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Influence of vegetation types and ground cover on soil water infiltration capacity in a high-altitude *páramo* ecosystem

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Abstract

Mountain ecosystems are receiving increasing attention due to their role in the regulation and supply of water for a growing human population, a pattern that is especially important in high altitude ecosystems of the northern Andes (páramo). Although it is commonly accepted that the capacity of soils to retain and regulate water is mostly given by their structure and organic matter content, it could be also influenced by the differences in the depth and nature of plant ground cover in different vegetation types. By performing a series of water infiltration essays in soils under different vegetation or land-use categories in an Ecuadorian *páramo*, we evaluated the relative contribution of ground vegetation cover to water infiltration capacity. Water infiltration was extremely high under shrubland vegetation and *Polylepis* forest, and decreased markedly under grassland, Pine plantations, and cattle trails. In all cases, the layer of ground vegetation made a significant contribution to total infiltration capacity, as shown by the lower infiltration rates of the essays performed after this layer was removed. Management and restoration of mountain ecosystems should concentrate in the recovery of landscape-level heterogeneity and the protection of the ground vegetation layer that regulates soil micro-climate, and provides additional water storage capacity.

Keywords. Ecuador, páramo, soil, water infiltration capacity, soil cover.

Resumen

Los ecosistemas de montaña están recibiendo mucha atención debido a su importancia en la provisión y regulación de los recursos hídricos, un fenómeno que es especialmente importante en los ecosistemas de altura de los Andes del norte (páramos). Si bien es ampliamente aceptado que la capacidad de los suelos para regular los flujos hidrológicos está básicamente dada por su estructura y su contenido de materia orgánica, esta capacidad también podría estar influenciada por las diferencias en la naturaleza y espesor de la cobertura del suelo en diferentes tipos de vegetación. Mediante una serie de ensayos de infiltración de agua en el suelo en localidades con diferentes tipos de vegetación o usos del suelo en un páramo ecuatoriano, evaluamos la contribución relativa de la cobertura de vegetación rastrera a la capacidad de infiltración de agua en el suelo. Las tasas de infiltración fueron extremadamente altas en las zonas arbustivas y en el bosque de *Polylepis*, pero decrecieron marcadamente en los pajonales, los bosques de pino y los senderos de paso de ganado. En todos los casos, la capa de vegetación rastrera contribuyo significativamente a la capacidad total de infiltración, como se demuestra por la disminución de las tasas de infiltración que reportamos cuando esa capa fue removida experimentalmente. El manejo y la restauración de los ecosistemas de montaña se debería concentrar en la recuperación de la heterogeneidad a nivel del paisaje y en la protección de las capas vegetales rastreras que regulan los microclimas del suelo y proveen una mayor capacidad de infiltración de agua.

Palabras Clave. páramo, Ecuador, suelo, capacidad de infiltración de agua, cobertura de suelo

Introduction

During the past two decades, high altitude ecosystems across the world have received special attention partially due to the ever-increasing threats that they are experiencing, but also to their crucial role in the regulation of important ecosystem services such as carbon storage,

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soil stabilization, and water supply [1–4]. In the particular case of the northern Andes (Venezuela, Colombia, Ecuador and northern Perú), attention has been centered in the disproportionate role that high-altitude ecosystems (>3200 m), hereafter termed páramo, have in water storage and regulation of hydrological flows [5–7]. Despite the isolated and fragmented occurrence of pára-mo over the Andean highlands, it has been estimated that these ecosystems provide water for irrigation, hydropower generation, and human consumption for at least 15 million people across the northern Andes, constituting more than 80% of the total water supply for large capital cities such as Bogotá and Quito [8]. To a large extent, this capacity of páramo ecosystems to regulate hydrological flows has been attributed to their deep soils, with excellent structure and high concentrations of organic matter [9, 10]. As a consequence, these soils can store large amounts of water that are slowly released into the streams. However, páramo soils and the vegetation that they support can be very heterogeneous, influencing eco-system functions such as water storage and regulation [7, 11]. In this study, we evaluated the relative contribution of different vegetation types in a high-altitude páramo ecosystem to soil water infiltration capacity as a measure of ecosystem function in this Andean ecosystem.

Previous studies about the hydrological function of páramo ecosystems have focused on the role of soils in controlling water infiltration capacity and on the effect of human activities in this ecosystem function [7, 9, 12–14]. Although the magnitude of these impacts might vary according to site particularities and the intensity of human intervention [5], the majority of studies have shown significant impacts such as decreased levels of infiltration or soil water retention capacity, reduced water yields, or increased erosion rates associated with cropping [6, 9, 14], burning and grazing [6, 14, 15], and afforestation with exotic species [16, 17]. Similarly, most of these studies have found that the decrease in hydrological functioning in páramo ecosystems is usually associated with losses in soil organic matter content, further emphasizing the role that this component has in the regulation of water retention and movement through páramo ecosystems [18]. Thus, although the influence of soil properties in the behavior of soil water is not to be questioned, emphasis in this aspect could lead us to ignore the potential contribution of ground vegetation cover to the water movement and retention in páramo soils.

The role of vegetation on soil water infiltration capacities has been evaluated in several locations around the world. Orradottir et al. [19] found that infiltration rates were significantly lower in grasslands than in Birch dominated woodlands in Iceland. Jimenez et al. [20] reported that undisturbed Andisols in Tenerife Island under native vegetation cover had significantly higher infiltration capacities than soils where the vegetation had been removed for establishment of tree plantations or agricultural fields. In general, a strong relationship has been found in which soil water infiltration capacities increase as a power law function of and above-ground biomass in water limited ecosystems [21]. Conversely, in mesic areas this relationship does not hold as stated, and variations in infiltration capacity seem to be predominantly explained by soil type. Although this pattern has been tested across a wide range of ecosystem types [21], it has not been evaluated in heterogeneous tropical montane areas where the combination of high altitude, cold and wet climate, and steep topography create a diverse range of vegetation types, and a large spatial variation in their biomass and distribution. Up to date, the extent to which this variation could influence local rates of soil water infiltration remains unexplored. In this paper we use the ecological heterogeneous setting of the high Andes of northeastern Ecuador to assess if different vegetation types in a páramo locality exhibit different soil water infiltration rates, and the relative contribution of ground vegetation cover to the infiltration capacity of soils under different vegetation types.

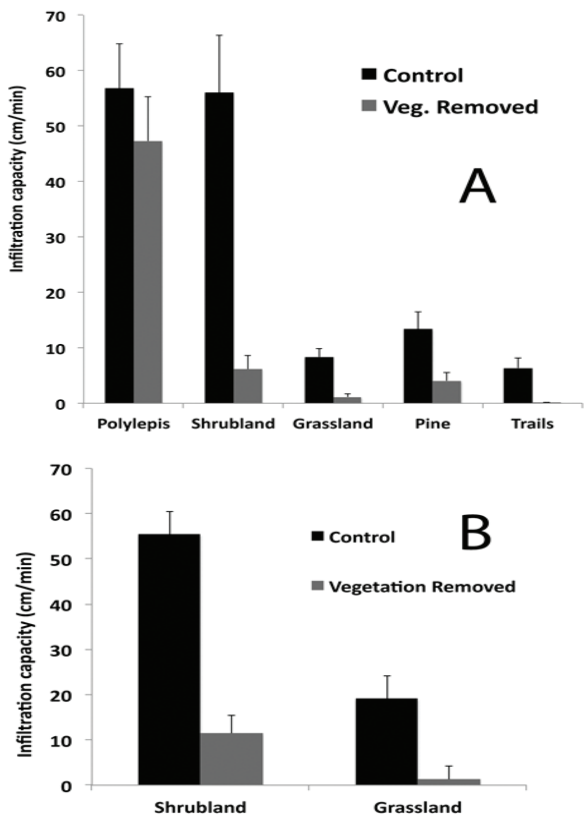

Figure 1: Relative contribution of ground vegetation cover to water infiltration rates in different vegetation or land-use types in a high-altitude páramo ecosystem in northeastern Ecuador. Each bar represents the average (+ standard error) of ten infiltration essays performed in paired soil samples during the dry season of 2010 (A) and wet season of 2011 (B). The first essay of each pair was performed in intact soil, while the second was performed in an adjacent spot in which ground vegetation cover had been removed.

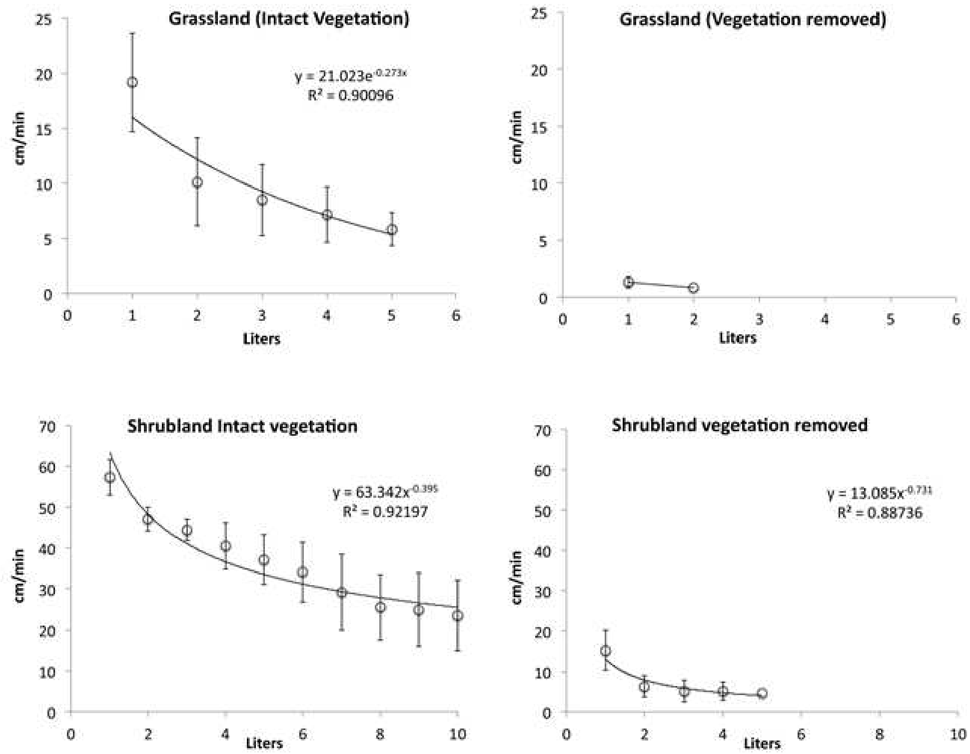

Figure 2: Soil water saturation surveys carried out under shrubland and grassland vegetation in a high-altitude páramo ecosystem in northeastern Ecuador. Essays where performed on intact soils and on soils from which upper vegetation layer had been removed.

Materials and Methods

Study area

This study was carried out in the Paluguillo area, a páramo watershed on the eastern mountain range of the Andean cordillera in northern Ecuador (00° 18.421 S; 078° 13.963 W). Our study sites are located in the west-facing slope of the mountain range, at altitudes between 3600 and 3900 m, and they experience annual means of temperature and precipitation of 6°C and 1300 mm respectively (Estación Meteorológica Paluguillo; Universidad San Francisco de Quito). The native vegetation is characterized by a heterogeneous matrix of páramo grasslands (primarily *Festuca* sp. and *Calamagrostis* sp.), with patches of forest dominated by *Polylepis* spp. and *Gynoxis* sp., and shrublands with a diverse array of woody species such us *Hypericum laricifolium*, *Diplostephium ericoides*, *Pentacalia peruviana*, *Baccharis* spp, and *Loricaria ferruginea*. The area also exhibits patches of vegetation altered by human activities such as roads or trails commonly dominated by dense mats of *Lachemilla orbiculata*, or mono-specific plantations of exotic trees (*i.e. Pinus* or *Eucalyptus*). In addition to striking differences in structure and richness of native species, all this vegetation types and land cover categories differ markedly in the nature and composition of the ground cover vegetation, from large mats of bryophytes and herbaceous vegetation up to 15 cm in thickness in shrub dominated patches, to bare ground or dense mono - specific carpets of grazing resistant species such as *Lachemilla orbiculata*, which are mainly distributed in cattle trails or roads.

In order to asses potential differences in water infiltration capacities of soils under different vegetation types or coverage, we selected representative patches of the following categories: *Polylepis* forest, *Diplostephium ericoides* shrubland; páramo grassland, Pine forests, and hiking trails. This particular order roughly reflects a gradient of increasing levels of human impact from the less disturbed vegetation of the *Polylepis* forest, to the drastically altered vegetation found in cattle trails. All patches were located on flat terrain or exhibited moderate slopes (25-30°) and occurred over typical Andosols, rich in organic matter and derived from volcanic materials.

Infiltration essays

We used a modified infiltration-ring methodology that allows ample replication and large spatial coverage. Although this method cannot be used to estimate infiltration capacities under normal field conditions (the volumes of water poured into the rings are much larger than the volumes that fall during typical rain events), it is useful to characterize potential differences between soils under contrasting vegetation types. We performed a series of infiltration essays using a metal infiltration ring (diameter = 0,17 m). For each essay, we pushed the infiltration ring 10 cm into the soil, trying to cause the least possible disturbance to soil structure. Then, we poured 1L of fresh water, collected in adjacent streams, into the ring, and recorded the time needed for all water to be absorbed by the soil. Although infiltration rates were extremely high for most soils, in the cases where they were slow we waited for a maximum of ten minutes and then recorded the volume of water remaining in the ring. In no case did we observe lateral flow of water out of the infiltration ring.

In each vegetation type or land-cover category, we carried out ten pairs of randomly located infiltration essays. The first essay of each pair was performed on intact soils in which we conserved the ground cover intact, while the second essay of the pair was performed 2 m away from the location of the first essay, in a spot in which undecomposed organic materials, surface leaf litter (O horizon) and plant ground cover wrere carefully removed (avoiding disturbance of lower layers) to a depth in which the A horizon was exposed. These essays were performed during the dry season of 2010, between June 28^{th} and September 29^{th}. This period was mostly characterized by very small and sporadic precipitation events, which did not exceed 56 mm per month. The mean difference in water infiltration rates between intact and bare soil sampling spots was used to estimate the relative contribution of ground vegetation cover to water infiltration capacity in each vegetation or land-cover category. In order to assess potential seasonal differences in the patterns of water infiltration capacities, we performed a second set of infiltration essays during the wet season, in April 2011. Because of logistical constraints, essays in this period were restricted to the shrubland and grassland vegetation types.

During the second sampling period we performed four individual soil-saturation tests in shrubland and grassland vegetation types. The purpose of these tests was to estimate the volume of water needed to saturate these páramo soils, both when vegetation cover is intact and when it has been removed. For each tests, we placed the infiltration ring as described above, and successively poured individual 1L-volumes of water, recording in each case the time needed for all the water to infiltrate the soil. We kept adding additional water volumes, until the infiltration time for the last liter of water exceeded 5 minutes. Four saturation tests were performed with the ground vegetation layer intact (control), and four were performed after this layer had been removed.

In addition to the infiltration essays, we collected the ground cover layer removed from each sample during the water infiltration essays. These samples were taken to the laboratory, dried for 24 hours at 70°C, and weighed to estimate total biomass in this layer. Immediately after the infiltration essays of the dry season, we collected soil samples (0-10 cm) in five of the sampling spots used for the water infiltration essays in each vegetation or land-cover category. These samples were air dried, passed through a sieve (mesh-size 2 mm) and analyzed for organic matter content using the Walkley-Black acid digestion method.

The effects of vegetation type and the presence or absence of the ground vegetation cover on water infiltration rates were evaluated through a two-way analysis of variance, whereas the influence of organic matter and the biomass of ground vegetation cover were assessed by ANCOVA, in which the amount of organic matter (%) was treated as covariate. All the analyses were performed on un-transformed data after assumptions of equal variance and normal distributions were tested.

Results

During the dry season, water infiltration rates differed significantly between vegetation or land-cover categories (Table 1) and achieved the highest values in the undisturbed páramo vegetation (*Polylepis* forest and páramo shrubland), averaging 56 cm/min (Figure 1). These infiltration capacities in undisturbed vegetation were between four and five times higher than comparable values measured in the páramo grassland (mean $\pm$ SE = 8.4 cm/min $\pm$ 1.5), the pine plantation (13.4 cm/min $\pm$ 3.0) and the trails (6.4 cm/min $\pm$ 1.7; Figure 1). In all land cover categories, water infiltration rates were higher in the control treatments, than in the infiltration essays performed after removing the ground vegetation layer (Figure 1). These differences were especially large in the shrubland, grassland, and Pine forest categories, where the infiltration rates in the control essays were between three and eight times higher than those estimated in the vegetation removal treatments.

Water infiltration capacities measured during the wet season in the shrubland (55.5 cm/min $\pm$ 2.6) and grassland (19.17 cm/min $\pm$ 4.5) vegetation types, were extremely similar to those measured during the dry season (Figure 1). Differences between control and infiltration essays performed after removal of the ground vegetation layer were also similar to those measured during the first sampling period (Figure 1). These patterns

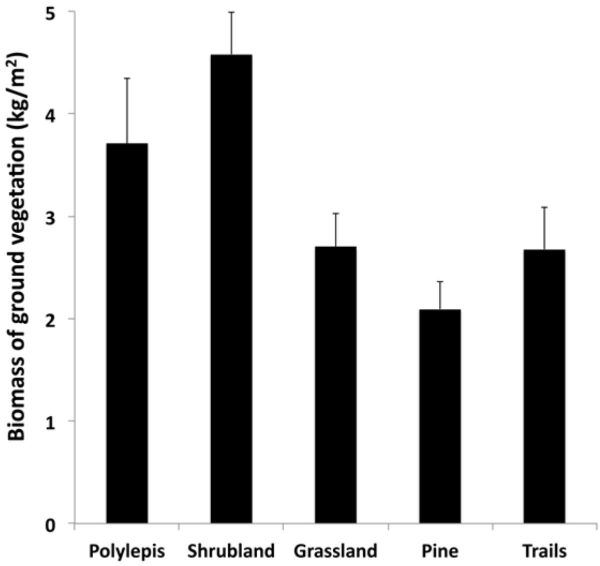

Figure 3: Biomass of the ground vegetation layer in different vegetation or land-use types in a high-altitude páramo ecosystem in northeastern Ecuador. Each bar represents the average (+ standard error) of ten samples.

	DF	SS	Mean Square	F	Pr > F
Intercept	1	322.6	322.6	392.01	0.000000
Vegetation Type	4	148.0	37.0	44.96	0.000000
Treatment	1	69.0	69.0	83.89	0.000000
Vegetation Type *Treatment	4	21.3	5.3	6.49	0.000123
Error	90	74.0	0.8		

Table 1: Results of ANOVA performed on the rates of soil water infiltration in different vegetation or land-cover categories in a high-altitude páramo ecosystem in northeastern Ecuador. Infiltration rate was the dependent variable, analyzed against five levels of the factor "vegetation type" and two levels of the factor "treatment": intact soil infiltration essays, versus removal of the ground surface vegetation cover before the infiltration essay.

were also observed during the soil saturation essays performed during the wet season. When the ground vegetation cover was intact, soil saturation followed a shallow power or exponential function, which retained considerable infiltration capacities even after more than 5 L of water had been poured in the infiltration ring, especially under shrubland vegetation (Figure 2). Saturation essays performed after removal of the ground vegetation were extremely short and demanded only 2 to 5 lt of water to saturate the soil (Figure 2).

Biomass of the ground vegetation differed among vegetation and land-cover types, and exhibited the highest values in the shrubland and *Polylepis* patches (3.7-4.5 kg/m^2; Figure 3). In the case of the these vegetation types, the ground cover was characterized by a thick mat of mosses (up to10 cm high) and partly decomposed plant materials (mainly Bryophytes) which completely covered the soil, leaving virtually no bare ground. In the páramo grassland, a dense mat of decomposing grass leaves and roots predominantly composed the grassland ground cover, which was not continuous and reached approximately 70 to 80% of the area of the interstices between grass tussocks. The biomass of ground plant cover in the pine forest and the trails did not differ significantly from the biomass in the grassland patches (Figure 3), but its nature is different. In the case of the Pine forests, a thick layer of pine needles formed it, whereas in the trails it was composed of a dense mat of *Lachemilla orbiculata* (Rosaceae), a grazing resistant plant that forms extremely dense carpets in disturbed páramo ecosystems.

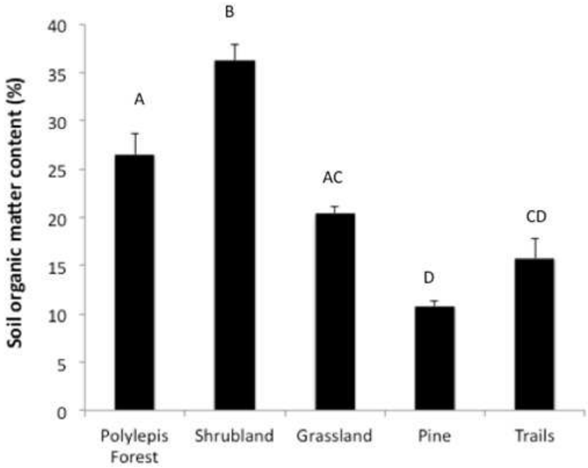

Figure 4: Soil organic matter content under different vegetation or land-use types in a high-altitude páramo ecosystem in northeastern Ecuador. Each bar represents the average (+ standard error) of five samples taken randomly from the first 10 cm of soil.

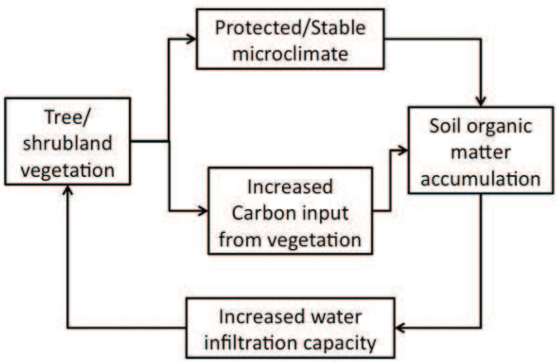

Figure 5: Schematic representation of the hypothesized relationships between plant cover, soil organic matter, and water infiltration capacity in páramo ecosystems in the Ecuadorian Andean páramo.

Soil organic matter content was very high in the undisturbed vegetation patches, averaging 36% $\pm$ 1.7 in the shrubland vegetation, and 26% $\pm$ 2.2 in the *Polylepis* forest (Figure 4). These values differed significantly from those measured in the disturbed vegetation patches, achieving the lowest organic matter contents in the Pine forest soils (10.8% $\pm$ 0.6; Figure 4). Despite these significant differences in organic matter content among land cover categories (Figure 4; Table 2), this variable was not a significant predictor of water infiltration capacities. On the contrary, the analysis of covariance performed on infiltration data, showed that the best predictor of soil infiltration capacity was the biomass of the ground vegetation layer, whereas the organic mater content, treated as a covariate, showed no significant effects (Table 2).

Conclusions

Differences in soil water infiltration capacities have been frequently related to the amounts of organic matter stored in the soil, especially in mesic regions where well - developed soils with large stocks of organic material usually exhibit higher water storage capacities and infiltration rates [21]. This relationship, however, minimizes the potential role that ground vegetation cover could have in the hydrological behavior of soils, a role that could be significant in mountain regions where the topographical and altitudinal gradients produce an extremely

Source	**DF**	**Type III SS**	**Mean Square**	**F**	**Pr > F**
Vegetation Type	4	6983.4	1745.8	69.57	<0.0001
Organic matter (%)	1	38.5	38.5	1.53	0.2314
Biomass (g)	1	164.4	164.4	6.55	0.0197

Table 2: Results of ANCOVA performed on the rates of soil water infiltration in different vegetation or land-use types in a high-altitude páramo ecosystem in northeastern Ecuador. Infiltration rate was the dependent variable, analyzed against five levels of the factor "vegetation type" and the biomass (g) of the ground surface vegetation cover and content of soil organic matter (covariate) as independent variables. Organic matter * Biomass interaction was not significant and consequently was dropped from the model.

heterogeneous vegetation matrix. In this context, the main purpose of our study was to assess if contrasting vegetation or land-use categories in an Andean páramo exhibit different soil water infiltration capacities.

Our results confirmed the extremely high infiltration capacities that commonly characterize organic matter-rich soils in general, and Andean Andosols in particular. The infiltration rates that we measured in the shrubland páramo and the *Polylepis* forest (20 and 50 cm/min) are almost one order of magnitude higher than common infiltration rates reported for other Andosols [20]. Interestingly, these high infiltration capacities did not varied significantly between dry and rainy seasons, suggesting that they are not an artifact of soil water content at the moment of our sampling. This conclusion is further supported by the saturation essays that we performed during the wet season, which showed that intact pára-mo soils, such as those found in our study site, can receive large volumes of water without altering significantly their water infiltration capacities. According the models developed during these essays (Figure 2), the volume of water needed to decrease the initial infiltration capacity by 50% were 2.5 litters for the grassland vegetation, and 7.5 litters for the shrubland vegetation.

Our data suggest that the hydrological behavior of high-altitude Andean ecosystems is extremely heterogeneous and is influenced by the nature of the vegetation cover and type of land-use. More specifically, in this study we show that common land-use practices that are currently affecting páramo ecosystems, such as afforestation with exotic species, or the burning and accompanying cattle rising, are associated with i) changes in the structure of the vegetation, including the vegetation ground layer, ii) a significant decrease of soil organic matter content, and iii) a drastic reduction in the water infiltration capacity of the soil (Figures 1 and 2). Although the scale of our study is different, our results support previous research that reports changes in the hydrological behavior of páramo soils exposed to land-use changes. For example, Buytaert et al. [16] reported that an Ecuadorian páramo watershed planted with the exotic *Pinus patula*, exhibited water yields that were 50% smaller than those in a control watershed. At the local level, these watershed-scale changes are probably related to losses of organic matter and water retention capacities of the soil as those reported by [15] in overgrazed páramo ecosystems, or [7] in páramo pine plantations, and to increased erosion and reduction in infiltration capacities such as those reported in this study (Figure 1), and in other Ecuadorian páramo ecosystems exposed to burning and grazing [14].

The water infiltration capacities that we measured in the shrubland páramo and the *Polylepis* forests are extremely high. In accordance to previous studies [7, 9, 10], we attribute this pattern to the high content of organic matter (25 to 35%; Figure 4) and to the excellent structure that characterize the Andosols in our study area and in other páramo localities. However, our results also suggest that soil organic matter content alone cannot explain the great variation and the extremely high infiltration capacities that we report in this study. In fact, the biomass and the characteristics of the ground vegetation layer that covers the soil were a more powerful predictor of soil water infiltration capacities that we measured in the field. From this perspective, the modification in vegetation structure that follows land-use change in the páramo (i.e. removal of *Polylepis* forests or shrubby vegetation by repeated fires, and the homogenization of grasslands or establishment of exotic tree plantations), affects the hydrological behavior of páramo ecosystems not only by reducing the content of SOM, but also by changing the nature of the ground vegetation cover of the soil.

Although previous studies have already highlighted the influence of aboveground biomass on the water infiltration capacity of soils, emphasis has been commonly put on the effects of total aboveground biomass [19, 21–23]. Although in our study area the vegetation types with higher infiltration capacities (*Polylepis* and shrubland) were also those with higher aboveground biomass (R. Sierra and E. Suárez, pers. obs.), in this study we highlight the influence of a more specific ecosystem component, the layer of plant materials covering the soil surface. This layer made a significant contribution to the total infiltration capacity of soil under the majority of the vegetation types that we analyzed. In fact, our data showed that its removal resulted in water infiltration rates that were between two and six times slower than the rates obtained from control infiltration essays (Figure 1). We hypothesize that this contribution of the plant ground cover to total infiltration capacities are probably due to the capacity of this layer of to absorb water when its plant materials (dead and alive) are not saturated; and, the creation of a complex and dense spatial structure which serves as a sponge, providing additional space for water storage.

From this perspective, we suggest that the maintenance of the thick ground layer could be crucial in terms of sustaining the water regulation capacity of páramo and other high-altitude ecosystems. In the case of the páramo, and based on available information [24–27], we suggest that the persistence and magnitude of this layer might be dependent on the microclimate created by the closed canopy of the shrubs or trees that dominate areas with low levels of human intervention. In these areas, thick vegetation cover might ameliorate the huge temperature variations that characterize these ecosystems, keeping a higher moisture content which facilitates development of a thick layer of mosses and other ground vegetation (Figure 5). Together with increased inputs of plant materials to the soil, a more stable and humid microclimate might promote higher accumulation of soil organic matter, further increasing the water infiltration capacity of the soil, and the conditions that ultimately favor the persistence of shrubland or forest vegetation in the páramo. In the same way, elimination of the shrubland vegetation as occur after repeated fires, or forest clearing, would start a negative feedback that alters the microclimate and organic matter inputs to the soil, reducing the content of soil organic matter, and water infiltration capacities. Although some of the proposed links along this feedback chain (Figure 5) have not been analyzed, this framework could provide a useful way to think about restoration of the hydrological properties of páramo soils that have been degraded by human activities. In the case of the Andean páramos and other mountain ecosystems around the world, this will become increasingly important as the human demand for water resources increase, along with the land-use pressures that currently affect high-altitude ecosystems [5, 28, 29].

For this study, we used a modified infiltration-ring methodology that allows ample replication and large spatial coverage. This method cannot be used to estimate infiltration capacities under normal field conditions, because the volumes of water poured into the rings are much larger than the volumes that fall during typical rain events. From this perspective, the high infiltration capacities that we measured in this study must be considered cautiously, specially regarding their contribution to large-scale hydrological behavior, and should not be extrapolated to watershed-level calculations. Our discussion emphasizes not the overall magnitude of the water infiltration rates in our study sites, but the relative differences between vegetation types, and the role of the ground vegetation cover. New studies should be conducted to evaluate the magnitude of the infiltration patterns under normal field conditions.

In conclusion, our data suggest that the large differences observed in water infiltration capacities of soils under different vegetation or land-cover categories, could have significant impacts in the hydrological behavior of páramo ecosystems. An area dominated by shrubland or *Polylepis* forest, for example, could have a better capacity for water regulation than a comparable area dominated by páramo grassland, or Pine plantations. Current management practices, however, tend to homogenize the páramo ecosystems, favoring the development of large tracts of grasslands, with low coverage of shrublands and native forests. From this perspective, we suggest that future management and restoration initiatives should be aimed at trying to restore a more complex matrix of grasslands, shrublands and native forests, which likely will favor both, biodiversity conservation, and the maintenance of the critical ecosystem services that we draw from mountain ecosystems.

Acknowledgments

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