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Impact analysis of pine plantations on Ecuador's páramo and corresponding stakeholder perceptions

Carlos Alberto Quiroz Dahik

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List of abbreviations

ABU	adult bovine unit
AG	aboveground
AIC	Akaike Information Criteria
AW	water availability
BA	basal area
BD	bulk density
BIC	Bayesian Information Criteria
BG	belowground
C	carbon
CCA	Canonical Correspondence Analysis
CD	canopy density
CDM	Clean Development Mechanism
Cs	conservation status
DBH	diameter at breast height (1.3 m)
EN	endangered specie
ES	ecosystem services
Eq	equation
FC	field capacity
FSS	fine soil stock
G	grazed páramo
H	herbaceous
GW	gravitational water
IPCC	Intergovernmental Panel on Climate Change
Ksat	saturated hydraulic conductivity
LC	least concern specie

Lf	life form
LMM	linear mixed model
NG	páramo natural grassland
Ni	specie not included in the Red List
NT	near threatened specie
pH	potential hydrogen
Pi	pine plantation site
PROFAFOR	Programa FACE de Forestación del Ecuador S. A.
SOC	soil organic carbon
SOM	soil organic matter
StC	saturation point
TD	tree density
TH	tree height
UNFCCC	United Nations Framework Convention on Climate Change
VU	vulnerable specie
W	woody plant
WP	wilting point

Abstract

High tropical montane ecosystems, of which the páramo is one of the most important and widespread, play an important role in ecosystem services, the provision and regulation of water supply, the conservation of biodiversity, and soil carbon storage. The establishment of pine plantations for carbon sequestration and wood production recently sparked the debate about the potential impact of afforestation on paramo's ecosystem services. This research aimed to inventory and analyze the impacts caused by the establishment of pine plantations in the páramos of South Ecuador.

Afforestation of the páramo is a complex socio-economic process, and we started with the analysis of the stakeholders to probe their different interests and perspectives. The results revealed four main groups of stakeholders: landowners, local government officials, foresters, and nature conservationists. Although almost all of them acknowledge the ecosystem functions of plantations, their perceptions on specific functions vary between or/and within the groups. While most of the landowners perceived that their plantations were not going to be productive, the rest of the stakeholders had the opposite perception. Also, while the majority of landowners perceived that the plantations helped to regulate water flows, the rest of the stakeholders perceived the opposite. Furthermore, while the majority of the interviewed from the four groups of stakeholders perceived that plantations positively affect the sequestration and storage of carbon, only in the group of nature conservationists, there were negative perceptions. As our analysis revealed the perceptions of the stakeholders vary and are mainly due to the lack of sound scientific local knowledge (e.g., if plantations enhance total carbon stock, improve the regulation of water flows, degrade native vegetation habitat). Therefore, we expect that regional studies like this can contribute to more sustainable management of the páramo ecosystem by reconciling the different perceptions of the stakeholders, and the identification of the aspects that require further investigation.

The study area of the research includes seven locations within an elevational range from 2700 to 3800 m a.s.l. of the páramo ecosystem. In each location, the characteristics of three types of land use were compared. The land uses

considered were sites with natural vegetation, grazed and pine plantation sites. The sites with natural vegetation were characterized as in good conservation status and consisted of tussock grasses (mainly *Calamagrostis* spp. and *Festuca* spp.) in the higher zones of the páramo and by a mixture of grasses and shrubs in the lower zone, called subpáramo. The grazed sites were characterized by cattle grazing, with more intense management in the lowlands. The plantations were all composed by *Pinus patula* Schltdl. & Cham. mostly of the same age and with similar management.

One of the main ecosystem services that the páramo provides and that turned out to be one of the ecosystem services with diverging perceptions between the stakeholders is the provision of water and the regulation of supply. The hydrological service is closely related to the soil's hydro-physical properties and soil organic matter (SOM). Consequently, we analyzed the saturated hydraulic conductivity (K_{sat}), the water retention capacity and the SOM of the three land uses. Most of the plantations registered significantly higher values for K_{sat}, a decrease of SOM, and an increase in soil bulk density (BD). While the plantations established in a degraded páramo site registered the opposite results.

Another important ecosystem service of the páramo is the storage of carbon. Whereas most of the plantations have been established to sequester carbon, a main issue of this research was to analyze, if the afforestation with pine resulted in a higher total carbon stock compared to the other predominant land uses. For this purpose, we measured and compared the aboveground, belowground, and soil organic carbon (SOC) pools of the three types of land use. For an accurate estimation of the biomass carbon of the pine trees, we developed our own allometric equations (above and belowground biomass). We found significant differences between the amounts of carbon pools stored above- and belowground in the three types of land use. Pine plantations (Pi) revealed the highest amounts of above- and belowground carbon followed by natural grassland (NG) and grazed (G) páramo sites. Concerning the SOC pool of the plantations, most of the locations registered significantly lower values of carbon than NG and G. It was concluded that afforestation in the highest zones of the páramo for the purpose of CO_2 mitigation is not an advisable option.

Finally, our study considered also the conservation of biodiversity. In addition to the fact that the páramo is recognized for hosting the richest high mountain flora in the world, the stakeholders had controversial perceptions about the impacts of the plantations on this. To research the impact of plantations on páramo's ecosystem services, we contrasted the natural vegetation in páramo natural grassland with the natural regeneration growing inside pine plantations. The results showed a significantly higher plant diversity in páramo natural grassland. Also, the results showed that herbaceous species richness tended to rise with increasing elevation, while woody species had the opposite tendency. In addition, in the plantations, the increment of K_{sat}, basal area, and canopy density of the pines, caused a decrease in the extent and richness of herbaceous species. Nevertheless, native herbaceous and woody species including endemic species prospered inside the plantations.

The results of this research constitute a significant step forward in a better understanding of the afforestation impacts on the páramo ecosystem with pines, particularly for programs of carbon sequestration. In addition, it is believed that the integration and consideration of the perceptions of the stakeholders found in this research shall enrich and facilitate the development of future páramo management policies. Ultimately findings can contribute to the development of adequate silvicultural practices of the plantations in the páramo, resulting in a more global sustainable management of this ecosystem.

Keywords: Andes, páramo, natural grassland, ecosystem services, pine plantation, stakeholders, hydraulic conductivity, soil water retention, carbon stocks, aboveground carbon, belowground carbon, soil organic carbon, species richness.

Zusammenfassung

Hochmontane tropische Ökosysteme, von denen der Páramo eines der bedeutendsten und verbreitetsten ist, spielen eine wichtige Rolle bei der Bereitstellung von Ökosystemdienstleistungen, vor allem für die Sicherung und Regulierung der Wasserversorgung, den Schutz der Biodiversität sowie die Kohlenstoffspeicherung. Die Anlage von Plantagen im Páramo zur Kohlenstoffspeicherung und Holzproduktion hat jüngst eine intensive Debatte über die möglichen Auswirkungen solcher Aufforstungen auf die Ökosystemleistungen ausgelöst. Die vorliegende Studie hat es sich deshalb zur Aufgabe gemacht, Auswirkungen von Kiefernaufforstungen im Páramo Südecuadors zu erfassen und zu analysieren.

Aufforstungen im Páramo stellen einen komplexen sozio-ökonomischen Prozess dar. Den Anfang dieser Studie bildete deshalb eine Analyse der Interessen und Perspektiven der verschiedenen Akteure. Danach können vier Hauptakteursgruppen identifiziert werden: Landbesitzer, Vertreter lokaler Regierungsbehörden, Forstleute und Naturschützer. Obwohl fast alle Gruppen die Erfüllung von Ökosystemfunktionen auch durch Plantagen anerkennen, variiert ihre Sicht bezüglich bestimmter Funktionen sowohl innerhalb als auch zwischen den Gruppen zum Teil deutlich. Während die meisten Landbesitzer die Plantagen als nicht gewinnbringend bezeichnen, unterstellten alle anderen Gruppen eine ertragreiche Nutzung. Im Gegensatz zu den anderen Gruppen gingen die Landbesitzer auch von einem positiven Beitrag der Plantagen zur Regulierung des Wasserabflusses aus. Für die Mehrheit aller Befragten leisten die Plantagen einen positiven Beitrag zur Bindung und Speicherung von Kohlenstoff. Lediglich die Naturschützer sahen auch negative Auswirkungen. Wie unsere Analyse erbrachte, sind die unterschiedlichen Wahrnehmungen vor allem auf den Mangel an fundierten wissenschaftlichen Erkenntnissen zurückzuführen.

Das Untersuchungsgebiet dieser Studie umfasst sieben Páramo-Standorte in Ecuador in Höhenlagen von 2700 bis 3800 m. An jedem Standort wurden die Charakteristika folgender drei Landnutzungsarten verglichen: ´natürlicher Páramo´ (NG), beweideter Páramo (G) und Kiefernplantagen (Pi). ´Natürlicher

Páramo´ umfasst Standorte in gutem natürlichem Erhaltungszustand (mit hauptsächlich *Calamagrostis* spp. und *Festuca* spp.) in den höheren Lagen und einer Mischung aus Gräsern und Büschen in den niedrigeren Zonen (subpáramo). Bei den beweideten Flächen handelt es sich um Rinderweiden mit geringerem Besatz in den höheren und intensiverem in den niederen Lagen. Bei allen Plantagen handelt es sich um Aufforstungen mit Kiefern (*Pinus patula* Schltdl. & Cham.) in nahezu gleichem Alter mit ähnlicher Bewirtschaftung.

Eine der wichtigsten Ökosystemdienstleistungen des Páramo ist die Bereitstellung von Wasser und die Regulierung von dessen Abfluss. Diese hydrologischen Funktionen sind eng mit den physikalischen Eigenschaften der Böden und der organischen Bodensubstanz verbunden. Deshalb wurden in den Untersuchungsflächen aller drei Nutzungsarten die gesättigte hydraulische Leitfähigkeit (Ksat), das Wasserretentionsvermögen sowie die organische Bodensubstanz (SOM) analysiert. Die meisten Plantagenstandorte wiesen im Vergleich zu den anderen Nutzungsarten signifikant höhere Ksat-Werte, niedrigere SOM-Gehalte und erhöhte Lagerungsdichten auf. Plantagen auf degradierten Standorten zeigten dagegen gegenteilige Ergebnisse.

Eine weitere wichtige Ökosystemleistung des Páramo ist die Speicherung von Kohlenstoff. Da die meisten der untersuchten Plantagen zum Zweck der Kohlenstoffbindung etabliert wurden, war ein Hauptziel dieser Studie zu untersuchen, ob die Aufforstungen im Vergleich zu den anderen Nutzungen zu einem erhöhten Gesamtkohlenstoffvorrat geführt haben. Zu diesem Zweck wurden C-Vorräte in der oberirdischen, der unterirdischen Biomasse sowie der organischen Bodensubstanz aller drei Nutzungstypen untersucht und verglichen. Für die Abschätzung der ober- und unterirdischen Biomasse der Kiefern wurden mittels eigener Biomasseerhebungen allometrische Gleichungen entwickelt. Die Ergebnisse zeigen signifikante Unterschiede zwischen den ober- und unterirdischen Kohlenstoffpools der verschiedenen Landnutzungen. Die Kiefernplantagen (Pi) wiesen die höchsten C-Vorräte in der ober- und unterirdischen Biomasse auf (55.4 und 6.9 tC/ha), gefolgt von den natürlichen Páramoflächen (NG) (23.1 und 2.7 tC/ha) und den beweideten Standorten (G) (9.1 und 1.5 tC/ha). Die SOC-Vorräte der Plantagen waren jedoch an den meisten Standorten signifikant niedriger als in den NG und G-Flächen, so dass sich die

Gesamtkohlenstoffvorräte an den meisten Standorten nicht signifikant unterscheiden. In den höheren Lagen des Páramo sind daher Aufforstungen zur CO2-Bindung keine empfehlenswerte Option.

Um die Auswirkungen der Aufforstungen auf die Biodiversität zur erfassen, wurden an sechs Standorten vergleichende Analysen der Verjüngung in Kiefernplantagen und benachbarten natürlichen Páramoflächen durchgeführt. Die Ergebnisse erbrachten eine signifikant höhere Pflanzendiversität in den natürlichen Páramoflächen. Es zeigte sich auch, dass die Vielfalt an krautigen Pflanzen mit der Höhenlage zunahm, während die der hölzernen Arten abnahm. In den Plantagen führten ein Anstieg der hydraulichen Leitfähigkeit der Böden, eine Zunahme der Grundfläche und der Bestandesdichte zu einem Rückgang der Ausdehnung und der Vielfalt an krautigen Arten. Nichtsdestotrotz gedeihen auch in den Plantagen einheimische krautige und hölzerne Arten, einschließlich endemischer.

Die Ergebnisse der Studie stellen einen wichtigen Schritt zum besseren Verständnis der Folgen von Páramoaufforstungen mit Kiefern in Ecuador dar, vor allem im Hinblick auf spezifische Programme zur Kohlenstoffbindung. Sie zeigt auch, dass die Berücksichtigung der Interessen und Sichtweisen wichtiger Akteure eine wichtige Maßnahme sind, um politische Programme zum künftigen Management von Páramoflächen zu verbessern. Regionale Studien wie die vorliegende, können einen wichtigen Beitrag dazu leisten, die unterschiedlichen Sichtweisen der Akteure zu harmonisieren, weiteren Forschungsbedarf zu identifizieren und ein nachhaltigeres Management von Páramo-Ökosystemen zu erreichen.

Schlüsselwörter: Anden, Páramo, natürliches Grasland, Ökosystemleistungen, Kiefernplantage, Interessengruppen, hydraulische Leitfähigkeit, Bodenwasserretention, Kohlenstoffvorräte, oberirdischer Kohlenstoff, unterirdischer Kohlenstoff, organischer Kohlenstoff im Boden, Artenreichtum.

Resumen

Los ecosistemas tropicales de alta montaña, de los cuales el páramo es uno de los más importantes y extendidos brindan importantes servicios ecosistémicos como; el suministro y regulación del agua, la conservación de la biodiversidad y el almacenamiento de carbono en el suelo. El establecimiento de plantaciones de pinos en los páramos para el secuestro de carbono y la producción de madera ha provocado el debate sobre el impacto potencial de la forestación sobre los servicios eosistémicos del páramo. Esta investigación tuvo como objetivo inventariar y analizar los impactos causados por el establecimiento de plantaciones de pino en los páramos del sur de Ecuador.

La forestación del páramo es un proceso socioeconómico complejo, en nuestro estudio comenzamos con el análisis de los actores para sondear sus diferentes intereses y perspectivas. Los resultados revelaron cuatro grupos principales de actores: propietarios de las plantaciones, gobiernos locales, forestales y conservacionistas de la naturaleza. Aunque casi todos estos actores reconocen las funciones ecosistémicas de las plantaciones, sus percepciones sobre funciones específicas varían entre y / o dentro de los grupos de actores. Si bien la mayoría de los propietarios percibieron que sus plantaciones no iban a ser productivas, el resto de los actores la percepción opuesta. Asimismo, mientras que la mayoría de los propietarios percibió que las plantaciones ayudaron a regular los caudales de agua, el resto de los actores percibió lo contrario. También, si bien la mayoría de los entrevistados de los cuatro grupos de actores percibieron que las plantaciones afectan positivamente el secuestro y almacenamiento de carbono, solo en el grupo de conservacionistas de la naturaleza hubo percepciones negativas. Como nuestro análisis reveló, las percepciones de los actores varían y esto se deben principalmente a la falta de conocimiento científico local sólido (por ejemplo, si las plantaciones aumentan las existencias de carbono total, mejoran la regulación de los flujos de agua, degradan el hábitat de la vegetación nativa). Por lo tanto, esperamos que estudios regionales como este puedan contribuir a una gestión más sostenible del ecosistema del páramo al conciliar las diferentes percepciones de los actores y la identificación de los aspectos que requieren mayor investigación.

El área de estudio de la investigación incluye siete localidades dentro de un rango de elevación de 2700 a 3800 m s.n.m. del ecosistema de páramo. En cada lugar, se compararon las características de tres tipos de uso del suelo. Los usos del suelo considerados fueron sitios con vegetación natural, sitios de pastoreo y plantaciones de pinos. Los sitios con vegetación natural se caracterizaron como en buen estado de conservación y consistieron en pajonales (principalmente *Calamagrostis* spp. y *Festuca* spp.) en las zonas altas del páramo, y por una mezcla de pajonales y arbustos en la zona baja, denominada subpáramo. Los sitios de pastoreo se caracterizaron por el pastoreo de ganado, con un manejo más intenso en las tierras bajas. Todas las plantaciones fueron compuestas por *Pinus patula* Schltdl. & Cham. en su mayoría de la misma edad y con un manejo similar.

Uno de los principales servicios ecosistémicos que brinda el páramo y que resultó ser uno de los servicios ecosistémicos con percepciones divergentes entre los actores es la provisión y regulación del suministro del agua. Este servicio hidrológico está estrechamente relacionado con las propiedades hidrofísicas del suelo y la materia orgánica del suelo. En consecuencia, analizamos la conductividad hidráulica saturada (Ksat), la capacidad de retención de agua y la materia orgánica de los tres usos del suelo. La mayoría de las plantaciones registraron valores significativamente más altos de Ksat, una disminución de la materia orgánica y un aumento en la densidad aparente del suelo. Mientras que las plantaciones establecidas en un páramo degradado registraron resultados opuestos.

Otro servicio ecosistémico importante del páramo es el almacenamiento de carbono. Si bien la mayoría de las plantaciones se han establecido para secuestrar carbono, un tema principal de esta investigación fue analizar, si la forestación con pino resultó en una mayor reserva total de carbono en comparación con los otros usos predominantes de la tierra. Para este propósito, medimos y comparamos los depósitos de carbono orgánico sobre el suelo, subterráneo y del suelo de los tres tipos de uso de la tierra. Para una estimación precisa del carbono de la biomasa de los pinos, desarrollamos nuestras propias ecuaciones alométricas (biomasa aérea y subterránea). Encontramos diferencias significativas entre las cantidades de reservas de carbono almacenadas encima y debajo del suelo en los tres tipos de uso de la tierra. Las plantaciones de pino (Pi) revelaron las mayores cantidades de carbono encima y debajo del suelo, seguidas de los pastizales naturales (NG) y los sitios de páramo de pastoreo (G). En cuanto a los bancos de carbono orgánico del suelo de las plantaciones, la mayoría de las localidades registraron valores de carbono significativamente menores que NG y G. Se concluyó que no es una opción aconsejable la forestación en las zonas más altas del páramo con el propósito de secuestrar el CO2.

Finalmente, nuestro estudio consideró también la conservación de la biodiversidad. Además del hecho de que el páramo es reconocido por albergar la flora de alta montaña más rica del mundo, los actores tenían percepciones controvertidas sobre los impactos de las plantaciones en la biodiversidad. Para investigar el impacto de las plantaciones en este servicio ecosistémico del páramo, contrastamos la vegetación natural en los pajonales naturales de páramo con la regeneración natural que crece dentro de las plantaciones de pinos. Los resultados mostraron una diversidad de plantas significativamente mayor en los pajonales naturales de páramo. Además, los resultados mostraron que la riqueza de especies herbáceas tendió a aumentar con la elevación, mientras que las especies leñosas tuvieron la tendencia opuesta. Asimismo, en las plantaciones, el incremento de Ksat, área basal y densidad de copa de los pinos, provocó una disminución en la extensión y riqueza de especies herbáceas. Sin embargo, especies herbáceas y leñosas nativas, incluidas especies endémicas, prosperaron dentro de las plantaciones.

Los resultados de esta investigación constituyen un importante paso adelante en una mejor comprensión de los impactos de la forestación con pino en el ecosistema de páramo, particularmente para los programas de secuestro de carbono. Además, se cree que la integración y consideración de las percepciones de los actores encontrados en esta investigación enriquecerá y facilitará el desarrollo de futuras políticas de manejo del páramo. En definitiva, los hallazgos pueden contribuir al desarrollo de prácticas silviculturales adecuadas de las plantaciones en el páramo, resultando en una gestión sostenible más global de este ecosistema.

Palabras clave: Andes, páramo, pajonales naturales, servicios ecosistémicos, plantación de pinos, actores, conductividad hidráulica, retención de agua del

suelo, reservas de carbono, carbono sobre el suelo, carbono bajo el suelo, carbono orgánico del suelo, riqueza de especies.

Publication's overview

This dissertation is based on four peer-reviewed publications (*Publication I – IV*). For each of these publications the original abstract, journal information and author's contribution are provided in the following. Original versions of Publication I – IV can be found in the Appendix or be accessed via the respective DOI listed below.

Publication I

Quiroz Dahik C, Crespo P, Stimm B, Murtinho F, Weber M, Hildebrandt P. 2018. Contrasting Stakeholders' Perceptions of Pine Plantations in the Páramo Ecosystem of Ecuador. Sustainability 10:1707.

DOI: 10.3390/su10061707

Journal impact factor: 2.592 (2018)

Abstract: The páramo, a collection of Neotropical alpine ecosystems, plays a prominent role in ecosystem services (ESs), providing water supply and regulation, conservation of biodiversity, and carbon storage in soil. The establishment of pine plantations for carbon sequestration and wood production has recently raised questions concerning the possible impact on the paramo's ES. This study identifies the main stakeholders in this field and compares and contrasts their perceptions of the impact of pine plantations on the paramo's ES, because the disparity among stakeholders' perceptions must be addressed to achieve sustainable management. The data were gathered using 56 semi-structured interviews and were qualitatively analyzed. The results show that the main stakeholder groups (landowners, local government officials, foresters, and nature conservationists) acknowledge the important ES of the plantations. The perception of plantation impact varies among and within stakeholder groups, however, on specific functions, such as water provision, carbon storage, erosion prevention, and habitat function for wildlife and natural vegetation. Consideration and integration of these perceptions can help policy makers and organizations develop sustainable policies for the future management of the páramo ecosystem.

Author's contribution: C.Q.D., P.C. and P.H. developed the study design; C.Q.D. collected the data; C.Q.D., M.W. and P.H. analyzed the data; C.Q.D. wrote the paper; all authors contributed to the paper's structure and provided extensive revision. All authors read and approved the final manuscript.

Publication II

Marín F, Quiroz Dahik C, Mosquera G, Feyen J, Cisneros P, Crespo P. 2018. Changes in Soil Hydro-Physical Properties and SOM Due to Pine Afforestation and Grazing in Andean Environments Cannot Be Generalized. Forests 10:17.

DOI: 10.3390/f10010017

Journal impact factor: 2.221 (2020)

Abstract: Andean ecosystems provide important ecosystem services including streamflow regulation and carbon sequestration, services that are controlled by the water retention properties of the soils. Even though these soils have been historically altered by pine afforestation and grazing, little research has been dedicated to the assessment of such impacts at local or regional scales. To partially fill this knowledge gap, we present an evaluation of the impacts of pine plantations and grazing on the soil hydro-physical properties and soil organic matter (SOM) of high montane forests and páramo in southern Ecuador, at elevations varying between 2705 and 3766 m a.s.l. In total, seven study sites were selected and each one was parceled into undisturbed and altered plots with pine plantation and grazing. Soil properties were characterized at two depths, 0–10 and 10–25 cm, and differences in soil parameters between undisturbed and disturbed plots were analyzed versus factors such as ecosystem type, sampling depth, soil type, elevation, and past/present land management. The main soil properties affected by land use change are the saturated hydraulic conductivity (Ksat), the water retention capacity (pF 0 to 2.52), and SOM. The impacts of pine afforestation are dependent on sampling depth, ecosystem type, plantation characteristics, and previous land use, while the impacts of grazing are primarily dependent on sampling depth and land use management (grazing intensity and tilling activities). The site-specific nature of the found relations suggests that extension of findings in response to changes in land use in montane Andean

ecosystems is risky; therefore, future evaluations of the impact of land use change on soil parameters should take into consideration that responses are or can be site specific.

Author's contribution: C.Q.D. and P.C. (Patricio Crespo) developed the study design. F.M. and C.Q.D. collected and analyzed the samples; F.M. analyzed data and wrote the manuscript; P.C. (Patricio Crespo) designed and supervised the study; G.M.M., P.C. (Pedro Cisneros) and P.C. (Patricio Crespo) provided a critical revision of the manuscript; J.F. and G.M.M. edited the manuscript. All authors read and approved the final manuscript.

Publication III

Quiroz Dahik C, Crespo P, Stimm B, Mosandl R, Cueva J, Hildebrandt P, Weber M. 2021. Impacts of pine plantations on carbon stocks of páramo sites in Southern Ecuador. Carbon Balance Manag. 16:5.

DOI: 10.1186/s13021-021-00168-5

Journal impact factor: 4.067 (2020)

Abstract: Since the 1990's, afforestation programs in the páramo have been implemented to offset carbon emissions through carbon sequestration, mainly using pine plantations. However, several studies have indicated that after the establishment of pine plantations in grasslands, there is an alteration of carbon pools including a decrease of the soil organic carbon (SOC) pool. The aim of this study is to investigate the impact of the establishment of pine plantations on the carbon stocks in different altitudes of the páramo ecosystem of South Ecuador.
Results: At seven locations within an elevational gradient from 2780 to 3760 m a.s.l., we measured and compared carbon stocks of three types of land use: natural grassland, grazed páramo, and *Pinus patula* Schlltdl. & Cham. plantation sites. For a more accurate estimation of pine tree carbon, we developed our own allometric equations. There were significant ($p < 0.05$) differences between the amounts of carbon stored in the carbon pools aboveground and belowground for the three types of land use. In most of the locations, pine plantations revealed the highest amounts of aboveground and belowground carbon (55.4 and 6.9 tC/ha)

followed by natural grassland (23.1 and 2.7 tC/ha) and grazed páramo sites (9.1 and 1.5 tC/ha). Concerning the SOC pools, most of the locations revealed significant lower values of plantations' SOC in comparison to natural grassland and grazed páramo sites. Higher elevation was associated with lower amounts of pines' biomass.
Conclusions: Even though plantations store high amounts of carbon, natural páramo grassland can also store substantial amounts above and belowground, without negatively affecting the soils and putting other páramo ecosystem services at risk. Consequently, plans for afforestation in the páramo should be assessed case by case, considering not only the limiting factor of elevation, but also the site quality especially affected by the type of previous land use.

Author's contribution: CQD, PC, BS, RM and MW made substantial contribution to the conception and design of the work. CQD collected and analyzed the data. CQD and JC performed the analysis of the data. CQD wrote the original draft of the manuscript. MW was the supervisor and PC and PH were the co-supervisors. All authors contributed to the paper's structure and provided extensive revision. All authors read and approved the final manuscript.

Publication IV

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DOI: 10.3390/f10090745

Journal impact factor: 2.221 (2020)

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 decreased; 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.

Author's contribution: 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.

1 Introduction

1.1 General background

A specific vegetation type is present between the upper limit of continuous forest and the upper limit of plant life in the tropical belt of the three continents (América, Africa and Oceania) (Luteyn et al. 1999). In the Andes, this vegetation is called "*páramo*" a high tropical montane vegetation (Lauer 1981; Monasterio and Sarmiento 1991). Based on the vegetation structure and elevation, the páramo has been categorized into three broad zones: the subpáramo, the páramo grassland and the superpáramo (Cuatrecasas 1968; Ramsay 1992; Luteyn et al. 1999; Llambí 2015). The subpáramo is located between 2800 and 3500 m a.s.l. and represents the transition ecotone between the montane forest below and the páramo grassland above. In the lower parts it is dominated by tall shrubs and small scattered trees, and in the upper parts by dwarf shrubs, grasses, and herbs (Llambí 2015). The most predominant zone of the páramo is the páramo grassland (Luteyn et al. 1999), which is mainly composed of tussock grasses dominated by *Calamagrostis* spp. and *Festuca* spp. The superpáramo is the zone located above the páramo grassland, found from 4000 to 5000 m a.s.l. to the snow landscape. Its vegetation grows on rocky scree and sandy soils. Among the páramo zones, this is the one with the lowest air temperature, precipitation, soil water retention capacity and nutrient content, as well as the highest solar radiation (Baruch 1984). Above the subpáramo ecotone, at heights between 3500 and 4200 m a.s.l. exist small isolated patches of forests mainly composed of *Polylepis* spp., which shares some shrub elements of the subpáramo, but have a different and less diverse woody composition (Llambí 2015).

The páramo provides important ecosystem services such as water supply and regulation, carbon storage and biodiversity conservation (Buytaert et al. 2011; Hofstede et al. 2014). As the páramo has a higher precipitation regime than the lowlands (Viviroli et al. 2007), it provides high-quality water to the Andean settlements. For instance, Quito and Bogotá, the capital cities of Ecuador and Colombia receive around 85% and 95% of superficial water from their regional páramo (Buytaert et al. 2011). Besides, the páramo soils possess a high water retention capacity (Mena V. et al. 2001; Poulenard et al. 2003) and its soil acts as a sponge that holds and releases the water gradually but constantly (Molina and

Little 1981; Luteyn et al. 1999). Another very important aspect of páramo soils is that they act as a carbon pool. Carbon is accumulated in the soil organic matter due to the cold and wet climate, low atmospheric pressure, and the formation of organometallic complexes that are resistant to microbial breakdown (Buytaert, Deckers, et al. 2006). Additionally, the páramo ecosystem presents the richest high mountain flora (Smith and Cleef 1988), as well as the fastest average net diversification rates of all biodiversity ´hotspots´ (Myers et al. 2000; Madriñán et al. 2013). It is estimated that 60% of páramo's vascular plants are endemic (Luteyn and Balslev 1992).

The páramo has been intervened for thousands of years. Before the arrival of the Incas, it was used as a ceremony and hunting place. Then, with the development of the Inca culture, it was used for grazing with Andean camelids and for potato cultivation. Later, with the arrival of the Spaniards, it was used for cattle and sheep grazing in addition to cereal cultivation. Currently, the activities that generate the greatest impacts on the páramo are the expansion of the agricultural frontier, mining, and afforestation with exotic species (Llambí and Cuesta 2014). Afforestation with non-native species in Ecuador started in 1875 when *Eucalyptus* spp. were introduced with the objective to produce timber, fuel and to restore degraded Andean soils (Dickinson 1969; Gade 1999; Doughty 2000; Rhoades 2006). Then, approximately in 1928, the Department of Agriculture introduced seventy species of conifers including some *Pinus* spp., to perform adaptation tests and to select given the local conditions the best species for forestation programs. After several years of testing, among the selected species were *Pinus radiata* and *Pinus patula*, with which important national afforestation programs were implemented through the 60, 70, and 80s (Hofstede et al. 1998; Farley 2010). The aim of these programs was to encourage the establishment of plantations, in most cases for timber production with full or partial economic assistance from the state. These programs were especially significant for rural communities and many small landowners (Farley 2007). Later on, by means of plantation subsidies or tax incentives, the conditions became more appealing to large tenants as larger plantations were considered potentially important timber producers (Farley 2007).

In the last decades, international funding replaced governmental financing, which caused a rise in the creation of new plantations. Many of them have been established to capture and fix carbon dioxide from the atmosphere under the auspices of the PROFAFOR program (Programa FACE de Forestación). PROFAFOR is an Ecuadorian company acting in the extension of the Forest Absorbing Carbon Dioxide Emissions (FACE) consortium, financed by the Dutch electricity companies to offset their carbon emissions. Since its establishment in 1993, PROFAFOR signed 152 afforestation contracts with private and community landowners. Until 2003, 22,000 ha of plantations were established in the Andean highlands from which most (94%) are pine plantations (Farley 2007; Wunder and Albán 2008). Most PROFAFOR plantations are exempted from the guidelines of the United Nations Clean Development Mechanisms (CDM) program, called the Kyoto protocol, as the year of planting falls before the year set in the protocol (Wunder and Albán 2008).

In Ecuador, non-native plantations were established mainly to ameliorate the economic viability by timber production. Also, these types of plantations have been created for erosion prevention, improvement of soil conditions, furtherance of water quantity and quality, watershed protection, mushroom harvesting, and carbon sequestration (Farley et al. 2004; Rudel et al. 2005; Buytaert, Iñiguez, et al. 2007). However, several studies have shown negative effects of these plantations on paramo's soil water retention and carbon storage (Hofstede, Groenendijk, et al. 2002; Farley et al. 2004; Farley et al. 2005; Buytaert, Iñiguez, et al. 2007; Ochoa-Tocachi et al. 2016). Other studies also identified negative effects of afforestation on the floristic composition and species diversity of the páramo (Ohep and Herrera 1985; van Wesenbeeck et al. 2003). Therefore, there is an increasing concern about the effects of pine plantations and future forestation strategies on the Ecuadorian páramo (Granda 2006; Ramos and Bonilla 2008; Merchán 2013 Nov 17).

1.2 Research questions

This thesis attempted to answer the following research questions:

- Who are the main stakeholders involved in afforestation of the Ecuadorian páramo and what are their perceptions of the impact of this activity on the páramo ecosystem services?

- What are the impacts of the change in land use, from páramo natural grassland to páramo grazing and afforestation, on páramo ecosystem services such as water regulation, biodiversity conservation, and carbon storage?

1.3 Objectives and hypothesis

The general aim of the thesis was to determine the impacts that forestation has on the ecosystem services of the páramo in the Southern Andes of Ecuador and to ascertain the perceptions that the society has about afforestation of the páramo. Based on this aim, the following four specific objectives were postulated:

1. To identify the main groups of stakeholders related to the establishment of pine plantations in the páramo ecosystem, and to explore and contrast their perceptions regarding the impacts of plantations on the páramo ecosystem services.
2. To evaluate the impact of pine afforestation and grazing on the hydro-physical properties and soil organic matter (SOM) content of the surface horizons of páramo soils.
3. To assess and compare the carbon stocks and soil bulk density of the different land uses of the páramo.
4. To analyze the regeneration of natural vegetation in the afforested sites and to evaluate the impacts of pine plantation attributes (basal area, canopy density, and soil properties) on the vegetation in three elevation bands.

The thesis is guided by the following hypotheses:

- There are disparities between the perceptions of different stakeholders about the impacts of forestation in the páramo ecosystem.
- Forestation in the páramo ecosystem changes the physical properties of the soil, alters the carbon storage and the composition and structure of the vegetation.

Based on previous considerations, a conceptual framework as shown in Figure 1 was developed.

1.4 Setting of the research

All investigations were conducted within the framework of the project PAK 824/B3 (WE 2069/7-1 and /7-2), "Improvement of forest management key strategies: a contribution to conservation and sustainable land use", funded by German Research Foundation (DFG), ETAPA, University of Cuenca, and the Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación del Ecuador (SENESCYT).

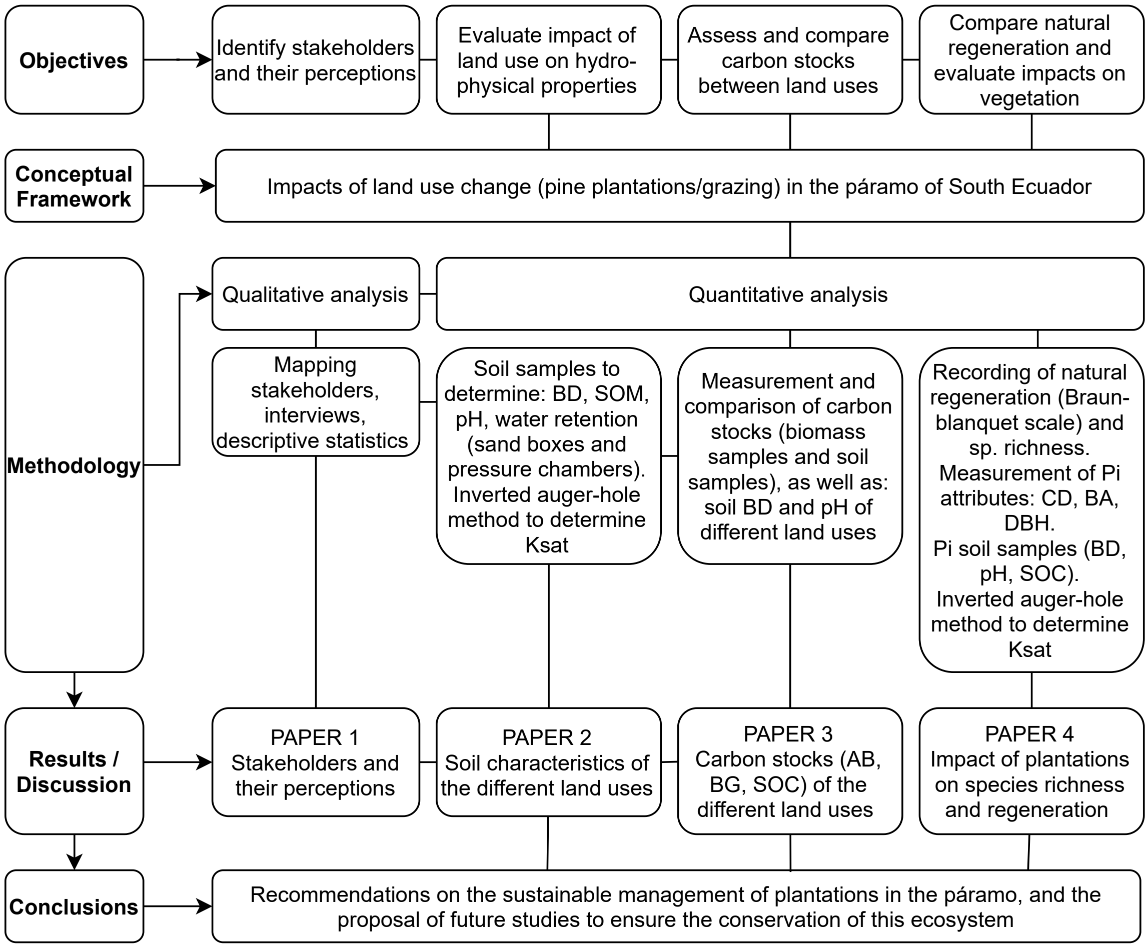

Figure 1. Conceptual framework of the research. BD = soil bulk density, SOM = soil organic carbon, K_{sat} = saturated hydraulic conductivity, CD= canopy cover, BA= basal area, DBH= diameter at the breast hight, AG = aboveground, BG = belowground, SOC = soil organic carbon, NG = páramo natural grassland, G= grazed páramo site, Pi = pine plantation site.

2 State of Research

This chapter provides a brief review of recent literature on the stakeholders' perceptions of forestation in the páramo, and their impacts on páramo ecosystem services. To develop concepts for a sustainable management of forestation in the páramo ecosystem, it is necessary to construct a clear idea of the stakeholders and their perceptions. Until recently, articles on ecosystem services centered on the biophysical and economic aspects instead of the values and perceptions and handling of the stakeholders (Menzel and Teng 2009). This research is the first one highlighting the variation in perceptions of the stakeholders about the impacts of forestation in the páramos of Ecuador (Publication I).

2.1 Perceptions of the impacts of pine plantations on páramo ecosystem services

Ecosystem services are the material and nonmaterial benefits nature provides to human well-being (Millennium Ecosystem Assessment 2005). The range of the páramo ecosystem services extends over several property boundaries which requires widespread stakeholder cooperation (Cowling et al. 2008). However, the stakeholders may have different perceptions of ecosystem service values, approaches and events (Turner and Daily 2008). For example, while in the last decades' pine plantations were established and promoted in the páramos (Farley 2007), some environmental non-governmental organizations have blamed the pine plantations for diminishing the water supply and for producing negative economic impacts to the landowners (Granda 2006; Ramos and Bonilla 2008). In recent years, also the scientific community has expressed concerns since some studies revealed negative impacts caused by plantations on local biodiversity, soil organic carbon and hydrological alterations such as a reduction of total water yield (Hofstede, Groenendijk, et al. 2002; Farley et al. 2004; Buytaert, Iñiguez, et al. 2007; Ochoa-Tocachi et al. 2016). However, actually, there is no sound information about the major stakeholders and their perceptions.

2.2 Impacts of afforestation on páramo ecosystem services

In the 60s, when the first national afforestation programs in the Andes began, its objectives were timber production and the recovery of some ecosystem services such as the recovery of degraded soil properties (Hofstede et al. 1998; Farley

2010). Some of these afforestation programs were established in the páramos, changing its land cover and land use. Only in the last decades, scientists recognized that land use changes are altering the ability of biological systems to support human needs (Vitousek et al. 1997). Since then, several studies have been conducted to investigate the effects of land use changes in the páramo.

Regarding water regulation and supply, some studies revealed a tendency of afforested páramo soils to become drier due to the high-water absorption capacity of the trees. This loss of humidity facilitates the decomposition of SOM (Hofstede, Groenendijk, et al. 2002; Farley and Kelly 2004; Buytaert, Iñiguez, et al. 2007), and reduces the soil water retention capacity (Harden et al. 2013). However, other studies reported no change or even an increment of SOM (Chacón et al. 2009; La Manna et al. 2016).

Concerning carbon storage, studies of the impacts of afforestation on SOC showed different results. A global synthesis (Paul et al. 2002) of these impacts revealed decreases as well as increases of SOC, while the global meta-analysis of Berthrong et al. (2009) showed decreases in SOC due to afforestation with pines. Several regional investigations in the páramo found a decrease in SOC (Hofstede, Groenendijk, et al. 2002; Farley et al. 2004; Farley et al. 2013; Bremer et al. 2016), but Chacón et al. (2009) suggested that the planted trees may not be the reason because pine plantations were mostly planted on degraded sites. Also, impacts of land use change on SOC depend on the soil properties and the environmental conditions, which can be unique for each region; in consequence the results should not be generalized (Hofstede, Groenendijk, et al. 2002; Holmes et al. 2006). In relation to biodiversity, key delegates at the International Congress for Conservation Biology were interviewed and had different views on the conservation of biodiversity, while some were in favor of conserving biodiversity on all areas, also including non-native species and highly modified landscapes, other delegates preferred conservation only of pristine nature in protected areas (Holmes et al. 2017). Similarly, researchers are still debating the impact of afforestation on páramo biodiversity conservation. Some studies found that páramo understory vegetation grew scarce under dense pine plantations due to the lack of light passing through the close canopy of the plantations (Ohep and Herrera 1985). Also, it has been found that páramos` native species biodiversity decreased when the area covered by plantations increased, or when the plantations crown coverage was too dense (Cavelier and Santos 1999; van Wesenbeeck et al. 2003). On the other hand, in other studies (Hofstede, Groenendijk, et al. 2002; Bremer 2012) no significant difference was found between the vegetation growing inside the plantation and in natural páramo grassland.

3 Study Area: General Context and Experimental Design

3.1 Study area

The study was carried out in southern Ecuador, in the Azuay province (2°57′-3°19′S, 79°5′-79°19′W), in an area whose height varies between 2700 and 3800 m a.s l. In this region, seven locations were selected and all of them correspond to the páramo ecosystem (Figure 2). Generally, the climate of the páramo is wet and

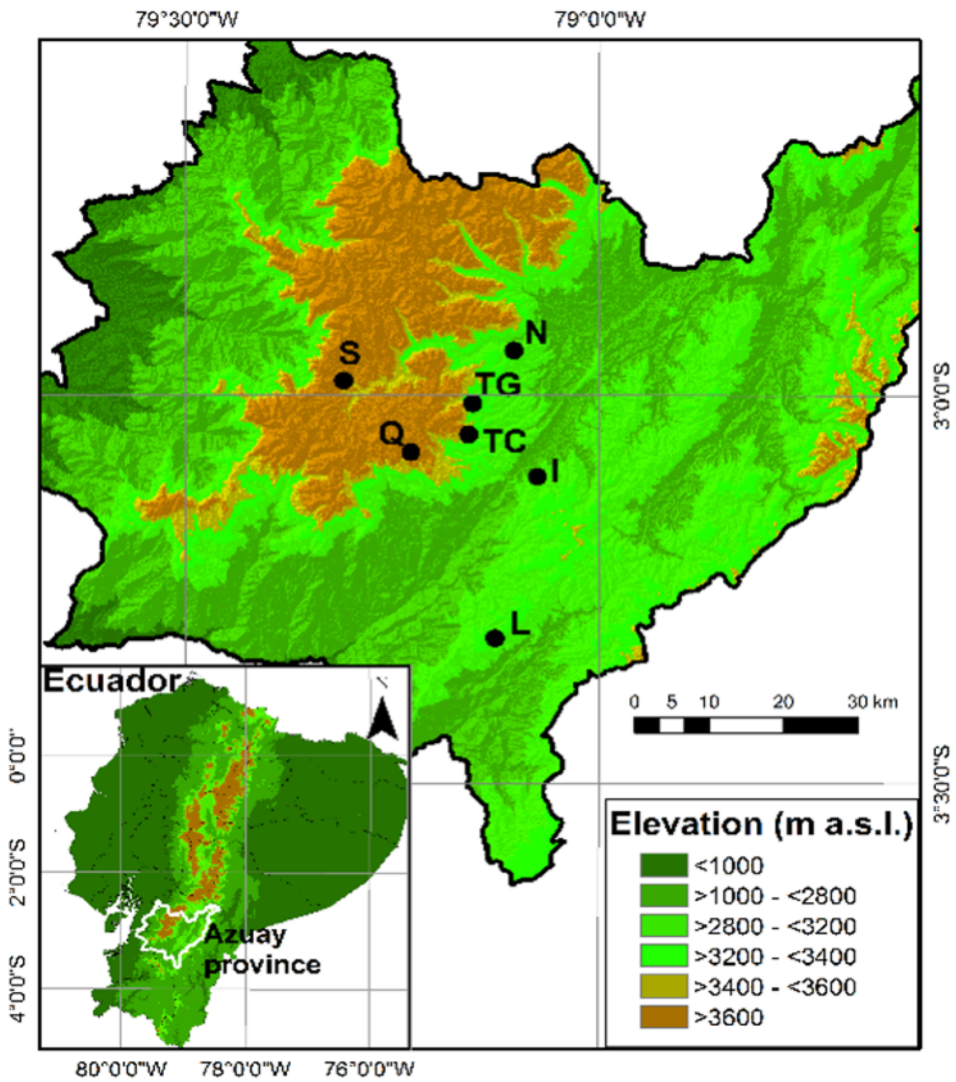

Figure 2. Map of Azuay province showing the seven locations of the study and its elevation: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S) (Publication III).

humid with a mean relative humidity of 91% (Padrón et al. 2015). Rainfall ranges between 900 and 1600 mm per year and is characterized by frequent low volume events. The climate regime is bimodal with a rainy season from December to

January and fewer rains from August to September (Buytaert, Deckers, et al. 2007; Quichimbo et al. 2012; Padrón et al. 2015). The change in average temperature with elevation is between 0.6 and 0.7°C per 100 m elevation difference. At 3600 m a.s.l., the average temperature is 8°C (Buytaert, Célleri, et al. 2006; Buytaert, Deckers, et al. 2007), is rather constant over the year but associated with high day-night variations (Buytaert et al. 2005).

The geological material in this region corresponds mainly to the Tarqui, Turi, and Saraguro mountain formations, which are composed of a variety of lithological andesite rocks, ash-flow tuffs, pyroclastic flows, and volcanic rocks. These formations belong to the Miocene, which is the first geological epoch of the Neogene period (Hungerbühler et al. 2002). Most of the soils are classified as Andosols of volcanic origin presenting Hydric and Histic properties with low volcanic glass content (Buytaert et al. 2002). 3000 years BP these soils have been rejuvenated by a thin layer of fine ash covering the bedrock. The volcanic ash protected the humus against decomposition through the formation of organic-mineral complexes (Dahlgren et al. 2004). Besides, the cold and humid weather and the low atmospheric pressure (Buytaert, Deckers, et al. 2007) favored the accumulation of soil organic matter (between 10 and 40%). The combination of the organic matter and the volcanic ash constitute the prevalent soil types in the páramo (Podwojewski and Poulenard 2004), which are black, humid and acid with porous structure, low bulk density (BD) of around 0.3 t/m^3 (Buytaert et al. 2005), and high water retention capacity (more than 0.4 cm^3/cm^3) (Poulenard et al. 2003; Quichimbo et al. 2012).

People living in the study area tend to have a low average income; the main livelihood comes from agriculture, cattle grazing and the utilization of pine plantations (Jokisch 2002; Buytaert, Iñiguez, et al. 2007; Farley et al. 2011). In brief, the people depend on the use of their land.

3.2 Experimental setup

For the study, seven locations were selected: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S) (Figure 2). The locations are situated in three elevation ranges: I, N, and L in 2700 - 3400 m a.s.l., TC and TG in 3400 - 3600 m a.s.l., and Q and S in 3600 - 3800 m a.s.l. At each location three types of land uses were compared: páramo natural grassland (NG), grazed páramo (G), and pine plantations (Pi). All sites were selected so that the site characteristics were as similar as possible with exception for the type of land use. For each location six NG sites (n=42), six G sites (n=42) and five Pi sites were selected, except for the locations of TG and S, where ten Pi sites were chosen (instead of five as in the other locations) (n=45).

3.3 Selection and implementation of study sites

The Pi sites were established first, and later the NG and G sites between 20 m and 2 km adjacent to the corresponding Pi site. For the establishment of the Pi we selected nine *P. patula* plantations located in the seven locations. The local forestry department provided an outdated forest register of the area, which we updated with the help of PROFAFOR and the landowners. From the updated list, we interviewed 19 plantation owners who make up approximately 70% of the plantation owners in the region. Based on the results of these interviews (Publication I), nine plantations were selected. The criteria for selecting the plantations were: the willingness of the landowners to collaborate with the study, location of the plantations in similar elevational ranges, similar silvicultural management, and degree of accessibility to the study area. For the location of five inventory plots inside each plantation, orthophotos were used. The orthophotos were provided by the Ministry of Agriculture "Sistema Nacional de Información y Gestión de Tierras Rurales e Infraestructura Tecnológica SIGTIERRAS del Ministerio de Agricultura y Ganadería". The orthophotos had a spatial resolution of 0.3 m, and were used to randomly locate the inventory plots inside each plantation.

Pine plantation sites (Pi) (Figure 3): in each site, one square plot with a side length of 24 m was constructed. All plantations were planted with *P. patula* sp, the first rotation with 3 x 3 m spacing with a median age of 19 years at the time of the forest inventory. The management of the plantations varied from no management to different intensities of pruning. Thinning was applied in a limited area in two plantations, and therefore this type of management was not further considered (Table 1). Generally, these types of plantations are harvested on a 25-year rotation. Seven out of the nine plantations mentioned that the plantations were established under contracts with the company PROFAROR Latinoamericana S.A.

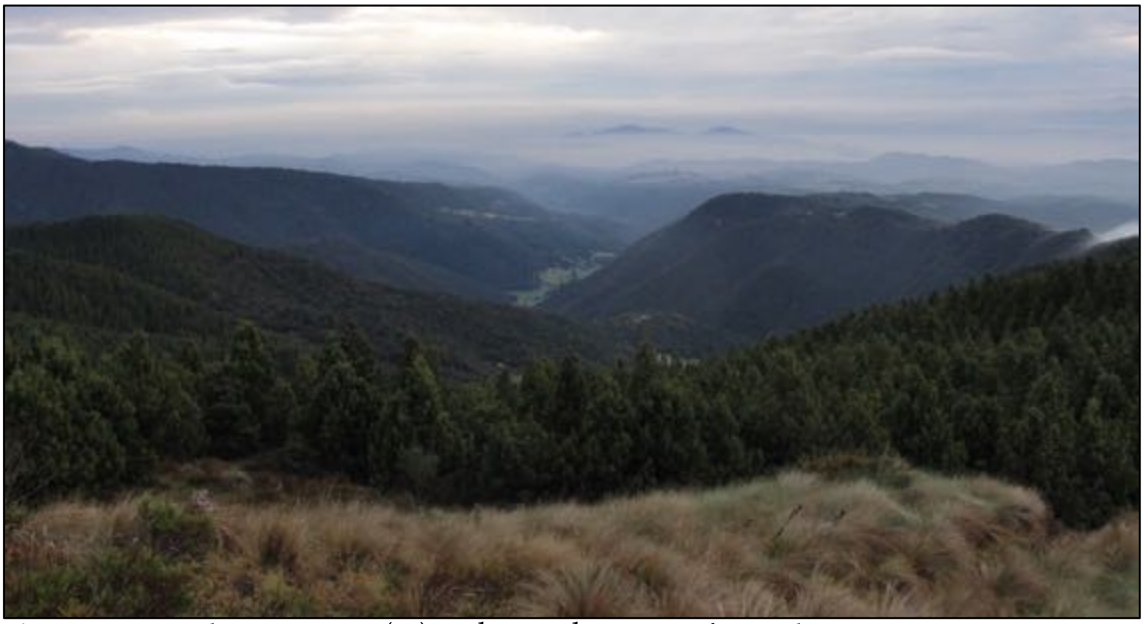

Figure 3. Pine plantation site (Pi) in the south region of Ecuador.

Table 1. Characteristics of the pine plantations sites (Pi), type of land use before their establishment and type of native vegetation found adjacent to the plantations in the undisturbed sites (NG) (Publication III).

Location		Altitud (m a.s.l.)	Age (years)	Size (ha)	Slope (%)	Trees per ha.	DBH (cm)	Tree height (m)	Management	Type of land use before the establishment of the plantation	Type of vegetation of the undisturbed sites (NG)
Irquis		2780	29	25	46.8	611	26.0	19.2	None	NG	Shrubs, woody veg.
Nero		3260	18	30	21.2	694	20.2	11.3	None	NG	Shrubs, woody veg.
La Paz		3380	17	46	12.8	850	21.2	9.3	Pruned	G	Tussock grass, shrubbs
Tutupali Chico		3420	16	350	22.4	712	20.8	9.7	Pruned	G	Tussock grass, shrubbs
Tutupali Grande	Pi1	3460	22	300	26.4	781	17.1	9.0	Pruned	G	Tussock grass
	Pi2	3540	20	300	41.1	806	15.8	7.6	None	G	Tussock grass
Quinsacocha		3690	19	123	23.3	573	9.5	4.9	Pruned	G	Tussock grass, shrubbs
Soldados	Pi1	3760	16	240	20.5	458	12.6	4.8	None	G	Tussock grass
	Pi2	3720	19	100	16.8	569	11.2	5.0	Pruned	NG	Tussock grass

Páramo natural grassland (NG) (Figure 4): these sites contained tall tussock grasses, mainly *Calamagrostis* spp. and *Festuc*a spp., and the NG located in the lower altitudes represents the common vegetation for the transition zone (subpáramo) between the upper Andean forest and the open páramo or páramo grassland. The sites of the lower altitude were dominated by shrubby or woody vegetation bushes. All NG sites did not show signs of recent disturbances such as grazing and burning. In each site, one NG plot was established adjacent (distance 20 m to 2 km) to the pine plantations. We did not include small forest patches of *Polylepis* spp. because these were too far away from the pine plantations.

Figure 4. Páramo natural grassland (NG; in the front) in the south region of Ecuador.

Grazed sites (G) (Figure 5): these sites represent extensively grazed páramo grassland (less than three animals per hectare), being the most common land use in the area. Burning of the grasses every two to three years to provide new succulent shoots to the cattle is a common practice in many regions of the páramo (Harden et al. 2013). In our selected sites we found signs of recent burning in two locations (Tutupali Chico and Tutupali Grande). At the higher elevational range, the sites are dominated by natural tussock grasses and introduced grasses such as *Lolium* sp and *Dactylis* sp; at the lower altitudes most of the vegetation is dominated by introduced species of *Trifolium* and grasses such as *Pennisetum* c*landestinum*, *Dactylis* sp, and *Lolium* sp. In the majority of the sites, in addition to fertilization, pre-tilling and reduced tilling activities are applied. In each site, one plot was established adjacent to the pine plantations (distance between 20 m and 2 km) (Table 2).

Figure 5. Extensively grazed páramo grassland in the south region of Ecuador.

Table 2. General description of the grazed sites (G) including their average elevation (ABU/ha= Adult bovine unit per ha and per year) (Publication III).

Location	Altitude (m a.s.l.)	Slope (%)	Pre-tilling and tilling activities	Type of land use before grazing	Grassland age	Grass	Animal load (ABU/ha)
Irquis	2830	22.5	Preparation through plowing, liming, and organic fertilization	NG	>10	*Pennisetum clandestinum*	1
Nero	3200	26.2	Preparation through plowing, organic and inorganic fertilization, and pastures irrigation and rotation	NG	>10	*Dactylis* sp., *Trifolium* sp. *and Lolium* sp.	2
La Paz	3320	22.5	Forest logging and burning, solid preparation was made using plowing discs.	NG	3	*Dactylis* sp. *and Pennisetum clandestinum*	1
Tutupali Chico	3480	31.5	Tussock grass burn	NG	<3	*Calamagrostis intermedia*	<0.2
Tutupali Grande	3470	27.7	Tussock grass burn	NG	<3	*Calamagrostis intermedia*	<0.2
Quinsacocha	3600	20.0	Vegetable cover cleaning, soil preparation through plowing and poultry fertilization	NG	5	*Lolium* sp.	0.5
Soldados	3750	14.2	Ground preparation through harrow and adding of vegetal material into the soil.	NG	7	*Lolium* sp. and *Dactylis* sp.	0.4

4 Methods

4.1 Identification of the main stakeholders and their perceptions

In order to identify the main stakeholders, they were defined as individuals within a system "who affect, and/or are affected by policies, decisions, and actions of the system; they can be individuals, communities, social groups or institutions of any size, aggregation or level in society. The term includes according to (Grimble and Chan 1995), policy-makers, planners and administrators in government and other organizations, as well as commercial and subsistence user groups. First, we identified and contacted public and private organizations related to forestry in the páramo and/or being involved in the conservation and sustainable management of the páramo. We created a map of stakeholders to identify the main groups of stakeholders, and for each group a list of potential interview subjects was compiled. The list was constantly updated using the snowball technique (Russell 2006). Following standard procedures, a substantial number of key informants were interviewed (Payne and Payne 2004) with a semi-structured and open-ended interview. The interviews were conducted in person between June 2013 and June 2015. The collected information that was related to the perceptions of the stakeholders about the impacts of the plantations on the páramo ecosystem services was coded following the categories of ecosystem services used by (TEEB 2010): provisioning, regulating, supporting, and cultural ecosystem services. The data, obtained from the interviews, was mainly qualitatively analyzed (Publication I).

4.2 Evaluation of the impacts of pine plantations and grazing on the hydro-physical properties and soil organic matter (SOM)

4.2.1 Soil properties characterization

First, a qualitative description of the soils in the NG sites was made according to the Food and Agriculture Organization of the United Nations guide (Jahn et al. 2006). The qualitative description included the collection of disturbed soil samples (0.5 kg) of the 0-10 cm and 10-25 cm layers for physical and chemical analysis. Second, for each of the three types of sites (NG, G, Pi) two undisturbed soil samples (100 cm^3 Kopecky rings) were randomly taken to determine soil hydro-physical properties and SOM in the layers 0-10 and 10-25 cm. In the case of the Pi sites, in each plot were the samples collected next to three trees randomly selected. At each of these trees two samples were taken, one at 0.75 m distance from the trunk and the second at 1.5 m distance; from these two samples an average was derived. Finally, the saturated hydraulic conductivity (K_{sat}) was determined in-situ using the inverted auger-hole method (Oosterbaan and Nijland 1994). Similar to the soil sampling, two measurements of K_{sat} were taken at two depths (0-10 cm and 10-25 cm) in each plot of the three land uses (NG, G, Pi). In the case of Pi, the measurements were taken next to the same three trees selected for soil sampling at the two distances (0.75 and 1.5 m) from the trunk.

Due to coordination difficulties with the landowners of the grazed (G) sites in the location of Tutupali Chico (TC), we were unable to perform hydraulic conductivity tests, nor were we able to take soil samples to determine the soil water retention characteristic.

4.2.2 Laboratory analyses

The disturbed soil samples were dried at room temperature (<30°C) and passed through a 2-mm sieve. The color was determined using the Munsell color table, the pH was measured with the potentiometer in a 1:2.5 soil:distilled water solution (Van Reeuwijk 2002), and the SOM content was determined through ignition of the soil at 410°C for 16 hours (Grimshaw 1989). Bulk density and water retention capacity were determined on the undisturbed samples and were reported as pF values (the logarithm of the negative pressure head) corresponding to pF 0 (saturation point; pressure 1cm H_2O), pF 0.5 (pressure 3.1 cm H_2O), pF 1.5 (31 cm H_2O), and pF 2.52 (field capacity; pressure 330 cm H_2O). Water content at saturation was considered as a proxy of porosity. For the measurement of the water retention below field capacity at pF 3.4 (2509 cm H_2O), and pF 4.2 (wilting point; 15300 cm H_2O) and the SOM content, disturbed sieved soil samples were used. To measure the water retention in the pF range 0.5 to1.5 sandboxes were used (Topp and Zebchuk 1979), and pressure chambers for pF 2.52, 3.4, and 4.2 (Van Reeuwijk 2002). Gravimetric water contents were transformed into volumetric contents. Gravitational water (GW) and water available for plants (AW) were calculated as the difference between the soil water contents corresponding to pF 0 and pF 2.52, and pF 2.52 and pF 4.2, respectively.

4.2.3 Data analysis

To determine if elevation and site, in addition to sampling depth have an impact on the interpretation of observations, the Spearman correlation analysis was carried out between elevation, hydro-physical properties, and SOM content measured respectively at the depths 0-10 and 10-25 cm under undisturbed natural cover. Afterward, the soil properties located at the same elevation and depth were compared among the seven study sites (Publication II).

To determine if the soil properties were affected by land use of pine plantations (Pi) and extensively grazed páramo (G), the soil characteristics at the two depths were compared with the soil characteristics of páramo natural grassland (NG) using the Kruskal-Wallis test ($p<0,05$). If significant differences were identified, the Nemenyi post hoc test ($p<0.05$) was applied. In Pi plots, the Mann-Whitney *U* test was applied to determine the differences between the properties measured at 0.75 and 1.5 m distance from the pine's trunk. If there were no significant differences, the data set was grouped. Likewise, the Mann-Whitney *U* test was performed to evaluate differences between the means of the two depths. The Spearman correlation analysis was performed for a better interpretation of the impacts of afforestation (Pi) on the soil properties. This analysis was conducted between the variables of all trees with the hydro-physical soil properties and SOM content at both depths. A similar analysis was applied to evaluate the impact of páramo extensively grazed grassland (G) (Publication II).

All statistical analyses were carried out using the R program version 3.3.2 (R Development Core Team 2016).

4.3 Evaluation of the impact of pine plantations on páramo carbon stocks

To evaluate the impacts of pine plantations on páramo carbon stocks, we measured and compared carbon stocks of páramo natural grassland (NG), pine plantations (Pi), and grazed páramo grassland (G). The carbon stocks were composed of the following carbon pools: aboveground biomass (including dead wood and litter), belowground biomass, and soil organic carbon (SOC) according to the United Nations Climate Change Secretariat (UNFCCC) (2015).

4.3.1 Biomass sampling

Trees and understory vegetation assimilate carbon dioxide (CO_2) from the atmosphere and store C in plant biomass. Among several methods are the allometric equations the most frequently used for determining tree biomass (Gower et al. 1999; Daba and Soromessa 2019). Tree allometry establishes quantitative relationships (equations) between the whole tree and a part of it (independent variable) that is easy to measure. The most common variables used in allometric equations are diameter at breast height (DBH) and height (Karlik and Chojnacky 2014; Mosseler et al. 2014). Allometric biomass equations have been developed for several tree species worldwide (Pastor et al. 1984; Chave et al. 2005; Díaz-Franco et al. 2007). Nevertheless, environmental variability (physiographic and edaphic conditions) play a fundamental role in biomass variation among different forest sites (Alves et al. 2010; He et al. 2018; Daba and Soromessa 2019). Therefore, since no allometric equation has been developed for *P. patula* in the high lands of Ecuador, to accurately quantify biomass and carbon storage in the pine plantations of the study, allometric equations were developed with a small but representative sample of trees from each plantation (Publication III). Equivalent to other studies (Díaz-Franco et al. 2007; Rojas-García et al. 2015), with the biomass obtained from the harvested trees (Schreiber and Schmid 2015), two equations for aboveground (Ba) and belowground biomass (Bb) were derived:

Eq. 1: $$B_{a[kg]}=Exp(-0.453)\ \times (DBH^2 \times h)^{0.649}$$

Eq. 2: $$B_{b[kg]}=Exp(-0.321)\ \times (DBH^2 \times h)^{0.316}.$$

The biomass estimation curves of both equations were compared with allometric equations for *P. patula* developed in other regions (Castellanos et al. 1996; Díaz Franco 2005; Rodriguez-Laguna et al. 2009; Figueroa-Navarro et al. 2010; Usuga et al. 2010; Pacheco 2011; Rodríguez-Ortiz et al. 2012) (Publication III).

For the calculation of the ground vegetation biomass three aligned subplots (0.5 x 0.5 m) were established inside each of the plantation plots. For the sampling of the aboveground biomass in the non-plantation sites, one subplot (0.5 x 0.5 m) per plot was used. Total aboveground biomass in the non-plantation sites was calculated as the sum of aboveground biomass of ground vegetation, dead wood, and litter. (Publication III).

4.3.2 *Soil carbon*

Undisturbed soil samples were collected at three depths: 0 - 15, 15 - 30, and 30 - 45 cm. The samples were processed in the laboratory of the University of Cuenca in Ecuador. The samples were dried and sifted to separate fine soil from stones and roots. Of each dried sample was the bulk density (BD) calculated. A portion of 120 gr of dry fine soil from each depth was collected and transferred to the Technical University of Munich (Germany), where all samples were grounded using the Retsch Mixer Mill MM200. These samples were used to measure C concentrations by the dry combustion method using the analyzer Vario EL III. To avoid overestimations of the SOC values, we did not use soil bulk density for the quantification of SOC (Wendt and Hauser 2013). The quantification of SOC stock was made with the following equations as done by for example Poeplau et al. (2017):

$$FSS_i = \frac{mass_{fine\ soil}}{volume_{sample}} \times depth_i \ ,$$

$$SOC_{stock_i} = SOC_{con_{fine\ soil}} \times FSS_i \ ,$$

where FSS_i is the fine soil stock of the investigated soil layer (t/ha), $depth_i$ is the depth of the respective soil layer (cm), $\mathrm{SOC_{stock_i}}$ is the SOC stock of the investigated soil layer (i) (t/ha), and $\mathrm{SOC_{con_{fine\ soil}}}$ is the content of SOC in the fine soil (%) (Publication III).

4.3.3 *Data analysis*

The allometric equations between tree biomass and the independent variable (squared DBH multiplied by tree height (D^2H)) were developed using curve fitting with the software SPSS, v. 24.0 (IBM Corp. 2016). The data were checked for normality with the Kolmogorov-Smirnov test, and for equality of variances with Levene’s test. One-way ANOVA was used when these assumptions were met. Where differences among land uses were significant, Kruskal-Wallis one-way ANOVA on ranks analysis was used to compare means. The significance of the relationship among soil properties was tested using Pearson´s product-moment correlation test (R) and regressions were calculated with the function resulting in the highest coefficient determination (r^2). Except for the development of the allometric equations, all other statistical analyses were conducted with the programming environment R v. 3.5.3 (R Core Team 2019) (Publication III).

4.4 Evaluation of pine plantations impact on the páramo vegetation diversity (structure and composition) across an elevational gradient

In this section of the study, we did not consider the lowest location Irquis because the vegetation of this location was different from the other locations as this one was located in the lower strip of the subpáramo zone, which is the transition ecotone between the montane forest and the páramo grassland above. The vegetation of Irquis is characterized by tall shrubs and small scattered trees. Therefore, we considered the six remaining localities grouped into the three elevational ranges (Figure 2). To evaluate the impact of the plantations on the vegetation, we compared species richness, composition, and structure of the natural regeneration between the plantations and natural grassland across the elevational gradient. In addition, we identified the plantations' attributes and soil properties that influenced the vegetation composition and cover. Fieldwork was carried out from July to November 2015. For the recording of the natural regeneration in both types of land use (NG and Pi), twenty independent square shaped plots with 24 m sides were randomly located and established in each elevational 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: a) two subplots of 100 m^2 (10 x 10 m) located in each corner of the diagonal of the plot, each for woody species including non-prostrate shrubs, treelets, and trees only; b) three subplots of 25 m^2 (5 x 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 (2001). Above 3600 m a.s.l. woody plant composition was not registered because of the low abundance of this type of vegetation. Cover vegetation for all species was estimated using the Braun-Blanquet scale (Braun-Blanquet 1979).

In each Pi plot, canopy density (CD) was measured using a convex spherical densitometer (Lemmon 1956). In addition, we measured basal area (BA), slope, and slope aspect.

4.4.1 *Edaphic properties*

To characterize the soil properties, we used the information of the collected soil samples at 0-10 cm depth in the plantations, described in section 4.2.1 to 4.2.3. The determination of the saturated conductivity (K_{sat}) of the plantations' soil is described in sections 4.2.1 to 4.2.3.

4.4.2 *Data analysis*

A linear mixed model (LMM) was used to detect effects of elevation and land use change on species richness and plant cover (Publication IV). This analysis was performed using the R package nlme (Pinheiro et al. 2019). Ranks species abundance curves were used for evaluating the composition and floristic assembly of plant communities. A Canonical Correspondence Analysis (CCA) was performed to evaluate the relationship between the attributes of Pi and soil properties and plant species (herbaceous and woody) and their cover, in the three elevation ranges. For this analysis, the vegan package (Oksanen et al. 2019) from R software was used. All statistical analyses were performed with the R Project program version 3.2.3 (R Development Core Team 2016) (Publication IV).

5 Results

5.1 Stakeholders and their perceptions

5.1.1 Stakeholder classification

According to our analysis the stakeholders can be classified into four groups: landowners, local governments, foresters, and nature conservationists. While the landowners´ and local governments are directly located within the páramo area of South Ecuador, the groups of foresters and nature conservationists are represented by local, regional, national, and international organizations (Table 3).

Table 3. Stakeholder classification in relation to pine plantations (Pi) in the páramo ecosystem of Ecuador (Publication I).

Stakeholder classification	Stakeholders	Institutional level	Environmental interest
Landowners	Pine plantation owners	Local on site	Timber production, conservation
Local governments	Local authorities	Local	Biodiversity conservation, timber production, conflict avoidance
Foresters	Companies	Local, regional, national	Climate change mitigation, sustainable forestry, advice on the creation and implementation of sustainable forest management policies, profit
	Forest departments	Local, regional, national	Plantation productivity, sustainable management of commercial plantations
	Universities	Local, regional, national	Research, sustainable management of plantations
	Wood industry	Regional, national	Plantation productivity
Nature conservationists	Consortium	Regional, national, international	Applied research, information exchange and policy development
	Corporation	Regional, national, international	Research, training and technical support of the sustainable management of the páramo
	Environmental departments	Local, national	Forestry regulation on protected areas
	NGOs	Regional, national, international	Preservation and restauration of ecosystems in the highlands
	Private mercantile trust	Local, regional	Research, monitoring, forest restoration and planting in the highlands
	Universities	Regional, national	Research, sustainable management of the páramo

The ´landowners´ include property owners and land managers with primary decision-making authority for the property (plantations), which have a direct and continuous relationship with the property. The group of the ´local governments´ comprises representatives from local governments decentralized from the central government. The local governments have under their jurisdiction the protection and sustainable use of the environment; therefore, they are in charge to develop and implement conservation programs including afforestation and reforestation. In addition, local governments are tasked with coordinating environmental management with public and private entities.

The group of ´foresters´ is represented by forestry professionals and researchers working for public institutions, private organizations or companies, and universities active in the páramo. The national and regional forestry departments are part of the public institutions since they are in charge of promoting and regulating commercial forestation activities. Timber producing companies and others specialized in carbon capture through afforestation belong to the private sector.

The last group, the nature conservationists, is represented by researchers and professionals involved in the conservation of natural resources. From the public institutions, the national department of ecological restoration was included. In the case of the private sector, institutions specialized in research, management, and conservation of the páramo ecosystem were invited to participate.

5.1.2 Characteristics of the plantations

The plantations of the 19 interviewed landowners cover a total area of 4886 ha. Excluding a single plantation of 2400 ha, the 18 remaining plantations varied in size between 19 and 350 ha with an average size of 138 ha. 70% of the plantations are located above 3500 m a.s.l. The plantation ages range from 16 to 29 years with an average of 19.5 years. Fourteen plantations are under contracts with PROFAFOR, four are managed autonomously and one has a contract with a local government institution. The contracts with PROFAFOR were signed between 1994 and 2000 for a rotation time of 20 years. Although the contracts oblige the owners to thin and prune the plantations, 80% of them have not received any thinning and only 20% a partial one. Only 33% of the plantations have received complete pruning.

5.1.3 *Stakeholders' perceptions of the impacts of plantations*

89% of the landowners stated that they established their plantations for the purpose of wood production. This statement corresponds with the perceptions of the other stakeholders (local governments, foresters, and nature conservationists), 70% of whom perceived wood production and 11% carbon sequestration as the main motivation for the planting of pines. Also, almost 75% of nature conservationists and landowners agreed in their perceptions that the land use before the establishment of the plantations was categorized as extensively grazed páramo grassland, characterized by tussock grass with signs of frequent burning and the presence of cattle.

The different stakeholders assigned four categories of ecosystem services to the plantations: provisioning, regulating, supporting, and cultural services. The most important subcategories mentioned were provisioning wood, regulating carbon sequestration and storage, regulating water flows, prevention of erosion, maintenance of soil fertility, and supporting habitat for species (Table 4).

Table 4. Summary of categories, subcategories, and a brief description of the ecosystem services mentioned by the interviewees. The table includes the percentage of respondents that mentioned each ecosystem service in the context of the research. Table based on (TEEB 2010), supplemented by the results of our stakeholder interviews (Publication I).

Category	Subcategory	Brief description	Respondents (%)
Provisioning	Raw materials (wood)	Ecosystems provide a great diversity of materials including wood.	91
	Freshwater	Ecosystems regulate the flow and purification of water. Vegetation and forests influence the quantity of water available locally.	2
Regulating	Carbon sequestration and storage	Ecosystems regulate the global climate by storing and sequestering greenhouse gases. Forest ecosystems are carbon stores.	27
	Water flows	Ecosystems and living organisms create buffers against natural disasters, thereby preventing possible damage. For example, wetlands can soak up flood water. Regulation of natural drainage, irrigation and drought prevention.	45
	Erosion prevention and maintenance of soil fertility	Soil erosion is a key factor in the process of land degradation and desertification. Vegetation cover prevents soil erosion. Soil fertility is essential for plant growth.	57

Supporting	Habitat for species (refugium)	Habitats provide everything that an individual plant or animal needs to survive: food, water, and shelter. Each ecosystem provides different habitats that can be essential for a species' lifecycle.	70
Cultural	Ecotourism	Ecosystems and biodiversity play an important role for many kinds of tourism which in turn provides considerable economic benefits. Cultural and eco-tourism can also educate people about the importance of biological diversities.	4

In more detail the stakeholders had the following perceptions:

Provisioning wood: As Figure 6 shows there is an obvious discrepancy in the perception of the stakeholder groups about the profitability of the plantations. While 79% of the landowners were dissatisfied with the profitability of the wood produced by their plantations, especially in the higher altitudes, 70% of the other stakeholders perceived provisioning wood as a profitable service (Figure 6). Only three landowners with plantations in lower altitudes (2800 – 3200 m a.s.l) who enjoyed better growth conditions, evaluated provisioning wood as positive.

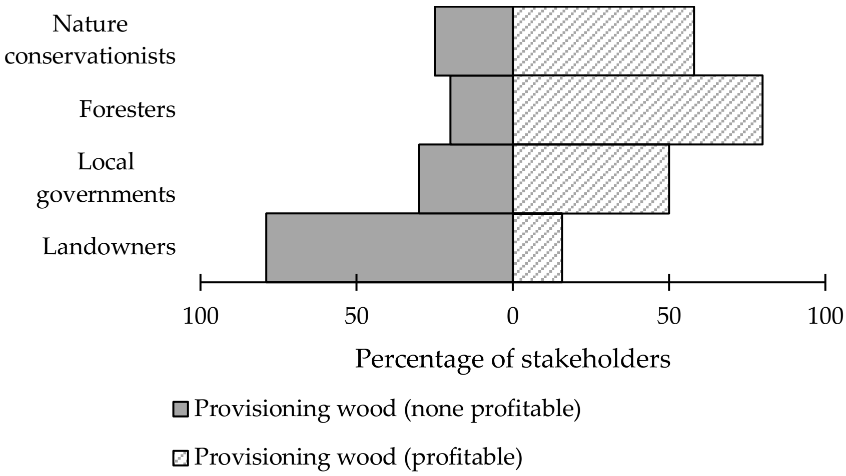

Figure 6. Stakeholder perceptions about the profitability of wood provision of pine plantations (Publication I).

Regulating water flows: all the nature conservationists and local government interviewees, as well as the majority of foresters, had a negative perception of the impact of the plantations on regulating water flows. They suppose a negative effect of the plantations on the hydrological balance due to greater water consumption. In contrast, the majority of the landowners perceived a positive effect, especially in the springs. One landowner expressed: "with the establishment of the plantations the springs recovered"(Publication I), which is similar to other studies (Murtinho et al. 2013; Farley and Bremer 2017) in the páramo, where several inhabitants of this environment had expressed that the plantations favor the retention of water and even increase rainfall.

Regulating carbon sequestration and storage: although most of the plantations were established under a forestation program for carbon sequestration, only 23% of all interviewees believed that the plantations positively affected the ecosystem services (75% of the interviews did not mention this topic). Only within the group of nature conservationists there were negative perceptions indicating that local studies are needed to know what impacts the plantations are causing especially on the carbon stored in the soil.

Regulating erosion prevention and maintenance of soil fertility: only the group of the local governments had a negative perception of the plantations impact on both of these ecosystem services; in the other groups the perceptions were varying. Most of the positive perceptions referred to the fact that the plantations established in highly degraded páramos stopped erosion. On the contrary, among the most mentioned negative impacts, was the acidification of the soil by the pines, and the fact that the soils in the plantation lose their water retention capacity.

Supporting habitat: here, two main perceptions were reported, one regarding fauna and the other regarding flora. In relation to fauna, all groups of stakeholders, especially most of the landowners (89%), perceived that the plantations serve as a refuge for native animals. All landowners mentioned the sighting of deer, rabbits, or guinea pigs on their plantations, and some have even seen the mountain tapir and the cougar. On the other hand, they also perceived that the plantations are causing the disappearance of native vegetation (Publication I).

5.2 Impacts of pine plantations and grazing on the hydro-physical properties and soil organic matter (SOM)

5.2.1 *Soil properties of páramo natural grassland*

The majority of the soil study sites were classified as Andosols, except for the location in Irquis, where the soil was identified as Cambisol. The morphological characteristics of the superficial horizons are described in Table 5. The surface horizon (A) of the Cambisol was characterized by a thickness ranging between 36 and 50 cm, low root density, a brownish color (7.5 YR 3/2-10Yr2/2), low SOM, an acidic pH, an intermediate to fine texture and a structure ranging from block-like to granular (Table 5). The surface horizon (Ah) of the Andosols was defined by a thickness varying from 34 to 106 cm, with high root density, black color (10YR 1.7/1 to 7.5YR 1.7/1), high SOM content, pH values ranging slightly from acidic to very acidic, and a structure between granular to block (Table 5).

Table 5. The median of the hydro-physical properties and SOM content of the soils in the natural grassland cover areas (NG).

Location (m a.s.l.)	Type of horizon	Thickness of the horizon (cm)	Number of roots per dm^2	pH	SOM (%)	Structure	Texture
Irquis (2800)	A	36-50	11-36	4.58-5.64	7.09-14.75	B-Gr	Fac-FacAr
Nero (3230)	Ah	34-106	30-200	4.89-5.72	17.08-39.63	B-Gr	F
La Paz (3340)	Ah	44-82	10-40	5.05-5.23	13.53-16.11	Gr-B	F-Fac
Tutupali Chico (3450)	Ah	50-57	32-64	5.06-5.19	19.58-29.85	Gr	Fac
Tutupali Grande (3480)	Ah	38-45	50-100	5.69-6.32	20.98-37.50	Gr-B	FL-F
Quimsacocha (3640)	Ah	28-55.5	84->200	5.00-5.49	40.15-42.49	Gr	Fac-FL
Soldados (3720)	Ah	20-38	30-110	5.08-5.82	11.38 -23.71	Gr	F-FL

Legend: A = Folic horizon; Ah = Andic horizon. SOM = Soil organic matter content. Structure: Gr = granular; B = block. Texture: F = silt; FL = loamy silt; Fac = loamy clay; FacAr = loamy clay sand.

At each location, the top layer (0-10 cm) presented higher values for K_{sat}, water retention (pF0 to 2.52), gravitational water (GW), available water (AW), and SOM as compared to the values of the same properties measured in the deeper layer, except for BD, which increased (Table 6). Water retention capacity at pF 0 was greater in the upper soil layer. There was a significant negative correlation between the elevation and K_{sat} (ρ = -0.74, p<0.05) and a positive correlation with the water retention capacity in the tension range of pF 0 to pF 2.52 (ρ = 0.66 – 0.71, p<0.05), also with the AW (ρ = 0.73, p<0.05).

Table 6. The median of the hydro-physical properties and SOM content of the soil at seven locations in the natural grassland areas (NG). The properties correspond to two depths: 0-10 cm and 10-25 cm.

	Properties	Irquis (2800)	Nero (3230)	La Paz (3340)	Tutupali Chico	Tutupali Grande (3480)	Quimsacocha (3640)	Soldados (3720)
0-10 cm soil layer	K_{sat} (cm/h)	12.91	4.92	17.3	7.26	3.33	1.38	1.92
	BD (g/cm³)	0.97	0.38	0.72	0.67	0.51	0.32	0.6
	0pF (cm³/cm³)	0.65	0.71	0.7	0.72	0.75	0.87	0.73
	0.5pF (cm³/cm³)	0.64	0.69	0.69	0.7	0.75	0.85	0.72
	1.5pF (cm³/cm³)	0.54	0.6	0.6	0.65	0.73	0.81	0.66
	2.52pF (cm³/cm³)	0.47	0.49	0.46	0.6	0.64	0.69	0.58
	3.4pF (cm³/cm³)	0.46	0.4	0.37	0.49	0.47	0.55	0.35
	4.2pF (cm³/cm³)	0.4	0.36	0.33	0.47	0.42	0.48	0.33
	GW (cm³/cm³)	0.17	0.21	0.24	0.14	0.11	0.18	0.17
	AW (cm³/cm³)	0.08	0.11	0.12	0.14	0.2	0.21	0.25
	SOM (%)	10.16	33.69	15.36	25.83	20.57	41.15	15.47
10-25 cm soil layer	K_{sat} (cm/h)	2.98	1.59	1.84	1.44	0.17	0.3	0.37
	BD (g/cm³)	1.18	0.5	0.92	0.72	0.56	0.43	0.88
	0pF (cm³/cm³)	0.6	0.68	0.62	0.7	0.74	0.82	0.63
	0.5pF (cm³/cm³)	0.58	0.67	0.61	0.7	0.73	0.82	0.61
	1.5pF (cm³/cm³)	0.54	0.59	0.52	0.64	0.71	0.78	0.53
	2.52pF (cm³/cm³)	0.49	0.52	0.41	0.57	0.63	0.67	0.46
	3.4pF (cm³/cm³)	0.45	0.47	0.4	0.54	0.48	0.51	0.38
	4.2pF (cm³/cm³)	0.41	0.41	0.35	0.46	0.43	0.48	36
	GW (cm³/cm³)	0.12	0.14	0.2	0.1	0.11	0.15	0.17
	AW (cm³/cm³)	0.06	0.11	0.06	0.1	0.2	0.21	0.09
	SOM (%)	8	28.73	13.19	18.98	19.02	36.65	8.83

Legend: K_{sat} = Saturated hydraulic conductivity; BD = bulk density; 0 - 4.2 pF = Retention capacity in pF 0 to pF 4.2; GW = Gravitational water; AW = Available water; SOM = Soil organic matter content.

5.2.2 *Hydro-physical properties and SOM content under pine afforestation (Pi) and grazed sites (G).*

In the plantation sites (Pi), the sampling distances (75 and 150 cm) from the trees had not any significant effect on the measured values and therefore the samples were merged. When comparing the hydro-physical properties and SOM of Pi and G with natural grassland areas (NG), pine afforestation led to significant differences mainly in the hydro-physical properties. The majority of the plantation's hydro-physical soil properties registered lower values. Also, when significant differences were registered in a location, in most cases changes were recorded for various soil properties. The most notorious case is the La Paz plantation where significant lower values of the water retention and SOM content accompanied by higher values of BD were measured. On the contrary, in the plantations of Soldados, the changes were positive, since higher values of the water retention capacity, SOM content, and hydraulic conductivity, accompanied with lower values of BD were recorded. In the case of the grazed sites (G), most of the significant differences in the soil hydro-physical properties were obtained mainly for K_{sat} and the water retention capacity.

Saturated hydraulic conductivity (K_{sat}). In the plantation sites (Pi), K_{sat} of the upper soil layer of Irquis and Nero was significantly lower, and in the locations of Tutupali Grande and Quimsacocha K_{sat} was significantly higher. In the deeper soil layer, K_{sat} showed a significant lower value in La Paz; and significant higher values in Irquis, Nero, Tutupali Grande and Quimsacocha (Figure 7). In the case of the grazed sites (G), K_{sat} in the upper soil layer was significant lower in Irquis and Tutupali Grande, while significant larger in Quimsacocha. K_{sat} was significant lower in the deeper soil layers in Irquis, La Paz, Quimsacocha and Soldados (Figure 7).

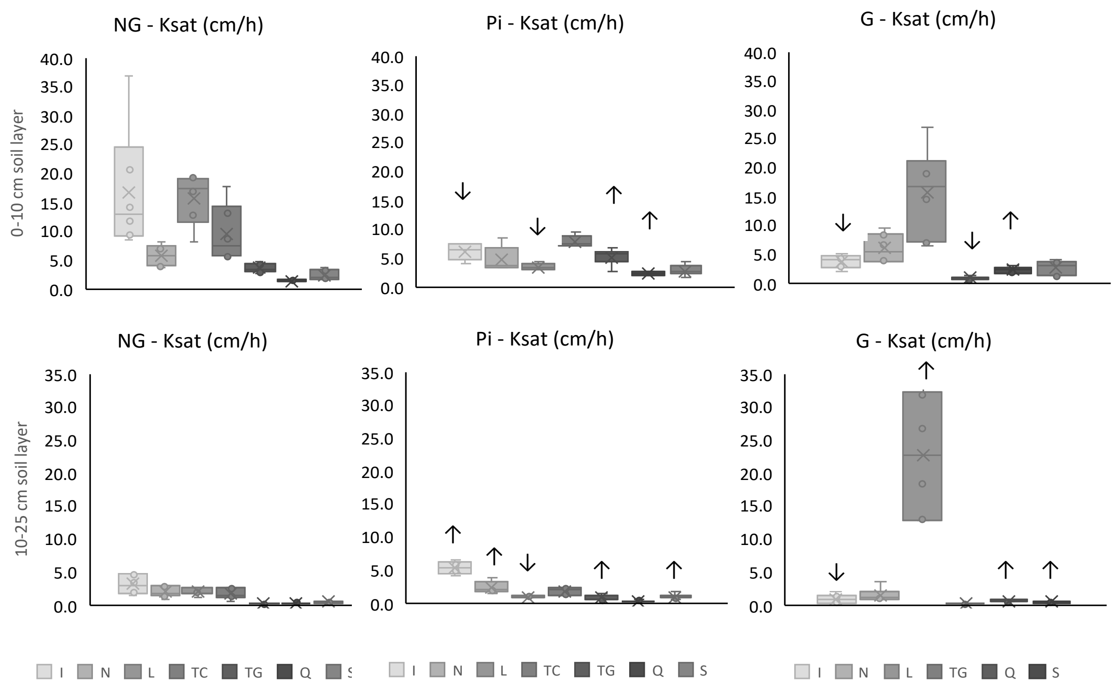

Figure 7. Box plots of the saturated hydraulic conductivity (K_{sat}) of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G) measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC),

Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ (p<0.05 value) when comparing Pi or G vs. NG.

Bulk density (BD). The BD in the topsoil of the plantations (Pi) in La Paz was significantly higher than in NG. In the case of the deeper soil layer, in Soldados BD was significantly less dense, and in La Paz BD was significantly denser (Figure 8). In the case of the grazed sites (G), in the upper soil layer BD was significantly higher in Nero and La Paz. In the deeper soil layer BD was significantly lower in Soldados (Figure 8).

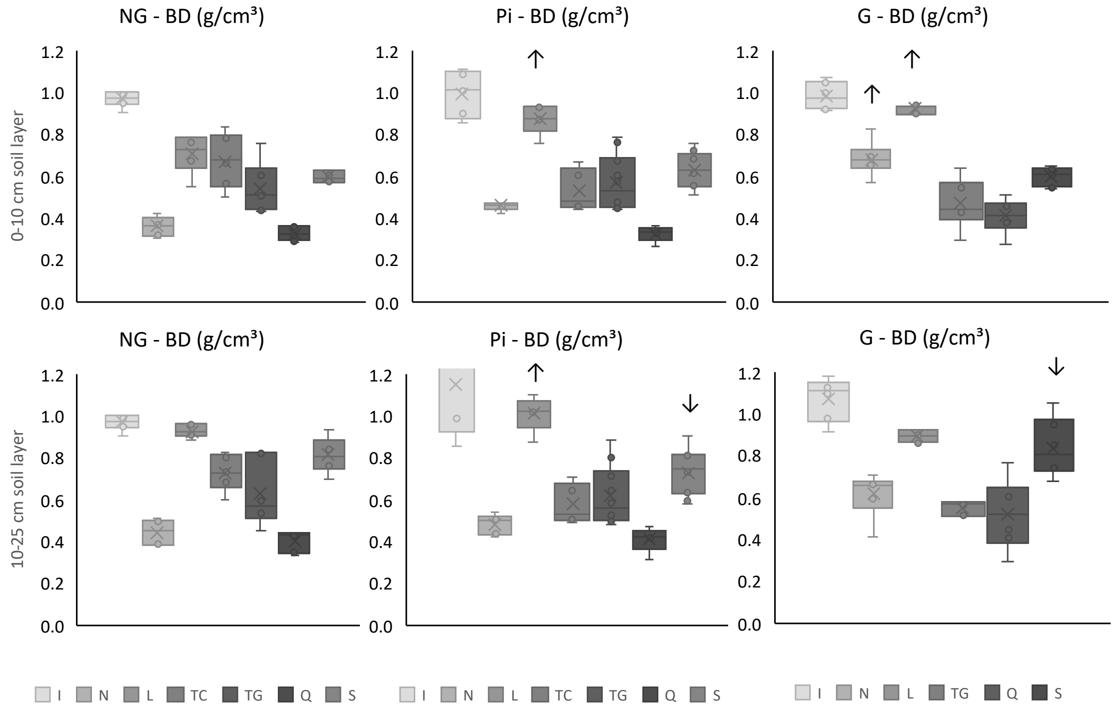

Figure 8. Box plots of soil bulk density (BD) of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ (p<0.05 value) when comparing Pi or G vs. NG.

Water retention capacity. In the plantations, the water retention capacity at saturation (pF 0) of the upper soil layer was significantly lower in Irquis, La Paz, Quimsacocha, and Soldados, and significantly higher in Nero. In the deeper soil layer a significantly lower value (pF 0) was found in Irquis, while significantly higher values in Nero and Soldados (Figure 9).

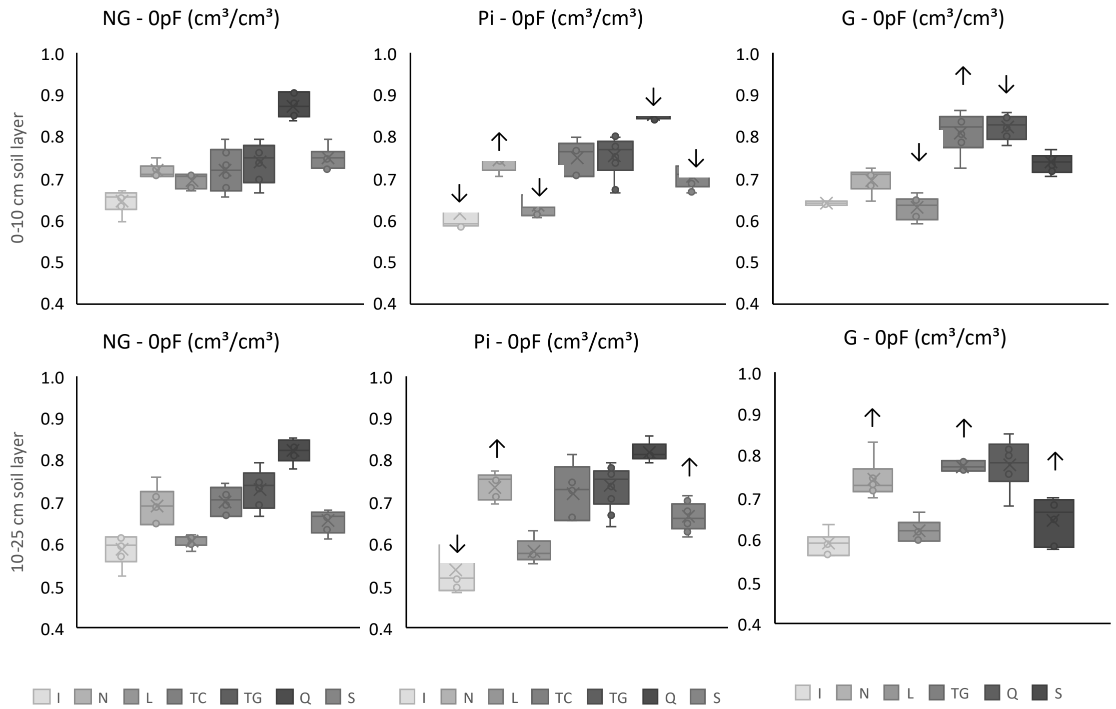

Figure 9. Box plots of the soil water retention capacity at pF 0 of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ ($p<0.05$ value) when comparing Pi or G vs. NG.

The tendency of the water retention capacity in the pF range 0.5 to 2.52 of the upper soil layer was similar to the tendency of the water retention capacity at pF 0. At the deeper soil layer, water retention capacity in the pF-range 0.5 to 1.5 was similar to those of pF 0 (Figure 10). The soil water retention at field capacity (pF 2.52) depicted only significant differences at the deeper soil layer revealing significant lower values in Irquis, La Paz and Quimsacocha, and a significant higher value in Nero (Figure 11). The soil water retention of the upper soil layer at pFs' 3.4 and 4.2 was significant higher in Soldados. In the deeper soil layer, significant lower values were recorded in Irquis and Tutupali Chico, while a significant higher value in Soldados (Figures 11 and 12). Gravitational water (GW) was significant higher in the upper soil layer in Tutupali Chico, Tutupali Grande and Quimsacocha, while no significant differences were observed in the lower soil layer (Figure 12). In La Paz and Soldados, the available water capacity (AW) of the upper soil layer was significant lower, while in the lower soil layer significant higher values were recorded in Nero and Tutupali Chico (Figure 13).

In the case of the grazed sites (G), the water retention capacity at saturation (pF 0) of the upper soil layer was significant lower in La Paz and Quimsacocha, while significant higher at Tutupali Grande. In the deeper soil layer, pF 0 showed significant higher values in Nero, Tutupali Grande, and Soldados (Figure 9). The differences in water retention capacity at pF 0.5 and pF 1.5 in the upper and lower soil layers showed the same trends as at pF 0 (Figure 10). The soil water retention capacity at pF 2.52 in the upper soil layer showed significant lower values in La Paz, Quimsacocha, and Soldados, while in Nero a significant higher value was recorded. In the deeper soil layer, pF 2.52 showed significant higher values in Nero and Quimsacocha (Figure 11). The water retention capacity at pF 3.4 in the upper soil layer showed a significant lower value in La Paz, while significant higher values were measured in Nero, Tutupali Grande, and Soldados. In the deeper soil layer, there was a significant lower value in La Paz, while Nero showed a significant higher value (Figure 11). At the wilting point (pF 4.2) the trend of the water retention in the upper soil layer was similar to that at pF 3.4. In the deeper soil layer, La Paz registered a significant lower value, while Nero registered a significant higher value (Figure 12).

Soil organic matter (SOM). In the plantations (Pi), SOM content in both soil layers was significant higher in Soldados, and in both soil layers it was significant lower in Irquis, Nero, and La Paz (Figure 13). In the case of the grazed sites (G), only La Paz registered a significant lower value for the SOM content in the upper soil layer (Figure 13).

The tree development variables (DBH, height, and canopy density) were positive correlated with the soil bulk density, and negative with the water retention capacity and SOM.

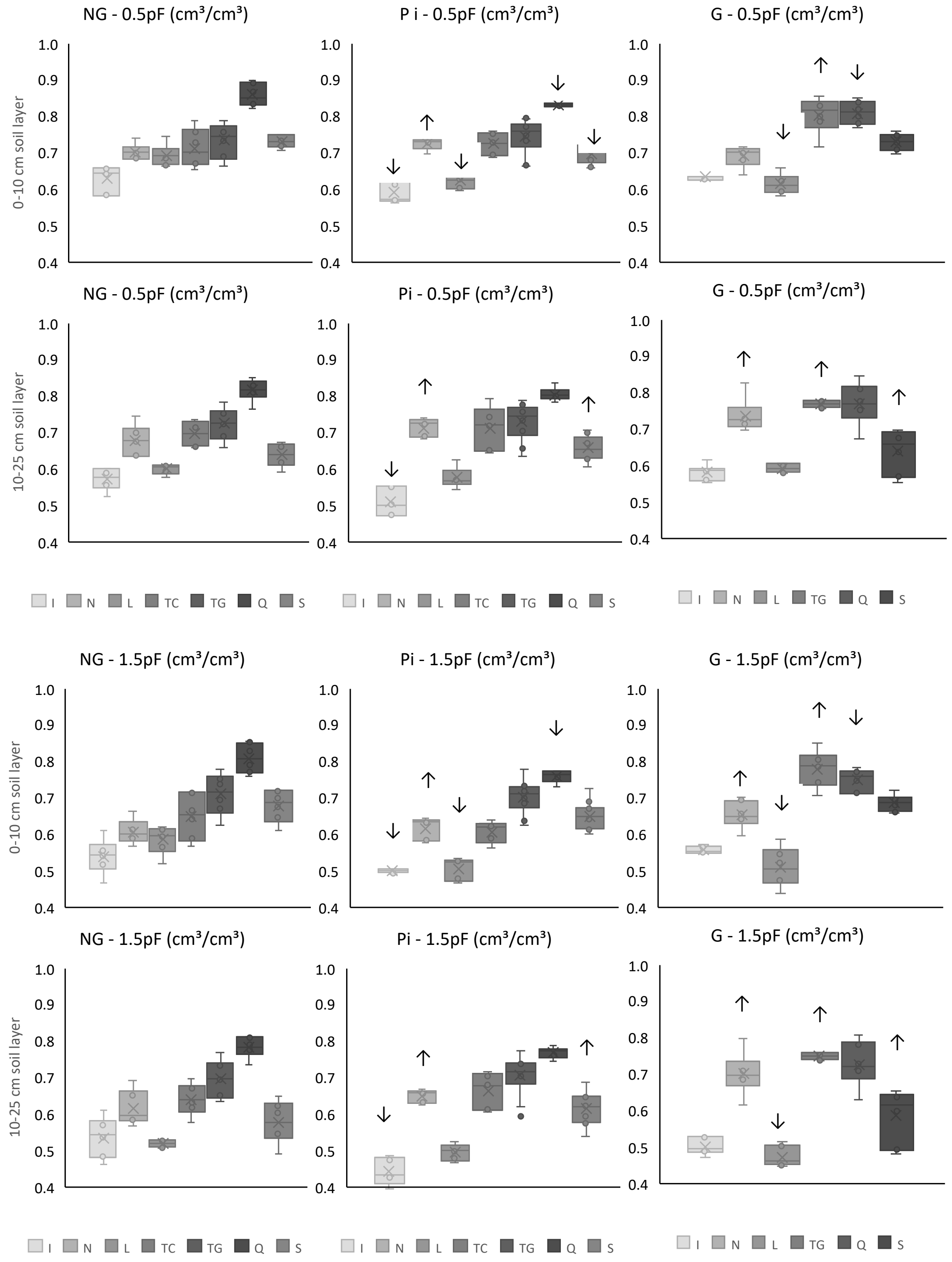

Figure 10. Box plots of the water retention capacity at pF 0 and pF 1.5 of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ ($p<0.05$ value) when comparing Pi or G vs. NG.

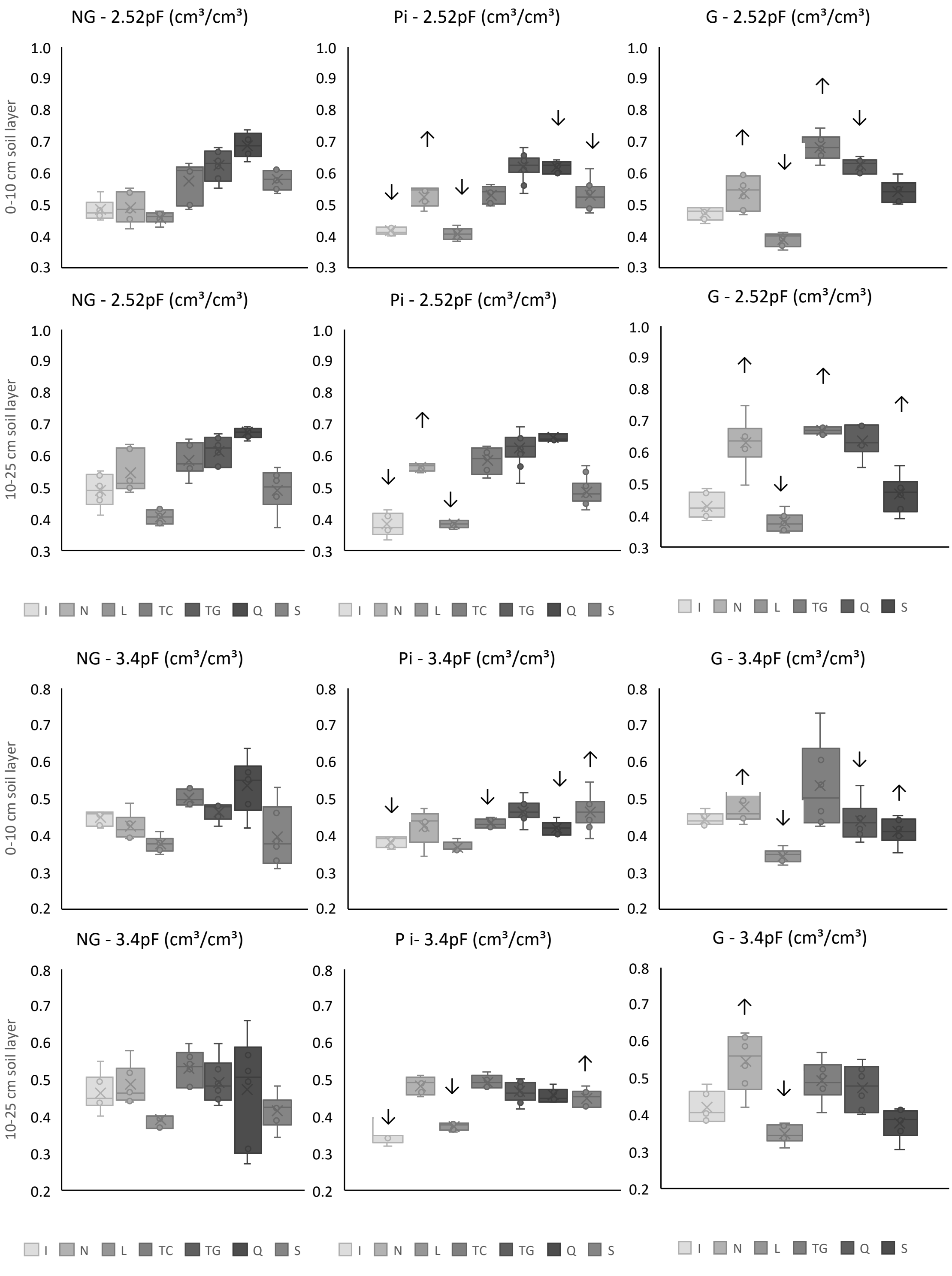

Figure 11. Box plots of the water retention capacity at pF2.52 and pF3.4 of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ ($p<0.05$ value) when comparing Pi or G vs. NG.

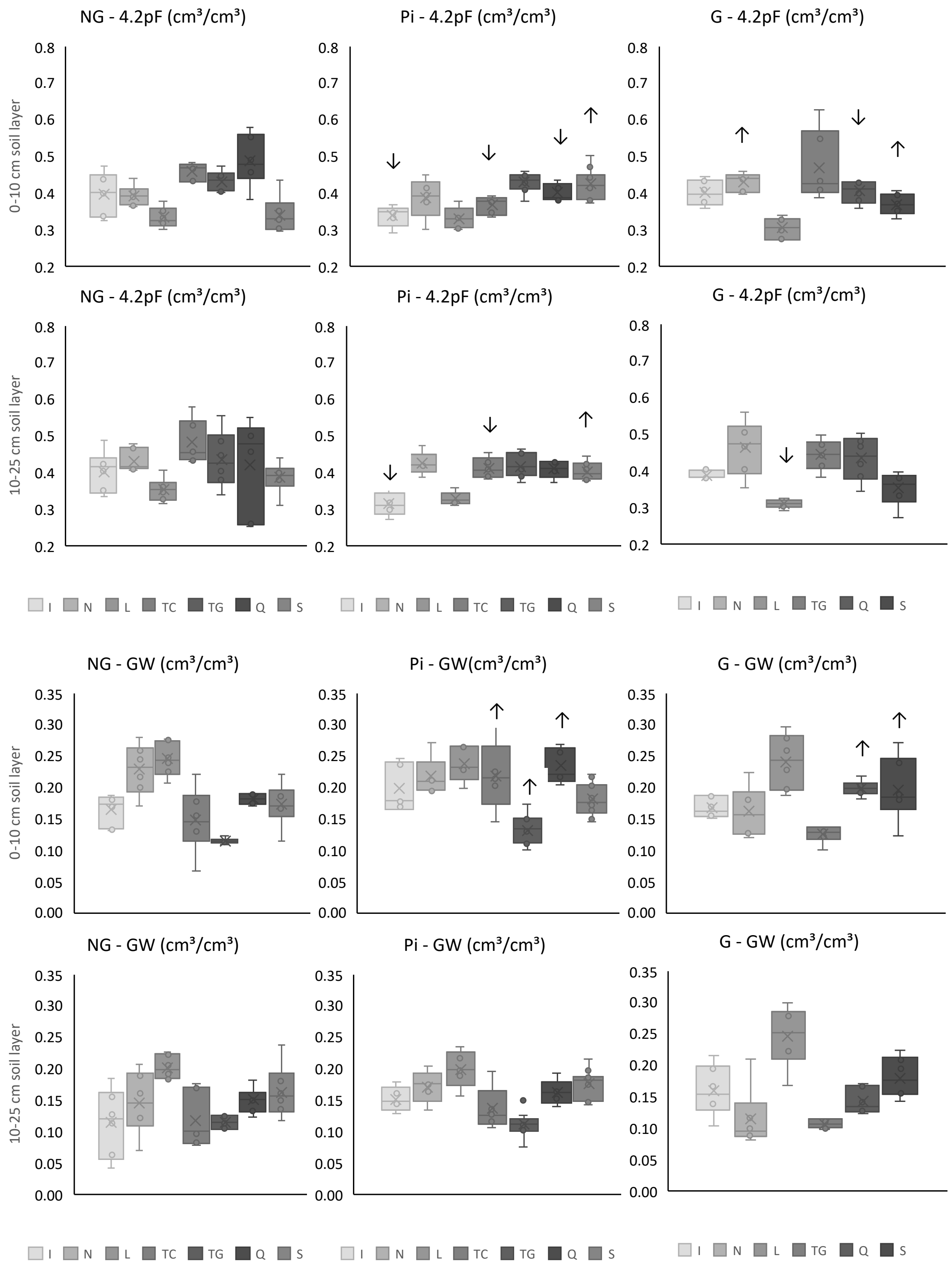

Figure 12. Box plots of the water retention capacity at pF4.2 and GW of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ ($p<0.05$ value) when comparing Pi or G vs. NG.

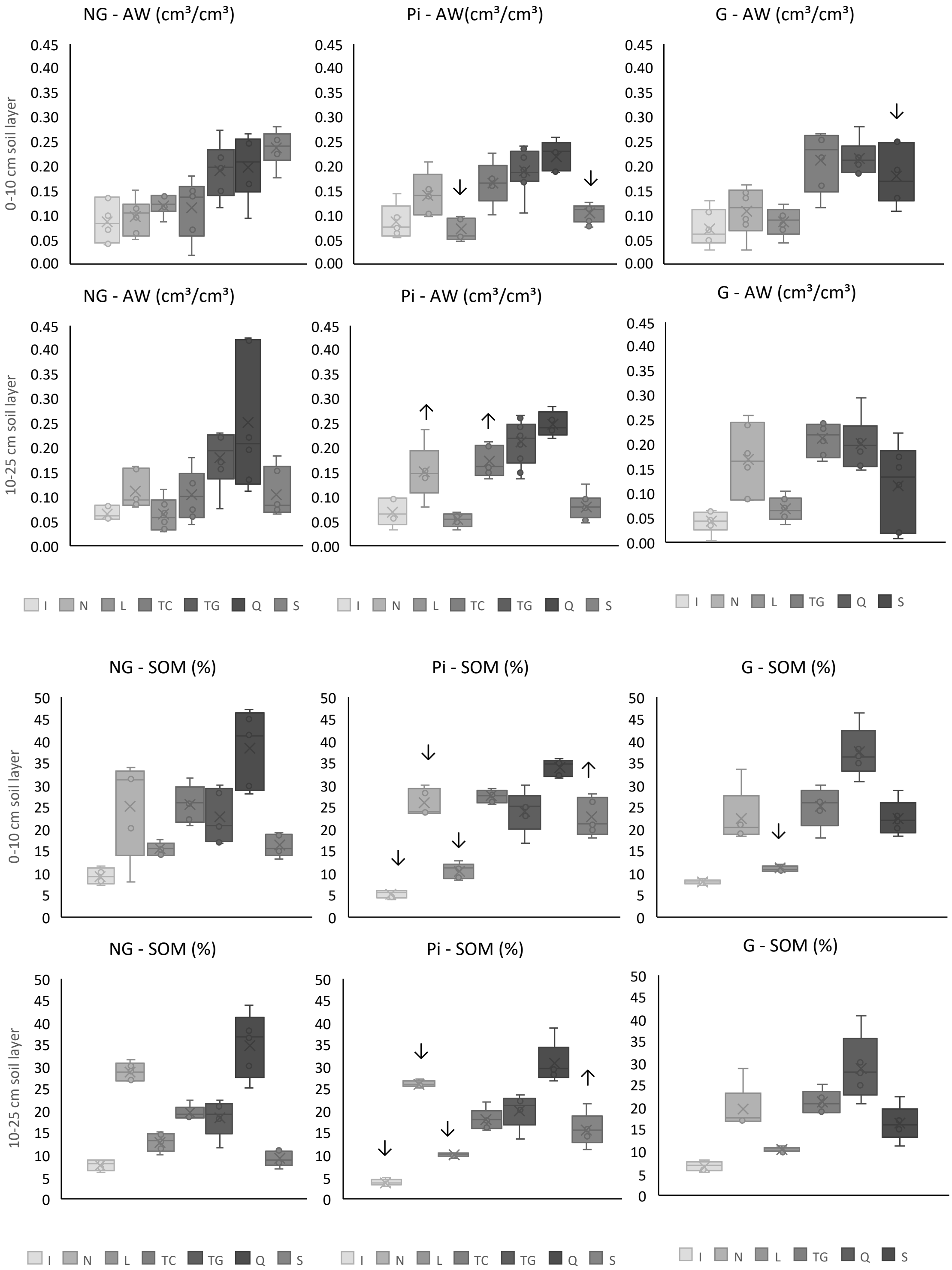

Figure 13. Box plots of AW (plant available water) and SOM (soil organic matter) of the soil layer 0-10 cm and 10-25 cm in natural grassland (NG), pine plantations (Pi), and grazed grassland (G), measured at seven locations: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S). ↓ or ↑ ($p<0.05$ value) when comparing Pi or G vs. NG.

5.3 Impacts of pine plantations on páramo carbon stocks

Table 5 provides an overview of the mean carbon stocks investigated in the different compartments and the three types of land use. SOC represents the dominant part in all the land uses (91.5% in NG, 96.4% in G, and 80.6% in Pi). Pine plantations (Pi) revealed the highest mean aboveground and total carbon stock. Nonetheless, the differences in carbon in biomass are clearly overcompensated by the high SOC share.

Table 7. Mean carbon and standard deviation (between brackets) in tons per hectare: AG = aboveground, BG = belowground, SOC = soil organic carbon (0-45 cm).

Land use	*Aboveground C*		*Total AG carbon*	*Belowground C*		*Total BG carbon*	*Total SOC*	*Total carbon stock*
	Ground vegetation (litter + herbs + shrubs)	*Pines (trunk, branches, leaves)*		*Roots*	*Pine roots*			
NG	23.1 (17.1)	--	23.1 (17.1)	2.7 (1.6)	--	2.7 (1.6)	275.6 (75.9)	301.3 (76.3)
G	9.1 (5.3)	--	9.1 (5.3)	1.5 (1.3)	--	1.5 (1.3)	282.6 (91.3)	293.2 (91.8)
Pi	14.5 (7.4)	40.9 (27.9)	55.4 (26.8)	3.9 (3.1)	3 (1.3)	6.9 (2.6)	258.0 (78.8)	320.2 (74.0)

The total aboveground C pools are significantly highest in almost all plantations at the different locations, except for those in Soldados. Soldados, the highest location, depicts similar amounts of aboveground carbon in Pi (35.6 t/ha) as NG (38.2 t/ha) (Table 8). At all locations the aboveground carbon of the grazed sites (G) is lower than the NG sites, even at five locations (Irquis, La Paz, Tutupali Chico, Quimsacocha and Soldados) at a significant level (Table 8). The belowground C pools reveal a similar trend, being highest in all Pi locations, followed by NG, while most of the grazed sites (G) had significantly lower values (Table 8). With respect to the SOC amount (0-45 cm depth), the Pi sites at three locations in the lower elevations (Irquis, La Paz and Tutupali Chico) showed significant lower amounts than NG and G, while at the highest location in Soldados, Pi1 registered a significant higher SOC values than NG and G (Table 8).

Table 8. Mean carbon pools and standard deviation (between brackets) in the different components (Aboveground biomass (AG), Belowground biomass (BG), and SOC) of the total C-stock for each land use within each location. NG = natural grassland, G = grazed páramo, Pi = pine plantation. Different letters are significantly different from each other (p<0.05).

Location (m a.s.l.)	Land use	Aboveground C (t/ha): (hebs+shrubs+ litter+dead wood)	Aboveground C (t/ha): Pines	Aboveground C (t/ha): Total AG	Belowground C (t/ha): Roots	Belowground C (t/ha): Pine roots	Belowground C (t/ha): Total BG	SOC (t/ha): 0-15 cm	SOC (t/ha): 15-30 cm	SOC (t/ha): 30-45 cm	SOC (t/ha): Total SOC	Carbon stock (AB + BG + SOC)
Irquis (2800)	NG	15.0 (3.8)^{a}		15.0 (3.8)^{b}	1.2		1.2 (0.4)^{b}	85.8 (21.1)^{a}	72.8 (17.0)^{a}	61.1 (14.9)^{a}	219.7 (50.7)^{a}	235.9 (48.1)^{a}
	G	9.0 (2.7)^{b}		9.0 (2.7)^{c}	0.6		0.6 (0.3)^{c}	67.5 (11.4)^{a}	58.1 (11.7)^{a}	46.0 (12.8)^{a}	171.5 (32.5)^{a}	181.1 (33.6)^{b}
	Pi	14.5 (5.7)^{ab}	91.7	106.2 (14.8)^{a}	2.7	4.4	7.1 (1.1)^{a}	46.4 (12.3)^{b}	39.4 (6.3)^{b}	32.8 (3.4)^{b}	118.6 (21.4)^{b}	231.9 (30.7)^{a}
Nero (3230)	NG	21.3 (12.6)^{a}		21.3 (12.6)^{b}	4.4		4.4 (1.7)^{b}	109.8 (23.0)^{a}	105.6 (15.1)^{a}	94.0 (17.8)^{a}	309.4 (46.4)^{a}	335.1 (52.9)^{a}
	G	18.3 (5.5)^{a}		18.3 (5.5)^{b}	1.4		1.4 (0.3)^{c}	142.9 (53.1)^{a}	114.8 (30.0)^{a}	106.0 (15.6)^{a}	363.7 (85.1)^{a}	383.4 (81.8)^{a}
	Pi	16.9 (7.4)^{a}	51.6	68.5 (15.6)^{a}	2.6	3.5	6.1 (1.2)^{a}	106.9 (19.8)^{a}	105.6 (12.3)^{a}	105.4 (23.1)^{a}	317.9 (45.7)^{a}	392.5 (52.1)^{a}
La Paz (3340)	NG	25.1 (18.4)^{a}		25.1 (18.4)^{b}	2.9		2.9 (1.4)^{b}	101.2 (18.0)^{a}	95.8 (15.2)^{a}	77.4 (10.9)^{a}	274.5 (42.4)^{a}	302.5 (42.8)^{a}
	G	6.3 (1.4)^{b}		6.3 (1.4)^{c}	1.5		1.5 (0.3)^{c}	94.9 (26.4)^{a}	89.1 (24.1)^{a}	84.0 (31.9)^{a}	267.9 (81.5)^{ab}	275.7 (80.6)^{a}
	Pi	13.9 (2.4)^{a}	54.7	68.6 (22.0)^{a}	2.7	4.0	6.7 (1.6)^{a}	77.8 (18.4)^{a}	81.3 (14.3)^{a}	65.5 (7.0)^{a}	224.6 (28.9)^{b}	299.9 (35.1)^{a}
Tutupali Chico (3450)	NG	28.0 (17.2)^{a}		28.0 (17.2)^{b}	3.1		3.1 (1.5)^{b}	135.2 (15.0)^{a}	124.7 (13.2)^{a}	113.3 (16.0)^{a}	373.2 (24.5)^{a}	404.3 (33.7)^{a}
	G	8.5 (4.5)^{b}		8.5 (4.5)^{c}	1.4		1.4 (0.3)^{c}	125.6 (14.2)^{a}	124.6 (7.8)^{a}	103.8 (7.1)^{a}	354.0 (24.2)^{a}	363.9 (22.6)^{b}
	Pi	9.1 (1.7)^{b}	50.0	59.1 (19.0)^{a}	4.5	3.5	8.0 (1.6)^{a}	123.4 (20.5)^{a}	102.6 (10.6)^{b}	88.7 (13.5)^{b}	314.7 (27.5)^{b}	381.8 (32.9)^{ab}
Tutupali Grande (3480)	NG	18.8 (15.2)^{a}		18.8 (15.2)^{b}	2.3		2.3 (0.5)^{b}	99.8 (18.0)^{a}	79.1 (27.0)^{a}	78.6 (25.3)^{a}	257.5 (49.5)^{a}	278.6 (54.4)^{a}
	G	9.5 (4.8)^{ab}		9.5 (4.8)^{b}	1.2		1.2 (1.3)^{b}	95.0 (52.9)^{a}	96.8 (8.7)^{a}	72.7 (38.0)^{a}	264.5 (92.2)^{a}	275.2 (92.4)^{a}
	Pi1	9.0 (4.1)^{ab}	46.2	55.2 (12.9)^{a}	1.9	3.5	5.4 (0.3)^{a}	117.5 (46.6)^{a}	101.0 (39.9)^{a}	80.4 (33.6)^{a}	299.0 (119.2)^{a}	359.6 (120.4)^{a}
	Pi2	6.0 (2.6)^{b}	34.2	40.2 (12.9)^{a}	1.9	3.1	5.0 (1.3)^{a}	118.9 (29.3)^{a}	113.8 (23.8)^{a}	72.0 (5.7)^{a}	304.7 (51.8)^{a}	349.9 (49.9)^{a}
Quimsacocha (3640)	NG	15.2 (6.6)^{a}		15.2 (6.6)^{b}	1.8		1.8 (0.3)^{b}	114.6 (18.8)^{a}	110.5 (19.3)^{a}	95.6 (22.2)^{a}	320.7 (58.7)^{a}	337.7 (55.1)^{a}
	G	4.7 (1.2)^{b}		4.7 (1.2)^{c}	0.4		0.4 (0.4)^{c}	130.9 (14.3)^{a}	114.2 (36.3)^{a}	91.9 (24.9)^{a}	337.0 (52.9)^{a}	342.1 (53.5)^{a}
	Pi	14.8 (2.6)^{a}	14.8	29.6 (15.4)^{a}	5.5	1.8	7.3 (2.9)^{a}	93.3 (12.2)^{b}	109.0 (25.3)^{a}	89.4 (23.1)^{a}	291.7 (38.4)^{a}	328.6 (49.8)^{a}
Soldados (3720)	NG	38.2 (28.5)^{a}		38.2 (28.5)^{a}	3.0		3.0 (2.3)^{b}	88.0 (28.7)^{b}	70.0 (21.6)^{a}	16.1 (10.1)^{a}	174.0 (50.0)^{b}	215.2 (60.9)^{a}
	G	7.5 (1.2)^{b}		7.5 (1.2)^{b}	3.8		3.8 (0.4)^{b}	115.2 (14.3)^{ab}	90.4 (36.3)^{a}	14.1 (24.9)^{a}	219.6 (52.9)^{ab}	230.9 (53.5)^{a}
	Pi1	22.6 (10.4)^{a}	12.6	35.2 (9.9)^{a}	4.5	1.6	6.1 (0.6)^{a}	120.4 (7.5)^{a}	94.5 (20.7)^{a}	13.1 (4.1)^{a}	228.0 (25.1)^{a}	269.3 (29.9)^{a}
	Pi2	23.3 (4.5)^{a}	12.5	35.8 (11.5)^{a}	8.5	1.4	9.9 (4.6)^{a}	119.0 (22.9)^{a}	90.5 (27.8)^{a}	13.3 (2.8)^{a}	222.7 (44.6)^{ab}	268.4 (51.2)^{a}

Concerning the influence of the elevation on the biomass of the pines, the data show a continuous decrease with increasing elevation.

5.4 Impacts of pine plantations on páramo vegetation

The observations show that herbaceous species richness significantly ($p<0.001$) increases with elevation (Table 9, Figure 14a), and that herbaceous species richness is significantly higher ($p<0.001$) in natural grassland (NG) than in pine plantations (Pi) (Table 9, Figure 14a). The percentage of plant cover differed significantly among the three elevational ranges, with a marked difference between 3200-3400 and 3400 and 3600 m a.s.l, and between (NG) and (Pi) (Figure 14b).

Table 9. Influence of elevation range and type of vegetation on species richness and percentage of plant cover of the herbaceous vegetation according to the ANOVA analysis obtained from a linear mixed model (LMM) (Publication IV).

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

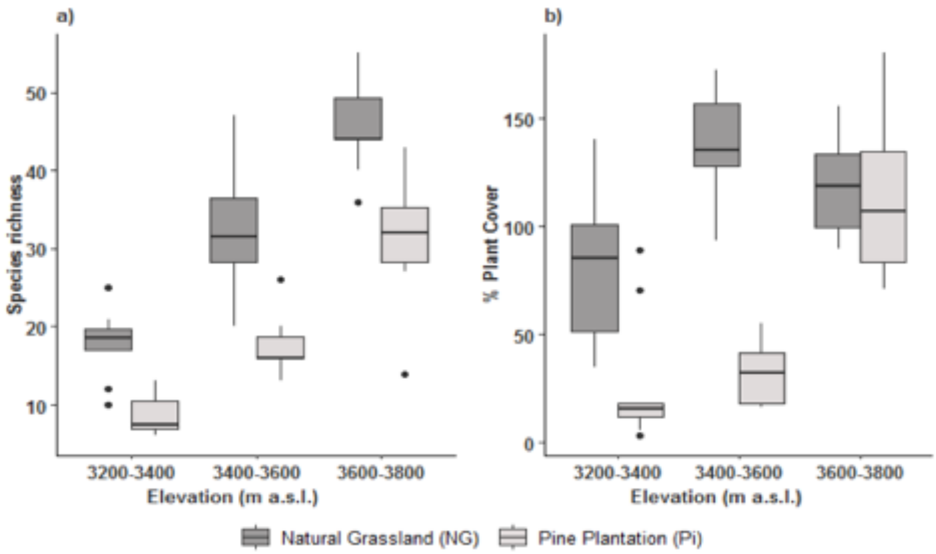

Figure 14. Box plots showing the effects of elevation range (3200-3400,3400-3600, and 3600-3800 m a.s.l.) and land use (plantations (Pi) and natural grassland (NG)) on (a) the herbaceous species richness, and (b) the percentage ground cover with herbaceous vegetation.

In contrast to the herbaceous vegetation, woody species richness and land cover had the tendency to decrease with elevation, and the interaction between elevation and type of land use was statistically significant (Table 10), indicating that the interaction between both factors is important when evaluating the variables of species richness and plant cover (Table 10, Figure 15a,b). Species richness and plant cover showed significantly higher values in NG than Pi (Figure 15a,b). (Publication IV).

Table 10. Influence of elevation range and land use 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 land use	1	77.7789	<0.0001
Elevational range	1	3.2464	0.3226
Type of land use: Elevational range	1	17.3	0.0002
Woody plant cover			
Intercept	1	48.5569	<0.0001
Type of land use	1	64.7345	<0.0001
Elevational range	1	1.3268	0.4551
Type of land use: Elevational range	1	4.9888	0.032

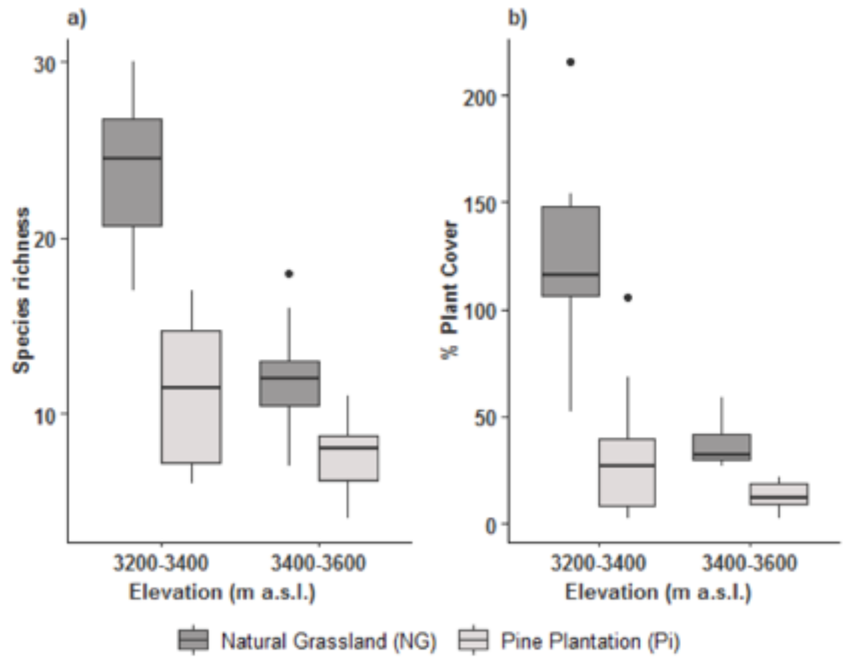

Figure 15. Box plots illustrating the effects of elevation range (3200-3400 and 3400-3600 m a.s.l.) and land use (pine plantations (Pi) and natural grassland (NG)) on (a) woody species richness and (b) woody plant cover.

In total thirteen endemic species were recorded in the observation plots, eight species under Pi and eleven in NG. Eleven of them are included in the Red List of Threatened Species of the International Union for Conservation of Nature and Natural Resources (IUCN 2019) (Publication IV). According to rank-abundance curves, a marked difference of herbaceous dominant species was found between NG and Pi, primarily at the lower and middle elevational ranges; the three dominant species do not coincide in both types of land use. In NG, the dominant species in the three elevational ranges were *Calamagrostis intermedia*, one of the most common species in grasslands of the páramo. In Pi, *Calamagrostis* spp, was a dominant species in the higher elevational range, while in the other two ranges the understory of the plantations is dominated by species such as *Triniochloa stipoides*, and *Cerastium danguyi*, which are not representative species from the páramo (Figure 16).

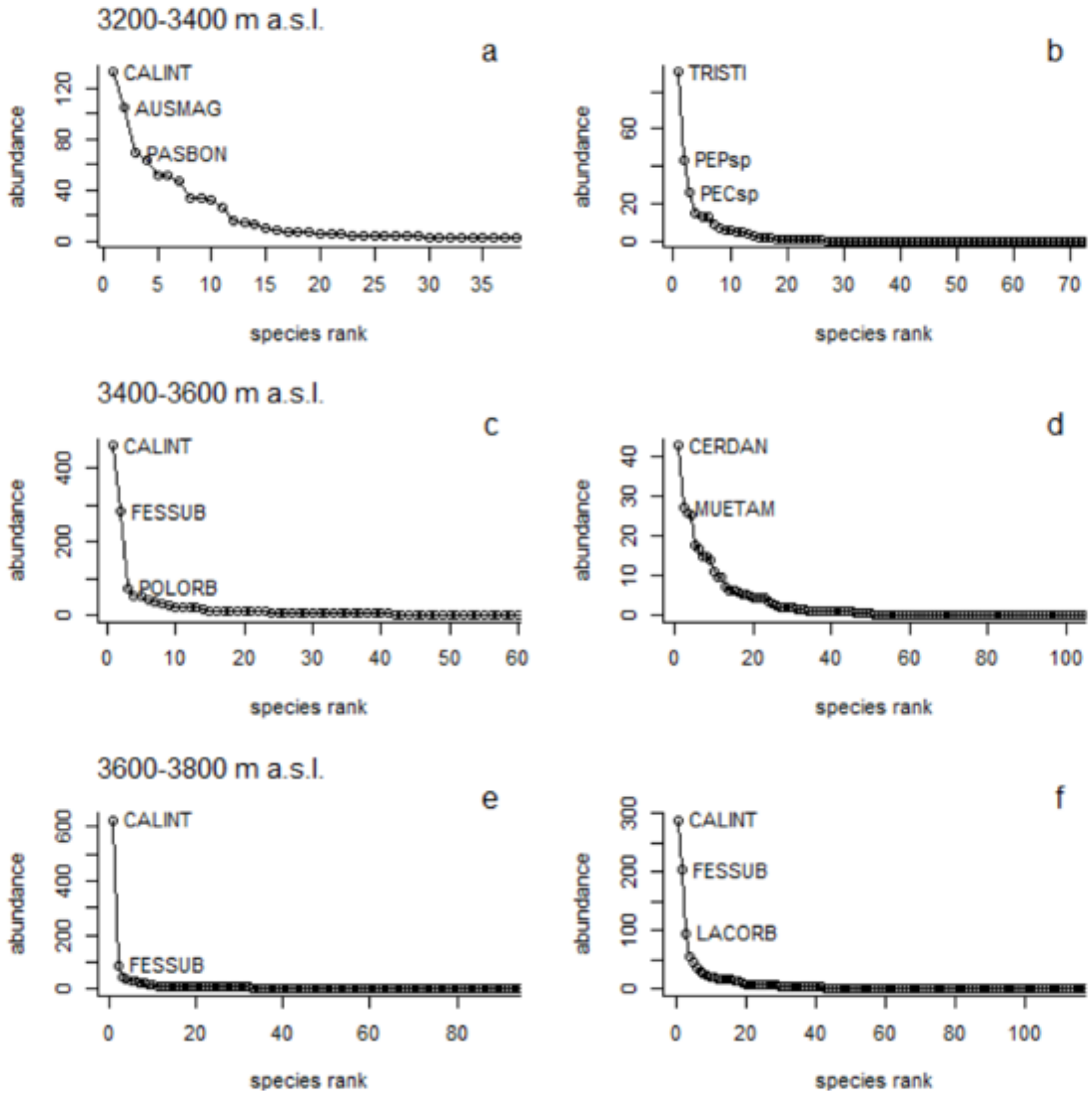

Figure 16. Abundance rank of herbaceous species in natural grassland (NG) (a,c,e) and pine plantations (Pi) cover (b,d,f) across three different elevational gradients (3200-3400, 3400-3600, and 3600-3800 m a.s.l.) CALINT = *Calamagrostis intermedia,* AUSMAG = *Austrolycopodium magellanicum, PASBON* = *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* (Publication IV).

In the case of woody species at the lower elevational range *Myrsine dependens* (Ruiz & Pav.) Spreng was in both land uses (NG and Pi) the dominant specie. In the higher elevational range, the composition of woody species differed completely between land uses. While *Valeriana hirtella* and *Morella parvifolia* dominated in NG, *Miconia crocea* and *Gynoxys* sp, dominated in the plantations (Pi) (Figure 17) (Publication IV).

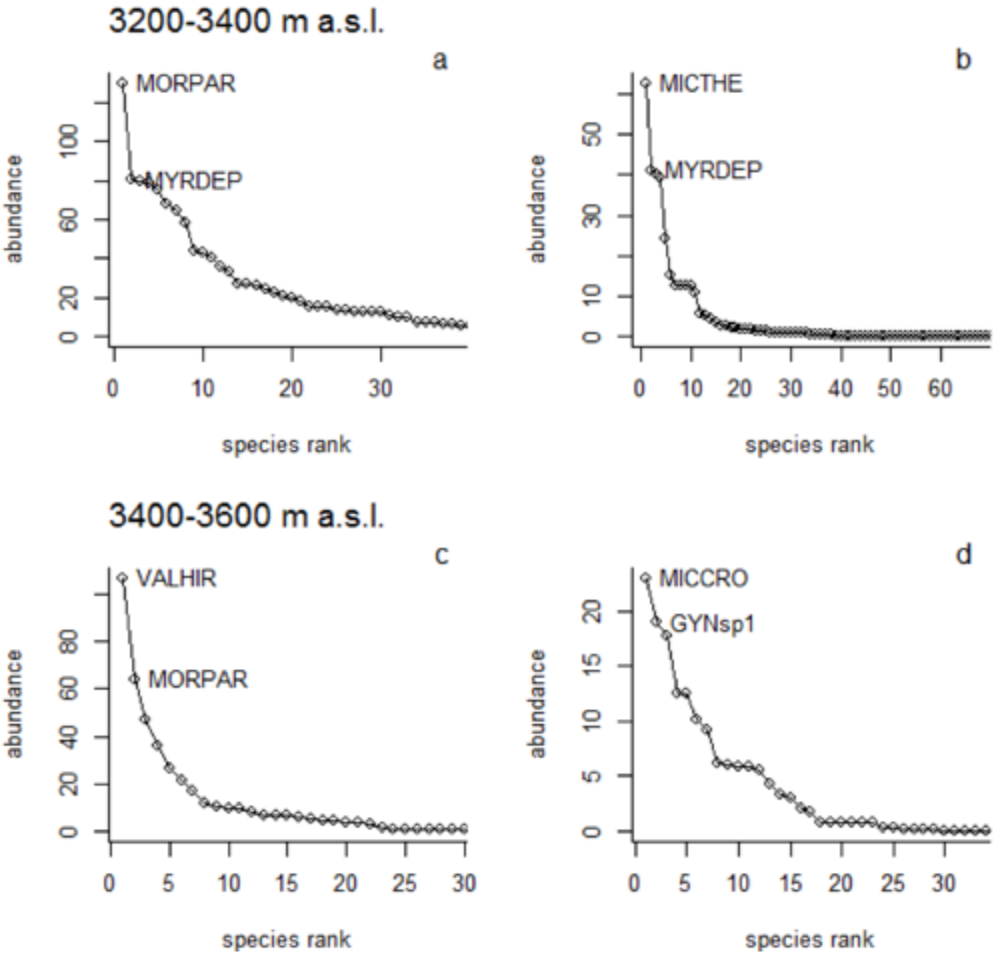

Figure 17. Abundance rank of woody species in natural grassland (NG) (a,c) and pine plantation (Pi) cover (b,d) across three different elevational gradients (3200-3400 and 3400-3600 m a.s.l.). MORPAR = *Morella parvifolia*, MYRDEP = *Myrsine dependens*, MICTHE = *Miconia theaezans*, VALHIR = *Valeriana hirtella*, MICCRO = *Miconia crocea*, GYNsp1 = *Gynoxys* sp. (Publication IV).

Also, the richness and cover of herbaceous species decreased significantly ($p<0.001$) with the increase of canopy density (CD), basal area (BA), K_{sat} (saturated hydraulic conductivity), and soil acidity. On the other end, the richness and cover of woody species decreased significantly ($p<0.01$) with the acidification of the soil, and are both negatively correlated with K_{sat} (Publication IV).

6 Discussion

6.1 Previous land use

One of the first discrepancies that we found (Publication I) between the stakeholders is related to the condition of the land before the establishment of pine plantations. Most of the landowners and the nature conservationists claimed that the pine plantations are realized on disturbed lands, mostly extensive grazing areas, while a minor percentage of the stakeholders do not share this perception, and rather claim that a major percentage of plantations have been established in undisturbed páramo grassland. Nevertheless, the landowners and nature conservationists perception corresponds with the findings of most of the studies (Hofstede, Groenendijk, et al. 2002; Chacón et al. 2009), which state that the plantations have been predominantly established in already disturbed grasslands. At present, the exact degree of intervention that the páramo of this region have had before the establishment of the plantations is uncertain, since human activities date back to the Holocene (Molina and Little 1981; Luteyn et al. 1999; White 2013). Nevertheless, it is still under discussion, whether the presence of the páramo grassland at certain altitudes have had an anthropogenic influence or occurred under natural processes (Llambí 2015). Therefore, it is important to consider previous land use in any type of study or program of reforestation, even more as worldwide studies on plantations established in grasslands indicate that the soil conditions of the plantations may depend on the previous conditions of the terrain (Paul et al. 2000).

6.2 Productivity of the plantations

Another important discrepancy identified between landowners and the other stakeholders was related to the provision of wood by the plantations. While all the owners of plantations located over 3100 m a.s.l. abnegated the profitability of their plantations, the other stakeholders perceive the plantations as a profitable land use. Nevertheless, the landowners' perception coincides with the recommendations of several authors who do not recommend afforesting over 3500 m a.s.l. because of the poor development of the trees above this elevation (Morris 1985; Medina et al. 2000). This is also demonstrated in our study (Publication III), in which the biomass of the pines tends to decrease with the increase in elevation. In addition, the plantations at the highest localities have a lower density of pines (Publication III) making plantations at higher elevations even less productive in terms of wood production.

Other reasons that could sustain the negative perception of the landowners on the productivity are the inefficient management of the plantations, the lack of the genetic management of the seeds, and the establishment of the plantations on land inappropriate for the production of wood (Publication I). On the contrary, the rest of the stakeholders had a positive perception of wood production, possibly due to the fact that there is a company successfully producing wood on approximately 10,000 ha of pine plantations in the páramos of central Ecuador (Aglomerados Cotopaxi S.A.). However, the successful management of this company does not represent the management of the plantations in this study, which are predominantly managed by farmers (Publication I).

6.3 Water regulation and supply

Another discrepancy between the landowners and the rest of the actors is related to their belief on the way pine plantations regulate water flows. Most of the landowners' perception that the plantations have a positive effect on the control of water flows is contrary to the results of the majority of studies in other regions and also in the Andean region (Bosch et al. 1982; Farley et al. 2005; Buytaert, Iñiguez, et al. 2007; Crespo et al. 2010). These studies demonstrated that the establishment of plantations in grasslands caused a reduction in the basin production of water. In our study (Publication II), we registered significant lower values of water retention capacity in the majority of the locations (Irquis, La Paz, Tutupali Chico and Quimsacocha) suggesting a reduction of the water storage capacity (Podwojewski and Poulenard 2004) of the plantation´s soils, and consequently altering the regulation and supply of water flows. Additionally, in our study the lowest values of water retention were attributed to a greater development of the pine trees, together with a decrease in SOM and increase in BD (Publication II). Another cause for the reduction of the water content of the soil is the increase of the hydraulic conductivity (Buytaert, Célleri, et al. 2006), which was registered in five locations (Irquis, Nero, Tutupali Grande, Quimsacocha and Soldados). The decline in water content and consequently of soil moisture is probably also negatively affected by the large amounts of water use by the rapidly growing trees (Fahey and Jackson 1997). This loss of soil moisture causes also a greater decomposition of the SOM content.

Nevertheless, studies exist that support the positive perception of the landowners. For instance, the study of Ilstedt et al. (2007) and Bauhus et al. (2010) illustrate that afforestation in degraded soils can recover the hydrological functioning of the soil. This could be the case in the plantation of Soldados, which registered significant higher values in most of the water retention capacity parameters, in addition to significantly higher values of SOM and lower values (only at the deeper soil layer) of BD (Publication II). It is also known that this area has been highly intervened, as in the year that the plantation of Soldados was established, a study (Hofstede, Coppus, et al. 2002) concluded that the status of conservation of the páramo of this region was one of the most degraded of the country.

Considering the grazed sites, in our study at the locations of Irquis, Tutupali Grande and Quimsacocha, K_{sat} values were significantly lower, contrary to the studies carried out by Alarcón et al. (2010) in Andosols in Chile. Probably, Alarcón did not find any type of change in the K_{sat}, because the study was limited to the impacts of grazing in the summer season when less rainfall and less water content in the soil are recorded. The reduction of the K_{sat} in the location of Irquis could be due to the loss of stability of the soil aggregates and the grazing density, while in the case of Tutupali Grande the consequence of the frequent burning of the tussock grass resulting in drying and crusting of the soil (Poulenard et al. 2001). The higher values of K_{sat} registered in Quimsacocha are probably due to the formation of preferential flows formed by soil tillage, which has been applied at this site (Bodner et al. 2013).

The significantly higher values of BD in Nero and La Paz are directly related to a higher grazing intensity (ABU ha^{-1} of 2 and 1, respectively), similar to the findings of Donkor et al. (2002). Our results of water retention are in line with the findings of Daza Torres et al. (2014), who found that the decrease in water retention was due to a loss in SOM content.

6.4 Regulating carbon sequestration and storage

Most of the interviewees perceived that the plantations have a positive effect in sequestering and storing carbon. Only the group of nature conservationists have an opposite view and perceived that the plantations may change the soil carbon dynamics, inducing a loss of soil carbon that could be large enough to offset the gains in biomass carbon (Publication I). Our results support the suggestion that SOC is the most important carbon pool in each studied land use. Other studies in the Ecuadorian páramo (Bremer 2012; Bremer et al. 2016), revealed similar results. However, in relation to the studies of afforestation in the Ecuadorian páramos, they showed a decrease in SOC (Hofstede, Groenendijk, et al. 2002; Farley and Kelly 2004; Farley et al. 2013). Similarly in our study (Publication III) the results showed significant lower values of total SOC (0-45 cm) for the plantations at the locations of Irquis, La Paz, Tutupali Chico, and in the superficial layer of SOC (0-15 cm) of the Quimsacocha Pi site compared to NG and G. On the contrary, in the location of Soldados, one of the plantations presented significant higher values of SOC (0-45 cm) (Publication III). Some studies (Bashkin and Binkley 1998; Wenjie et al. 2011) demonstrated that afforestation is expected to increase SOC when plantations have been established on cultivated or degraded soils. As stated earlier in this chapter, the soils of the region of Soldados have been classified as degraded, which could explain the increase of SOC.

The perception of the vast majority of the interviewees that plantations have a positive effect on carbon stock shows the lack of knowledge of the stakeholders about the latest studies that have been carried out in the páramo. The positive perception of the stakeholders can probably be explained by their belief that most of the programs of afforestation, reforestation, and avoided deforestation focused on the storage of carbon in the aboveground biomass (Razak et al. 2009; Gibbon et al. 2010). And when considering only the aboveground carbon pool trees develop much more biomass than grasslands, as evidenced by our study (Publication III), dismissing the tradeoffs of carbon between the soil and aboveground pines biomass.

6.5 Supporting habitat for native vegetation

All the interviewees who mentioned this topic believe that the plantations degrade the habitat of the native vegetation (Publication I). This perception is supported by studies in the páramos of Venezuela (Ohep and Herrera 1985) and Colombia (van Wesenbeeck et al. 2003), which found an inverse correlation between pine coverage and native vegetation diversity. Similarly, our research (Publication IV) shows that pine plantations (Pi) had a negative impact on natural regeneration. Nonetheless, as in other studies (Hofstede, Groenendijk, et al. 2002; Bremer 2012) native herbaceous and woody species were prospering inside the plantations (Publication IV).

We found the most pronounced shift in species composition between NG and Pi at the two lower elevational ranges, which could be related to the amount of light reaching the understory. In the case of the more dense plantations with bigger tree canopies, there is less light that penetrates to the understory, facilitating the establishment of shade-tolerant species, such as *Triniochloa stipoides*, a species commonly described in the growth on the floor of pine forest (González-Espinosa et al. 1991; Fuentes-Moreno et al. 2017).

Similar to comparable studies (Hofstede, Groenendijk, et al. 2002; Lemenih et al. 2004; Corredor-Velandia and Vargas Ríos 2007) our results showed that larger canopy density and basal area of the plantations reduced herbaceous species richness and cover. Additionally, the plantations with high hydraulic conductivity (K_{sat}) and therefore causing a loss of SOM (Publication II; Pesántez et al. 2018), restrained the development of herbaceous and woody species richness and cover (Publication IV). In line with the study of van den Berg et al. (2005) and Riesch et al. (2018) we found that the more acidic the soil, the richness and cover of woody species declines (Publication IV). And as shown in previous studies in the páramo (Ramsay 1992; Luteyn et al. 1999; Bader 2007), all vegetation experiences a significant influence of elevation. While elevation had a positive influence on the herbaceous richness and cover, it had a negative influence on the woody vegetation (Publication IV).

7 Conclusions and recommendations

Our first hypothesis that there are disparities between the perceptions of different stakeholders about the impacts of forestation with pines in the páramo could be confirmed. To reconcile different perceptions scientific evidence should be used as a starting point in planning processes as well as early stakeholder involvement. Foresters and nature conservationists should better communicate the ongoing studies and their results between them, and to the rest of stakeholders (local governments and landowners).

The second hypothesis that the pine plantations have changed the physical properties of the soil, altered the carbon storage and, the composition and structure of the vegetation could also be verified. Compared to the NG and G sites most of the plantation's sites had lower values of the water retention capacity of the soil and higher values of the hydraulic conductivity of the soil which was associated with a greater development of the pine trees together with a decrease in soil organic matter. These changes degraded the physical properties of the soil, and therefore they negatively affect the ecosystem service of the páramo of regulating and supplying water.

Most of the plantations revealed higher aboveground carbon values and lower soil organic carbon values than the other land uses. Therefore, it was concluded that there is a tradeoff of carbon between these carbon pools, and that the plantations are altering negatively the soil organic carbon pool. Consequently, we conclude that any quotation of the carbon budget of afforestation projects for carbon sequestration in the páramo, must include soil organic carbon pools.

Finally, the results show that pine plantations hold less plant diversity and cover, and a different composition of herbaceous and woody species than NG. Also, the plantations with high hydraulic conductivity restrained the development of herbaceous and woody species. Nevertheless, in the plantations that were established on natural grassland and had very little or no intervention, native vegetation was flourishing in the understory. We concluded that the replacement of páramo natural grassland by pine plantations negatively affects its biodiversity, but that the plantations that are already established, through adequate silvicultural management (adequate seed resources, pruning, thinning) could contribute to the ecological restoration of this ecosystem.

It is recommended that the results of this research be disseminated among the stakeholders so that a dialogue is generated based on the results of the study, and thus disparate perceptions can be reconciled.

In addition, since the plantations located above 3500 m a.s.l. have not been developed adequately and therefore probably will not generate any income for their landowners, it is recommended that further research should be carried out on alternative management and utilization options that can generate some type of economical return to the landowners without generating any negative impact on the páramo ecosystem services. One possible option could be to consider converting these plantations into ecological restoration spaces. Since in most plantations there is natural vegetation thriving in the understory, these plantations could be managed in a way that they gradually could become patches of native vegetation. However, such plantations must become part of existing and newly generated compensation programs for ecosystem services.

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9 Appendix

9.1 Publication I

Title: Contrasting Stakeholders' Perceptions of Pine Plantations in the Páramo Ecosystem of Ecuador.

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Article

Contrasting Stakeholders' Perceptions of Pine Plantations in the *Páramo* Ecosystem of Ecuador

Carlos Quiroz Dahik [1,2,*], Patricio Crespo [1], Bernd Stimm [2], Felipe Murtinho [3], Michael Weber [2] and Patrick Hildebrandt [2,4]

1 Departamento de Recursos Hídricos y Ciencias Ambientales, Facultad de Ciencias Agropecuarias, Facultad de Ingeniería, Universidad de Cuenca, Av.12 de abril s/n, Cuenca 0101168, Ecuador; patricio.crespo@ucuenca.edu.ec
2 Institute of Silviculture, Center of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; stimm@mytum.de (B.S.); m.weber@tum.de (M.W.); hildebrandt@tum.de (P.H.)
3 International Studies and Institute of Public Service, Seattle University, 901 12th Avenue, Seattle, WA 98122-1090, USA; murtinhf@seattleu.edu
4 Institute of Forest Management, Center of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
* Correspondence: caquirozd@hotmail.com; Tel.: +49-08161-71-4690

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Abstract: The *páramo*, a collection of Neotropical alpine ecosystems, plays a prominent role in ecosystem services (ESs), providing water supply and regulation, conservation of biodiversity, and carbon storage in soil. The establishment of pine plantations for carbon sequestration and wood production has recently raised questions concerning the possible impact on the *páramo's* ES. This study identifies the main stakeholders in this field and compares and contrasts their perceptions of the impact of pine plantations on the *páramo's* ES, because the disparity among stakeholders' perceptions must be addressed to achieve sustainable management. The data were gathered using 56 semi-structured interviews and were qualitatively analyzed. The results show that the main stakeholder groups (landowners, local government officials, foresters, and nature conservationists) acknowledge the important ES of the plantations. The perception of plantation impact varies among and within stakeholder groups, however, on specific functions, such as water provision, carbon storage, erosion prevention, and habitat function for wildlife and natural vegetation. Consideration and integration of these perceptions can help policy makers and organizations develop sustainable policies for the future management of the *páramo* ecosystem.

Keywords: Andes; ecosystem services; exotic plantations; *Pinus patula*

1. Introduction

Tropical alpine ecosystems, of which the *páramo* is one of the most important and widespread, provide ecosystem services (ESs) to more than 100 million people [1]. The most prominent ESs the *páramo* provides are water supply and regulation, biodiversity conservation, and carbon storage [2]. The majority of the main cities in the northern Andes benefit from these services for domestic and industrial water supply, irrigation, and the generation of hydroelectric power [3]. In addition to providing these ESs, the *páramo* is important for the establishment of economic activities. The *páramo* has long been used for grazing llamas and alpacas, and in the last few centuries, sheep, cattle, and horses [4,5]. In the last century, the *páramo* has also seen use for plantations, predominantly of pine. These plantations have varied purposes, including wood production, restoration of degraded land, and in the last few decades, generation of carbon credits as part of the Climate Change Kyoto Protocol, which has caused an increase in the rate of plantation establishment [6,7].

Given the potential positive impact of wood production both for local communities and for carbon sequestration, pine plantations have been broadly recognized as a valuable use of land in the high altitudes of the Andes [6,8]. Several recent studies have, however, raised critical views on *páramo* pine afforestation, taking into consideration their potential negative effects on water regulation and carbon storage [9–13]. More recently, some environmental non-governmental organizations (NGOs) and public media adhering to these views have criticized plantations of pine trees on *páramo* sites. For example, an Ecuadorian newspaper [14] published an article entitled "*Pinos destructores*" (destructive pines), in which pine plantations on *páramo* sites were blamed for the loss of native forests and biodiversity. Several environmental NGOs have also condemned the plantations for diminishing the water supply, drying the soil, and producing a negative economic impact on landowners [15,16].

Opinions on the benefits and risks of pine afforestation on *páramo* sites are both inconsistent and divergent, which presents a challenge to policy makers. The current high level of uncertainty about the future establishment and management of pine plantations is a direct consequence of these divergent opinions. Urgenson [17] emphasizes that the comprehension of stakeholder perceptions is an important means of understanding the opportunities and constraints of ecosystem conservation. Future management of the *páramo* therefore depends largely on reconciling the different stakeholder perceptions. In Ecuador, for example, Gonzales [18] describes how the country's new constitution (approved in 2008) created regulations that guarantee the active and ongoing participation of indigenous nationalities, local communities, forest stakeholders, and the general public in the planning, execution, and control of all forestry activities.

The objectives of this study were (i) to identify the main groups of stakeholders related to the establishment of pine plantations in the *páramo* ecosystem of Ecuador; (ii) using qualitative analysis, to explore and contrast stakeholder perceptions of both the negative and positive impacts of pine plantations on *páramo* ESs in Ecuador. This analysis contributes to the environmental management literature by illustrating the main differences in stakeholder perceptions and current scientific knowledge, ultimately emphasizing the need for additional knowledge. The results of this study are intended to improve public discussions of better management practices for future and already established plantations in *páramo* ecosystems.

2. Materials and Methods

2.1. Study Area

The Neotropical alpine ecosystem *(páramo)* is a high mountain ecosystem situated between the upper limit of the continuous closed forest and the upper limit of plant life, mostly distributed in the northern Andes; the traditional natural vegetation consists of tussock grasses, large rosette plants, shrubs with evergreen, coriaceous and sclerophyllous leaves, and cushion plants [19]. The *páramos* of northern and central Ecuador are found generally from 3500 masl, and in the south they can be found from 2800 masl and higher [20]. In the *páramos* of Ecuador, the annual precipitation varies widely (between 500 and 2000 mm) [19,21] even within rather short ranges, due to the complex topography of the mountains system [22]. In most of the territory, precipitation presents a bimodal pattern with rainy seasons from February to May and from October to December. *Páramos* have a generally cold and humid climate with sudden changes in weather and diurnal fluctuation in temperature oscillating from below freezing to 25 °C, with an annual average that varies between 2 and 10 °C [19,21,23,24]. Soil is one of the most important characteristics of the *páramo*; *páramo* soils act as huge carbon pools, storing and accumulating organic carbon, due to the formation of organometallic complexes that physically protect the humus against decomposition [25].

Interaction between humans and the *páramo* goes back 10,000 years, when parts of the *páramo* were used for hunting and gathering. The most important human impact on the Ecuadorian *páramo* began with the arrival of the Incas, who began to use the lower parts of the *páramo* for agriculture, as well as for grazing llamas and alpacas [4]. Later, Spanish invaders took the most productive lands in the valleys and displaced the native inhabitants to the highlands, some of them into the *páramo*. The Spanish also replaced the south American camelids with sheep, cattle, and horses and began burning large tracts of *páramo* to encourage the growth of tender forage [5]. Although the *páramo's* primary production is not high, as a whole it produces enough plant material to be partially usable for livestock grazing and supplies part of the population's demand for meat and milk [26]. More than 500,000 people, most of them from indigenous communities, live near the *páramo* and use it for productive agriculture [27]. As in other areas in the Ecuadorian Andes, people living inside or close to the *páramo* ecosystem tend to be relatively marginalized. Their main livelihood is agriculture, including cattle grazing, although in some cases they have off-farm income [28].

Pines were introduced to Ecuador in the 1920s as part of governmental forestation programs. At the beginning, these forestation programs focused mainly on meeting the need for fuel, restoring degraded landscapes and, in the case of some large plantations, contributing to economic development [6]. In recent decades, the establishment rate of plantations increased, mainly to generate carbon credits in the context of the clean development mechanism (CDM) [7]. This program promoted the plantation of pines in the *páramo*, based on the belief that they were effective at sequestering carbon from the atmosphere [29]. In Ecuador, the private company PROFAFOR Latinoamérica S.A. (Programa FACE de Forestación del Ecuador S.A.) created and funded by the Face Foundation (Forest Absorbing Carbon Dioxide Emissions), a foundation founded by a consortium of Dutch electricity companies (SEP), is the largest company currently compensating for CO_2 emissions through forestry. Since 1993, PROFAFOR has signed 152 forestation contracts with private and community landowners for carbon sequestration through reforestation and afforestation, 95% of which are located in the Andean highlands [29]. Up to 2003, 22,000 ha of plantations were established in the Ecuadorian highlands, of which 94% are pine plantations [30]. Most of the contracts were signed for 20 years, the expected rotation period for these pines. Landowners are compensated for the costs of the seedlings and their planting and are given an annual visit by a technician. Landowners are obliged to protect their plantations with a firewall and to manage them by pruning and thinning. At harvest time, the landowners receive 70% of the revenue and in the event they want to reforest the area, the full revenue [29].

The interviews given to pine plantation owners and local government authorities were carried out in the Azuay province, situated in southern Ecuador (Figure 1). *Páramo* landowners in the Azuay province include indigenous communities and mestizo farmers (of mixed Spanish and indigenous descent) [31]. This area was chosen because of the establishment of extensive pine plantations in the *páramo* and the society's dependence on the *páramo's* ESs. One of the most critical ESs this region provides is the water for the Paute hydroelectric complex, the oldest and largest in the country [32]. The local University of Cuenca, in collaboration with Belgian and German universities, developed a water resources program that became the main point of reference for ecohydrological research in the *páramo* [4].

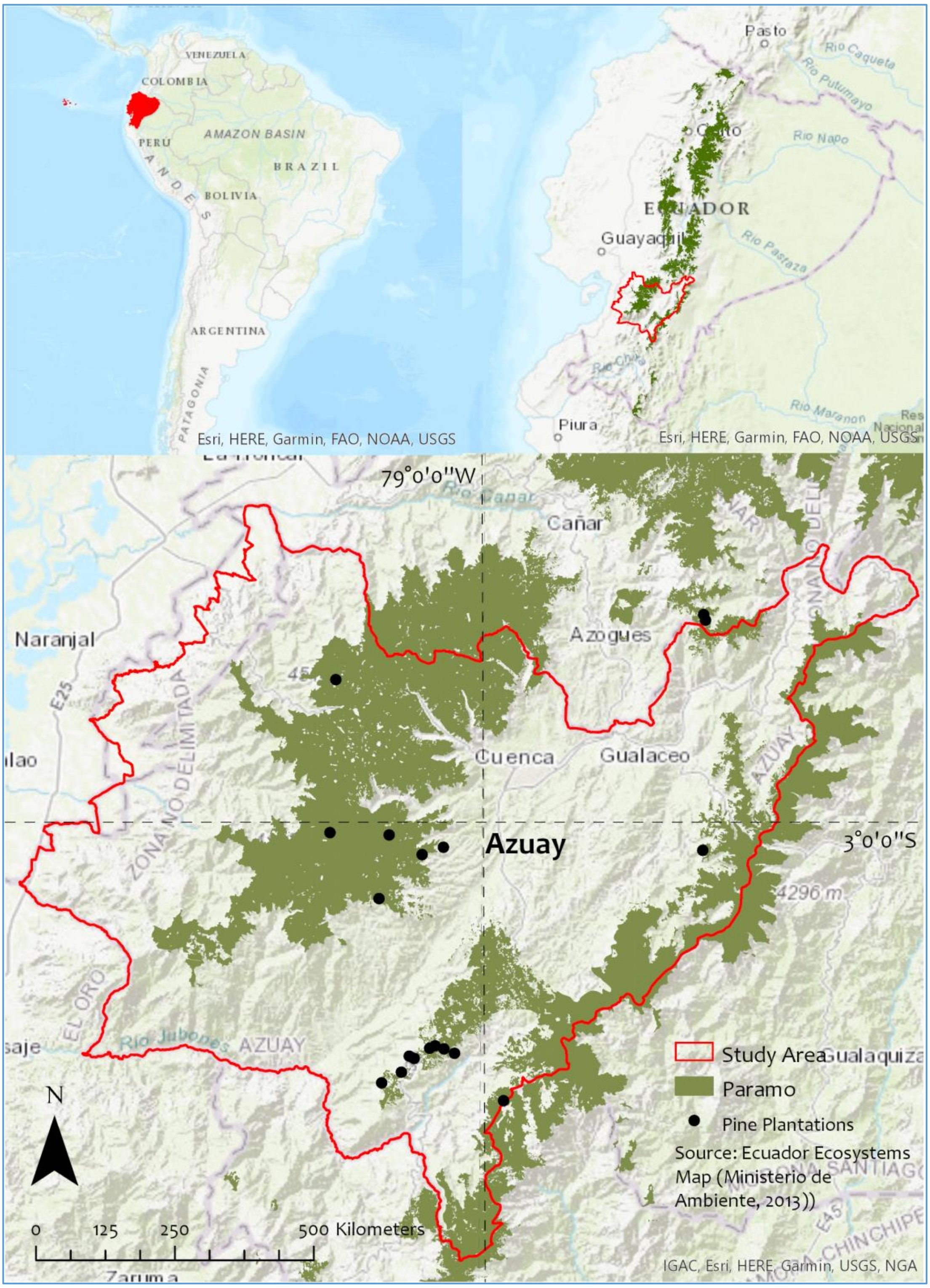

Figure 1. Map of Ecuador indicating the extent of the *páramo* ecosystem and the location of pine plantations corresponding to the group of landowners.

2.2. Methodology

To assess stakeholder perceptions, we followed the definition of Grimble and Chan [33], in which stakeholders are individuals within a system "who affect, and/or are affected by, the policies, decisions and actions of the system; they can be individuals, communities, social groups or institutions of any size, aggregation or level in society. The term thus includes policy makers, planners and administrators in government and other organizations, as well as commercial and subsistence user groups". We identified and contacted public and private organizations that either deal with forestry in the *páramo* and/or are involved in the conservation and sustainable management of the *páramo.* We created a map of stakeholders to identify the main actors in relation to pine plantations in the *páramo*. After the mapping, we identified four main groups of stakeholders: landowners, local governments, foresters, and nature conservationists. We made a list of potential interview subjects from each group of stakeholders. This list was verified and streamlined [33], as each interviewee was also asked to recommend other interviewees, using a snowball sampling technique [34], so that only those who were essential to the analysis were included. Availability also determined the final sample of interview subjects. Following standard practice, a substantial number of key informants from each group were interviewed [35], including: 19 landowners, 15 foresters, 12 nature conservationists, and 10 interviewees from local governments.

The interviews were semi-structured and used open-ended questions to guide the interview. We developed two interview formats: Appendix A.1, which was applied to the owners of the plantations and Appendix A.2 for the rest of the interviewees (Appendixes A.1 and A.2). The difference between the formats was that A1 collected more detailed information about the owners' plantations while A2 collected information about the plantations in the *páramos* in general. With the exception of certain specific information in A1, the rest of the questions were similar in such a way that the information could be compared. The interviews included an introduction to the research project and also assured confidentiality. We conducted 56 interviews in Spanish between June 2013 and June 2015, and collected information on: (1) the characteristics of the plantations (date and place of establishment, extension, type of agreement if it is the case, etc.) and the applied management activities (this information was collected only from landowners); (2) the motivation for establishing pine plantations; (3) the land conditions before planting (the response from landowners related to their own plantations, the replies of the other stakeholders were related to their own experience with pine plantations); (4) the perceptions of the plantations' positive and negative impacts (these perceptions were coded following the categories of ESs used by The Economics of Ecosystems and Biodiversity [36]; provisioning, regulating, supporting, and cultural ES); and (5) future plantations. Interviews were conducted in person by one or two members of our team. One interview was conducted via Skype. The interviews lasted between 26 and 90 min, depending on the availability of the interview subject. Where consent was granted, interviews were recorded (32 interviews) and transcribed (all 56 interviews).

3. Results

Results were grouped in two main categories: (i) stakeholder classification; and (ii) information collected in the interviews.

3.1. Stakeholder Classification

We classified the stakeholders in four groups: landowners, local governments, foresters, and nature conservationists. Stakeholders from the groups of landowners and local governments were located in the *páramos* of Southern Ecuador, while stakeholders from the groups of foresters and nature conservationists were represented by local, regional, national, and international organizations (Table 1).

- Landowners; this group was represented by property owners or land managers with primary decision-making authority for the property. The properties included pine plantations located in the highlands of South Ecuador.
- Local governments; this group was represented by representatives from the Juntas Parroquiales Rurales, the autonomous local governments decentralized from the central government; they are in charge of the protection and sustainable use of the environment and the biodiversity of their jurisdiction. For this reason, they have to promote plans and programs of conservation, afforestation, reforestation, and other actions tending towards the fulfillment of this objective. Additionally, local

governments have to coordinate environmental management with other entities (public and/or private) and prevent the generation of conflicts derived from inadequate management of natural resources. For this study, we considered only local governments from territories with pine plantations (established in private properties) in the *páramos* of southern Ecuador.

- Foresters; this group was represented by forestry professionals and forestry researchers working for public institutions, private organizations or companies, and universities. Of the public institutions, we selected the national and regional forestry departments, which are the entities in charge of promoting and regulating commercial forestation activities. The private companies consisted of timber companies and others that specialized in the establishment of plantations for climate change mitigation and the sustainable management of plantations. The universities included were involved in research and education. All of them were involved in activities in the *páramos*.
- Nature conservationists; this group was represented by researchers and professionals engaged in the conservation of natural resources from both the public and private sectors or universities. From the public institutions we included the national department that is in charge of forest restoration. The private institutions considered were specialized in research, managements and conservation of the *páramo* ecosystem. Some of them were international NGOs that had local representation.

Table 1. Stakeholders classification in relation to pine plantations in the *páramo* ecosystem of Ecuador.

Stakeholder Classification	Stakeholder	Institutional Level	Environmental Interest
Landowners	Pine plantation owners	Local on-site	Timber production, conservation
Local governments	Local authorities	Local	Biodiversity conservation, timber production, and conflict avoidance
Foresters	Companies	Local, regional, national	Climate change mitigation, sustainable forestry, advice on the creation and implementation of sustainable forest management policies
	Forest departments	Local, regional, national	Plantation productivity, sustainable management of commercial plantations
	Universities	Local, regional, national	Research, sustainable management of plantations
	Wood industry	Regional, national	Plantation productivity
Nature conservationists	Consortium	Regional, national, international	Applied research, information exchange and policy development
	Corporation	Regional, national, international	Research, training, and technical support of the sustainable management of the *páramo*
	Environmental departments	Local, national	Forestry regulation on protected areas
	NGOs	Regional, national, international	Preservation and restauration of ecosystems in the highlands
	Private mercantile trust	Local, regional	Research, monitoring, forest restoration, and planting in the highlands
	Universities	Regional, national	Research, sustainable management of the *páramo*

3.2. Information Collected in the Interviews

3.2.1. Characteristics and Management of the Plantations

The plantations of the 19 interviewed landowners cover a total area of 4886 ha. Excluding a single plantation of 2400 ha, the 18 remaining plantations varied in size between 19 and 350 ha with an average size of 138 ha. Of the plantation area, 70% is located above 3500 masl. The average size of the plantations increased with altitude, from 90 ha (2800–3200 masl), over 152 ha (3200–3500 masl) to 172 ha above 3500 masl. In all, 4 landowners manage their plantations autonomously, 14 have management contracts with PROFAFOR, and 1 has a contract with a local governmental institution.

The contracts with PROFAFOR were signed between 1994 and 2000 for an assumed rotation time of 20 years. One of the four autonomously managed plantations has been completely harvested and two of the plantations with PROFAFOR contracts harvested a minimum percentage of their area (one 7% and the other 0.7%). Although the contracts obligate the owners to thin and prune the plantations, 80% of the plantations had not received any thinning and 20% only received thinning in limited areas. Similarly, only 33% of the plantations had received a complete pruning, while 54% had been pruned only in selected parts of the plantation and 13% had not been pruned at all. Two plantations, both located above 3500 masl, received neither thinning nor pruning.

3.2.2. Motivation for the Establishment of Plantations

Although multiple answers were possible, the results show that the majority of landowners (89%) established their plantations for the purpose of wood production, nearly a third for carbon sequestration (as part of the PROFAFOR program), while a quarter mentioned both reasons, and just one (5%) mentioned erosion prevention. These results correspond with the perception of the other stakeholders (local governments, foresters, and nature conservationists), 70% of whom perceived wood production and 11% carbon sequestration as the main motivation for establishment. They also included other purposes such as erosion prevention (14%) and water regulation and supply (8%) (Figure 2).

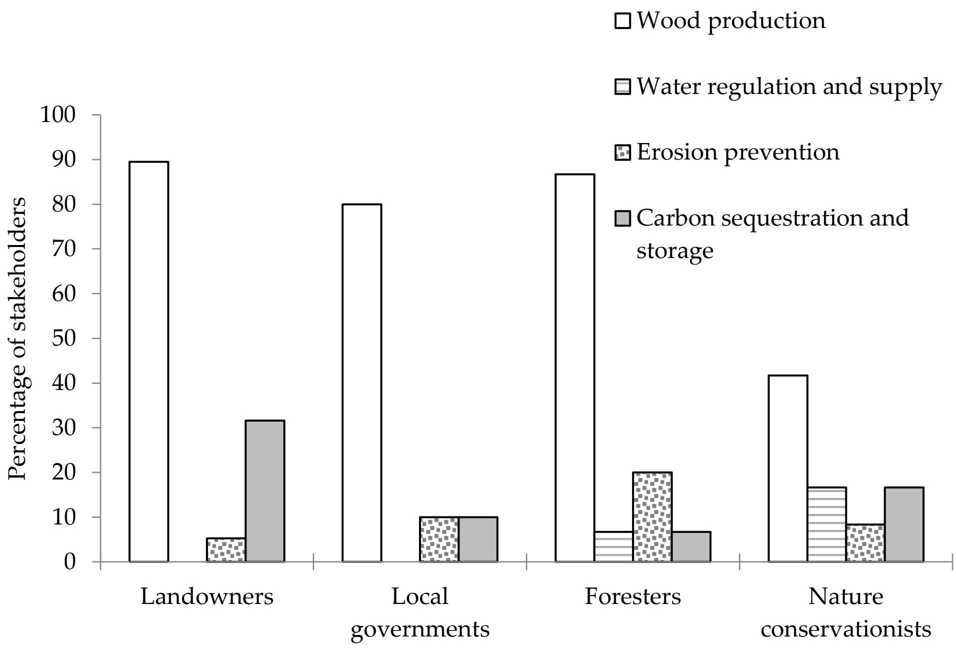

Figure 2. Stakeholder motivations (landowners) and perceptions (local governments, foresters, and nature conservationists) for the establishment of pine plantations in the highlands of Ecuador (multiple answers possible).

3.2.3. Stakeholder Perceptions of the Land Condition Previous to Afforestation

To characterize the land conditions before afforestation, we referred to the categories established by Hofstede et al. [21] in their study of the Ecuadorian *páramo.* Nature conservationists (75%) and landowners (74%) agreed in their perception that the category of the land used for the afforestation was "grazed *páramo*," characterized by tussock grass with signs of frequent burning and the presence of cattle. Only a few landowners (21%) and foresters (7%) perceived that the plantations were established in conserved *páramo*, characterized by tall tussock grasses, without any signs of burning, without cattle, and with the presence of native vegetation. More than half of the foresters (60%) and half of the local government (50%) perceived that most plantations were established on both types of *páramo* (Figure 3).

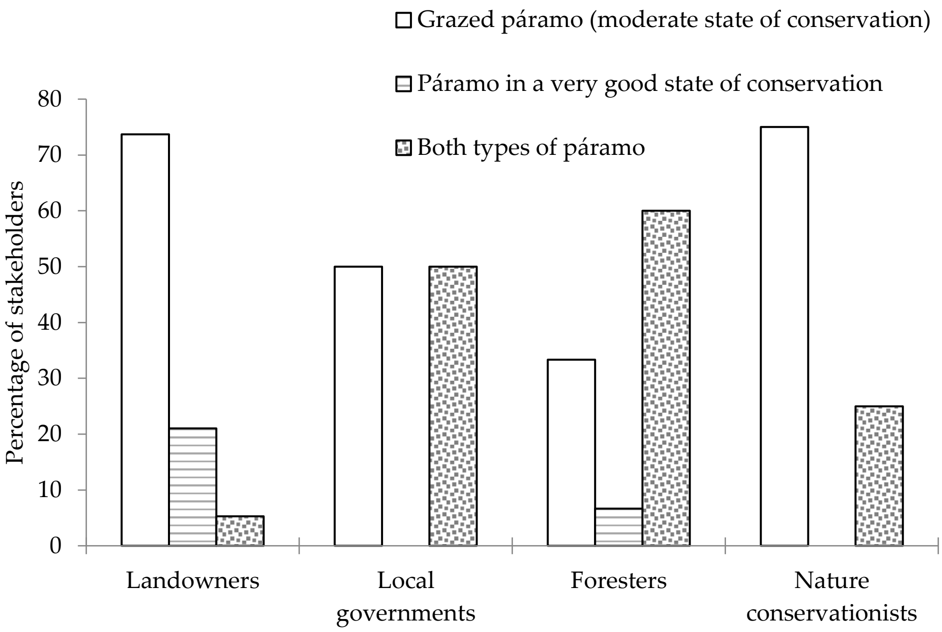

Figure 3. Stakeholder observations (landowners) and perceptions (local governments, foresters, and nature conservationists) about the prior condition of the land before the establishment of pine plantations in the highlands of Ecuador.

3.2.4. Stakeholder Perceptions of the Impacts Caused by Pine Plantations

In interviews, the stakeholders noted four categories of ESs: provisioning, regulating, supporting, and cultural services. Among the ESs mentioned by at least 25% of the interview subjects, the most important subcategories were: providing wood, regulating carbon sequestration and storage, regulating water flows, regulating erosion prevention or maintenance of soil fertility, and supporting habitat for species (Table 2).

Table 2. Summary of categories, subcategories, and brief description of the ESs mentioned by the interviewees. The table includes the percentage of respondents that mentioned each ES in the context of the research. Adapted from [36] and interviews with stakeholders.

Category	Subcategory	Brief Description	Respondents (%)
Provisioning	Raw materiales (wood)	Ecosystems provide a great diversity of materials including wood.	91
	Freshwater	Ecosystems regulate the flow and purification of water. Vegetation and forests influence the quantity of water available locally.	2
Regulating	Carbon sequestration and storage	Ecosystems regulate the global climate by storing and sequestering greenhouse gases. Forest ecosystems are carbon stores.	27
	Water flows	Ecosystems and living organisms create buffers against natural disasters, thereby preventing possible damage. For example, wetlands can soak up flood water. Regulation of natural drainage, irrigation and drought prevention.	45
	Erosion prevention and maintenance of soil fertility	Soil erosion is a key factor in the process of land degradation and desertification. Vegetation cover prevents soil erosion. Soil fertility is essential for plant growth.	57

Table 2. *Cont.*

Category	Subcategory	Brief Description	Respondents (%)
Supporting	Habitat for species (refugium)	Habitats provide everything that an individual plant or animal needs to survive: food, water, and shelter. Each ecosystem provides different habitats that can be essential for a species' lifecycle.	70
Cultural	Ecotourism	Ecosystems and biodiversity play an important role for many kinds of tourism, which in turn provides considerable economic benefits. Cultural and eco-tourism can also educate people about the importance of biological diversity.	4

- Provisioning wood

While 70% of local governments, foresters, and nature conservationists perceived provisioning wood to be a profitable service of pine plantations in the Ecuadorian *páramo*, 79% of landowners were dissatisfied with the profitability of the wood produced by their plantations (Figure 4). Some landowners were dissatisfied with the current level of development of their trees, especially in the higher altitudes. As one landowner stated, "in the upper part of the plantation the pines are small, in these places the pines have not grown". The same group of landowners complained about the high cost of managing their plantations. As one landowner expressed it, "according to the contract we had to carry out three prunings and one thinning, but we do not have enough economic resources, we just did one pruning in the entire plantation. It is clear that there will be no profits, so we are just protecting the plantation". Regarding the management of plantations, one local government representative stated, "it is not profitable, because the income produced does not cover the cost of management", and one nature conservationist argued "it was a great deception practiced on many communities, they all had subsidies for the establishment of the plantations, but nobody had financing for the management". A landowner noted that some other landowners have encountered problems with the environmental authorities, "to extract the wood we need to make some roads, but the authorities do not allow this and they do not allow us to make roads because it will damage the environment, so the trees will remain where they are". Only three landowners with plantations in lower altitudes (2800–3200 masl), who enjoyed better growth conditions, assessed provisioning wood as positive, because they had already obtained revenue from harvesting or thinning their stands.

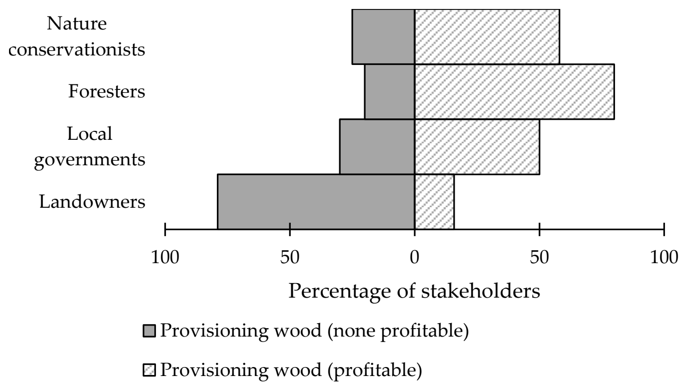

Figure 4. Stakeholder perceptions of the impact of pine plantations on provisioning wood.

- Regulating water flows

Nature conservationists (50%) and local government (60%) interview subjects had only negative perceptions of the impact of the plantations on regulating water flows (Figure 5). Of the foresters, 27% also had negative perceptions, with just 7% expressing positive assessments. Landowners, on the other hand, had more positive (37%) than negative perceptions (5%; Figure 5). Foresters and nature conservationists referred specifically to the negative impact. As one of them commented: "the generally rapid growth of exotic plantations is having a negative effect on the hydrological balance due to the greater use of water". One landowner and some representatives of local governments also mentioned that "water sources near pine plantations have dried up"; "now there is drought around the plantations". However, one of the foresters claimed that "plantations regulate the watershed water balance". The perceptions of most of the landowners referred to their impact on springs. They explained, for example, "previously the springs were drying up; now, they are not dry, and the water flows permanently"; some of them stated that "with the establishment of the plantations the springs have recovered".

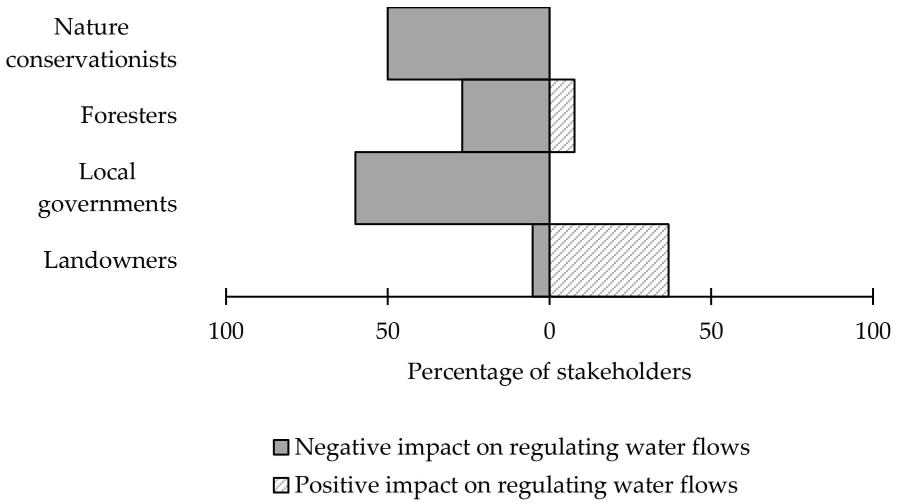

Figure 5. Stakeholder perceptions of the impact of pine plantations on regulating water.

- Regulating carbon sequestration and storage

Although 32% of the landowners said that carbon sequestration was a motivating factor for establishing a plantation, plantation impact on carbon sequestration was positively perceived by only 23% of the interviewees from among all the groups of stakeholders; 8% of the nature conservationists even expressed negative views (Figure 6). One of them explained that "in the *páramo,* approximately 90% of the carbon is stocked in the soil, and some studies showed that the capture of carbon in the biomass of the pines is causing a change in the soil carbon dynamics, causing a loss of soil carbon that could be large enough to offset the gains in biomass carbon". The interview subject emphasized, "this may lead to the failure of this type of project".

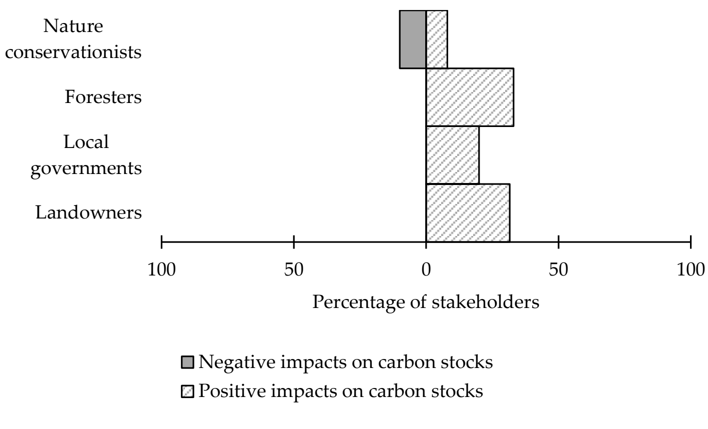

Figure 6. Stakeholder perceptions of the impact of pine plantations on regulating carbon sequestration and storage.

- Regulating erosion prevention and maintenance of soil fertility

Only the representatives of local governments were limited to negative perceptions of erosion prevention and maintenance of soil fertility; the other stakeholders had diverse perceptions (Figure 7). Positive perceptions were related to the recovery of degraded land. A landowner commented, "the plantations caused soil recovery, the pine needles help generate humus and shelter a diversity of insects"; one forester mentioned a case in which the control of desertification was attributed to the planting of pines, stating, "the process of desertification that comes from the Jubones river would have continued to advance if we would not have built a natural barrier using pines". The negative perceptions focused on the alteration of the soil properties, specifically its acidity (pH). A nature conservationist mentioned, "there is an acidification of the soil and a reduction of the water retention of the soil". On this matter, foresters and nature conservationists both observed that the impact depends on what is compared. The plantations may have a positive impact on degraded soils and a negative impact on well-preserved *páramo*.

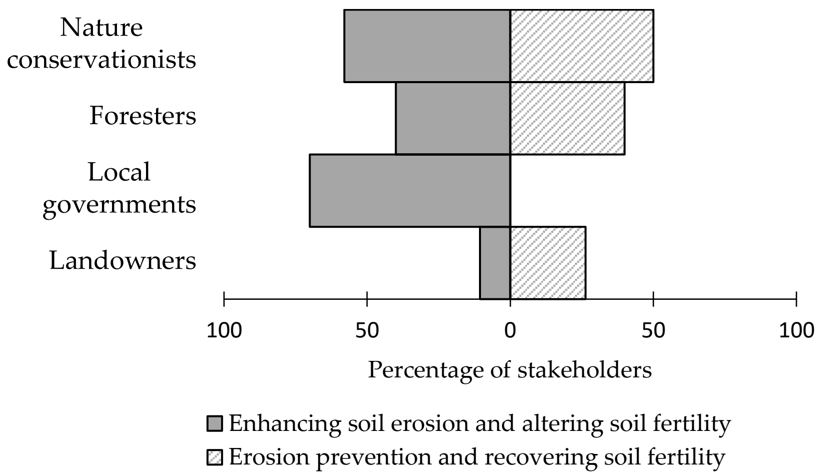

Figure 7. Stakeholder perceptions of the impact of pine plantations on regulating erosion and maintenance of soil fertility.

- Supporting habitat

Regarding this ES, two main perceptions were reported: one regarding fauna and the other one regarding flora. In relation to fauna, all stakeholders perceived that the plantations serve as a refuge for animals. Notably, almost all landowners (89%) had this perception and only 16% of local government representatives, foresters, and nature conservationists shared this perception. All landowners mentioned the presence of deer, rabbits, or guinea pigs on their plantations, and some even mentioned seeing rare mammals, such as the mountain tapir and cougar (Figure 8a). Concerning flora, all the interviewees perceived that the plantations are causing the disappearance of native plants. For example, one stated, "studies have shown alterations in the structure and composition of vegetation and a reduction of its biodiversity," and another said that "on plantations, the understory will not develop" (Figure 8b).

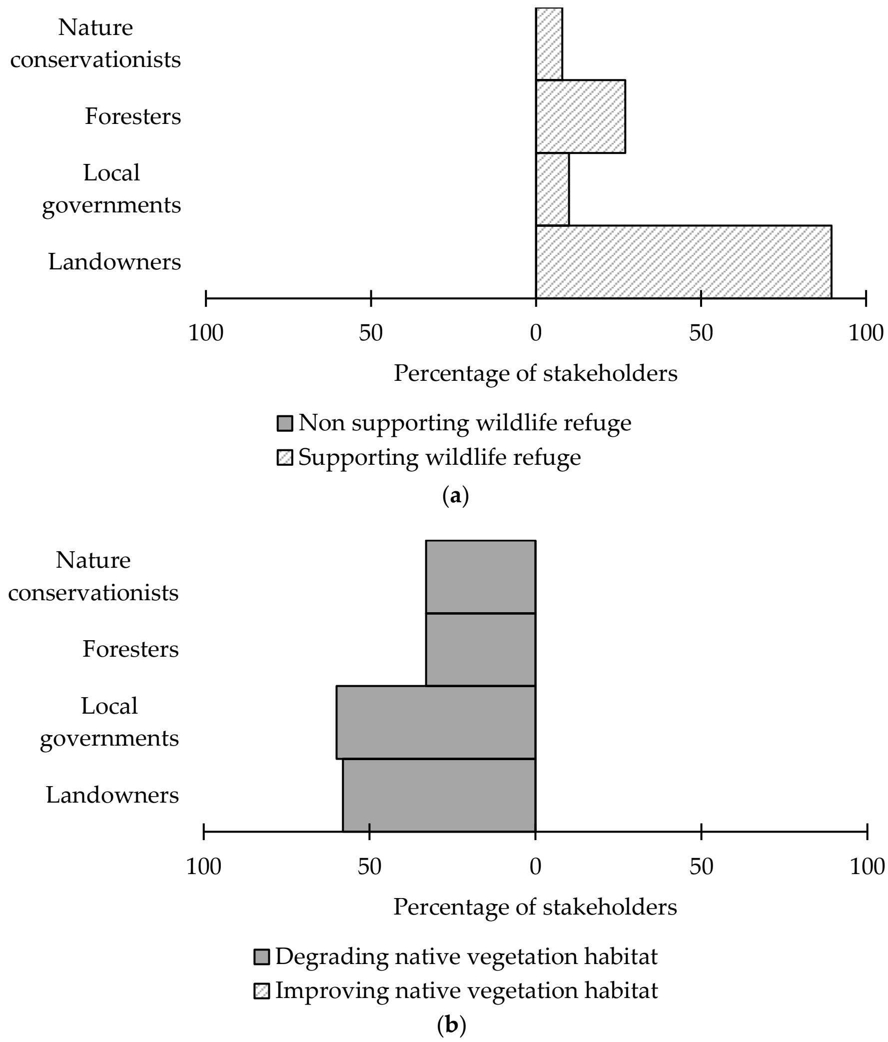

Figure 8. Stakeholder perceptions of the impact of pine plantations on supporting habitat. (**a**) Perceptions related to wildlife refuge, and (**b**) perceptions related to native vegetation.

3.2.5. Future Plantations

In this part, we collected technical information related to the future management of plantations by asking questions to local governments, foresters, and nature conservationists. The majority (67%) of representatives of local governments, foresters, and nature conservationists agree that future plantations should be established only in designated areas. A technical study by the Ministry of Agriculture (MAGAP) and the Ministry of Environment found that there was an area of 2.6 million ha available for the forest plantations to be established for commercial purposes [37]. This evaluation also specified the areas where commercial plantations cannot be established, namely, native forests or *páramo* located above 3500 masl (north of 3° latitude) and above 3000 masl (south of 3° latitude); as well as protected areas or places with slopes greater than 50°. The stakeholders interviewed further considered areas with degraded soils for plantation establishment (60% of local government representatives, 13% of foresters, and 33% of nature conservationists). However, they agreed with the MAGAP that *páramo* ecosystems (30% of local government representatives, 53% of foresters, 66% of nature conservationists), protected areas (30% of representatives of local governments, 47% of foresters, 42% of nature conservationists), and places with existing water sources (20% of representatives of local governments, 13% of foresters, 17% of nature conservationists) should not be afforested using plantations. Concerning the potential for improvement of the plantations, the interviewees highlighted four topics: the proper management of the plantations (38%), establishing plantations only in appropriate places for forestry (35%), the improvement of the genetics of the forest reproductive material (19%), and encouragement of research in the public sector (19%).

This section contains the information related to the interest of the stakeholders in future research. The different stakeholders clearly differentiated topics for further research. Most landowners (68%) were interested in practical aspects related to the management of the plantations, such as the silviculture and commercialization of the wood, and 26% on the impact of the plantations on the soil. The representatives of local governments were mainly interested in the impact of plantations on hydrology (50%), while the foresters had a special interest in the impact of plantations on carbon sequestration and storage (26%), in silviculture (20%), and the generation of work. Of the foresters, 13% were also interested in the impact on hydrology, soil, natural regeneration, and reforestation with native species. The nature conservationists prioritized the impact on hydrology (33%), natural regeneration (33%), and carbon capture (17%). Finally, all landowners expressed their willingness to provide their own plantations for any type of study to support the development of any kind of future research. All stakeholders were willing to collaborate and interact with researchers.

4. Discussion

In recent years the benefits of pine plantations in the *páramo* have been increasingly questioned [4,12], mainly due to the awareness of the importance of the *páramo*'s ESs [2,4]. Most stakeholders we interviewed agreed that the triggering factor for the establishment of pine plantations in the *páramo* is wood production. Pines were introduced to Ecuador in the 1920s, primarily to provide fuel and timber or to restore degraded soils, generally in the highlands, including the *páramo*. Throughout the 1970s and 1980s, the government also promoted the establishment of planations for the same objectives [7]. Since 1993, plantations were established under contract with PROFAFOR, which are mostly located in the highlands (95%) [29], with the purpose of sequestering CO_2 from the atmosphere to generate emissions-reduction credits that could be sold to industrialized countries. However, the amount of carbon credits generated depends on the amount of biomass produced and soil organic carbon stocked, which makes this aspect very important if this type of project is to be successful.

There was a discrepancy between landowners and other stakeholders in their perception of the condition of the land before afforestation. Hofstede et al. [9] and Chacon et al. [38] found in their studies that the plantations in the *páramo* were generally established on extensively grazed areas, which supports the landowners' perceptions and downplays the idea that most plantations damaged *páramo* sites that had good conservation status.

The ES of provisioning wood was mentioned by almost all interviewees. Our study revealed an astonishing discrepancy between the landowners and the other stakeholders in their perceptions of provisioning wood. In contrast with the latter, all landowners with plantations located between 3100 and 3800 masl (79% of the plantations) were dissatisfied with the profitability of their plantations, which could be due to the unexpectedly slow growth of trees at higher elevations. This led to the fact that today, afforestation above 3500 masl is no longer recommended, as previously mentioned [39,40]. Another reason that could have affected the productivity of the plantations is deficient management practices due to the high cost of thinning and pruning. 68% of the plantations did not undertake any thinning and just 32% of the landowners have pruned their entire plantation. Other important points that should be considered and mentioned by the stakeholders are the necessity of improving the genetics of the seeds and the establishment of plantations on land suitable for wood production, rather than degraded land. On the other hand, the positive perceptions in relation to this ES could be that the interviewees associate wood productivity with the levels of production of the wood company Aglomerados Cotopaxi S.A. This company was established in 1978 in the highlands of the north-central area of Ecuador. Currently, the company has approximately 10,000 ha of pine plantations and is one of the biggest manufacturer of medium-density fiberboard (MDF) panels in the Andean region [41]. But in this case, the management of these plantations meets high standards of quality. They produce

3.6 million seedlings per year, they prepare the soil with its own substrate and apply pruning and thinning, and have forest roads to facilitate timber extraction [42]. Moreover, the company saves production costs by locating the plantations next to the production plant and has guaranteed the sale of its wood. On the contrary, all the plantations from this research located from 3460 to 3800 masl had very precarious roads that did not meet the minimum standards of forest roads [43]), which makes the commercialization of their timber even more complicated.

Concerning the regulation of water flows, in contrast to the other stakeholders and most studies, most landowners had a positive perception of this ES. Bosch et al. [44] reviewed 94 catchment experiments worldwide and found that afforestation decreases water yield. In a global synthesis of the effects of afforestation, Farley et al. [11] found reductions of annual runoff when grasslands and shrublands became afforested. The few studies done in the *páramo* ecosystem revealed similar results. Buytaert et al. [12] and Crespo et al. [3] studied the impact of afforestation with *Pinus patula* on the water yield in a *páramo* site in the south of Ecuador. They compared the water yield of a cultivated and a natural catchment and their results indicated an approximately 50% reduction in the water yield of the catchment covered with pines. In the scientific community, it is accepted that the total water consumption of forests is larger than that of short vegetation such as grasslands [12]. Furthermore, as trees have larger leaf area indexes and roughness, they produce higher evapotranspiration; trees' deeper and better-developed root systems also allow them to access deeper water levels, reducing the water yield. Nevertheless, other studies support the perception of some landowners that the afforestation of degraded land can lead to improvements in the properties of the soil and therefore to the recovery of hydrological functions [45,46]. A possible reason why most of landowners perceived a positive effect of the plantations on this ES could be linked to an increase of precipitation in the area after the establishment of the plantations. In a similar study, Farley and Bremer [5] obtained a similar response from an interviewee who mentioned that on his property, pines had caused more rain than before. In a study in the Colombian Andes, Murtinho et al. [47] found that local people related changes of water scarcity with rainfall. We compared rainfall averages from 5 hydrological stations in the area [48], within the period of 1960–1994 (years of the establishment of the plantations) with the period of 1995–2013 (years of the interviews). The comparison of the averages resulted in an increase in precipitation. From 1960 to 1994 the average was 714 mm year^{-1}, while from 1995 to 2013 it was of 1036 mm year^{-1}. To determine the factors that caused the increase in precipitation, more research would be needed, but this fact could justify the positive perception of landowners.

The ES of regulating carbon-sequestration and -storage was the less mentioned by the interviewees. It was positively perceived by 25% of the interviewees, most of them landowners (43%), probably because the landowners assume that their plantations are contributing positively to carbon sequestration and storage, since all of these landowners have a contract with PROPAFOR and surely are familiar with the company's program. The only negative perception came from the group of nature conservationists. The majority of positive perceptions were probably influenced by the promotion of carbon sequestration; in general, conifer forests are considered major terrestrial carbon reservoirs [49]. Nevertheless, studies worldwide have shown that the afforestation of grasslands can have differing outcomes depending on the previous condition or use of the land [50]. For instance, Berthrong et al. [51] found in a meta-analysis that afforestation with pines decreased stocks of soil organic carbon (SOC). Most studies in the Ecuadorian *páramo* [9,52–54] found a decrease in SOC, although Chacon et al. [38] found no change. Local studies are therefore recommended, as SOC may also be affected by climate and parental material, which may vary among regions [55]. The reduced number of interviewees that mentioned this ES could be explained because there is not much information concerning this topic, as more studies are still needed to better understand the effects of land use change on SOC stocks [54,56].

The foresters and nature conservationists had diverging perceptions of the impact of plantations on erosion prevention and maintenance of soil fertility of the *páramo*. Both groups stated that the impact depends on the characteristics of the soil when the plantation is established: if the soil is degraded, the impact of a plantation could be positive, but if the soil is in good state of conservation, then its impact is more likely to be negative. As an example of a positive impact, some foresters and nature conservationists mentioned the plantation of pines established in the dry *páramo* of Palmira (Chimborazo province in central Ecuador). It is believed that this plantation halted the advance of sand dunes. This argument was stated in a technical report [57]. Hofstede [58] mentioned that it is obvious that pine plantations have prevented soil erosion in some *páramo* areas. For the moment, these perceptions are not based on sound scientific studies; we therefore recommend a conclusive study to assess the impact of pine plantations on erosion in one of these sites. On the other hand, the perception that erosion is enhanced or soil fertility is altered by changes in soil properties is supported by most Ecuadorian studies [9,24,59], which have shown that, for different *páramo* study sites throughout the country, the soil is considerably drier in pine plantations. Farley and Kelly [52] found more acid soils at plantations. Nevertheless, most landowners felt that the pines had led to an improvement in soil fertility. Another important factor that affects this ES is the frequency of burning commonly associated with grazed *páramo*. The perceptions of the stakeholders vary depending on what type of burning management is compared. A grassland that has been burned frequently and had intensive grazing will present few remnants of original vegetation and will have big patches of bare ground. In this type of management, erosion will be enhanced [60]. A different management with sporadic burning and extensive grazing would have less impact on this ES.

The concern of many stakeholders that the plantations may have negative effects on supporting habitats for native vegetation thanks to a degradation of such habitats has been supported by some studies in the *páramo* of Venezuela [61] and Colombia [62]; which have found that as pine coverage increases, species diversity of native vegetation decreases. In Ecuador, Hofstede et al. [9] found different results; in some plantations, the vegetation was similar to *páramo* grassland, and in others the understory was completely lacking. Farley and Bremer [5] found that in pine plantation sites plant species richness vary from lower to higher and plant species composition had large changes. Other studies [63] have also found that the type and quantity of solar radiation available in a forest influences numerous physiological, morphogenetic, and reproductive processes of plants. This effect depends on the density of the plantation, the age (the taller the pines, the less light they allow to fall on the soil), and the management of the plantation (without pruning and/or thinning, less light passes through). Concerning the function of the plantations in supporting habitat for wildlife (animals), landowners differed considerably from the other stakeholders. Almost all the landowners expressed this perception, but there is very limited research to support this belief. Molina [64] studied the biology of the white-tailed deer in the *páramo* of Venezuela, finding that the largest number of deer sightings occurs in the plantations and 70% of the inhabitants interviewed said that pine plantations benefit deer by providing refuge. According to Molina [64], these plantations are playing a positive ecological role for the preservation of the deer and the presence of this animal will depend on the renovation of these plantations. In our research, it was the landowners who highlighted the same function that the plantations are possibly providing to the animals.

Related to the future management of the plantations, the stakeholders believed that the productivity of the plantations could improve by: enhancing their management, establishing them in sites suitable for forestation, improving the genetic quality of the seeds, and supporting more research. All of these aspects corroborate the information already collected. In relation to the stakeholders' interest in future research, the results showed, as indicated Hein et al. [65], that stakeholders at different spatial scales have different interests in ESs. The landowners were mainly interested in the productivity of their plantations (management and commercialization) which also corroborates the intention for which most of them established their plantations. The local governments were interested in studies on the impact of the plantations on water resources, as water is one of the most valuable resources in rural areas. Foresters and nature conservationists were more interested in topics related to their areas of expertise such as the impact on carbon stocks and natural regeneration.

5. Conclusions

This study is one of the first to classify stakeholders in relation to pine plantations in the *páramos* of Ecuador and to report and contrast stakeholder perceptions of the impact of these plantations on the *páramo* ecosystem services. There are five main findings:

- Scientific evidence should be the starting point to reconcile the different perceptions between the stakeholders. Therefore, foresters and nature conservationists should communicate the results and nature of their research with the other stakeholders [66].
- The local knowledge provided by the perceptions of the landowners was fundamental [67] to identify gaps of knowledge related to the ES of provisioning wood and supporting habitat (wildlife refuge for animals).
- Perceptions among stakeholders differ on several aspects, such as: wood production, water regulation and supply, and support of habitat. Even within stakeholder groups, perceptions were not uniform on topics such as the regulation of erosion prevention and the maintenance of soil fertility. This disparate views should be reconciled by more interaction between stakeholders, which will facilitate linkage and information flow [68].
- Because wood production has been the main objective for the establishment of pine plantations in the *páramo*, their management must be improved; for example by establishing the plantations in lands designated for forestation, providing financial plans and silvicultural treatment, ensuring adequate road access to plantations and the fair commercialization of wood.
- It is quite unlikely that the emission-reduction objectives intended in the contracts can be achieved, especially for the plantations located in higher altitudes. Furthermore, it must be noted that the plantations may have negative effects on the provision of other ESs, such as supporting habitats for native species and regulating water flows. Consequently, the establishment of new plantations should take into account these possible trade-offs [5,69].

Identifying these perceptions may help avoid future conflicts in the management of the natural resources of the *páramo* and the design of effective conservation policies. In an Andean country like Ecuador, where awareness of the importance of *páramo* ESs has rapidly increased and is expected to continue doing so, the validation of such perceptions in future studies is important and could ultimately result in sustainable management and improved conservation of the *páramo*.

Author Contributions: C.Q.D., P.C. and P.H. developed the study design; C.Q.D. collected the data; C.Q.D., M.W. and P.H. analyzed the data; C.Q.D. wrote the paper; 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

Appendix A.1. Interviews Applied to Landowners

Fecha:
Entrevistador:

1. Información general

A pesar de la importancia que tienen los páramos para el desarrollo socio-económico y ambiental de la zona Austral. Desde hace varios años estos ecosistemas están siendo alterados, donde la forestación con especies exóticas como el pino han sido comúnmente usadas para diversos objetivos que van desde el secuestro de carbono hasta la conservación de agua. Sin embargo, estas prácticas no han sido evaluadas y su manejo ha sido muy deficiente. Por esta razón, esta investigación tiene como objetivo evaluar las diferentes prácticas de manejo forestal sobre la producción de madera, biodiversidad vegetal, secuestro de carbono y regulación de agua. Para ellos varias parcelas de monitoreo serán instaladas en la zona de Yanuncay al sur del Ecuador. Al final del proyecto se espera poder dar sugerencias sobre las prácticas de manejo forestal evaluadas para que se pueda realizar un manejo sostenible en las zonas de páramo

(La información obtenida en esta entrevista servirá para investigación científica y será anónima).

1.1. Nombre del propietario:
1.2. Lugar de la plantación:
1.3. Coordenadas y altitud:
1.4. Extensión de la propiedad: de la plantación:
1.5. ¿Existe algún tipo de convenio?
No___ Si ___
Tipo: Socio Bosque___ Créditos de carbón___ Otro:___
Institución:
Fecha: De _____________a_____________ Área:
1.6. Otras actividades que se realicen en la propiedad (ganadería, agricultura . . .)

2. Plantación

2.1. Motivo por el cual se realizó la plantación
2.2. Fecha del establecimiento de la plantación (Si hay varias plantaciones en diferentes épocas, especificar):
2.3. Especies de plantas utilizadas en la plantación:
2.4. ¿Cuáles fueron los criterios para seleccionar a esta especie? ¿Se consideraron otras especies, si es así cuales? ¿Por qué no se tomaron en cuenta otras especies?
2.5. Número de árboles por hectárea (distancia entre plantas):
2.6. ¿Cuál es la procedencia genética de los plantines? (en donde se cosecharon las semillas)
2.7. ¿En dónde se adquirieron los plantines?
2.8. Antes de la plantación, ¿Qué tipo de manejo tenía el terreno? (bosque, páramo, agricultura, ganadería, etc.)
2.9. Antes de plantar, ¿se preparó de alguna manera el terreno? (macheteo, desyerbar, abonar, herbicidas, etc.)
2.10. ¿Cuál fue el tamaño de los plantines en el momento de sembrarlos?
2.11. ¿Quién fue el responsable de realizar la plantación, y quién está a cargo ahora?
2.12. ¿Quién realizó la plantación? (mano de obra local capacitada, etc.)
2.13. Costos
Plantines:
De cada plantin_____
plantines/ha____

costo por ha____
de ha ____
costo total____
Trabajadores:
Pago diario por trabajador____
#de trabajadores diarios____
Salarios diarios____
de días contratados____
Costo total por trabajadores____
Gastos por contratación de técnicos:
Pago por cada asistencia____
(#)_____asistencias en ____ años
Costo total por contratación de técnicos____
Otros gastos:
Inversión total:
Existió algún tipo de subvención, o crédito

3. Manejo

3.1. ¿Existen algún tipo de regulación en cuanto al manejo?
No___ Si___
¿Cuáles son las regulaciones de manejo, o las condiciones legales que se deben cumplir?
3.2. ¿Cuenta con asesoría técnica?
No___ Si___
¿Quién?
¿Frecuencia de la asesoría?
¿Costos?
3.3. ¿Qué tipo de manejo ha tenido la plantación? (raleo, poda, tala, ninguno):
¿En qué área se hizo el manejo (en una sección o en toda la plantación)?
¿Cuál fue la intensidad?
¿Cuál fue el rendimiento?
¿Hubo algún ingreso?
3.4. Si ha tenido manejo, ¿con qué frecuencia se lo ha realizado?
3.5. Costo aproximado del manejo:
3.6. ¿Se han presentado algún tipo de plagas?
No___ Si___
¿Cuándo?
¿En qué extensión?
¿Se aplico algún tipo de tratamiento?
¿Cuál fue el resultado?
¿Fue reembolsado este gasto, por quién, en cuánto tiempo y qué porcentaje?
3.7. ¿Han ocurrido incendios?
No___ Si___
¿Cuándo?
¿En qué extensión?
¿Quién se encargó de controlarlo?
¿Tuvo algún costo por parte de la entidad que lo controló?
3.8. ¿Ha observado algún tipo de impacto generado por la plantación sobre la flora o fauna del lugar? ¿Si es así, se han tomado algún tipo de medidas para regular estos efectos?

4. Manejo futuro

4.1. ¿Cuál es el objetivo de manejo en su plantación?

Producción de madera ___
Protección del suelo (erosión) ___
Conservación del ciclo del agua ___
Secuestrar carbono ___
Producción de otros productos no maderables (¿cuáles, con qué frecuencia y cuáles serían las ganancias?)

4.2. ¿Qué actividad realizará en los próximos 10 años?
Ninguna ___
Poda ___
Raleo ___
Tala ___
No se sabe todavía ___

4.3. ¿Qué actividad realizará en los próximos 20 años?
Ninguna ___
Poda ___
Raleo ___
Tala ___
No se sabe todavía ___

4.4. ¿Existe algún interesado en comprar la madera? (¿Quién y con qué fines, a qué precio por metro cúbico?)

4.5. ¿Existe algún tipo de convenio para conservar la plantación? (¿con qué organismo y por qué?)

4.6. Otro tipo de manejo:

5. Estudio

Para realizar este estudio posiblemente se van a requerir realizar diferentes tipos de manejo (poda, raleo, enriquecimiento con especies nativas) en determinadas parcelas de las plantaciones. La superficie de las parcelas será de 24 m $\times$ 24 m aproximadamente, se estima que para todo el estudio se requerirán 50 parcelas aproximadamente.

5.1. ¿Cuál ha sido la mayor dificultad que ha tenido con la plantación?

5.2. ¿Le parece importante que se realice este tipo de investigación?
No___ Si___
¿Por qué?

5.3. ¿Estaría dispuesto a que se realice estos tipos de manejo en parcelas que se seleccionen en su propiedad?
No___ Si___
¿En cuántas parcelas de la plantación se podría realizar el estudio?
¿Cuáles actividades sería posible hacer?

5.2. Observaciones y/o comentarios.

Appendix A.2. Interviews Applied to Local Governments, Foresters and Nature Conservationists

Fecha:
Entrevistador:
Entrevistado:

A pesar de la importancia que tienen los páramos para el desarrollo socio-económico y ambiental de la zona Austral. Desde hace varios años estos ecosistemas están siendo alterados, donde la forestación con especies exóticas como el pino han sido comúnmente usadas para diversos objetivos que van desde el secuestro de carbono hasta la conservación de agua. Sin embargo, estas prácticas no han sido evaluadas y su manejo ha sido muy deficiente. Por esta razón, esta investigación tiene como objetivo evaluar las diferentes prácticas de manejo forestal sobre la producción de madera, biodiversidad vegetal, secuestro de carbono y regulación de agua. Para ellos varias parcelas de monitoreo serán instaladas en la zona de Yanuncay al sur del Ecuador. Al final del proyecto se espera poder dar sugerencias sobre las prácticas de manejo forestal evaluadas para que se pueda realizar un manejo sostenible en las zonas de páramo.

(La información obtenida en esta entrevista servirá para investigación científica y será anónima).

1. ¿Conoce cuándo se realizaron las primeras plantaciones de plantas exóticas (pino), y cuál fue el motivo (reforestación, producción de madera, protección del suelo, etc.)?
2. ¿Cuáles fueron los criterios para seleccionar a esta especie? ¿Por qué no se tomaron en cuenta otras especies?
3. ¿Se consideraron otras especies? ¿Cuáles?
4. ¿Cuál es la procedencia de los plantines, por qué se escogió esta procedencia?
5. ¿Qué tipo de terrenos se seleccionaron para las plantaciones, hubo algún tipo de preparación del terreno antes de la plantación?
6. ¿Bajo qué marco legal se están manejando las plantaciones, qué tipo de convenios existen, quienes son los responsables, qué tipo de regulaciones existen?
7. En la actualidad, ¿cuáles serían los impactos positivos que se han generado gracias a las plantaciones? (ambientales, económicos, sociales)
8. ¿Cuáles serían los principales impactos negativos, y qué medidas se han tomado o se están tomando? (ambientales, económicos y sociales)
9. ¿Cuál es el objetivo de manejo de las plantaciones forestales (protección, producción, secuestro CO_2, etc.)?
10. ¿Qué actividades se planifica realizar en los próximos años? (tipo de manejo, estudios, etc ...)
11. A la institución a la cual usted representa, ¿cuáles son los aspectos que más le interesan, respecto a las plantaciones (pino)? (estudios, ventajas/desventajas, protección, producción, captura carbono, reintroducción especies nativas, etc.)
12. ¿Cuáles son las desventajas que se presentan a futuro para las plantaciones (de pino)?
13. ¿Cómo cree que las plantaciones se podrían mejorar y/o acelerar?
14. ¿Cree que las plantaciones forestales podrían mejorar la situación económica de los propietarios, industrias forestales?
15. ¿Cómo su institución podría mejorar esta situación, esta la institución activamente participando en este proceso o planea hacerlo?
16. ¿Qué áreas deberían designarse para plantaciones forestales, y cuáles no? (especificar pino)
17. ¿Apoya su institución el establecimiento de plantaciones forestales, con qué especies? (económicamente, asesoría técnica, pago por servicios ambientales, etc.)

Observaciones y/o sugerencias.

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9.2 Publication II

Title: Changes in Soil Hydro-Physical Properties and SOM Due to Pine Afforestation and Grazing in Andean Environments Cannot Be Generalized

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Changes in Soil Hydro-Physical Properties and SOM Due to Pine Afforestation and Grazing in Andean Environments Cannot Be Generalized

Franklin Marín [1,2], Carlos Quiroz Dahik [1,3], Giovanny M. Mosquera [1,2,4], Jan Feyen [1], Pedro Cisneros [5] and Patricio Crespo [1,2,5,*]

1. Departamento de Recursos Hídricos y Ciencias Ambientales, Universidad de Cuenca, 010207 Cuenca, Ecuador; franklin.marinm@ucuenca.edu.ec (F.M.); carlos.quiroz@tum.de (C.Q.D.); giovanny.mosquerar@ucuenca.edu.ec (G.M.M.); jan.feyen@ucuenca.edu.ec (J.F.)
2. Facultad de Ingeniería, Universidad de Cuenca, 010203 Cuenca, Ecuador
3. Institute of Silviculture, Center of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
4. Institute for Landscape Ecology and Resources Management (ILR), Research Centre for BioSystems, Land Use and Nutrition (IFZ), Justus Liebig University Giessen, 35392 Giessen, Germany
5. Facultad de Ciencias Agropecuarias, Universidad de Cuenca, 010203 Cuenca, Ecuador; pedro.cisneros@ucuenca.edu.ec

* Correspondence: patricio.crespo@ucuenca.edu.ec

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Abstract: Andean ecosystems provide important ecosystem services including streamflow regulation and carbon sequestration, services that are controlled by the water retention properties of the soils. Even though these soils have been historically altered by pine afforestation and grazing, little research has been dedicated to the assessment of such impacts at local or regional scales. To partially fill this knowledge gap, we present an evaluation of the impacts of pine plantations and grazing on the soil hydro-physical properties and soil organic matter (SOM) of high montane forests and páramo in southern Ecuador, at elevations varying between 2705 and 3766 m a.s.l. In total, seven study sites were selected and each one was parceled into undisturbed and altered plots with pine plantation and grazing. Soil properties were characterized at two depths, 0–10 and 10–25 cm, and differences in soil parameters between undisturbed and disturbed plots were analyzed versus factors such as ecosystem type, sampling depth, soil type, elevation, and past/present land management. The main soil properties affected by land use change are the saturated hydraulic conductivity (K_{sat}), the water retention capacity (pF 0 to 2.52), and SOM. The impacts of pine afforestation are dependent on sampling depth, ecosystem type, plantation characteristics, and previous land use, while the impacts of grazing are primarily dependent on sampling depth and land use management (grazing intensity and tilling activities). The site-specific nature of the found relations suggests that extension of findings in response to changes in land use in montane Andean ecosystems is risky; therefore, future evaluations of the impact of land use change on soil parameters should take into consideration that responses are or can be site specific.

Keywords: andosols; high montane forests; páramo; anthropogenic activities; land use change

1. Introduction

High montane forests and páramo [1], typical Andean ecosystems, provide important services such as water supply regulation and carbon storage [2]. The hydrological services provided by Andean ecosystems have been closely related to the characteristic functions played by their soils at watershed scale [3–5]. These characteristics include: high soil organic matter (SOM) content [6], overall low bulk density (BD) (<0.6 g cm^{-3}) [7], and high-water retention capacity [7–12]. Despite the important role soils play with respect to the provision of ecosystem services in the Andean region, they have been increasingly altered by anthropogenic activities since pre-Hispanic times [13], and only a limited number of evaluations of the effects of anthropogenic land-use changes on soil properties exist.

In the Andean region, afforestation and grazing are the main anthropogenic activities affecting montane ecosystems [12,14–16]. Afforestation, primarily with pine, has been carried out to produce timber and reduce pressure on native ecosystems [16–19], as well as to capture carbon [19–21]. Without focus on the possible impact on soil and water resources, the majority of pine plantations were established on sites of important hydrological and ecological value to the Andean population. Grazing in the montane Andean ecosystems has been carried out since pre-Hispanic times (XV century), and this practice results mainly from extensive to intensive animal farming (cattle, horses, and sheep) [13]. In some cases, grazing is carried out directly in natural cover, considering tussock grass as fodder, or after burning to convert the land, whether or not accompanied with the introduction of more productive grass species [22], into suitable pasture where cattle can obtain more nutritious fodder [18].

Pine plantations and grazing interventions in Andean ecosystems have led to significant changes in the hydro-physical properties and SOM content, in particular of the top soil at depths lower than 30 cm [19,20,23,24]. Modifications in soil properties are causal factors of a reduction in water yield and variations in the hydrological response of montane Andean basins [25,26]. In the case of pine afforestation, the soils tend to dry out because of the high water absorption capacity of the trees, which favors SOM decomposition [19,20] and reduces the soil's water retention capacity [15]. Furthermore, preferential flows created by root growth increase the saturated hydraulic conductivity (K_{sat}) of soils [27]. Despite existing investigations, there still exists indistinctness and contradictions about the effect of anthropogenic impacts, such as pine plantations and grazing, on the soil properties of Andean ecosystems [28]. Some studies reported an increment in SOM in the Andosols of pine plantations [28], while other studies found no evidence of changes [29]. Additionally, in most studies, important factors capable of influencing changes in soil hydro-physical properties, such as previous land-use practices as evidenced by La Manna et al. [30], have not been considered. Similarly, the effects of livestock grazing, whether or not accompanied by burning, have been interpreted in different ways. Some authors claim that greater solar radiation exposure leads to soil drought, an increase in BD, SOM loss [19,23,31], and a reduction in soil water retention [23,32]; while a reduction of K_{sat} enhances water erosion [28]. Despite previous findings, under grazing activities some authors have shown, probably due to pre-tilling activities, a reduction in the BD and an increment in SOM [28,33]. Such discrepancies could be due to the intensity of grazing. In some cases, extensive grazing is not considered a source of stress on high Andean ecosystems [34].

Considering the role of soil properties in the provision of ecosystem services in Ecuador's Andean environments, and the past and present anthropogenic pressures resulting from afforestation and grazing activities, the main objective of this study was to evaluate the impact of pine afforestation and grazing on the hydro-physical properties and SOM content of the surface horizons of high montane forest and páramo soils. The study was guided by the following research hypotheses: (1) to properly assess anthropogenic impacts it is recommended to collect information of unaltered and altered plots on neighboring comparable sites to avoid that interpretation of results is biased by local site differences and (2) the impact of land-use change on the hydro-physical soil properties is not unique and often masked by other factors such as antecedent land-use, spatial variability, texture, elevation, climate, among other site-specific factors. The evaluation of both these hypotheses will not only improve the research quality and the capability to generalize research findings, but also the effectiveness of future decision making and conservation policies of high-elevation ecosystems in the Andean region.

2. Materials and Methods

2.1. Study Area

The study was conducted in the province of Azuay, southern Ecuador, in an area whose elevation varies between 2705 and 3766 m above sea level (a.s.l.) (Figure 1). The area is dominated by two Andean montane ecosystems—high montane forest and páramo. The high montane forest consists of evergreen vegetation with an arboreal stratum between 3 and 10 m tall, a great variety of vegetation and a high epiphyte density [35,36]. The predominant species there belong to the Solanaceae, Melastomataceae, Rosaceae, Ericaceae, Chlorantaceae, Myrtaceae, Lauraceae and Podocarpaceae families [8]. The páramo comprises predominantly herbaceous shrub-type vegetation (*Calamagrostis intermedia* (J. Presl) Steud.) and cushion-like grass varieties (*Azorella pedunculata* (Spreng.) Mathias & Constance and *Plantago rigida* Kunth) [13,26,37,38].

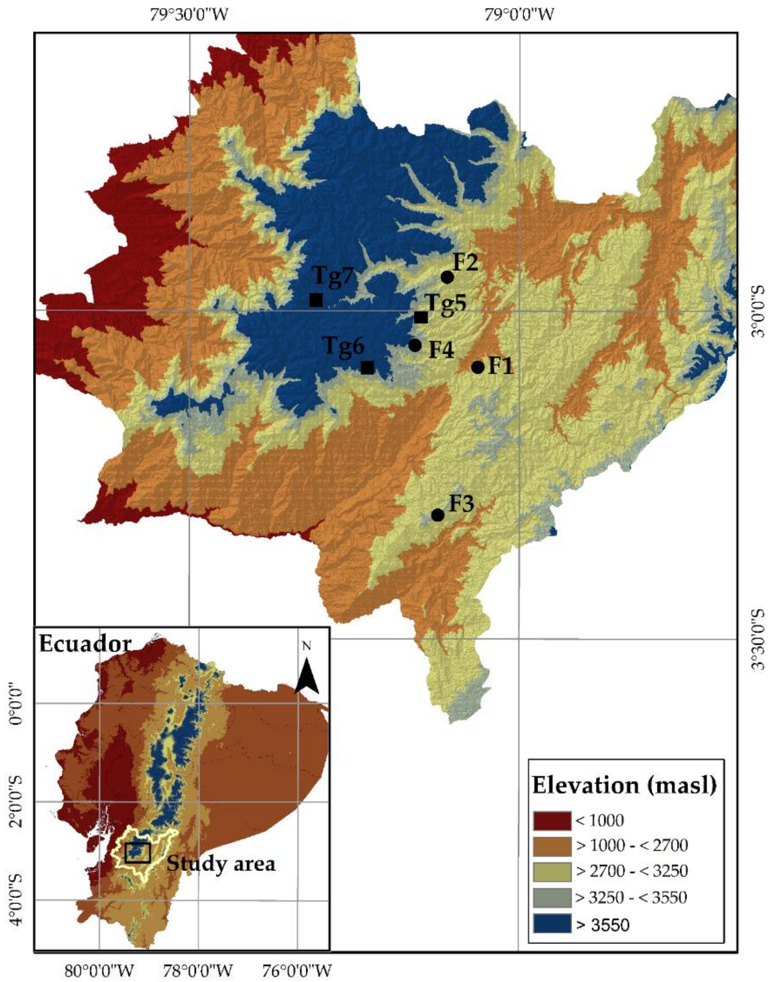

Figure 1. Study area and sampling sites in Azuay province, southern Ecuador. F = High montane forest; Tg = Páramo.

Climate at the study area is influenced by the Pacific coast regime and the Atlantic air currents [6,39]. Average annual solar radiation varies from 11.35 to 14.5 MJ m^{-2} day^{-1}, average daily temperature from 12.5 to 6 °C, and average annual precipitation from 900 to 1600 mm at elevations between 2600 and 4100 m a.s.l. [26,40]. The climate regime is bimodal with a rainy season from December to January and a less rainy season from August to September [41]. Rainfall variation is controlled by elevation and topographic parameters [12,26]. The geological material in southern Ecuador corresponds mainly to the Tarqui, Turi, and Saraguro mountain formations, which date back to the Miocene in the Neogene period. These formations are composed of a wide variety of lithological andesite rocks, ash-flow tuffs, pyroclastic flows and volcanic rocks [42].

Andosol soils of volcanic origin predominate within the study area; their depth ranges from 0.12 to >2 m [7,14,43]. Andosols are known for their Andic surface horizon (Ah), characterized by low BD [44], high porosity [11], high K_{sat}, and a SOM content that can exceed 40% [28,34]. This is why this horizon has a dark color, a high-water retention capacity [10,26,45], and controls to a certain extent the soil's water regulation capacity [4]. Land use consists mainly of two anthropogenic activities: (1) afforestation with pine (*Pinus patula* Seem.) [14] and (2) conversion to permanent grassland (*Lolium perenne* L., *Pennisetum clandestinum* Hochst. ex Chiov. and *Dactylis* sp.) or in some areas grazing on burnt grasslands [15,28].

2.2. Selection and Implementation of Study Sites

Seven study sites (Figure 1) expanding between 2705 and 3766 m a.s.l. were selected at three elevation zones: (1) F1 and F2, located below 3250 m a.s.l. corresponding to the high montane forest ecosystem; (2) F3, F4, and Tg5, located between 3250 and 3550 m a.s.l. representing the transition zone between high montane forest and páramo; and (3) Tg6 and Tg7 located above 3550 m a.s.l. being occupied by páramo.

These sites were selected given that they presented intervened zones afforested with pine and converted to grass land nearby undisturbed natural cover zones, all possessing similar topographic and edaphic conditions. We considered undisturbed natural cover in high montane native forest (F) as those sites covered with tree species having a tilted growth, accompanied by a high density of epiphytes and moss, as well as leaf litter accumulation in the ground [36]. In the páramo (Tg), we considered areas with tussock grass >50 cm high and without the presence of anthropogenic intervention indicator-plants, such as *Lachemilla orbiculata* (Ruiz & Pav.) Rydb. [8], as undisturbed natural cover. Information was collected from pine plantations and grazing areas through field visits and interviews with the landowners [46]. At each pine plantation, the previous land-use, management, plantation age, and the slope of the land, were registered. In the case of grazing, the previous land-use, pre-tilling, and tilling activities, the slope (Sl) of the land, the age of pastures, as well as the animal load (reported as adult bovine units per hectare, ABU Ha^{-1}), were registered. A total of 17 plots with a dimension of 24 $\times$ 24 m were implemented over the 3 elevation zones, with the exception of a grazing plot in the F4 transition band between high montane forest and páramo due to the complex topographical situation, very much different from the topography of undisturbed natural cover at this elevation band. The location (geographical coordinates and elevation) and slope (Sl) of each plot, and the density or number of trees per plot (SD) were determined. The diameter at breast height (DBH), height (Ht) and canopy diameter (CD) of each tree were also measured using a tape measure and a hypsometer.

2.3. Soil Properties Characterization

A first step in the soil characterization was limited to a qualitative description of the soils in the undisturbed natural cover plots following the Food and Agriculture Organization of the United Nations-guide [47]. The qualitative description focused on the surface horizon and included measurement of the thickness, the number of roots per dm^2, and the structure and texture by touch. A disturbed soil sample (0.5 kg) was collected in the layer 0–10 and 10–25 cm for physical and chemical analysis. In a second prospection and sampling phase the soil hydro-physical properties and SOM content of the 0–10 and 10–25 cm surface layers of the areas with undisturbed natural cover and the areas with impacts of pine afforestation and grazing were determined. Only these two surface layers of the profile were considered since they represent the zone with highest root density and influence of tilling activities. At each surface layer of each undisturbed natural cover and grazing plot, two undisturbed soil samples (100 cm^3 Kopecky rings) were randomly collected together with a disturbed sample of 0.5 kg. In the case of pine plots, the samples were taken at a distance of 75 and 150 cm from the tree trunks. The tree selection was random with a number of 3 trees per plot. At a similar density, K_{sat} was measured by means of the inverted auger-hole method [48] (3 repetitions per site, data shown represent the average of the repetitions). To avoid the effect on the measurement of the water-filled auger below 10 and 25 cm, respectively, the bottom of the upper and lower top layer, a plastic pipe with closed bottom was inserted in the auger holes after saturation of the soil. This enabled measuring subsequently the saturated horizontal hydraulic conductivity of both surface layers. Given the overall low bulk density of the organic top layers the soil can be considered isotropic, assuming that the vertical and horizontal saturated hydraulic conductivity are similar.

2.4. Laboratory Analyses

The disturbed samples taken during the qualitative characterization of the soil in the undisturbed natural plots were dried at room temperature (<30 °C) and passed through a 2-mm sieve. The color, pH, and SOM content were determined; the soil color was determined on wet samples using the Munsell color table. The pH was measured with a potentiometer on a 1:2.5 soil:distilled water solution [49], and the SOM content was determined through ignition of the soil at 410 °C for 16 h [50]. The BD and water retention capacity at pressure heads above field capacity were determined on undisturbed samples and are reported as pF values (or the logarithms of the negative pressure heads) corresponding to pF 0 (saturation point; pressure 1 cm H_2O), pF 0.5 (pressure 3.1 cm H_2O), pF 1.5 (31 cm H_2O) and pF 2.52 (field capacity; pressure 330 cm H_2O). Water content at saturation was considered as a proxy of porosity. Disturbed sieved soil was used for the measurement of the water retention below field capacity at pF 3.4 (2509 cm H_2O) and pF 4.2 (wilting point; 15300 cm H_2O), and the SOM content. The equipment used for the measurement of water retention was composed of sandboxes (pFs 0.5–1.5) [51] and two pressure chambers (low pressure for pF 2.52 and high pressure for pFs 3.4 and 4.2; Soilmoisture Equipment Corp., Goleta, CA, USA) [49]. Gravimetric water contents were transformed into volumetric contents. Gravitational water (GW) and water available for plants (AW) were calculated as the difference between the soil water contents at pF 0 and pF 2.52 and at pF 2.52 and pF 4.2, respectively. BD and pF at saturation were considered as proxies for soil compaction.

2.5. Statistical Analyses

For the characterization of the pine plantations and vegetation in the grazing plots and the soils in all three land uses, the median and the 25 and 75 percentiles of the distributions were defined given the lack of normality in most of the datasets as evidenced by the results of the Shapiro-Wilk test ($p < 0.05$). To define if elevation and differences in site as well as sampling depth have an impact on the interpretation of observations, a Spearman correlation analysis ($p < 0.05$) was performed between elevation, hydro-physical properties, and SOM content measured respectively at 0–10 and 10–25 cm depth under undisturbed natural cover. Subsequently, the soil properties located at the same elevation and depth were compared among the seven study sites. To this end, we applied non-parametric Kruskal-Wallis test [52] ($p < 0.05$) given the lack of normality in the datasets. If significant differences were identified, the Nemenyi post hoc test [53] ($p < 0.05$) for multiple pair comparisons was performed. The Mann-Whitney *U* test [54] ($p < 0.05$) was applied to evaluate differences in properties between the depth of 0–10 cm versus 10–25 cm.

The soil characteristics of the 0–10 and 10–25 cm soil layers of the land-use-change affected plots were compared to the same characteristics determined in the undisturbed natural cover plots to assess if the soil properties in high Andean ecosystems were affected by pine afforestation and grazing. In the pine afforested plots, first a screening was made between the properties measured at 75 and 150 cm from the trunk. The datasets were grouped if no significant differences were detected. Similarly, comparisons between the measured characteristics were made for both sampling depths (0–10 cm and 10–25 cm). Comparisons were made using the Mann-Whitney *U* test ($p < 0.05$). For a better interpretation of the impacts of afforestation, the relationship between the development of pine plantations and the soil properties was analyzed by means of the Spearman correlation analysis and linear regression ($p < 0.05$). Those analyses were performed on the variables of all trees with the hydro-physical soil properties and SOM content at both depths. The variables that did not present a normal distribution prior to the linear regression analysis were transformed to a normal distribution by Box-Cox method [55]. An analogue approach was followed to assess the impact of grazing. Per study site, soil characteristics at both depths at undisturbed natural cover and grazing plots were compared using the Mann-Whitney *U* test ($p < 0.05$).

To better identify and visualize the impacts of pine afforestation and grazing, forest plot graphs were built based on the differences of the medians of the pine plantations (Xtrat) vs. the undisturbed natural cover (Xcn) [56]. For grazing (Xtrat), the same procedure was followed; the differences were transformed into percentages as described by the following equation [56]:

$$\text{Effects } (\%) = [(\text{Xtrat} - \text{Xcn})/\text{Xcn}] \times 100 \quad (1)$$

Positive percentages represent an increase in the soil properties due to pine afforestation or grazing, while negative percentages represent a decrease, except for the BD. All statistical analyses were carried out by using the R program, version 3.3.2 [57].

3. Results

3.1. General Description of the Experimental Sites

In the following description of the pine afforested and grazing sites, there is always reference made to the previous land-use and/or native vegetation, as to highlight the changes introduced by respectively the introduction of pine plantation and the occupation of the land by cattle.

Table 1 presents the general characteristics of the pine plantations in the different study sites. The F1Pi, F2Pi and Tg6Pi plantations were established on sites where previous land-use comprised native vegetation cover. The slope on those sites varied from 43 to 20, and 22%, respectively. The F3Pi, F4Pi, and Tg7Pi plantations were established on sites where extensive-grazing had taken place for more than 5 years with an animal load <1 ABU Ha^{-1}. These plantations had a slope of 12%, 16%, 34% and 20%, respectively. The majority of the plantations were 16 to 19 years old, except in the F1Pi and Tg5Pi sites where the age of the trees varied between 20 and 29 years. The number of trees per plot (SD refers to the number of trees per 576 m^2) varied from 30 to 49 trees. The SD on the F1Pi, Tg6Pi, and Tg7Pi sites was smaller and varied between 30 and 34 trees. F2Pi, F3Pi, F4Pi and Tg5Pi had a greater SD (40–49 trees) (Table 1). Tree development was greater at F1Pi, F2Pi and Tg7Pi with a diameter at breast height (DBH) >18 cm, a tree height (Ht) >9 m, and a canopy diameter (CD) $\geq$5 m. The pine trees had slower growth in the Tg5Pi, Tg6Pi and Tg7Pi plantations, with an average DBH <18 cm, a Ht <8.5 m and a CD <5 m. In general, the management of the plantations was deficient because of the high associated costs; the F1Pi, F2Pi, Tg5Pi and Tg7Pi plantations did not receive any kind of management, while the only intervention in the F3Pi, F4Pi and Tg6Pi sites was the sporadic pruning of the trees.

Table 2 provides a general description of the grazing activity on each site controlled by cattle farming. Grazing takes place primarily on established sites with introduced grasses (G) (F1G, F2G, F3G, Tg6G and Tg7G) except on the Tg5G * site where the cattle grazed the native cover of tussock grass (G *). In all cases, the previous land use corresponded to native vegetation. The type and intensity of pre-tillage and management tasks were different at each site (Table 2). The age that land was converted to pasture was greater than 10 years in F1G and F2G, unlike F3G, Tg6G and Tg7G where it was shorter, between 3 and 7 years. In Tg5G *, the grassland renewal time was <3 years because of burning. Extensive grazing took place at the Tg5G *, Tg6G and Tg7G sites, with an animal load between 0.5 and <0.2 ABU Ha^{-1}, while in F1G, F2G and F3G grazing was intensive with an animal load between 1 and 2 ABU Ha^{-1}.

Table 1. General description and median values of the dendrometric variables in the pine plantations (Azuay province, southern Ecuador).

Elevation Range (m a.s.l.)	Code	Elevation (m a.s.l.)	Previous Land-Use	Sl (%)	Age (years)	SD (# of trees/plot)	DBH (cm)	Ht (m)	CD (m)	Management
<3250	F1Pi	2770	Native forest	43	29	34	25.6	19.4	5.1	Without management
	F2Pi	3260	Native forest	20	18	40	20.2	11.3	5.2	Without management
>3250–<3550	F3Pi	3359	Tussock grass subjected to equine grazing	12	17	49	18.4	8.8	5.15	Pruning
	F4Pi	3408	Tussock grasses subjected to bovine grazing	16	16	41	23.1	9.2	5	Pruning
	Tg5Pi	3485	Soils under extensive bovine grazing in burnt tussock grasses pasture.	34	21	47	16.8	8.3	3.88	Without management
>3550	Tg6Pi	3692	Tussock grass	22	19	33	8.75	4.45	1.58	Pruning
	Tg7Pi	3724	Compacted and eroded soil due to bovine grazing in burnt tussock grass	20	17.5	30	11.99	5	2.99	Without management

Legend: FxPi = pine plantation in high montane forest; TgxPi = pine plantation in the páramo; where x = 1–7 indicates sites 1–7; Sl = slope; SD = number of trees per 576 m^2 plot; DBH = diameter at breast height; Ht = tree height; CD = canopy diameter.

Table 2. General description of the grazing sites.

Elevation Range (m a.s.l.)	Code	Elevation (m a.s.l.)	Previous Use	Pre-Tilling and Tilling Activities	Grassland Age (years)	Grass	Animal Load (ABU Ha^{-1})
<3250	F1G	2836	Native forest	Preparation through ploughing, liming, and organic fertilization	>10	*Pennisetum clandestinum*	1
	F2G	3211	Native forest	Preparation through plowing, organic and inorganic fertilization, and pastures irrigation and rotation	>10	*Dactylis* sp., *Trifolium* sp. and *Lolium* sp.	2
>3250–<3550	F3G	3330	Native forest	Forest logging and burning, solid preparation was made using plowing discs	3	*Dactylis* sp. and *Pennisetum clandestinum*	1
	Tg5G *	3477	Tussock grass	Tussock grass burn	<3	*Calamagrostis intermedia*	<0.2
>3550	Tg6G	3628	Tussock grass	Vegetable cover cleaning, soil preparation through plowing and poultry fertilization	5	*Lolium* sp.	0.5
	Tg7G	3755	Tussock grass	Ground preparation through harrow and adding of vegetal material into the soil	7	*Lolium* sp. and *Dactylis* sp.	0.4

Legend: FG = Grazing in high montane forest; TgG = Grazing in the páramo; TgG * = Tussock grass altered by burning and grazing; ABU Ha^{-1} = Adult bovine unit per Ha and per year.

3.2. Soil Properties in Undisturbed Natural Cover Sites

The soils in most of the study sites (F2–Tg7) are identified as Andosols (>80%), except in F1 where they were identified as Cambisols. The deepest soils corresponded to the high montane forest sites (0.73–>2.28 m), while the shallower soils are in the páramo (0.46–1.67 m). The thickness of the surface horizon in the Andosols (Ah) varies from 34 to 106 cm, whereas in the páramo the surface horizon was less thick than 55 cm (Table 3). The root density in this horizon was lower in high montane forest sites (10–64 roots dm^{-2}) than in the páramo (30–200 roots per dm^{-2}). In both ecosystems, the Ah horizon is black (10YR 1.7/1 to 7.5YR 1.7/1), with a high SOM content (11.38%–42.49%), pH values ranging slightly from acidic to very acidic (6.32 to 4.89), and a structure between granular to block (Table 3). The texture ranged from loam to clay loam in the high montane forest and from loam to loamy silt in the páramo. The surface horizon in the Cambisols (A) is characterized by a thickness ranging between 36 and 50 cm, low root density (11–33 roots dm^{-2}), a brownish color (7.5YR 3/2–10YR 2/2), relatively low SOM content (7.09%–14.75%), and an acidic pH (4.58–5.64). Its texture is intermediate to fine, and the structure ranges from block-like to granular (Table 3).

Table 3. Morphological characteristics of the superficial horizons of the soils in the natural undisturbed land cover areas (F = High montane forest; Tg = Páramo).

Elevation Range (m a.s.l.)	Site Code	Type of Horizon [a]	Horizon Thickness (cm)	Number of Roots by dm^{-2}	pH	SOM [b] (%)	Structure [c]	Texture [d]
<3250	F1	A	36–50	11–33	4.58–5.64	7.09–14.75	B-Gr	Fac-FacAr
	F2	Ah	34–106	30–200	4.89–5.72	17.08–39.63	B-Gr	F
>3250–<3550	F3	Ah	44–82	10–40	5.05–5.23	13.53–16.11	Gr-B	F-Fac
	F4	Ah	50–57	32–64	5.06–5.19	19.58–29.85	Gr	Fac
	Tg5	Ah	38–45	50–100	5.69–6.32	20.98–37.50	Gr-B	FL-F
>3550	Tg6	Ah	28–55.5	84–>200	5.00–5.49	40.15–42.49	Gr	Fac-FL
	Tg7	Ah	20–38	30–110	5.08–5.82	11.38–23.71	Gr	F-FL

Legend: [a] A = Folic horizon; Ah = Andic horizon; [b] SOM = Soil organic matter content; [c] Gr = Granular; B = Block; [d] F = Silt; FL = Loamy silt; Fac = Loamy clay; FacAr = Loamy clay sand.

The hydro-physical properties and SOM content of the 0–10 cm and 10–25 cm soil layer, of the 20 study sites are listed in the Appendix A (Table A1 depicts the data for the undisturbed natural cover areas, Table A2 illustrates the same data for the pine afforested sites, and Table A3 for the pasture sites). Those tables show the median and 25 and 75 percentile value for each of the soil layers and 11 soil parameters evaluated. As revealed in Table A1, depicting for each depth the parameter values for the 7 sites in undisturbed natural cover area, the Kruskal-Wallis test ($p < 0.05$) showed significant differences between pairs of study sites. Also, the Nemenyi post-hoc test showed significant differences in the characteristics of the 0–10 cm surface layer. For example, K_{sat} values in the F1 and F3 sites in the high montane forest were higher than (12.91 and 17.30 cm h^{-1}) and differed significantly from the K_{sat} in the Tg6 and Tg7 sites situated in the páramo (1.38 and 1.92 cm h^{-1}). The water retention capacity between pF 0 and pF 2.52 was lower for F1, F2 and F3 (<0.73 cm^3 cm^{-3} at pF 0 and <0.52 cm^3 cm^{-3} at pF 2.52), differing significantly from the respective values for Tg6 (0.85 cm^3 cm^{-3} at pF 0 and 0.66 cm^3 cm^{-3} at pF 2.52). The highest contents of GW were found for F2 and F3 (0.21 and 0.24 cm^3 cm^{-3}, respectively), whereas the lowest was identified at Tg5 (0.11 cm^3 cm^{-3}). On the other hand, the AW content for F1 and F2 were the lowest (0.08 and 0.11 cm^3 cm^{-3}, respectively), whereas the highest was for the Tg7 site (0.25 cm^3 cm^{-3}). In addition, for the BD, water retention capacity at pF 3.4 and pF 4.2, and SOM content, significant differences were recorded regardless of the type of ecosystem. For example, the water retention capacity at pF 3.4 and pF 4.2 in Tg6 was significantly higher than in Tg7 even though both are located in the páramo.

The differences between study sites are smaller at a depth of 10–25 cm. The high montane forest sites presented higher K_{sat} values than the soil in the páramo plots. Important differences were observed in F1 (2.98 cm h^{-1}) against Tg5, Tg6 and Tg7 which are characterized by lower K_{sat} values (<0.46 cm h^{-1}). The highest volume of GW was found in F3 (0.24 cm^3 cm^{-3}), much different from the low GW volume in Tg5 (0.11 cm^3 cm^{-3}). The AW values of the F1 (0.06 cm^3 cm^{-3}) and F3 (0.06 cm^3 cm^{-3}) sites were significantly lower with respect to the AW values in the Tg5 and Tg6 sites (0.20 and 0.21 cm^3 cm^{-3}, respectively). Similarly, the water retention capacity in the tension range of pF 0 to pF 3.4, and the SOM content of the sites showed significant differences, regardless of the ecosystem type (Appendix A: Table A1). On the other hand, the water retention capacity at wilting point (pF 4.2) did not show significant differences among the different study sites. Furthermore, at each study site the top layer (0–10 cm) presented higher values for K_{sat}, water retention (pF 0 to 2.52), GW, AW, and SOM as compared to the values of the same properties measured in the second layer (10–25 cm), except for the BD, which increased. According to the Mann-Whitney *U* test ($p < 0.05$), K_{sat} differed significantly between the two depths at each study site (Appendix A: Table A1). Likewise, BD increased significantly in the second soil layer at the F1, F3, Tg6 and Tg7 sites. The water retention capacity at pF 0 was greater in the 0–10 cm soil layer and tended to decrease significantly in the layer below (10–25 cm below surface) on the F1, F3 and Tg6 sites (Table 3). Correlation of the median parameter values and the elevation of the sites, using the Spearman test, showed that most of the parameters and SOM content were strongly correlated with the elevation (Table 4). The strongest correlations were found for the surface layer (0–10 cm), reflecting a negative correlation of the elevation with K_{sat} ($\rho = -0.74$, $p < 0.05$) and a positive correlation with the water retention capacity in the tension range of pF 0 to pF 2.52 ($\rho = 0.66$–0.71, $p < 0.05$), as well as with the AW ($\rho = 0.73$, $p < 0.05$). The hydro-physical properties and SOM content in the 10–25 cm layer showed weaker correlations with elevation, with the exception of K_{sat} ($\rho = -0.66$, $p < 0.05$).

Table 4. Spearman correlation coefficients (ρ) between elevation and the hydro-physical properties and SOM content of the soil layer at 0–10 cm and 10–25 cm in the undisturbed natural cover areas.

Properties (0–10 cm)	ρ	Properties (10–25 cm)	ρ
K_{sat} 1 (cm h^{-1})	−0.74 *	K_{sat} 2 (cm h^{-1})	−0.66 *
BD 1 (g cm^{-3})	−0.29 *	BD 2 (g cm^{-3})	−0.15
0pF 1 (cm^3 cm^{-3})	0.68 *	0pF 2 (cm^3 cm^{-3})	0.34 *
0.5pF 1 (cm^3 cm^{-3})	0.66 *	0.5pF 2 (cm^3 cm^{-3})	0.33 *
1.5pF 1 (cm^3 cm^{-3})	0.71 *	1.5pF 2 (cm^3 cm^{-3})	0.28 *
2.52pF 1 (cm^3 cm^{-3})	0.70 *	2.52pF 2 (cm^3 cm^{-3})	0.23
3.4pF 1 (cm^3 cm^{-3})	0.08	3.4pF 2 (cm^3 cm^{-3})	−0.19
4.2pF 1 (cm^3 cm^{-3})	0.04	4.2pF 2 (cm^3 cm^{-3})	−0.11
GW 1 (cm^3 cm^{-3})	−0.27 *	GW 2 (cm^3 cm^{-3})	0.11
AW 1 (cm^3 cm^{-3})	0.73 *	AW 2 (cm^3 cm^{-3})	0.37 *
SOM 1 (%)	0.32 *	SOM 2 (%)	0.20

Legend: K_{sat} = saturated hydraulic conductivity; BD = bulk density; 0–4.2 pF = water retention capacity at pF 0 to pF 4.2; GW = gravitational water; AW = available water; SOM = soil organic matter content; 1 = 0–10 cm depth; 2 = 10–25 cm depth; * = significant correlations ($p < 0.05$).

3.3. Changes in Hydro-Physical and SOM Content under Pine Afforestation

The properties found at each of the pine afforested and grazing sites in the 0–10 and 10–25 cm soil layers are presented in the Appendix A, in Table A2 (pine plantation) and Table A3 (grazing). According to the Mann-Whitney *U* test ($p < 0.05$), the properties in the pine plantations in the 0–10 cm layer were significantly different from the characteristics measured in the 10–25 cm soil layer. Therefore, the impacts of pine afforestation were evaluated considering both depths. On the other hand, there were no significant differences ($p > 0.05$) in the properties between sampling distances (75 and 150 cm) from the trees in each of the pine plantations (Table A4), suggesting that sampling could have been carried out at either of these distances. Therefore, the properties' values measured at a distance of 75 and 150 cm from the tree trunk were grouped by depth.

Pine afforestation produced significant changes in the hydro-physical properties and SOM content in both layers as depicted in the forest plots of Figure 2 and Appendix A Table A2. K_{sat} of the upper layer decreased significantly in the F1Pi and F3Pi plantations (61.72% and 79.06%, respectively), which are located in the high montane forest area. In the páramo plantations, the K_{sat} value increased significantly in two of the three plantations (Tg5Pi and Tg6Pi) by 25.23 and 59.22%, respectively (see Figure 2a). The BD value did not show significant changes in most of the sites except for F3Pi which increased significantly by 18.42% (Figure 2b). As further depicted in Figure 2c, the water retention capacity at saturation (pF 0) in the upper layer decreased significantly in the F1Pi, F3Pi, Tg6Pi and Tg7Pi sites, with a reduction between 2.53% and 11.10%, while in F2Pi the water content at saturation increased significantly by 6.30% (Figure 2c). The changing tendency in water retention capacity in the pF range from 0.5 to 2.52 (see Figure 2d–f) was similar to the change in the water retention capacity at pF 0 in most of the plantations, supporting the conclusion that pine afforestation led to significant changes in the soil's hydro-physical properties. The water retention capacity at pF 3.4 and pF 4.2 (Figure 2g,h) decreased meaningfully between 12.21% and 27.52% in the F1Pi, F4Pi, and Tg6Pi sites, but differently in the Tg7Pi site where the increase was significant, varying between 15.54% and 44.31%. The GW in F4Pi, Tg5Pi and Tg6Pi increased significantly (13.15%–39.37%) (Figure 2i), while AW decreased considerably in F3Pi and Tg7Pi, with a reduction varying between 42.50% and 57.64%, (Figure 2j). The SOM content in F1Pi, F2Pi and F3Pi decreased considerably, by 28.97%, 29.00% and 47.90% (Figure 2k); while in Tg7Pi the SOM content was significantly reduced by 77.62%.

The K_{sat} increased significantly in the 10–25 cm layer in the F1Pi, F2Pi, Tg5Pi and Tg6Pi sites by 84.64%, 30.28%, 305.24% and 140%, respectively; while in F3Pi the K_{sat} was significantly reduced by 52.98% (Figure 2a). There was a significant increase of BD in F3Pi (9.81%), in contrast to Tg7Pi where there was a significant reduction of 2.47% (Figure 2b). Regarding the water retention capacity at saturation, F1Pi declined significantly by 10.62%, contrasting with F2Pi and Tg7Pi where there was a significant increment by 9.60% and 6.32%, respectively (Figure 2c). Similar results were obtained for water retention capacity in pF 0.5 to pF 1.5 (Figure 2d,e). Water retention at field capacity decreased significantly in F1Pi, F3Pi and Tg6Pi by 18.92%, 5.68% and 2.2%, respectively, whereas it increased significantly at F2Pi by 9.06% (Figure 2f). The retention capacities at pFs 3.4 and 4.2 decreased significantly between 2.62% and 30.35% at sites F1Pi and F4Pi (Figure 2g,h); whereas they increased significantly between 3.90 and 25.56% at site Tg7Pi. The GW did not show significant changes in any of the plantations. AW in the F2Pi and F4Pi plantations presented a significant increase of 51.55% and 79%. The SOM content in F1Pi, F2Pi and F3Pi decreased considerably by 55.50%, 9.32% and 23.50%, respectively, differently from Tg7Pi where there was a significant increase by 77.62% (Figure 2k).

Correlation analysis revealed that K_{sat} in the 0–10 cm and 10–25 cm layers presents strong correlations with tree development variables DBH, Ht and CD, and there is clearly an increase of K_{sat} with increasing tree height (data not shown). Likewise, the BD in both layers was also positively correlated with the tree development variables ($\rho \geq 0.31$, $p < 0.05$). That is to say, with an increase in tree growth, there is a significant increment in soil BD. On the other hand, water retention capacity and SOM contents are negatively correlated with tree development variables ($\rho \geq 0.31$, $p < 0.05$). That is, in both soil layers (0–10 and 10–25 cm), water retention capacity and SOM content decrease significantly with tree development.

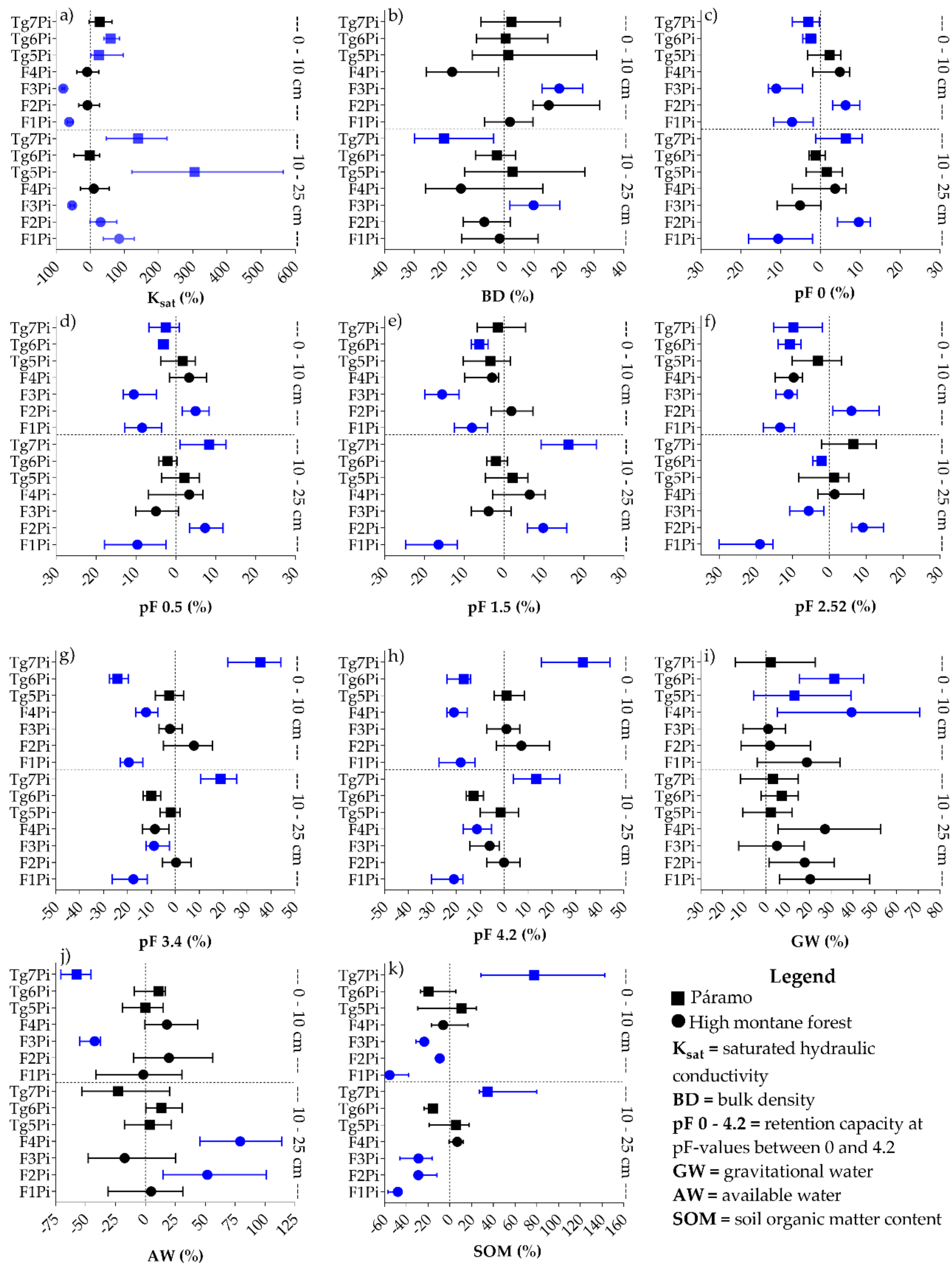

Figure 2. Forest and páramo plots showing the percentage change in hydro-physical properties and SOM content (increase or decrease) of the soils' surface horizons (0–10 and 10–25 cm) due to pine afforestation. Site codes: FPi = pine plantation in the high montane forest; TgPi = pine plantation in páramo. Blue-colored lines represent a significant change ($p < 0.05$) and black-colored lines represent a non-significant change ($p > 0.05$) in the variable.

3.4. Changes in Hydro-Physical and SOM Content under Grazing

The Mann-Whitney *U* test ($p < 0.05$) revealed significant changes in the soil's hydro-physical properties under grazing, which was reflected mainly in the K_{sat} and water retention capacity (Appendix A: Table A3). There were a higher number of sites with significant changes in the studied soil hydro-physical properties in the 0–10 cm surface layer, than in the 10–25 cm soil layer (Figure 3). In the upper layer, K_{sat} decreased significantly in the F1G and Tg5G * sites by 68.87% and 75.75%, respectively, while there was a significant increase of 55.19% in Tg6G (Figure 3a). With respect to the BD in F2G and F3G, there was a significant increase of 64.29% and 28.25% (Figure 3b). The water retention capacity at saturation in F3G and Tg6G decreased significantly by 10.10% and 5.18%, respectively, while it increased significantly by 8.97% in Tg5G * (Figure 3c). The changes in water retention capacity at pF 0.5 and pF 1.5 were similar to those at pF 0 (Figure 3d,e). Water retention capacity at pF 2.52 decreased significantly in the F3G, Tg6G and Tg7G sites by 13.11%, 8.61% and 9.77%, respectively. On the other hand, there was a significant increment of 10.46% at F2G (Figure 3f). The water retention capacity at pF 3.4 increased significantly at the sites F2G, Tg5G * and Tg7G by 17.38%, 6.15% and 20.46%, respectively. Conversely, the water retention at field capacity decreased by 7.36% in F3G. The changes in water retention at wilting point (pF 4.2) were similar to those at pF 3.4 (Figure 3g,h) at the sites with significant changes, except for F3G. Changes in GW (Figure 3i) were noticed in the Tg6G and Tg7G sites, with an increase of 10.59% and 36.12%, respectively. The AW (Figure 3j) and the SOM content (Figure 3k) did not show significant changes in the majority of the study sites, except the for SOM content in site F3G where there was a significant reduction of 30.47%.

In the soil layer 10–25 cm, K_{sat} decreased significantly by 71.01% in the F1G site, by 1120.09% in F3G, by 121.28% in Tg6G, and by 61.35% in the Tg7G site (Figure 3a). The BD did not show significant changes in the grazing sites, except for Tg7G where it decreased significantly by 18.63% (Figure 3b). The water retention capacity at pF 0 increased significantly by 10.71%, 4.67% and 9.57% in the F2G, Tg5G * and Tg7G sites (Figure 3c). At these sites, the trends followed by the changes in water retention capacity at pF 0.5 and pF 1.5 were similar to those at pF 0 (Figure 3d,e). At pF 2.52, the water retention capacity at F2G and Tg5G * increased significantly by 19.17% and 5.92%, respectively (Figure 3f). The water retention capacity at pF 3.4 increased significantly by 12.92% at site F2G, unlike F3G where a significant reduction of 13.78% was found (Figure 3g). Most sites did not display significant changes in the water retention capacity at wilting point, except for F3G, where there was a significant reduction of 12.06% (Figure 3h). Finally, GW, AW, and the SOM content did not show significant changes at all study sites (Figure 3i–k).

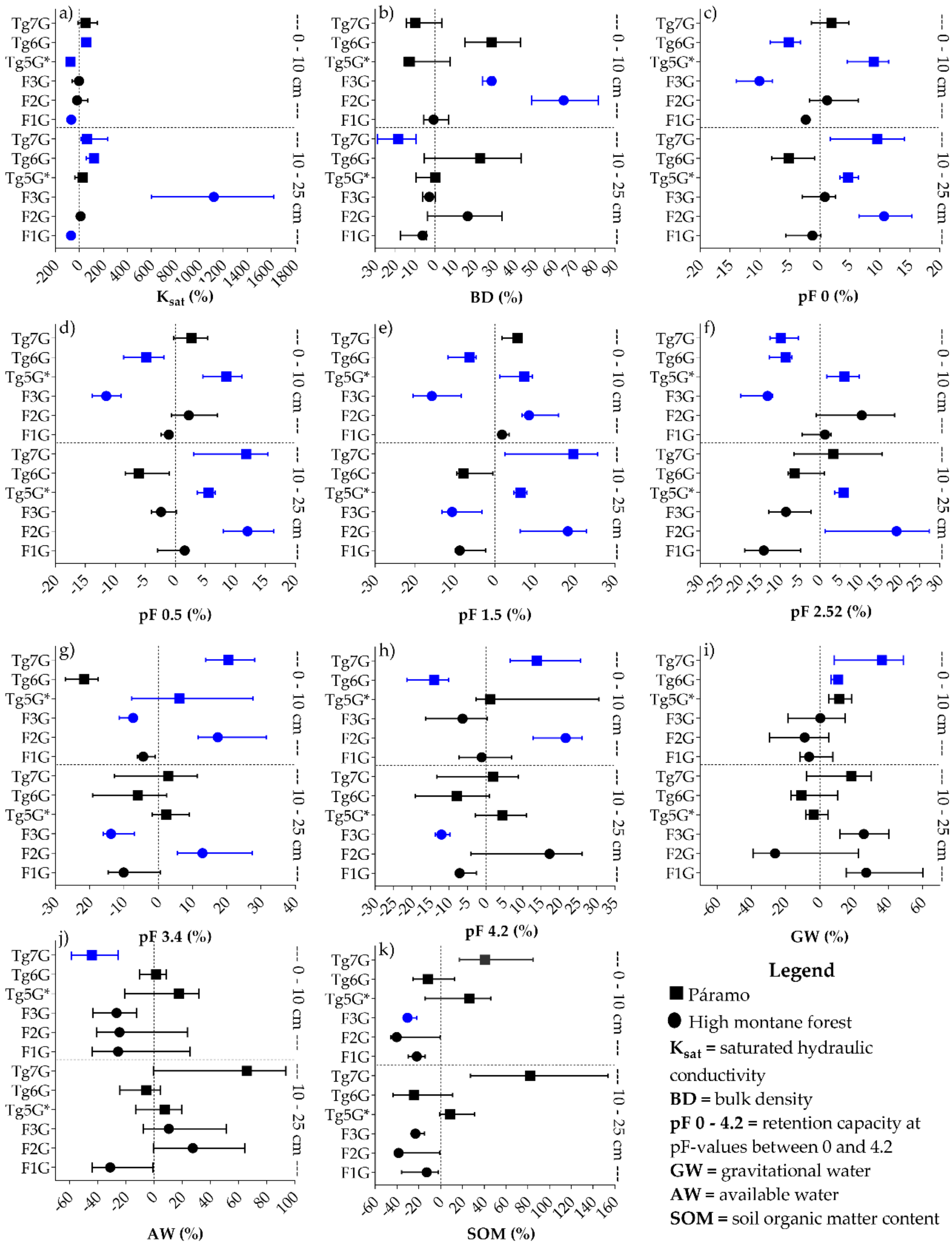

Figure 3. Forest and páramo plots showing the percentage change in the hydro-physical properties and SOM content (increase or decrease) of the soils' surface horizons (0–10 and 10–25 cm) due to grazing. Site codes: FG = grazing in high montane forest; TgG = grazing in the páramo; TgG * = grazing in tussock grass subject to burning. Blue-colored lines represent a significant change ($p < 0.05$) and black-colored lines represent a non-significant change ($p > 0.05$) in the variable.

4. Discussion

Some studies in sites close to the study presented herein evaluated the impacts of anthropogenic activities by grouping soils by their conditions of natural undisturbed land cover, without considering their elevation and sampling depth [19,28,29]. In our study, results suggest that in order to evaluate the impacts of any anthropogenic activity, it is essential to examine the spatial variability of soils under natural conditions or at least to avoid evaluating the impacts based on sampling sites located in different places. In other words, the impacts of anthropogenic activities on soils should be done in adjacent sites, which would guarantee similar geomorphological and climatic conditions [58]. Even the spatial variability of soils is often the cause that the hydrological performance of Andean ecosystems can be extremely heterogeneous [26,59]. That is, the high variability of soils under natural conditions can even cause variability in the functioning of basins.

An aspect often discussed in monitoring the impact of afforestation on soils is at what distance from the trunk and what depth should samples preferably be collected. A previous study in Andean highlands suggested that changes in soil properties in pine plantations differ depending on the sampling distance from the trunk of the tree [15]. However, in all the plantations within our study area, the hydro-physical properties did not differ between the tested sampling distances of 75 and 150 cm away from the trunk. These results are consistent with what Wilcox, Breshears & Turin [60] and Ruiz et al. [61] reported. Wilcox et al. [60] stated that the K_{sat} of the soil under the canopy and between the canopy of the pine trees did not show significant differences. Likewise, Ruiz et al. [61] reported that the water retention capacity and AW in the soil did not differ between 50 cm from the base of the trunk vs. under the crown of the tree. On the other hand, according to our results, the hydro-physical properties and the SOM content showed significant differences between the two sampling depths (0–10 cm and 10–25 cm) in each of the plantations, a finding in line with the results of Ghimire et al. [62]. Our results suggest that pine afforestation effectively impacts in a different way the soil properties as a function of depth, but not as a function of the distance samples are collected from the tree trunk.

The comparisons of the properties of each plantation with their respective adjacent natural cover revealed that the intervention of the soils through, for example, pine afforestation in the Andean ecosystems mainly affects K_{sat}, water retention capacity between saturation (pF 0) and field capacity (pF 2.52), and SOM content, and this at both sampling depths but at a different intensity. Due to these changes, pine plantations could directly alter the ecosystem services such as water regulation and storage [25,26] and the carbon sequestration by soils [63]. However, findings could not be generalized, showing dependencies mainly in the sampling depth, ecosystem type, characteristics of the plantations, and previous land-use. This implies a complexity in assessing the impacts of plantations and limits the generalization capability of changes in soil properties caused by pine plantations in high Andean ecosystems.

According to Alarcón et al. [64], changes due to grazing were not statistically evident in the K_{sat} measured in the 0–10 cm soil layer in Andosols. However, our results partially contradict this because 2 (F1G and Tg5G *) of the 6 study sites showed a significant reduction in K_{sat} up to 70%, while in the Tg6G site a significant increase of 52.67% was registered. The reduction in K_{sat} at the F1G site could be due to the loss of stability of the soil aggregates and grazing density, while the reduction in K_{sat} at Tg5G * is likely the consequence of the frequent burning of tussock grass resulting in a drying and crusting of the soil surface [65]. On the other hand, although the increase in K_{sat} was not significant at Tg7G, this percentage increase was very similar to that at the Tg6G site (Figure 3a). The increase at both these sites is likely related to preferential flows between the clods formed by soil tillage [66] during the preparation and sowing of pasture. However, this situation could apparently change over time due to the structural deterioration of the soil.

Despite the lack of significant evidence, it was observed that in 6 of the 7 pine plantations, BD tended to increase in the 0–10 cm soil layer, which certainly cannot be the consequence of the use of heavy machinery for maintenance since the associated high costs and the difficult topographic conditions prevent the use of machines [67]. Rather the drying of the soil by evapotranspiration [68] and the weight of the trees [69] are responsible for the increase in BD, which is confirmed in our study by a greater increase in BD in the sites where the pine plantation is characterized by high SD and CD (e.g., F2Pi and F3Pi in high montane forest and Tg5Pi in páramo). The BD at 10–25 cm depth was not affected in most of the plantations; however, most plantations showed a decreasing trend ranging from 2% to 18%. This tendency is attributable to the increase of porosity generated by the pine subsurface root system. On the other hand, two plantations (F3Pi and Tg5Pi) showed an increase which is attributable to the compaction by the pressure exerted by the biomass of the plantation on the soil, due to its high SD, which translates into a greater number of trees, increasing the transpiration, and resulting in soil contraction.

The compaction of the soil by grazing is normally directly reflected in an increase of the BD [70,71]. However, this effect was only observed in two study sites (F2G and F3G) and the direct consequence of the greater grazing intensity at these sites (ABU Ha^{-1} of 2 and 1, respectively), parallel to a decomposition of SOM. Our findings are consistent with those of Donkor et al. [72] where an increase in compaction was directly related to a greater grazing intensity. In páramo, the trampling effect of cattle was not reflected in the measurements, which was consistent with the results of Alarcón et al. [64] and Podwojewski et al. [23]. Their results and our study suggest that Andosols (due to their high SOM content) have a greater resilience to compaction [73] given the overall low-grazing intensity (ABU Ha^{-1} of <0.5). Because of the lack of significant evidence, our results do not permit to conclude that grazing significantly compacted the soil at the 10–25 cm depth. This may be due to the high SOM content of the Andosols. In the case of Tg7G, where BD decreased significantly by 18.63%, this decrease is likely caused by the incorporation of tussock grass biomass during tillage.

Pine plantations alter the water retention capacity of soils according to Farley et al. [20]. This is confirmed by the results of this study, with the difference that the alteration is not only dependent on associated changes in the SOM content, but also on elevation, ecosystem type, the development level of the plantation and land-use, as reported in other ecosystems [56,63,74]. The highest reduction percentages in our study were attributed to a greater development of the plantations (DBH >18 cm, Ht >8 m and CD >5 m), together with a decrease in SOM and increase in BD. In the three plantations that were established on soils whose previous use was grazing (F4Pi, Tg5Pi and Tg7Pi), the changes in water retention capacity were very variable, observing significant increases or decreases between pF 0 and pF 2.52, notwithstanding the SOM content tended to increase. This variation in the changes could be due to a mixture of changes between the previous use of the soil and the growth of the plantation [61,74]. This apparent overlap of impacts [62] hinders generalization of changes. On the other hand, our data show an increase in water retention is not necessarily always related to an increase in SOM content, but can also be the consequence of an increase in clay content due to the weathering of the soil [75,76]. In general, pine afforestation goes hand in hand with an increase in GW and a decrease in AW, suggesting that soils under pine plantations rapidly lose moisture after a rainfall event, which further enhances soil drying and decomposition of SOM [77]. On the other hand, according to Buytaert et al. [22], land use change could increase the AW of soils of volcanic origin by 30%. On the contrary, Hofstede et al. [19] reported a decrease in AW as a consequence of pine afforestation. Nevertheless, in our study, only two pine plantations showed a significant decrease (F3Pi and Tg7Pi).

Under grazing, it has been shown that the loss of water retention is mainly a result of a reduction in SOM content. Increases in water retention capacity were explicitly related to increases in SOM content due to burning and/or the incorporation of tussock grass during soil preparation. This finding is in line with Daza et al. [32] who reported that in their study the decrease in soil water retention was due to a loss of SOM content. However, in the F2G site the increase of the water retention capacity was the result of the easy weathering of volcanic glass, leading to the formation of montmorillonite clay [76]. The latter indicates that in order to correctly assess changes in, for example, the hydro-physical properties in soils, it is essential to evaluate the full spectrum of soil properties such as SOM, soil texture, type of management, among others.

Notwithstanding that several studies associate the reduction of SOM content with pine afforestation [19,20,58], our findings indicate that pine plantations could help the recovery of SOM in the 0–10 cm soil layer of former grazing sites, though the effect seems also to depend on the elevation of the site and the SD of the plantation. Although the SOM content did not show significant changes under grazing, a reduction in most of the study sites was detected. This slightly decreasing trend would imply that, over time, the soils under grazing in the Andean region could lose a considerable amount of SOM, and thus, reduce their capacity to retain water.

5. Conclusions

Andosols with their black Andic horizon are the predominant soils in Andean montane ecosystems. Our research clearly revealed that this horizon, with high water retention capacity and SOM content, is not that uniform under natural unaltered conditions. Differences in hydro-physical properties, such as K_{sat} and the water retention capacity, are related to the type of ecosystem and elevation of the terrain. Differences in properties not only occur between sites, but also within sites at different depths of sampling. As a result, higher values of K_{sat}, water retention capacity and SOM content were recorded in the 0–10 cm surface layer. The natural spatial variability in environmental conditions and the accompanied heterogeneity in soil properties requires that for the correct assessment of the impact of land use change, data are collected on neighboring comparable, unaltered and altered sites. Doing so will facilitate and help guarantee that a correct assessment of the causal factors that positively or negatively affect the soil hydro-physical properties by land use change, is drawn. Furthermore, the multitude of observations and their analyses clearly revealed that the impact of land-use change on the hydro-physical soil properties is not unique and often masked by other factors such as the antecedent land-use, spatial variability, pre-tilling and tilling activities, soil texture, elevation, climate, among other site-specific factors. Due to these differences, it is rather difficult to evaluate the impacts of pine plantations and grazing on properties at regional scale, and therefore any evaluation of the impacts of anthropogenic activities must be carried out in adjacent sites, which would guarantee similar geomorphological and climatic conditions. This conclusion clearly points out that generalization of findings related to the impacts of land use change on soil properties is not free of risks. Similarly, it also hinders the comparison of findings with published results.

The study further revealed that pine afforestation affects either in a positive or negative way the K_{sat}, the water retention capacity in the range pF 0 to 2.52 and the SOM content of the soil surface layer. The change and the order of magnitude of the change varies with sampling depth. Similarly, grazing causes positive and negative changes in K_{sat} and in the water retention capacity, and as in pine plantations, the recorded changes vary with sampling depth. Other controlling factors that define the impact of grazing are evidently pre-tilling and tilling activities in combination with cattle density. Soil spatial heterogeneity and diversity in local factors complicates the interpretation and extrapolation of observed phenomena to Andean montane ecosystems at a regional scale. Correct assessment of land use change impacts is not only of crucial importance for extrapolating findings, it also serves as a basis for the accurate estimation of socio-economic and ecological impacts that anthropogenic-induced changes might have on the water regulation and water storage functionalities of the Andic soils.

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

Appendix A Appendix

Table A1. Median and the 25th and 75th percentile of the hydro-physical properties and SOM content of the soil in the undisturbed natural cover areas (Azuay province, southern Ecuador).

	Elevation	**<3250 m a.s.l.**		**>3250–<3550 m a.s.l.**			**>3550 m a.s.l.**	
	Properties	**F1**	**F2**	**F3**	**F4**	**Tg5**	**Tg6**	**Tg7**
0–10 cm soil layer	K_{sat} (cm h^{-1})	12.91 (9.34–20.55) Aa	4.92 (3.34–7.10) Aab	17.30 (12.70–19.18) Aa	7.26 (5.62–13.08) Aab	3.33 (2.47–4.12) Aab	1.38 (1.29–1.49) Ab	1.92 (1.65–2.82) Ab
	BD (g cm^{-3})	0.97 (0.95–1.00) Ba	0.38 (0.34–0.55) Ab	0.72 (0.67–0.78) Bab	0.67 (0.56–0.78) Aab	0.51 (0.43–0.64) Aab	0.32 (0.29–0.36) Bb	0.60 (0.59–0.63) Bab
	0 pF (cm^3 cm^{-3})	0.65 (0.63–0.66) Ab	0.71 (0.67–0.73) Ab	0.70 (0.68–0.71) Ab	0.72 (0.67–0.76) Aab	0.75 (0.70–0.79) Aab	0.87 (0.85–0.90) Aa	0.73 (0.72–0.75) Aab
	0.5 pF (cm^3 cm^{-3})	0.64 (0.58–0.66) Ab	0.69 (0.66–0.72) Ab	0.69 (0.67–0.70) Aab	0.70 (0.67–0.76) Aab	0.75 (0.70–0.79) Aab	0.85 (0.83–0.89) Aa	0.72 (0.71–0.73) Aab
	1.5 pF (cm^3 cm^{-3})	0.54 (0.52–0.56) Ab	0.60 (0.57–0.64) Ab	0.60 (0.57–0.61) Ab	0.65 (0.59–0.71) Aab	0.73 (0.68–0.77) Aa	0.81 (0.77–0.85) Aa	0.66 (0.64–0.69) Aab
	2.52 pF (cm^3 cm^{-3})	0.47 (0.46–0.49) Ab	0.49 (0.46–0.52) Ab	0.46 (0.45–0.47) Ab	0.60 (0.50–0.62) Aab	0.64 (0.60–0.66) Aa	0.69 (0.66–0.72) Aa	0.58 (0.55–0.59) Aab
	3.4 pF (cm^3 cm^{-3})	0.46 (0.43–0.46) Aab	0.40 (0.39–0.43) Bab	0.37 (0.36–0.38) Ab	0.49 (0.48–0.53) Aa	0.47 (0.46–0.48) Aab	0.55 (0.48–0.57) Aa	0.35 (0.30–0.39) Ab
	4.2 pF (cm^3 cm^{-3})	0.40 (0.34–0.44) Aab	0.36 (0.34–0.40) Bab	0.33 (0.32–0.35) Ab	0.47 (0.43–0.48) Aa	0.42 (0.40–0.45) Aab	0.48 (0.46–0.55) Aa	0.33 (0.26–0.35) Ab
	GW (cm^3 cm^{-3})	0.17 (0.13–0.18) Aab	0.21 (0.18–0.25) Aa	0.24 (0.23–0.27) Aa	0.14 (0.13–0.18) Aab	0.11 (0.11–0.12) Ab	0.18 (0.18–0.19) Aab	0.17 (0.14–0.18) Aab
	AW (cm^3 cm^{-3})	0.08 (0.04–0.13) Ab	0.11 (0.08–0.15) Ab	0.12 (0.11–0.14) Aab	0.14 (0.07–0.15) Aab	0.20 (0.17–0.25) Aab	0.21 (0.16–0.25) Aab	0.25 (0.22–0.30) Aa
	SOM (%)	10.16 (8.24–11.57) Ab	33.69 (31.06–37.66) Aa	15.36 (13.92–17.38) Aab	25.83 (20.64–31.61) Aab	20.57 (16.75–29.93) Aab	41.15 (29.49–47.22) Aa	15.47 (14.95–18.44) Aab
10–25 cm soil layer	K_{sat} (cm h^{-1})	2.98 (1.93–4.62) Ba	1.59 (0.92–2.07) Bab	1.84 (1.80–2.62) Bab	1.44 (1.20–2.46) Bab	0.17 (0.15–0.18) Bc	0.30 (0.29–0.31) Bbc	0.37 (0.34–0.46) Bbc
	BD (g cm^{-3})	1.18 (1.06–1.25) Aa	0.50 (0.41–0.58) Ab	0.92 (0.91–0.96) Aa	0.72 (0.68–0.80) Aab	0.56 (0.51–0.78) Aab	0.43 (0.35–0.44) Ab	0.88 (0.77–0.94) Aa
	0 pF (cm^3 cm^{-3})	0.60 (0.57–0.62) Bb	0.68 (0.64–0.70) Aab	0.62 (0.60–0.62) Bb	0.70 (0.67–0.73) Aab	0.74 (0.69–0.77) Aa	0.82 (0.81–0.84) Ba	0.63 (0.60–0.67) Ab
	0.5 pF (cm^3 cm^{-3})	0.58 (0.56–0.60) Ab	0.67 (0.63–0.69) Aab	0.61 (0.59–0.61) Bb	0.70 (0.66–0.73) Aab	0.73 (0.68–0.76) Aa	0.82 (0.81–0.84) Aa	0.61 (0.58–0.64) Bb
	1.5 pF (cm^3 cm^{-3})	0.54 (0.49–0.57) Ab	0.59 (0.57–0.64) Aab	0.52 (0.51–0.53) Bb	0.64 (0.62–0.67) Aab	0.71 (0.65–0.74) Aa	0.78 (0.77–0.81) Aa	0.53 (0.51–0.59) Bb
	2.52 pF (cm^3 cm^{-3})	0.49 (0.46–0.54) Aab	0.52 (0.50–0.57) Aab	0.41 (0.39–0.43) Bb	0.57 (0.56–0.64) Aab	0.63 (0.58–0.66) Aa	0.67 (0.66–0.68) Aa	0.46 (0.41–0.50) Bb
	3.4 pF (cm^3 cm^{-3})	0.45 (0.44–0.49) Aab	0.47 (0.44–0.51) Aab	0.40 (0.37–0.40) Aab	0.54 (0.48–0.56) Aa	0.48 (0.46–0.52) Aab	0.51 (0.31–0.57) Aab	0.38 (0.34–0.43) Ab
	4.2 pF (cm^3 cm^{-3})	0.41 (0.35–0.42) Aa	0.41 (0.40–0.46) Aa	0.35 (0.33–0.37) Aa	0.46 (0.43–0.53) Aa	0.43 (0.38–0.47) Aa	0.48 (0.26–0.51) Aa	0.36 (0.31–0.39) Aa
	GW (cm^3 cm^{-3})	0.12 (0.06–0.16) Aab	0.14 (0.11–0.17) Bab	0.20 (0.18–0.22) Ba	0.10 (0.08–0.17) Aab	0.11 (0.10–0.12) Ab	0.15 (0.13–0.16) Bab	0.17 (0.14–0.20) Aab
	AW (cm^3 cm^{-3})	0.06 (0.06–0.08) Ab	0.11 (0.08–0.15) Aab	0.06 (0.04–0.09) Bb	0.10 (0.06–0.14) Aab	0.20 (0.16–0.22) Aa	0.21 (0.13–0.42) Aa	0.09 (0.07–0.13) Bab
	SOM (%)	8.00 (6.14–8.36) Ab	28.73 (26.64–31.39) Ba	13.19 (11.35–14.39) Aab	18.98 (18.30–22.45) Aab	19.02 (11.45–22.50) Aab	36.65 (25.19–43.98) Aa	8.83 (8.22–10.93) Bb

F = high montane forest; Tg = páramo; K_{sat} = saturated hydraulic conductivity; BD = bulk density; 0–4.2 pF = retention capacity at pF-values between 0 and 4.2; GW = gravitational water; AW = available water; SOM = soil organic matter content. The letters accompanying each property value represent the results of statistical comparisons. By properties: (1) different capital letters represent the significant differences ($p < 0.05$) between the two depths in each study site (i.e., 0–10 cm versus 10–25 cm), (2) different lower-case letters represent significant differences ($p < 0.05$) between sites at the same depth, (3) combinations of lower-case letters represent intermediate groups between two ranges. Letter denotation order was used from highest to the lowest value.

Table A2. Median and the 25th and 75th percentile of the hydro-physical properties and SOM content of the soil in the high montane forest and páramo converted to pine plantation (F = high montane forest; Tg = páramo).

	Elevation	**<3250 m a.s.l.**		**>3250–<3550 m a.s.l.**			**>3550 m a.s.l.**	
	Properties	**F1Pi**	**F2Pi**	**F3Pi**	**F4Pi**	**Tg5Pi**	**Tg6Pi**	**Tg7Pi**
0-10 cm soil layer	K_{sat} (cm h^{-1})	4.94 (4.32–6.41) A↓	4.52 (3.25–6.22) A	3.62 (2.99–4.30) A↓	6.59 (4.45–9.069) A	4.17 (3.38–6.53) A↑	2.19 (1.92–2.55) A↑	2.46 (1.85–3.14) A
	BD (g cm^{-3})	0.99 (0.91–1.07) B	0.44 (0.42–0.50) A	0.86 (0.81–0.91) B↑	0.55 (0.50–0.66) A	0.52 (0.45–0.67) B	0.32 (0.29–0.37) B	0.62 (0.55–0.71) B
	0 pF (cm^3 cm^{-3})	0.61 (0.58–0.64) A↓	0.75 (0.73–0.78) A↑	0.63 (0.61–0.67) A↓	0.75 (0.70–0.77) A	0.77 (0.73–0.79) A	0.85 (0.83–0.86) A↓	0.71 (0.68–0.73) A↓
	0.5 pF (cm^3 cm^{-3})	0.59 (0.56–0.62) A↓	0.73 (0.71–0.75) A↑	0.62 (0.60–0.66) A↓	0.72 (0.69–0.75) A	0.76 (0.72–0.79) A	0.83 (0.82–0.83) A↓	0.70 (0.67–0.72) A↓
	1.5 pF (cm^3 cm^{-3})	0.50 (0.48–0.52) A↓	0.61 (0.58–0.64) B↑	0.50 (0.48–0.53) A↓	0.63 (0.59–0.64) B	0.71 (0.66–0.75) A	0.76 (0.74–0.78) A↓	0.65 (0.61–0.69) A
	2.52 pF (cm^3 cm^{-3})	0.41 (0.39–0.43) A↓	0.52 (0.49–0.55) B↑	0.41 (0.39–0.42) A↓	0.55 (0.52–0.56) B	0.62 (0.58–0.66) A	0.61 (0.59–0.63) B↓	0.52 (0.49–0.57) A↓
	3.4 pF (cm^3 cm^{-3})	0.37 (0.35–0.39) A↓	0.43 (0.38–0.46) B	0.37 (0.35–0.38) A	0.43 (0.41–0.46) B↓	0.46 (0.43–0.49) A	0.42 (0.40–0.44) B↓	0.47 (0.43–0.50) A↑
	4.2 pF (cm^3 cm^{-3})	0.33 (0.29–0.35) A↓	0.39 (0.35–0.43) A	0.33 (0.30–0.35) A	0.37 (0.35–0.39) B↓	0.42 (0.40–0.45) A	0.40 (0.36–0.41) B↓	0.43 (0.38–0.47) A↑
	GW (cm^3 cm^{-3})	0.21 (0.17–0.23) A	0.22 (0.19–0.26) A	0.25 (0.22–0.26) A	0.20 (0.15–0.25) A↑	0.13 (0.11–0.16) A↑	0.24 (0.21–0.26) B↑	0.17 (0.14–0.21) A
	AW (cm^3 cm^{-3})	0.08 (0.05–0.11) A	0.13 (0.10–0.18) A	0.07 (0.05–0.08) A↓	0.16 (0.14–0.20) A	0.20 (0.16–0.23) A	0.23 (0.19–0.24) A	0.10 (0.07–0.13) A↓
	SOM (%)	5.29 (4.36–5.34) A↓	23.92 (23.44–29.71) A↓	10.91 (8.32–12.84) A↓	27.57 (25.59–29.06) A	24.98 (16.62–28.94) A	34.70 (31.33–35.16) A	20.87 (19.64–27.82) A↑
10-25 cm soil layer	K_{sat} (cm h^{-1})	5.50 (4.12–6.82) A↑	2.07 (1.58–2.82) B↑	0.87 (0.76–0.98) B↓	1.60 (1.04–2.25) B	0.70 (0.38–1.14) B↑	0.29 (0.16–0.38) B	0.89 (0.55–1.20) B↑
	BD (g cm^{-3})	1.17 (1.02–1.32) A	0.46 (0.43–0.51) A	1.01 (0.94–1.09) A↑	0.62 (0.53–0.81) A	0.58 (0.49–0.72) A	0.42 (0.39–0.44) A	0.71 (0.62–0.85) A↓
	0 pF (cm^3 cm^{-3})	0.53 (0.49–0.59) B↓	0.74 (0.71–0.76) A↑	0.58 (0.55–0.62) B	0.73 (0.66–0.75) A	0.75 (0.71–0.78) A	0.81 (0.80–0.83) B	0.67 (0.63–0.70) B↑
	0.5 pF (cm^3 cm^{-3})	0.52 (0.47–0.56) B↓	0.71 (0.69–0.74) A↑	0.58 (0.55–0.61) B	0.72 (0.65–0.74) A	0.75 (0.71–0.77) A	0.80 (0.78–0.82) B	0.67 (0.62–0.69) B↑
	1.5 pF (cm^3 cm^{-3})	0.45 (0.41–0.48) B↓	0.65 (0.63–0.68) A↑	0.50 (0.48–0.53) A	0.68 (0.62–0.70) A	0.72 (0.67–0.75) A	0.77 (0.75–0.79) A	0.62 (0.58–0.66) A↑
	2.52 pF (cm^3 cm^{-3})	0.40 (0.34–0.42) A↓	0.57 (0.55–0.60) A↑	0.38 (0.36–0.40) B↑	0.58 (0.55–0.63) B	0.64 (0.58–0.67) A	0.66 (0.64–0.67) A↑	0.49 (0.45–0.52) B
	3.4 pF (cm^3 cm^{-3})	0.37 (0.33–0.40) A↓	0.47 (0.44–0.50) A	0.36 (0.35–0.39) A↓	0.49 (0.46–0.52) B	0.47 (0.45–0.49) A	0.46 (0.44–0.48) A	0.45 (0.42–0.48) B↑
	4.2 pF (cm^3 cm^{-3})	0.33 (0.29–0.34) A↓	0.41 (0.38–0.44) A	0.33 (0.30–0.35) A	0.40 (0.38–0.43) A↓	0.42 (0.38–0.45) A	0.42 (0.40–0.44) A	0.41 (0.37–0.44) A↑
	GW (cm^3 cm^{-3})	0.15 (0.13–0.18) B	0.17 (0.15–0.19) B	0.21 (0.17–0.23) B	0.13 (0.11–0.15) B	0.11 (0.10–0.12) B	0.16 (0.15–0.17) A	0.18 (0.15–0.20) A
	AW (cm^3 cm^{-3})	0.07 (0.04–0.08) A	0.16 (0.12–0.21) A↑	0.05 (0.03–0.07) B	0.18 (0.15–0.22) A↑	0.21 (0.17–0.25) A	0.24 (0.21–0.27) A	0.07 (0.04–0.11) B
	SOM (%)	3.56 (3.32–4.95) B↓	26.05 (25.84–26.71) A↓	10.09 (9.06–10.52) A↓	17.82 (15.73–22.15) B	21.05 (13.42–23.64) B	29.41 (26.82–38.63) A	15.68 (11.34–21.40) B↑

FPi = pine plantation in high montane forest; TgPi = pine plantation in páramo. K_{sat} = saturated hydraulic conductivity; BD = bulk density; 0–4.2 pF = retention capacity at pF-values between 0 and 4.2; GW = gravitational water; AW = available water; SOM = soil organic matter content. The letters accompanying each property value represent the results of statistical comparisons. By properties: (1) different capital letters represent the significant differences ($p < 0.05$) between the two depths in each study site (i.e., 0–10 cm versus 10–25 cm). Letter denotation order was used from highest to the lowest value. ↓ or ↑ stand for a significant decrease or increment ($p < 0.05$ value) when comparing pine plantations vs. undisturbed natural cover.

Table A3. Median and the 25th and 75th percentile of the hydro-physical properties and SOM content of the soil in the high montane forest and páramo under cattle grazing (F = high montane forest; Tg = páramo).

	Elevation	**<3250 m a.s.l.**		**>3250–<3550 m a.s.l.**		**>3550 m a.s.l.**	
	Properties	**F1G**	**F2G**	**F3G**	**Tg5G ***	**Tg6G**	**Tg7G**
0–10 cm soil layer	K_{sat} (cm h^{-1})	4.02 (2.67–4.38) A↓	3.92 (3.61–8.36) A	16.58 (6.99–19.20) A	0.81 (0.52–0.96) A↓	2.14 (1.77–2.40) A↑	2.91 (1.65–4.80) A
	BD (g cm^{-3})	0.97 (0.92–1.04) A	0.62 (0.56–0.69) A↑	0.93 (0.89–0.93) A↑	0.44 (0.43–0.55) A	0.41 (0.37–0.46) A	0.54 (0.51–0.62) B
	0 pF (cm^3 cm^{-3})	0.64 (0.63–0.64) A	0.72 (0.69–0.75) A	0.63 (0.61–0.65) A↓	0.82 (0.79–0.84) A↑	0.82 (0.80–0.84) A↓	0.75 (0.72–0.77) A
	0.5 pF (cm^3 cm^{-3})	0.63 (0.63–0.64) A	0.71 (0.69–0.74) A	0.61 (0.59–0.63) A↓	0.81 (0.78–0.83) A↑	0.81 (0.78–0.84) A↓	0.74 (0.72–0.76) A
	1.5 pF (cm^3 cm^{-3})	0.55 (0.54–56) A	0.65 (0.64–0.70) A↑	0.50 (0.47–0.55) A↓	0.79 (0.74–0.80) A↑	0.76 (0.71–0.77) A↓	0.70 (0.67–0.70) A
	2.52 pF (cm^3 cm^{-3})	0.48 (0.45–0.49) A	0.54 (0.48–0.58) B	0.40 (0.37–0.40) A↓	0.68 (0.65–0.70) A↑	0.63 (0.60–0.64) A↓	0.52 (0.51–0.55) A↓
	3.4 pF (cm^3 cm^{-3})	0.44 (0.43–0.45) A	0.47 (0.45–0.53) B↑	0.35 (0.33–0.35) A↓	0.50 (0.44–0.60) A	0.43 (0.40–0.45) A↓	0.42 (0.40–0.45) A↑
	4.2 pF (cm^3 cm^{-3})	0.40 (0.37–0.43) A	0.44 (0.41–0.46) A↑	0.30 (0.27–0.33) A	0.42 (0.41–0.55) A	0.41 (0.38–0.43) A↓	0.37 (0.35–0.41) A↑
	GW (cm^3 cm^{-3})	0.16 (0.15–0.19) A	0.19 (0.15–0.22) A	0.24 (0.20–0.28) A	0.13 (0.12–0.14) A	0.20 (0.19–0.20) A↑	0.23 (0.18–0.25) A↑
	AW (cm^3 cm^{-3})	0.06 (0.05–0.10) A	0.08 (0.07–0.14) A	0.09 (0.07–0.11) A	0.23 (0.16–0.26) A	0.21 (0.19–0.22) A	0.14 (0.10–0.18) A↓
	SOM (%)	7.94 (7.14–8.72) A	20.11 (18.31–33.54) A	10.68 (10.19–12.00) A↓	25.98 (17.67–30.03) A	36.35 (30.74–46.42) A	21.79 (18.14–28.58) A
10–25 cm soil layer	K_{sat} (cm h^{-1})	0.86 (0.32–1.27) B↓	1.72 (1.17–2.19) B	22.50 (12.93–31.70) A↑	0.22 (0.11–0.26) B	0.66 (0.47–0.73) A↑	0.60 (0.41–1.24) B↑
	BD (g cm^{-3})	1.11 (0.98–1.13) A	0.58 (0.48–0.66) A	0.89 (0.86–0.92) A	0.56 (0.51–0.58) A	0.52 (0.40–0.61) A	0.72 (0.63–0.80) A↓
	0 pF (cm^3 cm^{-3})	0.59 (0.56–0.60) B	0.75 (0.72–0.78) A↑	0.62 (0.60–0.63) A	0.77 (0.76–0.79) A↑	0.78 (0.76–0.82) A	0.69 (0.64–0.72) B↑
	0.5 pF (cm^3 cm^{-3})	0.59 (0.56–0.59) B	0.75 (0.72–0.77) A↑	0.59 (0.58–0.61) A	0.77 (0.76–0.78) A↑	0.77 (0.75–0.81) A	0.69 (0.63–0.71) B↑
	1.5 pF (cm^3 cm^{-3})	0.49 (0.49–0.53) B	0.70 (0.63—0.73) A↑	0.46 (0.45–0.50) A↓	0.75 (0.74–0.76) A↑	0.72 (0.71–0.78) A	0.64 (0.55–0.67) B↑
	2.52 pF (cm^3 cm^{-3})	0.42 (0.40–0.47) A	0.62 (0.53–0.66) A↑	0.37 (0.35–0.40) A	0.67 (0.66–0.68) A↑	0.63 (0.62–0.68) A	0.48 (0.43–0.53) B
	3.4 pF (cm^3 cm^{-3})	0.41 (0.39–0.45) A	0.53 (0.49–0.60) A↑	0.34 (0.34–0.37) A↓	0.49 (0.47–0.52) A	0.48 (0.41–0.52) A	0.39 (0.33–0.42) A
	4.2 pF (cm^3 cm^{-3})	0.38 (0.38–0.40) A	0.48 (0.39–0.52) A	0.31 (0.30–0.32) A↓	0.45 (0.41–0.47) A	0.44 (0.39–0.48) A	0.37 (0.31–0.39) A
	GW (cm^3 cm^{-3})	0.15 (0.14–0.19) A	0.11 (0.09–0.18) B	0.25 (0.22–0.28) A	0.11 (0.10–0.11) B	0.14 (0.13–0.17) B	0.20 (0.16–0.22) A
	AW (cm^3 cm^{-3})	0.04 (0.04–0.06) A	0.13 (0.11–0.17) A	0.06 (0.05–0.09) A	0.22 (0.18–0.24) A	0.20 (0.16–0.22) A	0.15 (0.09–0.18) A
	SOM (%)	6.98 (5.13–7.84) A	17.66 (16.85–28.56) A	10.14 (9.85–11.24) A	20.71 (18.85–24.95) A	27.74 (20.63–40.71) A	16.08 (11.24–22.40) A

FG = grazing in high montane forest; TgG = grazing in páramo. K_{sat} = saturated hydraulic conductivity; BD = bulk density; 0–4.2 pF = retention capacity at pF-values between 0 and 4.2; GW = gravitational water; AW = available water; SOM = soil organic matter content. The letters accompanying each property value represent the results of statistical comparisons. By properties: (1) different capital letters represent the significant differences ($p < 0.05$) between the two depths in each study site (i.e., 0–10 cm versus 10–25 cm). Letter denotation order was used from highest to the lowest value. ↓ or ↑ stand for a significant decrease or increment ($p < 0.05$ value) when comparing grazing vs. undisturbed natural cover.

Table A4. *p*-values of the comparisons of the hydro-physical properties between 75 and 150 cm of sampling distance in each of the pine plantations in the study area. Elevation: <3250 m a.s.l., >3250–<3550 m a.s.l., >3550 m a.s.l.

	Elevation	<3250 m a.s.l.		>3250–<3550 m a.s.l.			>3550 m a.s.l.	
	Properties	**F1Pi**	**F2Pi**	**F3Pi**	**F4Pi**	**Tg5Pi**	**Tg6Pi**	**Tg7Pi**
0–10 cm soil layer	K_{sat}	0.16	0.59	0.19	0.18	0.36	0.45	0.66
	BD	0.62	0.82	0.92	0.76	0.92	0.79	0.91
	0 pF	0.48	0.4	0.38	0.74	0.76	0.3	0.93
	0.5 pF	0.97	0.43	0.59	0.9	0.76	0.53	0.94
	1.5 pF	0.97	0.8	0.71	0.08	0.77	0.55	0.93
	2.52 pF	0.65	0.95	0.36	0.24	0.97	0.42	0.79
	3.4 pF	0.18	0.53	0.27	0.25	0.24	0.88	0.45
	4.2 pF	0.32	0.74	0.42	0.19	0.18	0.37	0.93
	GW	0.93	0.43	0.48	0.32	0.68	0.77	0.58
	AW	0.8	0.71	0.2	0.81	0.52	0.59	1
10–25cm soil layer	K_{sat}	0.56	0.9	**0.03**	0.38	0.54	0.82	0.21
	BD	0.97	0.76	0.97	0.93	0.97	0.84	0.91
	0 pF	0.98	0.74	0.6	1	0.97	0.76	0.89
	0.5 pF	0.92	0.66	0.51	0.92	0.9	0.82	0.84
	1.5 pF	0.9	0.58	0.74	0.88	0.92	0.95	0.78
	2.52 pF	0.66	0.34	0.68	0.79	0.8	0.87	0.94
	3.4 pF	0.88	**0.03**	0.19	0.69	0.68	0.77	1
	4.2 pF	0.6	0.14	0.93	0.25	0.76	0.12	0.58
	GW	0.66	0.53	0.3	0.9	0.79	0.79	0.91
	AW	0.51	0.19	0.49	0.2	0.87	0.12	0.67

The names of the variables are defined in Table 4. The values in bold indicate that the properties are significantly different between both depths ($p < 0.05$).

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9.3 Publication III

Title: Impacts of pine plantations on carbon stocks of páramo sites in Southern Ecuador.

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Impacts of pine plantations on carbon stocks of páramo sites in southern Ecuador

Carlos Quiroz Dahik[1,2*], Patricio Crespo[2], Bernd Stimm[1], Reinhard Mosandl[1], Jorge Cueva[1], Patrick Hildebrandt[1] and Michael Weber[1]

Abstract

Background: Since the 1990's, afforestation programs in the páramo have been implemented to offset carbon emissions through carbon sequestration, mainly using pine plantations. However, several studies have indicated that after the establishment of pine plantations in grasslands, there is an alteration of carbon pools including a decrease of the soil organic carbon (SOC) pool. The aim of this study is to investigate the impact of the establishment of pine plantations on the carbon stocks in different altitudes of the páramo ecosystem of South Ecuador.

Results: At seven locations within an elevational gradient from 2780 to 3760 m a.s.l., we measured and compared carbon stocks of three types of land use: natural grassland, grazed páramo, and *Pinus patula* Schlltdl. & Cham. plantation sites. For a more accurate estimation of pine tree carbon, we developed our own allometric equations. There were significant ($p < 0.05$) differences between the amounts of carbon stored in the carbon pools aboveground and belowground for the three types of land use. In most of the locations, pine plantations revealed the highest amounts of aboveground and belowground carbon (55.4 and 6.9 tC/ha) followed by natural grassland (23.1 and 2.7 tC/ha) and grazed páramo sites (9.1 and 1.5 tC/ha). Concerning the SOC pools, most of the locations revealed significant lower values of plantations' SOC in comparison to natural grassland and grazed páramo sites. Higher elevation was associated with lower amounts of pines' biomass.

Conclusions: Even though plantations store high amounts of carbon, natural páramo grassland can also store substantial amounts above and belowground, without negatively affecting the soils and putting other páramo ecosystem services at risk. Consequently, plans for afforestation in the páramo should be assessed case by case, considering not only the limiting factor of elevation, but also the site quality especially affected by the type of previous land use.

Keywords: Carbon sequestration, Land use change, Carbon pools, Aboveground biomass, Belowground biomass, Soil organic carbon

Background

Afforestation with non-native species in Ecuador started in 1875, when the first species of *Eucalyptus* were introduced with the intention to produce timber, fuel and to restore degraded Andean soils [1–3]. Later, around 1928, seventy species of conifers were introduced including some *Pinus* spp., and after several years of testing, the government implemented afforestation programs with the best adapted species such as *Pinus patula* and *Pinus radiata*. These programs were implemented between the 60's and 80's, had total or partial economic assistance, and their main objective was to develop the economy of small producers and rural communities through the production of wood [4–6]. Over the last decades, many pine plantations have been established in order to capture and fix carbon dioxide from the atmosphere through the program PROFAFOR (Programa FACE de Forestación).

*Correspondence: caquirozd@hotmail.com
[1] Department of Ecology and Ecosystem Management, Technical University of Munich, Munich, Germany
Full list of author information is available at the end of the article

PROFAFOR is an Ecuadorian company acting as extension of the Forest Absorbing Carbon Dioxide Emissions (FACE) consortium, financed by the Dutch electricity companies to offset their carbon emissions. Since its establishment in 1993, PROFAFOR has signed 152 afforestation contracts with private and community landowners. Until 2003, 22,000 ha of plantations were established in the Andean highlands from which 94% correspond to pine plantations [4, 7]. Most of PROFAFOR ´s plantations are not eligible under the framework of the Clean Development Mechanism (CDM) under the Kyoto Protocol, as their year of planting predates that established in the protocol [7].

While much attention has been focused on the carbon (C) sequestration by growing trees, little attention has been paid to the environmental tradeoffs that are associated with these activities [8]. Most of the programs through afforestation, reforestation, and avoided deforestation have mainly focused on increasing the storage of aboveground biomass (C) [9, 10], without adequately considering soil organic carbon (SOC), even though it can constitute a large fraction of the total C stock [11, 12]. Therefore, there is a growing demand to accurately estimate soil carbon stocks [13] such as páramo soils to evaluate their role as carbon stores. The effects of land use change on soil C are also poorly understood [14], especially in the case of the páramo ecosystem [15, 16].

The páramo, a neotropical high montane ecosystem located between Costa Rica and northern Perú is composed mostly of grasses and shrubs and occurs above the limits of the continuous forest [17–19]. The páramo provides multiple ecosystem services (ES), the most prominent being water supply and regulation, biodiversity conservation, provisioning food for grazing and carbon storage [20–22]. The páramo soils are considered huge carbon stores, because there is a great accumulation of organic matter, due to low temperatures and high humidity that slow down the microbial activity which restricts the decomposition processes [23]. The organic matter, half of which is carbon, generates thick superficial horizons of black or dark tones, classified mostly as Andisols [24]. Recent studies have raised critical views on páramo pine afforestation, considering the potential negative effects on the ES of carbon storage [25, 26].

Research on soil C with afforestation show different outcomes. For example, in a global synthesis Paul et al. [27] found increases and decreases in SOC after afforestation. A subsequent global meta-analysis found that afforestation with pines demonstrated a clear decrease in SOC and nitrogen (N) [28]. The few studies that have been done in the Ecuadorian páramo have found a decrease of SOC [11, 15, 16, 25]. Additionally, in a study in an area of southern Ecuador, Chacón et al. [29] suggested that pines are usually planted on degraded areas or in extensively grazed páramos [25], and for this reason may not be the driver for decreasing SOC. In addition, the effects of land use change on SOC depend on soil properties and environmental conditions, therefore the effects should not be generalized across other regions [25, 30].

With the growing international interest in carbon sequestration, programs for carbon sequestration and conservation are continuously developing [31, 32]. Although currently the establishment of plantations in Ecuadorian páramos is prohibited [33], PROFAFOR contracts on plantations in the páramos allow their landowners to renew the contracts after the harvesting of the plantations [34]. Hence, in order to evaluate the future applicability of these type of programs, it is critical to identify the effects of pine plantations on the carbon stocks of the páramo ecosystem of the region. We have focused our research on pine plantations as they have been the most common land use change for carbon capture promoted in the South region of Ecuador. We especially address the following questions: (i) what are the sizes of carbon stocks and how are they distributed above and below ground in the different types of land use? (ii) what are the effects of different types of land use on the different components of the carbon stock? For this purpose, we have compared three types of land use: natural grassland, which is the dominant vegetation type in the páramo ecosystem studied under natural conditions, *P. patula* plantations, and grazed páramo, which is the most frequent former land use before pine establishment [19].

Methods

Study area

This research took place in the páramo of Azuay province (2° 57′–3° 19′ S, 79° 5′–79° 19′ W), Ecuador (Fig. 1) within an elevational range from 2700 to 3800 m a.s.l. In general the climate in the páramo is wet and humid, and the change in average temperature with elevation is between 0.6 and 0.7 °C for each 100 m of variation in altitude [35]. In this region at 3600 m a.s.l. the average temperature is 8 °C and at 2800 m a.s.l. it is 13.2 °C, while the mean relative humidity is 91% [36, 37]. Rainfall is characterized by frequent low volume events and ranges between 900 and 1600 mm/year [37–39].

The páramo of this region belongs to a landscape that was characteristically shaped by the last glacial period [24, 40]. These soils have been recently (3000 years BP) rejuvenated by a thin layer of fine ash covering the bedrock, most likely due to the activity of the Tungurahua and Sangay volcanos [40]. The volcanic ash is responsible for protecting the humus against decomposition through the formation of organic-mineral complexes [15,

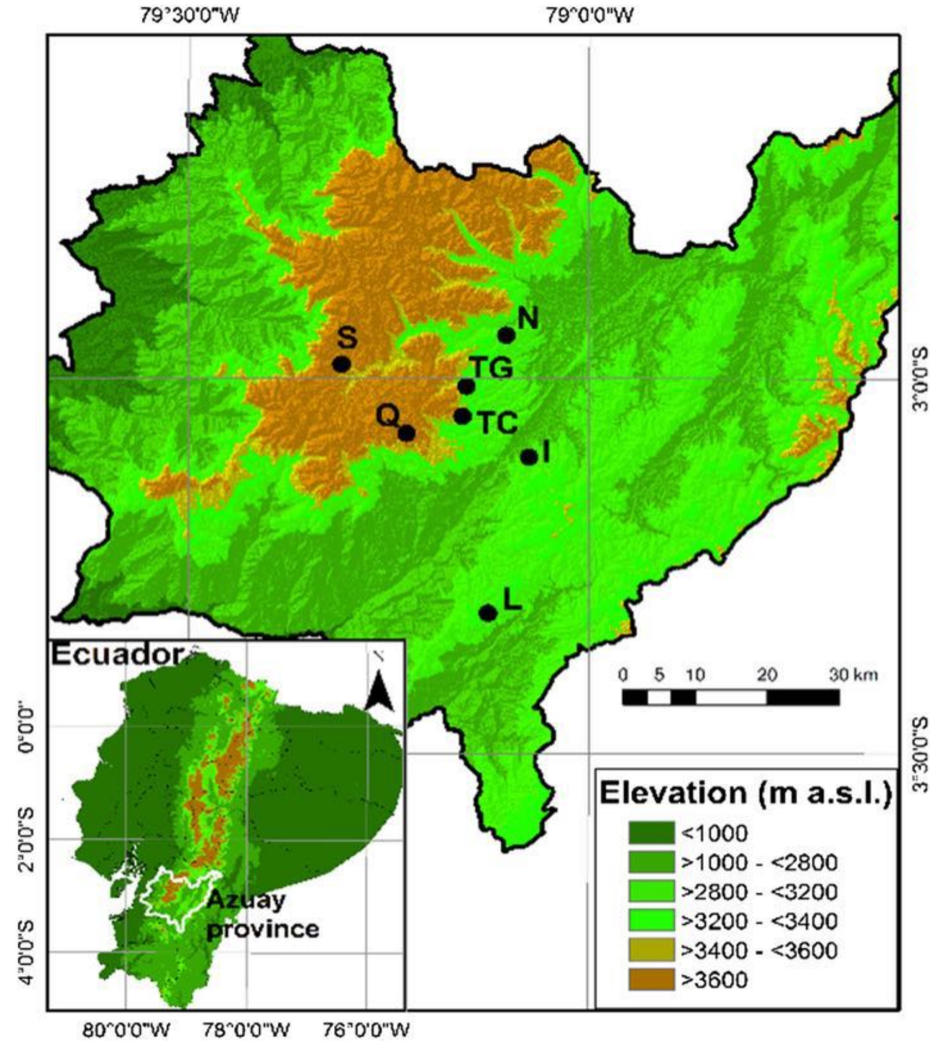

Fig. 1 Map of Azuay province showing the seven locations of the study from the lowest to the highest in elevation: Irquis (I), Nero (N), La Paz (L), Tutupali Chico (TC), Tutupali Grande (TG), Quimsacocha (Q) and Soldados (S)

41]. The humid and cold weather and low atmospheric pressure [36] have also favored the store of soil organic matter. This organic matter together with the accumulated volcanic ash are responsible for the formation of black, humid, and acid soils with porous structure, low bulk density, and high water retention capacity [24, 36, 39]. These soils have been classified as non-allophanic Andisols [16, 24]. The study area is located next to the Girón-Paute deflection where the Andes to the south breaks down into smaller mountains whose peaks do not exceed 4.000 m a.s.l., and the treeline is located at a lower elevation [42, 43]. The vegetation is characterized by tussock grass layers, mainly *Calamagrostis* spp. and *Festuca* spp. [44], covering the entire soil surface. Besides these grass species, dwarf shrubs (*Myricaceae*, *Primulaceae*, *Caprifoliaceae*) [44], can be found. The lowest zone of the páramo, located between 2800 and 3500 m a.s.l, is called subpáramo, and it is the transition zone from the Andean forest to the páramo [19]. The vegetation in this zone is composed of elements from the forest below and the grass páramo above. This zone is very difficult to define since the páramo has been affected by human activities since the Holocene (11,000 year BP) [19, 45, 46]. Human activities have changed much of this zone in such a way that now most of the subpáramo zone occur in areas that were probably covered with upper montane forest in the past [47]. The subpáramo communities are predominantly composed of shrubby or woody vegetation that is lacking or limited in the Andean forest below as well as small scattered trees [19, 48]. People living inside or close to the páramo ecosystem tend to have a low average income and depend from their land. Their main livelihood is agriculture, cattle grazing, and in some cases, they have off-farm income [21, 49].

Experimental setup

To investigate the differences among the C-pools stored in pine plantations and the other land uses, we compared *P. patula* plantation sites (Pi) and adjacent (between 20 m and 2 km) non-plantation sites. We selected two types of non-plantation sites: natural grassland vegetation (NG) which are almost undisturbed sites with the dominant vegetation type in the life zone studied under natural conditions as our control sites, and grazed páramo sites (G), which is the most frequent former land use in the region. All sites were selected so that the main site characteristics (age and management of the plantations, elevation, slope, aspect and soil) were as similar as possible, except for the type of land use. We selected seven locations between 2700 and 3800 m a.s.l., where the three types of land use could be found. In five locations one plantation was selected, and in two locations (Tutupali Grande and Soldados) two plantations were selected.

To measure the characteristics of the plantations, we did a plantation inventory in each one. For the inventory, we used the simple random sampling method. We treated each plantation as single population of N units. From the population a sample of n non-overlapping fixed-area sampling units (plot) were used. Each plot was randomly chosen. To select each sample plot, we used orthophotos of the plantations as a sampling frame. The orthophotos had a spatial resolution of 0.3 m and were taken in 2010, and proportionated by the "Ministerio de Agricultura, Ganadería, Acuacultura y Pesca". Each plantation was divided into a grid of square plots, the plots were numbered and randomly selected.

To calculate the sample size, a preliminary sampling was carried out to give an indication of the variability of the population, in which we calculated the coefficient of variation (CV) of pine density per hectare. With this preliminary information we calculated the sample size using a standard method [50]:

$$n = \frac{t^2(CV)^2N}{\left(N(E\%)^2 + t^2(CV)^2\right)}, \tag{1}$$

where n is number of sampling units measured, t is the Student's t distribution for desired probability level, CV is the coefficient of variation (CV = 100 multiplied by standard deviation and divided by the sample mean), N is the total number of sampling units in the population (the plantation), and $E\%$ is the allowable error as percent of the mean. t-value was associated with the 0.95 probability and 4 degrees of freedom, and we set $E\%$ to a maximum of 20% of the mean based on logistical and cost limitations. In most of the plantations n was equal to five. To perform this calculation, we put together the plantations that were at the same elevational range.

Inside each of the nine plantations five plots of 24×24 m were established. At each location adjacent to the plantation, we further established six square plots (0.5×0.5 m) per land use type (in total 42 plots for G and NG sites along various elevations). Inside each plantation plot we measured the tree height and diameter at breast height (DBH) of all trees to enable the calculation of the biomass of the pines. The coordinates and altitudes were recorded with a GPS for each plot.

Experimental sites

The páramo has been intervened for thousands of years, a recent study suggests that páramo hunter-gatherers would have actively manipulated the páramo grassland through the use of fire [46]. Until the arrival of the Incas it was used as a ceremony and hunting place. Later, with the development of the Inca culture, it was used for grazing with Andean camelids and for potato cultivation. Then, with the arrival of the Spaniards, it was used for cattle and sheep grazing in addition to cereal cultivation. Currently, the activities that generate the greatest impacts on the páramo are: the expansion of the agricultural frontier, mining, and afforestation with exotic species [51]. For our study we selected three types of land use which correspond to different intensities of human intervention.

Natural grassland sites (NG)

Páramo natural grassland sites had characteristics similar to the *páramo in good state of conservation* as described by Hofstede et al. [52] in an evaluation of the conservation status of the Ecuadorian páramo. Natural grassland sites in our study are characterized by the presence of tall tussock grasses, with no recent disturbances such as grazing and burning, a high content of organic matter, and the presence of native fauna. The NG sites in our study were predominantly characterized by tussock grasses, mainly *Calamagrostis* spp. and *Festuca* spp. In the lower altitudes the NG sites presented a vegetation typical for the transition zone between the upper Andean forest and the open páramo. These sites were dominated by shrubby or woody vegetation. Thus, the NG sites were not homogenous over the whole elevational range. We did not include small patches of *Polylepis* spp. because they were distant from the pine plantations.

Table 1 Characteristics of the pine plantations (Pi) for each location

Location	Altitud (m a.s.l)	Age (years)	Size (ha)	Slope (%)	Trees per ha	DBH (cm)	Tree height (m)	Management	Type of land use before the establishment of the plantation	Type of vegetation of the undisturbed sites (NG)
Irquis	2780	29	25	46.8	611	26.0	19.2	None	NG	Shrubs, woody veg
Nero	3260	18	30	21.2	694	20.2	11.3	None	NG	Shrubs, woody veg
La Paz	3380	17	46	12.8	850	21.2	9.3	Pruned	G	Tussock grass, shrubbs
Tutupali Chico	3420	16	350	22.4	712	20.8	9.7	Pruned	G	Tussock grass, shrubbs
Tutupali Grande										
Pi1	3460	22	300	26.4	781	17.1	9.0	Pruned	G	Tussock grass
Pi2	3540	20	300	41.1	806	15.8	7.6	None	G	Tussock grass
Quinsacocha	3690	19	123	23.3	573	9.5	4.9	Pruned	G	Tussock grass, shrubbs
Soldados										
Pi1	3760	16	240	20.5	458	12.6	4.8	None	G	Tussock grass
Pi2	3720	19	100	16.8	569	11.2	5.0	Pruned	NG	Tussock grass

ha hectare, *DBH* diameter at breast height of the pines, *NG* páramo natural grassland sites

Pine plantation sites (Pi)

The plantations were selected based on a forest register provided by the regional forestry department. After contacting 19 plantation landowners, nine of them were selected considering various factors such as plantation size, date of the establishment, average altitude of the plantations, accessibility of the plantation, and the interest of the landowners in cooperating in the research. All selected nine plantations were first rotation *P. patula* plantations with 3 × 3 m spacing located between 2700 and 3800 m a.s.l. The ages of the selected plantations range from 16 to 29 years, with a median age of 19 years. The management of the plantations varied from no management to different intensities of pruning. Thinning was applied in two plantations but in a very limited area which was not significant; so we did not further consider this type of management. These plantations are generally harvested on a 25-year rotation. Six of the plantations were established on extensively grazed páramo (G) and three on páramo natural grassland (NG) (Table 1). Seven plantations were established by the company PROFAFOR Latinoamericana S.A., which is the largest company in Ecuador currently compensating for CO_2 emissions through afforestation, mostly with *Pinus* species [34].

Grazed sites (G)

These sites represent the most common former land use in the highland area, grazed páramo grassland [53]. The sites at the higher elevations were dominated by tussock grasses and introduced grasses, *Lolium* sp. and *Dactylis* sp. and in the lower elevations most of the vegetation was dominated by introduced species of *Trifolium* and grasses such as *Pennisetum clandestinum*, *Dactylis* sp. and *Lolium* sp. The sites at the higher locations were managed with extensive cattle grazing and at the lower locations there were higher concentration of animals (two or less animals per ha). There were no signs of recent burning, even though burning of the grasses is a common practice [54]. In most of the sites pre-tilling and reduced tilling activities took place in addition to fertilization (Table 2).

Biomass sampling

As no allometric equation to quantify the biomass of *P. patula* in the study region has been developed, and because available equations were developed in different ecosystems [55], we decided to take a small sample of trees to measure their biomass and develop an allometric equation that could be compared and evaluated with the most suitable equations that have been developed. According to Picard et al. [56], even small samples could be valid very locally. Therefore, in each of the nine plantations, one tree with an average DBH and total height for each plantation was selected in the context of the detailed forest inventory realized in each plantation [57].

The selected trees were felled between May and July 2014. From each sample tree, we measured tree height and DBH, then the trees were divided into their components: crown (upper part of the trunk with a diameter < 7 cm), trunk (diameter ≥ 7 cm), branches, needles, and roots. All components were weighed fresh in the field, and a sample of approximately 10% of the weight of each component was taken to the laboratory to be dried. Once the tree was felled, we cut the crown, and then the trunk was cut into 2 m sections. At each trunk section the upper and lower diameter was measured to calculate the volume of each section. At the end of each trunk section a disc was cut, weighed, and taken to the laboratory in order to determine the wood density by dividing the dried mass by the volume (obtained through displacement). All branches of the respective trunk section were weighed and counted, and three representative branches were selected for each trunk section. From the three selected branches, the needles were separated, and then branches and needles were weighed. With these two measurements, we calculated a proportion of weight correspondent for needles and branches. Representative samples from branches and needles were taken to the laboratory. Later the stump was excavated, weighed and a disc sample was taken from it. For the quantification of the biomass of the roots (diameter ≥ 5 mm), two perpendicular axes that crossed in the center axis of the stump were marked and the surface was divided in four quadrants. From two opposite quadrants, one located uphill and the other downhill, all roots were dug out. The roots were classified into three groups, roots with diameters < 7 mm, from 7 to 12 mm, and bigger than 12 mm. Each group was weighed and a sample of 10% of the weight was taken to the laboratory [57]. With the biomass obtained from the nine trees harvested, two equations were fitted, Eq. 2 to estimate aboveground biomass (kg), and Eq. 3 to estimate belowground biomass (kg).

$$\mathrm{Ba} = \mathrm{Exp}(-0.453) \times \left(DBH^2 \times h\right)^{0.649}, \tag{2}$$

where DBH is the diameter at breast height and h is the height of the pine tree.

$$Bb = \mathrm{Exp}(-0.321) \times \left(DBH^2 \times h\right)^{0.316}, \tag{3}$$

where DBH is the diameter at breast height and h is the height of the pine tree.

We collected fresh samples from each tree component and dried them at the laboratory. The samples from the

Table 2 General description of the grazed páramo sites (G) including their average elevation and slope

Location	Altitud (m a.s.l.)	Slope (%)	Pre-tilling and tilling activities	Type of land use before grazing	Grassland age (years)	Grass	Animal load (ABU/ha)
Irquis	2830	22.5	Preparation through ploughing, liming, and organic fertilization	NG	> 10	*Pennisetum clandestinum*	1
Nero	3200	26.2	Preparation through plowing, organic and inorganic fertilization, and pastures irrigation and rotation	NG	> 10	*Dactylis* sp., *Trifolium* sp. and *Lolium* sp.	2
La Paz	3320	22.5	Forest logging and burning, solid preparation was made using plowing discs	NG	3	*Dactylis* sp. and *Pennisetum clandestinum*	1
Tutupali Chico	3480	31.5	Tussock grass burn	NG	< 3	*Calamagrostis intermedia*	< 0.2
Tutupali Grande	3470	27.7	Tussock grass burn	NG	< 3	*Calamagrostis intermedia*	< 0.2
Quinsacocha	3600	20.0	Vegetable cover cleaning, soil preparation through plowing and poultry fertilization	NG	5	*Lolium* sp.	0.5
Soldados	3750	14.2	Ground preparation through harrow and adding of vegetal material into the soil	NG	7	*Lolium* sp. and *Dactylis* sp.	0.4

ABU/ha: adult bovine unit per hectare and per year

crown, trunk, branches, and roots were dried for 72 h at 75 °C to obtain their dry weight, and needles for 48 h at 75 °C. We used the dried samples to calculate the dry/wet ratio, which was later used to extrapolate the dry weight of the entire components. With the biomass obtained from the nine trees, two equations between tree component biomass and the independent variable [squared DBH multiplied by the tree height (D^2H)] were developed, in the same way as it was done in other studies [55, 58].

The sampling of the ground vegetation was conducted between August and December 2014. For the calculation of its biomass, we aligned and established three subplots (0.5 × 0.5 m) inside each plantation plot, two in the opposite corners and one in the middle of the plot. For the sampling of the aboveground biomass in the non-plantation sites, one plot (0.5 × 0.5 m) was used. For the calculation of the biomass carbon of the ground vegetation, we put together dead wood, litter, and aboveground biomass pools. Dead wood included all non-living woody biomass not contained in the litter either standing or lying on the ground. Aboveground biomass included all living biomass above the soil [59]. All biomass samples were harvested and weighed. We brought the samples from each subplot and plot to the laboratory where we dried them at 75 °C until they reached a constant weight, and they were used to calculate the dry/wet ratio. The biomass of roots was calculated by the collection of one soil sample at three depths: 0–15 cm, 15–30 cm, and 30–45 cm, in each subplot of the plantations and in each plot of the other land uses. We collected the soil samples with soil cores (5 cm in diameter and 5.1 cm length, 100 cm^3). Soil samples were placed in plastic bags immediately after being taken, and later they were transported to the laboratory. At the laboratory, we sieved the samples with a 2 mm mesh size and all roots were collected, washed, dried (72 h, 75 °C), and weighed using a precision scale. We estimated the biomass carbon content using a standard coefficient of 0.5 [60]. We upscaled dry matter values to t/ha basis.

Soil sampling

We conducted the soil sampling between August and December 2014. Similar to the root sampling, one soil core was taken in each subplot and in each control plot using metal rings with 100 cm^3 volume to collect undisturbed soil samples at three depths: 0–15 cm, 15–30 cm, and 30–45 cm. We took the samples to the laboratory of the University of Cuenca in Ecuador, where they were air-dried and passed through a 2 mm sieve to separate fine soil from stones and roots. Fresh fine soil, stones, and roots were weighed. Later the fresh fine soil was oven dried for 72 h at 60 °C to obtain dry fine soil samples. Roots and stones were dried for 72 h at 72 °C. For each dried sample, we calculated the soil bulk density (BD, oven-dry mass of soil per unit of volume) using a standard method:

$$BD = \frac{mass_{fine\ soil}}{volume_{sample} - volume_{coarse\ fragments}}, \quad (4)$$

where BD is bulk density, $mass_{fine\ soil}$ is the mass of the fine soil (dried soil that has passed through a 2 mm sieve), $volume_{sample}$ is the total volume of the sample, and $volume_{coarse\ fragments}$ is the volume of rock fragments and/or roots bigger than 2 mm.

We quantified the volume of the rock fragments and roots by displacement in a water bath. The dry fine soil samples from each depth of the three subplots were mixed for measurement of SOC concentration due to economic reasons. We collected and transferred a portion of 120 g of each soil sample to the Technical University of Munich (Germany), where all samples were ground in a mill (Retsch Mixer Mill MM200) at a vibrational frequency of 25/s for 2 min to obtain a homogeneous sample. These samples were used to measure C concentrations by the dry combustion method using an analyzer Vario EL III. To avoid overestimations of the SOC values, we did not use soil bulk density for its calculations [61]. The quantification of SOC stock was made with the following equations as done by, e.g., Poeplau et al. [62]:

$$FSS_i = \frac{mass_{fine\ soil}}{volume_{sample}} \times depth_i, \quad (5)$$

where FSS_i is the fine soil stock of the investigated soil layer (t/ha), depth is the depth of the respective soil layer (cm); and:

$$SOC_{stock_i} = SOC_{con_{fine\ soil}} \times FSS_i, \quad (6)$$

where SOC_{stock_i} is the SOC stock of the investigated soil layer (i) (t/ha), and $SOC_{con_{fine\ soil}}$ is the content of SOC in the fine soil (%), and FSS_i is the fine soil stock of the investigated soil layer (t/ha).

Data analysis

We developed allometric equations between tree component biomass and the independent variable [squared DBH multiplied by the tree height (D^2H)] using curve fitting with the software SPSS, v. 24.0 [63]. The data were checked for normality with the Kolmogorov–Smirnov test, and for equality of variances with Levene's test. We used one-way ANOVA when these assumptions were met. Where differences among land uses were significant, Kruskal–Wallis one-way ANOVA on ranks analyses were used to compare means. The significance of the relationships among soil properties was tested using Pearson's product-moment correlation test (R) and regressions calculated with the function resulting in the highest coefficient determination (r^2). Except for the development of the allometric equations, the rest of the statistical analyses were done with programming environment R v. 3.5.3 [64] using the *agricolae* package [65], with differences in the $p < 0.05$ significance level. Mean values for sites or properties were given with the standard deviation in parenthesis.

Results

Figure 2 shows the results of the aboveground biomass estimation curves derived from the tree biomass analysis in relation to other allometric equations presented in Table 3.

As the values obtained with Eq. 2 were within the range of the results based on the equations found in the literature [66–72], we used our Eqs. 2 and 3 for the further biomass quantifications. Even though most of the equations have been developed in Mexico (Table 3), the relationship between DBH and biomass varied greatly between them. In addition, for the higher values of DBH

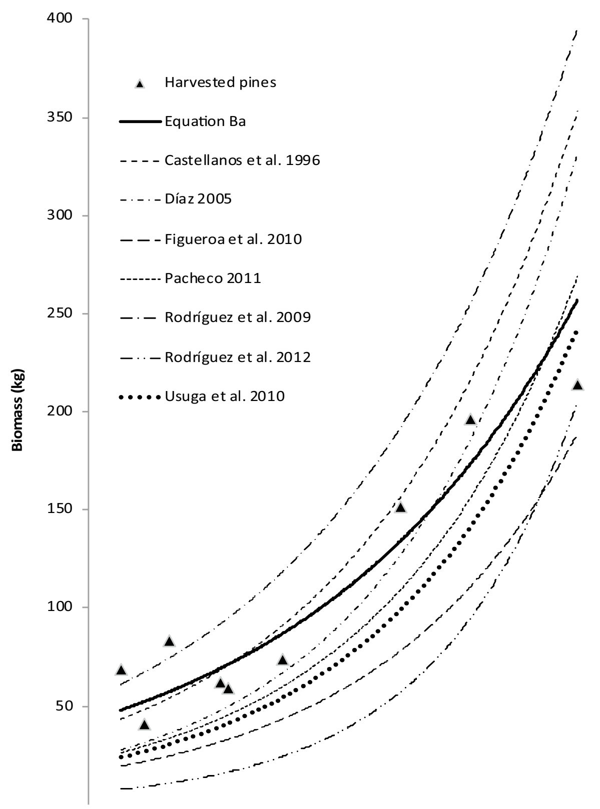

Fig. 2 Aboveground biomass estimation curves calculated with the allometric equations developed for *P. patula* including the data calculated with Ba (Eq. 2). The graph includes the biomass of the nine harvested pine trees

Table 3 Information about the studies that have determined allometric equations to estimate the aboveground biomass of *P. patula* trees

Research	Location (state, country)	Elevation (m a.s.l.)	Type of forest	Sampling size (trees)
Castellanos et al. [66]	Puebla, México	2400	Pine forest	27
Díaz Franco [67]	Tlaxcala, México	2875	Pine forest	25
Figueroa et al. [68]	Hidalgo, México	2800	Pine-Oak forest	18
Pacheco [69]	Oaxaca, México	2000	Pine-Oak forest	18
Rodríguez-Laguna et al. [70]	Tamaulipas, México	1800	Pine-Oak forest	111
Rodríguez-Ortiz et al. [71]	Oaxaca, México	2550	Cultivated forest	30
Usuga et al. [72]	Angostura-Manizales, Colombia	2230	Cultivated forest	54

our Eq. 2 revealed smaller increases in biomass compared to the other equations. This variability between the equations and the risk of overestimating data when using other equations justifies the use of our own equations.

Table 4 provides an overview on the mean carbon stocks in the different compartments and three investigated land uses. In all three land uses SOC represented the dominant part (NG: 91.5%; G: 96.4%; Pi: 80.6%) of the total C stock. The pine plantations revealed the highest mean aboveground and total carbon stock. Nevertheless, the higher aboveground C-stock of the plantations could only partially compensate the substantially lower amount of SOC.

The differences in carbon pools among the locations

At all localities, except Soldados, the total aboveground C pools were significantly highest in the plantation sites (Pi) compared to the other types of land use (Table 5). Furthermore, the highest values were recorded in the locations with the lowest altitude: Irquis (106.2 tC/ha), Nero (68.5 tC/ha), and La Paz (68.6 tC/ha). In Soldados, the highest location, the amounts of aboveground carbon were similar between NG (38.2) and Pi1 (35.2) and Pi2 (35.8).

The carbon in the ground vegetation of the plantations is linked with tree density. The less dense plantations such as the ones of Soldados, Quimsacocha, Irquis and Nero (513, 573, 611 and 694 trees per ha, respectively) had the highest amounts (Soldados 22.6/23.3, Quimsacocha 14.8, Irquis 14.5, and Nero 16.9 tC/ha). In contrast, the denser plantations (Tutupali Chico and Tutupali Grande with 712 and 793 tress per ha, respectively) registered the lowest amounts of understory carbon (9.1 and 9.0/6.0 tC/ha, respectively). At all locations the aboveground carbon of the grazed sites (G) was lower than that of the NG sites, at five locations on a significant level, and also the variation among the G sites was much lower.

Regarding the total belowground C pool, there was a clear trend: C pools were highest in all Pi locations, followed by NG, independent from the elevation.

Concerning total SOC stocks (0–45 cm deep), the situation varied among the land uses. At three locations (Irquis, La Paz, Tutupali Chico) the Pi sites had significantly lower SOC pools than the NG and G sites, while at Soldados one plantation (Pi1) had a significant higher pool. At the other locations the SOC pools did not show significant differences. Regarding the share of the deepest tier (30–45 cm) in the total SOC stock it is striking that at the highest location Soldados, it contributed only between 5.7 and 9.3% to the total SOC, while at the remaining locations it was between 23.6 and 33.2%

Despite the differences among the compartments of the several sites regarding the total carbon stock, only the locations of Irquis and Tutupali Chico registered significant differences between the land uses (Table 5).

Table 4 Mean values of carbon in tons per hectare followed by the standard deviation for each land use

Land use	Aboveground C		Total AG carbon	Belowground C		Total BG carbon	Total SOC	Total carbon stock
	Ground vegetation (litter + herbs + shrubs)	Pines (trunk, branches, leaves)		Roots	Pine roots			
NG	23.1 (17.1)	–	23.1 (17.1)	2.7 (1.6)	–	2.7 (1.6)	275.6 (75.9)	301.3 (76.3)
G	9.1 (5.3)	–	9.1 (5.3)	1.5 (1.3)	–	1.5 (1.3)	282.6 (91.3)	293.2 (91.8)
Pi	14.5 (7.4)	40.9 (27.9)	55.4 (26.8)	3.9 (3.1)	3 (1.3)	6.9 (2.6)	258.0 (78.8)	320.2 (74.0)

AG aboveground, *BG* belowground, *SOC* soil organic carbon (0–45 cm)

Table 5 Mean carbon values of the components of each carbon pool (± standard deviation) [aboveground (AG), belowground (BG) and SOC], for each land use within each location

Location (m a.s.l.)	Land use	Aboveground C (t/ha)			Belowground C (t/ha)			SOC (t/ha)				Carbon stock (AG + BG + SOC)
		(hebs + shrubs + litter + dead wood)	Pines	Total AG	Roots	Pine roots	Total BG	0–15 cm	15–30 cm	30–45 cm	Total SOC	
Irquis (2800)	NG	15.0 (3.8)^{a}		15.0 (3.8)^{b}	1.2		1.2 (0.4)^{b}	85.8 (21.1)^{a}	72.8 (17.0)^{a}	61.1 (14.9)^{a}	219.7 (50.7)^{a}	235.9 (48.1)^{a}
	G	9.0 (2.7)^{b}		9.0 (2.7)^{c}	0.6		0.6 (0.3)^{c}	67.5 (11.4)^{a}	58.1 (11.7)^{a}	46.0 (12.8)^{a}	171.5 (32.5)^{a}	181.1 (33.6)^{b}
	Pi	14.5 (5.7)^{ab}	91.7	106.2 (14.8)^{a}	2.7	4.4	7.1 (1.1)^{a}	46.4 (12.3)^{b}	39.4 (6.3)^{b}	32.8 (3.4)^{b}	118.6 (21.4)^{b}	231.9 (30.7)^{a}
Nero (3230)	NG	21.3 (12.6)^{a}		21.3 (12.6)^{b}	4.4		4.4 (1.7)^{b}	109.8 (23.0)^{a}	105.6 (15.1)^{a}	94.0 (17.8)^{a}	309.4 (46.4)^{a}	335.1 (52.9)^{a}
	G	18.3 (5.5)^{a}		18.3 (5.5)^{b}	1.4		1.4 (0.3)^{c}	142.9 (53.1)^{a}	114.8 (30.0)^{a}	106.0 (15.6)^{a}	363.7 (85.1)^{a}	383.4 (81.8)^{a}
	Pi	16.9 (7.4)^{a}	51.6	68.5 (15.6)^{a}	2.6	3.5	6.1 (1.2)^{a}	106.9 (19.8)^{a}	105.6 (12.3)^{a}	105.4 (23.1)^{a}	317.9 (45.7)^{a}	392.5 (52.1)^{a}
La Paz (3340)	NG	25.1 (18.4)^{a}		25.1 (18.4)^{b}	2.9		2.9 (1.4)^{b}	101.2 (18.0)^{a}	95.8 (15.2)^{a}	77.4 (10.9)^{a}	274.5 (42.4)^{a}	302.5 (42.8)^{a}
	G	6.3 (1.4)^{b}		6.3 (1.4)^{c}	1.5		1.5 (0.3)^{c}	94.9 (26.4)^{a}	89.1 (24.1)^{a}	84.0 (31.9)^{a}	267.9 (81.5)^{ab}	275.7 (80.6)^{a}
	Pi	13.9 (2.4)^{a}	54.7	68.6 (22.0)^{a}	2.7	4.0	6.7 (1.6)^{a}	77.8 (18.4)^{a}	81.3 (14.3)^{a}	65.5 (7.0)^{a}	224.6 (28.9)^{b}	299.9 (35.1)^{a}
Tutupali Chico (3450)	NG	28.0 (17.2)^{a}		28.0 (17.2)^{b}	3.1		3.1 (1.5)^{b}	135.2 (15.0)^{a}	124.7 (13.2)^{a}	113.3 (16.0)^{a}	373.2 (24.5)^{a}	404.3 (33.7)^{a}
	G	8.5 (4.5)^{b}		8.5 (4.5)^{c}	1.4		1.4 (0.3)^{c}	125.6 (14.2)^{a}	124.6 (7.8)^{a}	103.8 (7.1)^{a}	354.0 (24.2)^{a}	363.9 (22.6)^{b}
	Pi	9.1 (1.7)^{b}	50.0	59.1 (19.0)^{a}	4.5	3.5	8.0 (1.6)^{a}	123.4 (20.5)^{a}	102.6 (10.6)^{b}	88.7 (13.5)^{b}	314.7 (27.5)^{b}	381.8 (32.9)^{ab}
Tutupali Grande (3480)	NG	18.8 (15.2)^{a}		18.8 (15.2)^{b}	2.3		2.3 (0.5)^{b}	99.8 (18.0)^{a}	79.1 (27.0)^{a}	78.6 (25.3)^{a}	257.5 (49.5)^{a}	278.6 (54.4)^{a}
	G	9.5 (4.8)^{ab}		9.5 (4.8)^{b}	1.2		1.2 (1.3)^{b}	95.0 (52.9)^{a}	96.8 (8.7)^{a}	72.7 (38.0)^{a}	264.5 (92.2)^{a}	275.2 (92.4)^{a}
	Pi1	9.0 (4.1)^{ab}	46.2	55.2 (12.9)^{a}	1.9	3.5	5.4 (0.3)^{a}	117.5 (46.6)^{a}	101.0 (39.9)^{a}	80.4 (33.6)^{a}	299.0 (119.2)^{a}	359.6 (120.4)^{a}
	Pi2	6.0 (2.6)^{b}	34.2	40.2 (12.9)^{a}	1.9	3.1	5.0 (1.3)^{a}	118.9 (29.3)^{a}	113.8 (23.8)^{a}	72.0 (5.7)^{a}	304.7 (51.8)^{a}	349.9 (49.9)^{a}
Quimsacocha (3640)	NG	15.2 (6.6)^{a}		15.2 (6.6)^{b}	1.8		1.8 (0.3)^{b}	114.6 (18.8)^{a}	110.5 (19.3)^{a}	95.6 (22.2)^{a}	320.7 (58.7)^{a}	337.7 (55.1)^{a}
	G	4.7 (1.2)^{b}		4.7 (1.2)^{c}	0.4		0.4 (0.4)^{c}	130.9 (14.3)^{a}	114.2 (36.3)^{a}	91.9 (24.9)^{a}	337.0 (52.9)^{a}	342.1 (53.5)^{a}
	Pi	14.8 (2.6)^{a}	14.8	29.6 (15.4)^{a}	5.5	1.8	7.3 (2.9)^{a}	93.3 (12.2)^{b}	109.0 (25.3)^{a}	89.4 (23.1)^{a}	291.7 (38.4)^{a}	328.6 (49.8)^{a}
Soldados (3720)	NG	38.2 (28.5)^{a}		38.2 (28.5)^{a}	3.0		3.0 (2.3)^{b}	88.0 (28.7)^{b}	70.0 (21.6)^{a}	16.1 (10.1)^{a}	174.0 (50.0)^{b}	215.2 (60.9)^{a}
	G	7.5 (1.2)^{b}		7.5 (1.2)^{b}	3.8		3.8 (0.4)^{b}	115.2 (14.3)^{ab}	90.4 (36.3)^{a}	14.1 (24.9)^{a}	219.6 (52.9)^{ab}	230.9 (53.5)^{a}
	Pi1	22.6 (10.4)^{a}	12.6	35.2 (9.9)^{a}	4.5	1.6	6.1 (0.6)^{a}	120.4 (7.5)^{a}	94.5 (20.7)^{a}	13.1 (4.1)^{a}	228.0 (25.1)^{a}	269.3 (29.9)^{a}
	Pi2	23.3 (4.5)^{a}	12.5	35.8 (11.5)^{a}	8.5	1.4	9.9 (4.6)^{a}	119.0 (22.9)^{a}	90.5 (27.8)^{a}	13.3 (2.8)^{a}	222.7 (44.6)^{ab}	268.4 (51.2)^{a}

NG natural grassland, *G* grazed páramo, *Pi* pine plantation

Different letters are significantly different from each other ($p < 0.05$)

Concerning the influence of the elevation on the biomass of the pine trees Table 5 shows that above- and below-ground biomass of the pine trees decreased clearly with increasing elevation.

For the three types of land use, the values of SOC got lower with increasing depth (Table 5).

Discussion

The results of this study provide estimates of carbon stocks of the southern Ecuadorian páramo ecosystem under three types of land use: natural grassland (NG), grazed páramo (G), and pine plantations (Pi). With mean total carbon stocks (above- + below-ground + SOC in the top 45 cm) between 179.3 and 404.3 tC/ha (Table 5), the study confirms the high capacity of the páramo ecosystem as a carbon stock [10, 73]. The most important C-pool of the páramo in all land uses is the soil: in NG an average of 91.5% of the carbon stocks corresponded to SOC, in G 96.4%, and in Pi 80.6%, respectively.

Comparison of carbon pools among land use types

Aboveground carbon

The most noticeable difference in C stock among the land use types in our study occurred in the above- and below-ground biomass carbon pool. Similar to other studies in the Ecuadorian Andes [11, 74], we registered the highest amount of aboveground C in the plantations (Pi). Other studies obtained similar results with native trees [19, 75, 76]. In relation to the different elevation ranges, pines progressively decreased in size with the increase of elevation. The carbon values of the pine trees that we recorded at our two highest elevations (12.5 to 14.8 tC/ha) are similar to those (14 tC/ha) reported in a study conducted in a close area of the páramo at a similar elevation (3800 m a.s.l.) with *Pinus radiata* D. Don [77]. At the lowest elevation (2800 m a.s.l.) the stock was considerably higher (91.7 tC/ha) and compatible with those obtained by Bremer [74] (99–122 tC/ha). However, our values are lower than those reported in two other studies [11, 78]. This could be explained by the fact that these studies measured much older pines (40 years) and native species adapted to high elevations. Another reason for the difference could be that our own allometric equation for the pine's biomass estimation revealed a lower inclination with increasing diameter compared to the other curves (Fig. 2).

The C stocks of the natural grassland sites, except for the location of Soldados, are similar to those obtained by Bremer [74] (23.9 tC/ha) registered in tussock grass sites dominated by *Calamagrostis intermedia*, burned over 45 years ago and used for extensive Alpaca grazing as well as to those obtained by Farley et al. [11] (19.4–22.9 tC/ha) in páramo grassland burned 9 years ago with Alpaca grazing and burned 15 years ago with no grazing. We registered the highest value of C (38.2 t/ha) in NG at our highest elevation (3720 m a.s.l.). This was caused by the fact that the tussock grasses were very long and dense, in addition to the presence of tall shrubs in two study plots. Shrubs' biomass can considerable increase aboveground carbon, as was registered in the páramos of the Yacuri National Park that is located in a southern region from our study area [79].

The carbon stock obtained in grazed sites (G) ranged from 4.7 to 9.5 tC/ha, except for the location of Nero which revealed an extremely high value of 18.3 tC/ha. These values are similar to those obtained by Hofstede et al. [80] in a study of the páramos of Colombia, in the Parque Nacional de los Nevados. In this study, Hofstede distinguished several categories of páramo: in 'moderately grazed and burned páramo' he registered 10.6 tC/ha, in 'heavily grazed and burned páramo' 4.3 tC/ha, and in páramo 'heavily grazed without recent burning history' 7.7 tC/ha. In another study located 150 km north-east from our study area, in the Andes of Central Ecuador, Ramsay [75] measured the biomass of a páramo grassland extensively grazed by cattle and horses, and regularly burned every 2 to 4 years. In his study Ramsay measured 4.0 to 4.2 tC/ha. These values are lower than ours, probably because Ramsay did not include litter in his measurements, which is an important component of the grasslands. Furthermore, he estimated a low net annual productivity for these páramo sites, mainly attributed to physiological water limitation.

When the elevation increases, also the physical conditions of the habitat change dramatically. These changes are collectively known as elevational gradients. They are associated with changing components such as temperature, wind velocity, atmospheric gas composition, water availability, nutrient deposition and cycling, soil weathering, and solar irradiance [81]. All of these components influence the vegetation type, composition and primary production, and through this, the input of SOC. In addition, accumulation of carbon is directly influenced by temperature, soil weathering and water availability.

Native Páramo plants are well adapted to the extreme temperatures occurring in the páramo, mainly low night temperatures followed by strong solar radiation during the day [76], while this may not be true to the introduced pines at the higher elevations. Correspondingly, in our study we observed a negative effect of increasing elevation on tree biomass of pines (above and below-ground). However, our study did not examine enough environmental factors at the different elevations to conclude that elevation is the responsible factor for limiting pines growth. Nevertheless, the poor development of the pines established in the highest regions of this study is consistent with the observations made by Morris [82] in which he recognized restricted development of planted pines in areas above 3500 m a.s.l, in this region. Moreover, across the treeline ecotone, which is the zone where the plantations of the higher locations were established, stand density and tree vitality decreases with increasing elevation [83].

Belowground carbon

All the aforementioned studies related to carbon stock estimations included aboveground carbon pools. However, they did not consider the calculation of belowground carbon pools, probably because it is very laborious and demands much time and effort [84, 85].

In a study [77] carried out in the central zone of the Ecuadorian páramo in an elevational range between 3790 and 4100 m a.s.l, only 0.15 tC/ha of belowground biomass were registered in *P. radiata* plantations, and 0.17 tC/ha in NG. In our study, the belowground biomass carbon represents 2.7% of the total Pi carbon stock and less than 1% of the NG and G total carbon stock. Probably the values of Cargua et al. [77] are lower than those of our study most likely because they were performed in a higher elevation range. Although the belowground biomass does not contribute a significant part to the total C stock the difference of 5.4 tC/ha between the Pi and G sites and 4.2 tC/ha to the NG sites justifies the consideration of this compartment when the land uses are compared.

Soil organic carbon

We found that total soil organic carbon (0–45 cm depth) was high across all sites (118.6 to 373.2 tC/ha) and at five locations significant differences exist among the three land uses. Similar to previous studies [11, 15, 28], our results revealed significant lower values of total SOC (0–45 cm) for the plantations at the locations of Irquis, La Paz, Tutupali Chico and in the superficial layer of SOC (0–15 cm) of Quimsacocha compared to G and NG. In contrast, in the location of Soldados, both plantations (Pi1 and Pi2) presented significant higher values of SOC at the superficial layer. According to some studies [86, 87], afforestation is expected to increase SOC when plantations have been established on degraded or cultivated soils. In the case of the two plantations of Soldados, none of them (Pi1 and Pi2) were established on cultivated lands. In the same year that the plantations of Soldados were established, a study [88] was carried out to evaluate the state of conservation of the Ecuadorian páramos. Through transects all over the páramo, including the location of Soldados, several factors were evaluated such as: the degree of burning and grazing, other anthropic disturbances, erosion of the place, content of organic matter and biological activity in the soil. The study classified the region of Soldados as one of the most degraded páramos. This would explain the accumulation of SOC caused by the plantations of Soldados. Although the intention of these plantations was not to recover the soils, they obviously fulfilled this function. Nevertheless, as has been shown in a study in the Peruvian Andes [89], native species can be more successful in regenerating degraded soils.

The differences in SOC values that occur within each elevation range, and within some sites, highlight the heterogeneity that can exist between the categories of land use. In Hofstede's study [25], in which the impact of pine plantations on soil carbon along the Ecuadorian páramo was studied, it was concluded that it is difficult to generalize the effects of the plantations since they vary based on environmental factors, land use history, and management of the plantations [25]. In addition to the aforementioned factors, other researcher suggest that the effects are also be influenced by edaphic and pedogenic factors [16].

Conclusion

This study indicates that afforestation with *P. patula* in the páramo has enhanced biomass carbon stocks in comparison with natural grassland and grazed páramo. The plantations stored more biomass aboveground, mainly in the sites located in the lower elevational areas. In the higher areas, however, the pines' biomass production was very limited. Furthermore, as in other studies [11, 15, 28] in most of the locations we registered a loss of soil carbon, as well as compaction and acidification of the soil. Therefore, afforestation in the highest zones of the páramo for the purpose of CO_2 mitigation is not an advisable option.

Besides the tradeoff of belowground for aboveground carbon, the carbon stored in the pines is more vulnerable to be released to the atmosphere caused by fire in comparison to the carbon stored in the soil, which is a more stable pool over a longer period of time. Even though most of the carbon afforested stocks were higher, those of natural grassland were also high, which confirms that native grasslands can be an effective carbon store as well [15, 90, 91]. This study suggests that forestry plans should be assessed case by case, considering not only the limiting factor of elevation, but also the site quality especially affected by the type of previous land use. It is important to consider that the overall assessment of carbon sequestration projects depends not only on the development of the trees but also on the socioeconomic factors. If the demands and the local timber market are not considered, these projects create false expectations and disappointment on the part of the landowners [34]. Furthermore, these land use changes compromise other páramo ecosystem services such as water regulation and supply and biodiversity conservation which are factors that should be included when assessing the feasibility of these projects.

Abbreviations

ABU: Adult bovine unit; AG: Aboveground; BD: Bulk density; BG: Belowground; C: Carbon; CDM: Clean Development Mechanism; DBH: Diameter at breast height; Eq: Equation; FSS: Fine soil stock; G: Grazed páramo; IPCC: Intergovernmental Panel on Climate Change; NG: Páramo natural grassland; Pi: Pine plantation site; SOC: Soil organic carbon; UNFCCC: United Nations Framework Convention on Climate Change.

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Authors' contributions

CQD, PC, BS, RM and MW made substantial contribution to the conception and design of the work. CQD collected and analyzed the data. CQD and JC performed the analysis of the data. CQD wrote the original draft of the manuscript. MW was the supervisor and PC and PH were the co-supervisors. All authors contributed to the paper's structure and provided extensive revision. All authors read and approved the final manuscript.

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Availability of data and materials

The data supporting our conclusions are available either in the paper itself or in the links listed in the references. Additional data may be requested from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1] Department of Ecology and Ecosystem Management, Technical University of Munich, Munich, Germany. [2] Departamento de Recursos Hídricos y Ciencias Ambientales, Universidad de Cuenca, Cuenca, Ecuador.

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Publisher's Note

9.4 Publication IV

Title: 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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Article

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

Carlos Quiroz Dahik [1,2], Franklin Marín [1], Ruth Arias [1], Patricio Crespo [1], Michael Weber [2] and Ximena Palomeque [1,*]

1 Departamento de Recursos Hídricos y Ciencias Ambientales, Facultad de Ciencias Agropecuarias, Facultad de Ingeniería, Universidad de Cuenca, Av. 12 de abril s/n, 0101168 Cuenca, Ecuador
2 Institute of Silviculture, Center of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany
* Correspondence: ximena.palomeque@ucuenca.edu.ec

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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).

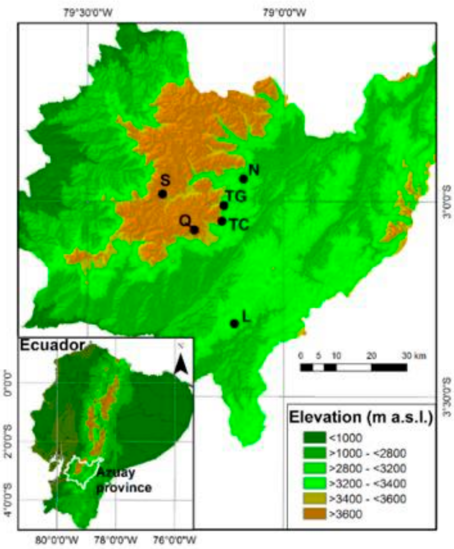

Figure 1. Location map of the study area showing the sites that correspond to natural grassland and pine plantations in three different elevational ranges: N (Nero) and L (La Paz) from 3200 to 3400 m a.s.l., TC (Tutupali Chico) and TG (Tutupali Grande) from 3400 to 3600 m a.s.l. and Q (Quimsacocha) and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

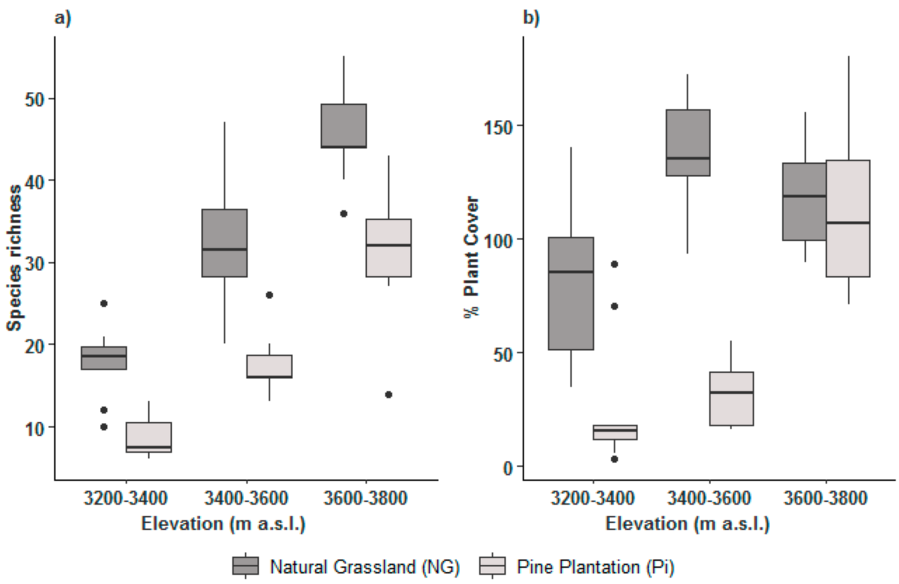

Figure 2. Box plots for the effects of elevational range (3200–3400, 3400–3600, and 3600–3800 m a.s.l.) and vegetation (Pi, NG) on (**a**) herbaceous species richness and (**b**) percentage of herbaceous vegetation cover.

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

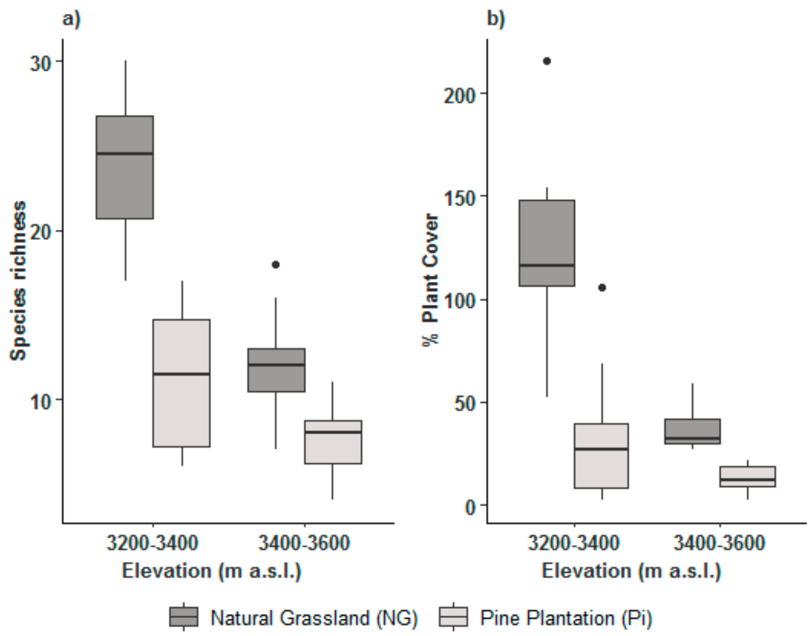

Figure 3. Box plots for the effects of elevational range (3200–3400 and 3400–3600 m a.s.l.) and type of vegetation (Pi and NG) on (**a**) woody species richness and (**b**) woody plant cover.

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).

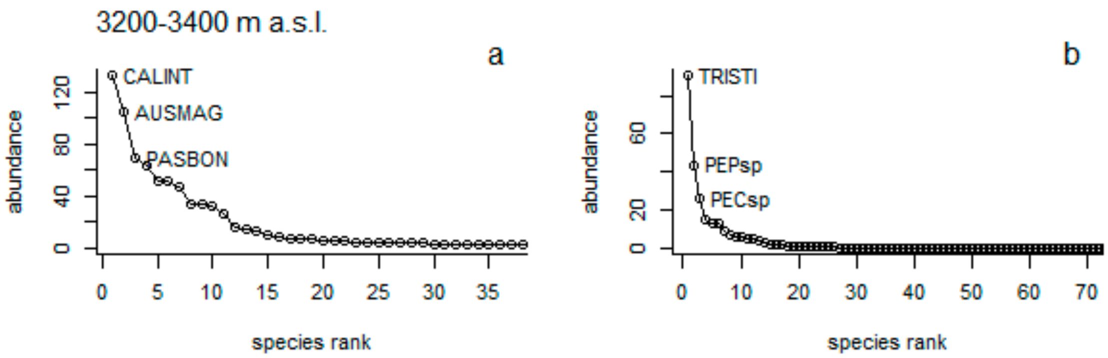

Figure 4. *Cont.*

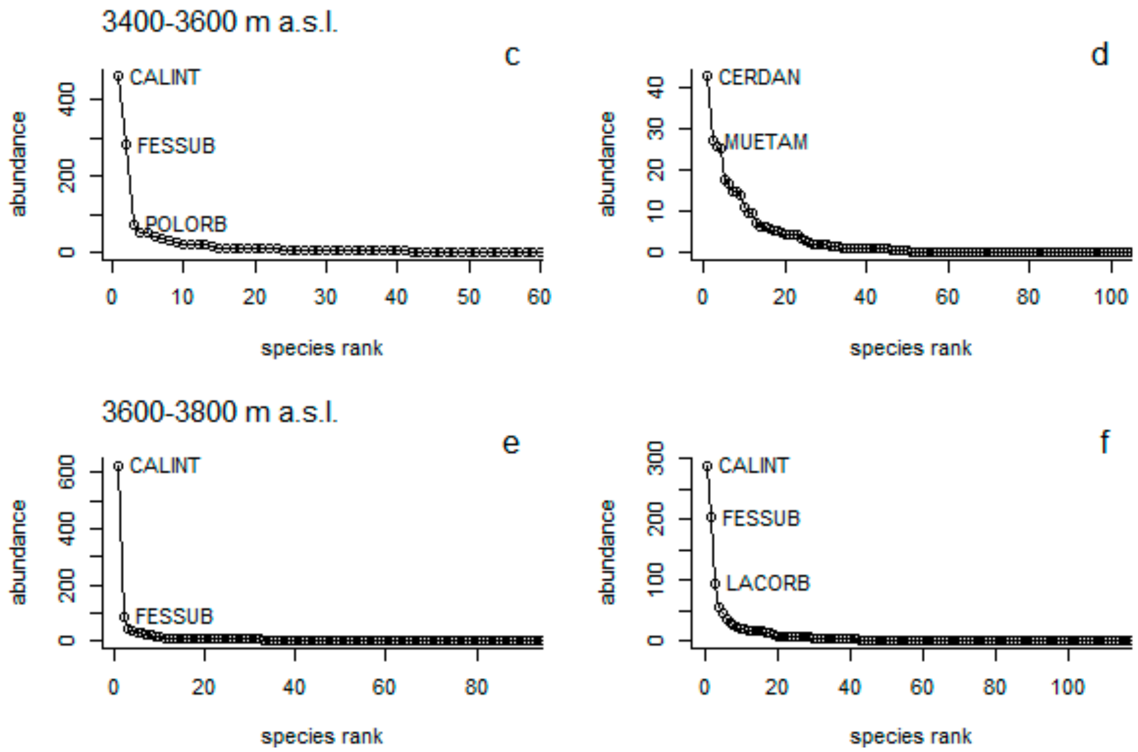

Figure 4. Herbaceous species abundance rank at natural grassland (NG) cover (**a**,**c**,**e**) and pine plantations (Pi) cover (**b**,**d**,**f**) across three different elevational gradients (3200–3400, 3400–3600, and 3600–3800 m a.s.l.).CALINT = *Calamagrostis intermedia*, AUSMAG = *Austrolycopodium 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).

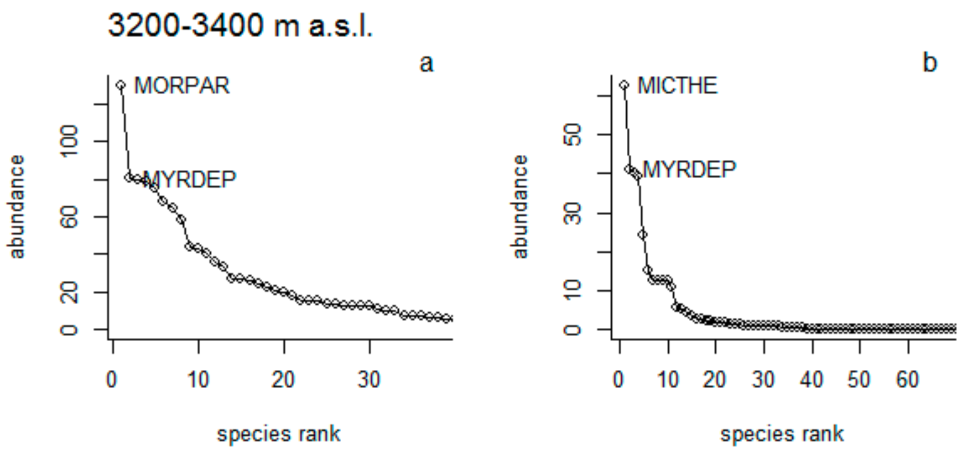

Figure 5. *Cont.*

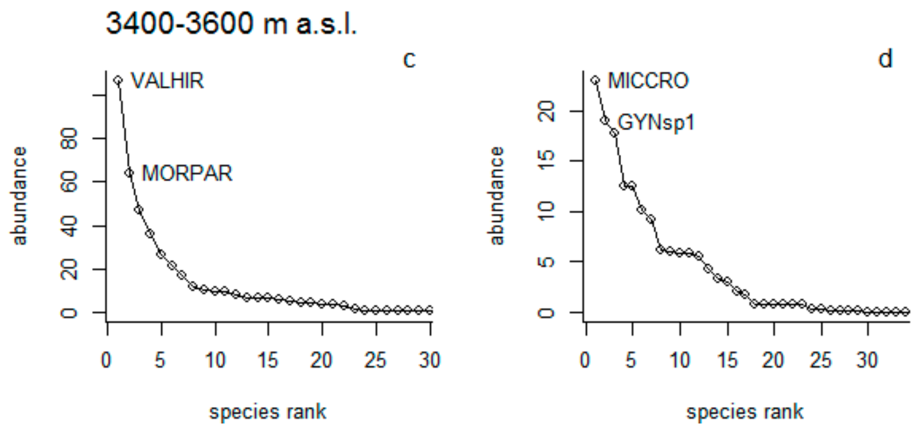

Figure 5. Woody species abundance rank at natural grassland (NG) cover (**a**,**c**) and pine plantation (Pi) cover (**b**,**d**) across three different elevational gradients (3200–3400 and 3400–3600 m a.s.l.). MORPAR = *Morella parvifolia*, MYRDEP = *Myrsine dependens*, MICTHE = *Miconia theaezans*,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

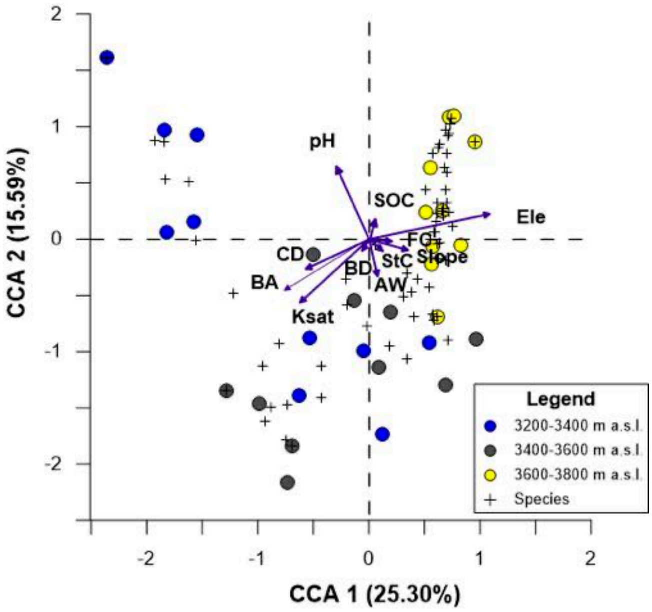

Figure 6. Canonical Correspondence Analysis (CCA) showing ordination of herbaceous species richness and their plant cover (+), plot (circles), and attributes of pine plantation and their physical and chemical soil characteristics across an elevational range (arrows). Abbreviations are as follows: CD = 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.

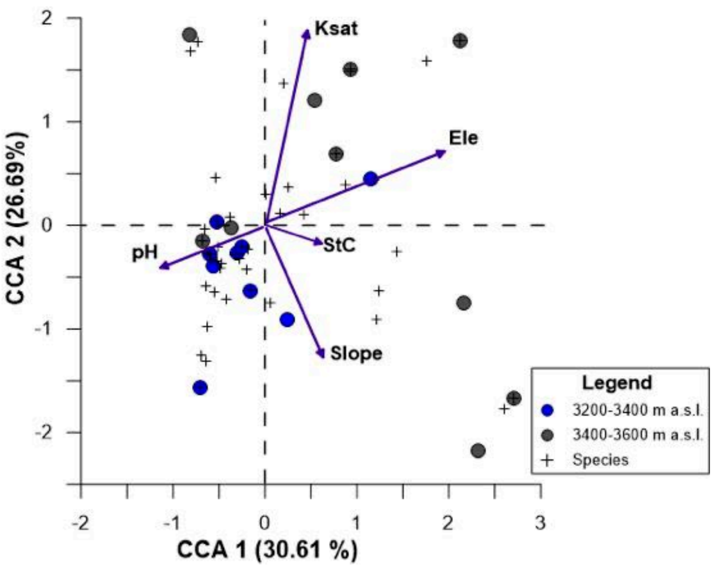

Figure 7. Canonical Correspondence Analysis (CCA), showing ordination of woody species richness and their plant cover (+), plot (circles) and attributes of pine plantation and their physical and chemical soil characteristics across an elevational range (arrows). Abbreviations are as follows: CD = canopy 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 sibbaldioides* 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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