Effects of Climate Change on Key Ecosystem Services provided by the Ecuadorian Páramo Ecosystems

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Doctor of Philosophy

University of York

Environment and Geography

September 2018

Abstract

The Ecuadorian páramo ecosystems play an important role in providing the local population with drinking water, irrigation, hydropower generation, carbon storage, and agricultural production. In Ecuador, páramo vegetation has suffered significant degradation and loss due to land use change. This has had a major impact on the capability of the ecosystems to resist or adapt to external pressures such as climate change. This research aims to understand the effects of climate change on the Ecuadorian páramo ecosystems and the potential consequences on the ecosystem services they provide.

This study applies state-of-the-art techniques to evaluate: a) the impact of climate change on the climatic niche distribution of the páramo ecosystems based on future greenhouse gas concentration scenarios; b) the amount of carbon stored in both soil and vegetation for key types of páramo ecosystems; and c) the future exposure of the Ecuadorian páramos to land use pressures, considering climate as a determining factor for increases or decreases in the farming frontier.

The research show that in 30 (2050) to 50 (2070) years, páramo ecosystems with isolated or restricted distribution could suffer significant niche contraction (>60%) or niche extinction (100%), while ecosystems with a broad distribution seem less vulnerable (<60%). The carbon (C) estimates show that C in soils could vary from 87.7 to 278.9 ton C/ha, while in vegetation could range from 5.3 to 8.9 ton C/ha in grassland and shrubland vegetation, and 96.3±32.4 ton C/ha in forest. Soil C stock is influenced by altitude and climatic conditions such as precipitation and temperature. The farming frontier could increase in 23% (2050) to 35% (2070) towards and within the páramo areas, most of them occurring in areas without protection (16%-21%). This study reveals considerable challenges for the future of the Ecuadorian páramo, highlighting the need to implement adaptation strategies in these natural areas.

List of Contents

List of Tables

(Short titles)

Chapter I

Chapter II

Chapter III

Chapter IV

List of Figures

(Short titles)

Chapter I

Chapter II

Chapter III

Chapter IV

List of Supplementary Material

(High Resolution Maps)

Chapter I

- Figure 1. 1 Spatial distribution of the páramo ecosystems in the Andes Cordillera.
- Figure 1. 2 Spatial distribution of the páramo ecosystems in Ecuador
- Figure 1. 3 Spatial distribution of the Ecuadorian páramo soils by order

Chapter II

- Figure 2. 1 Location of the Andes Biogeographic Region in Ecuador
- Figure 2. 1 Location of the Andes Biogeographic Region in Ecuador.
- Figure 2. 6 Location of Climatic Niche Impact on ecosystem HsSn02
- Figure 2. 7 Location of Climatic Niche Impact on ecosystem AsSn01.
- Figure 2. 8 Location of Climatic Niche Impact on ecosystem RsSn01.
- Figure 2. 9 Location of Climatic Niche Impact on ecosystem BsSn01.
- Figure 2. 10 Location of Climatic Niche Impact at National scale, based on “without consensus” approach, according to future scenario RCP 4.5 and RCP 8.5.
- Figure 2. 11 Location of Climatic Niche Impact at National scale based on “high consensus” approach, according to future scenario RCP 4.5 and RCP 8.5.
- Figure 2. 12 Location of Páramo Climatic Niche shifts in the Andes of Ecuador
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem AsAn01
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsSn04.
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsN03.
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsSn03.
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsNn01
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsNn02
- Figure 2. 13 Location of Climatic Niche Impact on ecosystem HsSn01.

Chapter III

- Figure 3. 1 Location of Carbon data sites respect to the Eastern and Western Andes Cordillera.

Chapter IV

Acknowledgements

First, I would like to thank to God for always being the best companion in every adventure that I undertake. Without His guidance, His love and His wisdom the achievement of this goal would not have been possible.

This research was funded by the National Secretariat of Higher Education, Science, Technology, and Innovation (SENESCYT- Ecuador). The funding for this research is gratefully acknowledged and made this entire project possible to investigate.

I would like to thank Professor Piran White for supervising my work. Thank you to my co-supervisors Dr Colin McClean and Dr Sylvia Toet for their guidance throughout my PhD. I also thank the administrative staff at the Department of Environment and Geography for all the facilities provided. Thank you also to the York Advanced Research Computing Cluster (YARCC), led by the IT Department, at the University of York. Thank you in particular to Dr Andrew Smith for his kindness and incredible technical support.

Thank you to the staff from the Ministry of Agriculture, Livestock, Aquaculture, and Fisheries (MAGAP) in Ecuador for all the information and technical advice. Thank you in particular to Eng. Blanca Zimbaña, Eng. Santiago González, Eng. Cristina Iglesias, and Eng. Yánez.

Thanks you to the people and friends from Ecociencia Foundation, National Secretariat for Planning and Development (SENPLADES) and Consortium for Sustainable Development of the Andean Ecoregion (CONDESAN) for sharing their information, experience, and advice to improve my research. A special thanks to Christian Martínez, Marjorie Villaroel, Patricio Mena, Rossana Manosalvas, Juan Calles, Fernando Rodríguez, Leonardo Espinosa, Verónica Santillán, Alexandra Cruz, and Francisco Cuesta.

Thank you to all the lovely PhD friends I met along these four years in the Department of Environment and Geography. You made this PhD a special and fun journey. A very special thank you to Hie Ling, Talia, Rosa, Rebecca, Lena, Tar, Syu and Alda. A big thank you everyone in the office 128, the best office I could have ever dream off with. Your support, positivity, and love helped me to finish my journey.

A big thank you to my green-STEMS girls, Maria, Giulia, and Ruth, your friendship, love, and support meant the world to me. I love you girls, you were my family away from home. Many thanks to all my friends from Ecuador and other parts of the world who were supporting my dream.

Thanks to my family at Calvary Chapel for their love and prayers. A special thank you to Mike, Karina and Helen. I would also like to thank to all my friends and instructors from York Sport Village. You all were an important part of my daily life here in York. I am immensely grateful with Michelle, Anuk, Sam, Anika, and Neil. I had a lot of fun with you guys.

Finally, the most special thank goes to my family for their unconditional support, advice, and love during all these years that I have been away from home. You are the main reason that I am able to finish my PhD.

The LORD is my rock, my fortress, and my saviour; my God is my rock, in whom I find protection. He is my shield, the power that saves me, and my place of safety.

Psalm 18:2

Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

Karla E. Beltrán Valenzuela

Chapter I
General Introduction

1. Introduction

The tropical Andes are characterized by containing a mosaic of ecosystems with an extraordinary biological and cultural diversity (Josse et al., 2009). The complex topography of the region results in diverse physical conditions that create unique habitats (Marengo et al., 2009). For more than 10,000 years, the well-being of human populations has been linked to the functioning of tropical Andean ecosystems. At present, millions of people depend on the Andean ecosystems as a source of fresh water, food, cultural importance, ecosystem goods, and services (Josse et al., 2009). Recently, in the tropical Andes, ranges of natural climatic variability have been recorded that exceed the historically documented thresholds (Anderson et al., 2017). In turn, there is concern about the general warming trends that are occurring and their implications for the integrity of the ecosystems and the human populations that depend on them. This study focuses on one of the most vulnerable Andean ecosystems known as páramos.

The páramo ecosystems consist of neo-tropical alpine vegetation ranging from Colombia to northern Peru along the Andes region, generally above 3,500 m.a.s.l (Buytaert et al., 2005b). These ecosystems are characterized by high endemism and diversity of their tropical high mountain flora which are linked to their evolutionary history (Hooghiemstra et al., 1995). The gradual rise of the Andes and the effects of glacial cycles in Pliocene and Pleistocene periods shaped this landscape (Hooghiemstra et al., 1995). The páramo landscape consists of uneven plains and valleys of glacial origin with a great variety of lagoons, wetlands and wet meadows (Mena and Ortiz, 2006). The páramo vegetation is dominated by herbaceous and shrubby plants communities located between the upper limit of the Andean forest and the perpetual snow (Molinillo and Monasterio, 2003; Hofstede et al., 2014).

The páramo region provides important ecosystem services for all Andean populations including water provision and regulation, carbon storage and livestock production, among others (Hofstede et al., 2003; Hofstede et al., 2014). The páramo vegetation constitutes the main source of water for the highlands of the Andes (Buytaert et al., 2006b). In fact, these ecosystems are considered the main source of water for the Andean region of Colombia and Ecuador and to a lesser extent also of Venezuela and Peru (Buytaert et al., 2006a). The vegetation functions as a giant sponge, storing and releasing water during the year, thereby ensuring the provision of water during dry periods in Andean regions (Buytaert et al., 2005b). This property is mainly due to the large accumulation of organic matter and the morphology of páramo plants (Mena et al., 2000). These plants are characterized by the predominance of small thick leaves with abundant trichomes which favour water accumulation (Llambí et al., 2012). Páramo soils are capable of regulating water flow from precipitation and snow melting from the glaciers (Mena et al., 2000), allowing their permanent use for irrigation, hydropower generation, and agricultural production (Smith and Cleef, 1988; Mena and Hofstede, 2006; Hofstede et al., 2014; Malagón and Pulido, 2000). Due to the great accumulation of organic matter in soils favoured by the cold and humid climate as well as by the low atmospheric pressure (Buytaert et al., 2006b), the páramo ecosystem is considered as a globally important reservoir of organic carbon and a natural mitigator of climate change (Winckell et al., 1991; Hofstede et al., 2014; Mena et al., 2000).

For decades, the Ecuadorian páramo ecosystem has suffered significant degradation and loss due to intensive land use pressure and land conversion, which has damaged the vegetation’s biophysical properties and reducing its capability to provide and regulate water, and to store carbon (Buytaert et al., 2011; Buytaert et al., 2005b; Buytaert et al., 2006b). These impacts are likely to be exacerbated in the future due to population growth, increases in living standards, expansion of the agricultural frontier and intensification of livestock grazing (Buytaert et al., 2011; Buytaert et al., 2006a). These anthropogenic interventions have caused not only severe impact on the ecosystem services provision but have also reduced the ecosystem’s capability to resist or adapt to external pressures such as climate change (Mena and Hofstede, 2006; Buytaert et al., 2006b; Hofstede et al., 2014).

Although the effects of climate change have been widely documented in all continents over the years, the published information is still scarce for the tropical Andes, making forecasts about the fate of the Andean ecosystems difficult (Herzog et al., 2012). There is a high level of uncertainty about the magnitude of the effects of climate change in Andean regions; however, the impacts of this phenomenon are certainly exacerbated in high mountain ecosystems (Beniston et al., 1997; Urrutia and Vuille, 2009; Solman et al., 2008; Marengo et al., 2009). In ecosystems with highly specialized habitat, limited environmental tolerance and a high dependence on the resources they provide, as in the páramo ecosystems, the level of vulnerability to climate change is high (Herzog et al., 2012). In theory, global warming and changes in precipitation patterns could lead to diverse ecosystem responses including tolerance and adaptation, migration to emerging gradients, or extinction due to an inability to adapt or move (Herzog et al., 2011, Parmesan and Yohe, 2003, Thomas et al., 2004). Temperature increases, increased seasonality and reduction in precipitation due to climate change could also alter the páramo's hydrological function since the key to high infiltration and water storage lies in the slow decomposition of soil organic matter which depends directly on cold weather and permanent humidity (Buytaert et al., 2006b; Buytaert et al., 2009). Influenced by future global warming, the capacity of páramo ecosystems to store and sequester carbon from the atmosphere could be reduced transforming them into net emitters of greenhouse gases (e.g. CO_2 and CH_4) (Herzog et al., 2012). The magnitude and consequences of these changes for the ecosystem services provided by the páramo vegetation are poorly understood.

Understanding the factors that are causing changes in ecosystems and ecosystem services is essential to design strategic interventions to minimize negative impacts (Millennium Ecosystem Assessment, 2005). The evaluation of ecosystem services requires the measurement, modelling and monitoring of ecosystem functions as a basis to promote the sustainable use of biodiversity, ecosystems, and natural resources in general (Carpenter et al., 2009). Among the variety of methodological approaches aimed at exploring the functions of ecosystems, biophysical models have excelled due to the multitude of uses for scientists, managers, and policymakers who investigate and govern natural processes (Bellocchi et al., 2011). The biophysical models are considered the most objective and effective way to project future ecological consequences caused by diverse drivers such as climate change (Wainwright and Mulligan, 2005); for this reason, they were used as main basis for the analyses.

One of the main strengths of the models is the exploration of interactions and feedback of natural and semi-natural systems (Wainwright and Mulligan, 2005), which help identify uncertainties in areas that lack knowledge. The accuracy of a model is determined, on the one hand, by the authenticity of the algorithms used to describe the real-world processes and also by the quality of the input data and the data used to evaluate the results (Bellocchi et al., 2011). Sadly, in most places (such as Ecuador), modellers often face with deficient databases because data monitoring is usually limited to a few points where the samples are collected and analysed with some intermittent frequency affecting the robustness of the models (Bellocchi et al., 2011).

Models are a simplification of a real natural system in which only the components that are considered relevant to the problem in question are represented (Wainwright and Mulligan, 2005). Consequently, one of the main problems of the models is the exclusion of important factors in their construction, including socio-economic and political variables that could influence future impacts and consequences on natural systems. Unfortunately, it is impossible to model all the potential motive forces affecting natural systems (Araújo et al., 2005) due to information constraints and since running complex models requires resources so expensive that relatively few countries (e.g. USA, UK and Japan) can afford them (Lahsen, 2005).

Models uncertainty is of great relevance in evaluating the impacts of climate change (Beven, 2007). Uncertainty could be caused by small errors in the input data that, although they do not affect the adjustment of the model in the time frame for which historical data are available, when they are extrapolated for longer periods of time they could cause significant deviations. The uncertainty linked to model predictions is often ignored by scientists and decision makers, or interpreted as a mere disagreement between experts; although, it is an important criterion in decision making (Beven, 2007). With this in mind, this study endeavoured to reduce the uncertainty surrounding climate change projections available for the Andes (Buytaert et al., 2009; Tovar et al., 2013) by using an ensemble approach based on two time horizons (2050 & 2070), two GHG emission concentration scenarios (RCP 4.5 & RCP 8.5) and several Global Climate Models (GCMs). This decision allowed for the control of errors and uncertainties in the individual models (Araújo and New, 2007). Models were also evaluated in terms of their predictive capacity and validated by comparing the simulated data with the real observation data as suggested by experts (Risbey et al., 1996; Pérez-Maqueo et al., 2006).

Although models inevitably present limitations linked with simplified assumptions and uncertainty (Wiens et al., 2009), not using them is not really an option because it results better than simply guessing what the future may hold and expect to be right. When model limitations are well-understood it is possible to make good use of them (Whittaker et al., 2005; Heikkinen et al., 2006). Model based investigations could constitute an important source of information by which scientists can interact and influence policy at local, regional, national, and international levels. Models are also considered beneficial in cases in which the collection of primary data is costly (Eigenbrod et al., 2010b) or limited, as in the case of Ecuador. In this context, biophysical models were used to communicate the diverse trajectories that páramo ecosystems could take in the coming decades due to climate change based on certain assumptions. The generation of models in this study is considered a significant contribution that favoured the exploration of some of the aspects that are currently influencing the behaviour of páramo ecosystems with results well-adjusted to the empirical data.

This research was designed to contribute to the need for scientific information on three main aspects related to some of the strategic ecosystem services provided by the Andean páramo ecosystems. In the first place, this study considers páramo biodiversity as a fundamental element to support ecosystem services (Balvanera et al., 2006; Haines-Young and Potschin, 2018). It contemplates that any alteration to the structural diversity of ecosystems can directly influence the provision of environmental services, such as provisioning and maintenance of habitat, reducing the resilience of ecosystems to environmental change (Millennium Ecosystem Assessment, 2005; Chapin III et al., 2000). Secondly, the potential of páramo ecosystems as providers of regulating services focused on their role as natural carbon sinks is evaluated. From a socioenvironmental point of view, páramo ecosystems function as provider of food was also analysed from the perspective of the impact that farming expansion could have on these natural area**s.** In this context, this study was focused on:

a) Predicting the impact of climate change on the climatic niche distribution of the eleven types of páramo ecosystems existing in the Ecuadorian Andes, considering current (1950-2000) and future (years 2050 & 2070) environmental conditions.
b) Quantifying the carbon stocks, in both soil and vegetation for ten key types of páramo ecosystems located in the Andes of Ecuador, based on secondary information compiled from literature generated over 15 years.
c) Analysing future changes induced by climate change in edapho-climatic suitability for three common Andean crops (i.e. potato, soft maize, and quinoa), as indicators of potential land use threats to the survival of the Andean páramo ecosystems.

To provide a background to the research objectives and put the results in context, general information about the páramo ecosystems is presented below. The following aspects are included: the origin of the Andean páramo ecosystems, current spatial distribution of the páramo ecosystems in the Andes, climatic conditions found in the Ecuadorian Andes as well as description of the eleven páramo ecosystems and páramo soils existing in Ecuador. Finally, an explanation of the ecosystem services provided by the Ecuadorian páramo ecosystem, and the anthropogenic pressures and the effects of climate change on the region are presented.

2. Recent Frameworks on Ecosystem Services

Ecosystem services are understood as the benefits that functional ecosystems provide to people (Millennium Ecosystem Assessment, 2005; Costanza et al., 1997). This simple definition appeared in the 1970s but it was not until the 1990s that it gained great momentum in the scientific literature (De Groot, 1992; Costanza et al., 1997; Daily, 1997). Parallel to these events, the concept of natural capital was developed (Costanza and Daly, 1992; Jansson, 1994; Dasgupta et al., 2000). Natural capital consider non-renewable resources, renewable resources, and ecosystem services as the biophysical basis for social and economic development (Common and Perrings, 1992; Arrow et al., 1996). The concept of ecosystem services has continued to evolve over the years. Boyd and Banzhaf (2007), for example, introduced the concept of "final ecosystem service" understood as "*the components of nature, directly enjoyed, consumed, or used to yield human well-being*" (Boyd and Banzhaf, 2007). Fisher (2008), contributed by separating ecosystem services into intermediate and final services and benefits, explaining that in accounting and valuation exercises only the benefits generated by the final services can be aggregated, and hence, avoid double counting.

More recently, Braat (2013) stated that ecosystem processes and functions should not be considered synonymous of ecosystem services. Ecosystem processes and functions should be understood as the biophysical relationships that exist independently of any benefit they may offer to humanity. In contrast, ecosystem services are processes and functions that benefit people, consciously or unconsciously, directly or indirectly (Braat, 2013). Haines-Young and Potschin (2018) suggested to frame the concept of ecosystem services by differentiating between: a) "final ecosystem services" understood as natural, semi-natural or artificial contributions of ecosystems to human well-being; b) "ecosystem good or product" as the things that people create from these final services contributing to human well-being ; and c) "benefit" to refer to human access to some good or product provided by the ecosystem producing well-being.

Given the growing interest in ecosystem services, over time appeared necessary to facilitate the discussion and systematic analysis of ecosystem services. Thus, in 2002, De Groot et al. (2002) proposed a classification system specifying the relationship and transitions of ecosystem processes and components and their transition to goods and. Later on, in 2005, the concept of ecosystem services was put into practice through the Millennium Ecosystem Assessment (MEA) (Millennium Ecosystem Assessment, 2005) by classifying the ecosystem services into four categories: provisioning, regulation, cultural and support. This classification included both those direct contributions to human wellbeing from the biotic and geotic structure of ecosystems, such as food or water (provisioning services); indirect contributions to human well-being from the functioning of ecosystems, such as water regulation or air purification (regulatory services), soil formation, photosynthesis and nutrient cycling (supporting services); and non-material and intangible contributions that society obtains through direct experience with ecosystems and biodiversity, such as sacred sites or recreation (cultural services) (De Groot et al., 2010a; Millennium Ecosystem Assessment, 2005).

Various classifications of ecosystem services have been developed since the MEA, launched by the United Nations Environmental Programme (UNEP) and criticized for not having considered the economic aspects of ecosystem change (De Groot et al., 2010b). Thus, in 2008, the Economics of Ecosystems and Biodiversity (TEEB) study (European Communities, 2008), an important European initiative, proposed a framework considering the global economic benefits of biodiversity, highlighting the increasing costs of biodiversity loss and ecosystem degradation (De Groot et al., 2010b; Balmford et al., 2008; Ring et al., 2010). Nowadays, conceptual frameworks continue to develop, such as the Common International Classification of Ecosystem Services (CICES) proposed by the European Environment Agency (EEA). CICES focuses on developing a hierarchically consistent, and science-based classification to be used for ecosystem mapping and accounting purposes (Haines-Young and Potschin, 2018). Other similar approaches like the Final Ecosystem Goods and Services Classification System (FEGS) developed by the U.S. Environmental Protection Agency have also emerged. This American initiative is focused on providing a foundation for measuring, quantifying, mapping, modelling, and valuing ecosystem services applicable at multiple scales (Costanza et al., 2017).

Until now, there is no agreement about the adequate differentiation between ecosystem functions and services, and their appropriate classification and quantification (Daily, 1997; Boyd and Banzhaf, 2007; Wallace, 2007; Fisher et al., 2009). Discussions continue around the place of biodiversity in the framework, the adequate differentiation of ecosystem from landscape functions and services, the way of valuing services provided by natural systems versus those cultivated (e.g. fish from the ocean versus fish from aquaculture), and the understanding of “Land use function” (Pérez-Soba et al., 2008) or ''Land function'' (Bakker and Veldkamp, 2008; Verburg et al., 2009), where the latter combines functions, services and benefits (De Groot et al., 2010a). Despite some differences in the details, the classification systems that have been proposed worldwide in the last twenty one years are very similar and have not deviated significantly from the original list of ecosystem services suggested by Costanza back in 1997 (Costanza et al., 2017). It would appear that it is time to accept that no classification is capable of capturing the many ways in which ecosystems support human life and contribute to human well-being (De Groot et al., 2010b). However, for an ecosystem assessment on a global scale, having terminology and standard classifications remains a necessity (De Groot et al., 2010b).

3. The Origin of the Andean Páramo Ecosystems

The entire flora located in Andean habitats above the treeline, is presumed to be very young and derived from habitats located in lower altitudes (Simpson, 1983). It is believed that the floristic differences in the vegetation of the Andes are due to the reception of propagules from different regions of the world and the different rates of survival of immigrant species (Simpson, 1983). The northern Andes received a more diverse range of settlers than any other high-altitude region across the Andes, providing more suitable habitats for species establishment and survival (Simpson, 1983). Several plant species that colonized the Andean habitats experienced autochthonous radiation, causing endemic speciation within certain habitat groups (Simpson, 1983). In the specific case of the páramo flora, its evolution has been determined by its tertiary volcanic history as well as by biophysical factors such as geographic isolation, moisture regimes, mother rock substrates (igneous over metamorphic), habitat diversity and human influence (Simpson, 1974; Vuilleumier and Monasterio, 1986; Luteyn and Balslev, 1992). The high diversity and endemism of the páramo flora is directly linked to its evolutionary history caused by the gradual ascent of the Andes and glacial events that occurred during the Pliocene and Pleistocene periods (Hooghiemstra et al., 1995; Van der Hammen and Cleef, 1986).

During the glaciations, the páramo vegetation located in the Northern Andes, became more diverse compared to mountainous flora located along the Southern Andes (Simpson, 1983). The climatic events during the Pleistocene era significantly influenced the levels of autochthonous speciation (Simpson, 1983). This speciation was caused by the retraction and dispersion of the genera during periods of isolation (Simpson and Todzia, 1990). The composition of páramo's original flora is neotropical and characterized by species coming from temperate areas of both hemispheres with a greater contribution from the northern hemisphere (Sklenář et al., 2011). Volcanism also played an important role in the formation, population and distribution of ecosystems in the Andes (Sklenář et al., 2010; Salamanca, 1992). Differences could be found between páramo vegetation located in the Andes of Venezuela, the

Eastern Cordillera of the Andes in Colombia and certain parts of the Central Cordillera versus páramo flora found in Western and Central Andes of Colombia and the majority of the Ecuadorian Andes. These differences are a consequence of non-volcanic and volcanic origin across the regions (Clapperton, 1993; Graham, 2009).

4. Spatial Distribution of the Andean Páramo Ecosystems

The páramo vegetation extends discontinuously along the High Andean region of Venezuela, Colombia, Ecuador and Peru between latitudes of 11° north and 8° south with small and disconnected extensions as far as Costa Rica and Panamá, covering in total 37,424 km^2 (Table 1.1 and Fig. 1.1) (Buytaert et al., 2006a; Hofstede et al., 2003). In Central America, the páramo vegetation occupies an area equivalent to 170 km^2, distributed along the Talamanca Cordillera between Costa Rica and Panama reaching altitudes between 3,000 and 3,819 m.a.s.l. (Hofstede et al., 2014). In Venezuela, páramo ecosystems cover an area of approximately 2,660 km^2 and can be found in the Mérida Cordillera, Serranía de Tamá, Serranía de Trujillo, and Sierra de Perijá regions (Hofstede et al., 2014). Most of the Venezuelan páramo vegetation is located above 3,000 m.a.s.l., except for that located in the south of Merida State, central-south of Táchira and Trujillo-Lara frontier (Molinillo and Monasterio, 2003). Peruvian páramo vegetation covers an extension of 462 km^2 and is located along the Andes and the Guamaní Cordilleras between 3,000 m.a.s.l. and 3,600 m.a.s.l (Hocquenghem, 1998; Hofstede et al., 2014) (Table 1.1 and Fig. 1.1).

The countries that have the largest area of páramo vegetation are Colombia and Ecuador. In Colombia, the páramo land covers and extension of 19,330 km^2 and extends over the entire Andean stretch and the Sierra Nevada of Santa Marta (Morales, 2007; Hofstede et al., 2014) (Table 1.1 and Fig. 1.1). Colombian páramos vegetation is generally found above 3,000 m.a.s.l., except for certain a-zonal páramo patches located from 2,500 m.a.s.l. (Hofstede et al., 2014). In Ecuador, the páramo vegetation extends from the border with Colombia to the North and to the Peruvian border to the South, covering 14,802 km^2 equivalent to 5.8% of national territory (MAE, 2013b). Ecuadorian páramo vegetation is distributed above the forest tree line along Eastern and Western Andes cordillera (Hofstede et al., 1998) (Table 1.1 and Fig. 1.1).The Eastern Cordillera has the greatest extension of páramo vegetation, forming an uninterrupted páramo complex from Carchi to Cañar (Fig. 1.1). Páramo vegetation located in the Western Cordillera is more fragmented; however, they include a non-fragmented páramo patch located between the provinces of Tungurahua, Chimborazo, and Bolivar (Fig. 1.1). In terms of altitudinal range, páramo ecosystems located at the centre and north of the country are generally found above the 3,500 m.a.s.l., whereas páramo ecosystems located at the south (Azuay and Loja provinces) are found at 2,800/3,000 m.a.s.l. (Hofstede et al., 2014; Smith and Cleef, 1988).

Figure 1.1 Spatial distribution of the páramo ecosystems in the Andes Cordillera.

Table 1.1 Area of Páramo Vegetation per Country.

Country	Location	Páramo Area (km^2)	%*
Panama	Central America	20	0.1
Costa Rica	Central America	150	0.4
Peru	South America	462	1.2
Venezuela	South America	2,660	7.1
Ecuador	South America	14,802	39.6
Colombia	South America	19,330	51.7
Total		**37,424**	**100**

** Percentage with respect to the total páramo area.*

5. Climatic Conditions in the Ecuadorian Andes

The Ecuadorian Andes have a climate influenced by several processes that occur on a large scale (Vuille et al., 2000). In the south-west of the Andes, the Humboldt Pacific current brings masses of cold and dry air, producing a semi-arid climate. Towards the northern Andes there is a tropical humid climate caused by the masses of warm and humid air that occur in the equatorial Pacific as well as the eastern slopes of the Andes which are permanently humid due to the influence of the Amazon basin (Vuille et al., 2000). In contrast, the inter-Andean valley is typically drier than the eastern side of the Andes due to the loss of humidity of the air masses during the orographic uplift that occurs on the outer slopes of the Andes (Vuille et al., 2000; Buytaert et al., 2010). Precipitation and temperature variability at inter-annual time scale in the Andes Cordillera is largely dominated by the tropical Pacific sea surface temperature (SST), with the presence of El Niño phenomenon causing inter-annual warmer and drier conditions in most of the Ecuadorian Andes except at the southwest of the Andes where opposing conditions tend to prevail because of the La Niña phenomenon (Francou et al., 2004; Vuille et al., 2000; Buytaert et al., 2010).

In general, the páramo region is characterized by a tropical climate typical of high mountain areas in South America (Buytaert et al., 2006a). Due to the páramo’s proximity to the equator, the daily solar radiation is intense and almost constant throughout the year (Buytaert et al., 2006a). Páramo ecosystems depend considerably on direct solar radiation as their main contributor of temperature while cloud cover reduces insolation drastically (Ramsay, 1992). During the night, cloudiness reduces thermal loss through long wave radiation, dampening temperature variation, restricting both the maximum and minimum temperatures (Ramsay, 1992). Despite the high radiation typical of these altitudes and latitudes, the evapotranspiration is very low, ranging between 1 to 1.5 mm day. These conditions are favoured by the abundance of xerophytic grasses and herbs with low transpiration characteristics (Buytaert, 2004).

In the páramo region, annual average temperature ranges between 2°C to 10°C, with daily variations ranging from below 0°C to >25°C being common (Hofstede et al., 2002a; Llambí et al., 2012; Mena et al., 2000). There are noticeable temperature variations in both Cordilleras marked by altitudinal floors (Camacho, 2014). The rate of average temperature change in relation to altitudinal variation is typically between 0.5 to 0.6 °C for each 100 metres (Buytaert et al., 2006a). Páramo vegetation located in the Central (Eastern Andes) and Western Cordilleras, at 3,000-3,600 m.a.s.l. and at 3,200-3,900 m.a.s.l., respectively, experience temperatures ranging from 6°C to 12°C. In contrast, temperatures between 3°C to 6°C are present in vegetation located from 3,600 (Eastern Andes) and 3,900 m.a.s.l. to 4,700 m.a.s.l. (Western Andes) (Cañadas Cruz, 1983). From 4,000 to 5,000 m.a.s.l, temperatures under zero are commonly registered at night, causing frost, although, below this altitude, this phenomenon rarely occurs (Buytaert et al., 2006a).

In the Ecuadorian Andes, precipitation has typically high frequency and low intensity and is determined by orography and the influence of wind, which causes a high spatial and temporal variability (Buytaert et al., 2010; Buytaert, 2004). Annual precipitation varies from less than 500 mm in the inter-Andean valley and the southwestern Pacific slopes, to more than 3000 mm in the outer Amazonian slopes (Hofstede et al., 2002a; Llambí et al., 2012; Luteyn and Balslev, 1992; Mena et al., 2000). The Humboldt Current brings drier air masses from the Pacific so páramo vegetation located in the Western, Central, and Southern Cordilleras receive less precipitation than in the North (Vuille et al., 2000). In contrast, the Eastern Cordillera is dominated by humid winds from the Tropical Atlantic and the Amazon basin causing a predominantly humid and hyper-humid rainy climate (Vuille et al., 2000; Vuille et al., 2008). In addition, the relative humidity in the páramo region is often very high, around 80% to 98% during most of the day (Mena et al., 2000). The constant humidity in the páramo region is mainly caused by indirect forms of precipitation, such as fog and drizzle, which results in permanent moisture in the soil (Mena et al., 2000). Humidity has a variable and seasonal pattern registering its maximum value in the rainy season (January to April) and its lowest value during the dry period (July and August) with continuous presence of fog through the year (Hofstede et al., 2014).

6. Ecuadorian Páramo Ecosystems

The Andean páramo ecosystems are considered to have the richest tropical mountain flora in the world (Smith and Cleef, 1988). This vegetation is characterized by a high degree of endemism in terms of species and genera (Sklenar and Ramsay, 2001). In general, a total of

3,595 páramo plant species have been reported of which 42% (1,524 species) can be found in Ecuador, making it the country with the most diverse páramo flora with respect to its national area (Sklenář et al., 2005). Of the total Ecuadorian páramo species, 17% (628 species) are endemic which represents 15% of the national endemic flora (León-Yánez et al., 2011). Around 75% of the páramo endemic species are threatened but approximately half of them (48%) have been protected as part of the National System of Protected Areas of Ecuador (Mena, 2017).

According to Mena (2011), the páramo vegetation could be divided by altitudinal range and predominant plant composition in three macro-zones. The first zone is *sub-páramo*, which constitutes the transition zone between the Andean forest and the actual páramo vegetation. This could be located as low as 2,800 m.a.s.l. (e.g. south of Ecuador) or as high as ≥ 4,000 m.a.s.l. (centre or north of Ecuador). This zone is characterized by a combination of grasslands, shrubs, and trees that diminish in size with altitude. The second zone *páramo*, is generally located between 3,500 m.a.s.l. to 4,400 m.a.s.l. It is characterized by continuous vegetation formed mainly by grasslands (e.g. *Calamagrostis intermedia*), giant rosettes (i.e. *Espeletia pycnophylla*), dwarf shrubs (e.g. *Arcytophyllum and Neurolepis aristata*), cushion plants (e.g. Azorella) and a variety of mosses. The third zone, *super-páramo*, corresponding to the vegetation belt that grows on the summits of the highest mountains is found generally above 4,400 m.a.s.l. on rocky, thick, and sandy soils, below the limit of perpetual snow. This zone presents the lowest temperatures, the poorest soils, the highest radiation and frequency of frost in comparison with the other two vegetation belts.

The latest classification of páramo ecosystems, defined for Ecuador in 2013, considers diagnostic factors such as climate, geoforms, flood areas, biogeography and land use combined with cutting-edge satellite information. Bibliographic information, expert knowledge, and field verification were also employed in the classification system (MAE, 2013b). According to this classification, which is applicable at national and regional (Andes) scale, Ecuador has 11 different types of páramo ecosystems. The most representative ecosystems in terms of area are *Páramo Grassland (HsSn02)* followed by *Páramo Evergreen Shrubland and Grassland (AsSn01)* covering 71.1% and 15.6% of the Ecuadorian páramo area, respectively. The remaining types of páramo vegetation are less representative in terms of area (0.6% to 4.5% of the Ecuadorian páramo area) showing typical patch isolation, characteristic of many of the páramo remnants found in Ecuador. The most restricted ecosystems are *Southern Páramo High Montane Evergreen Shrubland (AsAn01)* and *Sumaco Volcano's Páramo Grassland and Evergreen Shrubland (HsSn01)* representing 0.01% and 0.03% of the Ecuadorian páramo vegetation, respectively (Table 1.2 and Fig. 1.2).

Table 1.2 Description, Area and Representativeness of the Ecuadorian Páramo Ecosystems based on the national classification established for Continental Ecuador (MAE, 2013c).

Nº	Páramo Ecosystem	Páramo Ecosystem Code	Description	Altitude range (m.a.s.l.)	Area* (km^2)	%**
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	This ecosystem is also known as highland dwarf forest. Its vegetation is like that of the upper montane forest but smaller in height due to extreme environmental, topographic, and edaphic conditions. This vegetation is mainly composed of thorny species, small trees (*Polylepis*), and woody shrubs that do not exceed 3 metres in height. Its floristic composition is characterized by a mixture of species with thorns of the genera *Hesperomeles*, *Rubus*, *Ribes*, *Berberis*, *Desfontainia* and woody shrubs belonging to the families Ericaceae, Rosaceae, Asteraceae and Polygalaceae (Lozano, 2002).	2,800 – 3,300	2.1	0.01
2	Sumaco Volcano's Páramo Grassland and Evergreen Shrubland	HsSn01	This plant community is dominated by herbs (*Nertera granadensis*), shrubs (*Monticalia andicola* and *Vaccinium floribundum*), scattered grasses (*Cortaderia nitida*), and a thick layer of bryophytes and pteridophytes typical of very humid areas (*Blechnum* loxense and *Elaphoglossum* spp.). This community grows in isolation from other páramo vegetation on top of Sumaco Volcano and under almost no anthropogenic influence.	3,250 – 3,800	3.9	0.03
3	Páramo Evergreen Forest	BsSn01	This ecosystem is composed of dense evergreen forests with heights between 5 and 7 metres (Jørgensen and Ulloa, 1994) and with peculiar trees that grow crooked and highly branched due to climatic conditions, usually covered by bryophytes, lichens, and epiphytes. This type of ecosystem occurs as isolated patches within herbaceous or shrubby high-mountain vegetation (Beltrán et al., 2009). The arboreal stratum is dominated by species of the genera *Polylepis*, *Gynoxys*, and *Buddleja (Hofstede et al., 1998)*. The shrub-herbaceous stratum is dense and generally composed of species of the genera *Arcytophyllum*, *Barnadesia*, *Berberis*, *Puya*, *Brachyotum*, *Calamagrostis*, *Cortaderia*, *Diplostephium*, *Disterigma*, *Greigia*, *Pernettya*, *Senecio*, and *Valeriana (Jørgensen and Ulloa, 1994)*.	3,200 –4,100	87.8	0.6
4	Humid Subnival Páramo Grassland	HsNn01	This ecosystem is composed of dispersed grasslands restricted to the highest parts of the Ecuadorian Andes on periglacial slopes. The predominant life forms in this ecosystem are short-stemmed grasses, acaulescent rosettes, and cushioned grasses. The ecosystem is dominated by cushion plants (*Xenophyllum rigidum*), sclerophyllous shrubs (*Chuquiraga jussieui* and *Loricaria ilinissae*), prostrate shrubs (*Astragalus geminiflorus* and *Baccharis caespitosa*), erect shrubs (*Valeriana alypifolia*), and short-stemmed grasses (*Calamagrostis mollis* and *Agrostis tolucensis*)(Sklenář and Lægaard, 2003).	4,200 (West Chimborazo) 4,500 - 4,900	88.8	0.6

№	**Páramo Ecosystem**	**Páramo Ecosystem Code**	**Description**	**Altitude range (m.a.s.l.)**	**Area* (km^2)**	**%****
5	Floodable Páramo Grassland	HsSn04	A-zonal ecosystem primarily made up of flooded grasslands composed of cushions plants or isolated patches of floating vegetation (Cleef, 1981; Bosman et al., 1993). In high humidity conditions the dominant communities are *Sphagnum* spp., *Breutelia* sp., and *Campylopus cucullatifolius*. In less humid areas the vegetation is dominated by *Lophozia laxifolia* and *Cortaderia sericantha*. At higher altitudes, cushion plants grow combined with woody elements dominated by *Distichia muscoides*, *Plantago rigida*, *Werneria humilis*, *W. rigida, W. crassa, Oreobolus* spp., and *Eryngium humile*. In the upper stratum communities of Juncaceae and Cyperaceae are found (Bosman et al., 1993; Cleef, 1978; Cleef, 1981; Rangel, 1995; Jørgensen and Ulloa, 1994).	3,300 – 4,500	112.6	0.8
6	Ultra-humid Subnival Páramo Grassland	HsNn02	Vegetation dominated by prostrate shrubs or scattered cushion plants. Due to the influence of the Amazon, this ecosystem presents a significant number of bryophytes and a high diversity of species (Ramsay, 1992; Sklenář and Lægaard, 2003). The families Asteraceae and Poaceae are dominant. Vegetation located in the eastern cordillera and western cordillera in northern Ecuador is dominated by: *Huperzia rufescens*, *Nertera granadensis*, *Loricaria complanata*, *Calamagrostis guamanensis*, *C. ecuadoriensis*, *Draba spruceana*, and *Xenophyllum sotarense* (Sklenář and Balslev, 2005).	4,400 – 4,900	175.3	1.2
7	Humid High Upper Montane Páramo Grassland	HsSn03	Open-grassland vegetation dominated by species of the genera *Stipa*, *Senecio*, and *Plantago* (Sklenar and Balslev, 2007). Due to extreme weather conditions the richness and diversity of this ecosystem is lower than in more humid páramo grasslands. They are in volcanic enclaves at the bottom of glacial valleys (glacis). The aridity produced by wind erosion gives the landscape a desert-like appearance (Ramsay, 1992). The ecosystem is characterized by plant communities composed primarily of associations of *Agrostis breviculmis* and *Lachemilla orbiculata*, (Poulenard et al., 2001; Podwojewski et al., 2002; Poulenard et al., 2004).	3,500 – 4,200	361.5	2.4
8	Páramo Caulescent Rosettes (*frailejones*) and Grassland	RsSn01	Shrubs, grasses, and giant-rosette plants (up to 10 metres high) characterize its flora. This ecosystem is found in plains of glacial origin characterized by the presence of moraines that form crest-like depressions of variable dimensions. In the lower stratum, its vegetation is dominated by *Calamagrostis intermedia* and *Espeletia pycnophylla* (Ramsay, 2001). At higher altitudes the low vegetation is replaced by associations of *Agrostis* and *Espeletia* in fractured areas with very humid soils (northern Ecuador)(Ramsay, 1992).	3,350 – 4,100	463.0	3.1

Nº	**Páramo Ecosystem**	**Páramo Ecosystem Code**	**Description**	**Altitude range (m.a.s.l.)**	**Area* (km^2)**	**%****
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	This vegetation is locally known as *superpáramo* and is mainly composed of sclerophyllous semi-prostrate shrubs with a height from 0.5 to 1.5 metres (Cleef, 1981; Van der Hammen and Cleef, 1986; Sklenář, 2000). It usually occurs in moraines, glacier circuses, and steep slopes. The vegetation is fragmented, with bare soil between patches, and restricted to the northern Andes. At lower altitude, the dominant life forms are composed of dwarf sclerophyllous shrubs (*Loricaria*, *Pentacalia*, *Diplostephium*), cushions (*Xenophyllum*, *Azorella*, *Distichia*, *Plantago*) and short-stemmed grasses (*Poa*, *Stipa*, *Calamagrostis*)(Sklenář and Balslev, 2005). Shrubs and tussocks disappear gradually along the elevation gradient and are replaced by cushion plants, acaulescent rosettes, prostrate shrubs, and short-stemmed grasses (Cleef, 1981; Ramsay and Oxley, 1997; Luteyn et al., 1999; Harling, 1979; Cuatrecasas, 1954).	4,100 – 4,500	672.7	4.5
10	Páramo Evergreen Shrubland and Grassland	AsSn01	This ecosystem is located on the treeline and consists of shrubs of up to 3 metres high, mixed with tussock grasses of about 1.20 metres. Its composition and structure vary at lower altitudes due to the increase in the height of the bushes, number of trees, and species richness. The ecosystem is characterized by the presence of *Calamagrostis* spp. and shrubs of the genera *Baccharis*, *Gynoxys*, *Brachyotum*, *Escallonia*, *Hesperomeles*, *Miconia*, *Buddleja*, *Monnina*, and *Hypericum*. Species of Ericaceae such as *Disterigma acuminatum*, *D. alaternoides*, and *Themistoclesia epiphytica* are common in lower areas.	3,300 – 3,900 (North) 2,800 – 3,600 (South)	2,312.6	15.6
11	Páramo Grassland	HsSn02	This ecosystem comprises the largest extension of páramo vegetation in Ecuador (Beltrán et al., 2009; Valencia et al., 1999; Hofstede et al., 2003). Dense grassland vegetation is dominated by grasses taller than 50 cm. Its flora is characterized by rosette plants, xerophytic shrubs, and cushion plants. Generally located in glacial valleys and subglacial plains. Its vegetation is dominated by the genera *Calamagrostis*, *Agrostis*, *Festuca*, *Cortaderia*, and *Stipa*, along with shrubby patches of the genera *Diplostephium*, *Hypericum*, and *Pentacalia* as well as an abundant diversity of creeping and rosette-forming grasses (Ramsay and Oxley, 1997). In areas with a strong slope, landslide zones or in plains with hydromorphic soils, this ecosystem is characterized by pioneering bambusoid grassland communities dominated by *Chusquea* spp. that reach up to 3 metres in height (Ramsay, 1992).	3,400 – 4,300 (North) 2,900 – 3,900 (South)	10,522.1	71.1
			Total		**14,802.5**	**100**

** Area estimated based on the observed map.*

*** Percentage of representativeness with respect to the total national páramo area (14,802.52 km^2) based on the observed map.*

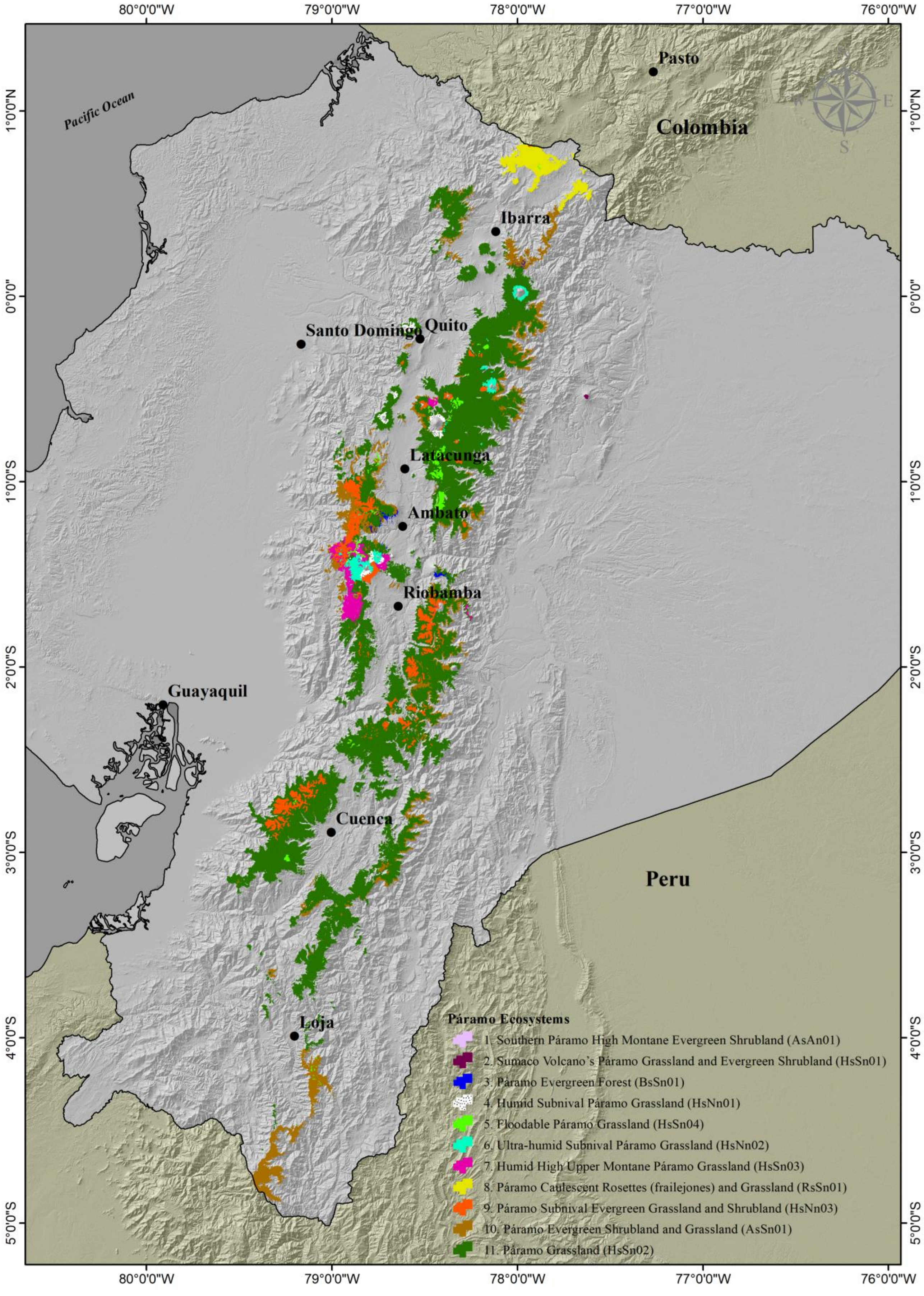

Figure 1.2 Spatial distribution of the páramo ecosystems in Ecuador.

7. Ecuadorian Páramo Soils

The origin of the páramo soils in the Andes is volcanic and recent (10,000 years ago), it occurred during last glaciations (Pleistocene) as a result of rocks expelled in the form of lava and later fragmented and dragged by the action of the glaciers (Hofstede et al., 2014). In Ecuador, the páramo soils are located on volcanic deposits product of Quaternary volcanic eruptions (Winckell et al., 1991; Barberi et al., 1988; Sauer, 1957) towards the centre and north of the Andes (Podwojewski and Poulenard, 2000b). At the south, there are páramo soils resting on non-volcanic deposits at altitudes above 3,000 metres (Mena et al., 2000). Volcanic páramo soils, due to their geological characteristics are sparsely developed with poorly differentiated horizons and are relatively young due to active volcanism which continues to provide layers of ash and pyroclastic materials (Llambí et al., 2012; Podwojewski and Poulenard, 2000b). In contrast, soils of páramo with non-volcanic origin are old, do not have pyroclastic coverage, have well-differentiated horizons, and a superficial layer (>20 cm) rich in organic matter (Sourdat, 1986; Podwojewski and Poulenard, 2000b). Although in the south of the country there is no volcanic activity, in some places thin layers of young volcanic ash covering the lower layers of ancient weathered ashes can be found (Podwojewski and Poulenard, 2000b).

Despite some differences due to their complex geology and topography, in general, all páramo soils have a typical association between active aluminium and organic matter (Mena et al., 2000). The presence of homogeneous layers of volcanic ash (old and young) favours the organic matter accumulation by the formation of organometallic (aluminium and iron) structures and presence of crystallized minerals (e.g. quartz, imogolite and kaolinite) which makes the organic matter extremely resistant to microbial decomposition (Buytaert et al., 2006b; Nanzyo et al., 1993; Mena and Hofstede, 2006). Therefore, the páramo ecosystems constitute a huge carbon reserve due to the high amount of organic matter stored in their soils (Llambí et al., 2012; Buytaert et al., 2006b).

In general, páramo soils are characterized by dark colour, low evapotranspiration, low density (<0.9 g/cm^3), and porous structure (Buytaert, 2004). As a result, they can retain large water flows which are released slowly during long periods (Buytaert, 2004). Páramo soils vary in thickness ranging from a few centimetres to several metres (up to 3 metres) (Buytaert et al., 2006b). This is due to factors such as climate, lithology (i.e. parent rock), relief (e.g. terrain inclination), biological (e.g. bacteria) and atmospheric agents (e.g. erosion) (Crespo, 2004); conditions which vary across all the Ecuadorian Andes. The climatic conditions existing in the

Andean páramo region also play an important role in the evolution of páramo soils (Mena et al., 2000). The low average temperature (2°C to 10°C) causes the reduction of the soil's biological activity, favouring the accumulation and slow decomposition of organic matter (Llambí et al., 2012; Mena et al., 2000). On the other hand, the variable but permanent precipitation (500 to >3000 mm/year) combined with the constant presence of fog and drizzle constantly maintains the páramo soils' humidity which favours soils rapid evolution (Mena et al., 2000). In addition to climate, vegetation is an active and determining factor in the formation of páramo soils. Páramo plants and roots contribute to the soil organic matter that later decomposes slowly due to the low temperatures, high humidity and the action of living organisms (e.g. worms and insects) (Llambí et al., 2012). In addition, vegetation promotes soil weathering, improves soil infiltration and porosity and produces CO_2 through shoot and root (Branson et al., 1981).

Based on the National Soil map of Ecuador (1: 250,000 scale) (MAGAP, 1986), 81% of the páramo soils have mineral composition while 6.3% are organic. The Ecuadorian soils have been classified according to the soil taxonomic legend established by the United States Department of Agriculture (USDA, 1999) based on morphological, physical, chemical and mineralogical properties (Velásquez, 2008). According to this classification, the Ecuadorian páramo soils represent six different soil orders including vertisols, alfisols, entisols, mollisols, histosols, and inceptisols. The most representative soils in terms of area are inceptisols covering 73.4% of the Ecuadorian páramo area. These soils are young with one or more underdeveloped horizons and have minerals such as carbonates (Llambí et al., 2012; USDA, 1999). They have an acidic pH, poor drainage conditions and may contain amorphous/allophane clay minerals, making them able to store water for long periods of time (Llambí et al., 2012). Inceptisols present accumulation of organic materials on the surface due to low degradation conditions (USDA, 1999). Histosols or peat soils cover 6.3% of the total páramo area of Ecuador and can be found in water-saturated páramo areas with less volcanic activity (e.g. southern Andes) at altitudes between 3,700 to 4,300 m.a.s.l. Histosols are dominated by cushion plants, bryophytes and herbaceous plants (Buytaert et al., 2006b; Bosman et al., 1993). These soils have developed through the accumulation of undecomposed or partially decomposed organic matter caused by low temperatures, high humidity conditions, and water saturation that prevents aerobic decomposition (Llambí et al., 2012). Since they are almost entirely formed by organic matter, these soils have a very high water retention capacity, low pH and very low bulk density (0.04-0.2) g/cm^3 (Llambí et al., 2012). The remaining 7.9% of the páramo soils are characterized by other types of mineral soils present in pure form or combined with other soils (Table 1.3 and Fig. 1.3).

Table 1.3 Description of the Ecuadorian páramo soils per soil order.

Soil Order		Composition	Description	Area (km^2)*	%**	Description Source
Inceptisol		mineral	Inceptisols occur in equatorial to tundra regions on relatively active landscapes, such as mountain slopes and river valleys. These soils have one or more underdeveloped horizons, acidic pH, and poor drainage conditions. Inceptisols may contain amorphous orallophane clay minerals, making them able to store water for long periods of time. This soils present high accumulation of organic materials on the surface due to low degradation conditions.	10,866.5	73.4	(USDA, 1999)
Histosol		organic	Histosols are often referred to as "peat soils" and occur in low elevation wet areas. This type of soil has low bulk density (<0.1 g/cm^3) and have very high content of organic matter in the upper 80 cm to 1 metre of the soils and no permafrost. The organic materials in histosols rest on rock or pumiceous materials, which do not oxidize because they are under water. In tropical mountainous areas, histosols occur at elevated flat elevations on impermeable rocks.	935	6.3	(IUSS Working Group and WRB, 2015; Buringh, 1979; USDA, 1999)
Other mineral soils	Vertisol	mineral	Vertisols are heavy, dark, clay soils (>30%) developed in large flat areas with a pronounced dry season**.** These soils have high bulk density when the soils are dry and low hydraulic conductivity when the soils are moist. These soils have a dark surface layer caused by the combination of organic matter (≥1%) with clay particles. The soil has a high water retention capacity, but relatively small amount of water is accessible for plant growth. They exist in subtropical and tropical climates with a wide range in rainfall.	1,174.4	7.9	(Buringh, 1979; Kilmer, 1982; USDA, 1999)
	Alfisol	mineral	Alfisols are soils with a combination of an ochric or umbric epipedon, an argillic or natric horizon, a medium to high supply of bases in the soils, and water available to mesophytic plants. They have a light coloured superficial horizon, usually acid and low in organic matter. Their moisture regime could be udic, ustic, or xeric, and in some cases they present aquic conditions.			(Kilmer, 1982; USDA, 1999)
	Entisol	mineral	The virtual absence of diagnostic horizons is characteristic of Entisols. Entisols are young, shallow and have a mineral nature. Soil colour varies from light to dark, depending on the original material. These soils occur on terraces and younger alluvial fans, along some valley bottoms, and on stream floodplains. These soils can present any type of mineral parent material, vegetation, age, or moisture regime and any temperature regime except permafrost.			(USDA, 1999; Boettinger, 2017)
	Mollisol	mineral	Mollisols are mineral soils recognized among the most fertile soils in the world. They are commonly found in temperate zones, but some occur in the tropics and subtropics. Mollisols found at high latitudes formed in late-Pleistocene or Holocene deposits. The mollic-epipedon has a thick dark surface horizon high in humus and nitrogen content. These soils have been subject to limited leaching and their organic matter and nutrient levels are high.			(Kilmer, 1982; USDA, 1999)
rocky outcrops, snow/ice, and water bodies (natural or artificial)				1,826.6	12.3	
			Total	**14,802.52**	**100**	

** Area estimated based on the observed map.*

*** Percentage of representativeness with respect to the total national páramo area (14,802.52 km^2) based on the observed map.*

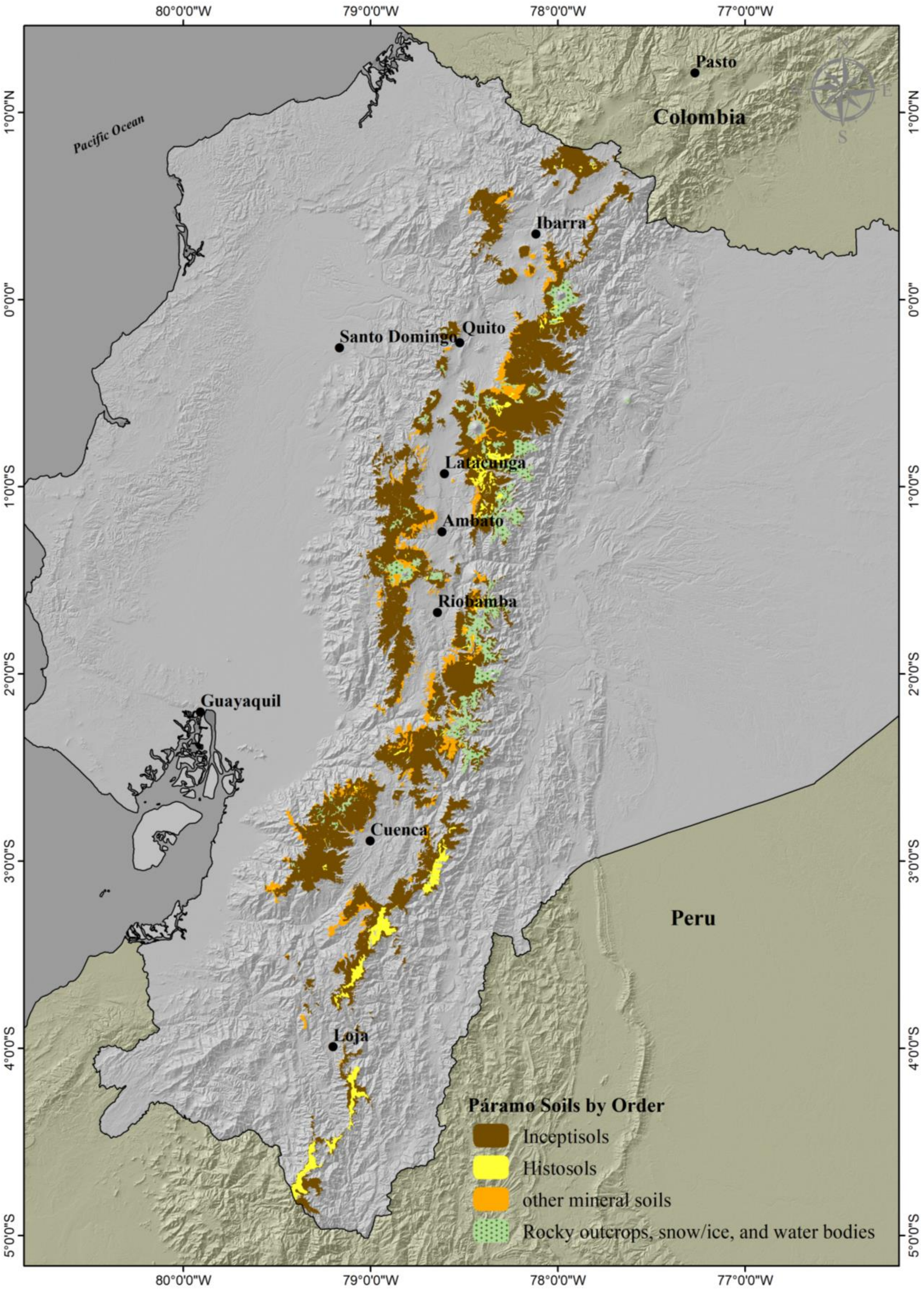

Figure 1.3 Spatial distribution of the Ecuadorian páramo soils by order.

8. Ecosystem Services provided by the Ecuadorian Páramo Ecosystems

A brief description of some of the most important ecosystem services provided by the páramo ecosystems is included below. There are more than thirty different ecosystem services provided by the Andean páramos covering all categories: supporting, provisioning, regulating and cultural (Nieto et al., 2017; Hofstede, 2008). The following description does not cover all of them but rather highlights the most important services provided by páramo ecosystems as a basis for understanding the present study.

In Ecuador, millions of people depend directly or indirectly on the continued ecological functioning of the páramo, demonstrating its economic, environmental, and social relevance (Buytaert et al., 2006a). Among the most important ecosystem services provided by the páramo vegetation is the capability to store and regulate water from rainfall and melting glaciers (Mena et al., 2000). This particular function of the páramo vegetation is directly linked to the large accumulation of organic matter in the soils and the morphology of certain páramo plants as discussed earlier (Mena et al., 2000). Water regulation by the páramo ecosystems is very important during dry seasons (July-August) since the ecosystem can slowly release water stored during rainy seasons (January-April) (Hofstede et al., 2014). These Andean ecosystems provide water for human consumption, irrigation, and hydroelectricity generation for Andean cities and for the population located in the Amazonian and coastal region of Ecuador. In fact, 85% of water sources necessary to cover Quito's[1] requirements come from páramo areas such as Papallacta and Antisana, located at 3,900 m.a.s.l (Buytaert et al., 2006a). Furthermore, the water provided by páramo vegetation is an important source for hydroelectric generation. Due to its topography and water availability a significant number of dams are located along the páramo region. Indeed, 25%-40% of water provision for the largest hydroelectric power plant (Amaluza) of Ecuador comes from páramo ecosystems located in the Central and Western Andes Cordillera (Buytaert et al., 2006a). The electricity capacity of Amaluza's[2] dam is 1,075 MW which represents 60% to 80% of the electricity used by the country (Southgate and Macke, 1989).

As explained previously, páramo soils accumulate significant quantities of organic carbon, which largely make páramo ecosystems net natural carbon sinks and may therefore be

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[1] Quito is the capital of Ecuador, and the second most populated city with 2,239,199 inhabitants (Census, 2010).

[2] Amaluza's dam is located in Paute's basin at 1,994 metres with a capacity of about 120 10^6 m^3.

important contributors to climate change mitigation (Winckell et al., 1991; Podwojewski and Poulenard, 2000a). According to the Global Peatlands Initiative, the peatlands are considered the world's largest terrestrial organic carbon stock (GPI, 2017). In the case of the páramo vegetation, peatlands occupy large areas and continue to grow, playing an important role as carbon storers and fixers (Hofstede et al., 2003; Mena et al., 2000). Although páramo's plant biomass is also a carbon sink, it is not as significant as the carbon stored in soil (Hofstede et al., 2003). Although not extensive in area, the forested masses, present in the páramo vegetation, efficiently fix atmospheric CO_2 (Hofstede et al., 2003). It is estimated that páramo forest species such as *Polylepis* could capture up to two tons of carbon per hectare per year (Fehse et al., 2002).

In terms of social and economic importance, the páramo vegetation is relevant for tourism and food provision. The diversity of páramo landscapes attracts millions of national and foreign tourists, representing an important source of income for the Andean countries and an alternative source of work for the local population (Hofstede et al., 2003). Furthermore, in Ecuador, approximately 500,000 people live in the páramo region (Josse et al., 1999) with most of them dedicated to productive activities including farming and livestock. The total area cultivated in the Northern Andes[3] reached 4.4 million hectares in 2001 (Dixon et al., 2001). Production in this region of the Andes is mainly focused on maize, potatoes, cereals, various vegetables, cereals, pastures, and cattle. Producers in the lower areas of the Andes tend to be relatively wealthy compared to producers in higher areas who live in severe poverty (Dixon et al., 2001). The páramo's population depend on agricultural activities for auto-consumption and commercial purposes. The traditional and modern uses of certain species of flora and fauna found in the páramo region are also indicators of the páramo's socio-ecological importance. The local population, including peasants, and indigenous communities use dozens of typical páramo plant species for consumption, medicine, crafts, or tools (Hofstede et al., 2003). Therefore, the role of the páramo vegetation as provider of natural resources and food has a significant social relevance especially now that Andean production has become increasingly important for food security, in developing countries such as Ecuador (Kleinwechter et al., 2016).

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[3] The Northern Andes, encompasses the Ecuadorian, Colombian, and Venezuelan cordilleras.

9. Human Impact on the Andean Páramo Vegetation

Over the last decades, the ecosystem services provided by the Andean páramo vegetation have been significantly altered (Buytaert et al., 2006b; Buytaert, 2004; Crespo et al., 2010). The major impacts are caused by intense anthropogenic activities such as farming, livestock, mining, introduction of exotic species (e.g. pine) and badly planned tourism (Crespo et al., 2010; Hofstede et al., 2014; Llambí, 2010; Mena and Hofstede, 2006), which have all contributed to increased fragmentation of the landscape and decline in ecosystem services. The anthropogenic pressure on the Ecuadorian páramo areas is evidenced by the advance of the agricultural frontier. The main causes of this continued expansion are population growth, social inequalities, and the intensification of agricultural techniques (Arellano et al., 2000). In 2000, it was estimated that around 40% (8,000 km^2) of the Ecuadorian páramo areas (20,000 km^2), above 3,000 m.a.s.l., were massively transformed by agriculture (Hofstede et al., 2003). Páramo vegetation represents enormous risks for agricultural development due to their extreme fragility, low productivity of soils, and high frequency of frost. Nevertheless these natural areas have increasingly and severely been impacted by farming activity (Llambí, 2010; Mena et al., 2008). Intensive livestock practices have been also impacting these natural areas, especially since cattle trampling causes soil compaction which damages the soils' infiltration capacity (Hofstede et al., 2014). Linked with the livestock practice, the páramo areas are also affected by burning, for the purpose of providing greener and tender pastures for cattle (Hofstede et al., 2014). This has led to the loss of native vegetation and alteration of habitat for local species such as the Andean bear (*Tremarctos ornatus*), the jambato frog (*Atelopus ignescens*), the Andean condor (Vultur gryphus), and the mountain tapir (*Tapirus pinchaque*) (Luteyn and Balslev, 1992).

Agricultural production systems in the Andes of Ecuador are highly variable, ranging from traditional subsistence, set-aside farming to intensive agro-commercial systems favoured with technology and capital investment (Llambí, 2010; Mena and Hofstede, 2006). Although the major impact on the páramo ecosystems in terms of area used is livestock, crop production (potatoes, maize, vegetables, fruits, cereals and tubers), causes the most significant ecological, economic and social impacts (Hofstede et al., 2003). Land-use change has significantly decreased the base flow of streams (Buytaert et al., 2006b). It is estimated that intensive grazing and farming could decline the water regulation capacity of páramo catchments by 40% (Buytaert et al., 2005b; Buytaert et al., 2004). In addition, as a result of excessive grazing, trampling, and burning, páramo soils could also be affected by accelerated runoff and erosion

(Buytaert et al., 2006b). In areas of national importance for water supply such as the páramo region, these problems can become critical, as in the case of the Paute's river basin located in southern Ecuador, where high sediment loads in rivers have caused erosion, affecting the quality and quantity of urban water supply and putting at risk hydroelectric power projects (Buytaert et al., 2006b). Mining activities taking place in the páramo region may also impact the ecosystem, especially by consumption of large amounts of water that subsequently re-enter the hydrological cycle with a high load of pollutants (Messerli et al., 1997). Additionally, the introduction of non-native woody species such as *Eucalyptus* and *Pinus* in the páramo region is causing water loss and base flow reduction (Célleri et al., 2004) as well as acidification and loss of carbon from soils (Farley and Kelly, 2004). Even though the intensive and extensive use of the páramo areas continues to this day, a greater collective awareness of the social and environmental situation occurring in the páramo region has promoted the development of initiatives for participatory conservation, research and sustainable management, which could be a sign of positive change for the future management and survival of the mountain ecosystems of the Andes (Llambí et al., 2013; Hofstede, 2011; Hofstede et al., 2014).

10. Páramo Ecosystems and Climate Change

During the last decades, the climatic variability in the Tropical Andes has begun to overcome the historically documented thresholds (Vuille et al., 2008). In the last 25 years, there has been a significant increase of 0.5°C per decade in comparison with the 0.1°C-0.2°C registered per decade over the last century (Anderson et al., 2011; Herzog et al., 2012). As future climate simulations have predicted, temperature increases in the Andes could range from 1°C (A1B[4] scenario) up to 3°C (A2[5] scenario) in the next 20 to 60 years, respectively (Cuesta et al., 2012a). In contrast, there are substantial uncertainties regarding precipitation trends in the Andes. While certain regional analyses based on rainfall series show no future substantial changes (Buytaert et al., 2010), other simulation models have predicted either an increase or a reduction in the volume of rainfall (Viviroli et al., 2011). Despite the discrepancies, changes in precipitation patterns have been already registered in the Eastern and Western slopes of the Andes as well as in the inter-Andean valleys (Anderson et al., 2011). It is expected that the changes in temperature, precipitation regimes and seasonal climate patterns predicted under

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[4] A1B= Global emissions scenario that predicts rapid economic growth but with a parallel introduction of new technologies.

[5] A2=Global emissions scenario that predicts a very heterogeneous world, with a continually increasing global population.

future climate change scenarios, will affect the regular functioning of the Andean ecosystems (Hofstede et al., 2014).

For the páramo region specifically, temperature is estimated to increase by 4°C-5°C towards the end of the 21st century (Buytaert et al., 2010). Climate stations located in páramo areas at high elevations are reporting clear trends towards the increment of daily maximum temperature, close to 1°C per decade, while at low elevations stations are registering an increase between 0.3°C and 0.6°C per decade (Hofstede et al., 2014). This confirms that at a higher altitude the increase in temperature is greater; correspondingly the effects of these changes are likely to be greater (Urrutia and Vuille, 2009; Buytaert et al., 2010; Herzog et al., 2012). Future temperature trends are not yet estimated for the Ecuadorian páramo region, however, in the period 1960-2006, Ecuador has experienced significant increases in mean annual temperature, absolute maximum temperature, and absolute minimum temperature, by about 0.8°C, 1.4°C and 1.0°C, respectively (MAE, 2011). Therefore, it is expected that similar temperature increases could have occurred in Ecuador's páramo region.

Climate change scenarios agree in predicting major changes of water flow with consequences for water supply and integrity of freshwater ecosystems (Vuille et al., 2008; Herzog et al., 2012). Changes in temperature and humidity, could led to the disappearance of the inter-tropical glaciers in the next 15 years, with adverse effects on water availability and hydropower generation (Ramirez et al., 2001; IPCC, 2014a). Prior to 2007, several water disputes had already been registered between different stakeholders in countries such as Peru, Bolivia, and Ecuador (Painter, 2007). In Ecuador, even small changes in glacial water’s contribution to river discharge will affect páramo’s water regulation, especially during the dry season (Herzog et al., 2012; Favier et al., 2008). As the climate warms, an increase in atmospheric water vapour concentrations from páramo ecosystems could be expected, exacerbating the greenhouse effect (Buytaert et al., 2006b). Future increases in temperature in a range from 3°C-4°C, as predicted for the Andes region, could cause the loss of páramo habitat of about 60% with the resultant extinction of certain plant species (Herzog et al., 2012). Altered climatic conditions could affect the location of páramo altitudinal belts, promoting the appearance or disappearance of species (Araújo and Rahbek, 2006; Anderson et al., 2010; Cuesta et al., 2012c; Cuesta et al., 2012a). At species level, there are three general responses expected including movement, adaptation, or local extinction (Parmesan and Yohe, 2003; Buytaert et al., 2010). Displacements of species such as those predicted for the páramo ecosystems could have consequences on the ecosystems’ structure and functioning (Herzog et al., 2012).

In the Ecuadorian Andes, a moderate rising trend in rainfall and humidity has been already observed (Hofstede et al., 2014; Huntington, 2006). Between 1960 and 2006, records provided by weather stations revealed that the amount of annual precipitation tended to increase in several parts of the Ecuadorian Andes (MAE, 2011). Changes in precipitation regimes could cause increases in runoff, sedimentation, erosion, and landslides (Herzog et al., 2012). Global warming could cause an increase in the proportion of vertical precipitation (rain) compared to horizontal precipitation (fog) affecting water retention and filtration capacity in páramo vegetation (Herzog et al., 2012). Future drier conditions could cause soil shrinkage (Poulenard et al., 2002), acceleration of organic matter decomposition (Price and Waddington, 2000; Waddington and Roulet, 2000) and hydrophobicity (Poulenard et al., 2004), affecting páramo soils' ability to regulate and store water.

Páramo soils are very dependent on low temperatures (mean minimum of 8 °C and mean maximum of 12 °C) to store carbon in the long-term (Buytaert et al., 2006a). Therefore, warming could accelerate organic matter decomposition and could increase CO_2 and CH_4 emissions to the atmosphere (Batjes, 1996; Eswaran et al., 1993; Lal, 2004), altering its role as a natural carbon sink (Peña Salamanca et al., 2013; Bellamy et al., 2005). Anthropogenic pressures on the páramo ecosystems could be also exacerbated by global climate change affecting the normal provision of ecosystem services (Hofstede et al., 2014). The increase in warming could lead to lengthening of crop growing seasons and optimal temperatures for assimilation, factors that could benefit the expansion of productive areas currently limited by low temperatures (Hijmans, 2003). Furthermore, changes in precipitation (increases or reductions) and greater concentrations of atmospheric CO_2, expected in the next decades, may promote crop yields (Nonhebel, 1994). Since land use change is the main driver of environmental degradation in the Andes, a potential expansion of productive areas towards páramo areas favoured by these changes could be expected (Adams et al., 1998). Due to growing demand of Andean products, at local and global scale, it is expected that producers will be forced to search for new productive lands, threatening the remaining natural ecosystems (Hijmans, 2003; Walker et al., 2011). The population's reliance on natural resources for their livelihoods makes them vulnerable (Painter, 2007).

11. The Thesis

11.1 Aims of the Study

The aim of this research is to analyse the effects of climate change on key ecosystem services provided by the Ecuadorian páramo ecosystems. To achieve this goal, the objectives of this study are:

- To predict the impacts of climate change on the climatic niche distribution of the Ecuadorian páramo ecosystems considering current (1950-2000) and future climatic conditions (2050 and 2070) and medium (RCP 4.5) and high (RCP 8.5) greenhouse gas (GHG) concentration scenarios.
- To quantify the carbon stocks, in both soil and aboveground vegetation for ten key types of páramo ecosystems located in the Andes of Ecuador, based on secondary information collected over 15 years, exploring a range of key factors influencing carbon stock variations.
- To determine the degree of future exposure of the Ecuadorian páramos to land use pressures, considering climate as a determining factor for increases or decreases in the farming frontier, based on future climate projections (2050 and 2070) and two greenhouse gas (GHG) concentration scenarios: RCP 4.5 (medium) and RCP 8.5 (extreme).

11.2 Thesis Structure

In order to achieve the objectives outlined for this study, a number of interdisciplinary approaches and techniques were undertaken. In Chapter I, a brief literature review of the state of the ecosystem services is presented. General data on páramo vegetation explaining its origin in the Andes, current spatial distribution, and climatic conditions found in the Andes is included in this chapter. A description of the páramo ecosystems and páramo soils existing in Ecuador is also included. In this chapter the importance of páramo vegetation as a provider of ecosystem services is highlighted. The vegetation’s vulnerability to human pressures and climate change is described.

In Chapter II, the páramo climatic niches are modelled under current (1950-2000) and future (years 2050 & 2070) environmental conditions oriented to understand ecosystems' vulnerability influenced by climate change. The research applies state-of- the-art techniques, based on the maximum entropy principle (MAXENT) to generate climatic niche models. In the analysis, six global climate models (GCMs) and two representative concentration pathways

(RCP), representing a moderate (RCP 4.5) and an extreme (RCP 8.5) greenhouse gas (GHG) emission scenario, are considered.

In Chapter III, the estimates of carbon stocks in páramo soil (at depth intervals of 0-30 cm +/- 5 cm) and aboveground vegetation (biomass + necromass) for ten key types of páramo ecosystems located in the Andes of Ecuador are presented. The carbon stocks quantification is based on secondary information compiled from literature collected over 15 years (2002 to 2016) at different páramo sites along the Ecuadorian Andes. An examination of differences in carbon storage influenced by vegetation type, soil order, altitudinal variation, and climatic conditions is also included.

In Chapter IV, the future exposure of the Ecuadorian páramo ecosystems to land use pressures induced by climate change is addressed. The impact is measured by analysing the edapho-climatic ranges of three common Andean crops (potato, soft maize, and quinoa) as indicators of potential threats from agriculture to the survival of the páramo vegetation. The analysis considered climate as the determining factor for increases or decreases in the agricultural frontier while soil conditions were assumed unchangeable. To simulate future changes, two GHG concentration scenarios, RCP 4.5 (moderate) and RCP 8.5 (extreme), are considered based on Global Climate Model CCSM4. The expansion of future farming land into páramo areas with and without protection is also evaluated.

In Chapter V, the aims of the research alongside with a summary of the key findings from the previous chapters are presented. The implications of the results obtained through this research, recommendations for future management of the páramo ecosystems as well as suggestions for future research are included in this chapter, along with final concluding remarks.

Chapter II

Predicting the Impacts of Climate Change on the Climatic Niche Distribution of the Ecuadorian Páramo Ecosystems

1. Introduction

The negative impacts of anthropogenic climate change on global biodiversity have generated widespread concern. Scientific evidence suggests that climate change could significantly affect the distribution of species and the composition of ecosystems due to changes in temperature and precipitation (Campbell et al., 2009; Bellard et al., 2012). Changes in species composition could alter the structure and functioning of ecosystems and therefore decrease the quality and quantity of ecosystem services available to the population (Campbell et al., 2009; Garavito et al., 2015). Global concern has mainly focused on the high risk of species extinction. It has been suggested that many species will become more prone to extinction as they will be unable to migrate or adapt fast enough to their environment in the face of rapid climate change (Garavito et al., 2015). In mountain regions, ecosystem composition and functioning depend mainly on air temperature, the spatial distribution of precipitation, atmospheric CO_2 concentrations, and radiation (Buytaert et al., 2011). Any climatic alteration that interrupts or alters these processes would force sensitive species to move towards new areas with the required climatic niche or otherwise would cause the species' decline and ultimate extinction (Buytaert et al., 2011). In the Andes specifically, climate warming is occurring at a rate of almost twice the world average (Vuille et al., 2003) confirming that warming is increased at high altitudes (Solomon, 2007). A high level of uncertainty surrounds the future of Andean ecosystems under the effects of climate change since knowledge is limited and predictions are highly variable. Continued exposure to climate change could lead to diverse responses at species level, including tolerance and adaptation, migration to emerging gradients, or extinction due to inability to adapt or move (Herzog et al., 2011; Parmesan and Yohe, 2003; Thomas et al., 2004).

Among the most vulnerable mountain ecosystems are the páramo vegetation; alpine neo-tropical vegetation discontinuously located along the Andes cordillera (Hofstede and Aguirre, 1999). These flora is characterized by high endemism and floristic diversity linked with the historical gradual rise of the Andes and the Pliocene/Pleistocene glacial cycles (Hooghiemstra et al., 1995). The high rates of diversity and endemism of páramo ecosystems linked with orography and differential climatic patterns in combination with intensive land use and hydrological regime alteration have made them highly vulnerable to climate change (Herzog et al., 2011). The páramo ecosystems play an important role in sustaining the life of millions of people providing environmental goods and services such as drinking water, irrigation, power generation, carbon storage and fertile land for agricultural production (Buytaert et al., 2006b; Bradley et al., 2006). However, climatic changes as well as anthropogenic threats (e.g. deforestation, expansion of the agricultural frontier, urban growth, and mining, among others) are putting at risk the resilience of the páramo vegetation and the population that depends on their ecosystem services. Studies suggest that the alteration of environmental conditions including rising mean temperature, temperature variability, rainfall, and humidity at various temporal and spatial scales will influence páramo vegetation distribution and persistence (Herzog et al., 2011). These extreme climatic changes could affect the páramo ecosystems causing significant habitat loss, physiological stress, fecundity alterations, abundance shifts, species invasion, migration and extinction (Herzog et al., 2011).

There are major concerns about the rapid and imminent decline of biodiversity and its consequences on ecosystems functioning, ecosystem services provision, and human well-being (Schläpfer and Schmid, 1999; Chapin III et al., 2000; Loreau et al., 2001; Díaz et al., 2005; Balvanera et al., 2006). As a result, over the two last decades several methodological approaches have been applied to examine the potential effects of climate change on biodiversity, including dynamic ecosystem models (Woodward and Beerling, 1997), biogeochemistry models (Peng, 2000), spatially explicit mechanistic models (Hill et al., 2001), physiologically based models (Sykes et al., 1996; Walther et al., 2005) and bioclimatic niche models (Box et al., 1993; Huntley et al., 1995; Iverson and Prasad, 1998; Pearson et al., 2002; Pearson et al., 2004; Thuiller, 2003; Thuiller et al., 2005; Vieilledent et al., 2016; Sales et al., 2017). Among all these alternatives, bioclimatic models are the most widely used to predict the spatial range of organisms as a function of climate (Jeschke and Strayer, 2008). This modelling technique focuses on defining the climatic niche that best describes the limits of the spatial range for any chosen species through the correlation between the current species distribution with selected climatic variables (Beaumont and Hughes, 2002; Pearson and Dawson, 2003; Thuiller, 2003; Huntley et al., 2004).

Bioclimatic models fail to consider climate as the sole determinant of the distribution of species when in reality factors such as extensive habitat fragmentation, species dispersal limitations, increase of atmospheric CO_2 (Woodward and Beerling, 1997; Iverson and Prasad, 2002), changes in soil and presence of fires (Brereton et al., 1995; Iverson and Prasad, 1998; Crumpacker et al., 2001), among others, are playing a determining role in the distribution of the species (Heikkinen et al., 2006). However, they can provide more accurate and realistic predictions than those offered by other types of species modelling techniques (Iverson and Prasad, 1998). In this study, bioclimatic models were used as the basis of all the analyses, focusing on the advantages previously mentioned, as well as on their high predictive power and capability to perform relatively quick analyses for numerous individual species (Iverson and Prasad, 2002; Pearson and Dawson, 2003; Gavin and Hu, 2005). Models were used for the evaluation of future bioclimatic ranges of páramo ecosystems considering the climatic variables that best describe the current niche distribution to simulate the future distributions of páramo niches under climate change scenarios (Bakkenes et al., 2002; Peterson et al., 2002a; Peterson et al., 2002b; Peterson et al., 2004; Thuiller, 2003; Pearson et al., 2004; Thomas et al., 2004; Thuiller et al., 2005).

Although through the years, several modelling approaches have been applied aimed at analysing the impact of climate change on Andean vegetation based on different climatic scenarios (Tovar et al., 2013; Cuesta et al., 2008; Cuesta, 2007; Ramirez-Villegas et al., 2014), the impact on specific Andean ecosystems remains poorly understood. The knowledge gap persists hand in hand with the improvement of data and the development of more accurate global climate model (GCM) projections. This study aimed to contribute to filling the existing knowledge gap by analysing the potential impact of climate change on the climatic niches of the eleven types of páramo ecosystems existing in the Ecuadorian Andes. This research applied state of the art modelling techniques (MAXENT) to generate climatic niche distribution models under current and future environmental conditions. Future projections were based on six different global climate models (GCMs) and two representative concentration pathways (RCP), a moderate (RCP 4.5) and an extreme (RCP 8.5) greenhouse gas (GHG) concentration scenario, representing two of the latest emission scenarios recognized by the IPPC in the Fifth Assessment Report (AR5). This research analyses the impact of climate change on páramo niches from two points of view: a) impact on the future distribution of climatic niches according to four categories of impact: unchanged, lost, expanded and extinct; and b) future impact on climatic niches shared among páramo ecosystems.

2. Materials and Methods

2.1 Study Region

Most niche models tend to define study areas according to countries geographical or political borders to promote regional or local conservation actions. By doing so, the resultant models ended up calibrated with a limited range of environmental conditions that do not capture the total species niche neither their real environmental tolerance (Raes, 2012; Titeux et al., 2017). This could cause the under-representation of areas of adequate habitats, and reduces the predictive power of the models (Sánchez-Fernández et al., 2011; Thuiller et al., 2004). It is therefore recommended the use of biogeographic boundaries for niche modelling purposes as an attempt to represent most of the species distribution ranges (Raes, 2012).

Under these circumstances, the Andes biogeographic region geographically defined for Ecuador was selected as the modelling boundary. In Ecuador, this natural boundary covers an area of approximately 102,450 km^2, including the Eastern and Western Cordillera of the Andes, ranging from the border with Colombia in the North to the Peruvian border in the South (Fig. 2.1). This region represents ecological and climatic characteristics necessary to guarantee the presence of these Andean vegetation (Brown and Lomolino, 1998; Radosavljevic and Anderson, 2014). Although, the Andean region offers a flexible spatial range for current and future niche predictions, it excludes páramo ecosystems existing in other countries such as Colombia and Peru. This decision was made since there were no maps of páramo ecosystems available for other páramo countries consistent with the scale and level of detail offered by the Ecuadorian map.

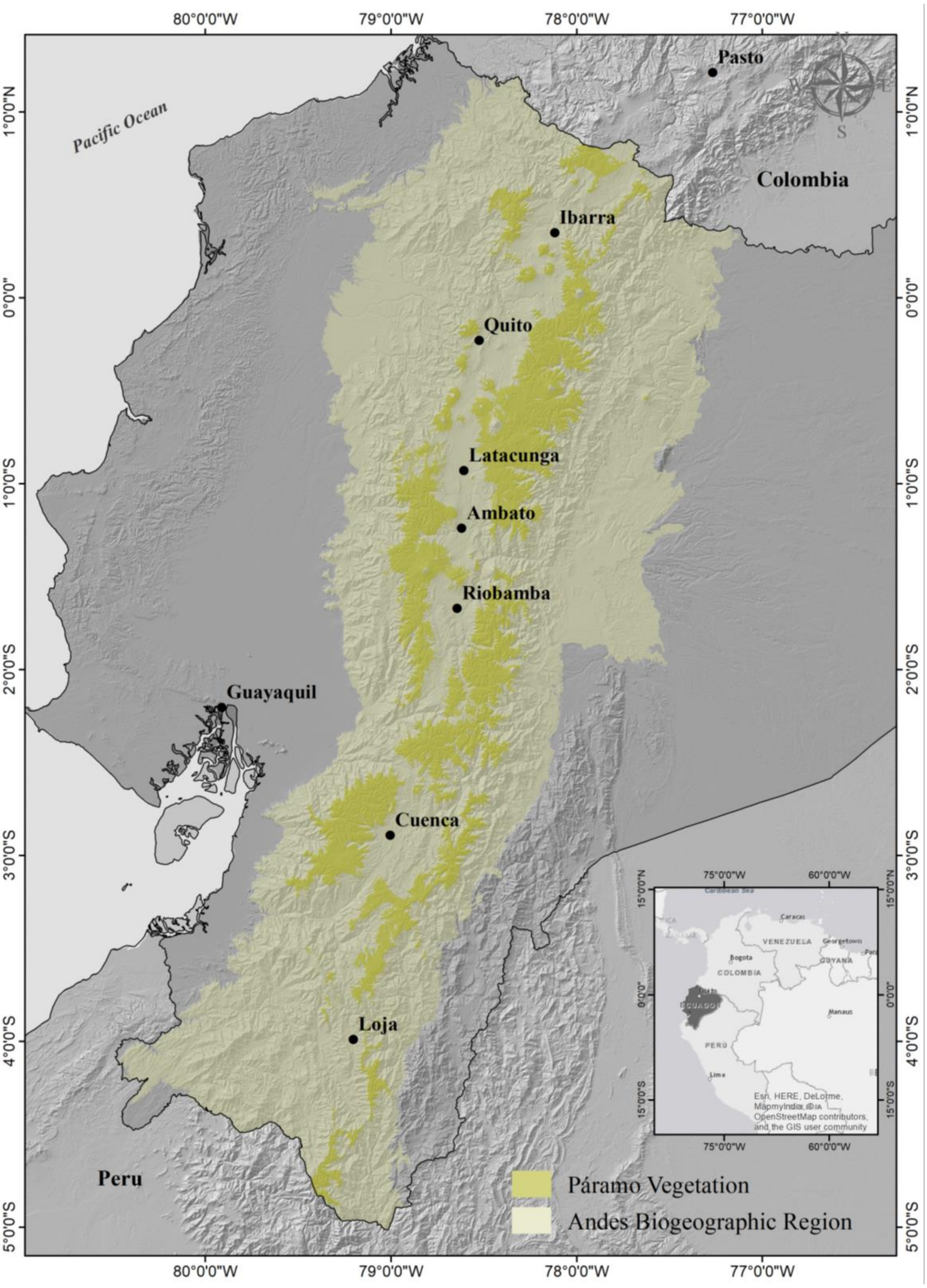

Figure 2.1 Location of the Andes Biogeographic Region in Ecuador.

2.2 Modelling Methods

2.2.1 Generation of Páramo Presence Records

In developing countries, the majority of species records are scattered, opportunistic and are mainly recorded in museum catalogues, personal collections, and literature (El-Gabbas and Dormann, 2018). In these countries, including Ecuador, due to the lack of funds dedicated to conservation, there is no systematic sampling scheme to collect biological information at national or regional level. Therefore, developing countries do not share their biodiversity data, causing a low representation of their species in international databases (e.g. Global Biodiversity Information Facility - GBIF) (Newbold, 2010). The scarcity of species records together with clear signs of sampling bias and limited local environmental gradients, make it difficult to establish distribution models based on solid records of species for a variety of taxonomic groups at national and regional scales.

Due to these circumstances, the *Map of Ecuadorian Continental Ecosystems,* scale 1:100,000 (MAE, 2013a), generated by the Ministry of the Environment of Ecuador (MAE) in 2013, was used to generate the records of presence for modelling the eleven páramo ecosystems (Table 2.1). The presence datasets varied in size (12 to 19,999 presence records, i.e. number of km^2) due to the variability in area of the different páramo types (See Chapter I - Table 1.2). Presence points were generated individually per type of vegetation, removing duplicates and ensuring a minimum distance of 1km in between points in agreement with climatic data resolution.

Table 2.1 Páramo Ecosystems, codes and number of presence records used for modelling.

Nº	**Páramo Ecosystem**	**Ecosystem Code**	**# Presence Records**
1	Sumaco Volcano's Páramo Grassland and Evergreen Shrubland	HsSn01	12
2	Southern Páramo High Montane Evergreen Shrubland	AsAn01	33
3	Humid Subnival Páramo Grassland	HsNn01	345
4	Ultra-humid Subnival Páramo Grassland	HsNn02	518
5	Floodable Páramo Grassland	HsSn04	560
3	Páramo Evergreen Forest	BsSn01	605
7	Humid High Upper Montane Páramo Grassland	HsSn03	827
8	Páramo Caulescent Rosettes (*frailejones*) and Grassland	RsSn01	854
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	2,124
10	Páramo Evergreen Shrubland and Grassland	AsSn01	8,699
11	Páramo Grassland	HsSn02	19,999

2.2.2 Selection of Niche Predictor Variables

Bioclimatic variables were used as predictor variables to capture annual climatic patterns, seasonality and extreme environmental conditions for each páramo remnant (O'Donnell and Ignizio, 2012; WorldClim, 2005). The set of variables was chosen based on previous literature on tropical ecosystem modelling (Tovar et al., 2013; Cuesta, 2007; Cuesta et al., 2008; Ramirez-Villegas et al., 2014) and due to their applicability for estimating potential effects of climate change on species distribution (O'Donnell and Ignizio, 2012; Pearson and Dawson, 2003). All climatic layers were provided by WorldClim (Version 1.4) at 30 seconds (~1 km^2) resolution. Current climatic conditions are based on interpolations of observed data representative of the 1950-2000 period. For future climatic projections, years 2050 (average for 2041-2060) and 2070 (average for 2061-2080) were considered (Table 2.2). In Ecuador, the WorldClim database has been verified and used in several climatic studies (e.g. Ecuador's Bioclimatic Model) and analyses led by local institutions (Cuentas, 2013; Melo et al., 2011), proving to be a reliable source of information. Despite certain limitations linked to the lack of broad coverage of the climatic stations in the Ecuadorian territory, WorldClim results more adequate to the scale of this study than other global data sets, such as PRECIS and TL959, which present much lower resolution (50 km^2) (Bustamante, 2017).

Although many of these variables are correlated, the entire bioclimatic set (19) was retained considering the complexity of diverse climatic requirements for all páramo remnants located along both cordilleras. Studies also reveal that in MAXENT under-parameterization has a stronger negative effect on models performance than when models are over-parameterized suggesting that it is better to allow the MAXENT algorithm to control model parameterization (Warren and Seifert, 2011). This criterion was applied for all models except for the ones with ≤ 40 occurrences. Several authors have suggested that when there are fewer occurrences, a simple model may be applied (Tovar et al., 2013; Ramirez-Villegas et al., 2014; Warren and Seifert, 2011), where the number of parameters does not exceed the number of points of occurrence used in the construction of the models (Warren and Seifert, 2011). The simpler models were applied for spatially-restricted vegetation types *Grassland and Evergreen Shrubland of Sumaco's Volcano Páramo* (HsSn01) and *High Montane Evergreen Shrub of Southern* Páramo (AsAn01), for which a selection of 7 (Bio1, Bio2, Bio 12, Bio14, Bio15, Bio18 and Bio19) out of the 19 bioclimatic variables was used based on correlation analysis (Pearson correlation coefficient cut-off 0.8). These decisions were informed by similar modelling exercises performed in the Andes (Tovar et al., 2013; Ramirez-Villegas et al., 2014; Cuesta, 2007).

Table 2.2 Bioclimatic Variables used to represent climatic niche under current (1950-2000) and future climatic conditions (2050 & 2070)

N°	**Code**	**Variable**	**Unit**
1	Bio1*	Annual Mean Temperature	°C
2	Bio2*	Mean Diurnal Range	°C
3	Bio3	Isothermality	°C
4	Bio4	Temperature Seasonality	°C
5	Bio5	Max Temperature of Warmest Month	°C
6	Bio6	Min Temperature of Coldest Month	°C
7	Bio7	Temperature Annual Range	°C
8	Bio8	Mean Temperature of Wettest Quarter	°C
9	Bio9	Mean Temperature of Driest Quarter	°C
10	Bio10	Mean Temperature of Warmest Quarter	°C
11	Bio11	Mean Temperature of Coldest Quarter	°C
12	Bio12*	Annual Precipitation	mm
13	Bio13	Precipitation of Wettest Month	mm
14	Bio14*	Precipitation of Driest Month	mm
15	Bio15*	Precipitation Seasonality	%
16	Bio16	Precipitation of Wettest Quarter	mm
17	Bio17	Precipitation of Driest Quarter	mm
18	Bio18*	Precipitation of Warmest Quarter	mm
19	Bio19*	Precipitation of Coldest Quarter	mm

**Variables used for simpler models*

2.2.3 Selection of Global Climate Models (GCMs) and Representative Concentration Pathways (RCPs) for Future Niche Spatial Distribution Prediction

Based on the assumption that as the number of independent models considered increases, the errors tend to be cancelled (Tebaldi and Knutti, 2007); six Global Climate Models (GCMs) were included to predict the future spatial distribution of páramo niches. The GCMs were selected based on the availability and completeness of the bioclimatic variables required to run the models in MAXENT. All GCMs were downscaled and calibrated by WorldClim using the current climate as baseline, assuming that the changes in climate have high spatial autocorrelation (Hijmans et al., 2005) (Table 2.3). Representative concentration pathways (RCPs) were considered to understand alternative futures for the páramo vegetation. RCPs considered the effects of implementing international policies or agreements aimed at mitigating emissions and other socio-economic and technology assumptions. There are four RCPs known as RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5, named according to their radiative forcing target level established for year 2100 (Van Vuuren et al., 2011). Only RCPs 4.5 and RCP 8.5 were considered, representing one moderate and extreme scenario respectively. The other two scenarios were excluded since according to the Intergovernmental Panel on Climate Change

(IPCC), RCP 2.6 is unlikely to be achieved and RCP 6.0 does not consider additional efforts to limit emissions (IPCC, 2014a; Van Vuuren et al., 2011) (Table 2.4).

Table 2.3 Global Climate Models (GCMs) considered for future scenarios

N	Modelling Centre	Abbreviation
1	Beijing Climate Center	BCC-CSM1-1
2	University Corporation for Atmospheric Research	CCSM4
3	Met Office Hadley Centre	HadGEM2-ES
4	Institut Pierre Simon Laplace	IPSL-CM5A-LR
5	Japan Agency for Marine, Earth Science and Technology, University of Tokyo and National Institute for Environmental Studies	MIROC-ESM
6	Meteorological Research Institute	MRI-CGCM3

Table 2.4 Representative Concentration Pathways (RCPs) Assumptions, b*ased on: (Van Vuuren et al., 2011), (Wayne, 2013), (Moss et al., 2008) & (Moss et al., 2010)*

Pathway	Radiative Forcing	Characteristics	Pathways	Emissions CO_2 equiv (p.p.m)	Expected Temperature Anomaly (°C)
RCP 8.5	>8.5 W/m^2 in year 2100	very high GHG concentration scenario, exclude any additional efforts to limit emissions	Rising	~1,370 ppm CO_2 eq.	4.9
RCP 4.5	~4.5 W/m^2 at stabilization after year 2100	intermediate scenario	Stabilization without overshoot	~650 ppm CO_2 eq.	2.4

2.2.4 Model Fitting and Implementation

The climatic niche models were generated through MAXENT software, version 3.3.3k. MAXENT is an estimation technique based on the maximum-entropy principle and extensively used in estimating species distributions under specific environmental dimensions (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2010; Franklin et al., 2013; Elith et al., 2006). MAXENT performs extremely well in predicting occurrences by finding the largest spread (maximum entropy) in a geographic dataset of local occurrences in relation to a set of environmental variables that limits species presence/occurrence (Steinbach, 2002; Elith et al., 2011). Among the advantages of this modelling technique are the use of only presence data, given that absence data are rarely available or unreliable (Phillips et al., 2006; Elith et al., 2011; Phillips and Elith, 2013). MAXENT results are continuous making it easier to distinguish and interpret the changes (Phillips et al., 2006). Unlike other techniques based on discriminative approaches, MAXENT applies a generative approach using the environmental data of the entire study area, which is an advantage when presence data are limited (Phillips and Elith, 2013). In addition, MAXENT is relatively unaffected by spatial errors associated with location data, it requires few occurrence data to build useful models and it has robust algorithms (deterministic) designed to efficiently achieve the maximum entropy distribution (Baldwin, 2009).

In contrast, there are some drawbacks associated with MAXENT. The main limitation is the possibility of over-fitting, which limits the ability of the model to adequately generalize independent data (Radosavljevic and Anderson, 2014). Although, MAXENT tries to address this limitation through its “regularization multiplier” parameter which limits the complexity of the model and generates a less localized prediction (Phillips and Dudík, 2008). Despite the limitations, it has been proven that MAXENT obtains a better discrimination of suitable versus unsuitable areas for the species than other presence-only modelling approaches such as the Genetic Algorithm for Rule-Set Prediction (GARP)(Phillips et al., 2006). The various points in its favour make MAXENT an appropriate modelling technique for this study.

Models were run according to default parameters with the exception of key settings used as optimization factors oriented to avoid over and under-prediction problems (Warren and Seifert, 2011; Ramirez-Villegas et al., 2014; Martínez, 2010; Lobo et al., 2008; Radosavljevic and Anderson, 2014). Parameter modifications were applied to groups of páramo ecosystems which were partitioned according to their number of presence records (Table 2.5). Key settings adjustment began with the identification of background points used to define the areas where the ecosystem has not developed. For this analysis, background points (pseudoabsences) where randomly sampled by MAXENT from the entire study region. All models were run with 10,000 background points (default value) with the exception of *Páramo Grassland vegetation (HsSn02)* for which it was increased to 20,000 background points in order to maintain a good discrimination between ecosystem presence and absence (VanDerWal et al., 2009; Isaac et al., 2009).

The replication type was selected considering the differences in MAXENT performance regarding internal usage of occurrence data (Phillips, 2005). Cross-validation was used for vegetation with > 40 occurrences, since this splits the occurrence data randomly into equal-size groups (10 folds), using all data for validation purposes (Radosavljevic and Anderson, 2014; Phillips, 2005). Bootstrapping was applied in cases with ≤ 40 occurrences, since this selects the training data by using the presence points with the number of samples being equal to the total number of presence points (Phillips, 2005). Models were run 10 times (replicates), except for vegetation with occurrences ≤ 40 for which models were run only 5 times (Young et al., 2011; Ramirez-Villegas et al., 2014). The random seed option was selected true for all cases to allow the program to use a different random seed for each run. Hence a different random test/train partition was made and a different random subset of the background was used (Phillips, 2005). Models were run simultaneously under the Linux operating system using batch mode available for MAXENT, in collaboration with the York Advanced Research Computing Cluster (YARCC) led by the IT Department at the University of York.

Models were set to 5,000 maximum iterations to provide sufficient time for convergence and to avoid over and under-prediction (Young et al., 2011). All models used the default regularization multiplier (1) except for the models with occurrences >2,000 to which a higher value (2.5) was assigned in order to achieve optimal model complexity and reduce overfitting in more general models (Elith et al., 2010; Radosavljevic and Anderson, 2014; Phillips, 2005). This analysis applied the criterion of unlimited dispersal for future climatic niche distribution (Thomas et al., 2004, Ramirez-Villegas et al., 2014), based on the assumption that all páramo ecosystems can migrate and occupy any site that becomes climatically suitable in the future. For this purpose, the extrapolate option was selected as true to allow models to predict into regions of environmental space beyond the climatic restrictions encountered during training (Phillips, 2005). Finally, a threshold rule was defined to obtain binary maps of niche distribution. This was useful to differentiate the areas of presence (1) and absence (0) of the ecosystems predicted. The threshold rule selected was one that maximizes the sum of sensitivity and specificity of training points, minimizing omission and commission errors (Manel et al., 2001; Freeman and Moisen, 2008), and equivalent to the closest optimal point on the Receiver Operating Characteristic curve (ROC) (Cantor et al., 1999). This threshold has demonstrated good performance in similar studies (Liu et al., 2005; Jiménez-Valverde and Lobo, 2007; Cao et al., 2013).

Table 2.5 MAXENT Key Settings defined for each modelling group

Group*	Páramo Ecosystem Code	Presence Records (#)	Replicated Run Type	Replicates Number	Background Points	Folds	Regularization Multiplier
1	HsSn01	12	Bootstrap	5	10,000	---	1
	AsAn01	33					
2	HsNn01	345	Cross-validation	10	10,000	10	1
	HsNn02	518					
	HsSn04	560					
	BsSn01	605					
	HsSn03	827					
	RsSn01	841					
3	HsNn03	2,123	Cross-validation	10	10,000	10	2.5
	AsSn01	8,690					
4	HsSn02	19,999	Cross-validation	10	20,000	10	2.5

**All groups were modelled by considering a maximum number of iterations equal to 5,000 and "Maximum training sensitivity plus specificity" as the threshold rule.*

2.2.5 Model Ensemble and Consensus

Numerous niche predictions and projections were generated through MAXENT based on current and future climatic conditions. There were 30 results for each páramo type, and 330 results in total. Under the assumption that all independent models could be considered flawed, however, many of them contain some degree of partial truth (McNees, 1992; Winkler, 1989; Araújo and New, 2007). Model combination was based on the ensemble of all binary outputs (i.e. 1 - 0) obtained from the six GCMs into a single map. Binary maps were combined according to the corresponding period (2050 & 2070), RCP (4.5 & 8.5) and type of páramo ecosystem based on two approaches. First, *without consensus (a)*, considers all predicted niche areas without discriminating consensus level among the six GCM. Thus, all pixels identified as presence (i.e. 1) by any of the six GCMs were considered as the true presence of the ecosystem. Second, *with consensus (b)*, groups the pixels of presence (i.e. 1) according to the level of agreement reached among the six GCMs. Thus, presence pixels predicted coincidentally by 1 to 2 GCMs were considered as low consensus, 3 to 4 GCMs as medium consensus and 5 to 6 GCMs as high consensus. Areas of niche predicted over areas of current human intervention (i.e. urban, agricultural and deforested areas) were discarded by using the intervention mask available on the *Map of Ecuadorian Continental Ecosystems* (MAE, 2013a). ArcGIS software version 10.4.1 was used to perform the spatial analysis required.

2.2.6 Evaluation of Model Performance

The models' performance was evaluated by using the area under the receiver operating characteristic curve (AUC) (Mateo et al., 2011; Phillips et al., 2006; Guisan and Zimmermann, 2000; Hanley and McNeil, 1982). AUC values can vary between 0 to 1, where 1 indicates perfect model discrimination, 0.5 indicates that the model's predictive discrimination is not better than random and values < 0.5 indicate performance worse than a random selection (Young et al., 2011; Elith et al., 2006). Despite limitations highlighted by several experts showing that the AUC could reflect a good predictive accuracy even in models that reflect a poor performance in estimating the underlying biology (Lobo et al., 2008; Warren and Seifert, 2011), the AUC remains a useful metric when it comes to prioritising areas in terms of their relative importance as species' habitat (Elith et al., 2006). Since models were run five to ten times, the calculation of AUC average (Appendix II.A) for test and training sets was performed for each dataset and subsequently for each consensus model (Radosavljevic and Anderson, 2014). Models with average AUC ≥ 0.7 were considered robust and consequently used for further analyses as suggested by similar studies (Ramirez-Villegas et al., 2014; Elith et al., 2006).

2.3 Climate Change Impact

2.3.1 Impact on Climatic Niche Distribution

The evaluation of the impact of climate change on páramo niches distribution was based only on niche areas identified as high consensus among the six GCMs results (at least 5 of 6 GCMs in agreement). Based on similar studies (Tovar et al., 2013; Broennimann et al., 2006; Ramirez-Villegas et al., 2014; Loehle and LeBlanc, 1996; Peterson et al., 2001), niche pixels were analysed and classified into four categories of impact. The first category was *unchanged niche (1)*, where climatic conditions remain stable. Thus, climatic niches (pixels) that were overlapping, due to their constant presence in the current scenario and future scenarios were considered as unchanged. The second category was *lost niche (2)*, where optimal climatic conditions are likely to decrease. Hence, climatic niches (pixels) that were present in the current scenario but are reduced in future scenarios were identified as lost. The third category was *expanded niche (3)*, where change to climatic conditions does not occur in the present but could probably occur in the future. Thus, climatic niches (pixels) that were absent in the current scenario but were present in future scenarios were considered as potential niche expansion . The fourth category was *extinct niche* (4), where optimal climatic conditions totally disappear. Hence, climatic niches (pixels) that were present in the current scenario but totally absent in future scenarios were identified as extinct.

Impact analysis was performed at two levels: individually per type of páramo vegetation and at national scale. At páramo ecosystem level, the impact was evaluated based only on pixels of niche presence identified under *high consensus* category. The decision was made to increase the reliability of the results since there is a high level of uncertainty associated with climate change. The impact at national scale was based on both ensemble approaches, *without consensus* and with *high consensus*, allowing some degree of flexibility in the evaluation of the impact. Therefore, the national impact was based on all pixels identified as presence by any GCMs without consensus and pixels of niche presence identified under the high consensus category (with consensus across all GCMs). Based on each approach, models were combined into one, without discrimination of vegetation type to show the national impact. ArcGIS software version 10.4.1 was used to perform the spatial analysis required.

2.3.2 Climatic Niche Shifts

The variation in time and space of páramo ecosystems sharing the same climatic niche was considered important in the evaluation of global change impact on páramo's vegetation biodiversity. Climatic niche shifts were estimated by accounting (pixel by pixel) the number of páramo ecosystems overlapping (sharing) climatic niches across future scenarios. For this purpose, only niche areas (pixels) previously identified under high consensus (i.e. 5 to 6 GCMs in agreement) were considered. Models were combined into one without discrimination of vegetation type. The assignation of value of one to each pixel of presence was required to facilitate the posterior quantification of niche shifts. Thus, the niche shifts could range from a minimum of 1 which represents climatic niches occupied by only one páramo ecosystem to a maximum of 11 representing climatic niches occupied by all eleven páramo ecosystems. ArcGIS software version 10.4.1 was used to perform the spatial analysis required.

3. Results

3.1 Models Evaluation

3.1.1 Statistical Evaluation

The niche distribution models suggested good performance according to the average AUC training and test showing values >0.9 for nine of the eleven páramo vegetation types. Despite having more presence records (occurrences) than the rest, niche distribution models for ecosystem types *Páramo Evergreen Grassland and Shrubland* (*AsSn01*) and *Páramo Grassland* (*HsSn02*) showed poorer statistical performance, however, AUC values were still ≥0.7 (Table 2.6).

Table 2.6 AUC- Statistical Evaluation for Current Scenarios

Nº	Ecosystem Code	# Presence Records	Training AUC average	Test AUC average
1	HsSn01	12	0.9994	0.9994
2	AsAn01	33	0.9981	0.9981
3	HsNn01	345	0.9807	0.9786
4	HsNn02	518	0.9725	0.9707
5	HsSn04	560	0.9647	0.9593
6	BsSn01	605	0.9549	0.9489
7	HsSn03	827	0.9589	0.9567
8	RsSn01	854	0.9633	0.9626
9	HsNn03	2,124	0.9112	0.9093
10	AsSn01	8,699	0.7344	0.7309
11	HsSn02	19,999	0.7240	0.7219

3.1.2 Variability of Climate Niche Predictions across Global Climate Models (GCMs)

Across the six GCMs used, climatic niche predictions varied significantly (Table Fig 2.7 and Fig 2.2). Considering scenario RCP 4.5 (year 2050) as an example, the niche area projected for ecosystem *HsSn01* (modelling group 1), varied from a minimum of 12 km^2 based on GCM *MRI-CGCM3* to a maximum of 489 km^2 according to GCM *IPSL-CM5A-LR*. A standard deviation (SD) of 190 km^2 was obtained by considering the variation in climatic niche area across all GCMs. Ecosystem *HsNn02* (modelling group 2), registered niche area variations ranging from a minimum of 476 km^2 according to GCM *CCSM4* to a maximum of 1,156 km^2 based on GCM *MRI-CGCM3*. In this case, the variation of climatic niche area across all GCMs represented a SD of 280 km^2. Ecosystem *AsSn01* (modelling group 3), experienced variations in climatic niche area ranging from a minimum 18,776 km^2 based on GCM *IPSL-CM5A-LR* to a maximum of 21,997 km^2 according to GCM *MRI-CGCM3*. A SD equal to 1,237 km^2 was obtained when all climatic niche areas, predicted by all GCMs, were considered. In the case of ecosystem *HsSn02* (modelling group 4), areas of niche reflected variations ranging from a minimum 21,479 km^2 based on GCM *IPSL-CM5A-LR* to a maximum of 25,307 km^2 according to BCC-CSM1-1. Niche variation across all GCM showed a SD of 1,401 km^2 (Table 2.7 and Fig 2.2). As observed in the examples, the same GCM (e.g. *MRI-CGCM3)* predicting the smallest niche area for one ecosystem (e.g. *HsSn01)* was predicting the largest niche area for another ecosystem (e.g. *AsSn01*). The rest of the páramo ecosystems experienced similar variation in climatic niche areas under scenario RCP 4.5 (Table 2.7) and scenario RCP 8.5 (Fig 2.3 and Appendix II.B); showing smaller or larger areas of climatic niche depending on the GCM used. There was no clear pattern leading to the exclusion of a particular model, justifying the model ensemble performed.

Table 2.7 Climatic niche area predicted for each Global Climate Model (GCM) under GHG emission scenario RCP 4.5 (years 2050 and 2070) per type of páramo ecosystem (code).

Modelling Group	**N°**	**Páramo Ecosystem Code**	**RCP 4.5 (~km^2)**																	
			Year 2050									**Year 2070**								
			BCC-CSM1-1	**CCSM4**	**HadGEM2-ES**	**IPSL-CM5A-LR**	**MIROC-ESM**	**MRI-CGCM3**	**SD**	**Min**	**Max**	**BCC-CSM1-1**	**CCSM4**	**HadGEM2-ES**	**IPSL-CM5A-LR**	**MIROC-ESM**	**MRI-CGCM3**	**SD**	**Min**	**Max**
1	**1***	HsSn01	**42**	**22**	**30**	**489**	**20**	**12**	**190**	**12**	**489**	35	8	200	546	165	23	204	8	546
	2	AsAn01	48	80	51	0	16	194	69	0	194	174	87	0	1	105	437	163	0	437
2	**3**	HsNn01	633	585	322	200	1,516	1,668	621	200	1,668	468	371	322	137	50	1,323	457	50	1,323
	4*	HsNn02	**1,156**	**476**	**580**	**579**	**808**	**1,056**	**280**	**476**	**1,156**	1,465	162	692	377	497	852	456	162	1,465
	5	HsSn04	4,954	3,697	2,914	4,696	4,760	4,332	781	2,914	4,954	4,491	4,433	1,395	3,272	3,607	4,154	1,162	1,395	4,491
	6	BsSn01	3,711	7,356	2,626	1,805	2,933	4,740	1,981	1,805	7,356	3,999	8,330	2,546	676	880	2,440	2,818	676	8,330
	7	HsSn03	812	1,248	230	171	3,290	2,328	1,238	171	3,290	188	205	10	2	1	1,644	645	1	1,644
	8	RsSn01	2,169	393	3,056	2,411	1,932	2,553	912	393	3,056	4,372	185	2,472	2,516	830	2,594	1,482	185	4,372
3	**9**	HsNn03	3,049	2,314	1,534	1,072	2,413	2,758	749	1,072	3,049	2,595	2,105	871	764	1,919	1,887	723	764	2,595
	10*	AsSn01	**20,501**	**18,841**	**19,775**	**18,776**	**19,183**	**21,997**	**1,237**	**18,776**	**21,997**	19,511	16,314	15,914	13,589	21,135	22,639	3,466	13,589	22,639
4	**11***	HsSn02	**25,307**	**23,856**	**22,911**	**21,479**	**21,800**	**23,225**	**1,401**	**21,479**	**25,307**	23,915	21,022	21,053	19,501	23,808	21,695	1,730	19,501	23,915

** Ecosystems used to exemplify climatic niche variation across Global Climate Models (GCMs).*

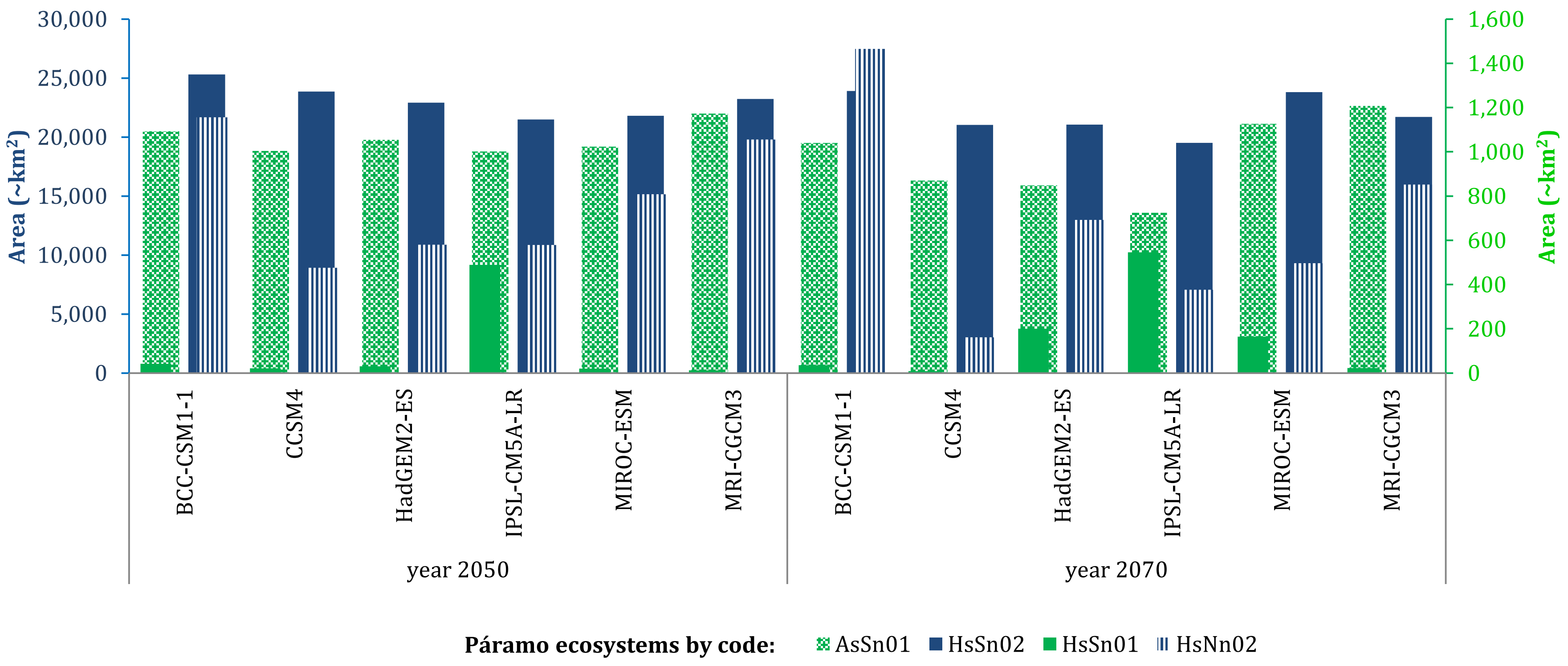

Figure 2.2 Example of variation in climatic niche area across Global Climate Models (GCMs) based on future scenario RCP 4.5 (moderate), years 2050 and 2070. Green coloured bars represent páramo ecosystems corresponding to modelling groups 1 (*HsSn01*) and 3 (*AsSn01*), while blue coloured bars represent páramo ecosystems corresponding to modelling groups 2 (*HsSn02*) and 4 (*HsSn02*).

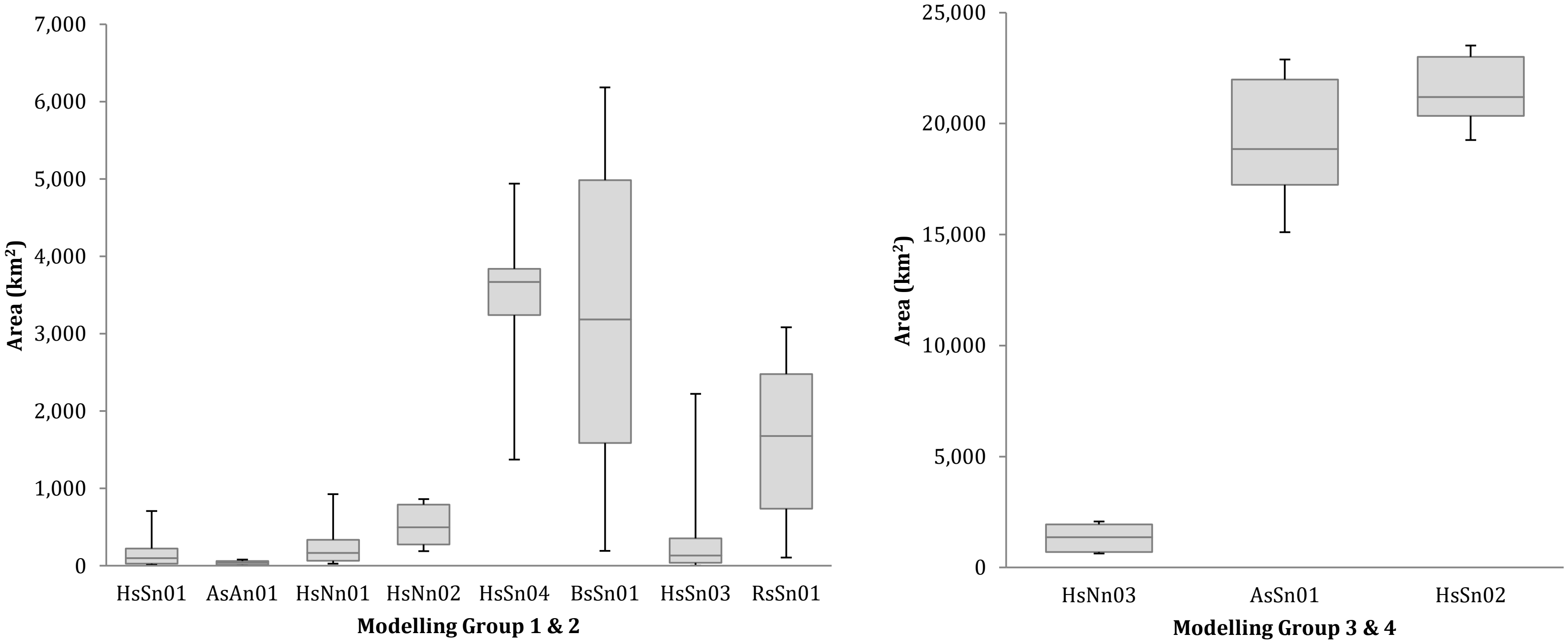

Figure 2.3 Example of variation in climatic niche area predicted across the six GCMS per páramo ecosystem (code) based on future scenario RCP 8.5 (extreme), year 2050. The graph from the left corresponds to Modelling Groups 1 and 2 while the graph from the right corresponds to Modelling Groups 3 and 4. The graphs represent minimum, first quartile, median, third quartile, and maximum values.

3.1.3 Differences in Climatic Niche Area by level of Consensus

The niche predictions obtained for the current scenario showed in general, a trend towards over-prediction with respect to the observed niche. The majority of climatic niche areas predicted for the current scenario reached high consensus. The proportion of niche area under high consensus varied differently across páramo modelling groups. The results showed that for páramo ecosystems with the highest number of occurrences (i.e. Group 3 and 4, Fig. 2.4), the proportion of niche areas reaching high consensus was ≥ 85%. The proportion of areas under high consensus was reduced for páramo ecosystems with an intermediate number of occurrences (i.e. Group 2, Fig. 2.4) showing niche areas under high consensus > 60% and ≤ 85%. For the group of ecosystems with the lowest number of occurrences (i.e. Group 1, Fig. 2.4), the proportion of niches reaching high consensus was < 60%. Future projections behaved differently compared to the current predictions. For modelling groups 3 and 4, the percentages of niche area reaching high consensus was still significant (Fig. 2.5). Ecosystems *HsSn02* (Group 4) and *AsSn01* (Group 3), had percentages >70% and <90% and >40% and <70% of niche areas reaching high consensus, respectively, when all future scenarios were compared (Table 2.8). In this modelling group, the exception was ecosystem *HsNn03* (Group 3) that reflected smaller percentage (>20% and <40%) of niche areas under high consensus (Table 2.8), throughout all future scenarios. For modelling groups 1 and 2 (Fig 2.5), the percentages of niche areas under high consensus varied differently according to the páramo ecosystem modelled. In these groups, percentages were not as significant as in the other modelling groups, reporting null percentages of niche under high consensus (e.g. *AsAn01*) to a maximum of 30% (e.g. *HsNn02*) (Table 2.8).

Table 2.8 Climatic niche area predicted and projected for current and future scenarios (RCP 4.5 and RCP 8.5) by level of consensus (high, medium, and low) reached across GCMs. Percentages of representativeness of climate niche areas by consensus level with respect to the total niche area predicted by páramo ecosystem (code) are also shown.

Modelling Group	N°	Páramo Ecosystem Code	Observed Niche (~km^2)*	RCP 4.5																											
				Year 2050														Year 2070													
				Current Niche							Future Niche							Current Niche							Future Niche						
				High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)
1	**1**	HsSn01	12	13	28	5	11	29	62	**47**	3	1	26	5	463	94	**492**	13	30	7	16	23	53	**43**	9	1	42	6	640	93	**691**
	2	AsAn01	33	155	44	77	22	120	34	**352**	0	0	0	0	298	100	**298**	166	47	69	20	115	33	**350**	0	0	0	0	604	100	**604**
2	**3**	HsNn01	345	3,788	79	480	10	536	11	**4,804**	225	10	472	21	1,605	70	**2,302**	3,361	66	1,127	22	594	12	**5,082**	46	3	256	17	1,223	80	**1,525**
	4	HsNn02	518	3,757	76	518	11	638	13	**4,913**	442	30	355	24	669	46	**1,466**	3,928	76	656	13	590	11	**5,174**	273	17	350	22	981	61	**1,604**
	5	HsSn04	560	5,693	85	387	6	652	10	**6,732**	2,302	29	1,394	18	4,138	53	**7,834**	5,386	83	438	7	675	10	**6,499**	1,454	21	2,292	33	3,273	47	**7,019**
	6	BsSn01	605	7,211	64	1,894	17	2,076	19	**11,181**	1,287	14	2,041	23	5,701	63	**9,029**	6,910	61	2,485	22	1,910	17	**11,305**	474	5	2,058	23	6,549	72	**9,081**
	7	HsSn03	827	3,593	79	428	9	546	12	**4,567**	165	5	1,001	29	2,247	66	**3,413**	3,530	80	393	9	492	11	**4,415**	1	0	38	2	1,612	98	**1,651**
	8	RsSn01	854	1,069	85	89	7	98	8	**1,256**	534	12	935	20	3,129	68	**4,598**	1,105	81	83	6	184	13	**1,372**	422	8	1,239	24	3,426	67	**5,087**
3	**9**	HsNn03	2,124	6,380	84	511	7	660	9	**7,551**	1,335	38	1,085	31	1,123	32	**3,543**	6,635	89	366	5	415	6	**7,416**	807	27	1,094	37	1,052	36	**2,953**
	10	AsSn01	8,699	20,458	89	1,121	5	1,417	6	**22,996**	13,854	65	4,401	21	3,059	14	**21,314**	19,676	87	1,480	7	1,567	7	**22,723**	11,029	52	5,431	25	4,846	23	**21,306**
4	**11**	HsSn02	19,999	22,636	95	492	2	587	2	**23,715**	18,285	86	1,375	6	1,545	7	**21,205**	19,688	84	3,152	13	530	2	**23,370**	17,011	82	2,004	10	1,680	8	**20,695**

Modelling Group	N°	Páramo Ecosystem Code	Observed Niche (~km^2)*	RCP 8.5																											
				Year 2050														Year 2070													
				Current Niche							Future Niche							Current Niche							Future Niche						
				High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)	High consensus (~km^2)	%	Medium consensus (~km^2)	%	Low consensus (~km^2)	%	Total (~km^2)
1	**1**	HsSn01	12	13	30	6	14	24	56	**43**	7	1	9	1	853	98	**869**	12	57	1	5	8	38	**21**	4	0	26	1	3,432	99	**3,462**
	2	AsAn01	33	139	41	124	37	75	22	**338**	0	0	0	0	162	100	**162**	138	49	56	20	85	30	**279**	0	0	0	0	263	100	**263**
2	**3**	HsNn01	345	3,273	70	780	17	626	13	**4,679**	32	3	163	16	796	80	**991**	2,868	63	670	15	1,027	22	**4,565**	4	1	65	14	391	85	**460**
	4	HsNn02	518	3,656	74	552	11	727	15	**4,935**	192	18	374	35	492	47	**1,058**	3,890	77	451	9	720	14	**5,061**	77	23	123	37	136	40	**336**
	5	HsSn04	560	5,439	82	524	8	649	10	**6,612**	1,176	16	1,565	21	4,755	63	**7,496**	5,602	79	697	10	782	11	**7,081**	339	5	1,365	19	5,464	76	**7,168**
	6	BsSn01	605	8,324	70	1,710	14	1,881	16	**11,915**	465	6	2,823	34	4,969	60	**8,257**	7,763	73	1,173	11	1,704	16	**10,640**	15	0	1,029	17	5,114	83	**6,158**
	7	HsSn03	827	3,470	78	351	8	652	15	**4,473**	0	0	73	3	2,056	97	**2,129**	3,574	80	331	7	562	13	**4,467**	0	0	4	0	1,179	100	**1,183**
	8	RsSn01	854	1,122	79	65	5	233	16	**1,420**	340	8	827	20	2,948	72	**4,115**	1,097	85	98	8	103	8	**1,298**	4	0	670	12	5,058	88	**5,732**
3	**9**	HsNn03	2,124	6,385	85	591	8	526	7	**7,502**	656	27	942	39	812	34	**2,410**	6,317	85	581	8	576	8	**7,474**	180	27	183	27	303	45	**666**
	10	AsSn01	8,699	20,245	88	1,253	5	1,409	6	**22,907**	12,665	60	4,981	24	3,466	16	**21,112**	20,531	88	1,251	5	1,440	6	**23,222**	8,746	45	6,541	34	4,132	21	**19,419**
4	**11**	HsSn02	19,999	22,745	97	424	2	398	2	**23,567**	16,690	82	1,860	9	1,901	9	**20,451**	22,443	96	489	2	430	2	**23,362**	13,675	76	2,106	12	2,181	12	**17,962**

**Observed niche is correspondent to the occurrence points obtained from the observed Ecosystems map and used for model generation.*

***Percentages of representativeness of niche area were calculated with respect to the total niche area predicted per scenario.*

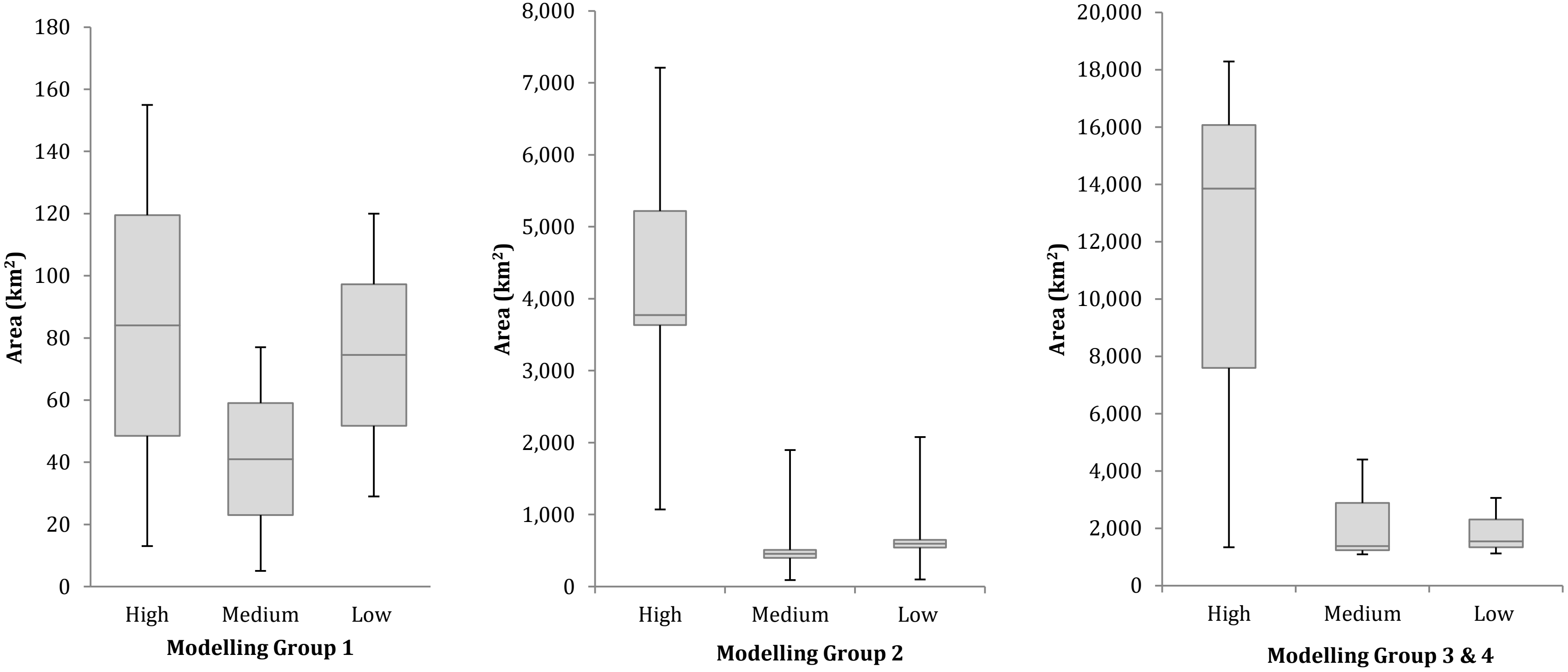

Figure 2.4 Example of proportion of climatic niche area under high, medium, and low consensus, based on current scenario per páramo modelling group. The graph from the left corresponds to Modelling Group 1, and the graph from the centre represents Modelling Group 2, while graph from the right correspond to Modelling Groups 3 and 4. The graphs represent minimum, first quartile, median, third quartile, and maximum values.

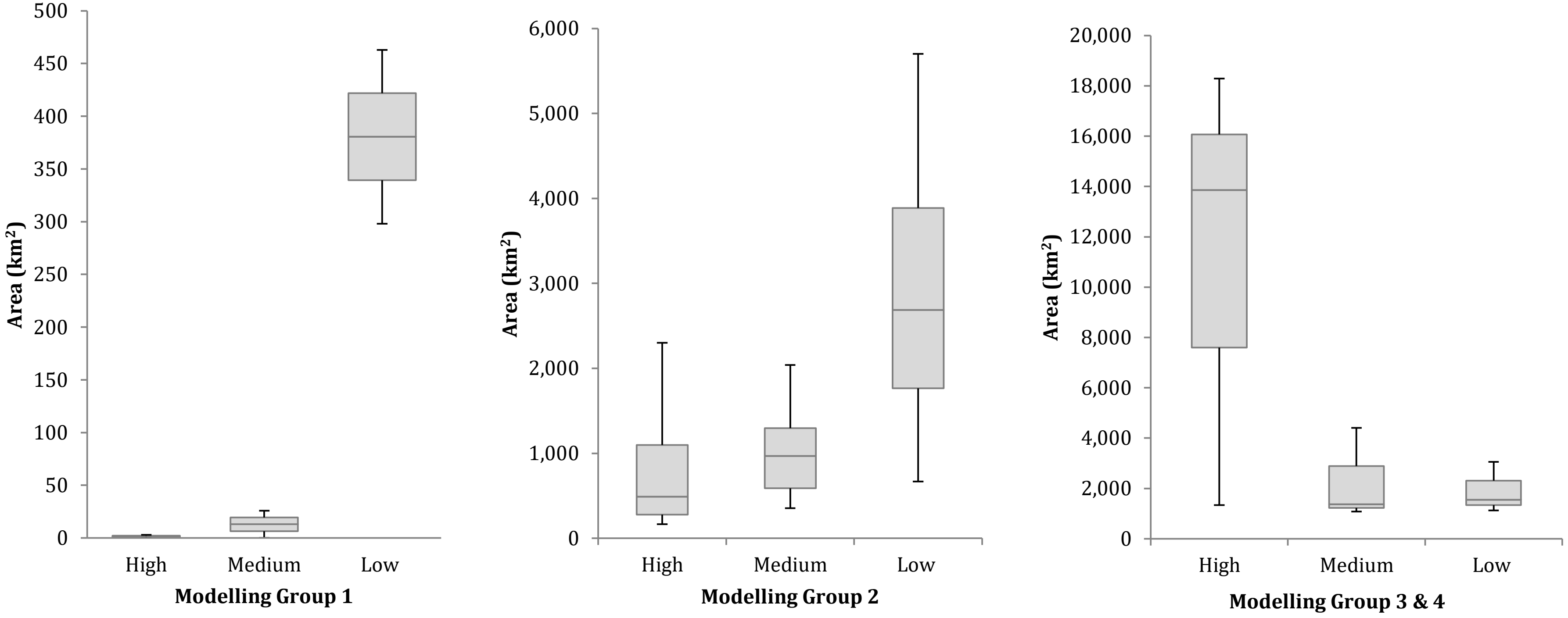

Figure 2.5 Example of proportion of climatic niche area under high, medium, and low consensus, based on future scenario RCP 4.5 (moderate), year 2050, per páramo modelling group. The graph to the left corresponds to Modelling Group 1.The graph in the centre represents Modelling Group 2. The graph to the right corresponds to Modelling Groups 3 and 4. The graphs represent minimum, first quartile, median, third quartile, and maximum values.

3.2 Climate Change Impact

3.2.1 Impact on Climatic Niche Distribution per type of Páramo Ecosystem

Based on “high consensus” niches, by 2050, under RCP 4.5 (*moderate*), one out of the eleven páramo ecosystems (i.e. *HsSn02*) could experience niche losses ≤ 25%. Niche losses > 25% and ≤ 75% were reported for three páramo ecosystems (i.e. *AsSn01, RsSn01 & HsSn04).* Six ecosystems presented niche losses > 75% (i.e. *HsSn01, HsNn03, BsSn01, HsNn02, HsNn01 & HsSn03*). Total niche extinction was reported for ecosystem *AsAn01*. Percentages of niche expansion are still very low (<4%) and probable only for four ecosystems (i.e. *BsSn01*, *HsSn04, RsSn01 & AsSn01*). By 2070, patterns were similar; however, niche losses were more significant in most cases. Páramo ecosystem *HsSn02* was predicted to experience niche losses ≤ 25%. Niche losses > 25% and ≤ 75% were reported for four páramo ecosystems (i.e. *HsSn01*, *AsSn01 and RsSn01 & HsSn04)*. Five ecosystems (i.e. *HsNn03, BsSn01, HsNn02 & HsNn01*) reported niche losses >75%, where many of them could experience losses significantly close to their extinction. Total niche extinction was registered for two páramo ecosystems (i.e. *AsAn01 and HsSn03)*. In terms of potential expansion, percentages were still very low (≤ 4%) and probable only for three ecosystems (i.e. *RsSn01, AsSn01 & HsSn04*) (Table 2.9). Under RCP 8.5 (*extreme*) projections reflected higher niche losses and lower probability of niche expansion across all ecosystems in comparison to the moderate intensity scenario (RCP 4.5). By year 2050, considering only “high consensus niches”, niche losses start with losses >25% and ≤ 75% reported for four páramo ecosystems (i.e. *HsSn02, AsSn01, HsSn01 & RsSn01*). Five páramo ecosystems (i.e. *HsSn04, HsSn03, BsSn01, HsNn02* & *HsNn01*) presented niche losses >75%, where many of them could experience losses close to their total extinction. Total niche extinction was predicted for two páramo ecosystems (i.e. *HsSn03 & AsAn01)*. In terms of expansion, the percentage is low (≤ 4%) and seems probable only for three ecosystems (i.e. *BsSn01, AsSn01 & HsSn04*). By 2070, niche losses >25% and ≤ 75% are reported for three páramo ecosystems (i.e. *HsSn02, AsSn01 & HsSn01*). Three ecosystems presented niche losses >75% (i.e. *HsSn04, HsNn03 & HsNn02*), where all of them could experience losses close to their total extinction. For this case in particular, five ecosystems (i.e. *AsAn01, HsNn01, BsSn01, HsSn03 & RsSn01*) were identified under risk of total niche extinction. In terms of expansion, the probability is lower than the rest of scenarios (<2%) and with this result probable only for three páramo ecosystems (i.e. *HsSn02, AsSn01 & HsSn04*) (Table 2.9 and Fig. 2.6 – Fig. 2.9). For detailed information regarding the spatial location (maps) of the impact for all páramo ecosystems, see the supplementary material.

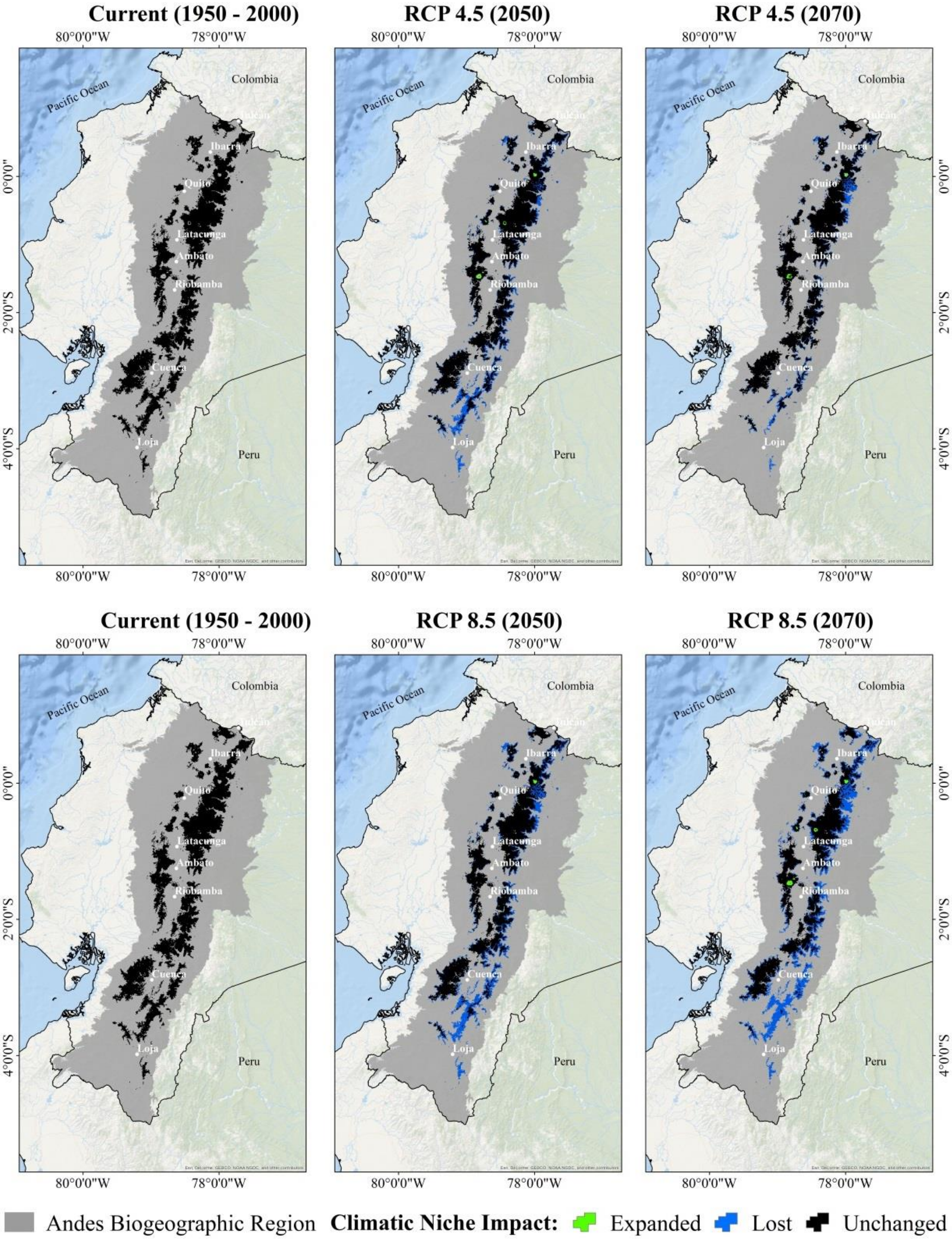

Figure 2.6 Location of Climatic Niche Impact on ecosystem *Páramo Grassland* (*HsSn02*) according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

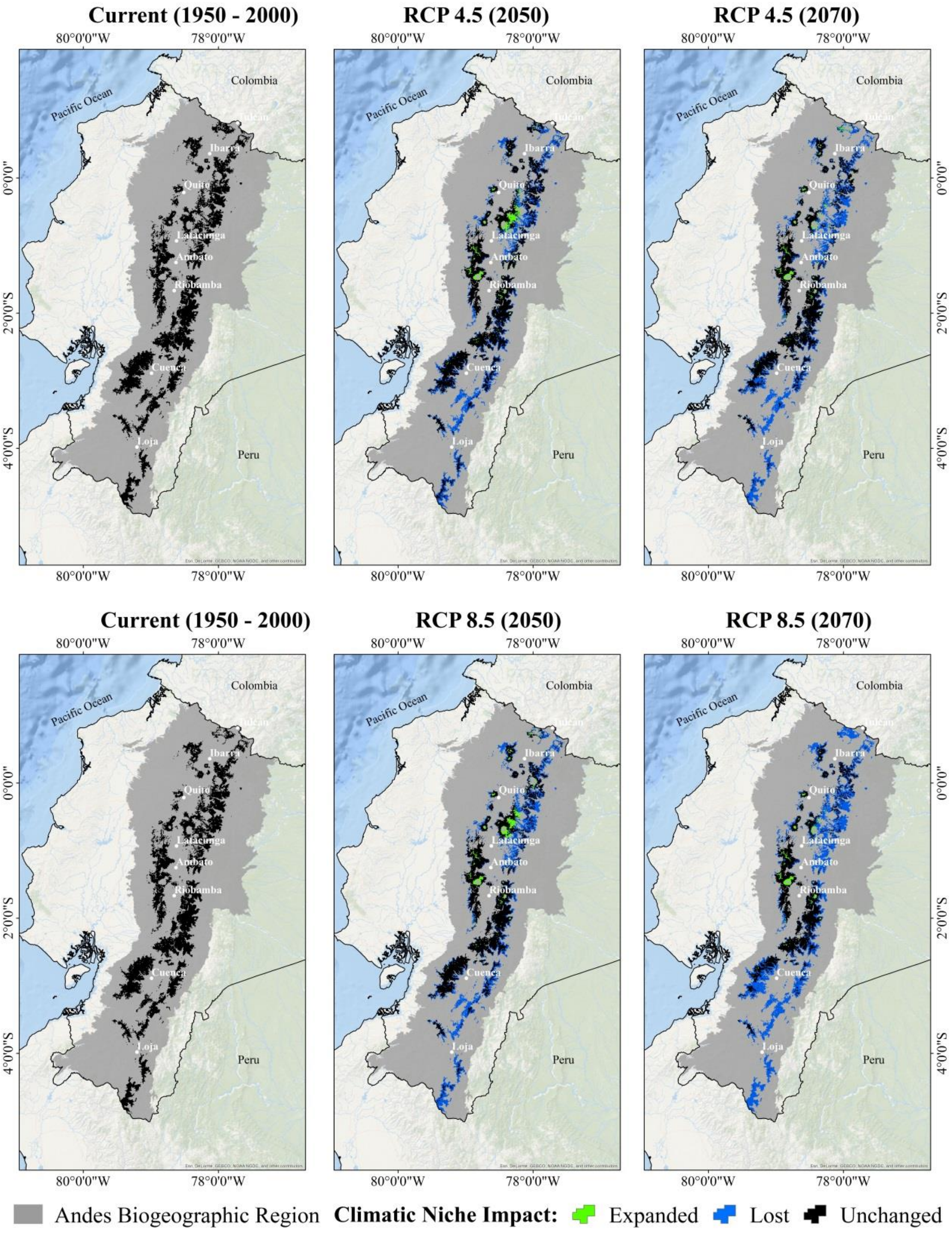

Figure 2.7 Location of Climatic Niche Impact on ecosystem *Páramo Evergreen Shrubland and Grassland* (AsSn01) according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

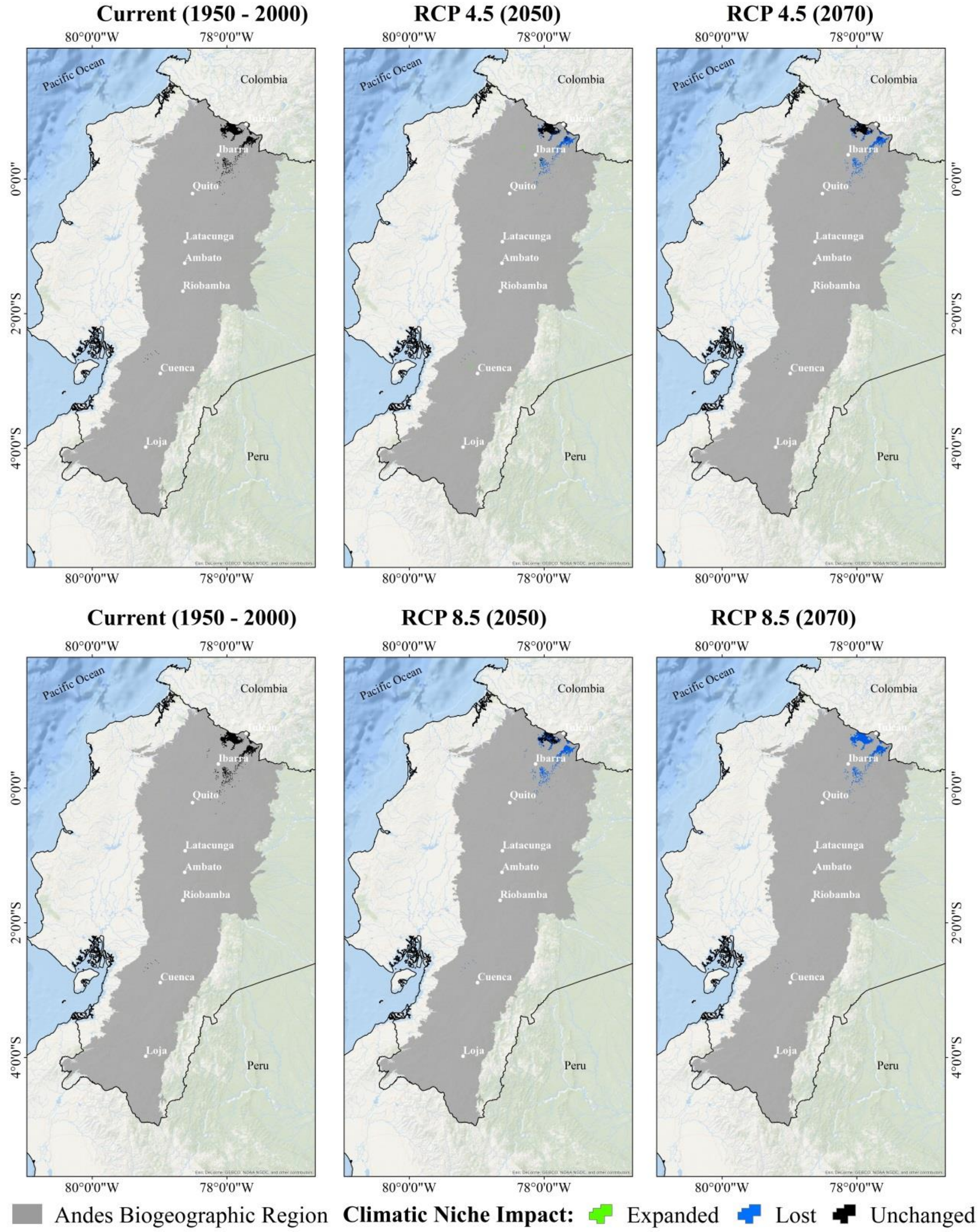

Figure 2.8 Location of Climatic Niche Impact on ecosystem *Páramo Caulescent Rosettes (frailejones) and Grassland* (*RsSn01*) according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

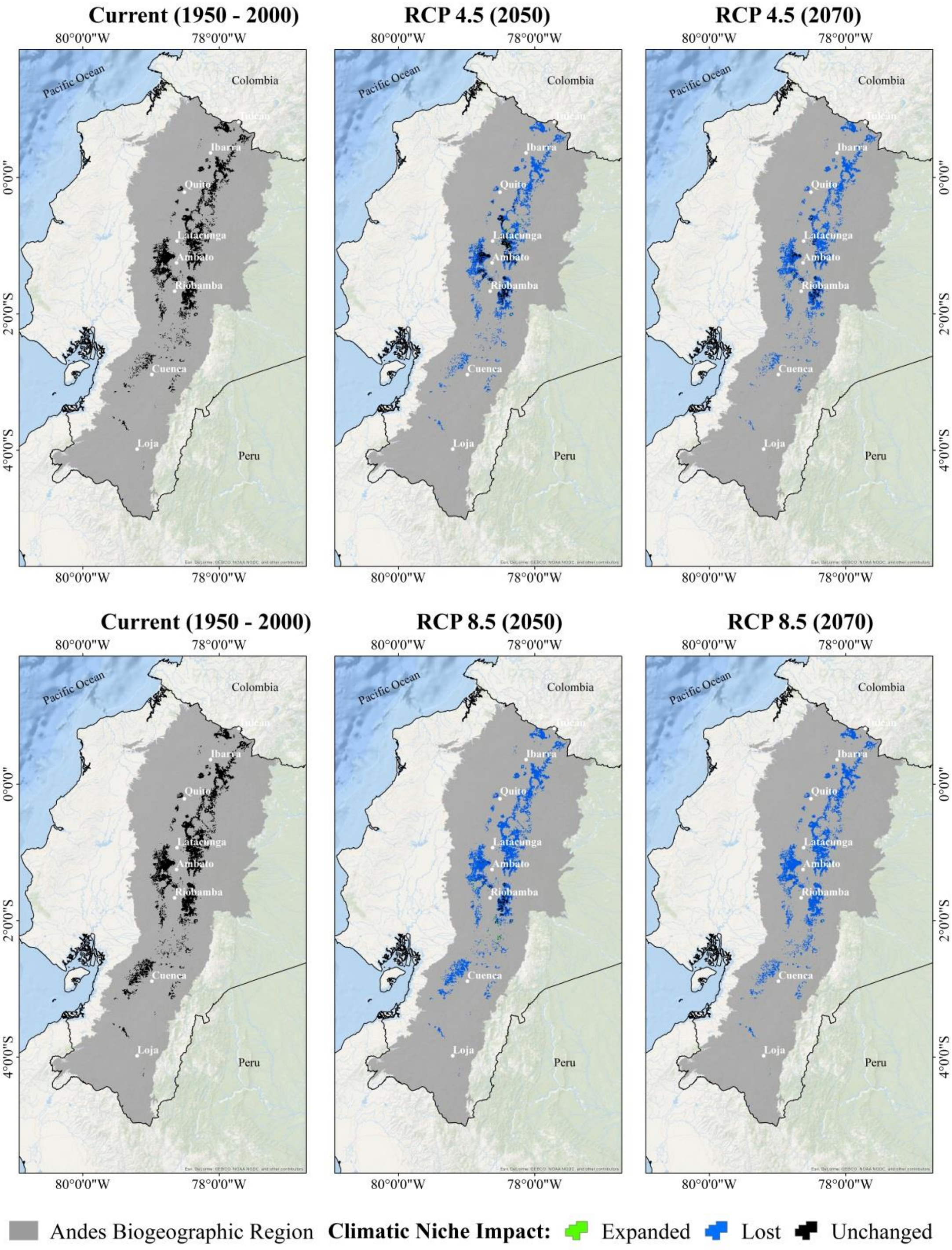

Figure 2.9 Location of Climatic Niche Impact on ecosystem *Páramo Evergreen Forest* (*BsSn01*) according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

Table 2.9 Impact of Climate Change on Páramos Climatic Niche Distribution by type of páramo ecosystem (code) under future scenarios (years 2050 & 2070) RCP 4.5 (moderate) and RCP 8.5 (extreme)

N°	Páramo Ecosystem Code	RCP 4.5												RCP 8.5											
		Year 2050						Year 2070						Year 2050						Year 2070					
		Unchanged (~km^2)	Unchanged (%)**	Lost (~km^2)	Lost (%)**	Expanded (~km^2)	Expanded (%)**	Unchanged (~km^2)	Unchanged (%)**	Lost (~km^2)	Lost (%)**	Expanded (~km^2)	Expanded (%)**	Unchanged (~km^2)	Unchanged (%)**	Lost (~km^2)	Lost (%)**	Expanded (~km^2)	Expanded (%)**	Unchanged (~km^2)	Unchanged (%)**	Lost (~km^2)	Lost (%)**	Expanded (~km^2)	Expanded (%)**
1	HsSn01	3	23	10	77	0	0	9	69	4	31	0	0	7	54	6	46	0	0	4	33	8	67	0	0
2	AsAn01*	0	0	155	100	0	0	0	0	0	100	0	0	0	0	139	100	0	0	0	0	0	100	0	0
3	HsNn01*	225	6	3,563	94	0	0	46	1	3,315	99	0	0	32	1	3,241	99	0	0	4	0	2,864	100	0	0
4	HsNn02	441	12	3,316	88	1	0	273	7	3,655	93	0	0	192	5	3,464	95	0	0	77	2	3,813	98	0	0
5	HsSn04	2,133	37	3,560	63	169	3	1,232	23	4,154	77	222	4	956	18	4,483	82	220	4	248	4	5,354	96	91	2
6	BsSn01*	1,227	17	5,984	83	60	1	464	7	6,446	93	10	0	396	5	7,928	95	69	1	12	0	7,751	100	3	0
7	HsSn03*	165	5	3,428	95	0	0	1	0	3,529	100	0	0	0	0	3,470	100	0	0	0	0	0	100	0	0
8	RsSn01*	495	46	574	54	39	4	409	37	696	63	13	1	340	30	782	70	0	0	4	0	1,093	100	0	0
9	HsNn03	1,335	21	5,045	79	0	0	801	12	5,834	88	6	0	656	10	5,729	90	0	0	167	3	6,150	97	13	0
10	AsSn01	13,045	64	7,413	36	809	4	10,525	53	9,151	47	504	3	11,853	59	8,392	41	812	4	8,322	41	12,209	59	424	2
11	HsSn02	18,180	80	4,456	20	105	0	16,928	86	2,760	14	83	0	16,648	73	6,097	27	42	0	13,507	60	8,936	40	168	1

**Páramo ecosystems showing signs of potential niche extinction.*

***Percentages were calculated with respect to each corresponding current niche scenario (high consensus) presented in Table 2.8.*

3.2.2 Impact on Climatic Niche Distribution at National Scale

Based on the “*without consensus*” ensemble approach, the climatic niche available for páramo vegetation at national scale could reach in average 25,896 km^2 (SD 95 km^2). By year 2050, 12% to 14% of the total climatic niche area, currently suitable for páramo vegetation, could be lost under RCP 4.5 (*moderate*) and RCP 8.5 (*extreme*), respectively. By year 2070, climatic niche losses could reach 13% to 21% when considering scenario RCP 4.5 (*moderate*) and RCP 8.5 (*extreme*), respectively. The percentage of niche expansion reported for 2050 varied from 2% to 3% and from 3% to 8%, based on RCP 4.5 (*moderate*) and RCP 8.5 (*extreme*), respectively (Fig. 2.10 and Appendix II.C).

In contrast, based on “*high consensus*” ensemble approach, the climatic niche available for páramo vegetation at national scale could reach in average 24,580 km^2 (SD 613 km^2). By year 2050, 21% to 28% of the total climatic niche area, currently suitable for páramo vegetation, could be lost under RCP 4.5 (*moderate*) and RCP 8.5 (*extreme*), respectively. By year 2070, climatic niche losses could reach 23% to 40% when considering scenario RCP 4.5 (*moderate*) and RCP 8.5 (*extreme*), respectively. The percentage of niche expansion reported across all scenarios was null (Fig. 2.11 and Appendix II.C).

3.2.3 Climatic Niche Shifts

According to the current scenario, there are up to eight páramo ecosystems sharing the same climatic niche. The highest percentage of climatic niche area is shared by two (35% in average) to three (21% in average) páramo ecosystems, while 3% and 2% of the total niche area is shared by 7 and 8 ecosystems, respectively. By 2050, there are between seven to five páramo ecosystems sharing the same niche, according to scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. Under both future scenarios (RCP 4.5 & RCP 8.5), the largest niche area is now occupied by two to one páramo ecosystems reaching 42% and 23% of the total niche area available at that time, respectively. By year 2070, there is a maximum of six to four páramo ecosystems sharing niches, based on scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. At that time, two ecosystems are found occupying the majority of the total niche area available, reaching 38% or 29%. The percentage of area occupied by only one ecosystem increases to 28% to 29%, according to RCP 4.5 and RCP 8.5, respectively. The area of niche shared by more than two ecosystems is progressively reduced across all future scenarios (Table 2.10 and Fig 2.12).

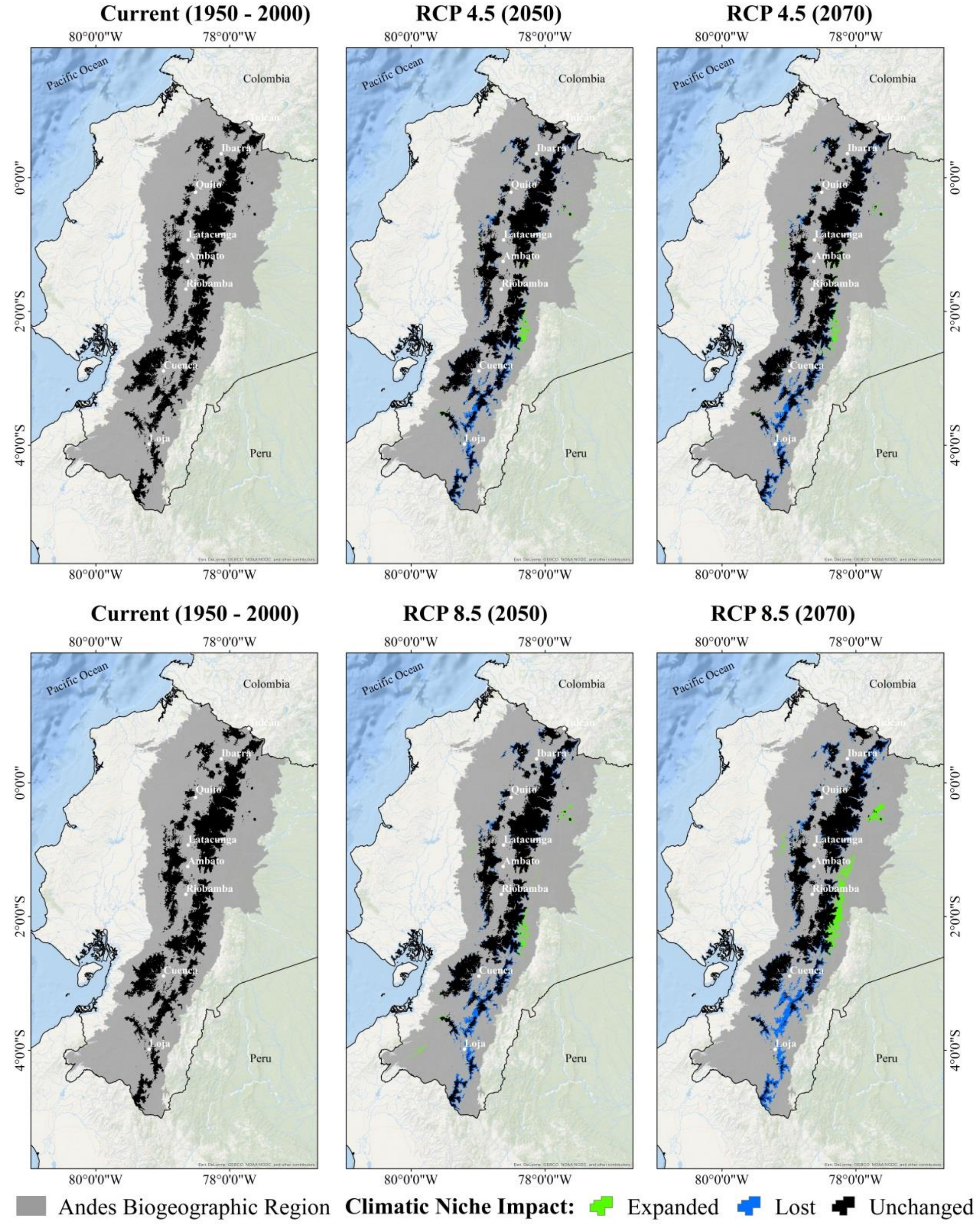

Figure 2.10 Location of Climatic Niche Impact at National scale, based on "without consensus" approach, according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

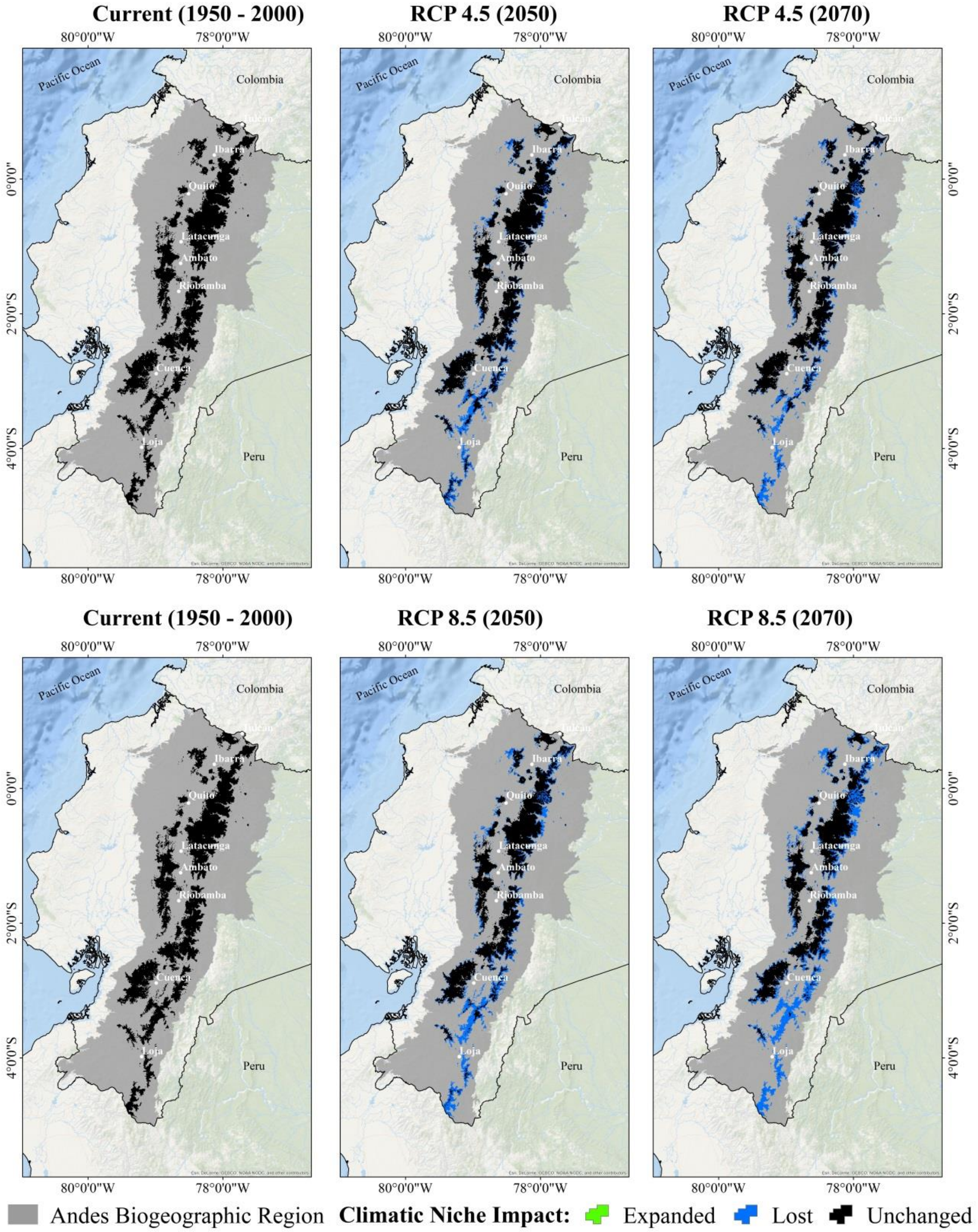

Figure 2.11 Location of Climatic Niche Impact at National scale, based on "*high consensus*" approach, according to future scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), year 2050 & 2070.

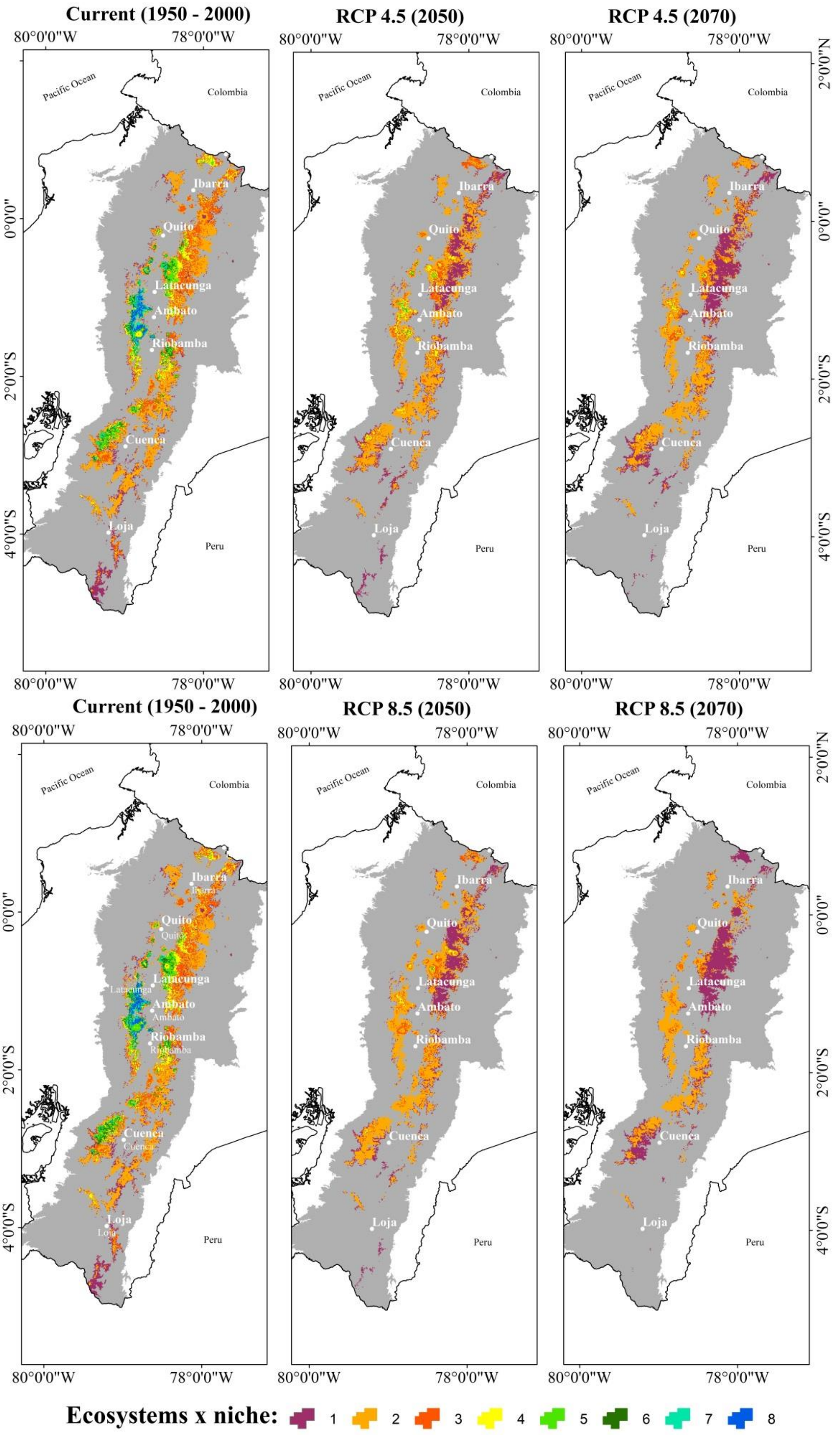

Figure 2.12 Location of Páramo Climatic Niche shifts in the Andes of Ecuador

Table 2.10 Climatic Niche Shifts under future scenarios (years 2050 & 2070) RCP 4.5 (moderate) and RCP 8.5 (extreme).

Number of Páramo Ecosystems in the Niche	RCP 4.5										RCP 8.5									
	Current Scenario		Year 2050			Current Scenario		Year 2070			Current Scenario		Year 2050			Current Scenario		Year 2070		
	Area (~km^2)	%	Area (~km^2)	%*	Variation (%)**	Area (~km^2)	%*	Area (~km^2)	%*	Variation (%)**	Area (~km^2)	%*	Area (~km^2)	%*	Variation (%)**	Area (~km^2)	%*	Area (~km^2)	%*	Variation (%)**
1	3,546	14	5,762	23	62	4,237	18	7,012	28	65	3,638	15	5,779	23	59	3,414	14	7,156	29	110
2	9,249	37	10,458	42	13	7,651	32	9,450	38	24	8,802	35	10,493	42	19	9,087	37	7,352	29	-19
3	5,083	20	2,123	9	-58	4,822	20	1,224	5	-75	5,248	21	1,286	5	-75	5,090	21	321	1	-94
4	2,590	10	1,051	4	-59	2,660	11	436	2	-84	2,701	11	355	1	-87	2,899	12	36	0.1	-99
5	1,916	8	190	1	-90	1,907	8	36	0.1	-98	1,916	8	36	0.1	-98	1,892	8	----	----	-100
6	1,079	4	28	0.1	-97	1,004	4	3	0.01	-100	1,277	5	----	----	-100	1,083	4	----	----	-100
7	914	4	9	0.04	-99	894	4	----	----	-100	773	3	----	----	-100	817	3	----	----	-100
8	581	2	----	----	-100	492	2	----	----	-100	546	2	----	----	-100	513	2	----	----	-100

**Percentages were calculated with respect to each corresponding current niche scenario (high consensus).*

***the minus sign "−" represents reduction, and, likewise, the plus sign "+" represents increment.*

4. Discussion

4.1 Climate Change Impact

The climatic niche projections obtained through this research reflect an unpromising future for the Ecuadorian páramo ecosystems, in agreement with previous studies carried out in the Andes (Cuesta, 2007; Cuesta et al., 2008; Tovar et al., 2013; Feeley and Silman, 2010). As reported in previous research, this study showed that in approximately 30 (2050) to 50 (2070) years, according to moderate (RCP 4.5) and extreme (RCP 8.5) GHG concentration scenarios, the páramo ecosystems are at high risk of abrupt niche changes. In the Andes, the most vulnerable vegetation is those with isolated or restricted spatial distribution, highly endemic biota and significant fragmentation (Herzog et al., 2011; Herzog et al., 2012; Cuesta et al., 2008; Thuiller et al., 2005), which causes greater contraction of climate niche and in some cases local extinction (Williams and Jackson, 2007; Williams et al., 2007; Tovar et al., 2013). This work is in agreement with this assertion as signs of potential extinction were shown in five (i.e. *AsAn01*, *HsSn03, HsNn01, BsSn01 & RsSn01*) páramo ecosystems. In contrast, páramo vegetation with broad distribution such as *Páramo Grassland* (*HsSn02*) and *Páramo Evergreen Shrubland* & Grassland (*AsSn01*) appeared less vulnerable to future changes across all scenarios. This could be seen as an explanation of their current predominance along the Ecuadorian Andes, as well as an indicator of their future tolerance to extreme climatic conditions such as those suffered in the past during the Pliocene-Pleistocene (Luteyn, 2002; Young et al., 2002; Van der Hammen and Cleef, 1986).

Across all future scenarios, the impacts of climate change on the páramo climatic niches reported by this study showed four potential trends of change, including unchanged niches, lost niches, expanded niches, and extinct niches. By 2050, six (RCP 4.5) or five (RCP 8.5) ecosystems could experience niche losses > 75%. Among these critical ecosystems, two (RCP 4.5) and four (RCP 8.5) ecosystems reflected niche losses close to extinction (≥90%). In 2050, total niche extinction could happen in one (RCP 4.5) or two (RCP 8.5) páramo ecosystems. Potential niche expansion ≤ 4% was reported as probable only for four (RCP 4.5) and three (RCP 8.5) ecosystems. By 2070, five (RCP 4.5) or three (RCP 8.5) ecosystems could experience niche losses ≥75%. Among these critical ecosystems, three (RCP 4.5) or three (RCP 8.5) reflected losses close to extinction (>90%). In 2070, the total extinction of two (RCP 4.5) or five (RCP 8.5) ecosystems could be expected. Regarding a potential niche expansion, percentages are still not significant (≤4%) and probable only for three ecosystems under both scenarios (RCP 4.5 & RCP 8.5). As expected, under the extreme scenario (RCP 8.5), projections reflected higher niche losses, lower probability of niche expansion and higher number of ecosystems at risk of extinction, across all ecosystems in comparison to the moderate scenario (RCP 4.5). The percentages of niche loss presented here are in agreement with similar studies (Cuesta et al., 2012c), indicating an average reduction of climatic niche in Andean ecosystems of 80% to 100% (potential extinction), by years 2020 and 2050 (under emission scenario A2), respectively.

The impact on the páramo climatic niche at national scale, showed a niche-decreasing tendency across all future scenarios. Impacts were more critical when only high consensus niches were considered. By 2050, climatic niche losses based on the "*without consensus*" approach could reach 12% (RCP 4.5) or 14% (RCP 8.5), whereas by 2070, niche losses could increase to 13% (RCP 4.5) or 21% (RCP 8.5). Based only on "*high consensus*" niches, by 2050, niche losses could represent 21% (RCP 4.5) or 28% (RCP 8.5). By 2070, niche reductions could reach 23% (RCP 4.5) or 40% (RCP 8.5). The probabilities of niche expansion were highly unlikely according to "*without consensus*" niches and null based on "*high consensus*". In terms of spatial location of the impact, patterns of niche loss were identified across the entire Andes Cordillera of Ecuador. However, páramo vegetation located at the Southeast of the Ecuadorian Andes seemed to be more vulnerable showing significant niche losses and so requires special attention.

Regarding climatic niche shifts induced by climate change, the results showed a clear trend towards a reduction in climatic niche shared by more than one páramo ecosystem across all future scenarios analysed. Climatic niche shifts varied from 8 ecosystems sharing the same climatic niche under current climatic conditions to a minimum of 5 (RCP 4.5) or 4 (RCP 8.5), by 2050. By 2070, the number of ecosystems sharing the same niche may not exceed 4 (RCP 4.5) to 3 (RCP 8.5). Consequently, an increase in the proportion of the area occupied by only 2 (RCP 4.5) to 1 (RCP 8.5) páramo ecosystems was evident across all future scenarios; this increase goes hand in hand with the corresponding reduction of the area of niche available in the future. This could be seen as a sign that most páramo ecosystems will find it difficult to adapt to climate changes. These results confirmed the high vulnerability of high mountain vegetation leading to species upward movement and species loss (Herzog et al., 2011). These findings are consistent with assertions made by several authors (Araújo and Rahbek, 2006; Anderson et al., 2011) regarding the potential impact of climate change not only in terms of the location of vegetation altitudinal belts but also regarding the appearance or disappearance of species according to their level of tolerance to new climatic conditions.

4.2 Emerging Hypotheses

This study recognizes that besides climatic changes there are other ecological factors that could influence the response of ecosystems at the species or community level including specie's ability of dispersion, competition, and their physiological response to stress leading to different consequences (Ramirez-Villegas et al., 2014). The level of impact on páramo ecosystems will depend on the response of their species to future changes. Páramo species would adapt to new ecological conditions and changing landscapes if they are mobile enough to track the geographic displacement of their climatic niches, they are capable of rapid evolutionary change or they have a wide range of abiotic tolerances (Broennimann et al., 2006). In contrast, very specialized páramo species (i.e. species that can thrive only in a narrow range of environmental conditions) or species showing low colonization capacity could result unable to adapt (Travis, 2003; Opdam and Wascher, 2004). Páramo landscapes are permanently transformed, due to diverse anthropogenic activities including livestock, agriculture and burning, which affects possible emerging areas of some ecosystems, the ability of species to move, increases the fragmentation of the habitat and reduces their capacity for recovery (Tovar et al., 2013).

The results of this study project a significant reduction of páramo's climatic niche across all future scenarios. Doubt remains as to the possibility that a replacement between ecosystems could happen in the future. In post-glacial times, ecosystems such as forests and páramo vegetation have already experienced upward displacements (Bush et al., 2004; Bush et al., 2005; Hooghiemstra and Van der Hammen, 2004; Valencia et al., 2010). However, given the speed at which climatic changes are occurring, ecosystems will require species to migrate faster. Otherwise, many populations of Andean species might decrease while novel species assemblages might emerge (Feeley and Silman, 2010). This study, like many others, supposes that species will become extinct in those areas predicted as climatically inadequate for them (Ohlemüller et al., 2006), without considering the adaptive responses at the species or population level that could reduce the negative effects (Harte et al., 2004).

Due to its geographic location in the highest part of the Andes, páramo areas are considered highly vulnerable to climate change due to the lack of upslope area for migration (Tovar et al., 2013). The establishment of an ecosystem in emerging niche areas is a process that can take decades (Tovar et al., 2013). In the process, species representative of each ecosystem would be established, as well as functional species or nurse plants that would facilitate the colonization process (Nuñez et al., 1999). The migration of certain individuals will also depend on processes such as pollination and dispersion to ensure their reproduction. In the same way, migratory species will have to face competition with the currently existing species. Species competition will be stronger if the new climatic conditions are sufficiently variable to cover the previous climatic conditions making the establishment of migratory species more difficult (Valencia et al., 2010).

4.3 Implications for Management and Policy

Impact as predicted by this study could represent the alteration of páramo ecosystems in terms of composition, relative abundance, functional diversity, and in some degree taxonomic species diversity (Millennium Ecosystem Assessment, 2005). In countries highly dependent on páramo ecosystem services, as Ecuador, the reduction or disappearance of páramo natural areas could seriously compromise water supply, flow regulation, irrigation and hydroelectric generation (Bradley et al., 2006; Vergara et al., 2007). Any alteration of biodiversity affects key ecosystem processes including biomass production, nutrient, and water cycling, and soil formation and retention, among others. Therefore, the quality and stability of páramo ecosystem services would be significantly compromised.

Furthermore, the total niche extinction for five types of páramo ecosystems, as was predicted here, could represent the loss of abundant and less common species reducing the ecosystem's capacity to cushion the impacts caused by physical and biological changes under climate change (e.g. changes in precipitation and temperature). The changes in the exchange of climatic niches between the páramo ecosystems evidenced in this study could be seen as a potential sign of future invasion of high resistance páramo vegetation in altitudinal ranges where previously they were not found. These changes could affect the carbon capture capacity of páramo ecosystems since the characteristics of resident species determine the amount of carbon that ecosystems assimilate and release into the atmosphere (Millennium Ecosystem Assessment, 2005). The significant reduction of the climatic niches as was predicted showed evidence of a potential increase in the fragmentation and isolation of páramo patches. Although some páramo ecosystems showed signs of greater tolerance to future climatic conditions, this does not prevent significant losses from their original niches being recorded, cancelling the possibility of connecting with adjacent páramo patches, as predicted by other studies in the past (Cuesta, 2007; Young, 2009; Ramirez-Villegas et al., 2014).

Conservation and sustainable management strategies are crucial to minimize future impacts. Páramo areas should be prioritized by level of vulnerability based on these results. Connectivity between remnant páramo patches should be also considered when implementing protection strategies in order to promote the maintenance of local populations. Based on the assumption that vegetation patches linked or connected by a corridor decrease the rate of extinction and have a greater value for conservation than isolated habitats (Noss, 2006), the establishment of ecological corridors is recommended. Corridors should include different environmental gradients and be sufficiently representative of the species habitat to facilitate the dispersal of plants and animals, the recovery of landscape matrices, the survival of diverse species (Donald and Evans, 2006). The awareness of all social actors involved directly (e.g. indigenous communities and farmers) or indirectly (e.g. urban population) in the management of the páramo areas is crucial when planning and implementing strategies for sustainable management and conservation of these natural resources (Adger, 2003).

Conservation and sustainable management strategies are crucial to minimize the future impacts on páramo ecosystems. For this purpose, it is necessary to prioritize areas of intervention by differentiating ecosystems by level of vulnerability as was identified here. The patches of vegetation linked or connected by a corridor decrease the rate of extinction and have a greater value for conservation than isolated habitats (Noss, 2006). Thus, the connectivity between páramo patches through ecological corridors should be also considered when implementing protection strategies to promote the maintenance of local populations and address the problem of habitat fragmentation that was evidenced in this study. Corridors in páramo areas should include different environmental gradients and be representative enough of the species habitat to facilitate: the dispersal of plants and animals, the recovery of landscape matrices, and the survival of diverse species (Donald and Evans, 2006). In humanized landscapes as páramo lands, the involvement of social actors (e.g. indigenous communities, farmers, and urban population) is important to implement adequate strategies for conservation and sustainable management (Adger, 2003).

4.4 Model Approach

In this analysis, climatic aptitude (bioclimate) was considered as the key factor for páramos survival (Buytaert et al., 2011). However, this study acknowledges that in reality the different páramo ecosystems are influenced by several factors including dispersal capacity, interactions (competition) or their physiological response to climatic stress (Ramirez-Villegas et al., 2014), among others. For ecosystems still under study such as the páramo vegetation, the inclusion of these factors is difficult due to a lack of information. Consequently, the analysis was limited to measuring the level of environmental tolerance (i.e. bioclimatic conditions) of the páramo ecosystems under climate change conditions expected in the future. These limitations might have been reflected in the contradictory results obtained for *Sumaco Volcano's Páramo Grassland and Evergreen Shrubland* (*HsSn01*) under RCP 4.5 (moderate scenario), showing a "beneficial" effect (i.e. lower niche losses) over the climatic niche area by 2070 compared to 2050. This could be an indicator of GCM limitations when it comes to predicting climatic conditions for periods over 30 years or could simply be a reflection of the analysis limitations in terms of modelling scale. If this unexpected result is due to analysis limitations, this highlights the need for microclimatic data for highly restricted-endemic vegetation. Similar limitations have been faced before by other páramo niche studies (Feeley and Silman, 2010; Cuesta et al., 2012c), highlighting the high sensitivity of these ecosystems and the need to develop specific studies that promote a better understanding of their vulnerability. As in previous studies (Cuesta et al., 2008; Ramirez-Villegas et al., 2014), the "unlimited dispersal" criterion was applied, assuming that species can migrate and occupy new niches that become suitable under future climatic conditions. Despite this being an unrealistic scenario, the results in this study reflected the high vulnerability of the páramo vegetation in the face of future climate changes even when considering the best possible conditions for ecosystems survival.

Current niche results proved that having a greater number of presence records did not necessarily guarantee the better statistical performance of the model. In fact, AUC values showed lower model performance for ecosystems with higher number of presence records, as was highlighted in the past by several authors (Phillips and Dudík, 2008; Elith et al., 2006). Although statistically the number of records seems to have no relevance, the niche spatial coherence seems to be affected for ecosystems with a lower number of presence records. This is the case of ecosystem *HsSn01,* which despite having a high AUC value (i.e. 0.9), niche predictions reflected obvious contradictions among scenarios. In contrast, the two ecosystems with the largest number of occurrences (i.e. *HsSn02* & *AsSn01*), which despite reporting the lowest AUC values (i.e. 0.7), had robust niche predictions across all scenarios. Therefore, this study agrees with several authors (Fourcade et al., 2014; Lobo et al., 2008; Jiménez-Valverde et al., 2013; Jiménez-Valverde, 2014) who recommend being cautious and not relying solely on statistical indicators to include or exclude a model, but rather conjoining them with an adequate "spatial" evaluation of the results based on specialized knowledge of the ecosystem under study. The generation of models was carried out independently for each páramo ecosystem in order to reflect the individual behaviour of each type of vegetation under climate change scenarios. Thereby, it is recognized that results are reporting areas of climatic niche that could be also occupied by other ecosystems depending on their dispersion capacity and other ecological factors.

Considering the high level of uncertainty surrounding future climate change projections for the Andes (Buytaert et al., 2009; Tovar et al., 2013), an ensemble approach considering two time horizons (2050 & 2070), two GHG emission concentration scenarios (RCP 4.5 & RCP 8.5) and six different GCMs, was applied by this study. No future models were discarded based on the premise that all independent models could be considered flawed, however, many of them contain some degree of partial truth (McNees, 1992; Winkler, 1989; Araújo and New, 2007). This allows for the control of errors and uncertainties in the individual models (Araújo and New, 2007). Based on the significant variation of niche area obtained across the six GCMs, this research highlights the importance of using more than one GCM to generate more robust and reliable predictions. The discrimination of niche areas by categories of consensus (high, medium and low) is presented as a good alternative for the evaluation of climate change impact, given that allows the reduction or partially cancelation of individual errors (Tebaldi and Knutti, 2007; Thuiller, 2004; Araújo and New, 2007; Elith et al., 2010; Araújo et al., 2006). This approach allows showing differences on the magnitude of the impact as well as on the niche expansion plausibility, which in practice could lead to different conclusions. This study confirmed in the evaluation of impact at national scale, that by considering all niche areas without discrimination of GCM consensus, the impact could be somehow underestimated, minimizing the losses and maximizing the probability of niche expansion. In contrast, impact based on niche areas identified under high consensus could overestimate the impact, this time maximizing the losses and minimizing the probability of niche expansion. Notwithstanding, based on the large percentage of future niche area reported under low consensus, the results presented here, based only on high consensus niches, could have increased the reliability of the impact reported. Finally, the use of RCPs as the basis for the future projection of the climatic niches allowed the intrinsic consideration of socio-economic factors that could influence the impact of climate change at regional and global scale. Despite being a contribution to the understanding of the páramo vegetation behaviour under these new premises, the results showed that mitigation efforts as assumed in scenario RCP 4.5 do not seem to reduce the impact of climate change on the Andean páramo ecosystems.

Finally, this study recognizes that the failure to include points of occurrence of páramo ecosystems from other Andean countries could have caused only a partial representation of the Andean páramo niches. Although, several studies suggest that the accuracy of the model can be improved by increasing sampling across certain underrepresented areas (Loiselle et al., 2008), others (Kadmon et al., 2004; Raes, 2012) state that an area of greater sampling may not be required when the climatic gradients of the species/ecosystems are relatively well represented, or when there is a relatively large number of presence locations (e.g. >100), as in the case of the present study. Based on the good coverage of presence points used for Ecuador and the similarities existing between páramo ecosystems found across the entire Andes region (Hofstede et al., 2014), it is presumed that the results presented here continue to be a significant contribution to the understanding of the potential impacts of climate change on páramo niches.

5. Conclusion

This research recognizes the uncertainty surrounding the results presented. The study acknowledges the limitations of climatic niche distribution models produced in Maxent (Pearson et al., 2006; Elith et al., 2010; Elith et al., 2011) mainly in climatically complex regions such as the Andes. The accuracy of the predictions could be improved in future studies by building better climate models based on improved data. Therefore, it is important to promote the collection and evaluation of climate data from different elevations along the Ecuadorian Andes to facilitate a better representation of local and temporal climatic changes (e.g. temperature and precipitation patters, cloud formation, orography influence, etc.). Future research should consider niche areas identified as high and medium consensus to increase the reliability of the results. In the future, efforts should be focused on carrying out páramo niche modelling at a regional scale, including the six countries (i.e. Panama, Costa Rica, Peru, Venezuela, Ecuador, and Colombia) presenting páramo ecosystems in their territories to guarantee the total representation of the niches and their future tolerance range more precisely.

Despite the limitations, the results obtained are a rational estimation of the potential effects of climate change on the páramo ecosystems confirming their high vulnerability to climate change. The findings can inform decision makers and could promote the sustainable management of the páramo ecosystems. Future efforts should be focused on the implementation of priority measures in páramos areas identified under niche extinction risk or considered highly vulnerable. Complementary analyses referring to páramo socio-economic importance (e.g. fresh water, hydropower, irrigation, among others) are also needed to focus resources on the most vulnerable sites.

Chapter III

Estimates of Carbon in Soil and Vegetation of the different Ecuadorian Páramo Ecosystems

1. Introduction

Terrestrial carbon (C) plays a significant role in regulating many ecosystem services and contributing to human well-being (Schimel, 1995). Large amounts of C are stored in living vegetation, necromass and in organic matter in soils (Bellamy et al., 2005). In vegetation, C accumulates as a net result of input (i.e. photosynthesis) and loss (e.g. respiration, fire, or harvest) processes (Batjes, 1996). In contrast, in soils, the amount of organic C stored depends on the balance of two biotic processes, the production of organic matter by terrestrial vegetation and the decomposition of organic matter by soil organisms (Post et al., 2001; Batjes, 1996). Soil C is of particular importance since soils are among the largest terrestrial C deposits playing an important role in global C sequestration (Bernhardt and Schlesinger, 2013). It is estimated that the global amount of C contained in the terrestrial vegetation is in the order of 550 ± 100 Gt C (Jobbágy and Jackson, 2000), while the world's soils contain between 900 Gt C (at 2 metres depth) and 1,500 Gt C (at 1 metres depth) (Kirschbaum, 2000). Thus the global C content in soils could represent two to three times the C found in vegetation.

Terrestrial sinks (soil and vegetation) remove about 190±55 Gt C from the atmosphere annually, which represents 28% of the total atmospheric C content (Le Quéré et al., 2017). Climatic conditions, in particular temperature and precipitation, have a great influence on the amount of C stored in vegetation and soils, due to their influence on plant productivity and degradation rates of organic matter (Schlesinger 1997). Therefore, C densities (carbon mass per unit area) of vegetation and soils will differ between climatic regions (e.g. boreal, temperate, or tropical) (Blais et al., 2005). Many other variables could affect the C stored in terrestrial ecosystems. In the short to medium term, land use change is playing a determinant role in C fluxes between land, water and the atmosphere (Brown et al., 1993). Long term carbon fluxes are mainly influenced by increases in atmospheric concentrations of CO_2, changes in temperatures and precipitation, and alteration of patterns and magnitudes of chemical inputs in the atmosphere (Brown et al., 1993).

Global climate change could affect the C stored in vegetation and soils (Cramer et al., 2001; Le Quéré et al., 2017; Houghton, 2007; IPCC, 2014c; Joos et al., 2001). Besides global warming, precipitation patterns may also change around the world, which may even change soils from a net C sink into a net source of C due to changes in soil moisture and alterations in underground hydrological processes (Heisler and Weltzin, 2006). However, there is still uncertainty in the amount of C stored in and potentially emitted by many terrestrial ecosystems now and in the future (Scharlemann et al., 2014). Knowledge about the nature and size of current carbon stocks will help to adequately parameterize models to estimate net future carbon changes (Post et al., 2001). Considering the influence of the carbon reserves of the terrestrial soil in atmospheric carbon chemistry and global warming, the reliable evaluation of ecosystems current carbon storage as well as estimating its potential future change is a priority (Gianelle et al., 2010; Baldocchi, 2008).

In this regard, the Biodiversity Strategy to 2020 highlights the urgent need to represent ecosystem services through biophysical mapping and valuation (Maes et al., 2012; Mubareka et al., 2013). Over the years, great advances have been made in the development of ecosystem service modelling and mapping approaches aimed at understanding stocks, demands and flows of ecosystem services at different spatial and temporal scales (Burkhard et al., 2013). Ecosystem service maps can be generated based on representative samples of the entire study region, modelled surfaces based on primary data or by proxies based on land cover and modelled surfaces using prior knowledge (Eigenbrod et al., 2010b). For this purpose, a wide range of tools such as thematic mapping, GIS, remote sensing, multiple criteria analysis and geo-biophysics and decision process models are currently available (Burkhard et al., 2013). However, due to the lack of available data, most ecosystem service maps are based on gross estimates (proxies) (Naidoo et al., 2008).

Knowledge of the distribution of carbon content in areas where ecosystem services are thought to be of local or global importance is essential (Minasny et al., 2006). Therefore, in the last two decades, there has been substantial progress in the quantification of carbon content. Worldwide, consistent global databases based on observations of carbon in vegetation biomass have allowed the generation of proxies for carbon storage for several biomes (Naidoo et al., 2008). Unfortunately, some carbon proxies not only have used global carbon data published more than 30 years ago (Olson and Dinerstein, 1998) but they represent by one single value the carbon stored in just a few types of globally mapped biomes (Naidoo et al., 2008). In addition, the majority of these global Initiatives have been mainly focused on the quantification of carbon in forest ecosystems with a view to implementing REDD (Reducing

Emissions from Deforestation and Degradation) projects, leaving aside other important ecosystems.

Many global soil information systems are currently available for modelling SOC stocks and estimating C sequestration, including the harmonized global soil database (HWSD) and the soil and land database (SOTER), among others. More recently, Batjes (2016) produced more complete estimates of global SOC populations using the WISE30sec databases improving results spatial resolution (~0.86 km^2). However, WISE30sec data have been identified as not very useful for many global simulation models and decision making systems (Hengl et al., 2017). Although, global data sets have considerable potential to improve estimates of carbon flux in the soil in a changing climate, they present certain deficiencies. Global data sets may not be able to capture the local and regional heterogeneity resulting from the complex interaction of environmental drivers (Vitharana et al., 2019). Frequently, soil profile data used in global soil mapping are collected over different periods of time and through a variety of soil analytical methods. Additionally, there are geographical gaps caused by the unequal spatial distribution of the global soil profile data sets (Batjes, 2016). As a result of these limitations, unreliable and coarse global estimates are obtained, making it difficult to use at national level.

Developing countries, such as Ecuador, require solid estimates of carbon stocks for the successful implementation of climate change mitigation policies (Saatchi et al., 2011). Sadly, the collection of primary and site-specific data result expensive and time consuming (Plummer, 2009). The scarcity of information at relevant scale and good resolution has been a major obstacle to understanding, valuing and protecting the Ecuadorian ecosystems. Consequently, for decades, Ecuador has been using gross carbon estimates based on low-resolution global carbon maps (e.g. Saatchi et al. (2011) and Baccini et al. (2012)), which do not adequately represent the finely grained mosaic of vegetation present in this megadiverse country. Despite limitations, in 2008, Ecuador produced its first national map of carbon for forest ecosystems. The estimates of carbon values per forested area were obtained by applying remote sensing techniques based on the use of satellite images (Landsat and MODIS) of coarse (500 m) to medium (30m) resolution combined with plots obtained from the National Forestry Inventory (Bertzky et al., 2010). The map was based on the updated stratification of forest vegetation and estimates of biomass (belowground and aboveground) carbon content (Bertzky et al., 2010). Although this study provided a wealth of valuable data, it does not account for the variation of carbon stocks found across other types of Andean ecosystems including páramo ecosystems.

Among the terrestrial ecosystems with limited information on carbon stocks are the páramo ecosystems, which are potentially an important net C sink (Winckell et al., 1991; Podwojewski and Poulenard, 2000a). These ecosystems can be found in the humid tropics of the Andes from Colombia to northern Peru, predominantly above 3,500 m.a.s.l. (Buytaert et al., 2005b). The high mountain vegetation is dominated by grassland and shrubs. The C storage in the soils and the vegetation are influenced by geographical isolation, and biophysical, geological and climatic factors (Luteyn and Baslev, 1992). Although the plant mass of the páramo ecosystems are considered as an overall C sink, the soil is assumed to be a more important C store (Hofstede et al., 2014). Unfortunately, climate change and agricultural intervention could alter the regular functioning of páramo ecosystems causing loss of organic matter in surface horizons, reduction of water retention capacity and alteration of microbial biomass and soil biota (Cuesta et al., 2014; Buytaert et al., 2006b). The anthropogenic pressures could alter the role of the páramo ecosystems as natural CO_2 sinks causing the potential loss of C stored in soils and vegetation to the atmosphere (Buytaert et al., 2011).

Therefore, this study identified the need to produce carbon stocks proxies for the Ecuadorian páramo ecosystems to facilitate the adequate planning, policy formulation, and sustainable management of these natural areas. An alternative method known as "benefits transfer" was considered a good option to estimate and map the carbon stocks in Ecuador, since this country is constrained by lack of data and information on this matter. This approach is applicable for studies in which the ecosystem services to be mapped are homogeneous and when results are aimed at simply classifying and mapping the ecosystems' relative importance (Eigenbrod et al., 2010a). In this study, specifically, benefit transfer mapping allowed to extrapolate the values of carbon stored in soil and vegetation from small páramo areas to larger páramo areas of the same kind. For this purpose, the adaptation of information from original investigations carried out in several páramo sites across the Andes of Ecuador was required. This study was able to summarise all the available data on C stocks in the soil and aboveground vegetation of the key types of páramo ecosystems existing in Ecuador. The study also assessed how vegetation type (Bunker et al., 2005; Sombroek et al., 1993), soil characteristics (Pribyl, 2010), altitude (Townsend et al., 1995), geographical location (Spracklen and Righelato, 2014) and climatic conditions (Jones, 1973), impact on these C stocks.

2. Materials and Methods

2.1 Study Area

The study area comprises all the páramo ecosystems of Ecuador, distributed along the Eastern and Western Cordilleras from the border with Colombia in the north to the Peruvian border in the south, covering an area of 1,297,979 ha, equivalent to 5.1% of Ecuador's national territory (Cuesta et al., 2012b) (Fig 3.1). These ecosystems are usually found above the tree line (Andean Forest) above 3,500 m.a.s.l, in the centre and north of the country, and above 3,000 m.a.s.l in the south (Hofstede et al., 2014; Mena and Hofstede, 2006). In the páramo region, climate together with the Andes geological history (e.g. age of rise, type of rock and presence of volcanism) and geographical aspects such as geomorphology and glaciation are determinant factors influencing the C stocks in both soil and vegetation (Buytaert et al., 2005a; Llambí et al., 2012; Jørgensen and Ulloa, 1994; Mena et al., 2000). The precipitation in the Andes is determined by the Andean orography and the influence of locally prevailing winds, which determines its high temporal and spatial variability (Buytaert et al., 2010). The Humboldt Current brings drier air masses from the Pacific, which causes that páramo vegetation located in the Western, Central, and Southern Cordilleras to receive less precipitation than in the north (Vuille et al., 2000). The Eastern Cordillera is dominated by humid winds from the Tropical Atlantic and the Amazon basin causing a predominantly humid and hyper-humid rainy climate (Vuille et al., 2000; Vuille et al., 2008). Consequently, the páramo region is characterized by precipitation that varies significantly between 500 to >3,000 mm/year and an annual average temperature between 2°C-10°C with daily variations ranging from below zero to >25°C (Hofstede et al., 2002a; Llambí et al., 2012; Mena et al., 2000). Temperature in both Cordilleras are marked by altitudinal floors (Camacho, 2014). Thus, páramo vegetation located in the Central (Eastern Andes) and Western Cordilleras, at 3,000-3,600 m.a.s.l. and at 3,200-3,900 m.a.s.l., respectively, experience temperatures ranging from 6°C-12°C. In contrast, vegetation located from 3,600 (Eastern Andes) and 3,900 m.a.s.l. to 4,700 m.a.s.l. (Western Andes), experience temperatures between 3°C to 6°C (Cañadas Cruz, 1983).

In Ecuador, páramo soils located in the Northern and Central Andes rest on volcanic deposits, product of Quaternary volcanic eruptions (Winckell et al., 1991; Barberi et al., 1988; Sauer, 1957), and differ from southern Andes soils that are resting on non-volcanic deposits at altitudes above 3,000 metres (Mena et al., 2000). Influenced by these geological characteristics northern/central páramo soils are sparsely developed and relatively young due to active volcanism that continues to provide layers of ash and pyroclastic materials (Llambí et al., 2012). Depending on geographical location, the páramo soils vary in thickness ranging from a few centimetres to several metres (up to 3 metres) and have a dark colour due to their high organic matter content (Buytaert et al., 2006b). In general, all páramo soils have a high content of organic matter (>5%) (Hofstede et al., 2014). Ecuadorian páramo soils have mineral and organic composition with presence of organometallic complexes resistant to microbial degradation which enforces the organic matter accumulation (Buytaert et al., 2006b). The most representative páramo soils in Ecuador are inceptisols and histosols (peat), covering 85.7% and 7.2% of the total páramo region (Table 3.1) (See soils description in Chapter I).

Due to extreme weather (i.e. cold and humid environmental conditions), the páramo vegetation is dominated by tall-structured grassland and shrubland vegetation interspersed with patches of páramo giant rosettes (frailejones) and evergreen páramo forests (e.g. *Polylepis*, *Gynoxys*, and *Buddleja)* (Hofstede et al., 1998; Mena et al., 2001; Mena and Hofstede, 2006). Páramo ecosystems are well adapted to low temperature and high ultraviolet radiation which is reflected in low biomass with slow decomposition of organic matter and high accumulation of dead plant material (necromass) in the soil (Camacho, 2014; Hofstede et al., 1995; Monasterio and Sarmiento, 1991; Smith and Young, 1987). Necromass is preserved as part of growing plant structures such as tussock grasses and stem rosettes (Smith, 1979; Monasterio and Sarmiento, 1991). Up to 70% of the aboveground biomass could be constituted by "standing dead" material (Cardozo and Schnetter, 1976; Hofstede et al., 1995). The most predominant páramo ecosystems in Ecuador are *Páramo Grassland (HsSn02)* and *Páramo Evergreen Shrubland and Grassland (AsSn01)* covering 71.5% and 16.5% of the Ecuadorian páramo region, respectively. Evergreen Páramo Forest and the remaining types of shrubland and grassland ecosystems are less representative covering 12.6% of the total páramo region (Table 3.1).

Table 3.1 Páramo ecosystems in Ecuador versus soil order, *based on the Map of Ecuadorian Continental Ecosystems, scale 1:100,000 (MAE, 2013a) and National Soil map of Ecuador, scale1: 250,000 (MAGAP, 1986).*

Nº	**Páramo Ecosystem**	**Ecosystem Code**	**Soil Order**	**Area (ha)***	**Soil Representativeness by Ecosystem (%)**	**% Vegetation Representativeness in the Ecuadorian Páramo Region (%)**
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	Inceptisol	211.0	99.8	2E-02
			Entisol	0.5	0.2	
	Subtotal			**211.5**	**100**	
2	Sumaco Volcano's Páramo Grassland and Evergreen Shrubland	HsSn01	Inceptisol	392.0	100	3.0E-04
	Subtotal			**392.0**	**100**	
3	Evergreen Páramo	BsSn01	Inceptisol	5,953.2	71.6	0.6

№	Páramo Ecosystem	Ecosystem Code	Soil Order	Area (ha)*	Soil Representativeness by Ecosystem (%)	% Vegetation Representativeness in the Ecuadorian Páramo Region (%)
	Forest		Entisol	824.0	9.9	
			Other mineral soils	1,504.7	18.1	
			Histosol	28.0	0.3	
	Subtotal			**8,310.0**	**100**	
4	Humid Subnival Páramo Grassland	HsNn01	Inceptisol	3,555.3	69.1	0.4
			Entisol	1,575.5	30.6	
			Histosol	14.9	0.3	
	Subtotal			**5,145.7**	**100**	
5	Floodable Páramo Grassland	HsSn04	Inceptisol	5,979.9	55.9	0.8
			Entisol	311.6	2.9	
			Other mineral soils	123.5	1.2	
			Histosol	4,283.7	40.0	
	Subtotal			**10,698.7**	**100**	
6	Ultra-humid Subnival Páramo Grassland	HsNn02	Inceptisol	2,189.0	48.8	0.3
			Entisol	2,258.7	50.3	
			Other mineral soils	29.3	0.7	
			Histosol	10.1	0.2	
	Subtotal			**4,487.0**	**100**	
7	Humid High Upper Montane Páramo Grassland	HsSn03	Inceptisol	30,799.4	93.2	2.5
			Entisol	1,932.3	5.8	
			Other mineral soils	123.0	0.4	
			Histosol	178.5	0.5	
	Subtotal			**33,033.1**	**100**	
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	Inceptisol	45,175.4	97.8	3.6
			Other mineral soils	273.1	0.6	
			Histosol	751.8	1.6	
	Subtotal			**46,200.3**	**100**	
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	Inceptisol	46,605.2	96.3	3.7
			Entisol	1,190.0	2.5	
			Other mineral soils	483.8	1.0	
			Histosol	132.5	0.3	
	Subtotal			**48,411.5**	**100**	
10	Páramo Evergreen Shrubland and Grassland	AsSn01	Inceptisol	171,086.0	80.1	16.5
			Entisol	2,948.2	1.4	
			Other mineral soils	11,690.1	5.5	
			Histosol	27,811.4	13.0	
	Subtotal			**213,535.6**	**100**	
11	Páramo Grassland	HsSn02	Inceptisol	800,952.6	86.4	71.5
			Entisol	22,561.0	2.4	

Nº	Páramo Ecosystem	Ecosystem Code	Soil Order	Area (ha)*	Soil Representativeness by Ecosystem (%)	% Vegetation Representativeness in the Ecuadorian Páramo Region (%)
			Other mineral soils	43,756.0	4.7	
			Histosol	60,284.5	6.5	
	Subtotal			**927,554.1**	**100**	
	Total Páramo Region			**1,297,979.5**		**100**

** Area of páramo ecosystems excluding rocky outcrops, snow/ice, and water bodies (natural or artificial), which amounts to 182,272.4 ha.*

2.2 Benefit Transfer Mapping

The quantification and evaluation of ecosystem services can play an important role in conservation planning and ecosystem-based management (Plummer, 2009). Unfortunately, the collection of primary and site-specific data is expensive and time consuming (Plummer, 2009). Thus, alternative methods such as "benefits transfer" are a good option for studies where information is scarce. Benefits transfer adapts information from an original investigation and apply it in a different context of study (Rosenberger and Loomis, 2003). Most benefit transfer studies focus on estimating the economic values of ecosystem services. However, its use can be much broader including ecosystem services mapping. This technique is applicable when the ecosystem services to be mapped are homogeneous and results are aimed at simply classifying and mapping the ecosystems' relative importance (Eigenbrod et al., 2010a). The most common benefit transfer applies an estimate of the value per hectare to all areas that have the same land cover or habitat type. It estimates the value of ecosystem services in different landscapes from a standard set of categories of ecosystem services (e.g. carbon storage) and landscape types (e.g. páramo) that are then linked to a set of benefits (e.g. carbon sequestration) that are supposed to provide (Plummer, 2009).

This methodological approach presents several advantages including low cost and easy-quick application (Barbera, 2010). However, it is particularly susceptible to generalization errors resulting from lack of correspondence (Plummer, 2009). The three main generalization errors that this type of approach could generate are known as uniformity, sampling, and regionalization (Plummer, 2009; Eigenbrod et al., 2010a; Eigenbrod et al., 2010b). Uniformity error happens when values are considered constant (uniform) for each type of ecosystem without considering additional factors such as biophysical differences. Sampling error is caused when sampling sites are limited and biased to certain areas which increases the risk of errors in the estimates (Eigenbrod et al., 2010a). The third typical error is known as regionalization error (Plummer, 2009; Eigenbrod et al., 2010a), caused by the differences in representativeness of the sampling areas in relation to the area being mapped (Eigenbrod et al., 2010a).

In the case of Ecuador, this methodological approach appeared very attractive due to the difficulty of applying more complex models to estimate reserves and carbon fluxes (e.g. GefSoc, Century, and RothC). Complex models lack spatial dimensions and do not include parameters adjusted to the specificities found in the páramo region (Sevink et al., 2014), such as porosity and bioturbation (Elzein and Balesdent, 1995; Smith et al., 1997; Jenkinson et al., 2008). More importantly, these models are based on fractions of soil organic matter (SOM) and decomposition processes that are not representative of the volcanic ash soils existing in páramo lands (Sevink et al., 2014). Most of the existing carbon models focus on estimating the carbon content in the upper layer of the soil (<25 cm depth), which constitutes a great barrier to its application given that páramo soils store a large amount of organic carbon at greater depths (Sevink et al., 2014).

In addition, knowledge about the carbon reserves in the various compartments of páramo ecosystems and their dynamics is really scarce (Bertzky et al., 2010; Sevink et al., 2014). The data currently available on páramo carbon stocks are the result of small, isolated, and biased research efforts unrepresentative of the variety of carbon stocks existing in this type of vegetation (Sevink et al., 2014). Under these circumstances, benefit transfer was considered a good option for this study due to its applicability for studies with limited information. Specifically, this approach was used to quantify and map the carbon stored in páramo soil and vegetation by extrapolating values of carbon content per hectare to páramo ecosystems presenting similar habitat type. Further explanation on the application of this technique is presented below.

2.3 Carbon Data Compilation

Carbon data were compiled from literature (27 sources reviewed; 14 used) produced by researchers and institutions over 15 years (2002 to 2016) at different páramo sites along the Ecuadorian Andes (Eastern and Western Cordillera). Web-based data compilation was focused on collecting sampling data on soil and vegetation biomass (aboveground biomass and necromass) to determine carbon stocks of ten key páramo ecosystems existing in Ecuador. For this purpose, the following information was included in the compilation: sampling site name and geographical location (coordinates), sampling vegetation stratum, soil sampling depth from soil surface, percentage of soil organic matter (SOM), soil organic carbon content per unit soil area (SOC), soil bulk density and depending on data availability carbon content per unit soil area in aboveground biomass and aboveground necromass. Due to lack of a common protocol for soil data collection the information available varied in depth ranges between sources. Based on the assertion that most types of soil contain more than 50% of the stored carbon in the top 25 cm of the soil (Eswaran et al., 1995; Garnett et al., 2001), this study defined as standard depth intervals of 0-30 cm with a depth variation range of +/- 5 cm to enable the comparison between secondary sources and to increase the reliability of the carbon stock estimation. In making this decision, the calculation included most of the organic horizon of inceptisols and histosols which are the most predominant páramo soil orders in Ecuador (Table 3.1).

Once compiled, quality control was applied to discard plots lacking spatial location or presenting incomplete data. In cases where geographical coordinates were not available, approximate locations were assigned based on the location maps and description of the sampling sites found in the secondary sources consulted. There were few cases in which mapping scale conflicts were identified for which spatial modification of the sampling points was required. Spatial modifications respected the limit defined according to the páramo ecosystems mapping scale (1:100,000) corresponding to the minimum value of horizontal accuracy equivalent to +/- 50.8 metres (Burrough, 1986), beyond which no spatial alteration was permitted. Based on this, the discrimination of sampling sites by level of spatial accuracy and precision was considered necessary (Appendix III.A). An accurate site was considered when the site coordinates match the true location whereas a site was considered precise when the sources included good attribute information reflected in a detailed coordinates description (e.g. coordinates including degrees, minutes and seconds; coordinate system and datum).

Despite the elimination of several data, it was possible to collect sufficient information to characterize the soil carbon content for 8 out of the 10 types of páramo ecosystems (13 different sites and 51 sampling points in total) covering 95.4% (1,238,477 ha) of the total páramo area of Ecuador (Table 3.2a). The solution found to fill gaps in soil information for the other two páramo ecosystems (i.e. *HsSn04* and *HsNn03*) included in the estimate is explained later (Section 2.3). In the case of vegetation biomass (aboveground biomass and aboveground necromass) data was available for 5 páramo ecosystems (5 different sites and 48 sampling points in total); allowing the characterization of 89% (1,154,757 ha) of the total Ecuadorian páramo land (Table 3.2b). The solution found to fill gaps in biomass information for the other five páramo ecosystems (i.e. *HsSn04*, *HsNn03, HsNn02, HsSn03,* and *RsSn01)* included in the estimate is explained later (Section 2.3). Due to lack of information on carbon content on soil and vegetation, *Sumaco Volcano's Páramo Grassland and Evergreen Shrubland* (*HsSn01*) was excluded from all carbon stock estimates. However, this ecosystem covers only 392 ha which is 0.03% of the total Ecuadorian páramo area. The final data were classified, completed, standardised (units and terminology) and finally mapped based on the geographical coordinates available (Fig. 3.1). For calculation purposes, sampling data were spatially linked with the corresponding type of páramo vegetation and soil order with the purpose of differentiating their specific carbon contribution, using the *Map of Ecuadorian Continental Ecosystems* (MAE, 2013a) and the *National Soil map of Ecuador* (MAGAP, 1986). ArcGIS software version 10.4.1 was used to locate all sample points and to perform the spatial analysis required.

Table 3.2a Data compiled for the estimation of Soil Carbon Stock by páramo ecosystem.

N°*	Code	Ecosystem	# Sites	Site	Soil Order	Plot Code	# Sampling Plots	Sampling Range Depth (cm)	Andes Location	Reference
1	AsAn01	Southern Páramo High Montane Evergreen Shrubland	1	El Tiro-Cajanuma	Inceptisol	CJN13,CJN14, CJN16	3	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
				El Tiro-Cajanuma	Entisol	CJN11, CJN12, CJN9	3	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
3	BsSn01	Evergreen Páramo Forest	1	Ecuadorian Andes	Inceptisol	BA	12	0-30	Eastern and Western Cordillera	(Hofstede et al., 2002b)
4	HsNn01	Humid Subnival Páramo Grassland	1	Yanacocha Reserve 1	Inceptisol	YAC2	1	0-30	Western Cordillera	(Calderón et al., 2013)
6	HsNn02	Ultra-humid Subnival Páramo Grassland	1	Pulingui	Inceptisol	PLG9, PLG10	2	0-25	Western Cordillera	(Muñoz Alcívar, 2016)
7	HsSn03	Humid High Upper Montane Páramo Grassland	1	Chimborazo Volcano	Inceptisol	CHV1 - CHV2	2	0-30	Western Cordillera	(Podwojewski et al., 2002)
8	RsSn01	Páramo Caulescent Rosettes (frailejones) and Grassland	2	El Angel 2	Inceptisol	GEL	1	0-30	Western Cordillera	(Poulenard et al., 2003)
				Chiles Volcano	Inceptisol	P2 A, P2 B, P3 A, P3B	4	0-30	Western Cordillera	(Ipial, 2013)
10	AsSn01	Páramo Evergreen Shrubland and Grassland	1	El Tiro-Cajanuma	Inceptisol	CJN6,CJN8,CJN15	3	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
				El Tiro-Cajanuma	Entisol	CJN3, CJN10	2	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
11	HsSn02	Páramo Grassland	5	El Tiro-Cajanuma	Inceptisol	CJN5,CJN7	2	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
				Ningar		NI4	1	0-30		(Buytaert et al., 2006c)
				Cuenca		CUE	1	0-30	Western Cordillera	(Poulenard et al., 2003)
				Machángara Catchment		MA5	1	0-30		(Buytaert et al., 2007)
				Western Cordillera (north to south)		CH3	1	0-30		(Buytaert et al., 2005a; Buytaert et al., 2007)

N°*	Code	Ecosystem	# Sites	Site	Soil Order	Plot Code	# Sampling Plots	Sampling Range Depth (cm)	Andes Location	Reference
			2	Western Cordillera (north to south)	Histosol	PD	2	0-30	Western Cordillera	(Buytaert et al., 2005a; Buytaert et al., 2007)
				Eastern Cordillera (north to south)		JI	2	0-34	Eastern Cordillera	(Buytaert et al., 2005a; Buytaert et al., 2007)
			1	El Tiro-Cajanuma	Entisol	CJN2,CJN4,CJN1	3	0-25	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)

** For comparative purposes the initial numbering presented in Table 3.1 was retained.*

Table 3.2b Data compiled for the estimation of Vegetation Carbon Stock (aboveground biomass + aboveground necromass) by páramo ecosystem.

N°	Code	Ecosystem	Site	# Sites	Plot Code	# Sampling Plots	Andes Location	Reference
1	AsAn01	Southern Páramo High Montane Evergreen Shrubland	El Tiro-Cajanuma	1	CJN9,CJN11,CJN12,CJN13,CJN14,CJN16	6	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
3	BsSn01	Evergreen Páramo Forest	Pifo	1	PIF1	4	Eastern Cordillera	(Fehse et al., 2002)
4	HsNn01	Humid Subnival Páramo Grassland	Yanacocha Reserve 1	2	YAC2	1	Western Cordillera	(Calderón et al., 2013)
			Yanacocha Reserve 2		PP15	4	Western Cordillera	(Albán Molina and Granda Garzón, 2013)
10	AsSn01	Páramo Evergreen Shrubland and Grassland	El Tiro-Cajanuma	1	CJN3,CJN6,CJN8,CJN10,CJN15	5	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)
11	HsSn02	Páramo Grassland	Illinizas	4	C-1,C-2,C-3,C-4,C-5,C-6,C-7,C-8,C-9,C-10,C-11,C-12,C-13,C-14	14	Western Cordillera	(Ecociencia, 2011)
			Yanacocha Reserve 1		YAC1	1	Western Cordillera	(Calderón et al., 2013)
			Yanacocha Reserve 2		PP01,PP02,PP06,PP09,PP10,PP13,PP14,PP23	8	Western Cordillera	(Albán Molina and Granda Garzón, 2013)
			El Tiro-Cajanuma		CJN2,CJN4,CJN1,CJN5,CJN7	5	Eastern Cordillera	(Santín Aguirre and Vidal González, 2012)

** For comparative purposes the initial numbering presented in Table 3.1 was retained.*

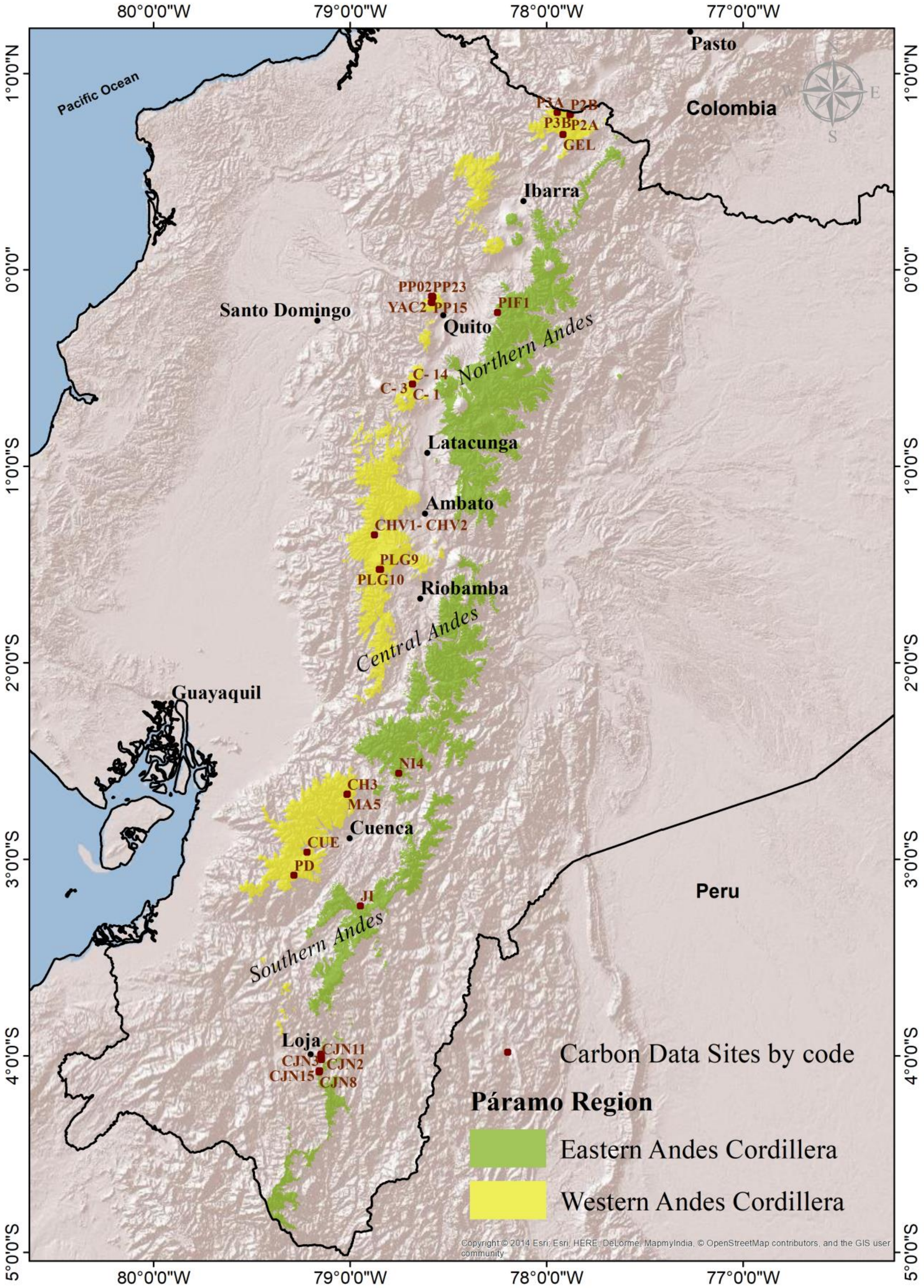

Figure 3.1 Location of Carbon data sites per code with respect to the Eastern and Western Andes Cordillera.

2.4 Solution of Carbon Data Gaps

Carbon data gaps were resolved based on three criteria: a) spatial proximity; b) vegetation similarity; and c) edaphic similarity. The spatial proximity criterion took into account the geographic closeness of the ecosystems without information versus ecosystems with available information. It was assumed that vegetation that grows close and at similar altitudinal ranges could be influenced by similar environmental conditions; therefore, could present similar C contents in soil and vegetation. For the vegetation similarity, the descriptions of páramo ecosystems (See ecosystems description in Chapter I) were evaluated in order to identify similarities at macro level assuming that similar species give rise to similar biomass contents. The criterion of edaphic similarity was related to the presence of soils of similar order between ecosystems with and without information. The three criteria were applied to solve the information gaps identified in six páramo ecosystems (2 without C data in soil and vegetation and 3 without information on biomass) (Table 3.3).

Based on the criteria established to fill the gaps, the vegetation C stock of *Humid Subnival Páramo Grassland (HsNn01)* was used for *Humid High Upper Montane Páramo Grassland* (*HsSn03*) and *Ultra-humid Subnival Páramo Grassland* (*HsNn02*). *Páramo Caulescent Rosettes (frailejones) and Grassland (RsSn01)* was assumed to have similar vegetation C stock to that of *Páramo Grassland (HsSn02).* For ecosystems *Floodable Páramo Grassland (HsSn04),* and *Páramo Subnival Evergreen Grassland and Shrubland (HsNn03)* there were no C data available for either soil or vegetation. Therefore, stock C values obtained for *Páramo Grassland (HsSn02)* were used as reference for the overall carbon estimation for *Floodable Páramo Grassland (HsSn04).* While for ecosystem *Páramo Subnival Evergreen Grassland and Shrubland (HsNn03)* the calculation was based on the average of soil C stocks obtained for *Humid Subnival Páramo Grassland* (*HsNn01*) and *Ultra-humid Subnival Páramo Grassland* (*HsNn02*). In the particular case of *Evergreen Páramo Forest (BsSn01)*, vegetation C content was based on the average of above-ground biomass obtained from four samples of *Polylepis* forest with different ages (6, 15, 30 & 45 years old) reported by Fehse (2002); combined with a referential value of necromass provided by Calderón (2013) (Table 3.3).

Table 3.3 Criteria and solutions applied to solve carbon data gaps in soil and vegetation carbon data.

Nº	**Páramo Ecosystem without information**	**Páramo Ecosystem Code**	**Carbon Data Gap**	**Ecosystem Equivalency**	**Spatial Proximity**	**Vegetation Similarity**	**Edaphic Similarity**
5	Floodable Páramo Grassland	HsSn04	soil and vegetation	Páramo Grassland (HsSn02)	North and South of Western and Eastern Cordillera (3,300 – 4,500 m.a.s.l)	Grassland vegetation with presence of cushions plants	Inceptisol, histosol, entisol and other mineral soils
6	Ultra-humid Subnival Páramo Grassland	HsNn02	vegetation	Humid Subnival Páramo Grassland (HsNn01)	North and South of Western and Eastern Cordilleras (4,200 – 4,900 m.a.s.l)	Grassland subnival vegetation	Not required
7	Humid High Upper Montane Páramo Grassland	HsSn03	vegetation	Humid Subnival Páramo Grassland (HsNn01)	South of Western Cordillera (Chimborazo volcano) (3,500 – 4,900 m.a.s.l)	dispersed grasslands with exposed soil surface	Not required
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	vegetation	Páramo Grassland (HsSn02)	North of Western and Eastern Cordilleras (3,350 – 4,300 m.a.s.l)	Grassland vegetation with presence of caulescent Rosettes	Not required
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	soil and vegetation	Humid Subnival Páramo Grassland (HsNn01) & Ultra-humid Subnival Páramo Grassland (HsNn02)	North of Western and Eastern Cordilleras (4,100 – 4,900 m.a.s.l)	Subnival grassland vegetation	Inceptisol, histosol, entisol and other mineral soils

** For comparative purposes the initial numbering presented in Table 3.1 was retained.*

Additionally, to estimate the soil C stock it was necessary to discriminate the páramo ecosystems by four main categories of soil order including inceptisol, histosol (peat), entisol and “other mineral soils” (i.e. alfisols, vertisols, mollisols). This study had enough information to characterize the C content in inceptisols for the great majority of páramo ecosystems (8 out of the ten ecosystems). However, the information was limited for histosol, entisol and soils grouped under the category "other mineral soils". For histosols, the average value of the soil C stock obtained for *Páramo Grassland (HsSn02)* and corresponding to 210.1±62.6 ton C/ha was used as a referential value for histosols across all páramo ecosystems. This was intended to capture the histosols carbon variability present in both Cordilleras (Eastern and Western). Similarly, with information for entisols for which the average of soil C stocks from three ecosystems with data available (i.e. *HsSn02, AsSn01* and *AsAn01*) and equivalent to 82.5± 8.5

ton C/ha was used to fill the gaps in the rest of ecosystems. For soils identified under "other mineral soils" category, based on edaphic similarities, they were assumed to be similar to inceptisols, therefore, the specific value of soil carbon content estimated for each ecosystem was used. The soil C stock estimate was estimated differently for *Evergreen Páramo Forest (BsSn01)* as the calculation could not be differentiated by soil type and was solely based on the average of 12 samples of *Polylepis* forest reported by Hofstede (2002b).

Among the ecosystems presenting C data gaps was also the *Sumaco Volcano's Páramo Grassland and Evergreen Shrubland* (*HsSn01*). This páramo vegetation covers only 0.03% (392 ha) of the total Ecuadorian páramo area. This ecosystem represents a very young pioneer vegetation settled in geologically young lava fields with striking similarities with other communities of pioneer plants in adjacent páramo areas (Løjtnant and Molau, 1983). However, its soils are quite particular, possessing a relatively thin upper soil layer, high organic carbon (at 5 cm depth), relatively low values of essential nutrients (i.e. nitrogen and phosphorus) and surprisingly high content of potassium due to the presence of nephelitic tephrites rich in feldtspatoids exclusive of the Sumaco volcano in the entire Andean region (Løjtnant and Molau, 1983). Due to its isolated and remote location, the vegetation has not been disturbed by livestock grazing or any form of human activity, which is an unusual condition for the páramo vegetation in Ecuador. The soils of this ecosystem, have been studied only at 5 cm deep by Løjtnant and Molau (1983) and their C content in biomass has not yet been estimated. Based on these particular conditions, this ecosystem was excluded from all carbon stock estimates (soil C and vegetation C) since it represents unique vegetation difficult to link with any other type of páramo ecosystem. Despite the data limitations and assumptions made in this analysis, it is expected that the general estimate of C for both soil and vegetation was not considerably affected since the 6 páramo ecosystems (including the ecosystem excluded *HsSn01*) with data limitations represent only 11% of the entire páramo region of Ecuador.

2.4 Quantification of Carbon Stocks

2.4.1 Carbon Stock in Soils

Calculation of carbon stocks in soil (in ton C/ha) was based on the application of the Rosenzweig and Hillel equation (Eq.[1]) (Rosenzweig and Hillel, 2000). Prior to the application of the formula, soil organic carbon (SOC) values were adjusted according to the standard sampling depth of 0-30 cm defined for this study. For cases in which the site or sample layers differ from the standard depth in ± 5 cm (i.e. between 25-35 cm depth), SOC values were proportionally increased or decreased in order to obtain the C content corresponding to the selected standard depth of 0-30 cm. Once adjusted, SOC values and bulk densities were averaged for each individual páramo ecosystem. On the other hand, for cases in which data were limited to percentage of soil organic matter (SOM) a conversion factor of 2 was used to obtain SOC (Eq.[2]). Through this factor it was assumed that organic matter contains 50% of C which is currently considered more accurate than the conventional factor of 1.724 (Van Bemmelen, 1890); identified by several studies as too low for most soils (Brady and Weil, 1999; Gortner, 1916; Pribyl, 2010; Broadbent, 1953; Van Reeuwijk, 2002). Data originally calculated using the old conversion factor (1.724) was updated based on this criterion. Soil C stocks (in ton C/ha) were estimated individually based on Eq.[1] for each type of páramo ecosystem. The soil C stock for the entire páramo region of Ecuador (in ton C/ha) was obtained according to the relative contribution of each individual soil C stock of each ecosystem to the overall Ecuadorian páramo area based on Eq.[3]. Soil C stocks included the standard error as a measure of the accuracy of the estimate performed when data for more than one site were available.

$$Cstock_{soil} = SOC * d * BD \qquad [1]$$

Where:

$Cstock_{soil} = soil\ carbon\ stock\ (ton\ C/ha)$

$SOC = soil\ organic\ carbon\ concentration\ (\%)$

$d = sampling\ depth\ (cm)$

$BD = bulk\ density\ (g/cm^3)$

$$SOC\ (\%) = \frac{SOM(\%)}{2} \qquad [2]$$

Where:

$SOC = soil\ organic\ carbon\ concentration\ (\%)$

$SOM = soil\ organic\ matter\ concentration\ (\%)$

$2 = conversion\ factor$

$$\mathrm{Regional}_{\mathrm{Cstock_{soil}}} = \sum_{i=1}^{n=10} \frac{\mathrm{A_i}}{\mathrm{A_t}} * \mathrm{C_{stock_{soil_i}}} + \ldots\ldots\ldots + \frac{\mathrm{A_{n\text{-}1}}}{\mathrm{A_t}} * \mathrm{C_{stock_{soil_{n\text{-}1}}}} + \frac{\mathrm{A_n}}{\mathrm{A_t}} * \mathrm{C_{stock_{soil_n}}} \qquad [3]$$

Where:

$Regional_{Cstock_{soil}} =\ soil\ carbon\ stock\ for\ the\ entire\ páramo\ region\ (ton\ C/ha)$

$Cstock_{soil_i} = soil\ carbon\ stock\ for\ ecosystem\ i\ (ton\ C/ha)$

$A_i = area\ of\ páramo\ ecosystem\ i\ (ha)$

$A_t = total\ area\ of\ the\ páramo\ region\ of\ Ecuador\ (ha)$

2.4.2 Carbon Stock in Vegetation

For the estimation of carbon stocks in páramo vegetation, aboveground biomass and aboveground necromass were included. Following the traditional approach, the estimation of C in vegetation was based on the assumption that the C concentration in a plant sample (g C/g sample) is 50% (Eq.[4]) (Calderón et al., 2013). Therefore, the widely used coefficient (f) of 0.5 was used for the conversion of biomass (aboveground biomass + aboveground necromass) into carbon, as suggested by several authors (MacDicken, 1997; Hollinger et al., 1993; Brown, 1997). Based on Eq.[4], the vegetation C stocks were determined for each type of páramo ecosystem (in ton C/ha). Subsequently, the vegetation C stock for the entire páramo region was estimated from the individual vegetation C stocks (in ton C/ha) but proportional to the area of each páramo ecosystem using Eq.[5]. Vegetation C stocks included the standard error as a measure of the accuracy of the estimate performed when data for more than one site were available.

$$Cstock_{vegetation} = W * f \qquad [4]$$

Where:

$Cstock_{vegetation} = vegetation\ carbon\ stock\ (ton\ C/ha)$

$W = dry\ weight\ of\ biomass\ (ton\ /ha)$

$f = conversion\ factor\ of\ carbon\ concentration\ in\ biomass = 0.5$

$$\mathrm{Regional}_{\mathrm{Cstock_{vegetation}}} = \sum_{i=1}^{n=10} \frac{A_i}{A_t} * \mathrm{C_{stock_{vegetation_i}}} + \ldots\ldots + \frac{A_{n\text{-}1}}{A_t} * \mathrm{C_{stock_{vegetation_{n-1}}}} + \frac{A_n}{A_t} * \mathrm{C_{stock_{vegetation_n}}} \; [5]$$

Where:

$Regional_{Cstock_{vegetation}} = vegetation\ carbon\ stock\ for\ the\ entire\ páramo\ region\ (ton\ C/ha)$

$Cstock_{vegetation_i} = vegetation\ carbon\ stock\ for\ ecosystem\ i\ \ (ton\ C/ha)$

$A_i = area\ of\ páramo\ ecosystem\ i\ (ha)$

$A_t = total\ area\ of\ the\ páramo\ region\ of\ Ecuador\ (ha)$

2.4.3 Total Carbon Stock

The estimation of the total C stock was based on the summary of both the C stored in soil and in aboveground vegetation individually for each páramo ecosystem (Eq. [6]). The total C stock was also estimated for the entire páramo region for which the same approach applied for regional soil and C stocks was applied, based on the summary of the individual total C stocks but proportional to the area of each páramo ecosystem using Eq.[7] .

$$Total\ C_{Stock} = C\ stock_{soil} + C\ stock_{vegetation} \qquad [6]$$

Where:

$Total\ C_{Stock} = total\ content\ of\ organic\ carbon\ in\ soil\ and\ vegetation\ (ton\ C/ha)$

$Cstock_{soil} = content\ of\ soil\ organic\ carbon\ (ton\ C/ha)$

$Cstock_{vegetation} = content\ of\ carbon\ stored\ in\ vegetation\ \ (ton\ C/ha)$

$$\mathrm{Regional}_{\mathrm{Total\ C_{stock}}} = \sum_{i=1}^{n=10} \frac{\mathrm{A_i}}{\mathrm{A_t}} {}^*\mathrm{Total\ C_{stock_i}} + \ldots\ldots + \frac{\mathrm{A_{n\text{-}1}}}{\mathrm{A_t}} {}^*\mathrm{Total\ C_{stock_{i_{n-1}}}} + \frac{\mathrm{A_n}}{\mathrm{A_t}} {}^*\mathrm{Total\ C_{stock_n}} \qquad [7]$$

Where:

$\mathrm{Regional}_{\mathrm{Total\ C\ stock}}$ = total content of organic carbon for the entire páramo region (ton C/ha)

$Total\ C\ stock_{ecosystem_i} = total\ content\ of\ organic\ carbon\ for\ ecosystem\ i\ (ton\ C/ha)$

$A_i = area\ of\ \text{páramo}\ ecosystem\ i\ (ha)$

$A_t = total\ area\ of\ the\ \text{páramo}\ region\ of\ Ecuador\ (ha)$

2.4.4 Carbon Stored by Páramo Ecosystem Area

To evaluate the contribution of the different páramo ecosystems in terms of the carbon stored in their area, the multiplication of the total carbon stock (soil + vegetation) of each ecosystem was multiplied by its corresponding area (Eq. [8]). In addition, the regional carbon store was calculated by summation of the individual ecosystem values (Eq. [9]). The percentage of carbon contribution was also estimated for each ecosystem and for the entire páramo region of Ecuador.

$$C_{storage} = A * \ Total\ Carbon_{Stock} \qquad [8]$$

Where:

$C_{storage} = carbon\ storage\ per\ ecosystem\ area\ \ (ton\ C)$

$A =\ \text{páramo}\ ecosystem\ area\ (ha)$

$Total\ C_{Stock} = total\ content\ of\ organic\ carbon\ in\ soil\ and\ vegetation\ (ton\ C/ha)$

$$\mathrm{Regional}_{\mathrm{C_{storage}}} = \sum_{i=1}^{n=10} \frac{\mathrm{A_i}}{\mathrm{A_t}} {}^*\mathrm{C_{storage_i}} + \ldots\ldots + \frac{\mathrm{A_{n\text{-}1}}}{\mathrm{A_t}} {}^*\mathrm{C_{storage_{n\text{-}1}}} + \frac{\mathrm{A_n}}{\mathrm{A_t}} {}^*\mathrm{C_{storage_n}} \qquad [9]$$

Where:

$Regional_{C\ storage}\ =\ carbon\ storage\ in\ the\ entire\ \text{páramo}\ region\ area\ (ton\ C)$

$C_{storage_i} =\ carbon\ storage\ per\ ecosystem\ i\ \ in\ the\ area\ (ton\ C)$

$A_i = area\ of\ \text{páramo}\ ecosystem\ i\ (ha)$

$A_t = total\ area\ of\ the\ \text{páramo}\ region\ of\ Ecuador\ (ha)$

2.4.5 Controls on Soil Carbon Stocks

Potential environmental controls on the soil C stocks of the Ecuadorian Andes were explored. Climatic layers (i.e. bio 1 and bio 12) provided by WorldClim (Version 1.4) at 30 seconds (~ 1 km^2) resolution were used for climatic characterization. ArcGIS software version 10.4.1 was used to perform the spatial analysis required. In this way, annual precipitation and annual surface air temperatures (over 1950-2000) were identified for each individual site.

The influence of altitude on soil C stocks was also assessed (Townsend et al., 1995). For this purpose, the entire set of inceptisols data available for the eight páramo ecosystems were used (31 records in total) (Appendix III.B). Linear regression was carried out to determine whether there was a linear relationship between the soil C stock for annual precipitation, annual air temperature, and altitude.

3. Results

3.1 Quantification of Carbon Stocks

3.1.1 Carbon Stock in Soils

The national C stock in páramo soils amounted to 189.3 ton C/ha based on the soil stocks estimated for ten out of the eleven páramo ecosystems covering 99.9% (1,238,869 ha) of the total páramo area in Ecuador (1,297,979 ha). By analysing the results per ecosystem type*,* *Páramo Caulescent Rosettes (frailejones) and Grassland* (*RsSn01*) had the highest C stock expressed per ha (278.9 ton C/ha). *Evergreen Páramo Forest* (*BsSn01*) had the second highest C stock amounting to 212.1 ton C/ha; followed by the most predominant vegetation *Páramo Grassland (HsSn02)*, covering 71.5% of the total páramo area, with 207.9 ton C/ha. The lowest stock of C in soil was observed in subnival ecosystems located at the highest altitude (above 4,000 m.a.s.l,), *Ultra-humid Subnival Páramo Grassland* (*HsNn02*), *Páramo Subnival Evergreen Grassland and Shrubland* (*HsNn03*) and *Humid Subnival Páramo Grassland (HsNn01),* amounting to 87.7 - 103.5 ton C/ha, respectively (Table 3.4 and Fig. 3.2).

In terms of bulk density across all ecosystems values were relatively low. The overall estimate resulted in an average bulk density of 0.5 g/cm^3 for the entire páramo region. Differences in bulk density per soil order showed that organic soils (i.e. histosols) had on average (± SE) the lowest bulk density (0.4 g/cm^3 ± 0.3) while the highest were observed among mineral soils, inceptisols (0.7 g/cm^3 ± 0.1) and entisols (1.0 g/cm^3 ± 0.1). In terms of SOC (%), the average value obtained for the páramo region was 16.4%. The highest percentage of SOC was 19.9% reported for *Páramo Grassland (HsSn02),* while the lowest was 3.0% registered for *Ultra-humid*

Subnival Páramo Grassland (*HsNn02*). Regarding the C stock per type of soil, when considering inceptisols which are the most predominant soils in the Ecuadorian páramos, the average (± SE) C stock amounted to 162.5 ± 23.3 ton C/ha, based on eight páramo ecosystems with data. Entisols had a lower average (± SE) C stock corresponding to 82.8±8.5 ton C/ha, based on three páramo ecosystems with data available. Histosols had the highest average (± SE) C stock of 210.1 ± 62.6 ton C/ha based on information available only for the most predominant vegetation *Páramo Grassland* (*HsSn02*).

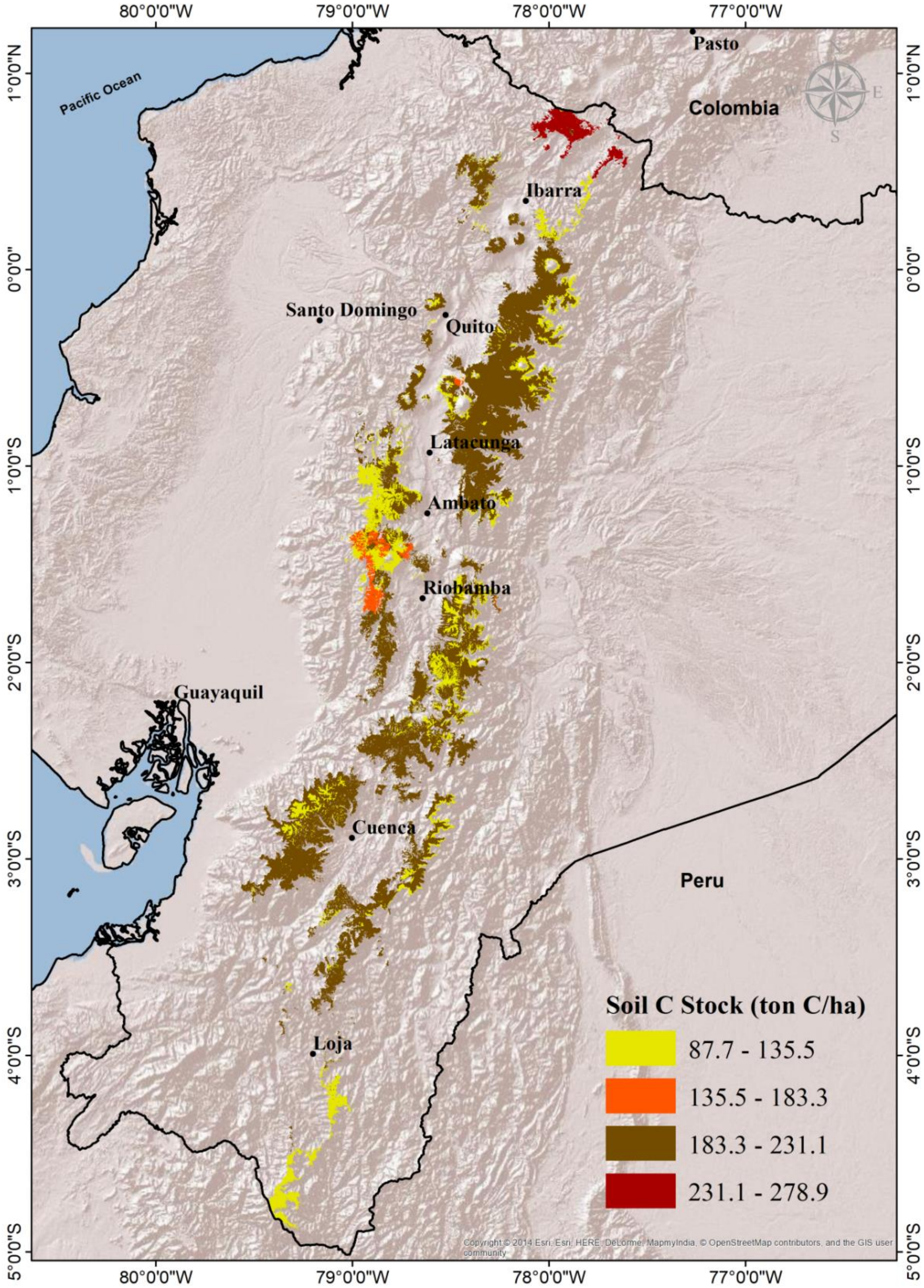

Figure 3.2 Location of Soil Carbon Stocks in the Ecuadorian Páramo Region.

Table 3.4 Soil C stock (ton C/ha) estimated at standard depth (30 cm) per type of páramo ecosystem. The table includes bulk density (g/cm^3), SOC (%) and standard error (± SE) where data for more than one site were available.

Nº	Páramo Ecosystem	Ecosystem Code	Soil Order	Area (ha)*	Standardised Depth (cm)	Bulk Density (g/cm^3)	SOC (%)	Soil C Stock (ton C/ha)
6	Ultra-humid Subnival Páramo Grassland	HsNn02	Inceptisol	2,189.0	30	1.0	3.2	92.2
			Entisol[Ɔ]	2,258.7	30	1.0 ± 0.1	2.8 ± 0.5	82.8 ± 8.5
			Other mineral soils	29.3	30	1.0	3.2	92.2
			Histosol[Π]	10.1	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem HsNn02			**4,487.0**	**30**	**1.0**	**3.0**	**87.7**
9	Páramo Subnival Evergreen Grassland and Shrubland[φ]	HsNn03	Inceptisol	46,605.2	30	1.0	3.2	102.2 ± 10.0
			Entisol[Ɔ]	1,190.0	30	1.0 ± 0.1	2.8 ± 0.5	82.8 ± 8.5
			Other mineral soils	483.8	30	1.0	3.2	102.2 ± 10.0
			Histosol[Π]	132.5	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem HsNn03			**48,411.5**	**30**	**1.0**	**3.2**	**102.0**
4	Humid Subnival Páramo Grassland	HsNn01	Inceptisol	3,555.3	30	1.0[φ]	3.2[φ]	112.2
			Entisol[Ɔ]	1,575.5	30	1.0 ± 0.1	2.8 ± 0.5	82.8 ± 8.5
			Histosol[Π]	14.9	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem HsNn01			**5,145.7**	**30**	**1.0**	**3.1**	**103.5**
10	Páramo Evergreen Shrubland and Grassland	AsSn01	Inceptisol	171,086.0	30	0.8	4.6	103.7
			Entisol	2,948.2	30	0.9	3.7	99.7
			Other mineral soils	11,690.1	30	0.8	4.6	103.7
			Histosol[Π]	27,811.4	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem AsSn01			**213,535.6**	**30**	**0.7**	**6.0**	**117.5**
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	Inceptisol	211.0	30	0.9	5.5	135.7
			Entisol	0.5	30	1.1	2.4	73.5
	Total Ecosystem AsAn01			**211.5**	**30**	**0.9**	**5.5**	**135.5**
7	Humid High Upper Montane Páramo Grassland	HsSn03	Inceptisol	30,799.4	30	0.8	6.2	153.0
			Entisol[Ɔ]	1,932.3	30	1.0 ± 0.1	2.8 ± 0.5	82.8 ± 8.5
			Other mineral soils	123.0	30	0.8	6.2	153.0
			Histosol[Π]	178.5	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6

Nº	Páramo Ecosystem	Ecosystem Code	Soil Order	Area (ha)*	Standardised Depth (cm)	Bulk Density (g/cm^3)	SOC (%)	Soil C Stock (ton C/ha)
	Total Ecosystem HsSn03			**33,033.1**	**30**	**0.8**	**6.0**	**149.2**
5	Floodable Páramo Grassland [φ]	HsSn04	Inceptisol	5,979.9	30	0.5 ± 0.1	20.6 ± 4.6	211.3 ± 24.4
			Entisol	311.6	30	1.1	2.3	75.2
			Other mineral soils	123.5	30	0.5 ± 0.1	20.6 ± 4.6	211.3 ± 24.4
			Histosol	4,283.7	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem HsSn04			**10,698.7**	**30**	**0.5**	**18.1**	**206.9**
11	Páramo Grassland	HsSn02	Inceptisol	800,952.6	30	0.5 ± 0.1	20.6 ± 4.6	211.3 ± 24.4
			Entisol	22,561.0	30	1.1	2.3	75.2
			Other mineral soils	43,756.0	30	0.5 ± 0.1	20.6 ± 4.6	211.3 ± 24.4
			Histosol	60,284.5	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem HsSn02			**927,554.1**	**30**	**0.5**	**19.9**	**207.9**
3	Evergreen Páramo Forest	BsSn01	Inceptisol	5,953.2	30	0.6	12.5	212.1
			Entisol	824.0	30			
			Other mineral soils	1,504.7	30			
			Histosol	28.0	30			
	Total Ecosystem BsSn01			**8,310.0**	**30**	**0.6**	**12.5**	**212.1**
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	Inceptisol	45,175.4	30	0.5 ± 0.1	18.6 ± 2.7	280.1 ± 50.4
			Other mineral soils	273.1	30	0.5 ± 0.1	18.6 ± 2.7	280.1 ± 50.4
			Histosol [Π]	751.8	30	0.4 ± 0.1	15.6 ± 2.3	210.1 ± 62.6
	Total Ecosystem RsSn01			**46,200.3**	**30**	**0.5**	**18.5**	**278.9**
	Total Páramo Region [ʌ]			**1,297,587.5**	**30**	**0.5**	**16.4**	**189.3**

** For comparative purposes the initial numbering presented in Table 3.1 was retained and organised by ascendant order in Soil C Stock (ton C/ha).*

***Areas of páramo ecosystems excluding rocky outcrops, snow/ice, and water bodies (natural or artificial)*

[φ] *Values are only referential due to lack of data.*

[Π] *Values are only referential based on ecosystem HsSn02.*

[Ɔ] *Values are only referential based on entisol carbon stocks for ecosystems: HsSn02, AsSn01, and AsAn01.*

[ʌ] *Area of páramo region excluding ecosystem Sumaco Volcano's Páramo Grassland and Evergreen Shrubland (HsSn01).*

Note: values that do not present standard errors are corresponding to ecosystems with only one value available per site.

3.1.2 Carbon Stock in Aboveground Vegetation

The average value of C in aboveground biomass and necromass for grassland and shrubland vegetation types, amounted to 3.8 ton C/ha and 3.5 ton C/ha, respectively (Table 3.5). The highest stock of C in aboveground biomass among these vegetation types (grassland and shrubland) was reported for *Southern Páramo High Montane Evergreen Shrubland* (*AsAn01*), (7.7 ton C/ha, Table 3.5). In terms of aboveground necromass, the highest value was estimated for *Humid Subnival Páramo Grassland* (*HsNn01*), amounting to an average (± SE) of 4.3±4.0 ton C/ha, while the lowest was observed in *Páramo Evergreen Shrubland and Grassland* (*AsSn01*) with 0.9 ton C/ha (Table 3.5). Among all grassland and shrubland vegetation types, the lowest C stock in aboveground biomass was reported for the most predominant vegetation, *Páramo Grassland* (*HsSn02*), amounting to an average (± SE) of 3.6±0.6 ton C/ha (Table 3.5). However, the low C stored in biomass was compensated with the C stocked in necromass, which was on average (± SE) 4.0±2.2 ton C/ha (Table 3.5). This indicates that the inclusion of aboveground necromass could double the C stock in aboveground vegetation as noted in seven of these páramo types (i.e. grassland and shrubland). In the case of forests, the C in aboveground biomass and necromass amounted to averages (± SE) of 94.3±32.4 and 2.0 ton C/ha, respectively (Table 3.5). This shows that in páramo forests, the content of C in aboveground necromass was not as significant as that of aboveground biomass, contrary to what happened with the other types of páramo vegetation. By considering all páramo vegetation types, the aboveground biomass carbon and aboveground necromass estimated for the páramo region amounted to averages of 4.4 ton C/ha and 3.5 ton C/ha, respectively (Table 3.5).

Aboveground C stock in vegetation (biomass + necromass) was on average 7.3 ton C/ha for grassland and shrubland vegetation types. Among these type of vegetation (grassland and shrubland), *Humid Subnival Páramo Grassland* (*HsNn01*) had the highest C stock in aboveground vegetation with an average (± SE) of 8.9±2.4 ton C/ha, whereas the lowest was reported for *Páramo Evergreen Shrubland and Grassland* (*AsSn01*) with 5.3 ton C/ha (Fig 3.3). In the case of *evergreen Páramo Forest* (*BsSn01*) the C stock in aboveground vegetation amounted to an average (± SE) of 96.3 ± 32.4 ton C/ha (Fig 3.3). Although *Evergreen Páramo Forest* had more than 10 times higher C stock than the other ecosystems, it only covers 0.6% of total Ecuadorian páramo area. The most predominant páramo vegetation, *Páramo Grassland* (*HsSn02*), had on average (± SE) 7.6±2.4 ton C/ha of C stored in aboveground vegetation (Fig 3.3). When all páramo ecosystems were considered, the overall aboveground vegetation C stock at regional scale amounted to 7.9 ton C/ha (Table 3.5).

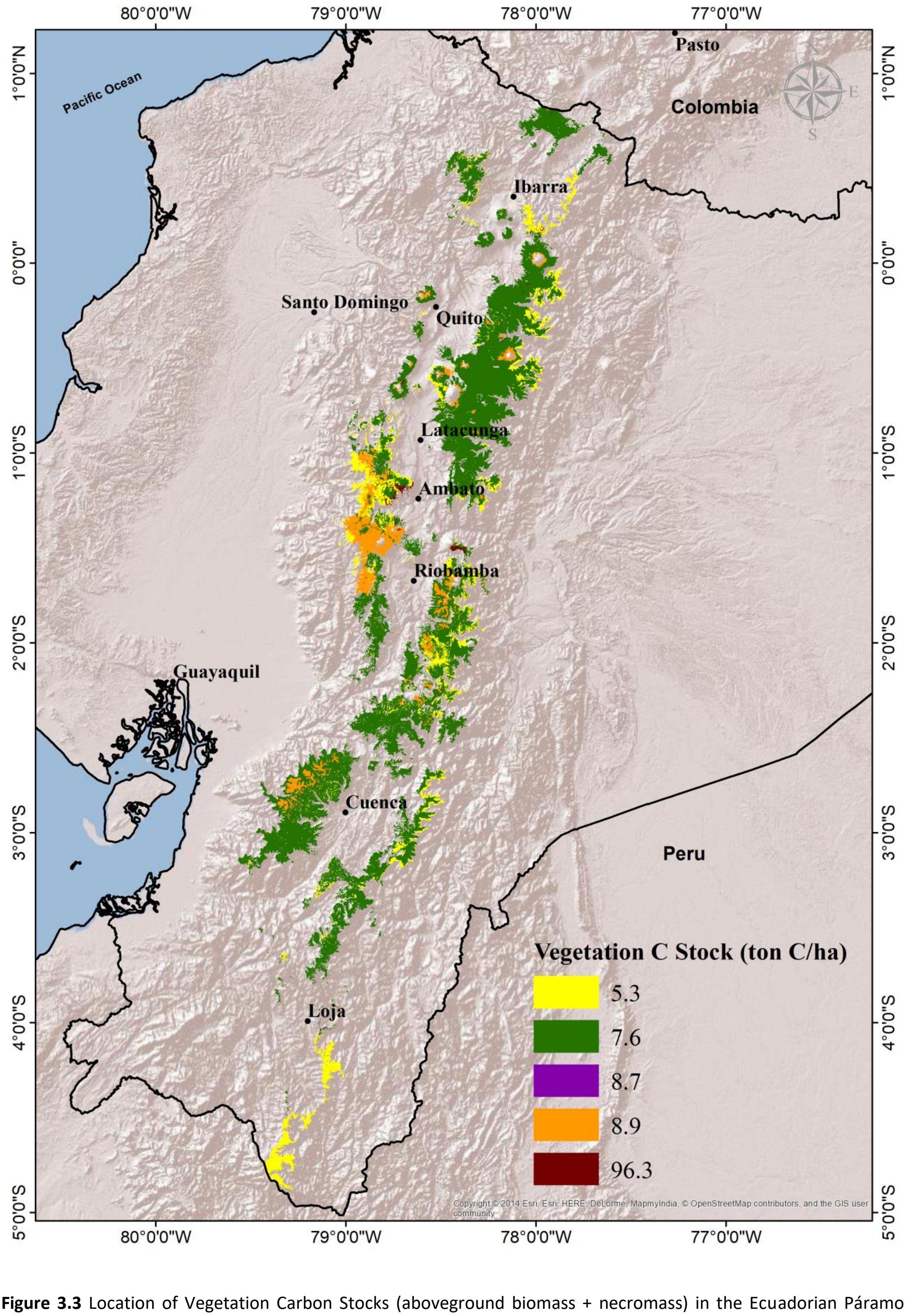

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Figure 3.3 Location of Vegetation Carbon Stocks (aboveground biomass + necromass) in the Ecuadorian Páramo Region.

Table 3.5 Aboveground vegetation C stock (biomass + necromass) (ton C/ha) by páramo ecosystem. The table includes biomass C (ton C/ha), necromass C (ton C/ha) and standard error (± SE) where data for more than one site were available.

Nº*	Páramo Ecosystem	Ecosystem Code	Area (ha)**	Aboveground Biomass C (ton C/ha)	Aboveground Necromass C (ton C/ha)	Vegetation C Stock (ton C/ha)
10	Páramo Evergreen Shrubland and Grassland	AsSn01	213,535.6	4.4	0.9	5.3
5	Floodable Páramo Grassland	HsSn04	10,698.7	3.6$^{\varphi}$	4.0$^{\varphi}$	7.6$^{\varphi}$
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	46,200.3	3.6$^{\varphi}$	4.0$^{\varphi}$	7.6$^{\varphi}$
11	Páramo Grassland	HsSn02	927,554.1	3.6 ± 0.6	4.0 ± 2.2	7.6 ± 2.4
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	211.5	7.7	1.0	8.7
7	Humid High Upper Montane Páramo Grassland	HsSn03	33,033.1	4.7$^{\varphi}$	4.3$^{\varphi}$	8.9$^{\varphi}$
6	Ultra-humid Subnival Páramo Grassland	HsNn02	4,487.0	4.7$^{\varphi}$	4.3$^{\varphi}$	8.9$^{\varphi}$
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	48,411.5	4.7$^{\varphi}$	4.3$^{\varphi}$	8.9$^{\varphi}$
4	Humid Subnival Páramo Grassland	HsNn01	5,145.7	4.7 ± 1.7	4.3 ± 4.0	8.9 ± 2.4
Total Grassland and Shrubland Vegetation			**1,289,277.5**	**3.8**	**3.5**	**7.3**
3	Evergreen Páramo Forest	BsSn01	**8,310.0**	**94.3 ± 32.4**	**2.0**	**96.3 ± 32.4**
	Total Páramo Region$^{\wedge}$		**1,297,587.5**	**4.4**	**3.5**	**7.9**

** For comparative purposes the initial numbering presented in Table 3.1 was retained and organised by ascendant order respect to vegetation carbon (ton C/ha).*

***Areas of páramo ecosystems excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

$^{\varphi}$ *Values are only referential due to lack of biomass carbon data.*

$^{\wedge}$ *Area of páramo region excluding ecosystem Sumaco Volcano's Páramo Grassland and Evergreen Shrubland (HsSn01).*

Note: values that do not present standard errors are corresponding to ecosystems with only one value per site.

3.1.3 Total Carbon Stock

Among grassland and shrubland ecosystems, the highest value of total C stock (soil + aboveground vegetation; aboveground vegetation: aboveground biomass and litter) was reported for *Páramo Caulescent Rosettes (frailejones) and Grassland* (*RsSn01*) amounting to 286.5 ton C/ha, whereas the lowest value was for *Ultra-humid Subnival Páramo Grassland* (*HsNn02*) with 96.6 ton C/ha (Fig. 3.4). For the most predominant páramo vegetation, *Páramo Grassland* (*HsSn02*), the total C stock amounted to 215.5 ton C/ha (Fig. 3.4). In all cases, the largest amount of C was stored in soils rather than in the vegetation. In fact, soil C stocks, in grassland and shrubland ecosystems, were 10 to 37 times higher than those in aboveground vegetation. The total C stock in *Evergreen Páramo Forest* (*BsSn01*), was the highest (308.4 ton C/ha, Fig. 3.4). In this case, the C stock in soil was only twice as high as that in aboveground vegetation. When all páramo ecosystems were considered, the overall total C stored in the entire páramo region of Ecuador amounted to 197.2 ton C/ha (Table 3.6).

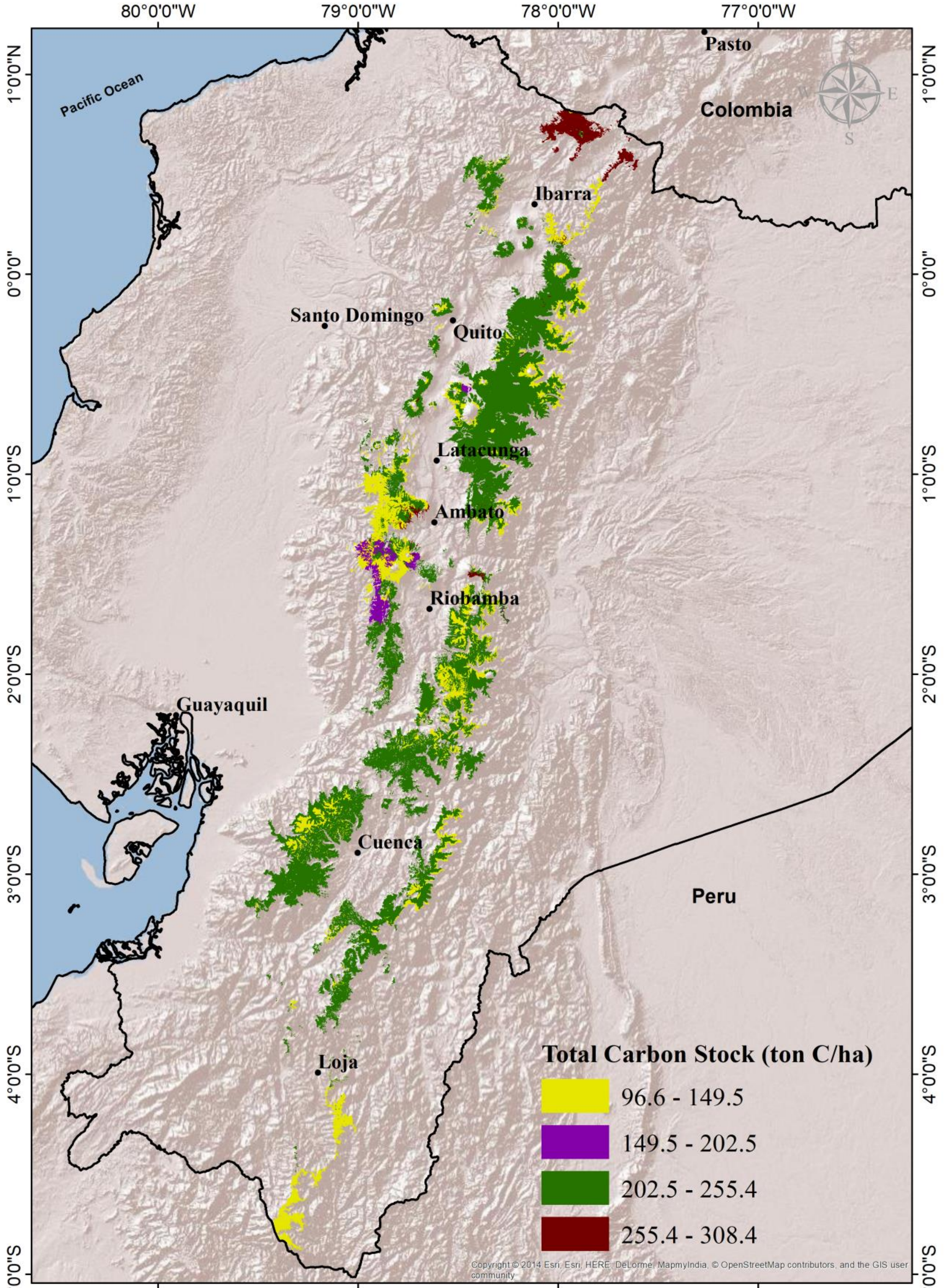

Figure 3.4 Location of Total Carbon Stocks in the Ecuadorian Páramo Region.

Table 3.6 Total C Stock (soil C + aboveground vegetation C (aboveground biomass + necromass) (ton C/ha) by páramo ecosystem. The table includes soil C stock (ton C/ha) and aboveground vegetation C stock (ton C/ha).

Nº*	**Páramo Ecosystem**	**Ecosystem Code**	**Area (ha)****	**Soil C Stock (ton C/ha)**	**Vegetation C Stock (ton C/ha)**	**Total C Stock (ton C/ha)**
6	Ultra-humid Subnival Páramo Grassland	HsNn02	4,487.0	87.7	8.9[φ]	96.6[φ]
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	48,411.5	102.0[φ]	8.9[φ]	110.9[φ]
4	Humid Subnival Páramo Grassland	HsNn01	5,145.7	103.5	8.9	112.4
10	Páramo Evergreen Shrubland and Grassland	AsSn01	213,535.6	117.5	5.3	122.8
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	211.5	135.5	8.7	144.2
7	Humid High Upper Montane Páramo Grassland	HsSn03	33,033.1	149.2	8.9[φ]	158.1[φ]
5	Floodable Páramo Grassland	HsSn04	10,698.7	206.9[φ]	7.6[φ]	214.5[φ]
11	Páramo Grassland	HsSn02	927,554.1	207.9	7.6	215.5
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	46,200.3	278.9	7.6[φ]	286.5[φ]
3	Evergreen Páramo Forest	BsSn01	8,310.0	212.1	96.3	308.4
	Total Páramo Region[ʌ]		**1,297,587.5**	**189.3**	**7.9**	**197.2**

** For comparative purposes the initial numbering presented in Table 3.1 was retained and organised by ascendant order respect to vegetation carbon (ton C/ha).*

***Areas of páramo ecosystems excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

[φ] *Values are only referential due to lack of carbon data.*

[ʌ] *Area of páramo region excluding ecosystem Sumaco Volcano's Páramo Grassland and Evergreen Shrubland (HsSn01).*

Note: values that do not present standard errors are corresponding to ecosystems with only one value per site.

3.1.4 Carbon Stored by Páramo Ecosystem Area

When the area covered by the páramo ecosystems was also taken into account in the C stock estimates, the ecosystem that stored the largest amount of C is *Páramo Grassland* (*HsSn02*). This ecosystem stored 199.9 Mt C which equates to 78.1% of the C stored in the entire páramo-covered area of Ecuador (Table 3.7). In second place is *Páramo Evergreen Shrubland and Grassland (AsSn01*), storing 26.2 Mt C and contributing with 10.3% of the C stored by all ten páramo ecosystems (Table 3.7). The carbon stored in the area of the remaining páramo ecosystems was 29.7 Mt C, which was 11.6% of the overall C stored in the páramo vegetation of Ecuador (Table 3.7). In the total area of all ten páramo ecosystems in Ecuador 255.9 Mt C was stored.

Table 3.7 Carbon stored by páramo ecosystem area (Mt C). The table includes total C stock (ton C/ha) and C contribution (%) with respect to the national C contribution.

Nº*	Páramo Ecosystem	Ecosystem Code	Area (ha)**	Total C Stock (ton C/ha)	C Stored (Mt C)ƒ	C Contribution (%)
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	211.5	144.2	0.03	0.01
6	Ultra-humid Subnival Páramo Grassland	HsNn02	4,487.0	96.6	0.4	0.2
4	Humid Subnival Páramo Grassland	HsNn01	5,145.7	112.4	0.6	0.2
5	Floodable Páramo Grassland	HsSn04	10,698.7	214.5	2.3	0.9
3	Evergreen Páramo Forest	BsSn01	8,310.0	308.4	2.6	1.0
7	Humid High Upper Montane Páramo Grassland	HsSn03	33,033.1	158.1	5.2	2.0
9	Páramo Subnival Evergreen Grassland and Shrubland	HsNn03	48,411.5	110.9	5.4	2.1
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	46,200.3	286.5	13.2	5.2
10	Páramo Evergreen Shrubland and Grassland	AsSn01	213,535.6	122.8	26.2	10.3
11	Páramo Grassland	HsSn02	927,554.1	215.5	199.9	78.1
	Total Páramo Region^		**369,821.9**	**197.2**	**255.9**	**100**

** For comparative purposes the initial numbering presented in Table 3.1 was retained and organised by ascendant order respect to carbon stored per ecosystem area (ton C).*

***Areas of páramo ecosystems excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

ƒValues presented in Mega tonnes of Carbon.

^ Area of páramo region excluding ecosystem Sumaco Volcano's Páramo Grassland and Evergreen Shrubland (HsSn01).

3.2 Controls on Soil Carbon Stocks

Soil C stock showed a significant positive linear relationship with altitude, when including the entire dataset (R^2= 0.297, p= 0.002, n=31; Fig. 3.5). In addition, soil C stocks showed a significant negative linear relationship with annual mean air temperature (R^2= 0.358, p= 0.0004; Fig. 3.6) and a significant positive linear relationship with annual precipitation (R^2= 0.255, p= 0.004; Fig. 3.7)

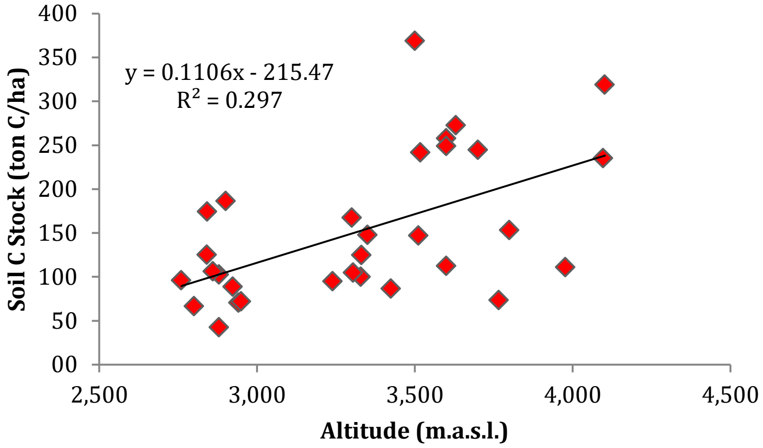

Figure 3.5 Soil C stock as a function of altitude for the entire dataset of the Ecuadorian páramo ecosystems all soil samples (linear regression: p= 0.002).

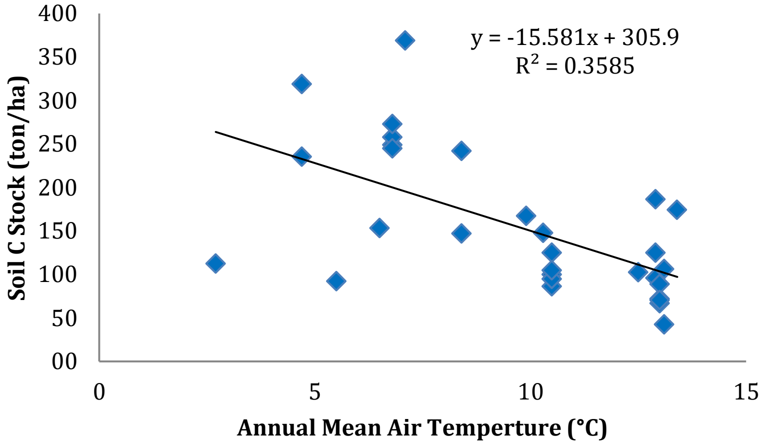

Figure 3.6 Soil C stock as a function of annual mean air temperature (°C) for the entire dataset of the Ecuadorian páramo ecosystems all soil samples (linear regression: p= 0.0004).

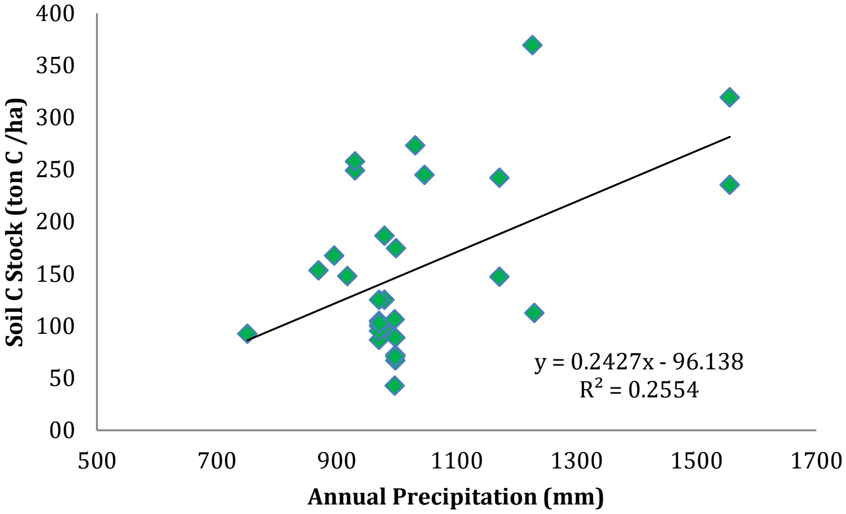

Figure 3.7 Soil C stock as a function of annual precipitation (mm) for the entire dataset of the Ecuadorian páramo ecosystems all soil samples (linear regression: p= 0.0004).

4. Discussion

4.1 Carbon Stock Estimates

In agreement with previous studies (Farley, 2010; Farley and Kelly, 2004; Hofstede et al., 2014), the C estimates obtained by this research confirmed that páramo vegetation was not a significant contributor of C in comparison with their soils. This study estimated that in the Ecuadorian páramo area as a whole the average C stock in soil was 189.3 ton C/ha while in aboveground vegetation (biomass + necromass) it was on 7.9 ton C/ha, which means that the C stock in the Ecuadorian páramo soils was on average 24 times higher than in the vegetation. However, this difference might be overestimated due to insufficient data on belowground plant biomass to be included in the C stock estimates. Nevertheless, these findings confirm that the plant mass of the páramo vegetation is a much smaller C stock than the soils (Hofstede et al., 2014).

Global carbon data estimates a SOC concentration for tropical grasslands varying between 110 to 117 ton C/ha (Lal, 2004). Based on the average SOC estimated for páramo ecosystems (i.e. 189.3 ton C/ha), this could represent an underestimation of 38% to 42% of the soil carbon content present in the páramo soils, confirming that the global estimates do not adequately fit this type of tropical vegetation. In terms of soil C variation influenced by soil order characteristics, results showed that inceptisols contained on average (± SE) 162.5 ± 23.3 ton C/ha, whereas histosols and entisols 210.1±62.6 ton C/ha and 82.8±8.5 ton C/ha, respectively.

In contrast, global SOC estimates reported by Lal (2004) per type of soil, show a concentration of SOC in inceptisols, histosols, and entisols corresponding to 148 ton C/ha, 1,170 ton C/ha and 42 ton C/ha, respectively. Global reports seem to approximate quite well the páramo estimates in the case of inceptisols with only 9% less carbon reported globally. For entisols, 49% less carbon is reported globally compared to this study. In contrast, global estimates report 82% more carbon in histosols than the reported by this study. These differences highlight the importance of generating carbon studies on a local scale that allow a better reflection of the influence of parent material on C content in soil. Results also highlight the relevance of soil type discrimination in the estimation of carbon stocks.

Despite methodological differences (e.g. soil sampling depth), páramo vegetation particularities and the influence of other factors (e.g. micro-climate), the soil C stocks obtained here mostly fell within the ranges observed in the other countries (Table 3.8). For example, this study estimated a soil C stock for *Evergreen Páramo Grassland* (top 30 cm) (i.e. 207.9 ton C/ha) that falls within the range of stocks in other *Páramo Grasslands* located in the Andes of Peru and Colombia (i.e. 119-181.4 ton C/ha at 0-20/0-33 cm depth; Table 3.8) (Zimmermann et al., 2010; Vásquez et al., 2014; Rangel, 2000). Similarly, the estimate obtained for *Evergreen Páramo Forest* (i.e. 212.1 ton C/ha) was in the range of those reported by similar studies (i.e. 118-397 ton C/ha; Table 3.8).

Table 3.8 Comparison between Soil C Stocks estimated in this study versus previous studies performed in different countries with páramo sites along the Andes (error bar indicates SE).

Country	Andes Location	Site	Páramo Ecosystem	Altitude (m.a.s.l)	Depth (cm)	Soil C Stock (ton C/ha)	Source
Peru	Eastern	Manu National Park	Páramo Forest	3,370	0-20	118±15	(Zimmermann et al., 2010)
	Eastern	Nor Yauyos Cochas National Park		4,200	0-20	397±69	(Vásquez et al., 2014)
Ecuador	Eastern and Western	Ecuadorian Andes		3,600	0-30	212.1	This study
Colombia	***	Sierra Nevada	Páramo Grassland	3,460	0-33	150.2	(Rangel, 2000)
	Centre	Cordillera Central		3,090	0-27	181.4	
Peru	Eastern	Manu National Park	Páramo Grassland	3,547	0-20	119±8	(Zimmermann et al., 2010)
Ecuador	Eastern and Western	Various sites		2,800-3,600	0-30	207.9	This study

At the ecosystem level, there were notable differences in the soil C stocks depending on the type of páramo ecosystem considered. Soil C stocks ranged from 87.7 to 278.9 ton C/ha, while vegetation C stocks varied from 5.3 to 8.9 ton C/ha, in grassland and shrubland páramo types, and it amounted to 96.3±32.4 ton C/ha in the *Evergreen Páramo Forest*. *Páramo Grassland* and *Páramo Evergreen Shrubland and Grassland*, were identified as the most representative C sinks storing 78% (199.9 Mt C) and 10.3% (26.2 Mt C) of the total carbon stored in the Ecuadorian páramo region, respectively. Both ecosystems together store 88.3% of the entire carbon stored while the remaining ecosystems contribute as a whole with only 11.6% (29.7 Mt C).

Regarding vegetation C stocks, according to global estimates, aboveground C stocks for tropical grasslands could amount to 29 ton C/ha, whereas for tropical forests they ranged from 120 ton C/ha to 194 ton C/ha (Prentice et al., 2001). These values seemed overestimated when compared with aboveground C stocks calculated by this study for *Páramo Grassland* vegetation, which only ranged between 5.3 ton C/ha and 8.9 ton C/ha. However, these estimates fell within the ranges reported for several *Páramo Grassland* sites in Peru showing values between 3.35 and 7.5 ton C/ha (Table 3.9). Regarding *Evergreen Páramo Forest* this study estimated a vegetation C stock with an average (± SE) of 96.3±32.4 ton C/ha which was much closer to the global estimates (i.e. 194 ton C/ha). In the same way, this estimate showed good agreement with aboveground C stocks reported for Peruvian páramo forest (i.e. 19-99 ton C/ha) by similar studies (Vásquez et al., 2014; Girardin et al., 2010; Román-Cuesta et al., 2011; Gibbon et al., 2010; Oliveras et al., 2014).

Most of the studies included the aboveground necromass (if it was present) as part of C stocks of the soil profile (O horizon) (Table 3.9). Except for Gibbon et al. (2010), who included necromass (litter) and mosses in the vegetation C stock estimate of páramo grasslands in Peru (63.4±5.2 ton C/ha in páramo forest and 7.5±0.7 in páramo grassland; Table 3.9). Gibbon findings are closer to those presented by this study (94.3 ± 32.4 ton C/ha in páramo forest and 4.0±2.2 ton C/ha in páramo grassland; Table 3.9). Other páramo grassland sites across the Andes (Vásquez et al., 2014; Girardin et al., 2010; Román-Cuesta et al., 2011; Gibbon et al., 2010; Oliveras et al., 2014), reported C in aboveground biomass between 3.35 to 7.5 ton C/ha, which, despite methodological differences, are within the range of the estimates presented here (Table 3.9). For *Evergreen Páramo Forest* (*BsSn01*), the aboveground C stock estimated in this study was in agreement with similar studies performed in páramo sites along the Peruvian Andes (Table 3.9). This study concludes that the inclusion of aboveground necromass could double the C stock in aboveground vegetation, as noted in seven páramo grassland-shrubland types. Therefore, it is relevant to be taken into account in future carbon estimates.

Table 3.9 Comparison between Aboveground Vegetation C Stocks estimated in this study versus previous studies performed in different páramo sites along the Andes.

Country	Andes Location	Site	Páramo Ecosystem	Altitude (m.a.s.l)	Aboveground Biomass C Stock (ton C/ha)	Source
Peru	Eastern	Nor Yauyos Cochas National Park	Páramo Forest	4,200	19	(Vásquez et al., 2014)
		Kosñipata valley		3,020	47	(Girardin et al., 2010)
				3,025	65	
		Manu National Park, Challabamba		3,100	99	(Román-Cuesta et al., 2011)
				3,400	84.5	
		Manu National Park		3,345	63.4±5.2$^{\varphi}$	(Gibbon et al., 2010)
Ecuador	Eastern	Pifo		3,600	94.3 ± 32.4	This study
Peru	Eastern	Manu National Park	Páramo Grassland	3,540	7.5±0.7$^{\varphi}$	(Gibbon et al., 2010)
		Manu		3,300	3.35±0.1	(Oliveras et al.,

Country	Andes Location	Site	Páramo Ecosystem	Altitude (m.a.s.l)	Aboveground Biomass C Stock (ton C/ha)	Source
		National Park				2014)
Ecuador	Eastern and Western	Various sites		2,800-4,043	4.0±2.2	This study

[φ] *Including aboveground biomass, litter, and moss.*

The carbon estimates reported in this study highlight the importance of the páramo ecosystems as C sinks. However, there are many factors that can put the stability of the C stored in these terrestrial ecosystems at risk. In the páramo region, land use change is playing a determinant role in altering C fluxes. The transformation of páramo ecosystems into agricultural lands could cause a rapid loss of carbon in biomass and soil due to the elimination of the natural vegetation that protects the soil, decreasing the entry of organic matter into the soil and increasing the rate of decomposition of plant residues (Don et al., 2011). In addition, C fluxes are significantly influenced by climate change affecting the structure and functionality of ecosystems (Smith and Shugart, 1993). Changes in ecosystems composition could cause an increase or decrease in their capacity to absorb carbon (Cramer et al., 2001; Cox et al., 2000; Smith and Shugart, 1993; Joos et al., 2001). In this context, based on the national C stocks estimated here for the Ecuadorian páramo ecosystems, the release of the entire C stored in soil and vegetation (i.e. 197.2 ton C/ha) would represent a contribution of 256 Mt C to the atmosphere. Therefore, the role of páramo ecosystems in capturing carbon and stabilizing atmospheric emissions needs to be recognized, emphasizing the collateral social and environmental benefits of soil conservation that go beyond carbon mitigation (e.g. provision and regulation of water) (Dumanski, 2004).

4.2 Controls on Soil Carbon Stocks

In the Ecuadorian Andes, the SOC is influenced by humid air currents from the oceans (Humboldt Current) and the Amazon basin, determining humid conditions in the north and centre of the Andes and relatively drier conditions in the south (Rivera Ospina and Rodríguez Murcia, 2011; Luteyn et al., 1999; Sarmiento, 1986). This study was able to prove the influence of climatic conditions such as precipitation and temperature in páramo soil C stocks as has been highlighted by previous studies (Hofstede et al., 2014; Llambí et al., 2012; Mena et al., 2000). Climatic influence was reflected on the results by showing a significant negative linear relationship of soil C stock with annual mean temperature (R^2= 0.3585, p= 0.0004) and a significant positive relationship of soil C stock with annual precipitation (R^2= 0.2554, p= 0.0044) based on all the data available. Both climatic factors influence vegetation composition and productivity, as well as the quantity and turnover of soil organic matter (SOM) (Dai and Huang, 2006). Therefore, both factors have significant impact on the C stocks in páramo soils.

Regarding altitude, the regression analysis based on the entire dataset showed a significant positive linear relationship of soil C stock with altitude (R^2= 0.297, p= 0.002). These results agree with other studies around the globe (Sims and Nielsen, 1986; Tate, 1992; Dai and Huang, 2006; Jenny and Raychaudhuri, 1969). The relevance of altitudinal variation found across all páramo soils support the observations that the climatic variables annual precipitation and annual temperature, are key drivers in C stocks, as air temperature decreases and precipitation increases with increasing altitude (Dai and Huang, 2006; Don et al., 2011). while younger páramo soils at higher altitude will present less accumulation of organic matter (Hofstede et al., 2014).

The study acknowledges the existence of other factors influencing the soil C stocks such as the incidence of active volcanism in the Northern part of the Andes Cordillera and the absence of this activity in the Southern mountain range (Podwojewski and Poulenard, 2000b). Hofstede et al (2014), for example, states that soils in humid páramo ecosystems and developed on volcanic deposits, as in the North and Centre of the Ecuadorian Andes, will have greater accumulation of organic matter, therefore, more C in their soils. Hence, the influence of parent material on soil C stocks needs to be further explored.

4.3 Approach Limitations & Recommendations for further study

Most benefit transfer studies focus on estimating the economic values of ecosystem services, however, this study proved its usefulness in ecosystem carbon mapping. Benefit transfer technique presents several advantages including low cost and easy and quick application (Barbera, 2010). However, this approach is capable to cause generalization errors (Plummer, 2009; Eigenbrod et al., 2010a; Eigenbrod et al., 2010b). In this study, uniformity error could have been caused by considered constant (uniform) the carbon stocks for each type of ecosystem without considering some biophysical differences across páramo patches of the same type such as climatic variations along the Andes Cordillera (e.g. humid at the North and dry at the South), management history and level of anthropogenic intervention, among others. Having a small number of field measurements available increases the risk of errors in the estimates (Eigenbrod et al., 2010a). Therefore, sampling error might be present in the results as well, since for some páramo ecosystems the number of sampling sites to estimate the carbon values was limited and biased to certain areas of the Andean Cordillera. Furthermore, regionalization error might have happened caused by the differences in representativeness of the sampling areas in relation to the area being mapped (Eigenbrod et al., 2010a). It has been shown that the relationships between ecosystem services demonstrate geographic variation (Anderson et al., 2009). Therefore, the generalization of sampled páramo areas to the entire páramo ecosystems area may have introduced particular extrapolation problems, preventing results to show these differences. Based on the aforementioned, the results presented here must be used with discretion, avoiding its use for identifying hotspots or priority areas for multiple services (Eigenbrod et al., 2010b).

Linking the different sampling stratum reported by the secondary sources with the new categories of páramo vegetation represented a major challenge due to the inaccuracy in the geographical location of the sampling sites (i.e. coordinates, in some cases non-existent) provided by some of the secondary sources. The lack of a common protocol for soil sampling among the studies, may also have increased inaccuracies in the C stock estimates as both sampling approaches with either strict depth intervals or with soil horizons were both included (Calderón et al., 2013). The inaccurate geographical location and the depth constriction led to the exclusion of 13 of the 27 studies consulted. In this study, soil C stocks were evaluated at a standard depth range of 0 – 30±5 cm, considering that more than 50% of the soil C is present in the first 25 cm as several authors have suggested (Eswaran et al., 1995; Garnett et al., 2001). This decision was made to generate robust C stock calculation and to facilitate the data comparability among the different sources consulted.

The compiled data covered both Andes Cordilleras from north to south, however, 71% of the data was from the Western flank, whereas data for the Eastern side was limited and mostly from the far south. This was due to the exclusion of certain studies that did not meet the requirements established by this study (e.g. soil depth). The collection of soil data in páramo regions that present information gaps (in particular the Eastern Cordillera) is considered relevant given the variation of soil C contents identified with respect to their location in the Andes. This could facilitate the evaluation of other control factors that could not be explored due to these limitations, such as parent material (e.g. volcanic versus non-volcanic deposits). Additionally, the generation of a study especially focused on the estimation of carbon contents in histosols is required due to the special characteristics that these organic soils present in the páramo region (e.g. soil depth of potentially ≥4 metres). Similarly, more C stock information regarding biomass and necromass across the Andes of Ecuador is still required. This could help in the future to keep exploring the relevance in terms of C of certain types of páramo ecosystems versus others. Despite the limitations, the most predominant páramo vegetation

(HsSn02), covering 71.5% of the páramo region, was well-represented by the data compiled for both soil and vegetation. It is believed that data gaps have not significantly affected the C estimates generated for this study. Therefore, the C stocks presented here could be considered a rational approximation of the C stocks currently present in the Ecuadorian páramo region.

Soil information has long been considered one of the least developed environmental data at a global scale, with data available only at approximate resolutions and with limited accuracy (Sanchez et al., 2009; Grunwald et al., 2011). Most global SOC maps have been coarse both in spatial resolution and in terms of number of soil parameters considered (Meentemeyer et al., 1985; Brus et al., 2017), making difficult to use for national studies. However, global estimates could be improved by systematically collecting more data on soil profiles and including sampling at greater depths (Scharlemann et al., 2014). The standardization of sampling methods and the availability of national data would facilitate in the future the combination, complementarity, and comparison of data from different sources providing better global, regional, and local carbon assessments. To this end, several global initiatives focused on improving soil data are in progress implemented by institutions such as the United Nations Convention to Combat Desertification (UNCCD) and the Global Soil Organic Carbon led by FAO. Thus, global soil datasets are expected to become increasingly accurate, complete and reliable (Brus et al., 2017).

For countries like Ecuador, global soil maps can be also useful for filling gaps in areas where data collection is limited by budget or accessibility such as in the Andes region. Global soil datasets could contribute to the improvement of national carbon stock maps allowing researchers to identify areas of great differences that should be considered for further investigation (Scharlemann et al., 2014). In the same way, the comparison of global results with those obtained locally could increase the degree of confidence in the use of the estimates of these maps for the regions where there is a consensus among the maps. At the national level, global SOC estimates can be used as a reference of soil carbon stocks, with the aim of refining national inventories of greenhouse gases and assessing the sensitivity of soils to degradation and climate change (Brus et al., 2017). To date, national level inventory of SOC páramo stocks has not been reported. Thus, the spatially-explicit estimates of SOC stocks reported in this study, can serve in the future as a basis for process-based simulation models which intends to predict anthropogenic and climatic impacts on soil systems. Further, the estimates and maps produced here can improve the process of páramos carbon budgeting and reporting in line with global initiatives oriented to minimize greenhouse gas emission and thus the impacts of climate change.

5. Conclusion

The present study summarised all available C stock data of soils, aboveground plant biomass and aboveground plant necromass according to the new national classification of páramo ecosystems. The estimates presented mostly fit well with within the range of C stocks found in soil and vegetation in páramo ecosystems in the Andes. Through this effort, it was possible to confirm that C stocks in páramo ecosystems are clearly influenced by type of vegetation, as well as, soil characteristics (soil order), climate and altitude. Therefore, any C estimate that does not acknowledge these aspects in the calculation would tend to underestimate the C stocks. It is clear that there is a considerable margin for the improvement of C inventories for both soil and vegetation. The generation of C data under a standard methodology, prioritizing páramo ecosystems with information gaps (e.g. *Floodable Páramo Grassland* and *Páramo Subnival Evergreen Grassland and Shrubland*) or important to population in terms of ecosystem services (e.g. drinking water/hydropower) is a priority. An accurate assessment of C stored in páramo ecosystems is essential to understand their role as sources or sinks of atmospheric CO_2. Future studies should aim to reduce uncertainty in the amount of C stored in páramo histosols (peatlands). Exploring the alteration of the C reserves due to anthropogenic pressures such as land use, fires, and cattle, in humanized ecosystems such as the páramos, is a must in order to design appropriate strategies for future management of these natural areas.

Given the potential importance of changes in páramo C stocks for atmospheric C chemistry and global warming, a reliable global assessment of current C storage and estimates of probable changes in the future are necessary. This will imply the development of strategies for monitoring and the construction of a solid C stock database at national and regional level in order to promote informed decision making and to link páramo ecosystems to the C market. Immediate efforts to mitigate the negative consequences of climate change and other stressors in the Andean páramo region should be encouraged. Sustainable management strategies should be implemented, aimed to reduce páramo ecosystems vulnerability to climate change and human intervention, ensuring the future provision of critical ecosystem services. Efforts should be aimed at restoring degraded soils in order to increase SOC and sequestering C within the terrestrial ecosystems (Lal et al., 2000). The promotion of sustainable agricultural practices (e.g. crop rotation) could also reduce the intensity of the alteration and help avoid erosion and loss of C in soils and vegetation (Horowitz et al., 2010).

Chapter IV

Future Exposure of the Ecuadorian Páramo Vegetation to Land Use Pressures influenced by Climate Change

1. Introduction

The global footprint of agriculture is expanding rapidly, especially in South America (Laurance et al., 2014). Cropland and grazing areas are currently occupying an area equivalent to the size of South America and Africa, respectively (Foley et al., 2005). Given the magnitude and accelerated rate of agricultural impact on ecosystems, it is predicted that an "agricultural bomb" is looming in the coming era. The origin of this bomb will be the tropics, due to the great population growth that is projected in these region (United Nations, 2013). Increasing food consumption per capita driven by the improvement of population living standards (Bruinsma, 2009; Kastner et al., 2012). The problem posed by the growing demand for ecosystem services is compounded by an increasingly severe degradation in the capacity of ecosystems to provide services.

In the coming decades, the pressures to increase food production will be enormous and the constant agricultural expansion will continue to exert pressure on tropical ecosystems (Tilman et al., 2001; Dobrovolski et al., 2011). By 2050, the world population could reach 10 billion people with the greatest increases in tropical developing countries (United Nations, 2013). The exponential population growth comes hand in hand with the increase in per capita food consumption. In 2050, global food needs could increase by 70 to 110 % (Tilman et al., 2001; Bruinsma, 2009). These needs must be met by agricultural systems struggling with climate change (Nelson et al., 2009). This will imply a significant increase in the demand and consumption of biological products and physical resources, as well as the escalation of impacts on ecosystems and the services they provide (Millennium Ecosystem Assessment, 2005; Laurance et al., 2014). The agricultural expansion would be favoured by the creation of new roads, intensifying the conflicts between food production and nature conservation (Laurance et al., 2014).

The Tropical Andes have been considered an important source of cultivated plants used for food, medicine and industry for more than 10,000 years (Saavedra and Freese, 1986). In the

Andes, cultural and anthropogenic activities have mainly been developed in páramo areas. Despite their rugged topography and extreme climatic conditions, these natural areas have proved to be quite favourable for the establishment of human population, leading to habitat loss, urban expansion and anthropogenic transformation (Morales-Betancourt and Estévez-Varón, 2006). Farming is present in the páramo areas of all countries in the Northern Andes (Llambí, 2010). The páramo areas where the use of land has impacted the most are: the Mérida Cordillera in Venezuela, the Santanderes, Boyacá, Antioquia and Nariño-Carchi regions in Colombia, and the Imbabura and Chimborazo provinces in Ecuador (Hofstede et al., 2003).

During the first decades of the 20th century, the expansion of the agricultural frontier in páramo areas occurred, causing major changes in the Andean landscape (Suárez et al., 2011). Large-scale intensification characterized by monocultures, extensive cattle raising and agricultural smallholdings were gradually occupying the fertile Andean valleys and peripheral landscapes with subsequent replacement of the original mountain ecosystems (Suárez et al., 2011). During the 1940s and 1950s, significant processes of transformation and expansion of the agricultural frontier occurred (Llambí, 2010). This situation was encouraged by the agrarian reform, applied during the 1960s and 1970s, focussed on solving two interrelated problems, the concentration of land ownership in few owners and low agricultural productivity due to the non-use of technologies and land prices speculation that was preventing or rejecting at that time the productive use of land (Llambí, 2010). The reform led to the modernization of practices, intensification of agriculture, and promoted the use of agrochemicals (Llambí, 2010). After the agrarian reform and impulse by demographic growth, the use of the land became even more intensive. Indigenous communities and peasant associations applied inappropriate farming techniques in the páramo lands (e.g. intensive livestock) (Murra, 2002). The application of the agrarian reform and its amendments caused accelerated processes of agricultural small-holdings (mini-fundio) and micro-holdings (micro-fundio), increasing deforestation, erosion and loss of soil fertility in the Andes (Murra, 2002).

Intensive alteration in the Andes continued to increase until the late 1980s, a period in which the agricultural expansion in some areas of the tropical Andes started to decline due to the increase of agricultural imports in all Andean countries (Suárez et al., 2011). During the 1980s and 1990s, in Ecuador, migratory processes occurred as a result of agrarian reform reflected in lack of access to resources (water and land), land degradation, lack of access to credit and technical assistance aggravated by periods of drought (Lasso, 2009). The large haciendas typical of the early 20th century progressively disappeared, although, until now there are haciendas occupying extensive areas maintained since colonial or republican times (Lasso, 2009). New páramo owners with business vision bought large areas for agro-industrial purposes based on monocultures such as potatoes, garlic, livestock, and forest plantations.

Intensification of land use and natural resources in the Andes continues today, leading to greater loss, fragmentation and degradation of habitat (Corrales, 2001; Palminteri and Powell, 2001). As a result of transformation and replacement of ancestral cultures by Western civilization in the Andes, traditional systems of land use have also changed (Young, 2008). This has led to modifications to the soil and caused loss of animal and plant species as well as elimination of much of the original vegetation (Young, 2008; Herzog et al., 2012). It is estimated that 24% of the Andean region has been altered by human intervention (Josse et al., 2009). Current trends in land use change are substantially increasing habitat loss and fragmentation in mountain ecosystems, and also contributing to the negative impacts of climate change on biodiversity (Báez et al., 2012). In 2005, it was estimated that approximately 30% of páramo areas in the Andes region had been completely transformed, 40% were partially modified and only 30% remained well preserved (Llambí, 2010). Anthropogenic intervention has significantly affected associated páramo ecosystem services such as water regulation, supply of drinking water and carbon storage (Hofstede, 2001; Hofstede et al., 2003; Podwojewski et al., 2002). Several studies in the Andes have shown that after agricultural and livestock intervention in páramo forests, the regeneration and natural recovery of forest areas are severely constrained by the limited capacity for recolonization of woody species, favouring the colonization of a less diverse herbaceous vegetation (Vargas and Mora, 2009).

Climate change scenarios project a significant increase in average temperatures (>4 C°) in the twenty-first century, accompanied by more frequent extreme weather events, such as droughts and heat waves (IPCC, 2014b). Higher temperatures increase the water requirement for crops, which, together with changes in rainfall patterns, could generate higher risks of drought stress for several crops (Schafleitner et al., 2011). Studies suggest that in tropical countries such as Ecuador, it is unlikely that current crop varieties will continue to be produced in the future under extreme conditions (Challinor et al., 2005; Challinor et al., 2010; Byjesh et al., 2010), since they are very sensitive to changes and variations in climates (Lane and Jarvis, 2007). However, there is evidence that climate change in the Andes is influencing agricultural activities, causing conflicts between the use of land required for productive purposes and the priorities of conservation of natural areas (Bradley et al., 2006; Báez et al., 2012). It is expected that productive activities will exacerbate the negative effects of climate change on biodiversity, causing fragmentation of ecosystems while decreasing their probability of survival (Young, 2009). Plausible climate change scenarios consider increases in temperature and changes in precipitation (increase or reduction) as well as higher concentrations of CO_2 in the atmosphere which could lead to the expansion of productive land towards páramo areas (Adams et al., 1998).

At the moment there is no consensus on the magnitude of the impacts of climate change on crop production, mainly due to the lack of understanding of crop growth processes and limitations (Ramirez-Villegas et al., 2013). Due to the lack of precise methods to evaluate the response of crops to the climate, there are several important crops at the regional level that have been little investigated. Given the need to assess the influence of climate change on land use as changes to land use may threaten natural areas, several researchers have used suitability indexes as an indicator to evaluate the response of crops to environmental factors (Lane and Jarvis, 2007; Nisar Ahamed et al., 2000; Schroth et al., 2009; Ramirez-Villegas et al., 2013). Crop's suitability studies based on bioclimatic approaches have been developed as good proxies to quantify the relationship between climate and crop yield when no detailed information is available (Ramirez-Villegas et al., 2013).

For Ecuador, generating key information to guide adaptation processes in the field is a challenge, mainly in crops located in the páramo region where there is a clear competition between agricultural expansion and natural areas of great importance for ecosystem services provision. Therefore, this research was concerned with exposure of the Ecuadorian páramo vegetation to land use pressures from agricultural crops, since climate could be a determining factor of potential expansion of the farming frontier. Due to data limitations, a bioclimatic approach was considered appropriate. For this purpose, three common Andean crops including potato, soft maize, and quinoa were used as indicators of potential land use threats to the survival of the páramo vegetation. For the representation of the agricultural frontier, páramo areas were characterized in terms of their edaphic and agro-climatic properties to identify areas edapho-climatically suitable for crops under present and future conditions. Edaphic suitability was based on páramo soils´ characterization according to critical parameters necessary for crop growth. Soil requirements were defined by the Food and Agriculture Organization of the United Nations (FAO) and adapted to in-situ conditions by local Institutions. The Ecocrop module in DIVA-GIS was used to evaluate the agro-climatic suitability for the Andean crops under current (1950-2000) and future (2050 and 2070) climatic conditions. To simulate the future conditions, two greenhouse gas (GHG) concentration scenarios, RCP 4.5 (moderate) and RCP 8.5 (extreme), were considered; both are officially recognized by the Intergovernmental Panel on Climate Change (IPCC) in the latest assessment Report (AR5) (IPCC, 2014a). Given the nature of the study, the discrimination of the future farming land in areas under or without protection was necessary to better understand the level of vulnerability of páramo areas which may be exposed to land use threats in the future.

2. Materials and Methods

2.1 Study Region

The study focuses on evaluating the pressures of land use change on the natural páramo areas of Ecuador. The study area comprises the entire Ecuadorian páramo region located along the Andes region covering an area of approximately 14,799.3 km^2, equivalent to 5.8% of Ecuadorian national territory (256,775.7 km^2) (MAE, 2013b). Páramo areas are locally distributed from the border with Colombia in the North to the Peruvian border in the South (Cuesta et al., 2012b). Páramo vegetation in Ecuador is distributed above the forest tree line along Eastern and Western Andes cordillera (Hofstede et al., 1998) at 3,700 and 3,400 m.a.s.l., respectively. Páramo vegetation located in the Ecuadorian Eastern Cordillera covers a higher extension forming an almost undisrupted vegetation patch that goes from the provinces of Carchi in the North to Cañar in the South (Fig 4.1). On the Western Cordillera, páramo patches are in general fragmented with the exception of a significant patch of vegetation located between Tungurahua, Chimborazo and Bolívar provinces (Hofstede et al., 2014).

The major impacts on páramo areas are caused by intense anthropogenic activities such as farming, livestock and mining (Crespo et al., 2010; Hofstede et al., 2014; Llambí, 2010; Mena and Hofstede, 2006), which have all contributed to increasing fragmentation of the landscape and declining ecosystem services. In Ecuador, the continued expansion of the agricultural frontier towards páramo areas is evidently driven by population growth, social inequalities, and the intensification of agricultural techniques (Arellano et al., 2000)(Fig 4.1).

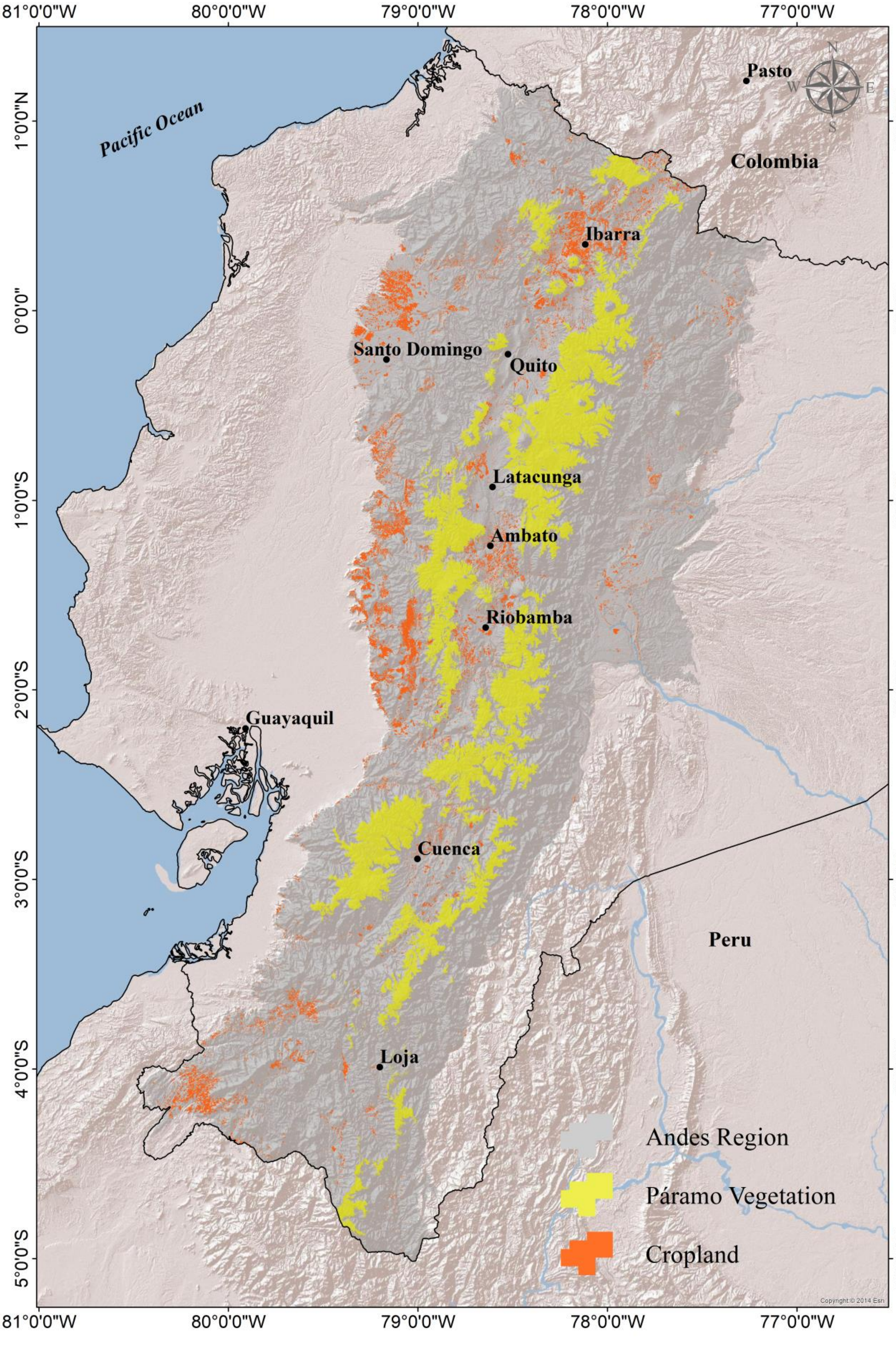

Figure 4.1 Location of the páramo vegetation and cropland in the Andes Region of Ecuador.

2.2 Modelling Methods

2.2.1 Selection of Andean Crops for Modelling

The selection of Andean crops for modelling purposes was based on three criteria: a) the crop needed to be traditionally grown in the Andean region and pose a threat to páramo ecosystems; b) the crop should be sensitive to climatic variations (i.e. temperature and precipitation); and c) the historical behaviour of the crop should reflect changes in terms of sowed and harvested area that could indicate advance of the agricultural frontier over time. Based on the criteria above, three common Andean crops, potato (*Solanum tuberosum L.*), soft maize (*Zea mays amylacea*) and quinoa (*Chenopodium quinoa*), were used as exemplars to representing the potential impact of land use change in the Ecuadorian páramo areas.

The potato crop was particularly relevant because it is the most cultivated Andean product in the páramo region of Ecuador. Also for the interest of exploring the veracity on an imminent advance of this crop towards páramo areas potentially favoured by climate change, as it has been manifested by several authors (Hofstede et al., 2003; Morales, 2007; Cuesta et al., 2012a; Hofstede et al., 2014). Soft maize was also chosen due to its high sensitivity to climatic variations (Adams et al., 1998; Bassu et al., 2014), resulting interesting to explore under climate change scenarios. Quinoa crop was included in the modelling due to its high tolerance to extreme environmental conditions (Ruiz et al., 2014; Jacobsen et al., 2003), and because of its significant increase in production registered in recent years (MAGAP-INEC, 2017), making it a potential source of future impact on páramo areas. Another decisive factor in the selection of these three crops was the availability of information for the evaluation of both edaphic and climatic suitability. Although intensive livestock farming is one of the main threats, its exclusion from this analysis is due to data limitations. There was no information on edaphic and climatic parameters defined for specific páramo grasses (e.g. *Dactylis glomerata*) used for cattle ranching in the Andes. Background information on each crop is presented below to put the subject in context based on national statistics only due to the lack of homogeneous information at better scale (e.g. province) for the three crops.

Potato (*Solanum tuberosum L.*) was selected since it is one of the most important crops grown in the inter-Andean region (between 2,600 to 3,500 m.a.s.l.) and has been for millennia a high priority crop in Ecuador, playing an important role in the population's diet (MAGAP, 2014a). Potato crops have optimum temperatures ranging from 15°C (min) to 25°C (max) and optimum precipitation from 500 mm (min) to 800 mm (max) (Hijmans et al., 2001). Potato is very sensitive to late frosts. If the temperature falls to -1°C, the plants can die although they may re-sprout (Basantes Morales, 2015; Hijmans et al., 2001). Historical data (MAGAP-INEC, 2017) show that over the last 17 years, potato cultivation in Ecuador has undergone variations but with a downward trend in terms of the areas sowed and harvested (Table 4.1 and Fig. 4.2), which may be seen as an indicator of the existence of factors (environmental or social) that are directly affecting the crop areas. Despite the reduction of potato growing area (sowed and harvested), there has been an increase of 75% in production from 2000 to 2016, which could reflect a trend towards the intensification of land use. This intensification of production on a nearly constant area of cultivated land could be slowing down the spread of potato cultivation to other areas including the páramo land.

Soft Maize (*Zea mays amylacea*) or highland maize was considered for modelling purposes since it is a basic component of the Andean population's diet and plays an important role in national internal production. In Ecuador, soft maize is generally grown on irregular terrain with slopes ranging from 0% to 50% located in altitudes ranging from 2,200 and 3,000 m.a.s.l. Highland maize persists in the Andean region despite multiple problems such as low fertility of soils, pests, and diseases which in some cases can lead to low yields. Highland maize has optimum temperatures ranging from 20°C (min) to 27°C (max) and optimum precipitation between 600 mm (min) and 1200 mm (min) (Basantes Morales, 2015; Hijmans et al., 2001). However, periods of drought and high temperatures can cause early maturation (Basantes Morales, 2015). According to official data (MAGAP-INEC, 2017), over the last 17 years, the level of soft maize cultivation has been variable, with both increases and decreases in its cultivation area (sowed and harvested) (Table 4.1 and Fig. 4.2). As with potato, despite registering a reduction of growing area (sowed and harvested), there has been an increase in production of 44% in the period 2000-2016, which could reflect a trend towards the intensification of land use.

Quinoa crop (*Chenopodium quinoa*) was included in the modelling since it has been under increasing demand in the last few decades, positioning Ecuador among the largest quinoa producers behind Bolivia and Peru (Basantes Morales, 2015). This traditional crop has been cultivated for around 7,000 years and it is appreciated for its nutritional value and high resistance to difficult environmental conditions (Jacobsen, 2002). Quinoa crops are generally found between 2,600 to 3,500 m.a.s.l. (Basantes Morales, 2015) on irregular terrain with slopes greater than 45% located across the inter-Andean and sub-Andean floors (Jacobsen, 2002). The optimum temperatures for quinoa crop ranges between 14°C (min) and 18°C (max);

however, it is able to withstand frosts up to -8 °C (Hijmans et al., 2001). The optimum precipitation for this crop ranges from 500 mm (min) to 1000 mm (max) (Hijmans et al., 2001). In terms of soil, quinoa adapts to a wide range of well-drained soils rich in organic matter (Basantes Morales, 2015). Although quinoa crops can resist extreme climatic conditions including prolonged periods of drought, during the phases of germination, flowering and grain formation, the crops require good moisture conditions (Basantes Morales, 2015). Unlike potato and soft maize, quinoa cultivation has shown an increase in sowed and harvested area during the last 17 years (2000-2016) (Table 4.1 and Fig. 4.2). Through this period, there have been no significant differences between the sowed and harvested area, which may be indicative of the crop's good resistance. In terms of production, quinoa crop has experienced an increase of 6 times the production registered in 2000, which could represent a trend towards more intensive production for this particular crop.

Table 4.1 Sowed Area (km^2), Harvested Area (km^2) and Production (MT) by type of Andean Crop per year.

Year	Potato			Soft Maize			Quinoa		
	Sowed Area (km^2)	Harvested Area (km^2)	Production (MT)	Sowed Area (km^2)	Harvested Area (km^2)	Production (MT)	Sowed Area (km^2)	Harvested Area (km^2)	Production (MT)
2000	497.19	425.54	239,714	309.77	261.59	43,168	13.00	13.00	650
2001	527.30	476.12	248,580	284.83	250.16	41,496	6.50	6.50	320
2002	539.39	509.82	254,385	160.25	155.61	32,888	7.00	7.00	350
2003	514.95	498.44	378,667	154.88	143.51	32,332	10.00	10.00	519
2004	609.68	571.68	412,365	238.36	216.85	43,107	8.00	8.00	400
2005	506.81	478.62	337,465	204.79	182.63	39,886	9.15	9.15	652
2006	534.62	510.77	358,300	203.24	194.57	50,323	10.20	10.20	721
2007	468.70	457.85	313,134	168.13	159.26	40,719	9.64	9.64	711
2008	440.66	425.87	264,542	147.40	137.27	30,850	9.98	9.98	1,114
2009	506.16	487.58	286,401	194.19	189.20	44,323	13.63	13.63	995
2010	468.65	434.60	384,234	146.74	139.00	34,557	15.29	15.29	1,162
2011	473.97	427.99	334,630	198.81	181.33	47,552	22.25	22.25	1,424
2012	355.55	341.09	284,630	204.24	192.66	50,271	22.70	22.70	1,453
2013	486.93	466.88	343,344	192.97	178.99	37,218	25.74	25.74	1,802
2014	333.28	325.47	417,178	222.68	201.95	55,361	57.00	49.01	7,436
2015	314.90	292.39	393,526	323.74	280.32	68,722	77.55	70.57	12,680
2016	323.01	292.92	418,546	227.95	198.89	61,955	26.79	21.53	3,822

Data for potato was provided by (MAGAP-CGSIN, 2014b) and (MAGAP-INEC, 2017).
Data for soft maize was provided by (MAGAP-CGSIN, 2014a) and (MAGAP-INEC, 2017).
Data for quinoa provided by (SIA-MAGAP, 2014), (BCE-MAGAP, 2014), (DPA-MAGAP, 2014) and (MAGAP-INEC, 2017).

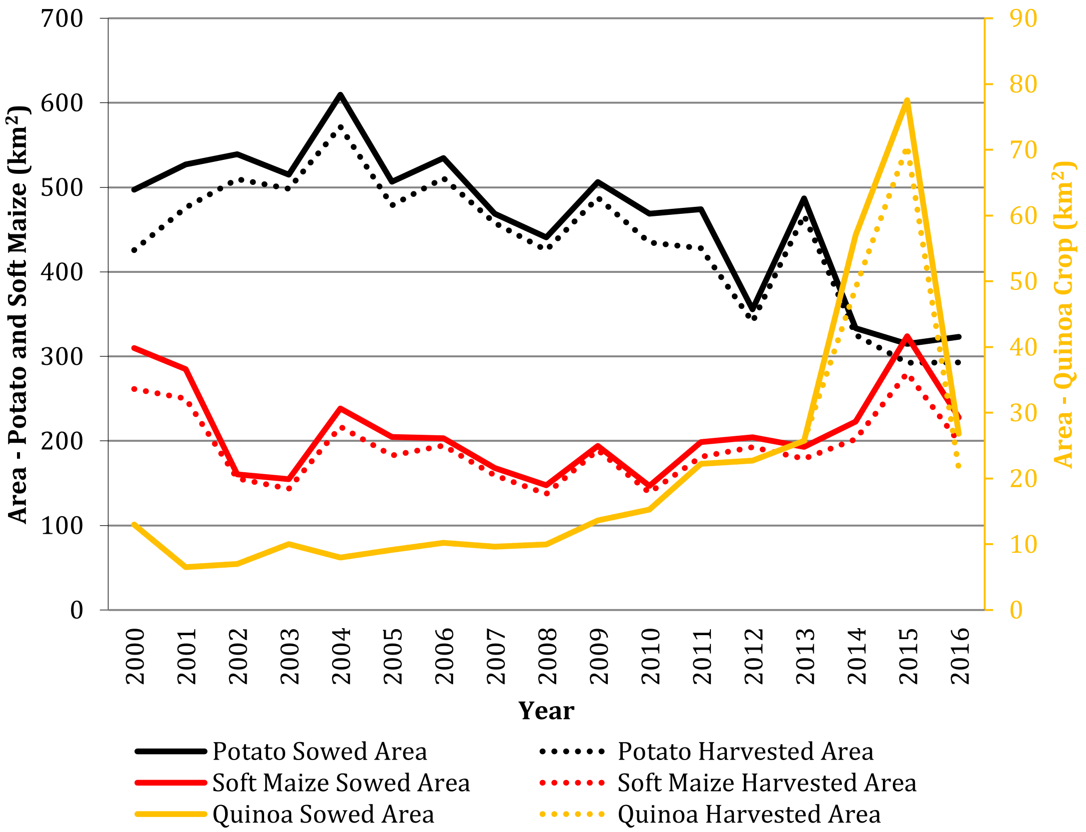

Figure 4.2 Historical behaviour of Sowed and Harvested Area (km^2) by type of Andean crop.

2.2.2 Modelling Land Suitability for Crops

The identification of suitable areas for the cultivation of potato, soft maize, and quinoa in the Ecuadorian páramo areas was based on the evaluation of edaphic (soil) and climatic conditions that are required for the adequate growth of these Andean crops. The analysis included the separate assessment of edaphic and climatic suitability and the subsequent integration of both in order to obtain the edapho-climatic suitability for each crop considering current and future climatic conditions.

2.2.2.1 Edaphic Suitability

The analysis of edaphic suitability considered ten edaphic parameters that are critical for the adequate growth of potato, soft maize, and quinoa (See parameter descriptions in Appendix IV.A). Each soil requirement was defined by the Food and Agriculture Organization of the United Nations (FAO) and adapted to specific local conditions by the Ministry of Agriculture, Livestock and Fisheries (MAGAP) and the National Institute of Agricultural Research of Ecuador (INIAP). The edaphic characterization for each of the three Andean crops was based on the map of soil of Ecuador, scale 1: 250,000 (MAGAP, 1986), transformed into raster format (pixels) with 1 km^2 resolution. Edaphic parameters (in raster format) were evaluated independently according to their category of edaphic suitability by assigning a numerical value as follows: optimal (3), moderate (2), marginal (1) and not suitable (0) (Table 4.2). Based on the numerical value assigned, all ten edaphic parameters were integrated into one, based on the assumption that all parameters considered are equally important to guarantee the potential growth of the crop. Therefore, an area (pixel) was considered optimal only if all edaphic parameters were classified as optimal (i.e. value 3). In this way, the combination of suitability values among variables (per pixel) always tended to consider the lower value as the decisive factor of their suitability. This analysis did not include the variable salinity since it was verified that the entire study area was optimal. Due to lack of information on soil, the páramo complex located in the Sumaco volcano (northeast of the Ecuadorian Andes) was not included in the analysis. However, the Sumaco páramo covers only 392 ha (0.03% of the total páramo area). The boundary of the Ecuadorian páramo areas was used for the spatial delimitation of the analysis, based on the map of Ecuadorian Continental Ecosystems, scale 1:100,000 (MAE, 2013a). Areas identified as rocky outcrops, snow/ice, and water bodies (natural or artificial), were discarded. ArcGIS software version 10.4.1 was used to perform the spatial analysis required.

Table 4.2 Edaphic requirements for growing potato (*Solanum tuberosum L.*), soft maize (*Zea mays amylacea*) and quinoa (*Chenopodium quinoa*) in Ecuador by level of edaphic suitability (MAGAP, 2014a; MAGAP, 2014b; INIAP, 2000; FAO, 1997 ; INIAP, 2018).

Crop	Variable	Edaphic Suitability			
		Optimal	**Moderate**	**Marginal**	**Not suitable**
Potato	**Slope**	0-12%	12-25%	25-50%	>50%
	Texture	sandy loam (fine to coarse), silty loam, loam, silty, clay loam (> 35%), clay loam (<35% clay), silty clay loam, sandy clay loam	sandy clay, silty clay	loamy sand	sandy (fine, medium, coarse), clay, clay (> 60%)
	Depth	deep	moderately deep	limited deep	superficial
	Stoniness	non-stony	slightly stony	stony	highly stony
	Drainage	good	moderate	excessive	bad
	Phreatic Level	deep	moderately deep	limited deep	superficial
	pH	slightly acid, neutral	slightly alkaline	moderately alkaline, acid	highly acid, alkaline
	Toxicity	null	light	medium	high
	Organic Matter	very high, high	medium	low, very low	---
	Fertility	high	medium, low	very low	---
Soft Maize	**Slope**	0-25%	25-50%	50-70%	>70%
	Texture	loam, silty, clay loam (<35% clay), silty clay loam, sandy clay loam	sandy loam (fine to coarse), sandy clay, silty clay, silty loam, clay	loamy sand	clay (> 60%), sandy (fine, medium, coarse)
	Depth	deep, moderately deep	limited deep, superficial	---	---
	Stoniness	non-stony	slightly stony	stony	highly stony
	Drainage	good	moderate	bad	excessive
	pH	neutral	slightly acid	moderately alkaline, acid	highly acid, alkaline

Crop	Variable	Edaphic Suitability			
		Optimal	Moderate	Marginal	Not suitable
Soft Maize	Phreatic Level	deep	moderately deep	limited deep	superficial
	Toxicity	null	light	medium	high
	Organic Matter	very high	high, medium	low	very low
	Fertility	high	medium	low	very low
Quinoa	Slope	0-25%	25-50%	50-70%	>70%
	Texture	sandy (fine, medium, coarse), loamy sand, sandy loam (fine to coarse), silty loam, loam, silty, clay loam (<35% clay), sandy clay loam, silty clay loam	clay loam (> 35%)	clayey, sandy clay, silty clay	clayey (> 60%)
	Depth	deep, moderately deep, limited depth	superficial	---	---
	Stoniness	non-stony	slightly stony	stony	highly stony
	Drainage	good, moderate	excessive	bad	---
	Phreatic Level	deep, moderately deep	limited deep	superficial	---
	pH	slightly acid, neutral, moderately alkaline	acid	highly acid	alkaline
	Toxicity	null, light	medium	---	high
	Organic Matter	very high, high, medium	low	very low	---
	Fertility	high, medium	low	very low	---

2.2.2.2 Agro-Climatic Suitability

The EcoCrop model available under DIVA-GIS software (Version 7.5) was used to analyse the agro-climatic suitability for the Andean crops selected. This model has been used previously by several studies (Ramirez et al., 2011; Van den Bergh et al., 2010; Sparks et al., 2014; Lane and Jarvis, 2007; Ramirez-Villegas et al., 2013; Nyabako and Manzungu, 2012) to understand areas of crop suitability in different parts of the world and how these may shift in response to climate change. EcoCrop is a relatively simple suitability-based model based on the FAO-EcoCrop database of crop ecological requirements (Hijmans et al., 2001), which predicts the distribution of suitable conditions for a specific crop over a specific geographic area. The model performs the calculations for temperature and precipitation separately for the defined growth season based on the climatic thresholds defined for each variable (Hijmans et al., 2012; Hijmans et al., 2001). EcoCrop identifies optimal conditions as those when during a growing season a site is between the minimum and maximum optimum for both variables (precipitation and temperature) (white area, Fig. 4.3). Unsuitable conditions occur when a site is either above or below the absolute (or marginal) thresholds for either temperature or precipitation (light grey area, Fig. 4.3). Whereas marginal areas, occur where conditions are between the optimum and absolute thresholds (dark grey area, Fig. 4.3) (Challinor et al., 2015; Ramirez-Villegas et al., 2013). Models were run on a pixel basis to calculate the so-called suitability index through linear regression, assigning 100% to the optimal and 0% to the unsuitable sites, respectively. The index classifies suitability in six categories as follows: “excellent” (index= 80-100), “very suitable” (index= 60-80), “suitable” (index= 40-60) , “marginal” (index= 20-40), “very marginal” (index= 1-20) and “not suitable” (index=0) (Le Page et al., 2017).

For the purposes of this study, the agro-climatic suitability was modelled by applying the EcoCrop algorithm on a pixel basis for current and future climatic conditions to reflect the potential impact of climate change on the distribution of suitable areas for each crop. Temperature and precipitation thresholds as well as length of growing season were left as default for all modelled crops (Table 4.5). As required by Ecocrop, the models were run using mean monthly temperature, mean maximum monthly temperature, mean minimum monthly temperature, and mean monthly precipitation data. Climatic variables for the current scenario were based on interpolations of observed data from the 1950-2000 period. For future climatic conditions, years 2050 (average for 2041-2060) and 2070 (average for 2061-2080) were considered based on the Global Climate Model “CCSM4” (Table 4.3). In addition, two of the latest greenhouse gas (GHG) concentration scenarios, known as representative concentration pathways (RCPs), were included in the analysis. RCP 4.5 and RCP 8.5 are moderate and extreme scenarios, respectively (Van Vuuren et al., 2011). Further explanation can be found in Chapter II - Section 2.2.3. Climatic data were provided by WorldClim (Version 1.4) at 1 km^2 resolution in raster format (Table 4.4). Once the suitability indices were generated, the areas (pixels) were reclassified in four classes to facilitate further analysis as follows: a) *optimal*, which includes areas identified as "excellent" and "very suitable" (i.e. index= 61-100); b) *moderate*, which includes areas classified as "suitable" (i.e. index= 41-60); c) *marginal*, which includes areas categorised as "marginal" and "very marginal" (i.e. index= 1-40) and; d) *not suitable*, which includes the areas identified as "not suitable" (i.e. index= 0). Areas identified as rocky outcrops, snow/ice, and water bodies (natural or artificial), were excluded from the analysis. ArcGIS software version 10.4.1 was used to perform the spatial analysis when required.

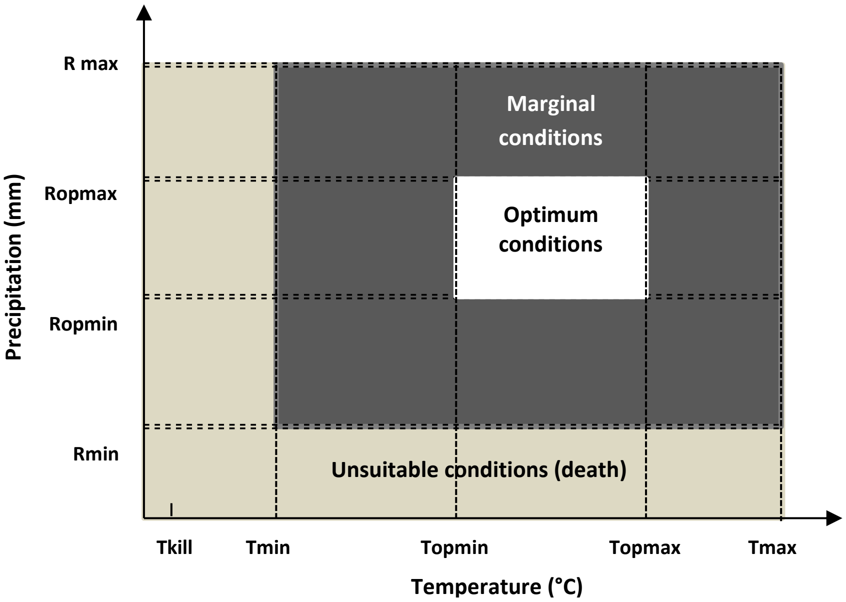

Figure 4.3 EcoCrop Suitability Thresholds.
Based on: (Ramirez-Villegas et al., 2013).

Table 4.3 Global Climate Model (GCM) and Representative Concentration Pathways (RCPs) considered in the analysis.

GCM	Modelling Centre	Year	RCP	Type	Spatial Resolution	Information Source
CCSM4	University Corporation for Atmospheric Research	2050 & 2070	4.5 & 8.5	Raster	1 km^2	WorldClim Version 1.4

Table 4.4 Variables used for modelling current and future climatic conditions.

Variables	Type	Spatial Resolution	Information Source
monthly minimum temperature (tn)	Raster	1 km^2	WorldClim Version 1.4
monthly maximum temperature (tx)	Raster	1 km^2	WorldClim Version 1.4
monthly total precipitation (pr)	Raster	1 km^2	WorldClim Version 1.4

Table 4.5 Default Parameters used for modelling agro-climatic suitability per type of Andean crop based on Hijmans (2001).

Crop	Length of growing season (# days)*			Temperature Thresholds (°C)*					Precipitation Thresholds (mm)*			
	GMin	GMax	Gavg	Tkill	TMin	TOPmin	TOPmax	Tmax	Rmin	ROPmin	ROPmax	Rmax
Potato	90	160	125	-1	7	15	25	30	250	500	800	2000
Soft Maize	90	140	115	0	12	20	27	45	450	600	1200	1800
Quinoa	90	240	165	-8	2	14	18	35	250	500	1000	2600

**See description of EcoCrop variables in Appendix IV.B.*

2.2.2.3 Evaluation of Agro-climatic Models

Areas were potato is currently farmed where used to evaluate the performance of ECoCrop models in predicting agro-climatic areas under the current scenario. Potato crop areas were obtained from the map of Land Use of Ecuador (1:100,000 scale) generated by local institutions through satellite imagery interpretation and in-situ validation (MAE-MAGAP, 2015). For evaluation purposes, the agro-climatic suitability for potato was run for the entire Andes region of Ecuador to have a larger area for evaluation. Areas of potato from the map were transformed into points (64,204 points in total) in order to quantify the percentage of crop samples (points) that occur inside or outside areas (pixels) modelled as suitable. Therefore, the model was considered reliable only if the percentage of real crop samples (points) predicted in non-suitable areas was low. It was acknowledged that in reality there are many other factors influencing the location of the crops (e.g. population growth or profit). However, this approach considered agro-climate as a determinant factor in the location of the crops. Maize and Quinoa crops were not considered in this evaluation due to the lack of information on the real location of these crops in the Ecuadorian páramo region.

2.2.3 Future Exposure of the Páramo Vegetation to Land Use Pressures

The potential exposure of the páramo vegetation to land use pressures, was based on the integration of edaphic and agro-climatic suitability maps (raster format) to obtain edapho-climatically suitable areas for each Andean crop. Based on this analysis, it was assumed that páramo areas that were suitable under both criteria (soils and agro-climate) could be considered potentially vulnerable to land use pressures. For this purpose, edaphic suitable areas previously identified from optimal to marginal were used as mask to clip the agro-climatic suitable areas identified from optimal to moderate. Given the common use of soils not suitable for cultivation in the páramo region (Poulenard et al., 2004; Podwojewski and Poulenard, 2000a; Hofstede, 2001) (Appendix IV.C), a flexible range of edaphic suitability categories (i.e. optimal to marginal) were included in the analysis. Marginal agro-climatic areas were excluded to avoid overestimating the representation of future land use pressure. The analysis was performed by type of crop considering its respective current and future (2050 and 2070) emission scenarios (RCP 4.5 moderate and 8.5 extreme). Edaphic conditions were considered stable across all future scenarios analysed due to lack of data to reflect these changes in the future. Finally, based on the assumption that páramo areas under protection are less likely to be converted to use for crops, areas of potential land use pressure (i.e. edapho-climatically suitable areas) with or without protection were distinguished. In this analysis, the discrimination of type of crops was considered irrelevant. Therefore, all edapho-climatic suitability areas were integrated into one. Protected areas were represented by the national map of Protected Areas of Ecuador, scale 1:250,000, provided by the Ministry of Environment of Ecuador (MAE, 2017) and used as mask to clip the edapho-climatic suitability areas. ArcGIS software version 10.4.1 was used to perform the spatial analysis required.

3. Results

3.1 Evaluation of Agro-climatic Models

The evaluation of the agro-climatic model performance showed that only 10% (6,149 out of 64,204 crop samples) from the total number of real crop samples were located in areas identified by EcoCrop as not suitable. By considering the rest of categories of agro-climatic suitability, it was found that 56% (36,208 crop samples)of potato crop samples coincided with areas identified as optimal (28% of crop samples) and moderate (28% of crop samples). Whereas 34% (21,847 crop samples), corresponded to areas of marginal suitability (Table 4.6). Based on these results, the overall performance of the current agro-climatic models was considered robust. Therefore, these agro-climatic models could be used with some degree of confidence for predictions of agricultural cropping pressures under future climatic conditions.

Table 4.6 Comparison between modelled potato suitability and real potato crop samples by level of agro-climatic suitability.

Crop	Agro-climatic Suitability Category	Crop Sample Points (#)	(%)*
Potato	Optimal	18,152	28
	Moderate	18,056	28
	Marginal	21,847	34
	Non suitable	6,149	10
	Total	**64,204**	**100**

** Percentage calculated with respect to total number of crop samples.*

3.2 Crop Suitability

3.2.1 Edaphic Suitability

The analysis of edaphic suitability showed the limitations of the soils in the páramo land for growing the three crops (i.e. potato, soft maize, and quinoa). In the case of potato crop, when considering categories from optimal to marginal, only 27% (3,548 km^2) of the soils were suitable for growing potato. Of this percentage, 0.2% (24 km^2) was considered optimal, 1% (118 km^2) moderate and 26% (3,406 km^2) marginal. Similar limitations were reflected for growing soft maize, for which no páramo soils were optimal, 3% were moderately suitable, and 59% were marginal reaching a total of 62% (7,957 km^2) when considering all suitability categories. In the case of quinoa, only 1% (139 km^2) of páramo soils were optimal, 26% (3,380 km^2) were moderate and 39% (5,090 km^2) were marginal, reaching a total of 66% (8,609 km^2) when considering all suitability categories (Table 4.7 and Fig. 4.4).

Table 4.7 Areas of páramo (km^2) according to edaphic suitability per type of crop.

Crop	Current							
	Optimal (km^2)	%*	Moderate (km^2)	%*	Marginal (km^2)	%*	Not suitable (km^2)	%*
Potato	24	0.2	118	1	3,406	26	9,428	73
Soft Maize	0	0	353	3	7,605	59	5,019	39
Quinoa	139	1	3,380	26	5,090	39	4,367	34

**Percentage of representativeness respect to the total area of páramo vegetation excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

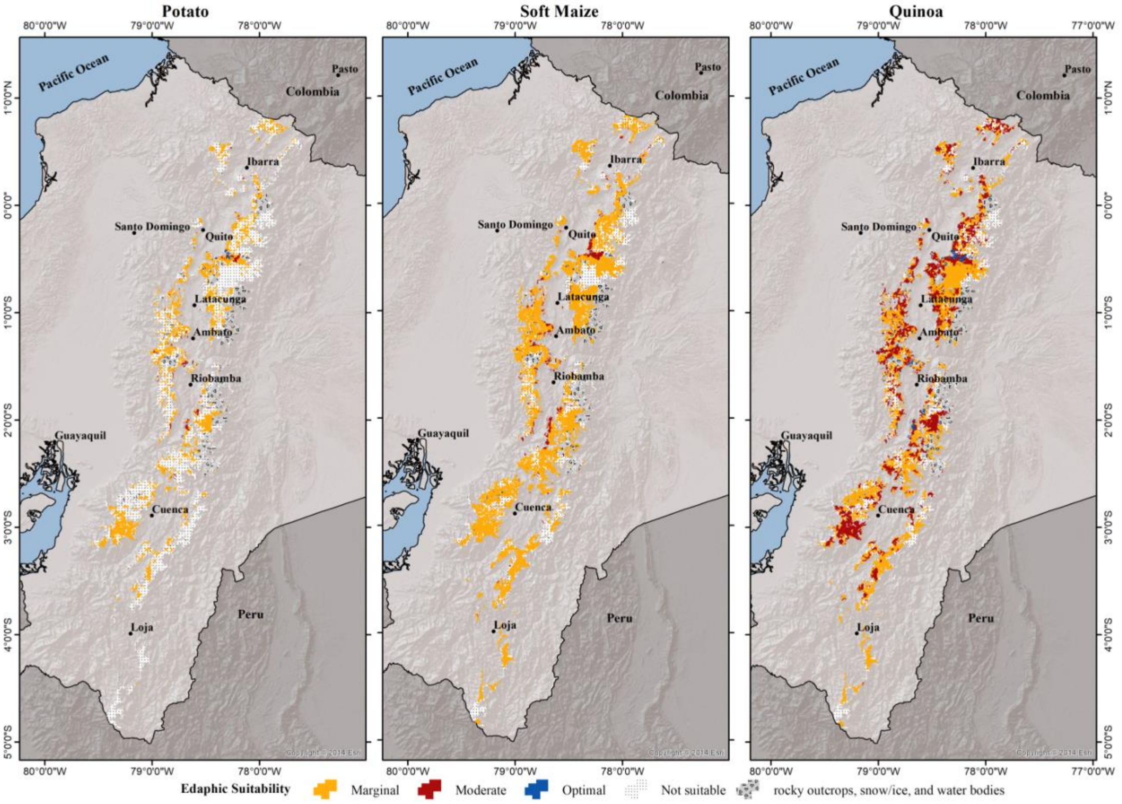

Figure 4.4 Location of areas edaphically suitable for potato, soft maize, and quinoa.

3.2.2 Agro-climatic Suitability

In terms of agro-climatic suitability, based on current scenario, 13% (1,723 km^2) of the páramo areas presented optimal to moderate climatic conditions favourable for potato cultivation (Fig. 4.5). Agro-climatic conditions were not favourable for soft maize cultivation presenting optimal to moderate conditions in only 0.03% (4 km^2) of the páramo areas. In contrast, optimal to moderate conditions for quinoa cultivation were present in 49% (6,400 km^2) of the páramo land. By 2050, optimal to moderate areas for potato cultivation could increase to 25% (3,302 km^2) or 30% (3,956 km^2) under scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Fig. 4.5). Climatic conditions seemed to remain quite restrictive for the cultivation of soft maize, presenting optimal to moderate conditions only in 0.2% (22 km^2) or 0.3% (38 km^2) of the páramo areas when considering scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. In contrast, páramo areas could continue to be climatically favourable for quinoa cultivation, showing 82% (10,636 km^2) or 90% (11,619 km^2) of optimal to moderate suitable areas under scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively.

In 2070, the agro-climatic conditions seem to be changing in favour of potato crop cultivation by presenting optimal to moderate suitability in 28% (3,646 km^2) or 44% (3,111 km^2) of the páramo land under scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Fig. 4.5). In the case of soft maize, the agro-climatic suitability in páramo areas is still not significant by 2070; páramo areas with optimal to moderate climatic conditions for soft maize could occupy only 0.2% (29 km^2) or 1% (119 km^2) under scenario RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. In contrast, optimal to moderate climate favourable for quinoa cultivation could occupy 87% (11,261 km^2) or 98% (12,721 km^2) of the páramo areas under RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.8 and Fig. 4.6). For detailed information regarding the spatial location (maps) of agro-climatic suitable areas for all crops, see the supplementary material.

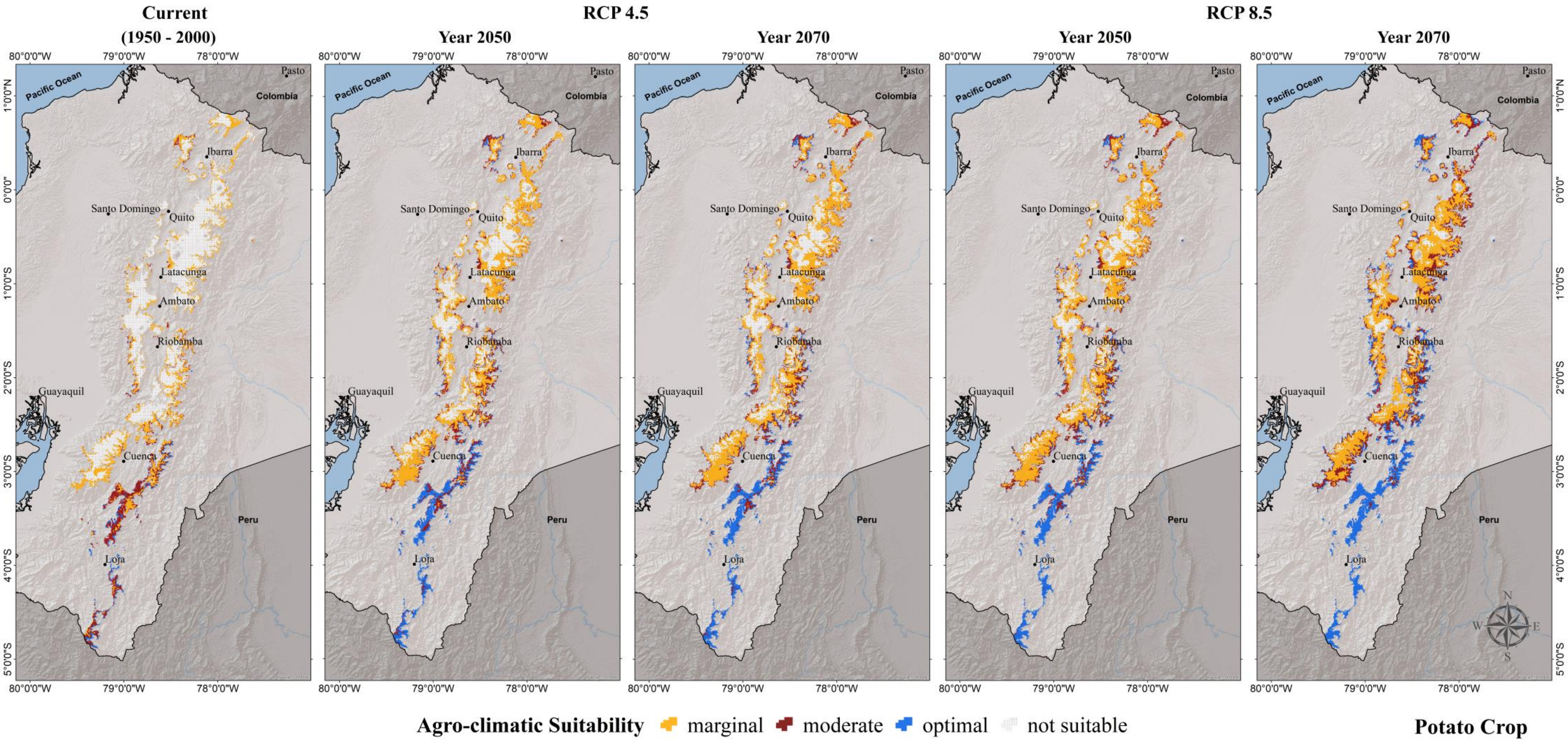

Figure 4.5 Location of areas agro-climatically suitable for potato in the páramo region based on current (1950-2001) and future climatic conditions (2050 & 2070, considering emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme).

Table 4.8 Agro-climatic suitable areas (km^2) per type of crop based on current (1950-2001) and future climatic conditions (2050 & 2070) under scenario RCP 4.5 (moderate) and RCP 8.5 (extreme).

Crop	**Current (km^2)***			**Future (km^2)***											
				RCP 4.5						**RCP 8.5**					
	(1950-2001)			**2050**			**2070**			**2050**			**2070**		
	Optimal	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**
Potato	317.5	1,405.4	3,142.9	1,623.1	1,679.0	5,669.6	1,934.0	1,711.7	6,041.8	2,075.7	1,880.5	6,224.0	2,948.6	2,720.6	6,438.7
Soft Maize	0.2	3.7	162.5	2.3	19.4	1,082.6	4.1	25.3	1,437.4	5.0	33.2	1,390.4	18.3	100.3	2,421.7
Quinoa	2,547.6	3,852.8	6,567.4	4,619.1	6,016.4	2,339.4	5,153.5	6,107.1	1,715.0	5,587.5	6,031.0	1,357.0	7,772.5	4,948.7	254.6

**Areas exclude rocky outcrops, snow/ice, and water bodies (natural or artificial).*

*** Percentage of representativeness respect to the total area of páramo vegetation excluding rocky outcrops, snow/ice, and water bodies (natural or artificial) are presented in Appendix IV.D.*

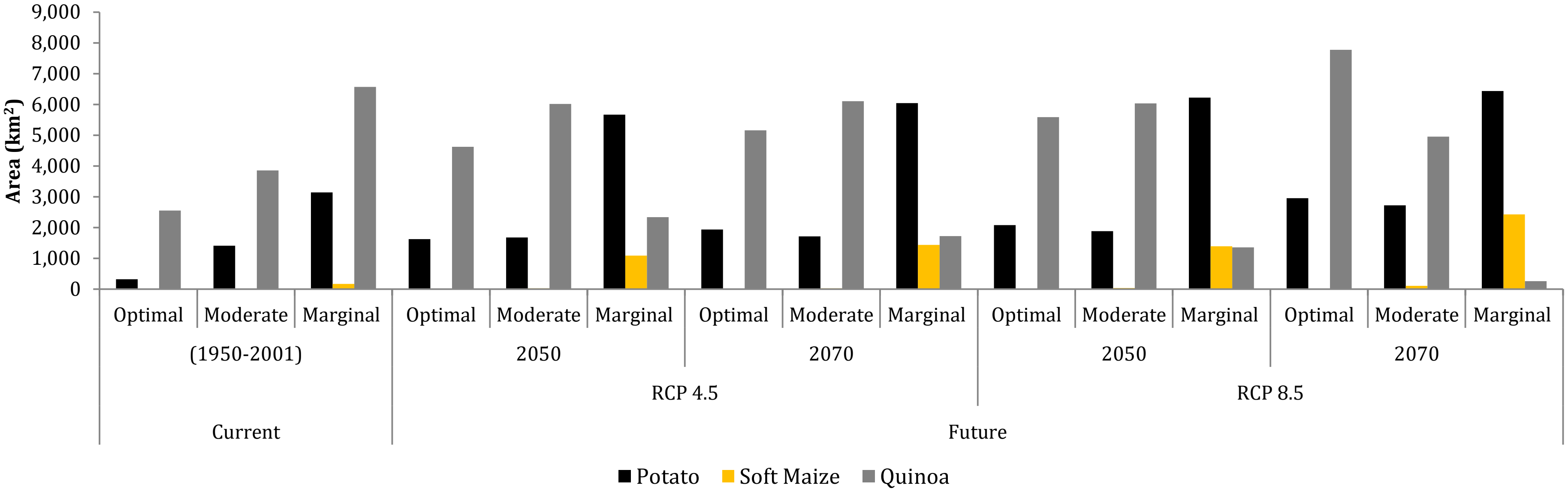

Figure 4.6 Variation of Agro-climatic Suitability per type of crop based on current (1950-2001) and future climatic conditions (2050 & 2070) under scenario RCP 4.5 (moderate) and RCP 8.5 (extreme).

3.3 Future Exposure of the Páramo Vegetation to Land Use Pressures

3.3.1 Land Use Pressure by type of Andean Crop

In the case of potato cultivation, the results showed that currently, areas with optimal to moderate edapho-climatic conditions represent only 2% (245 km^2) of the total páramo areas of Ecuador (Table 4.9). By 2050, potato-suitable areas could amount to 4% (540 km^2) or 5% (702 km^2) under emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. In 2070, suitable areas for potato growth could occupy 5% (621 km^2) or 9% (1,212 km^2) of the páramo land, when considering emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.9 and Fig. 4.7). Regarding soft maize, currently, optimal to moderate edapho-climatic conditions are practically non-existent and continue to be very restrictive across all future scenarios analysed (Table 4.9 and Fig. 4.7). In contrast, areas suitable for quinoa appeared to be extensive (Table 4.9 and Fig. 4.7). Under current conditions, areas with optimal to moderate edapho-climatic conditions for quinoa could be found in 28% (3,611 km^2) of the total páramo land (Table 4.9 and Fig. 4.7). In 2050, favourable conditions for quinoa cultivation could remain present, occupying 49% (6,374 km^2) or 54% (6,988 km^2) of the páramo areas, according to emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.9 and Fig. 4.7). By 2070, favourable conditions for quinoa could continue to expand in the páramo areas; occupying potentially 52% (6,783 km^2) or 56% (7,219 km^2) of the páramo land, based on emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.9 and Fig. 4.8). Information regarding the spatial location (high-resolution maps) of land use pressures (i.e. edapho-climatic suitable areas) for all scenarios is also presented as supplementary material.

Table 4.9 Páramo Areas (km^2) with optimal to moderate edapho-climatic conditions suitable for potato, soft maize and quinoa, based on current (1950-2001) and future climatic conditions (2050 & 2070) considering RCP 4.5 (moderate) and RCP 8.5 (extreme) scenarios.

Scenario	Period	Andean Crops					
		Potato (km^2)	%*	Soft Maize (km^2)	%*	Quinoa (km^2)	%*
Current	(1950-2001)	245	2	0.02	0	3,611	28
RCP 4.5	2050	540	4	2	0.01	6,374	49
	2070	621	5	3	0.03	6,783	52
RCP 8.5	2050	702	5	6	0.05	6,988	54
	2070	1,212	9	33	0.3	7,219	56

**Percentage of representativeness respect to the total area of páramo vegetation excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

*** Edapho-climatic suitability areas per all categories (optimal, moderate, and marginal) are presented in Appendix IV E.*

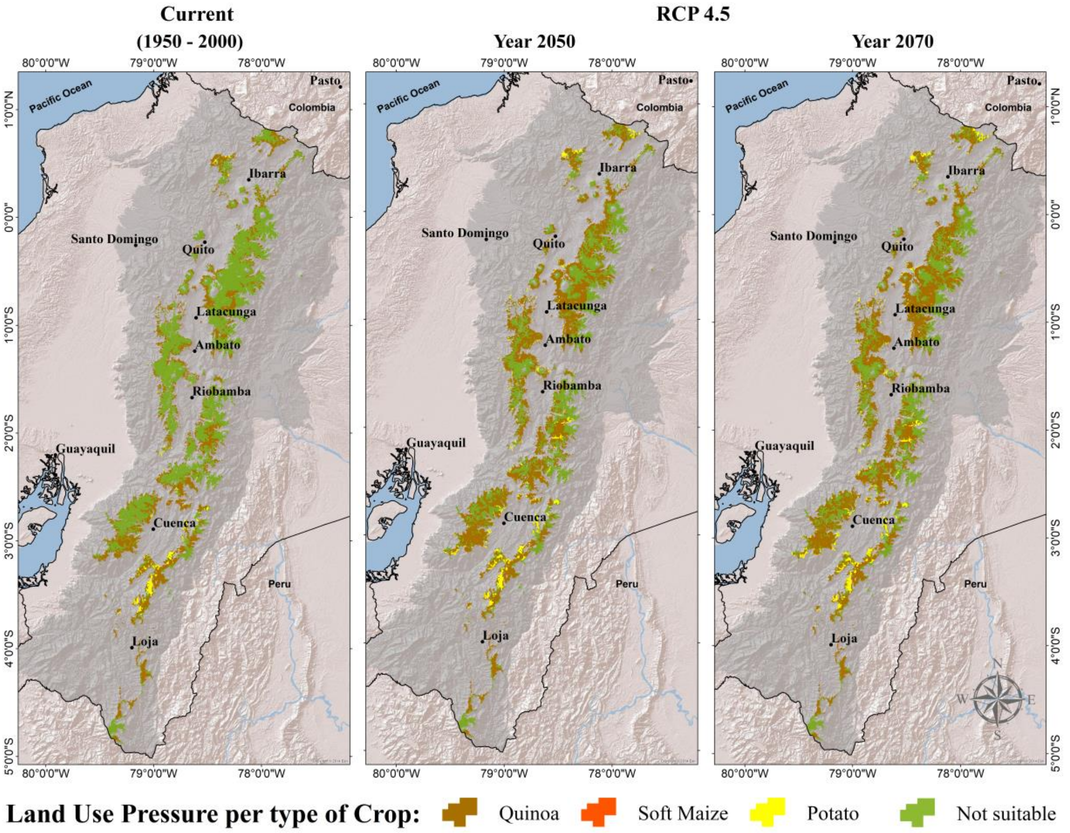

Figure 4.7 Location of land use pressure represented by areas with edapho-climatic suitability (optimal to moderate) for the three Andean crops (potato, soft maize and quinoa), based on current (1950-2001) and future (2050 & 2070) emission scenario RCP 4.5 (moderate).

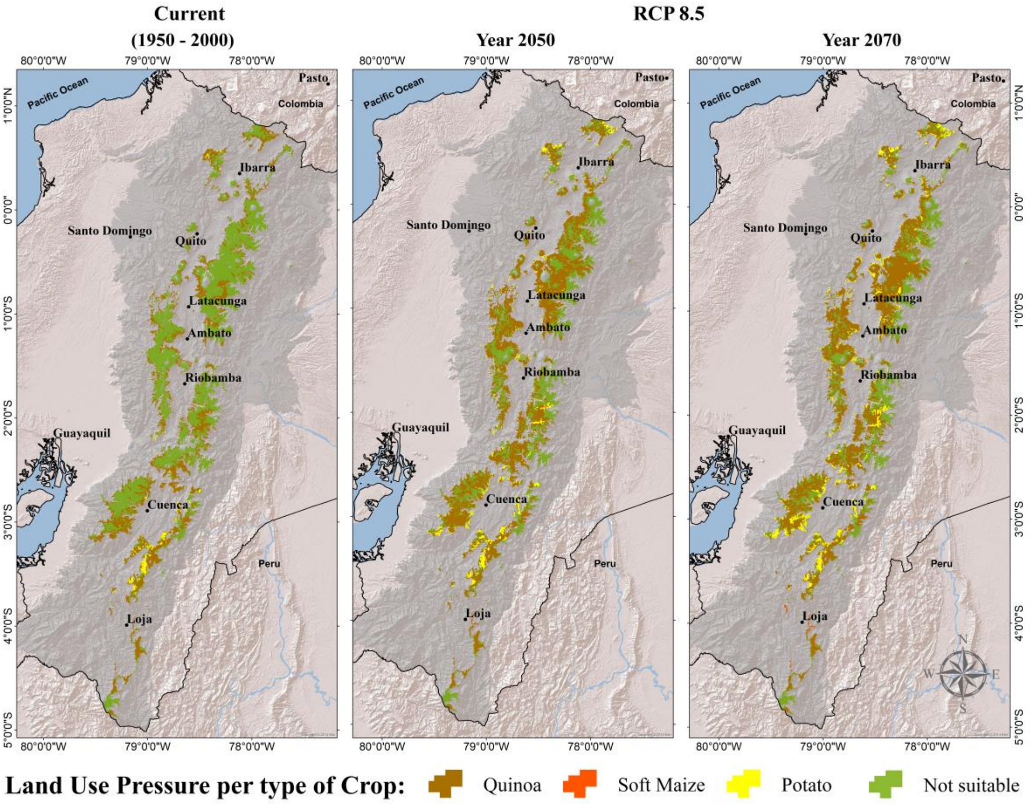

Figure 4.8 Location of land use pressure represented by areas with edapho-climatic suitability (optimal to moderate) for the three Andean crops (potato, soft maize and quinoa), based on current (1950-2001) and future (2050 & 2070) emission scenario RCP 8.5 (moderate).

3.3.1.1 Land Use Pressure versus National Protected Areas

Considering the three crops as a representation of the potential impact of agricultural land use change in the páramo areas of Ecuador, páramo areas with optimal to moderate edapho-climatic conditions for farming are currently found in 30% (3,855 km^2) of the total páramo area of Ecuador (12,976 km^2) (Table 4.10 and Fig. 4.9). Of this potentially suitable land, 22% (2,856 km^2) occurs in places without any type of protection (Table 4.10 and Fig. 4.9). By 2050, under the influence of climate change, the area suitable for cultivation could occupy 53% (6,916 km^2) or 59% (7,697 km^2) of the páramo areas when considering emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.10 and Fig. 4.9). Of this percentage, 37% (4,757 km^2) or 40% (5,226 km^2) could be in areas without protection (Fig. 4.10 and Fig. 4.11). By 2070, suitable farming areas increased amounting to 57% (7,408 km^2) or 65% (8,464 km^2) under emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively (Table 4.10 and Fig. 4.9). Of this land, 39% (5,063 km^2) or 44% (5,750 km^2) is unprotected (Fig. 4.10 and Fig. 4.11). Information regarding the spatial location (high-resolution maps) of land use pressures versus protection for all scenarios is also presented as supplementary material.

Table 4.10 Areas suitable for cultivation (km^2) versus National Protected Areas, considering current (1950-2001) and future (2050 & 2070) scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme).

Scenario	Period	Protected (km^2)	%*	Unprotected (km^2)	%*	Total (km^2)	%*
Current	**(1950-2001)**	999	8	2,856	22	3,855	30
RCP 4.5	**2050**	2,159	17	4,757	37	6,916	53
	2070	2,345	18	5,063	39	7,408	57
RCP 8.5	**2050**	2,471	19	5,226	40	7,697	59
	2070	2,714	21	5,750	44	8,464	65

**Percentage of representativeness respect to the total area of páramo vegetation excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

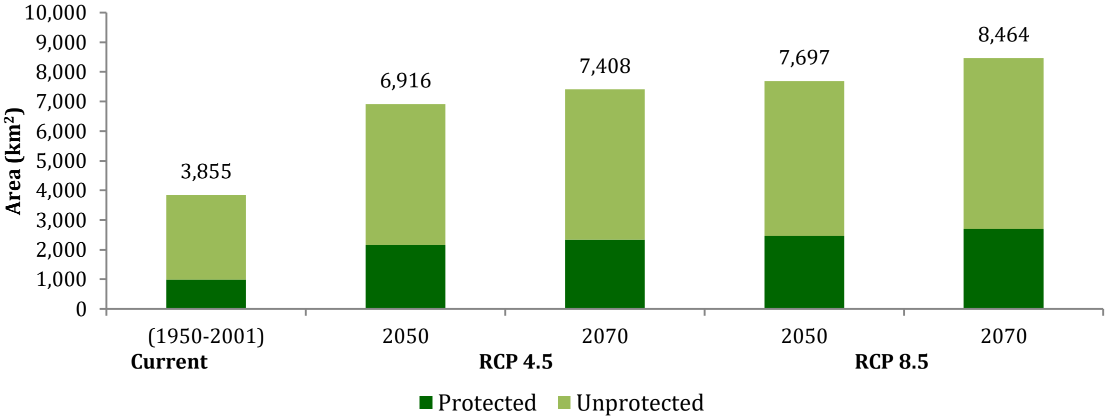

Figure 4.9 Variation of areas suitable for cultivation (km^2) with or without protection, based on current (1950-2001) and future (2050 & 2070) scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme).

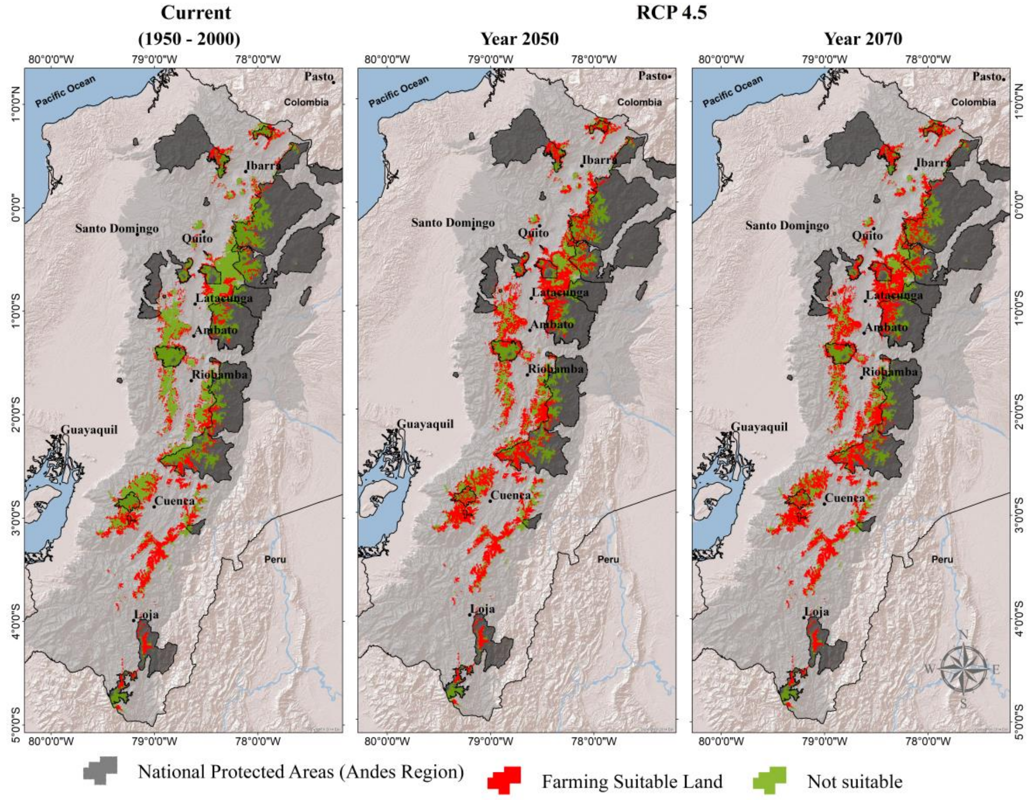

Figure 4.10 Location of Páramo Areas (km^2) suitable for farming (potato+ soft maize+quinoa) based on current (1950-2001) and future (2050 & 2070) emission scenario RCP 4.5 (moderate) versus National Protected Areas located in the Ecuadorian Andes Region.

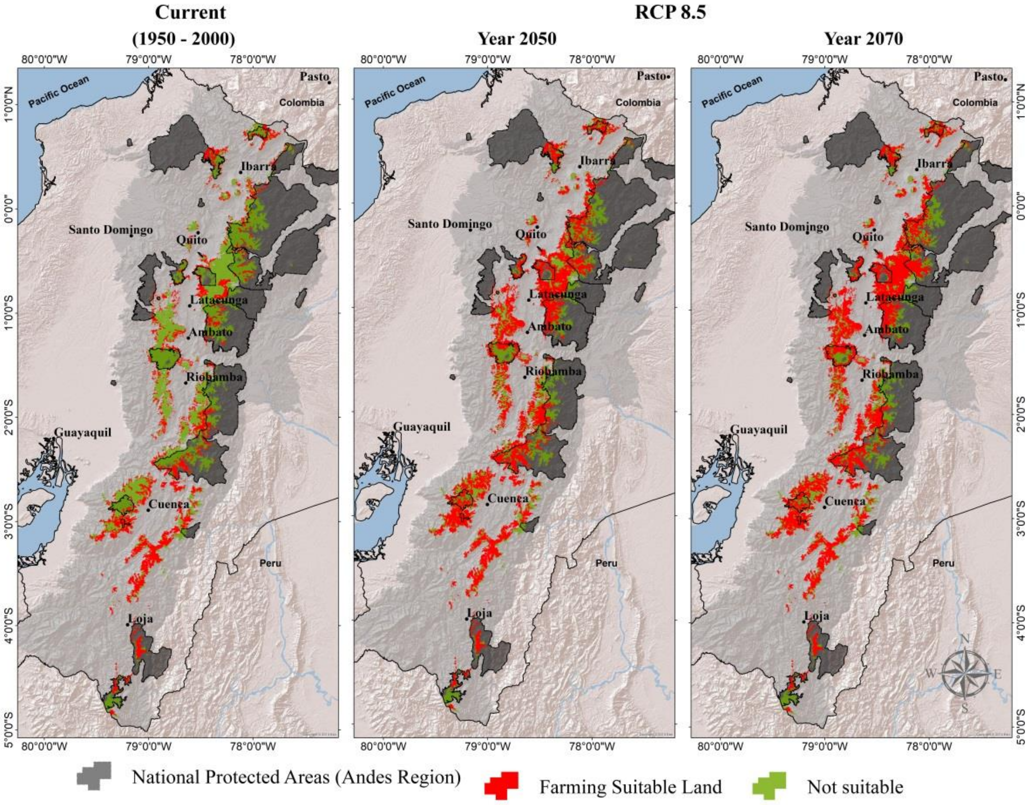

Figure 4.11 Location of Páramo Areas (km^2) suitable for farming (potato + soft maize + quinoa) based on current (1950-2001) and future (2050 & 2070) emission scenario RCP 8.5 (moderate) versus National Protected Areas located in the Ecuadorian Andes Region.

4. Discussion

4.1 Edaphic and Agro-Climatic Suitability

This study suggests that the future expansion of the crops towards and within the páramo areas in Ecuador may be constrained by edaphic limitations, in agreement with previous statements about the unsuitability of páramo soils for cultivation (Poulenard et al., 2004; Podwojewski and Poulenard, 2000a; Hofstede, 2001). Edaphic limitations for the three Andean crops were confirmed, showing marginal edaphic suitability in 26% (potato), 59% (soft maize), and 39% (quinoa) of the total páramo area. In terms of agro-climate, the páramo land appeared to be in some degree favourable for potato and quinoa but very restrictive for soft maize. Agro-climatic models showed that optimal to moderate conditions beneficial for potato and quinoa could be found in 13% and 49% of the páramo areas. In contrast, for soft maize optimal to moderately suitable conditions, were currently inexistent. However, future climatic changes are likely to have differing implications for the three crops considered. By 2050, under the influence of climate change, areas agro-climatically suitable for potato could occupy 25% or 30% of the páramo land under scenarios RCP 4.5 and RCP 8.5, respectively. In the case of soft maize, agro-climatic conditions could continue to be very restrictive, occupying less than 0.5% of the páramo areas under both future scenarios (RCP 4.5 & RCP 8.5). In contrast, quinoa continue to be favoured by agro-climatic conditions present in the páramo land, showing optimal to moderate conditions in 82% or 90% of the páramo areas according to scenario RCP 4.5 and RCP 8.5, respectively. By 2070, the agro-climatic area suitable for the three Andean crops is likely to have expanded further. The most significant expansion may continue to occur for quinoa cultivation, presenting favourable agro-climate in 87% or 98% of the páramo land under RCP 4.5 and RCP 8.5, respectively. In the case of potato crop, agro-climatically suitable areas could occupy 28% or 44% of the páramo land according to scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme), respectively. Regarding soft maize, the agro-climatic conditions seemed to remain restrictive under both future scenarios (RCP 4.5 & RCP 8.5), with suitable conditions for the crops' growth occupying a maximum of 1% of the páramo land.

4.2 Future Exposure of the Páramo Vegetation to Land Use Pressures

This study is in agreement with previous studies which have stated that climate change will improve the potential agricultural productivity of páramo lands, intensifying their vulnerability and leading to the possible extinction of many species (Travis, 2003; Valencia, 2000; Young et al., 2012). Considering the changes on edapho-climatic suitability (optimal to moderate conditions), as an indicator of future pressure of land use change on the Ecuadorian páramo region, quinoa was identified as the greatest potential threat followed by potato. Soft maize was not predicted to exert significant pressure on these natural areas. In terms of the magnitude of this pressure, based on the expansion of optimal to moderate edapho-climatically suitable areas, quinoa could expand from 28% (current scenario) to 49% (RCP 4.5) or 54% (RCP 8.5) along the páramo region, by 2050. Quinoa expansion could continue in 2070, occupying 52% (RCP 4.5) or 56% (RCP 8.5) of the páramo areas. The results reflect the good tolerance of quinoa to adverse climatic and edaphic conditions as stated by other authors previously (Ruiz et al., 2014; Jacobsen et al., 2003). This study adds to the evidence which shows quinoa as a potential threat to the páramos in the future. However, this would only happen if the interest of quinoa producers is increased by national or global demand or by government incentives. This occurred in 2015, when the sowed area registered its highest production peak due to Ecuadorian government incentives aimed at increasing the export of cereals internationally (El Telégrafo, 2015) (Table 4.1). The future of Andean quinoa and its impact on the páramo areas, will also depend on other factors including pests and diseases, farmer adaptation capacity and market uncertainty (Jacobsen, 2002).

Potato, on the other hand, could exert some pressure in the páramo region, with a potential expansion of edapho-climatically suitable areas, varying from 2% (current scenario) to 4% and 5%, by year 2050. By 2070, the ideal areas for potato cultivation could occupy up to 5% or 9% of the páramo areas. The results presented here are in agreement with studies that have suggested that at high latitudes, global warming is likely to cause changes in the location of potato crops towards areas where production is currently not suitable (Hijmans, 2003; Walker et al., 1999; Leemans and Solomon, 1993). Although potato is being already cultivated in the Andes at altitudes higher than 4,000 meters above sea level (Hofstede et al., 2014), this study proved that the expansion of suitable areas for potato cultivation in páramo areas is not as significant as expected. Results seemed to agree with the downward trends of the sowed and harvested area of potatoes registered in recent years in Ecuador (Table 4.1). The downward trend could be also a reflection of other aspects such as the difficulty faced by producers to adapt to climatic changes, pests, and social challenges. However, despite the edapho-climatic limitations identified for potato crop, it could continue to be a latent threat to páramo areas, due to high potato demand and the progressive development of varieties increasingly resistant to frost and temperature variations associated with climate change (Morales, 2007; Hofstede et al., 2014). In the case of soft maize, edapho-climatic conditions (optimal to moderate) are scarce in the páramos land, occupying currently less than 0.5% of the páramo areas, without showing any changes that could favour the crop’s expansion across all future scenarios analysed. The results reflect the lack of favourable edaphic and agro-climatic conditions for this crop in páramo areas and could be representing the high sensitivity of maize crop to temperature changes (Bassu et al., 2014; Adams et al., 1998), limiting its expansion over these natural areas. Given that a conservative increase of 2°C could cause the reduction of 8% to 14% of world maize production (Bassu et al., 2014), it seems that this particular crop could present instead a social threat by putting food security at risk.

This study was also interested in evaluating how much of the ideal (optimal to moderate) areas identified as edapho-climatically suitable for cultivation would be located in protected areas, assuming that areas under protection are less likely to be converted to use for crops. Based on the exemplar crops, the results showed that currently favourable conditions for farming could be found in 30% of the Ecuadorian páramo areas. Of this percentage, 22% could occur in areas without protection. By 2050, suitable areas for farming could occupy 53% (RCP 4.5) or 59% (RCP 8.5) of páramo areas, of which 37% (RCP 4.5) or 40% (RCP 8.5) could occur in unprotected areas. By 2070, the expansion of areas suitable for cultivation could occupy 57% (RCP 4.5) or 65% (RCP 8.5) of páramo land, of which 39% (RCP 4.5) or 44% (RCP 8.5) could happen in unprotected areas.

In general, across all future scenarios, protected areas appear to be less threatened by farming expansion. This could be reflecting the fact that protected areas in tropical regions such as Ecuador are generally located in inaccessible areas with low human pressure (Mulongoy and Chape, 2004; Andam et al., 2008; Joppa and Pfaff, 2010). These results call into question the effectiveness of protected areas in the face of the global changes as it has been widely discussed (Southworth et al., 2004; Ferraro and Pattanayak, 2006; Joppa et al., 2008; Wright, 2010; Rayn and Sutherland, 2011; Rodríguez et al., 2013). Therefore, the success of future investments in conservation will depend on the expansion of protected areas in regions where rapid changes in land use are anticipated due to anthropogenic pressures (Forero-Medina and Joppa 2010; Hoffmann 2011).

4.3 Implications for Management and Policy

Management plans aimed at maintaining valuable ecosystem services and mitigating the negative impacts of climate change, should focus efforts on natural areas where climate change is projected to be more severe (Huber et al., 2013; Polasky et al., 2008), and in areas whose loss could have a greater impact on the provision of ecosystem services (Bullock et al., 2011; Dickie et al., 2011; Vihervaara et al., 2010). In this respect, the capacity of the future models generated here is crucial to explore policy alternatives, given that all adaptation and mitigation initiatives require a long-term commitment. In spite of limitations, future projections presented here result useful to identify potential hotspots of pressure caused by farming activity on the páramo areas. By doing so, policy makers could adequately invest the resources oriented to conservation and sustainable management in critical areas (e.g. areas without protection).

It is known that an effective and sustainable conservation of the páramo lands will only be achieved with structural changes at political, educational, and social levels. In humanized landscapes such as páramo lands restoration practices could be an effective strategy to recover the structure and functioning of páramo areas subject to farming intervention. The creation of corridors between remnants of páramo patches combined with the monitoring of areas of national importance could also curb the impacts of intervention. Stopping the future expansion of cultivated lands in the páramo region will represent a challenge for local authorities and all the social actors involved (e.g. indigenous communities and landowners). Therefore, management strategies based on participatory processes are recommended in order to increase the population's awareness of páramo areas in terms of environmental services, promoting the sustainable management of these natural areas.

4.4 Modelling Approach

One of the main constraints of EcoCrop, is its application of a simplistic approach that fails to capture the whole set of interactions that occur within the plant at the physiological level (e.g. plant-soil water flow) (Ramirez-Villegas et al., 2013). Therefore, the suitability indices and changes generated here should be interpreted simply as an approximate and general representation of the capacity of a given environment to allow the growth of a crop. Among other limitations is the fact that the agro-climatic models were generated based on monthly data, however it is known that stressful conditions can occur in shorter periods of time (e.g. weeks) (Ramirez-Villegas et al., 2013). On the other hand, due to data limitations, the models do not take into account drought, waterlogging, excessive heat or cold during key physiological periods (e.g. flowering), which could have led in certain cases to an overestimation of climatic suitability.

This study was limited by the uncertainty that characterizes global climate data sources such as those used here (e.g. WorldClim). It is very likely that the crops current scenarios would have been affected by the uncertainty linked to the limited number of meteorological stations (Hijmans et al., 2005) existing in the Andes of Ecuador. In addition, limitations liked with the interpolation algorithm (Hutchinson and De Hoog, 1985), the quality of the historical records and the geographical distances between stations might have also influenced in the results. It is believed that future climate data has also generated a certain degree of uncertainty, mainly because predicted changes in climate (e.g. temperatures and rainfall) show considerable variability among Global Climate Models (Pierce et al., 2009; Quiggin, 2008).

The number of papers about suitability of land for crops has grown significantly in recent years (Ramirez et al., 2011; Ramirez-Villegas et al., 2013; Sparks et al., 2014; Läderach et al., 2013). However, most of the approaches are concerned with analysing the suitability of the crops as a risk against food security. This approach, on the other hand, was focused on analysing changes in land suitability, induced by climate change, in páramo natural areas as a threat against ecosystem services provision. Unlike previous studies performed in different regions of the world (Hijmans, 2003; Teixeira et al., 2013; Parry et al., 2004), based solely on the repercussion of climatic variations on crops, this study also included consideration of edaphic limitations that could directly affect the crop's suitability. This decision was made by taking into account the views of other authors who highlighted the omission of soil conditions as a limiting factor that affects the accuracy of the results obtained by EcoCrop (Ramirez-Villegas et al., 2013). Additionally, the inclusion of two representative concentration pathways (RCPs) in the analysis was an advantage because results could be interpreted under two emission perspectives; a moderate one (RCP 4.5) that considers global action against climate change and another pessimistic but more realistic one where society does not change its trend of polluting emissions (RCP 8.5). The use of RCPs in the analysis was novel since they represent the latest greenhouse concentration scenarios launched by IPCC, which have not been extensively used in previous studies in Ecuador. Although the use of RCPs in this study could be seen as innovative, it also made it difficult to compare the results generated since similar studies based on RCPs are still scarce.

The projections obtained by EcoCrop were found to perform well when predicting agro-climatically suitable areas under current conditions. Therefore, it is probable that similar levels of accuracy were achieved in the future projections. However, future predictions must be taken with caution due to the level of uncertainty surrounding the climate change phenomenon. Although the inclusion of edaphic characteristics should have increased the reliability of the prediction, the assumption of soil conditions as constant across all future scenarios remains a great limitation for this type of modelling approach. This limitation can be improved upon in future studies. It was acknowledged that the inclusion of marginal conditions could over-predict the edaphic suitability results. This decision was based on the intensive use of páramo areas for agricultural crop production, despite edaphic restrictions. This fact was verified in this study as it was found that 85% of real potato samples were located in areas with marginal edaphic suitability (Appendix IV.C).

This study recognizes as limitation the exclusion of key factors in this analysis, including population growth, road density, and irrigation. The variable population growth was excluded because the administrative units defined for population mapping in Ecuador (i.e. province, canton, and parish) are to general in comparison with the spatial representation of the páramo areas used in this study (Villacís and Carrillo, 2012). In addition, projections of future population available for Ecuador have been generated for a period different (i.e. 2020) from that established in this study (i.e. 2050 and 2070) and only reach the cantonal scale, making it difficult to be included in this study.

Regarding road density, it was acknowledge that agricultural expansion could be favoured by the creation of new roads (Laurance et al., 2014). However, the information of roads was not included due to differences regarding the road's mapping scale and the lack of information on future road projects required for the analyses under future climate scenarios that were contemplated in this study. However, in the Ecuadorian páramos, most existing roads are precarious and limited to the transit of small cars, except in some provinces (e.g. Cotopaxi and Carchi) were accessibility is an important factor of pressure.

In terms of irrigation, it is known that it has a positive influence on agricultural expansion (Lambin et al., 2001; Lambin et al., 2003). Unfortunately, data limitations prevented its inclusion as an explanatory factor in this analysis. The future inclusion of these socio-economic factors and others (e.g. crop demand, market prices, fertilization effect of CO_2 emissions and farming policies), could lead to more robust results. These factors could influence the location of the crops, potentially over and above the biophysical factors considered here. Nevertheless, the results are a rational representation of future land use trends that could potentially affect the páramos areas, based on a flexible approach that can be continuously improved.

5. Conclusion

This study confirmed the high vulnerability of the páramo vegetation to land use impact as a result of climate change. In general, across all future scenarios, results showed a trend in the increase of farming land towards and within the páramo areas. Among the three Andean crops analysed, quinoa seemed to represent a greater threat to the páramo areas followed by potato cultivation, while, in contrast, a potential expansion of soft maize crops towards páramo areas seemed unlikely. Despite these differences, there was an agreement among RCPs in predicting a potential increase in the area of edapho-climatic suitability for the crops, favouring the future expansion of the farming frontier towards the páramo areas induced by climate change. The most extreme emission scenario (RCP 8.5) reflected a greater increase of edapho-climatically suitable areas across all scenarios and Andean crops considered. This could mean that the higher the greenhouse gas emissions to the atmosphere, the greater the favourable conditions to cultivate in the páramo areas and therefore the higher the future land use impact.

Contrary to other studies based solely on the influence of agro-climatic factors (Ramirez-Villegas et al., 2013; Sparks et al., 2014; Schafleitner et al., 2011), the areas of potential crop expansion presented here are more conservative. This could have been caused by the restrictive edaphic conditions typical of the páramo areas as shown on the observed soil map used in the analysis and by considering the edaphic conditions as unaltered across all future scenarios. Although the approach faced limitations due to the use of secondary data and by the great uncertainty surrounding soil responses to climate change, these results are a rational representation of the potential impact of land use threats in the páramo land induced by climate change. This study highlights not only the vulnerability of páramo areas to land use change but also the importance of conservation efforts that should consider potential future displacements of productive areas when planning conservation and sustainable management strategies for these natural areas.

Chapter V

General Discussion

1. Summary of Thesis Aims and Results

This research aimed to increase the understanding of potential threats to the páramo ecosystems in the Andes of Ecuador as a consequence of climate change. In this final Chapter, the major findings and implications of this work are brought together and discussed in light of the original research objectives.

Chapter I provided background information highlighting the importance of the páramo ecosystems in terms of ecosystem services. As starting point, a brief literature review of the state of the ecosystem services literature was included. Subsequently, general data on páramo vegetation explaining their origin, current geographical distribution, and characteristic climatic conditions were included. A detailed description of the different types of páramo existing in Ecuador was also presented to explain their floristic characteristics and the specific ecological requirements necessary to guarantee their future existence. Particular emphasis was given to the description of páramo soils to emphasize their importance as carbon sinks. This chapter emphasized the importance of the present research focused on páramo ecosystems putting in context the results obtained through it.

In Chapter II, the páramo climatic niches were modelled under current (1950-2000) and future (years 2050 & 2070) environmental conditions oriented to understand ecosystems' vulnerability influenced by climate change. State of the art modelling techniques, based on the maximum entropy principle (MAXENT) was used to generate climatic niche models for the eleven páramo ecosystems found in Ecuador. Six global climate models (GCMs) and two representative concentration pathways (RCP) representing a moderate (RCP 4.5) and an extreme (RCP 8.5) greenhouse gas (GHG) concentration scenario were considered. The modelling performed showed that in approximately 30 (2050) to 50 (2070) years, the eleven páramo ecosystems could be at high risk of abrupt niche changes based on moderate (RCP 4.5) and extreme (RCP 8.5) GHG concentration scenarios. Across all future scenarios, páramo niches showed four potential trends of change including unchanged niches, lost niches, expanded niches, and extinct niches. Páramo vegetation with an isolated or restricted distribution, highly endemic biota, and significant fragmentation proved to be most vulnerable, with signs of potential extinction shown in five out of the eleven páramo ecosystems. On the contrary, páramo vegetation with a broad distribution appeared less vulnerable to future climatic changes across all scenarios. The probability of climatic niche expansion appears remote for most páramo ecosystems analysed. Results on niche shifts confirmed the possibility of a potential appearance or disappearance of species according to their level of tolerance to new climatic conditions. Overall, this study demonstrated the high vulnerability of Andean mountain ecosystems to climate change as previously highlighted by several authors in the past (Cuesta, 2007; Cuesta et al., 2008; Tovar et al., 2013; Feeley and Silman, 2010)

In Chapter III, the benefit transfer approach was applied to estimate the carbon stocks in páramo soil (at depth intervals of 0-30 cm +/- 5 cm) and aboveground vegetation (biomass + necromass) for ten key types of páramo ecosystems located in the Andes of Ecuador. The C stocks quantification was based on secondary information compiled from literature collected over 15 years (2002 to 2016) at different páramo sites along the Ecuadorian Andes. An examination of differences in carbon storage influenced by vegetation type, soil order, altitudinal variation, and climatic conditions was also included. Based on the estimates obtained, the Ecuadorian páramo vegetation as a whole could be accumulating C in soil (at 30 cm depth) equal to 189.3 ton C/ha, whereas in aboveground vegetation the C stock could amount 7.9 ton C/ha. This demonstrated that the C stock in the páramo soils could result 24 times higher than that of vegetation. Depending on the type of páramo ecosystem, soil C stocks ranged from 87.7 to 278.9 ton C/ha. Vegetation C stocks could vary from 5.3 to 8.9 ton C/ha, in grassland and shrubland páramo types, and it could amount to 96.3±32.4 ton C/ha in the páramo forest. This study suggested that the release of the entire C stored in soil and páramo vegetation (i.e. 197.2 ton C/ha) would represent a contribution of 256 Mt C to the atmosphere. Regarding the influence of climatic conditions on soil C stocks, the influence of precipitation and temperature on soil C Stocks (Hofstede et al., 2014; Llambí et al., 2012; Mena et al., 2000) was confirmed. This study contributed to a better understanding of the role of the páramo ecosystems as carbon sinks, highlighting the variability of C stocks that could be found in this Andean vegetation.

Chapter IV addressed the future exposure of the Ecuadorian páramo ecosystems to land use pressures induced by climate change. The impact was measured by analysing the edapho-climatic ranges of three common Andean crops (potato, soft maize, and quinoa) as indicators of potential threats from farming to the survival of the páramo vegetation. The analysis considered climate as the determining factor for increases or decreases in the farming frontier while soil conditions were assumed unchangeable. Future changes were simulated based on Global Climate Model (GCM) CCSM4 and two greenhouse gas (GHG) concentration scenarios, RCP 4.5 (moderate) and RCP 8.5 (extreme). Among the main findings, the edaphic limitations for the three exemplar crops existing in páramo areas were confirmed. The agro-climatic conditions (optimal to moderate) in the páramo land were to some degree favourable for potato and quinoa but very restrictive for soft maize. Based on future edapho-climatic suitability, quinoa was identified as the greatest potential threat in the Ecuadorian páramo region. A potential expansion of potato cultivation was also confirmed, however, its expansion does not seem significant, whereas soft maize does not show signs of becoming a threat to these natural areas. In general, results showed that the farming frontier could increase in 23% (2050) to 35% (2070) towards and within the páramo areas, most of them occurring in areas without protection (16%-21%). These findings reflected not only the high vulnerability of these natural areas to future land use intervention but also called into question the effectiveness of protected areas in the face of the global changes.

2. Implications for Ecosystem Services Provision

If the impact of climate change on climatic niches predicted in Chapter II is confirmed, it is highly probable that the biodiversity of páramo vegetation will be altered in terms of composition, relative abundance, functional diversity and, to a lesser extent, taxonomic diversity of the species (Millennium Ecosystem Assessment, 2005). The loss of biodiversity of small or large magnitude reduces the ability of ecosystems to adapt to changing environments (Hofstede et al., 2014; Mena and Ortiz, 2006). Although the stability of an ecosystem depends mainly on the characteristics of the dominant species, the less abundant species also contribute to its long-term functioning (Millennium Ecosystem Assessment, 2005). In the Andes, populations have long depended on ecosystem services related to biodiversity (Fjeldså, 2007). Therefore, the loss of sensitive species and the displacement of páramo ecosystems as predicted could affect the composition of ecological communities with direct implications on ecosystem services provision. Knowing that any alteration of biodiversity affects key ecosystem processes, it is expected that the quality and stability of páramo ecosystem services, such as biomass production, nutrient and water cycling, and soil formation and retention, will be significantly compromised. For Ecuador, a country highly dependent on páramo ecosystems services, the reduction or disappearance of these natural areas could compromise water supply, flow regulation, irrigation, and hydroelectric generation (Bradley et al., 2006; Vergara et al., 2007).

The future changes in páramo climatic niches predicted here, showed evidence of potential increase in the fragmentation and isolation of the páramo patches in agreement with previous studies (Young, 2009). Although some páramo ecosystems showed signs of greater tolerance to future climatic conditions increasing their representativeness in certain sites along the Andes, this does not prevent their original niches from being reduced annulling the possibility of connecting with adjacent páramo patches as has been suggested by other studies (Young, 2009). Moreover, changes in ecosystems composition could cause an increase or decrease in their capacity to absorb carbon (Cramer et al., 2001; Cox et al., 2000; Smith and Shugart, 1993; Joos et al., 2001). This study coincide with previous studies (Thuiller et al., 2005; Killeen et al., 2007) highlighting as plausible the extinction of species restricted to high elevations and confirms the reduction of niche sharing among ecosystems. Since vegetation characteristics and predominance of species in an ecosystem determine the amount of carbon absorbed (i.e. assimilation) or released (i.e. decomposition, combustion) into the atmosphere (Millennium Ecosystem Assessment, 2005), it seems clear that there will be serious repercussions for the role of páramo vegetation as carbon sinks. The replacement of páramo biodiversity by the most predominant vegetation (e.g. páramo grassland), as was predicted (Chapter II), could represent alterations in terms of belowground and aboveground storage. Therefore, a net reduction of the carbon stored in the páramo region could be expected.

The magnitude of a potential contribution of carbon to the atmosphere by páramo ecosystems was estimated in Chapter III, generating concern about the factors that can put at risk the stability of the carbon stored on these terrestrial ecosystems. In the long term, carbon fluxes are significantly influenced by climate change affecting the structure and functionality of ecosystems (Smith and Shugart, 1993). Increases in temperature, for example, will tend to increase the rates of decomposition of soil organic matter due to microbial activity with effects of unknown magnitude in different types of soils (Powlson, 2005). The accelerated decomposition of organic matter in páramo soils could become a significant source of atmospheric CO_2 (Buytaert et al., 2006b). The release of this carbon into the atmosphere as CO_2 or methane could cause serious impacts on the global climate (Peña Salamanca et al., 2013; Bellamy et al., 2005). Furthermore, a reduction in total precipitation and a stronger or longer dry season could cause drier soils and consequently faster decomposition of organic matter (Buytaert et al., 2011). Drier conditions could cause soil shrinkage (Poulenard et al., 2002), acceleration of organic matter decomposition (Price and Waddington, 2000; Waddington and Roulet, 2000) and hydrophobicity (Poulenard et al., 2004). However, the speed and equilibrium conditions in which these processes could occur will depend on local conditions (Buytaert et al., 2006b).

In the short to medium term, land use change is playing a determinant role in altering carbon fluxes (Brown et al., 1993). It is plausible that increasing temperature will lead to the replacement of páramo vegetation with agricultural lands as was explored in Chapter IV, therefore, leading to reductions in above and below-ground carbon (Dercon et al., 2007; Vanacker et al., 2003). Changes in land use are the second most important source of man-induced greenhouse gas emissions, mainly due to deforestation of natural areas in the tropics and subtropics (Don et al., 2011). In Chapter IV, this research shows the plausible and potential displacement of the farming frontier towards areas currently occupied by natural páramo vegetation due to the influence of climate change. Processes of conversion of páramo ecosystems into farming such as those predicted by this study could significantly alter landscape structure contributing to fragmentation, habitat reduction, and biodiversity loss (Quinn and Harrison, 1988; Cuesta et al., 2014). The transformation of páramo vegetation into crops would cause a rapid loss of carbon in biomass and soil due to the elimination of the natural vegetation that protects the soil, decreasing the entry of organic matter into the soil and increasing the rate of decomposition of plant residues (Don et al., 2011). This farming activity induces significant modifications in structural properties of páramo soils such as texture and water retention capacity, losses of organic matter in the most superficial horizons and in key compartments such as the microbial biomass and alterations in the structure and functional diversity of the soils (Jaimes and Sarmiento, 2002; Sarmiento and Smith, 2011; Sarmiento and Llambí, 2011).

Vegetation and soil resilience will depend critically on local environmental conditions, duration, extension, and intensity of the disturbance (Poulenard et al., 2001; Ferwerda, 1987; Sarmiento and Llambí, 2011; Sarmiento and Smith, 2011; Jaimes and Sarmiento, 2002). The latest studies based on rates of change in the structure and abundance of species estimate that to recover the structure of the páramo to a state prior to conversion of farming could take 30 years or more (Sarmiento and Llambí, 2011), while the recovery of 90% of native species richness could take at least 12 years (Jaimes and Sarmiento, 2002). This implies that páramo vegetation can regenerate rapidly under adequate measures of protection, recovery, and sustainable management (Sarmiento and Llambí, 2011; Jaimes and Sarmiento, 2002). Although the structure and diversity of the natural ecosystem could regenerate to a large extent, some alterations in terms of species dominance could prevail (e.g. shrubs) (Jaimes and Sarmiento,

2002) with direct implications for ecosystem functioning and services including water retention and regulation. Despite the relatively fast recovery of páramo vegetation after farming, the impact of farming on the hydro-physical properties of their soils is irreversible and affects their capacity to retain water (Buytaert et al., 2002). If mechanized cultivation is implemented, páramo soils could face decrease in porosity, dehydration, and aggregation as well as increased susceptibility to erosion (Dorel et al., 2000). These constraints along with socioeconomic aspects such as population growth, changes in land tenure and migration could intensify the anthropogenic expansion putting at risk the resilience of these natural areas and the ecosystem services provided to the population (López Sandoval, 2004).

3. Implications for Policy and Management

Conservation and sustainable management strategies are crucial to minimize future impacts. Strategies should be implemented in a differentiated manner for those ecosystems in danger of extinction and those that show signs of greater resistance to future climatic changes. Criteria for prioritizing affected areas and connectivity between remnant páramo patches should be considered when implementing protection strategies in order to promote the maintenance of local populations. This would also address the problem of habitat fragmentation predicted by this study. Based on the assumption that vegetation patches linked or connected by a corridor decrease the rate of extinction and have a greater value for conservation than isolated habitats (Noss, 2006), the establishment of ecological corridors is recommended. Such measures would also prevent the massive and uncontrolled expansion of the agricultural frontier (Cuesta et al., 2014). Corridors should include different environmental gradients and be sufficiently representative of the species habitat to facilitate the dispersal of plants and animals, and the recovery of landscape matrices, promoting the survival of diverse species and therefore the restoration of ecosystem benefits (Donald and Evans, 2006).).

The important role played by the páramo ecosystems as carbon dioxide sinks justifies the need to implement conservation and sustainable management strategies in these mountain areas. Strategies should be designed to avoid the potential emission of carbon stored in the páramo vegetation into the atmosphere. Efforts should be aimed at increasing carbon capture in soils and biomass through policies for the sustainable management of high altitude areas (Peña Salamanca et al., 2013). In humanized landscapes as páramo lands, restoration practices could be an effective strategy for recovering the structure and functioning of páramo areas subject to agricultural intervention. Ecological restoration of degraded soils and vegetation is an efficient strategy for increasing soil organic carbon content (SOC) and sequestering carbon within the terrestrial ecosystems (Lal et al., 2000; Castañeda-Martín and Montes-Pulido, 2017). Soil restorative measures in páramo areas could include the recovery of native vegetative cover in damaged areas, thereby increasing the quantity of biomass into the soil and contributing to the recovery of their original functionality of the ecosystems (Hobbs and Cramer, 2008).

Considering the pressure of agricultural activities in the Ecuadorian páramo, the implementation of agricultural practices that reduce tillage, the maintenance of soils permanently covered with vegetation and the promotion of sustainable agricultural practices (e.g. crop rotation) could reduce the intensity of change and help avoid erosion and loss of carbon in soils and vegetation (Horowitz et al., 2010). In addition, promoting less intensive and extensive agricultural practices among small and medium Andean farmers could reduce carbon loss in páramo soils (Castañeda-Martín and Montes-Pulido, 2017). The restoration of abandoned farmland previously occupied by páramo vegetation and where intervention has not been severe could be a complementary strategy that would facilitate the creation of corridors (Cramer et al., 2008). Conservation efforts should consider potential future displacement of productive areas, as the ones predicted here, when planning adaptation and mitigation measures to promote the sustainable use of páramo ecosystems.

National and global mitigation plans should recognize the role of páramo ecosystems in capturing carbon and stabilizing atmospheric emissions, emphasizing the collateral social and environmental benefits of soil conservation that go beyond carbon mitigation (e.g. provision and regulation of water) (Dumanski, 2004). Strategies of sustainable management in these natural areas must be combined with adequate monitoring focused on those areas under the greatest risk of anthropogenic intervention, such as the ones identified in this study (Chapter II and Chapter IV).Actions should be oriented to establish protected areas and natural corridors in areas that provide key environmental services to the population (e.g. drinking water and hydropower). Stopping the expansion of cultivated lands in the páramo region will represent a challenge to local authorities and all social actors involved (e.g. indigenous communities and landowners). Therefore, management strategies should include participatory processes aimed at raising population awareness of the importance of páramo areas in terms of environmental services, while identifying sustainable alternatives through consensus between stakeholders (Adger, 2003).

3. Future Research

The present investigation generated key information on the future challenges that climate change will pose for the Ecuadorian páramo vegetation. However, there are still many unexplored topics that require further investigation. Niche modelling in the Andean regions could significantly benefit from building better climate models based on improved data (e.g. microclimate). Promoting the collection and evaluation of climate data from different elevations along the Andes will significantly improve the models' representation of local and temporal climatic changes (e.g. temperature and precipitation patterns, cloud formation, orographic influences, etc.) that influence the behaviour of páramo ecosystems.

On the other hand, it was identified the need to carry out páramo niche modelling at international scale, including the six countries (i.e. Panama, Costa Rica, Peru, Venezuela, Ecuador and Colombia) that present páramo ecosystems in their territories. A cross-boundary initiative would guarantee the total representation of the niches and their future tolerance range more precisely. To this end, it would be necessary to promote an improved and systematic sampling of the occurrence of species in regions where there are currently only biased and scarce data available. The regional mapping of páramo ecosystems under a standard methodology, legend, and scale could also facilitate this type of studies in the future.

In addition, empirical analyses characterizing páramo fragmentation and connectivity (structural and functional) could provide useful information when implementing conservation strategies such as ecological corridors. In countries with limited resources for conservation such as Ecuador, it is important to prioritize the areas of strategic intervention. Therefore, complementary analyses aimed at identifying which of the areas identified as vulnerable by this study are a priority from a socio-economic point of view (e.g. fresh water, hydropower, irrigation, among others) and are needed in order to focus resources most effectively.

Future efforts have to be made to collect information on vegetation carbon content. The information currently available is limited and focuses only on certain páramo types and specific areas of the Andes which does not allow discrimination of the different varieties of species found on both flanks of the cordillera (i.e. Eastern and Western). In terms of soil carbon data, the need for a National protocol that regulates soil data collection is evident since soil information was limited and biased to certain sites in the Ecuadorian Andes. Therefore, it would be appropriate to establish an organized strategy to fill information gaps in the future, considering the differences in soil carbon content across the Andes as was highlighted in this study. This could promote the construction of a comprehensive soil database that facilitates the comparison, analysis and monitoring of páramo areas at local, national and regional scale. Studies aimed at better understanding the environmental (e.g. climate, parent material, and slope) and pedological (e.g. type of soil, texture, and pH) factors that control the regional and vertical distribution of the soil organic carbon would be useful for better understanding and modelling of current and future carbon fluxes from páramo ecosystems.

A more detailed mapping of soils that better discriminates the location and representativeness of histosols (peat) in the Andes would allow a better estimation of the carbon content in páramo lands, facilitating the prioritization of conservation efforts in these areas rich in carbon. Little is known about páramo soils in terms of changes in their storage and carbon capture capacity under the influence of climate change. Therefore, in-situ monitoring and experimental studies in this subject are required. Although the first steps have been taken in terms of regional monitoring (e.g. Gloria Andes initiative), it will still be some years before these data will be available for modelling and conclusions can be drawn to define adequate mitigation and adaptation strategies under these new considerations. In general, efforts should be oriented to build more accurate estimates of the storage of terrestrial carbon in Andean ecosystems. This would allow researchers to quantify possible sources of terrestrial CO_2 and CH_4 with implications for emissions at national and global scale.

Modelling the behaviour of soils under the influence of climate change is yet to be conducted on the Andes ecosystems. Studies of this nature could help researchers understand the impact of the climate phenomenon on future agricultural practices. In this context, it is important to re-evaluate the páramo lands destined for productive uses in contrast with the real socioeconomic benefits the population would obtain from agriculture. This could lead to better territorial planning and therefore slow down the advance of the agricultural frontier in the páramo region. For this, the adequate mapping of actors, the understanding of ancestral agricultural practices as well as the identification of crop varieties resistant to future biophysical conditions would allow the authorities to guide farmers towards better practices that balance conservation and social well-being. Finally, complementary studies contrasting the pressures of land use with páramo areas of high socioeconomic importance would be extremely useful to focus sustainable management strategies in these critical sites.

4. Conclusion

The first aim of this research was to predict the impacts of climate change on the climatic niche distribution of the Ecuadorian páramo ecosystems under current and future environmental conditions. The analysis considered current (1950-2000) and future climatic conditions (years 2050 and 2070) by applying niche-based modelling. This analysis included six different Global Climate Models (GCMs) predictions and two greenhouse gas (GHG) concentration scenarios: RCP 4.5 (moderate) and RCP 8.5 (extreme). The second aim was to estimate the carbon stocks in páramo soils and aboveground vegetation for ten key types of páramo ecosystems located in the Andes of Ecuador, based on secondary information generated over 15 years. The analysis was focused on reflecting the diversity of carbon stocks in soil and vegetation that could be found across different types of páramo ecosystems, as well as to offer an insight into the factors that influence the carbon stocks in the páramo region. The third aim was to explore the potential exposure of the Ecuadorian páramo vegetation to land use pressures, considering climate as a determining factor of a potential expansion of the farming frontier. Páramo areas were characterized in terms of the edaphic and agro-climatic suitability in order to identify areas edapho-climatically suitable for crops under current and future climatic conditions.

Among the main contributions of this research are the novel use of representative concentration pathways (RCPs) which constitute the latest GHG emission scenarios recognized by the Intergovernmental Panel on Climate Change (IPCC) in the Fifth Assessment Report (AR5). This allowed not only the updating of páramo niche predictions under the new global considerations but also the testing of the new emission scenarios in the Andean region. The estimation of the carbon stocks in soils and vegetation constitutes a significant effort to integrate independent/isolated efforts to achieve a carbon stock quantification at a national scale, highlighting the global importance of páramo areas as carbon sinks. The goal of predicting the impacts of farming influenced by climate change by applying an innovative approach that considers edaphic and agro-climatic limitations is a solid improvement in this type of analysis, still scarce in Ecuador. This study has highlighted the vulnerability of páramo ecosystems to climate change. Areas of particular vulnerability to loss of climatic niches and future anthropogenic intervention occur in unprotected páramo remnants at the south of the eastern cordillera. Páramo areas of interest for carbon capture are located along both cordilleras, and some of them are already under protection. It is hoped that the material generated by this study will contribute to a greater understanding of the vulnerability of the Andean ecosystems to climate change, motivating the adoption of adaptation and mitigation measures designed to guarantee the future provision of páramo ecosystem services for the Ecuadorian population.

Appendices

Appendix II.A Average Training and Test average AUC obtained by current scenario models run for each páramo ecosystem (code)

N°	Páramo Ecosystem Code	Training AUC																								SD	AUC average of predictions
		Average AUC 1	Average AUC 2	Average AUC 3	Average AUC 4	Average AUC 5	Average AUC 6	Average AUC 7	Average AUC 8	Average AUC 9	Average AUC 10	Average AUC 11	Average AUC 12	Average AUC 13	Average AUC 14	Average AUC 15	Average AUC 16	Average AUC 17	Average AUC 18	Average AUC 19	Average AUC 20	Average AUC 21	Average AUC 22	Average AUC 23	Average AUC 24		
1	HsSn01	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.0000	0.9994
2	AsAn01	0.998	0.998	0.999	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.0003	0.9981
3	HsNn01	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.98	0.981	0.981	0.98	0.981	0.981	0.981	0.981	0.981	0.981	0.981	0.0003	0.9807
4	HsNn02	0.972	0.973	0.973	0.973	0.973	0.972	0.973	0.973	0.973	0.973	0.972	0.972	0.973	0.973	0.973	0.973	0.973	0.973	0.972	0.972	0.973	0.973	0.973	0.973	0.0003	0.9725
5	HsSn04	0.964	0.965	0.964	0.965	0.966	0.964	0.966	0.964	0.965	0.964	0.965	0.967	0.964	0.964	0.965	0.965	0.965	0.965	0.964	0.964	0.965	0.965	0.966	0.965	0.0007	0.9647
6	BsSn01	0.954	0.955	0.955	0.955	0.956	0.955	0.955	0.955	0.954	0.954	0.954	0.955	0.955	0.955	0.955	0.956	0.956	0.956	0.955	0.956	0.955	0.955	0.954	0.955	0.0006	0.9549
7	HsSn03	0.959	0.959	0.959	0.96	0.959	0.959	0.96	0.959	0.959	0.959	0.958	0.959	0.959	0.959	0.958	0.959	0.959	0.959	0.959	0.96	0.959	0.959	0.959	0.959	0.0004	0.9589
8	RsSn01	0.964	0.963	0.964	0.963	0.964	0.963	0.963	0.963	0.963	0.963	0.963	0.963	0.963	0.963	0.963	0.964	0.963	0.963	0.963	0.964	0.964	0.963	0.963	0.963	0.0002	0.9633
9	HsNn03	0.911	0.911	0.911	0.912	0.911	0.911	0.911	0.912	0.912	0.911	0.911	0.911	0.911	0.911	0.912	0.911	0.911	0.911	0.912	0.912	0.911	0.911	0.911	0.911	0.0003	0.9112
10	AsSn01	0.734	0.736	0.733	0.735	0.734	0.735	0.733	0.734	0.735	0.733	0.736	0.735	0.735	0.733	0.734	0.732	0.734	0.735	0.735	0.735	0.734	0.735	0.733	0.735	0.0010	0.7344
11	HsSn02	0.727	0.65	0.727	0.728	0.727	0.727	0.727	0.727	0.727	0.727	0.727	0.727	0.728	0.728	0.728	0.728	0.727	0.728	0.727	0.727	0.727	0.727	0.727	0.727	0.0157	0.7240

N°	Páramo Ecosystem Code	Test AUC																								SD	AUC average of predictions
		Average AUC 1	Average AUC 2	Average AUC 3	Average AUC 4	Average AUC 5	Average AUC 6	Average AUC 7	Average AUC 8	Average AUC 9	Average AUC 10	Average AUC 11	Average AUC 12	Average AUC 13	Average AUC 14	Average AUC 15	Average AUC 16	Average AUC 17	Average AUC 18	Average AUC 19	Average AUC 20	Average AUC 21	Average AUC 22	Average AUC 23	Average AUC 24		
1	HsSn01	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.0000	0.9994
2	AsAn01	0.998	0.998	0.999	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.998	0.0003	0.9981
3	HsNn01	0.979	0.979	0.979	0.979	0.979	0.978	0.979	0.979	0.98	0.979	0.979	0.978	0.978	0.978	0.979	0.979	0.978	0.977	0.978	0.979	0.978	0.979	0.978	0.978	0.0006	0.9786
4	HsNn02	0.97	0.97	0.97	0.971	0.97	0.97	0.97	0.971	0.971	0.971	0.97	0.97	0.971	0.971	0.971	0.972	0.971	0.971	0.969	0.971	0.971	0.971	0.971	0.971	0.0005	0.9707
5	HsSn04	0.959	0.96	0.958	0.96	0.961	0.959	0.96	0.959	0.96	0.959	0.959	0.961	0.959	0.958	0.96	0.959	0.959	0.959	0.959	0.959	0.96	0.958	0.961	0.959	0.0009	0.9593
6	BsSn01	0.948	0.95	0.949	0.95	0.949	0.948	0.948	0.95	0.948	0.947	0.949	0.948	0.95	0.949	0.948	0.951	0.95	0.949	0.95	0.95	0.949	0.949	0.948	0.949	0.0009	0.9489
7	HsSn03	0.957	0.957	0.957	0.958	0.957	0.957	0.958	0.956	0.957	0.956	0.956	0.957	0.957	0.956	0.956	0.957	0.957	0.957	0.956	0.957	0.957	0.957	0.957	0.957	0.0005	0.9567
8	RsSn01	0.963	0.963	0.963	0.963	0.963	0.962	0.962	0.963	0.963	0.963	0.963	0.962	0.962	0.963	0.963	0.963	0.962	0.963	0.962	0.963	0.963	0.963	0.962	0.962	0.0002	0.9626
9	HsNn03	0.91	0.909	0.909	0.91	0.909	0.909	0.91	0.91	0.91	0.909	0.91	0.91	0.909	0.91	0.91	0.909	0.909	0.909	0.91	0.91	0.909	0.91	0.909	0.909	0.0005	0.9093
10	AsSn01	0.731	0.732	0.73	0.731	0.731	0.732	0.73	0.731	0.732	0.73	0.733	0.732	0.732	0.73	0.731	0.729	0.73	0.731	0.732	0.731	0.731	0.732	0.73	0.731	0.0010	0.7309
11	HsSn02	0.725	0.649	0.724	0.726	0.725	0.725	0.725	0.725	0.725	0.725	0.725	0.724	0.726	0.725	0.726	0.726	0.725	0.726	0.725	0.725	0.725	0.725	0.725	0.726	0.0156	0.7219

Appendix II.B Differences of Future Páramo Niche Area (~km^2) projected by Global Climate Model (GCMs) under RCP 8.5 (extreme scenario), years 2050 and 2070

Modelling Group	N°	Páramo Ecosystem Code	RCP 8.5 (~km^2)																	
			Year 2050									Year 2070								
			BCC-CSM1-1	CCSM4	HadGEM2-ES	IPSL-CM5A-LR	MIROC-ESM	MRI-CGCM3	SD	Min	Max	BCC-CSM1-1	CCSM4	HadGEM2-ES	IPSL-CM5A-LR	MIROC-ESM	MRI-CGCM3	SD	Min	Max
1	**1**	HsSn01	25	28	240	707	166	12	267	12	707	15	28	40	3,203	557	6	1,273	6	3,203
	2	AsAn01	7	81	65	2	32	47	31	2	81	0	14	279	40	65	58	103	0	279
2	**3**	HsNn01	372	54	228	28	102	926	339	28	926	77	93	48	0	108	345	120	0	345
	4	HsNn02	847	245	371	190	622	860	297	190	860	253	6	127	115	232	248	98	6	253
	5	HsSn04	4,939	3,866	1,373	3,751	3,126	3,583	1,176	1,373	4,939	2,187	5,156	1,272	2,058	1,322	3,233	1,468	1,272	5,156
	6	BsSn01	3,439	5,497	2,929	191	1,137	6,185	2,350	191	6,185	263	4,786	453	4	1,127	4,056	2,091	4	4,786
	7	HsSn03	223	40	397	0	40	2,221	863	0	2,221	1	0	6	0	100	1,132	455	0	1,132
	8	RsSn01	2,551	106	2,251	3,084	616	1,100	1,181	106	3,084	6,050	37	46	2,497	1	1,104	2,378	1	6,050
3	**9**	HsNn03	1,904	665	821	628	2,077	1,953	703	628	2,077	602	124	242	196	336	456	178	124	602
	10	AsSn01	19,367	15,110	16,868	18,343	22,884	22,857	3,158	15,110	22,884	14,657	17,122	13,902	7,768	21,329	18,939	4,720	7,768	21,329
4	**11**	HsSn02	23,520	20,409	20,323	19,262	21,975	23,351	1,750	19,262	23,520	20,297	17,394	16,330	13,539	17,799	17,880	2,219	13,539	20,297

Appendix II.C Impact of Climate Change on Páramos Climatic Niche Distribution at National Scale under future scenarios (years 2050 & 2070) RCP 4.5 (moderate) and RCP 8.5 (extreme), based on models ensemble approach a) (without consensus) and b) (high consensus)

Without Consensus

Observed Niche (~km2)*	RCP 4.5																RCP 8.5															
	2050								2070								2050								2070							
	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)
25,292	26,036	23,425	22,883	88	3,153	12	542	2	25,824	23,159	22,476	87	3,348	13	683	3	25,869	23,035	22,332	86	3,537	14	703	3	25,856	22,250	20,305	79	5,551	21	1,945	8

High Consensus

Observed Niche (~km2)*	RCP 4.5																RCP 8.5															
	2050								2070								2050								2070							
	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)	Current Niche (~km^2)	Future Niche (~km^2)	Unchanged (~km^2)	Unchanged (%)	Lost (~km^2)	Lost (%)	Expanded (~km^2)	Expanded (%)
25,292	24,958	19,621	19,618	79	5,340	21	3	0	23,667	18,161	18,142	77	5,525	23	19	0	24,901	17,949	17,948	72	6,953	28	1	0	24,795	14,865	14,863	60	9,932	40	2	0

***Percentages were calculated with respect to each corresponding current niche scenario.*

Appendix III.A Carbon Data Sites: Coordinates, Precision and Accuracy of the coordinates

Sample Code	Site Name	Longitude X	Latitude Y	Precision	Accuracy
JI	Central Cordillera (north to south)	-78.9465	-3.2364	Low	High
P2A	Chiles Volcano	-77.8783	0.7907	Good	Good
P2B	Chiles Volcano	-77.8787	0.7904	Good	Good
P3A	Chiles Volcano	-77.9438	0.8014	Good	Good
P3B	Chiles Volcano	-77.9442	0.8017	Good	Good
CHV1- CHV2	Chimborazo Volcano	-78.8752	-1.3491	Low	Low
CUE	Cuenca	-79.2181	-2.9636	Good	Good
GEL	El Angel	-77.9153	0.6894	Low	Low
CJN1	El Tiro-Cajanuma	-79.1453	-4.0170	Good	Low
CJN2	El Tiro-Cajanuma	-79.1451	-4.0196	Good	Good
CJN3	El Tiro-Cajanuma	-79.1556	-4.0761	Good	Low
CJN4	El Tiro-Cajanuma	-79.1450	-4.0181	Good	Low
CJN5	El Tiro-Cajanuma	-79.1447	-4.0048	Good	Low
CJN6	El Tiro-Cajanuma	-79.1552	-4.0781	Good	Good
CJN7	El Tiro-Cajanuma	-79.1462	-3.9915	Good	Good
CJN8	El Tiro-Cajanuma	-79.1559	-4.0824	Good	Good
CJN9	El Tiro-Cajanuma	-79.1456	-4.0182	Good	Low
CJN10	El Tiro-Cajanuma	-79.1550	-4.0764	Good	Good
CJN11	El Tiro-Cajanuma	-79.1448	-4.0161	Good	Low
CJN12	El Tiro-Cajanuma	-79.1448	-4.0160	Good	Low
CJN13	El Tiro-Cajanuma	-79.1471	-3.9945	Good	Low
CJN14	El Tiro-Cajanuma	-79.1464	-3.9917	Good	Low
CJN15	El Tiro-Cajanuma	-79.1550	-4.0796	Good	Good
CJN16	El Tiro-Cajanuma	-79.1469	-3.9955	Good	Good
C- 1	Illinizas	-78.6805	-0.5807	Good	Good
C- 2	Illinizas	-78.6805	-0.5807	Good	Good
C- 3	Illinizas	-78.6805	-0.5807	Good	Good
C- 4	Illinizas	-78.6805	-0.5807	Good	Good
C- 5	Illinizas	-78.6804	-0.5807	Good	Good
C- 6	Illinizas	-78.6804	-0.5807	Good	Good
C- 7	Illinizas	-78.6804	-0.5807	Good	Good
C- 8	Illinizas	-78.6805	-0.5807	Good	Good
C- 9	Illinizas	-78.6805	-0.5807	Good	Good
C- 10	Illinizas	-78.6805	-0.5807	Good	Good
C- 11	Illinizas	-78.6805	-0.5807	Good	Good
C- 12	Illinizas	-78.6805	-0.5807	Good	Good
C- 13	Illinizas	-78.6805	-0.5807	Good	Good
C- 14	Illinizas	-78.6804	-0.5808	Good	Good
MA5	Machángara Catchment	-79.0122	-2.6673	Low	High
NI4	Ningar	-78.7508	-2.5620	Low	High
PIF1	Pifo	-78.2478	-0.2171	Low	Low
PLG9	Pulingui	-78.8496	-1.5247	Good	Low
PLG10	Pulingui	-78.8444	-1.5240	Good	Low
CH3	Western Cordillera (north to south)	-79.0149	-2.6690	Low	High
PD	Western Cordillera (north to south)	-79.2851	-3.0816	Low	High
PP01	Yanacocha Reserve 2	-78.5804	-0.1356	Good	Good
PP02	Yanacocha Reserve 2	-78.5799	-0.1357	Good	Good
PP06	Yanacocha Reserve 2	-78.5810	-0.1345	Good	Good
PP09	Yanacocha Reserve 2	-78.5830	-0.1338	Good	Good
PP10	Yanacocha Reserve 2	-78.5829	-0.1332	Good	Good
PP13	Yanacocha Reserve 2	-78.5814	-0.1335	Good	Good
PP14	Yanacocha Reserve 2	-78.5807	-0.1339	Good	Good
PP15	Yanacocha Reserve 2	-78.5766	-0.1387	Good	Good
PP23	Yanacocha Reserve 2	-78.5800	-0.1369	Good	Good
YAC1	Yanacocha Reserve 1	-78.5848	-0.1652	Low	Low
YAC2	Yanacocha Reserve 1	-78.5826	-0.1668	Low	Low

** Geographic Coordinate System: WGS 1984*

Appendix III.B Carbon Data used for Soil Carbon Stock Estimate by Páramo Ecosystem

								Original Carbon Data			**Adjusted Carbon Data**				
N°*	**Páramo Ecosystem**	**Ecosystem Code**	**Soil Order**	**Site/Plot Code**	**Site**	**Altitude (m.a.s.l.)**	**Andes Location**	**Depth Range**	**Depth (cm)**	**Soil C Stock (ton C/ha)**	**Depth (cm)**	**Bulk Density (g/cm^3)**	**SOM (%)**	**SOC (%)**	**Soil C Stock (ton C/ha)**
11	Páramo Grassland	HsSn02	Histosol	PD	Western Cordillera (north to south)	3,630	Western Cordillera (South)	0–12	12	119.8	12	0.5	43.4	21.7	119.8
								12–30	18	153.0	18	0.6	30.9	15.5	153.0
							Sample Plot total				**30**	**0.5**	**35.9**	**18.0**	**272.7**
				JI	Eastern Cordillera (north to south)	3,350	Eastern Cordillera (South)	0–15	15	86.4	15	0.3	33.9	17.0	86.4
								15–34	19	77.4	15	0.4	19.4	9.7	61.1
							Sample Plot total				**30**	**0.4**	**26.7**	**13.3**	**147.6**
							Sites Average Histosol				**30**	**0.4±0.1**	**31.3±4.6**	**15.6±2.3**	**210.1±62.6**
			Inceptisol	CJN5	El Tiro-Cajanuma	2,880	Eastern Cordillera (South)	0-25	25	85.3	30	1.1	6.3	3.1	102.4
				CJN7	El Tiro-Cajanuma	2,842	Eastern Cordillera (South)	0-25	25	145.2	30	0.9	12.9	6.5	174.3
							Site replicates average				**30**	**1.0**	**9.6**	**4.8**	**138.3**
				CUE	Cuenca	3,700	Western Cordillera (South)	0-30	30	244.7	30	0.4	46.6	23.3	244.7
				MA5	Machángara Catchment	3,600	Western Cordillera (South)	0–30	30	257.5	30	0.3	59.2	29.6	257.5
				CH3	Western Cordillera (north to south)	3,600	Western Cordillera (South)	0–30	30	248.8	30	0.3	57.2	28.6	248.8
				NI4	Ningar	3,300	Eastern Cordillera (South)	0–30	30	167.3	30	0.3	33.8	16.9	167.3
							Sites Average for Inceptisol				**30**	**0.5±0.1**	**41.3±9.1**	**20.6±4.6**	**211.3±24.4**

N°*	Páramo Ecosystem	Ecosystem Code	Soil Order	Site/Plot Code	Site	Altitude (m.a.s.l.)	Andes Location	Original Carbon Data			Adjusted Carbon Data				
								Depth Range	Depth (cm)	Soil C Stock (ton C/ha)	Depth (cm)	Bulk Density (g/cm^3)	SOM (%)	SOC (%)	Soil C Stock (ton C/ha)
			Entisol	CJN2	El Tiro-Cajanuma	2,800	Eastern Cordillera (South)	0-25	25	55.5	30	1.1	4.0	2.0	66.6
				CJN4	El Tiro-Cajanuma	2,923	Eastern Cordillera (South)	0-25	25	73.9	30	1.0	6.0	3.0	88.7
				CJN1	El Tiro-Cajanuma	2,941	Eastern Cordillera (South)	0-25	25	58.7	30	1.1	4.1	2.1	70.5
				Site replicates average for Entisol							**30**	**1.1**	**4.7**	**2.3**	**75.2**
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	Inceptisol	CJN13	El Tiro-Cajanuma	2,841	Eastern Cordillera (South)	0-25	25	104.1	30	1.2	6.9	3.5	124.9
				CJN14	El Tiro-Cajanuma	2,760	Eastern Cordillera (South)	0-25	25	79.9	30	0.4	14.5	7.3	95.8
				CJN16	El Tiro-Cajanuma	2,901	Eastern Cordillera (South)	0-25	25	155.2	30	1.1	11.3	5.6	186.3
				Site replicates average for Inceptisol							**30**	**0.9**	**10.9**	**5.5**	**135.7**
			Entisol	CJN11	El Tiro-Cajanuma	2,880	Eastern Cordillera (South)	0-25	25	35.4	30	1.1	2.7	1.3	42.5
				CJN12	El Tiro-Cajanuma	2,860	Eastern Cordillera (South)	0-25	25	88.4	30	1.0	7.3	3.6	106.1
				CJN9	El Tiro-Cajanuma	2,949	Eastern Cordillera (South)	0-25	25	59.9	30	1.1	4.2	2.1	71.9
				Site replicates average for Entisol							**30**	**1.1**	**4.7**	**2.4**	**73.5**
8	Páramo Caulescent Rosettes (frailejones) and Grassland	RsSn01	Inceptisol	P2A	Chiles Volcano	3,518	Western Cordillera (North)	0-30	30	241.7	30	0.5	31.6	15.8	241.7
				P2B	Chiles Volcano	3,512	Western Cordillera (North)	0-30	30	146.8	30	0.3	35.0	17.5	146.8
				Site replicates average							**30**	**0.4**	**33.3**	**16.6**	**194.3**
				P3A	Chiles Volcano	4,097	Western Cordillera (North)	0-30	30	235.2	30	0.5	29.6	14.8	235.2
				P3B	Chiles Volcano	4,102	Western Cordillera (North)	0-30	30	318.9	30	0.5	41.7	20.8	318.9
				Site replicates average							**30**	**0.5**	**35.6**	**17.8**	**277.0**

N°*	Páramo Ecosystem	Ecosystem Code	Soil Order	Site/Plot Code	Site	Altitude (m.a.s.l.)	Andes Location	**Original Carbon Data**			**Adjusted Carbon Data**				
								Depth Range	**Depth (cm)**	**Soil C Stock (ton C/ha)**	**Depth (cm)**	**Bulk Density (g/cm^3)**	**SOM (%)**	**SOC (%)**	**Soil C Stock (ton C/ha)**
				GEL	El Angel	3,500	Western Cordillera (North)	0– 30	30	**368.9**	30	**0.6**	**42.4**	**21.2**	**368.9**
				Sites Average for Inceptisol							**30**	**0.5±.1**	**37.1±2.7**	**18.6±1.4**	**280.1±50.4**
6	Ultra-humid Subnival Páramo Grassland	HsNn02	Inceptisol	PLG10	Pulingui	3,766	Western Cordillera (Centre)	0-25	25	61.3	30.0	1.0	5.0	2.5	73.5
				PLG9	Pulingui	3,977	Western Cordillera (Centre)	0-25	25	92.4	30.0	1.0	7.7	3.9	110.9
				Site replicates average for Inceptisol							**30**	**1.0**	**6.4**	**3.2**	**92.2**
10	Páramo Evergreen Shrubland and Grassland	AsSn01	Inceptisol	CJN6	El Tiro-Cajanuma	3,329	Eastern Cordillera (South)	0-25	25	83.2	30	1.0	6.9	3.5	99.8
				CJN8	El Tiro-Cajanuma	3,424	Eastern Cordillera (South)	0-25	25	72.0	30	0.8	7.2	3.6	86.4
				CJN15	El Tiro-Cajanuma	3,331	Eastern Cordillera (South)	0-25	25	104.1	30	0.6	13.4	6.7	124.9
				Site replicates average for Inceptisol							**30**	**0.8**	**9.2**	**4.6**	**103.7**
			Entisol	CJN3	El Tiro-Cajanuma	3,305	Eastern Cordillera (South)	0-25	25	87.1	30	0.9	8.0	4.0	104.5
				CJN10	El Tiro-Cajanuma	3,240	Eastern Cordillera (South)	0-25	25	79.1	30	0.9	7.0	3.5	94.9
				Site replicates average for Entisol							**30**	**0.9**	**7.5**	**3.7**	**99.7**
7	Humid High Upper Montane Páramo Grassland	HsSn03	Inceptisol	CHV1	Chimborazo Volcano	3,800	Western Cordillera (Centre)	0-15	15	77.1	15	0.7	13.9	7.0	77.1
				CHV2	Chimborazo Volcano	3,800	Western Cordillera (Centre)	15-30	15	75.9	15	0.9	10.9	5.4	75.9
				Sample Plot total for Inceptisol							**30**	**0.8**	**12.4**	**6.2**	**153.0**
3	Evergreen Páramo Forest	BsSn01	****	BA	Andes	3,000-4,000	Eastern and Western Cordillera	0-30	30	212.1	**30**	**0.6**	**24.9**	**12.5**	**212.1**
4	Humid Subnival Páramo Grassland	HsNn01	Inceptisol	YAC2	Yanacocha Reserve 1	3,600	Western Cordillera (North)	0-30	30	112.2	**30**	**N/A**	**N/A**	**N/A**	**112.2**

** For comparative purposes the initial numbering presented in Table 3.1 was retained*

Appendix III.C Carbon Data used for Vegetation Carbon Stock Estimate by Páramo Ecosystem (aboveground biomass & aboveground necromass)

N°*	Ecosystem	Ecosystem Code	Site Code	Site	Altitude (m.a.s.l.)	Andes Location	Aboveground Biomass Carbon (ton C/ha)	Aboveground Necromass Carbon (ton C/ha)	Vegetation Carbon Stock (ton C/ha)
11	**Páramo Grassland**	HsSn02	C- 1	Illinizas	3,811	Western Cordillera (Centre)	6.1	0.4	6.5
			C- 2	Illinizas	3,807	Western Cordillera (Centre)	4.2	0.1	4.3
			C- 3	Illinizas	3,805	Western Cordillera (Centre)	0.7	0.1	0.8
			C- 4	Illinizas	3,802	Western Cordillera (Centre)	3.2	0.3	3.5
			C- 5	Illinizas	3,807	Western Cordillera (Centre)	4.2	0.2	4.5
			C- 6	Illinizas	3,807	Western Cordillera (Centre)	3.0	0.4	3.4
			C- 7	Illinizas	3,801	Western Cordillera (Centre)	2.5	0.4	2.9
			C- 8	Illinizas	3,805	Western Cordillera (Centre)	3.9	0.4	4.3
			C- 9	Illinizas	3,805	Western Cordillera (Centre)	3.4	0.3	3.7
			C- 10	Illinizas	3,810	Western Cordillera (Centre)	1.1	0.2	1.3
			C- 11	Illinizas	3,808	Western Cordillera (Centre)	4.4	0.3	4.7
			C- 12	Illinizas	3,804	Western Cordillera (Centre)	4.0	0.4	4.4
			C- 13	Illinizas	3,798	Western Cordillera (Centre)	3.9	0.3	4.2
			C- 14	Illinizas	3,807	Western Cordillera (Centre)	2.2	0.5	2.7
			Site replicates average				**3.4**	**0.3**	**3.7**
			PP01	Yanacocha Reserve	4,028	Western Cordillera	3.0	6.6	9.5

N°*	Ecosystem	Ecosystem Code	Site Code	Site	Altitude (m.a.s.l.)	Andes Location	Aboveground Biomass Carbon (ton C/ha)	Aboveground Necromass Carbon (ton C/ha)	Vegetation Carbon Stock (ton C/ha)
11	**Páramo Grassland**	HsSn02		2		(North)			
			PP02	Yanacocha Reserve 2	4,043	Western Cordillera (North)	2.1	8.0	10.1
			PP06	Yanacocha Reserve 2	4,028	Western Cordillera (North)	2.6	10.5	13.2
			PP09	Yanacocha Reserve 2	3,943	Western Cordillera (North)	3.4	5.1	8.6
			PP10	Yanacocha Reserve 2	3,938	Western Cordillera (North)	2.6	10.0	12.6
			PP13	Yanacocha Reserve 2	3,994	Western Cordillera (North)	3.4	5.3	8.8
			PP14	Yanacocha Reserve 2	4,025	Western Cordillera (North)	1.8	3.1	4.9
			PP23	Yanacocha Reserve 2	4,067	Western Cordillera (North)	4.2	9.9	14.2
				Site replicates average			**2.9**	**7.3**	**10.2**
			CJN2	El Tiro-Cajanuma	2,800	Eastern Cordillera (South)	4.3	0.6	4.8
			CJN4	El Tiro-Cajanuma	2,923	Eastern Cordillera (South)	2.3	0.6	2.9
			CJN1	El Tiro-Cajanuma	2,941	Eastern Cordillera (South)	4.0	0.8	4.7
			CJN5	El Tiro-Cajanuma	2,880	Eastern Cordillera (South)	3.4	1.3	4.7
			CJN7	El Tiro-Cajanuma	2,842	Eastern Cordillera (South)	3.8	0.8	4.5
				Site replicates average			**3.5**	**0.8**	**4.3**
			YAC1	Yanacocha Reserve 1	3,600	Western Cordillera (North)	4.8	7.5	12.3
				Sites Average for Ecosystem HsSn02			**3.6±0.6**	**4.0±2.2**	**7.6±2.4**
10	Páramo Evergreen Shrubland and	AsSn01	CJN3	El Tiro-Cajanuma	3,305	Eastern Cordillera	3.2	1.4	4.6

N°*	Ecosystem	Ecosystem Code	Site Code	Site	Altitude (m.a.s.l.)	Andes Location	Aboveground Biomass Carbon (ton C/ha)	Aboveground Necromass Carbon (ton C/ha)	Vegetation Carbon Stock (ton C/ha)
	Grassland					(South)			
			CJN6	El Tiro-Cajanuma	3,329	Eastern Cordillera (South)	3.0	1.3	4.3
			CJN8	El Tiro-Cajanuma	3,424	Eastern Cordillera (South)	4.2	0.2	4.4
			CJN10	El Tiro-Cajanuma	3,240	Eastern Cordillera (South)	7.4	1.3	8.8
			CJN15	El Tiro-Cajanuma	3,331	Eastern Cordillera (South)	4.0	0.5	4.6
			Sites replicates Average for Ecosystem AsSn01				**4.4**	**0.9**	**5.3**
1	Southern Páramo High Montane Evergreen Shrubland	AsAn01	CJN9	El Tiro-Cajanuma	2,949	Eastern Cordillera (South)	6.8	1.5	8.3
			CJN11	El Tiro-Cajanuma	2,880	Eastern Cordillera (South)	4.2	1.1	5.4
			CJN12	El Tiro-Cajanuma	2,860	Eastern Cordillera (South)	5.8	1.3	7.1
			CJN13	El Tiro-Cajanuma	2,841	Eastern Cordillera (South)	13.9	0.6	14.5
			CJN14	El Tiro-Cajanuma	2,760	Eastern Cordillera (South)	8.0	1.3	9.4
			CJN16	El Tiro-Cajanuma	2,901	Eastern Cordillera (South)	7.5	0.2	7.6
			Sites replicates Average for Ecosystem AsAn01				**7.7**	**1.0**	**8.7**
3	Evergreen Páramo Forest	BsSn01	PIF1 (6 years forest)	Pifo	3,600	Eastern Cordillera (North)	45.0	2.0	47.0
			PIF1 (15 years forest)	Pifo	3,600	Eastern Cordillera (North)	46.5	2.0	48.5
			PIF1 (30 years forest)	Pifo	3,600	Eastern Cordillera (North)	103.0	2.0	104.9
			PIF1 (45 years forest)	Pifo	3,600	Eastern Cordillera (North)	182.8	2.0	184.8
			Sites replicates Average for Ecosystem BsSn01				**94.31±32.4**	**2.0**	**96.3±32.4**

N°*	Ecosystem	Ecosystem Code	Site Code	Site	Altitude (m.a.s.l.)	Andes Location	Aboveground Biomass Carbon (ton C/ha)	Aboveground Necromass Carbon (ton C/ha)	Vegetation Carbon Stock (ton C/ha)
4	**Humid Subnival Páramo Grassland**	HsNn01	PP15	Yanacocha Reserve 2	4,242	Western Cordillera (North)	1.7	0.0	1.7
			PP15	Yanacocha Reserve 2	4,242	Western Cordillera (North)	0.9	0.0	0.9
			PP15	Yanacocha Reserve 2	4,242	Western Cordillera (North)	2.1	0.1	2.3
			PP15	Yanacocha Reserve 2	4,242	Western Cordillera (North)	1.6	0.0	1.6
			Site replicates average				**6.3**	**0.2**	**6.5**
			YAC2	Yanacocha Reserve 1	3,600	Western Cordillera (North)	3.0	8.3	11.3
			Sites Average for Ecosystem HsNn01				**4.7±1.7**	**4.3±4.0**	**8.9±2.4**

** For comparative purposes the initial numbering presented in Table 3.1 was retained.*

Appendix IV.A Description of Edaphic Parameters considered for the Analysis of Edaphic Suitability (Rulebase, 2015)

Agro-ecological Requirement	Description	Information Source
Slope	Slope is the inclination of the land surface from the horizontal.	Glossary (2016) by U.S. Department of Agriculture, Natural Resources Conservation Service
Texture	Texture represents the relative proportions of three sizes of grains in a mass of soil: sand, silt and clay. The surface layer of the soils at a depth of approximately 25 cm is the part of the soil most used by crop plants.	NAL Glossary (2014) by United States Department of Agriculture, National Agricultural Library(Rasheed and Venugopal, 2009)
Depth	The depth of a soil profile is measured from the top to parent material or bedrock or to the layer of obstacles for roots. It differs significantly for different soil types.	Glossary of Soil Terms (2012) by European Commission
Stoniness	Stoniness is the relative proportion of coarse particles (larger than 2 mm diameter) in the soil or on soil surface.	Glossary of Soil Terms (2012) by European Commission
Drainage	Drainage is the manner in which the water of an area passes or flows off by surface streams or subsurface conduits.	Energy Glossary and Acronym List (2016) by U.S. Geological Survey
pH	pH means the symbol for the negative logarithm of the hydrogen ion concentration, which is a measure of the degree of acidity or alkalinity of a solution.	Food Code Definitions (2001) by Idaho Department of Health and Welfare & The State of Idaho
Toxicity	The degree to which a substance or mixture of substances can harm humans or animals.	Glossary of Environmental Terms (2016) by Arizona Department of Environmental Quality
Organic Matter	That fraction of the soil that includes plant and animal residues at various stages of decomposition, cells and tissues of soil organisms, and substances synthesized by the soil population.	Glossary of Wildland Fire Terminology (2012) by National Wildfire Coordinating Group
Salinity	Salinity is the amount of soluble salts in a soil.	NAL Glossary (2014) by United States Department of Agriculture, National Agricultural Library
Fertility	Fertility is a measure of the ability of soil to provide plants with sufficient amount of nutrients and water, and a suitable medium for root development to assure proper plant growth and maturity.	Glossary of Soil Terms (2012) by European Commission
Phreatic level	Upper surface of an unconfined aquifer (e.g. the top sand layer in a dike) at which the pressure in the groundwater is equal to atmospheric pressure.	Glossary of Coastal Terminology (2003) by The United States Army

Appendix IV.B EcoCrop Variables: Units and description based on Hijmans (2012)

EcoCrop	Variables	Units	Description
Length of the Growing Season	Gmin	days	start of growing season
	Gmax	days	end of growing season
	Gavg	days	length of growing season ((Gmax+Gmin)/2)
Temperature Threshold	Tkill	°C	absolute temperature that will kill the plant
	Tmin	°C	minimum average temperature at which the plant will grow
	TOPmin	°C	minimum average temperature at which the plant will grow optimally
	TOPmax	°C	maximum average temperature at which the plant will grow optimally
	Tmax	°C	maximum average temperature at which the plant will cease to grow

EcoCrop	Variables	Units	Description
Precipitation Threshold	Rmin	mm	minimum rainfall (mm) during the growing season
	ROPmin	mm	optimal minimum rainfall (mm) during the growing season
	ROPmax	mm	optimal maximum rainfall (mm) during the growing season
	Rmax	mm	maximum rainfall (mm) during the growing season

Appendix IV.C Verification of Edaphic Limitations

To evaluate the edaphic limitations existing in the páramo areas, the percentage of coincidence between the areas identified as edaphically suitable (pixels) and the real location of potato crops was analysed. The results showed that from the total sample of potato crops currently located in páramo areas (8,093 samples in total), 85% and 14% were located in soils identified as marginal and moderate, respectively, while only 1% was located in areas identified with optimal soils. It is acknowledged that in reality there are many factors influencing the location of the crops (e.g. population growth and profit). However, the results could be representing some of the biophysical limitations that occur in reality like inadequate soils.

Real potato crops located in páramo areas versus areas of edaphic suitability by category of suitability

Crop	Edaphic Suitability Category	# Crop sample points	(%)*
Potato	Optimal	102	1
	Moderate	1,143	14
	Marginal	6,848	85
Total		**8,093**	**100**

** Percentage calculated with respect to total number of crop samples in páramo areas*

Appendix IV.D Percentage of Representativeness of agro-climatic suitable areas per type of crop based on current (1950-2001) and future climatic conditions (2050 & 2070) under scenario RCP 4.5 (moderate) and RCP 8.5 (extreme)

Crop	**Current**				**Future**															
					RCP 4.5								**RCP 8.5**							
	(1950-2001)				**2050**				**2070**				**2050**				**2070**			
	Optimal (%)	**Moderate (%)**	**Marginal (%)**	**Not suitable (%)**	**Optimal (%)**	**Moderate (%)**	**Marginal (%)**	**Not suitable (%)**	**Optimal (%)**	**Moderate (%)**	**Marginal (%)**	**Not suitable (%)**	**Optimal (%)**	**Moderate (%)**	**Marginal (%)**	**Not suitable (%)**	**Optimal (%)**	**Moderate (%)**	**Marginal (%)**	**Not suitable (%)**
Potato	2.4	10.8	24.2	62.5	12.5	12.9	43.7	30.9	14.9	13.2	46.6	25.3	16.0	14.5	48.0	21.5	22.7	21.0	49.6	6.7
Soft Maize	0.002	0.03	1.3	98.7	0.02	0.1	8.3	91.5	0.03	0.2	11.1	88.7	0.04	0.3	10.7	89.0	0.1	0.8	18.7	80.4
Quinoa	19.6	29.7	50.6	0.1	35.6	46.4	18.0	0.01	39.7	47.1	13.2	0.002	43.1	46.5	10.5	0.002	59.9	38.1	2.0	0.000

*** Percentage of representativeness respect to the total area of páramo vegetation excluding rocky outcrops, snow/ice, and water bodies (natural or artificial).*

Appendix IV.E Edapho-climatic Suitable areas (km^2) per type of crop and suitability category (optimal, moderate, marginal), based on current (1950-2001) and future climatic conditions (2050 & 2070) under emission scenarios RCP 4.5 (moderate) and RCP 8.5 (extreme)

Crop	**Current (km^2)***			**Future (km^2)***											
				RCP 4.5						**RCP 8.5**					
	(1950-2001)			**2050**			**2070**			**2050**			**2070**		
	Optimal	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**	**Optimal**	**Moderate**	**Marginal**
Potato	28	217	756	227	313	1,809	270	351	1,959	286	416	2,040	458	754	2,125
Soft Maize	0	0	51	0	2	521	0	3	723	0	6	683	1	32	1,296
Quinoa	1,432	2,179	4,751	2,652	3,722	1,692	2,989	3,794	1,201	3,291	3,697	912	4,815	2,404	145

**Areas exclude rocky outcrops, snow/ice, and water bodies (natural or artificial).*

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