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I declare that I wrote this thesis by myself with advice of my supervisor. All literature sources are mention in literature cited. Print version is identical to electronic version in SIS.

In Frýdštejn, 18. 8. 2011

Summary

Paramo is the name of the region encountered in the upper belt (3 000m – 4 800m) of the Andean mountain ridges from Venezuela to the North of Peru. Paramo ecosystem occupies only 2% of the area of those countries. Nevertheless, paramo flora is the richest high mountain flora of the world (over 3500 species, 60% of endemism). High mountain region of the Northern Andes were almost uninhabited until the arrival of the Conquistadores. At the time of the conquest, livestock and new crops were introduced to the Andean ecosystems. Since that time, paramo has been used mainly for extensive cattle grazing and cultivation of potatoes and onions. During the last three centuries an abrupt intensification of the agricultural practices has occurred. The main aim of this study is to investigate the effects of human intervention, by mean of farming, on species diversity of the paramo vegetation. The study area was selected in the paramo belt of Santurban, Colombian Eastern Cordillera. Ordination techniques were applied to analyze the relation between plant species composition, environmental variables and management variables. We found plant species diversity is influenced by cattle grazing and cropping, but the vegetation changes are mainly determined by the altitudinal gradient. Intensity of human impact is also related to altitude. In Santurban, intensity of human impact decrease with increasing altitude whereas diversity of plants increase with increasing altitude.

Keywords: paramo, diversity, human influence, paramo vegetation, human impact, plant diversity, Santurban.

Abstrakt

Paramo je ekosystém nacházející se pod vrcholy And, přibližně mezi 3000 a 4800 m n. m., od Venezuely do severní části Peru. Paramo zaujímá pouze 2% z celkové rozlohy těchto zemí, přesto je jeho flora nejbohatší ze všech tropických alpínských ekosystémů na světě (přes 3500 druhů cévnatých rostlin, z nich 60% jsou druhy endemické). Zavedení nových zemědělských systémů během kolonizačních období Andskou krajinu hluboce zasáhlo. Od té doby je oblast parama využívána zejména na extenzivní chov dobytka či pěstování brambor a cibulí. Během posledních tří set let dochází k prudkému trendu intenzifikace zemědělské produkce. V této studii byl zkoumán antropogenní vliv na druhovou diverzitu paramových rostlin. Studijní oblast se nachází v severní části východní Kolumbijské Kordillery, v tzv. Komplex Paramo de Santurban. V Komplexu Paramo de Santurban, se vzrůstající nadmořskou výškou druhová diverzita rostlin roste a intenzita lidského zásahu naopak klesá. Korespondenční analýzy ukazují vztah mezi druhovou diverzitou rostlin a intenzitou pastvy a pěstování. Nicméně, druhové složení vegetace je silně vázáno na nadmořskou výšku.

Chapter 1

Introduction

The Andes ranges are considered a biodiversity hotspot. This fact has two meanings. First of all, it is a biologically rich region with a unique diversity of species. Secondly, all this richness is threatened by changing environmental parameters. A region is considered a hotspot when it meets two conditions: at least 0.5% of its vascular plant must be endemic species and at least 70% of the primary vegetation has already been destroyed (Myers et al 2000). There are more than thirty biodiversity hotspots all over the world and there are several International Organizations that are working in many ways to conserve these regions.

Paramo is the name of the regions located in the upper belt of the Andean ridges (3000 to 4800 m. s. l) from Venezuela to the northern of Peru (Van der Hammen & Cleef 1986). The paramo flora is by far the richest one from high mountains in the World. Although the paramo ecosystem occupies no more than 2% of land area of the countries in which it is found; more than 3500 species of vascular plants are encountered there (Luteyn 1999, Sklenár et al 2011).

In addition to the biological value that is related to its diversity of species, one of the main ecological values of the natural paramo is its high water retention capacity: precipitation surplus in wet periods is stored in vegetation and soils, which can be liberated in dryer periods (Hofstede 1995). By far the majority of the population of Ecuador and Colombia is dependent on drinking water directly from paramo or from streams which originate there. Hydroelectric power plants, which are frequently constructed at high altitude, are also dependent of the paramo stream water.

The paramo was a little inhabited region until the Spanish conquer time (Monasterio 1981). The spectacular sceneries of these upper Andean regions were even considered such as a sacred place for some native cultures in the past. Today the paramos are inhabited by some ethnic groups and peasants who work mainly in potato cultivation and cattle farming. These activities have followed different socio economical processes directed to the intensification of the agriculture practices (Brush 1982).

The main aim of this study is to investigate the effects of human intervention, by mean of livestock and cropping on species diversity of the paramo vegetation. The study area was selected in the paramo belt of Santurban, Colombian Eastern Cordillera. The study was carried out by quantifying plant species composition and estimating intensity of human impact. Ordination techniques were used to analyze the relation between vegetation, human impact and environmental variables.

The following aims were formulated:

1) Estimate the species composition and species diversity of the vegetation of the paramo Santurban.

2) Estimate the intensity of human intervention related to cropping and grazing in the paramo Santurban.

3) Estimate the effect of those activities on the plant species richness and plant species diversity of the paramo Santurban.

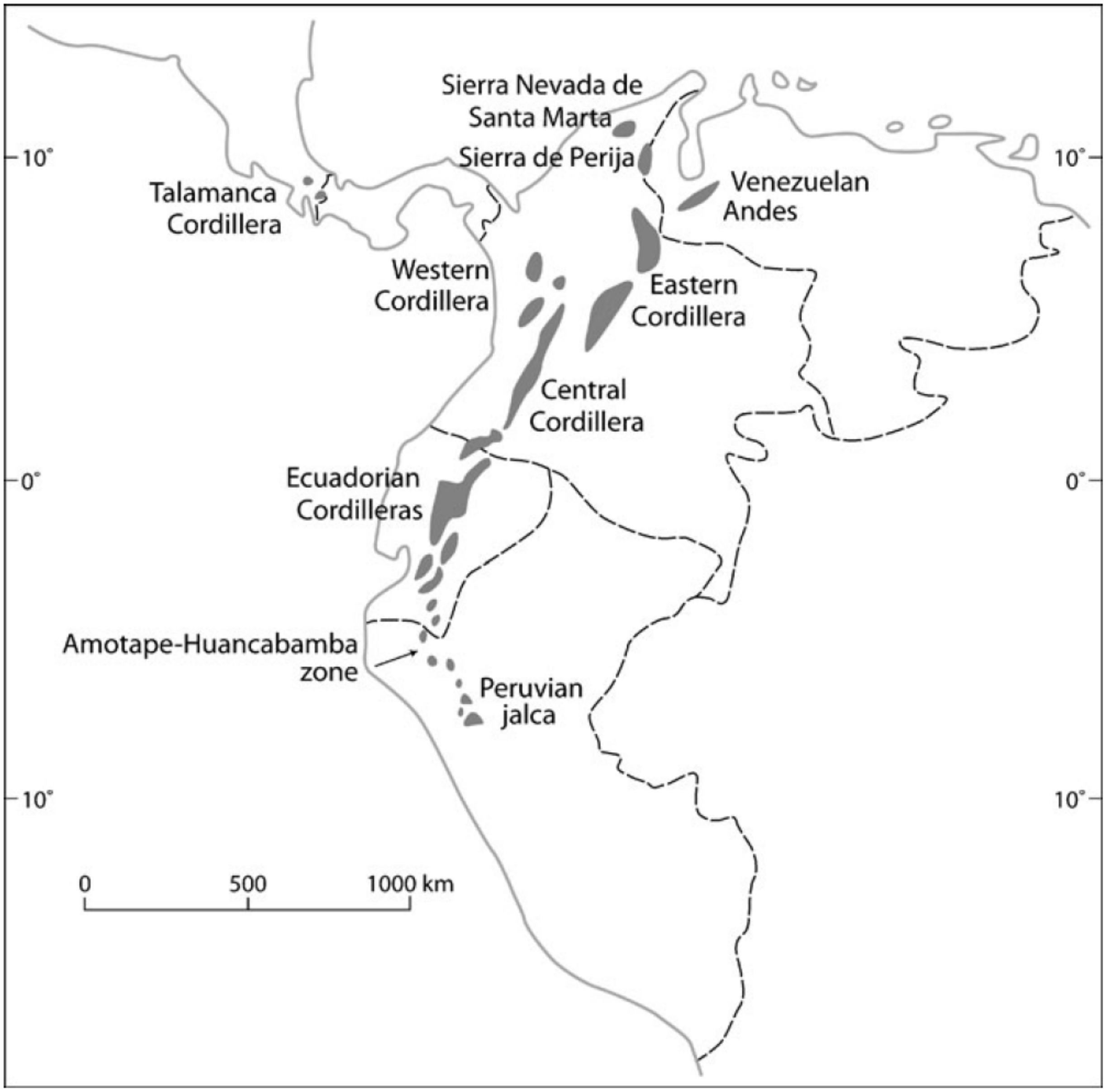
4) Estimate the changes on vegetation caused by grazing and cropping.

Chapter 2

Literature Review

Tropical alpine ecosystems are regions encountered between the upper limit of continuous, closed-canopy forest (often around 3000-3900 m) and the upper limit of plant life (often around 4600 - 4900 m) (Rundel et al 2008). Tropical alpine ecosystems of the Northern Andes are called “paramo”. The Northern Andes stretch from Venezuela and Colombia to the Amotape-Huancabamba zone in northern Peru. Paramo ecosystem is discontinuously distributed, the main extension is found in Colombia and outliners are encountered in Panama, Costa Rica and Northern Peru (fig. 1) (Van der Hammen & Cleef 1986). The lower boundary of is difficult to define since the natural timberline has been eliminated by man in a lot of mountains. The word paramo comes from the Latin word “Paramus” (Ellenberg 1979). The early Spanish conquistadores used that word to define the north Andean areas that were high, cold and inhospitable. They associated those areas with the arid plain of Castile, which was called “paramera”. Nowadays, in Colombia, Ecuador and Venezuela, we found some words expressions as: "estoy emparamado", that one might say, when is getting wet because of rain and cold. "paramitos" referred to atmospheric moisture in the form of drizzle. The term "parameando" has come to mean is "it is raining" (Monasterio 1981, Ramsay 1992, pers. observations).

Figure 1. Geographic delimitation of the paramo ecosystem in Central and South America with names of the major mountain ranges (Sklenar et al. 2011).



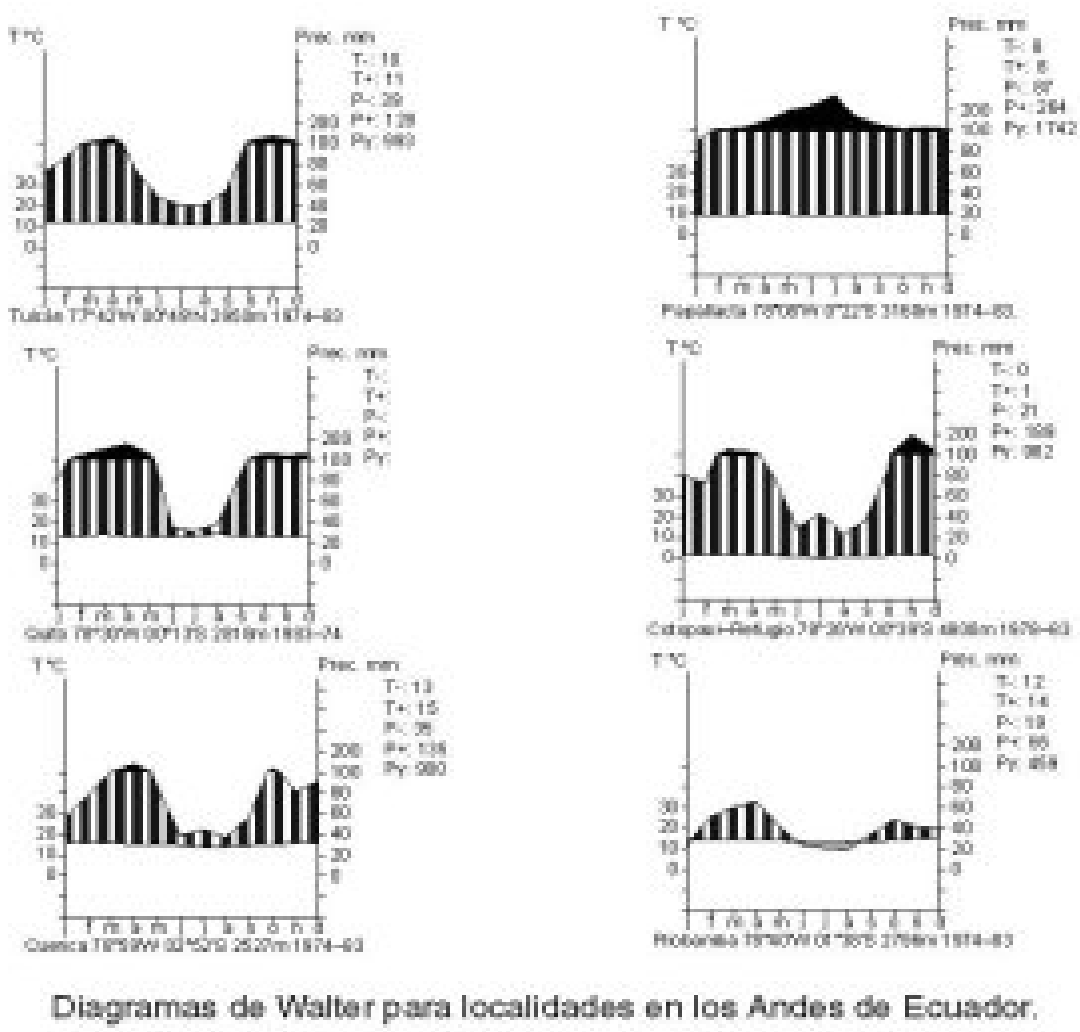
2.1. Climatic characteristic of the paramo ecosystem

Climate of the tropical high Andes is characterized by pronounced daily and minimal seasonal temperature oscillations. Diurnal ranges of temperature change are commonly 3-10 times greater than seasonal changes. This contrasts markedly from alpine environments in high latitudes where seasonal temperature changes are large and diurnal changes relatively small. Seasonal changes in temperature reply to global pattern of irradiance. Low tropical latitudes are regions of net heat gain and have relatively constant levels of solar irradiance over annual cycles. Over a 12-month cycle at the equator, for example, the daily maximum irradiance is only 13% higher than the minimum level. This ratio remains relatively small up to the latitudes of the Tropic of Cancer and Tropic of Capricorn where it reaches about 60% but thereafter increases much more sharply toward higher latitudes (Rundel et al 2008).

Paramos regions have a generally cold and humid climate with sudden changes in the weather and a diurnal fluctuation in temperature from below freezing to as much as 30°C (Fig.2). Paramo of regions of Venezuela, Colombia and Ecuador are influenced by the intertropical convergence of air masses, because of their geographical location near the Equator. They are generally humid throughout all or most months of the year (with a few notable exceptions) and highly stable seasonal patterns of change in both maximum and minimum monthly temperatures. Many regions receive more than 2000 mm of rain on their exposed slopes (absolute range 500-ca. 3000 mm/year). They have a high relative humidity averaging 70-85% (absolute range 25-100%). Paramo becomes driest near its southern limits in southern Ecuador and northern Peru, where they are influenced by two air masses, one from the Amazon Basin, which has already released its moisture on the eastern slopes, and another dry cool air mass from the West under the influence of the Humboldt Current. Local microclimates may strongly influence regional weather patterns (Luteyn 1999).

Although overall mean annual temperatures of paramo range from 2°C to 10°C, there is much greater contrast in the climate of higher elevation areas than the climate found in lower zones of the same mountain ranges. Therefore, the environment becomes harsher and more severe for plant life as altitude increases. (Luteyn 1999).

Figure 2. Overall climate of paramo by the use of climate diagrams from some localities in Ecuador (Luteyn 1999).



2.2. Characteristic of the soils

Most paramo soils are relatively young and only slightly developed, and are broadly classified into the orders Andosols, Inceptisols, Histosols, Entisols, and Mollisols (Cleef 1981). Andosols are soils derived from volcanic ashes, are wet, black coloured and have a low bulk density. Particularly in Andosols, decomposition is seriously retarded because of the protection of soil organic matter against bio-degradation by the formation of organic-metallic complexes. Consequently the total stock of nutrients may be high, but the amount of nutrients available for the plant is low (Hofstede 1995). Histosols are highly organic soils and are found in very wet places such as bogs and swamps. Entisols are soils that have little or no evidence of development (i.e., absence of horizons) and have a highly mineral nature. These are often found near snow line and Mollisols are a less common soil group in the paramo, are very dark colored and base-rich. Paramo soils at the highest elevations are very shallow and coarse with a high percentage of soil and sand. They are extremely infertile, have low water retention and practically no ability to hold exchangeable cations since are so poor in organic matter. Furthermore, at high altitudes, soil-moving phenomena such as frost-heaving and thawing and sorting of material is common. Paramo soils at lower elevations are relatively deep, humid, black or dark brownish, and acidic with pH ranging from about 3.7 to 5.5 (Luteyn 1999).

2.3. Paramo vegetation

The paramo flora is the richest high mountain flora of the world (Sklenár et al 2011, Tab. 1). Although the paramo ecosystem occupies no more than 2% of the land area of the countries in which it is found, the flora is extremely divers. The recently compiled species list of paramos, ranging from Costa Rica to northern Peru, includes 1298 and 3399 species of non-vascular and vascular plants, respectively (Luteyn 1999). General floristic diversity of paramo flora is presented in table 2. Asteraceae and Poaceae are the largest family in numbers of species and genera, followed by. Four of the five most speciose paramo genera of Asteraceae are: *Pentacalia*, *Senecio*, *Diplostephium* and *Espeletia*. The largest genera of Poaceae are *Festuca*, *Calamagrostis*, *Agrostis*, and *Poa* (Luteyn 1999, Sklenár et al 2005).

Tab. 1. Vascular plant diversity in tropical alpine floras of Central and South America (paramo), Africa (Afroalpine), and New Guinea with estimated ages in Mya of respective alpine habitats (Sklenar et al. 2010).

	Páramo	Afroalpine	New Guinea
Families	127	44	84
Genera	509	139	226
Species	3,564	371	1,118
Estimated age	3–5 Mya	0.1–23 Mya	~1.8 Mya

Table 2. Fifteen largest families and genera of paramo flowering plants (Luteyn 1999)

Family (no. gen./spp.)	**Genus (and family) (no. spp.)**
Asteraceae (101/858)	*Pentacalia* (Asteraceae) (89)
Poaceae (41/227)	*Senecio* s.s. (Asteraceae) (69)
Orchidaceae (25/152)	(*Senecio* s.l. =172)
Scrophulariaceae (14/144)	*Diplostephium* (Asteraceae) (70)
Melastomataceae (9/107)	*Calceolaria* (Scrophulariaceae) (65)
Gentianaceae (4/93)	*Espeletia* s.s. (Asteraceae) (61)
Ericaceae (16/79)	(*Espeletia* s.l. =123)
Bromeliaceae (6/78)	*Lupinus* (Fabaceae) (56)*
Rosaceae (10/77)	*Valeriana* (Valerianaceae) (54)
Fabaceaea (9/76)	*Hypericum* (Clusiaceae) (54)
Brassicaceae (13/71)	*Miconia* (Melastomataceae) (54)
Cyperaceae (8/70)	*Gentianella* (Gentianaceae) (48)
Apiaceae (15/61)	*Puya* (Bromeliaceae) (48)
Solanaceae (8/58)	*Gynoxys* (Asteraceae) (46)
Clusiaceae (2/56)	*Baccharis* (Asteraceae) (45)
	Draba (Brassicaceae) (45)
	Geranium (Geraniaceae) (43)

*Rupert Barneby, who studied *Lupinus*, felt there are only about 15 species in the genus. If this is true the overall family number drops to ca. 35 species.

2.3.1. Evolution of paramo flora

Paramo flora is linked to the Andes orogeny. Andes emerged above treeline near the end of the Pliocene (3–5 Mya). During uplift, a semi-open vegetation is believed to have occurred on hilltops in the Andean region, determined by local climate or edaphic conditions. This hypothetical preparamo vegetation contained elements of savanna and subandean forest and might have been an important source of the neotropical element in modern paramo. By gradual enrichment of protoparamo the modern paramo ecosystem evolved during the Pleistocene. During the pleistocene, vegetation zone were shifted altitudinally as many glacial cycles occurred. Many of the isolated paramos merged, and the ecosystem as a whole covered an area many times larger than the present one. (Van der Hammen & Cleef 1986).

For the evolution of the paramo flora, speciation within paramo groups has been very important. Species evolution within paramo groups has been enhanced by several mechanisms as: repeated isolation and expansion of plant populations due to climatic oscillations during the Plio-Pleistocene, interaction with pollinators leading to diversified flower morphology, and habitat heterogeneity. Fascinating examples of adaptive radiation are found in several taxa as the composite subtribe Espeletiinae, *Valeriana*, *Gentianella*, and *Lupinus* (Cuantrecasas 1986, Luteyn 1999, Sklenár et al 2011).

2.3.2 Physiognomy of paramo vegetation

Most high elevation tropical plant communities have a characteristic physiognomy, which repeats in geographically disjunctive areas of the world where they occur, for example, South America, East Africa, and Hawaii. The growth forms that characterize this physiognomy are examples of convergent evolution: the forms evolved independently in several different plant families on distant continents in response to the unique high altitude tropical environments. These growth forms often result from ecological and morphological adaptation (Hedberg & Hedberg, 1979, Ramsay & Oxley 1997)

Paramo has its own important and conspicuous growth forms, although not all of which are strictly found in paramo. The presence of rosette plants (some of giant size) is probably a good general indicator of paramo and seems to be one of the clearest distinctions between high elevation areas of tropical and temperate latitudes. According to Hedberg and Hedberg (1979) and Ramsay and Oxley (1997) the most characteristic growth forms of the high elevation paramos are summarized below.

Rosette Plants - Two kinds of rosette plants have been described: Stem rosette. The most typical and well known growth form of paramo is the columnar woolly rosette plant. Members of the genus *Espeletia* (Asteraceae), are the classical example. These plants produce an erect, normally unbranched, thick-woody stem tightly encased by the dense bases of old leaves . The erect stems may be as tall as 15 meters in undisturbed paramo. Lateral inflorescences are produced from the single aerial meristem.

Acaulescent rosette. These plants develop thick, perennial, tap-roots and a dense rosette of leaves at the ground level. The flowering stems may be very short with the flowers hidden in and amongst the leaf bases, or longer thereby lifting the flowers above the ground surface. Some plants, such as *Puya* spp. (Bromeliaceae), produce giant, bulky inflorescences several meters tall. In all cases, the buds that form the flowers originate in the axils of the rosette leaves, which are sunken a few centimeters below the ground. Acaulescent plants thereby protect their buds from fire and frost. Some examples are: genera *Hypochaeris* , *Paepalanthus* (Eriocaulaceae) *Acaena cylindristachya* (Rosaceae) and *Valeriana plantaginea* (Valerianaceae).

Cushion Plants - These plants form a flat, convex, or hemispherical cushion as the result of the regular outward branching of dense radially oriented buds. Each branch has a small rosette of leaves at the tip and only the outer and upper leaves are green and living; the interior of the cushion consists of a peaty mass, the remains of dried leaves, accumulated humus, dust, soil, and rain water, all of which protect the buds and stems from wind, desiccation and predation, and provide a reservoir of water and nutrients. Like in rosette plants, the mean temperature is higher within the cushion than at the cushion surface, thereby protecting the buds from cold temperatures. The plants are often very prickly and hard to the touch, yet firm enough that one is able to walk on top of certain species, such as in *Azorella* (Apiaceae), *Plantago* (Plantaginaceae).

Tussock Grasses - This growth form is the most widespread in the paramo. In undisturbed areas, grasses may average 1-1.5 m tall with a coverage of up to 100%. Members of the grass and sedge families frequently form tufts or dense bunches of stems with rigid, pointed, tubular or inrolled leaves. These dense tufts in which the dead leaves are maintained and decay on the plant, along with the culms, provide good insulation for the buds and young leaves from cold temperatures, high radiation, evaporation, and high heat of fires to 500°C (Ramsay, 1992; Ramsay & Oxley, 1996). Much of their regeneration takes place through the production of vegetative buds near the ground. Here the tufts are very dense and living shoots are found along with dead culms and leaves. These tufts protect the vegetative buds. The most common species are *Calamagrostis recta* and *C. effusa* (Poaceae); other important genera and species are *Carex, Cortaderia* spp., *Festuca spp.*.

Microphyllous Shrubs - These shrubs are characterized by dense foliage of small, xeromorphic leaves, sometimes with many of the following combinations of adaptations in the same species, all acting as protection from ultraviolet light and/or the reduction of transpiration. Examples of genera and/or species with hard or sclerophyllous leaves include *Miconia summa* (Melastomataceae), *Chuquiraga* (Asteraceae), *Hypericum laricifolium* (Clusiaceae), and *Valeriana microphylla* (Valerianaceae).

Prostrate Dwarf Shrubs - These are small, woody plants that rarely produce shoots over 0.75 m tall. The special feature separating them from microphyllous shrubs is that they have a larger part of their branch system protected below or upon the soil surface. They are often prostrate, growing laterally along the ground. Sometimes entire branching systems occur underground and only the current year's growth is seen above ground. This growth form often has its regenerative buds below ground where they are protected from fire and frost. Some examples are *Disterigma* (Ericaceae) and *Arcytophyllum* (Rubiaceae).

Geophytes - These are herbs that survive the unfavorable periods of the year by means of subterranean organs, such as succulent roots, rhizomes, stolons, tubercules, or bulbs (Lægaard, 1992). Examples of geophytes include *Orthrosanthus chimboracensis* (Iridaceae) and *Gomphychis* (Orchidaceae).

Certain trends are held in common between the vegetation physiognomy across the high Andes. The most widespread vegetation structure is the tussock grass páramo. Here, the vegetation typically consists of a tussock grass layer (up to 1-1.5 m tall, *Calamagrostis ssp.*, *Festuca ssp*.) with a high coverage (up to 100%). Between the tussocks, the ocurrence of dwarf shrubs (Hypericaceae, Ericaceae, Asteraceae) and accaulescent rosettes is typical. Stem rosettes are by far the most characteristic aspect of tropical alpine vegetation. For the páramo from northern Ecuador to Venezuela the most typical and well known growth form is the giant rosette of the genus *Espeletia* (Asteraceae). Isolated pockets of true closed canopy forest composed of *Polylepis* (Rosacea) and other species can occur well above the general treeline in the Andes at elevations up to 4300 m, typically occupying sheltered talus slopes (Rundel et al 2008).

Based on altitudinal zonation and vegetation structure several classifications have been proposed (Acosta-Solis 1986, Cuatrecasas 1958, Jorgensen & Ulloa, 1994). The latter two authors proposed three main types of vegetation above the tree line. In the treeless areas between 3400 and 4000 m grass paramo or "pajonal" and forest patches occur. Between 4000-4500 m the second vegetation type called shrub and cushion paramo occur. It is dominated by cushion plants, in particular species of *Azorella*, *Plantago*, and *Werneria*, sclerophylous shrubs like and scattered tussock grasses. Above 4500 m desert paramo is present. The vegetation is scarce, plants grow in isolated small patches, and only on stabilized ground may the vegetation be better developed. Rather, communities appear to vary continuously along climatic and edaphic gradients, with few distinct discontinuities. However, very few quantitative data on spatial variation in community structure are available for tropical alpine areas (Baruch 1984, Rundel et al 2008).

2.3.3. Phytogeography and Origins

A multiple origin of the paramo flora was documented already three decades ago (Cleef, 1981). Two main elements have are distinguished, 1) allochthonous: temperate plant groups that immigrated, often through long-distance dispersal, to the tropics from higher latitudes, 2) autochthonous: plant groups evolved by adaptation of lower elevation plants to high elevation (Cleef 1981, Van der Hammen & Cleef 1986).

Four main chorological flora element are also distinguished in the paramo flora:
1) Tropical paramo element comprise those taxa that entered high-altitude habitats from lower elevations of the (neo)tropical region by adapting to environmental conditions as mountains rose to present height. One necessary step in that adaptive process must have been evolution of the ability to survive subzero temperatures, which is a year-round phenomenon in high-altitude paramo. Evolution of new adaptations by tropical plant lineages, such as frost resistance, is believed to have been the limiting factor in colonization of paramo habitats, 2) Endemic Element includes genera confined to the paramo ecosystem and radiating within it, although occasionally some species may be found in montane forest 3) Temperate element comprise those taxa from temperate zones of southern hemispheres, 4) Cosmopolitan element include taxa that have a worldwide distribution. Tropical and temperate genera contributed equally to modern species richness of the paramo flora. Among temperate genera, the northern hemisphere genera gave rise to more species in paramo than did genera from the southern hemisphere (Smith & Cleef 1988, Sklenár et al 2011)(Tab. 3).

Table 3. Species richness of paramo genera with tropical, north temperate, and south temperate origin (Sklenár et al 2011)

	Element		
	Tropical	Temperate (north/south)	Total
Number of Genera	18	16 (9/7)	34
Páramo Species Richness	464	363 (275/88)	827
Mean Species Richness (± SD)	25.8±29.6	22.7±23.1 (30.6±21.1/12.6±21.5)	24.3±26.8
Proportion per Genus (%)	3.1±3.58	2.7±2.79 (3.7±2.55/1.5±2.6)	2.9±3.24

2. 4. Human in the paramo environment

It’s very probable that somebody who has been any time in an Andean country won’t doubt about the grandeur of its mountains. From any point of view, the Andean mountains fill the space, their high plateaus are opened like the hand palms where their villages were settled and the ranges are spread like fingers showing the deep valleys and canyons by the way. They join together the villages, cities and countries, not only geographically but also historically. The Andes give the form to the landscape and, although the fact I am not a human ecologist, as a native person from the Andes region, I can assure that the culture of these people have been also shaped by the mountains. Even most of the inhabitants there haven’t been conscious about this due to some failures in the educative system, such us the lack of programs about our ancestors cultures and in general there are some ‘hollows’ in the knowledge of the Andean villages history. When we ignore the history, we can lose the identity and the belonging sense. This is the first step in the degradation process of the natural environment in the Andes regions. The intensive exploitation of the Andean ecosystems is a recent matter. Especially in the case of paramos, which was inhabited by human beings the first time about 15000 years ago and it lasted almost unoccupied until the Spanish conquer epoch more than 500 years ago (Ellenberg 1979). The following discussion summarizes what we should know about the history of man's presence in the paramo, with the purpose of a better comprehension about the changes generated by men in the paramo environment.

Pre-Columbian Period. The native inhabitants of the Andes constituted a trading and peasant society, living mainly at mid-altitude on mountain slopes. The highest mountains and paramos were mostly considered sacred, often with mystical qualities, and their main use was for religious purposes and to bury the prominent dead. In Colombia, the pollen record shows that human activity in the paramos around Bogotá began about 800 years ago. However, probably paramos were mostly uninhabited, there were no permanent settlements until colonial times (Van der Hammen 1968). Pre-Columbian agriculture was concentrated below 2000 m. The cultures that developed in or near the paramos were dedicated to agriculture and gathering. Paramo was used for the cultivation of some tuber crops (potatoes, corn, oca, and ullucu) and as a crop-storage area. Paramo was also used as corridors or as hunting areas (Monasterio 1980).

Colonial and Independence Period. Conquistadores settled the New World in the 16th century. They introduced exotic animals that were totally new to the northern Andes (cows, sheep, goats, horses, and donkeys. Exotic plants were also introduced by Europeans for cultivation at the cooler high elevations, especially the grains wheat and barley, but also vegetable crops such as broad, lentils, peas, carrots, radishes, onions, and garlic (Ellenberg1979). Early colonists (including pre-Columbian man) founded their villages and towns primarily in the cooler inter-andean valleys along rivers, where their crops were grown in the fertile floodplains (corn) and along the adjacent upland slopes (potatoes and grains). Cattle reached the Andes of Venezuela and Colombia in the late 1500s, but probably were not introduced into the paramos until the early 1700s, and then only to ca. 3000 m. The cattle foraged in the paramo grasslands above the forest, several hours or days walk from their homes. Thus it would seem that in the early 1700s the paramos of the northern Andes were still not to much utilized. However, during the late Colonial period and into the Independence period, agriculture and cattle grazing became common (Brush 1982).

Modern Period. During the 20th century population densities in the interandean valleys increased and people began to colonize new areas in order to satisfy their needs (Ellenberg 1979, Hofstede 1995, Molinillo & Monasterio 1997). Because of land and agrarian reform policies during the 1960s and 1970s, most parts of Colombia, Venezuela, Ecuador, and northern Peru have experienced two recent tendencies: the upward movement of agriculture into the paramo belt between 3000 m and 4000 m, and the intensification of animal production in the lower paramo belts (Hess 1990, Laegaard 1992). At the end of the last century, regional growth in urbanization occurred, with farmers abandoning the countryside to cities such as Mérida, Bogotá, Quito, etc. This has resulted in greater demand and increased pressure upon fewer farmers throughout the Andes to cultivate new land to produce more food. As natural soil fertility decreased in the paramo, usage of chemical fertilizers, insecticides, pesticides, and fungicides increased, followed by soil contamination (Luteyn 1992). Along with the upward movement of agriculture and increased livestock production, has come the continued lowering of the forest line. Other recent developments that have led to additional paramo disturbance include construction of aqueducts, drainage systems, and roads, mining and afforestation projects. (Luteyn 1992, pers. observ.).

2.5. Impact of agricultural practices on paramo ecosystem

One of the problems confronted by introduction of European cattle into paramo environments, and Andean environments in general, was the forage quality of the dominant vegetation. Up to 80% of the above ground biomass of the tussock cover is dead material. The low efficiency of European animals for digesting natural forage, with a large proportion of dry material limited potential areas for grazing. Thus animals were concentrated in a low number of suitable pasture areas or vegetation was modified to improve forage quality. Forage palatability and accessibility was improved by burning the pastures (Laegaard 1992, Hofstede 1995).

2.5.1. The effects of cattle grazing and burning on paramo vegetation

Burning and grazing go hand-in-hand in most high elevation areas of the northern Andes. Burning results in concentrated disturbance in the form of grazing and trampling by livestock (Velazquez 1992, Verweij & Budde, 1992, Hofstede 1995 Laegaard 1992). Fires in the grass paramo promote a disturbance mosaic pattern, made up of patches of previously burned vegetation in various stages of recovery (Ramsay & Oxley 1996, Ramsay 1999). Plant survival of fires depends partly on plant growth form (tussocks and rosette plants are favored over woody species), but also on factors such fire intensity and fire frequency (Legaard 1992, Ramsay & Oxley 1996). Survival following fire does not guarantee a plant's persistence in the community, since both tussock grasses and intertussock species show significant mortality rates in the months following fire (Hofstede 1995).

When fires are followed by continued grazing or overgrazing, short matted grasses and forbs increase and a gradual transformation into other communities occurs - Short-grass communities (*Agrostis, Festuca, Paspalum*), rosaceous species (*Acaena* and Lachemilla orbiculata), and species of low or matted herbs such as *Eryngium humile* (Apiaceae), *Bidens* and *Hypochaeris* (Asteraceae). These plants are better adapted to cattle grazing and to more exposure of bare ground. (Cleef 1981, Hofstede 1995, Ramsay 1992, Verweij & Budde 1992, Verweij & Kok1992).

Some investigations have been dedicated to the study of effects of bunrninf and grazing on the stem rosettes of the Espeletiinae. Pérez (1992) found that cattle browsing could cause a decrease of 37% in rosette cover of *Coespeletia timotensis* (Asteraceae: Espeletiinae) in Venezuela. Suarez & Medina (2001) and Verweij & Kok (1992) studied the effects of burning and grazing on *Espeletia pycnophylla* and *Espeletia hartwegiana,* respectively. They found that the highest densities of stems occurred at sites with intermediate disturbance. They attributed that high stem density to the abrupt increase of space, light, and nutrients after the fire or when a stem rosette is knocked down by cows. They summarized the impacts of fire and grazing on population dynamics as follows: most juveniles (over 80%) are killed immediately after the fire, but are quickly replaced by individuals benefitting from the extra amount of space, light, and nutrients. Adults have a higher risk of being killed by fire or by rubbing.

2.5.2. The effects of cattle grazing and burning on soil properties

Undisturbed paramo has a larger water-storage capacity than burned and grazed paramo, a continuously wet plant layer is important for maintaining the large soil storage for dryer periods (Hofstede 1995). With grazing and burning, however, vegetation cover disappears and is replaced by a low growing, ground cover that cannot hold as much moisture since the paramo soils are more compressed, dryer, less acidic, and somewhat less organic (Hofstede 1995). Verweij and Budde (1992) also found that during the first 1.5-5 years following fire the percentage of bare soil increased over 10%, depending on the vegetation structure and grazing intensity. Meanwhile vegetation is trampled and compacted, and the turf is broken-up by cattle (Hofstede 1995), thus favoring erosion, loss of soil, and micro-terracing, especially on slopes (Pérez 1992).

Grazing and especially burning practices can also result in faster decomposition and mineralization due to dryer soils and higher maximum soil temperatures. This does not necessarily lead to higher nutrient contents of soils and plant tissues. On a short-term basis, mineralized nutrients may become available for immediate plant regrowth, but generally they are very quickly unavailable in the soil due to immobilization especially of phosphorus, volatilization especially of nitrogen and sulphur, or less importantly to erosion or leaching. Therefore, the vegetation remains nutrient poor (Hofstede 1995, Verweij & Kok 1992).

Chapter 3

Methods

3.1. Study site

The Santurban paramo complex is a paramo belt encountered in the northern of the Eastern Colombian cordillera (74°4'W, 4°35'N). The maximum elevation of the Santurban complex is 4290 m and its area is aprox. 82664 ha. The regional is associated with rocks that have a high degree of dynamic thermal metamorphism, intruded by Mesozoic and Cenozoic. Most of the soils are inceptisols, which are slightly developed and relative young. Annual precipitation rates of Santurban are one of the lowest of the Colombian paramos, typically receives between 600 and 1000 mm of rain annually. Mean annual temperatures in the paramo belt vary from 13-14 C° to 0 C° (Cleef 1981, Rangel 2000).

The main economics activities in this region are cultivation of crops (mainly potatoes and onions), cattle farming and mining. Fish production is other important economic activity. The rainbow trout (*Oncorhynchus mykiss*) was introduced in the 80's and was a good business until the 90's, but in the last 10 years it has decreased due to the water contamination, as well as, others cultivations such as potatoes and onions for the same reason (Internet 1).

Research for this study was conducted nearby two villages: Berlin and Vetas. Berlin has the major agricultural production of the region. The potato production has been estimated 18 ton/year and potato fields cover 2779 ha. According to an official report by the agriculture ministry in 2005, inadequate use of agrochemical supplement makes a lower quality of the product and exposes the good health of the consumers. Inhabitants of Vetas are primarily dedicated to exploitation of gold an silver. Mining has being practiced in an artisan way since the pre-columbian times. The biggest gold deposits were exploited out during the Spanish conquer period. After this historical period, the mining exploitation went on in a reduced way and with little incomes for the local producers. This is the reason why some foreign companies which have new techniques based on are interested in the gold exploitation in the area, but without any limits in the balance environment damage (Internet 2).

3.2. Sampling and data analyses

Field work for this project was performed between September and November 2008 and 2009. Research place (15km x 5 km) was located along an unpaved road that connects Berlin and Vetas towns. At each plot altitude, azimuth and slope were measured and percentage of bare ground and rocky habitat were estimated. Floristic composition was described by estimation of species coverage according to Braun-Blanquet scale (r = 0.05%, += 0.5%, 1= 2.5%, 2a=10%, 2b = 20%, 3=37.5%, 4=62.5%, 5=87.5%). To describe human impact following variables were used: occurrence of fields, occurrence of house, occurrence of fences, distance to path, number of cows and number of cow droppings (Verweij&Budde 1992, Hofstede 1995). Distance to path is the distance measured from the center point of each phytosociological relevé to the nearest path. According to that distance, probability density function was used to define 5 categories: 5 m - 30 m, 30 m – 125 m, 125 m – 300 m, 300 m – 500 m, 500 m – 1000 m.

Vegetation analysis - To estimate floristic composition, importance value for each species was calculated as mean cover + percent frequency (Keating 1999, Keating 1984). Mean cover of a particular species is obtained by dividing the total cover of that species by its frequency. Frequency is the number of plots, where the species occurs. The Percent frequency is found by multiplying each relative frequency value by 100. Relative frequency of a particular species is found by dividing the frequency by the number of observations. Shannon-Wiener index (Peet 1974) was calculated for each plot to estimate α diversity of the vegetation. Species richness was estimated as the total number of species recorded in each plot.

Analysis of human influence – Influence between vegetation data, environmental variables and management variable were analyzed by means of ordination analyses. The statistical package CANOCO (Braak & Smilauer 1998) was employed. Detrended correspondence analysis (DCA) was run first to demonstrate the position of the species in the ordination space. Then, explanatory power of the categorical variables was tested by means of canonical correspondence analysis (CCA). Stepwise multiple linear regression analysis was performed to examine the relationship between species diversity, environmental variables, and variables related to human impact.

Chapter 4

Results

4.1. General floristic diversity

Over the study site a total of 70 relevés were made, in which 141 plant species were found. The most common species was *Acaena cylindristachya* (Rosaceae), that was registered in 48 plots, followed by *Hypochaeris sessiliflora*, *Noticastrum marginatum* which were found in 40 sample plots (Tab. 4). More than a half of all the species (57%) were present in less than six sample plots.

Tab 4. The most frequent species in Santurban paramo (frequency >20). Frequency is the number of plots (out of 70), where each specie was recorded.

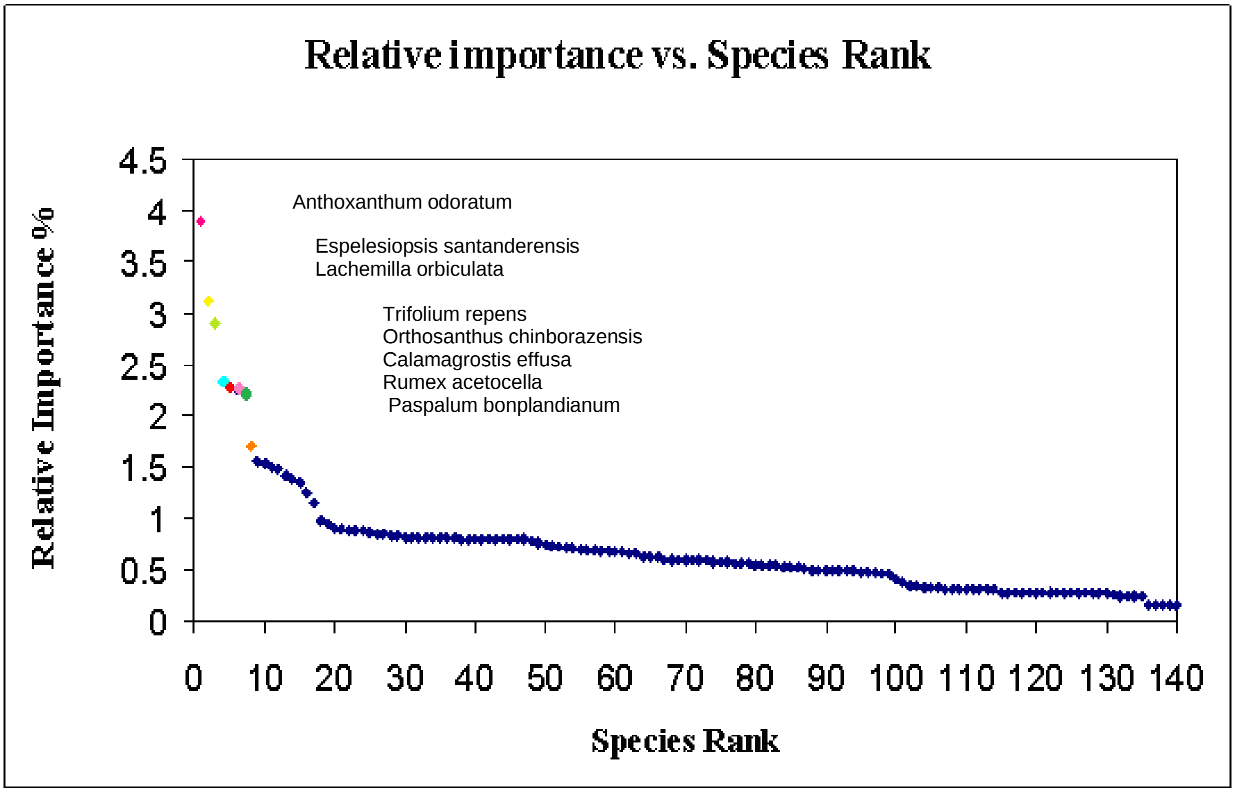
Species	***Frequency***
Acaena cylindristachya	48
Hypochaeris sessiliflora	40
Noticastrum marginatum	40
Hypericum mexicanum	37
Anthoxanthum odoratum	37
Calamagrostis effusa	37
Baccharis tricuneata	34
Agrostis sp.	31
Geranium multiceps	29
Espeletiopsis santanderensis	27
Orthosanthus chimboracensis	27
Paspalum bonplandianum	26
Halenia sp.	26
Plantago monticola	23
Aciachne sp.	22
Lachemilla orbiculata	21
Rumex acetocella	21
Bidens andicola	21

Importance value of each species is calculated as mean coverage of the specie + percent frequency. Total relative importance values (%) for each species are plotted against their rank (Fig. 3). Species with relative importance values above 1% are listed in Table 5. Only seven species (5%) accounted for more than 2% of the total importance. The vast majority (86.5%) of all species were locally rare since they have relative importance values below 1%.

Table 5. Important plant species in the Santurban paramo. Relative importance values (RIV) are given as percentages over the entire site. Importance values were determined as (cover + frequency).

Species	***Relative Importance Value %***
Anthoxanthum odoratum	3.9
Espeletiopsis santanderensis	3.1
Lachemilla orbiculata	2.9
Triforium repens	2.3
Orthosanthus chinboracensis	2.3
Calamagrostis effusa	2.2
Rumex acetocella	2.2
Paspalum bonplandianum	1.7
Hypericum lancifolium	1.5
Hypochaeris sessiliflora	1.5
Acaena cylindristachia	1.5
Baccharis prunifolia	1.5
Arcytophillum nitidum	1.4
Baccharis tricuneata	1.4
Noticastrum marginatum	1.3
Hypericum mexicanum	1.2
Agrostis sp.	1.1
Total	33.3

Figure 3. Overall relative importance of each plant species versus its rank. The most important species are presented in colored symbols. Relative importance was calculated for 141 species that occurred in the 70 plots inventoried.



The species with high relative importance values belong also to the species with high frequency values. However, some species with the highest relative importance value do not belong to the most common species. This is the case of *Hypericum lancifolium* registered in 12 plots and *Arcytophyllum nitidum* registered in 15 plots. Both of them are quite tall upright shrubs, their high important value is related to their high coverage. In the opposite way, the most common species, i.e., *Acaena cylindristachya, Hypochaeris sessiliflora*, *Noticastrum marginatum* and *Hypericum mexicanum*, do not have the highest relative importance values because they are all low herbaceous plants (ground rosettes, creeping or ascending herbs) with lower values of coverage

The plant species registered belong to 31 families, 16 of which contained only one species. The most diverse families with at least six species are: *Asteraceae* (41), *Poaceae* (17), *Rosaceae* (8), *Apiaceae* (7), *Hypericaceae* (6), *Ericaceae* (6), *Cyperaceae* (6), and *Lamiaceae* (6) (Table 6). The families *Gentianaceae, Geraniaceae* and *Rubiaceae* contained four species each, whereas *Fabaceae*, *Iridaceae* and *Plantaginaceae* contained between two or three species. In terms of the overall importance (a relative measure comprising cover + frequency), the most important families were *Asteraceae* (27.3%), *Poaceae* (16.7%), and *Hypericaceae* (7.2%), which together accounted for almost 50%. Less important but still among the highest ranking and most diverse families are *Rosaceae* (6.1%), *Ericaceae* (4.3%), *Cyperaceae* (3.2%), together accounting for 13.1%. The ten most important woody species and ten most important herbaceous species (grasses included) are presented in table 7. Woody species account for 11.3% of the total relative importance.

Table 6. Important plant families in the paramo of Santurban. Only the families with total relative importance (RIV) >1.0 % over the entire site are listed. Relative importance values were determined as (cover + frequency). Total RIV for each family was determined by summing individual importance values for all species within the family.

Family	RIV (%)	No. of species
Asteraceae	27.3	41
Poaceae	16.7	17
Hypericaceae	7.2	6
Rosaceae	6.1	8
Ericaceae	4.3	6
Cyperaceae	3.2	6
Lamiaceae	3	6
Rubiaceae	2.9	4
Fabaceae	2.9	2
Iridaceae	2.3	2
Gentianaceae	2.8	4
Polygonaceae	2.2	1
Apiaceae	2	7
Plantaginaceae	1.6	2
Orchidaceae	1.1	2
Remaining 16 families	14.2	29
Total	100	141

Table 7. The most important herbaceous and woody species in the Santurban paramo. Relative importance values (RIV) are given as percentages over the entire site. Importance values were determined as (cover + frequency)

The most important herbaceous species		***The most important woody species***	
Species	**RIV(%)**	**Species**	**RIV(%)**
Anthoxanthum odoratum	3.9	*Hypericum lancifolium*	1.5
Espeletiopsis santanderensis	3.1	*Bacharis prunifolia*	1.5
Lachemilla orbiculata	2.9	*Arcytophillum arbusto*	1.4
Trifolium repens	2.3	*Baccharis tricuneata*	1.4
Orthosanthus chimboracensis	2.3	*Hypericum mexicanum*	1.2
Calamagrostis effusa	2.2	*Castilleja arbusto*	0.9
Rumex acetocella	2.2	*Vaccinum sp.*	0.9
Paspalum hirtum	1.7	*Hypericum hileras*	0.8
Hypochaeris sessiliflora	1.5	*Calceolaria sp.*	0.8
Acaena cylindristachia	1.5	*Pernettya prostrata*	0.8
Total	23.7	**Total**	11.3

Seven life forms of plants were recognized: graminoids (grasses and sedges), ground rosettes, upright shrubs, upright herbs, creeping herbs, prostrate shrubs and trees. In terms of relative importance, graminoids (23.6%) is the most important life form (Table 8). In terms of species richness, the most important is the “upright herbs” category (32). Ground rosettes is the second most important life form and “upright shrubs” category is the third most important, both in terms of overall importance and in terms of species richness. Trees category is after “creeping shrubs” category the most rare with only two species which account for 0.9% of the overall importance.

Table 8. Plant life forms at páramo de Santurbán. Total relative importance (RIV) was determined for each category by adding relative importance values for all species within the life form category.

Life form	**RIV(%)**	**Number of species**
Graminoids	23.6	28
Ground rosettes	20.6	27
Upright shrubs	17.1	24
Upright herbs	16.6	32
Creeping herbs	15.6	22
Prostrate shrubs	5.6	6
Trees	0.9	2
Total	100	141

4.2. Intensity of human impact

Seven variables related to human influence were recorded at the same sample sites, where vegetation data was collected. Those variables are: occurrence of fields, occurrence of house, occurrence of fences, distance to path, number of cows and number of cow droppings.

Occurrence of fields was characterized by the presence or absence of fields within an area of 10000 m² measured from the center point of each phytosociological relevé. Fields were encountered in the vicinity of 27.2% of sample plots, mostly below 3600 m.

Above 3700 m any field was recorded. Occurrence of houses was recorded within an area of 90000 m² measured from the center point of each phytosociological relevé. Above 3800 m s l. houses were never found. House was registered in 20 of 70 plots recorded for the whole study area.

Occurrence of fences was recorded within an area of 10000 m² measured from the center point of each phytosociological relevé. Fences occurred nearby 30 of the plots in the study area. Most fences (19) were located between 3300 m and 3600 m whereas above 3600 only 5 fences were recorded (Tab.9).

Table 9. Intensity of human inpact through altitudinal gradient. Intensity of human influence characterized by occurrence of fields, house and fences.

Altitudinal intervals (m)	Total number of sample plots	Number of plots with presence of fields	Number of plots with presence of houses	Number of plots with presence of fences
3300-3400	2	2 (100%)	2 (100%)	2 (100%)
3400-3500	11	6 (54.5%)	2 (18%)	6 (54,5%)
3500-3600	15	6 (40%)	9 (60%)	11 (73.3%)
3600-3700	13	5 (38.5%)	6 (46.1%)	6 (46.1%)
3700-3800	9	0	1 (11.1%)	3 (33.3%)
3800-3900	11	0	0	1(9.1%)
3900-4000	9	0	0	1(11.1%)
Total	**70**	**19 (27.2%)**	**20 (28.6%)**	**30 (42.8%)**

Number of cows was recorded at the same places as plots within an area of 10000 m² measured from the center point of each phytosociological relevé. Cows were encountered in 42.8% of the sample plots, mostly below 3700 m. Cow droppings were counted within an area of 100 m². These were also found mostly below 3700 m, in 70% of the sample plots (Tab. 10). Usually more than five cows were found by sample plot (Fig. 4). The number of cow feces counted by plot used to vary from 4 to 12 droppings (Fig. 5).

Table 10. Distribution of cows and cow dropping within the altitudinal gradient.

Altitudinal intervals (m s. l.)	*Number of plots with presence of cows*	*Number of cows*	*Number of plots with presence of cows droppings*	*Number of cow dropping*
3300-3400	2 (100%)	15	2 (100%)	14
3400-3500	7 (63.6%)	50	11 (100%)	96
3500-3600	9 (60%)	49	13 (86.6%)	104
3600-3700	7 (53.8%)	48	9 (69.2%)	60
3700-3800	2 (22.2%)	8	5 (55.5%)	21
3800-3900	1 (9.1%)	3	4 (36.4%)	21
3900-4000	2 (22.2%)	8	4 (44.4%)	12
Total	30 (42.8%)		49 (70%)	

Figure 4. Histogram of the number of cows.

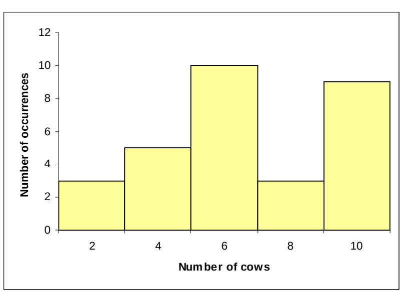
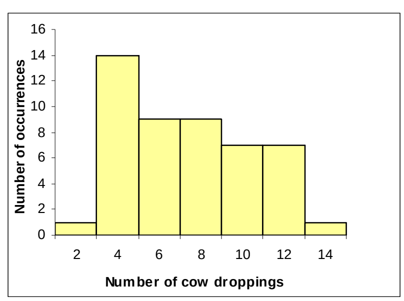


Figure 5. Histogram of the number of cow droppings.



Distance to path was measured from the center point of each phytosociological relevé to the nearest path. According to that distance five categories were distinguished: 5 m - 30 m, 30 m – 125 m, 125 m – 300 m, 300 m – 500 m, 500 m – 1000 m. Most of the paths recorded were situated between 30 m and 500 m far from the sample plot (Fig.6). At low elevations, below 3700 m, paths were usually situated close to the sample plots, in a distance between 5 m to 125 m from the center of the sample plot. Above 3700 m, paths were usually found at least 300 m far from the sample plots (Fig. 7).

Figure 7. Distance to path within each altitudinal intervals. Five categories were distinguished according to the distance from center point of each phytosociological relevé to the nearest: 5–30 m, 30–125 m, 125–300 m, 300– 00 m, 500–1000 m.

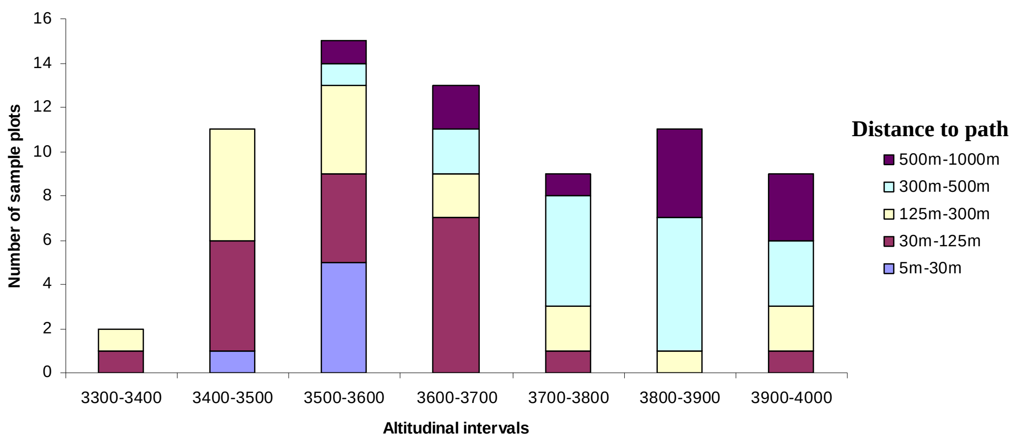
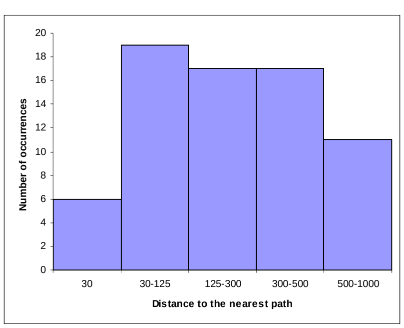


Figure 6. Histogram of the distance measured from the center point of the phytosociological relevé to the nearest path

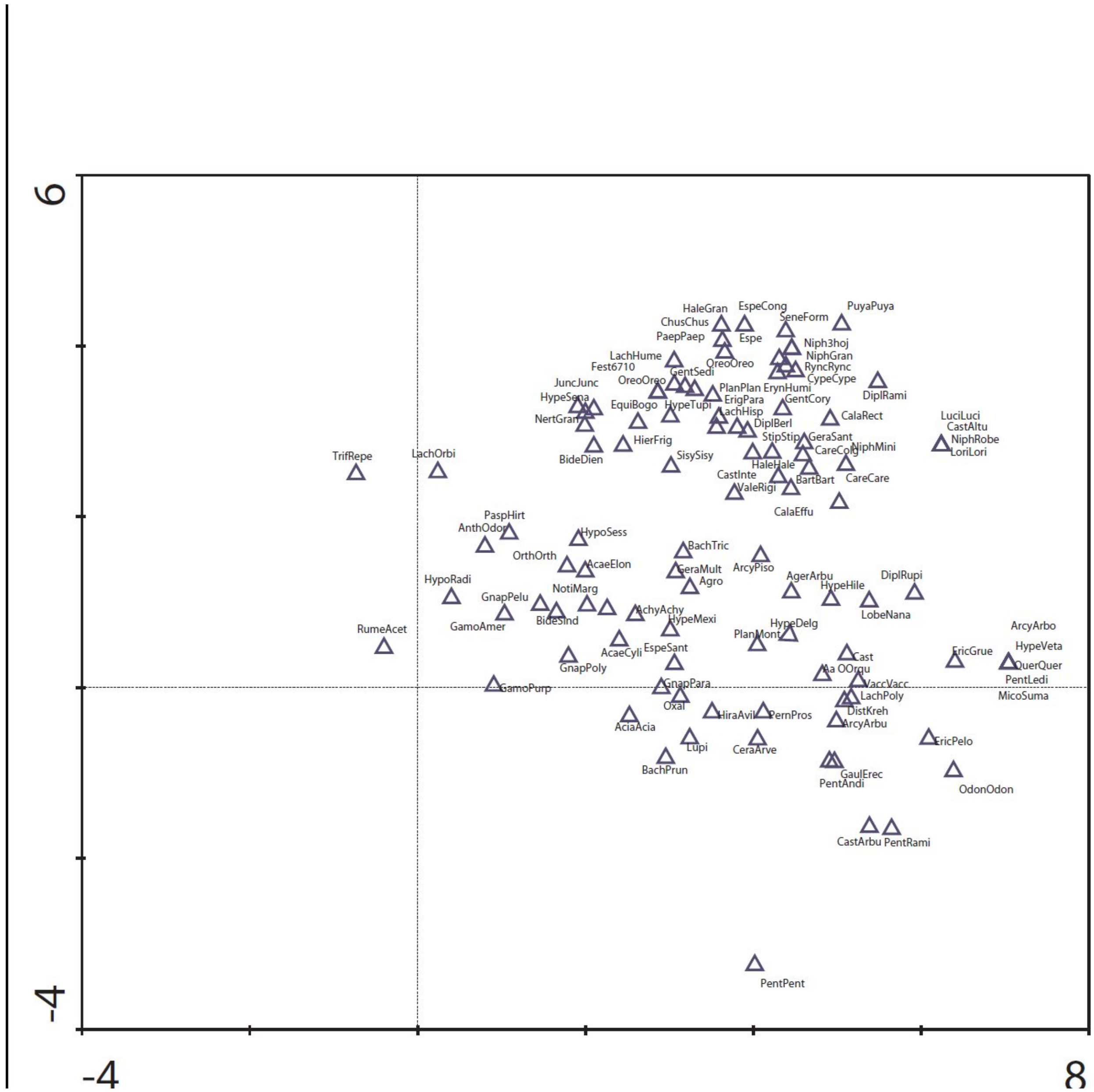


4.3. Human influence on vegetation

Species composition data from the sample plots, environmental data (altitude, exposition, azimuth, slope, rock, bare soil), and data related to human influence (occurrence of fields, houses, fencing, and distance to path, number of cows and number of cow droppings) were analyzed by means of ordination analyses.

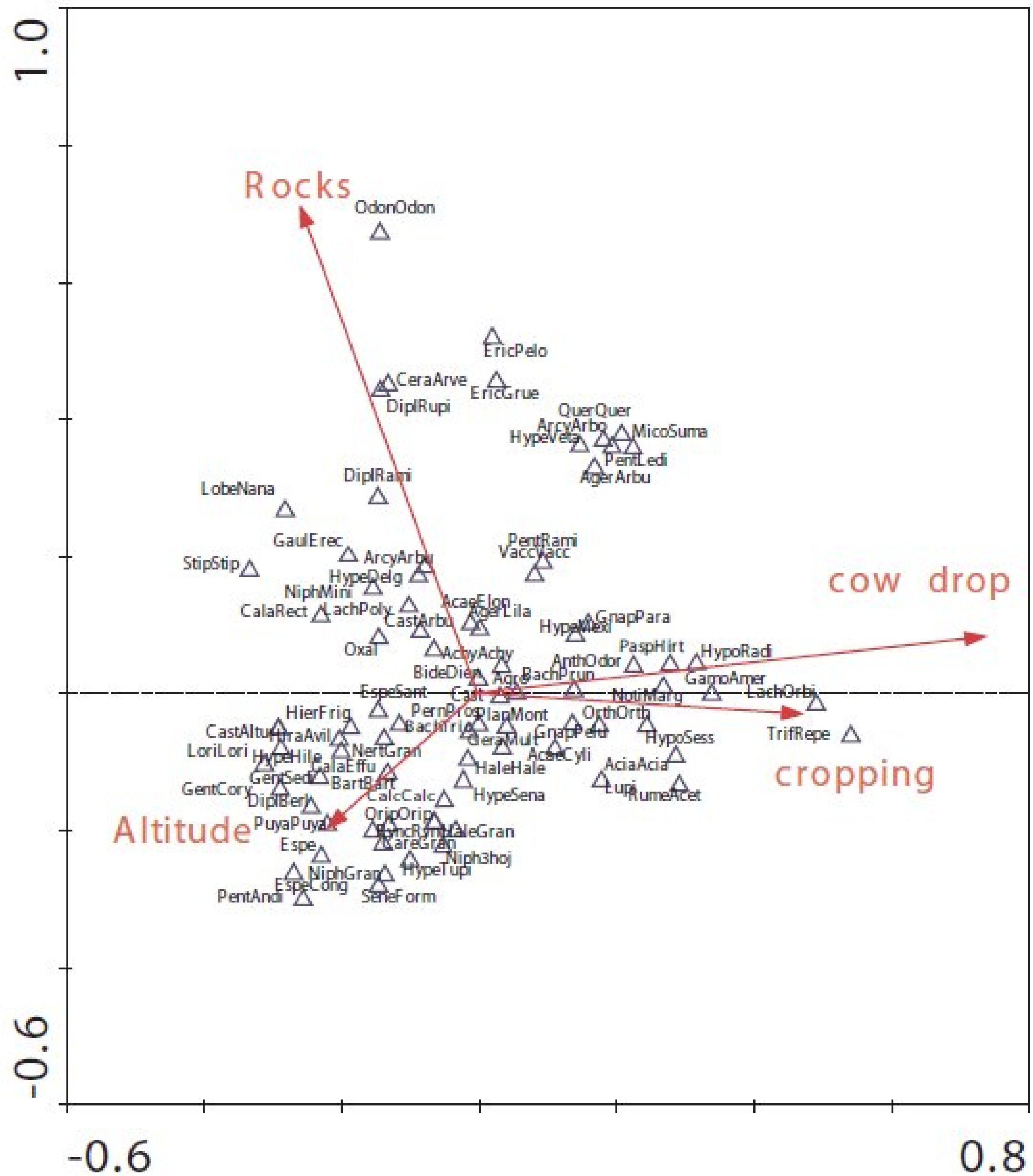
The DCA ordination revealed major trends in the species composition of the vegetation (Fig. 8). The species in the left side of the ordination diagram are found in plots with high intensity of human impact whereas species in the right side of the diagram are present in plots with low human impact. The first ordination axis thus depicts the gradient of human impact. The species ordination along the second axis shows species relation to the altitudinal gradient.

Figure 8. Species composition of the paramo vegetation presented in an ordination diagram of a detrended correspondence analysis (DCA), the first axis correlates to the gradient of human impact , λ1=0.567, λ2=0.314, total inertia = 4.191.



In the CCA ordination diagram environmental variables that significantly correlated to species composition are displayed. (Fig. 9). The first ordination axis accounts for 5.2% of the total variability of vegetation data. It is correlated to human impact, represented by the occurrence of fields and number of cow droppings, and partly to altitude. The second axis accounts for 3.3 % total variability of vegetation data and is correlated to the occurrence of rocky habitats. The arrow for cow droppings and occurrence of fields point to the right of the diagram, this indicates that those variables are largely correlated. The species in the right side of the diagram are positively correlated with increasing human impact, those are, for example, *Acaena cylindristachya*, *Rumex acetocella*, *Lachemilla orbiculata, Trifolium repens, Paspalum bonplandium, Hypochaeris sessiliflora*. Species in the left side of the diagram, such as *Calamagrostis effussa* and *Gentianella corymbosa*, are negatively correlated to human impact and are also correlated to increasing altitude. *Diplostephium rupicola* and *Odontoglossum sp.* and a few other species are strictly confined to rocky habitats.

Figure 9. Canonical correspondence analysis of the 70 samples collected in the Santurban paramo indicates that species composition of the vegetation correlates to human impact measured as occurrence of fields and number of cow droppings and environmental variables, such as altitude and occurrence of rocky habitats; λ1=0.218 (F=3.398, P=0.002), λ2=0.138 (F=2. 2099, P=0.002), total inertia =4.191.



4.4. Human influence on species diversity

Number of species and Shannon-Wiener index of diversity was calculated for each phytosociological réleve to characterize species diversity of vegetation in paramo Santurban. Mean number of species for all réleves (16.6) characterize species richness of paramo Santurban. Arithmetic mean of the Shannon-Wiener index (0.94) characterizes species diversity of the vegetation in Santurban.

Stepwise multiple linear regression analysis was performed to examine the relationship between species diversity, environmental variables, and variables related to human impact. Altitude was the only significant variable for both, species diversity measuared with species richness (Fig.10; R^2=0.262) and Shannon-Wiener index (Fig.11; R^2=0.239) . Both measures of diversity increase with increasing altitude. (Fig. 10 and Fig. 11). The increase of plant species diversity with increasing altitude in Santurban paramo can be explained by the decrease of human impact within higher altitudes.

Figure 10. Linear regression plot between altitude and species richness.
y= -48.585+1.777.10^{-2}x. R^2=0.262.

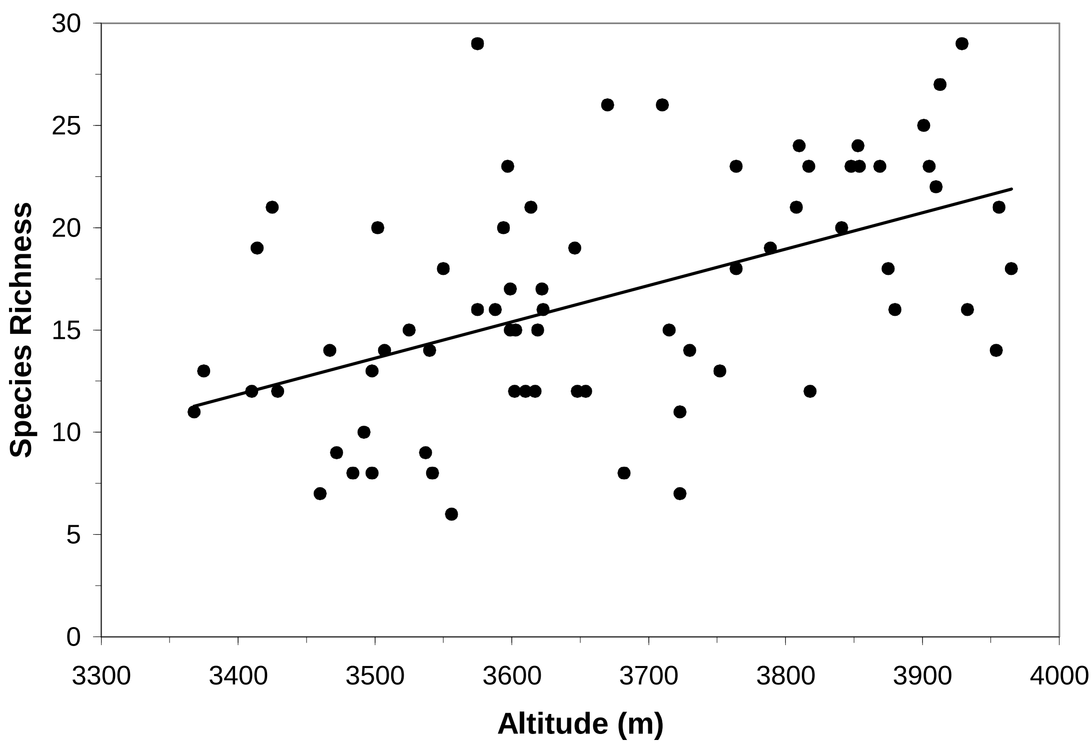
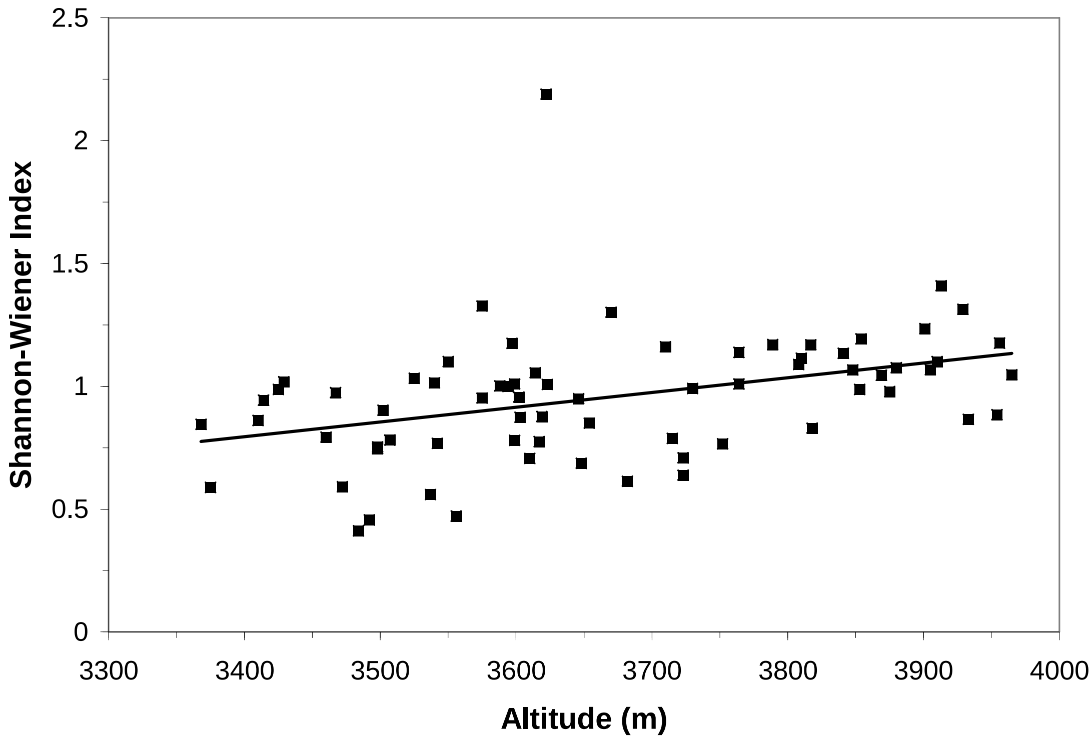


Figure 11. Community diversity measured as Shannon-Wiener index increases with altitude in the Santurban páramo, Colombian Eastern Cordillera; $y = -1.378+6.312.10^{-4}x$. $R^2=0.262$.



Chapter 5

Discussion

Attempts to measure human impact, have been made by different authors. In this study, a group of variables were selected to characterize the intensity of human influence. The selection of those variables was made on the basis of the studies performed by Verweij and Budde (1992) and Hofstede (1995). Collected data are primarily related to cattle grazing and cropping. As others authors did, we could not consider disturbance history, because it is difficult to assess it accurately. Estimation of human impact was performed in relation to the altitudinal gradient. This allows us to find a relation between intensity of human impact and altitude. We found the intensity of human impact was lower at high elevations and increase with decreasing altitude. Lower parts of the paramo are more productive, both for plants and for livestock, therefore farmers' efforts tend to be concentrated in the grass paramo (Sklenar & Ramsay 2001).

The correspondence analysis showed the main floristic variation was related to the altitudinal gradient. It is difficult to test the influence of other parameters on the floristic variation, because most parameters are also related to altitude. Intensity of cropping and grazing was also found to be an important factor determining changes of the vegetation. These results agree with the conclusions of other authors (Ramsay 1999, Sklenar & Ramsay 2001, Baruch 1984, Keating 1999).

Ordinations diagrams were useful to distinguish species related to high intensity of human influence and species related to lower human impact.

Species related to high intensity of human influence. *Lachemilla orbiculata* has been described as an important element of plant communities occurring in intensively grazed paramos (Cuatrecasas1958, Cleef 1981, Verweij & Budde 1992, Hofstede 1995). In Santurban paramo, this creeping herb was one of the most important species in terms of relative importance. It was found at all altitudes but reached the highest abundance at lower elevation in intensively grazed sites. In the CCA diagram it is found correlated with increasing number of droppings and occurrence of fields.

Acaena cylindristachya is a conspicuous low-rosette herb usually growing associated with the small xerophytic cushion grass *Aciachne pulvinata* (Cleef 1981). Both species were widely distributed in Santurban paramo. *Acaena cylindristachya* was the most common species occurring in 48 of 70 (68.6%) phytosociological réleves. Cleef 1981 suggested that the natural habitats of *Acaena cylindristachya* and *Aciachne pulvinata* are the dry sites with thin top soil and explained their wide distributions is a result of intensive grazing and cropping, in combination with a shallow soil. Other authors have also suggested *Acaena cylindristachya* to be related to intensive disturbances (Verweij & Budde 1992). According to them, we suggest that the wide distribution of *Acaena cylindristachya* in Santurban is caused by: 1) the natural dry conditions in Santurban and 2) the intensive cattle grazing and cultivation.

In general, our results and observation of fieldwork agree with Cleef's conclusions: where tussock cover disappear a herbaceous meadow is developed. In these herbaceous communities *Acaena cylindristachya*, *Lachemilla orbiculata* or *Aciachne pulvinata* can dominate. We presume *Aciachne pulvinata* occurs only in dry sites of the paramo a can dominate in driest sites. *Lachemilla orbiculata* will dominate on slightly humid ground and principally in sites, where intensive cattle farming continue even after tussock cover loss. According to our results, *L. orbiculata* is strongly correlated with number of cow droppings. Moreover, Verweij and Budde (1992) found a positive reaction of *L. orbiculata* to grazing intensity. *Acaena cylindristachya* occurs from the driest sites to slightly humid sites and can dominate in the intermediately dry sites. Nevertheless, these are just interpretation based on our and others authors observations. Further studies are necessary to determine the relation between soil properties and vegetation.

Other species occurring at places strongly influenced by man, usually associated with *Acaena cylindristachya*, *Lachemilla orbiculata* and *Aciachne pulvinata* are: *Hypochaeris sessiliflora*, *Noticastrum marginatum*, *Hypochaeris radicata* and *Paspalum bonplandium* (Cleef 1981, Verweij & Budde 1992, Sarmiento et al 2003). The relation between those species can be can be seen in the CCA a DCA diagram.

Orthosanthus chimboracensis was another species found in Santurban, which correlated with increasing human influence. *Orthosanthus chimboracensis* is an endemic plant for the Northern Andes occurring in the dry sites of the mountains. Their large tufts can become dominant in the communities established at intensively disturbed places. Probably its distribution is restricted to low elevations (Cleef 1981). In Santurban, *O. chimboracensis* was one of the most important species (RIV=2.3). The species was recorded at lower elevations, at strongly disturbed places with reduced cover of tussock grasses. *Orthosanthus chimboracensis* has been reported to occur in disturbed sites of the paramos over the Eastern Colombian cordillera (Cleef 1981). Nevertheless, further investigation is necessary to clarify the relation of this specie to disturbance.

Anthoxanthum odoratum was introduced to the Americas as a pasture grass. In terms of relative importance, was the most important species (RIV=3.9) in Santurban. *Anthoxanthum odoratum* is also wide distributed in other paramos of Venezuela and Ecuador.

Species related to low intensity of human influence. *Calamagrostis effusa* was found within the whole altitudinal gradient but the highest abundance values were recorded above 3700 m, where dense graminoids communities were formed. We attribute the lower abundance values of *Calamagrostis effusa* at lower altitudes to the high human impact that occurred in those elevations.The effect of grazing on tussock grasses growth was studied by Hofstede (1995). He demonstrated that the productivity of tussock grasses was lower at intensively grazed sites.

Bartsia is a widely distributed genus that can occur at any altitude (Luteyn 1999). Only one of the species of *Bartsia* was recorded and was found rarely, always associated with *Calamagrostis effusa*. In Santurban, it is possible that its actual apparently restricted distribution to higher elevations is a consequence of the intensive human impact in lower elevations. Laegaard (1992) also suggested that *Bartsia* is not able to survive strong fires. *Bartsia* was present in the dense tussock cover, where it is protected against fires (Laegaard 1992, Cleef 1981). Similarly, *Hieracium avilae* and *Gentianella corymbosa* were encountered rarely and in less disturbed sites. *Hieracium* was found, hidden between the tufts of *Calamagrostis effusa*, similar to *Bartsia, Gentianella corymbosa* grew in dense cushion plants.

In Santurban most of the woody species (members of *Vaccinium*, *Pentacalia* and *Diplostephium* genus) occurred rarely. They were mostly confined to less accessible sites with extreme climate and unfavorable topographic conditions. Woody vegetation is probably the most influenced by man in paramo environment. After fire there is a high mortality of shrubs and trees (Laegaard 1992, Luteyn 1999). Moreover, due to the limited sources of fuelwood and timber, woody plants are intensively cut and collected. Probably the actual distribution of woody species in Santurban is mainly related to environmental variables, such as altitude. Nevertheless, we consider that some species can also be related to low human impact, since they are more wide distributed in other paramos surrounding Santurban (Sanchez R. pers. communication).

Plant species diversity

Due to the scarcity of vegetation studies in the paramos, it is difficult to evaluate and compare the results related to the plant species composition of paramo Saturban.

Cleef 1981, Rangel 2000 and Galvan 2001(unpublished data) performed vegetation studies in paramos of the Eastern Colombian cordillera. In their studies, they also found the families Asteraceae and Poaceae to be the largest in numbers of species and genera. Cleef 1981 and Rangel 2000, have also reported the families Hypericaceae, Rosaceae and Ericaceae to occur very commonly in other paramos of the Eastern Colombian cordillera.

Species richness and diversity (Shannon-Wiener index) was calculated to characterize α-diversity of the communities. Number of species over all 70 phytosociological relevés varies from 6 to 29 and Shannon-Wiener index varies from 0.41 to 1.04. Few studies have analyzed patterns of vegetation diversity in tropical Andes. Sklenár and Ramsay (2001) examined plant diversity of Ecuadorian paramos. They reported Simpson's diversity index ranged from 0.48 to 1.8 and an average of 20 species by plot. Baruch (1999) reported an average of 16 species by plot and Shannon-Wiener index ranged from 0.77 to 0.85. Similar scores have been reported by Keating (1999) and Sarmiento (2003), also for an Ecuadorian and a Venezuelan paramo, respectively. Nevertheless, the comparison between different studies must be interpreted carefully, because each author made use of different methodologies to select sample sites and to collect vegetation.

Both measures of α-diversity, species richness and Shannon-Wiener index, increase with increasing altitude. This increase of species diversity with increasing altitude is apparently related to the decrease of intensity of human influence at higher altitudes. In Santurban, high intensity of human influence found at low elevations had a big impact on the tussock grass vegetation. Short fallow cultivation and intensive cattle grazing lead to the fragmentation of tussock cover and reduction of leaf growth (Hofstede 1995). When tussock cover disappears a dense meadow of herbs is developed (Cleef 1981, Hofstede 1995, Molinillo & Monasterio 1997). These communities, presented in Santurban, were species poor, since only a few pioneer species (*Lachemilla orbiculata*, *Rumex acetocella*, *Trifolium repens*, *Acaena cylindristachya*, *Hypochaeris sessilifloa)* used to dominate. High abundances of those species at early successional stages have been described by several authors (Cleef 1981, Hofstede 1995, Verweij & Budde 1992, LLambí et al. 2003, Monasterio et al. 2011, Sarmiento et al 2003.).

At higher altitudes, the lower intensity of human influence leaded to a reduction of the tussock cover, but not to its complete loss. When tussock cover is reduced, new open and dryer habitats appear and some species can develop (Cleef 1981, Hofstede 1995) Further studies are needed to understand the influence of disturbance on grass paramo. Nevertheless some authors have also suggested that moderate fires and moderate grazing of the grass paramo result in an increase of species richness paramo (Cleef 1981, Beck et al. 1986, Ramsay & Oxley 1996, Ramsay, 1999, Sklenár & Ramsay 2001).

The species diversity at higher altitudes was probably enriched with the species of shrubs and small trees, which occurred mostly at higher elevations probably enhanced . Shrubs and small tress can be killed by fires (Laegaard 1992), therefore they use to be present at high elevations, which are less susceptible to fire and related disturbances because there is not sufficient plant material to sustain fires. Some authors have described a narrow belt of dwarf shrubs (*Pentacalia*, *Diplostephium*, and *Chuquiraga*) occurring between the grass paramo and the superparamo (Sklenár & Ramsay 2001, Keating 1999).

Conclusion:

The influence of grazing and cropping on the vegetation can be summarized as follows:

1) High intensity of cattle grazing and cropping lead to the loss of tussock cover. This conclusion is supported by the results of other investigations (Hofstede 1995, Verweij &Budde 1992, Sarmiento et al 2003).
2) Intensive cropping and intensive cattle grazing lead to the develop of a low herb vegetation. *Lachemilla orbiculata*, *Trifolium repens*, *Acaena cylindristachya*, *Rumex acetocella, Hypochaeris sessiliglora, Paspalum bonplandium* are characteristic in those communities. Other authors have also reported the relation of those species to disturbance (Verweij & Budde 1992, Sarmiento et al 2003, LLambí et al 2003, Hofstede 1995, Suarez&Medina 2001).
3) Shrubs and trees are related to low human impact, as has been suggested by other authors (Laegaard 1992, Suarez&Medina 2001, Ramsa&Oxley 1996).

We suggest intensive cropping and grazing can lead to a decrease of α diversity since the plant communities developed at strong disturbed places are dominated by a few low herbs with high abundance values. Although, the impact of the vegetation depends on the intensity of those agricultural practices (Suarez&Medina 2001, Ramsa&Oxley 1996, Sarmiento et al 2003, Sklenár&Ramsay2001). The vegetation encountered at lower altitude is probably the most threatened since the human impact is concentrated at low elevations. This agree with the conclusions of some authors, who suggest the natural tree line has been shifted to lower elevations by human intervention (Ellenberg 1979, Leagaard 1992, Rundel et al 2008). Nevertheless, further studies are necessary to determine the relation of the vegetation to the different environmental parameters. Investigations of the human influence on paramo vegetation, at landscape level and on particular plant communities and species are also necessary.

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