Plant diversity and vegetation of the Andean Páramo

Gwendolyn Peyre

ADVERTIMENT. La consulta d'aquesta tesi queda condicionada a l'acceptació de les següents condicions d'ús: La difusió d'aquesta tesi per mitjà del servei TDX (**www.tdx.cat**) i a través del Dipòsit Digital de la UB (**diposit.ub.edu**) ha estat autoritzada pels titulars dels drets de propietat intel·lectual únicament per a usos privats emmarcats en activitats d'investigació i docència. No s'autoritza la seva reproducció amb finalitats de lucre ni la seva difusió i posada a disposició des d'un lloc aliè al servei TDX ni al Dipòsit Digital de la UB. No s'autoritza la presentació del seu contingut en una finestra o marc aliè a TDX o al Dipòsit Digital de la UB (framing). Aquesta reserva de drets afecta tant al resum de presentació de la tesi com als seus continguts. En la utilització o cita de parts de la tesi és obligat indicar el nom de la persona autora.

ADVERTENCIA. La consulta de esta tesis queda condicionada a la aceptación de las siguientes condiciones de uso: La difusión de esta tesis por medio del servicio TDR (**www.tdx.cat**) y a través del Repositorio Digital de la UB (**diposit.ub.edu**) ha sido autorizada por los titulares de los derechos de propiedad intelectual únicamente para usos privados enmarcados en actividades de investigación y docencia. No se autoriza su reproducción con finalidades de lucro ni su difusión y puesta a disposición desde un sitio ajeno al servicio TDR o al Repositorio Digital de la UB. No se autoriza la presentación de su contenido en una ventana o marco ajeno a TDR o al Repositorio Digital de la UB (framing). Esta reserva de derechos afecta tanto al resumen de presentación de la tesis como a sus contenidos. En la utilización o cita de partes de la tesis es obligado indicar el nombre de la persona autora.

WARNING. On having consulted this thesis you're accepting the following use conditions: Spreading this thesis by the TDX (**www.tdx.cat**) service and by the UB Digital Repository (**diposit.ub.edu**) has been authorized by the titular of the intellectual property rights only for private uses placed in investigation and teaching activities. Reproduction with lucrative aims is not authorized nor its spreading and availability from a site foreign to the TDX service or to the UB Digital Repository. Introducing its content in a window or frame foreign to the TDX service or to the UB Digital Repository is not authorized (framing). Those rights affect to the presentation summary of the thesis as well as to its contents. In the using or citation of parts of the thesis it's obliged to indicate the name of the author.

Plant diversity and vegetation of the Andean Páramo

Diversidad de plantas y vegetación del Páramo Andino

By

Gwendolyn Peyre

A thesis submitted for the degree of Doctor from the University of Barcelona and Aarhus University

University of Barcelona, Faculty of Biology, PhD Program Biodiversity

Aarhus University, Institute of Bioscience, PhD Program Bioscience

Supervisors: Dr. Xavier Font, Dr. Henrik Balslev

Tutor: Dr. Xavier Font

March, 2015

Aux peuples andins

Summary

The páramo is a high mountain ecosystem that includes all natural habitats located between the montane treeline and the permanent snowline in the humid Northern Andes. Given its recent origin and continental insularity among tropical lowlands, the páramo evolved as a biodiversity hotspot, with a vascular flora of more than 3400 species and high endemism. Moreover, the páramo provides many ecosystem services for human populations, essentially water supply and carbon storage. Anthropogenic activities, mostly agriculture and burning-grazing practices, as well as climate change are major threats for the páramo's integrity. Consequently, further scientific research and conservation strategies must be oriented towards this unique region. Botanical and ecological knowledge on the páramo is extensive but geographically heterogeneous. Moreover, most research studies and management strategies are carried out at local to national scale and given the vast extension of the páramo, regional studies are also needed. The principal limitation for regional páramo studies is the lack of a substantial source of good quality botanical data covering the entire region and freely accessible. To meet the needs for a regional data source, we created VegPáramo, a floristic and vegetation database containing 3000 vegetation plots sampled with the phytosociological method throughout the páramo region and proceeding from the existing literature and our fieldwork (Chapter 1). We made VegPáramo accessible online through a webportal, www.vegparamo.com, from which the data can be freely consulted and downloaded. We then used the VegPáramo data to conduct a regional vegetation classification of the páramo (Chapter 2). We used a clustering technique and classified the region into 17 clusters, 14 representing natural phytogeographical units of one or several plant communities and 3 artificial ensembles. We characterized the 17 clusters and calculated the alpha diversity and beta diversity to highlight species richness and floristic similarities. Our last study focused on the plant diversity patterns in the páramo region (Chapter 3). We used the VegPáramo data and our classification results to estimate and compare plant diversity at local and regional scale in the altitudinal belts of the páramo. We evaluated the importance of the environment as driver of species richness using regression models. Finally, we modeled the predicted species richness in the páramo region and highlighted biodiversity hotspots. Our project contributes to a better understanding of the páramo biogeography and makes primarily suggestions for conservation. We believe further research should focus on the climate change impacts on the páramo flora and vegetation.

Keywords: Biogeography, Northern Andes, Biological Database, Vegetation Classification, Plant Diversity.

Sammenfatning

Páramoen er et højalpint økosystem, som omfatter alle naturlige habitater mellem den alpine trægrænse og den permanente snegrænse i det nordlige, fugtige del af Andesbjergene. Som følge af dens nylige opståen og kontinentale isolation blandt tropiske lavområder har páramoen udviklet sig til et biodiversitivt hotspot med en vaskulær flora bestående af mere end 3400 plantearter samt en høj grad af endemisme. Endvidere varetager páramoen mangfoldige økosystematiske funktioner for menneskelige befolkninger, herunder navnlig tilvejebringelsen af vand samt lagringen af kulstof. Páramoens beståen trues af antropogeniske aktiviteter, såsom navnlig landbrug og udsættelse af jorden for afbrænding og græsning, samt af klimaforandringer. Som en konsekvens heraf bør denne unikke region gøres til genstand for yderligere videnskabelig opmærksomhed samt bevaringsstrategier. Botanisk og økologisk viden om páramoen er omfattende men geografisk heterogen. Dertil kommer, at de fleste forskningsprojekter og håndteringsstrategier udføres på en lokal til national skala. I lyset af den betragtelige udstrækning af páramoen er regionale studier imidlertid også påkrævede. Manglen på tilgængelige substantielle kilder til botaniske data af høj kvalitet omfattende den samlede region udgør en primær begrænsning for regionale studier af páramoen. For at afhjælpe denne mangel på regionale datakilder har vi etableret VegPáramo – en floristisk og vegetativ database indeholdende 3000 vegetation plots indsamlet ved hjælp af den phytosociologiske metode i hele páramoregionen, som hviler på eksisterende litteratur samt vores feltarbejde (Kapitel 1). VegPáramo er gjort tilgængelig online på portalen www.vegparamo.com hvorfra oplysningerne kan tilgås og downloades frit. Vi har anvendt data fra VegPáramo til at opstille en regional klassifikation af páramoen (Kapitel 2). Ved hjælp af en cluster-teknik har vi klassificeret regionen i 17 clusters, hvoraf 14 repræsenterer naturlige phytogeografiske enheder af en eller flere plantefællesskaber samt 3 kunstige sammensætninger. Vi har beskrevet de 17 clusters samt udregnet alfa- og betadiversiteten for at belyse forekomsten af arter samt floristiske ligheder. Vores sidste studie fokuserer på plantevariationsmønstre i páramoregionen (Kapitel 3). Vi har anvendt data fra VegPáramo og vores klassifikation resulterer i en vurdering og sammenligning af plantediversitet på en lokal og regional skala i páramoens højdeintervaller. Vi har evalueret betydningen af miljøet som en fremmende faktor for rigdom af arter ved hjælp af regressionsmodeller. Endelig har vi modelleret den forventede rigdom af arter i páramoregionen og belyst hotspots for biodiversitet. Vores projekt bidrager til en bedre forståelse af páramoens biogeografi og opstiller grundlæggende forslag med hensyn til bevaring. Efter vores opfattelse bør fremtidig forskning fokusere på betydningen af klimaforandringer for páramoens flora og vegetation.

Stikord: Biogeografi, Den nordlige Andesregion, Biologisk database, Vegetation klassifikation, Plante diversitet.

Resumen*

Introducción

La región biogeográfica que incluye los ecosistemas naturales y semi-naturales de alta montaña distribuidos entre el bosque montano y las nieves perpetuas en los Andes del Norte recibe el nombre de páramo, el cual es considerado un hotspot de biodiversidad, con más de 3400 especies de plantas vasculares y un alto grado de endemismo. La gran biodiversidad del páramo se debe en gran parte a su reciente origen y evolución asociados al levantamiento final de los Andes septentrionales en el Neógeno que permitió el desarrollo de ecosistemas con características particulares encima de los bosques de altitud, primero como un proto-páramo durante el Mioceno y luego como un páramo verdadero durante el Plioceno. Los sucesivos ciclos glaciales que tuvieron lugar durante el Pleistoceno, modelaron considerablemente los ecosistemas de páramo, favoreciendo la especiación vegetal en los periodos glaciares, y la radiación altitudinal de especies tropicales y latitudinal de especies templadas en los periodos interglaciares. En la actualidad, el páramo se distribuye en islas biogeográficas en una matriz de tierras bajas tropicales, lo que promueve su alta biodiversidad y su alta endemicidad.

La región de páramo se extiende en los Andes de Venezuela, Colombia, Ecuador y el norte de Perú, y se distribuye sobre varias cordilleras andinas, separadas por barreras biogeográficas latitudinales y longitudinales. Consideramos la depresión de Huancabamba en Perú como límite sur de la distribución del páramo, aunque este tema sigue en debate. El páramo se divide en tres pisos altitudinales, según la zonación clásica propuesta por Cuatrecasas (1958), que son el ecotono arbustivo inferior o *sub-páramo,* el piso intermedio o *páramo,* dominado por pajonales, arbustales, frailejonales y chuscales, y el piso superior o *super-páramo,* con vegetación escasa sometida a un severo estrés ambiental.

El ambiente de páramo es muy inhóspito con temperaturas bajas, alta humedad, vientos fuertes y alta radiación UV. La estacionalidad decadal, interanual o anual influye en los patrones climáticos de la región, pero es la estacionalidad diaria la que más impacta los organismos parameros, alternando horas de gran insolación y temperaturas altas, y horas de gran nubosidad y temperaturas muy bajas. También los suelos en el páramo tienen una gran influencia sobre las plantas, ya que estos suelen ser relativamente productivos, con gran capacidad de retención de agua y de carbono en las zonas bajas, y en las zonas altas son poco desarrollados, muy improductivos, y sufren de erosión y heladas periódicas.

---

*para referencias bibliográficas, referirse al texto de la disertación

El páramo tiene una gran diversidad florística, aunque no esté completamente registrada todavía. Las angiospermas están muy diversificadas, entre las familias más representativas tenemos las Asteraceae, las Poaceae y las Orchidaceae. También en el páramo podemos encontrar numerosas formas de vida adaptadas a estos ambientes y una alta diversidad beta que se refleja en numerosas comunidades vegetales, las cuales están organizadas en mosaicos complejos en el paisaje.

Los páramos andinos proporcionan muchos servicios ecológicos a las poblaciones humanas, sobretodo en el subministro de agua y el secuestro de carbono. La actividad antrópica en el páramo está afectando considerablemente al equilibrio del ecosistema, tanto en su biodiversidad como en su capacidad de proporcionar sus servicios ecológicos. El impacto antrópico aumenta con el tiempo y se estima que las consecuencias se agraven en combinación con el cambio climático.

Consecuentemente, es imprescindible aumentar nuestro conocimiento científico y proponer nuevas estrategias de gestión y de conservación. La mayoría de estudios botánicos y ecológicos sobre el páramo, y al igual que los planes de gestión, se desarrollan a escala local hasta nacional. Aunque estos estudios son obviamente aportaciones de gran valor, también es importante considerar el ecosistema en toda su extensión con el objetivo de obtener unos resultados y patrones validos en la región biogeográfica. Los estudios regionales sobre la biogeografía de plantas en el páramo son muy escasos, siendo las principales limitaciones la dificultad de establecer colaboraciones científicas y de gestión internacionales, y la falta de fuentes de datos biológicos de buena calidad y de libre acceso. Con este proyecto, proporcionamos una nueva base de datos biológicos para el páramo y nos enfocamos en dos temáticas biogeográficas importantes, que son la diversidad de la flora y de la vegetación de este ecosistema.

Objetivos

Objetivo 1. Construir *VegPáramo*, una base de datos de flora y vegetación para el páramo, basada en inventarios de vegetación y de libre acceso mediante su portal web.

Objetivo 2. Clasificar la vegetación de páramo, para destacar las principales unidades fitogeográficas de la región y compararlas a nivel de diversidad alpha y beta.

Objetivo 3. Analizar la diversidad florística del páramo, comparando los pisos altitudinales de páramo y super-páramo a escala local y regional, evaluando la influencia del ambiente en la variación de la riqueza florística y modelando la riqueza potencial en la región.

Capitulo 1: *VegPáramo*, una base de datos de flora y vegetación para el páramo andino

Introducción

Las bases de datos biológicas son herramientas muy útiles en biogeografía, porque proporcionan grandes volumenes de información revisada y actualizada, que pueden sostener numerosos estudios científicos a diferentes escalas. En la actualidad, existen varias bases de datos florísticas enfocadas en los Neotrópicos que ofrecen información en forma de citas florísticas, fotografías de plantas vivas y fotografías de especímenes de herbario, entre otras. No obstante, las bases de datos de vegetación en Sur America siguen siendo muy escasas y son sobretodo de acceso restringido. Los datos de vegetación generados en el páramo por científicos locales e internacionales proceden de muestreos efectuados con metodologías heterogéneas y no cubren el territorio de manera uniforme.

Para facilitar los avances científicos y de conservación en el páramo, proponemos *VegPáramo*, una base de datos biológica con información de flora y vegetación para toda la región de páramo y de libre acceso.

Material y métodos

Los datos contenidos en *VegPáramo* son inventarios de vegetación muestreados con el método fitosociológico, metodología que pretende caracterizar una comunidad vegetal mediante sus especies diagnósticas, es decir mediante las especies con una presencia preferencial en esta comunidad. El método de muestreo de estos inventarios consiste en definir una parcela en un área representativa de la comunidad vegetal, listar las especies presentes y estimar su grado de cobertura en la parcela. Este método ha tenido mucho éxito en Europa y menos en los trópicos, porque no es el más adecuado frente a la fisonomía compleja de los bosques tropicales, pero si conviene a la estructura relativamente sencilla de las comunidades del páramo.

Programamos *VegPáramo* en SQL y Java, siguiendo el modelo del *Sistema de Información de la Vegetación Ibérica y Macaronésica* (SIVIM). La base de datos contiene seis tablas principales conectadas por una clave primaria: la tabla central de los inventarios, la tabla con la georeferenciación, la tabla de atributos, la tabla de procedencia y dos tablas de tesauros, un tesauro taxonómico y otro sintaxonómico. Los tesauros contienen listas de nombres aceptados y sinonimos para taxones de plantas y comunidades vegetales (sintaxones) y permiten revisar y actualizar los nombres empleados en los inventarios. Construimos el tesauro de taxones sumando y revisando los catálogos florísticos de la región. En la actualidad, contiene 15,000 nombres de especies registradas para la zona de páramo y un amplio ecotono inferior. El tesauro de sintaxones contiene los nombres de comunidades vegetales descritas por los fitosociólogos. El tesauro de sintaxones no es exhaustivo y almacena 400 nombres en la actualidad.

Resultados y discusión

VegPáramo contiene 3,000 inventarios de vegetación, de los cuales 2,700 proceden de la literatura científica, correspondientes al periodo de 1955-2010. Los 300 inventarios restantes son inéditos y proceden de nuestras campañas de muestreo realizadas entre 2011 y 2013, con el objetivo de muestrear los páramos menos estudiados en Perú, Ecuador y Venezuela. Los 3,000 inventarios cubren la mayoría de las áreas de páramo, pero no están distribuidos de manera uniforme, siendo unos páramos muy muestreados, como el páramo de Chingaza en Colombia, y otros poco muestreados, como los páramos peruanos. Creemos que para ser representativa, el volumen cantidad de datos debería ser positivamente correlacionada con la extensión y la riqueza florística del páramo de cada país. Los países con más datos son Colombia y Ecuador que tienen una gran extensión de páramo y una flora muy rica. En contraste, Venezuela que tiene relativamente una gran extensión de páramo, pero una flora pobre, y Perú que tiene una pequeña extensión de páramo con una flora rica, están menos representados en los datos de *VegPáramo*. Alrededor de 2,220 especie están presentes en los datos de *VegPáramo*, lo que corresponde entre el 50% y el 65% de las estimaciones de la flora paramera total. En los datos, las familias más importantes en término de número de especies son las Asteraceae, Poaceae, Orchidaceae y Melastomataceae, que juntas representan un 40% del total de la flora. A nivel genérico, se observan muchos géneros con pocas especies y pocos géneros con muchas especies. Finalmente, pocas especies están muy representadas en los datos, mientras la mayoría de especies aparecen en pocos inventarios.

VegPáramo (GIVD Nº SA-00-002) es de acceso libre y está disponible en www.vegparamo.com, donde se pueden consultar los datos por búsquedas taxonómicas, sintaxonómicas y geográficas y descargarlos. Los resultados de las búsquedas muestran para un taxón su ficha biológica y distribución geográfica, para un sintaxón su lista de especies y distribución geográfica y para una área geográfica su lista de taxones y de sintaxones. Los resultados se pueden descargar como citas florísticas o como inventarios de vegetación, y ser utilizados en numerosos tipos de estudios científicos en botánica y ecología, y también podrán ser útiles para desarrollar estudios de gestión del páramo.

Capitulo 2: Clasificación de la vegetación en la región de páramo

Clasificar la vegetación de un área y particularmente de una región biogeográfica aporta una contribución científica esencial y de soporte para desarrollar investigación en biogeografía y en ecología. Este tipo de estudios se basa, en la mayoría de casos, en la composición de especies como criterio para segregar comunidades vegetales, como ocurre en el sistema sintaxonómico en fitosociológica. Varias clasificaciones de la vegetación paramera han sido propuestas en los diferentes países andinos durante las últimas décadas. No obstante, aunque estas clasificaciones son de gran interés, no se pueden extrapolar sus resultados a toda la región, ya que la validez de los resultados dependen de la escala de trabajo, lo que puede influenciar las interpretaciones. Consecuentemente, con el fin de definir un marco biogeográfico valido para todo el páramo en base a la vegetación, es importante efectuar una clasificación considerando toda la región basada en un gran volumen de datos.

En este estudio realizamos una clasificación regional de la vegetación zonal en el páramo, basada en los datos de *VegPáramo*, y comparamos la diversidad alpha y beta entre las unidades fitogeográficas obtenidas.

Material y métodos

Usamos un conjunto de datos procedente de *VegPáramo*, que no contiene datos de vegetación azonal (según la descripción del autor original de los datos). En primer lugar, empleamos una metodología que combina la técnica de clasificación no jerárquica K-means para dividir los datos en la mejor partición de grupos (*clusters*) y el cálculo del índice de fidelidad Ochiai para destacar las especies diagnósticas de cada grupo obtenido. En segundo lugar, comparamos los grupos a nivel de riqueza florística (diversidad alpha) usando un test de Kruskal-Wallis con un post hoc test bilateral de Steel-Dwass-Critchlow-Fligner y también a nivel de diversidad beta, calculando el índice de Similitud de Sørensen por pares.

Resultados y discusión

La partición en 17 grupos fue la más adecuada para dividir los datos, y representa bien la zonación altitudinal con 9 grupos de páramo, 4 de super-páramo y 2 de sub-páramo, y también uno de vegetación azonal y uno de vegetación intervenida. Los grupos de páramo cubren las principales comunidades vegetales de la región, incluyendo los pajonales de Perú y Ecuador, las comunidades mixtas de pajonal-frailejonal de Colombia, y los frailejonales de Venezuela. Los grupos de super-páramo también representan a las principales comunidades vegetales a gran altitud, principalmente de Ecuador y Colombia. Incluyen a las comunidades de cojines y/o de arbustos concentradas en el ecotono super-páramo inferior y a las comunidades desérticas del super-páramo superior. Nuestra clasificación no pudo segregar bien las diversas comunidades de sub-páramo y sospechamos que se debe a que los datos de *VegPáramo* no alcanzan a ser suficiente representativos de la alta diversidad florística y de vegetación. Una clasificación a nivel genérico quizás podría dividir mejor la vegetación del sub-páramo con estos datos. La clasificación generó un grupo de vegetación azonal de cojines, cuyos inventarios no quitamos de los datos originales porque sus autores no los describieron como azonales. Finalmente, la clasificación generó un grupo de vegetación intervenida, que agrupa diversos inventarios con una componente de especies comunes ruderales importante. Consideramos 14 de los grupos obtenidos como naturales, y representando unidades fitogeográficas en la región y 3 grupos como artificiales. Los grupos artificiales fueron generados por la agrupación de inventarios sin las especies diagnósticas que hubieran permitido que se junten a otros grupos y esto es un efecto secundario de las clasificaciones realizadas sobre un juego de datos muy heterogéneo. Las unidades fitogeográficas con una distribución restringida y caracterizadas por especies diagnósticas con altos valores de índice Ochiai podrían presentar alta endemicidad y deberían recibir una atención particular.

Respeto a la diversidad, observamos mucha variación dentro y entre los grupos. Los grupos ecuatorianos y venezolanos suelen ser más ricos que sus homólogos colombianos, lo cual es sorprendente dado que los páramos colombianos son los más húmedos y podría ser debido al muestreo. También nos parece que se puede distinguir un patrón altitudinal de riqueza de tipo *hump-shaped*, con un máximo al ecotono entre páramo y super-páramo, seguramente debido a su situación en el estrato superior de condensación. Desde el punto de vista de la biodiversidad beta, cada grupo tiene más similitud florística con los grupos latitudinalmente y altitudinalmente cercanos, lo que podría sugerir que los grupos con una baja similitud florística con los demás sean potencialmente ricos en endemismos.

Capitulo 3: Patrones de diversidad de plantas en el páramo

Introducción

Los estudios sobre la diversidad de plantas en los trópicos siguen siendo escasos, lo que contrasta con su gran biodiversidad por lo que merecen una mayor atención científica. Los pocos estudios que se han realizado en el páramo están generalmente enfocados a un grupo taxonómico concreto y restringido geográficamente. Entender la diversidad de plantas a nivel regional es importante porque permite entender los grandes patrones de diversidad, que se pueden relacionar con otros gradientes ecológicos; además permite destacar unos hotspots de biodiversidad, que deberían ser prioritarios para la conservación. En las montañas tropicales, la diversidad de plantas esta principalmente correlacionada con factores ambientales, sobretodo los patrones de precipitación a bajas altitudes, y los patrones combinados de precipitación y temperatura a altitudes altas. La hipótesis que el ambiente es el mayor determinante que causa los patrones de diversidad es generalmente aceptada y tiene dos versiones, una *climática*, afirmando que el ambiente afecta directamente a la fisiología de los organismos, y otra de *productividad*, afirmando que al ambiente actúa indirectamente sobre los organismos a través de su fitness.

En este estudio, queremos destacar y entender los patrones de riqueza florística en la región de páramo. Comparamos la diversidad de plantas en el páramo y el super-páramo a dos escalas focales complementarias, la escala local (diversidad alpha) y la escala regional (diversidad gamma). Evaluamos el poder explicativo del ambiente, en su versiones climática y de productividad. Finalmente, predecimos la riqueza florística a toda la región.

Material y métodos

Usamos un conjunto de datos procedentes de VegPáramo, que dividimos en los pisos altitudinales de páramo y super-páramo, basándonos en la clasificación obtenida previamente (Capitulo 2), y eliminamos los inventarios de sub-páramo y de vegetación azonal e intervenidos. Al usar el método fitosociológico, el área del inventario de vegetación no es un parámetro fijo, sino que depende a la práctica de la fisionomía de la vegetación, así que es necesario evaluar su importancia como potencial factor explicativo, lo que hacemos mediante un análisis de regresión simple. Para comparar la riqueza florística a escala del inventario de vegetación (diversidad alpha) entre páramo y super-páramo, empleamos un test t de Student. Además, para comparar la diversidad gamma a escala de la región entre páramo y super-páramo, efectuamos un análisis de pseudo-rarefacción, que permite relacionar el área total muestreada y la riqueza florística total. Evaluamos el poder explicativo del ambiente en la variación de la riqueza florística con modelos de regresión por Mínimos Cuadrados Generalizados (GLS) evaluados por el Criterio de Información Akaike (AIC) bajo cuatro escenarios diferentes: efecto del área del inventario, efecto del ambiente en la versión clima, efecto del ambiente en la versión productividad y efecto del ambiente total (incluyendo todos los previos factores). Para construir los modelos, definimos previamente la componente climática del ambiente como una selección de variables bioclimáticas de temperatura y precipitación procedentes de Worlclim. De manera similar, definimos la componente de productividad del ambiente con variables seleccionadas de evapotranspiración y de déficit hídrico procedentes del CGIAR-CSI. Finalmente, empleamos metamodelos Kriging con un rendimiento óptimo a gran escala, para predecir la riqueza florística en toda la región de páramo. Modelamos la riqueza predicha con tres enfoques: un primer enfoque puramente espacial con un Kriging Ordinario, un segundo considerando únicamente el ambiente con el mejor GLS previamente obtenido y un tercero combinando las dimensiones espaciales e ambientales con un Kriging Universal.

Resultados y discusión

En cuanto a la diversidad alpha, no observamos diferencias significativas en la riqueza florística entre el páramo y el super-páramo, y consecuentemente no encontramos el patrón de disminución de la riqueza con la altitud generalmente observado en montañas altas. Quizás este resultado se debe al ecotono entre los dos pisos altitudinales, aquí incluido con el super-páramo y que podría compensar un super-páramo superior más pobre. En cuanto a la diversidad gamma, se observa que existe, a igual área, una gran diferencia entre páramo y super-páramo, siendo el páramo mucho más diverso. Concluimos que esta diferencia se debe a una diversidad beta mucho mayor en el páramo ya que el mosaico de hábitats está muy extendido, por causas naturales (microclima y topología) y artificiales (actividades antrópicas). Nuestro juego de datos refleja bastante bien la diversidad beta del super-páramo, pero para acercarse a la beta diversidad máxima en el páramo se requieren datos adicionales.

Según la Suma de Cuadrados de nuestros modelos GLS, el ambiente tiene mucho poder explicativo de la riqueza florística en ambos pisos altitudinales, y sobretodo en el super-páramo. Los resultados de los modelos GLS mostraron que el ambiente en su conjunto es el mejor predictor y que el clima es especialmente importante en el super-páramo, lo que coincide con las conclusiones clásicas; consecuentemente, estos ecosistemas serian particularmente vulnerables a cambios climáticos. En comparación, la productividad tiene más poder predictivo en el páramo que en el super-páramo, lo que podría reflejar un efecto del paisaje en mosaico usualmente mantenido por actividades antrópicas con comunidades vegetales de productividad vegetal diferentes.

El Kriging Universal dio los mejores resultados prediciendo la riqueza florística en la región de páramo. Observamos una disminución de la riqueza florística desde el Sur hacia el Norte con numerosas excepciones locales a este patrón regional. Generalmente, los páramos secos suelen tener una riqueza menor que los páramos húmedos. Además, pudimos identificar unas áreas de alta riqueza que calificamos preliminarmente de hotspots de biodiversidad. Estos hotspots están sobretodo concentrados en el sur de la región, en los páramos del este del Ecuador y también en los páramos del extremo Este de Venezuela. Los páramos colombianos están descritos como extremamente diversos en cuanto a flora y hábitats y son en mayoría húmedos por estar localizados en el área central de la Zona de Convergencia Intertropical, consecuentemente estamos sorprendidos de no encontrar en nuestros resultados unos hotspots en Colombia. Consideramos por ello que los datos colombianos contenidos en *VegPáramo* requieren una revisión y quizás aportes adicionales para confirmar el patrón de riqueza encontrado. A partir de nuestro estudio, podemos proponer que los patrones de diversidad de plantas en montañas tropicales dependen más de las condiciones microambientales que de los gradientes macroclimáticos.

Conclusiones y perspectivas de futuro

Nuestro trabajo generó una base de datos botánicos para el páramo (*VegPáramo*) y dos estudios biogeográficos sobre toda la región de páramo como primeros elementos hacia una mejor caracterización del paramo en su conjunto.

VegPáramo con sus 3,000 inventarios de vegetación ofrece una fuente importante de datos botánicos, accesibles a través de su página web de libre acceso. Es importante que la base de datos siga mejorando y creciendo con nuevos datos, especialmente de las áreas con alta riqueza florística pero poco muestreadas, como son los páramos peruanos. Estamos trabajando para desarrollar nuevos atributos que sean de interés ecológico, como las categorías IUCN de los taxones y nuevas herramientas que permitan facilitar el uso del portal y de los datos. Las opciones online de *feedback* y comentarios ayudan a la interacción entre usuarios y a mejorar la base de datos.

La clasificación regional de la vegetación de páramo nos permitió destacar las grandes unidades fitogeográficas de vegetación zonal de páramo. Los resultados de diversidad alpha parecen apoyar la alta riqueza florística de las comunidades vegetales del ecotono entre páramo y super-páramo que se ya ha sido observado en otros estudios. Sería interesante profundizar esta temática porque los ecotonos son ecológicamente frágiles y en este caso, como dependen directamente del estrato superior de condensación que podría estar muy afectado por el cambio climático, estarían a su turno impactados. Mientras que la clasificación dividió satisfactoriamente los pisos altitudinales de páramo y super-páramo, no pudo segregar bien las comunidades del sub-páramo. Este ecotono esta caracterizado por su gran biodiversidad pero es especialmente frágil y esta frecuentemente muy intervenido o incluso destruido por las actividades antrópicas. Es imprescindible que estudios futuros se enfoquen en el sub-páramo, muchas veces descuidado por los biólogos, para que se caracterice y pueda ser evaluado con más precisión a fin de promover su conservación. Las unidades fitogeográficas de nuestra clasificación, con su significado ecológico, pueden utilizarse solas o combinadas como base para nuevos estudios

científicos. También, nos parece importante efectuar una clasificación regional de los tipos de vegetación azonal de páramo, especialmente de los amenazados bosques de *Polylepis* y de la vegetación hidrófila, que a pesar de tener una distribución muy restringida a escala local, se extienden ampliamente a lo largo de los Andes.

Nuestro estudio de diversidad de plantas en el páramo destaco un patrón general de disminución de la riqueza florística de Sur a Norte con muchas excepciones locales, lo que apoya la importancia de las condiciones microambientales en montañas tropicales. Creemos que los datos de Colombia necesitan una revisión y nuevos inventarios fitosociológicos para comprobar la baja riqueza florística de estos páramos a pesar de su reconocida alta diversidad de ambientes y hábitats. A fin de captar la máxima diversidad de comunidades vegetales en la región, es necesario aumentar el esfuerzo de muestreo, particularmente en el piso altitudinal del páramo. Pensamos que nuestros modelos predictivos podrían mejorar tomando en cconsideración además del ambiente otros factores explicativos, como procesos evolutivos o interacciones bióticas y sobretodo incluyendo una dimensión temporal. Los hotspots de biodiversidad propuestos en este estudio son candidatos primarios a la conservación, no obstante es importante notar que el concepto de riqueza florística no diferencia entre áreas naturales y antropizadas. Consecuentemente una manera de valorar la calidad de nuestros hotspots, seria correlacionar los patrones de riqueza florística con patrones de endemicidad. Finalmente, se ha demostrado que los patrones regionales de riqueza especifica estan sobretodo definidos por las especies comunes y sería interesante afinar nuestros resultados destacando el balance entre especies comunes y raras, y evaluando su importancia relativa a la hora de modelar los patrones de riqueza florística a gran escala.

Queremos llamar la atención sobre les ecosistemas relativamente prístinos del super-páramo presentan una flora muy especializada, endémica y frágil, y siguen bien conservados por la falta de actividades antrópicas a estas altitudes. El cambio climático es la mayor amenaza para las plantas del super-páramo por la limitación de sus nichos ecológicos y de su capacidad evolutiva, pero también por el avance de las actividades antrópicas a mayores alturas. Consecuentemente, nos parece imprescindible estimar la respuesta potencial de estos ecosistemas frente al cambio climático.

Palabras claves: Biogeografía, Andes del Norte, Base de datos biológica, Clasificación de la vegetación, Diversidad de plantas.

Acknowledgments

I am deeply thankful to all the people that have helped and supported me during the fieldwork, analyses and writing phases of my PhD thesis. I would like to express my special appreciation and thanks to my supervisors Dr. Xavier Font and Dr. Henrik Balslev who, with their kindness, patience and professionalism made this project possible. Thank you both for helping me grow as a researcher.

I am very grateful to my collaborators in South America who helped me get over the many obstacles encountered on the way to the mountain top, and made me a stronger person. Many thanks to Dr. Pablo Lozano, Dr. Nidia Cuello, Dr. Isidoro Sánchez-Vega and Ing. Omar Cabrera for their considerable support and for taking the time to share their research, experiences and ideas with me. Many thanks to Dr. José Campos de la Cruz, Dr. Katya Romoleroux, Dr. Renato Valencia, Dr. Javier Estrada and Dr. Juan Gaviria for their trust and considerable help with the administrative work of collecting and exporting permits procedures, and with organizing the fieldwork campaigns.

My thanks go to Dr. Petr Sklenář, Dr. Antoine Cleef and Dr. Paul Ramsay who have inspired my work and taken the time to receive me and discuss páramo research. A special thank goes to my collaborator and friend Dr. Sebastian Tello with whom I developed the Plant diversity study and who has taught me much about Macroecology. I would like to thank Dr. Rainer Bussmann and Dr. David Rivera for sharing their data and participating in the development of *VegPáramo*. Many thanks to David Martí and Rafael Quadrada for their considerable help building the *VegPáramo* webportal.

I would also like to express my gratitude to the expert taxonomists Dr. Simon Lægaard, Dr. Benjamin Øllgaard, Dr. Mats Gustafsson, Dr. Nicholas Hind, Dr. Ulf Molau, Dr. Benito Briceño, Dr. Robbin Moran, Dr. Paola Pedraza and Dr. Carmen Ulloa whose help identifying the plant samples was greatly appreciated.

Many thanks to my fieldwork collaborators and friends Walter Vargas, Raiza Garcia, Rene López, Dr. Manuel Albán, Dionys Sánchez, Dr. Gilberto Morillo, Marina Mazón, Roberto Rueda, Roberto Carrillo, Dr. Jerome Mwinyelle, Dennis Pedersen, Jonathan Mucherino and the local people who accompanied us on the field, with whom were shared extreme páramo adventures that will never be forgotten.

I would like to thank everybody involved in the double degree administrative process from the University of Barcelona and Aarhus University, especially Dr. Maria-José López Fuster, Birte Tofte, Liselotte Kaspersen and Carmela Ruz who have endured my many questions and doubts, and always responded nicely and efficiently. Many thanks also to Dr. Ramón Massalles, Dr. Josep Ninot and Dr. Ignasi Soriano of my PhD commission at the University of Barcelona for their guidance.

My gratitude is also extended to the staff of the herbariums where I identified my plant samples, Aarhus University Herbarium, CPUN Herbarium at the National University of Cajamarca, the Herbarium at the Royal Botanic Gardens Kew, the Herbaria MERC and MERF at the University of the Andes, the Missouri Botanical Garden Herbarium, the New York Botanical Garden Herbarium, the PORT Herbarium at the National Experimental University of the Llanos Ezequiel Zamora, the QCA Herbarium at the Pontifical Catholic University of Ecuador and the San Marcos University Herbarium. A special thank to Jette Bargholz and Birgitte Bergmann in Aarhus who have helped handling my specimens.

I gratefully acknowledge the PhD grant (2011FI_B 00190) and the traveling grant (BE-DGR 2011) that I received from the Agency for Administration of University and Research Grants (AGAUR) from the Generalitat de Catalonia (Spain) and also the traveling grants from the University of Barcelona that financed my PhD, my fieldwork and my participation to conferences.

A special thanks to my parents Emmanuel and Béatrice Peyre, my brother Alexandre and my sister Yoorana for their unconditional love and support in all circumstances.

I am indebted to all my friends, who have supported me over the last few years. A special thank goes to Javier Castillo, Francisco Santiago and Anne Funck for always being there for me and endure my ups and downs. I would not have made it without you.

Last, but certainly not least, I must acknowledge with tremendous and deep thanks Dr. Timothy McDowell who inspired me when I deeply needed it and took me to the páramo for the first time, in 2009. And the fascination began……

Merci à tous

Index

Introduction

The Neotropics host the highest biodiversity on Earth (Antonelli & Sanmartín 2011) and are particularly diverse in mountain areas (Jiménez *et al.* 2009), where the Andean páramo is found. The páramo is a biogeographic region that includes all natural and semi-natural ecosystems located between the montane treeline and the permanent snowline in the humid Northern Andes (Luteyn 1999). The páramo is characterized as a fast evolving hotspot (Hughes & Eastwood 2006; Madriñán *et al.* 2013), with the richest tropical high mountain flora (Smith & Cleef 1988; Sklenář *et al.* 2014), high endemism (Luteyn 1992) and ecologically fragile (Balslev & Luteyn 1992).

Origin of the páramo

The páramo has a recent geological origin and was topographically modeled by glacial activity (Baruch 1984). During the Miocene, circa 10 Ma, the Northern Andes started their last upheaval and a proto-páramo with shrubby vegetation started developing above the montane treeline at lower altitude than the páramo today. The region reached its ultimate elevation during the Pliocene (5–2.5 Ma) and by the end of the Neogene, real páramo vegetation was recorded, according to fossils (van der Hammen & Cleef 1986). The glaciation dynamics during the Pleistocene, and especially the short 100,000 years cycles in the last million years, shaped the páramo as it is today (Hooghiemstra & van der Hammen 2004; Hughes & Eastwood 2006). During interglacial epochs, páramo areas were extended and connected, promoting the radiation of species. General radiation trends included (i) for tropical taxa to move upwards from the adjacent Amazon basin and western lowlands and (ii) for temperate taxa, from the Holarctic and Austro-Antarctic regions, to move longitudinally along the Andes (Simpson 1975; Hooghmiestra *et al.* 2006). During glacial epochs, páramo areas were easily isolated, like archipelagos of continental islands, promoting isolation and speciation, which explains the high endemism (*e.g.* Simpson & Todzia 1990; Myers *et al.* 2000). Most of the Northern Andes have been affected by volcanism, directly or indirectly, with events that still condition the páramo ecosystems in their structure and dynamics today (Hofstede *et al.* 2003; Sklenář *et al.* 2010).

Study Area

The páramo region extends accross the Andes of Venezuela, Colombia, Ecuador and northern Peru, but it also includes extra-Andean areas such as the Sierra de Talamanca in Costa Rica (Luteyn 1999). Moreover, specific páramos, or *paramillos,* are also extraordinarily located on lower mountains, such as isolated high volcanoes in the Amazon basin (Løjtnant & Molau 1983) and the coastal Cordillera in Venezuela (Vareschi 1955). The southern limit of the páramo remains a debated topic. The depression of Huancabamba in northern Peru partially interrupts the high Andes and is usually considered the separation point between the humid Northern Andes and dry Central Andes (Josse *et al.* 2011). This area is a biogeographical barrier for many high mountain plant taxa (Molau 1988; Richter *et al.* 2009) and therefore it is also considered a major barrier for páramo habitats (Weigend 2002; Sánchez-Vega & Dillon 2006). South of the depression of Huancabamba, the high Andes are dominated by ecosystems of jalca and puna that differ from the páramo by having a drier climate and a more pronounced dry season (> 5 months) (Lauer 1979; Vuilleumier & Monasterio 1986). Nonetheless, humid mountain conditions also happen at these latitudes, for example on the Amazonian slope of the Andes, and lead to ecosystems that resemble the páramo (García & Beck 2006; Rangel-Churio *et al.* 2006). A revision of these habitats is therefore needed, but we will focus here on the traditional Andean distribution of the páramo (Fig. I.1, Appendix 1).

In Peru, the páramo is confined to the Amatope-Huancabamba zone, a biogeographic area shared with Ecuador that extends to the Paute-Girón valley in the north (Weigend 2002). From this point, the páramo is mainly found on two parallel cordilleras, the eastern and western Ecuadorian cordilleras (Hofstede *et al.* 2002). Further north at the node of Pasto, the Andes divide into three cordilleras, the western, central and eastern Colombian cordilleras, which all present páramo. The eastern Colombian cordillera in turn divides at the node of Pamplona into the Cordillera de Mérida in the east and the Sierra de Périja-Sierra Nevada de Santa Marta isolated complex in the north (Rangel-Churio 2000a). The Cordillera de Mérida extends east in Venezuela and contains most páramos in the country, other smaller areas including part of the Sierra de Périja and Táma (Monasterio & Reyes 1980).

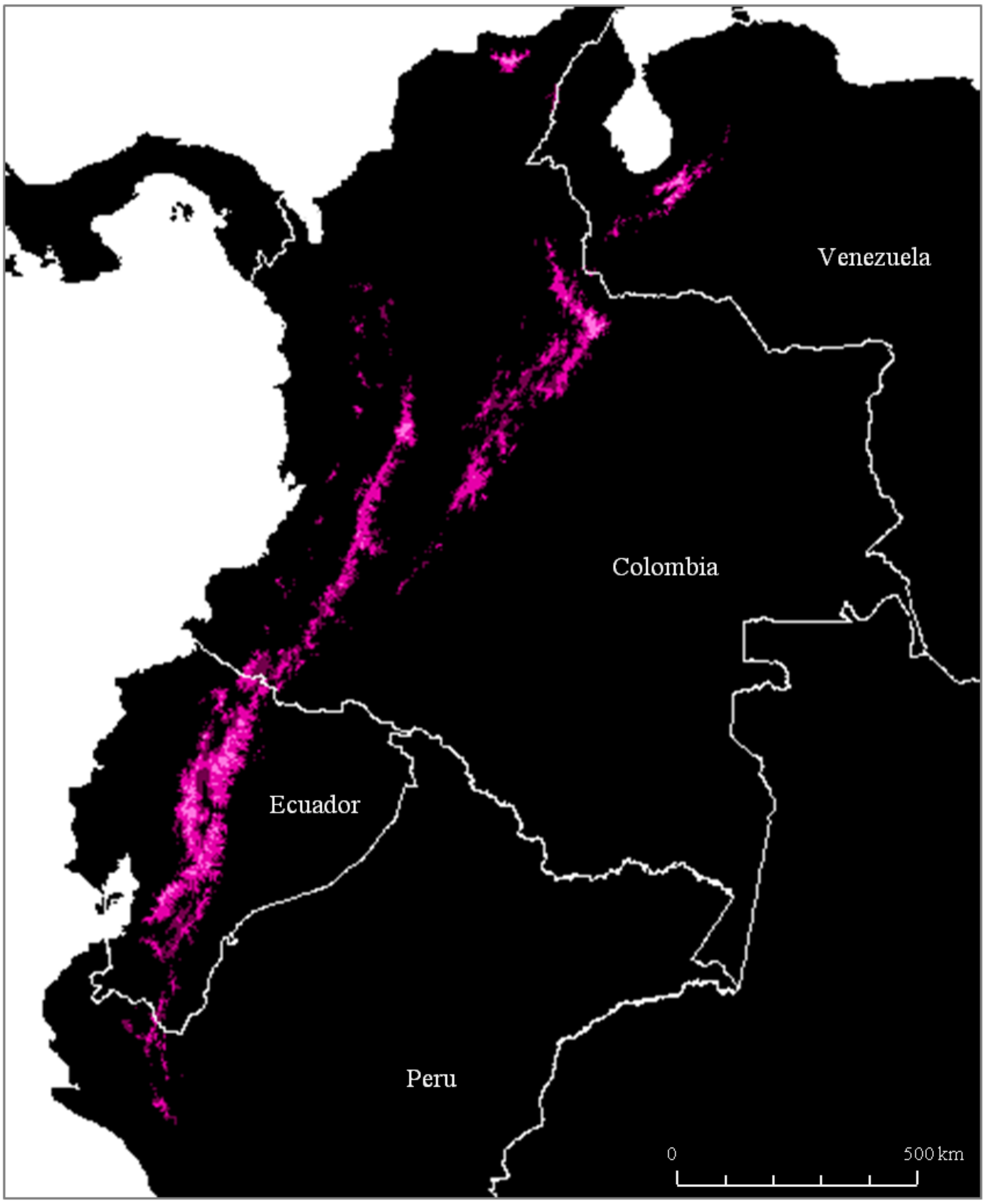


Figure I.1. Potential distribution of the páramo region in the Northern Andes (> 3000 m). Altitudinal zonation: sub-páramo (dark pink), páramo (bright pink) and super-páramo (light pink).

A general approximation of the páramo altitudinal distribution is the 3000–5000 m elevation range. Traditionally, the páramo has been divided into three altitudinal belts, sub-páramo (~ 3000–3500 m), páramo (~ 3500–4000 m) and super-páramo (~ 4000–5000 m), a zonation proposed by Cuatrecasas (1958) that has been largely debated (*e.g.* Monasterio & Reyes 1980; Acosta-Solís 1984) but is usually accepted (*e.g.* Cleef 1981; Balslev & Luteyn 1992; Lutyen 1999). The sub-páramo forms the ecotone between montane forest and páramo and manifests as a shrubby transitional vegetation. It is often artificially fragmented and sometimes removed by agriculture and the expansion of páramo grasslands downward, or *paramerization*, which is associated to frequent burning (Ramsay 1992). The páramo forms a relatively continuous belt in the region, except for the western Colombian cordillera and the isolated Périja-Santa Marta complex. The páramo belt mostly contains grasslands and shrublands and it is very pressured by anthropogenic activities including agriculture and pasture (Ramsay & Oxley 1996; Molinillo & Monasterio 2002). The super-páramo occupies a much smaller area in the Andes and it is reduced to continental islands on the higher mountains of Ecuador, Colombia and Venezuela (Sklenář & Jørgensen 1999). In general, the super-páramo habitats present scarce vegetation and are less disturbed by human activities due to their stressful environment (Sklenář & Ramsay 2001).

Environment

Climate

The climate in the region is severe and stressful for páramo life, and its characteristics include high humidity, cold temperatures, strong winds and intense solar radiation (Luteyn 1999; Buytaert *et al.* 2011). The páramos usually stay humid throughout most of the year with great moisture intakes (70–90%) in form of vertical precipitation (rain) and mostly horizontal precipitation (clouds and mists) (Luteyn 1999). There are two climatic buffer zones, which are the lower and upper condensation belts, located at the altitudinal levels of respectively the upper montane forest and the ecotone between páramo and super-páramo (Cleef 1981). Páramos can be classified according to annual rainfall, as pluvial (> 4000 mm), per-humid (4000–3000 mm), humid (1800–3000 mm), semi-humid (1800–1200 mm) and dry (< 1200 mm) (Rangel-Churio 2000b). Temperature decreases with elevation, usually at a rate of 0.6ºC per 100 m, and ranges from 9ºC in average in the sub-páramo belt, to 6ºC in the páramo belt and 3ºC or less in the super-páramo belt (van der Hammen & Otero-García 2007). Moreover, at these elevations, the pressure in O_2 and CO_2 gases is low and the UV radiation is at its highest intensity due to the equatorial location of these mountains. Temperature and especially precipitation are primordial factors shaping the páramo plant diversity (Kessler *et al.* 2011) and their general patterns are highly influenced by winds and topography. The northern páramos in Venezuela and in the Périja-Santa Marta complex are usually dry páramos as they are exposed to the northeast Caribbean trade winds (Lauer 1979). However the easternmost páramos in Venezuela are also submitted to the Orinoquia winds that make them per-humid (Monasterio & Reyes 1980; Hofstede *et al.* 2003). In the tropics, the differences between the east-west slopes of mountains are usually steeper than between the north-south slopes, as precipitation usually goes leeward and windward (Smith 1978). This explains for instance why the slopes facing the Amazon or the

Chocó are wetter than the inter-Andean Cauca and Magdalena valleys in Colombia or the inter-Andean plateau in Ecuador (Rangel-Churio 2000b; van der Hammen & Otero-García 2007). Further south in the Amotape-Huancabamba zone, the Andes are wetter on the eastern slope bordering the Amazon basin and drier on the western slope, which is submitted to the cold Humboldt Current (Jørgensen & Ulloa-Ulloa 1994). Moreover, the region shows a wide panel of microclimatic conditions, including steep gradients in temperature and humidity that are mostly conditioned by the complex topography (Antonelli *et al.* 2009; Young *et al.* 2011).

In terms of seasonality, the Northern Andes are submitted to different timescales of climatic variation that are usually driven by the main oceanic currents (Marengo *et al.* 2004). At decadal scale, the northwestern Andes are submitted to the Pacific Decadal Oscillation (PDO) that periodically cools and warms the Pacific Ocean and has a direct influence on the western winds (Mantua & Hare 2002). The PDO effects are combined with the primary impacts of the inter-annual changes in the El Niño Southern Oscillation (ENSO) (Martínez *et al.* 2011). The ENSO events usually lead to fewer rains during the warm El Niño phenomenon and stronger rains during the cold La Niña phenomenon in the region (Vuille *et al.* 2000; Poveda *et al.* 2004). Annual seasonality in the páramo varies substantially depending on the area, slope and microclimate. One of the main factors of seasonal variability is the latitudinal oscillation of the dynamic Inter-tropical Convergence Zone (ITCZ) (Martínez *et al.* 2011). The ITCZ is where the southern and northern winds converge and its precipitation equator is located approximately 2–5ºN of the geographic equator (Sarmiento 1986). However, the ITCZ is not static and it latitudinally migrates during the year, covering the 6ºS–12ºN range (Mitchell & Wallace 2012), which conditions the precipitation annual seasonality regimes. In fact, the precipitation regimes of the southern and northern páramos have a unimodal tendency (two seasons) as the ITCZ passes over once a year, and the central páramos have a bimodal tendency (four seasons) as the ITCZ passes over twice (Ramsay 1992), but these precipitation regimes are latitudinally and altitudinally variable (Rangel-Churio 2006). The southernmost páramos in Ecuador and Peru show the strongest seasonality as they border the dry Central Andes (Martínez *et al.* 2011). The more challenging seasonality for organisms and plants in particular, is the diurnal cycle (Smith & Young 1987). Diurnal climatic variation is associated to the convection effect that causes moisture advection during the day and cooling and drying processes at night (Ruiz *et al.* 2009). These cycles can encompass changes of up to 30ºC in temperature and go from high insolation to dense fogs (Hedberg 1969; Luteyn, 1999), with the steepest variations in the super-páramo belt, in the drier páramos and during the dry season (Sklenář 2000). Temperature oscillations around the freezing point are primordial for páramo plants and their frequency helps shaping the species composition and distribution at high elevation (Sklenář & Balslev 2005). Frost and snowfall usually take place at night and are correlated with elevation, slope and seasonality. In general, diurnal frost occurs from 4300–4500 m in the super-páramo (Baruch 1984; Salamanca *et al.* 1993).

Soils

The soils are very diverse in the páramo region and they are mostly conditioned by geology and climate. Two important trends in the formation of the páramo soils are *andolization* (presence of volcanic ashes) and *hydromorphism* (saturation in water) that lead to the pedogenesis of the Andisols and Histosols respectively (Malágon & Pulido 2000). The sub-páramo belt is where the highest diversity of soils can be found. These soils, mostly Andisols and Inceptisols, are generally productive. In the páramo belt, the common soils, essentially Andisols and Inceptisols, are dark acidic soils with high contents in organic matter and a constant saturation in water (Cleef 1981; Poulenard *et al.* 2003). They are also moderately productive as the low temperatures limit the soil microbial and fungal activity (Ramsay 1992). In addition, peat soils, or Histosols, are often found in small depressions and around stagnant water, preferentially in the páramo belt. In the super-páramo belt, and especially in the upper zone, the soils are mostly cryic Entisols and volcanic Andisols that are poorly developed. These rocky and sandy soils with almost no organic horizon are very infertile and have little water-retention capacity. They also suffer from severe periglacial phenomena such as solifluction and needle-ice activity (Luteyn 1999; Sklenář 2000).

Flora and vegetation

The páramo hosts an incredible flora of more than 1300 non-vascular plant species and 3400 vascular plant species (Luteyn 1999). Other estimates for the regional páramo flora, but including the Central American páramos, count over 5000 vascular plant species (Rangel-Churio 2000c). Species are still being discovered in the tropics, including the high Andes, and the information on hybridization and species limits remains incomplete; therefore, these approximations of the páramo flora are not final and the páramo could be even more diverse. Even though authors do not agree on taxa numbers, they usually do agree on the proportions and importance of the different taxa in the flora. Of the recognized páramo vascular plant species, 10 % are Pteridophytes, 1 % are Gymnosperms and 89% are Angiosperms, of which 21% are Monocots and 79% are Dicots (based on Luteyn 1999). The most important Pteridophyte families in term of species number are Dryopteridaceae, Lycopodiaceae and Polypodiaceae, whicht are represented in most páramo habitats. Gymnosperms are naturally rare in the páramo, with Ephedraceae being the only widespread family and Podocarpaceae occasionally present in the sub-páramo. For Angiosperms, Asteraceae, Poaceae and Orchidaceae are the most diverse families. Asteraceae are well represented throughout the páramo region and almost all habitats. Poaceae are also widely distributed, but they are most diversified in the páramo belt. Orchidaceae are still under-estimated and mostly found in the sub-páramo belt but also in the páramo belt where they usually adopt a terricole form. The páramo flora has multiple origins thanks to the complex orogeny of the Northern Andes and the ratio of temperate *vs.* tropical taxa varies along the latitudinal and altitudinal gradients. In general, the more humid páramos of the equatorial zone show a more balanced ratio of 50/50 (van der Hammen & Cleef 1986; Smith & Cleef 1988), whereas the drier and more seasonal páramos present a higher proportion of temperate taxa, as stated in Ecuador where the ratio becomes 70/30 according to Ramsay (1992). In addition, the temperate component presents usually more Holartic taxa in the northern páramos and more Austral-Antarctic elements in the southern páramos (Sklenář 2000). Along the altitudinal gradient, the ratio of temperate *vs.* tropical taxa increases with elevation. For example, tropical families such as Melastomataceae, Bromeliaceae and Orchidaceae are more diverse in the sub-páramo and temperate families such as Brassicaceae, Apiaceae and Caryophyllaceae are better represented in the super-páramo (Jørgensen & Ulloa-Ulloa 1994).

The past and present insular situations of the páramo have promoted high endemism in the region, especially in the more isolated areas such as the Sierra Nevada de Santa Marta (Carbono & Lozano-Contreras 1997). Along the altitudinal gradient, endemism peaks in the sub-páramo, which presents high diversity of habitats (Luteyn 1999), and also in the geographically more isolated super-páramo (Berg 1998). No family has become endemic of the páramo due to its recent origin (van der Hammen & Cleef 1986), but 5% of the genera are endemic and regional estimates of endemism at species level reach 60% (Luteyn 1992; Luteyn 1999). However, the number of species, limits and distribution are too poorly known to give a realistic estimate of the páramo endemism.

The páramo flora can be classified into ten principal growth-forms: stem rosettes, basal rosettes, acaulescent rosettes, tussock plants, cushions and mats, upright shrubs, prostrate shrubs, erect herbs, prostrate herbs and trailing herbs (Ramsay & Oxley 1997), to which we add the less represented epiphytes and trees (Appendix 2). Among the rosette forms, stem rosette plants are characteristic of tropicalpine ecosystems (Smith & Young 1987) and present a tall woody stem with a large apical rosette of leaves, basal rosette plants have a large basal rosette of leaves from which a flowering stem eventually arises, and acaulescent rosette plants present a small basal rosette of leaves and no developed stem. Tussock plants are grasses with rigid leaves that grow in dense clumps or bunches. Cushions and mats are dense hemi-spherical to flat structures made of relatively small plants with stems hidden into the peat center of the cushion and small rigid leaves on the surface. Shrubs in the páramo can be upright or prostrate and very often present microphyllous sclerophyllous leaves. Trees are rare in the páramo and usually present hard wood due to their slow growth and sclerophyllous leaves. Herbs have a variety of forms and can be erect, prostrate or trailing and climbing on other plants. Finally, vascular epiphytes are usually small Orchids and Bromeliads found in the sub-páramo belt. The many growth forms found in the páramo are well adapted to the severe environment (Ramsay 1992). Some common adaptations include pubescence on stems and leaves to reduce transpiration and regulate temperature, isolation with dead leaves of live parts of the cormus and sclerophyllous leaves to limit dessication (*e.g* Baruch 1984) (Fig. I.2).

Figure I.2. Examples of plant adaptations, sclerophyllous leaves with glabrous stems on (a) *Chuquiraga jussieui* J.F. Gmel. and with pubescent stems on (b) *Aragoa lucidula* S.F.Blake. Leaves with tomentose hair on (c) *Espeletia schultzii* Wedd. Protective dead leaves on (d) *Coespeletia timotensis* (Cuatrec.) Cuatrec.

The páramo is also very diverse in terms of plant communities (*e.g.* Sturm & Rangel-Churio 1985; Rangel-Churio 2000d) that are representing different vegetation physiognomies (Fig. I.3). Páramo landscapes are dominated by *zonal* vegetation, which is determined by the macro- and meso-environments (Cleef 1981) and presents many vegetation types such as bunch grasslands, shrublands, rosette communities, bamboo communities, cushion communities, meadows and high altitude desert. In contrast, *azonal* vegetation is geographically restricted and associated to specific micro-environments. Examples of azonal vegetation in the páramo are the bogs and mires developing around local stagnant water that usually consist of cushion plants and small herbs (Cleef 1981; Bosman *et al.* 1993). Other examples of azonal vegetation are the remnant *Polylepis* forests that are usually found in little-accessible areas in the páramo belt. The zonal or azonal character of these forests is still debated as records show these forests could have been largely distributed in the past forming the upper treeline at 4000 m and were then drastically reduced and fragmented by anthropogenic activities (Fjeldså 1992; Kessler 2006). For simplicity reasons, we consider the *Polylepis* forests azonal.

Ecosystem services

The páramo provides numerous ecosystem services that serve a large human population in million inhabitant cities, such as Quito and Bogota, countless smaller cities and also many Andean indigenous communities (Célleri & Feyen 2009; Buytaert *et al.* 2006). According to the Millenium Ecosystem Assessment (2005), ecosystem services can be categorized as provisioning, regulating, supporting and cultural services (Anderson *et al.* 2011). Following this classification, the main provisioning and regulating service that the páramo provides is water supply thanks to the tremendous water-retention and regulation capacity of the soils, especially in the páramo belt (Buytaert *et al.* 2006; Vuille *et al.* 2008). Other páramo provisioning services are food, timber and fiber supplies that are mostly useful for the local Andean communities. An example of important regulating service the páramo offers is carbon storage, which is facilitated by the volcanic component of most soils that increases the soil capacity to capture and retain atmospheric carbon dioxide (Podwojewski *et al.* 2002). The páramo also provides natural supporting services like soil formation, nutrient cycling and photosynthesis. Finally, its spiritual value for the Andean communities and its undeniable landscape value that makes it attractive for tourism are the most important cultural services the páramo offers (Anderson *et al.* 2011).

Figure I.3. Main vegetation physiognomies in the páramo, (a) bunch grasslands, (b) rosette communities, (c) cushion communities, (d) shrublands, (e) high altitude deserts, (f) bamboo communities, (g) meadows, (h) forests.

Ecological threats

The páramo region is ecologically fragile and its homeostasis is critically threatened by the combined effects of anthropogenic activities at local scale and Climate change at global scale (Hofstede *et al.* 2003).

Anthropogenic activities

Human occupation in the high Northern Andes goes back to the pre-Columbian period. Since the arrival of the Spanish and especially since the 1960s, the traditional land use was progressively replaced, intensified, and diversified into more modern practices of agriculture and pasture, in form of burning and grazing, with a strong impact on the natural ecosystems (Vásconez & Hofstede 2006) (Fig. I.4). Agriculture in the páramo is mostly revolving around resistant tuber crops such as potatoes, oca and mashua; however crops of legumes, like quinoa, and cereals are also developed in the lower elevations (Nieto & Estrella 2000; Mena-Vásconez & Medina 2001). Agriculture has a very strong impact on the ecosystem as the vegetation cover is removed and the soil exposed and gradually affected by erosion and agrochemicals, reducing its content in nutrients and its water-retention capacity (Molinillo & Monasterio 2002). Moreover, opportunist species are sometimes introduced through crops and become invasive, such as *Rumex acetosella* L. in the Cordillera de Mérida (Molinillo & Monasterio 1997). The upper agriculture border is rising quickly in the páramo region to satisfy the local communities' development and reaches the ecotone between páramo and super-páramo in some areas, where the severe climate and unfertile soils become limiting. Pasture practices, which include alternating phases of burning and grazing, is relatively less impacting than agriculture but also affects the vegetation and soils (Molinillo & Monasterio 2002). The main impacts of burning include losses of biodiversity, impoverishment of the soils and regressive vegetation succession, for example from shrublands to bunch grasslands and finally to dry meadows. Burning can homogenize the landscape on large extensions but also create spatial and temporal heterogeneity within the landscape (Ramsay & Oxley 1996; Suaréz & Medina 2001). Grazing, on the other hand, is generally carried out by cows or sheep and causes soil contamination and plant species selection (Hoftstede *et al.* 2003). Other activities include deforestation of remnant *Polylepis* forests, which are now reduced to a mere 10% of their original cover (Kessler 2006), and extended reforestation of the páramo grasslands with *Pinus,* which among other things dries and acidifies the soils (Farley *et al.* 2004). Mining is also developed in some páramo areas and causes abrupt removal of the ecosystems and contamination (Vélasquez 2012). Finally, tourism is less impacting on the páramo ecosystems, especially in areas where it is regulated (Rangel-Churio *et al.* 2006).

Figure I.4. Example of anthropogenic activities in the páramo: burning, grazing and pine plantation (Salinas, Bolívar, Ecuador).

Consequently, human influence plays a significant role in shaping and maintaining most of the páramo landscapes, principally in the sub-páramo and páramo belts (Hofstede *et al.* 2003). With human population growth, the anthropogenic pressure on the páramo will intensify and accelerate the degradation of ecosystems (Balslev & Luteyn 1992; Hofstede *et al.* 2003).

Climate change

Tropical mountains are classified as highly vulnerable to the impact of Climate change (IPCC 2007) and might be the most affected areas in the world due to their inter-tropical situation and high elevation (Young *et al.* 2011). In the Northern Andes, the overall picture of climatic evolution remains uncertain (Anderson *et al.* 2011) but a general increase in temperature combined with different trends of change in the precipitation patterns are expected (Urrutia & Vuille 2009; Buytaert *et al.* 2009). Among the most dramatic consequences of Climate change in the region are the accelerated retreat of glaciers (Vuille *et al.* 2008) and the lift of the condensation belts associated with a diminution of cloud cover (Meehl *et al.* 2007; Ruiz *et al.* 2009). Changes in the climatic conditions will have a direct impact on biodiversity in the páramo. The vulnerability of a species to Climate change is defined by its susceptibility (intrinsic biological traits), exposure (area), and adapting capacity (Hole *et al.* 2011). Therefore páramo plant species will respond by either changing their abundances and distribution, plastically evolving or becoming extinct (Pearson & Dawson 2003; Jørgensen *et al.* 2011). Species will respond individually to Climate change, and even if their biotic interactions might condition their response, ecosystems will not shift intact (Parmesan 2006; Young *et al.* 2011). Consequently, no-analog vegetation could develop and opportunist invasive species could take advantage of the newly available niches (Williams & Jackson 2007). Climate change will also have repercussions on the ecosystem services of the páramo, for example the melting of glaciers and increased insolation could lead to a gradual xerification of the páramo, which will affect its water retention and regulation capacity (Vuille *et al.* 2008). Human behavior is already altering the páramo ecosystem services and it will be modified in reaction to these changes, which will probably lead to an accelerated degradation of the páramo, for example with artificial solutions to regulate water supply (Anderson *et al.* 2011).

Conservation state

The conservation state of the páramo is overall critical but very geographically variable. A good taxonomic and ecological knowledge is required prior to taking conservation measures, but in the region, some knowledge gaps on the páramo flora and species distributions create limitations (Jørgensen *et al.* 2011). There are few international programs focusing on páramo conservation, the most active being the *Andean Páramo Project* (www.condesan.org/ppa) which includes collaborative institutions in the four páramo countries and conducts substantial research and integrative management in the region (*e.g.* Cuesta & Becerra 2009; Josse *et al.* 2009). At national scale, the páramo has been recently included in national management programs of the Ministries of the Environment in Colombia and Ecuador. Creating protected areas is the most common measure used in conservation and it is an efficient strategy to preserve the páramo ecosystems, which to date are represented in seven protected areas in Venezuela, fourteen in Colombia, seven in Ecuador and one in Peru (Hofstede *et al.* 2003). Designation of these areas should be based on a biodiversity criterion, ideally combining species richness and endemism; however, more protected areas are created on the basis of socio-political opportunities rather than on the basis of pristine habitats (Hole *et al.* 2011). Other important tools for monitoring and prioritizing the páramo plant species for conservation are the comprehensive Red Lists that are scarcely available in the tropics (Pitman & Jørgensen 2002) and for the páramo countries have only been published and updated in Ecuador (*e.g.* Valencia *et al.* 2000) and Peru (Léon *et al.* 2006). As the páramo is a region under human influence (Balslev & Luteyn 1992), its management and conservation strategies should be integrative and developed in adequate politico-legal framework and socio-economical framework that promote sustainable development and active participation of the population (Hole *et al.* 2011).

In the future, conservation measures will have to develop tools to take into account Climate change in order to minimize losses of biodiversity and key ecological processes (Araújo *et al.* 2004; Buytaert *et al.* 2011). For example in Colombia, Climate change is already becoming an explicit component of future conservation planning (Hoffmann *et al.* 2011). Depending on the threat severity, some areas might require a strict protection of their fragile habitats and species, while others will be suitable to develop integrative conservation and management strategies.

Study goals

Tropical ecosystems are in overall under-studied, which contrasts with their high biodiversity and often critical vulnerability that should capture most scientific attention (Field *et al.* 2009; Lenoir *et al.* 2014). Botanical and ecological research on the páramo is relatively well developed, however, most studies are conducted at local scale (up to national scale), and even though they have great scientific value, their results and conclusions are difficultly comparable and cannot be extrapolated to the entire region (Kessler *et al.* 2011). Therefore, there is a need to increase regional studies that will characterize the páramo as a region.

The scarcity of regional studies in the páramo are due to two main causes, (i) the difficulty to establish joint international research collaborations, which implies data and results sharing agreements and (ii) the limited availability of open access data-sources containing substantial amounts of good quality data able to sustain broad-scale studies. Páramo plant data, in form of floristic and vegetation records, are relatively scarce and scattered, with floristic data contained in monographs, checklists and smaller floristic works (*e.g.* Luteyn 1999; Pedraza-Peñalosa *et al.* 2005) and vegetation data contained mostly in vegetation characterization works that use different sampling methods (*e.g.* Cleef 1981; Salamanca *et al.* 2003). Therefore, there is a need to compile, homogenize and revise the existing data, and generate new data in the areas with less information. Our first objective in this project was to provide a data source of substantial good quality floristic and vegetation data for the páramo that would be freely available to researchers and conservationists (Chapter 1).

We are moreover very interested in the biogeography of plants in the páramo region, a subject that is still emerging for the Northern Andes (*e.g.* Sklenář & Balslev 2005; Mutke *et al.* 2014). We believe that understanding the spatial and temporal broad-scale patterns of species distribution, assemblages and richness in the páramo is important in order to characterize the region and promote conservation (*e.g.* Whittaker *et al.* 2005). The páramo vegetation has been extensively described, with different definitions, criteria and terminologies, and also classified into plant communities, which are fundamental work units in ecology and biogeography.

However, these classification studies are scale-dependant and consequently partially valid if not conducted on the entire region (Chytrý *et al.* 2002). As regional classifications are lacking, we proposed as second objective of our study to classify the páramo vegetation at regional scale in order to reveal the main páramo phytogeographical units (Chapter 2). Finally, understanding the global patterns of species richness is a great challenge in biogeography (Tello & Stevens 2010) and these studies are, beyond evident research interest, also fundamental for conservation as they provide information on hotspots for biodiversity. Studies on species richness patterns in the páramo and their determinants are very scarce and geographically restricted (Kessler *et al.* 2011). Consequently, we focused the third and last study of this PhD project on understanding the regional patterns of plant diversity in the páramo region (Chapter 3).

This PhD dissertation resumes the principal findings and conclusions of the three research studies developed in the framework of this integrative project on páramo flora and vegetation.

References

Acosta-Solís M (1984) Los páramos andinos del Ecuador. Publicaciones científicas MAS, Quito.

Anderson EP, Marengo J, Villalba R, Halloz S, Young B, Cordero D, Gast F, Jaimes E, Ruiz D (2011) Consequences of climate change for ecosystems and ecosystem services in the tropical Andes. Climate change and Biodiversity in the Tropical Andes. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 1–5.

Antonelli A, Sanmartín I (2011) Why are there so many plant species in the Neotropics?. Taxon 60(2): 403–414.

Antonelli A, Nylander JA, Persson C, Sanmartín I (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution.Proceedings of the National Academy of Sciences, 106(24): 9749–9754.

Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve selection methods. Global Change Biology 10: 1618–1626.

Balslev H, Luteyn JL (1992) Páramo – An Andean Ecosytem Under Human Influence. Academic Press, London.

Baruch Z (1984) Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan páramos. Vegetatio 55(2): 115–126.

Berg A (1998) Pflanzengesellschaften und Lebensformen des Super-páramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157–203.

Bosman AF, van der Molen PC, Cleef AM (1993) Ecology of a páramo cushion mire. Journal of Vegetation Science 4: 633–640.

Buytaert W, Cuesta-Camacho F, Tobón C (2011) Potential impacts of climate change on the environmental services of humid tropical alpine regions. Global Ecology and Biogeography 20(1): 19–33.

Buytaert W, Célleri R, de Bièvre B, Cisneros F, Wyseure G, Deckers J, Hofstede R (2006) Human impact on the hydrology of the Andean páramos. Earth-Science Reviews 79(1): 53–72.

Carbono E, Lozano-Contreras G (1997) Endemismos y otras singularidades de la Sierra Nevada de Santa Marta, Colombia. Posibles causas de origen y necesidad de conservarlos. Revista de la Academia Colombiana de Ciencias 21(81): 409–419.

Célleri R, Feyen J (2009) The Hydrology of Tropical Andean Ecosystems: Importance, Knowledge Status and Perspectives. Mountain Research and Development 29: 350–355.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of vegetation science 13: 79–90.

Cleef AM (1981) The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae (61), University of Amsterdam, Amsterdam.

Cuatrecasas J (1958) Aspectos de la vegetación natural de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 10(40): 221–268.

Cuesta F, Becerra MT (2009). Atlas de los Andes del norte y centro. Secretaría General de la Comunidad Andina, Lima.

Farley KA, Kelly EF, Hofstede RG (2004) Soil organic carbon and water retention after conversion of grasslands to pine plantations in the Ecuadorian Andes. Ecosystems 7(7): 729–739.

Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Tirner JRG (2009) Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36(1): 132–147.

Fjeldså J (2002) Polylepis forests–vestiges of a vanishing ecosystem in the Andes. Ecotropica 8(2): 111–123.

García EE, Beck SG (2006) Puna. In: Moraes M, Ollgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, pp 51–76.

Hedberg O (1969) Evolution and speciation in a tropical high mountain flora. Biological Journal of the Linnean Society 1(1–2): 135–148.

Hoffmann D, Oetting I, Arnillas CA, Ulloa R (2011) Climate change and Protected Areas in the Tropical Andes. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 311–325.

Hofstede RGM, Segarra P, Mena-Vásconez P (eds) (2003) Los páramos del mundo. Proyecto Atlas Mundial de los Páramos. GPI/NC-IUCN/EcoCiencia, Quito.

Hofstede R, Coppus R, Vásconez PM, Segarra P, Wolf J, Sevink J (2002). El estado de conservación de los páramos de pajonal en el Ecuador. Ecotropicos 15(1): 3–18.

Hole DG, Young KR, Gomez-Wichtendahl C, Hoffmann D, Schutze-Paez K, Sánchez S, Muchoney DA, Grau HR, Ramirez E. Adaptive Management for Biodiversity Conservation under Climate change – a Tropical Andean Perspective. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 19–46.

Hooghiemstra H, Wijninga VM, Cleef AM (2006) The paleobotanical record of Colombia: implications for biogeography and biodiversity. Annals of the Missouri Botanical Garden 93(2): 297–325.

Hooghiemstra H, van der Hammen T (2004) Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. Philosophical Transactions of the Royal Society B: Biological Sciences 359: 173–181.

Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Sciences 103(27): 10334–10339.

IPCC (2007) Climate change 2007 – impacts, adaptation and vulnerability. Cambridge University Press, Cambridge.

Jiménez I, Distler T, Jørgensen PM (2009) Estimated plant richness patterns across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. Ecography 32: 433–448.

Jørgensen PM, Ulloa-Ulloa C, León B, León-Yánez S, Beck SG, Nee M, Zarucchi JL, Celis M, Bernal R, Gradstein R (2011) Regional Patterns of Vascular Plant Diversity and Endemism. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 192–203.

Jørgensen PM., Ulloa-Ulloa C (1994) Seed plants of the high Andes of Ecuador: a checklist. AAU Reports (No. 34), Aarhus.

Josse C, Cuesta F, Gonzalo N, Barrena V, Becerra MT, Cabrera E, Chacón-Moreno E, Ferreira W, Peralvo M, Saito J, Tovar A, Naranjo LG (2011) Physical Geography and Ecosystems in the Tropical Andes. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 152–169.

Josse C, Cuesta F, Navarro G, Barrena V, Cabrera E, Chacón E, Tovar A (2009) Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, RUMBOL SRL, Lima.

Kessler M (2006) Los bosques de Polylepis. In: Moraes M, Ollgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, pp 51–76.

Kessler M, Grytnes JA, Halloy SRP, Kluge J, Krömer T, León B, Macía MJ, Young KR (2011) Gradients of plant diversity: local patterns and processes. In: Herzog SK, Martinez R, Jørgensen PM, Tiessen H (eds) Climate change and Biodiversity in the Tropical Andes. Sao José dos Campos, pp 204–219.

Lauer W (1979) La posición de los páramos en la estructura del paisaje de los Andes tropicales. In: Salgado-Labourian (ed) El Medio Amabiente Páramo, Ediciones CEA-IVIC, Caracas, pp 29–45.

Lenoir J, Svenning J-C (2014) Climate-related range shifts–a global multidimensional synthesis and new research directions. Ecography 37: 1–14.

León B, Pitman N, Roque J (2006) Introducción a las plantas endémicas del Perú. Revista peruana de biología 13(2): 9–22.

Løjtnant B, Molau U (1983) Analysis of a virgin páramo plant community on Volcán Sumaco, Ecuador. Nordic Journal of Botany 2(6): 567–574.

Luteyn J (1992) Páramos: why study them? In: Balslev H, Luteyn J (eds) Páramo. An Andean ecosystem under human influence, Academic Press, London, pp 1–14.

Luteyn J (1999) Páramos: A checklist of plant diversity, geographic distribution, and botanical literature. Memoirs of the New York Botanical Garden (84), New York.

Madriñan S, Cortés AJ, Richardson JE (2013) Páramo is the world's fastest evolving and coolest biodiversity hotspot. Frontiers in Genetics 4: 1–6.

Malagón D, Pulido C (2000) Suelos del páramo colombiano. Colombia Diversidad Biótica III. La región de vida paramuna. Universidad Nacional de Colombia. Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá.

Mantua NJ, Hare SR (2002) The Pacific decadal oscillation. Journal of Oceanography 58(1): 35–44.

Marengo J (2004) Interdecadal variability and rends of rainfall across the Amazon basin. Theoretical and Applied Climatology 78: 79–96.

Martínez R, Ruiz D, Andrade M, Blacutt L, Pabón D, Jaimes E, León G, Villacís M, Quintana J, Montealegre E (2011) Synthesis of the climate of the tropical Andes In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 97–109.

Meehl G, Coey C, Delworth T, Latif M, McAvaney B, Mitchell JFB, Stouffer RJ, Taylor KE (2007) The WCRP CMIP3 multimodel data set: a new era in climate change research. Bulletin of the American Meteorological Society 88: 1383–1394.

Mena-Vásconez P, Medina G (2001) La biodiversidad de los páramos en el Ecuador. In: Mena Vásconez P, Medina G, Hofstede R (eds) Los Páramos de Ecuador. Particularidades, Problemas y Perspectivas,. Editorial Abya Yala, Quito, pp 27–52.

Millenium Ecosystem Assessment (2005) Ecosystems and human well-being. Island Press, Washington DC.

Mitchell TP, Wallace JM (1992) The annual cycle in the equatorial convection and sea surface temperature. Journal of Climate 5: 1140–1156.

Molau U (1988) Scrophulariaceae Part I. Calceolarieae. Flora Neotropica Monograph (47): 1–325.

Molinillo M, Monasterio M (2002) Vegetation and grazing patterns in páramo environment. Ecotropicos 15(1): 19–34.

Molinillo M, Monasterio M (1997) Pastoralism in páramo environments: practices, forage, and impact on vegetation in the cordillera of Merida, Venezuela. Mountain Research and Development 197–211.

Monasterio M, Reyes S (1980) Diversidad ambiental y variación de la vegetación en los páramos de los Andes venezolanos. In: Monasterio M (ed) Estudios ecológicos en los páramos andinos, pp 47–91.

Mutke J, Jacobs R, Meyer K, Henning T, Weigend M (2014) Diversity patterns of selected Andean plant groups correspond to topography and habitat dynamics, not orogeny. Evolutionary and Population Genetics 5: 1–15.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403(6772): 853–858.

Nieto C, Estrella J (2000) La agrobiodiversidad en los ecosistemas de páramo: Una primera aproximación a su inventario y su situación actual. Serie Páramo (Biodiversidad) 7: 31–53.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37: 637-669.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. Global ecology and biogeography 12(5): 361–371.

Pedraza-Peñalosa P, Betancur J, Franco-Rosselli P (2004) Chisacá, un recorrido por los páramos andinos. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

Pitman NCA, Jørgensen PM (2002) Estimating the size of the world's threatened flora. Science 298(5595): 989–989.

Podwojewski P, Poulenard J, Zambrana T, Hofstede R (2002) Overgrazing effects on vegetation cover and properties of volcanic ash soil in the páramo of Llangahua and La Esperanza (Tungurahua, Ecuador). Soil Use and Management 18(1): 45–55.

Poulenard J, Podwojewski P, Herbillon AJ (2003) Characteristics of non-allophanic Andisols with hydric properties from the Ecuadorian páramos. Geoderma 117(3): 267–281.

Poveda G (2004) La hidroclimatología de Colombia: una síntesis desde la escala inter-decadal hasta la escala diurna. Revista de la Academia Colombiana de Ciencias 28(107): 201–222.

Ramsay PM (1992) The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes. PhD. Thesis, University of Wales, Bangor.

Ramsay PM, Oxley ERB (1997) The growth form composition of plant communities in the Ecuadorian páramos. Plant Ecology 131(2): 173–192.

Ramsay PM, Oxley ERB (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Vegetatio 124(2): 129–144.

Rangel-Churio JO (2000a) Visión integradora sobre la región del páramo. In: Rangel JO (ed) Colombia Diversidad Biótica III, La Región de Vida Paramuna. Instituto de Ciencias Universidad Nacional de Colombia-Instituto Alexander von Humboldt. Bogotá, pp 837–866.

Rangel-Churio JO (2000b) La región paramuna y franja aledaña en Colombia. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica III: La región de vida paramuna. Instituto de Ciencias Naturales, Instituto Alexander von Humboldt, Bogotá, pp 1–23.

Rangel-Churio JO (2000c) Biodiversidad en la región del páramo: con especial referencia a Colombia. Congreso Mundial de Páramos. MMA, CAR, IDEAM y Colombia, C. Paipa I: 168–200.

Rangel-Churio JO (2000d) La diversidad beta: tipos de vegetación. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica III. La región de vida paramuna. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, pp 658–719.

Rangel-Churio JO (2006) The biodiversity of the Colombian páramo region and its relation to antropogenic impact. In: Spehn E, Lieberman M, Körner C (eds) Land use change and mountain biodiversity. CRC Press. Taylor & Francis Group, pp. 103–118.

Richter M, Diertl KH, Emck P, Peters T, Beck E (2009) Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador. Landscape Online 12: 1–35.

Ruiz D, Arroyave MP, Molina AM, Barros JF, Gutierrez ME; Zapata PA (2009). Signals of climate variability/change in surface water supply of high-mountain watersheds-case study: Claro River high mountain basin, Los Nevados Natural Park, Andean Central Mountain Range, Colombia. World Bank Group, pp 4355–4373.

Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: van der Hammen T, dos Santos AG (eds) La Cordillera Central Colombiana. Transecto Parque los Nevados. Studies on Tropical Andean Ecosystems, J. Cramer. Berlin-Stuttgart 5: 1–77.

Sánchez-Vega I, Dillon MO (2006) Jalcas. In: Moraes RM, Øllgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica Económica de los Andes Centrales. Herbario Nacional de Bolivia, Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, pp 81–94.

Sarmiento G (1986) Ecologically crucial features of climate in high tropical mountains. In: Vuilleumier, F., Monasterio, M. (eds) High Altitude Tropical Biogeography, Oxford University Press, Oxford, pp 11–45.

Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian super-páramos. PhD thesis, Charles University, Prague.

Sklenář P, Hedberg I, Cleef AM (2014) Island biogeography of tropical alpine floras. Journal of Biogeography 41(2): 287–297.

Sklenář P, Kovář P, Palice Z, Stančík D, Soldán Z (2010) Primary succession of high-altitude Andean vegetation on lahars of Volcan Cotopaxi, Ecuador. Phytocoenologia 40(1): 15–28.

Sklenář P, Balslev H (2005) Super-páramo plant species diversity and phytogeography in Ecuador. Flora-Morphology, Distribution, Functional Ecology of Plants 200(5): 416–433.

Sklenář P, Ramsay PM (2001) Diversity of zonal páramo plant communities in Ecuador. Diversity and Distributions 7: 113–124.

Sklenář P, Jørgensen PM (1999) Distribution patterns of páramo plants in Ecuador. Journal of Biogeography 26(4): 681–691.

Simpson BB (1975) Pleistocene changes in the flora of the high tropical Andes. Paleobiology 273–294.

Simpson BB, Todzia CA (1990) Patterns and processes in the development of the high Andean flora. American Journal of Botany 1419–1432.

Smith AP, Young TP (1987) Tropical alpine plant ecology. Annual Review of Ecology and Systematics 18: 137–158.

Smith JMB, Cleef AM (1988) Composition and origins of the world's tropicalpine floras. Journal of Biogeography 15: 631–645.

Smith NP (1978) Longshore currents on the fringe of Hurricane Anita. Journal of Geophysical Research: Oceans (1978–2012) 83(C12): 6047–6051.

Suárez E, Medina G (2001) Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. Arctic, Antarctic, and Alpine Research 33(2): 158–164.

Sturm H, Rangel O (1985) Ecología de los páramos andinos: una visión preliminar integrada. Universidad nacional de Colombia, Bogotá.

Tello JS, Stevens RD (2010) Multiple environmental determinants of regional species richness and effects of geographic range size. Ecography 33(4): 796–808.

Urrutia R, Vuille M (2009) Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. Journal of Geophysical Research: Atmospheres (1984–2012) 114(D2).

Valencia R, Pitman N, León-Yánez S, Jørgensen PM (eds) (2000) Libro Rojo de las Plantas Endémicas del Ecuador 2000. Editorial Pontificia Universidad Católica del Ecuador, Quito.

van der Hammen T, Otero-García J (2007) Los páramos: archipiélagos terrestres en el norte de los Andes. In: Morales M, Otero-García J, van der Hammen T, Torres A, Cadena C, Pedraza C, Rodríguez N, Franco C, Betancourth JC, Olaya E, Posada E, Cárdenas L (eds) Atlas de páramos de Colombia. Instituto de Investigación de Recursos Biológicos Alexander con Humboldt, Bogotá, pp 25–31.

van der Hammen T, Cleef AM (1986) Development of the high Andean páramo flora and vegetation. In: Vuilleumier F, Monasterio M (eds) High altitude tropical biogeography, Oxford University Press, New York, New York, pp 153–201.

Vareschi V (1970) Flora de los Páramos de Venezuela. Universidad de los Andes, Mérida.

Vareschi V (1955) Monografias geobotánicas de Venezuela I Rasgos geobotánicos sobre el Pico de Naiguatá, Caracas.

Vásconez PM, Hofstede RGM (2006) Los páramos ecuatorianos. In: Moraes MR, Øllgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica económica de los Andes Centrales. Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, pp 91–109.

Velásquez TA (2012) The science of corporate social responsibility (CSR): Contamination and conflict in a mining project in the southern Ecuadorian Andes. Resources Policy 37(2): 233–240.

Vuille M, Fraucou B, Wagnon P, Juen I, Kaser G, Mark BG, Bradley RS (2008). Climate change and tropical Andean glaciers: Past, present and future. Earth-Science Reviews 89(3): 79–96.

Vuille M, Bradley RS, Keimig F (2000) Climate variability in the Andes of Ecuador and its relation to tropical Pacific and Atlantic sea surface temperature anomalies. Journal of Climate 13: 2520–2535.

Vuilleumier F, Monasterio M (eds) (1986) High altitude tropical biogeography. Oxford University Press, Oxford.

Weigend M (2002) Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. The Botanical Review 68(1): 38–54.

Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JE, Willig KJ (2005) Conservation biogeography: assessment and prospect. Diversity and distributions 11(1): 3–23.

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5(9): 475–482.

Young BE, Young KR, Josse C (2011) Vulnerability of tropical Andean ecosystems to climate change. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 170–181.

Objectives

Objective 1. Build a database for páramo flora and vegetation, called *VegPáramo*, which contains phytosociological data in form of vegetation plots and is available online through an open-access webportal (Chapter 1).

Objective 2. Conduct a regional classification of the páramo vegetation in order to reveal the main phytogeographical units and compare them at alpha diversity and beta diversity levels (Chapter 2).

Objective 3. Study plant diversity in the páramo region by comparing species richness in the páramo and super-páramo altitudinal belts, evaluating the influence of the environment on species richness and predicting species richness in the region (Chapter 3).

Chapter 1: *VegPáramo*, a flora and vegetation database for the Andean páramo

Introduction

Biological databases are useful tools for research as they contain substantial amounts of information that is uniform and frequently updated (Font *et al.* 2009; Dengler *et al.* 2011). There are several floristic databases focusing on the tropics worldwide (e.g. *TROPICOS*, Missouri Botanical Garden, www.tropicos.org) and some focusing especially on the Neotropics, providing pictures of herbarium specimens (*e.g. Neotropical Herbarium specimens*, Field Museum, fm1.fieldmuseum.org) or picture of live plants (*e.g. Neotropical Live Plant Photos*, Field Museum, fm2.fieldmuseum.org/plantguides; *Neotropical Plants Image Database*, Royal Botanic Gardens at Kew, www.kew.org/science/tropamerica/ imagedatabase). In addition, there are national and smaller scale floristic databases available, such as the National Colombian Herbarium Collections (www.biovirtual.unal.edu.co). Regarding vegetation data, the *Global Index of Vegetation-Plot Databases* covers 42 tropical vegetation plot databases, 10 of which are South American but mostly of restricted access (Dengler *et al.* 2011). Of particular relevance here is the recent *Colombian Páramo Vegetation Database* that compiles 1000 vegetation plots resulting from the considerable field work carried out during the past decades in the Colombian páramo, but so far it is not publicly accessible (Rangel-Churio & Pinto-Zárate 2012). Vegetation plot databases are becoming increasingly attractive to botanists and ecologists (Schaminée *et al.* 2009; Dengler *et al.* 2011) as they can sustain numerous large-scale applications, such as vegetation classification, floristic diversity studies, and vegetation mapping.

To meet the need of intensifying research and conservation in the northern high Andes, we here present *VegPáramo* as a significant new data source for flora and vegetation data for the páramo. We constructed *VegPáramo* to contain phytosociological data, from which vegetation plots and floristic records can be obtained. We created an open access webportal for the database.

Materials and methods

Structure of VegPáramo

The phytosociological plot, or *relevé*, is the basic data unit in *VegPáramo*. The phytosociological method aims at characterizing a plant community by its taxa in a representative area of the vegetation present in a territory by means of cover and occasionally sociability (Braun-Blanquet 1951). This method has been widely used in Europe but less in the tropics due to the complex stratification of most plant communities, often including many lianas and epiphytes (Schilling & Batista 2008). Nonetheless, botanists consider the use of phytosociology suitable in the páramo as it presents a simpler physiognomy (Cleef 1981; Pinto-Zárate 2010). Phytosociological fieldwork involves defining a plot, noting the environmental and geographic characteristics and listing the plant species in each vegetation layer. Each species is then assigned a cover coefficient, usually following the scale: + (less than 1% cover), 1 (up to 5%), 2 (up to 25%), 3 (up to 50%), 4 (up to 75%), or 5 (up to 100%). The categorized cover variable has to be carefully manipulated in statistics (Podani 2006) but is flexible in transformations (*e.g.* abundance, presence/absence). The standard plot size depends on the vegetation physiognomy and is based on the principles of representativity in the vegetation patch, uniformity and minimal area (Mueller-Dombois & Ellenberg 1974). The latter criterion is defined by the traditional species area curve indicating the area for which the number of species reaches an asymptote. Therefore, plot size usually ranges from 1–500 m^2, corresponding to short meadows and forests respectively.

We programmed *VegPáramo* in SQL and Java following the *Iberian and Macaronesian Vegetation Information System* model (Font *et al.* 2009). The database contains six main tables interconnected via one single primary key: the central *Plot data* table, the secondary *Georeferences* and *Attributes* tables, the *Plot source* table, as well as two checklists, the *Taxon list* and the *Syntaxon list*. The *Plot data* table refers to the original plot species list and their designated phytosociological coefficients. The *Georeferences* table contains the plot geographic characteristics such as its UTM coordinates (mostly at 1x1 km scale) and its exact locality (Municipality, Province/Department and Country). The *Attributes* table holds for each plot the associated information on vegetation physiognomy, or layers, in terms of height (in cm) and cover (in %) as well as other environmental characteristics such as slope, orientation or soil. The *Plot source* table contains the published and unpublished references in which the plot data was first displayed. The two checklists *Taxon list* and *Syntaxon list*, are lists of codified names for plant taxa and plant communities (referred to as *syntaxa* in phytosociology), with their updated validity status (accepted, rejected, dubious, etc). Both files check the original names used in the *VegPáramo* data and update them automatically to their actual accepted form based on the most recent source. The taxon checklist contains names of about 15,000 species, 1700 genera and 188 families of vascular plants, synonyms included, which were recorded in the páramo region. This exhaustive list is based on several sources from which the information was extracted after definition of the interested geographical area (country, province and elevation above 2800 m). The bibliographical sources used are: the *Páramo Checklist* (Luteyn 1999), the *Catalogue of the Ecuadorian Vascular Plants* (Jørgensen & León-Yánez 1999), the *Catalogue of the Flowering Plants and Gymnosperms of Peru* (Brako & Zarucchi 1993) and the *Catalogue of the*

Flowering Plants of the Venezuelan Páramos: Dicots and Monocots (Briceño & Morillo 2011a; Briceño & Morillo 2011b). We gave priority to the most recent source in case of synonymy. Additional smaller sources were consulted and their information added for specific taxa. Names were then revised and updated using the *TROPICOS* website and *The Plant List* (www.plantlist.org). Due to the selection process, the taxon checklist also includes taxa from the upper montane ecotone in certain areas and taxa from the jalca transition from the northern Peruvian departments. To date, the taxon checklist does not provide synonymy for non-vascular plants. The syntaxon checklist contains almost 400 synonymized names of plant communities described in the literature. In phytosociology, the syntaxonomy refers to the hierarchical classification of plant communities into classes, orders, alliances and associations, the latter being the basic unit similarly to species in taxonomy (for more details see Chapter 2). The synonymy provided here is partial and the syntaxonomic affiliation of the plots if only provisional as there is no actual global syntaxonomic revision of the páramos.

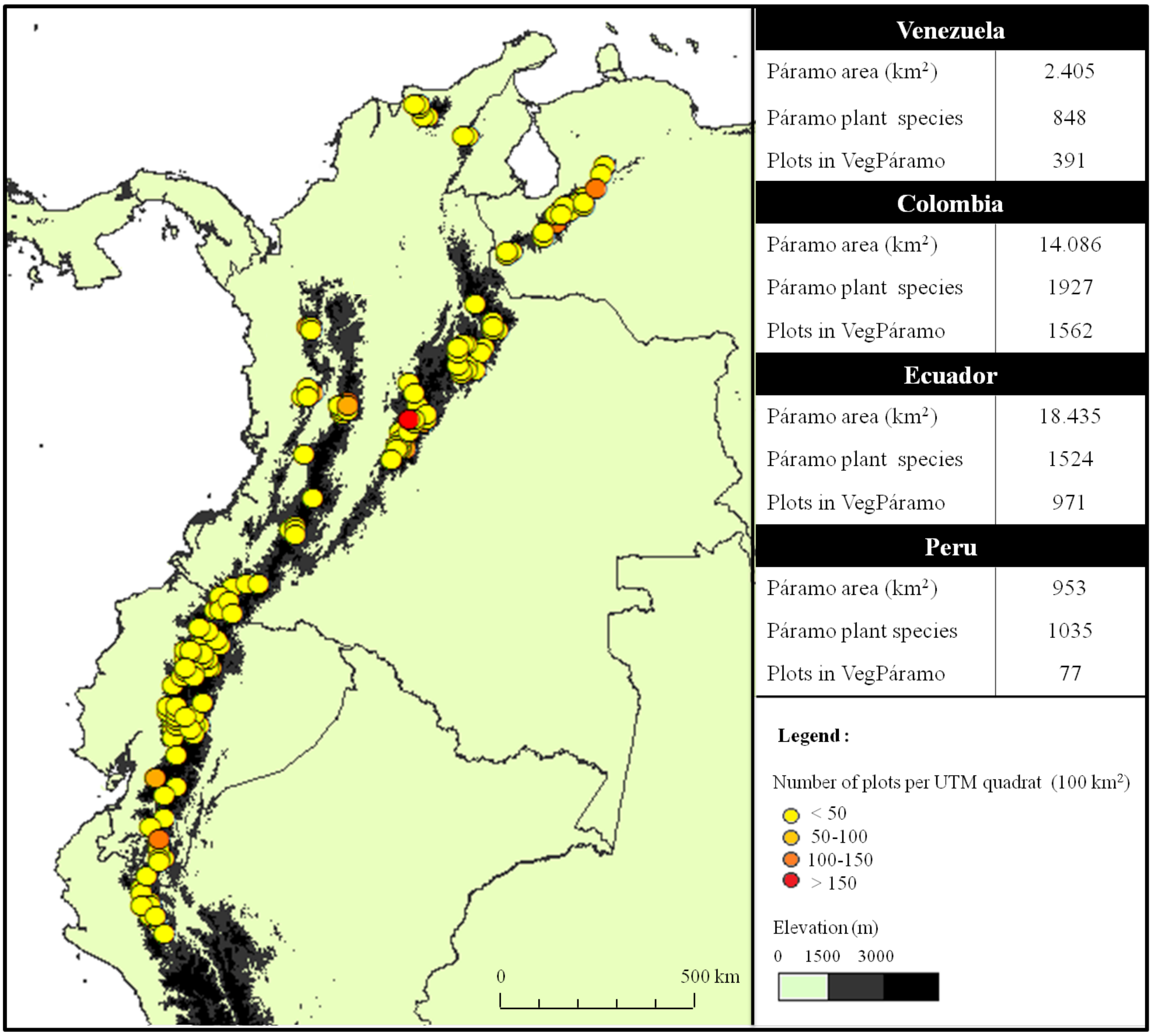
Origin of the data

The 3000 data plots contained in *VegPáramo* come from multiple sources. We retrieved 2700 plots from the existing literature on páramo vegetation in South America including published bibliography, thesis and scientific reports covering the period 1955–2010. We took into account all plots obtained with the phytosociological method and sampled preferentially in both zonal and azonal plant communities. Most data from Colombia come from the extensive phytosociological fieldwork carried out in the páramos by local and international botanists within major research projects such as the *ECOANDES* (*e.g.* van der Hammen & Ruiz 1986; van der Hammen 2008). In Ecuador and Venezuela, even though there is a long tradition of floristic and vegetation studies in páramos (*e.g.* Acosta-Solís 1968; Monasterio & Reyes 1980), the interest in the phytosociological method is more recent and relatively few researchers have used it in the páramo (*e.g.* Ramsay 1992; Cuello & Cleef 2009). We found no data for Peru, as the method has not yet been used in the Peruvian páramos where biological studies are in general scarce and scattered (*e.g.* Sabogal & Quinteros 2013). After mapping the spatial distribution of the literature plots in the study area, we added our own 300 plots obtained between 2011–2013, in order to cover the less sampled páramo areas in Peru, Ecuador and Venezuela (Appendix 3).

Results and discussion

Data contents in VegPáramo

The *VegPáramo* data are contained in 489 UTM quadrats of 1 km^2, spread throughout the estimated 35,000 km^2 potential páramo area (Fig. 1.1).



Venezuela	
Páramo area (km^2)	2.405
Páramo plant species	848
Plots in VegPáramo	391
Colombia	
Páramo area (km^2)	14.086
Páramo plant species	1927
Plots in VegPáramo	1562
Ecuador	
Páramo area (km^2)	18.435
Páramo plant species	1524
Plots in VegPáramo	971
Peru	
Páramo area (km^2)	953
Páramo plant species	1035
Plots in VegPáramo	77

Figure 1.1. Distribution of the VegPáramo plots and details of the páramo area (Josse *et al.* 2009), flora (Sklenář *et al.* 2005) and plot numbers in Venezuela, Colombia, Ecuador and Peru.

The distribution of the plots is not uniform because páramo fieldwork expeditions were mostly driven by floristic interest and facility of access. As a result some páramos are over-sampled, such as Chingaza in Colombia, whereas others are under-sampled, like the Peruvian páramos. However, even if the *VegPáramo* data is unequally spread between the four northern Andean countries, it should be representative of their respective páramo area and corresponding plant diversity. In Venezuela, the páramo is geographically limited and has the lowest floristic diversity of the four countries, partly due to the desertic conditions of the high páramos in the Cordillera de Mérida (Monasterio & Reyes 1980). Venezuelan data currently account for 13% of the total *VegPáramo* plots. Colombia hosts the richest páramo flora (Rangel-Churio 2006) and represents 52% of the *VegPáramo* data. Ecuador has the largest páramo extension running from north to south and covering 30% of its territory. In our data, the Ecuadorian páramo is also numerically and geographically well represented. Although geographically limited and confined in the Amotape-Huancabamba zone in Peru (Weigend 2002), the southernmost páramos are extremely diverse ecosystems thanks to their relatively isolated situation, older geology, lower elevation and relatively limited human disturbance (Keating 2008; Lozano *et al.* 2009). Our data for this area remain incomplete, representing a mere 3% of all *VegPáramo* plots.

The data contained in *VegPáramo* represent 123 vascular plants families, 504 genera and 2220 species. While at family and genus level, *VegPáramo* is rather complete, it remains fairly incomplete at species level representing a little less than 50% of the total páramo flora estimate by Rangel-Churio (2000) and 65% of Luteyn's estimate (1999). This under-representation at species level is most likely due to the limited data availability and the sampling method that focuses on the main vegetation types. In *VegPáramo,* Asteraceae, Poaceae, Orchidaceae and Melastomataceae are the most important páramo plant families in terms of species number and the four families account for about 40% of the total páramo floristic diversity (Table 1.1).

VegPáramo		**Luteyn (1999)**		**Rangel-Churio (2000)**	
Asteraceae	21%	Asteraceae	22%	Asteraceae	27%
Poaceae	8%	Poaceae	5%	Orchidaceae	12%
Orchidaceae	5%	Orchidaceae	5%	Poaceae	5%
Melastomataceae	5%	Melastomataceae	4%	Melastomataceae	5%

Table 1.1. Relative importance in terms of species of the main plant families in the páramo in this study and two previous reports.

Whereas the relative importance of the most important families generally agrees with other estimates (Luteyn 1999; Rangel-Churio 2000), we note that orchids must have been overlooked in the *VegPáramo* plots, maybe because of their minor importance in vegetation structure. The expression of plant species within the páramo area covered by *VegPáramo* plots follows the traditional logarithmic series distribution (Fig. 1.2).

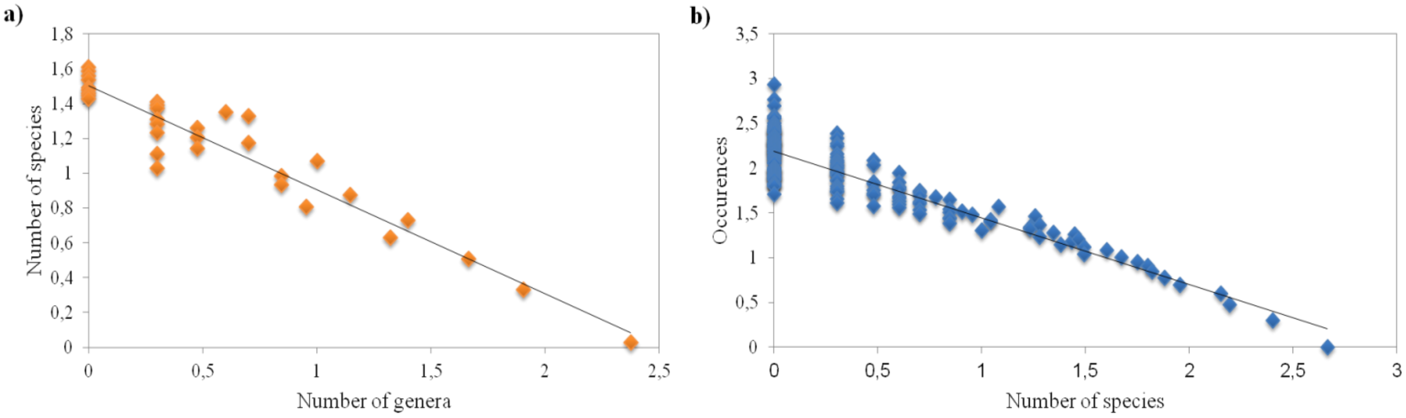


Figure 1.2. Log-Log plots of a) species number per plant genus and b) number of occurrences in the *VegPáramo* plots per species.

Almost half of the genera are represented by only one species in *VegPáramo* and only 5% of the genera are represented by more than 10 species, among the richest, *Diplostephium* (Asteraceae), *Miconia* (Melastomataceae), *Huperzia* (Lycopodiaceae) and *Elaphoglossum* (Dryopteridaceae). Similarly, few species are widely distributed, like *Pernettya prostrata* Cav. (DC.) (Ericaceae) present in 851 plots and *Calamagrostis effusa* (Kunth) Steud. (Poaceae) present in 586 plots, while most species are only represented in a few plots and 450 of them in one plot.

The VegPáramo webportal

VegPáramo (GIVD Nº SA-00-002) is a free, open access biological database, accessible from the webportal www.vegparamo.com in English and Spanish. The database is part of the *BIODIVER* databases complex developed by the *Biosystematics and Vegetal Biodiversity Research Group* at the University of Barcelona that includes the *Information System for Iberian and Macaronesian Vegetation (SIVIM)*, the *Biodiversity data bank of Catalonia (BDBC)*, the *Information System for Andorran biodiversity (SIBA)* or most recently the *Atlas of the Pyrenean Flora (POCTEFA)* (biodiver.bio.ub.es). From the webportal, floristic data (taxonomic record) and vegetation data (vegetation plots) can be consulted via online searches and downloaded. The webportal is designed for online searches by taxon name (genus, species), plant community (syntaxon name or combination of diagnostic species) or geographic area (UTM quadrat or locality). Any search will lead to the record of the searched item, with its geographical distribution, taxonomic contents and description when available (Fig. 1.3).

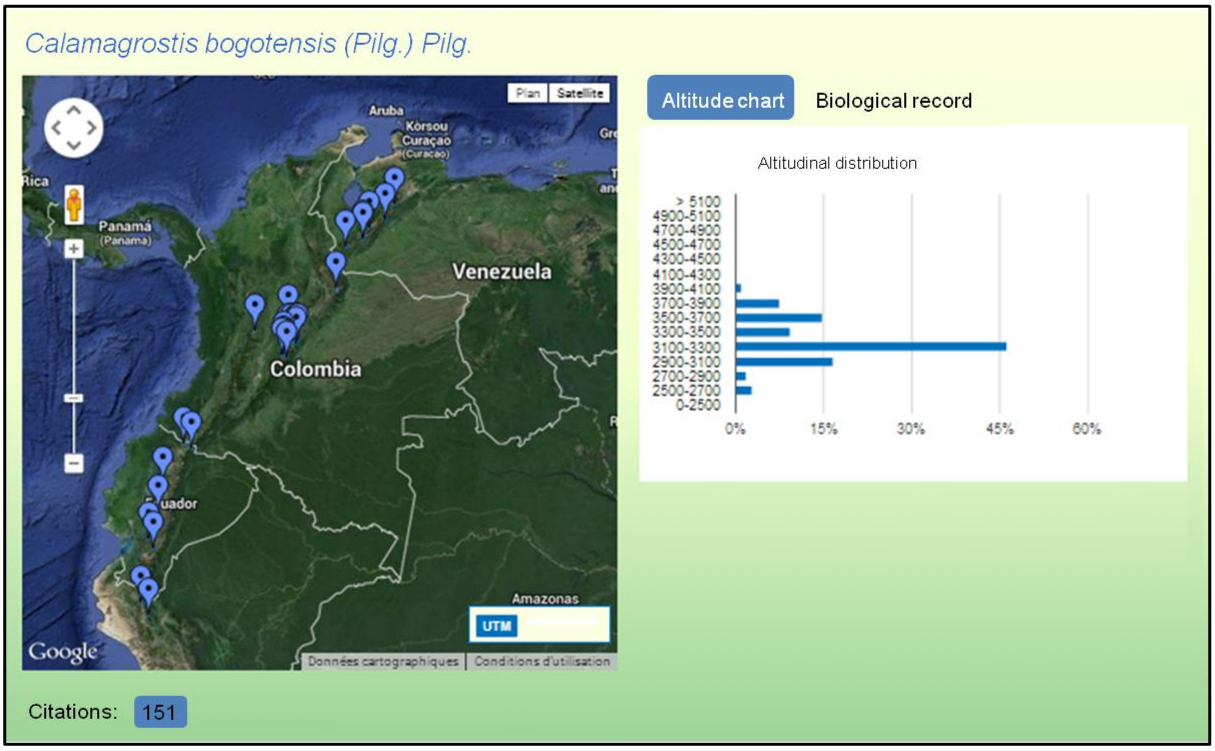


Figure 1.3. Example of a taxon search on the *VegPáramo* webportal.

Names on the portal are always checked by either the taxon or the syntaxon checklist so to allow the user to work with updated valid names. Finally, the results of any search can be downloaded in XML or TXT tabulated format, making their export to data edition/analysis programs easy.

Future perspectives

The páramo ecosystem, with its great biodiversity, is unique but also critically threatened by anthropogenic activities and Climate change. Consequently, a better scientific understanding and conservation of this singular neotropical environment is needed. Towards this goal, *VegPáramo* provides a substantial botanical data source for the páramo that is freely accessible through the webportal. The *VegPáramo* data is well distributed and geographically representative of the páramo region. Nonetheless, the floristic contents of the database and especially the large amount of low-occurrence species indicate that *VegPáramo* still needs to grow in floristic representativeness. We hope the sampling effort on páramo vegetation will continue, especially in the less studied areas such as northern Peru, so that *VegPáramo* can be improved with additional data and grow in scientific significance.

The *VegPáramo* data can be used in many different kinds of ecological research involving flora and/or vegetation. For example, diversity studies can be done on a taxonomic group (*e.g.* Ericaceae), a specific area (*e.g.* southern Ecuador), a plant community (*e.g. Polylepis* forests) and also comparing units (*e.g.* comparison of the floristic diversity of the different *Calamagrostis* grasslands in the páramo region). Mapping the current distribution of a taxon or a plant community can be done easily, using a sub-dataset of *VegPáramo*. Furthermore, modelling species' actual or future distributions, after compilation of a GIS, can be done using many techniques thanks to the versatility of the phytosociological data. The most common use of large phytosociological datasets is the classification of vegetation into plant communities, or *types* (Bruelheide & Chytrý 2000; Knollová *et al.* 2005).

Conservation plans and strategies rely on data analysis from research carried out in research or management-oriented institutions. On one hand, research institutions massively produce useful publications on broad scale studies and methods, but these results are not always easy to apply and may be difficult to synthesize regularly for management planners (Guisan *et al.* 2013). In addition, the data used can be kept away from the public, especially in tropical areas, sometimes because of the numerous time and economic costs associated with the sampling, plant identification and bureaucracy. This limitation makes it difficult to repeat a study or explore the data further. On the other hand, research carried out in management-oriented institutions is more easily applicable to case studies for conservation but sometimes miss the global ecological context and it is often limited by the lack of large amounts of quality biological data (Cayuela *et al.* 2009). In this way, *VegPáramo* provides a novel approach in terms of quantity and quality of data, in spite of the multiple data sources, thanks to the overall taxonomic revision and the georeferencing of the data. Moreover, vegetation plot sampling is especially useful as it gives abundance as well as presence/absence data, which can be particularly important when studying the geographic distribution of endangered species. Conservation measures and plans are increasing and improving their organization in the páramo region, but given the enormous task, efforts must be joined and collaborations developed, nationally as well as internationally (Hofstede *et al.* 2003). We hope the opportunity of using *VegPáramo*'s data will help increase the activity of conservationists and ease the communication with researchers.

In addition to expanding *VegPáramo* and fill in the blanks in the highly diverse páramo's distribution, we are developing new statistical tools for the webportal (diversity, fidelity index, etc) that we believe will be useful for exploratory analyses online and also new features of ecological interest, such as the IUCN status of species when available, which is valuable information for conservation prioritization not only of a specific taxon but also of habitats. We encourage new plot contributions and data revision in order to improve the quality and relevance of *VegPáramo*. Finally, we invite comments, updates and references through the interactive feedback option online that will allow any user to participate in the advances of *VegPáramo*.

References

Acosta-Solís M 1968 *Divisiones Fitogeográficas y Formaciones Geobotánicas del Ecuador*. Publicaciones Científicas MAS, Quito.

Balslev H, Luteyn JL (1992) Páramo - An Andean Ecosytem Under Human Influence. Academic Press, London.

Beck SG (1995) El páramo yungueño de Bolivia, datos de la flora y vegetación. In: Congreso Ecuatoriano de Botánica. Resumen II, Pontificia Universidad Católica del Ecuador.

Brako L, Zarucchi JL (1993) Catalogue of the flowering plants and gymnosperms of Peru: Catálogo de las angiospermas y gimnospermas del Perú Vol. 45. Missouri Botanical Garden. St. Louis

Braun-Blanquet J (1951) Pflanzensoziologie. Grundzfige der Vegetationskunde, 2nd edn. Springer, Vienna

Briceño B, Morillo G (2011a) Catálogo abreviado de las plantas con flores de los páramos de Venezuela. Parte I. Dicotiledóneas (Magnoliopsida). Acta Botánica Venezuelica 25(1): 1–46.

Briceño B, Morillo G (2011b) Catálogo de las plantas con flores de los páramos de Venezuela. Parte II. Monocotiledóneas (Liliopsida). Acta Botánica Venezuelica 29(1): 89–134.

Bruelheide H, Chytrý M (2000) Towards unification of national vegetation classifications: A comparison of two methods for analysis of large data sets. Journal of Vegetation Science 11: 295-306.

Cayuela L, Golicher DJ, Newton AC, Kolb M, de Alburquerque FS, Arets EJMM, Alkemade JRM, Pérez AM (2009) Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. Tropical Conservation Science 2(3):319–352.

Cleef AM (1981) The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae (61), University of Amsterdam, Amsterdam

Cuello NL, Cleef AM (2009) The páramo vegetation of Ramal de Guaramacal, Trujillo State, Venezuela. 1. Zonal communities. Phytocoenologia 39(3): 295–329.

Dengler J, Janse F, Glöckler F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Lopez-González G, Finckh M, Mucina L, Rodwell JS, Schaminée JHJ, Spencer N (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. Journal of Vegetation Science 22: 582–597.

Font X, Rodríguez-Rojo MP, Acedo C, Biurrun I, Fernández-González F, Lence C, Loidi J, Ninot JM (2009) SIVIM: an on-line database of the Iberian and Macaronesian vegetation. Waldökologie, Landschaftsforschung und Naturschutz 9: 1–22.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney R, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. Ecology letters 16(12): 1424–1435.

Hofstede RGM, Segarra P, Mena-Vásconez P (eds) (2003) Los páramos del mundo. Proyecto Atlas Mundial de los Páramos. Global Peatland Initiative/NC-IUCN/EcoCiencia, Quito

Jørgensen PM, León-Yánez S (1999) Catalogue of the vascular plants of Ecuador. Monographs in Systematic Botany from the Missouri Botanical Garden (75), Missouri Botanical Gardens Press, Saint Louis.

Josse C, Cuesta F, Navarro G, Barrena V, Cabrera E, Chacón-Moreno E, Tovar A (2009) Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, RUMBOL SRL, Lima.

Keating PL (2008) The Floristic Composition and Biogeographical Significance of A Megadiverse Páramo Site in The Southern Ecuadorian Andes 1. The Journal of the Torrey Botanical Society 135(4): 554–570.

Knollová I, Chytrý M, Tichý L, Hájek O (2005) Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. Journal of Vegetation Science 16: 479-486.

Lozano P, Cleef AM, Bussmann RW (2009) Phytogeography of the vascular páramo flora of Podocarpus National Park, south Ecuador. Arnaldoa 16(2): 69–85.

Luteyn J (1999) Páramos: A checklist of plant diversity, geographic distribution, and botanical literature. Memoirs of the New York Botanical Garden (84), New York.

Monasterio M, Reyes S (1980) Diversidad ambiental y variación de la vegetación en los páramos de los Andes venezolanos. In: Monasterio M (ed) Estudios ecológicos en los páramos andinos, pp. 47–91.

Mueller-Dombois D, Ellenberg H (1974) Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Pinto-Zárate JH (2010) Conservación y sostenibilidad de los ecosistemas de alta montaña en Latinoamérica. Foro Electrónico ‘Biodiversidad en Montañas’, CONDESAN, Quito.

Podani J (2006) Braun-Blanquet's legacy and data analysis in vegetation science. Journal of Vegetation Science 17(1): 113–117.

Ramsay PM (1992) The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes. PhD. Thesis, University of Wales, Bangor

Rangel-Churio JO (2000) Biodiversidad en la región del páramo: con especial referencia a Colombia. Congreso Mundial de Páramos. MMA, CAR, IDEAM y Colombia, C. Paipa I: 168–200.

Rangel-Churio JO (2006) The biodiversity of the Colombian páramo region and its relation to antropogenic impact. In: Spehn E, Lieberman M, Körner C (eds) Land use change and mountain biodiversity. CRC Press. Taylor & Francis Group, pp 103–118.

Rangel-Churio JO, Pinto-Zárate JH (2012) Colombian Páramo Vegetation Database (CPVD)-the database on high Andean páramo vegetation in Colombia. In: Dengler J, Olderland J, Jansen F, Chytrý M, Ewald J, Finckh M, Glöckler F, Lopez-Gonzalez G, Peet RK, Schaminée JHJ (eds) Vegetation databases for the 21st century. Biodiversity and Ecology 4: 275–286.

Sabogal A, Quinteros Y (2013) Diversidad vegetal y uso antrópico de los páramos de Samanga (Sectores Espíndola y El Toldo) y San Juan de Cachiaco (Caseríos San Juan y Totora), Ayabaca, Piura. Ecología Aplicada 12(1): 9–17.

Schaminée JH, Hennekens SM, Chytrý M, Rodwell JS (2009) Vegetation-plot data and databases in Europe: an overview. Preslia 81(3): 173–185.

Sklenář P, Luteyn JL, Ulloa-Ulloa C, Jørgensen PM, Dillon MO (2005) Flora genérica de los páramos: guía ilustrada de las plantas vasculares. New York Botanical Garden, New York.

van der Hammen T (ed) (2008) Studies on tropical Andean ecosystems. Vol 7. La Cordillera Oriental Colombiana Transecto Sumapaz. J. Cramer, Berlin-Stuttgart.

Weigend M (2002) Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. The Botanical Review 68(1): 38–54.

Chapter 2: Regional classification of the páramo vegetation

Introduction

Even though vegetation is generally a continuum, plant communities can be segregated and characterized by the habitat they occupy and by the species they contain (de Cáceres & Wiser 2012). Vegetation classifications are one of the fundamental contributions of phytogeography and they are essential to research in botany and ecology (Mucina 1997). Such classifications are base on division criteria such as species composition, physiognomy or life forms. Among the methodologies used, the phytosociological method has received much interest, particularly in Europe where researchers embraced the concept of hierarchical classifications (Syntaxonomy) and faithful species (Braun-Blanquet 1951). Syntaxonomy, in a similar way to taxonomy of taxa, aims at organizing plant communities and rank them from *coarse* units (*e.g.* all *Calamagrostis* grassland) to *fine* units (*e.g. Calamagrostis intermedia* grassland from dry areas in southern Ecuador). Nowadays, the term *diagnostic* species is preferred over the term *faithful* as it includes the constancy factor (Dufrêne & Legendre 1997; de Cáceres *et al.* 2008). A diagnostic species is defined by having a niche preference and its presence can be used as indicator of a particular plant community (de Cáceres *et al.* 2010). Consequently, a species that is highly diagnostic of a fine plant community will also be characteristic, but to a lesser extent, of the higher level community in the hierarchical classification, and respectively a highly diagnostic species of a coarse community will be characteristic of its included finer communities (Chytrý *et al.* 2002; Willner *et al.* 2009). At first, botanists were describing plants communities and their classification based on field observations (see Géhu & Rivas-Martínez 1981). Nowadays, statistical tools allow us to revise these classifications and describe new communities (Grabherr *et al.* 2003; Peyre & Font 2011).

Several vegetation classifications have been conducted for the páramos of Venezuela (*e.g.* Monasterio & Reyes 1980; Cuello & Cleef 2009), Colombia (*e.g.* Cleef & Rangel-Churio 2008; Pinto-Zárate & Rangel-Churio 2010) and Ecuador (*e.g.* Acosta-Solís 1984; Sklenář 2000). So far, no classification exists for the Peruvian páramo. A large number of plant communities have been recognized and classified, and most classifications in the páramo region have used the phytosociological method, which allows fast and efficient sampling and is particularly adequate to sample vegetation with relatively simple structure. To date, more than 500 fine plant communities have been described for the páramo.

In vegetation science, researchers often look for general patterns in distribution, species composition and dynamics of plant communities, whose first definition is highly context-dependant (Dengler *et al.* 2011). Local vegetation classifications are very valuable and offer a detailed insight; however, the geographical or political restriction of such studies often makes it impossible to extrapolate the results. Moreover the statistical results must be handled with caution as values obtained for the study case with no context of comparison might not reflect absolute values (Chytrý *et al.* 2002; Tichý & Chytrý 2006). Therefore, to obtain valid biogeographical frameworks based on vegetation, classifications should be made in a broad context and sustained by large amounts of representative and good quality data. Such classifications provide relevant biogeographical divisions that are essential for macroecological research and conservation (*e.g.* Olson *et al.* 2001; Kreft & Jetz 2010).

Our goal in this study is to classify and define the main plant communities in the páramo region. We conducted a broad-scale classification of a large vegetation dataset representative of the entire páramo range that revealed the main páramo types in the area and highlighted their floristic characteristics and relations by evaluating the alpha and beta diversity.

Materials and methods

Vegetation data

We used a dataset of 3000 vegetation plots from *VegPáramo* that we edited by removing the bryophytes, undetermined taxa, supra-specific taxon names and species with few occurrences (> 2). In addition, infra-specific taxa were merged to species level. In this study, we focus on the main páramo vegetation types, *i.e.* the zonal plant communities, and therefore we removed the azonal vegetation plots, based on their author's description. To reduce the sampling heterogeneity bias, we conducted a preferential stratified resampling on a geographic base, including the UTM quadrat and altitudinal 200 m strata (Knollová *et al.* 2005; Michalcová *et al.* 2011). These consecutive data reductions lead to a final dataset of 1854 plots. Finally, to minimize the collector effect on plant cover estimates, we transformed the phytosociological scale into a presence/absence binary scale and we paid a posteriori attention to the dominant taxa (Kočí *et al.* 2003; Willner *et al.* 2009).

Statistical analyses

To classify our dataset, we chose the non-hierarchical agglomerative clustering technique K-means (MacQueen 1967), which is much used and appropriate for classifying heterogeneous data that represent many, and not necessarily hierarchically related, plant communities (Chytrý *et al.* 2002; de Cáceres & Wiser 2012). We converted our species/plot matrix into a plot/plot distance matrix using the Bray-Curtis distance (Bray & Curtis 1957) and performed the classification in partitions of two to k clusters, with 10,000 iterations. We set k at 150, as already many clusters in the previous partitions were not ecologically interpretable. Then, we calculated the Ochiai fidelity index (OI) (Ochiai 1957) to estimate the diagnostic value of every species in each cluster independently of the other clusters, and repeated the calculus in all partitions (de Cáceres *et al.* 2008). We used a 0.3 threshold value to consider a species diagnostic but also looked at rare exclusive species (Peyre & Font 2011). The quality of diagnostic values varies with the choice of index but mostly with the context of comparison, which here is set to the entire páramo range and in this case assures regional diagnostic values (Chytrý *et al.* 2002). The resulting clusters of vegetation plots with their list of diagnostic species can usually be assigned to páramo vegetation units. Niche breath varies and while some species are better diagnostics of coarse plant communities, with a high OI in a cluster of a little divided partition, others will be better diagnostics of a fine plant community, with a high OI in a cluster of a very divided partition. Consequently, the increasing number of partitions can normally be assimilated to stages of a hierarchical classification as in the syntaxonomic system. However, because our dataset represents many different plant communities, we suspect one partition will hardly show an equal division with clusters at the same hierarchical level but more evidently clusters at different levels; for example keeping all the *Festuca* grasslands in one cluster dividing the *Calamagrostis* grasslands into many clusters. Over the years, several criteria, mostly based on number and value of the diagnostic species, have been suggested to determine the optimal partition of division (de Cáceres & Wiser 2012). However in an exploratory context and with the structure of the dataset previously unknown, there is no generally approved criterion (Tichý *et al.* 2010). Because of the great heterogeneity in our dataset, we believe it makes sense to select the partition that contains most clusters at the same hierarchical level and agrees with a coarse regional vegetation classification. We expect the clusters, at this level of division, to be more representative of phytogeographical units, with similar environmental conditions, than plant communities directly. To sharpen our analysis, we compared the selected *coarse partition* with another partition of higher division that reflects fine plant communities and correlated them via their plot composition. To represent the *fine partition*, we selected the most detailed valid division available, *i.e.* the last partition before the appearance of clusters with one plot only. After defining the fine clusters and listing their diagnostic species, we correlated them to already described plant communities from the literature. Consequently, by merging the clusters of the fine partition into the clusters of the coarse partition based on plot composition distances, we could extrapolate the contents in plant communities to each coarse cluster. This partition was only used to complement the first partition and would be invalid on its own to characterize the páramo because although our data is geographically representative of the region, there are few chances it represents all the fine plant communities.

To assess the floristic diversity and affinities between the clusters of the coarse partition, we estimated the local alpha diversity at plot level and the turnover in species, or beta diversity, between clusters. For alpha diversity, we calculated the species richness in plots for each cluster and compared them using the non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952) with the post hoc Steel-Dwass-Critchlow-Fligner bilateral test (Hollander & Wolfe 1999). For beta diversity, we calculated the Sørensen Similarity Index in pairs (Mueller-Dombois & Ellenberg 1974) to compare the clusters.

Results

Description of the clusters

The partition of 17 clusters gave the most coherent results for a coarse classification of our dataset, while the partition of 89 clusters was chosen as the complementary fine partition (Appendix 4,5). We recognized nine páramo, four super-páramo, two sub-páramo, one azonal and one disturbed vegetation clusters and drew a list of diagnostic species for each (Table 2.1, Table 2.2). We briefly describe the 17 coarse clusters obtained, from north-east to south-west:

We observed a general latitudinal gradient in the páramo landscape (Clusters 1–9) going from rosette dominated communities in Venezuela to mixed grasslands with rosettes in Colombia to tussock grasslands in Ecuador.

Cluster 1 — Cordillera de Mérida rosette páramo (Venezuela) — This cluster included the main plant communities from the páramo and super-páramo belts of the Cordillera de Mérida. The common páramo vegetation was dominated by giant Asteraceae rosettes such as the diagnostic *Espeletia schultzii* with some shrubs like *Chaetolepis lindeniana* and *Hypericum caracasanum* and a poor herbaceous stratum with *Senecio formosus, Orthrosanthus acorifolius* and *Acaena cylindrostachya*. The super-páramo was geographically restricted and characterized by desertic communities of Espeletiinae such as *Coespeletia moritziana* and *C. timotensis* with few herbs such as *Hinterhubera imbricata* and *Draba pulvinata*.

Cluster 2 — Périja-Santa Marta páramo (Colombia-Venezuela) — The two isolated massifs, Sierra de Périja and Sierra de Santa Marta, form a biogeographic unit host great biodiversity and endemism (Pinto-Zárate & Rangel-Churio 2010). The lower páramo was dominated by mixed grasslands of *Calamagrostis spp.* with Espeletiinae like *Espeletia perijaensis* and shrubs, such as the diagnostic *Hypericum magdalenicum* (Santa Marta) and *H. stenopetalum* (Périja). The *Calamagrostis effusa* grassland with *Lachemilla polylepis* from the upper Santa Marta páramo belt was segregated in the fine partition. Our dataset did not contain higher elevations plots from the area and therefore no super-páramo community was detected.

Cluster 3 — Eastern cordillera páramo grasslands (Colombia) — This cluster contained most páramo grasslands from the Colombian eastern cordillera. The páramos on the Amazonian slope are generally humid and dominated by bamboo communities, while the western slope páramos are drier and dominated by *Calamagrostis effusa* grasslands with shrubs (Rangel-Churio 2000). Both types were included in this cluster and characterized by the diagnostic *Espeletia grandiflora* with shrubs like *Diplostephium phylicoides* and *Arcytophyllum nitidum* and the herbs *Calamagrostis bogotensis, Bartsia santolinifolia* and *Castratella piloselloides.*

Cluster 4 — C*entral and western cordilleras dry páramo grasslands (Colombia) —* The eastern slopes of the western and central Colombian cordilleras are relatively dry, whereas their western slopes are more humid (Rangel-Churio 2000). Cluster 4 included the dry páramos from both cordilleras as well as the dry Nariño páramos. These communities were mostly grasslands of *Calamagrostis effusa* with *Espeletia hartwegiana*, shrubs like *Hypericum laricifolium* or *Monticalia vaccinioides* and often the fern *Blechnum loxense*. Other shrubs like *Diplostephium schultzii* or *Monnina revoluta* were diagnostic. The mixed grasslands of *Calamagrostis effusa* and *C. macrophylla* from Puracé were also included.

Cluster 5 — Mixed group of humid páramo grasslands (Colombia) — This cluster did not represent a coherent biogeographical unit and included several botanically and geographically distinct plant communities. The plots were grouped because they associated *Calamagrostis effusa* and *Pernettya prostrata*, both very common species, with *Arcytophyllum muticum*. The cluster did not have real valid diagnostic species, as the high-presence species were common species and the low-presence species were not overall representative. However, there was a common humid character to these plots, as revealed by the bamboo *Chusquea tessellata* and herbs like *Arcytophyllum muticum* and *Carex bonplandii*. Cluster 5 showed clear floristic affinities with Clusters 3 and 4 and was probably generated by regrouping plots that lacked the diagnostic species of Clusters 3 and 4 and could neither create a new valid cluster.

Cluster 6 — Ruiz-Tolima upper páramo grassland (Colombia) — This cluster represented an upper páramo community from Ruiz-Tolima at the ecotone between the lower grasslands of *Calamagrostis effusa* and the super-páramo (Salamanca *et al.* 2003). This distinctive grassland was dominated by *Calamagrostis recta*, mixed with *Espeletia hartwegiana* and shrubs, like the diagnostic *Pentacalia vernicosa* and *Baccharis rupicola*. The associated herbs were common species such as *Oreomyrrhis andicola* and *Hypochaeris sessiliflora*.

Cluster 7 — Carchi páramo grassland (Ecuador-Colombia) — At the Andean Ecuador-Colombia border, the páram communities are mostly humid *Calamagrostis effusa* grasslands with the southernmost Espeletiinae, *Espeletia pycnophylla* (Moscol-Olivera & Cleef, 2009) and were represented here. The shrubs *Brachyotum lindenii, Diplostephium floribundum* and the herbs *Chaptalia cordata, Lupinus pubescens* were diagnostic. Our dataset did not include super-páramo data and therefore no super-páramo community was detected.

Cluster 8 — Ecuadorian páramo grasslands — Most Ecuadorian páramos suffer intensive burning and grazing that promote the dominance of *Calamagrostis intermedia* grasslands (Hofstede *et al.* 2003). The distinctive páramos running on the Amazonian slope or in the extreme south are less disturbed and present also other dominant vegetation types in the landscape such as bamboo communities and shrublands (Ramsay 1992). Cluster 8 contained the common *Calamagrostis intermedia* grasslands with diagnostic shrub species of *Pentacalia, Diplostephium* and *Monnina. Galium corymbosum* and *Senecio chionogeton* were examples of diagnostic species.

Cluster 9 — The mixed grassland with cushions from Ecuador — Cluster 9 contained the upper páramo humid grasslands with cushions that form the lower ecotone on the humid slope of some Ecuadorian mountains (Sklenář & Ramsay 2001). These mixed communities consisted of small tussocks of *Calamagrostis* spp. such as *C. intermedia* and *C. fibrovaginata* alternating with other grasses like *Festuca andicola* and *Poa cocullata* among cushions of *Azorella pedunculata* and *A. aretioides*. Diagnostic herbs included *Gentianella cerastioides* and *Cerastium imbricatum*.

Diagnostic species	
Cluster 1	*Espeletia schultzii* Wedd. (0.70), *Hinterhubera imbricata* Cuatrec. & Aristeg. (0.49), *Lachemilla sprucei* (L.M.Perry) Rothm. (0.48), *Aciachne acicularis* Laegaard (0.44), *Oxylobus glanduliferus* (Hemsl.) A.Gray (0.38), *Baccharis prunifolia* Kunth (0.38), *Arenaria venezuelana* Briq.(0.38), *Poa petrosa* Swallen (0.36), *Azorella julianii* Mathias & Constance (0.32), *Draba pulvinata* Turcz. (0.35), *Echeveria venezuelensis* Rose (0.30), *Lachemilla moritziana* Damm. (0.29), *Calamagrostis pittieri* Hack.(0.29)
Cluster 2	*Hypericum magdalenicum* N. Robson (0.41), *Pentacalia albotecta* (Cuatrec.) Cuatrec.(0.41), *Sisyrinchium pusillum* Kunth (0.33), *Ranunculus spaniophyllus* Lourt. (0.38), *Lourteigia stoechadifolia* (L.f.) R.M.King & H. Rob. (0.35), *Hypericum baccharoides* Cuatrec. (0.33), *Bejaria nana* A.C.Sm. & Ewan (0.32), *Hypericum stenopetalum* Turcz. (0.31), *Sericotheca argentea* (L. f.) Rydb.(0.29), *Draba cheiranthoides* Hook. f. (0.28), *Lupinus carrikeri* C. P. Sm. (0.27), *Espeletia perijaensis* Cuatrec. (0.26), *Lachemilla polylepis* (Wedd.) Rothm.(0.24)
Cluster 3	*Espeletia grandiflora* Humb. & Bonpl. (0.67), *Arcytophyllum nitidum* (Kunth) Schldl. (0.51), *Diplostephium phylicoides* (Kunth) Wedd.(0.74), *Calamagrostis bogotensis* (Pilg.) Pilg.(0.52), *Bartsia santolinifolia* (Kunth) Benth.(0.46), *Castratella piloselloides* (Bonpl.) Naudin (0.52), *Aragoa abietina* Kunth (0.47), *Geranium santanderiense* R. Knuth (0.47), *Jamesonia bogotensis* H. Karst. (0.52), *Paepalanthus columbiensis* Ruhland (0.32)
Cluster 4	*Niphogeton ternata* (Willd. ex Schult.) Mathias & Constance (0.42), *Diplostephium schultzii* Wedd. (0.40), *Calamagrostis macrophylla* (Pilg.) Pilg. (0.40), *Monnina revoluta* Kunth (0.37), *Lachemilla pectinata* (Kunth) Rothm. (0.36), *Baccharis macrantha* Kunth (0.32), *Gynoxys tolimensis* Cuatrec. (0.28)
Cluster 6	*Calamagrostis recta* (Kunth) Trin. ex Steud. (0.65), *Pentacalia vernicosa* (Sch. Bip. ex Wedd.) Cuatrec. (0.48), *Gentianella dasyantha* (Gilg) Fabris (0.42), *Lachemilla galioides* (Benth.) Rothm.(0.41), *Carex peucophila* Holm (0.39), *Baccharis rupicola* Kunth (0.36), *Hypericum lancioides* Cuatrec.(0.33), *Festuca procera* Kunth (0.32)
Cluster 7	*Espeletia pycnophylla* Cuatrec. (0.89), *Diplostephium rhododendroides* Hieron. (0.75), *Lupinus pubescens* Benth. (0.66), *Puya hamata* L.B.Sm. (0.65), *Brachyotum lindenii* Cogn. (0.52), *Chaptalia cordata* Hieron. (0.40), *Neurolepis aristata* (Munro) Hitchc. (0.29)
Cluster 8	*Calamagrostis intermedia* (J.Presl) Steud (0.58)., *Lupinus prostratus* J. Agardh (0.52), *Galium corymbosum* Ruiz & Pav.(0.45), *Carex pygmaea* Boeck. (0.33), *Senecio chionogeton* Wedd. (0.32), *Ranunculus peruvianus* Pers. (0.28), *Geranium campii* H. E. Moore (0.26), *Dorobaea pimpinellifolia* (Kunth) B. Nord. (0.24), *Arcytophyllum filiforme* (Ruiz & Pav.) Standl. (0.24), *Hypericum aciculare* Kunth (0.22)
Cluster 9	*Geranium multipartitum* Benth. (0.62), *Werneria nubigena* Kunth (0.59), *Gentianella cerastioides* (Kunth) Fabris (0.58), *Festuca andicola* Kunth (0.57), *Cerastium imbricatum* Kunth (0.54), *Azorella pedunculata* (Spreng.) Mathias & Constance (0.51), *Calamagrostis fibrovaginata* Laegaard (0.44), *Plantago sericea* Ruiz & Pav. (0.38), *Calamagrostis jamesonii* Steud. (0.36), *Ranunculus praemorsus* Kunth ex DC. (0.35)

Table 2.1. List of diagnostic species for the valid páramo clusters.

The super-páramo (Clusters 10–13) can be divided into (1) the lower super-páramo (~4000–4300 m) located in the humid upper condensation belt where shrubs and cushion plants develop and (2) the upper super-páramo (> 4400m) with very stressful environmental conditions for plants' growth resulting in more desertic vegetation (Cleef 1981).

Cluster 10 — Ruiz-Tolima super-páramo (Colombia) — The cluster mostly represented the super-páramo communities from Ruiz-Tolima and included the lower transitional community of *Loricaria columbiana* with *Valeriana pilosa* and shrubs, the higher blue grasslands dominated by *Agrostis araucana* and *Lupinus alopecuroides* as well as the desertic upper super-páramo with few diagnostic species such as *Senecio isabelis* and *Draba hallii* (Salamanca *et al.* 2003). Few plots from the vicariant humid Sumapaz super-páramo, with *Loricaria complanata*, *Draba rositae* and *Senecio niveo-aureus*, were also found in this cluster and only discriminated as a community in the fine partition.

Cluster 11 — Lower humid super-páramo (Ecuador-Colombia) — This cluster contained zonal cushion plant communities from northern/eastern Ecuador and southern Colombia. Cushion communities are mostly azonal, when associated with locally running or standing water, however they can be zonal when covering great extensions like in the lower very humid super-páramos, where environmental humidity is constant, soils are deep and frost is limited (Bosman *et al.* 1993; Sklenář & Balslev 2005). Cushion plants like *Xenophyllum humile* or *Plantago rigida* are dominant and create a favorable environment for other species (Sklenář 2009), like the diagnostic shrubs *Diplostephium rupestre* and *Loricaria thuyoides* and herbs such as *Festuca asplundii* or *Valeriana pilosa that* were diagnostic. Sometimes, the *Loricaria* shrubs are absent like in some Ecuadorian super-páramos (Quintanilla 1983) and sometimes the *Loricaria* shrublands do not have cushions plants, such as the Ruiz-Tolima communities that were included in Cluster 10 (Cleef 1981).

Cluster 12 — Humid upper super-páramo from Ecuador — In the upper super-páramo, the climatic conditions, permanent night frost and great solifluction confine the vegetation to few microsites. There are two general tendencies, the humid one, when communities show little vegetation cover (< 30%), or the dry one, where vegetation cover drops (< 20%) (Sklenář 2000). Cluster 12 included the humid communities, essentially found on the Ecuadorian eastern cordillera and in Cajas. The vegetation is organized in small patches of herbs and low shrubs with diagnostic species like *Culcitium canescens* and *Cerastium floccosum*. The humid trend characterizing the cluster was driven by plants like *Calamagrostis ligulata* and *Ourisia muscosa*.

Cluster 13 — Dry upper super-páramo from Ecuador — This cluster grouped the dry Ecuadorian upper super-páramo communities often found on the slopes facing the inter-Andean valley but also in high rain-shadow deserts (Sklenář & Laegaard 2003). These communities are desertic and consist of a few shrubs like *Chuquiraga jussieui*, few grasses such as *Calamagrostis mollis* and *Agrostis tolucensis* and prostrate plants, for example the diagnostic *Astragalus geminiflorus* or *Nototriche jamesonii*.

	Diagnostic species
Cluster 10	*Erigeron chionophilus* Wedd. (0.58), *Pentacalia gelida* (Wedd.) Cuatrec. (0.47), *Agrostis araucana* Phil. (0.43), *Senecio latiflorus* Wedd. (0.41), *Festuca ulochaeta* Nees ex Steud. (0.40), *Senecio isabelis* S. Díaz (0.37), *Poa trachyphylla* Pilg. (0.31), *Draba pennell-hazenii* O. E. Schulz (0.27), *Loricaria columbiana* Cuatrec. (0.18)
Cluster 11	*Azorella aretioides* (Spreng.) DC.(0.57), *Lachemilla hispidula* (L. M. Perry) Rothm.(0.56), *Festuca asplundii* E.B. Alexeev (0.47), *Carex* gr. *aciculares* (Kük.) G.A. Wheeler (0.47), *Aciachne flagellifera* Laegaard (0.45), *Diplostephium rupestre* (Kunth) Wedd.(0.44), *Oritrophium peruvianum* (Lam.) Cuatrec.(0.44), *Gentianella nummulariifolia* (Griseb.) Fabris (0.39), *Calamagrostis guamanensis* Escalona (0.37), *Valeriana bracteata* Benth.(0.36)
Cluster 12	*Erigeron ecuadoriensis* Hieron. (0.48), *Calamagrostis ligulata* (Kunth) Hitchc. (0.42), *Ourisia muscosa* Benth. (0.41), *Draba aretioides* Kunth (0.42), *Lupinus rupestris* Kunth (0.36), *Elaphoglossum yatesii* (Sodiro) H. Christ (0.32), *Senecio culcitioides* Sch. Bip. (0.25), *Lupinus purdieanus* C.P. Sm. (0.24), *Calamagrostis aurea* (Munro ex Wedd.) Hack. ex. Sodiro (0.22)
Cluster 13	*Astragalus geminiflorus* Bonpl. (0.72), *Valeriana alypifolia* Kunth (0.60), *Nototriche jamesonii* A.W. Hill (0.58), *Draba depressa* Hook. f. (0.50), *Calamagrostis mollis* Pilg. (0.49), *Werneria pumila* Kunth (0.49), *Viola polycephala* H.E. Ballard & P. Jorg. (0.44), *Geranium ecuadoriense* Hieron. (0.42), *Perezia pungens* (Bonpl.) Less. (0.38), *Monticalia microdon* (Wedd.) B. Nord. (0.33), *Lupinus smithianus* Kunth (0.33), *Castilleja nubigena* Kunth (0.32), *Xenophyllum rigidum* (Kunth) V.A. Funk (0.29)
Cluster 15	*Chusquea angustifolia* (Soderstr. & C.E.Calderón) L.G.Clark (0.78), *Ruilopezia lopez-palacii* (Ruiz-Terán & López-Fig.) Cuatrec.(0.78), *Hypericum paramitanum* N.Robson (0.65), *Rhynchospora guaramacalensis* M.T.Strong (0.56), *Libanothamnus griffinii* (Ruiz & López) Cuatrec.(0.43), *Neurolepis glomerata* Swallen (0.43), *Puya aristiguietae* L.B.Sm. (0.32)

Table 2.2. List of diagnostic species for the valid super-páramo and sub-páramo clusters.

Our classification gave non-consistent results for the sub-páramo range and divided the altitudinal belt into two clusters (Clusters 14–15).

Cluster 14 — Widespread sub-páramo (Peru-Ecuador-Colombia-Venezuela) — Many different communities were included in this cluster due to their lack of floristic coherence and similarity with the other 16 clusters. Cluster 14 is unresolved and no list of valid diagnostic species could be suggested. Most communities should be classified as sub-páramo as they present a shrubby physiognomy and come from low elevation plots (< 3500 m). Sub-páramo communities are often mixed, very diverse and with many endemics, nonetheless, certain constancy is observed at genus level, e.g. *Weinmannia, Miconia, Diplostephium, Epidendrum* and *Stelis* (Cuello *et al.* 2010). In the fine partition, many valid clusters were recognized; however one heterogeneous cluster with 75 plots remained unresolved and requires a further division. One cluster included plots of mixed shrublands with *Chusquea angustifolia* bromeliads and orchids from the Nepes sub-páramo in the eastern Andes of Venezuela. Another cluster contained the shrubby sub-páramo of *Chaetolepis microphylla* from Cruz Verde (eastern cordillera, Colombia). The diverse sub-páramo with *Gaultheria anastamosans, Maclaenia rupestris* and *Weinmannia* spp. from Chingaza (eastern cordillera, Colombia) also appeared as a cluster. In Ecuador, the only sub-páramo cluster distinguished was a mixed shrubland and a *Neurolepis laegaardii* bamboo community from the Podocarpus National Park in southern Ecuador (Bussmann 2002). Two sub-páramo clusters representing never described sub-páramo communities were differentiated for Peru, (1) a mixed shrubland with *Brachyotum naudinii, Gaultheria reticulata* and *Arcytophyllum rivetii,* from the Cajamarca department and (2) a mixed grassland of *Calamagrostis tarmensis* with shrubs like *Arcytophyllum setosum* and *Hypericum sprucei* from the Piura department.

Cluster 15 — the Guaramacal sub-páramo (Venezuela) — This cluster mostly represented the very humid Guaramacal sub-páramo (Trujillo). These communities are mixed tall shrublands and their diagnostic species included *Ruilopezia lopez-palacii* and the bamboo *Chusquea angustifolia.* The fern *Blechnum schomburgkii* and grass *Cortaderia nitida* are also structuring the community, however they are not diagnostic. Cluster 15 also contained few plots from the humid Zumbador sub-páramo (Táchira), where similar vegetation grows.

Finally, our partition contained two clusters that corresponded to azonal (16) and disturbed (7) vegetation that were not intended to be classified. In both cases, the validity of the clusters' characterization is partial.

Cluster 16 — Azonal cushions from Colombia — The plots included were of azonal vegetation but was not recognized as such by its authors, therefore they remained in the original dataset. The vegetation types represented in this cluster were dominated by chamaephyte cushion plants such as *Plantago rigida, Oreobolus obtusangulus* and *Distichia muscoides* forming bogs and mires around páramo stream and lakes. Similar communities dominated by bryophytes, essentially *Sphagnum* spp., also exist (*e.g.* Bosman *et al.* 1993) but as bryophytes were originally removed from our dataset, we could not distinguish them. The herbs *Oritrophium limnophilum* and *Floscaldasia hypsophila* and the shrub *Loricaria lagunillensis* are diagnostic species.

Cluster 17 — Widespread disturbed vegetation — This cluster was not overall coherent and was based on plots sampled in heavily disturbed vegetation, mostly in the páramo belt, and with high contents in common species. Species characterizing the cluster are mostly herbs, such as *Lachemilla orbiculata, Rumex acetosella, Paspalum bonplandianum* and *Bidens triplinervia,* some of which are introduced. Such species are indicators of high anthropogenic disturbance and some are even invasive, like *Rumex acetosella* in Venezuela (Sarmiento 2006). The fine partition differentiated clusters showing different kinds of disturbances, such as the *Lachemilla orbiculata* meadows or the *Aciachne* spp. meadows implying intense grazing in the humid and dry páramos respectively.

Plant diversity

We compared the species richness per plot in each cluster of the coarse partition (Fig. 2.1.).

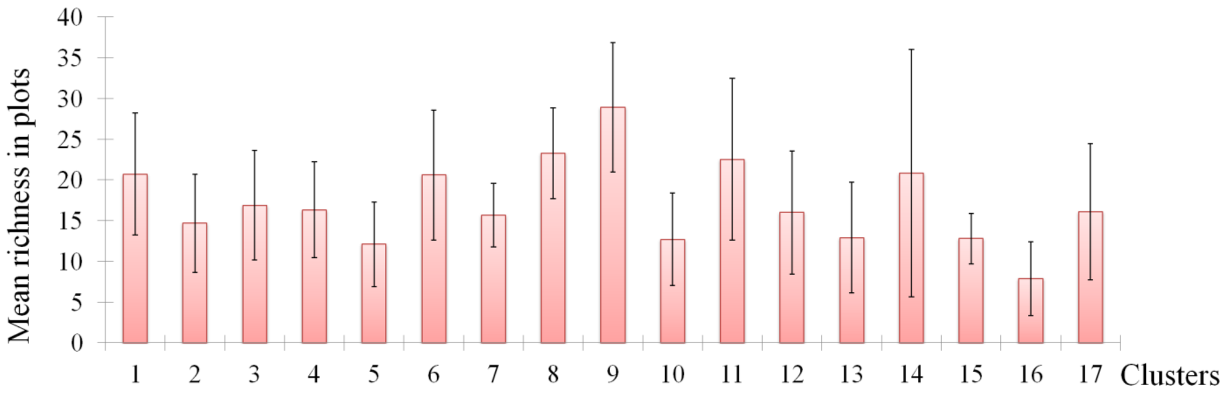


Figure 2.1. Mean observed floristic richness for the 17 clusters.

The standard deviation was generally wide for these mean values, which could reflect the phytosociological non-standardized plot size bias, a heterogeneous sampling quality that could be expected from a multiple data-sources dataset, or simply a lack of consistence in the cluster (Chytrý & Otýpková 2003; Dengler *et al.* 2009). Species richness values in the clusters differed significantly and we observed an overall large variability within and between clusters. We did not observe a monotonous decrease in richness with altitude, but distinguished, when omitting Cluster 10, a possible hump-shaped altitudinal pattern from the páramo belt to the super-páramo belt, with a maximum at the ecotone (Cluster 9). In the three altitudinal belts, it seems that the Venezuelan and Ecuadorian clusters were richer than the Colombian clusters. The azonal Cluster 16 was the poorest cluster, while the mixed grassland with cushions Cluster 9 is significantly the richest (see Appendix 6 for the results of the Kruskal-Wallis post hoc bilateral test). Finally, the most heterogeneous clusters were the general sub-páramo Cluster 14 and the disturbed vegetation Cluster 17.

For beta-diversity, the super-páramo clusters were generally consistent together (mean SI: 0.363), slightly more than the páramo clusters were together (mean SI: 0.330) and more than with the páramo clusters (mean SI: 0.258) (Table 2.3).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2	0.375															
3	0.350	0.469														
4	0.317	0.327	0.372													
5	0.321	0.401	0.500	0.515												
6	0.253	0.264	0.273	0.428	0.401											
7	0.159	0.306	0.228	0.274	0.515	0.238										
8	0.273	0.377	0.456	0.441	0.314	0.372	0.156									
9	0.244	0.200	0.172	0.264	0.254	0.358	0.257	0.428								
10	0.201	0.185	0.175	0.296	0.296	0.746	0.221	0.232	0.327							
11	0.212	0.213	0.196	0.353	0.369	0.346	0.251	0.461	0.520	0.339						
12	0.142	0.129	0.117	0.235	0.215	0.335	0.239	0.305	0.483	0.379	0.490					
13	0.102	0.088	0.047	0.120	0.113	0.216	0.175	0.224	0.404	0.232	0.272	0.463				
14	0.311	0.285	0.237	0.304	0.294	0.170	0.109	0.341	0.189	0.114	0.213	0.120	0.068			
15	0.183	0.161	0.230	0.157	0.127	0.083	0.146	0.062	0.043	0.053	0.060	0.056	0.037	0.083		
16	0.233	0.173	0.235	0.250	0.290	0.307	0.220	0.189	0.251	0.298	0.308	0.249	0.210	0.114	0.129	
17	0.318	0.316	0.287	0.357	0.382	0.366	0.232	0.483	0.444	0.272	0.392	0.256	0.214	0.310	0.088	0.219

Table 2.3. Sørensen Index values (SI) of beta-diversity among the 17 clusters.

Each cluster seemed floristically closer to the latitudinally closer cluster, such as Cluster 2 from the Périja-Santa Marta complex and Cluster 3 from the Colombian eastern cordillera, followed by the altitudinally closer cluster, like the Ruiz-Tolima upper páramo Cluster 6 and super-páramo Cluster 10. The highest similarities with more than half of the species shared included the páramo/super-páramo transition clusters from Ruiz-Tolima (6, 10), the páramo/super-páramo transition humid clusters from Ecuador (9, 11), and the mixed Colombian grasslands Cluster 5 with the other *Calamagrostis effusa* Colombian grassland clusters (3, 4, 7). The sub-páramo clusters (14, 15) showed little floristic affinity with each other and with the rest. The azonal Cluster 16 was similar to the humid ecotone páramo/super-páramo clusters (6, 10, and 11). Finally, the disturbed vegetation Cluster 17 was closer to the páramo clusters (mean SI: 0,349), especially the Ecuadorian grassland clusters (8, 9), than to the super-páramo clusters (mean SI: 0,283).

Discussion

Our exploratory vegetation classification highlighted the main phytogeographical units in the páramo region. In our study, we delimited 17 coarse clusters of which, 14 were *natural* (aggregation of plots with similar species contents) and three were *artificial* (aggregation of plots due to lack of similarity with other clusters). Artificial groups are a side effect of statistical classifications conducted on very heterogeneous data because each plot must fit into a cluster (Andrés & Font 2011). We consider Clusters 5, 14 and 17 to be artificial. The other clusters represent natural zonal vegetation units, with the exception of the azonal Cluster 16. The geographic distribution of the zonal natural clusters plus the widespread sub-páramo Cluster 14 is resumed in Figure 2.2.

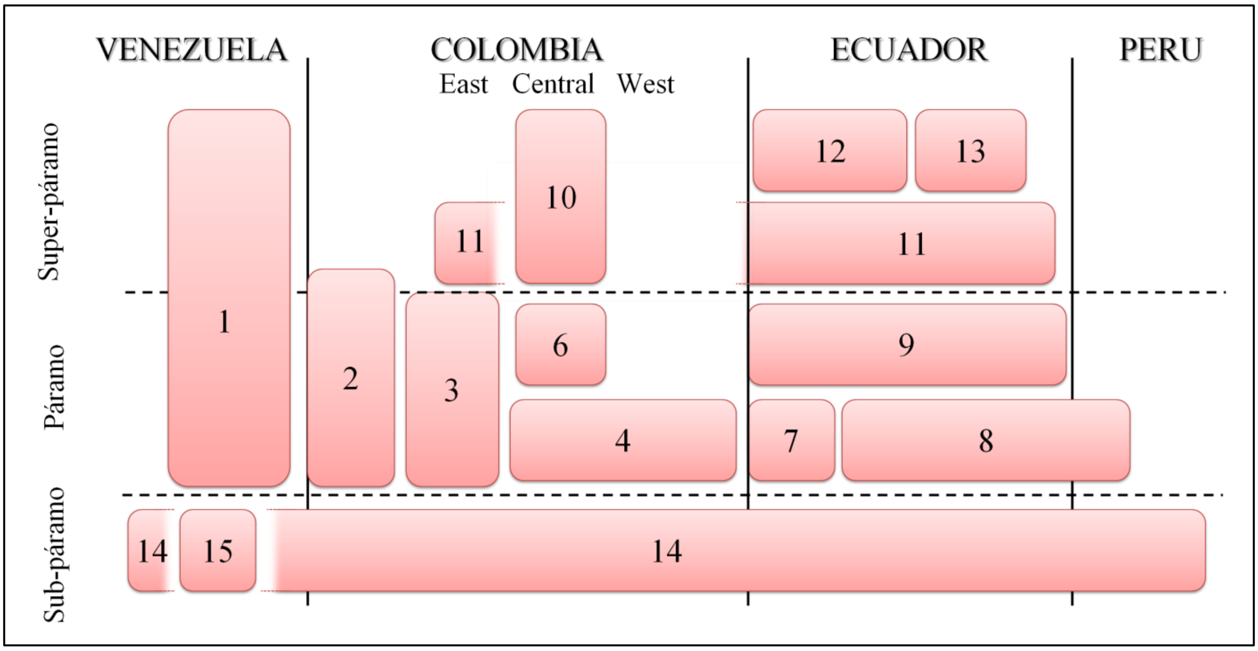


Figure 2.2. Distribution of the zonal natural clusters and the widespread sub-páramo. East (Eastern Cordillera), West (Western Cordillera), Central (Central Cordillera).

The zonal natural clusters are comparable to phytogeographical units that vary in geographical distribution, and plant community composition. We suppose that if a phytogeographical unit is restricted geographically and is recognized in a coarse vegetation classification like ours, it means the flora it contains is specialized and probably endemic. Such units would have diagnostic species with high diagnostic value in the case it contains few different plant communities (*e.g.* Cluster 7) or moderately high values if it contains many plant communities (*e.g.* Cluster 2). It would be important to focus future research on these phytogeographical units, as their source of narrowly distributed flora could be a fundamental criterion towards their conservation.

Our analysis revealed the altitudinal zonation including three altitudinal belts: sub-páramo, páramo and super-páramo, itself divided into lower and upper super-páramo (Sklenář & Jørgensen 1999). Our alpha-diversity analysis showed that, independently of the elevation and even though Colombia hosts the richest overall páramo flora (Rangel-Churio 2000), the Colombian clusters were generally poorer in species than the Ecuadorian and Venezuelan clusters. We suspect that this result might be due either a lack of data to represent the Colombian páramo flora or to a sampling effect. We recognized a general altitudinal hump-shaped pattern of species richness, but our results alone cannot affirm the pattern. This would support the previous findings suggesting a richer páramo/super-páramo ecotone, where communities present floristic elements from both belts and are less disturbed than in the lower páramo but not as environmentally stressed as in the upper super-páramo (Sklenář & Ramsay 2001).

The super-páramo was in general well divided by our method, except for areas where data was scarce. Because of the insularity of the super-páramo, its flora is highly endemic and organized into complex plant communities with narrow distribution (Sklenář & Balslev 2005). In general, the lower humid super-páramo, corresponding to low shrublands with or without cushions, was revealed and differentiated from the desertic upper communities. In turn, the upper super-páramo was generally divided into drier and more humid super-páramos, as clearly seen in Ecuador. We could not observe such clear separation for the Colombian upper super-páramo with our coarse partition, probably for lack of data, nonetheless, the fine partition revealed communities falling into both categories. The Venezuelan super-páramo vegetation could not be differentiated from the páramo vegetation in our coarse partition. The dry character of the higher Venezuelan mountains implies a gradual transition between páramo and super-páramo, with no specific upper condensation belt communities. In this case, both upper páramo and super-páramo belt share a similar physiognomy consisting of giant Espeletiinae rosettes including species of *Espeletia*, *Coespeletia* and *Ruilopezia*, and a poor herbaceous stratum (Monasterio & Reyes 1980). Whereas *Espeletia schultzii* is the dominant species in many Venezuelan páramos, many other Espeletiinae, of more restricted distribution, dominate also in the super-páramo (Berg 1998). One main radiation center for the Espeletiinae tribe is the Cordillera de Mérida, which can explain the large amount of speciation in the super-páramo and therefore the large amount of plant communities (Diazgranados 2012). We believe further efforts should be directed towards research in the Colombian super-páramos, on which sampling is still scarce in some areas. Envisaging that super-páramo communities are the first threatened and probably the most affected by Climate change makes the understanding of their structure and ecosystem functions crucial.

Unlike the super-páramo, the páramo is highly disturbed by anthropogenic activities, which fragment the natural vegetation and with time homogenize the landscape (Ramsay & Oxley 1996; Molinillo & Monasterio 2002). The Colombian páramos are typically more humid than the Ecuadorian and Venezuelan páramos, a climatic pattern well illustrated by the general latitudinal vegetation pattern going from grass-dominated communities in Peru and Ecuador, to more humid mixed grass and rosette communities in Colombia and to drier rosette dominated communities in Venezuela (Monasterio & Reyes 1980). In the páramo belt, the main vegetation types can often be recognized by their dominant species, contrarily to the super-páramo belt, as there is generally low equitativity (Sklenář & Ramsay 2001). For example, two species of *Calamagrostis, C. intermedia* and *C. effusa*, differentiate one drier southern and one more humid northern domain in the region, while the *Espeletia* species divide the northern domain into smaller phytogeographical units, for instance in Colombia with *Espeletia grandiflora* in the eastern cordillera and *E. hartwegiana* in the western (ssp. *hartwegiana*) and central cordilleras (ssp. *centroandina*). Nonetheless, classifying the relatively continuous páramo communities in Colombia is challenging, due to the great importance of the bamboo *Chusquea tessellata* that indicates a humid character and tends to outweigh the characteristics of the different biogeographic sectors. Moreover, proportions of these flora elements, in the same altitudinal belt vary within the cordilleras, essentially between the eastern and western slopes (Cleef 1981; Rangel-Churio 2000). As highlighted by the beta diversity test, invasive species are a real issue in the páramo belt (Monasterio & Molinillo 2002) and we think it would be useful to monitor these species in the region and predict their advances to limit niche competition and species replacement in the páramo plant communities.

Finally, our technique could not easily separate the sub-páramo into valid vegetation types. Apart from the Guaramacal páramo that stood out from the rest due to its high endemism and isolated situation (Cuello & Cleef 2009), all others sub-páramos were included into the same cluster. We understand that the high equitativity and remarkable diversity of these shrublands at a local scale due to a great mosaic of habitats (climate, soils), make them difficult to segregate, especially with a dataset not highly representative of this altitudinal belt. We believe that, in this case, a classification at genus level would be more appropriate to bring out the main vegetation types. Our beta-diversity analysis highlighted the little floristic similarity of the sub-páramo clusters with the other clusters, although we should not jump to conclusion given the great heterogeneity in the general sub-páramo cluster. This difference might reveal very different habitats from the páramo habitats and it would be interesting to also evaluate the montane component in the sub-páramo flora. The sub-páramo is a very fragile natural ecotone and it is especially threatened by the advances of agriculture and pasture that promote the downhill expansion of grasslands (páramo) and retraction of shrublands (sub-páramo) on most mountains (Ramsay 1992; Luteyn 1999). However, in some areas, especially low and difficultly accessible mountains (*e.g.* eastern Venezuela, southern Ecuador, Peru), the sub-páramo communities are still relatively well preserved and can dominate the landscape (Weigend 2002; Cuello *et al.* 2010). They are also often considered hotspots for biodiversity and areas of high endemism (Bussmann 2002; Lozano *et al.* 2009). Consequently, further studies on the sub-páramo vegetation complexity and floristic diversity are urgent in order to increase the scientific knowledge on these particular communities and promote conservation measures to slow down their degradation.

References

Acosta-Solís M (1984) Los páramos andinos del Ecuador. Publicaciones científicas MAS, Quito.

Andrés M, Font X (2011) Agrupacions de plantes vasculars segons la seva distribució a Catalunya. Botànica Pirenaica-cantàbrica; Actes del IX Col·loqui Internacional de Botànica Pirenaico-cantàbrica a Ordino, Andorra 31–44.

Berg A (1998) Pflanzengesellschaften und Lebensformen des Super-páramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157–203.

Bosman AF, van der Molen PC, Cleef AM (1993) Ecology of a páramo cushion mire. Journal of Vegetation Science 4: 633–640.

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological monographs 27(4): 325–349.

Bussmann RW (2002) Estudio Fitosociológico de la Vegetación en la Reserva Biológica de San Francisco (ECSF), Zamora Chinchipe. Herbario Loja 8: 1–106.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of vegetation science 13: 79–90.

Chytrý M, Otýpková Z (2003) Plot sizes used for phytosociological sampling in European vegetation. Journal of Vegetation Science 14: 563–570.

Cleef AM (1981) The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae (61), University of Amsterdam, Amsterdam.

Cleef AM, Rangel-Churio JO (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds) La Cordillera Occidental colombiana. Transecto de Tatamá. Estudios de Ecosistemas Tropandinos 6: 377–468.

Cuello N, Cleef AM (2009) The páramo vegetation of Ramal de Guaramacal, Trujillo State, Venezuela I: Zonal communities. Phytoceonologia 39(3): 295–329.

Cuello N, Cleef AM, Aymard G (2010) Phytogeography of the vascular páramo flora of Ramal de Guaramacal (Andes, Venezuela) and its ties to other páramo floras. Anales del Jardin Botanico de Madrid 67(2): 177–193.

de Cáceres M, Font X, Oliva F (2008) Assessing species diagnostic value in large data sets: A comparison between phi-coefficient and Ochiai index. Journal of Vegetation Science 19(6): 779–788.

de Cáceres M, Legendre P, Moretti M (2010) Improving indicator species analysis by combining groups of sites. Oikos 0: 1–11.

de Cáceres M, Wiser SK (2012) Towards consistency in vegetation classification. Journal of Vegetation Science 23(2): 387–393.

Dengler J, Löbel S, Solnik C (2009) Species constancy depends on plot size-a problem for vegetation classification and how it can be solved. Journal of Vegetation Science 20: 754–766.

Dengler J, Janse F, Glöckler F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Lopez-González G, Finckh M, Mucina L, Rodwell JS, Schaminée JHJ, Spencer N (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. Journal of Vegetation Science 22: 582–597.

Diazgranados M (2012) A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae). PhytoKeys 16: 1–52.

Dufrêne M, Legendre P (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological monographs 67(3): 345–366.

Géhu JM, Rivas-Martínez S (1981) Notions fondamentales de phytosociologie. Sintaxonomie. In: Dierschke H. (ed) Ber. Int. Symp., Rinteln (1980). Cramer, Vaduz, pp 5–53.

Grabherr G, Reiter K, Willner W (2003) Towards objectivity in vegetation classification: the example of the Austrian forests. Plant Ecology 169: 21–34.

Hofstede RGM, Segarra P, Mena-Vásconez P (eds) (2003) Los páramos del mundo. Proyecto Atlas Mundial de los Páramos. Global Peatland Initiative/NC-IUCN/EcoCiencia, Quito.

Hollander M, Wolfe DA (1999) Nonparametric statistical methods, 2nd ed. Wiley, New York.

Knollová I, Chytrý M, Tichý L, Hájek O (2005) Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. Journal of Vegetation Science 16: 479–486.

Kočí M, Chytrý M, Tichý L (2003) Formalized reproduction of an expert-based phytosociological classification: a case study of subalpine tall-forb vegetation. Journal of Vegetation Science 14: 600–610.

Kreft H, Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. Journal of Biogeography 37(11): 2029–2053.

Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. Journal of the American statistical Association 47(260): 583–621.

Lozano P, Cleef AM, Bussmann R (2009) Phytogeography of the vascular páramo flora of Podocarpus National Park, south Ecuador. Arnaldoa 16(2): 69–85.

Luteyn J (1999) Páramos: A checklist of plant diversity, geographic distribution, and botanical literature. Memoirs of the New York Botanical Garden (84), New York.

MacQueen J (1967) Some methods for classification and analysis of multivariate observations. Proceedings of the fifth Berkeley symposium on mathematical statistics and probability 1(14): 281–297.

Michalcová D, Lvoncik S, Chytrý M, Hájek O (2011) Bias in vegetation database) A comparison of stratified-random and preferential sampling. Journal of Vegetation Science 22(2): 281–291.

Molinillo M, Monasterio M (2002) Vegetation and grazing patterns in páramo environment. Ecotropicos 15(1): 19–34.

Monasterio M, Reyes S (1980) Las formaciones vegetales de los páramos de Venezuela. In: Monasterio M (ed) Estudios ecológicos en los páramos andinos, Editorial de la Universidad de los Andes, Mérida, pp 93–158.

Moscol-Olivera MC, Cleef AM (2009) A phytosociological study of the páramo along two altitudinal transects in El Carchi province, northern Ecuador. Phytocoenologia 39(1): 79–107.

Mucina L (1997) Classification of vegetation: Past, present and future. Journal of Vegetation Science 8(6): 751–760.

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation analysis. J. Wiley & Sons, New York.

Ochiai A (1957). Zoogeographic studies on the soleoid fishes found in Japan and its neighbouring regions. Bulletin of the Japanese Society of Scientific Fisheries 22(9): 526–530.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D’Amico JA., Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51: 93–938.

Peyre G, Font X (2011) Syntaxonomic revision and floristic characterization of the phytosociological alliances corresponding to subalpine and alpine grasslands of the Pyrenees and Cantabrian Mountains (classes Caricetea curvulae, Carici-Kobresietea, and Festuco-Seslerietea). Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 145(sup1): 220–232.

Pinto-Zárate JH, Rangel-Churio JO (2010) La vegetación de los páramos del norte de Colombia (Sierra Nevada de Santa Marta, Serranía de Perijá). In: Rangel-Churio JO (ed) Colombia diversidad biótica X: Cambio global (natural) y climático (antrópico) en el páramo colombiano, Instituto de Ciencias Naturales, Bogotá, pp 289–410.

Quintanilla V (1983) Observaciones fitogeograficas en el páramo de la Cordillera Oriental del Ecuador. Bulletin de l'Institut Français d'Etudes Andines 12(1-2): 55–74.

Ramsay PM (1992) The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes. PhD Thesis, University of Wales, Bangor.

Ramsay PM, Oxley ERB (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Vegetatio 124(2): 129–144.

Rangel-Churio JO (2000) Biodiversidad en la región del páramo: con especial referencia a Colombia. Congreso Mundial de Páramos. MMA, CAR, IDEAM y Colombia, C. Paipa I: 168–200.

Rangel-Churio JO (2000) La diversidad beta: tipos de vegetación. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica III. La región de vida paramuna. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, pp 658–719.

Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: van der Hammen T, dos Santos AG (eds) La Cordillera Central Colombiana. Transecto Parque los Nevados. Studies on Tropical Andean Ecosystems, J. Cramer. Berlin-Stuttgart 5: 1–77.

Sarmiento G (1986) Ecologically crucial features of climate in high tropical mountains. In: Vuilleumier F, Monasterio M (eds) High Altitude Tropical Biogeography, Oxford University Press, Oxford, pp 11–45.

Sarmiento L (2006) Grazing impact on vegetation structure and plant species richness in an old-field succession of the Venezuelan Páramos. In: Spehn EM, Liberman M, Körner C (eds) Land use change and mountain biodiversity. CRC Press, pp 119–136.

Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian super-páramos. PhD thesis, Charles University, Prague.

Sklenář P (2009). Presence of cushion plants increases community diversity in the high equatorial Andes. Flora-Morphology, Distribution, Functional Ecology of Plants 204(4): 270–277.

Sklenář P, Jørgensen PM (1999) Distribution patterns of páramo plants in Ecuador. Journal of Biogeography 26: 681–691.

Sklenář P, Ramsay PM (2001) Diversity of zonal páramo plant communities in Ecuador. Diversity and Distributions 7: 113–124.

Sklenář P, Lægaard S (2003) Rain-Shadow in the High Andes of Ecuador Evidenced by Páramo Vegetation. Arctic, Antarctic, and Alpine Research 35(1): 8–17.

Sklenář P, Balslev H (2005) Super-páramo plant species diversity and phytogeography in Ecuador. Flora-Morphology, Distribution, Functional Ecology of Plants 200(5): 416–433.

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17(6), 809–818.

Tichý L, Chytrý M, Hájek M, Talbot S, Botta-Dukát Z (2010) OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. Journal of Vegetation Science 21: 287–299.

Weigend M (2002) Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. The Botanical Review 68(1): 38–54.

Willner W, Tichý L, Chytrý M (2009) Effects of different fidelity measures and contexts on the determination of diagnostic species. Journal of Vegetation Science 20: 130–137.

Chapter 3: Patterns of plant diversity in the páramo region

Introduction

Understanding the global patterns of species richness remains one of the greatest actual challenges in biogeography (Jiménez *et al.* 2009; Tello & Stevens 2010). Species richness studies are relatively scarce in the tropics, which contrast their record biodiversity for which reason they should receive most of the scientific attention (Hawkins *et al.* 2003; Field *et al.* 2009). With a latitudinal distribution extending over four countries in South America, the páramo is a perfect model to study regional species richness patterns in tropical and mountain areas. Studying these patterns in the region is particularly essential in order to locate hotspots for biodiversity that deserve priority in conservation. While there are few small-scale studies on pattern of plant species richness already conducted on altitudinal gradients in the páramo (*e.g.* Sklenář & Ramsay 2001), there are none on the regional latitudinal richness patterns (Kessler et al. 2011).

Even though the research field of Macroecology has shown great advances in the last decades and many hypotheses have been proposed to explain patterns of species richness based on ecology and evolution, no ultimate theory has been approved (*e.g.* Brown 1995; Whittaker *et al.* 2001). Most hypotheses rely on a combination of richness drivers that can be categorized as scale, environmental, historical and biological factors (*e.g.* Willig *et al.* 2003; Field *et al.* 2009; Jiménez *et al.* 2009). Scale is usually very important as the significance of the other factors is highly scale-dependant (Rosenweig 1995; Rahbek 2005; Nogués-Bravo *et al.* 2008). Traditionally, scale is divided into grain, or sampling unit, and extent, or study area, both aspects needing consideration (Lyons & Willig 2002; Field *et al.* 2009). Authors agree that the environment, independently of the study, always plays a significant role in shaping species richness pattern (*e.g.* Francis & Currie 2003; Hawkins *et al.* 2003; Willig *et al.* 2003; Currie *et al.* 2004). Environmental determinants include many correlated factors like the essential water and energy availability but also topography, soils and environmental heterogeneity (Currie 1991; Jiménez *et al.* 2009; Tello & Stevens 2010). Historical and evolutionary processes control species richness via speciation, expansion and diversification and are usually difficult to evaluate (*e.g.* Wiens & Donoghue 2004; Ricklefs 2005; Jablonski *et al.* 2006). Finally, biological factors include biotic interactions and population dynamics and known to be important, especially at local scale (*e.g.* Ricklefs 2004; Grytnes *et al.* 2008). For certain broad latitudinal gradients, geometric constraints are a crucial factor (Colwell & Lees 2000), nonetheless, in the case of the páramo, which extends in an equatorial area of the globe and in one altitudinal band, their effect is secondary (Lyons & Willig 2002). The relative importance of all these factors as drivers of species richness patterns varies substantially among taxonomic groups and study area (Whittaker *et al.* 2001; Willig *et al.* 2003). Moreover, some factors such as biotic interactions or dispersal can be difficult to quantify and evaluate, especially on broad extents and especially in the tropics (Field *et al.* 2009). Because it is not feasible to consider all the factors potentially influencing the richness patterns, we focus on the *environmental* hypothesis, which states that the environment is the main driver of species richness patterns, principally via gradients of energy and water availability (Wright *et al.* 1993; Lyons & Willig 2002; Currie *et al.* 2004). This hypothesis has been presented in two versions, one suggesting that the energy available, in form of climate, affects the physiology of organisms, whereas the other proposes that energy affects the productivity of plants and therefore the ecosystem (*e.g.* Rahbek & Graves 2001; Willig *et al.* 2003). Although dividing the environmental hypothesis into its two versions is less essential for plants than it is for animals (Hawkins *et al.* 2003), we believe it is important to take both of them into consideration as they might explain different parts of the variation (*e.g.* Mittelbach *et al.* 2001; Francis & Currie 2003).

Species richness in the tropics is usually highly correlated with regional humidity gradients (Hawkins *et al.* 2003), except for high elevations where energy also becomes a limiting factor (Lyons & Willig 2002). Therefore, we expect drier páramos to have lower species richness than the more humid páramos. We suppose that the main latitudinal patterns of plant species richness would follow the humidity trends in the region and be highest around the equator of the Inter-Tropical Convergence Zone in Colombia. We also think that plant diversity, including species richness and species turnover, would decrease with elevation as the environment becomes less favorable for plant development (Sklenář & Ramsay 2001). Finally, we believe that species richness would be higher in the páramos less affected by anthropogenic activities as their plant communities would be more diverse.

Our goal is to recognize the main patterns of plant diversity in the páramo region, which will increase our biogeographic knowledge for this diverse ecosystem and could have repercussions on its current management and conservation (Mace *et al.* 2010). We compared plant diversity in the páramo and super-páramo belts throughout the region using two complementary focal approaches, the local scale (alpha diversity) and the regional scale (gamma diversity) (Jetz *et al.* 2005; Kessler *et al.* 2011). We then evaluated the importance of the environment in explaining the variation of species richness. Finally, we modeled the predicted species richness in the region to highlight the principal patterns.

Material and Methods

Vegetation data

We used a dataset of 3000 vegetation plots from *VegPáramo*. A downside of the phytosociological method when doing studies on species richness is the varying plot size (Chytrý 2001). Plot size is determined in theory by the *species-area curve* (Guinochet 1973), sampling the minimal area for the quasi-saturation in species of the plant community, however in practice and prior to any knowledge of the area, plot size is usually defined based on the vegetation physiognomy (Ozenda 1982) and despite the use of different standard sizes, for example 9 m^2 for meadows, 25 m^2 for grasslands, 50 m^2 for shrublands and 250 m^2 for forests, it is sometimes defined subjectively. In our study, we summed infra-specific taxa and omitted the unidentified species, which we expect would not be significant in species richness estimates (Pos *et al.* 2014). We also converted the cover values to presence/absence records. Furthermore, we removed the plots located below 3000 m that surely represent montane forest and ecotonal vegetation. We also filtered the plots based on their species to avoid disturbed and azonal vegetation. We simplified the altitudinal gradient into páramo and super-páramo to reveal potential differences in plant diversity. To do so, we classified and divided our dataset using the previously obtained revised clusters (Chapter 2). We then verified the significance of our division by visualizing the geographical distribution of the plots and doing a two dimensions Non-metric Multidimensional Scaling (NMDS) based on pair Jaccard distances. Prior to our diversity models we delimited the distribution of the páramo and super-páramo units by classifying all 1 km^2 raster cells of our study area according to their mean altitude as páramo (< 4000 m) or super-páramo (> 4000 m).

Environmental data

Because patterns of species richness are usually grain dependant (Willig *et al.* 2003; Field *et al.* 2009), we took plot size into account. Extent here is a secondary factor as our results will be valid for the entire páramo region. All our plots are fine-grained sampled so we expected a good correlation between environmental variables and species richness (Rahbek & Graves 2000). Moreover, in phytosociology, the plots are supposed to represent the dominant vegetation types so we expect representative results for the region and minimal information losses (Currie 1991; Hawkins *et al.* 2003). Nonetheless, the differences in term of plot sizes used and sampling effort in the páramo and the super-páramo can significantly influence richness patterns (Jiménez *et al.* 2009). Therefore, we compared the plot sizes used in the two units and conducted a regression analysis to reveal the potential correlation between plot size and species richness. If the correlation is significant, our further analyses will have to include an area-correction.

We considered several environmental variables that may be important in shaping richness patterns in the páramo region. We define as *climatic* variables the ones that affect plants physiology directly through the climate and as *productivity* variables the ones that affect plants indirectly through their fitness. Productivity variables are usually calculated with climatic proxies (Hawkins *et al.* 2003) and are therefore considered together with climatic variables; however we believe it is important to study them separately and combined. Spatial autocorrelation of the variables must be considered as it can bias the results and alter our interpretation (Willig *et al.* 2003; Fortin & Dale 2005). For climatic variables, we used the 19 bioclimatic variables from Worldclim (Hijmans *et al.* 2005) and to reduce the dimensions of our data, synthetize the information and avoid colinearity and redundancy, we carried out a Principal Component Analysis (PCA) on these variables (Rangel *et al.* 2010). As for productivity variables, we considered evapotranspiration variables, min potential evapotranspiration, mean potential evapotranspiration and actual evapotranspiration, and also a water deficit factor that we all obtained from the *Consultative Group on International Agricultural Research Consortium for Spatial Information* (CGIAR-CSI) database (www.cgiar-csi.org). Unfortunately, we could not access other variables to include in our definition of the environment.

Statistical analyses

To compare plant diversity between the páramo and super-páramo belts, we had to consider that setting the spatial limits associated with alpha and gamma diversity is subjective and that the detection and strength of large-scale patterns are scale-dependant (*e.g.* Gaston & Blackburn 2000; Willig *et al.* 2003). Here, we define alpha diversity as the species richness at the finest scale available, which is plot size, whereas gamma diversity corresponds to the regional diversity in the páramo (Rahbek 2005). We did not directly evaluate beta diversity in our two units; however it was implied in the relation between gamma and alpha diversity (Whittaker *et al.* 2001). We compared the alpha diversity of our two units and evaluated the difference with a t-test. In order to remove the plot-size effect, we compared and evaluated the difference of species richness between páramo and super-páramo based on the residuals of the previous regression analysis (Lyons & Willig 2002). We then compared páramo and super-páramo by their gamma diversity by conducting a *pseudo-rarefaction*, which approaches the rarefaction techniques (Gotelli & Colwell 2001; Gotelli *et al.* 2013), and proceeds by n times randomly picks an equal amount of plots from both units and sums their area and corresponding species richness.

Consequently, this technique gives a comparable relation between total area sampled and total species richness for both páramo and super-páramo.

To understand the importance of the environment in shaping richness patterns in the páramo and the super-páramo separately, we built four regression models with different approaches (1) the area model, (2) the climatic model, (3) the productivity model and (4) the environmental model. In the area model, we only took into account the effect of plot size. For the climatic model, we performed a forward selection of the components explaining most variation and obtained from the previous PCA analysis with the *ordiR2step* function of the VEGAN software package (Oksanen *et al.* 2013). For the productivity model, we considered the four productivity variables coupled with two of the Worldclim bioclimatic variables that we expect to be highly correlated with plant productivity (BIO1, mean annual temperature and BIO 12, annual precipitation) and also selected the most significant variables. Finally, for the environmental model, we used a combination of variables including plot size, bioclimatic variables and energetic variables. For all models, we used the spatial regression method, or Generalized Least Squares (GLS) with an exponential covariance structure. One main advantage of this technique is that it controls spatial autocorrelation in our data, which is a regular downside of biogeographical data (Jetz & Rahbek 2002; Tognelli & Kelt 2004). We used the adjusted Akaike Information Criterion (AIC) to evaluate the models' performance.

To build predictive models of species richness in the páramo region, we focused on the Kriging metamodels interpolation techniques, whose performance is optimized at global scale (*e.g.* Kreft & Jetz 2007). To assure a good exploration of species richness, we used three different approaches. The first approach consisted of a simple space-based Ordinary Kriging model, which by residuals interpolation estimates species richness in non-sampled areas thanks to the proximity of the sampled points (Burrough & McDonnell 1998; Banerjee *et al.* 2003). The second approach used the best GLS model previously obtained and fitted to the empirical data. The third approach combined the components of both approaches into an integrative model, or Universal Kriging. Whereas the Ordinary Kriging alone might not be explicative enough, it becomes very useful when completing an easily over-predicting environmental model, such as our regression model, into a complete Universal Kriging (*e.g.* Miller 2005; Allouche *et al.* 2008).

Results

The units obtained by dividing the dataset were coherent with the páramo and super-páramo altitudinal belts (Fig. 3.1).

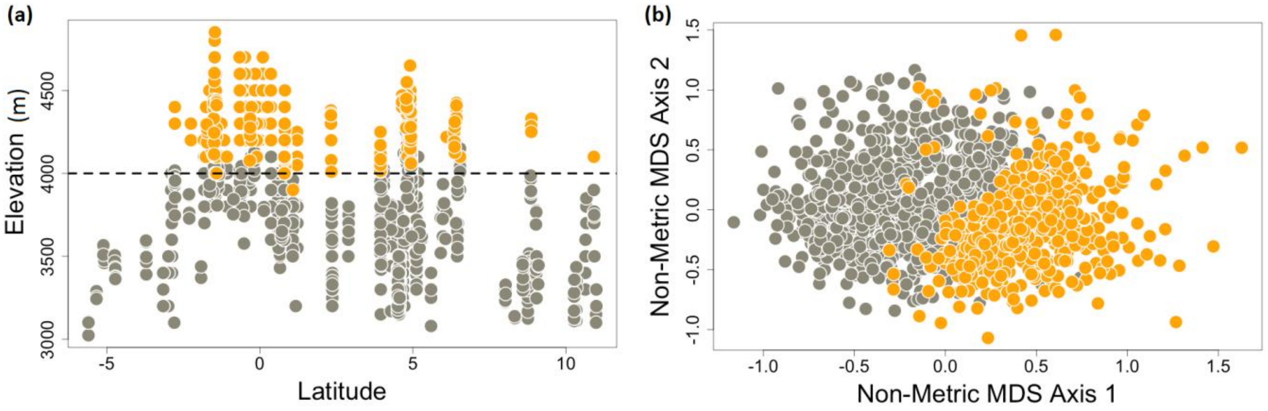


Figure 3.1. Differences in (a) elevation and (b) species composition of the páramo (gray) and super-páramo (orange) plots.

We observed that the distribution of the plots, both latitudinally and altitudinally, coincided with the geographical distribution of the altitudinal belts, with the páramo plots spread over the four Andean countries and the super-páramo plots with a more restricted distribution and lacking in Peru (Fig. 3.1a). The transition between the páramo and super-páramo units occured around 4000 m, with some páramo plots found up to 4200 m in Colombia and some super-páramo plots found below 4000 m in northern Ecuador. The two dimension NMDS separated the two units with little overlap based on their respective floras (Fig. 3.1b).

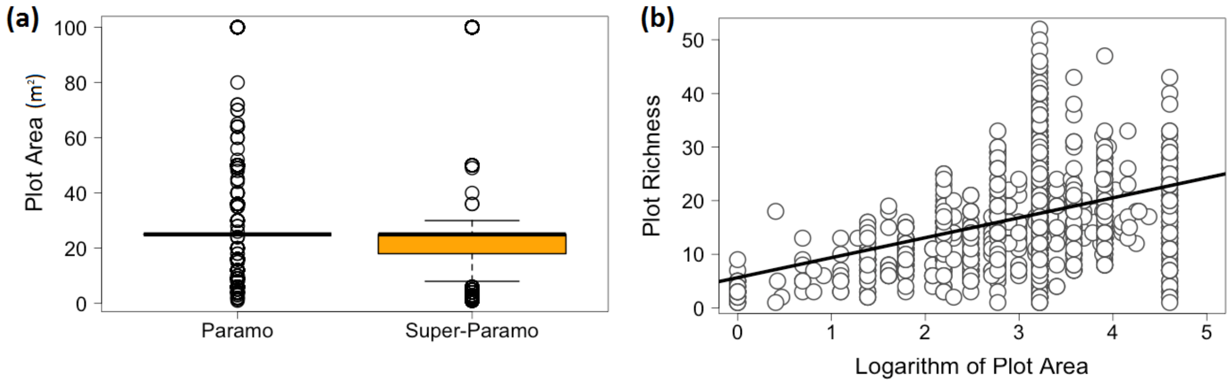


Figure 3.2. (a) Plot size used in the páramo and super-páramo units and (b) effect of plot size on local species richness.

Regarding plot size, we note that plots of 25 m^2 were more commonly used in both units, although super-páramo plots are often smaller (Fig. 3.2a). Plot size varied substantially in both units and the variation was more pronounced in the páramo. The regression analysis between species richness and plot area showed a clear positive correlation, therefore, we hould consider the plot size factor when modeling species richness in the region (Fig. 3.2b).

Local and regional diversity

Species richness at plot level was not significantly different between páramo and super-páramo, whether the comparison was based on real data (Fig 3.3a: t-test: 1.0902, p-value = 0.2759) or an area-corrected version of the data using the residuals of the last regression analysis (Fig. 3.3b: t-test: 0.1651, p-value: 0.8689).

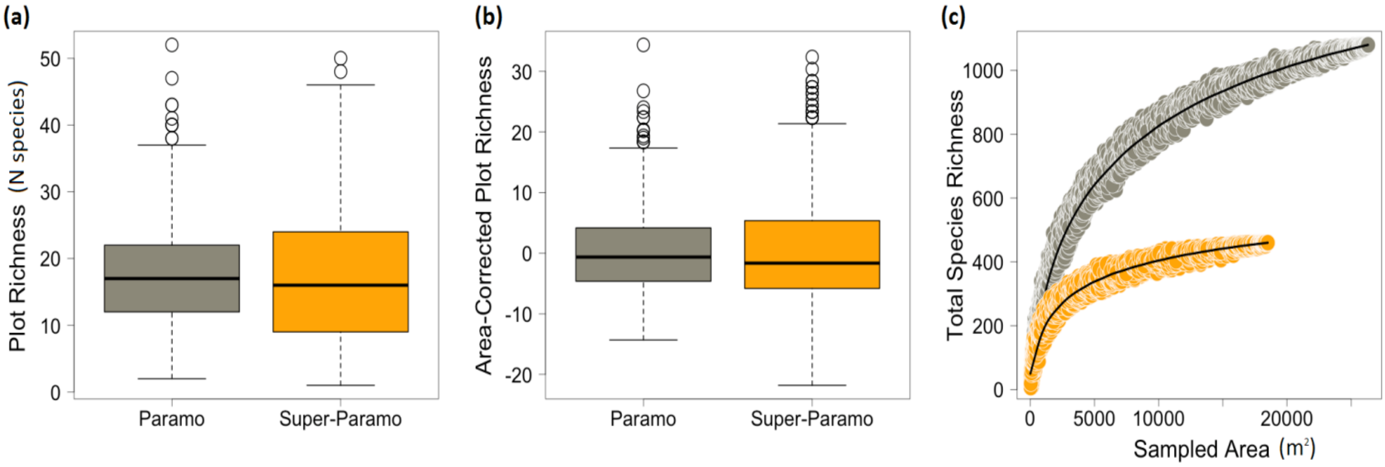


Figure 3.3. Comparisons of (a),(b) local (alpha) and (c) regional (gamma) diversity between páramo and super-páramo units.

For gamma diversity (Fig. 3.3c), we observed that most sampling effort had been directed towards the páramo, whose extension and accessibility is greater than that of the super-páramo. Moreover, the super-páramo curve tended to a quasi-asymptote, whereas the páramo curve was not. We observed that gamma diversity, independently of the total area sampled, was clearly higher in the páramo than in the super-páramo.

Predictions of species richness

The Sum of Squares (SS) of the regressions models, showed that the environment explained more of the species richness variation in the super-páramo (60%) than in the páramo (45%) (Fig. 3.4). For the páramo, the environmental model explained species richness better, whereas for the super-páramo, both the climatic and environmental models performed very well. The climate was a relatively better predictor for super-páramo richness than it was for páramo richness and productivity was a better predictor for the páramo richness than for the super-páramo richness. For both units, area alone was not a good predictor of species richness.

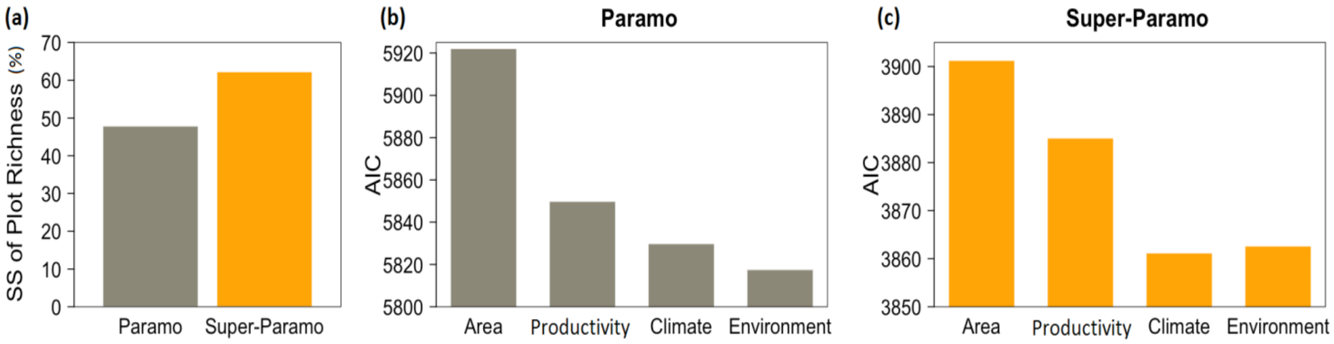


Figure 3.4. Richness-environment relationships in the páramo and super-páramo: (a) Sum of Squares of the models and (b),(c) performance of the models evaluated with the AIC.

These results confirm the importance of climate in the super-páramo and highlight productivity variables as non negligible factors for species richness in the páramo belt, probably through anthropogenic effects and maintenance of diversity. Therefore, we used the GLS complete environmental model for predicting species richness in non-sampled areas.

The predicted local species richness for a 25 m^2 standard plot differ between the three approaches, Ordinary Kriging model (Fig. 3.5a), environmental model summing the two environmental GLS models for páramo and super-páramo (Fig. 3.5b) and Universal Kriging combining both previous models (Fig. 3.5c). The Ordinary Kriging, which predicts richness without considering any explanatory gradient, tended to under-predict species richness overall, with most values varying from 10–15 species per plot. In contrast, the environmental GLS model was closer to reality with most areas containing 15–30 species per plot, but seemed to over-predict richness in large areas. The Universal Kriging model was the most realistic model, with contrasting values that highlighted the main patterns. In the predictions of the Universal Kriging model, we observed a general decrease of species richness from south to north with many exceptions to the global pattern. Drier areas such as the Chimborazo mountain in Ecuador (~Lat. -1; Long. -79) and the central range of the Cordillera de Mérida (~Lat. 9; Long. -71) usually had low species richness. In contrast, hotspots for floristic diversity concentrated in Ecuador, essentially on the humid slope of the eastern cordillera (*e.g.* the Llanganates area,~Lat. -2; Long. -78) and in the Amotape-Huancabamba zone (~Lat. -4; Long. -80). In addition, the low páramos of the eastern Andes in Venezuela seemed to have high species richness. One unexpected result is that all Colombian páramos seemed relatively poor in comparison to other páramos, with generally less than 20 species per plot.

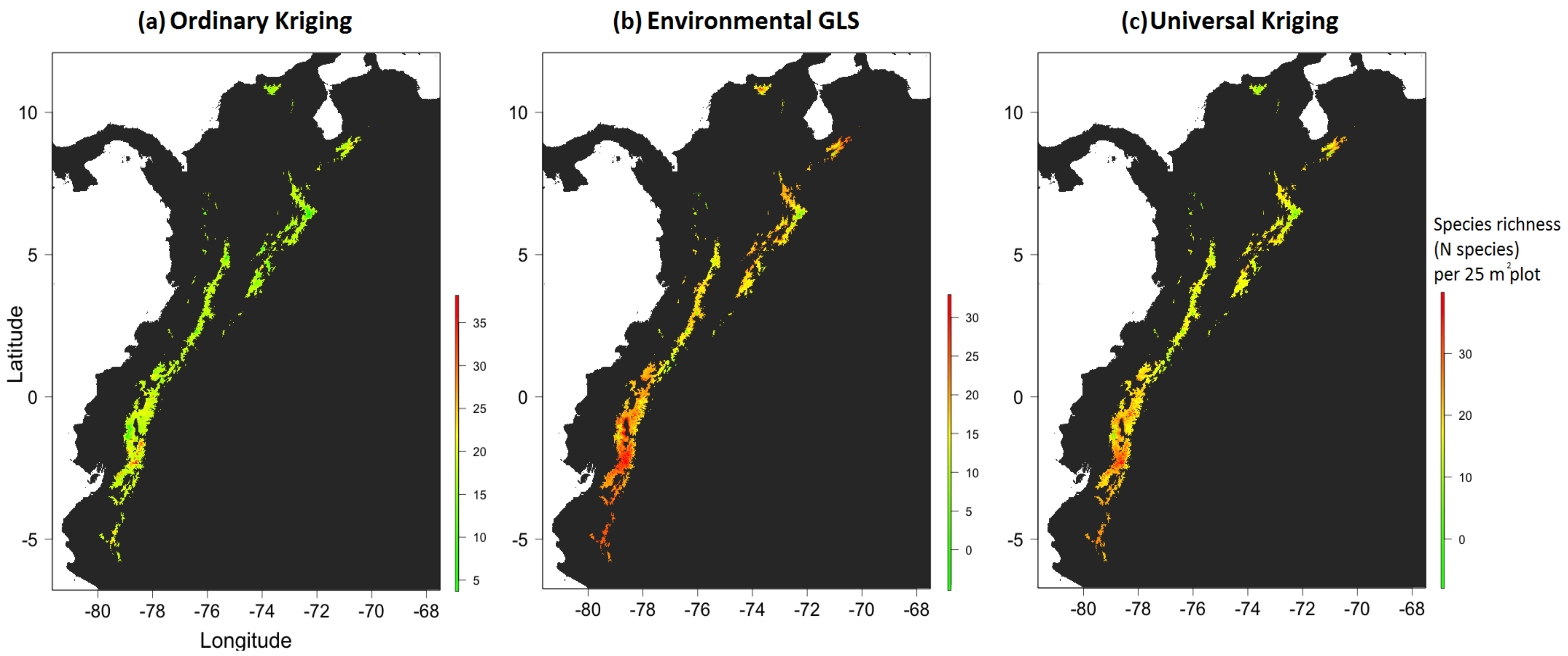


Figure 3.5. Expected geographic patterns of local species richness accross the entire páramo region according to (a) the Ordinary Kriging, (b) environmental GLS and (c) Universal Kriging models.

Discussion

The dataset division into páramo and super-páramo units agreed well with the geography and floristic composition of these two altitudinal belts. Regarding plot size, there was no noticeable difference between the two units, but we observed certain general variability. Although this is probably due to the great diversity of vegetation physiognomies found naturally in each altitudinal belt, some extreme values such as 1 m^2 for páramo plots and 100 m^2 for super-páramo plots, reveal necessarily a data collector effect. In fact, these plot sizes should be used for specific azonal plant communities, such as *Aciachne* meadows and *Polylepis* forest respectively, which have not been considered in the study. The regression analysis showed a clear correlation between plot size and species richness, a statement generalized in biogeography as the effect of grain on species richness. How species richness increases with grain is a controversial topic as, if truly in one same plant community, plots should quasi-saturate in species after a linear increase, while if it keeps increasing, the plot might be merging two or more plant communities together.

Local and regional diversity

We expected alpha diversity to be higher in the páramo than in the super-páramo as species richness usually decreases with altitude (Rahbek 2005), but our results did not support this hypothesis and did not reveal a significant difference. As some authors have recognized an overall decrease of species richness from páramo to super-páramo (*e.g.* Sklenář & Ramsay 2001) we believe our observed result could be due to the lower super-páramo compensating the upper super-páramo. In fact as the lower super-páramo is usually very diverse thanks to its ecotone situation, the upper super-páramo is in contrast species poor because of its very severe environment (see Chapter 2). Moreover, vegetation cover, a factor that we did not consider here, is generally low in the upper super-páramo and high in the lower super-páramo, and species richness is known to generally increase with vegetation cover in these environments (Sklenář & Jørgensen 1999). Consequently, the high variability in species richness observed for the super-páramo unit could be due to these two sub-units that were not segregated.

Gamma diversity was much higher in the páramo than in the super-páramo. The extent could have been a factor influencing species richness as it is greater for the páramo than for the super-páramo belt (*e.g.* Whittaker *et al.* 2001; Rahbek 2005), however, our analysis revealed a substantial richness difference between the two units at equal extent. As alpha diversity was not significantly different, we conclude the main driver of difference in diversity between the two units is beta diversity, meaning that the páramo contains many more plant communities and greater species turnover than the super-páramo. This result supports previous findings that the number of vegetation types in the páramo belt is higher than in the super-páramo belt (Rangel-Churio 2000a), maybe because of greater climatic and soil heterogeneity, which are both correlated to the topographic complexity, or thanks to the artificial habitat mosaic created with anthropogenic activities. Our results also imply that the dataset used here does not represent the overall diversity of plant communities in the páramo but represent well the super-páramo communities. Consequently, more sampling is needed in the region and especially in the páramo belt to include more ecosystems.

The environmental hypothesis

The different regression models allowed testing different theories on which component of the environment would be a better driver of species richness in the páramo and super-páramo belts. The environment generally explained more variation in species richness for the super-páramo than for the páramo. Climate was an important driver in both units, but was more essential in the super-páramo belt, which we saw presents extreme environments, especially in the upper super-páramo. It also means that super-páramo ecosystems would be more easily affected by Climate change. The productivity model performed better for the páramo belt than for the super-páramo. A primary interpretation could be that the decrease of anthropogenic disturbance with elevation affects plant productivity and therefore species richness (Ramsay & Oxley 1996; Nogués-Bravo *et al.* 2008). In fact, as anthropogenic disturbance modifies the landscapes by homogenizing extended areas but also by fragmenting and creating new habitats, it enhances the diversity of ecosystems and therefore the variability in the overall productivity.

Regional pattern of species richness

At regional level, we did not observe the two expected richness gradients converging in the Inter-Tropical Convergence zone but more likely a general decrease of species richness from south to north with many exceptions. Colombia aside, we see that species richness is higher in more humid páramos with little seasonality such as the páramos on the Amazonian slope of the eastern Cordillera in Ecuador. On the other hand, drier and more seasonal páramos, for example on the high peaks of the Cordillera de Mérida, seem to be poorer in species, hence generally agreeing with humidity being a primordial richness driver. It is important to remember that species richness is not a good indicator of ecosystem quality alone as it does not differentiate between disturbed and natural areas. We recognized some páramo areas with high species richness that are known to be in relatively good preservation state, such as the eastern Trujillo Andes in Venezuela (Cuello *et al.* 2010) and the Amotape-Huancabamba zone (Lozano *et al.*

2009; Richter *et al.* 2009); therefore, these areas could be primarily qualified as hotspots for biodiversity. The fact that Colombian páramos are extremely diverse, in terms of climate, flora and plant communities (Rangel-Churio 2000b), had us believe some areas would be highlighted as hotspots. From our analyses, the Colombian páramos seem species poor and we believe it would be important to revise the existing data and add new data from Colombia to see if the pattern remains unchanged. Finally, we can anticipate from our example that patterns of plant species richness in topographically complex areas in the tropics are driven mostly by local microclimates and less by regional climatic trends, which support previous findings (*e.g.* Kessler *et al.* 2011). However, any further interpretation should disentangle the natural from the anthropogenic effects, as human influence could have already permanently affected global species richness patterns (Nogués-Bravo *et al.* 2008; Kessler 2009).

References

Allouche O, Steinitz O, Rotem D, Rosenfeld A, Kadmon R (2008). Incorporating distance constraints into species distribution models. Journal of Applied Ecology 45 (2): 599–609.

Banerjee S, Gelfand AE, Sirmans CF (2003) Directional rates of change under spatial process models. Journal of the American Statistical Association 98(464): 946–954.

Brown JH (1995) Macroecology. The University of Chicago Press, London.

Burrough PA, McDonnell R., (1998) Principles of geographical information systems, Vol. 333. Oxford: Oxford university press.

Chytrý M (2001). Phytosociological data give biased estimates of species richness. Journal of Vegetation Science 12(3): 441-444.

Cleef AM (1981) The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae (61), University of Amsterdam, Amsterdam.

Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15:70–76.

Cuello N, Cleef AM, Aymard G (2010) Phytogeography of the vascular páramo flora of Ramal de Guaramacal (Andes, Venezuela) and its ties to other páramo floras. Anales del Jardin Botanico de Madrid 67(2): 177–193.

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist 137: 27–49.

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kerr JT, Oberdoff T, O'Brien E, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Tirner JRG (2009) Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36(1): 132–147.

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press.

Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. The American Naturalist 161(4): 523–536.

Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell, London.

Gillmann LN, Wright SD (2006) The influence of productivity on the species richness of plants: a critical assessment. Ecology 87(5): 1214–1243.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology letters 4(4): 379–391.

Gotelli NJ, Chao A, Levin S (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Encyclopedia of biodiversity 5: 195–211.

Grytnes JA, Beaman JH, Romdal TS, Rahbek C (2008) The mid-domain effect matters: simulation analyses of range-size distribution data from Mount Kinabalu, Borneo. Journal of Biogeography 35:2138–2147.

Guinochet M (1973). Phytosociologie. Masson, Paris.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guègan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated global terrestrial climate surfaces. International Journal of Climatology 25: 1965–1978.

Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314:102–106.

Jetz W, Rahbek C (2002) Geographic range size and determinants of avian species richness. Science 297: 1548–1551.

Jetz W, Rahbek C, Lichstein JW (2005) Local and global approaches to spatial data analysis in ecology. Global Ecology and Biogeography 14(1): 97–98.

Jiménez I, Distler T, Jørgensen PM (2009) Estimated plant richness patterns across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. Ecography 32:433–448.

Kessler M, Grytnes JA, Halloy SRP, Kluge J, Krömer T, León B, Macía MJ, Young KR (2011) Gradients of plant diversity: local patterns and processes. In: Herzog SK, Martinez R, Jørgensen PM, Tiessen H (eds) Climate change and Biodiversity in the Tropical Andes. Sao José dos Campos, pp 204–219.

Kessler M (2009) The impact of population processes on patterns of species richness: lessons from elevational gradients. Basic and Applied Ecology 10:295–299.

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences 104(14): 5925–5930.

Lozano P, Cleef AM, Bussmann R (2009) Phytogeography of the vascular páramo flora of Podocarpus National Park, south Ecuador. Arnaldoa 16(2): 69–85.

Lyons SK, Willig MR (2002) Species richness, latitude, and scale-sensitivity. Ecology 83: 47–58.

Mace GM, Balmford A, Boitani L, Cowlishaw G, Dobson AP, Faith DP, Gaston KJ, Humphries CJ, Vane-Wright RI, Williams PH (2000) It’s time to work together and stop duplicating conservation efforts. Nature 405: 393.

Miller J (2005) Incorporating spatial dependence in predictive vegetation models: residual interpolation methods. The Professional Geographer 57(2): 169–184.

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Nogués-Bravo D, Araújo MB, Romdal T, Rahbeck C (2008) Scale effects and human impact on the elevational species richness gradients. Nature Letters 453: 216–220.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2012) Vegan: community ecology package. R package version 2.0-4. http://CRAN.R-project.org/package=vegan

Ozenda P (1982) Les vegetaux dans la biosphere. Doin editeurs, Paris.

Pos E, Guevara-Andino JE, Sabatier D, Molino JF, Pitman N, Mogollón H, Neill D, Cerón C, Rivas G, di Fiore A, Thomas R, Tirado M, Young KR, Wang O, Sierra R, García-Villacorta R, Zagt R, Palacios W, Aulestia M, ter Steege H (2014) Are all species necessary to reveal ecologically important patterns? Ecology and evolution, 4(24): 4626–4636.

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Rahbek C, Graves GR (2001) Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Science of the United States of America 98:4534–4539.

Ramsay PM, Oxley ERB (1996). Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Vegetatio 124(2): 129–144.

Rangel-Churio JO (2000a) La diversidad beta: tipos de vegetación. In: Rangel-Churio (ed) Colombia Diversidad Biótica III. La región de vida paramuna. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, pp 658–719.

Rangel-Churio JO (2000b) Biodiversidad en la región del páramo: con especial referencia a Colombia. Congreso Mundial de Páramos. MMA, CAR, IDEAM y Colombia, C. Paipa I: 168–200.

Rangel TFLVB, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. Ecography 33:46–50.

Richter M, Diertl MK, Emck P, Peters T, Beck E (2009) Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador Landscape Online 12: 1–35.

Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1–15.

Ricklefs RE (2005) Phylogenetic perspectives on patterns of regional and local richness. In: Bermingham E, Dick CW, Moritz C (eds) Tropical rainforest: past, present, and future. University of Chicago Press, Chicago, pp 16–40.

Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, New York, NY.

Sklenář P, Ramsay PM (2001) Diversity of zonal páramo plant communities in Ecuador. Diversity and Distributions 7:113–124.

Sklenář P, Jørgensen P (1999) Distribution patterns of páramo plants in Ecuador. Journal of Biogeography 26: 681–691.

Tello JS, Stevens RD (2010) Multiple environmental determinants of regional species richness and effects of geographic range size. Ecography 33(4): 796–808.

Tognelli MF, Kelt DA (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. Ecography 27: 427–436.

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28: 453–470.

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639–644.

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273–309.

Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. Species diversity in ecological communities: historical and geographical perspectives 66–74.

Conclusions and future perspectives

Our project focuses on actual challenges for the region, including lack of substantial amounts of available biological data and need for regional ecological and biogeographic plant studies.

With 3000 vegetation plots, *VegPáramo* is a novel and substantial source of botanical data geographically representative of the páramo region. The database is freely accessible online through its webportal, from which the data can be consulted and downloaded. We hope to keep improving *VegPáramo* with new data, especially from narrowly distributed and very biodiverse under-sampled páramo areas such as the Peruvian páramos. We are working on developing new features of ecological interest for the webportal to provide valuable information on the endangered and endemism status of páramo species, which could guide future studies into the crucial monitoring and management challenges (León-Yánez 2000). We are also developing new useful tools online to conduct primary statistical analysis on *VegPáramo* data such as diversity calculus. We believe the feedback and comments feature offers a great opportunity for users to interact and work together to help improve the database.

Classifying the páramo vegetation at regional scale is a difficult task due to the great complexity of climatic, topographic, soil and land-use conditions. Our regional vegetation classification of the páramo could highlight the main phytogeographical units of zonal vegetation in the páramo and while it overall satisfactorily segregated the plant communities in the páramo and super-páramo altitudinal belts, it could not divide well the sub-páramo based on species, and we believe a classification at genus level could result in a better classification of the sub-páramo vegetation. This particular ecotone is known for its great biodiversity and habitat diversity but it is also very fragile and often heavily impacted by the anthropogenic pressure that play a significant role in modeling the montane treeline (Bader *et al.* 2007; Young & Leon 2007). Therefore, we consider important that future scientific studies focus on the sub-páramo, which to date is still largely overlooked, in order to characterize, evaluate and preserve these unique ecosystems. Our simple species richness analysis highlighted a potential altitudinal richness gradient with a maximum peak at the ecotone between páramo and super-páramo that would confirm previous findings (*e.g.* Sklenář & Ramsay 2001). It would also be important to focus future further research on this ecotone, which is in addition closely related to the upper condensation belt that risks being strongly impacted by Climate change and in turn affect the ecotone habitats (Hole *et al.* 2012). Our classification has overall biogeographic validity and provides valuable units, clusters of group of clusters, that can be used to sustain future botanical and ecological studies on the páramo. The azonal páramo ecosystems are especially valuable for biodiversity, ecosystem services and paleoecology among other things and they are particularly fragile and little represented in regional páramo research and management (Bosman *et al.* 1993; Kessler 2006). Moreover, their habitat is locally restricted but can be widely extended in the Andes (Cleef 1981), consequently, we believe more scientific attention should be paid to these ecosystems and a regional vegetation classification at a continental scale to characterize them would be very useful.

Our study on plant diversity in the páramo region supported the environmental hypothesis and highlighted a general decrease of species richness from south to north, with many local exceptions to the global pattern, which supports the importance of local environments on richness patterns in tropical mountains. We believe that a revision of the Colombian data and new data are necessary to confirm their relatively low local richness despite their great habitat diversity and overall high richness. More sampling effort is also required, especially in the páramo belt, in order to capture and represent a larger amount of plant communities and improve our beta diversity estimates for the region. We believe our understanding of species richness patterns may be improved using a more complete approach considering additional influencing factors in the models, such as biotic interaction and evolution processes, and also a temporal component (Rohde 1992; Willig *et al.* 2003). The biodiversity hotspots proposed in our study are primary candidates for conservation, however the concept of species richness does not discriminate between natural and anthropogenized habitats, therefore a promising way to evaluate their hotspot quality would be to correlate the richness patterns with patterns of endemism (Sklenář & Jørgensen 1999; Kessler *et al.* 2011). From a different point of view, it has been shown that overall species richness patterns are mostly driven by common species (Evans *et al.* 2005; Šizling *et al.* 2009) and we think it would be interesting to understand the commonness and rarity structure of the páramo flora as well as their respective share in explaining species richness patterns in the region. The consideration of dispersal/historical factors would then be primordial as these factors are essential in shaping patterns of endemics (Whittaker *et al.* 2001; Wiens & Donoghue 2004).

Finally, we would like to draw special attention to the super-páramo ecosystems, which host a very specialized, endemic and fragile flora and have so far remained well preserved as human impact is limited at these elevations. Climate change is a main challenge for super-páramo plants because of limitations in their ecological niches and evolutive capacity and also the upward advances of anthropogenic activities (Larsen *et al.* 2011). Consequently, we believe it is very important to dedicate more research and management effort on these particular ecosystems in order to understand, estimate and monitor their response to Climate change.

References

Bader MY, Rietkerk M, Bregt AK (2007) Vegetation structure and temperature regimes of tropical alpine treelines. Arctic, Antarctic, and Alpine Research 39(3): 353–364.

Bosman AF, van der Molen PC, Cleef AM (1993) Ecology of a páramo cushion mire. Journal of Vegetation Science 4: 633–640.

Cleef AM (1981) The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae (61), University of Amsterdam, Amsterdam.

Evans KL, Warren LPH, Gaston KJ (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80:1–25.

Hole DG, Young KR., Seimon A., Gomez C, Hoffmann D, Schutze–Paez K, Sanchez S, Muchoney D, Grau HR, Ramirez E (2011) Adaptive management for biodiversity conservation under Climate change In: Herzog SK, Martínez R, Jørgensen PM, Tiessen M (eds) Climate change and Biodiversity in the Tropical Andes. Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp 19–46.

Jørgensen PM, Tiessen H (eds) Climate change and Biodiversity in the Tropical Andes. Sao José dos Campos, pp 204–219.

Kessler M (2006) Los bosques de Polylepis. In: Moraes M, Ollgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, pp 51–76.

Kessler M, Grytnes JA, Halloy SRP, Kluge J, Krömer T, León B, Macía MJ, Young KR (2011) Gradients of plant diversity: local patterns and processes. In: Herzog SK, Martinez R,

Larsen TH, Brehm G, Navarrete H, Franco P, Gómez H, Mena JL, Morales V, Argollo J, Blacutt L, Canhos V (2011) Range Shifts and Extinctions Driven by Climate change in the Tropical Andes: Synthesis and Directions . In: Herzog SK, Martinez R, Jørgensen PM, Tiessen H (eds) Climate change and Biodiversity in the Tropical Andes. Sao José dos Campos, pp 47–67.

León–Yanéz S (2000) Páramos ecuatorianos. In: Josse C, Mena PA, Medina G (eds) La biodiversidad de los Páramos. Serie Páramo 7. GTP/Abya Yala, Quito, pp 7–20.

Luteyn J (1999) Páramos: A checklist of plant diversity, geographic distribution, and botanical literature. Memoirs of the New York Botanical Garden (84), New York

Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.

Šizling AL, Šizlingova E, Storch D, Reif J, Gaston KJ (2009) Rarity, Commoness, and the Contribution of Individual Species to Species Richness Patterns. The American Naturalist 174(1): 82–93.

Sklenář P, Jørgensen PM (1999) Distribution patterns of páramo plants in Ecuador. Journal of Biogeography 26: 681–691.

Sklenář P, Ramsay PM (2001) Diversity of zonal páramo plant communities in Ecuador. Diversity and Distributions 7: 113–124.

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28: 453–470.

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639–644.

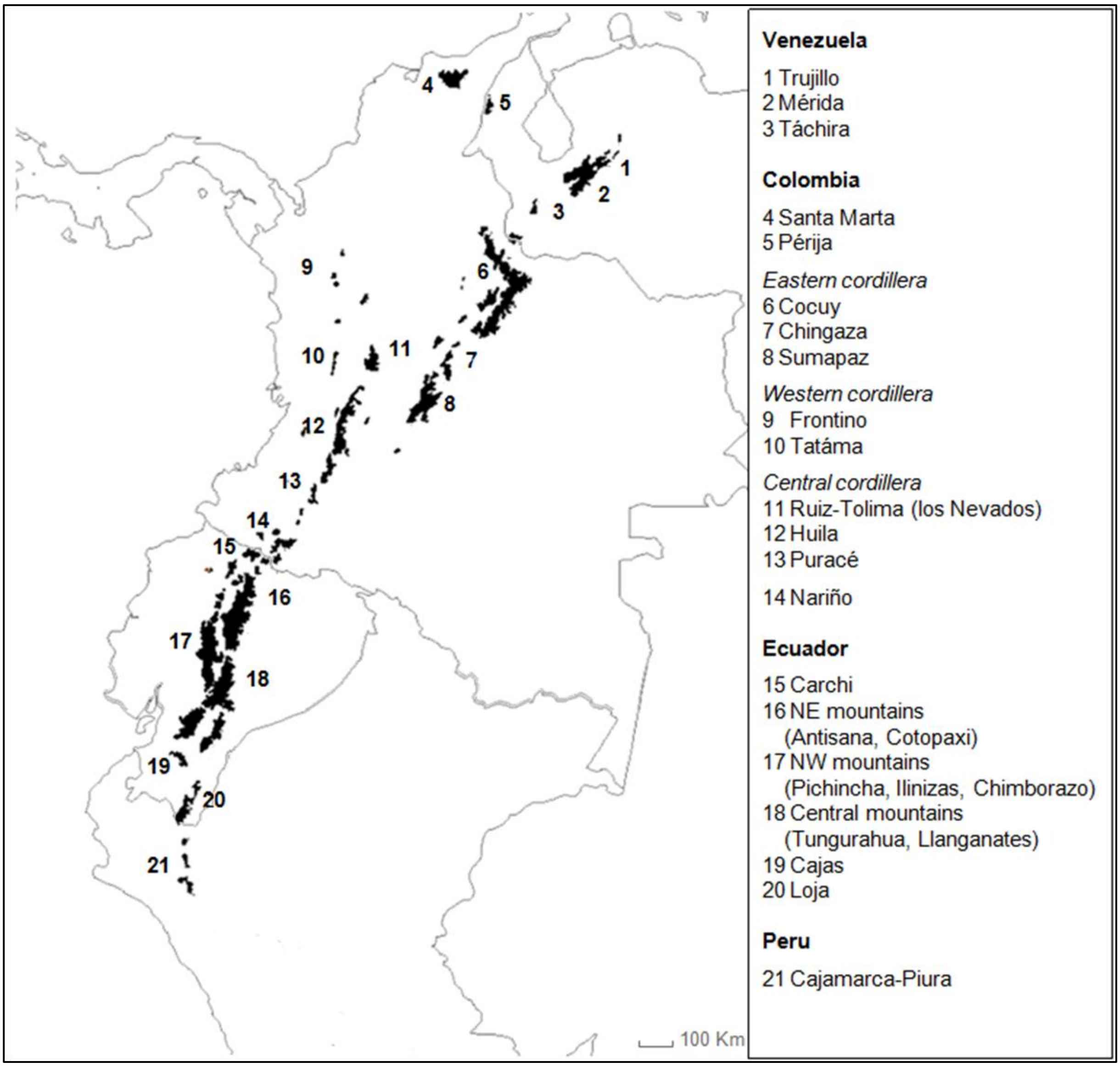
Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273–309.

Young KR, León B (2007) Tree–line changes along the Andes: implications of spatial patterns and dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 362(1478): 263–272.

Supplementary materials

Appendix 1

Distribution of the main páramo areas in the Northern Andes.



Appendix 2

Examples of common growth-forms in the páramo, (a) stem rosette (*Espeletia schultzii* Wedd.), (b) tussock plant (*Calamagrostis intermedia* (Presl) Steud.), (c) tree (young *Polylepis incana* Kunth), (d) erect shrub (*Diplostephium foliosissimum* Blake.), (e) erect herb (*Lamourouxia virgata* Kunth), (f), trailing herb (*Vicia andicola* Kunth), (g) basal rosette (*Puya trianae* Baker), (h) acaulescent rosette (*Viola bangii* Rusby), (i) prostrate shrub (*Baccharis caespitosa* (Lam.) Pers.), (j) cushion and mats (*Azorella pedunculata* (Spreng.) M.&C.), (k) prostrate herb (Geranium *sibbaldioides* Benth.),(l) epiphyte (*Racinaea* tetrantha (Ruiz & Pav.) M. A. Spencer & L. B. Sm.)

Appendix 3

Working plot-table for zonal páramo vegetation in Ecuador.

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30
Elevation (m)	4330	3945	3940	3797	3774	3612	3628	3778	3650	3869	3888	3959	3966	4077	4230	4276	3805	3807	3913	3944	4031	3990	3993	3993	4556	4605	4851	4257	4271	4222
Plot area	25	50	50	50	50	25	25	25	50	25	50	25	25	50	25	25	25	25	16	16	25	16	10	9	16	25	16	9	9	16
Slope (º)	25	10	0	5	5	45	25	5	20	55	30	25	25	10	10	15	70	50	20	30	30	75	10	5	20	40	30	10	0	5
Aspect	N	E	#	W	N	N	S	SW	SE	NE	NW	N	SW	NW	SE	E	S	SE	NW	SE	N	SE	W	N	SW	SW	SW	SE	#	W
Vegetation cover	98	90	100	85	85	100	100	100	98	95	95	90	98	100	100	98	98	70	75	100	65	90	100	98	10	40	25	55	80	5
Aa paleacea																							+							
Acaena elongata																														
Acaena ovalifolia		+																				+								
Achyrocline alata																														
Achyrocline hallii																	1													
Achyrocline satureioides																														
Achyrocline trianae																														
Aciachne pulvinata	1																													
Aetheolaena caldasensis														1	3															
Aetheolaena involucrata																														
Aetheolaena lingulata																														
Aetheolaena otophora																														
Aetheolaena rosana																														
Ageratina azangaroensis																														
Ageratina pichinchensis																														
Ageratina sodiroi																														
Agrostis breviculmis																														
Agrostis foliata								1							+	1														
Agrostis haenkeana																														
Agrostis perennans				1	1																									
Agrostis tolucensis										1												+	2					1		
Aira caryophyllea																			+											
Alnus acuminata																														
Altensteinia virescens																														
Anatherostipa rosea																														
Anthoxanthum odoratum							1	+				+																		
Anthurium sp.																														
Aphanactis jamesoniana																						1		+						
Aphanactis villosa									+																			+		
Arcytophyllum filiforme																														
Arcytophyllum setosum																														
Arcytophyllum vernicosum																														
Arenaria lanuginosa																														
Aristeguietia glutinosa																														
Asplenium oellgaardii																														
Astragalus geminiflorus																										3			2	1
Aulonemia hirtula																														

Plot number	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60
Elevation (m)	3982	3985	4019	4076	4125	4127	4139	3890	4389	4391	4444	4425	4331	4112	4004	4017	3984	3982	3962	3928	3935	3943	3956	3855	3817	3747	3787	3826	3905	3948
Plot area	16	16	16	16	9	25	16	36	25	16	16	25	25	9	25	25	50	25	50	25	16	16	25	25	50	25	25	30	25	25
Slope (º)	20	10	25	10	20	75	10	80	10	40	15	25	60	15	70	35	25	5	75	65	20	2	35	50	80	70	25	70	10	30
Aspect	SW	SW	SW	SE	SW	NE	SE	NW	SW	W	E	E	SE	E	S	SE	S	S	SW	NE	NE	NW	E	E	NE	NE	NE	N	E	NE
Vegetation cover	100	100	100	95	100	98	100	98	25	40	70	75	75	90	100	90	90	100	100	95	98	98	98	100	100	95	100	100	100	95
Aa paleacea																														r
Acaena elongata	1																													
Acaena ovalifolia																														
Achyrocline alata																														
Achyrocline hallii																														
Achyrocline satureioides																											1	+		+
Achyrocline trianae								1																						
Aciachne pulvinata																														
Aetheolaena caldasensis																														
Aetheolaena involucrata																														
Aetheolaena lingulata	+									+		r	+										+							
Aetheolaena otophora																														
Aetheolaena rosana																														
Ageratina azangaroensis								+																						
Ageratina pichinchensis																														
Ageratina sodiroi																														
Agrostis breviculmis							1																							
Agrostis foliata															+	2						3				1				
Agrostis haenkeana																														
Agrostis perennans																														
Agrostis tolucensis													+				+													
Aira caryophyllea														+																
Alnus acuminata																														
Altensteinia virescens																														
Anatherostipa rosea										2	1		3	4																
Anthoxanthum odoratum			+																									+	1	
Anthurium sp.																														
Aphanactis jamesoniana														1			1	3												
Aphanactis villosa																														
Arcytophyllum filiforme															+		+		+				1	1	+					
Arcytophyllum setosum																														
Arcytophyllum vernicosum																+										2				
Arenaria lanuginosa																														
Aristeguietia glutinosa																														
Asplenium oellgaardii																														
Astragalus geminiflorus									2		3	2	2																	
Aulonemia hirtula																														

Plot number	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90
Elevation (m)	3998	4025	3777	3787	3882	3792	3577	3742	3679	4406	4422	4430	4441	4439	4428	4412	3370	3391	3439	3422	3374	4187	4248	4267	4295	4185	4245	4115	3888	3957
Plot area	25	36	65	50	25	35	50	25	64	25	50	36	25	25	9	36	36	25	25	36	64	9	25	25	25	16	25	25	25	9
Slope (º)	40	50	25	25	10	10	55	55	40	20	40	60	5	15	5	40	20	40	30	10	5	5	15	70	55	25	50	35	60	45
Aspect	NW	S	W	S	SW	SE	SE	S	NE	W	SW	SW	NE	NW	NW	NE	W	SW	SW	S	SW	SE	SW	SE	W	NE	E	SE	E	S
Vegetation cover	100	92	100	99	100	100	100	98	97	98	98	100	95	98	100	95	90	90	95	90	95	100	100	97	98	98	98	98	99	100
Aa paleacea																														
Acaena elongata						1																								
Acaena ovalifolia																														
Achyrocline alata								1										+												
Achyrocline hallii																					+									
Achyrocline satureioides	+						+		+								+	+		r										
Achyrocline trianae																														
Aciachne pulvinata																														
Aetheolaena caldasensis																														
Aetheolaena involucrata																											1			
Aetheolaena lingulata																														
Aetheolaena otophora																														
Aetheolaena rosana																				1	1									
Ageratina azangaroensis																														
Ageratina pichinchensis							2		2								1			1	+									
Ageratina sodiroi																														
Agrostis breviculmis																														
Agrostis foliata														+													+			
Agrostis haenkeana																														
Agrostis perennans																	+	+		+										
Agrostis tolucensis																														
Aira caryophyllea																														
Alnus acuminata																														
Altensteinia virescens																		+			2									
Anatherostipa rosea																														
Anthoxanthum odoratum				+	1												+		2											
Anthurium sp.																														
Aphanactis jamesoniana																														
Aphanactis villosa																														
Arcytophyllum filiforme																														
Arcytophyllum setosum																														
Arcytophyllum vernicosum																														
Arenaria lanuginosa								1																						
Aristeguietia glutinosa																														
Asplenium oellgaardii																														
Astragalus geminiflorus																														
Aulonemia hirtula																														

Plot number	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Elevation (m)	3932	3762	3785	3865	3872	3874	3915	3901	3728	3391	3467	3477	3474	3466	3496	3586	3595	3879	3892	3953	3987	4044	3999	2878	2892	3753	3866	3844	3825
Plot area	50	25	25	16	16	36	30	36	25	25	36	25	16	16	36	25	9	25	9	50	9	50	25	50	16	25	9	25	25
Slope (º)	30	65	50	80	15	40	60	55	80	40	70	45	10	35	50	45	40	25	20	70	0	65	50	55	40	75	20	35	40
Aspect	W	E	SE	N	SE	SW	W	NW	SE	NE	S	SE	SE	E	N	E	SE	SW	SE	NE	#	SE	S	NW	NE	NE	W	SW	NE
Vegetation cover	98	90	98	95	95	83	97	98	85	90	98	99	99	92	98	98	97	97	80	97	100	98	96	100	97	90	99	100	100
Aa paleacea																										r	r		
Acaena elongata																													
Acaena ovalifolia																													
Achyrocline alata		1	+	+					2																	+		+	
Achyrocline hallii																													
Achyrocline satureioides																			+	r		2	r						
Achyrocline trianae																													
Aciachne pulvinata																													
Aetheolaena caldasensis																													
Aetheolaena involucrata																													
Aetheolaena lingulata				+																									
Aetheolaena otophora											+																		
Aetheolaena rosana																													
Ageratina azangaroensis																													
Ageratina pichinchensis																													
Ageratina sodiroi								2																		2		1	+
Agrostis breviculmis																			1										
Agrostis foliata																													
Agrostis haenkeana					1																								
Agrostis perennans										2		+	+		+														
Agrostis tolucensis		+				1										1													
Aira caryophyllea																										+			
Alnus acuminata										+																			
Altensteinia virescens																													
Anatherostipa rosea																													
Anthoxanthum odoratum																													
Anthurium sp.																								+					
Aphanactis jamesoniana																													
Aphanactis villosa																													
Arcytophyllum filiforme																													
Arcytophyllum setosum		3	+						2		+			1			+												
Arcytophyllum vernicosum																								1	3				
Arenaria lanuginosa																													
Aristeguietia glutinosa		+					4																					2	
Asplenium oellgaardii		1																											
Astragalus geminiflorus																													
Aulonemia hirtula											3																		

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Axinaea nitida																																																																																																																			|2|				
Azorella aretioides			+					1																							+	+									3																				+										2	2	2	+	2	2							1		2					1																														
Azorella biloba	2																																																								2																																																						+		3													
Azorella corymbosa																																																																																								2																																						
Azorella crenata																																																																													+								+																																																	
Azorella multifida																			1												1		+	+	2	+																								+			+		+																																																																		
Azorella pedunculata										+		1			1	3					+	1		1													2	1						2			+	+																														+		+	3		1	2							2		+		1	+	+														r	3				1				2		
Baccharis alaternoides																																						1																																																																																								
Baccharis arbutifolia											3																																				2																																																																															
Baccharis buxifolia				2													2				+	1																																										1		1																																																	4		2				3		1	1
Baccharis caespitosa																	+					1	+			1		+	+			2	2		1		1		+		2	1	1			+														+	1													2	2								2																												+				2						
Baccharis genistelloides																																																	+				1	+		+				+																		+																				+	+	+								+	r		+														
Baccharis latifolia																																																																					3																																																												
Baccharis macrantha									+																																																																																																																							
Baccharis padifolia																																																																			1																																																																				
Baccharis sp.																																																										2	1				1	+																																																																													
Baccharis tricuneata																																														1	+	1		1	1																																																																																						
Barnadesia spinosa																																																																																					2	2																																																						
Bartsia laticrenata																																																																																																|r|			|r|+|															|+|1|					
Bartsia melampyroides																																																																																																																											1		
Bartsia orthocarpiflora								+																																																																									1	1																																																	1	
Bartsia pedicularioides																																																																																										+																																											
Bartsia stricta																																																						r																																																																																	
Belloa longifolia					+													+																																																																																																													
Belloa piptolepis																													2																																																																																																							
Belloa radians																																																																																																				+																								
Berberis lobbiana																																																																																																		|1|2|1|																					
Berberis multiflora																																																																															1	+																																																														
Berberis paniculata																																																																			+																																																																							
Berberis pectinata																																																																																				2																																																									
Bidens rubifolia																																																																															1	+	r		+																																																										
Bidens triplinervia					+	+	+										+	+			+	1				+		+	+	+								+	1	1			1														+	+	+	r	+						1	+																														r			+																	r									1	+	1	+
Blechnum loxense										4	2	2																																																																																															1		+												1					
Blechnum violaceum																																																																																																								+		+						+														
Bomarea brachysepala																																																																																																																									+					
Bomarea chimboracensis																																																																																																																																
Bomarea glaucescens																																																																																										+																																											
Bomarea linifolia																																																																															1	1		+																																																										
Bomarea multiflora																																																										|1|				|+|				|+|1|																																																																												
Bomarea perglabra																																																																																																	|2|	|+|1|1|																					
Bomarea uncifolia																																																																																																														+													
Bothriochloa barbinodis																																																																																																												1															
Bowlesia lobata																																																																																																					2	1														+							
Brachyotum benthamianum																																																																																																								1	1		+	4										1				
Brachyotum jamesonii																																													1									1	3	+								2			3	2																																																												3	
Brachyotum ledifolium																																																										2	2					3					1	2									3	2		2																																																								
Brachyotum lindenii						3	3																																																																																																																												
Brachyotum rostratum																																																																																																										2																	
Brachypodium mexicanum																																																																																															1		1	+		+	+	1																						
Bromus lanatus												1								+				1				+			2				1	1	+						+				+													+	r																	r	+			r			1																																+						
Bromus pitensis										+													1																																											1																										1	+			+																				1			
Bulbostylis juncoides																																															+					1																																																																													
Caiophora contorta																																																																															+																				+																						
Calamagrostis bogotensis																																														+							1	+	+							+																								+															1																			
Calamagrostis effusa		5	4			3	3	4	5																																																																																																																	
Calamagrostis fibrovaginata	2																																																																								+	+	1	2							2	1							+																					+	r	1				2		
Calamagrostis heterophylla											2	1																																																																																																																			
Calamagrostis intermedia				5	5	2	3	2	2				5		2		5	4	2	5	4	4	2	5	1	1		2	2	1	4	2	5	2	4	5									5	3	3	1		4	3		5	2		3	1		2	2	1		1	3	5	5	2	2									3			2	1			1				4				2	3	4	5	4			2	3		5	5	2	1	4	2								1		1	4	2
Calamagrostis mollis																										+			+										1			2		1																																																																																									
Calamagrostis planifolia																																					+																																																																																																	
Calamagrostis recta																																																															4								2	+	+	3	+		3																								2	2																							
Calamagrostis rigescens																							1																																																																																																														
Calamagrostis rigida																																																																																														2																	5	2	3		3	2						

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Calamagrostis rupestris																																																																																																									r	+												
Calceolaria crenata																																																																		+	1																																																					+	
Calceolaria ericoides																																						2																																																				5					1	+		1	+	1																							
Calceolaria ferruginea																		+			1	1	1			+																	1																																																																															
Calceolaria gossypina										1	+	+																																																																																																													
Calceolaria hyssopifolia																																																																													1															1	2	+		+	1	2	1																					
Calceolaria lamiifolia																																																																																																																	1							
Calceolaria rosmarinifolia																																																																														1			1																																							
Campyloneurum amphostenon									+																																								+						1																																																															
Campyloneurum angustifolium																																																																																																			+																				
Campyloneurum solutum																																																																																																																															
Cardamine bonariensis																																																																		r																																																											
Cardamine jamesonii																																																																																																																															
Carex jamesonii																																															1	+																																																																															
Carex lemanniana																																																																																											1																											
Carex pichinchensis	+	2																					+								2																																		+																																						1				+												
Carex pygmaea																																														1						1							1	1	r																																	r	+	1			+	1			+						
Castilleja fissifolia						+	1	+													+		1																															+														+																							+		+		+			r																	1	1	
Castilleja nubigena																																								+		+	+	+																														+																																														
Castilleja pumila																																					1																																													+			+																																					
Castilleja virgata																																																																														+	r	+																									r																
Cerastium candicans															1																																																																																																															
Cerastium floccosum																					1															+				+			+	+																																									+																																					
Cerastium kunthii																																																																																												r																										
Cerastium mollissimum				+													+						+															+																																								+	+	+													+																						+			+
Cerastium trianae		1							+																																																																																																																				
Cestrum buxifolium																																																																																	2																																					
Chevreulia acuminata																																																																																														r	+																									
Chrysactinium acaule																																						1														1	+																													+														+		1		1						+	2		+													
Chuquiraga jussieui																		1				+				2	2		2	2			2						1		1	r	2	2					4													2	1								1	1	+				2														2	+	+	1																			3			1			3
Chusquea loxensis																																																																																																																			1					
Clethra ovalifolia																																																																																																																			+	+				
Clinopodium brownei																																																																														r																				+																							
Clusia alata																																																																																																																			1					
Columellia oblonga																																																																														+			2																																					
Conyza cardaminifolia																													+																1																																																																												1	r							+		
Coriaria ruscifolia																																																																			2		2																																																							
Cortaderia bifida																																																																																																				+	4			+	1														
Cortaderia nitida			2		2								3	2	1			1	1																																												1	1	2			3	2	3		1		1										+																																							2							
Cortaderia sericantha																																																				1																																																																							
Cotula mexicana																				1														1																										+			1																						+	1						1																												
Cuatrecasasiella isernii																																																																												1																1																					3								
Culcitium canescens																																								1																																																																																					
Culcitium nivale									+																		1															+																																																																																							
Cybianthus marginatus																																																																																																																			1					
Cystopteris fragilis																																																																					+																																															+			
Diplostephium ericoides																																																																																																					1																			
Diplostephium foliosissimum																																																							3																																																																			
Diplostephium glandulosum																																													1	+	1	+	2	2				+																																																																			
Diplostephium hartwegii		1	1																																																																																																							+	+	+	1	1													
Diplostephium rupestre	1	1	3					+							2	4	2																																																																										1													5	+																																						
Disterigma codonanthum	1										1																																																																																																																	
Disterigma empetrifolium										3		1																																	+																																																								2	2		1												
Distichia muscoides	2																																																																											1																																											
Dorobaea pimpinellifolia					+		+				+	1	+																																			1	1					1	r				+																																						+																										
Draba depressa																												+	+													1																																																																															
Draba pycnophylla																																						+						+																																																																																		
Draconanthes aberrans																																																																																																								+															
Echeveria quitensis																																																																																																			+																				
Elaphoglossum engelii						+				+		1																					+																																													+																																				+					
Elaphoglossum isophyllum																																																																																	+																																					
Elaphoglossum mathewsii																						+																				1															+		+	1																																					1		+																								
Elaphoglossum minutum																																																																														+																																									

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Elaphoglossum muscosum																																																																																																																								
Elaphoglossum ovatum													1			1																																																																																																				
Elaphoglossum rimbachii																																																																																																																								
Elymus cordilleranus																					1											+							+																					1										+									+			r											+	r																											
Ephedra americana																																																																																																													2										
Ephedra rupestris																					+																					1			+																																																																										
Epidendrum pseudosarcoglottis																																																																																																								1															
Epilobium denticulatum																																																																																									r		1																												
Equisetum bogotense										1	2																																																																+			+								+		r																			1			r						
Erigeron ecuadoriensis	1								1													1	+																	+		1																													+																														r	+																									
Eriocaulon microcephalum																																																																																																																	1							
Eriosorus flexuosus																																																																																																																				+					
Eriosorus rufescens																																																																																																																					1				
Eryngium humile										1		1						+	2	1	+			2							+	+			2	+	1							+									1	+			+	+		+	1	1							+							1			1	+														1	+																							
Escallonia myrtilloides																																																									1	3								+																																																				
Espeletia pycnophylla						1	2	3	2																																																																																																												
Eudema nubigena	+																														1																																																																																								
Festuca asplundii																																																																					3	1	2	+			1									1																																				
Festuca chimborazensis																																																																																		+	+		1												+																1								
Festuca glumosa																																					2																																																																																	
Festuca imbaburensis	1		+																																																																																																																			
Festuca parciflora																																															4	2	3																																																																				
Festuca procera																			3																																																																																																	3		1	3
Festuca sodiroana										2	1																																																																																																										
Festuca ulochaeta																																						4																				3	3	4	3	3		3	1	2													2	3	5	1	1					2	2		1																																	
Festuca vaginalis																																																																																																																			1						
Galium aparine																																																										+				+					+		+																																																		
Galium canescens																																																															+																														1																											
Galium hypocarpium						+	+																						+										+																+											1							+												+	+	r	+	1																+					+				+													
Galium obovatum																																																																		+																																																				
Galium pseudotriflorum					+																																																																												+	+								+		1							+												+		r		+							
Gamochaeta americana																																																																																							+						+													r															
Gamochaeta pennsylvanica																																																											+																																																											
Gamochaeta purpurea				+																																																																											1																r										+													+	+		
Gaultheria amoena																																																																																												+																										
Gaultheria erecta																																																																																																					1			+																
Gaultheria glomerata							+																																																																					1			+																																					+				
Gaultheria vaccinioides																																																																																																											2												
Gentiana sedifolia	1	+												+						+			+						+		+		+																		+	+	+																								+	+	1							+			+											r				+											+							
Gentianella cerastioides																		1			1			1																																						2	1																						2																												+	1		+		1				2	+	
Gentianella cernua																																										1	1																														1														1	1	+																																
Gentianella foliosa																																																																								+																																														
Gentianella hirculus																																														1					1	+		+																																																																	
Gentianella hyssopifolia																																																					1																																																																	
Gentianella limoselloides	+			+	+	r																																																																																																																	
Gentianella rapunculoides																																																																																												+		1	1		2	1																						
Gentianella rupicola																																																																																																1																							
Geranium campii																																																																																																				+		1	1	1	1		2														
Geranium diffusum			1																																			1																																																																																
Geranium ecuadoriense																												+										2		2	2																																																																												
Geranium humboldtii																																																																							1	+	+	1	2																																												
Geranium killipii																																																																				+																																																		
Geranium maniculatum																																																																																			+																																			
Geranium multipartitum																												3	2	1		+	2		+		+												+	1													+																															r																							1	+					+						
Geranium reptans				1	1					1	2	+																+																	2											1												1	2	2	1											+															2																				+	+							
Geranium sibbaldioides	+							1	2						2																																	1	1	+	+	1	2	1	2	2	2		+																+	2	1	1	2		2		r		r				1						+				+																			
Geranium stramineum					+			1							1	1	1																													1																																				+											+	+		2																					1									
Gnaphalium antennarioides																																																																													r																																									
Gnaphalium chimborazense																			+	+	+																																																																																														1		
Gnaphalium dombeyanum					2																																														+																																																																			
Gnaphalium dysodes						+	+																																																																				+																																									
Gunnera magellanica		2	1	+						4	4	4	1	2	+	2																	+		+																																																										1	2	3			2																											
Gynoxys buxifolia																																																																																																												+		1		2			+				

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Gynoxys cuicochensis																																																																																			1																																					
Gynoxys ferreyrae																																																	+				r		2	1																																																															
Gynoxys hallii										2				3																																																																			2	4			1	2	3																							
Gynoxys miniphylla																																													2		1		3																																														2																									
Gynoxys parvifolia						1		+	1																																																																																																				
Gynoxys sancti-antonii																																																																																																							1	1													
Gynoxys sodiroi																																						2																			2								1																																																					
Halenia brevicornis																																																																													+	+	+	+																																						
Halenia kalbreyeri																															2																										+	+	2	1	1	1	1				r																																																			+	
Halenia pulchella	2												+		+																																																																																																
Halenia serpyllifolia																																																				1				+																																																															
Halenia taruga-gasso																																													+																																																							2		+				1													
Halenia weddelliana																					1																2																																				2	+								+										+	+	1																							
Hedyosmum purpurascens																																																																																																																		2					
Hedyosmum racemosum																																																																																																					+	+																
Hesperomeles ferruginea																																																																		+			1																																1	+			3														
Hesperomeles obtusifolia											4	2																																																						1	1										1	1		2	1										+								r																+					
Hieracium frigidum						+	+																																						1	1	+	+	r												1	+		+						+																																																		
Hieracium peruanum																																																																																																				+		+		2	+	+	+														
Hieracium sprucei																																																																															+																																									
Holcus lanatus																																																																			2										1																																											
Huperzia brevifolia																																																																																																								+		+														
Huperzia columnaris																																														+																																																																								
Huperzia crassa	2		+										+	1	+																	2	1			1													+	+	+												3							1		2	1										+			+																									2								
Huperzia eversa									+																																																																																																											
Huperzia lindenii																						+																																																																																																
Hydrocotyle alchemilloides																																																																																																						1																
Hydrocotyle bonplandii																			+	+																+														+						3				1		1			+	2	2	+		+										+		+	1	+								3		2							+				+	+		+	+													2	1
Hypericum aciculare																																																		+	+																																																						2		+	2													
Hypericum decandrum																																																																																																				1		+																
Hypericum lancioides			+			1	2	+	1																																																																																													1			1					
Hypericum laricifolium					3																											2	+																											4	3	+	2			4			3	4	2	1									1	+		+	+																																					
Hypericum loxense				1																																																																																																														
Hypericum quitense																																																				1	+	+		+																																																													
Hypericum sprucei																																																																																								+								1																							
Hypochaeris radicata																																																																													+	+	+	+																																						
Hypochaeris sessiliflora						+		1		1		2					+	+	2	1		+	1	+	1	1			2	1	+	r			1	+	2		1	1	+	1	2	1		2										1				+	1										+	1	2	3	2		+	+	+	r		2	1	+	2	2	3			+		+		+	1				+										+				+						+
Hypochaeris sonchoides																																												1														1																																																													
Jamesonia goudotii																																														1																																																																								
Jamesonia pulchra																																																																																																				1																		
Jamesonia rotundifolia																																																																																																						1	r		+														
Jungia rugosa																																																																													+			1																																						
Lachemilla andina																																															+		1				1		+		1	+																				+	2												1						3	2	+																1				+		+	
Lachemilla angustata																																																				+		+																																																															
Lachemilla fulvescens																					+																																																																																																	
Lachemilla galioides												1																																																									1	1																																																
Lachemilla hirta					1																																	2																					+					1		1	2	1	+																					3			2	2																									
Lachemilla hispidula																																																																																				+	1	1	1	+																														
Lachemilla jamesonii		+		+				+	1				+				1		1																				+																+						2	2	+				+											2			1														+																									
Lachemilla mandoniana			+																																																									+				+																																															2								
Lachemilla nivalis	1		1					+						+																																																																																																					
Lachemilla orbiculata		+			1			+							+		3			2	2			4	2							2	+	1	1	1			+									1	2									+		2			1	1	2	3	1	+	1	+	+	2							2			3	+		+	1				r		+		+			+															2		+	+	+	3				4	+	
Lachemilla pectinata													2																																3																																																																										
Lachemilla perryana																																																																						2						2								2																																			
Lachemilla sprucei										+																																																																																																								
Lachemilla uniflora																																																													1																																							+	+	+	r																
Lachemilla vulcanica		1	1		2																	1	1																																									1																											+		r	+			+			2	+											1						2	1						
Lamourouxia virgata																																																																																												2							+																			+		r
Lasiocephalus ovatus	1									+																1														+		1	1																																+	1	2	2		1											2	1	+																															
Lepidium abrotanifolium																																												+			+	+																																																																						
Lobelia tenera																																																																														+																																								
Lophosoria quadripinnata																																																							1																																																															
Loricaria ilinissae															2	5																																																																																																								

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Loricaria thuyoides																																	2	4					1	2						1						2									3									+	4	4	2	3	1	2							+		3		1	1																1											+				
Lucilia kunthiana				+																																								2																																							1																																				
Lupinus microphyllus																								1				1	1						+		1		r	1		+								+	+	+																																																																			
Lupinus purdieanus																																																											+																																			r	+	+																							
Lupinus ramosissimus					+																																																																																																																		
Lupinus revolutus								+																																												+	2																																																					+													
Luzula gigantea											1	+																																																																																													+														
Luzula racemosa	1																				+	+		+																		+	1																																							r	1		r		r								r	+												r											
Luzula vulcanica			1																																																																																																																				
Lycopodium clavatum					2	1	2	+								+																	+																					1		+	2			1																																								1	1													1					
Lycopodium jussiaei																																																																																																					+														+				
Lycopodium magellanicum																																													+				+				1																																											+											1												
Lycopodium vestitum																																																																																																																			1				
Lysipomia montioides																																																																								2	1	1	1																																												
Lysipomia vitreola																																														3					2	+																																																																			
Macleania rupestris																																																																																																									1														
Margyricarpus pinnatus																																																																			1	+	+																							1							+																				
Maxillaria floribunda																																																																																																																		1					
Melpomene flabelliformis																+																																																																																																r					
Melpomene moniliformis											2																																																																			r																		1	+		+								+												
Melpomene peruviana				r																																																																																																																			
Miconia chionophila																																																																																																																							
Miconia latifolia																																																																																																																		1					
Miconia ligustrina																																																																																																																			+				
Miconia obscura																																																																																																																		1					
Miconia pernettifolia																																																																																																				+					+														
Miconia salicifolia																																															2		2						1																																													1																			
Mikania brachyphylla																																																																																																																		+					
Monnina arbuscula																																																																																																					+			+															
Monnina cestrifolia																																																																																	2																																						
Monnina crassifolia					1		1																															2																			2	+					1																										2		3																			1		+	r						
Monnina ligustrina																																																																																																	2	2																					
Monnina phillyreoides																																																																	+	1	1	1	2								1			+																																							1
Monticalia andicola									+			1	+	1		+																																																						3						3																														+													
Monticalia angustifolia																	+																																																																																			+				+							
Monticalia arbutifolia		+																																																					1																																	+			4					1		1														1	+						
Monticalia befarioides																																																																																				+																																			
Monticalia peruviana														2								1									2	2	2		+																											2								+	3															+	3									1												2											
Monticalia vaccinioides						+																																							+	+				1	3																																																																				
Morella parvifolia																																																									2																																																														
Morella pubescens																																																																													+	2		2	+																																						
Muehlenbeckia tamnifolia																																																																													+																																										
Muehlenbeckia volcanica																																						+																																																																																	
Myrsine dependens																																																																																																					1		1			1															
Myrteola phylicoides																																																																																																																		2					
Nassella brachyphylla																																																																																																													1			+							
Nassella inconspicua																	1																																						+																																																+																
Nertera granadensis					+	1	1	+						+	1																																																		2		2												r		r		1		1																														1			1					
Neurolepis aristata																																																																																																										3		2												
Neurolepis villosa																																																		2																																																																					
Niphogeton dissecta														2		1		1																																																							+		+		1		1		+		+																1												+					+							+		+		+	
Nototriche jamesonii																										1		1														1																																																																													
Oenothera multicaulis																																						1																																							+		1			+												r			+		+																								
Ophioglossum crotalophoroides								+																																																																																																															
Oreobolus goeppingeri							+			1																																					1						2			1																																														2				+		1				+												
Oreocallis grandiflora																																																																																																																		1		1				
Oreomyrrhis andicola	+																						1					+		1								+							1															r					+													r					1		+		1		+		+		+			1						+																							
Oreopanax ecuadorensis																																																																																	1																																						
Oritrophium crocifolium																																														2					1		+																																																			+												2				
Oritrophium peruvianum	1																					+		1																																																			1												+		+		r																															
Orthrosanthus chimboracensis																																																																													1			2		1		1																					r		+		1		1		+		+												
Oxalis corniculata																																																																	2		2																																																					
Oxalis eriolepis																																																																																																										+													

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Oxalis filiformis																																																																																																																	+	+
Oxalis lotoides																																																																																																2	2																					
Oxalis medicaginea			1	+																								+																																																														r																											
Oxalis rufescens																																											1																																																																											
Paranephelius uniflorus	+																																																																																																																						
Paspalum bonplandianum				3	1	2	3	2									+					+	2													1																	+						2		1	+							1	+	+	+	1									2	1	2	2																	2	2				1		1	2	+		1													
Pedicularis incurva																																													1						+																																																			1																
Pernettya prostrata		1	+		1	+	2	+	+				+	1	1	+					+			1								+	+		+	+		+												+	+	+	+		+	1	2	1	+	1	2	1	1			2		+									1	1		1					1	+								2	2	1	r	+		+	+			1	3			1		r		1	1						1
Phylloscirpus acaulis																																																																																																														2								
Pinguicula calyptrata																																																																																																				2				+															
Plagiocheilus peduncularis				+											+					+																																																		+														2																																				
Plantago australis																																																																													1			1	+									+	+																												
Plantago lanceolata																																																																																																																							r
Plantago linearis																												+																																																															+			r	1																				1		
Plantago rigida	2															1																5	3	2		+	1																																			1		+	1	3	4	+						1	3	1	2	3	1	r		5																						+								
Plantago sericea																												1	1	+																																																																																									
Plantago tubulosa																																											+																																																																											
Plutarchia ecuadorensis																																																																																																																			2					
Poa aequatoriensis	+																														+																																																																																							
Poa cucullata																+																																																							+	+																																																
Poa páramoensis												2																																																																																																											
Poa pauciflora																						1						+									+																																																																+		1	1		+					+	r								
Poa pratensis																							1																																																																																															
Poa subspicata																																																																										+		+																																														
Podocarpus oleifolius																																																																																																																			2					
Polylepis incana																																																																																								1																																
Polylepis lanuginosa																																																																																	1																																							
Polylepis reticulata																															r																		r					2																																																																
Polypodium quitense																																																	+																																																																					
Polystichum orbiculatum						1																1																																	1																						1		r	1							1		1					+	+		+	1	1												+			+								
Polystichum pycnolepis																																																																														+																																								
Puya clava.herculis								+	3				2																																	2			+	2	2		+	+																																																																	
Puya eryngioides																																																																																																																			1				
Puya pygmaea																																																																																																					2				2																
Puya vestita																																																																				3																																																		
Ranunculus geranioides					+	1							+																		+																													r																																																									
Ranunculus peruvianus				+		+	+	1																																																																																																													
Ranunculus praemorsus										2	2						+																				1																																2										r		+															+	r	+																+								
Rhynchospora hieronymii																																																																																																																			1				
Rhynchospora macrochaeta					2																																																																								1		+	2	2																																							
Rhynchospora ruiziana						3	3	1	+																																					1	2			1	1	+		+	1																																																r		2	2		+	r	1														
Ribes andicola														+																																																						2																																								1		+							
Ribes hirtum															1	+																																														1																																																+										
Ribes lehmannii																																																																																																																							
Rubus coriaceus																																																																																																																							
Rubus glabratus																																																																														1																																								
Rumex acetosella				+																			1																																																						r																+																									+	+
Salpichroa tristis																																																															+						2																																																		
Salvia corrugata																																																																													+			1	4										1							1																					
Satureja nubigena		1						+	1														1		1				+							1																1																																														+																				+							
Senecio chionogeton				+	+																																																																																																			+									2							
Senecio formosus		2		1					+																																																																																																															
Senecio sp.																																																													+				r																																																						
Senecio tephrosioides													+	1		+																																																																																																						
Sibthorpia repens									+				2								1																																	+				+																																				2	+						+	+																	+							
Silene thysanodes																																																																																																																				r		r	+
Sisyrinchium jamesonii													+																																																																					r																																					
Sisyrinchium tinctorium																																													+			+																																																										r			+																
Sisyrinchium trinerve							+																																																																																																															
Sphyrospermum cordifolium																																																																																																																			+					
Stachys elliptica																				+								1																																				+																							r		1																												
Stellaria recurvata													1																																													+				2																																																1		1	+					
Stellaria serpyllifolia				+	+																													+																														+	1		1		1								1			+									+		1		2					+	r																					

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97	I98	I99	I100	I101	I102	I103	I104	I105	I106	I107	I108	I109	I110	I111	I112	I113	I114	I115	I116	I117	I118	I119
Taraxacum officinale																			+	+			+																																																																					r																										r	
Trifolium repens																							+																																																									r										1									r																				
Trisetum irazuense																																																																														r																																									
Uncinia hamata		+	2																																																																						1																																														
Uncinia macrolepis																		+				+										1																																																		+	1																																				
Uncinia paludosa								+																																																																																																															
Uncinia phleoides																																																																																									2					+																									
Urtica echinata																																																																																																																											
Urtica leptophylla																																																																																																																+							
Vaccinium floribundum					1												1	3				1																							1	1			1					1			2	2					1				1											2																																					+				
Valeriana adscendens	+		1											1	1																																																																																																						
Valeriana alypifolia																										+																																																																																	
Valeriana aretioides	+																																																																																			1	+																																				
Valeriana cernua																																																																																																																											
Valeriana clematitis																																																																																																					+																		
Valeriana hirtella																																																																																																					+																		
Valeriana microphylla			3		2			+	1				1	2	1	1	2	1			2	2											+	2		1	+	2				1	2		1		1		1	2	1		1	+		1	2	1	2	1	+	2		2		2	1	2				1						1			+						1	2								1				1	+	+		+	+	+		2	3	2		2	1					+	
Valeriana pilosa																																																																																									3																																
Valeriana rigida																		1	2		1											+			1																			1		2				1	+																																		+	+																							
Valeriana tomentosa																																																																																	1																																						
Vicia andicola					+													r																																																																											2	r																									
Viola bangii																												1											+	+	1	1																																																																													
Viola dombeyana																																																																					+																																																		
Viola pygmaea																																														+																																																																									
Vulpia australis																			+																																																																																																				
Weinmannia elliptica																																																																																																								+										1					
Weinmannia reticulata																																																																																																																		1					
Werneria nubigena														1							2	1									2	1	1	1	2	+	2		2	+	2	2		1							3		1	2		+				+	+	2																				3																					2								+		2						
Werneria pumila																											+																																																																1												
Werneria pygmaea																				2								1	3																															+																																																			1								
Xenophyllum crassum			4					+																																																																																																																	
Xenophyllum humile	2														2																																																							1	1	2	1	1	2	1							2	+	+	2	+																																
Xyris subulata																																																																																																															4				1				

Locality:

I1 Páramo de Papallacta, Pichincha; I2 Páramo de Papallacta, Pichincha; I3 Páramo de Papallacta, Pichincha; I4 Laguna de Mojanda, Imbabura; I5 Laguna de Mojanda, Imbabura; I6 Páramo El Angel, Carchi; I7 Páramo El Angel, Carchi; I8 Páramo El Angel, Carchi; I9 Páramo El Angel, Carchi; I10 ladera Norte del volcan Tungurahua, Tungurahua; I11 ladera Norte del volcan Tungurahua, Tungurahua; I12 ladera Norte del volcan Tungurahua, Tungurahua; I13 Páramo de Papallacta, Pichincha; I14 Páramo de Papallacta, Pichincha; I15 Páramo de Papallacta, Pichincha; I6 Páramo de Papallacta, Pichincha; I17 Páramo, alrededores de Salinas, Bolívar; I18 Páramo, alrededores de Salinas, Bolívar; I19 Páramo, alrededores de Salinas, Bolívar; I20 Páramo, alrededores de Salinas, Bolívar; I21 Páramo, alrededores de Salinas, Bolívar; I22 Páramo, alrededores de Salinas, Bolívar; I23 Páramo, alrededores de Salinas, Bolívar; I24 carretera Ambato-El Arenal, Tungurahua; I25 ladera Norte del Volcan Chimborazo, Chimborazo; I26 ladera Norte del Volcan Chimborazo, Chimborazo; I27 ladera Norte del Volcan Chimborazo, Chimborazo; I28 El Arenal, Bolívar; I29 El Arenal, Bolívar; I30 El Arenal, Bolívar; I31 ladera Este del Pichincha, Pichincha; I32 ladera Este del Pichincha, Pichincha; I33 ladera Este del Pichincha, Pichincha; I34 ladera Este del Pichincha, Pichincha; I35 ladera Este del Pichincha, Pichincha; I36 ladera Este del Pichincha, Pichincha; I37 páramo, carretera San Juan-El Arenal, Chimborazo; I38 páramo, carretera San Juan-El Arenal, Chimborazo; I39 ladera SW del Chimborazo, Chimborazo; I40 ladera SW del Chimborazo, Chimborazo; I41 ladera SW del Chimborazo, Chimborazo; I42 ladera SW del Chimborazo, Chimborazo; I43 ladera SW del Chimborazo, Chimborazo; I44 ladera SW del Chimborazo, Chimborazo; I45 Parque Nacional Cajas, Azuay; I46 Parque Nacional Cajas, Azuay; I47 Parque Nacional Cajas, Azuay; I48 Parque Nacional Cajas, Azuay; I49 Parque Nacional Cajas, Azuay; I50 Parque Nacional Cajas, Azuay; I51 Parque Nacional Cajas, Azuay; I52 Parque Nacional Cajas, Azuay; I53 Parque Nacional Cajas, Azuay; I54 Parque Nacional Cajas, Azuay; I55 Parque Nacional Cajas, Azuay; I56 Parque Nacional Cajas, Azuay; I57 ladera S del Cerro Illiniza Sur, Cotopaxi; I58 ladera S del Cerro Illiniza Sur, Cotopaxi; I59 ladera S del Cerro Illiniza Sur, Cotopaxi; I60 ladera S del Cerro Illiniza Sur, Cotopaxi; I61 ladera S del Cerro Illiniza Sur, Cotopaxi; I62 ladera S del Cerro Illiniza Sur, Cotopaxi; I63 ladera S del Cerro Illiniza Sur, Cotopaxi; I64 ladera SE del Corazón, Pichincha; I65 ladera SE del Corazón, Pichincha; I66 ladera SE del Corazón, Pichincha; I67 ladera NE del Corazón, Pichincha; I68 ladera NE del Corazón, Pichincha; I69 ladera NE del Corazón, Pichincha; I70 ladera NW del Cerro Carihuairhazo, Tungurahua; I71 ladera NW del Cerro Carihuairhazo, Tungurahua; I72 ladera NW del Cerro Carihuairhazo, Tungurahua; I73 ladera NW del Cerro Carihuairhazo, Tungurahua; I74 ladera NW del Cerro Carihuairhazo, Tungurahua; I75 ladera NW del Cerro Carihuairhazo, Tungurahua; I76 ladera NW del Cerro Carihuairhazo, Tungurahua; I77 Páramo cerca de la comunidad Yerba Buena, Chimborazo; I78 Páramo cerca de la comunidad Yerba Buena, Chimborazo; I79 Páramo cerca de la comunidad Yerba Buena, Chimborazo; I80 Páramo cerca de la comunidad Yerba Buena, Chimborazo; I81 Páramo cerca de la comunidad Yerba Buena, Chimborazo; I82 Páramo en la via hacía de la comunidad Ambrosio Lasso, Chimborazo; I83 Páramo en la via hacía de la comunidad Ambrosio Lasso, Chimborazo; I84 Páramo en la via hacía de la comunidad Ambrosio Lasso, Chimborazo; I85 Páramo en la via hacía de la comunidad Ambrosio Lasso, Chimborazo; I86 Cerro Igualita, Tungurahua; I87 Cerro Igualita, Tungurahua; I88 Cerro Igualita, Tungurahua; I89 via San Juan-Vinchoa, Chimborazo; I90 Carretera San Martin-San Miguel, Chimborazo; I91 Carretera San Martin-San Miguel, Chimborazo; I92 Páramo cerca de la parroquia Achupallas, Chimborazo; I93 Páramo cerca de la parroquia Achupallas, Chimborazo; I94 Páramo cerca de la parroquia Achupallas, Chimborazo; I95 Páramo cerca de la parroquia Achupallas, Chimborazo; I96 Páramo cerca de la parroquia Achupallas, Chimborazo; I97 Páramo cerca de la parroquia Achupallas, Chimborazo; I98 Páramo cerca de la parroquia Achupallas, Chimborazo; I99 Páramo cerca de la parroquia Achupallas, Chimborazo; I100 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I101 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I102 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I103 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I104 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I105 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I106 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I107 Páramo, sendero de cresta desde carretera Loja-Saraguro, Loja; I108 borde Norte del lago Limpiopungo, Cerro Rumiñahui, Pichincha; I109 sendero ladera SE del Cerro Rumiñahui, Pichincha; I110 sendero ladera SE del Cerro Rumiñahui, Pichincha; I111 sendero ladera SE del Cerro Rumiñahui, Pichincha; I112 sendero ladera SE del Cerro Rumiñahui, Pichincha; I113 sendero ladera SE del Cerro Rumiñahui, Pichincha; I114 Parque Podocarpus, carretera Loja-Zamora, Loja; I115 Parque Podocarpus, carretera Loja-Zamora, Loja; I116 Laguna Quilotoa, Cotopaxi; I117 Laguna Quilotoa, Cotopaxi; I118 Laguna Quilotoa, Cotopaxi; I119 Laguna Quilotoa, Cotopaxi.

Appendix 3(2)

Working plot-table for zonal páramo vegetation in Venezuela.

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Elevation (m)	3323	3374	3396	3412	3862	3871	4304	4316	4328	4330	4247	4285	4250	3125	3167	3231	3277	3330	3296	3220	3225	3233	3275	3300	3329	3273	3227	3257	3296	3312	3335	2830	2867	2880	2903	2800	3850	3897	3966	3987	3880	3890	3893	3517	3450	3473	3446	3462	3491	3466	3496	3500	3762	3775	3766	3692	3622	3443	3378	3383	3394	3419	3247	3441	3446	3448	3332	2819	2845	2851	2883	2866	2838	2817	3276	3310	3295	3322	3369	3385	3436	3458	3467	3450	2948	3058	3065	3120	3113	3099	3095	3076	3127	3129	3139	3041	2945
Plot area	25	25	25	25	25	25	25	25	16	25	25	25	25	16	25	16	16	25	16	25	25	16	25	16	25	25	16	16	25	16	25	50	25	25	20	50	16	25	25	36	25	25	25	25	50	25	36	25	25	50	25	16	16	12	25	64	9	16	25	10	36	16	25	25	20	9	25	25	25	25	16	25	16	25	64	36	16	36	16	16	64	25	16	25	25	25	16	25	50	25	16	25	25	16	36	64	16
Slope (º)	75	70	65	60	25	35	50	15	45	55	20	60	50	20	10	15	80	65	50	70	65	35	30	55	15	55	20	35	60	10	40	30	20	5	75	50	35	50	60	65	45	50	55	20	45	45	65	30	80	40	10	75	5	0	20	25	15	10	25	15	15	10	10	15	0	0	30	40	70	55	60	60	50	75	55	40	80	50	20	35	30	50	25	0	10	45	30	10	0	25	35	25	40	15	30	35	30
Aspect	SW	W	SW	SW	N	NE	SW	SW	E	SW	NE	E	NE	SW	SW	W	E	N	W	S	W	SW	W	S	NW	N	S	SSW	NW	S	W	NNE	N	N	SW	SW	NE	E	NE	E	NW	W	SW	SE	N	NE	NE	NW	SSW	SW	SE	E	E	#	S	SE	S	N	NW	SSE	SE	SE	E	SW	#	#	SSE	NW	NW	N	W	NW	NW	S	SW	W	SSW	SW	SW	W	SW	NW	W	#	S	SE	SSE	E	#	S	SSE	NW	W	NW	SSE	E	NE
Vegetation cover	90	80	80	75	95	80	35	30	65	65	80	70	35	80	85	80	60	95	60	100	100	98	90	95	95	98	65	65	98	75	95	95	90	85	100	75	65	60	45	60	65	80	85	100	98	90	95	70	65	98	99	99	96	92	100	95	100	50	97	100	100	70	100	85	96	100	100	100	98	100	99	100	100	100	98	92	68	97	97	92	98	92	87	92	100	100	97	100	100	100	98	100	99	99	100	100	98
Aa paleacea																																																																													r																			
Acaena cylindristachya	2	1		2	2	2					+	+		+	1	1			2	+	r	+	1	1	1			1		2	+									1	1		1				1					1	+	1	1			+			2	+	1			+																	1									1	+		
Acaena elongata					+	2									1											1	+		+							1	+					2	2	1	+		1							2	+																			3		1			1			r												
Acaulimalva purdiaei						1			+	+	1	+																																					+		1																																											
Achyrocline gaudens																																																																																																1
Achyrocline lehmannii																			1															1		1	1																																																																	+
Achyrocline ramosissima		1																																																									+																			1						+		+														
Achyrocline satureioides	+																+															1				1																																			2								1																							
Aciachne acicularis					2	2				+	2	1																																											2		3	3	+		+						+	r	1																																					
Aegopogon cenchroides	+			+										4			+										2	1																																																			+		+																	
Ageratina aristeguietii																																																																											1	+																					
Ageratina articulata		2																																															2	1																																																
Ageratina gracilis																				2	2	1																																																															+												
Ageratina jahnii																																																																																															1				1
Ageratina theifolia																					1																																															1							2					1	2								3							
Ageratina tinifolia																											1				2																																																																		
Agrostis breviculmis											+																																																																																				
Agrostis ghiesbreghtii																																																																																															+				2
Agrostis mertensii																																																							2			1				2	+																																				
Agrostis perennans																																																								2											2	+																												
Agrostis subrepens																																																																									4	+																						
Agrostis tolucensis		1		+		1	2	1			1	+	1																										1	+	1															2											1	2																																
Agrostis trichodes																									1		+	1																									3	+	2	1	+		1				1					+																														
Alnus acuminata																																+			+																																																														+	
Anthoxanthum odoratum																																																																																												1					
Anthoxanthum redolens																																																													1																		+																			
Aragoa lucidula																																													3	1		2		2																																														
Arcytophyllum muticum																																																													+																																			
Arcytophyllum nitidum		+																		3	3	2	1	1							2	1		3			2																							1						4																						2	1			2	1					
Arenaria lanuginosa																											+																																																																					
Arenaria musciformis	+						+														+																													+	+																																											
Arenaria venezuelana		+		2							2	1	+																1									+		+	+	1	+	1	1												+			+			+			+										2	1																								
Asplenium polyphyllum																																													2											+																				+																					
Asplenium serra																																																																										+																						

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Athyrium filix-femina																																												+																								+																													
Azorella julianii					+						2										r		+																			2				1							+				+								+																																
Baccharis latifolia																															2																												+			+																							+												
Baccharis prunifolia	1	1	2	2		1					1			1		2	1												2					1				1			1	2	1	4	2	1	2		1			1											1	+			3																														
Baccharis tricuneata																									1																																			+					+																																+
Bartsia glandulifera	1	+	+																																																																									+																					
Bartsia laniflora												+																																																																												+									
Bartsia pedicularioides																																																+						+		1																																									
Bartsia santolinifolia																																																						+																																											
Bejaria aestuans																																1	+		1																																																														
Belloa longifolia									+		+																																								+																																														
Belloa piptolepis							+				+		+																																																																																				
Belloa radians																																																			1		+	r																																												
Berberis discolor																												1	+																																														1					+	1																
Berberis prolifica																																																								+																																									
Bidens triplinervia		2	1		2					+										1	+			1	+													+	1	2	1	2	1			+					+	+				1	+		+		+					1															1																
Blechnum auratum																																																																																					1	2	2		1	2	2						
Blechnum loxense																																	1	1																										1	+																																				
Bomarea pauciflora																																																																																					1	+			+		r						
Bomarea setacea																																																																				2																													
Brachypodium mexicanum	3	4	2																																			1		2	1	1	1			1	2		1	+																									1	2	+		2	+	2																
Bromus catharticus																																																				+																												+																	
Bromus lanatus																																																																			+																														
Bromus pitensis																																															+																																																		
Bulbostylis capillaris														2	2		+	1																		+																																																													
Calamagrostis bogotensis																2		3		1									1		1	2	1			2																							+	4	1		2																													+		2		+	
Calamagrostis chaseae	1																																																																																																
Calamagrostis coarctata									+																																																																																								
Calamagrostis effusa																			1	1			2	1	2	2						2													1	4			1										2	+	+																											2		2	+						5
Calamagrostis heterophylla											+	2	1																																																																																				
Calamagrostis meridensis																																													1			2																																																	
Calamagrostis pittieri	+				1																													2			1	+			1	1	1					2																																												+		2		+	1
Calamagrostis planifolia		2	2	2																																										2					+		2		+	1	+	1	+			1	+	1																	+	1																
Calceolaria microbefaria																																															2																													+							1														
Calceolaria nevadensis																																																																														+																			
Calceolaria perfoliata																																																																											1						+																
Campyloneurum amphostenon																															1																																												2			2	+	2																	
Campyloneurum angustifolium																																																																						+	+																										
Carex amicta												+		1	2											2		1		1																							1				2		1		+	1	+	+	+																													1			
Carex bonplandii																																																			2	2			1											2		1					2	+																1							
Carex jamesonii																																																																																							2										
Carex larensis																																2	2	2		1																																																													
Carex phalaroides																											2																																																																						
Castilleja breviflora							+	2																																																																																									
Castilleja fissifolia	+	+	2						2	2		2	1																			+				+		+	1	2	1		1										r	+																					+	+		r		r	+	+	+										1				
Castilleja meridensis																																1			2																																																														
Castilleja steyermarkii																				+	1		+	+	+																																																																								
Castilleja trujillensis																																																								1																																									
Cerastium cephalanthum										1		+	2																																																																																				
Cestrum buxifolium	2			+										2	+												1	1		1	+																		+							2											1				1									1															+	+	
Chaetolepis lindeniana															2	2		2	2	1	2	1		2		1	+	1	1	1	1														2		4			2		+						3	3				3				2														1						1		+	2	2	1	2		2	2	
Cheilanthes marginata	+			+																																																																								+		1																			
Chusquea angustifolia																																	3	2	1																																	5		1				3																							

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Chusquea spencei																																																																																									2		5		2	1				2		
Cinna poiformis																					2	2	+	2	+	1																																																																																		
Clethra fimbriata																																																																																					1	+										
Clusia multiflora																																																																								2																	+								
Coespeletia moritziana							3	2	3	2	4	3																																																																														
Coespeletia thyrsiformis																					2	2	2	2	2	2																																																																																		
Coespeletia timotensis											4	3	2																																																																														
Conyza bonariensis																	1																	+																																																														
Conyza uliginosa												+																																																							+																														
Coriaria ruscifolia																																																																												+																						
Cortaderia columbiana																																														1		4																													1		1		1		2	1		1													
Cortaderia hapalotricha																										3																																			+				2																	2			3					1	1						
Cortaderia nitida				1																																																																	2										1																	
Culcita coniifolia																																																																					+	1	1	+																											
Cybianthus marginatus																																																																					1		1														1	2			5										
Danthonia secundiflora																2							3		3						2			2		+	1																																																																						
Daucus montanus																																																																											1	+	+		2		+																	
Dendrophthora lindeniana																					+																																																								1																	1	2	
Dendrophthora Méridana																															1	+			+																																																										1				
Dendrophthora squamigera																																+																																																																			
Diplostephium obtusum																					r																																																																2					1						
Diplostephium venezuelense																																																													3																														2				1	
Disterigma acuminatum																																																																																							1										
Disterigma alaternoides																																																																																					2	1	1		2		2						
Draba pulvinata												+																																										1																																										
Drimys granadensis																															+																																																																		
Drymaria ovata																																																																											1	1				2	1																	
Drymaria villosa																				1																															+																																												
Eccremis coarctata																																																																																																	2
Echeveria venezuelensis	+	+	1	1								1					1										+			1							+	2	2	1		1	2						1																										+	+	r	+	+	+		+	2													
Elaphoglossum appressum																																															1																																																		
Elaphoglossum deorsum																																														1	1			+										+																						2	2													
Elaphoglossum inaequalifolium																	1	2								1	+		1																											+								+																														
Elaphoglossum lindenii																																													+		+																																																		
Elaphoglossum melancholicum																																																																					+	1				1																							
Elaphoglossum minutum																																				1									+																															+			+		+	+													
Elaphoglossum muscosum																																																																											+									+															
Elaphoglossum nivosum																																																																											+	1	1	1	1	1																		
Elaphoglossum tachirense																																1																									+												2																										
Elleanthus aurantiacus																																1																																																															1	
Epidendrum frutex																																																																																						2												
Epidendrum klotzscheanum																																																																								1																								
Epidendrum pittieri																																																																																						1												
Equisetum bogotense																																																				2																							r																						
Eriosorus flexuosus																																																																					+																												
Eriosorus rufescens				1																																																																																												
Eryngium humile		+				1																		+														+			+	+				+											+								1									2	2	+		1		+	+											1		2		
Escallonia myrtilloides																																																																										3	2																					
Espeletia aurantia																																																																																		2														
Espeletia marthae																																																										+	1	1	+	+		+	+																																	
Espeletia schultzii	3	3	3	4	3	3								3	3	4	2	2	2								3	3	3	4	1						1	2		2	2	3	3	3	1	2	1	3	1	1							1	2		+	4	2	5			1																											+	3				
Espeletiopsis angustifolia																																																																																												1					
Espeletiopsis pannosa																																																																																														4			

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Festuca coromotensis																																																																												+																						
Festuca tolucensis																																							1				+																																+	r	2	1	2		r	3	+	5													
Galium canescens	1																												2			+																																												r				+	+									+							
Galium hypocarpium	2	2	1	1	1	+								1	1	1		1	1	1	2	1		1	1		+	+	1		1	+				1	1	+			+			+	+	1	1		+	+	+	+			+	+		+			+		+				+			+			+	+	+	1		1			2	+										+		+	1	1	
Gamochaeta páramora				+																																																																																														
Gamochaeta purpurea		+														+											r			+																		+			1	r		+																											+																
Gaultheria anastomosans																																																																																												+					
Gaultheria buxifolia														1				1										1																																																									3											2	
Gaultheria erecta																				1		2				2						2	+		2	1										1																																								r	1				+	+				1	
Gaultheria glomerata																																				+																						1																																	1							
Gaultheria hapalotricha																																																																															+																				
Gaultheria oreogena																																																																																1																			
Gentiana sedifolia																																																																		r																															
Gentianella corymbosa																																																					1	+			1			+	+																																								
Geranium diffusum												1	1																																																																																						
Geranium meridense	+	1	2	2								+																																																							1								1	+		+	+	+	+																	
Geranium multiceps																		+	1																													+	+			2	2	1		1		+		2	2					2								1																							
Geranium sibbaldioides																						+		2	1	+																																																																							
Geranium stoloniferum																				2	2																																																																											
Geranium subnudicaule																																												1		+																																																			
Geranium velutinum																						2	2																																																																		1	+	2	1	1		2	
Gnaphalium antennarioides																												+		+																											1				+																																	r				
Gnaphalium dombeyanum	+	+	1	1																																	+	1	+	1	2	1	1								+					2								1			+																														
Gnaphalium Méridanum								+	+	1	+	1	+																								1		1																																																												
Gnaphalium meridense																																																					r	+	+			+				+																																				
Gnaphalium moritzianum		1	1	+																																											+		+																												2			r																			
Gomphichis traceyae																																																											1																					1																		
Greigia alborosea																																																																																							1												
Greigia aristeguietae																																																																				+																													
Gynoxys Méridana																																															3			r																																															2		
Gynoxys moritziana																													2		+																									2																																												
Habenaria gollmeri																																																																																													r					
Halenia brevicornis																																																																																																1			
Halenia subinvolucrata																																																																	r	1																														
Halenia viridis												+																																																																				1																		
Hesperomeles ferruginea																		1										1																																															2	2	+	+						r													
Hesperomeles obtusifolia																	3			+	1										2						2				1			2	2			2	2	3						2		+	+		+						2			+												+										+	+			1	
Hesperomeles sp.																				2		1		1																																																																									
Hieracium avilae																		r			+																									+			+	1								+			+						r																												+		
Hieracium erianthum												1																								+																																																													
Hieracium frigidum		+		1																																		1	1		1	+																																			r		+			+						1			r						
Hinterhubera imbricata							2	2	1	2	+	+	+										+																															1										+																																			r
Hinterhubera laseguei																																									+																																																									
Huperzia reflexa																																																																																								+												
Hydrocotyle bonplandii																																																													+																				2																
Hymenophyllum polyanthos																																														+																																																		
Hypericum caracasanum														+	+	+	+										+	+		+															+	+					r								1	+	+															1											2			+	+						
Hypericum chamaemyrtus																																	+		+																																																														
Hypericum juniperinum																								3																																																																									
Hypericum lancioides																																					2	3						2																																							1													
Hypericum laricifolium	1	+	2	+	4	2					2	3	3					1														1		3		+			2	2	2	2	3		+	1			1						3																										+	+															
Hypericum marahuacanum																																																									2																																												
Hypericum paramitanum																																2																																																																		

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Hypericum phellos																					2	4	+	2	2	r																																																																								
Hypericum stenopetalum																																																																																												2		2		
Hypericum tetrastichum																																																																																												1				
Hypericum thesiifolium														r																																																																														
Hypochaeris sessiliflora																					+	+	r		+																																																																								
Hypochaeris setosa		+	+	+	1	+			+	+	2		1																											+		+	+		+								+	+	+	r	1		2					+		r	r	+																																
Ilex myricoides																																																																							1	1	+																										
Jamesonia auriculata																																																																																															2	
Jamesonia bogotensis																																	2	2	2	+																																1																														
Jamesonia canescens																							2	2	1	1																															+		+		+	+				+																																2
Jamesonia imbricata																													2		2																																																													2	+				
Jamesonia laxa																																																																																																		
Juncus ecuadoriensis																																																												1						2																														
Lachemilla andina															+	+																																																																														
Lachemilla aphanoides																													2																																																																			
Lachemilla fulvescens																																																																		+																														
Lachemilla hirta																											2			+	+																								2												3								1	2			+		2			+																
Lachemilla hispidula																				1	1	+	+	1	+																																																																								
Lachemilla mandoniana																																									+										+														+																														
Lachemilla moritziana	1			+																	+																	+						+	+																r						+																														
Lachemilla polylepis												+	1																																																																																			
Lachemilla sprucei	+	+			3	2		+		+	1				+	+			1					+	+		1	+	+						+		1							+		1		+					1	1	r	r	1		1																															2															
Lachemilla verticillata												1																								1										2					+	+		1		2																																										1	
Laennecia filaginoides		+						+		2	1	2	1																+														1											+																																														
Lasiocephalus longepenicillatus											1		+																																														+																																						
Lasiocephalus sp.																																																	1																										1				+			1	1															
Lepechinia bullata														1	2		+											1			1																																																																			
Libanothamnus occultus																																														4			4																																														
Libanothamnus parvulus																																4	2		2	3																																																													
Libanothamnus spectabilis																																																																																															3	
Lobelia tenera	+	+	+	+																																	+		+	r	+	1											r					+	+			+				r																											r					
Lourteigia stoechadifolia			1	1																																														3																										+				+																			
Lupinus jahnii										2																																																																																				
Lupinus Méridanus		+	1	+																																																																																													
Lupinus peruvianus																																					+	+																																																										
Luzula gigantea																																													2												+																		+																							
Luzula racemosa	+	+	+	1		+	+																															1	1	+									+			1	1	1	1			r				+																																			
Lycopodium clavatum																		2	2	2	1		1		+	2	1				1				1	+																								+	+		r						+																1		+	1		+		+		1		4	
Lycopodium magellanicum																																																															+	+																																
Lycopodium thyoides																		+														2																																																																
Lysipomia bourgoini																																																					+																																											
Macleania rupestris																																																																														5						1				1							2	
Macrocarpaea bracteata																																																																					1	1	2	+																								
Melpomene flabelliformis																																														+	1			+																																														
Melpomene moniliformis																																																										1														1							+					r	+									+		
Melpomene peruviana																				2	2	+			+																																																																								
Miconia arbutifolia																																				1																																																												
Miconia latifolia																																1																																																																
Miconia mesmeana																																																																						1																										
Mikania stuebelii																																																																				+	1	2																										
Monnina meridensis			1																																																																								1					1																	
Monochaetum bonplandii																																				2																																																												
Monochaetum discolor																																1		+	1																																		3	3	3	2																								

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Monticalia apiculata																		1																							+	1				1				+																																															
Monticalia cachacoensis																																																																																							2	+			+		2						
Monticalia greenmaniana																					1																																			3																																															
Monticalia magnicalyculata																																																																																																+					
Monticalia pachypus																																													4		1	1																																																						
Monticalia quiroana																																																																																																			2		
Morella pubescens																																				2																																																													3				
Muehlenbeckia tamnifolia																																																																							1	2		1																							
Muehlenbeckia volcanica																																																								2				+	+														+			+					3														
Muhlenbergia ligularis																																																									4			+						4																															
Munnozia senecionidis																																																																					+	1	+																										
Myrcianthes myrsinoides																																																																											2	+	+	1																			
Myrica funckii																																																																							1																										
Myrsine coriacea																																1			2	2																																																															
Myrsine dependens																	1	2	2												1																			2																									2	1		2			2										2		+				
Nassella depauperata																																																			3	r															1																														
Nassella mucronata																																												2																															+				+																		
Nertera granadensis																				1	2	1		1																												r																+		2		1	1																	1		+			+	1	
Niphogeton dissecta		+																																												+							+																																												
Noticastrum marginatum					+	1								2		+						1	+	r	+		1																								1	+	r					r																																							
Oenothera epilobiifolia														+																							+														+				+																														2													
Oenothera multicaulis	+				1							1																																																																																				
Oreobolus goeppingeri																										1							1																																																																
Oreobolus venezuelensis																																																												1					r																					+	1											
Oreopanax discolor																																																																					+	1				+																								
Oreopanax reticulatus																																																																											1					3	1																
Oritrophium blepharophyllum																																				r																																																														
Oritrophium venezuelense																																																												2					1																																
Ortachne erectifolia																																																							1																																										
Orthrosanthus acorifolius	2	2	+	2										2	3	3		2	1				2	2	2	+	2	2	1	1	1																																					+					+																							
Orthrosanthus chimboracensis																																																			1	3			+			+		1	+		+				+									1						1													1	+	+
Oxalis medicaginea																																																																				1	+	+				4																							
Oxalis spiralis	+																											+	1	+	+						1						+	+	+		1	+		+		r			1	1		+			+			+			+																														
Oxalis tabaconasensis		1	1	2																																																																										2	1		1														
Oxylobus glanduliferus	+	1			2							+	2																								2	1		2	2	2	1			2	1			2																																														
Paepalanthus andicola																																1	+	+	1																																																													
Paepalanthus crassicaulis																																																																																																	+
Paepalanthus karstenii																																																+					+					+		+						+																				+		r					1			
Paspalum nutans														2	1	1	2	1	1								2	2		1																																																																			
Paspalum prostratum	2			2																																																															1																									2		2		+	
Passiflora mixta																																			2																																																														
Peperomia galioides			+																																									+			1			+						1																																									
Peperomia hartwegiana																																																																											1			+		2																	
Peperomia microphylla	+																																			1																						+																						1			+														
Peperomia rotundata																																																																																2			1														
Pernettya prostrata	1															2		1		+		2										1					2	2			2	2		+	1	1	2	+	1	+								r	+	+			+	+	1		2																		1				1	1			+		1		
Phoradendron undulatum																																																																											1						1																
Piptochaetium panicoides																																																																															1																		
Pityrogramma chrysoconia	1	1	1																																																																1																														
Pityrogramma tartarea																																																																												1						r															
Plantago australis																																																																																				+													
Plantago sericea		1																																				1																												+										3					2															
Poa mucuchachensis																																															1																																														1	1		1	+	

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Poa pauciflora																																																			1																																														
Poa petrosa		+		1																			r														+	1								+						1			+	+				r																																				
Polylepis sericea																																																		2																									2																							
Polypodium lasiopus																																			1																						1																																									
Polypodium murorum																												+																			1																																	2			2														
Polystichum orbiculatum																													1																																																																				
Polystichum pycnolepis																																																																																	2																	
Potentilla heterosepala																																																																																				1														
Psychotria eciliata																																																																					2	2		1																									1	
Pteridium arachnoideum																																1																																																																
Puya aristeguietae																																																				3								1	4																																				
Puya trianae																										2																																																																	3						
Puya venezuelana																																+																																																																	+
Racinaea tetrantha																																																																																																1	
Ranunculus bonariensis																																																				+																																												
Ranunculus praemorsus																																												1																																																				
Rhynchospora aristata																																																																																												2	1	+	+	3	2
Rhynchospora macrochaeta																				+	1	+		1		1							2	+	+	1																																								1																1		+	1						
Rhynchospora talamancensis																																																																																													+	2	+		
Ribes andicola			1																					+						+																																																																	
Ribes canescens																																													1																																																			
Roupala pseudocordata																																			2																																																													
Rubus bogotensis															1																																																					r		+																										
Rubus coriaceus																					1																																																					1															+								
Rubus nubigenus																																																																				r																												
Ruilopezia atropurpurea																																																																																																1	
Ruilopezia floccosa																																						+	2																																																									
Ruilopezia hanburiana																																																																																														2		2	1	1
Ruilopezia jabonensis																																	3	3																																																													
Ruilopezia jahnii																							2			3																																																													4	2			+						
Ruilopezia paltonioides																																																																				1	1	+		+	2	+																												
Rumex acetosella	1	+	1	2	1	1		2		3	2	2	2	1	+																1	1	+						2	2		1	+	+	+	1	+						2	+			2								r				+																																
Salvia rubescens																																																																																	+																	
Salvia sp.																																	+	1																																																													
Satureja nubigena																									+																														1																																									
Schizachyrium sanguineum																																	1	2																																																													
Senecio formosus			+		2	+		+	+	1	+	1	1																											1		+	2	1	1		+		+						1	1	+		2	1		+			r	r												+																								
Senecio funckii											1		1																																																																																				
Serpocaulon funckii																					1	1																																														2	2	2	2	2		2															+											
Serpocaulon loriceum																																																																																								+	+								
Sibthorpia repens																								1	1																																																																								
Siphocampylus reticulatus																																																																										+																						
Siphocampylus sceptrum																																																																											1		+						1													+		
Sisyrinchium alatum																																																			r																																													
Sisyrinchium jamesonii																			+																																				r	1	+		+	+			r	r				+																											+			1		
Sisyrinchium tinctorium	1	+	+	1							+	1			r												+	+						+			+		+	+				1			+																					+					1	+		1									1													
Smilax domingensis																																																																																					1													
Solanum colombianum		r																																																																																																
Sphyrospermum buxifolium																																																																							1	+																1			1			+					
Stachys venezuelana																																													2								1			1						r																																				
Stevia caracasana																												+		+																																																																			
Stevia lucida	2		+	1							1	+		2		2	2	2									3				1						2				+					1																						1										1	2	1							1														
Ternstroemia meridionalis																																																																																						+											

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57	I58	I59	I60	I61	I62	I63	I64	I65	I66	I67	I68	I69	I70	I71	I72	I73	I74	I75	I76	I77	I78	I79	I80	I81	I82	I83	I84	I85	I86	I87	I88	I89	I90	I91	I92	I93	I94	I95	I96	I97
Thalictrum podocarpum																																																																											1						1		+														
Themistoclesia dependens																																																																							4																									
Tillandsia biflora																																1				1																																																														
Tillandsia compacta																																																																				1	2	2	2	2		2																							
Tillandsia complanata																																																																					1		1																										
Tillandsia sp.																																																																					2	+	2		+																								
Tillandsia tovarensis																																			1																																																																
Triniochloa stipoides																											+	2	2	2																			2																								1	+	+	2		+																				
Trisetum irazuense																											+																	1	2							1																								1	+																					

Trisetum spicatum																																												+																																																										
Urtica ballotaefolia																																																								+																																														
Vaccinium corymbodendron															2	1		1	2																																																							+																								
Vaccinium floribundum	2	1	4	1		1															1	1	1			+			2																																																																					
Vaccinium meridionale																	1																																																																																		
Valeriana phylicoides		1																																				2							1																				2																																	
Valeriana rosaliana																				+																																																																															
Valeriana scandens																																																																												+						1																
Vallea stipularis																													+		1					1											1																														+		r			2															1	
Vicia andicola																													+																																																																				
Vriesea incurva																																																																												+																						
Vriesea tequendamae																																1			+	1																																					1																										
Vulpia bromoides	+			+																																															1	+																																																
Weinmannia karsteniana																																	+		1																																																														
Weinmannia lechleriana																																																																						2		1													2												
Xyris subulata																																																												2																												3	+		+							

Locality: I1 páramo de Mucuchies, Mérida; I2 páramo de Mucuchies, Mérida; I3 páramo de Mucuchies, Mérida; I4 páramo de Mucuchies, Mérida; I5 páramo de Piedras Blancas, Mérida; I6 páramo de Piedras Blancas, Mérida; I7 páramo de Piedras Blancas, Mérida; I8 páramo de Piedras Blancas, Mérida; I9 páramo de Piedras Blancas, Mérida; I10 páramo de Piedras Blancas, Mérida; I11 páramo de Piedras Blancas, Mérida; I12 páramo de Piedras Blancas, Mérida; I13 páramo de Piedras Blancas, Mérida; I14 Páramo de La Culata, Mérida; I15 Páramo de La Culata, Mérida; I16 Páramo de La Culata, Mérida; I17 Páramo de La Culata, Mérida; I18 Páramo de La Culata, Mérida; I19 Páramo de La Culata, Mérida; I20 Páramo las Rosas, Táchira; I21 Páramo las Rosas, Táchira; I22 Páramo las Rosas, Táchira; I23 Páramo las Rosas, Táchira; I24 Páramo las Rosas, Táchira; I25 Páramo las Rosas, Táchira; I26 Páramo las Rosas, Táchira; I27 Páramo La Culata, Mérida; I28 Páramo La Culata, Mérida; I29 Páramo La Culata, Mérida; I30 Páramo La Culata, Mérida; I31 Páramo La Culata, Mérida; I32 Páramo Las Rosas, Trujillo; I33 Páramo Las Rosas, Trujillo; I34 Páramo Las Rosas, Trujillo; I35 Páramo Las Rosas, Trujillo; I36 Páramo Cendé, Trujillo; I37 Páramo de Mifafí, Mérida; I38 Páramo de Mifafí, Mérida; I39 Páramo de Mifafí, Mérida; I40 Páramo de Mifafí, Mérida; I41 Páramo de Mifafí, Mérida; I42 Páramo de Mifafí, Mérida; I43 Páramo de Mifafí, Mérida; I44 Páramo de Mucubaji, Mérida; I45 Páramo de Mucubaji, Mérida; I46 Páramo de Mucubaji, Mérida; I47 Páramo de Mucubaji, Mérida; I48 Páramo de Mucubaji, Mérida; I49 Páramo de Mucubaji, Mérida; I50 Páramo de Mucubaji, Mérida; I51 páramo de Tuñame, Trujillo; I52 páramo de Tuñame, Trujillo; I53 páramo de Tuñame, Trujillo; I54 páramo de Tuñame, Trujillo; I55 páramo de Tuñame, Trujillo; I56 páramo de Tuñame, Trujillo; I57 páramo de Tuñame, Trujillo; I58 páramo de Guirigay, Trujillo; I59 páramo de Guirigay, Trujillo; I60 páramo de Guirigay, Trujillo; I61 páramo de Guirigay, Trujillo; I62 páramo de Guirigay, Trujillo; I63 páramo de Guirigay, Trujillo; I64 páramo Teta de Niquitao, Trujillo; I65 páramo Teta de Niquitao, Trujillo; I66 páramo Teta de Niquitao, Trujillo; I67 páramo Teta de Niquitao, Trujillo; I68 páramo de los Nepes, Trujillo; I69 páramo de los Nepes, Trujillo; I70 páramo de los Nepes, Trujillo; I71 páramo de los Nepes, Trujillo; I72 páramo de los Nepes, Trujillo; I73 páramo de los Nepes, Trujillo; I74 páramo de los Nepes, Trujillo; I75 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I76 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I77 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I78 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I79 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I80 Sierra Nevada de Mérida; Laguna Coromoto, Mérida; I81 Sierra Nevada de Mérida; camino Laguna Coromoto-Laguna Verde, Mérida; I82 Sierra Nevada de Mérida; camino Laguna Coromoto-Laguna Verde, Mérida; I83 Sierra Nevada de Mérida; camino Laguna Coromoto-Laguna Verde, Mérida; I84 Sierra Nevada de Mérida; camino Laguna Coromoto-Laguna Verde, Mérida; I85 páramo el Zumbador, Táchira; I86 páramo el Zumbador, Táchira; I87 páramo el Zumbador, Táchira; I88 páramo el Zumbador, Táchira; I89 páramo el Zumbador, Táchira; I90 páramo el Zumbador, Táchira; I91 páramo el Zumbador, Táchira; I92 páramo de San José; Pueblos del Sur, Mérida; I93 páramo de San José; Pueblos del Sur, Mérida; I94 páramo de San José; Pueblos del Sur, Mérida; I95 páramo de San José; Pueblos del Sur, Mérida; I96 páramo de San José; Pueblos del Sur, Mérida; I97 páramo de San José; Pueblos del Sur, Mérida.

Appendix 3(3)

Working plot-table for zonal páramo vegetation in Peru.

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Elevation (m)	3262	3276	3290	3259	3255	3243	3256	3261	3511	3523	3502	3529	3530	3460	3475	3558	3567	3509	3481	2812	2811	2799	2803	2795	2800	3506	3468	3458	3433	3466	3455	3425	3377	3373	3363	2634	2675	2756	2800	2828	2869	2920	2903	2912	3014	3049	3071	3086	2883	2925	2945	2912	2991	3024	3060	3108	3101
Plot area	60	80	10	15	55	25	10	15	20	40	10	25	30	45	0	5	10	15	45	60	65	5	60	55	60	55	0	35	15	80	75	40	50	25	55	50	45	45	30	35	25	0	5	5	30	35	5	50	30	15	55	65	25	70	20	75	30
Slope (º)	50	25	50	25	25	9	71	25	25	36	50	25	16	16	9	9	16	25	49	36	25	36	9	16	25	9	9	36	25	25	36	25	20	25	9	25	25	16	25	25	16	25	16	25	49	16	25	16	25	9	16	25	21	49	36	9	12
Aspect	S	SWW	SEE	SWW	NE	SSE	S	S	NNW	N	NWW	SWW	NW	E	#	SWW	NEE	E	SE	SSE	SE	SSW	NWW	SE	NWW	W	#	W	NW	SW	NW	NWW	NE	NNW	SW	S	NW	SW	S	SSW	W	#	NE	W	NNW	W	NW	SSE	NW	W	N	E	NNE	SE	SW	W	SW
Vegetation cover	95	100	100	98	75	80	70	100	97	99	98	90	99	96	97	98	98	100	90	80	98	95	87	85	85	99	100	96	97	100	98	98	99	97	99	99	95	85	100	99	95	100	98	99	98	99	100	95	100	96	99	100	86	99	100	99	92
Acaena ovalifolia	1						1											+																																							
Achyrocline alata	2						+																																+			2	+		+							+				+	
Achyrocline celosioides																																																					+				
Achyrocline hallii																																																			+	1					
Achyrocline satureioides		+										+																						1																							
Achyrocline trianae																					+																	+																			
Aciachne acicularis														1	3																																										
Aegopogon cenchroides																				r	+	+			+																									2							
Ageratina articulata																		+																								1					2								+		
Ageratina azangaroensis	1	r		+				+																																																	
Ageratina cutervensis																						+																																			
Ageratina exertovenosa				1																+	+				2			1			r	1	1						2	+											+				1		
Ageratina piurae							3				4																																														
Ageratina pseudochilca									2		3		1	3																																											
Ageratina scopulorum																																																		1		+					
Ageratina tambillensis							+																																																		
Agrostis breviculmis	+								1																	3																															
Agrostis foliata																														+																											
Agrostis perennans	1						+											2	1										+	+																											
Agrostis tolucensis	+								+					+		+	1				1			+																						+											
Alnus acuminata																																				+				+														2			
Antennaria linearifolia																								r																								1									1
Aphanactis villosa													+		+			+																																							
Arcytophyllum capitatum																																														1		1						1		2	
Arcytophyllum filiforme											+		+			2																		+																							
Arcytophyllum nitidum																	2																	+																							
Arcytophyllum rivetii							+													+			+																		1	+							3		2	2	2	1			
Arcytophyllum setosum		1	+	+		1		+																			1		1																												
Arcytophyllum vernicosum																																						1																			
Arenaria lanuginosa			+																												r																								r		
Aristeguietea sp.	1																																																								
Axinaea nitida																																												+										1			
Axonopus fissifolius																							2	1																																	

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Azorella biloba																										+	2						+																								
Azorella multifida	+															1	+									1																															
Azorella pedunculata																		+																																							
Baccharis alaternoides																			1	2	1	2																																			
Baccharis buxifolia										2								1																																							
Baccharis genistelloides								r															+																												+						
Baccharis obtusifolia	+																					+																1		+		2	1	1	+	1	+	+	+		+	+	1	+			
Baccharis peruviana																													1																												
Baccharis phylicoides							+														2																															2	1				
Baccharis sp.																												2	1	2																											
Baccharis tricuneata																			2																																						
Barnadesia dombeyana												1																																													
Bartsia crisafullii																																																		+		1	r				
Bartsia mutica																																				r																					
Bartsia santolinifolia													+			+																																									
Bartsia sericea	+	r																		+	+		1																																		
Bartsia tomentosa																																								+	+		+			+											
Bartsia trichophylla																										+	+			+																											
Bartsia weberbaueri																																														+		+									
Bejaria aestuans																																							r														1	+			
Berberis jelskiana																																																	+								
Berberis lobbiana									+	1	2		+																																												
Berberis podophylla																										1		1		+	1																										
Bidens triplinervia	r	+												+															+																	1				1							
Blechnum auratum					1															+																			1					1	+									+			
Blechnum cordatum																																				1																					
Blechnum lima																		1			+								+	+	2	+	1																								
Blechnum loxense																		1																																							
Blechnum violaceum																										1		+																													
Bomarea crocea											+																																														
Bomarea densiflora																			+																																						
Brachyotum andreanum																																	2	+	+																						
Brachyotum benthamianum																												2	+		+																										
Brachyotum grisebachii		2	2																																																						
Brachyotum jamesonii																							+		2																																
Brachyotum longisepalum				+																																																					
Brachyotum naudinii									r				2				+												1			1	1						1		1	2	+	1	+	+	2	2			1	1	+		1	+	1
Brachyotum rostratum										1	+							2	2																																						
Brachyotum tyrianthinum																																				2	2																				
Brachypodium mexicanum												r																																													
Bromus catharticus																																		+																							
Bulbostylis junciformis																		+																																							
Bulbostylis juncoides																							2	1																								+									
Calamagrostis bogotensis																	1																																								1
Calamagrostis effusa														1		1	1																																								
Calamagrostis intermedia	2			+	1	1	+	1			1		4													1	2		3	1		2	2	3	4														2	2	3	3	4	2	1	3	
Calamagrostis rigescens													1																																												
Calamagrostis rupestris																																										1					+										
Calamagrostis tarmensis		3	+													4	5	2		1	4	2	4	2	1													2	4	3	4		2		2	4	2	3									
Calandrinia ciliata																									1																																
Calceolaria nivalis	2							1																				+								1	2	+											1								
Calceolaria pilosa																				1																																					
Calceolaria rhododendroides									1	1		2																		+																											

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Calceolaria rotundifolia	1	1						+												1	1			+																		1						+			+		+		+		
Campyloneurum solutum																		+																																							
Carex bonplandii																		3										2																												
Carex jamesonii																				+																																				
Carex muricata													+																			1																								
Castilleja fissifolia													+	r	+																																									
Cavendishia bracteata																			1																									1												
Cerastium danguyi																																	+																							
Chevreulia acuminata																				+			+																												+					
Chrysactinium acaule													+															1					1																							
Chrysactinium amphothrix												+																																												
Chrysactinium caulescens		1		+				+												1	1	+	1	1																															1	+	
Chuquiraga jussieui												1																				3	2																							
Chusquea neurophylla																														2																										
Chusquea scandens																																			1																					
Clethra cuneata				r																		+																																		
Clethra fimbriata		2	+	+				1													1																							2									1	2	1		2
Clethra ovalifolia																			+																																					
Clinopodium obovatum																				1	+		+	+																																
Clusia ducuoides																			1													1																								
Clusia multiflora																																+																								
Coreopsis capillacea					2																																																			
Coreopsis oblanceolata		1		1				2														+	+	+	+																												1			+	+
Coreopsis piurana																																																				1				
Coriaria ruscifolia																			1																																					
Cortaderia bifida																			1	1	+			1																																
Cortaderia nitida																												1		+		1																								
Cortaderia sericantha																																															+					+				
Cotula mexicana																	1								2																															
Cuphea ciliata																					+																				+															
Dendrophthora densifolia						+																																																		
Desfontainia spinosa																														1																										
Diodia dichotoma																																				+																				
Dioscorea weberbaueri																																																	+							
Diplostephium callaense																																																								2
Diplostephium foliosissimum	2				+													1																																							
Diplostephium jelskii				2			2																																																	
Diplostephium meyenii												2																																												
Disterigma acuminatum																											2																	1	1		+									
Disterigma empetrifolium				1																					2	2		2	2	1	+	2	1	1													1					+				
Dorobaea pimpinellifolia											r																	+													r			r		+										
Dryopteris wallichiana	+																																			+																					
Eccremis coarctata																																					+																			
Elaphoglossum antisanae																								+					1																											
Elaphoglossum dendricola																			1										1																											
Elaphoglossum engelii	+	2		+	1			+		1		+						1								2																			1				+								
Elaphoglossum huacsaro																			1																																					
Elaphoglossum minutum	+																			+										1	1			+																	+					2	
Elaphoglossum ovatum																														1																										
Elleanthus aurantiacus				2	+															1	+	+		+											+				1					+								1	1		+	
Epilobium denticulatum																									+																	+														
Equisetum bogotense																	1																																							
Eriosorus cheilanthoides																												+	+					+	+																					

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Eriosorus elongatus	+									+											+																						+									+			
Eryngium humile													+								r		1	1	+		1											+	+										+				+	2				r
Escallonia myrtilloides																					1	1								3													1					3												
Festuca asplundii																																1				+																									
Festuca dolichophylla																																																			1		r		+				
Gaiadendron punctatum																																																			+					3			
Galinsoga quadriradiata	+																																																								
Galium corymbosum									r		r		+												+		1				+																							+		+					
Galium ferrugineum																			+																																						
Galium hypocarpium											+								+						+					+						+	+																+		
Gamochaeta americana	+																																																								
Gamochaeta purpurea															r				+							+	1	1				+																											
Gaultheria bracteata																																					2																						
Gaultheria erecta																					+					+				+	2	+		+					2												1			+	+		1
Gaultheria foliolosa																																					2																						
Gaultheria glomerata																																									1	1	1				+											
Gaultheria reticulata		1		1	+																2		+								1	2			+				2	2	2	2	2	+	1					2		3	+		+			1
Gaultheria rigida	1	1		1	+	+							+																																										
Gaultheria tomentosa																					+																																				
Gaultheria vaccinioides																			+												2																											
Gentiana sedifolia																															+																											
Gentianella androsacea																																					+																						
Gentianella iberidea																	1	+																																								
Gentianella liniflora								1																		r																		+								2								
Gentianella setipes									r		r	2		+																																											
Geranium ayavacense	1									+	+			+	+		+				+	+			+																								+										1		
Geranium campii																		r																		2																							
Geranium reptans		+																											+																														
Geranium sibbaldioides																1		+	+								2	+		1			1		1	2																							
Gnaphalium dombeyanum	1																																																								
Gomphichis koehleri																																							+																			
Gunnera magellanica																		2														+																										
Gynoxys buxifolia	1	+																	1	3							1		1		1	+																										
Gynoxys hallii							2					1	3																																												
Gynoxys hutchisonii																					+																																				
Gynoxys soukupii																							2																																		
Halenia pinifolia																						+																																			
Halenia sphagnicola																																																+								+
Halenia umbellata																															r				+	+																						
Halenia weddelliana	+								1		+		+		2	+	+																																							
Hedyosmum racemosum																			+																																						
Hesperomeles ferruginea																														1		2																									
Hesperomeles obtusifolia						+			+		2	2	1																									+		2			1							1				2			
Hieracium chilense																															1																											
Hieracium frigidulans																											+							+	+																							
Hieracium peruanum																							+	+																																
Hieracium sprucei														+																																										
Hieracium tallenganum								+																																																
Huperzia binervia																					1		+																																		
Huperzia brevifolia																																					1																					
Huperzia weberbaueri																	+																																								
Hydrocotyle bonplandii	+						+																																																	
Hydrocotyle humboldtii																						+	+			+				+	2			+	+					+									+		+									+	+	

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Hydrocotyle ranunculoides																		+																																							
Hypericum aciculare																													+																												
Hypericum callacallanum																										+	+																														
Hypericum decandrum					+	2																																										+									
Hypericum laricifolium																																				1	2	1		1	+		+		+	1	1						2	+	4		2
Hypericum silenoides	+																																																								
Hypericum sprucei	1	+	2					2	3	1	1		2			r	+																	1																							
Hypochaeris chillensis																																+											+					+		+							
Hypochaeris graminea								+																																																	
Hypochaeris sessiliflora														+																																											
Jamesonia goudotii													1																			+			1																						
Jamesonia rotundifolia									1										1																																						
Jarava ichu																									2																																
Juncus bufonius	+																												2																												
Lachemilla andina	1						+																		1																																
Lachemilla aphanoides	1													+				+																		+																					
Lachemilla fulvescens																		+									+			+				+																							
Lachemilla hirta	+																																																								
Lachemilla jamesonii																										2	+																														
Lachemilla nivalis																													2																												
Lachemilla orbiculata	+						r							+								1					+	2		1	1																										
Lachemilla pectinata																		2																																							
Lachemilla sprucei																										1	1																														
Lachemilla uniflora														+	+	1	+																																								
Lachemilla vulcanica	+								1				+																																												
Lilaea scilloides																										r			r																												
Lobelia tenera									+												r		+	+														+			+					+										+	+
Lomatia hirsuta			1	1				1			1									1													2												+							1		1			
Loricaria thuyoides																	1																																								
Lupinus foliolosus																																						+																			
Lupinus pubescens																																																	+								
Lupinus purdieanus																r																																							1	1	
Lupinus ramosissimus													r	+																2												2				1	1	+									
Lupinus revolutus																r																	+																								
Luzula ecuadoriensis																																															+										
Luzula gigantea										1		+						+	+							+				2	1																										
Lycopodium clavatum		1		+	+			1								+	+			1	+			+			r				+	+		2	+	+		1		3	+	2	+	1				+					2	2	2		+
Lycopodium magellanicum									1																																																
Lycopodium thyoides	+	2		1				2																	+													2			1	3				+			5		2		+			3	+
Lycopodium vestitum	+																																																								
Lysimachia andina																													2																												
Lysipomia sphagnophila																+														r																											
Lysipomia subpeltata																																	+																								
Macleania rupestris		1		+																					1											1																					
Malaxis andicola																					r																	r	r																		
Margyricarpus pinnatus	1														+																																										
Melpomene flabelliformis																										+																															
Melpomene moniliformis																	+			+																																					
Meriania furvanthera																					1	1																																			
Miconia aspergillaris							1														+	3			2																											2					
Miconia bracteolata							2																																																		
Miconia caelata																												1																													
Miconia cauingia			1																																																						

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Miconia hutchisonii		1	2					1																																																	
Miconia loxensis																			2																																						
Miconia rotundifolia															1																				+																						
Miconia salicifolia																													+																												
Monnina conferta										1	1																																														
Monnina decurrens										2	1																																														
Monnina ligustrina																						+																																			
Monnina salicifolia		1	+	2				1																																			2				1										
Monnina sandemanii																																																	+								
Monticalia arbutifolia																														1																											
Monticalia peruviana	1		3							4			1																																												
Morella pubescens			+	3				2												+																1																					
Muehlenbeckia tamnifolia																			+			+			+						1																								1		
Muehlenbeckia volcanica																												2																													
Muhlenbergia angustata																																																		3							
Myrcianthes fimbriata																																		3																							
Myrsine coriacea																																								1					1												
Myrsine dependens				1			1	1			2		+						2	1		2			+				+	+				1																							
Myrsine manglilla																						1																																			
Myrteola acerosa				1	2																																																				
Nassella depauperata																																																							2		
Nassella inconspicua				+		1		2	+		+	+			1					+				+																																	
Nassella mucronata														1	+																												+				+										
Nassella pubiflora	+													2							+																																				
Nertera granadensis																		1	2							2			2	+																											
Neurolepis nana																											1					5																									
Niphidium crassifolium	1																					1			+																								1			1					
Niphogeton smithii																																																							+		
Oncidium excavatum																																								+											+						
Oreithales integrifolia											r			r	+																																										
Oreobolus goeppingeri																1											1		2			1		+	2																						
Oreocallis grandiflora				2		+																1														+	1		+	2			3		r							3		2			
Oreopanax oroyanus							2																																																		
Oreopanax weberbaueri																									+																																
Oritrophium crocifolium																											1					+																									
Oritrophium limnophilum																	+																																								
Oritrophium repens																	1																															+									
Orthrosanthus chimboracensis	2	r		+			+	1	2	+	1	1	1	3			+	+	1		2	1		+					+	+				+	+			+																			
Ourisia chamaedrifolia																												2																													
Oxalis eriolepis																+	+																																								
Oxalis spiralis										+	2	+						1	+																																						
Oxalis subintegra																																				+																					
Oxalis tabaconasensis																															1																										
Panicum pantrichum																								+	1																																
Panicum stramineum																						+																																			
Paranephelius uniflorus						+		+														+	1	1																	1							1					1				
Paranephelius wurdackii																									+																																
Paspalum bonplandianum		+		1				+	1		r		1	1	2	2	1				+	2		2									+	2																							
Paspalum candidum																																					1	2																			
Paspalum pilgerianum																																							+		+	+	1		+	1	+	1			1	1		+	1	+	2
Passiflora cumbalensis																																															+										
Passiflora loxensis																															+																										
Pennisetum clandestinum																						2																																			

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Peperomia galioides																												+		1																											
Peperomia hartwegiana										+								+	2			+																																			
Peperomia rotundata																																															1										
Pernettya prostrata	1		1		+	2		+	1	2		1		+	+	1	1				+						1				2				+					2	2	1	1	2			+										
Persea brevipes																				1																																					
Phyllactis tenuifolia								+																																																	
Plagiogyria semicordata																		1		1																																					
Plantago linearis														1	r																																										
Plantago rigida																													+																												
Poa pauciflora																											+																														
Polylepis lanuginosa													1																																												
Polylepis weberbaueri			2				+		2																																																
Polystichum montevidense	+																																																								
Polystichum orbiculatum											1																																														
Pterichis galeata																																																					r				
Pteridium arachnoideum		1																			2	3	1		2											+	1	+	2	2	1	1	+	1	2		2	+	1		+						
Puya exigua																																									1										2						
Puya glaucovirens																					2			3																																	
Puya hamata																																1	+		1																						
Ranunculus nubigenus																		1																																							
Ranunculus praemorsus																										+																															
Rhynchospora kunthii								2													2	1		+	+																	1	2	+		+									2	+	+
Rhynchospora macrochaeta																		1																				1												2		+	+	+	2	+	2
Rhynchospora polyphylla																																				+	+																				
Rhynchospora ruiziana									+		+	+	+						1											1	+	1		2	3																						
Rhynchospora vulcani																											1		+																												
Ribes elegans																						r																																			
Ribes weberbaueri																												1																													
Rubus bogotensis																																					1																				
Rubus coriaceus																			+																																						
Rubus laegaardii																														+	+																										
Rubus megalococcus																			1																																						
Rubus nubigenus																						1			+																																
Rubus peruvianus							1																																																		
Rubus robustus										1																																+					+										
Salvia corrugata							2																																																		
Salvia griseifolia																									2																																
Saracha quitensis																						1																																			
Satureja guamaniensis		+	+	+			3	+																															1			+	+			1					1	+		+	+		+
Satureja revoluta										1		1		+				1																																							
Schizachyrium sanguineum																								2																										4		2	1				
Senecio chionogeton																											1							1	2															+							
Senecio piurensis																													+																												
Senecio usgorensis																					1	1	+	+									+																								
Sibthorpia repens																						+																																			
Siphocampylus sp.																			+																																						
Sisyrinchium caespitificum																													1																												
Sisyrinchium chilense																					+																													+			r				
Sisyrinchium tinctorium																	+																																								
Sisyrinchium trinerve																										+								r														1									
Smilax eucalyptifolia																																											r		+												
Solanum sanchez.vegae																												1																													
Stellaria serpyllifolia										+									+							+					+																										

Plot number	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	I11	I12	I13	I14	I15	I16	I17	I18	I19	I20	I21	I22	I23	I24	I25	I26	I27	I28	I29	I30	I31	I32	I33	I34	I35	I36	I37	I38	I39	I40	I41	I42	I43	I44	I45	I46	I47	I48	I49	I50	I51	I52	I53	I54	I55	I56	I57
Stenomesson aurantiacum				r																																																				1	
Stevia andina	1		1	1				+												+	+																																				
Stevia macbridei																							+															+			+					+	+	r									
Sticherus revolutus			2																	2																2																					
Tibouchina laxa																																				2	+	1				+															
Tillandsia sp.																				1																																					
Trichocline hieracioides																																																		1							
Triniochloa stipoides																																										+					1										
Trisetum irazuense	+																																																								
Trisetum spicatum															1																																										
Uncinia macrolepis												+	1														1						1																								
Uncinia paludosa																2	2																																								
Vaccinium crenatum																																						1													4	2	1			+	
Vaccinium floribundum		2		2	1	1		2	2		2	4	2							+					1							+	2	2															3								
Valeriana microphylla																											+	+	+						1													+									
Valeriana pilosa																		1											+																										3		
Vernonia sp1		2																																																							
Vernonia sp2								2																																																	
Veronica serpyllifolia																		+																																							
Viburnum incarum																																											+														
Vicia andicola																		+																																							
Viola arguta																																															3										
Viola dombeyana												+																																													
Weinmannia anisophylla		1			+																	1																																			
Weinmannia auriculata																															1																										
Weinmannia cymbifolia																				1		1																	3	+				2	2									2			
Weinmannia elliptica																				2																								2	2												
Weinmannia fagaroides		1	1	2																					1																																
Weinmannia glabra																																				1																					
Weinmannia jelskii																																				1																		1			
Werneria nubigena	+												r	+	3	2											2																														
Xyris subulata																	2																																								
Locality:	I1 Cuello del Inca, Piura; I2 Cuello del Inca, Piura; I3 Cuello del Inca, Piura; I4 Cuello del Inca, Piura; I5 Cuello del Inca, Piura; I6 Cuello del Inca, Piura; I7 Cuello del Inca, Piura; I8 Cuello del Inca, Piura; I9 camino hacia la Laguna Negra, Piura; I10 camino hacia la Laguna Negra, Piura; I11 camino hacia la Laguna Negra, Piura; I12 camino hacia la Laguna Negra, Piura; I13 camino hacia la Laguna Negra, Piura; I14 camino hacia la Laguna Negra, Piura; I15 camino hacia la Laguna Negra, Piura; I16 camino hacia la Laguna Negra, Piura; I17 camino hacia la Laguna Negra, Piura; I18 camino hacia la Laguna Negra, Piura; I19 camino hacia la Laguna Negra, Piura; I20 páramo de Cruz Chiquita, Piura; I21 páramo de Cruz Chiquita, Piura; I22 páramo de Cruz Chiquita, Piura; I23 páramo de Cruz Chiquita, Piura; I24 páramo de Cruz Chiquita, Piura; I25 páramo de Cruz Chiquita, Piura; I26 páramo de Espindola, Piura; I27 páramo de Espindola, Piura; I28 páramo de Espindola, Piura; I29 páramo de Espindola, Piura; I30 páramo de Espindola, Piura; I31 páramo de Espindola, Piura; I32 páramo de Espindola, Piura; I33 páramo de Espindola, Piura; I34 páramo de Espindola, Piura; I35 páramo de Espindola, Piura; I36 páramo de Colasay, Cajamarca; I37 páramo de Colasay, Cajamarca; I38 páramo de Colasay, Cajamarca; I39 páramo de Sallique, Cajamarca; I40 páramo de Sallique, Cajamarca; I41 páramo de Sallique, Cajamarca; I42 páramo de Sallique, Cajamarca; I43 páramo de Sallique, Cajamarca; I44 páramo de Sallique, Cajamarca; I45 páramo de Sallique, Cajamarca; I46 páramo de Sallique, Cajamarca; I47 páramo de Sallique, Cajamarca; I48 páramo de Sallique, Cajamarca; I49 páramo de Palambe, Cajamarca; I50 páramo de Palambe, Cajamarca; I51 páramo de Palambe, Cajamarca; I52 páramo de Palambe, Cajamarca; I53 páramo de Palambe, Cajamarca; I54 páramo de Palambe, Cajamarca; I55 páramo de Palambe, Cajamarca; I56 páramo de Palambe, Cajamarca; I57 páramo de Palambe, Cajamarca.																																																								

Appendix 4

Plot contents in the 17 clusters (coarse vegetation classification), with their location and source.

Clusters	Number of plots	Locality	Source
Cluster 1	16	Piedras Blancas, Mérida, VE	- Course BOTANE. Unpublished data - Peyre G. Unpublished data
	14	Media-Luna, Mérida, VE	- Berg AL (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157-203.
	11	Mucubají, Mérida, VE	- Peyre G. Unpublished data
	11	La Culata, Mérida, VE	- Peyre G. Unpublished data
	7	Mifafí, Mérida, VE	- Peyre G. Unpublished data
	7	Tuñame, Trujillo, VE	- Peyre G. Unpublished data
	5	Mucuchíes, Mérida, VE	- Vareschi V (1953) Sobre las superficies de asimilación de sociedades vegetales de cordilleras tropicales y extratropicales. Boletín de la Sociedad Venezolana de Ciencias Naturales, 14: 121-173. - Course BOTANE. Unpublished data
	5	Santo Cristo, Mérida, VE	- Berg AL (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157-203.
	5	Guirigay, Trujillo, VE	- Peyre G. Unpublished data
	4	Laguna Coromoto, Mérida, VE	- Peyre G. Unpublished data
	3	Espejo, Mérida, VE	- Berg AL (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157-203.
	3	Niquitao, Trujillo, VE	- Peyre G. Unpublished data
Cluster 2	47	Perijá, César, CO	- Rangel-Churio JO, Arellano-Peña H (2007) La Vegetación de la alta montaña de Perijá. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica V. Instituto de Ciencias Naturales-Corpocesar. Bogotá, pp. 163-189.
	37	Santa Marta, Magdalena, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM, Rangel-Churio JO (1984) La Vegetación del Páramo del Noroeste de la Sierra Nevada de Santa Marta. In: Van der Hammen T, Ruiz P (eds) Estudios de Ecosistemas Tropandinos, Vol. 2, Cramer, Vaduz, pp. 203-266. - Cleef AM, Rangel-Churio JO (1991) La vegetación del páramo del noroeste de la Sierra Nevada de Santa Marta. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 24-71.
	7	Cocuy, Boyacá, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	6	las Rosas, Táchira, VE	- Peyre G. Unpublished data
	3	Almorzadero, Santander	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.

Clusters	**Number of plots**	**Locality**	**Source**
Cluster 2(2)	3	la Sarna, Boyacá, CO	- Rangel-Churio JO, Aguirre JC (1986) Estudios ecologicos en la cordillera oriental colombiana, III La vegetación de la cuenca del Lago de Tota (Boyacá). Caldasia 15(71-75): 264-311.
	2	Sumapaz, Meta, CO	- Cleef AM, Rangel-Churio JO, Arellano H (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T (ed) Estudios de Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz, Vol. 7, J. Cramer, Stuttgart, pp. 799-913.
	2	Neusa, Cundinamarca, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	2	San José, Mérida, VE	- Peyre G. Unpublished data
	1	Belén, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	1	La Rusia, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	1	Pisva, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	1	Guasca, Cundinamarca, CO	- Cleef AM, Rangel-Churio JO (1991) La vegetación del páramo del noroeste de la Sierra Nevada de Santa Marta. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 24-71.
	1	lago de Tota, Boyacá, CO	- Rangel-Churio JO, Aguirre JC (1986) Estudios ecologicos en la cordillera oriental colombiana, III La vegetación de la cuenca del Lago de Tota (Boyacá). Caldasia 15(71-75): 264-311.
Cluster 3	71	Chingaza, Cundinamarca, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación del Parque Nacional Natural Chingaza. In: Rangel-Churio JO (ed) La región de vida paramuna. Colombia diversidad Biótica III. Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá, pp. 720-753. - Franco PR, Rangel-Churio JO, Lozano GC (1986) Estudios ecologicos en la cordillera oriental- II Las comunidades vegetales de los alrededores de la Laguna de Chingaza (Cundinamarca). Caldasia, 15(71-75): 219-243.
	40	Cruz Verde, Cundinamarca, CO	- Lozano GC, Schnetter R (1976) Estudios ecologicos en el páramo de Cruz Verde, Colombia: 2. Las comunidades vegetales. Caldasia 11(54): 53-68. - Rivera DO. Unpublished data
	22	Sumapaz, Meta-Cundinamarca, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM, Rangel-Churio JO, Arellano H (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T (ed) Estudios de Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz, Vol. 7, J. Cramer, Stuttgart, pp. 799-913.
	18	Monserrate, Cundinamarca, CO	- Vargas R, Zuluaga S (1985) La vegetación del Páramo de Monserrate. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada. Instituto de Ciencias Naturales, Universidad Nacional, Bogotá.
	3	La Rusia, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.

Clusters	Number of plots	Locality	Source
Cluster 3(2)	2	Guantiva, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	2	la Sarna, Boyacá, CO	- Rangel Churio JO, Aguirre JC (1986) Estudios ecologicos en la cordillera oriental colombiana, III La vegetación de la cuenca del Lago de Tota (Boyacá). Caldasia 15(71-75): 264-311.
Cluster 4	39	Tatamá, Chocó-Risaralda, CO	- Cleef AM, Rangel-Churio JO, Salamanca S, Ariza CL, van Reenen GBA (2005) La vegetación del Páramo del Macizo de Tatamá, Cordillera occidental, Colombia. In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds) La Cordillera Occidental Colombiana Tansecto Tatamá. Studies on tropical Andean ecosystems, Vol 6, J.Cramer, Berlin-Stuttgart. - Pinto-Zárate JH, Rangel-Churio JO (2010) La vegetación paramuna de la Cordillera Occidental colombiana I: Las formaciones zonales. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica X: Cambio global (natural) y climático (antrópico) en el Páramo colombiano. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, pp. 181-287.
	28	Puracé, Cauca, CO	- Rangel-Churio JO, Franco PR (1985) Observaciones fitoecologicas en varias regiones de vida de la cordillera central de Colombia. Caldasia, 14(67): 211-249. - Duque AN, Rangel-Churio JO (1991) Analisis Fitosociologico de la vegetación Paramuna del Parque Natural Puracé. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 256-276.
	23	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	9	Santo Domingo, Cauca-Huila, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Rangel-Churio JO, Franco PR (1985) Observaciones fitoecologicas en varias regiones de vida de la cordillera central de Colombia. Caldasia, 14(67): 211-249.
	5	Frontino, Antioquía, CO	- Rangel-Churio JO, Sánchez D, Ariza CL (2005) La vegetación del Páramo de Frontino. In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds). La Cordillera Occidental Colombiana Tansecto Tatamá. Studies on tropical Andean ecosystems, Vol 6, J.Cramer, Berlin-Stuttgart.
	2	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	1	Chingaza, Cundinamarca, CO	- Vargas OR, Rivera DO (1991) Comunidades vegetales del Parque Nacional Natural Chingaza: Sector I Río La Playa-Río Guatiquía (resultados preliminares). Cuadernos Divulgativos Univ. Javeriana, 23: 1-74.
	1	Sumapaz, Meta-Cundinamarca, CO	- Cleef AM, Rangel-Churio JO, Arellano H (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T (ed) Estudios de Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz, Vol. 7, J. Cramer, Stuttgart, pp. 799-913.

Clusters	Number of plots	Locality	Source
Cluster 5	46	Chingaza, Cundinamarca, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación del Parque Nacional Natural Chingaza. In: Rangel-Churio JO (ed) La región de vida paramuna. Colombia diversidad Biótica III. Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá, pp. 720-753. - Franco PR, Rangel-Churio JO, Lozano GC (1986) Estudios ecologicos en la cordillera oriental- II Las comunidades vegetales de los alrededores de la Laguna de Chingaza (Cundinamarca). Caldasia, 15(71-75): 219-243.
	35	Frontino, Antioquía, CO	- Rangel-Churio JO, Sánchez D, Ariza CL (2005) La vegetación del Páramo de Frontino. In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds). La Cordillera Occidental Colombiana Tansecto Tatamá. Studies on tropical Andean ecosystems, Vol 6, Ed. J.Cramer, Berlin-Stuttgart. - Pinto-Zárate JH, Rangel-Churio JO (2010) La vegetación paramuna de la Cordillera Occidental colombiana I: Las formaciones zonales. In: Rangel-Churio JO (ed) Colombia Diversidad Biótica X: Cambio global (natural) y climático (antrópico) en el Páramo colombiano. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, pp. 181-287.
	31	Sumapaz, Meta-Cundinamarca, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam. - Cleef AM, Rangel-Churio JO, Arellano H (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T (ed) Estudios de Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz, Vol. 7, J. Cramer, Stuttgart, pp. 799-913.
	29	Tatamá, Chocó-Risaralda, CO	- Cleef AM, Rangel-Churio JO, Salamanca S, Ariza CL, van Reenen GBA (2005) La vegetación del Páramo del Macizo de Tatamá, Cordillera occidental, Colombia. In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds) La Cordillera Occidental Colombiana Tansecto Tatamá. Studies on tropical Andean ecosystems, Vol 6, J.Cramer, Berlin-Stuttgart.
	21	Cocuy, Boyacá, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	7	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	6	Neusa, Cundinamarca, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	6	Puracé, Cauca, CO	- Duque AN, Rangel-Churio JO (1991) Analisis Fitosociologico de la vegetación Paramuna del Parque Natural Puracé. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 256-276.

Clusters	**Number of plots**	**Locality**	**Source**
Cluster 5(2)	6	Cruz Verde, Cundinamarca, CO	- Lozano GC, Schnetter R (1976) Estudios ecologicos en el páramo de Cruz Verde, Colombia: 2. Las comunidades vegetales. Caldasia 11(54): 53-68.
	4	La Rusia, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	3	los Nevados, Caldas-Tolima-Risaralda, CO	- Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	2	Papallacta, Pichincha, EC	- Peyre G. Unpublished data
	1	Monserrate, Cundinamarca, CO	- Vargas R, Zuluaga S (1985) La vegetación del Páramo de Monserrate. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada. Instituto de Ciencias Naturales, Universidad Nacional, Bogotá.
	1	Pisva, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
Cluster 6	96	los Nevados, Caldas-Tolima-Risaralda, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
Cluster 7	34	Guandera, Carchi, EC	- Moscol-Olivera MC, Cleef AM (2009) A phytosociological study of the Páramo along two altitudinal transects in El Carchi province, northern Ecuador. Phytocoenologia, 39(1): 79-107.
	19	El Angel, Carchi, EC	- Moscol-Olivera MC, Cleef AM (2009) A phytosociological study of the Páramo along two altitudinal transects in El Carchi province, northern Ecuador. Phytocoenologia, 39(1): 79-107. - Peyre G. Unpublished data
Cluster 8	20	Cajas, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	18	El Altar, Chimborazo, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	18	Cotacachi, Imbabura, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.

Clusters	**Number of plots**	**Locality**	**Source**
Cluster 8(2)	18	Comunidad Daldal, Chimborazo, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	14	Chiles, Carchi, EC	- Ramsay P (2001) The zonal Páramo vegetation of Volcán Chiles. In: Ramsay P (ed) The Ecology of Volcán Chiles High altitude ecosystems on the Ecuador-Colombia border. University of Plymouth. Pebble & Shell Publications, Plymouth, pp. 27-38. - Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor. - Peyre G. Unpublished data
	9	Zapote-Najda, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	8	Cumbe, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	8	Guamaní, Pichincha, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	7	Saraguro, Loja, EC	- Peyre G. Unpublished data
	4	San Francisco, Zamora-Chinchipe, EC	- Bussmann RW (2002) Estudio fitosociológico de la vegetación en la Reserva Biológica San Francisco (ECSF) Zamora Chinchipe. Publicaciones Herbario LOJA Nº8, Loja.
	4	Espindola, Piura, PE	- Peyre G. Unpublished data
	3	Oña, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	3	Achupallas, Chimborazo, EC	- Peyre G. Unpublished data
	3	Laguna Negra, Piura, PE	- Peyre G. Unpublished data
	2	Laguna de Mojanda, Imbabura, EC	- Peyre G. Unpublished data
	2	Salinas, Bolívar, EC	- Peyre G. Unpublished data
	2	Illinizas, Cotopaxi, EC	- Peyre G. Unpublished data
	1	Papallacta, Pichincha, EC	- Peyre G. Unpublished data
	1	Pichincha, Pichincha, EC	- Peyre G. Unpublished data
	1	Corazón, Pichincha, EC	- Peyre G. Unpublished data
Cluster 9	13	Pichincha, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Peyre G. Unpublished data
	13	Cotopaxi, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Balslev H, de Vries T (1991) Life forms and species richness in a bunch grass páramo on Mount Cotopaxi, Ecuador. In: Erdelen W, Ishwaran N, Muller PP (eds) Proceedings of the International and Interdisciplinary Symposium Tropical Ecosystems, Margraf Scientific Books, Weikersheim, pp. 45-58.

Clusters	Number of plots	Locality	Source
Cluster 9(2)	12	Chimborazo, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Peyre G. Unpublished data
	9	Antisana, Napo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	8	Illinizas, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Peyre G. Unpublished data
	4	San Juan, Chimborazo, EC	- Peyre G. Unpublished data
	3	Cayambe, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	3	Rumiñahui, Pichincha, EC	- Peyre G. Unpublished data
	2	Salinas, Bolívar, EC	- Peyre G. Unpublished data
Cluster 10	80	los Nevados, Caldas-Tolima-Risaralda, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	8	Sumapaz, Meta-Cundinamarca, CO	- Cleef AM, Rangel-Churio JO, Arellano H (2008) The páramo vegetation of the Sumapaz massif (Eastern Cordillera, Colombia). In: van der Hammen T (ed) Estudios de Ecosistemas Tropandinos: La Cordillera Oriental Colombiana-Transecto Sumapaz, Vol. 7, J. Cramer, Stuttgart, pp. 799-913.
Cluster 11	24	El Altar, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	20	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	15	Quilimas, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	12	Saraurcu, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	9	Llanganates, Tungurahua, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.

Clusters	Number of plots	Locality	Source
Cluster 11 (2)	9	Guamaní, Pichincha, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	7	Carihuairazo, Tungurahua, EC	- Peyre G. Unpublished data
	6	Imbabura, Imbabura, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	6	Yanaurcu, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	6	Cotacachi, Imbabura, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	5	Sumapaz, Meta-Cundinamarca, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	5	Antisana, Napo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	5	Cajas, Azuay, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	4	Cayambe, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	4	Puracé, Cauca, CO	- Duque AN, Rangel-Churio JO (1991) Analisis Fitosociologico de la vegetación Paramuna del Parque Natural Puracé. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 256-276.
	4	Chiles, Carchi, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	4	Papallacta, Pichincha, EC	- Peyre G. Unpublished data
	3	Cotacachi, Imbabura, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	3	Igualita, Tungurahua, EC	- Peyre G. Unpublished data
	2	San Juan, Chimborazo, EC	- Peyre G. Unpublished data
Cluster 12	24	Tungurahua, Tungurahua, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	10	Antisana, Napo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	10	Cayambe, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.

Clusters	Number of plots	Locality	Source
Cluster 12 (2)	10	Illinizas, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	9	Cotacachi, Imbabura, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	7	Chiles, Carchi, EC	- Sklenář P (2001) Superpáramo flora and vegetation of Volcán Chiles. In: Ramsay P (ed) The Ecology of Volcán Chiles High altitude ecosystems on the Ecuador-Colombia border. University of Plymouth. Pebble & Shell Publications, Plymouth, pp. 39-45. - Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	4	Chimborazo, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	4	El Altar, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	4	los Nevados, Caldas-Tolima-Risaralda, CO	- Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	3	Quilimas, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	3	Pichincha, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	2	Saraurcu, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	2	Cumbe, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
Cluster 13	46	Chimborazo, Chimborazo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague. - Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor. - Peyre G. Unpublished data
	9	Cotopaxi, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	5	Antisana, Napo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	3	El Arenal, Bolívar, EC	- Peyre G. Unpublished data
	1	Illinizas, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos.PhD thesis.Charles University, Prague.

Clusters	Number of plots	Locality	Source
Cluster 14	24	San Francisco, Zamora-Chinchipe, EC	- Bussmann RW (2002) Estudio fitosociológico de la vegetación en la Reserva Biológica San Francisco (ECSF) Zamora Chinchipe. Publicaciones Herbario LOJA Nº8, Loja.
	20	Chingaza, Cundinamarca, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación del Parque Nacional Natural Chingaza. In: Rangel-Churio JO (ed) La región de vida paramuna. Colombia diversidad Biótica III. Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá, pp. 720-753. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	13	Cruz Verde, Cundinamarca, CO	- Rivera DO. Unpublished data
	12	Puracé, Cauca, CO	- Duque AN, Rangel-Churio JO (1991) Analisis Fitosociologico de la vegetación Paramuna del Parque Natural Puracé. In: Rangel-Churio JO (ed) vegetación y Ambiente en tres gradientes montañosos de Colombia. PhD Thesis, University of Amsterdam, The Netherlands, pp. 256-276.
	10	Cocuy, Boyacá, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	10	Sallique, Cajamarca, PE	- Peyre G. Unpublished data
	9	Chingaza, Cundinamarca, CO	- Franco PR, Rangel-Churio JO, Lozano GC (1986) Estudios ecologicos en la cordillera oriental- II Las comunidades vegetales de los alrededores de la Laguna de Chingaza (Cundinamarca). Caldasia, 15(71-75): 219-243.
	9	Palambe, Cajamarca, PE	- Peyre G. Unpublished data
	8	Sierra Nevada de Mérida, Mérida, VE	- Berg AL (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157-203.
	8	Cuello del Inca, Piura, PE	- Peyre G. Unpublished data
	7	Frontino, Antioquía, CO	- Rangel-Churio JO, Sánchez D, Ariza CL (2005) La vegetación del Páramo de Frontino. In: van der Hammen T, Rangel-Churio JO, Cleef AM (eds). La Cordillera Occidental Colombiana Tansecto Tatamá. Studies on tropical Andean ecosystems, Vol 6, Ed. J.Cramer, Berlin-Stuttgart.
	7	los Nevados, Caldas-Tolima-Risaralda, CO	- Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	7	Chimborazo, Chimborazo, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor. - Peyre G. Unpublished data
	7	Nepes, Trujillo, VE	- Peyre G. Unpublished data

Clusters	Number of plots	Locality	Source
Cluster 14 (2)	6	Santo Domingo, Cauca-Huila, CO	- Rangel-Churio JO, Franco PR (1985) Observaciones fitoecologicas en varias regiones de vida de la cordillera central de Colombia. Caldasia, 14(67): 211-249.
	6	Lago de Tota, Boyacá, CO	- Rangel-Churio JO, Aguirre JC (1986) Estudios ecologicos en la cordillera oriental colombiana, III La vegetación de la cuenca del Lago de Tota (Boyacá). Caldasia 15(71-75): 264-311.
	6	Tungurahua, Tungurahua, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor. - Peyre G. Unpublished data
	6	Laguna Coromoto, Mérida, VE	- Peyre G. Unpublished data
	6	Laguna Negra, Piura, PE	- Peyre G. Unpublished data
	6	Cruz Chiquita, Piura, PE	- Peyre G. Unpublished data
	6	Espindola, Piura, PE	- Peyre G. Unpublished data
	4	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	4	Cajas, Azuay, EC	- Peyre G. Unpublished data
	4	Achupallas, Chimborazo, EC	- Peyre G. Unpublished data
	4	Zumbador, Táchira, VE	- Peyre G. Unpublished data
	4	San José, Mérida, VE	- Peyre G. Unpublished data
	3	Cotopaxi, Pichincha, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	3	las Rosas, Trujillo, VE	- Peyre G. Unpublished data
	3	Colasay, Cajamarca, PE	- Peyre G. Unpublished data
	2	Neusa, Cundinamarca, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	2	Illinizas, Pichincha, EC	- Peyre G. Unpublished data
	2	Saraguro, Loja, EC	- Peyre G. Unpublished data
	1	Antisana, Napo, EC	- Sklenář P (2000) Vegetation ecology and phytogeography of Ecuadorian superpáramos. PhD Thesis Charles University, Prague.
	1	Pisva, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	1	Yerba Buena, Chimborazo, EC	- Peyre G. Unpublished data
	1	San Martin, Chimborazo, EC	- Peyre G. Unpublished data
	1	Cendé, Trujillo, VE	- Peyre G. Unpublished data
	1	Niquitao, Trujillo, VE	- Peyre G. Unpublished data
Cluster 15	36	Guaramacal, Trujillo, VE	- Cuello NL, Cleef AM (2009) The Páramo vegetation of Ramal de Guaramacal, Trujillo State, Venezuela. 1. Zonal communities. Phytocoenologia, 39(3): 295-329.
	2	Zumbador, Táchira, VE	- Peyre G. Unpublished data
Cluster 16	22	Cocuy, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.

Clusters	Number of plots	Locality	Source
Cluster 16 (2)	9	Sumapaz, Meta-Cundinamarca, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	6	Nariño, Nariño, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Churio JO (ed) Colombia diversidad biótica III. La región paramuna de Colombia, Unibiblos, Universidad Nacional de Colombia, Bogotá, pp. 754-784.
	6	Pisva, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	6	Santo Cristo, Mérida, VE	- Berg AL (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. Phytocoenologia 28(2): 157-203.
	5	Almorzadero, Santander, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	5	La Rusia, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
	2	Lago de Tota, Boyacá, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam.
Cluster 17	21	los Nevados, Caldas-Tolima-Risaralda, CO	- Salamanca S (2003) Recovery of the páramo vegetation after the 1985 eruption on the Ruiz Volcano. In: van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	16	Cocuy, Boyacá, CO	- Sturm H, Rangel-Churio JO (1985) Estudios generales. In: Sturm H, Rangel-Churio JO (eds) Ecologia de los páramos andinos: Una visión preliminar integrada,Instituto de Ciencias Naturales, Universidad Nacional, Bogotá. - Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.
	11	Cruz Verde, Cundinamarca, CO	- Rivera DO. Unpublished data
	7	Cajas, Azuay, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor. - Peyre G. Unpublished data
	6	Almorzadero, Santander, CO	- Cleef AM (1981) The Vegetation of the páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae, University of Amsterdam, Amsterdam. - Salamanca S, Cleef AM, Rangel-Churio JO (2003) The páramo vegetation of the volcanic Ruiz-Tolima massif. In: Van der Hammen T, dos Santos A (eds) La Cordillera Central Colombiana Tansecto Parque Los Nevados. Studies on tropical Andean ecosystems, Vol 5, J.Cramer, Berlin-Stuttgart.

Clusters	Number of plots	Locality	Source
Cluster 17 (2)	4	Guamaní, Pichincha, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	4	Corazón, Pichincha, EC	- Peyre G. Unpublished data
	4	Yerba Buena, Chimborazo, EC	- Peyre G. Unpublished data
	3	El Altar, Chimborazo, EC	- Ramsay P (1992) The Páramo Vegetation of Ecuador: The Community Ecology Dynamics and Productivity of Tropical Grasslands in the Andes. Phd thesis, University of Wales, Bangor.
	3	Salinas, Bolívar, EC	- Peyre G. Unpublished data
	3	Quilotoa, Cotopaxi, EC	- Peyre G. Unpublished data
	2	Chingaza, Cundinamarca, CO	- Rangel-Churio JO, Ariza CL (2000) La vegetación del Parque Nacional Natural Chingaza. In: Rangel-Churio JO (ed) La región de vida paramuna. Colombia diversidad Biótica III. Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá, pp. 720-753.
	2	Pichincha, Pichincha, EC	- Peyre G. Unpublished data
	2	Illinizas, Pichincha, EC	- Peyre G. Unpublished data
	2	Achupallas, Chimborazo, EC	- Peyre G. Unpublished data
	2	Rumiñahui, Pichincha, EC	- Peyre G. Unpublished data
	1	San Martin, Chimborazo, EC	- Peyre G. Unpublished data

Appendix 5

Relations between the clusters of the 17 and 89 partitions according to their plot composition (pertinence of the smallest Bray-Curtis distance between clusters): VE Venezuela, CO Colombia, EC Ecuador, PE Peru.

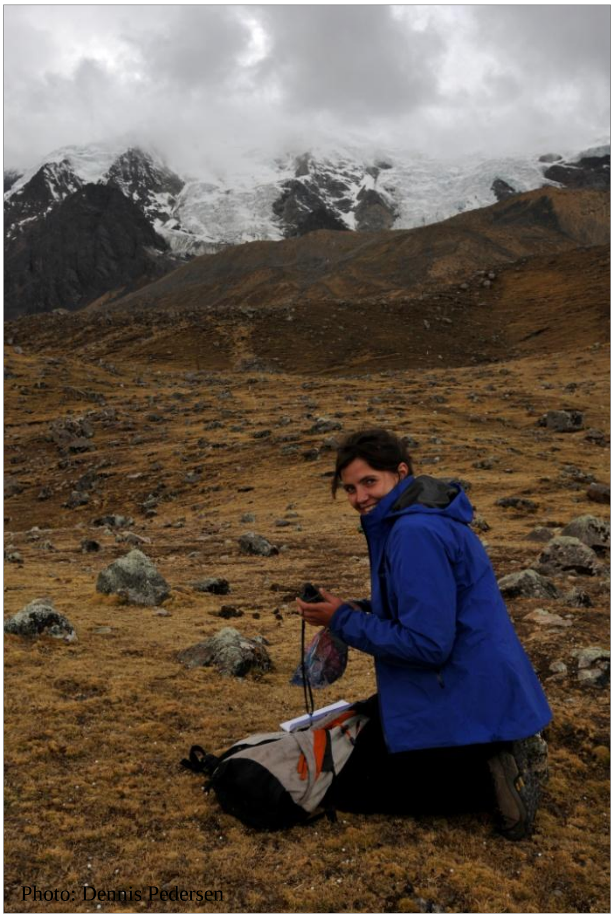
Partition 17 clusters	**Partition 89 clusters**
Cluster 1	Páramo *Espeletia schultzii* community with low shrubs and herbs (VE); Mixed community of *Chaetolepis lindeniana* and *Espeletia schultzii* (VE); Dry super-páramo of Espeletinae (VE)
Cluster 2	Humid upper C*alamagrostis effusa* grassland (1) (Santa Marta, CO); Humid upper C*alamagrostis effusa* grassland (2) (Santa Marta, CO); Mixed C*alamagrostis intermerdia* grassland with shrubs (1) (Périja, CO); Mixed C*alamagrostis intermerdia* grassland with shrubs (2) (Périja, CO); Dry páramo *Plantago sericea* community (Dpt. Boyacá, CO); Bamboo community with shrubs (Périja, CO); Mixed grassland of C*alamagrostis effusa* with *Espeletia colombiana/lopezii* (Dpt. Boyacá, CO)
Cluster 3	Mixed grassland of C*alamagrostis effusa* with *Espeletia grandiflora* and shrubs (Eastern Cordillera, CO); Mixed grassland of C*alamagrostis effusa* with *Arcytophyllum nitidum* and *Hypericum juniperinum* (Eastern Cordillera, CO); Humid C*alamagrostis effusa* grassland (Cruz Verde, CO); Humid shrubby páramo (Eastern Cordillera, CO); grassland with shrubs and bamboo (Cruz Verde, CO); Mixed grassland with bamboo (Chingaza, CO); Semi-humid C*alamagrostis effusa* grassland with *Espeletia grandiflora* and *Carex* spp. (Sumapaz, CO); Páramo mixed shrubland of *A. nitidum* and *E. argentea* (Eastern Cordillera, CO)
Cluster 4	Grassland of C*alamagrostis effusa* with *Blechnum loxense* and *Espeletia hartwegiana* (Nariño, CO); Grassland with shrubs (Western Cordillera, CO); Mixed páramo shrubland with bamboo (Western Cordillera, CO); Páramo D*iplostephium* spp. shrubland (Puracé, CO); Mixed *Calamagrostis* spp. grassland from Puracé (CO); Mixed páramo shrubland of *Diplostephium* spp. and *Hypericum* spp. with bamboo (CO); Poor Pernettya prostrata community (Central Cordillera, CO)
Cluster 5	Lower super-páramo *Loricaria complanata* community (CO); Mixed shrubland of *Hypericum spp.* with tussocks and rosettes (Chingaza, CO); Páramo shrubland with *Cortaderia nitida* (Sumapaz, CO); semi-humid C*alamagrostis effusa* grassland (Frontino, CO); C*alamagrostis effusa* grassland with *Espeletia frontinoensis* and shrubs (Frontino, CO); Mixed grassland (bamboo and *Calamagrostis*) with *Loricaria complanata* and shrubs (Tatama, CO); Humid páramo bamboo community (Chingaza, CO); poor secundary succession C*alamagrostis effusa* grassland (CO); Mixed shrubland of *Aragoa abietina* (Chingaza, CO)
Cluster 6	Upper páramo mixed C*alamagrostis recta* grassland with *Espeletia hartwegiana* (Nevados, CO); Upper páramo mixed grassland with shrubs (Nevados, CO); Páramo grassland of C*alamagrostis effusa* with *Espeletia hartwegiana* (Central Cordillera, CO); Páramo *Hypericum laricifolium* secundary succession community (EC-CO); Upper páramo meadow (Nevados, CO); Remnant shrublands of *Myrsine* and *Gynoxys* (Frontino, CO)
Cluster 7	Páramo C*alamagrostis effusa* grassland with *Espeletia pycnophylla* (Carchi, EC)
Cluster 8	Semi humid C*alamagrostis intermedia* grassland (1) (EC); Semi humid C*alamagrostis intermedia* grassland (2) (EC); Semi-dry C*alamagrostis intermedia* grassland (Loja, EC); Semi-humid C*alamagrostis intermedia* grassland (Cajas, EC); Humid C*alamagrostis intermedia* grassland (PE-EC); Semi-dry C*alamagrostis intermedia* grassland (Cotacachi, EC); Low altitude grassland (Podocarpus, EC); C*alamagrostis intermedia* disturbed grassland (EC)
Cluster 9	Upper páramo grassland with cushions (EC); Super-páramo meadows and pioneer vegetation (EC)
Cluster 10	Super-páramo blue meadows and subnival community (Nevados, CO); Upper super-páramo with *Agrostis* spp. (Nevados, CO); Lower super-páramo shrubland of Asteraceae (Nevados, CO); Lower humid super-páramo with low shrubs (Sumapaz, CO)

Partition 17 clusters	**Partition 89 clusters**
Cluster 11	Humid lower cushion and tussocks super-páramo (EC); Super-páramo cushion community (EC); Lower humid super-páramo with Ericaceae and *Loricaria* shrubs on cushions(CO-EC); Lower humid super-páramo of Asteraceae shrubs on cushions (EC-CO); Super-páramo cushion community (El Altar, EC); Super-páramo blue meadows (Puracé, CO)
Cluster 12	Pioneer humid super-páramo (Tungurahua, EC); Super-páramo *Calamagrostis ligulata* humid community (EC-CO); Semi-humid upper super-páramo (EC); Humid lower super-páramo (EC)
Cluster 13	Dry upper super-páramo (Chimborazo, EC); Pioneer super-páramo of *Monticalia microdon* (Cotopaxi, EC); Lower desertic super-páramo with *Chuquiraga jussieui* (Chimborazo, EC)
Cluster 14	Mixed group of several shrubby communities (PE-EC-CO-VE); Sub-páramo shrubland (Podocarpus, EC); Sub-páramo mixed shrubland with *Drimys granadensis* and *Weinmannia spp.* (Chingaza, CO); Sub-páramo shrubland (Cruz Verde, CO); Mixed *Calamagrostis tarmensis* grassland with shrubs (PE); Sub-páramo shrubland (Nepes, VE); Sub-páramo mixed shrubland (PE); Mixed sub-páramo shrubland (Chingaza, CO); Sub-páramo *Chusquea spencei* community (CO-VE)
Cluster 15	Sub-páramo (Guaramacal, VE); Sub-páramo shrubland (Zumbador, VE)
Cluster 16	Azonal páramo *Werneria pygmaea* bogs (CO); Azonal super-páramo *Werneria* cushion bog (Cocuy, CO); Azonal bogs of *Distichia muscoides* (CO); Azonal cushions communities of *Plantago rigida* (CO); Azonal *Carex amicta* mire (VE); Azonal *Oreobolus obtusangulus* bog (Eastern Cordillera, CO); Azonal *Muhlengergia fastigiata* meadow (CO)
Cluster 17	Semi-humid disturbed grasslands of *Calamagrostis rigida/Festuca ulochaeta* (Central Ecuador); Disturbed páramo meadows (Cruz Verde, CO); Disturbed meadows of *Aciachne pulvinata* and *Agrostis spp.* (Eastern Cordillera, CO)

Appendix 6

Multiple comparisons of the 17 clusters in pairs with the Steel-Dwass-Critchlow-Fligner bilateral test (Kruskall-Wallis test: obs.value 541. 327, p.value (< 0,0001).

Clusters	**mean of ranks**	**richness categories**							
16	311,310	1							
5	572,523		1						
15	625,408		1	1					
10	627,890		1	1					
13	668,847		1	1	1				
2	765,949			1	1				
17	840,841			1	1	1			
7	860,455			1	1	1			
12	874,374			1	1	1			
4	885,831				1	1			
3	915,185				1	1			
14	1051,088					1	1		
6	1150,971						1	1	
1	1168,597						1	1	
11	1206,069						1	1	
8	1358,304							1	
9	1554,515								1



Snowline is the limit…