Article

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Altitudinal zonation of mosses in west of the Sierra Nevada of Cocuy, Boyacá, Colombia

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ABSTRACT – (Altitudinal zonation of mosses in west of the Sierra Nevada of Cocuy, Boyacá, Colombia). This study was carried out with bryophyte populations in order to study the presence of populations and how they change over altitudinal gradients. Mosses were chosen as a model to do this study because they have a high sensitivity to climatic conditions and wide distribution. The western region of the Sierra Nevada del Cocuy, Boyacá, Colombia has a wide range of climate and ecosystems due to its complex topography. Plots were sampled every 200 m from the peak of Mount Mahoma at 4,200 m a.s.l. south to the Chicamocha River canyon at 1,200 m a.s.l. Diversity and cover are analyzed in each plot from soil, rock and bark substrates. We found 80 species distributed in 29 families, with Pottiaceae and Brachytheciaceae the most diverse families. Ours results show a tendency of the diversity and the coverage to increase with altitude, and we observed five altitudinal belts with three populations defined by mosses species. The Páramo and Superpáramo belts are the richest ones.
Keywords: altitudinal gradient, bryophytes, forest structure, Sierra Nevada del Cocuy, species richness and composition, substrate

RESUMO – (Zonação altitudinal de musgos no oeste da Sierra Nevada del Cocuy, Boyacá, Colombia). Este estudo foi realizado com populações de briófitas, a fim de estudar a presença e de como as populações mudam nos gradientes altitudinais. Os musgos foram escolhidos como modelo para realizar este estudo, pois apresentam alta sensibilidade às condições climáticas e ampla distribuição. A região oeste da Sierra Nevada del Cocuy, Boyacá, Colombia possui clima e ecossistemas diferenciados devido à sua complexa topografia. Parcelas em cada 200 m alt. foram instaladas a partir do pico do Monte Mahoma a 4.200 m alt. ao sul do desfiladeiro do rio Chicamocha a 1.200 m alt. A diversidade e a cobertura do solo, da rocha e da casca foram analisadas em cada parcela. Foram encontradas 80 espécies distribuídas em 29 famílias, sendo Pottiaceae e Brachytheciaceae as famílias mais diversas. Nossos resultados mostram uma tendência à diversidade e a cobertura aumentar com a altitude. Observamos cinco faixas altitudinais com três populações definidas pelas espécies de musgos. As faixas Páramo e Superpáramo são as mais ricas.
Palavras-chave: bryophytes, estrutura florestal, gradiente altitudinal, riqueza e composição de espécies, Sierra Nevada del Cocuy, substrato

Introduction

The knowledge of richness, abundance and distribution of species and how they are assembled along the altitudinal gradients help to promote the long-term conservation of natural species (Korner 2007). Zoning studies help to determine the distribution of biological populations by sampling zones in altitudinal belts where specific ecological characteristics of the site have been described (Kessler 2000). The belt classification of bryophytes has been widely studied and several schemes have been proposed with terminology that varies with the region of the geographical studied area (Frahm & Gradstein 1991)

Floristic composition in montane ecosystems, the distribution of the plants in them, and the factors that influence the local diversity provide us data to study the

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relationships between species diversity and climate change (McCain & Grytnes 2010, Graham *et al.* 2014, Nascimbene & Spitale 2017) and can be used to improve conservation strategies (Socolar *et al.* 2016).

Colombia has a relatively stable climate, in the tropical zone, with its temperature ameliorated by the relief of the Andes mountain range. This mountainous complex provides a variety of environmental conditions that drives the diversification of species, and to date more than 27,000 species of plants and lichens are known to exist in this area (Bernal *et al.* 2015). Boyacá has the highest mountains in Colombia and has a relief so abrupt that just within a few kilometers several thermal floors strongly differentiated by vegetation and temperature can be found (Governación de Boyacá 2018, IGAC 2008, León *et al.* 2000).

Mosses are very important plants within the Andean ecosystems because they fulfill vital functions such as water regulation, generation of organic matter, nitrogen fixation and soil protection (Churchill & Linares 1995, Glime 2001, Slack 1988). They are high diversified in tropical environments (Gradstein *et al.* 2001, Churchill & Linares 1995) and widely known to be bioindicators (Proctor & Tuba 2002) by their sensitivity to heavy metals (Taylor 1919, Glime 1994), soil acidity (Clymo 1987), air quality (Simijaca *et al.* 2014), water quality (Martínez-Abaigar *et al.* 1993), and UV-B radiation (Searles *et al.* 2002). Due their simple anatomy they can be extremely affected by environmental changes (Spitale 2016, Proctor 1990) thereby aiding in the evaluation and classification of altitudinal belts of environmental quality (Kessler 2000).

Mosses also play a wide range of interactions with other species in the ecosystem as they contribute to the renewal of forests by facilitating seed germination (Glime 2001), and by providing protection and food to several invertebrate groups (Gerson 1982, 1984, Glime 1994). Bryophytic relationships with roots and mycorrhizae form complex assemblages in some areas, achieving equilibrium in the ecosystem (Cornelissen *et al.* 2007). These features are totally related to altitudinal gradients due to changes in humidity, temperature and soil (Stehn *et al.* 2010).

Generally species richness increases with altitude, which is typically related to an increase in humidity (Lee & Roi 1979), microclimate variables (Raabe *et al.* 2010) and the variety of available substrates (Mills & Macdonald 2005). These variables influence moss communities more than forest structure (Márialigeti *et al.* 2009) even though bryophytes show tolerances to extreme conditions (Bruun *et al.* 2006).

The type of substrate has been widely discussed although it has been suggested that some species are substrate specialists (Söderström 1988, 1993) and others generalists (Frego & Carleton 1995). Substrate colonization preference is mediated by the response of mosses to the assemblages related to the micro- and macrohabitat, they are indicative of the importance of the microtopography of the substrate and the degree of light with respect to the gradient (Halpern *et al.* 2014).

Epiphytic mosses are more influenced by altitudinal gradient than terrestrial mosses (Spitale 2016, Chen *et al.* 2017). Halpern *et al.* (2014) emphasized the importance of including all substrate colonized in order to understand the abundance and diversity of bryophytes in forests once studies with this focus were carried out over very small altitudinal gradients and in countries with different climates in latitudes far from the Neotropics. The zonation of bryophytes was studied in Latin America by Wolf (1993), Van Reenen & Gradstein (1983), Gradstein & Frahm (1987), Frahm & Gradstein (1991), and Kessler (2000), Santos & Costa (2010) but no such study has been made in the eastern hills of Colombia.

This study compares the diversity of mosses along an altitudinal gradient on the west slope of the Sierra Nevada del Cocuy (Boyacá, Colombia). The aim is to determine the replacement and composition of species by means of a Bray-Curtis analysis (cluster) and to understand the variables that influence the distribution of mosses in this region by means of a multivariate analysis.

Material and methods

Study area and sampling design - Boyacá is a department located in the center of Colombia on the eastern mountain range of the Andes, its northern border is with Santander and there it hosts a mountainous complex called the Serranía del Cocuy with the tallest mountains of Colombia. This site has an enormous variety of ecosystems and climates due to its relief that ranges from 1,000 to 5,500 m a.s.l., the highest point is the top of Mount Mohammed at west side of the Sierra Nevada del Cocuy. This site includes the rural area of the municipalities of Cocuy, Panqueba, Guacamayas, El Espino and Boavita. The lowest points converge at the Chicamocha River, where it crosses the canyon south of the municipality of Tipacoque at 1,200 m a.s.l. (IGAC 2008).

Collections were made along an altitudinal gradient from 1,200 to 4,200 m a.s.l., the sampling plots (with 2 plots of 10 × 10 m on soil, rock and 10 tree trunks with a diameter at breast height - DBH - greater than 10 cm) were established every 200 altitudinal meters, with a total of 16 sampling points (figure 1). We collected data of relative humidity, temperature, vegetation characteristics, disturbance aspects, proximity to water tributaries among other aspects, following the methodology of BRYOLAT for altitudinal studies (Frahm & Gradstein 1991, Ah-Peng *et al.* 2014, Hernández-Hernández *et al.* 2017).

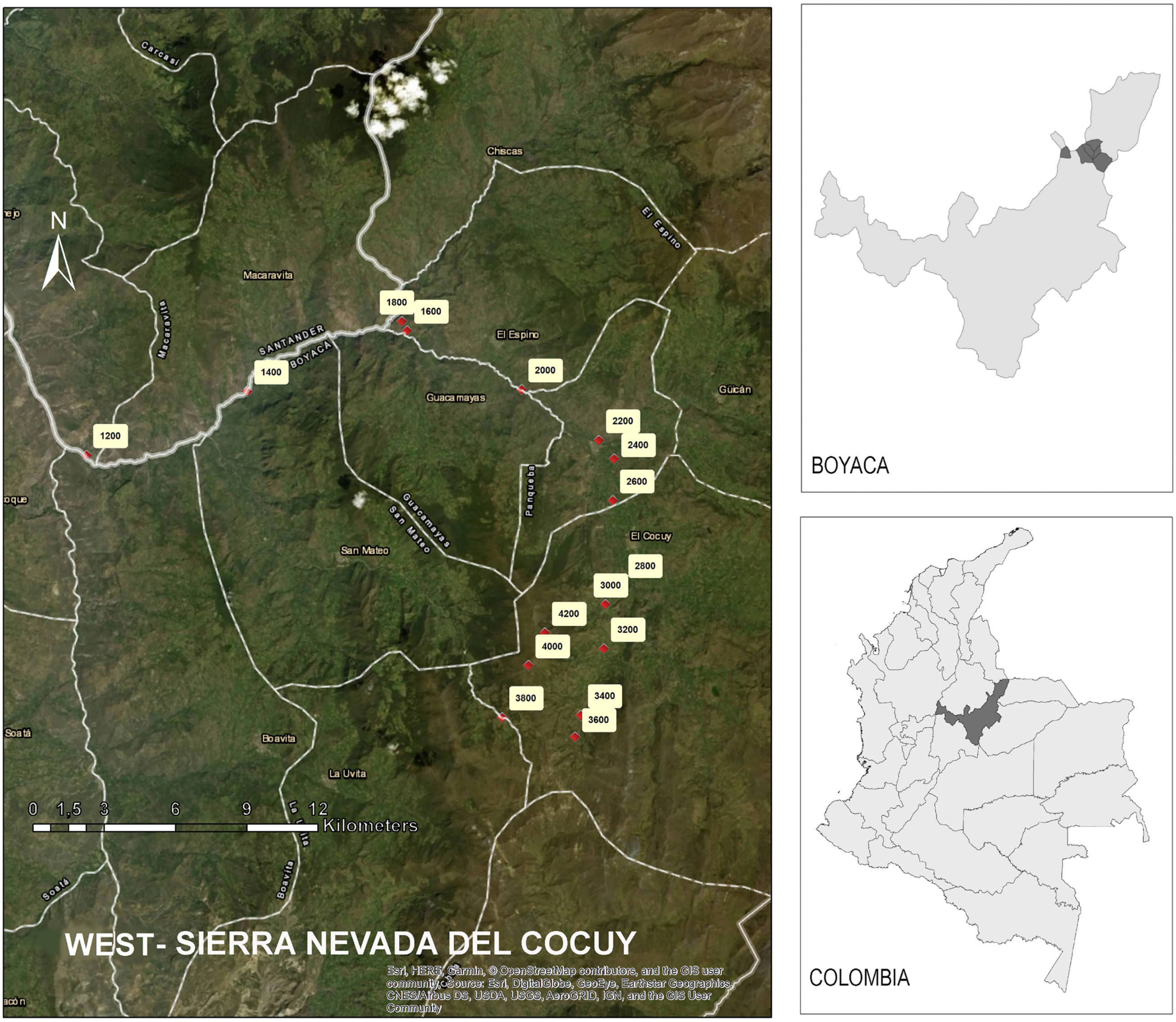

Figure 1. Location of the 16 points in the sampling area within the municipalities of El Cocuy, Panqueba, El Espino, Guacamayas and San Mateo, Department of Boyacá, Colombia.

Description and characterization of the altitudinal belts - Superpáramo (3,800 4,200 m a.s.l.) (figure 2 a): These areas have scarce vegetation that grows on rocks and sandy soils at the snow line. It is at the limit of three páramo zones: the temperatures are extreme and frequently dip to the freezing point, precipitation is incessant, winds often reach high speeds. Due to the extreme environmental conditions, access to these areas is difficult and thus there has been little disturbance by man. The superpáramo contains a very high level of endemism (Baruch 1984, Cleff 1978). There are no arboreal phorophytes, only small shrubs of *Polylepis*, *Pentacalia* and *Espeletia*, species of the family Ericaceae and Asteraceae, and large grasslands dominated by the genera *Calamagrostis* and *Agrostis* growing among rocks on the peaks of the mountains. Páramo (3,200 3,600 m a.s.l.) (figure 2 b): Tropical Subalpine Forest (Gradstein & Frahm 1987), fourth thermal floor (Van Reenen & Gradstein 1984), Subalpine Forest (Frahm 1990). This area is a particular tropical ecosystem characterized by low temperatures, high atmospheric pressure, intense radiation, high humidity and extreme changing conditions (Cuatrecasas 1968, Van der Hammen & Cleef 1986). The vegetation of the páramos comprises areas of low shrubs known as "pajonales" and "frailejonales" with *Espeletia*, *Puya*, *Polylepis*, *Pentacalia, Gynoxys*, *Werneria* and *Aciachne*. Subpáramo (2,600 3,000 m a.s.l.) (figure 2 c)**:** High tropical montane forest (Gradstein & Frahm 1987, Frahm 1991), third thermal floor (Van Reenen & Gradstein 1984), tropical subalpine forest (Frahm & Gradstein 1991). This is a transition zone between the high Andean forest and the páramo, characterized by being very humid and dominated by low shrubs such as the genus *Baccharis*, *Hypericum*, *Gaultheria* and *Sambucus*.

Figure 2. Zonal outline of the different sampling points. a. Superpáramo. b. Páramo. c. Subpáramo. d. High Forest. e. Low Montane Forest, Department of Boyacá, Colombia.

However, there are also scattered and isolated patches of forest that are dominated by the genera *Miconia*, *Escallonia*, and *Diplostephium* with height not exceeding 10 m (Cuatrecasas 1934, 1958). These areas are threatened by deforestation for agricultural exploitation and the creation of pastures for cattle grazing. High Andean forest (2,000 2,400 m a.s.l.) (figure 2 d)**:** Tropical montane forest (Gradstein & Frahm 1987, Frahm 1991), second thermal floor (Van Reenen & Gradstein 1984), Andean forest (Cuatrecasas 1958), high montane tropical forest (Frahm & Gradstein 1991). In these zones the climate becomes more temperate, plant cover increases considerably, and soils have a large amount of humid organic matter (Frahm & Gradstein 1991). The ground is sometimes covered with large grazing areas and epiphytic moss mats become prominent in the areas of woody vegetation of a greater height, dominated by trees of the genera *Escallonia*, *Salix*, *Quercus*, *Pinus*, *Eucalyptus*, *Schinus* and *Acacia*. These areas are strongly influenced by the presence of the Nevado River, with riparian forests among the tributaries and fog at the highest points. The mosses of this area are important for the conservation of water resources; they also contribute to the preservation of microhabitats for microfauna and facilitate seed germination of native species (Cornelissen *et al.* 2007). Montane-low forest (1,200 1,800 m a.s.l.) (figure 2 e)**:** Submontane tropical forest (Gradstein & Frahm 1987, Frahm 1991), first thermal floor (Van Reenen & Gradstein 1984), lowlands (Grubb & Whitmore 1967). This area consists primarily of very dry, desert areas of high temperatures with thorn scrub-type xerophytic to subxerophytic vegetation, although there are also forest types in the highest or transitional sites (Cuatrecasas 1958). The soils lack organic matter, and some authors have highlighted the presence of arid, cardonal pajonales and a vegetation typical of dry forests (Hernández *et al.* 1992, Rangel 1995). These forests contain a great diversity of cacti with *Opuntia*, *Wigginsia*, *Mammillaria* and *Echinopsis*; the common low trees are *Prosopis*, *Mielochia, Schinus*, *Gyrocarpus*, and *Lipia*, and grasses like *Cyperus*. This vegetation type has similarities with the tropical dry forest located towards the Caribbean coast and in the Patia Valley (Albesiano & Rangel 2006).

Collection and data analysis: The coverage of each of the samples were taken with a transparent acetate template of 20 × 22 cm with 1 cm quadrants (modified from Iwatsuki 1960). Specimens collected were air-dried (Churchill & Linares 1995, Gradstein *et al.* 2001) and deposited in the herbarium of Universidad Distrital "Francisco José de Caldas" (UDBC).

Specimen determinations follow Churchill & Linares (1965), Zander (1972), Monte (1977). Griffin & Morales (1983), Cárdenas (1995), Duarte (1997), Gradstein *et al.* (2001), Muñoz (1999), Allen (2002), Calabrese (2006) and Frahm (1991).

A matrix was constructed with: Sample number, coverage, coordinates, substrate, humidity, temperature, description of ecosystem and type of soil. R program was used to determine the relationships between the species and the zones based on Simpson and Shannon indexes and the clusters using Bray-Curtis similarity index. PCord program was carried out in order to establish which variables are affecting the composition and structure of the mosses in each altitudinal belt.

Results

A total of 752 samples were collected from the 16 established sampling plots. We found 29 families and 80 species (table 1), including eight new records to Colombia and 36 for Boyacá according to the list of Gradstein *et al.* (2018). 65% of the species correspond to acrocarps and most are found on soils and rocks. The highest host specificity was found in epiphytes, and the families with the most species richness are Pottiaceae (15 spp.) and Brachytheciaceae (10 spp.). The composition of the forest along the altitudinal gradient (4,200 m a.s.l. to 1,200 m a.s.l.) was marked by five altitudinal belts: superpáramo, páramo, subpáramo, high-Andean forest and low montane forest.

Variations in diversity and coverage along the altitudinal gradient The Shannon and Simpson diversity and abundance indices show that diversity has a tendency to increase with altitude. Páramo and superpáramo (figure 3) show the highest values, which reaffirms the importance of the conservation of these ecosystems and the value that this region has at an ecological level (Cleef 1978, Luteyn 1992). The diversity of mosses on soil in all the altitudes was greater than that of the epiphytes because terrestrial mosses are less subject to climatic variability (Spitale 2016, Spitale 2016). In the literature the increase in altitude is associated with lower temperatures, more humid and cloudy climates; these ecological characters are optimal for a great diversity of mosses (Lee & Roi 1979, Kessler 2000, Bruun *et al.* 2006).

The Simpson indices show a lower dominance of species in the highest belts (3600 4200 m) and a high dominance in the lowest belts (1200 1600 m) (figure 4). The low belts have a low presence of species because of dry forest conditions with *Pseudocrossidium replicatum* dominating on soil and *Fabronia ciliaris* as the dominant epiphyte.

Cover analysis - The moss cover in low montane forests has a low value in comparison with the other altitudinal belts, since at 2,200 m there is a remarkable increase in moss cover with it decreasing only when reaching the superpáramo (figure 5). This trend in cover was also observed by Van Reenen & Gradstein (1983) in the Sierra Nevada of Santa Marta and Frahm (1990) in Borneo.

Table 1. Species of mosses present in the west of the Sierra Nevada of Cocuy, Boyacá, Colombia.

Species	Growth form	Substrate	Altitud (m a.s.l.)
Anacolia laevisphaera (Taylor) Flowers	Acrocarpic	Rock-Soil	4000-3600-3400-2000-1600
Andreaea rupestris Hedw.	Acrocarpic	Rock	4200
Anomobryum prostratum (Müll. Hal.) Besch.	Acrocarpic	Soil	3400
Barbula integrifolia (R.S. Williams) R.H. Zander	Acrocarpic	Bark	3800
Brachymenium klotzchii (Schwägr.) Paris	Acrocarpic	Bark	2400
Brachytecium conostomun (Taylor) A. Jaeger	Pleurocarpic	Soil	3600
Brachythecium plumosum (Hedw.) Schimp.	Pleurocarpic	Bark-Rock-Soil	3400-3000-2600
Brachythecium poadelphus Müll. Hal.	Pleurocarpic	Soil	3600
Brachythecium ruderale (Brid.) W.R. Buck	Pleurocarpic	Bark-Rock-Soil	3000-2800-2000
Brachythecium rutabulum (Hedw.) Schimp.	Pleurocarpic	Soil-Rock	3800-3000-2600
Brachythecium sp.	Pleurocarpic	Soil	3000
Breutelia polygastrica (Müll. Hal.) Broth.	Acrocarpic	Soil	4200
Bryum andicola Hook.	Acrocarpic	Bark-Rock-Soil	4200-4000-3800-3600-3200-3000-2800-2600-2400-2200-2000-1800
Bryum argenteum Hedw.	Acrocarpic	Bark-Rock-Soil	3600-2600-2400-1800
Campylopus andersonii (Müll. Hal.) A. Jaeger	Acrocarpic	Rock	2800
Campylopus fragilis Bruch & Schimp.	Acrocarpic	Rock -Soil	1600
Campylopus nivalis (Brid.) Brid.	Acrocarpic	Rock-Soil	4200
Campylopus sp.	Acrocarpic	Soil	3200
Catagonium brevicaudatum Müll. Hal. ex Broth.	Pleurocarpic	Bark-Rock	4200
Chryso-hypnum elegantulum (Hook.) Hampe	Pleurocarpic	Rock	2000
Cryphaea patens Hornsch. ex Müll. Hal.	Pleurocarpic	Bark	3200
Cryphaea ramosa (Mitt.) Mitt.	Pleurocarpic	Bark-Soil	4000-3800-3600-3400
Daltonia pulvinata Mitt.	Pleurocarpic	Bark	4000
Dicranum frigidum Müll. Hal.	Acrocarpic	Rock-Soil	4200
Entodon jamesonii (Taylor) Mitt.	Pleurocarpic	Bark-Rock-Soil	3600-3200-3000-2000
Erpodium beccari Müll. Hal.	Pleurocarpic	Bark	1400-1200
Erythrodontium longisetum (Hook.) Paris	Pleurocarpic	Bark-Rock	2600-2400-2200
Fabronia ciliaris (Brid.) Brid.	Pleurocarpic	Bark-Rock-Soil	2200-1800-1600-1400-1200
Fissidens angustelimbatus Mitt.	Acrocarpic	Soil	2000
Fissidens bryoides Hedw.	Acrocarpic	Soil	3400-1600
Fissidens curvatus Hornsch.	Acrocarpic	Soil	2200
Fissidens palmatus Hedw.	Acrocarpic	Soil	1600
Fissidens sp.	Acrocarpic	Soil	1200
Fissidens weirii Mitt.	Acrocarpic	Soil	2800
Fissidens zollingeri Mont.	Acrocarpic	Soil	3400
Grimmia donniana Sm.	Acrocarpic	Rock	3400 (New record to Colombia)
Grimmia elongata Kaulf.	Acrocarpic	Soil	4000-3400 (New record to Colombia)

continue

Table 1 (continuation)

Species	Growth form	Substrate	Altitud (m a.s.l.)
Grimmia fuscolutea Hook.	Acrocarpic	Rock	4000-3200 (New record to Colombia)
Groutiella chimborazensis (Spruce ex Mitt.) Florsch.	Acrocarpic	Bark	2000
Hedwigia ciliata (Hedw.) P. Beauv.	Acrocarpic	Rock	3400-3200 (New record to Colombia)
Hedwigidium integrifolium (P. Beauv.) Dixon	Acrocarpic	Rock	4200-4000-3800(New record to Colombia)
Hypnum cupressiforme Hedw.	Pleurocarpic	Bark-Rock-Soil	4200-4000-3800-3600-3400-3200-3000-2800
Leiomela aristifolia (A. Jaeger) Wijk & Margad.	Acrocarpic	Soil	4200
Leiomela bartramioides (Hook.) Paris	Acrocarpic	Rock-Soil	3800-3000-2800-2600-2400
Leptodontium flexifolium (Dicks.) Hampe	Acrocarpic	Bark-Soil	4200-4000-3800
Leptodontium proliferum Herzog	Acrocarpic	Bark	3600-3400
Leptodontium sp.	Acrocarpic	Bark-Rock-Soil	4200-3600-3200-3000
Leptodontium syntrichioides (Müll. Hal.) Kindb.	Acrocarpic	Bark	4000-3600
Leptodontium viticulosoides (P. Beauv.) Wijk & Margad.	Acrocarpic	Bark -Rock-Soil	4200-4000-3800-3600-3200-3000-2800-2600
Lepyrodon tomentosus (Hook.) Mitt.	Pleurocarpic	Bark	4000-3800
Leskeadelphus angustatus (Taylor) B.H. Allen	Pleurocarpic	Bark-Soil	2800-2600-2400-2200-2000-1800-1600
Macrocoma tenuis (Hook. & Grev.) Vitt	Acrocarpic	Bark-Soil	2000-1800
Macromitrium cirrosum (Hedw.) Brid.	Acrocarpic	Bark	4200-4000-2200
Macromitrium punctatum (Hook. & Grev.) Brid.	Acrocarpic	Bark	3800-2600
Macromitrium richardii Schwägr.	Acrocarpic	Bark	3800
Macromitrium scoparium Mitt.	Acrocarpic	Bark	3600
Macromitrium sp.	Acrocarpic	Bark	4200-3200
Meteoridium remotifolium (Müll. Hal.) Manuel	Pleurocarpic	Soil	2200-2000
Meteoridium tenuissimum (Hook. & Wilson) M.A. Lewis	Pleurocarpic	Bark	4000
Neckera ehrenbergii Müll. Hal.	Pleurocarpic	Bark	4000-3800-3600-3200-3000-2000
Palamocladium leskeoides (Hook.) E. Britton	Pleurocarpic	Bark-Soil	4200-4000
Philonotis sp.	Acrocarpic	Soil	1400
Pleurochaete squarrosa (Brid.) Lindb.	Acrocarpic	Soil	2400
Polytrichum juniperinum Hedw.	Acrocarpic	Soil	4200-4000-3800
Prionodon densus (Sw. ex Hedw.) Müll. Hal.	Pleurocarpic	Bark	4000
Pseudocrossidium replicatum (Taylor) R.H. Zander	Acrocarpic	Soil	1800-1600-1400-1200
Racomitrium crispipilum (Taylor) A. Jaeger	Acrocarpic	Soil	4200
Rhacocarpus purpuracens (Brid.) Paris	Pleurocarpic	Soil	4200
Rhynchostegium scariosum (Taylor) A. Jaeger	Pleurocarpic	Bark	3800-3400
Rhynchostegium serrulatum (Hedw.) A. Jaeger	Pleurocarpic	Soil	3000-3800-4000
Sematophyllum subpinnatum (Brid.) E. Britton	Pleurocarpic	Bark-Soil	3600-1600

continue

Table 1 (continuation)

Species	Growth form	Substrate	Altitud (m a.s.l.)
Streptocalypta lorentziana Müll. Hal.	Acrocarpic	Soil	1600 (New record to Colombia)
Synthrichia lacerifolia (R.S. Williams) R.H. Zander	Acrocarpic	Rock	2600 (New record to Colombia)
Syntrichia andicola (Mont.) Ochyra	Acrocarpic	Bark-Soil	3600
Syntrichia fragilis (Taylor) Ochyra	Acrocarpic	Bark-Rock-Soil	3600-3400-3200-3000-2800-2400-2200-2000-1800-1400
Syntrichia laevipila Brid.	Acrocarpic	Rock	3600 (New record to Colombia)
Syntrichia sp.	Acrocarpic	Rock	2600
Thuidium delicatulum (Hedw.) Schimp.	Pleurocarpic	Bark-Rock-Soil	4200-4000-3800-3600-2000
Thuidium peruvianum Mitt.	Pleurocarpic	Bark-Soil	3800
Zygodon sp.	Acrocarpic	Bark	4000

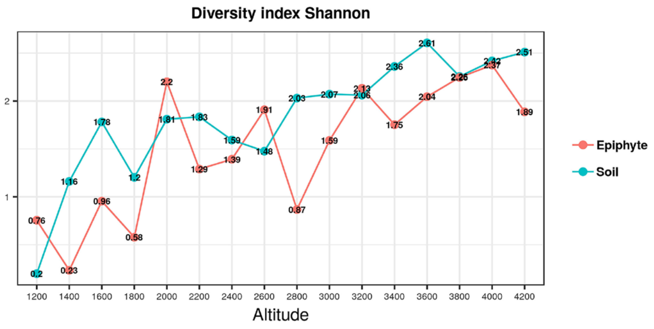

Figure 3. a. Behavior of the specific diversity index (Shannon-Wienner) along the altitudinal gradient. b. Specific diversity index (Shannon-Wiener) comparing epiphytic and soil mosses along the altitudinal gradient.

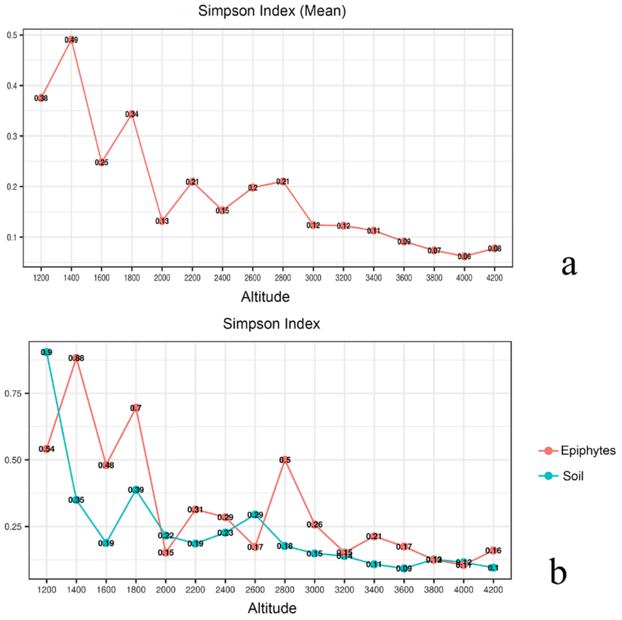

Figure 4. a. Species dominance (Simpson's Index) total along the altitudinal gradient. b. Species dominance (Simpson's Index) for epiphytic and soil mosses along the altitudinal gradient.

The moss cover shows an increase with altitude from the low montane forest to the high Andean forest with similar curves for soil and epiphytic substrates, and only at the páramo and superpáramo does the cover on soil become greater than that of epiphytic habitats (figure 6).

The Two-way analysis of Bray-Curtis (figure 7 a) shows well the structure in relation to the altitudinal zoning. Basically three groups are formed: (1) low montane forest (2) Andean high forest and parts of the sub-paramo and páramo (3) superpáramo and parts of the páramo. The zones with more unique elements correspond to the lower zones and the highest ones of the altitudinal gradient. The intermediate zones do not seem to have unique phytotaxonomic elements but rather the species composition is the result of the replacement and overlap of species from the surrounding altitudinal belts.

Cluster Analysis of the species at altitude belts studied shows interrelationship associations between nearby plots and it does not clearly differentiate the belts studied and the confidence is greater than 0.5 (figure 7 b).

A multidimensional scale ordering (figure 8) comparing the abundances of the species in the altitudinal ranges sampled (Bray-Curtis) shows a structural map of the altitudinal zoning, where the mosses located east of the Sierra

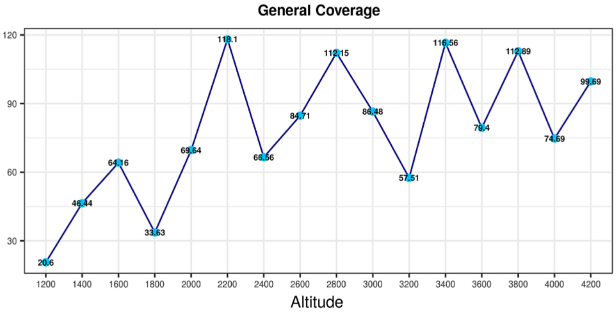

Figure 5. Total coverage of all species present at each altitudinal belt, Department of Boyacá, Colombia.

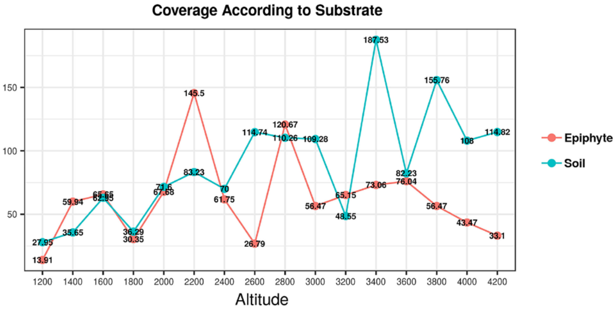

Figure 6. Average coverage of epiphytic and soil mosses for each altitudinal point, Department of Boyacá, Colombia.

Nevada de Cocuy have a fairly distributed dominance due to their large number of species and their variety of ecosystems. Indicator species of altitudinal or ecosystem conditions are pointed out, and some of these have been recognized in the literature, such as *Erpodium beccarii* indiative of dry tropical forests; the genera *Leptodontium*, *Grimmia* and *Andreaea* as typical to the páramos; and the genera *Brachymenium*, *Erythrodontium* and *Brachythecium* characteristic of humid tropical forests (Hernandez & Sanchez 1992: Churchill & Linares 1995).

The overlap of species between the altitudinal ranges show the assemblages among the niches available for the ecotone. There are three groups that share environmental characteristics and correspond to the species of low montane forest, high Andean forest and the páramos: the species with greater altitudinal ranges are acrocarpous ones from the families Pottiaceae, Bryaceae and Bartramiaceae (Stehn *et al.* 2010).

The analysis of canonical components of the vegetation shows the páramos (figure 9 a) as the richest in environmental variables with correspondingly greater diversity because they seem to be optimal for the growth and dispersal of mosses (Cleef 1978, Proctor *et al.* 2007, Glime 2017). Populations of low montane forest show a small group of mosses isolated from the rest due to habitat's high temperatures, low humidity and characteristic tropical dry forest vegetation (Albesiano *et al.* 2003, Smith & Stark 2014). The High Andean forest seems to contain a transitional or overlapping group of species between other altitudinal belts, with species adapted to temperate and warm climates as well described by Proctor (2000), Smith & Stark (2014) and Glime (2017) for species of dry ecosystems forming populations separated from the common niche.

The analysis of canonical components of the substrates (figure 9 b) shows relationships between the lower temperatures and higher humidity with rocks and soils clearly related to the large quantity of rocks and humus-rich, humid soils and the frequent fog at high elevations. The low relationship with the epiphytic species is because phorophyte size decreases with altitude, and woody substrates are more frequently colonized in low montane forests with dry conditions and generalists without a preferred substrate. This analysis shows how the populations of mosses distributed by substrate do not have a clear relation with environmental variables but rather their distribution is mediated by the availability of the resources found (Spitale 2016, Spitale 2017) within the type of forest and the geographical conditions of the place.

Description of communities and altitudinal belt exclusive mosses - Superpáramo (3,800 4,200 m a.s.l.): The coverage of mosses represents 23% of the total sampled with the superpáramo being the most diverse altitudintal belt with 21 families (Hypnaceae, Pottiaceae, Macromitriaceae, Neckeraceae, Brachytheciaceae, Bryaceae, Thuidiaceae, Bartramiaceae, Polytrichaceae, Dicranaceae, Cryphaeaceae, Grimmiaceae, Orthotrichaceae, Meteoriaceae, Lepyrodontaceae, Daltoniaceae, Prionodontaceae, Rhacocarpaceae, Catagoniaceae, Hedwigiaceae and Leucobryaceae). The highest indices were found at 4,000 m a.s.l. The coverage of epiphytic mosses is minimal due the scarce number of phorophytes. The indicator species exclusively found in this belt are *Racomitrium crispipilum*, *Leptodontium flexifolium*, *Macromitrium punctatum*, *Lepyrodon tomentosum*, *Leptodontium synthrichioides*, *Andreaea rupestri*s and *Grimmia elongata*.

Páramo (3,200 3,600 m a.s.l.): The coverage of mosses at this point remains stable at 23% of the total sample. The bryophytic epiphytes show a greater coverage with 17 families (Entodontaceae, Leucobryaceae, Hypnaceae, Leskeaceae, Pottiaceae, Hedwigiaceae, Grimmiaceae, Dicranaceae, Bryaceae, Neckeraceae, Brachytheciaceae, Cryphaeaceae, Macromitriaceae, Bartramiaceae, Fissidentaceae, Thuidiaceae, and Sematophyllaceae). The indicator species exclusive of this belt are *Hedwigia ciliata*, *Anomobryum prostratum*, *Syntrichia laevipila*, *Grimmia fuscolutea* and *Cryphaea ramosa*.

Subpáramo (2,600 3,000 m a.s.l.): The diversity of mosses increases slightly with respect to the high Andean forest in subpáramo. The epiphytic strata have less species than those of the soil; the coverage at this point represents 23%

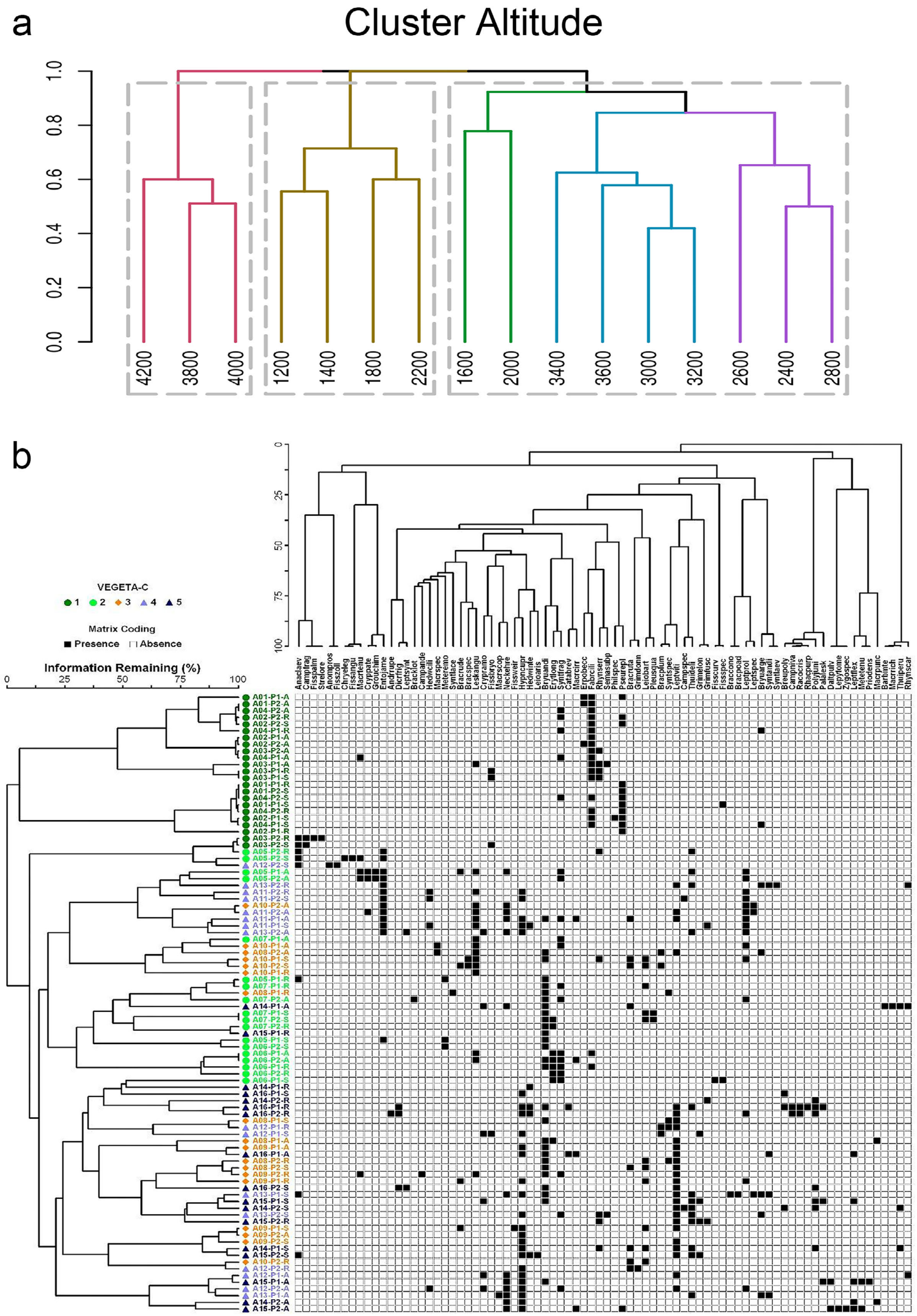

Figure 7. a. Cluster of altitudinal points (similarity index of Bray-Curtis). b. Analysis of presences and absences (Two-way) of Bray-Curtis.

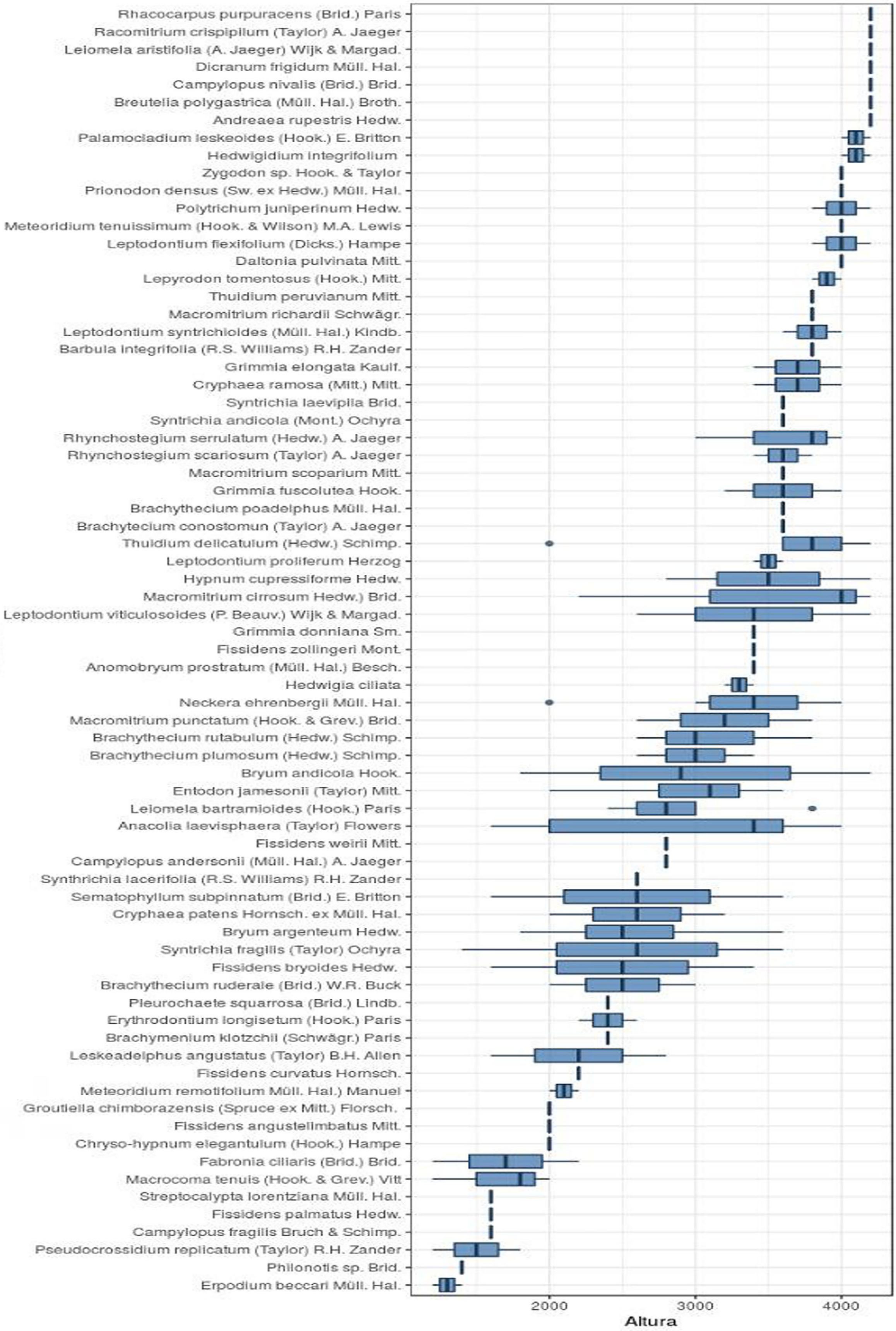

Figure 8. Ordination of species on a multidimensional scale using Bray Curtis.

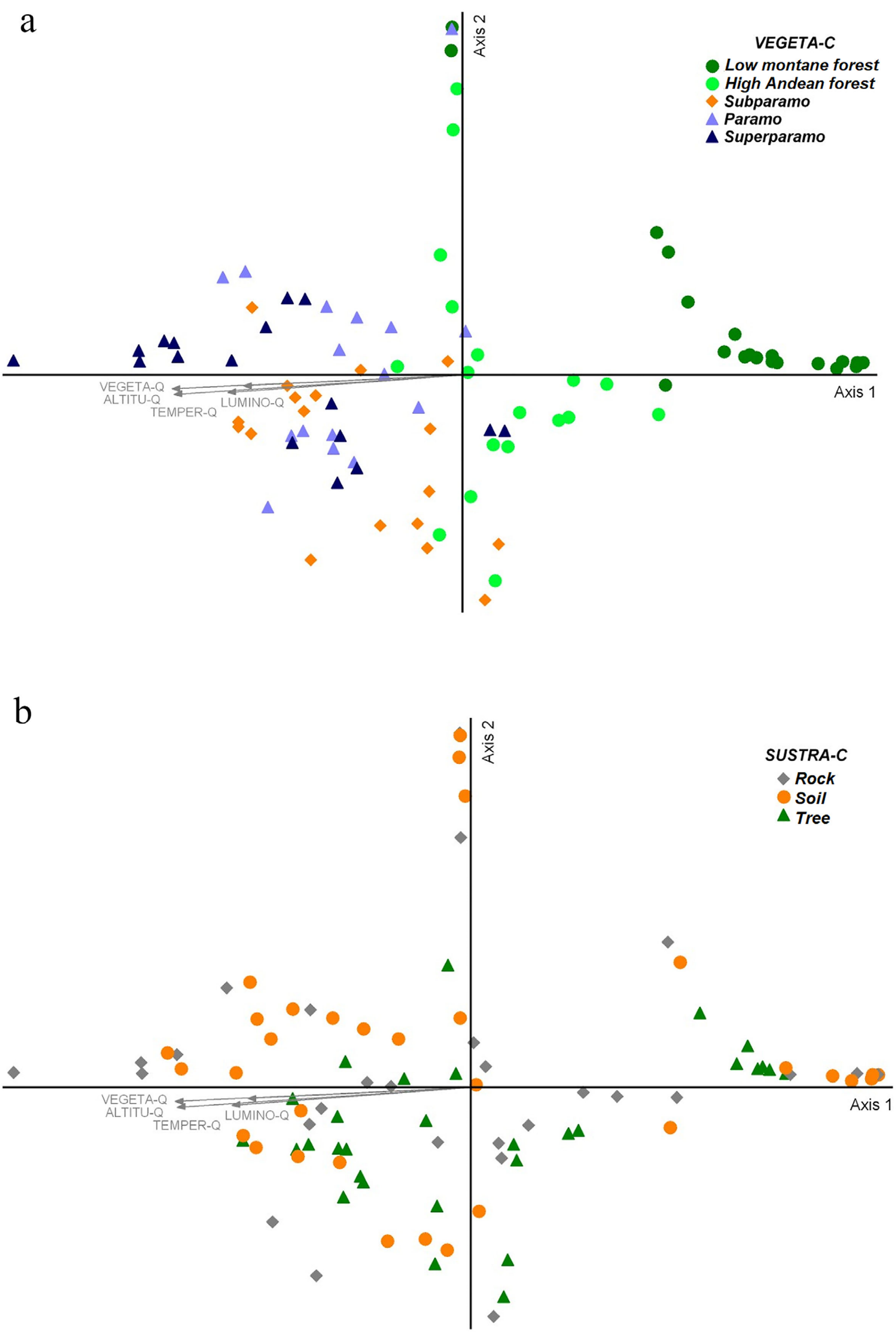

Figure 9. Analysis of canonical components. a. For altitudinal belts. b. For substrate.

of the sample and is represented mostly by soil mosses with 10 families (Pottiaceae, Bryaceae, Brachytheciaceae, Leskeaceae, Macromitriaceae, Entodontaceae, Hypnaceae, Leucobryaceae, Bartramiaceae and Neckeraceae). The indicator species exclusive of this belt are *Fissidens weirii*, *Pleurochaete squarrosa*, *Syntrichia lacerifolia* and *Leptodontium viticulosoides*.

High Andean forest (2,000 2,400 m a.s.l.): The coverage of mosses in this area is equal to 22% of the total sample. The epiphytic mosses have a greater coverage at this point and this also seems to explain the increase in the diversity of this point with respect to the Low montane forest. The diversity of bryophytes also increases with 11 families (Pottiaceae, Bartramiaceae, Leskeaceae, Entodontaceae, Fissidentaceae, Macromitriaceae, Thuidiaceae, Hypnaceae, Brachytheciaceae, Meteoriaceae and Cryphaeaceae). The exclusive species exclusive of this belt are *Erythrodontium longisetum*, *Chryso-hypnum elegantulum*, *Brachymenium klotzchii*, *Brachythecium rutabulum* and *Groutiella chimborazensis*.

Montane-low forest (1,200 1,800 m a.s.l.): The coverage of mosses in this place represents only 9% of total sampling. The epiphytic mosses represent a higher percentage of the total than those on soil in this area, and include rare species such as *Erpodium beccarii*, widely known for characterizing alternative algae forests (Churchill & Linares 1995) and which is a new record for Colombia. *Fabronia ciliaris* and *Fissidens bryoides* are new records for Boyacá. The diversity of mosses in this belt is low with only eight families of mosses recognized: Pottiaceae, Fabroniaceae, Erpodiaceae, Fissidentaceae, Bartramiaceae, Leucobryaceae, Brachytheciaceae and Sematophyllaceae. The indicator species exclusive of this belt are *Pseudocrossidium replicatum*, *Fabronia ciliaris* and *Erpodium beccarii*.

Discussion

The western region of the Sierra Nevada del Cocuy has a wide variety of ecosystems and climatic conditions that specifically influence the composition of moss populations. Our data show a marked difference between species composition of moss populations in all altitudinal belts and a varied preference in terms of available substrates. The diversity and coverage of mosses in this region increases with altitude, related to the decrease in temperature, the increase in humidity (Sporn *et al. 2*009, Stehn *et al.* 2010, Karger *et al.* 2012), and the high dominance of a few species at the lowest altitudinal points.

The change of species is very marked in all the altitudinal belts of this region although some species have very large distribution ranges such as *Bryum andicola*, which is present in all high mountain areas. Other species show a specificity for a particular environment and conditions, such as *Fabronia ciliaris* and *Erpodium beccarii* to the hot and arid climates in the low montane forest or *Andreaea rupestris* and *Dicranum frigidum* to climates of extreme cold and high humidity in the superpáramo. These distribution patterns are related to the adaptability of the mosses to a specific niche (Glime & Vitt 1986, Slack 1998, Pullian 2000). The behavior of mosses differs in terms of the climatic conditions of the sector and the availability of resources.

The five established forest types have resources and environmental conditions that allow the specific assembly of the moss species in the altitudinal gradient: the superpáramo has a great availability of rocks due to its steep slopes, the forests have the highest and most abundant vegetation, and the páramos have more humid soils, rich in organic matter. This explains the great population differences and the way mosses adapt to each specific ecosystem (Hylander 2005, Spitale 2016, Spitale 2017). In this study the epiphytic mosses stand out for having a high sensitivity and a greater number of specific species confined to this substrate. This may be due to greater exposure to climatic conditions (Sales *et al.* 2016, Chen *et al.* 2017) and to the great variety of sampled phorophytes given by the change in the structure of the forest.

As in most zoning studies with bryophytes, the zones with the greatest diversity are found in the highest altitudes (Frahm & Gradstein 1991, Kessler 2000, Sun *et al.* 2013). Our study shows that this is related to the type of forest and the increase in humidity and luminosity and the decrease in temperature. Places that did not meet these specific conditions lacked diversity and coverage. The mosses of dry ecosystems are totally different populations from those of montane climates. The latter have morphological adaptations so that their populations can survive in environments lacking water and humidity (Stark *et al.* 2009, Smith & Stark 2014). The type of substrate does not seem to be mediated by environmental variables, but this may be related to the type of forest and the resources provided by it (Stehn *et al.* 2010, Spitale 2016, Spitale 2017).

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