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Comparison of Natural Regeneration in Natural Grassland and Pine Plantations across an Elevational Gradient in the Páramo Ecosystem of Southern Ecuador

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Abstract: During the 1980s, reforestation programs using exotic species (*Pinus* spp.) were established in the páramo ecosystem of Ecuador. The aims of this study were: (1) to compare the natural regeneration between pine plantations (Pi) and natural grassland (NG) across an elevational gradient and (2) to identify the attributes of Pi and soil properties that were influencing herbaceous and woody plant composition and their plant cover. In total, six independent *Pinus patula* (Schltdl. & Cham. plantations (two per each elevation) were selected and distributed in an elevational range (3200–3400, 3400–3600, 3600–3800 m a.s.l.). Adjacent to Pi, plots in NG were established for recording natural regeneration. Both, namely the attributes and the soil samples, were measured in Pi. The results showed that natural regeneration differs significantly between both types of vegetation. As expected, NG holds more plant diversity than Pi; the elevational range showed a clear tendency that there was more herbaceous richness when elevation range increases, while the opposite was found for woody species. Moreover, attributes of Pi influenced herbaceous and woody vegetation, when saturated hydraulic conductivity (Ksat) in the soil, basal area (BA) and canopy density (CD) increased, herbaceous species richness and its cover decreseased; and when Ksat and the acidity in the soil increased, woody plants richness and its cover decreased. The plantations have facilitated the establishment of shade tolerant species. More studies are needed to evaluate if removal with adequate management of pine plantations can improve the restoration and conservation of the native vegetation of the páramo ecosystem.

Keywords: Andes; species richness; vegetation assemblage; plant cover; natural grassland; soil properties

1. Introduction

The Neotropical alpine ecosystem of the "páramo" provides several ecosystem services like water regulation and supply, carbon storage and biodiversity conservation [1,2]. Furthermore, the páramo ecosystem hosts the richest high mountain flora in the world [3], and the fastest average net diversification rates of all 'hotspots' or areas featuring exceptional concentrations of endemic species that are experiencing exceptional loss of habitat [4,5]. According to Hofstede et al. [2], 1,524 species of vascular plants have been registered in the páramo of Ecuador, from which approximately 628 are endemic (15% of Ecuadorian endemic plants). This great biodiversity of this ecosystem is related to the diversity of the ecological conditions linked to the glacial geomorphology that has resulted in a large number of different plant associations, each one with their typical species [6].

Elevation is an important factor that shapes plant diversity in the páramo. The elevational gradients combine sets of environmental conditions such as: temperature, wind velocity, atmospheric gas composition, water availability, nutrient deposition and cycling, soil weathering and solar radiation, all of which determine the composition and structure of vegetation [7]. Based on the influence of these factors and vegetation structure, the páramo has been divided into three zones, from lowest to highest: subpáramo, páramo (páramo grassland) and superpáramo [8]. The subpáramo, also called páramo forest, shrubby páramo, subpáramo woodland and subpáramo elfin forest [9], is the transition zone (ecotone) between the forest (upper montane cloud forest) and the páramo grassland [8–11]. The subpáramo is usually an entangle of shrubs and small dispersed trees, gradually reduced in size, that gives way to grasses and herbs [9]. The páramo vegetation zone, also called grass páramo or páramo grassland, is characterized by tussock grasses dominated by species of *Calamagrostis* and/or *Festuca*. Finally, above the páramo, there is the superpáramo, which is the zone located between the páramo and the permanent snow. In some cases, small isolated woodlands of *Polylepis* could be found above the subpáramo zone [9–11].

Unfortunately, human activities can significantly alter páramo biodiversity [12], associated with land use change and climate change, which are promoting loss of native grassland cover [13]. It is estimated that 40% of the original Ecuadorian páramo has been transformed into agroecosystems and that 30% is used for extensive livestock grazing [2]. Livestock has a negative effect on the vegetation structure by making it more open and less tall, and also on its composition by reducing shrubs and endemic plants [14,15]. Cattle raising is usually combined with burning of natural grassland to provide the cattle with fresh and more tender grasses [12,16]. The impacts of burning are a decrease in the productivity of the vegetation and a drastic change in its composition, depending on the frequency and intensity of the fires [2]. Woody species are the least resistant to burning, and the greater frequency and intensity of burning favors the establishment of exotic weed species [17]. Another activity that alters biodiversity is afforestation, which in the last decades has been promoted in the páramos of Ecuador for timber production and carbon sequestration with exotic species such as *P. patula* and *Pinus radiata* D. Don. Pine species have been selected because of their fast growth which make them more appreciated by local people also due to the limited forestry knowledge of native species [18–20].

In the scientific community, the debate of the impact of afforestation on biodiversity, specifically on the floristic composition due to the conversion of grassland into forest plantations, is still going on [21]. In the region of the study, the impact of these plantations on ecosystem services has generated disputed perceptions among their stakeholders [22], as most of them have been established on non-forest vegetation that alters the hydrology [23–25] and soil characteristics [18,19,26,27]. In terms of plant diversity, Ohep and Herrera [28] found that in the páramo of Venezuela not much understory vegetation was growing under dense pine plantations due to the lack of light passing through the canopies. In the highlands of Colombia, Van Wesenbeeck et al. [29] found that species diversity of native vegetation decreased when pine plantations coverage increased. Also, Cavalier and Santos [30] found few species growing under pine plantations because of the accumulation of needles and high biomass of fine roots. Nevertheless, in the páramo of Ecuador, Hofstede et al. [18] observed that in some cases the vegetation growing in some pine plantations was similar to the natural grassland; and Bremer [31] found that in one area, plant species richness was lower in pine plantations than in natural grasslands, but higher in another plantation area that was adjacent to a native forest.

In other regions of the world, there is enough evidence that plantations can provide protective functions and have a nurse effect for the natural forest regeneration by modifying both the physical and biological site conditions [32–34]. The importance of nurse plants lies in that they facilitate the growth and development of other plant species, offering a microhabitat with optimal conditions for seed germination and/or seedling recruitment, Ren et al. [34]. Therefore, plantations with exotic species could provide complementary conservation services [35].

Afforestation with pines reduces soil organic matter contents as a result of a faster decomposition due to a lower soil water content [1], however there is a lack of information of how soil properties under pine plantations impact the natural regeneration of both herbaceous and woody species. Several studies have shown changes in soil properties after the establishment of plantations on grasslands [18,19,36–39]. However, little is known about the effects on herbaceous and woody plant richness and composition. Besides, several authors agree that, in mountain regions, the elevational gradient explains the variation in soil properties [40,41].

Our study addressed the following questions: (1) Are there differences in herbaceous and woody floristic composition in an elevation range (3200–3400, 3400–3600, 3600–3800 m above sea level (a.s.l.) and in different types of vegetation (pine plantation and natural grassland) in the páramo ecosystem of Southern Ecuador? and (2) What are the effects of soil properties and plantation attributes on herbaceous and woody plant composition under pine plantations among different elevational ranges?

2. Materials and methods

The study area is located in the Azuay Province in Southern Ecuador. In total, six pine plantations of *Pinus patula* were chosen for the study in three different elevational ranges, and two different sites were selected in each of these ranges: La Paz and Nero from 3200 to 3400 m a.s.l., Tutupali Chico and Tutupali Grande from 3400 to 3600 m a.s.l. and Quimsacocha and Soldados from 3600 to 3800 m a.s.l. Additionally, natural grassland sites adjacent to these plantations were also selected for recording natural regeneration information (Figure 1).

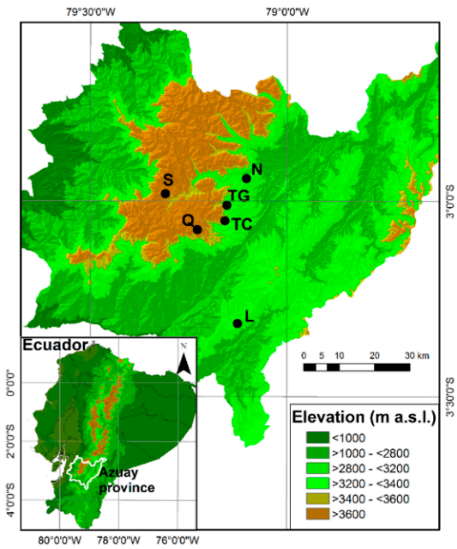

Figure 1. Location map of the study area showing the sites that correspond to natural grassland and pine plantations in three different elevational ranges: N (Nero) and L (La Paz) from 3200 to 3400 m a.s.l., TC (Tutupali Chico) and TG (Tutupali Grande) from 3400 to 3600 m a.s.l. and Q (Quimsacocha) and S (Soldados) from 3600 to 3800 m a.s.l.

In regard to climate conditions, the páramo ecosystem in the Azuay province is characterized by high differences in temperature during the day and night [9,25]. Rainfall presents a high spatial variability, it is well distributed year round, and seasonality is less pronounced at higher elevations; the mean annual precipitation ranges from 660 to 3400 mm [42]. The high variability depends on the geographic location with a high precipitation increment from west to east influenced by the Pacific regimen and air masses from the Atlantic [43]. Table 1 shows information of meteorological characteristics according to each elevational range in the study area.

Table 1. Characteristics of pine plantations across the elevational range in the study area. Except for temperature and precipitation, all variables include the median and, between parentheses, the quartiles Q1 and Q3. Bi = pine biomass, TD = tree density, DBH = diameter at breast height, TH = tree height, BA = basal area, CD = canopy density.

Elevational Range (m a.s.l.)	3200–3400		3400–3600		3600–3800	
Plantation	**Nero**	**La Paz**	**Tutupali Chico**	**Tutupali Grande**	**Quimsacocha**	**Soldados**
Mean annual temperature (minimum–maximum in °C) [a]	5–15		4–13		1–12	
Mean annual precipitation (mm) [b]	1100		1200		1250	
Slope (%)	20(15–25)	12(11–16)	16(12–28)	30(27–43)	22(22–26)	20(18–20)
Age (years)	18(18–18)	17(17–17)	16(16–16)	22(20–22)	19(19–19)	16(16–19)
Bi (t/ha) [c]	105.7(88.1–134.4)	107.8(77–5–162.0)	103.6(76.8–138.7)	90.7(70.8–93.6)	19.9(14.8–58.0)	22.2(14.6–46.4)
TD (trees/ha)	694.4(677.1–729.4)	850.3(833.3–920.0)	711.7(677.2–781.3)	781.3(711.7–955.1)	573.1(486.2–573.1)	555.6(486.2–607.5)
DBH (cm)	20.2(18.4–23.2)	19.7(17.3–26.0)	24.2(18.6–24.5)	16.5(15.6–18.9)	9.0(8.0–11.5)	10.5(9.8–11.9)
TH (m)	11.1(10.5–12.0)	8.8(8.5–10.2)	10.4(7.9–12.1)	7.3(7.3–8.0)	4.9(4.5–5.0)	4.6(4.5–5.1)
BA (m^2/ha)	19.9(16.7–22.1)	22.9(17.3–30.9)	26.6(24.0–28.4)	18.6(18.3–20.5)	3.7(3.0–4.8)	4.7(4.7–8.0)
CD (%)	82.7(75.7–87.7)	92.3(89.0–94.3)	97.3(97.0–97.3)	81.0(78.0–91.0)	19.3(12.7–24.0)	64.8(63.8–66.1)

[a] [44], [b] [42], [c] [45].

In the páramo of Southern Ecuador, soils are classified as Aluandic or Silandic Andosols presenting Hydric and Histic properties with low volcanic glass content [46]. These soils are dark, humid and have excellent water infiltration and retention; a high organic carbon content between 10 and 40%, and water storage capacities could be more than 0.4 cm^3/cm^3 [47].

2.1. Description of Natural Grassland and Pine Plantations

In general, the natural grassland (NG) is found between 3200 and 3800 m a.s.l. [48], dominated by tussock grasses, mainly *Calamagrostis* spp. and *Festuca* spp. A great diversity of herbs, sub-shrubs and shrubs grows under or between the tussocks. The presence of woody species was very low above 3600 m a.s.l. The only forest able to grow at such high elevation is the one formed by *Polylepis* spp. However, in our study area, we did not include this genus because they form specific patches mostly in concave sites in very protected places and distant from the pine plantations. We identified six NG sites situated near each plantation site.

The plantations of the study have been established for the purpose of timber production (its wood is used in plywood, chopsticks, and in the form of densified wood). Five of the plantations are part of a program of carbon sequestration through afforestation. Because the growth of *P. patula* in the highlands decreases at 25, harvesting is generally done between 20 and 25 years. The selected plantations were between 16 and 22 years old (in 2015) according to personal communication with the landowners. Most of the plantations were established on grazed páramo, all of them are first rotation with 3 × 3 m spacing, and they have been protected from grazing since their establishment. At each elevational range, the average biomass of the pines varied, showing a clear tendency of decreasing biomass with increasing elevation. Table 1 shows the characteristics of the pine plantations distributed in the elevational range.

2.2. Experimental Design and Data Collection

Fieldwork was carried out from July to November 2015. For recording natural regeneration in both types of vegetation (Pi and NG), 20 independent plots of 576 m^2 (24 × 24 m) were randomly located and established in each elevation range (total 60 plots for herbaceous and 40 plots for woody plants). In each plot, subplots were established to record different types of understory vegetation: (i) two subplots of 100 m^2 (10 × 10 m) located in each corner of the diagonal of the plot, each for woody species including non-prostrate shrubs, treelet and trees only; (ii) three subplots of 25 m^2 (5 × 5 m) located in each corner and in the center of the diagonal of the plot, each for herbaceous species including prostrate shrubs-sub shrubs and vines. The subplot size of 25 m^2 was based on the method used by Sklenar and Ramsay [49]. For the purposes of our study, we did not differentiate the type of natural regeneration (from self-sown seed, coppice shoots or root suckers).

In our study area above 3600 m a.s.l., woody plant composition was not registered because of the low abundance of this type of vegetation. Additionally, cover vegetation for all species was estimated using the Braun-Blanquet scale [50], (*r* = 0.01%, + = 0.1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100%) subsequently converted into percentage coverage for the respective analysis using their midpoint values. The plant identification was done at species level, but in some cases it was only possible to identify plants at the genus or family level.

In each plot of 24 × 24 m at Pi, five points were selected (four in the corners and one in the center) for measuring canopy density (CD) using a convex spherical densitometer [51]. The average of all the points per plot was calculated for the respective data analysis. The basal area (BA) was calculated based on all tree measurements using diameter at breast height (DBH) and the average of data per plot was calculated. The slope and the aspect were measured from the center of the plot using a Suunto compass. In order to avoid the influence of the slope aspect on the analysis, 90% of the plots were located facing East.

2.3. Soil Sampling

In Pi, the soil sampling was carried out between 0–10 cm of depth in three different subplots located randomly in each plot of 24 × 24 m. In each subplot, the soil samples were taken at a distance of 75 cm from the tree, one sample of 1 kg of disturbed soil and two samples with rings of 100 cm^3, each of undisturbed soil, were taken. The disturbed sample was used for analyzing the chemical properties of the soil, and the undisturbed samples were used for analyzing the physical properties.

Additionally, saturated hydraulic conductivity was determined in the field using three replicates through inversed auger-hole method [52]. All samples for physical analysis were carried to the soil laboratory at the University of Cuenca, and for chemical analysis to the soil laboratory of the Institute of Silviculture at the Technical University of Munich, Germany.

2.4. Soil Analysis

The disturbed soil samples were air-dried at room temperature and passed through a 2-mm sieve. The carbon-nitrogen ratio was calculated by determining the organic carbon and nitrogen with the wet combustion method using an elemental analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany). The pH was analyzed using a potentiometer with a soil-water ratio of 1:2.5. The undisturbed soil samples were used to determine water content at saturation point (StC) (pressure 1 cm H_2O) and water content at field capacity (FC) (pressure 330 cm H_2O) through pressure chambers. To determine the wilting point (WP), a saturated soil paste was made with disturbed soil, and later placed in a high pressure chamber at 15,300 cm H_2O [53]. The gravitational water (GW) was obtained as the difference between water content at saturation point and water content at field capacity, while the water availability (AW) was obtained as the difference between water content at field capacity and wilting point. Bulk density (BD) was determined with dried undisturbed samples at 105 °C for 24 h.

2.5. Data Analysis

In order to detect the effects of elevational range and type of vegetation on species richness and plant cover of herbaceous and woody species, a linear mixed model (LMM) was carried out. We used as fixed factors, the elevational range and type of vegetation, and as random factor, each site nested within the elevation. This model was selected based on previous running models with different combinations of fixed and random factors. Therefore, the best model with goodness of fit was chosen according to information criteria such as the widely used Akaike Information Criteria (AIC) and the Bayesian Information Criteria (BIC). This analysis was performed using R package nlme [54].

For evaluating the composition and floristic assembly of plant communities, rank species abundance curves were used. In both Pi and NG at each elevational range, the abundance value of each species was calculated at plot level using the average of the plant cover among subplots.

A Canonical Correspondence Analysis (CCA) was performed to evaluate the relationship between the attributes of Pi and soil properties (physical and chemical) and herbaceous and woody species richness and their cover, in three different elevational ranges. Box-Cox transformations were used due to the lack of normality according to the Shapiro test ($p < 0.05$). For this analysis, the vegan package [55] from R software was used. All statistical analyses were executed in the R Project program version 3.2.3 [56].

3. Results

3.1. Effects of Elevational Range and Type of Vegetation on Hebaceous and Woody Vegetation

Herbaceous vegetation: The results showed a clear tendency that species richness increases with elevational range (Table 2, Figure 2a) ($p < 0.0001$). As expected, NG had more species richness than Pi cover, showing a high statistical significance for both factors (elevation range and type of vegetation) ($p < 0.0001$) (Table 2, Figure 2a). However, the interaction of both factors did not show a high statistical significance ($p = 0.2304$), indicating that their combination did not contribute to the performance of natural regeneration. The percentage of plant cover differed significantly among the three elevational ranges ($p < 0.0001$) (Table 2), with a marked difference between 3200–3400 and 3400–3600 m a.s.l, and between NG and Pi (Figure 2b) which was highly significant ($p < 0.0001$). However, herbaceous vegetation cover under NG was reduced in the highest elevational range compared to the mid elevational range and it was similar to the herbaceous vegetation cover under Pi (Figure 2b). A list of herbaceous species is presented in Appendix A.

Table 2. Influence of elevational range and type of vegetation on species richness and percentage of plant cover of herbaceous vegetation according to the ANOVA analysis obtained from the linear mixed model (LMM).

Factor	DF	F Value	*p* Value
Herbaceous species richness			
Intercept	1	1219.2021	<0.0001
Type of vegetation	1	75.6021	<0.0001
Elevational range	2	98.7806	<0.0001
Type of vegetation: Elevational range	2	1.5084	0.2304
Herbaceous plant cover			
Intercept	1	564.1922	<0.0001
Type of vegetation	1	63.1343	<0.0001
Elevational range	2	24.4648	<0.0001
Type of vegetation: Elevational range	2	16.6442	<0.0001

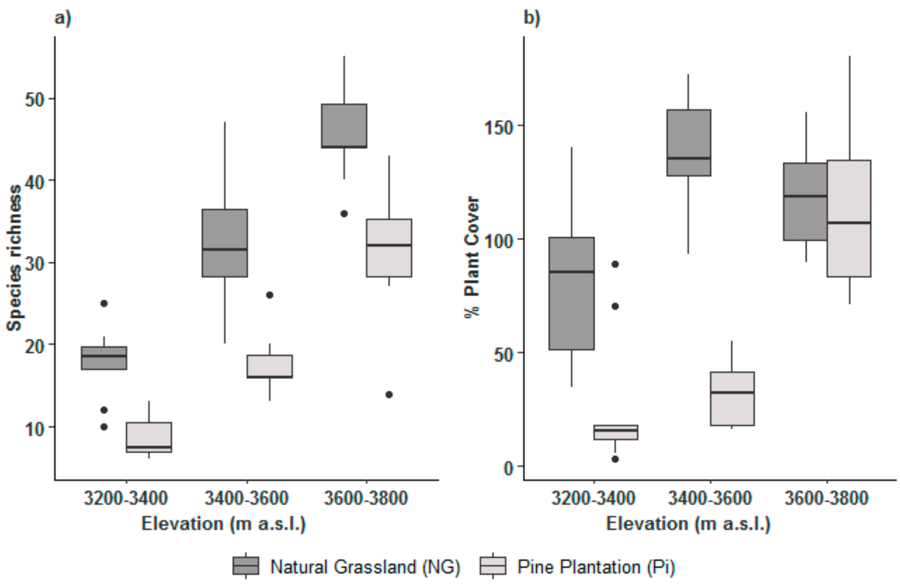

Figure 2. Box plots for the effects of elevational range (3200–3400, 3400–3600, and 3600–3800 m a.s.l.) and vegetation (Pi, NG) on (**a**) herbaceous species richness and (**b**) percentage of herbaceous vegetation cover.

Woody vegetation: In contrast to the herbaceous vegetation, woody species richness and their plant cover had the tendency to decrease with elevational range (the effect was not statistically significant, $p > 0.05$) (Table 3, Figure 3a,b); however, the interaction between elevational range and type of vegetation for species richness and plant cover was statistically significant ($p < 0.005$) (Table 3), indicating that the interaction of both factors plays an important role on evaluating the variables of species richness and plant cover. Besides species richness and plant cover were also higher at NG than Pi, showing high statistical significance ($p < 0.001$, Figure 3a,b). Appendix A presents a list of woody species.

Table 3. Influence of elevational range and type of vegetation on species richness and plant cover of woody vegetation according to an ANOVA analysis obtained from the linear mixed model (LMM).

Factor	DF	F Value	*p* Value
Woody species richness			
Intercept	1	54.4736	<0.0001
Type of vegetation	1	77.7789	<0.0001
Elevational range	1	3.2464	0.3226
Type of vegetation: Elevational range	1	17.30	0.0002
Woody plant cover			
Intercept	1	48.5569	<0.0001
Type of vegetation	1	64.7345	<0.0001
Elevational range	1	1.3268	0.4551
Type of vegetation: Elevational range	1	4.9888	0.032

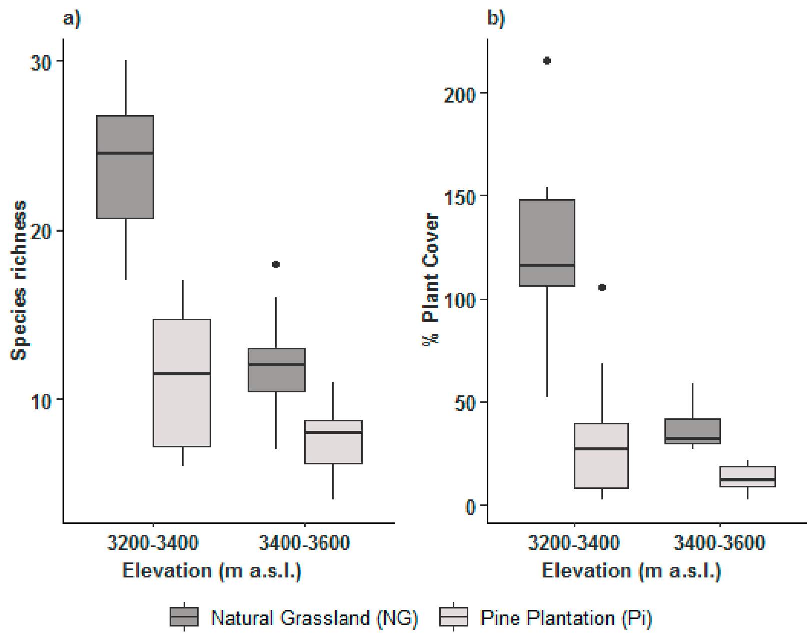

Figure 3. Box plots for the effects of elevational range (3200–3400 and 3400–3600 m a.s.l.) and type of vegetation (Pi and NG) on (**a**) woody species richness and (**b**) woody plant cover.

Endemic species: In total, thirteen endemic species were recorded in our observational plots, eight species under Pi cover and eleven species in the NG cover across all elevational ranges. From the endemic species registered eleven species are included in the International union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species [57]. Five species occurred exclusively in NG, from which *Lysipomia vitreola* McVaugh [58] and *Brachyotum jamesonii* Triana [59] are considered an endangered and a vulnerable species respectively; and *Gynoxys miniphylla* Cuatrec [60] and *Miconia pernettifolia* Triana [61] found only under Pi sites are considered vulnerable species according to the IUCN (Table 4).

Table 4. List of endemic species with their percentage of occurrence in the plots at natural grassland (NG) and pine plantation (Pi) sites in three different elevational ranges in m a.s.l. (Total 30 plots for herbaceous plants for each vegetation cover, and 20 plots for woody plants for each vegetation cover). Lf = life form, Cs = conservation status according to the IUCN Red List of Threatened Species [57], H = herbaceous plant, W = woody plant. LC = least concern, NT = near threatened, VU = vulnerable, Ni = not included in the Red List, EN = endangered.

Family	Endemic species	Lf	Cs	NG	Pi	NG	Pi	NG	Pi
				3200–3400		3400–3600		3600–3800	
ARALIACEAE	*Oreopanax andreanus* Marchal	W	LC [a]	50					
ARALIACEAE	*Oreopanax avicenniifolius* (Kunth) Decne. & Planch.	W	NT [b]	50	40	10	30		
ASTERACEAE	*Aphanactis jamesoniana* Wedd.	H	LC [c]			10		60	20
ASTERACEAE	*Gynoxys miniphylla* Cuatrec.	W	VU [d]		10				
ASTERACEAE	*Lasiocephalus lingulatus* Schltdl.	H	Ni			10		30	
CAMPANULACEAE	*Lysipomia vitreola* McVaugh	H	EN [e]					10	
DIOSCOREACEAE	*Dioscorea cf choriandra* Uline ex R. Knuth	H	Ni	20	10				
GENTIANACEAE	*Halenia taruga-gasso* Gilg	H	NT [f]	50		80		80	60
GROSSULARIACEAE	*Ribes lehmannii* Jancz.	W	VU [g]	40	20				
HYPERICACEAE	*Hypericum quitense* R. Keller	W	LC [h]			10			
MELASTOMATACEAE	*Miconia pernettifolia* Triana	H	VU [i]						10
MELASTOMATACEAE	*Brachyotum confertum* (Bonpl.) Triana	W	LC [j]	60	40	90	60		
MELASTOMATACEAE	*Brachyotum jamesonii* Triana	W	VU [k]	20					

[a] [62], [b] [63], [c] [64], [d] [60], [e] [58], [f] [65], [g] [66], [h] [67], [i] [61], [j] [68], [k] [59].

3.2. Vegetation Assemblages along Elevational Ranges and Type of Vegetation Cover

Herbaceous vegetation: According to rank-abundance curves, a marked difference of dominant species was found between NG and Pi, mainly at the lower and middle elevational ranges; all three dominant species do not coincide in both type of vegetation. For instance, at 3200–3400 m a.s.l. under NG *Calamagrostis intermedia* (J. Presl) Steud, *Austrolycopodium magellanicum* (P. Beauv) Holub, and *Paspalum bonplandianum* Flüggé had the highest abundance (Figure 4a), while under Pi it was *Triniochloa stipoides* (Kunth) Hitchc, *Peperomia* sp, and *Pecluna* sp. (Figure 4b). At 3400–3600 m a.s.l, *C. intermedia*, *Festuca subulifolia* Benth., and *Polystichum orbiculatum* (Desv) (Figure 4c), were the dominant species, while in Pi, there were *Cerastium danguyi* J.F. Macbr. and *Muehlenbeckia tamnifolia* (Kunth) Meisn. (Figure 4d). At 3600–3800 m a.s.l., the species, *C. intermedia* and *F. subulifolia* were presented in both types of vegetation (Figure 4e,f), while *Lachemilla orbiculata* (Ruiz & Pav.) Rydb. was observed with high dominance only under Pi (Figure 4f). Interestingly, *C. intermedia* was the dominant species present in all three elevational ranges at NG (Figure 4a,c,e).

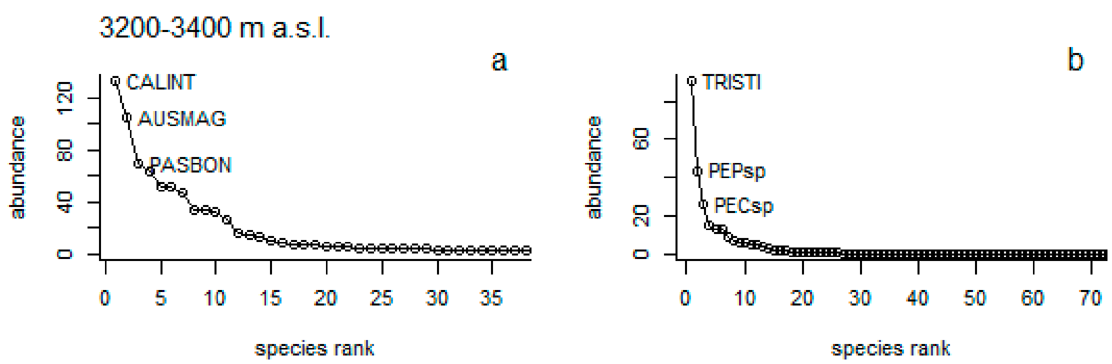

Figure 4. *Cont.*

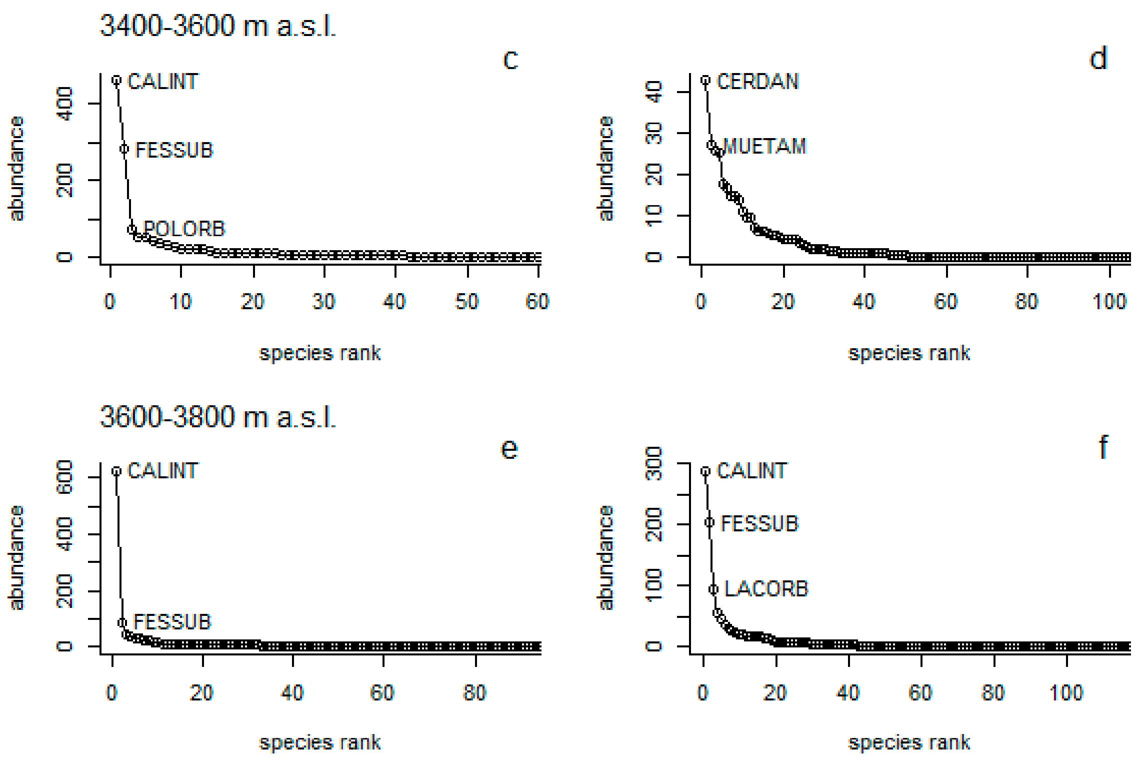

Figure 4. Herbaceous species abundance rank at natural grassland (NG) cover (**a**,**c**,**e**) and pine plantations (Pi) cover (**b**,**d**,**f**) across three different elevational gradients (3200–3400, 3400–3600, and 3600–3800 m a.s.l.).CALINT = *Calamagrostis intermedia*, AUSMAG = *Austrolycopodium magellanicum*, PASBON = *Paspalum bonplandianum*, TRISTI = *Triniochloa stipoides*, PEPsp = *Peperomia* sp, PECsp = *Pecluna* sp, FESSUB = *Festuca subulifoli*, POLORB = *Polystichum orbiculatum*, CERDAN = *Cerastium danguyi*, MUETAM = *Muehlenbeckia tamnifolia*, LACORB = *Lachemilla orbiculate*.

Woody vegetation: The results showed that within the lower elevational range, species such as *Morella parvifolia* (Benth.) Parra-Os. and *Myrsine dependens* (Ruiz & Pav.) Spreng. were dominant under NG (Figure 5a), while *Miconia theaezans* (Bonpl.) Cogn. and *M. dependens*, dominated in Pi (Figure 5b). In the higher elevational range, these species were not present in both types of vegetation cover. Here, the dominant species were *Valeriana hirtella* Kunth and *M. parvifolia* in the NG (Figure 5c), and *Miconia crocea* (Desr.) Naudin *and Gynoxys* sp. under Pi (Figure 5d).

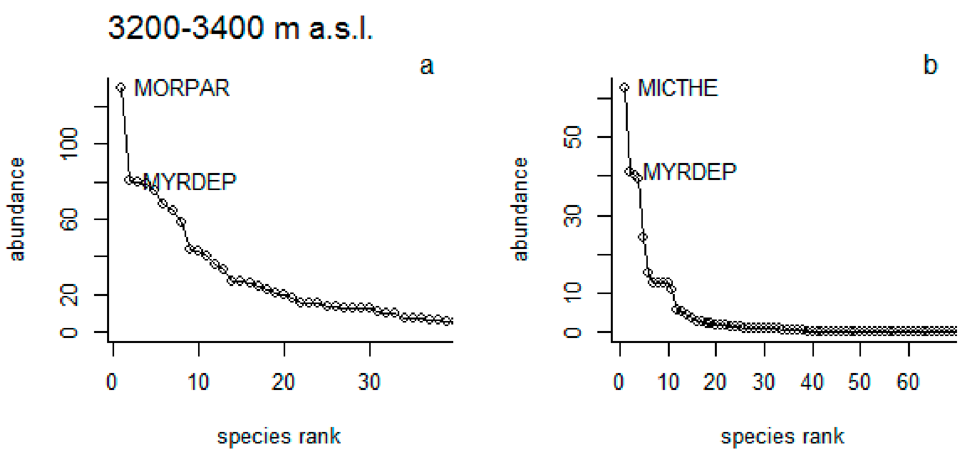

Figure 5. *Cont.*

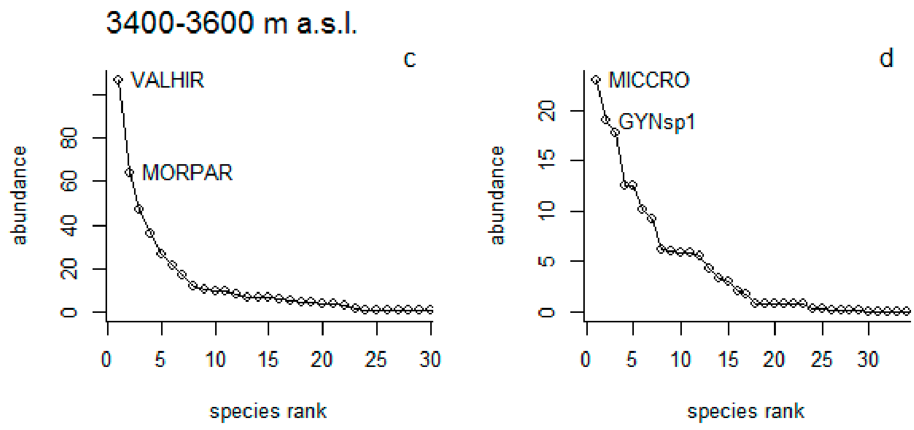

Figure 5. Woody species abundance rank at natural grassland (NG) cover (**a**,**c**) and pine plantation (Pi) cover (**b**,**d**) across three different elevational gradients (3200–3400 and 3400–3600 m a.s.l.). MORPAR = *Morella parvifolia*, MYRDEP = *Myrsine dependens*, MICTHE = *Miconia theaezans*, VALHIR = *Valeriana hirtella*, MICCRO = *Miconia crocea*, GYNsp1= *Gynoxys* sp.

3.3. Relationship between Herbaceous Species Richness and Its Vegetation Cover with Edaphic Properties and Attributes of Plantations

Herbaceous vegetation: In the CCA 40.89% of the variance was explained in the two axes. In the CCA1, the variables related to the attributes of Pi and soil characteristics with highest contribution were elevation (Ele), basal area (BA), saturated hydraulic conductivity (Ksat) and canopy density (CD), while in CCA2 pH was the variable with the highest contribution (Figure 6). According to CCA, herbaceous species richness and its cover showed that Ele was positively correlated ($p < 0.001$); therefore, herbaceous species richness increased with higher elevation. Moreover, there was a negative correlation between the herbaceous species richness and its cover with CD ($p < 0.001$), BA ($p < 0.001$) and Ksat ($p < 0.001$). On the other hand, the herbaceous species richness was lower in those plots where the pH was more acid ($p < 0.001$) (Figure 6).

Woody species: In the CCA, 57.30% of the variance was explained in the two axes. In the CCA1, the most relevant variables were Ele and pH in soil while in CCA2 the Ksat and slope had the highest contribution (Figure 7). The CCA also explained that, the woody species richness and its cover was negatively correlated to Ele ($p < 0.001$); indicating that number of these were lower at the highest elevational range. The Ksat variable showed the same tendency as well as Ele. The pH variable showed a positive relation with the woody species and its cover ($p < 0.01$) while the plots with steep slope showed a low presence of woody species ($p < 0.01$) (Figure 7). The soil properties of all pine plantations sites (Pi) are shown in Appendix B.

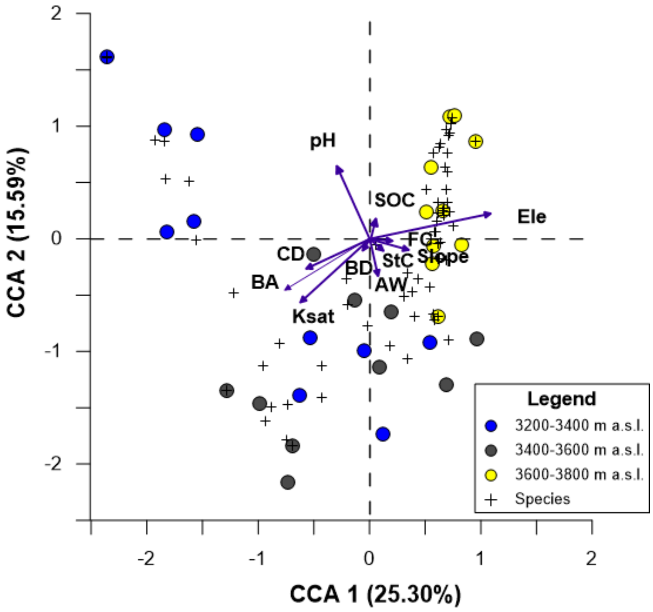

Figure 6. Canonical Correspondence Analysis (CCA) showing ordination of herbaceous species richness and their plant cover (+), plot (circles), and attributes of pine plantation and their physical and chemical soil characteristics across an elevational range (arrows). Abbreviations are as follows: CD = canopy density, BA = basal area, Ksat = saturated hydraulic conductivity, SOC = soil organic carbon, StC = water content at saturation point, FC = water content at field capacity, AW = available water capacity, pH = potential hydrogen, Ele = elevation, BD = bulk density.

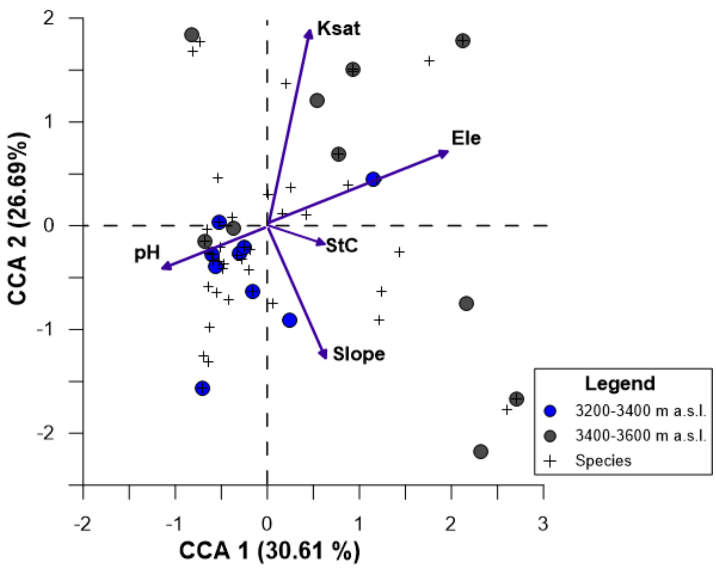

Figure 7. Canonical Correspondence Analysis (CCA), showing ordination of woody species richness and their plant cover (+), plot (circles) and attributes of pine plantation and their physical and chemical soil characteristics across an elevational range (arrows). Abbreviations are as follows: CD = canopy density, BA = basal area, Ksat = saturated hydraulic conductivity, SOC = soil organic carbon, StC = water content at saturation point, FC = water content at field capacity, AW = available water capacity, pH = potential hydrogen, Ele = elevation, BD = bulk density. The other variables that contributed little to the analysis are not visible here.

4. Discussion

4.1. Natural Regeneration under the Influence of Pine Plantations in an Elevational Gradient

Our results demonstrate that species richness and its cover were lower under Pi than NG across the elevational gradient and thus, pines have a negative impact on natural regeneration. Several authors found similar results with the establishment of pine plantations in the páramo ecosystem of Ecuador [18,31] and Colombia [29]. On a larger scale, Bremer and Farley [69] evaluated plant biodiversity on 11 afforested grasslands of different location around the world, and also found a reduction in plant species richness. On the other hand, we found that herbaceous and woody native and endemic species of plants were existing in the understory of Pi, taking advantage of the dense canopy of the pines that blocks solar radiation and creates an adequate microclimate for their development [32,69,70]. Nevertheless, these native species are shade tolerant with high physiological adaptation to the new conditions offered by Pi. In the same way, Hofstede et al. [18] and Bremer [31] found understories of native vegetation in several pine plantation plots which coincides with our results.

In our study, there was a significant influence of the elevation on herbaceous species richness and its cover, which increased at higher elevation while the opposite result was found for woody species richness and cover, even though it was not statistically significant for woody species. Several studies describe that above the tree line (below the subpáramo), the vegetation becomes smaller and scattered as the elevation increases, and shrubs become even more dispersed at the highest elevations [9,10,71]. Among the responsible factors that determine the marked distribution between woody and herbaceous species in an elevational gradient in the páramo are lower temperatures in the upper zones, especially frost which can occur year-round at night [72,73], strong solar radiation due to the combination of low latitude and high elevation [72], and variation of soil conditions (i.e., bulk density and water availability for plants) [74]. These factors may be responsible for the lower productivity of the pine plantations (smaller trees and less dense plantations) at the higher elevational range. Therefore, these plantations have more open areas with enough available light for the establishment of natural regeneration [75–77]. Probably, this is why we found similar herbaceous coverage between NG and Pi at the highest elevational range.

Regarding the composition of the species, the most important families in our study were Asteraceae containing 17% of the species, and Poaceae containing 9% of the species. These results are similar to the ones obtained by Ramsay [10] (20% of the species belonged to Asteraceae and 14% to Poaceae) in the research that covered most of the páramos of Ecuador. With regard to the herbaceous vegetation assemblage across the elevational gradient in the NG, it was observed that tussock grasses represented by *C. intermedia* were the most dominating species. In the two lower elevational ranges, *F. subulifolia* was one of the species also dominating the plant community. These two species are very typical in the páramo ecosystem [8–10,78]. Most likely, these species evolved to survive at the highest elevation, thereby demonstrating physiological mechanisms of adaptation. For example, due to the fact that in the higher elevations of the páramo, water is available only for few hours of the day, tussock grasses have developed long and thin leaves to avoid water loss by transpiration [79]. In addition, dead leaves are maintained and decay on the external part of the plant providing good insulation from cold temperatures and high heat, as well as protection from radiation, for the young leaves located in the inside of the plant [10,16,80]. Also these dead leaves retain nutrients that are used for the growth of the plants [10,81].

The shift in species composition that we found between NG and Pi at the two lower elevational ranges could be related once again to the amount of light that reaches the understory; in this case, the larger canopies block more light and facilitate the establishment of shade-tolerant species. There was limited information about the ecology of the dominant species found in the understory of the plantations. However, at the lower elevational range, we found that one of the dominant species, *T. stipoides*, has also been described as a common herbaceous species in the understory of Mexican pine forests [82,83]. In the case of the woody vegetation, it is known that *M. theaezans*, a dominant species in the understory of our study, is highly capable of natural regeneration and is a common species in secondary succession [84]. In the mid-elevational range, from the herbs that we registered, *M. tamnifolia*, one of our dominant species, has also been listed in most of the plant communities in a research carried out in the Colombian subpáramo [29], and it was one of the dominant species in an Andean forest of the same country [85]. Finally, in the higher elevational range, there were no important changes in species composition between NG and Pi.

The majority of the species was registered in NG (85%) of which 31.9% were registered only in NG, and 68% of the species were registered in Pi, of which 14.8% were registered only in Pi. In comparison to the studies of van Wesenbeeck et al. [29] and Bremer [31], the number of species that we found in Pi only is much higher, probably because our study covered a wider elevational range, which therefore included more species. In relation to endemic species, we found a 23% decrease of species between NG and Pi, which is less compared to what Bremer and Farley´s [69] found in their study. Among the endemic species registered, because of their status of conservation, *L. vitreola* [58] and *B. jamesonii*, [61] found only under NG, and *G. miniphylla* [62] and *M. pernettifolia* [61] found only under Pi, special consideration should be given to protect these natural grasslands and to manage the plantations in a way that will guarantee the conservation of these spp. Concerning introduced spp, we found five adventive herbs, *Anthoxanthum odoratum* L., *Holcus lanatus* L., *Rumex acetosella* L., *Euphorbia peplus* L. and *Taraxacum officinale* F.W. Wigg. (the last two species were found only inside the plantations). However, all the introduced species that we found in the study are considered indicators of human and grazing disturbances, and nowadays most parts of the Andean páramos are affected by these introduced plants from Europe [9,86]. It should be noted that we did not find any pine seedling in any of the two types of vegetation cover, so we do not consider this species as an invasive one.

4.2. Natural Regeneration Influenced by Pine Plantation Attributes and Soil Properties

Our results showed that herbaceous species richness and cover are influenced by the characteristics of pine plantations, finding a higher herbaceous species richness and cover in pine plantations with lower canopy density and basal area, which is consistent with the results reported in several studies [18,76,77]. With less CD and BA there is more availability of light and water for the development of herbaceous plants within Pi. According to Brockerhoff et al. [75], the characteristics of the plantations directly affect the availability of light, which is necessary for the development of understory vegetation within the plantations. In addition, due to high water requirements and the interception of rainfall by plantations [1], there is less water available in the soil for the germination, growth and establishment of herbaceous vegetation within the plantations. Also, the Ksat of pine plantation soils showed a negative relationship with the herbaceous species richness and its cover. This relationship is due to the fact that plantations with a high Ksat show a high speed of water movement in the soil, causing fast drying [74] and loss of SOM [87], limiting the development of herbaceous plants. Therefore, we can conclude that besides elevation, herbaceous species richness and its cover within plantations depend substantially on the attributes of the plantations as well as on the properties of the soils.

Woody species richness and its cover decreased when the Ksat of the soil increased and the pH was more acidic, which agrees with Riesch et al. [88], who found that one of the main properties of soils that control the composition and richness of woody plants is the pH. In addition, soils with very acidic pH show a lower availability of nutrients [89] with toxicity problems for plants [90] that directly affect species richness. Several studies from different parts of the world show that generally, afforestation of grasslands with pines leads to moderate soil acidification, on average 0.3 units [36,38]. According to Jobbágy et al. [91], the forestation of grasslands which generates higher rates of primary production, involves a greater sequestration of soil nutrients by the pines. This transference of nutrients and of other cations from the páramo soil towards the pine biomass would be accompanied by a release of acidity from the pines towards the soil to balance the charges [92]. This is consistent with our results, in which a lower woody species rischness and its cover were observed in plantations with very acidic soils (pH < 4.4). This highlights that certain plantations with soil acidification processes would cause a negative effect on the regeneration of woody plants.

4.3. Recommendations for Pine Plantation Management

Based on the differences of herbaceous and woody plant richness and its cover between páramo grassland and pine plantations, we suggest that these plantations should be gradually harvested. According to the understory biodiversity that we have found, these plantations could be managed for ecological restoration purposes. Some of the species registered in the plantations are being used in ecological restoration projects such as: *M. tamnifolia* [93], *M. theaezans* [94,95], *Lupinus* spp. [96], *Solanum* spp, [97]. However, the biodiversity that has been developed inside these plantations is threatened by the future harvesting of the plantation. Due to profitability reasons, the type of harvest practiced in the country is clear-cutting, which has negative consequences such as a very erosive effect on the soil [98–100]. In addition, the regeneration that has taken place will surely be destroyed with this type of harvesting [99]. Although the understory developed in the plantations is not the ideal model for conservation management with a proper silvicultural treatment that could support the restoration of the structural and functional attributes of the páramo. Future work should therefore include different silvicultural treatments in these plantations to develop the most appropriate management, thereby ensuring the conservation of the páramo biodiversity.

5. Conclusions

Afforested páramo grassland with *P. patula* showed a decrease in species richness and cover and a different composition of herbaceous and woody species compared to the natural páramo grassland. Nevertheless, in the plantations, which were established on natural grassland or grazed páramo and had none or very limited silvicultural management and have not been grazed since its establishment, native vegetation, including even endemic and endangered species was maintained. In addition, the presence of these species within the plantations has surely taken place because they have not been exposed to lifestock and fire since the establishement of the plantations. The impacts of these activities on the native vegetation will vary depending on the intensity of the grazing and the frequency of the burning. This highlights the importance of controlling these activities that are commonly practiced along the Andean páramo. Therefore, from this research we conclude that under suitable conditions these plantations in the páramos could also contribute to the ecological restoration programs of this ecosystem. This in no way implies that we are promoting any kind of afforestation in the páramo ecosystem. In order to conserve the native vegetation found within the plantations, we suggest that the plantations should be managed in a way that considers the factors that we found having a great influence on the richness, cover and composition of vegetation such as: basal area, canopy density and saturated hydraulic conductivity.

Author Contributions: Conceptualization, C.Q.D., P.C. and X.P.; data curation, C.Q.D., R.A. and F.M.; methodology, C.Q.D., R.A. and F.M.; formal analysis, F.M., R.A. and X.P.; writing of the original draft and preparation, X.P., C.Q.D. and F.M. Supervision, M.W. and X.P.; project administration P.C. and M.W.; writing of the paper, C.Q.D.; all authors contributed to the paper's structure and provided extensive revision. All authors read and approved the final manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Inventory of species classified by type of vegetation, natural grassland (NG) and pine plantation (Pi), and elevational range in m a.s.l. S = biogeographic current condition of the species in Ecuador (N = native, E = endemic, I = introduced), Lf = life form (H = herbaceous, H* = prostrate shrubs-sub shrubs and vines, W = woody plant). "X" represents the presence of the species.

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		3400–3600		3600–3800	
ADOXACEAE	*Viburnum triphyllum* Benth.	N	W	X	X		X		
ALSTROMERIACEA	*Bomarea* sp.	N	H	X	X	X	X	X	
APIACEAE	*Azorella biloba* (Schltdl.) Wedd.	N	H			X	X	X	X
APIACEAE	*Azorella* sp. 1	N	H			X	X	X	X
APIACEAE	*Eryngium humile* Cav.	N	H	X		X		X	X
APIACEAE	*Oreomyrrhis andicola* (Kunth) Endl. ex Hook. f.	N	H					X	X
APOCYNACEAE	*Matalea* sp.	N	H*	X	X				
ARALIACEAE	*Hydrocotyle* sp. 1	N	H		X	X	X	X	X
ARALIACEAE	*Hydrocotyle* sp. 2	N	H	X		X			
ARALIACEAE	*Hydrocotyle* sp. 3	N	H		X				
ARALIACEAE	*Hydrocotyle* sp. 4	N	H			X			
ARALIACEAE	*Oreopanax andreanus* Marchal	E	W	X					
ARALIACEAE	*Oreopanax avicenniifolius* (Kunth) Decne. & Planch.	E	W	X	X	X	X		
ARALIACEAE	*Oreopanax* sp. 3	N	W		X				
ARALIACEAE	*Oreopanax* sp. 4	N	W	X					
ASPLENIACEAEA	*Asplenium* sp. 1	N	H				X	X	
ASPLENIACEAEA	*Asplenium* sp. 2	N	H	X	X				
ASPLENIACEAEA	*Asplenium* cf	N	H						X
ASTERACEAE	*Achyrocline alata* (Kunth) DC.	N	H			X		X	
ASTERACEAE	*Ageratina* sp	N	W	X	X	X	X		
ASTERACEAE	*Ageratina* sp. 2	N	W	X					
ASTERACEAE	*Aphanactis jamesoniana* Wedd.	E	H			X		X	X
ASTERACEAE	*Aristeguietia cacalioides* (Kunth) R.M. King & H. Rob.	N	W	X	X	X			
ASTERACEAE	*Asteraceae* sp. 2	N	H					X	X
ASTERACEAE	*Asteraceae* sp. 3	N	H					X	
ASTERACEAE	*Asteraceae* sp. 4	N	W	X	X				
ASTERACEAE	*Baccharis caespitosa* (Ruiz & Pav.) Pers.	N	H*					X	X
ASTERACEAE	*Baccharis genistelloides* (Lam.) Pers.	N	H*	X		X		X	X
ASTERACEAE	*Baccharis* sp. 2	N	W	X					
ASTERACEAE	*Baccharis* sp. 3	N	W	X					
ASTERACEAE	*Baccharis* sp. 4	N	W	X					

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		**3400–3600**		**3600–3800**	
ASTERACEAE	*Baccharis tricuneata* (L. f.) Pers.	N	W	X					
ASTERACEAE	*Barnadesia arborea* Kunth	N	W	X			X		
ASTERACEAE	*Bidens andicola* Kunth	N	H	X		X	X	X	X
ASTERACEAE	*Chaptalia cordata* Hieron.	N	H			X	X	X	X
ASTERACEAE	*Chrysactinium acaule* (Kunth) Wedd.	N	H	X		X		X	X
ASTERACEAE	*Chrysactinium* sp.	N	H	X					
ASTERACEAE	*Chuquiraga jussieui* J.F. Gmel.	N	W	X		X			
ASTERACEAE	*Cotula mexicana* (DC.) Cabrera	N	H					X	X
ASTERACEAE	*Diplostephium glandulosum* Hieron.	N	H					X	X
ASTERACEAE	*Dorobaea pimpinellifolia* (Kunth) B. Nord.	N	H	X		X			X
ASTERACEAE	*Erato sodiroi* (Hieron.) H. Rob.	N	W	X	X				
ASTERACEAE	*Galinsoga* cf. *quadriradiata* Ruiz & Pav.	N	H				X		
ASTERACEAE	*Gamochaeta americana* (Mill.) Wedd.	N	H		X	X		X	X
ASTERACEAE	*Gamochaeta purpurea* (L.) Cabrera	N	H					X	X
ASTERACEAE	*Gnaphalium* sp.	N	H	X		X		X	
ASTERACEAE	*Guevaria sodiroi* (Hieron.) R.M. King & H. Rob.	N	H			X			
ASTERACEAE	*Gynoxys miniphylla* Cuatrec.	E	W		X				
ASTERACEAE	*Gynoxys* sp. 1	N	W	X	X	X	X		
ASTERACEAE	*Gynoxys* sp. 2	N	W	X	X				
ASTERACEAE	*Gynoxys* sp. 3	N	W	X	X				
ASTERACEAE	*Gynoxys* sp. 4	N	W	X		X			
ASTERACEAE	*Hieracium* sp. 1	N	H			X		X	X
ASTERACEAE	*Hieracium* sp. 2	N	H			X			
ASTERACEAE	*Hypochaeris sessiliflora* Kunth	N	H					X	X
ASTERACEAE	*Jungia* sp.	N	W			X	X		
ASTERACEAE	*Lasiocephalus lingulatus* Schltdl.	E	H			X		X	
ASTERACEAE	*Loricaria* sp.	N	W			X			
ASTERACEAE	*Monticalia empetroides* (Cuatrec.) C. Jeffrey	N	W			X			
ASTERACEAE	*Munnozia senecionidis* Benth.	N	W	X	X		X		
ASTERACEAE	*Oligactis coriacea* (Hieron.) H. Rob. & Brettell	N	W	X			X		
ASTERACEAE	*Oritrophium crocifolium* (Kunth) Cuatrec.	N	H					X	X
ASTERACEAE	*Senecio* cf	N	H	X					
ASTERACEAE	*Senecio cf chionogeton* Wedd.	N	H			X	X	X	X
ASTERACEAE	*Senecio* sp. 1	N	H	X		X			
ASTERACEAE	*Taraxacum officinale* F.H. Wigg.	I	H						X

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		**3400–3600**		**3600–3800**	
ASTERACEAE	*Werneria nubigena* Kunth	N	H					X	X
ASTERACEAE	*Werneria pygmaea* Gillies ex Hook. & Arn.	N	H						X
ASTERACEAE	*Xenophyllum humile* (Kunth) V.A. Funk	N	H					X	X
BERBERIDACEAEA	*Berberis cf lutea Ruiz* & Pav.	N	W		X				
BERBERIDACEAEA	*Berberis* sp. 1	N	W	X					
BERBERIDACEAEA	*Berberis* sp. 2	N	W	X					
BERBERIDACEAEA	*Berberis* sp. 3	N	W				X		
BERBERIDACEAEA	*Berberis* sp. 4	N	W	X	X				
BLECHNACEAE	*Blechnum* sp.	N	H	X		X	X		
BRASSICACEAE	*Draba* sp.	N	H					X	
BROMELIACEAE	*Bromeliaceae* 1	N	H	X					
BROMELIACEAE	*Bromeliaceae* 2	N	H	X					
BROMELIACEAE	*Guzmania* sp	N	H	X					
BROMELIACEAE	*Puya* sp. 1	N	H			X	X	X	X
BROMELIACEAE	*Puya* sp. 2	N	H			X			X
BROMELIACEAE	*Puya* sp. 3	N	H	X	X				
BROMELIACEAE	*Tillandsia* sp	N	H	X					
CAMPANULACEAE	Campanulacea cf	N	W	X					
CAMPANULACEAE	*Centropogon* sp.	N	W			X			
CAMPANULACEAE	*Lysipomia sphagnophila* Griseb. ex Wedd.	N	H					X	X
CAMPANULACEAE	*Lysipomia vitreola* McVaugh	E	H					X	
CAMPANULACEAE	*Siphocampylus giganteus* (Cav.) G. Don	N	W				X		
CAMPANULACEAE	*Lobelia tenera* Kunth	N	H	X					
CAPRIFOLIACEAE	*Valeriana hirtella* Kunth	N	W	X		X	X		
CAPRIFOLIACEAE	*Valeriana microphylla* Kunth	N	H			X	X	X	X
CAPRIFOLIACEAE	*Valeriana niphobia* Briq.	N	H			X		X	
CAPRIFOLIACEAE	*Valeriana pyramidalis* Kunth	N	H	X			X		
CAPRIFOLIACEAE	*Valeriana rigida* Ruiz & Pav.	N	H						X
CARYOPHYLLACEAE	*Arenaria* cf.	N	H					X	
CARYOPHYLLACEAE	*Cerastium* cf	N	H					X	
CARYOPHYLLACEAE	*Cerastium danguyi* J.F. Macbr.	N	H			X	X	X	X
CARYOPHYLLACEAE	*Stellaria recurvata* Willd. ex D.F.K. Schltdl.	N	H				X	X	
CELASTRACEAEA	*Maytenus cf verticillata* (Ruiz & Pav.) DC.	N	W	X	X				
CHLORANTHACEAE	*Hedyosmum luteynii* Todzia	N	W				X		
CLETHRACEAE	*Clethra* sp.	N	W	X					
CONVOLVULACEA	*Dichondra aff microcalyx* (Hallier f.) Fabris	N	H				X	X	

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		3400–3600		3600–3800	
CORNACEAEA	*Cornus peruviana* J.F. Macbr.	N	W	X	X				
CUNONIACEAE	*Weinmannia fagaroides* Kunth	N	W	X	X	X	X		
CYPERACEAE	*Carex crinalis* Boott	N	H	X		X	X	X	X
CYPERACEAE	*Carex ecuadorica* Kük.	N	H					X	X
CYPERACEAE	*Carex jamesonii* Boott	N	H	X		X	X	X	X
CYPERACEAE	*Carex pichinchensis* Kunth	N	H				X		X
CYPERACEAE	*Carex* sp. 3	N	H					X	X
CYPERACEAE	*Carex* sp. 4	N	H	X			X	X	X
CYPERACEAE	*Carex* sp. 5	N	H			X			
CYPERACEAE	*Carex tamana* Steyerm.	N	H			X		X	X
CYPERACEAE	*Carex tristicha* Spruce ex Boott	N	H	X		X		X	X
CYPERACEAE	*Eleocharis acicularis* (L.) Roem. & Schult.	N	H						X
CYPERACEAE	*Oreobolopsis inversa* Dhooge & Goetgh.	N	H	X				X	X
CYPERACEAE	*Oreobolus ecuadorensis* T. Koyama	N	H						X
CYPERACEAE	*Oreobolus goeppingeri* Suess.	N	H			X		X	X
CYPERACEAE	*Rhynchospora* sp. 1	N	H	X	X	X			X
CYPERACEAE	*Rhynchospora* sp. 2	N	H						X
CYPERACEAE	*Rhynchospora vulcani* Boeckeler	N	H	X	X	X	X	X	X
CYPERACEAE	*Uncinia tenuis* Poepp. ex Kunth Search in The Plant List	N	H			X		X	X
DENNSTAEDTIACEAE	*Pteridium arachnoideum* (Kaulf.) Maxon	N	H				X		
DIOSCOREACEAE	*Dioscorea cf choriandra* Uline ex R. Knuth	E	H	X	X				
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 1	N	H				X		
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 2	N	H			X			
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 3	N	H			X			
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 4	N	H	X					
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 5	N	H	X					
DRYOPTERIDACEAEA	*Elaphoglossum* sp. 6	N	H			X			
DRYOPTERIDACEAEA	*Polystichum orbiculatum* (Desv.) J. Rémy & Fée	N	H	X	X	X	X		
ELAEOCARPACEAE	*Vallea stipularis* L. f.	N	W	X	X		X		
EQUISETACEAE	*Equisetum myriochaetum* Schltdl. & Cham.	N	H	X	X	X			
ERICACEAE	*Bejaria resinosa* Mutis ex L. f.	N	W		X				
ERICACEAE	*Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hil.) Hoerold	N	W	X	X				
ERICACEAE	*Disterigma empetrifolium* (Kunth) Drude	N	H			X		X	X
ERICACEAE	*Gaultheria amoena* A.C. Sm.	N	H			X	X		
ERICACEAE	*Gaultheria erecta* Vent.	N	W			X			
ERICACEAE	*Gaultheria glomerata* (Cav.) Sleumer	N	W			X			
ERICACEAE	*Gaultheria reticulata* Kunth	N	W	X					
ERICACEAE	*Gaultheria* sp	N	W	X	X	X	X		

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		3400–3600		3600–3800	
ERICACEAE	*Gaultheria tomentosa* Kunth	N	W	X		X	X		
ERICACEAE	*Macleania rupestris* (Kunth) A.C. Sm.	N	W	X		X			
ERICACEAE	*Pernettya prostrata* (Cav.) DC.	N	H*				X	X	X
ERICACEAE	*Pernettya* sp.	N	W			X			
ERICACEAE	*Vaccinium floribundum* Kunth	N	H*	X	X	X	X	X	X
ERIOCAULACEAE	*Paepalanthus* sp.	N	H					X	X
ESCALLONIACEAE	*Escallonia myrtilloides* L. f.	N	W	X					
EUPHORBIACEA	*Euphorbia peplus* L.	I	H				X		
FABACEAE	*Lupinus tauris* Benth.	N	H			X	X	X	X
GENTIANACEAE	*Gentianella cerastioides* (Kunth) Fabris	N	H			X		X	X
GENTIANACEAE	*Gentianella rapunculoides* (Willd. ex Schult.) J.S. Pringle	N	H					X	X
GENTIANACEAE	*Halenia taruga-gasso* Gilg	E	H	X		X		X	X
GERANIACEAE	*Geranium diffusum* Kunth	N	H			X		X	X
GERANIACEAE	*Geranium maniculatum* H.E. Moore	N	H			X		X	X
GERANIACEAE	*Geranium multipartitum* Benth.	N	H					X	X
GERANIACEAE	*Geranium sibbaldioide*s Benth.	N	H			X	X	X	X
GROSSULARIACEAE	*Ribes* cf.	N	W			X	X		
GROSSULARIACEAE	*Ribes lehmannii* Jancz.	E	W	X	X				
HYPERICACEAE	*Hypericum aciculare* Kunth	N	W			X			
HYPERICACEAE	*Hypericum decandrum* Turcz.	N	H*			X	X	X	X
HYPERICACEAE	*Hypericum laricifolium* Juss.	N	W	X		X			
HYPERICACEAE	*Hypericum quitense* R. Keller	E	W			X			
IRIDACEAE	*Orthrosanthus chimboracensis* (Kunth) Baker	N	H	X	X	X	X	X	X
IRIDACEAE	*Sisyrinchum* sp.1	N	H			X		X	X
JUNCACEAE	*Juncus* sp.	N	H			X			
JUNCACEAE	*Luzula* sp.	N	H			X		X	
LAMIACEAE	*Clinopodium nubigenum* (Kunth) Kuntze	N	H			X		X	
LAMIACEAE	*Lepechinia rufocampii* Epling & Mathias	N	H	X					
LAMIACEAE	*Salvia corrugata* Vahl	N	W	X					
LAMIACEAE	*Stachys cf elliptica* Kunth	N	H				X	X	X
LAURACEAE	*Ocotea heterochroma* Mez & Sodiro	N	W	X	X				
LORANTHACEAE	*Gaiadendron punctatum* (Ruiz & Pav.) G. Don	N	W	X					
LYCOPODIACEAE	*Austrolycopodium magellanicum* (P. Beauv.) Holub	N	H	X	X	X	X	X	X
LYCOPODIACEAE	*Huperzia crassa* (Humb. & Bonpl. ex Willd.) Rothm.	N	H					X	
LYCOPODIACEAE	*Huperzia* sp. 1	N	H			X		X	X
LYCOPODIACEAE	*Huperzia* sp. 2	N	H					X	X

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		**3400–3600**		**3600–3800**	
LYCOPODIACEAE	*Lycopodium clavatum* L.	N	H	X	X	X	X	X	
LYCOPODIACEAE	*Lycopodium magellanicum* (P. Beauv.) Sw.	N	H	X	X	X			
MELASTOMATACEAE	*Miconia aspergillaris* (Bonpl.) Naudin	N	W		X				
MELASTOMATACEAE	*Miconia chionophila* Naudin	N	H			X	X	X	X
MELASTOMATACEAE	*Miconia crocea* (Desr.) Naudin	N	W	X			X		
MELASTOMATACEAE	*Miconia pernettifolia* Triana	E	H						X
MELASTOMATACEAE	*Miconia salicifolia* Naudin	N	W			X	X		
MELASTOMATACEAE	*Miconia* sp. 1	N	W	X	X				
MELASTOMATACEAE	*Miconia* sp. 3	N	W				X		
MELASTOMATACEAE	*Miconia* sp. 4	N	W	X			X		
MELASTOMATACEAE	*Miconia* sp. 6	N	W	X					
MELASTOMATACEAE	*Miconia theaezans* (Bonpl.) Cogn.	N	W	X	X	X			
MELASTOMATACEAE	*Brachyotum confertum* (Bonpl.) Triana	E	W	X	X	X	X		
MELASTOMATACEAE	*Brachyotum jamesonii* Triana	E	W	X					
MONNIMIACEAE	*Monnina ligustrifolia* Kunth	N	W			X			
MONNIMIACEAE	*Monnina* sp.	N	W	X	X		X		
MONOCOTILEDONEA	Monocotiledonea	N	H				X		
MYRICACEAE	*Morella parvifolia* (Benth.) Parra-Os.	N	W	X	X	X	X		
PRIMULACEAE	*Myrsine andina* (Mez) Pipoly	N	W	X		X	X		
PRIMULACEAE	*Myrsine dependens* (Ruiz & Pav.) Spreng.	N	W	X	X	X	X		
MYRTACEAE	*Myrtaceae* sp.	N	W		X				
ONAGRACEAE	*Fuchsia* sp.	N	W	X					
OPHIOGLOSSACEAE	*Ophioglossum cf crotalophoroides* Walter	N	H				X		
ORCHIDACEAE	*Aa* sp.	N	H					X	
ORCHIDACEAE	*Epidendrum* sp.	N	H	X	X				
ORCHIDACEAE	*Maxilaria* sp.	N	H	X		X			
ORCHIDACEAE	Orchidaceae	N	H	X	X	X			
ORCHIDACEAE	*Stellis* sp.	N	H	X					
OROBANCHACEAEA	*Bartsia laticrenata* Benth.	N	H			X		X	
OROBANCHACEAEA	*Bartsia* sp. 1	N	H			X		X	X
OROBANCHACEAEA	*Bartsia* sp. 2	N	H					X	
OROBANCHACEAEA	*Castilleja fissifolia* L. f.	N	H					X	X
OXALIDACEAE	*Oxalis* sp. 1	N	H	X	X	X	X		
OXALIDACEAE	*Oxalis* sp. 2	N	H				X		
OXALIDACEAE	*Oxalis* sp. 3	N	H					X	X
OXALIDACEAE	*Oxalis* sp. 4	N	H			X			
OXALIDACEAE	*Oxalis* sp. 5	N	H			X			

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		**3400–3600**		**3600–3800**	
PASSIFLORACEAE	*Passiflora* sp.	N	H*		X				
PINGUICULACEAE	*Pinguicula calyptrata* Kunth	N	H					X	
PIPERACEAE	*Peperomia* sp. 1	N	H	X	X	X	X		
PIPERACEAE	*Peperomia* sp. 2	N	H	X					
PIPERACEAE	*Peperomia* sp. 3	N	H	X	X				
PIPERACEAE	*Peperomia* sp. 4	N	H	X	X				
PIPERACEAE	*Peperomia* sp. 5	N	H	X					
PIPERACEAE	*Piper* sp.	N	W	X					
PLANTAGINACEAE	*Plantago cf tubulosa* Decne.	N	H						X
PLANTAGINACEAE	*Plantago australis* Lam.	N	H		X				
PLANTAGINACEAE	*Plantago linearis* Kunth	N	H			X		X	
PLANTAGINACEAE	*Plantago rigida* Kunth	N	H						X
PLANTAGINACEAE	*Plantago sericea* Ruiz & Pav.	N	H					X	
POACEAE	*Aciachne acicularis* Lægaard	N	H					X	X
POACEAE	*Agrostis breviculmis* Hitchc.	N	H						X
POACEAE	*Agrostis perennans* (Walter) Tuck.	N	H	X	X	X	X	X	X
POACEAE	*Agrostis* sp. 1	N	H			X		X	X
POACEAE	*Agrostis tolucensis* Kunth	N	H			X		X	X
POACEAE	*Anthoxanthum odoratum* L.	I	H	X	X	X	X	X	
POACEAE	*Bromus lanatus* Kunth	N	H					X	X
POACEAE	*Bromus pitensis* Kunth	N	H					X	
POACEAE	*Calamagrostis aff. recta* (Kunth) Trin. ex Steud.	N	H					X	X
POACEAE	*Calamagrostis intermedia* (J. Presl) Steud.	N	H	X	X	X	X	X	X
POACEAE	*Calamagrostis bogotensis* (Pilg.) Pilg.	N	H			X		X	
POACEAE	*Calamagrostis* sp.	N	H	X		X			X
POACEAE	*Cortaderia hapalotricha* (Pilg.) Conert	N	H			X		X	X
POACEAE	*Cortaderia jubata* (Lemoine) Stapf	N	H		X				
POACEAE	*Cortaderia nitida* (Kunth) Pilg.	N	H	X					
POACEAE	*Cortaderia sericantha* (Steud.) Hitchc.	N	H			X		X	
POACEAE	*Elymus cordilleranus* Davidse & R.W. Pohl	N	H			X		X	
POACEAE	*Festuca subulifolia* Benth.	N	H	X	X	X	X	X	X
POACEAE	*Holcus lanatus* L.	I	H		X		X	X	
POACEAE	*Paspalum bonplandianum* Flüggé	N	H	X	X	X	X	X	X
POACEAE	*Poa annua* L.	N	H						X
POACEAE	*Poa pauciflora* Roem. & Schult.	N	H			X		X	X
POACEAE	*Poaceae* sp. 1	N	H				X		
POACEAE	*Poaceae* sp. 2	N	H						X

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		3400–3600		3600–3800	
POACEAE	*Triniochloa stipoides* (Kunth) Hitchc.	N	H	X	X	X	X		
POACEAE	*Stipa rosea* Hitchc.	N	H	X		X	X	X	X
POLYGONACEAE	*Muehlenbeckia tamnifolia* (Kunth) Meisn.	N	H*	X	X	X	X		
POLYGONACEAE	*Rumex acetosella* L.	I	H		X		X	X	X
POLYGONACEAE	*Rumex* sp. 2	N	H	X					
POLYPODIACEAE	*Melpomene moniliformis* (Lag. ex Sw.) A.R. Sm. & R.C. Moran	N	H		X	X		X	X
POLYPODIACEAE	*Niphidium* sp.	N	H	X	X	X			
POLYPODIACEAE	*Pecluma* sp. 1	N	H			X	X		
POLYPODIACEAE	*Pecluma* sp. 2	N	H	X	X				
POLYPODIACEAE	*Pecluma* sp. 3	N	H		X				
POLYPODIACEAE	*Polypodium* sp.	N	H	X		X			
PROTEACEAE	*Lomatia hirsuta* (Lam.) Diels	N	W	X	X	X	X		
PROTEACEAE	*Oreocallis grandiflora* (Lam.) R. Br.	N	W	X	X	X	X		
PTERIDACEAE	*Eriosorus* sp.	N	H			X		X	
PTERIDACEAE	*Jamesonia* sp. 1	N	H	X		X	X	X	X
PTERIDACEAE	*Jamesonia* sp. 2	N	H			X			
PTERIDACEAE	*Pteridacea* sp.	N	H				X		
PTERIDOPHYTA	Pteridophyta	N	H				X		
RANUNCULACEAE	*Ranunculus peruvianus* Pers.	N	H			X			
ROSACEAE	*Hesperomeles ferruginea* (Pers.) Benth.	N	W	X					
ROSACEAE	*Hesperomeles obtusifolia* (Pers.) Lindl.	N	W	X	X	X			
ROSACEAE	*Lachemilla hispidula* (L.M. Perry) Rothm.	N	H			X		X	X
ROSACEAE	*Lachemilla orbiculata* (Ruiz & Pav.) Rydb.	N	H		X	X	X	X	X
ROSACEAE	*Lachemilla* sp. 1	N	H					X	
ROSACEAE	*Lachemilla* sp. 2	N	H			X	X	X	X
ROSACEAE	*Lachemilla vulcanica* (Schltdl. & Cham.) Rydb.	N	H					X	X
ROSACEAE	*Potentilla dombeyi* Nestl.	N	H					X	
ROSACEAE	*Rubus coriaceus* Poir.	N	H	X	X	X	X		X
ROSACEAE	*Rubus* sp. 1	N	W			X	X		
ROSACEAE	*Rubus* sp. 2	N	W			X			
ROSACEAE	*Rubus* sp. 3	N	W	X	X				
ROSACEAE	*Rubus* sp. 4	N	W		X				
RUBIACEAE	*Arcytophyllum filiforme* (Ruiz & Pav.) Standl.	N	H*	X		X	X	X	X
RUBIACEAE	*Arcytophyllum* sp. 2	N	H*	X		X	X		
RUBIACEAE	*Galium hypocarpium* (L.) Endl. ex Griseb.	N	H	X		X	X	X	X
RUBIACEAE	*Nertera granadensis* (Mutis ex L. f.) Druce	N	H						X

Table A1. *Cont.*

Family	Specie	S	Lf	NG	Pi	NG	Pi	NG	Pi
				3200–3400		**3400–3600**		**3600–3800**	
RUBIACEAE	*Palicourea* sp. 1	N	W	X					
RUBIACEAE	*Palicourea weberbaueri* K. Krause	N	W	X	X				
SCROPHULARIACEAE	*Sibthorpia repens* (L.) Kuntze	N	H		X	X	X	X	
SOLANACEAEA	*Iochroma cyaneum* (Lindl.) M.L. Green ex G.H.M. Lawr. & J.M. Tucker	N	W		X				
SOLANACEAEA	*Solanum* sp. 1	N	W		X		X		
SOLANACEAEA	*Solanum* sp. 2	N	W	X					
SYMPLOCACEAE	*Symplocos* sp. 1	N	W	X	X				
URTICACEAE	*Pilea* sp.1	N	H				X		
VERBENACEAE	*Citharexylum ilicifolium* Kunth	N	W	X					
VIOLACEAE	*Viola arguta* Willd. ex Roem. & Schult.	N	H	X					
VIOLACEAE	*Viola dombeyana* DC.	N	H					X	X
XYRIDACEAE	*Xyris subulata* Ruiz & Pav.	N	H					X	

Appendix B

Table A2. Species richness and coverage, and soil properties of pine plantations (Pi) sites across the elevational range. The data indicate the median and between parentheses quartiles (Q1 and Q3). HR = herbaceous richness, HC = herbaceous cover, WR = woody plant richness, WC = woody plant coverage, Ksat = saturated hydraulic conductivity, BD = bulk density, StC = water content at saturation point, FC = water content at field capacity, WP = wilting point, GW = gravitational water, AW = available water capacity, N = nitrogen, SOC = soil organic carbon, pH = potential of hydrogen, CN = carbon-nitrogen ratio.

Elevational Range (m a.s.l.)	**3200–3400**		**3400–3600**		**3600–3800**	
Plantations (Pi)	**Nero**	**La Paz**	**Tutupali Chico**	**Tutupali Grande**	**Quimsacocha**	**Soldados**
HR (%)	11 (9–12)	7 (7–7)	16 (16–20)	16 (16–18)	33 (32–33)	33 (27–36)
HC (%)	17.84 (17.68–17.84)	11.84 (5.68–15.17)	39.67 (17.35–41.84)	29.17 (19.85–35.18)	110.00 (101.36–130.18)	105.86 (73.84–136.03)
WR (%)	15(14–16)	7(6–8)	9(8–10)	7(6–8)		
WC (%)	40.84 (34.67–68.84)	8.17 (4.50–10.01)	12.17 (11.68–19.34)	8.84 (5.67–16.67)		
Ksat (cm/h)	3.61 (3.48–3.84)	3.77 (3.46–3.84)	6.55 (6.45–7.47)	4.71 (3.64–5.16)	2.11 (2.01–2.17)	2.20 (2.13–2.45)
BD (g/cm^3)	0.46 (0.45–0.47)	0.87 (0.86–0.90)	0.52 (0.52–0.65)	0.65 (0.48–0.76)	0.33 (0.33–0.36)	0.66 (0.57–0.66)
StC (cm^3/cm^3)	0.75 (0.74–0.76)	0.63 (0.62–0.64)	0.76 (0.70–0.77)	0.74 (0.67–0.78)	0.85 (0.84–0.85)	0.71 (0.69–0.72)
FC (cm^3/cm^3)	0.54 (0.51–0.55)	0.41 (0.39–0.41)	0.54 (0.51–0.55)	0.61 (0.55–0.64)	0.62 (0.6–0.63)	0.52 (0.50–0.55)
WP (cm^3/cm^3)	0.39 (0.38–0.41)	0.32 (0.32–0.33)	0.38 (0.35–0.38)	0.41 (0.41–0.42)	0.39 (0.38–0.40)	0.42 (0.41–0.45)
GW (cm^3/cm^3)	0.21 (0.19–0.21)	0.24 (0.23–0.26)	0.21 (0.19–0.21)	0.13 (0.12–0.14)	0.23 (0.21–0.25)	0.17 (0.16–0.20)
AW (cm^3/cm^3)	0.14 (0.10–0.15)	0.06 (0.06–0.08)	0.16 (0.16–0.18)	0.18 (0.18–0.22)	0.23 (0.21–0.24)	0.10 (0.10–0.10)
N (%)	0.87 (0.78–0.99)	0.34 (0.29–0.43)	1.12 (0.91–1.16)	0.66 (0.62–0.73)	1.25 (1.12–1.28)	0.89 (0.76–0.91)
SOC (%)	14.72 (13.87–17.23)	6.33 (4.82–7.45)	15.99 (14.84–16.86)	9.64 (9.26–12.77)	20.12 (18.17–20.39)	12.41 (11.79–16.14)
pH	4.52 (4.52–4.88)	4.14 (4.11–4.14)	4.40 (4.30–4.45)	4.10 (4.06–4.16)	4.15 (4.09–4.17)	4.77 (4.63–4.81)
CN	17.47 (14.29–17.88)	17.70 (16.48–18.15)	14.52 (14.23–16.06)	15.02 (14.71–15.6)	16.07 (15.9–16.29)	16.55 (16.33–17.47)

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