

Potential impacts of climate change on the environmental services of humid tropical alpine regions

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Abstract

1. Aim

Humid tropical alpine environments are crucial ecosystems that sustain biodiversity, biological processes, carbon storage, and surface water provision. They are identified as one of the most vulnerable terrestrial ecosystems to global environmental change. Despite their vulnerability, and the importance for regional biodiversity conservation and socio-economic development, they are among the least studied and described ecosystems in the world. This paper reviews the state of knowledge about tropical alpine environments, and provides an integrated assessment of the potential threats of global climate change on the major ecosystem processes.

2. Location

Humid tropical alpine regions occur between the upper forest line and the perennial snow border in the upper regions of the Andes, the Afroalpine belt, and Indonesia and Papua New Guinea.

3. Results and main conclusions

Climate change will displace ecosystem boundaries, and strongly reduce the total area of tropical alpine regions. Displacement and increased isolation of remaining patches will induce species extinction and biodiversity loss. Drier and warmer soil conditions will cause a faster organic carbon turnover, decreasing the below-ground organic carbon storage. Since currently most of the organic carbon is stored in the soils, it is unlikely that an increase of above-ground biomass will be able to offset soil carbon loss at an ecosystem level. Therefore a net release of carbon to the atmosphere is expected. Changes in precipitation patterns, increased evapotranspiration, and alterations of the soil properties will have a major impact on water supply. Many regions are in danger of a significantly reduced or less reliable stream flow. The magnitude and even the trend of most of these effects depend strongly on local climatic, hydrological and ecological conditions. The extreme spatial gradients in these conditions put the sustainability of ecosystem management at risk.

4. Main keywords

Tropical alpine regions, climate change, ecosystem services, biodiversity, soil properties, hydrology

1 Introduction

1.1 Occurrence of humid tropical alpine ecosystems

Humid alpine environments occur in tropical mountain ranges of the Andes, the Afroalpine belt, and to a lesser extent in Indonesia and Papua New Guinea (Fig. 1). They extend between the treeline border and the permanent snowline. This coincides with a lower limit between 3400 and 3600 m, and an upper limit of about 5000 m, depending on the latitude and local conditions.

The largest extension of tropical alpine ecosystems is found in the Northern Andes (e.g., Hofstede et al., 2003; Sklenář et al., 2008), where they are commonly known as *páramos*. They cover an area of about 36000 km² (Josse et al., 2009), forming a discontinuous belt that stretches from the páramo de Ávila near Caracas in Venezuela to the Huancabamba depression in North Perú (Fig. 1). To the south, the páramo is bordered by the jalca, which is a transition biome between the páramo and the drier puna that dominates highlands in south Peru and Bolivia (e.g., Weigend, 2002). Further north, two isolated systems occur. One of them is the Sierra Nevada de Santa Marta in Colombia (Cleef & Rangel-Churio, 1984) (about 1370 km²). In Costa Rica, around 70 km² of páramo stretches out over the Cordillera Central and the Cordillera Talamanca (Kappelle et al., 2005).

In Africa, afroalpine ecosystems occur as small and isolated patches in the mountains along the Great Rift Valley. The Sanetti Plateau in the Bale Mountains (Fig. 1), South-East Ethiopia, hosts the largest continuous afroalpine habitat, covering an area above 3500 m of about 1100 km² (Frankfurt Zoological Society, 2007). A second afroalpine ecosystem is found in the Simien mountains in northern Ethiopia (Rundel et al., 1994; Yimer et al., 2006a). Finally the volcanic peaks of Kenya, Tanzania and Uganda (Kilimanjaro, Mount Kenya, Rwenzori, Virunga, Mt. Elgon) contain limited patches of afroalpine vegetation (Beck et al., 1981; Hedberg, 1992; Young & Peacock, 1992; Miehe & Miehe, 1993; Hemp, 2002).

The only extent of tropical alpine regions in the Asian continent is a discontinuous patchwork along a 2000 km long mountain range in the highlands of New Guinea. The largest areas

occur around the Puncak Jaya peak (4884 m), which forms part of the Maoke mountains at the Indonesian side of the island (Fig. 1). Several other peaks host tropical alpine vegetation, such as Puncak Trikora (Mangen 1993) and Mount Wilhelm (Hope 1976, Hnatiuk 1994). In this part of the world the forest limit is located at about 3800 – 3900 m, which is higher than other tropical alpine regions. This may be attributed to the high humidity and cloudiness of the local climate, which causes milder temperatures and lower radiation. The total alpine habitat area in this part of the world is estimated at about 700 km² (Hope et al., 2003).

1.2 Environmental services

Despite their limited area, tropical alpine environments provide important environmental services on both local and global scales. The most important services are biodiversity conservation, carbon storage, and water supply for cities, agriculture and hydro-power. Tropical alpine regions host a unique fauna and flora, and are hotspots for biodiversity (Myers et al., 2000). Adaptation to the specific physio-chemical and climatic conditions, such as the low atmospheric pressure, large daily fluctuation of temperature, intense ultra-violet radiation, and the drying effects of wind has resulted a species endemism of up to 60% in the Andes.

Due to the orographic effect, high altitudinal mountain regions often receive higher amounts of precipitation, providing good conditions for the development of wetlands. The absence of trees and dense vegetation as in mountain forests emphasizes the importance of the soils and water bodies in the water cycle. Indeed, despite the low water storage and attenuation capacity of the vegetation, tropical alpine regions and particularly the páramos are known for an excellent water regulation capacity which converts the erratic precipitation regime into a constant base flow in rivers. Combined with the difficulties in extracting groundwater and the generally drier climatic conditions of the adjacent lowlands, surface water from alpine regions is often crucial for local water supply (Buytaert et al., 2006a). The wetlands also help to improving groundwater recharge, sediment accretion and pollution removal.

Finally, the soils of tropical alpine regions can be a considerable carbon sinks. Soil organic carbon accumulation is primarily caused by the continuous vegetation cover, low air temperature, the low atmospheric pressure and frequent water logging of the soils (Podwojewski et al., 2002; Poulénard et al., 2003). In addition, accumulation is often enhanced by the formation of resistant organometallic complexes with Al and Fe released by breakdown of volcanic parent material (Nanzoy et al., 1993).

1.3 Climate change

Global climate change is expected to have an important effect on the aforementioned ecosystem processes (Arnell, 1999). Despite widely diverging projections from different global circulation models, there is consistent trend towards an increase in temperature. At higher altitudes, enhanced warming effects are expected due to alterations of the lapse rate (Still et al., 1999; Urrutia & Vuille, 2009). Future projections of the precipitation regime are more variable, but often a higher precipitation variability is expected, resulting in longer and/or stronger dry seasons (Giorgi & Bi, 2005; Boulanger et al., 2007; Buytaert et al., 2009).

The combination of a fragile ecosystem and an enhanced climate change illustrate the potentially dramatic effect of global change on local system dynamics, affecting essential ecosystem processes such as streamflow (Jansky et al., 2002). In contrast, very little is known about climate, climate variability and its interaction with ecosystem services in tropical alpine regions.

This paper reviews the current state of knowledge on the functioning and vulnerability of ecosystem processes in tropical alpine environments in view of climate change. A first part gives a comprehensive overview of the main characteristics of tropical environments in the light of the main ecosystem services. In light of these characteristics, the second part discusses the expected impacts of global change on tropical alpine vegetation, soils and hydrology. We conclude by discussing the limitations of the currently available techniques to quantify and predict the effects of climate change on tropical alpine regions and outline the main needs for future scientific research.

2 The main characteristics of tropical alpine regions

2.1 Climate

A common feature among all tropical mountain wetlands is a cold and wet climate. In sharp contrast to wetlands of high latitudes, seasonal variability in temperature tends to be low because of the constant level of solar radiance throughout the year. Intraday variations dominate (a phenomenon which is often referred to as *summer every day and winter every night*, Hedberg, 1964). The diurnal cycle can be very strong in places with low cloud cover. For instance, in the Ethiopian Sanetti plateau, day-night temperature variations of up to 40°C have been recorded (-15°C to 26°C, Frankfurt Zoological Society, 2007). Temperature gradients with elevation are relatively constant in different mountain ranges. The modern lapse rate can range from 0.53 to 0.7°C 100 m⁻¹ (Mangen, 1993; van der Hammen & Hooghiemstra, 2000; Yimer et al., 2006a).

Precipitation patterns, on the other hand, are complex and difficult to generalise. The irregular topography and the large differences in slope, exposure and elevation give rise to strong gradients in temperature and precipitation, shading effects and local microclimates. In the Andean highlands, precipitation ranges from less than 500 mm in the dry páramos of central Ecuador (Acosta-Solís 1984) and Venezuela to more than 3000 mm on the outer slopes in the western and eastern Cordillera in Colombia. The outer slopes of the Andes have climate patterns that are determined by large scale climate systems over the Pacific and the Amazon. The inter-Andean valleys between the western and the eastern mountain range undergo a varying influence from oceanic and continental air masses, often resulting in complex, bimodal seasonal distribution (e.g., Celleri et al., 2007).

The climatic patterns in the alpine regions of the African rift valley are similarly variable. The slope of the Kilimanjaro has a precipitation pattern close to that of the rest of the East African region, exhibiting a pronounced bimodal seasonality (Basalirwa et al., 1999). Precipitation amounts are highly variable, depending on altitude, topography and exposure. On the south and south-eastern

slopes that get the highest precipitation levels, a maximum precipitation of around 1600 – 1800 mm year⁻¹ is found at an altitude of 2200 m. Further upslope, precipitation decreases rapidly, to around 550 mm year⁻¹ at 3900 m. Kibo station at 4571 m receives only 350 mm year⁻¹ (Røhr & Killington, 2003), while the summit (5893 m) receives less than 100 mm year⁻¹ (Hedberg, 1964). Mount Kenya has a wetter regime, with values of 850 mm year⁻¹ at the summit (5199 m) and a peak of 2500 mm year⁻¹ in the 1400 – 2200 m elevation range. Both mountains have similar temperature regimes, with an average temperature of 2°C at 4000 m (Hedberg, 1964).

The Ethiopian highlands are characterized by a higher precipitation and more cloudiness. The climate is bimodal with a main wet season from July to October and a smaller one from March to May. Stations at the slopes of the Bale mountains (around 2500 m altitude) record annual rates between 870 and 1065 mm year⁻¹ (Yimer et al., 2006a). In the Simien mountains, the closest records come from a catchment at an altitude between 3000 and 3500 m described by Liu et al. (2008), who report an average precipitation of 1467 mm year⁻¹ and a mean temperature of 12.6°C. Due to the strong bimodal season, daily reference evapotranspiration values can be very high in the dry season, with values up to 10 mm day⁻¹ (Liu et al., 2008).

The tropical alpine regions of New Guinea experience a climate that is very similar to wet tropical lowlands. Seasonal climate variability is low. Perennial heavy cloud cover, high atmospheric humidity, and mixing of slope air with that in the free atmosphere dampen daily temperature changes (Van Royen, 1980; Rundel et al., 1994). At the upper border of tropical mountain areas, the permanent snow line is very sharp. The limit for permanent frost is located at about 5000 m along the equator and slightly lower further north and south.

2.2 *Vegetation*

The isolated and fragmented occurrence of tropical mountain vegetation promotes high speciation and an exceptionally high endemism at the species and genera level (Sklenář & Ramsay, 2001). At the regional and landscape scales, climate, geological history, habitat diversity and also

human influence determine the diversity of biota (Vuilleumier & Monasterio, 1986; Luteyn et al., 1992). Local climatic gradients further complicate diversity patterns, with spatial community changes often occurring over short distances (Cleef, 1981; Ramsay, 1992, Sklenář & Balslev, 2005). The páramo ecosystem hosts 3595 species of vascular plants distributed in 127 families, and 540 genera, of which 14 are endemic to the Northern Andes (Sklenář & Balslev, 2005; Fig. 4). About 60% of these species are endemic to the Northern Andes (Luteyn, 1999).

The physiognomy of tropical alpine vegetation varies within and between regions but certain features are shared such as similar growth forms of the dominant plants (e.g., Cleef, 1978; Smith & Young, 1987; Ramsay, 2001). In the Andean páramos, three main units are generally identified above the upper forest line, according to the physiognomy and structure of the vegetation: (1) the subpáramo or shrub páramo, (2) grass páramo, tussocks and/or bamboos frequently dominated by giant rosettes of the genus *Espeletia* or *Puya* and (3) superpáramo. *Polylepis* woodlands, probable remnants of more extensive upper Andean forest in the past (Fjeldså, 1992; Laegaard, 1992), also contribute to the mosaic of the páramo habitats.

The subpáramo is dominated by upright and prostrate shrubs. The grass páramo is characterised by a dominance of tussock grasses, stem rosettes (e.g., *Espeletia*, *Puya*), small patches of upright sclerophyllous shrubs, and patches of monotypic or mixed forest of *Gynoxys*, *Diplostephium* or *Escallonia*. The super-páramo vegetation is primarily found in the Andes of Ecuador, Colombia and Venezuela, on the slopes of the highest mountains at 4100 – 4800 m altitude and can be divided in two altitudinal belts (Cleef, 1981; Sklenář, 2000). The lowermost superpáramo belt has a more or less closed vegetation of shrubs, cushions, acaulescent rosettes, and tussock grasses. At higher elevation, shrubs and tussock grasses are lacking and the plant cover is patchy. Topographic variations at site scale result in azonal habitats (cushion bogs, mires, aquatic vegetation) which occur at perhumid areas (Cleef, 1981).

Afroalpine flora displays striking similarities with the South American páramo due to convergent adaptation. The same lifeforms occur, dominated by giant rosettes, tussock grasses and

sclerophyllous shrubs. Vegetation zonation is also similar, with the grass páramo and the superpáramo corresponding to the afroalpine belt, and the subpáramo corresponding to the ericaceous belt (Hedberg, 1992). Giant rosettes (*Dendrosenecio*, *Carduus*, *Lobelia*) appear abundantly throughout all elevations up to 4600 m (Smith, 1994). Patches of arborescent *Dendrosenecio keniodendron* can form nearly closed canopy on the slopes of Mount Kenya, while *Erica arborea* bushlands occur in lower afroalpine regions of Ethiopia, and on Kilimanjaro and Mount Kenya (Hemp, 2002; Frankfurt Zoological Society, 2007). Upper limits of the afroalpine regions are dominated by short herbs, grasses and lichens. On wet slopes and seepage zones, cushion plants occur.

In the alpine regions of New Guinea, tussock grasslands are mostly composed of tussock grassland associations characteristic for the oceanic climate in the southern hemisphere, with species such as *Deschampsia* and *Poa*. Rich dwarf shrub (e.g., *Styphelia*, *Drapetes*) combined with mosses (*Racomitrium*) also occur abundantly. Hard cushion vegetation, and mire and moss communities dominate in the wetter areas. Some of the most conspicuous species occurring in the area are treeferns (*Cyathea*) and finger-line ferns (*Papuapteris linearis*), exposing a similar growth form as species of *Jamesonia* in the Andes (Van Royen, 1980; Mangen, 1993; Hnatiuk, 1994).

2.3 Soils

Many different soil types are found in tropical alpine regions. Around active volcanoes such as Cotopaxi and Sangay in Ecuador and volcanic formations such as the Bale Mountains, young volcanic ash deposits are found, resulting in vitric and silandic Andosols (Yimer et al, 2006a,b; FAO/ISRIC/ISSS, 1998). They accumulate little organic matter because of regular and debris deposition. Further away and near extinct volcanoes more developed volcanic soils are present. These soils contain the highest organic matter content. The abundance of organic matter and the relatively low pH prevents the formation of typical volcanic minerals such as allophane and imogolite, and the soils are often classified as Aluandic or even Histic Andosols (Buytaert et al.,

2006a; Poulénard et al., 2003; Zehetner & Miller, 2006).

In absence of volcanic substrates, e.g., south Ecuador, northern Peru, Venezuela, and New Guinea, soils still often develop Umbric or Histic properties, depending on the local climate conditions. These soils are found for instance in the tropical alpine regions of South Ecuador and North Peru, the Eastern, Central and Western Cordillera of Colombia, Venezuela and New Guinea (Van Royen, 1980, Poulénard et al., 2003; Buytaert et al., 2006b, 2007b). Soil development tends to decrease with altitude, such that in the highest parts, as well as on steep slopes, shallow soils with little soil development occur (Inceptisols or Leptosols, Regosols). Finally, soils near the snow border are often affected by cryoturbation, which limits vegetation growth.

2.4 Hydrology

Locally, tropical alpine regions are well known for their water supply. The Andean páramos provide reliable and high quality drinking water to the inter-andean valley. Large cities such as Quito and Bogotá, rely virtually completely (respectively around 85% and 95%) on surface water from the local páramos for their water supply and ubiquitous hydropower projects. Similarly, the Ethiopian highlands are important water sources for the dry lowlands. The small area of other African and Asian wetlands, as well as the wet climate in the lowlands of the latter, prevents them from playing an important role in the local water cycle. Nevertheless they can be important to sustain local ecosystems further downslope. Several mechanisms lead to the importance of afroalpine regions as “water towers” for the surrounding areas.

Similar to many other mountain regions in the world (Messerli et al., 2004; Viviroli et al., 2007), tropical mountain environments tend to have a higher precipitation regime than surrounding lowlands. For instance, Ecuadorian páramos (>3500 m) receive on average 16% more rainfall than stations in the interandean valley between 2500 and 3000 m (Fig. 3). The differences are more pronounced in mountain regions that have desertic lowlands, particularly the páramos of north Peru and the Ethiopian highlands.

Additionally, the low temperatures of highlands reduce evapotranspiration rates. In tropical alpine regions, transpiration is very low because of the frequency of fog, presence of cloud cover and high relative humidity, as well as the xerophytic properties of the vegetation. Literature values range from 0.7 to about 1.8 mm day⁻¹ (Hniatuk et al., 1976 in Van Royen, 1980; Hofstede et al., 1995). Therefore, the runoff ratio for tropical alpine regions is exceptionally high, ranging from 0.54 in the Simien mountains (Liu et al., 2008) up to 0.73 in Ecuador and Colombia (Buytaert et al., 2007b). In comparison, the entire Upper Blue Nile basin in Ethiopia, has a runoff ratio of only 0.18 (Conway, 2000), despite similar precipitation totals (resp. 1421 for Simien and 1467 mm year⁻¹ for the Upper Blue Nile basin, Conway, 2000; Liu et al., 2008).

The most remarkable feature of many tropical alpine regions, however, is their high water regulation capacity. Peak flow over base flow ratios can be as low as 5 for natural páramo catchments (Buytaert et al., 2004). Three main mechanisms for a high and constant baseflow are identified. First, temporal variability of rainfall is low in many tropical alpine regions, providing a relatively constant water input in the system. Furthermore, the very porous soils have a high infiltration and storage capacity, thus promoting subsurface runoff (Buytaert et al., 2006a, Villacis, 2008). Finally, the abundance of hydrologically disconnected areas in the irregular topography also gives rise to a large number of lakes and swamps, which further improve hydrological attenuation.

Snow cover and melt have only a very limited role in humid tropical wetlands. The lack of seasonality and strong diurnal temperature variations reduces snow cover to the night time, with little or no seasonal accumulation.

These specific hydrological processes are vulnerable to perturbation. Being headwater catchments, they rely entirely on meteorological water. Lacking the buffering role of groundwater contributions, changes in the spatial and temporal changes in the precipitation pattern may have a strong impact on hydrological processes, and therefore soil formation and ecosystem dynamics.

3 Past climate change in tropical Alpine environments

Tropical alpine regions have experienced strong climatic change in the past (Clapperton, 1993; Marchant et al., 2002; Hansen et al., 2003). In the tropical Andes, cool and wet conditions prevailed during the Middle Pleniglacial (60000 – 28000 years BP). These conditions favoured glacier extension down to 3500 – 3000 m, with some evidences occurring as low as 2900 m. During the subsequent Upper Pleniglacial (28000 – 14000 years BP), glaciers limits were forced upwards under much drier conditions (van der Hammen & Hooghiemstra, 2000; Thompson et al., 2000). Around 10000 years BP, the glacial limit was located at about 4000 m, from where it rapidly increased to its current location at about 5000 m above sea level (Thouret et al., 1996; van der Hammen & Hooghiemstra, 2000, Jomelli et al., 2009). In Colombia alone, the Pleistocene glaciation was around 2600 km², compared to the current 100 km² (Thouret et al., 1996). Similarly, ecological zones below the glaciers were located more downslope than present, which increased their areal coverage. For South America, an extensive overview is given by van der Hammen & Hooghiemstra (2000). The tropical glaciers of East Africa and Australasia have undergone a similar reduction. During the last glacial period, the Kilimanjaro glaciers reached down to an altitude of 3200 m. Since then they have gradually decreased in size, despite some intermittent periods of expansion. E.g., during the warm and wetter conditions of the African humid period (11 – 4 ka), most glaciers expanded (Thompson et al., 2002). Currently only discontinuous remnants occur above 4800 m (Kaser et al., 2004; Cullen et al., 2006). In New Guinea, the equilibrium line has increased from around 3600 – 4000 m during the last glacial maximum to around 4850 m (Prentice et al., 2005; Hastenrath, 2009).

Over the last decades, climatic and atmospheric changes have been observed for the entire tropics. Over the period 1960-1998, Malhi & Wright (2004) observed a temperature increase for the tropical rainforest regions of $0.26 \pm 0.05^{\circ}\text{C}$ per decade, with an intensification during the El Niño events. Rainfall has also changed in some tropical regions, declining about 4% per decade in northern tropical Africa and decreasing marginally in tropical Asia, while regional phenomena such as El Niño have increased in frequency (Malhi & Wright, 2004; Nepstad et al., 2004). However, it is

unknown to which extent these large scale trends, particularly in precipitation, are applicable to high mountain regions, which may show very different climate patterns than their surrounding lowlands (Urrutia & Vuille, 2009).

Locally, climate trends are often hard to prove. Trends of individual stations may not be statistically significant because of a lack of data, high natural variability, or both. The average temperature in the Colombian páramos of Cundinamarca, Tolima and Boyacá increased with 1°C, 0.9°C and 1.9°C respectively in the period from 1970 to 1990 (Castaño, 2002). At the same time, a decrease in monthly precipitation of about 5 - 10 mm was observed. Further south, in the Paute river basin the Ecuador Andes, no general precipitation trend could be observed, but a steady increase in seasonality was found (Timbe, 2004). In general, observed trends in most of the variables suggest an intensification of the water cycle during last decades (Huntington, 2006). Although scarce, these observations are consistent with projection of future climate change.

In the afroalpine regions, the longest meteorological time series are available from the Kilimanjaro. These records show a declining trend in precipitation since 1880, which was particularly pronounced at the end of 19th century (Kaser et al., 2004). An overall warming trend can be observed for most of the period since 1950 to present. Observations from neighbouring Amboseli indicate a local warming rate of 0.27°C per decade between 1976 and 2000. This is significantly higher than the global average (Agrawala et al., 2003). Both trends are consistent with empirical observations of enhanced glacier melt and fire risk over the last decades (Kaser, 1999; Thompson et al., 2002).

In New Guinea, meteorological time series are very scarce, but enhanced glacier melt has also been observed. The glacier limit on Mt. Jaya rose from 4620 m in 1947 to 4850 m in 2000, while the glacier on Puncack Madala has disappeared (Prentice et al., 2005; Hastenrath; 2009).

It is clear that these historical changes in climate patterns, and particularly the snow line, have had an important impact on the extension and characteristics of tropical alpine environments (e.g., Wille et al., 2002). Many current páramos were covered by glaciers during the last glacial

period. Therefore, soils and vegetation history are quite recent. For instance, the oldest tephra depositions found in the South Ecuador páramo coincide with local glacier retreat. Pollen records for the Laguna Pallcacocha (4060 m) of Cajas National Park start at about 15000 years BP. Those of the nearby Laguna Chorreras (3700 m) are about 2000 years older (Rodbell et al., 2002; Hansen et al., 2003). Similarly, the forest line has moved upwards from about 1500 m during the last glacial period to the current limit of about 3500 m.

Apart from areal extension, internal dynamics such as species composition and richness will have been affected. About this aspect far less information is available. Sediment cores suggest a similar herb vegetation during the late glacial period dominated by pteridophytes, Asteraceae and *Puya* spp. (Rodbell et al., 2002). Nevertheless, other evidence from pollen analysis suggests that historically wetter periods in the tropical Andes tended to have a higher biodiversity compared to dryer periods (van der Hammen & Hooghiemstra, 2000).

The information reviewed in this section can be used to relate the occurrence and characteristics of tropical alpine ecosystems to external conditions. However, it is questionable to which extent this information can be useful to predict the effects of global climate change. Future changes are expected to happen much quicker than historical changes, which is particularly important for biological processes such as species migration.

4 Expected climate change and its effects on tropical alpine ecosystems

4.1 Projections of future climate

It is expected that climate will warm over the coming century in response to changes in radiative forcing arising from anthropogenic emissions of greenhouse gases and aerosols (IPCC, 2007). However, small-scale temporal and spatial variability may still be dominated by natural fluctuations in the climate system or phenomena such as El Niño, anomalies of ocean heat or fluctuations in the thermohaline circulation.

Because of the high local variability, as well as limitations in climate models and data,

substantial uncertainty in future projections remains. Projections of temperature yield consistent results, with a mean increase in of about $3 \pm 1.5^{\circ}\text{C}$ over the Andes (Fig. 5). This increase is lower than over the Amazon basin, which may be due to the lack of adequate topographical representation, although regional climate model results suggest that warming over the Amazon is abnormally high due to local climate conditions (Urrutia & Vuille, 2009).

The projected precipitation changes are much more variable. For Ecuador and most of Colombia, on average an increase in yearly precipitation is expected, with values as high as 300 mm year^{-1} . Northern Colombia and Venezuela, regions that are primarily dominated by trade winds coming from the Caribbean basin, show an opposite trend with decreasing rainfall. The discrepancies between the different IPCC models, however are very high, typically often exceeding 50% (Fig. 5).

A major reason for the large discrepancy and low consistency of global circulation models is their inability to include the complex topography of the Andes, which may result in large prediction errors. The increase in air humidity related to increased temperatures and evapotranspiration is expected to lower the lapse rate. This means that higher altitudes may experience stronger warming. Reductions in albedo linked to decreasing snow and ice cover are also expected to increase the warming effect in high mountain areas (Fyfe & Flato, 1999), although in tropical mountains they may be relevant only at local scale. The complex topography finally results in steep gradients in local weather patterns, which are not properly represented in current GCMs.

4.2 Climate change effects on biodiversity

Tropical mountain ecosystems are classified as highly vulnerable to climate change impacts (IPCC, 2007) mainly due to the origin and actual spatial arrangement of the majority of the taxa, and the morphological and physiological adaptations of the species that evolved to allow them to live in a stress limiting environment. Many of these adaptations depend heavily in the air and leaf temperatures, on the spatial distribution of rainfall, atmospheric CO_2 level, and radiation. Climate

change is likely to disrupt and alter these processes, forcing species to move towards their new climatic niche or to die out. This is expected to result in higher rates of species loss and turnover under projected climate conditions. The impacts of the climate change in the tropical mountain biota are likely to act at different scales and in different forms, the most important of which are detailed in the following sections.

4.2.1 Shift in species ranges

At the species level, three general responses might occur due to climate change: movement, adaptation, or local extinction (Holt, 1990; Peterson et al., 2001). The effects of climate change will often reflect the interaction of these three mechanisms. Abrupt induced displacements of species distributions may ultimately lead to increased extinction rates as well as to significant impacts on the phenology and physiology patterns of any given area (Parmesan & Yohe, 2003).

However, individual species behaviour may differ widely. Mobile species may be able to track the geographic displacement of their ecological niches, while species that are capable of rapid evolutionary change or have a wide range of physiological tolerances, may adjust to changing ecological conditions and landscapes (Broennimann et al., 2006; Harrison et al., 2006).

In tropical alpine areas, certain life-history and niche characteristics might influence the likelihood that species will decline and suffer local extinction in the face of climate change. For instance, habitat specialists, especially those that exist in limited environmental space (Thuiller et al., 2005), such as at the tops of isolated mountains, are particularly susceptible to climate change (Foden et al. 2008). If the same patterns of range contraction and expansion, documented in other mountain systems (Grabherr et al., 1994; Peñuelas & Boada, 2003; Sanz-Elorza et al., 2003; Pauli et al., 2007) apply to the páramo flora, plant species associated to the super-páramo belt are the most threatened (e.g., species of the genera *Gentianella*, *Senecio*, *Draba*, *Azorella*, *Nototriche*) due to an expected contraction in their climate niche and the impossibility to migrate (Walther, 2003; Pauli et al. 2007). Many of them are restricted to small isolated páramo patches, thus the extinction of the

local population is the obliteration of the species in all of its range.

4.2.2 Shifts of major vegetation zones or biomes

Climate change impacts on geographical distribution of páramo vegetation are mainly determined by changes in temperature and humidity. An increase in temperature will induce an upward shift of altitudinal ecotone succession, leading to a loss of biodiversity at the ecosystem scale (beta and gamma diversity). With a constant lapse rate of about $0.6 - 0.7 \text{ } 100 \text{ m}^{-1}$, the current temperature projections would indicate that current temperature regimes will shift upward between about 140 and 800 m. Körner and Paulsen (2004) hypothesize that the upper forest line is limited by tissue growth as such, rather than photosynthesis or the carbon balance. The lower threshold temperature for tissue growth and development appears to be higher than 3°C and lower than 10°C , possibly in the $5.5 \pm 7.5^{\circ}\text{C}$ range, most commonly associated with seasonal means of air temperature at forest line positions. An increase on air temperature and solar radiation will enhance the temperature of páramo topsoil providing a feedback for an upward displacement of the upper forest line from its current position.

Changes in humidity will also have a significant impact. Increased air humidity may decrease the lapse rate, inducing stronger warming at high elevations (Urrutia & Vuille, 2009). Humidity has also a direct effect on ecosystem type and composition. The dependence of alpine regions on meteoric water and the resulting small storage capacity in many of the headwater catchments amplifies potential impacts of changes in precipitation and air humidity.

However, other external factors influencing ecosystem development and extension, such as geology, soil type and radiation, may further complicate the picture.

Finally, the extrapolations are hindered further by the existence of strong gradients in microconditions, determined by water climate variability, water table variations, and topographical conditions such as slope and wind sheltering. These microconditions may create ecological niches that may be characterized by positive feedback loops that stabilise their occurrence (i.e. Polylepsis).

spp and *Gynoxis* spp). Disturbance of such feedback loops may result in strongly non-linear ecosystem behaviour that hinders extrapolation.

4.2.3 Interactions between effects of climate change and habitat fragmentation

The fragmented, archipelago-like occurrence of the páramos is one of the major drivers of the high levels of endemism (Luteyn 1999). In the context of global change, this isolation is also one of the principal factors that make the páramo species highly vulnerable. The low genetic variability and low population numbers give the species a low genetic resilience. The continuous encroachment of pasture and croplands reduces the functional size of the páramo patches further. This decreases the connectivity with the upper montane forest, which eventually will be important to help species distribution shifts.

For relatively contiguous populations, adaptation to a warming climate will be aided by gene flow from populations in already warmer areas of the species range; for isolated populations, gene flow from neighbouring populations will be limited, as is the case for many páramo species. Therefore, the response of isolated populations to changing climate will depend on the level of climate-related variability already contained within the population. If the population contains considerable variability for the traits that determine the species response to climate (whether genetic or plastic), the population is likely to show a greater tolerance of changes in climate (in terms of plant fitness, Lynch & Lande, 1993; Rehfeldt et al., 1999) than if it were genetically less variable. We do not know the genetic resilience of tropical alpine plants and not even how isolated they are in terms of gene flow. More research is needed at the population scale to understand these processes, document the genetic variability of the most vulnerable páramo plants and suggest mitigation measures.

4.3 *Effects on soils and the carbon cycle*

Tropical alpine areas can be significant carbon stores, mainly below the land surface. No

detailed studies about the carbon storage in the vegetation layer are available. In open, temperate peatlands, dry biomass is around 760 g m^{-2} (Gorham, 1991). This is probably indicative for most tropical alpine regions dominated by grassland, although it may be higher in some specific regions such as bamboo páramos. Additionally, most páramos store large amounts of carbon in their soils. This is particularly the case in valley bottoms and depressions with deep soils, where peat accumulation is common and soil organic C concentrations may reach values over 40% (Buytaert et al., 2006b).

The impacts of climate change on soil organic carbon storage are twofold. Under climate change conditions, a new natural soil organic carbon equilibrium will be reached. As a secondary effect, climate change will induce land use and cover changes that also affect carbon storage. New equilibrium states are hard to generalize due to the highly variable and often unique soil properties and local settings. However, identifying trends between environmental conditions and soil organic carbon accumulation at a regional scale can be used to model the impact of climate change on soil organic carbon.

An increase in temperature will accelerate microbial and fungal activity, resulting in faster decomposition. A decrease in total precipitation and a stronger or longer dry season will induce dryer soil conditions during at least some part of the year, which may also accelerate decomposition. The velocity of this process, as well as the equilibrium conditions depend strongly on the local conditions. For wet, volcanic páramos in south Ecuador, Buytaert et al. (2006b) found that soil wetness may be of secondary importance in carbon accumulation compared to temperature and organometallic complexation (Fig 5a). However, significant correlations between precipitation trends and soil organic carbon accumulation are often present at a regional scale (Fig 5b).

For climate change induced land use and cover changes, different future scenarios need to be considered. If páramos are replaced by other natural biomes, a potential loss of belowground carbon storage may be compensated by increased aboveground storage. Tropical upper montane forests are the most common natural ecosystem below the páramo belt. Soil organic carbon tends to be lower

in soils of these forests, but these forests develop thick litter layers and store considerable amounts of carbon in the vegetation layer. As a result, the total carbon storage may reach levels similar to the páramos (see e.g., Davidson & Janssens, 2006, for a global discussion of this trade-off).

However many tropical alpine areas have considerable human activity. Due the high pressure for arable land (Dercon et al., 1998), an increasing temperature will therefore more likely lead to an encroachment of tropical alpine grassland by agriculture rather than forest. Land use types currently found in the zone below are mainly cattle grazing and smallholder farming. Carbon storage under these land uses, both above- and below ground, is low due to the lack of fertilisation and manuring combined with high erosion levels (Vanacker et al., 2003; Dercon et al., 2007). Such evolution would therefore lead to a net reduction of the carbon storage of tropical alpine regions.

In view of potential contributions to the greenhouse effect, the continuous CO₂ uptake of wetland soils is partly offset by the production and release of CH₄ and NH₂ which have a stronger warming potential than CH₄ (Gorham, 1991). Although this may result in some wetlands being carbon positive (Bragg, 2002), the impact of the world's wetlands on climate radiative forcing is thought to be negative with about -0.2 to -0.5 W m⁻² (Frolking & Roulet, 2007). Specific studies on mountain wetlands do not exist. The main factors influencing methane production are the available substrate, production and oxidation in the soil, and transport of methane to the atmosphere (Wania, 2007). The presence of organometallic complexes in many páramo soils may have an impact on substrate availability, while the different climate pattern and potentially different micro-organisms may affect metabolic reaction rates. As such, figures on methane emissions in temperate wetlands, where most research has been done, may be difficult to extrapolate to tropical mountain regions (van Huissteden, 2004). In future climate conditions, methane production in wetlands is expected to increase due increased temperatures (van Huissteden, 2004).

Finally, indirect responses to environmental change may provide positive or negative feedbacks on soil properties. Changes in soil properties are strongly related to their hydrology. Perennially saturated areas may start to experience unsaturated conditions during the year if

minimum rainfall falls below a certain level thus affecting both carbon sequestration and methane emission. Fire regimes, partly controlled by humidity and temperature, may change with humidity conditions and alter the vegetation. In current conditions, burning often has only a minor impact on soil properties due to the high water content of the soil (Hofstede, 1995). Drier soil conditions may thus increase damage caused by frequent fires.

4.4 Effects on the water cycle

Environmental change has a direct and strong effect on water resources (IPCC, 2007; Arnell, 1999). The higher temperatures and energy content of the atmosphere are expected to intensify the global water cycle, resulting in higher rainfall intensities and stronger temporal patterns in many places (Huntington, 2006). Climate change impacts include temperature, and timing, quantity and spatial distribution of precipitation. Being the headwaters of many mountain regions, tropical alpine regions are relatively independent from hydrological changes in other systems. One notable exception are regions with tropical glaciers, present in the Andes of Bolivia, Peru, Ecuador and Colombia, as well as Mount Kenya and Kilimanjaro in Africa. Stream discharge from many tropical glaciers is currently above the long-term average because of increased melting but it is expected to reduce drastically in the future due to the areal decrease or disappearance of many glaciers (Vuille et al., 2008).

In most humid tropical alpine regions, such as Colombia and Ecuador, the production of glacier runoff is minimal and only locally significant. The lower contribution of glacier melt may intensify the shift towards a drier páramo climate (Villacis, 2008). Also, local wetlands that rely strongly on water influx from glaciers may change drastically or disappear. In the drier highlands of Peru and Bolivia, the impacts of reduced glacier water production on water supply systems may be much more important (Bradley et al., 2006; Vuille et al., 2008).

Changes in precipitation patterns will affect the water cycle directly. As alpine regions have low evapotranspiration rates and therefore a relatively high water production (Buytaert et al.,

2007b), the absolute changes in the flow patterns will be higher than other ecosystems with similar precipitation patterns. Currently, the high water storage and regulation capacity of many páramos is able to bridge fairly large dry periods while maintaining a significant base flow (Buytaert et al., 2006a). However, the actual water residence time and therefore the water regulating capacity of páramos has never been quantified. Additionally, in the long term, the hydrophysical soil properties that provide the mechanism behind the high water storage and regulation may be negatively affected by accelerated organic matter decomposition, further reducing base flows.

Changes in groundwater recharge are likely to be small. Glacier compaction and abrasion have often resulted in a low permeability of the substrate of the headwater catchments, sharply contrasting to the high permeability of the topsoil layer. As such deep infiltration is limited by permeability rather than soil water content. Only in dry or very permeable locations such as morene deposits, the change in deep infiltration will be proportional to the change in precipitation.

The increase in temperature will affect evapotranspiration rates directly. Currently, evapotranspiration is low, mainly due to the frequency of fog in contact with páramo vegetation, and presence of cloud cover. These phenomena result in less solar radiation, a higher air humidity and a low temperature. Finally, the xerophytic properties of the vegetation play a role. In the abundant open water surfaces, temperature increases will have a maximum effect. In densely vegetated areas, the increase in evaporation may be aggravated by the replacement of indigenous low consumption species with exotic species that have less expressed or no xerophytic properties. The extent to which this will occur is not fully clear.

Finally, changes in the wetland ecosystem and other neighbouring ecosystems may have important feedbacks on the local climate pattern. However, these mechanisms are so complex that no successful efforts are known on quantifying or modelling the process. Changes in downslope cloud forest may either increase cloudiness (by higher evaporation), or decrease it (through higher interception) compared to other land covers.

A main obstacle for prediction these and other local impacts of climate change on

hydrological processes is the coarse resolution of current climate change projections (Fig. 5). Most GCMs currently have a resolution of several degrees, which is far too coarse as an input for hydrological models (e.g., Salathé Jr (2003) recommends a maximum resolution of 0.125 for hydrological simulations in mountainous catchments). The use of downscaling models, which may bridge the difference in resolution between global circulation models and hydrological models, is currently in their infancy, particularly in tropical regions.

5 Conclusions and future research

This overview shows that climate change has a potentially important impact on the environmental services of tropical alpine regions. Biodiversity will suffer, especially species that are unable to adapt to the fast changing conditions. The carbon cycle may evolve towards smaller carbon storage of the soils, while water production and local storage and regulation may decrease. The number of potential mitigation strategies is limited. From a water resources perspective, a degradation of the water regulation capacity can be counteracted by building storage reservoirs, but this is a very costly measure with serious impacts on the local environment. Additionally, technical adaptation strategies are currently constrained by a lack of knowledge. As long as no detailed predictions can be made, designing the technical details of adaptation measures is impossible.

However, many of the changes expected to happen in climate change conditions are very similar to the impacts observed by present human activities. Cultivation, forestry and intensive livestock grazing may also lead to biodiversity loss and soil carbon reduction in many tropical highlands (Yimer et al., 2007; Farley et al., 2004). Specific practices, such as artificial wetland drainage and the use of high water consuming pinus species in forestry, drastically reduce water production, particularly base flows (Buytaert et al., 2006a, 2007b). Removal of the original vegetation, intensive ploughing and draining often result in irreversible soil structure degradation, loss of organic carbon content and erosion (Poulenard et al., 2001; Podwojewski et al., 2002), intensifying the reduction of the soil water storage and regulation capacity. Consequently, the best

adaptation option may be the protection of those regions that either are very fragile to climate change and those which are most probable to survive in future conditions.

Irrespective of the choice for conservation or technical adaptation strategies, a better insight in the current processes and their interrelationships (Young & Lipton, 2006), is necessary for improved conservation of the páramos and their environmental services. From the foregoing discussion, the following research priorities are derived:

- Long term monitoring of biophysical conditions of tropical alpine ecosystems is necessary. Monitoring should focus particularly on water and carbon fluxes and biodiversity, as well as their temporal and spatial distribution. Monitoring of environmental processes in tropical alpine is very limited. Lack of resources, difficult conditions such as harsh weather and remoteness, and a low economic interest are reasons outside the scope of science. However, the extraordinary properties and high variability of tropical alpine regions often require a tailored approach. For instance, automatic soil moisture monitoring using time domain reflectometry probes is complicated by the high water content and swell and shrink properties of the soils (Topp & Davis, 1985). Methods need to be developed to cope with climatological extremes, and variability. New technologies such as wireless environmental sensor networks should be explored (Hart & Martinez, 2006).
- The development of process-level models that can extract maximum information from scarce and potentially low quality data. Many conceptual climatic, hydrological and ecological models developed for very different environments may not be applicable. For instance, very few precipitation downscaling techniques have been tested for tropical mountain regions (Fowler et al., 2007). Currently available methods are mainly based on point measurements, and will probably be unable to represent a high spatial variability (e.g., Céleri et al., 2007). New data availability such as remotely sensed precipitation images may be a useful additional source of information for such models (e.g., Bendix, 2000; Sklenář et al., 2008).
- The data scarcity of tropical alpine environments requires the development of simple and robust

decision support tools for ecosystem services management and conservation. Conceptually simple methods are often preferable over complex hydrological models, as the latter have data requirements that are hard to satisfy. Complex models are also difficult to calibrate and may contain large uncertainties due to equifinality of their parameters or low quality input data (Beven, 2006). However, a proper uncertainty analysis of such models can provide useful insights in the potential of new data to improve environmental predictions. This is essential for prioritizing research program resources (e.g., measurement campaigns) to target management decisions most efficiently.

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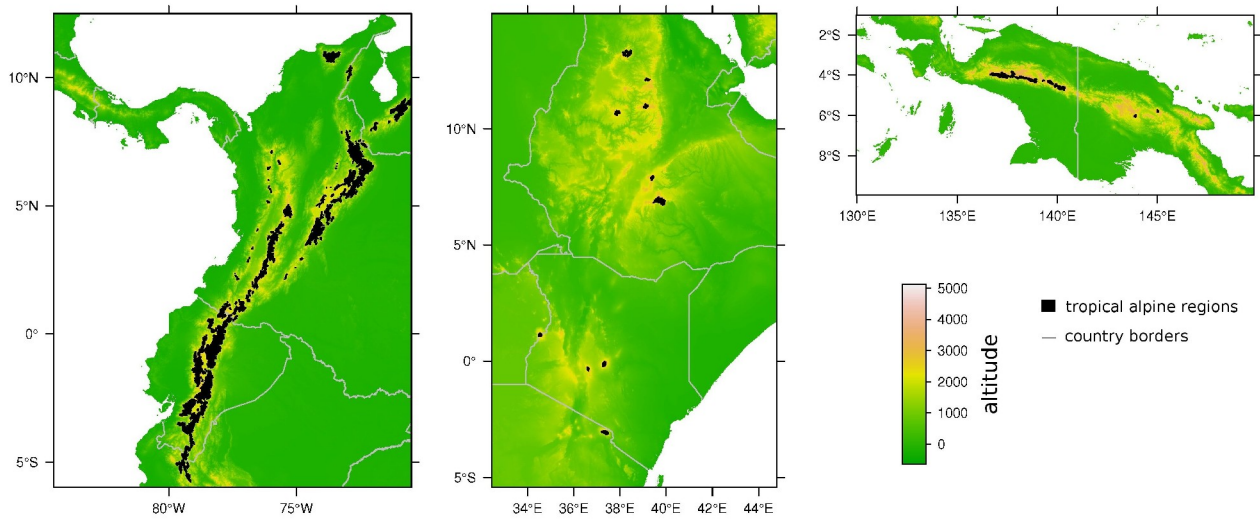


Figure 1: Extension of tropical alpine environments (black) in South America (left), East Africa (central) and New Guinea (right).



Figure 2: View over the páramos of Chingaza National Park, Colombia. Note the conspicuous *Espeletia killipii* in the foreground.

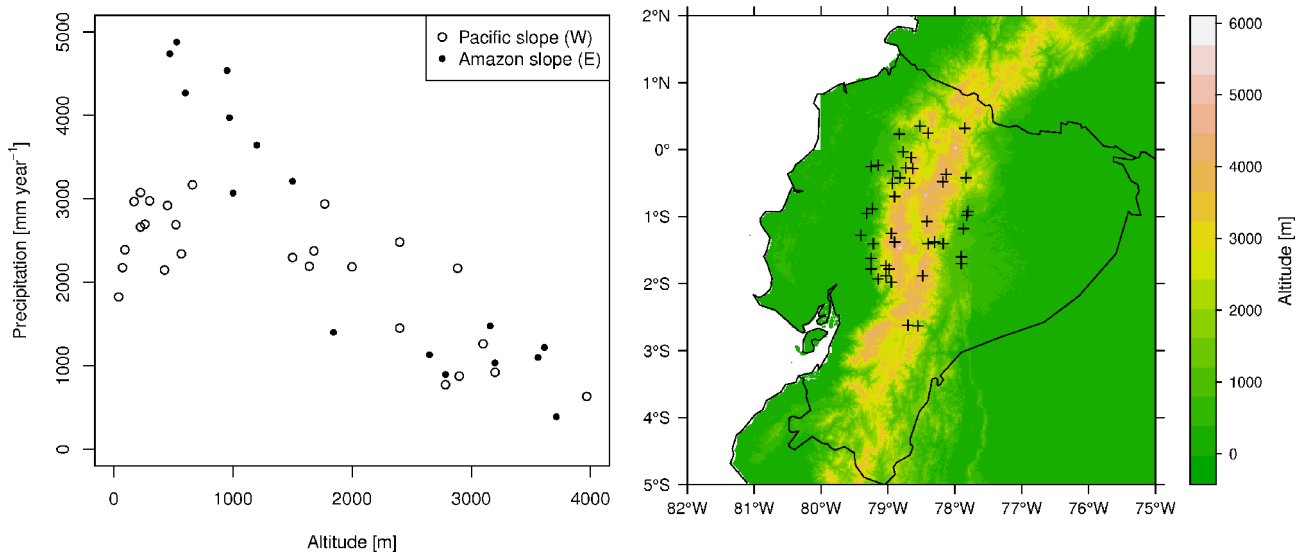


Figure 3: Left: Gradients of average yearly precipitation on the outside slopes of the north and central Ecuadorian Andes during the 1960 – 1980 period. Data are from the NOAA Global Historical Climatology Network. Right: location of the rain gauges.

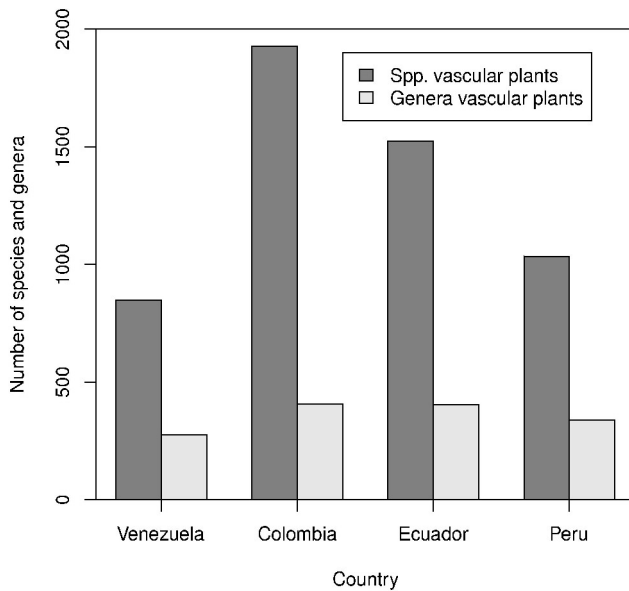


Figure 4: Number of species and genera of vascular plants registered for the Andean páramos per country (after Sklenář & Balslev, 2005).

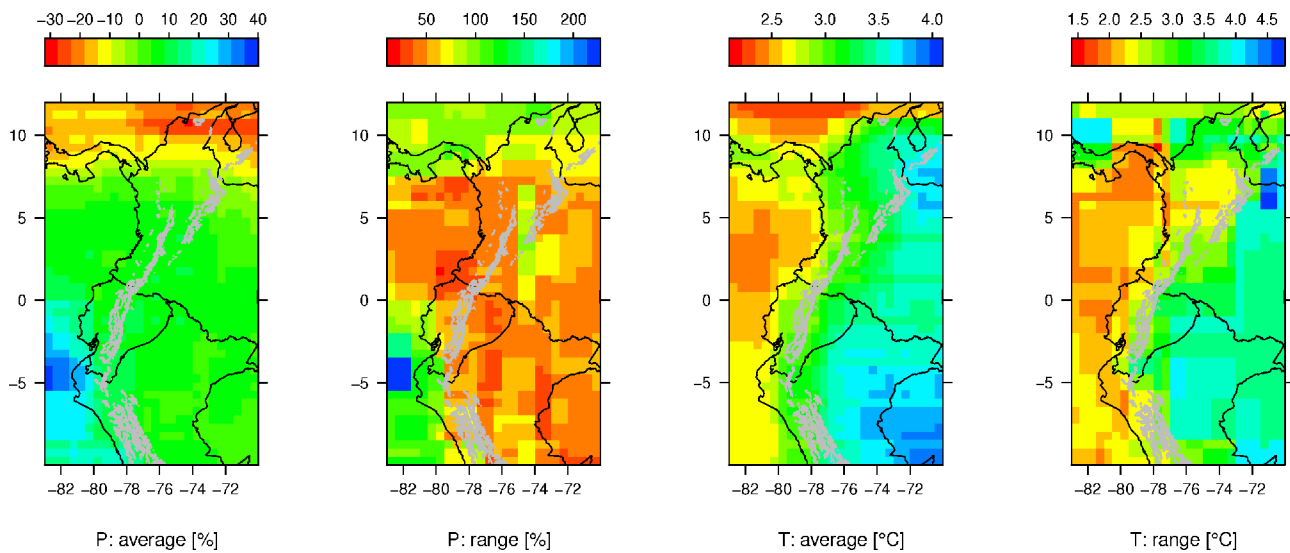


Figure 5: Average and range of the predicted anomalies in temperature (T) and precipitation (P) in the tropical Andes, during the period 2080 – 2099 and for the A1B emission scenario. The models used in the GCM ensemble are those of the IPCC 4th assessment report (IPCC, 2007): UKMO-HADCM3, UKMO-HADGEM1, NCAR-CCSM3, BCCR-BCM2, CCCMA-CGCM3.1-T47, CNRM-CM3, CONS-ECHO-G, CSIRO-MK3, GFDL-CM2, GFDL-CM2.1, INM-CM3, IPSL-CM4, LASG-FGOALS-G1.0, MPIM-ECHAM5, MRI-CGCM2.3.2, NASA-GISS-AOM, NASA-GISS-EH, NIES-MIROC3.2-HI, NIES-MIROC3.2-MED. All models were rescaled to a common resolution of 0.5° using the nearest neighbour approach before averaging. The limit of the tropical alpine region is delineated in grey. Data were obtained through the IPCC Data Distribution Centre (IPCC, 2007).

Table 1: Number of C3 and C4 species in the páramo bioma in the Northern and Central Andes (León and Young, 2007, pers. comm.).

Region	Family	C3	C4
Páramo	Poaceae	34	7
Puna	Poaceae	36	12