000; Buytaert et al. 2006). Large proportions of the human population in Venezuela, Colombia, and Ecuador depend on drinking water originating in the páramo (Hofstede et al. 2003).

The páramo ecosystem suffers a number of degrading processes (Ellenberg 1979; Balslev and Luteyn 1992; Medina and Mena 2001). High population growth over the past century has resulted in increased pressure to cultivate new land to satisfy growing demands for food. This has resulted in an upward movement of the agricultural frontier into the páramo and an intensification of agricultural production, involving increased use of chemical fertilizers and pesticides, indiscriminate use of fires, overgrazing, construction of drainage systems, and roads (Monasterio 1980; Hess 1990; Mena et al. 2008). The principal settlement of the páramo occurred during the European conquest, when introduction of livestock, new crops, and new socio-economic practices facilitated the colonization of the highlands (Monasterio 1980; Little 1981; Mena et al. 2008). Since the páramo originally had a sparse human population, its vegetation is quite sensitive to human influences particularly to burning (Lægaard 1992; Verweij and Budde 1992; Horn 1993; Ramsay and Oxley 1996) and grazing (Molinillo and Monasterio 1997; Suárez and Medina 2001). Burning wipes out most shrub and tree species (Williamson et al. 1986; Coblentz and Keating 2008), and tussock and inter-tussock species show significant post-fire mortality rates (Ramsay and Oxley 1996). When fires are followed by continued grazing or overgrazing the vegetation is transformed into a low ground cover of short grasses, including species of *Agrostis, Festuca, Paspalum*, and matted herbs such as *Lachemilla orbiculata,* and species of *Bidens,* and *Hypochaeris* (Cleef 1981; Verweij and Budde 1992). Increase in the number and abundance of exotic species has also been reported in places affected by human intervention (Olivera and Cleef 2009; Valencia et al. 2013). Changes of the vegetation cover are accompanied by compressed, dryer, and less organic soils, which are more prone to erosion and micro-terracing (Pérez 1992).

Despite the importance of páramo, little is known about the impact of anthropogenic activities on its plant diversity. Compositional vegetation changes are primarily determined by the elevational gradient (Troll 1968; Baruch 1984), which constitutes a complex set of elevation-related environmental gradients including temperature, precipitation, moisture, and land-use (Körner 2007). Diversity is expected to naturally decrease with elevation due to climate and to space and time constraints of evolution (Körner 2004). Several authors have suggested that human disturbance is one of the main factors determining species composition and structure of the páramo vegetation (Keating 1999; Sklenář and Ramsay 2001; Sarmiento et al. 2003; Valencia et al. 2013). However, since the factors controlling vegetation changes are strongly interrelated it is difficult to determine the role of human influence in shaping plant diversity patterns. The main objective of this study was to investigate the relative importance of human disturbance associated with cropping and cattle farming on plant species diversity and floristic composition in the páramo. After making a floristic inventory of the area, we asked the following specific questions: (1) How important are variables driven by human impact relative to variables driven by natural impact for the plant species variation? When all variables are taken together—both those driven by human impact and those driven by natural impact—(2) Which ones most strongly influence species composition? (3) Which ones affect plant diversity most strongly? Based on this, conservation implications of our findings are discussed.

Methods

Study site

We studied the cropping and cattle farming impacts in the Santurbán páramo in the northern part of the eastern Colombian cordillera (74°4′W, 4°35′N) at 3300–4000 m a.s.l. Here, the annual precipitation ranges from 600 to 1000 mm, the mean annual temperature vary from 0 to 13 °C, and the soils are slightly developed and relatively young (Cleef 1981). The village Berlin provides onion and potato in the region, and its surroundings are modified through agricultural activities. Another village, Vetas is surrounded by more pristine landscapes with steep slopes. Apart from agriculture, villagers are artisan gold and silver miners, and these metals have been extracted since pre-columbian times (Moreno 1999). The largest gold deposits were exhausted following the European conquest and since then, mining has continued with reduced intensity. Recently, the arrival of a Canadian mining company to Santurbán sparked serious controversy, which received international attention (Ochoa 2014).

Mining involves chemical and physical modifications of the environment that affect the vegetation directly or indirectly. Physical modifications of the land-surface result in the destruction of the vegetation cover (Ratcliffe 1974). Alteration of soil and hydrological conditions due to erosion, ground water and contamination discharges, exacerbate the problems of vegetation degradation (Chernaik 2010). The production of hazardous wastes such as cyanide, mercury, arsenic and lead, is one of the major environmental problems associated with gold-mining (Tarras-Wahlberg et al. 2000). In higher plants, cyanide contamination inhibit respiration, germination and growth (Eisler and Wiemeyer 2004). Mining impacts on vegetation differ with the scale of the mining project, the methods applied and the specific-site environmental conditions (Müezzinoğlu 2003). In the Páramo the Santurbán, the effects of gold-mining on the vegetation have not been studied. However, given the large scale of the current mining projects and the use of chemical metallurgical methods, severe impacts on vegetation may be expected.

Field sampling

Fieldwork was performed from September to November, both in 2008 and in 2009, in a 5 × 15 km rectangle along the gravel road connecting Berlin and Vetas. Plot locations (70) within the study rectangle were randomly generated with ArcGIS, followed by the exclusion of plots without vegetation and ones located closer than 10 m to each other. In each plot (5 × 5 m), variables driven by human impact (occurrence of field crops, occurrence of houses, occurrence of fences, signs of fire, proximity to path, number of cows, and number of droppings) and variables driven by natural impact (elevation, slope, and percentage of rocky habitat) were recorded along with floristic data (Table 1). Floristic composition was assessed using an 8-grade semiquantitative scale combining abundance and cover (Mueller-Dombois and Ellenberg 1974). Data were transformed to their mid-point values (r = 0.05 %, += 0.5 %, 1 = 2.5 %, 2a = 10 %, 2b = 20 %, 3 = 37.5 %, 4 = 62.5 %, 5 = 87.5 %) for further analysis. Past disturbance histories were not noted for lack of information.

Data analyses

Patterns in plant species composition were analyzed with CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002). Detrended correspondence analysis (DCA) was used to detect the length of the environmental gradient. After DCA, Canonical correspondence analysis

Table 1 Floristic, environmental and land use variables used to study human impact on plant diversity in the Santurbán páramo, Colombia

Category	Name	Unit	Description
Floristic1	Species names abbreviated as the first three letters of the generic and of the species name	Semiquantitative abundance-cover scale	(r = 0.05 %, += 0.5 %, 1 = 2.5 %, 2a = 10 %, 2b = 20 %, 3 = 37.5 %, 4 = 62.5 %, 5 = 87.5 %)
Variables driven by natural impact			
	Elevation	MASL	Meters above sea level
	Slope	°	Inclination of the surface to the horizontal
	Rock	%	Percentage of area covered of rocky habitat at each sampling plot
Variables driven by human impact			
	CowD	None	Number of cattle droppings per 100 m^2 [a]
	Fire	None	Presence of fire traces within the plot
	Fences	None	Presence of fences within an area of 10000 m^2 [a]
	Crop	None	Presence of field crops within an area of fields within an area of 10000 m^2 [a]
	Dstapath	m	Distance to the nearest path measured from the center point of the sampling plot
	House	None	Presence of houses within an area of 9000 m^2 [a]
	Cow	None	Number of cows within an area of 10000 m^2 [a]

[a] Area measured from the center point of the sampling plot

(CCA) was applied because the data set was relatively heterogeneous and therefore the length of the gradients in DCA was relatively long (Lepš and Šmilauer 2003). The significances of the first ordination axis and of the sum of all the canonical axes were evaluated with unrestricted Monte Carlo tests with 499 permutations. Partial CCA was used to assess the relative contribution of the variables driven by human impact and the variables driven by natural impact on species variation. Partial CCA estimates the variation in plant species that can be attributed to one set of variables after the effect of the other variables is partialed out. CCA and partial CCA with forward selection and Monte Carlo permutation test (499 unrestricted permutations) were used to determine the variables that best explain the species composition $P < 0.05$) (Thomsen et al. 2005). For each plot species richness (the number of species in each plot) was counted, along with two measures of within community diversity. Within-community diversity was estimated by computing the Shannon index (H) and within-community evenness with Shannon's equitability (E_H) (Peet 1974). The major determinants of plant diversity (i.e., Shannon indices and species richness) were assessed using forward stepwise multiple regressions on the full set of explanatory variables using OpenStat softwareVersion 3 (Miller 2008).

Results

Inventory

A total of 141 vascular plant species were encountered in the 70 sampling plots. They belonged to 31 families, 15 of which were represented by only one species. The most species rich families were Asteraceae (41 species) and Poaceae (17 species), followed by Rosaceae (8 species) and Apiaceae (7 species), and by Hypericaceae, Ericaceae, Cyperaceae, and Lamiaceae each with 6 species. In terms of the overall importance, a relative measure accounting for the sum of cover and frequency (Keating 1999, 2000), the most important species were *Espeletiopsis santanderensis, Lachemilla orbiculata, Trifolium repens* L., *Orthrosanthus chimboracensis, Calamagrostis effusa,* and *Rumex acetosella* L., each accounting for more than 1 % of the total relative importance. The vast majority (86 %) of all species had importance values below 1 %, indicating that they were locally rare.

How important are variables driven by human impact relative to variables driven by natural impact for the plant species variation?

The CCA with all nine explanatory variables explained 19 % of the total floristic variation (total inertia 4.854, $F = 1.553$, $P = 0.002$). The first ordination axis accounts for 7.2 % of the variance ($F = 4.635$, $P = 0.002$) and captures the gradient of human impact by means of agricultural practices (droppings, cattle, crops, fences, houses) along with elevation and the distance to the nearest path (Fig. 1). This axis separates species occurring in disturbed places, such as *Anthoxanthum odoratum* L., *Hypochaeris radicata* L., *Lachemilla orbiculata, Trifolium repens* L., and *Paspalum bonplandianum* Flüggé, from species occurring in undisturbed places, at higher elevation and partly also away from the paths, such as *Pentacalia andicola*, *Lobelia nana* and *Calamagrostis recta*. The second axis accounts for 2.2 % of variation and demonstrates a correlation to slope and percentage of rocky habitat, although the test of the second axis was not significant ($F = 1.617$, $P = 0.568$). Variance

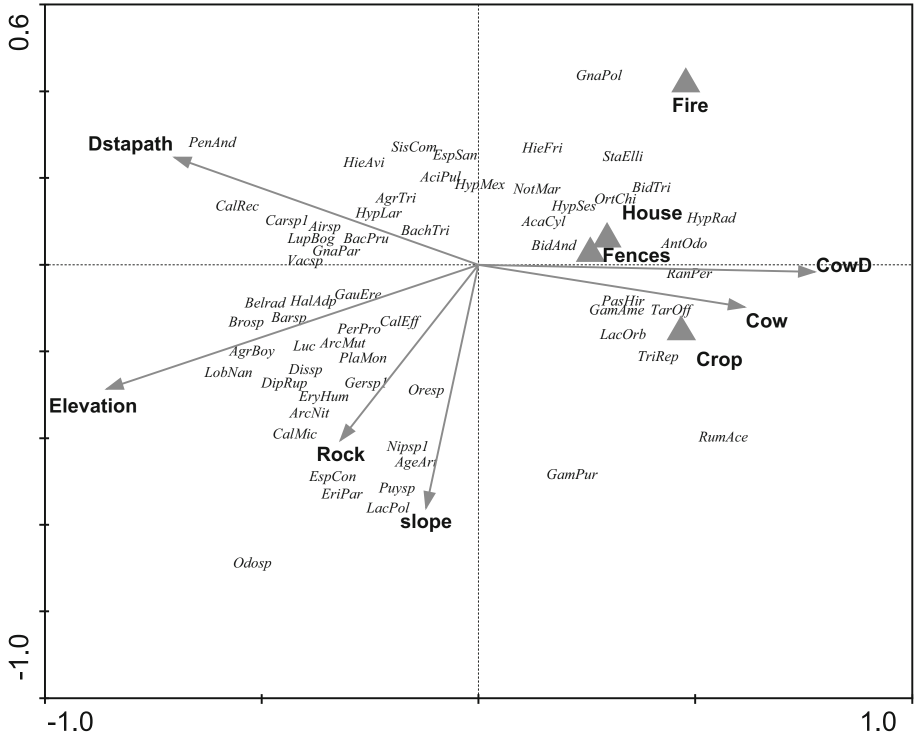

Fig. 1 Ordination biplot depicting the first two axes of the canonical correspondence analysis of the species assemblages in a páramo at Santurbán, Colombia. Only species with fits >4 % are shown

partitioning using partial CCA indicated that the variables driven by human impact alone described 55 % of the total variance explained (F = 1.281, P = 0.014), whereas the variables driven by natural impact alone accounted for 29 % of the total variance explained (F = 1.359, P = 0.012), and the variation that is jointly described by both set of variables is 16 %. Hence, the pure effect of human disturbance on species composition was almost twice as large as the pure effect of the variables driven by natural impact.

Which variables are the most important in determining species composition of the vegetation?

In the CCA with all nine explanatory variables, elevation (F = 4.09, P = 0.002) and distance to the nearest path (F = 1.76, P = 0.008) were selected by the forward procedure. In the partial CCA with the variables driven by human impact as explanatory variables and the variables driven by natural impact as covariable only distance to the nearest path was selected (F = 1.78, P = 0.004). In the partial CCA with forward selection with the variables driven by natural impact as explanatory variables and the variables driven by human impact as covariable elevation was selected (F = 1.75, P = 0.006). Thus, among the whole set of variables, elevation and distance to the nearest path best explain the variation in species composition (Table 2).

Table 2 Best explanatory variables of plant species composition, plant species diversity and species evenness in the Santurbán Páramo, Colombia

	Species composition	Species diversity		Evenness
		Shannon index (*H*)	Species richness	Shannon equitability (E_H)
Variable 1	Elevation	Elevation	Elevation	Elevation
Variable 2	Distance to the nearest path	Fire	Slope	Fire

Which variables affect plant diversity most strongly?

The number of plant species found in a single plot was 6–29. Shannon diversity (*H*) ranges from 0.41 to 2.18 and Shannon's equitability (E_H) from 0.18–1. Forward stepwise multiple regressions selected elevation and signs of fire as the best predictors of *H* (adj. $R^2 = 0.216$, $P < 0.0001$) and E_H (adj. $R^2 = 0.216$, $P < 0.0001$) (Table 3). *H* showed a significant positive correlation with elevation (std. $R = 0.393$, $P < 0.0001$) and a significant negative correlation with signs of fire (std. R = -0.304, $P < 0.006$). Likewise, E_H was positively correlated with elevation (std. $R = 0.451$, $P < 0.0001$) and negatively correlated with signs of fire (std. $R = -0.304$, $P < 0.006$). With respect to species richness three variables were selected as the best predictors: elevation, rocky habitat, and slope (adj. $R^2 = 0.318$,

Table 3 Results from a páramo at Santurbán, Colombia, of stepwise multiple regression of species richness, Shannon index *H* and Shannon equitability E_H

Species richness					
Regression statistics	R^2	SE	Adj. R^2	F	Prob.
0.059	0.348	4.763	0.318	11.749	0.000
Predictor	Std. Partial R	SE	Partial R	t	Prob.
Elevation	0.451	0.004	0.016	4.129	0.000
Slope	−0.282	0.045	−0.123	−2.759	0.008
Percentage of rocky habitat	0.236	0.07	0.150	2.156	0.035
Shannon index (*H*)					
Regression statistics	R^2	SE	Adj. R^2	F	Prob.
0.488	0.238	0.232	0.216	10.479	0.000
Predictor	Std. Partial R	SE	Partial R	t	Prob.
Elevation	0.393	0.000	0.001	3.684	0.000
Fire	−0.304	−0.341	0.119	−2.853	0.006
Shannon equitability (E_H)					
Regression statistics	R^2	SE	Adj. R^2	F	Prob.
0.488	0.238	0.106	0.216	10.479	0.000
Predictor	Std. Partial R	SE	Partial R	t	Prob.
Elevation	0.451	0.004	0.016	4.129	0.000
Fire	−0.304	0.055	−0.156	−2.853	0.006

Variables selected by forward method are shown

$P < 0.0001$) (Table 3). Species richness significantly increases with elevation (std. $R = 0.451$, $P < 0.0001$) and the percentage of rocky habitat (std. $R = 0.451$, $P = 0.035$), and decreases with increasing slope (std. $R = -0.282$, $P < 0.01$). On that account, elevation and fire were the main variables determining plant diversity in terms of H and E_H. Besides elevation, slope, and the extent of rocky habitat were also important for species richness (Table 2).

Discussion

How important are variables driven by human impact relative to variables driven by natural impact for the plant species variation?

Partial CCA showed that the relative contribution of the variables driven by human impact on plant species variation was almost twice as large as relative contribution of the variables driven by natural impact. This is congruent with the CCA outcomes which indicated that the main gradient in the floristic composition was related to the gradient of human impact (Fig. 1). While several studies have documented the major role of elevation in controlling compositional vegetation changes (Cuatrecasas 1968; Troll 1968; Baruch 1984), our results indicated that in a páramo under human influence floristic patterns are tightly associated to human disturbance. This lends support to previous findings which highlight the mosaic pattern in the páramo vegetation, suggesting that floristic composition is not only controlled by the elevational gradient but also by local environmental factors, such as land-use patterns and soil conditions (Olivera and Cleef 2009; Valencia et al. 2013).

Which variables are the most important in determining species composition of the vegetation?

The CCA and pCCA with forward selection showed that, from the whole set of variables, elevation and distance to the nearest path were the major determinants of floristic composition. Elevation is correlated with a wide range of environmental factors and thus, it constitutes a complex set of inter-correlated environmental gradients that exerts strong control over changes in the composition of the vegetation (Troll 1968; Körner 2007). Distance to the nearest path was the most important land-use variable for plant species composition, suggesting that the impact of human disturbance associated with cattle farming and cropping on floristic patterns is determined by the level of accessibility. This agrees with recent studies that demonstrate that inaccessible habitats can be used to infer the potential natural vegetation in the high Andes (Sylvester et al. 2014).

Which variables affect plant diversity most strongly?

Forward stepwise multiple regressions showed that plant diversity, in terms of species richness, Shannon diversity (H), and Shannon equitability (E_H), was most strongly correlated with elevation. Contrary to the expected, we observed a significant increase of plant diversity with elevation (Table 3). We suggest that the cause of this pattern is the intensive human intervention at low elevations which may result in lower diversity. For instance, at 3300–3700 m, the occurrence of field crops or houses was noted in almost half of all sample plots, whereas above 3700 m no field crop were encountered and only a single

Table 4 Intensity of human impact throughout the altitudinal gradient in a páramo at Santurbán, Colombia

Altitudinal range	No. of plots	Plots with presence of fences (%)	Plots with presence of field crops (%)	Plots with presence of houses (%)	Average number of cattle droppings	Average number of cattle	Average distance to the closest path (m)
3300–3400	2	100	100	100	7	7.5	213
3400–3500	11	55	55	18	8.7	4.5	196
3500–3600	15	73	40	60	6.9	3.3	223
3600–3700	13	46	39	46	4.6	3.7	344
3700–3800	9	33	0	11	2.3	1.3	469
3800–3900	11	9	0	0	1.9	0.3	664
3900–4000	9	11	0	0	1.8	0.9	581
3300–4000	70	43	27	29	5	3	384

house was registered. Also, on average, the number of cattle droppings per plot was nearly three times larger below 3700 m than above 3700 m. The higher intensity of human intervention at lower elevations compared to higher ones is also reflected by the differences in the distance of the plot to the nearest path (Table 4). Fire was also shown to greatly affect plant diversity by reducing H and E_H. Fires assist most of agricultural practices, resulting in concentrated disturbance related to grazing, cropping, and in general to increasing accessibility (Lægaard 1992; Verweij and Budde 1992; Ramsay and Oxley 1996). The effect of burning on plant diversity is related to the different abilities of plant species to survive and recover from fires. Tussock grasses survive fires easily and regenerate within a few weeks or months after burning, whereas other species, especially shrubs and trees, may die (Williamson et al. 1986; Lægaard 1992; Coblentz and Keating 2008). Thus, fires affect species diversity and equitability by promoting a vegetation cover dominated by tussock grasses, in which the number of species and their abundances are limited (Sklenář and Ramsay 2001). Slope and rocky habitat were also significantly correlated to species richness. In our study species richness showed a significant increase with the extent of rocky habitat and a significant decrease with increasing slope (Table 3). Rocky terrain supports plant diversity by facilitating habitats for survival and colonization (Sklenář and Ramsay 2001; Coblentz and Keating 2008), and by limiting human disturbance, since it is not favorable for most agricultural activities. The negative correlation between species richness and slope may be related to the enhanced effects of grazing and trampling at the steeper slopes. Grazing on slopes caused loss of vegetation cover, whereas on flat parts, it produces a closed mat of short grasses and ground-covering forbs (Verweij and Budde 1992). Intensive agriculture at steep slopes accelerates soil erosion, leading also to the disappearance of the vegetation and hence of plant diversity.

Conclusion

Although vegetation changes are mainly controlled by the elevational gradient, which represents a complex set of interrelated factors, the pure effect of the variables driven by human impact on species composition is significantly greater than the pure effect of the variables driven by natural impact. Our results point to the major role of human disturbance in determining species composition. The effect of human disturbances on plant species composition was determined by the accessibility. Human disturbance also significantly affected plant diversity through a negative effect of fire. Human disturbance was more intensive at lower than at higher elevations, resulting in an increase of plant diversity with elevation. Based on our results, we strongly recommend managers to consider the influence of human impact when designing protected area zoning, which is a current issue in páramo conservation. Our results also suggest that strict protection should be granted to remote and upper sites of the páramo and that the restriction of fire and of agricultural practices along steep slopes may contribute to counteract the negative effects of human disturbance on tropical-alpine plant diversity in the northern Andes in the future.

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