UNIVERSIDAD DE INVESTIGACIÓN DE TECNOLOGÍA EXPERIMENTAL YACHAY

Escuela de Ciencias Biológicas e Ingeniería

TÍTULO: Estructura de la comunidad y relaciones espaciales de traqueofitas y briofitas en el páramo de El Ángel, sector "Lagunas del Voladero", Carchi, Ecuador.

Trabajo de integración curricular presentado como requisito para la obtención del título de Bióloga

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Daniela Salomé Pasquel Dávila

RESUMEN

Este estudio describe los patrones de estructura de la comunidad de traqueofitas y briofitas y sus relaciones espaciales en el páramo de El Ángel, sector “Lagunas del Voladero”, Carchi, Ecuador. En esta área, se establecieron *N*=60 parcelas (2 m × 2 m) para muestrear traqueofitas y briofitas. Estos dos linajes evolutivos fueron muestreados usando un diseño anidado en el cual las briofitas fueron solo muestreadas en el área central de 1 m × 1 m. Las parcelas (*N*) fueron establecidas en los siguientes hábitats: bosque (*N*=10), cima de colina con *Espeletia pycnophylla* (*N*=16), pendiente con *E. pycnophylla* (*N*=14), valle de humedal con *E. pycnophylla* (*N*=10) y valle de humedal casi sin *E. pycnophylla* (*N*=10). Para cada especie, la dominancia, medida como cobertura vegetal (cm^2), se estimó con una cuadrícula metálica. Se encontraron 111 especies de traqueofitas y 94 especies de briofitas. La familia de traqueofitas con más especies fue Asteraceae (19 spp.), mientras que la familia de briofitas con más especies fue Plagiochilaceae (10 spp.). Las familias más dominantes (en términos de cobertura vegetal) fueron Asteraceae y Poaceae para traqueofitas, y Bartramiaceae y Dicranaceae para briofitas. A nivel de especie, las traqueofitas más dominantes fueron *Calamagrostis intermedia* y *Espeletia pycnophylla*, mientras que las briofitas más dominantes fueron *Breutelia tomentosa* y *Riccardia amazonica*. Según las curvas de rarefacción especies-área, las traqueofitas tuvieron mayor densidad de especies que las briofitas, y ambos linajes evolutivos mostraron mayor densidad de especies en hábitats de tierras altas que en humedales. Los análisis de NMDS para traqueofitas y briofitas mostraron una estructura de la comunidad diferente para cada hábitat, excepto cima y pendiente que tuvieron la misma estructura. A nivel de parcela, la densidad de especies de briofitas se correlacionó positivamente con la densidad de especies de traqueofitas. Por otro lado, la dominancia de briofitas vs. la dominancia de traqueofitas no mostraron ninguna correlación. Además, a nivel de parcela, no hubo una correlación entre la dominancia de briofitas y la dominancia de formas de crecimiento de las traqueofitas comunes: tussoks, rosetas basales, arbustos postrados, o *Espeletia pycnophylla*. En conclusión, este estudio reporta los patrones de estructura de las comunidades de traqueofitas y briofitas y sus relaciones espaciales en el páramo de El Ángel. Este páramo ha sido bien estudiado en cuanto a la diversidad de traqueofitas, pero es relativamente inexplorado para briofitas. Los resultados de este estudio sobre la coexistencia de traqueofitas-briofitas en páramo son importantes para comprender mejor sus procesos ecológicos en este ecosistema.

Palabras claves: páramo, traqueofitas, briofitas, estructura comunitaria, relaciones espaciales

ABSTRACT

This study describes the community structure patterns of tracheophytes and bryophytes and their spatial relations in El Ángel páramo, “Lagunas del Voladero” area, Carchi, Ecuador. In this area, I established *N*=60 small plots (2 m × 2 m) to sample both tracheophytes and bryophytes. These two evolutionary lineages were sampled using a nested design in which bryophytes were only sampled in the center 1 m × 1 m. Plots (*N*) were established in the following habitats: forest (*N*=10), hilltop with *Espeletia pycnophylla* (*N*=16), slope with *E. pycnophylla* (*N*=14), wetland valley with *E. pycnophylla* (*N*=10) and wetland valley with almost no *E. pycnophylla* (*N*=10). For each species, dominance, measured as vegetation cover (cm^2), was estimated using a metallic grid. I found 111 tracheophyte species and 94 bryophyte species. The most speciose tracheophyte family was Asteraceae (19 spp.), whereas the most speciose bryophyte family was Plagiochilaceae (10 spp.). The most dominant families (in terms of vegetation cover) were Asteraceae and Poaceae for tracheophytes, and Bartramiaceae and Dicranaceae for bryophytes. At the species level, the most dominant tracheophytes were *Calamagrostis intermedia* and *Espeletia pycnophylla*, whereas the most dominant bryophytes were *Breutelia tomentosa* and *Riccardia amazonica*. According to species-area rarefaction curves, tracheophytes had higher species density than bryophytes, and both evolutionary lineages showed higher species density in upland habitats than in wetlands. NMDS analyses for both tracheophytes and bryophytes showed a community structure different for each habitat, except hilltop and slope which had the same structure. At the plot level, I found that bryophyte species density correlated positively with tracheophyte species density. On the other hand, dominance of bryophytes vs. dominance of tracheophytes did not show any correlation. Further, at plot level, there was no correlation between bryophyte dominance and the dominance of common tracheophyte growth forms: tussocks, basal rosettes, prostrate shrubs, or *Espeletia pycnophylla*. In conclusion, this study reports the community structure patterns of tracheophytes and bryophytes and their spatial relations in El Ángel páramo. This páramo has been well studied for tracheophyte diversity, but it is relatively unexplored for bryophytes. The results of this study about tracheophytes-bryophytes coexistence in páramo are important to better understand their ecological processes in this ecosystem.

Key words: páramo, tracheophytes, bryophytes, community structure, spatial relationships

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INTRODUCTION

In Neotropical ecosystems, the diverse communities of vascular plants, also known as **tracheophytes**, have caught the interest of naturalists for centuries. In contrast, non-vascular plants (mosses, liverworts and hornworts), also known as **bryophytes**, have not received as much attention. It is only in the last few decades that a renewed impulse to study these small plants has emerged, although they are actually omnipresent in many habitats. Today, growing interest by the Ecuadorian scientific community for plant discovery has developed into research hubs mostly located at different herbaria associated with universities or research centers.

TRACHEOPHYTE AND BRYOPHYTE COLLECTIONS IN ECUADOR

In the context of collections of tracheophytes, Jørgensen (1999) provides a good overview. During 1735–1743, Joseph de Jussieu, a French botanist, was the first to collect tracheophytes in Ecuador for scientific purposes. Soon, during the same XVIII century, he was followed by Pedro Franco Dávila (Ecuadorian), Thaddäus Haenke (Czech), Luis Née (French), Juan José Tafalla (Spanish) and Juan Agustín Manzanilla (Spanish). During the XIX century, dozens of botanists, mostly European, worked and lived in Ecuador, including Karl Theodor Hartweg (English), Thomas Edmonston (English), John Goodridge (English), among others. Early in that century, the renowned German geographer and naturalist Alexander von Humboldt collected many tracheophyte species in the context of biogeographical studies. Ecuadorians such as José Mejía del Valle and Luis Cordero (who was the 17th. President of Ecuador) also made important botanical contributions during that century. As a result of these efforts, the first flora of tracheophytes of Ecuador was published in 1885 by the British botanist William Jameson, who worked and lived in the vicinities of Quito from 1822 to 1873 (Jørgensen, 1999; León-Yánez et al., 2006). In the XX century, more than 900 botanists collected in Ecuador, totaling ca. 500 000 plant specimens (Jørgensen, 1999). Many of them are still active today in the XXI century, studying the flora using taxonomical, ecological, genetical or ethnobotanical approaches.

Thanks to all these collection efforts, the number of native tracheophyte species officially registered until a few years ago in Ecuador was near 18 000 (Neill, 2012; Ulloa et al., 2017). Some botanists argue that the total number of native tracheophyte species in the country might reach 25 000 (Neill, 2012). Peak diversity of trees and lianas is found in the tropical lowlands, while epiphyte species are certainly more numerous in mountain forests; herbs are particularly speciose in páramos and inter-Andean valleys (Jørgensen & León-Yánez, 1999). These patterns can be correlated to the distribution of certain taxonomic families and genera, which can be much more diverse in certain ecosystems than in others.

For bryophytes, the first scientific collections in Ecuador were made by William Jameson in the XIX century (Jørgensen, 1999; León-Yánez et al., 2006). Another British botanist, Richard Spruce, also focused on the non-vascular flora, mostly working in the provinces of Pastaza, Tungurahua and Guayas from 1857 to 1864 (León et al., 2003). In 1884, he published the book *Hepaticae of the Amazon and the Andes of Peru and Ecuador* (Spruce & Thiers, 1984). In the early and mid XX century, collection and study of bryophytes from Ecuador was conducted by relatively few scientists, among them Hampus Arnell (1848–1932), Gunnar W. Harling (1920–2010), Theodor K. G. Herzog (1880–1961) and Ynes Mexia (1870–1938) (Renner, 1993; Churchill, 1998; León-Yánez et al., 2006). Since the late XX century, botanists such as Steven P. Churchill and Robert Gradstein have contributed greatly to the knowledge of tropical bryophytes. In the current century, a number of local botanists, including Ángel Benítez (Universidad Técnica Particular de Loja), Michael Burghardt (Universidad de las Américas), Susana León-Yánez (Pontificia Universidad Católica del Ecuador), Thalía Morales and Elsa Toapanta, have become well known for their work on Ecuadorian bryophytes.

As a result of this taxonomic work on bryophytes, today it is estimated that 1650 species occur in continental Ecuador (Churchill, 1994; Churchill et al., 2000; León-Yánez et al., 2006) and approximately 200 species in the Galápagos Islands (Weber, 1975; Gradstein & Weber, 1982). These numbers significantly increased in the last few decades thanks to a number of local studies in different provinces of Ecuador, mostly from the Andean and Amazonian regions (e.g., Arts & Sollman, 1998; Kuc, 2000; Churchill et al., 2009; Mandl et al., 2010; Benítez & Gradstein, 2011; Toapanta, 2011; Schäfer-Verwimp et al., 2013; Castillo-Monroy & Benítez, 2015). Yet, there are still areas in Ecuador where bryophytes have not been extensively collected, such as the northern Andes and the entire Coastal region (A. Benítez, pers. comm.).

GAMMA(Γ)-DIVERSITY OF TRACHEOPHYTES AND BRYOPHYTES IN PÁRAMOS OF ECUADOR

The community structure and distribution of tracheophytes in Ecuadorian páramos has been extensively studied by many authors. A pioneer study by Ramsay & Oxley (1997) created a classification of growth forms of páramo plants and how they are distributed along altitudinal gradients in 12 different páramos. In the late 1990´s, several studies first formally characterized the vegetation structure of different páramos. For example, Keating (1999) studied the vegetation structure of the Podocarpus National Park páramos, while Sklenář & Jørgensen (1999) floristically analyzed the páramo plant communities of six mountains (Pichincha, Guamaní [Papallacta], Antisana, Cotopaxi, Chimborazo, and Cajas). In addition, Ramsay (2001) and Sklenář (2001) studied the tracheophyte communities of El Ángel páramo, including the superpáramo of the Chiles volcano, Sklenář & Ramsay (2001) presented an extensive survey of 30 different páramo locations (with more than 300 plots), and Sklenář & Balslev (2005) summarized the vascular vegetation structure in 18 superpáramos. The results of these ecological studies complemented the information provided by species checklists or field guides focused on tracheophytes (e.g., Ulloa & Jørgensen, 1993; Luteyn, 1999; Balslev, 2001; Sklenář et al., 2005; Aguilar et al., 2009; Ulloa et al., 2010; MECN - INB, 2015; Minga et al, 2016; Nth development, 2019). Luteyn (1999) estimated that ca. 3400 vascular plant species (tracheophytes) occur in the páramos of Ecuador.

Regarding bryophytes in Ecuadorian páramos and high Andean forests, just a handful of checklists and studies about community structure are available (Arts & Sollman, 1998; Toapanta, 2005; Toapanta, 2011; Schäfer-Verwimp et al., 2013). For example, Kuc (2000) analyzed the moss distribution in high elevations of the Chimborazo, Cotopaxi and Cajas mountains; Toapanta (2011) elaborated a checklist for mosses in Ecuador reporting 223 species, from which 30 species were reported for Carchi; Schäfer-Verwimp et al. (2013) also listed the distributional data of new Ecuadorian bryophyte taxa, including 26 species for Carchi; and Benítez et al. (2019) reported 28 bryophyte species in Podocarpus National Park páramo. In total, ca. 600 bryophyte species are known to occur in the páramos of Ecuador (Missouri Botanical Garden, 2020).

El Ángel páramo

El Ángel páramo, where this study is situated, is characterized by the dominant presence of *Espeletia pycnophylla* subsp. *angelensis*, commonly called “frailejón.” In

Ecuador, except for an isolated and small population occurring in the Llanganates cordillera (*Espeletia pycnophylla* subsp. *llanganatensis*), the distribution of frailejón-dominated páramo is restricted to the northernmost territory, near the border with Colombia. *Espeletia pycnophylla* is the only species of "frailejón" that occurs in Ecuador, but in Colombia and Venezuela the genus *Espeletia* is represented by more than 100 species. The vascular plant community (tracheophytes) of the frailejón páramo has been described by several studies (e.g., Ramsay & Oxley, 1997; Balslev, 2001; Moscol & Cleef, 2009; Beltrán et al., 2009), focusing on the effects of disturbance (e.g., Suárez & Medina, 2001; Ron, 2011) and climate change (e.g., Delgado & Suárez-Duque, 2009; León & Rodríguez, 2020). Only three studies (Toapanta, 2005; Beltrán et al., 2009; Moscol & Cleef, 2009) include bryophytes as part of the characterization of the plant communities at the El Ángel páramo or nearby areas. Indeed, the only plant field guide available for this páramo (Chimbolema et al., 2013), in which 85 vascular plant species are described, does not include bryophytes. For the province of Carchi at altitudes >3500 m, ca. 1300 vascular plant species have been reported (Chimbolema et al., 2013; Jørgensen & León-Yánez 1999 [web version database]). In contrast, studies have reported only close to 100 species of bryophytes for this province (León-Yánez et al., 2006; Toapanta, 2011).

Despite the importance of the El Ángel páramo as a provisioning area for nearby towns and cities, the area is ecologically vulnerable due to social, political, economical and environmental factors, including climate change. Human activities in the El Ángel Ecological Reserve and its buffer zone—such as hunting, fishing, uncontrolled tourism, agriculture and livestock—change the natural vegetation, increasing evapotranspiration and soil water loss (Espinosa & Rivera, 2016; MAE, 2015). In addition, it is expected that as climate change intensifies, it will provoke stronger rains, longer dry seasons and higher temperatures (MAE, 2015). In fact, temperature has increased by 0.11 °C each decade (Buytaert et al, 2014), which could be too fast to allow for species to adapt, thus compromising their survival. These factors put the plant species of this páramo at risk with them the fauna that depends on this ecosystem. In fact, a study estimates that by the year 2080, 26% of the flora will be lost from the Golondrinas Protected Forest and the El Ángel Ecological Reserve (Delgado & Súarez-Duque, 2009).

OBJECTIVES

In the spirit of the seemingly endless task that began in Ecuador more than three centuries ago, the general objective of this thesis is to describe the community structure and spatial relations of tracheophytes and bryophytes in the Lagunas del Voladero area, El Ángel Ecological Reserve, Carchi, Ecuador. In this context, the specific objetives of this study are:

1. Describe the taxonomic richness of tracheophyte and bryophyte plant communities, at the family and species levels.
2. Describe the dominance patterns (vegetation cover) of tracheophyte and bryophyte plant communities, at the family and species levels.
3. Characterize the species density patterns for the whole study area and among different habitats, for both tracheophyte and bryophyte plant communities.
4. Evaluate the variation of community structure among habitats, for both tracheophyte and bryophyte plant communities.
5. Assess the spatial relations between bryophytes and tracheophytes, in terms of vegetation cover (dominance).

HYPOTHESES

The first four specific objectives of this thesis are descriptive and thus no hypotheses will be tested for them. However, for the last objective (spatial relations), I propose to test the following two hypotheses with regard to the influence of tracheophyte growth forms on bryophyte distribution:

Hypothesis 1 (H1): There is a negative correlation between vegetation cover of bryophytes and vegetation cover of the most dominant species of tussocks, basal rosettes and prostrate shrubs (typical growth forms of tracheophytes in paramos).

> *Rationale:* Several studies have shown that the growth form of tracheophytes, in particular when they grow as grassland tussocks or basal rosettes, can affect the local dominance of bryophytes. For example, grassland tussocks of the genus *Calamagrostis*, along with other types of Poaceae, affect bryophytes directly by changing light and moisture conditions at ground level, negatively competing with them (Herben, 1987; Hellquist & Crow, 1999; BGCI, 2017). This competition can become more intense after a grassland fire, when young vascular plants start to grow very actively, reducing soil moisture (Hellquist & Crow, 1999). Species of basal

rosettes (e.g., *Puya*) and prostrate shrubs, could also exert a negative effect on bryophyte growth, as they occupy "large" areas of soil (from the point of view of bryophytes), causing strong competition for nutrients, water, and light, thus displacing bryophytes as a result. On the other hand, some erect herbs, such as *Festuca* and *Trifolium*, can have a positive effect on bryophyte growth, as a result of facilitation allowing coexistence (Ingerpuu et al., 2005; Rajandu, 2010).

Hypothesis 2 (H2): There is a positive correlation between bryophyte vegetation cover and vegetation cover of the common giant rosette *Espeletia pycnophylla*.

Rationale: In El Ángel páramo, the most characteristic vascular plant species is *Espeletia pycnophylla*, "frailejón." The species of *Espeletia* can avoid freezing by controlling their internal temperature in leaves, piths, and roots (Rada et al., 1985). These giant rosettes can regulate solar radiation effect reducing radiative heat loss and connective heat loss due to winds typical of páramo ecosystems; in turn, this increases the minimum soil temperature around the plant, preventing soil water freezing or ice formation (Pérez, 1989; Mora et al., 2019). In addition, they can stabilize soil conditions and preserve soil water availability, increasing water retention and organic matter on soil (Pérez, 1987). These conditions create a beneficial microhabitat, moist and nutrient rich, for young *Espeletia* and for surrounding plants, including bryophytes. In this context, Mora et al. (2019) showed that plant species richness and abundance was twice as high in the plant community with *Coespeletia timotensis*, compared to areas without it. Additionally, there is evidence that *Espeletia* seeds tend to germinate on bryophyte substrates (Gallego & Gómez, 2016).

METHODS

STUDY AREA

The study area (Figure 1) is located at El Ángel Ecological Reserve, in the páramo area known as Lagunas del Voladero, in the province of Carchi, western Andean cordillera, Ecuador (near the station of the Ministerio del Ambiente y Agua located at 0°40′38″N 77°52′37″W, 3722 m). The two “El Voladero” lakes are bordered by wetlands, surrounded by several hills. These hills are dominated by the presence of *Espeletia pycnophylla* subsp. *angelensis*, although small patches of evergreen high montane forest also occur.

The El Ángel Ecological Reserve, one of the 51 public protected areas in Ecuador, has an extension of 16591.6 ha, with an altitudinal range of 3200–4200 m, temperature range of 4–18°C, mean wind rate of 10.9 m/s, and annual precipitation range of 2000–3000 mm (Carrasco, 2012; MAE, 2015). There are two annual rainfall peaks: January–May and October–December. According to the reserve management plan (MAE, 2015), the following types of vegetation types can be recognized:

(i) “Rosetal caulescente, y herbazal montano alto y montano alto superior de páramo” (89.95% of the area), commonly referred as “páramo de frailejones” dominated by *Espeletia pycnophylla*.

(ii) “Herbazal inundable montano alto y montano alto superior de páramo” (3.17%), characterized by cushion growth forms such as *Plantago rigida*, *Oreobolus* spp., *Distichia muscoides*, and *Sphagnum* spp.

(iii) “Bosque siempre verde montano alto y montano alto superior de páramo” (0.59%) dominated by *Polylepis*, *Gynoxys* and *Buddleja*.

(iv) “Cuerpos de agua” which are the aquatic ecosystems (0.39%).

(v) Cultivated or livestock areas (5.90%).

Except for the last vegetation type, all the rest of broad vegetation types formed part of this research´s study area.

RESEARCH DESIGN

Plots size and distribution

Field work was conducted between January and March 2020. At the “Lagunas del Voladero” area, a total of 60 plots (2 m × 2 m quadrats) were established to sample the vegetation in different habitats. Each plot was georeferenced using a Garmin eTrex Legend® GPS, configured for decimal degrees. The number of plots in each habitat was determined by the geographic features that were represented in the landscape, as hereby described (Figure 1):

(i) In forest (F) habitat, 2 plots were established in each of 5 forest patches that still persisted along the slopes, for a total of 10 plots. They occur at altitudes of 3700–3791 m.

(ii) In hilltop habitat dominated by *Espeletia pycnophylla* (HE), 2–3 plots (separated by 15–20 m) were established in each of the 7 hilltops that surround "Lake 1", for a total of 16 plots. Hilltop plots were located at altitudes of 3770–3805 m.

(iii) In slope habitat also dominated by E. pycnophylla (SE), 2 plots (separated by 15–20 m) were established at approximately midway between each of the 7 hilltops and the lake, following a linear direction towards the lake, for a total of 14 plots. Slopes had an inclination of 10–20 degrees. Slope plots were located at altitudes of 3700-3785 m.

(iv) In wetland valley habitat where *E. pycnophylla* was commonly growing (WVE), 2 plots (separated by 15–20 m) were established at each of 5 random locations, for a total of 10 plots. Wetland valleys, relatively flat, occur at an average altitude of 3746 m.

(v) In wetland valley habitat that almost did not have any *E. pycnophylla* growing (WV), 2 plots (separated by 15–20 m) were established at each of 5 random locations, for a total of 10 plots. Note that this type of humid wetland valley has a limited distribution, being mostly located at the eastern shore of the lake, within 10 m of its edge, at an altitude of 3745 m (Figure 1).

For statistical purposes, a plot hereby is defined as a sampling unit or replicate, while the set of plots in a given habitat as a sample of such habitat.

Each plot was set up as a "perfect" square using measuring tape and the Pythagoras theorem. The 4 m^2 area (2 m × 2 m) matched the terrain inclination, not its horizontal projection. Further, to facilitate sampling, a plot was subsectioned into four triangles using rope and PVC tubes (Figure 2). The vertices of a plot corresponded to the four cardinal directions. One permanent PVC tube was left in the field at the center of each plot; this can help to locate the plot for future vegetation monitoring efforts. This PVC tube was painted (fluorescent red) and labelled with the plot number.

Sampling of tracheophytes and bryophytes

In each plot, tracheophytes were sampled within the whole 2 m × 2 m area (4 m^2), while bryophytes were only sampled within a 1 m × 1 m area (1 m^2) at the center of the plot (Figure 2). This nested design has been used in other studies with bryophytes (e.g., Jiang et al., 2015). Although sampling bryophytes in the whole 2 m × 2 m would have been ideal, it proved very challenging and time-consuming in the field. Yet, the area used to sample bryophytes (1 m × 1 m) falls well within the area that is usually recommended (see e.g., Ilić et al., 2018). I am assuming that bryophyte data taken in the 1 m^2 area is representative of the 4 m^2 area without falling into any serious sampling bias. The plot size here used to sample tracheophytes (2 m × 2 m) is smaller than that usually used to characterize their community structure in páramos (e.g., 5 m x 5 m; Ramsay, 2001; Sklenář, 2001). Yet, I opted for a 2 m × 2 m plot to sample tracheophytes because of the last objective of this study: to evaluate the spatial relations between the tracheophyte community and the bryophyte community. If I had used a larger plot size to sample tracheophytes, it would not have been representative of the microhabitat in which the bryophytes of a given plot were growing.

Species abundance was not estimated as density (number of individuals in a given area) because, for many growth forms in páramos, it is often difficult to distinguish among different individuals. Instead, I used vegetation cover, or dominance, as a proxy for abundance. For tracheophytes and bryophytes, this was measured as the number of square units (1 cm × 1 cm=1 cm^2) that the vertical projection of the whole plant structure had on the soil. This was estimated using a metallic grid placed on top of the vegetation (or at soil level for prostrate plants), in a given triangle of a plot (Figure 2). The use of a grid to estimate vegetation cover is commonplace in many studies (see e.g., Sun et al., 2013; Pauli et al. 2015).

Sampling always started in the northeastern triangle (T1, see Figure 2), and then followed clockwise for the rest of the triangles. Note that the cover of a given species could be measured in two or more triangles in the plot, depending on size and number of individuals. Each grid measurement of cover corresponded to a different entry in the database. In addition, for each plant observed, I recorded the following information: reproductive stage (fertile or not), habit (terrestrial, epiphyte, facultative epiphyte), substrate type (e.g., soil, bark, fresh leaves, litterfall, etc.), microenvironmental conditions at time of observation (e.g., under shade, no shade, etc.), and dominant associated species (if known). All this extra descriptive information was not analyzed, but was simply annotated to be included for the herbarium label description.

Collection and taxonomic identification of botanical specimens

Botanical vouchers were collected while vegetation cover was measured. Tracheophytes were collected using a hand pruner, then labelled (using vynil flagging tape), and immediately stored in a plastic bag. Bryophytes were collected along with substrate, labelled, and temporarily stored in ziplock plastic bags. To avoid confusion, each plastic bag always contained one plant specimen only. In a given plot, at least one voucher was collected for each different species present. Under certain conditions (e.g., if the plant was fertile), up to three duplicates from the same individual were collected. Each botanical voucher was labelled with the corresponding code in the database. When a new sampled plant evidently belonged to a species already collected in the same plot, it was linked in the database (field data sheet) to the corresponding voucher already collected. This practice reduced the amount of botanical specimens collected. In the lab, following standard protocols, tracheophytes were pressed in newspaper and then dried for a few days, whereas bryophytes were first photographed under a DMS 300 Leica stereoscope, at different magnifications, and then air-dried in 10 cm × 15 cm bond paper envelopes, as recommended by Gradstein et al. (2001).

To taxonomically identify tracheophytes, given the COVID-19 pandemic, specimens were examinated at home using a 14x triplet hand lens and bibliography such as general guides, plant systematics books (e.g., Gentry, 1996; Judd et al., 2016), or field guides of páramo flora (e.g., Ulloa et al., 2010; Werner & Mendieta-Leiva, 2011; Chimbolema et al., 2013; Fernández et al., 2015; Brito et al., 2019; Cruz et al., 2016). In addition, internet resources proved invaluable during this process, including the online database of the Catalogue of Vascular Plants of Ecuador in Tropicos® (Jørgensen & León-Yánez, 1999; Tropicos®, 2020), the database of the Global Biodiversity Information Facility (GBIF, 2020), and several virtual herbaria that contained high quality plant images, such us those from the Azuay Herbarium (HA), the Pontifical Catholic University of Ecuador Herbarium (QCA), the Missouri Botanical Garden Herbarium (MO), the New York Botanical Garden Herbarium (NY), The Field Museum of Chicago Herbarium (F), The Plant List website (TPL, 2020), among others.

For bryophytes, taxonomic work was more challenging and at this point can still be considered as work in progress. First, supported by stereoscope photographs and by physical vouchers, I created morphospecies that were informally named based on visible morphological characteristics. This preliminary classification was then reviewed by Dr. Ángel Benítez (UTPL professor) through online conferences; he is one of the few specialists on bryophytes and lichens in Ecuador. As a result, he scientifically identified some vouchers to species level, while identifying most vouchers to genus level. Representative vouchers of each species or morphospecies have been shipped to Dr. Benítez lab for further taxonomic work. In order to properly identify many of the specimens, he needs to prepare microscope slides to observe cell forms and arrangement. During the last weeks, he has been sending proper taxonomic identifications of some vouchers, and will continue to do so as his work advances.

Unidentified specimens were coded as “ZZZ” if family was unknown and “Zzz” if genus was unknown. All specimens that were not fully identified were temporarily assigned a morphospecies name (operational taxonomic units at the species level). In this document, usually the term “species” is meant to refer to both formally named species and informally named morphospecies. I followed the taxonomy of tracheophyte and bryophyte in The Plant List website (TPL, 2020), in order to avoid outdated or unaccepted names. In a post COVID-19 scenario, taxonomic identification of the botanical vouchers should be double checked in different herbaria, and, if in doubt, sent to specialists around the world for taxonomic confirmation. Eventually, I plan to deposit representative vouchers of the tracheophytes and bryophytes collected during this study at the Universidad Técnica Particular de Loja Herbarium (UTPL), the National Herbarium of Ecuador (QCNE), the Catholic University Herbarium in Quito (QCA), the Catholic University Herbarium in Ibarra (ECCA), and the Berlin-Dahlem (B) Herbarium in Germany.

DATA ANALYSES

Data was recorded and organized using Excel and its different data handling functions. Data was handled in two independent databases: one for tracheophytes, and one for bryophytes. A few entries (<1%) were taken out from the databases because they did not have a physical collection associated to them (due to human error), which made it impossible to assign a taxonomic name for such entry. In order to obtain a vegetation cover value for a given species in a plot, all cover values of the different entries of that species, in all four triangles of a plot, were added.

Taxonomic richness

The number of species, genera and families of tracheophytes and bryophytes found in all habitats combined and in each habitat, along with the number of species per family and number of genera per family, were tabulated using dynamic tables in Excel.

Dominance

To evaluate the dominance of families and species, total vegetation cover of each taxon was calculated for each plot and for each habitat.

Species density

I used species density (number of species/area; Gotelli & Colwell 2011) to assess the plant diversity patterns of the tracheophyte and bryophyte plant communities, for all habitats combined, and for each habitat independently. These comparisons were made using species-area rarefaction curves obtained in EstimateS® 9.1 (Colwell, 2019), by inputting a matrix of sites × species filled with presence [1] / absence [0] of a species in a plot (incidence data). To generate the curves, I ran 100 permutations without replacement. Following the criteria of Gotelli & Colwell (2011) and Colwell et al. (2012), statistical comparison of plot-based species-area rarefaction curves was inferred by using confidence intervals at 84%, which represent an α significance level of 0.05, conservatively (Colwell et al. 2012). The comparisons between confidence intervals were made at the point in which the same number of plots were sampled.

In addition, I compared the number of species of tracheophytes vs. bryophytes, per plot, by correlating them using a Spearman non-parametric test, given that the data did not follow a normal distribution according to a Shapiro-Wilk test. These analyses were run in Past 4.03 (Hammer et al., 2001).

Community structure

To assess the variation in community structure, I applied Nonmetric Multidimensional Scaling (NMDS), coupled with an Analysis of Similarities (ANOSIM).

NMDS and ANOSIM matrices—Before running the NMDS and ANOSIM, I created two matrices of sites × species filled with vegetation cover data (cm^2): one for the whole species dataset, and another for the species dataset without uniques (a “unique” is defined as the presence of one species in just one plot, sensu Colwell 2013). After all, the presence of a unique species cannot be ecologically interpreted as a definite preference of such species for a given habitat—it could be simply growing there just by chance. Following recommendations in the literature (see Kindt & Coe, 2005; Somerfield, 2008; Greenacre & Primicerio, 2014), the input matrices for the ordination were:

- *(i)* Matrices with no transformation—This gives each species a weight directly proportional to its original cover data (in cm^2), making it possible to evaluate how both common and rare species affect the ordination results.
- *(ii)* Matrices with percentage (%) transformation—This makes possible to directly compare between the tracheophyte and bryophyte plant communities, despite their different sampling unit areas (2 m × 2 m vs. 1 m × 1 m, respectively).
- *(iii)* Matrices with presence-absence transformation (incidence data)—This gives the same weight to all species in a plot, independently of their cover, and represents an extreme approach to minimize the potential effect that species that are very common or very rare can unduly have on the ordination (Kindt & Coe, 2005; Somerfield, 2008; Greenacre & Primicerio, 2014). Evidently, the sum of the presence values of a species (incidence data) is equal to the number of plots where it occurs, i.e., its total frequency.

NMDS—This ordination technique represents the variation among sites in a low dimensional space based on a matrix of dissimilarity pairwise distances among sites (Greenacre & Primicerio, 2014). The sites, in this study, are the plots, while the pairwise distances among them were calculated using the Bray-Curtis index, defined as:

$$D = 1 - 2\frac{\sum_{i=1}^{S} \min(a_{i\,,}\, b_i)}{\sum_{i=1}^{S}(a_i + b_i)}$$

where the site A contains S_i species with a_i species abundance for each species i, and the site B contains S_i species with b_i species abundance for each species i. Dissimilarity values between two sites can vary from 0 to 1, being 0 for complete similarity (no dissimilarity). This index is the most commonly applied in biological studies because it complies with a series of technical criteria (Clarke et al., 2006): coincidence, complementarity, relative invariance, independence of joint absence, localisation, and dependence on totals. In addition, this index can handle data based on density (counting of individuals), cover, or biomass (Greenacre & Primicerio, 2014).

ANOSIM—This analysis statistically tests if a sample (set of plots) of one habitat is significantly different from that of another habitat, as depicted in a NMDS graph. This non-parametric test uses the same dissimilarity matrix that a NMDS uses. An ANOSIM (like an ANOVA) compares the variation *between* habitats with the variation *within* habitats, summarizing the result in an R statistic, which can vary from 0 (no dissimilarity) to 1 (complete dissimilarity), and an associated P-value. In addition, I ran post-hoc multiple comparisons tests among all habitats, obtaining a P-value for each pairwise comparison between habitats. To conclude whether two habitats were significantly different (null hypothesis rejected), based on the Bray-Curtis dissimilarity index, I used two criteria: *(i)* no Bonferroni correction was applied (family-wise $\alpha = 0.05$), and *(ii)* a traditional or classical Bonferroni correction was applied (corrected family-wise α = pairwise α / number of comparisons). Given that the number of pairwise comparisons in this study was 10 (five different habitats are being compared among each other), the approximate family-wise Bonferroni error rate (α) was $0.05/10 = 0.005$.

Note that the application of a type of Bonferroni correction is not immune to critiques in the literature. The use of a Bonferroni correction has been popular in the last two decades for multiple comparison testing (Chen et al., 2017; Albers, 2019), in order to avoid the drastic increase of family-wise α error (Holm, 1979; Rice, 1989). This is the probability of committing a Type I error given that the null hypothesis is true (Lane et al., 2020). The traditional Bonferroni correction is strict in the sense that it significantly lowers the risk of a Type I error, but also unduly reduces the statistical power, thus increasing the probability of a Type II error (Abdi, 2010; Eitchteaded, 2013; Chen et al., 2017). An alternative to the traditional Bonferroni correction is the Sequential Bonferroni correction, which is less conservative and does not sacrifice much statistical power (Abdi, 2010; Chen et al., 2017). Yet, when differences are highly significant to start with, the application of a Sequential Bonferroni could result in similar conclusions as when no Bonferroni correction is applied (H. Romero-Saltos, pers. comm.). Many authors (Calbin & Mitchel, 2000; García et al., 2004; Jhon et al., 2012) have questioned the blind application of a Bonferroni correction, stressing that there is not a unique criterion on how to apply it, and that it is up to the researcher to envision its usefulness, depending on the study context. In this study, I opted, as explained above, to show the Results both without a Bonferroni correction, and with a traditional Bonferroni correction.

Spatial relations in terms of vegetation cover

I assessed the variation of percentage (%) vegetation cover (dominance), per plot, of bryophytes vs. tracheophytes, by correlating them using a Spearman non-parametric test, given that the data did not follow a normal distribution, according to a Shapiro-Wilk test. This approach was also applied to assess the correlation between dominance of bryophytes vs. dominance of the most common species of tussocks, basal rosettes and prostrate shrubs (see Hypothesis H1), and to assess the spatial relation between bryophyte dominance and *Espeletia pycnophylla* dominance (see Hypothesis H2). As mentioned before, the % transformation allowed the comparison between tracheophytes and bryophytes, given that, in each plot, their sampling area was different (4 m^2 vs. 1 m^2, respectively). All analyses were run in Past 4.03 (Hammer et al., 2001).

RESULTS

TAXONOMIC RICHNESS

Tracheophyte taxonomic richness

In all 60 plots of this study—each 4 m^2—I found 111 species of tracheophytes (including five morphospecies), represented by 70 genera and 37 families (Appendix 1). Two morphospecies could not be identified to family level and three were left identified to genus level. In addition, 28 species (25 fully identified species + 3 morphospecies) were uniques (only present in one plot). Among the 111 tracheophyte species, seven were endemic, among which five were considered in the conservation status of "Least Concern" (LC), one (*Brachyotum jamesonii*, Melastomataceae) was considered "Vulnerable" (VU), and one (*Solanum carchiense*, Solanaceae) was considered "Critically Endangered" (CR) (León-Yánez et al. 2011; IUCN, 2020).

For all habitats combined, the most speciose tracheophyte family was Asteraceae (19 species), followed by three families with six species each: Cyperaceae, Melastomataceae, and Polypodiaceae (Figure 3A). Asteraceae was also the family with the highest number of genera (11), while the remaining of families had only 1–4 genera (Figure 3A).

Regarding the floristic patterns of tracheophyte families per habitat (Figure 4A), Asteraceae was also the most speciose family in all habitats. In hilltop habitat, sedges (Cyperaceae) and grasses (Poaceae) had three and four species, respectively; whereas in slope habitat, Cyperaceae had only one species, and Poaceae occurred with four species (Figure 4A, Appendix 1). These two families were also present in the different wetland habitats, with 2–3 species per family. In forest, speciose families of ferns (Dryopteridaceae, Blechnaceae and Polypodiaceae) had 3–6 species each. Also, some fern families (Blechnaceae, Dryopteridaceae, Pteridaceae) were well represented in hilltop and slope habitats by 3–4 species. Melastomataceae and Ericaceae, constituted mostly by shrubs, were notably represented by four species in forest, 3–4 species in hilltop, and 2–3 species in slope (Figure 4A, Appendix 1).

Bryophyte taxonomic richness

In all 60 plots of this study—each 1 m^2—I found 94 species of bryophytes (including 56 morphospecies), represented by 43 genera and 35 families (Appendix 2). From these 94 bryophyte species, 53 species belong to the Phylum Marchantiophyta ("liverworts"), 41 species belong to the Phylum Bryophyta (“mosses”) and no species belong to the Phylum Anthocerotophyta (“hornworts”). All morphospecies were identified to family level, and all but one of the 56 morphospecies were identified to genus level. In addition, 34 species (1 fully identified species + 33 morphospecies) were uniques. Among the species fully identified, no species endemic to Ecuador was registered in this study; in addition, no bryophyte species has had its conservation status assessed (see León-Yánez et al., 2011; IUCN, 2020; Missouri Botanical Garden, 2020). Note however that there are many morphospecies still left to be fully identified.

The most speciose bryophyte family was Plagiochilaceae (10 species), followed by Dicranaceae (8 species) and four families with six species each: Bryaceae, Lepidoziaceae, Metzgeriaceae, and Sematophyllaceae (Figure 3B). There were only 1–3 genera among bryophyte families; i.e., no family was dominant in terms of number of genera per family (Figure 3B).

Regarding the floristic patterns of bryophyte families per habitat (Figure 4B), Plagiochilaceae was the most speciose family in forest and slope habitats; and it was also, along with other families, species-rich in hilltop habitats. Dicranaceae was always present among the families with highest species number in all habitats. Metzgeriaceae and Sematophyllaceae had the highest species richness in hilltops.

DOMINANCE

Tracheophyte dominance

The most dominant tracheophyte families for the whole study area were (Figure 5): Poaceae (35.61×10^4 cm^2), Asteraceae (32.35×10^4 cm^2), Ericaceae (7.25×10^4 cm^2) and Cyperaceae (4.23×10^4 cm^2).

In terms of the dominance of tracheophyte families in different habitats (Figure 6A), Poaceae and Asteraceae were the most dominant in nearly all habitats, although in forest Poaceae was not. There, Melastomataceae, along with Asteraceae, prevailed (Figure 6A). Accompanying Asteraceae and Poaceae, Bromeliaceae was also dominant in hilltops and slopes (Figure 6A). Cyperaceae was among the top most dominant families in wetlands (Figure 6A). Ericaceae was the fourth or third with highest dominance in all habitats, except in forest where it was less dominant (Figure 6A).

The two most dominant tracheophyte species were *Calamagrostis intermedia* and *Espeletia pycnophylla* (Table 1), although they did not grow in forest. Further, *C.*

intermedia was rare in wetland valleys. Other dominant species were *Cortaderia nitida* and *Disterigma empetrifolium,* which occurred in all habitats, but were scarce in forests and slopes. *Puya hamata,* a conspicuous Bromeliaceae clearly noticeable in the landscape because of its tall inflorescence, was also among the most dominant species, growing mostly in hilltops and slopes.

Bryophyte dominance

The most dominant bryophyte families for the whole study area were (Figure 5): Bartramiaceae (5.74×10^4 cm^2), Dicranaceae (3.44×10^4 cm^2), Aneuraceae (2.47×10^4 cm^2), and Hylocomiaceae (1.73×10^4 cm^2).

In terms of the dominance of bryophyte families (Figure 6B), Bartramiaceae was the most dominant in all habitats, except in forest where Hylocomiaceae prevailed instead (Figure 6B). Another family that was usually well represented was Dicranaceae (Figure 6B). Aneuraceae was between the third or the fourth most dominant in all habitats, with the exception of hilltops.

For bryophytes, the two most dominant species were *Breutelia tomentosa* and *Riccardia amazonica* (Table 2). They occurred in all habitats, although were less common in forest. The next three most dominant species (*Campylopus* "puitas 1", *Pleurozium schreberi* and *Lepidozia* "gema") were also widespread in all habitats. The rest of species with high dominance interestingly tended to be distributed either in upland or valley.

SPECIES DENSITY

According to the species-area rarefaction curves, species density of the whole tracheophyte plant community (111 species) was significantly higher, at an α level of 0.05, than the species density of the bryophyte plant community (94 species) (Figure 7). This conclusion can be reached because their 84% confidence intervals did not overlap (see Gotelli & Colwell [2011] and Colwell et al. [2012] for further explanation about this type of statistical inference). The rarefaction curves at the habitat level (Figure 8) showed that there was no significant difference in species density of tracheophytes among forest, hilltop and slope habitats (Figure 8A); whereas for bryophytes, hilltop habitat had significantly higher species density than slope habitat (Figure 8B). On the other hand, wetland habitats showed significantly lower species density than upland habitats, for both tracheophytes (Figure 8A) and bryophytes (Figure 8B). Species density of tracheophytes in wetland valley with *Espeletia* was significantly lower than the species density in wetland valley with almost no *Espeletia*, at the edge of the lake (Figure 8A). In contrast, species density of bryophytes was not significantly different between both kinds of wetland habitats (Figure 8B). By comparing the curves (and its corresponding confidence intervals) of tracheophytes and bryophytes in a given habitat (i.e., mentally overlapping Figures 8A and 8B), it can be observed that species density of tracheophytes was only significantly higher than that of bryophytes in forest and wetland habitats. This difference is particularly notable in wetland habitat without *Espeletia* (at the edge of the lake), where tracheophyte species density was twice as high as that of bryophytes.

Additionally, there was a positive correlation between bryophytes and tracheophytes in terms of number of species per plot (Spearman's ρ [rho]=0.31, P=0.016; Figure 9). The Spearman´s non-parametric test was applied here because Shapiro-Wilk normality tests only showed a normal distribution for bryophytes (W=0.9784, P=0.364), but not for tracheophytes (W=0.9476, P=0.012) (note that H_0, for a normality test, is defined as the normal distribution).

COMMUNITY STRUCTURE (NMDS AND ANOSIM)

For tracheophytes, the original matrix dimension was 60 plots × 111 species; when uniques were excluded, it got reduced to 60 plots × 83 species. For bryophytes, the original matrix dimension was 60 plots × 94 species; when uniques were excluded, it got reduced to 60 plots × 60 species.

NMDS analyses showed similar stress values between runs with uniques and runs without uniques (Table 3). For tracheophytes, stress values varied from 0.1560 to 0.1701; while for bryophytes, stress values varied from 0.2573 to 0.2856, depending on the type of transformation applied (Table 3). The variation on stress values among iterations of a given NMDS was minimal (hundredths of decimals), which means that the NMDS results were stable. Values of ANOSIM´s R were similar between datasets with and without uniques, with corresponding P-values all very low (P=0.0001) (Table 3). R values for tracheophytes were much higher than those for bryophytes, with both the lowest and highest R values occurring when the presence/absence transformation was applied (0.6822–0.7532 for tracheophytes vs. 0.3299–0.4914 for bryophytes). Therefore, there were just small differences on stress and R values between those analyses with uniques and those without uniques. Because of this, below I only present the results of the analyses without uniques.

For tracheophytes (dataset without uniques), ANOSIM´s post hoc multiple comparison tests among habitats in general showed a significant difference between two given habitats (usually *P*=0.0001; Table 4), with the exception of hilltop and slope habitats whose community structures were statistically indistinguishable. This pattern held when using raw vegetation cover data (in cm^2) and after applying the two data transformations (percentage and presence/absence). It was also independent of whether or not a Bonferroni corrected family-wise α was applied (Table 4). The NMDS graphs indeed tend to reflect these pairwise statistical differences among habitats: those that are significantly different occupy different areas in the multivariate space (Figure 10).

For bryophytes (dataset without uniques), the graphical distinction among habitats becomes relatively unclear in the NMDS graphs (Figure 11), as compared to those of tracheophytes (Figure 10). Indeed, ANOSIM´s *R* values for bryophytes were relatively low, but this does not mean that when pairwise comparisons were made, they did not turn out to be significantly different. In fact, *P*-values of the pairwise comparisons for bryophytes mostly showed a similar pattern as with tracheophytes, except that the *P*-values were sometimes not as low (Table 4). In addition, there were the following two particularities:

(i) Just like with tracheophytes, bryophytes from hilltop and slope habitats—except for the results based on presence/absence data—were not significantly different in terms of their community structure, independently of the Bonferroni correction (Table 4; see also Figure 11).

(ii) The bryophytes in the two types of wetlands did not differ significantly in terms of their community structure (Table 4; see also Figure 11), although with presence/absence transformation, there is a significant difference if no Bonferroni correction of family-wise α is applied to interpret the results (Table 4).

SPATIAL RELATIONS

The data of tracheophytes and bryophytes in terms of % vegetation cover did not follow a normal distribution according to a Shapiro-Wilk test (*W*=0.93, *P*=0.003 for tracheophytes; *W*=0.8, $P=1.41\times10^{-7}$ for bryophytes). Therefore, a Spearman non-parametric test was applied in order to analyze the correlation between % bryophyte cover and % vegetation cover. The result was that no correlation exists between these two variables (Spearman’s ρ [rho]=−0.02, *P*=0.857; Figure 12). In the more detailed analyses that are described below, in order to test Hypotheses 1 and 2, Spearman´s rank correlations were also always applied, given that % cover data did not follow a normal distribution.

In order to assess Hypothesis 1 related to the spatial relation between % bryophyte cover and % cover of dominant species of tussocks, basal rosettes and prostrate shrubs in each plot, it was first necessary to define what the most dominant species of tracheophytes in these growth forms were (see Table 1): for tussocks, *Calamagrostis intermedia* and *Cortaderia nitida* were selected; for basal rosettes, just *Puya hamata* was selected; and for prostrate shrubs, just *Disterigma empetrifolium* was selected.

The correlation between % bryophyte cover and % cover of tracheophyte species of tussocks, basal rosettes and prostrate shrubs, did not show any correlation, according to Spearman´s rank tests (ρ[rho]=−0.29 to +0.28; *P*-values=0.111 to 0.840; Table 5). Therefore, I fail to reject the null hypothesis of 0 (zero) correlation, and thus there is evidence that Hypothesis 1 (see Introduction) is not probably true. The correlation between % bryophyte cover and % cover of the dominant caulescente rosette*, Espeletia pycnophylla*, also yield a similar result (ρ[rho]=−0.12, *P*=0.437; Table 5), providing evidence that Hypothesis 2 (see Introduction) is not probably true, either.

DISCUSSION

To my knowledge, this is the first study in Ecuador that has explored, at the same time, the floristics and community structure of vascular plants (tracheophytes) and non-vascular plants (bryophytes) in páramos. Indeed, it is one of the few studies that has used the same sampling units (plots) to inventory these two evolutionary groups in terms of their taxonomic richness, dominance (as vegetation cover), species density, community structure and spatial relations.

TAXONOMIC RICHNESS

Tracheophyte taxonomic richness

Ten percent (10%) of regional species richness (γ-gamma diversity) of tracheophytes was detected in this study—The 111 tracheophyte species reported in this study (Appendix 1), in just 60 plots of 4 m^2 (Figure 1), represent 10% of the ca. 1100 tracheophytes species estimated for El Ángel Ecological Reserve (Chimbolema et al., 2013), 8% of the ca. 1300 tracheophytes known to occur in Carchi province at altitudes ≥3000 m (Jørgensen & León-Yánez, 1999), and ca. 3% of the 3400 species estimated to occur in all Ecuadorian páramos, including high-altitude forests (Luteyn, 1999).

Asteraceae was the most speciose tracheophyte family—In this study, with a total of 19 species recorded, the total number of Asteraceae species was more than double the number of the next most species-rich families (Figure 3A). It was also the most species-rich family in each of the habitats studied (Figure 4A), demonstrating that species in this family can live under many different environmental conditions. Asteraceae, along with Orchidaceae, are indeed the families with the highest number of species worldwide, certainly as a result of their close coevolutionary relation with insects (Evert & Eichhorn, 2013). In Ecuador, it is estimated that ca. 430 Asteraceae species occur at altitudes ≥3000m (Jørgensen & León-Yánez, 1999), and it is well-known that Asteraceae is one of the most speciose families in páramos (e.g., Jørgensen & León-Yánez, 1999; Ulloa et al. 2010). For example, 18 species of Asteraceae were reported in the grassland and wetland páramos in Antisana and Cotopaxi (FONAG, 2017), 11 species occurred in the Chimborazo páramo (Caranqui, 2014), 11–25 species were found in the Podocarpus National Park páramo (Aguirre-Mendoza et al., 2015; Eguiguren et al., 2015), and 85 species were found in the Cajas National Park páramo (Ulloa et al., 2010). These numbers are not directly comparable among them because of the different methodologies applied, but exemplify the point that Asteraceae is, in fact, very species-rich in páramos.

Bryophyte taxonomic richness

Total species richness of bryophytes was much higher than expected—The present study reports 94 bryophyte species (41 of which are mosses) sampled in 60 plots of 1 m^2 (Appendix 2). This number seems high considering that only 96 bryophyte species had been reported in the past for the whole province of Carchi: 30 species of mosses and 66 species of liverworts and hornworts (León-Yánez et al., 2006; Toapanta, 2011). The report of 30 moss species for Carchi (Toapanta, 2011) is however lower than the 41 moss species recorded in this study in just 60 small plots, clearly suggesting that there are many more species of mosses in northern Andean Ecuador yet to be registered. Indeed, the coastal and northern Andes of Ecuador are among the regions where further exploration of bryophytes is needed (Toapanta, 2011; A. Benítez, pers. comm.). The 94 bryophyte species found in this study represent 15.7% of the ca. 600 bryophyte species estimated to occur in all Ecuadorian páramos (Missouri Botanical Garden, 2020) and ca. 5% of the ca. 1900 bryophyte species known to occur in the whole Ecuadorian territory (Gradstein & Weber, 1982; Churchill, 1994; Churchill et al., 2000; León-Yánez et al., 2006). In addition, note that out of the 94 bryophyte species from this study, 56 (59.6%) are really morphospecies. This is a high % of unidentified species-level taxa, although all but one of them were successfully identified to genus level. Certainly, taxonomic identification of bryophytes to species level is difficult because it requires work under the microscope (histological cuts) and extensive comparative work with herbarium specimens. After such work is completed in the future, it is possible that the number of valid species may change (A. Benítez, pers. comm.). Comparative genomic analyses could also aid in this taxonomic effort. An updated checklist of all known bryophytes from Ecuador (mosses, liverworts and hornworts), categorized by province and type of ecosystem, is certainly eagerly needed.

Bryophyte families contributed more or less equitably to the number of species recorded—Even though there were bryophyte families that were relatively species-rich in certain habitats (such as Plagiochilaceae, Dicranaceae, Metzgeriaceae and Sematophyllaceae, to name a few), the difference in their relative contribution did not reveal a clear pattern (Figure 3B). This is certainly a very different pattern than what was observed in tracheophytes, where just one family, Asteraceae, clearly contributed many more species than other families.

Some of the most speciose bryophyte families were also speciose in other studies—The bryophyte families reported here with the highest species number had also been recorded as such in other studies, although a direct comparison is not possible because of the different methodologies applied. In any case, some examples can be highlighted. In the Cordillera del Cóndor in Zamora Chinchipe province—where 166 bryophyte species were reported—the most diverse families were Lepidoziaceae, Lejeuneaceae, Pilotrichaceae, Dicranaceae, and Sematophyllaceae. From these, Lepidoziaceae, Dicranaceae and Sematophyllaceae were also among the most species-rich in the present study (Figure 3B), depending on the habitat (Figure 4B). For the whole country, Toapanta (2011) reported 223 species of bryophytes, among which the families containing the highest number of species were Pilotrichaceae, Bryaceae and Bartramiaceae. In this study, Bryaceae and, to a lesser extent, Bartramiaceae, contained also relatively high species numbers (Figure 3B; Figure 4B). For the province of Carchi, Toapanta (2011) reported the following families as the most diverse: Dicranaceae, Bartramiaceae and Pottiaceae. From these, Dicranaceae and Bartramiaceae were also among the most species-rich in this study (Figure 3B; Figure 4B).

DOMINANCE

Tracheophyte dominance

Among tracheophytes, the most dominant families were Poaceae and Asteraceae—In terms of vegetation cover, the typical flora of northern Ecuadorian páramos is dominated by the families Poaceae and Asteraceae (Neill, 1999; Ramsay, 2001; Sylvester et al., 2019). The results from this study are not the exception, with Poaceae and/or Asteraceae being very dominant families in all habitats (Figures 5 and 6A).

In this study, the dominance of Poaceae in upland habitats (hilltop and slope) was mostly due to the high vegetation cover of *Calamagrostis intermedia* and *Cortaderia nitida* (Table 1; Appendix 1), both representative of the typical and common tussock growth form of páramos (e.g., Løjtnant & Molau, 1983; Ramsay & Oxley, 1997; Caro & Rivera, 2015; FONAG, 2017). This growth form, common in highly disturbed areas (Ramsay & Oxley 1997; Caranqui et al., 2016), is also common at El Ángel probably because of past practices of livestock and burning, which still occur but at lower intensities (MAE, 2015). It is well known that tussock growth forms can quickly recover and increase their dominance after a disturbance, probably outcompeting other species in grassland páramos (Ramsay & Oxley, 1996). In fact, just one individual of *Cortaderia nitida* can occupy a large area due to their long and erect tillers and tightly organized leaves (Ramsay & Oxley, 1997).

To a great extent, the dominance (vegetation cover) of the Asteraceae family is due to *Espeletia pycnophylla*, "frailejón" (Table 1; Appendix 1). *Espeletia* is an endemic genus of the páramo ecosystem, currently distributed from the páramos of western Venezuela to northern Ecuador (although an isolated population exists in the Llanganates mountains, further south in Ecuador). Nowadays, *Espeletia pycnophylla* is the only species of its genus in Ecuador, although two subspecies are recognized: *angelensis* and *llanganatensis* (Neill, 1999). The diversification in *Espeletia* is probably the result of past climatic fluctuations, through which species were adapted to different niches along altitudinal gradients (Padilla-Gonzales et al., 2017). This wind-dispersed genus (Berry & Calvo, 1989) occurs at El Ángel grassland páramo, including some wetland valleys, as long as they are not too waterlogged.

After Poaceae and Asteraceae, the common families Bromeliaceae, Melastomataceae, Cyperaceae and Ericaceae are also common in other Ecuadorian páramos—Along with Poaceae and Asteraceae, the families Bromeliaceae, Ericaceae and Melastomataceae (Neill, 1999; Ramsay, 2001). The dominance of Bromeliaceae (Figure 6A) is explained by the common presence of *Puya hamata*, which was abundant in the upland habitats of hilltop and slope (Table 1; Appendix 1), i.e. in the habitats that epitomize the classic view of a "páramo" (Miller & Silander, 1991). *Puya hamata* is also dominant in other Ecuadorian páramos (Neill, 1999), including the southernmost páramos such as that in Podocarpus National Park (Aguirre-Mendoza, 2015). The dominance of this species could be explained by its fire resistance, which reduces its mortality rate, and by the large area that one individual can occupy because of its thick, spirally arranged, leaves (García-Meneses & Ramsay, 2014). Regarding Melastomataceae, because it is a family characterized by species of shrubs and trees, it was evidently more dominant in forest. The dominance of Cyperaceae in wetland habitat was mainly related to the common presence of *Oreobolus ecuadorensis* (Table 1; Appendix 1), a cushion plant (Bosman et al., 1993). With respect to Ericaceae, it was a dominant family because of *Disterigma empetrifolium* (Table 1; Appendix 1), which some studies in fact report it as the most dominant woody species (e.g., Keating, 2000, Ramsay, 2001, Arellano-González et al., 2020). This species is a prostrate dwarf shrub, creeping along the soil with high density cover, sometimes forming cushions (Ramsay & Oxley, 1997).

Bryophyte dominance

Among bryophytes, Bartramiaceae was the most dominant family in all habitats, usually along with Dicranaceae, except in forest where Hylocomiaceae was the most dominant—Figure 6B shows that, in terms of vegetation cover (dominance), the bryophyte families Bartramiaceae, Dicranaceae and Hylocomiaceae were dominant or codominant in most habitats. In Guantiva-La Rusia, a Colombian páramo, Bartramiaceae and Dicranaceae were also the most dominant families, along with Bryaceae, Hypnaceae, Pottiaceae, and Meteoriaceae (Martínez et al., 2019). Regarding Bartramiaceae, it was a dominant family because of the high dominance of *Breutelia tomentosa* (Table 2; Appendix 2). This species is clearly a generalist with wide niche preferences. The second most dominant bryophyte species, *Riccardia amazonica* (Aneuraceae), is also a generalist widely distributed in all habitats. Regarding Dicranaceae, it became a dominant family because of the common presence of *Campylopus* spp. (Appendix 2), particularly the morphospecies *Campylopus* "puitas1" (Table 2; Appendix 2). Likewise, Hylocomiaceae became a dominant family because of *Pleurozium schreberi*, a widespread species particularly common in forest habitat (Table 2; Appendix 2), and which is in fact the only representative of this family (Appendix 2).

Strangely, Sphagnaceae was uncommon in the study area—It is peculiar in the present study that Sphagnaceae does not appear among the most dominant families in wetland valleys, where *Sphagnum* species are usually abundant (Evert & Eichhorn, 2013). Even in the Chiles páramo, which is actually part of the same páramo ecosystem of this study, *Sphagnum* spp. seem to have been very common in the boggy areas (Terneus, 2001). Further sampling of the wetlands around El Voladero lakes is certainly necessary to confirm the relative low abundance of *Sphagnum* in the present study.

Dominant species and families of bryophytes change in different páramos—The dominant species of bryophytes in this study are not among the most common bryophytes in other studies. For example, in Podocarpus National Park, the dominant species were *Plagiochila diversifolia* (Plagiochilaceae), *Leptotheca boliviana* (Rhizogoniaceae), *Breutelia chrysea* (Bartramiaceae) and *Frullania* sp. (Juvulaceae) (Urgiles-Gómez et al., 2001); while in a Colombian páramo, the dominant species were *Campylopus flexuosus*

(Dicranaceae), *Adelothecium bogotense* (Daltoniaceae), *Heterophyllum affine* (Sematophyllaceae) and *Leskeadelphus angustatus* (Leskeaceae) (Martínez et al., 2019). Thus, bryophyte species dominance seems to vary a lot among different páramo sites (in contrast to what is observed for tracheophytes, in which the most dominant species, or at least genera, tend to also dominate in páramo sites separated by hundreds of kilometers). This is not to say that many of the species or genera recorded in this study are not found in other sites. In fact, South American páramos contain many cosmopolitan genera (Griffin, 1990): *Bryum*, *Campylopus*, *Pleurozium* and *Sphagnum* are for example each represented by several species in this study. *Sphagnum magellanicum*, a widely spread cosmopolitan species, was recorded in this study as well.

SPECIES DENSITY

All habitats considered, tracheophytes show significantly higher species density than bryophytes, but the difference is rather small—In the area sampled by this study, tracheophytes had in total more species than bryophytes (111 vs. 94, respectively), which was a statistically significant difference, according to the rarefaction curves (Figure 7). This result could be expected given the larger regional species pool (γ-gamma diversity) (Ron et al., 2018) of tracheophytes as compared to bryophytes (León-Yánez et al., 2006; Toapanta, 2011; Chimbolema et al., 2013). Incomplete identification of bryophytes in the few studies that sampled them (e.g., Caranqui et al., 2014; Aguirre-Mendoza et al., 2015; FONAG, 2017), probably has also contributed to the perception that the diversity of bryophytes is much lower than that of tracheophytes, on a per area basis (α-alpha diversity). Bryophytes seem indeed less diverse than tracheophytes, but the difference does not seem to be very strong, although it is significant (Figure 7).

Both tracheophytes and bryophytes had significantly higher species density in uplands than in wetlands—Tracheophytes had higher species density in upland habitats (forest, hilltop, slope) than in wetland habitats (Figure 8A); and this same pattern was observed for bryophytes (Figure 8B). For tracheophytes, the low plant diversity observed in wetlands could be explained by a strong environmental filtering, such as lack of true soil and roots frequently facing waterlogging (anaerobic conditions). For bryophytes, a reason why they might be not diverse in wetlands could be that they do not easily grow on cushions (pers. obs.), a well adapted and common tracheophyte growth form in wetlands. Under stressful wetland conditions, it would be expected, according to the Stress Gradient Hypothesis, that the few specialized plant species that thrive there start to facilitate their mutual coexistence (Bertness and Callaway, 1994; Anthelme & Dangles, 2012).

At the plot level, species density of bryophytes correlated positively with species density of tracheophytes—There is a positive correlation between the number of species of bryophytes vs. tracheophytes (r=0.31, P<0.016; Figure 9). This pattern could be explained by the microenvironments that tracheophytes can create through their complex architecture and growth forms. Different bryophyte species can exploit these different niches, characterized for example by gradients of humidity, soil pH, substrate and light (e.g., During & Van Tooren, 1990; Corrales et al., 2010; Chantanaorrapint & Frahm, 2011). In fact, competition can allow the coexistence of bryophytes and tracheophytes, sometimes even resulting in a facilitating effect for bryophytes (Ingerpuu et al., 2005). But not only tracheophytes may affect the distribution of bryophytes—other macroenvironmental factors such as altitude, climate and soil can also control bryophyte diversity (Frantzen & Bouman, 1989; Gradstein, 1989; Eldridge & Tozer, 1997; Noriega et al., 2008; Ingerpuu et al., 2019). Community assembly experiments that manipulate the environment and its biotic interactions are needed to elucidate among the putative mechanisms that could influence species coexistence of tracheophytes and bryophytes.

COMMUNITY STRUCTURE (NMDS AND ANOSIM)

Tracheophyte community structure

Independently of whether uniques were included or not, or whether a data transformation was applied or not, the NMDS ordinations for tracheophytes (Figure 10; Table 3) had all relatively low stress values (ca. 0.16–0.17). Because these values were all <0.30, it means that the real variation is properly depicted in a multivariate two-dimensional space (Kindt & Coe, 2005). Also, it is interesting to note that the distances among plots within forest habitat (Figure 10) are larger than what is observed for other habitats. This means that there are actually quite different patterns of community structure among different forest patches, probably as a cause of strong microenvironmental variation among them and intense historical fragmentation (which can limit their ecological interconnectedness). This particular topic deserves further study, while controlling for potential sampling biases.

ANOSIM´s R, which can vary from −1 to +1, was close to 0.7 for all ordinations, with a significant difference among habitats (P=0.0001) (Table 3). This means that, the dissimilarity among habitats was significantly greater than that within habitats, as summarized by the Bray-Curtis index (Kindt & Coe, 2005).

ANOSIM´s pairwise comparisons among habitats showed that the tracheophyte communities of most habitats were significantly different, independently of whether or not a Bonferroni correction was applied (Table 4). The exception were the hilltop and slope habitats, which did not show a significant difference in their community structure (Table 4). This result makes sense given the visibly homogenous features of the landscape of hilltops and slopes: a grassland páramo dominated by *Espeletia pycnophylla* and *Calamagrostis intermedia*.

Bryophyte community structure

The NMDS ordinations for bryophytes (Figure 11; Table 3) had stress values relatively close to the threshold of 0.3 (ca. 0.26–0.29), above which the variation in the system would not anymore be properly depicted in a multivariate two-dimensional space (Kindt & Coe, 2005). ANOSIM´s *R* values of bryophytes (ca. 0.33–0.49) were much lower than those observed with tracheophytes (around 0.7), although still there was a significant difference among habitats (P=0.0001) (Table 3). Thus—even though *R* values were relatively low and the plots of different habitats overlap in the NMDS graphs—the dissimilarity among habitats according to the Bray-Curtis index was still significantly greater than that within habitats (Kindt & Coe, 2005).

Similar to tracheophytes, ANOSIM´s pairwise comparisons among habitats showed that the community structure of bryophyte communities of hilltops and slopes were, in general, not significantly different—although they were significantly different when presence-absence data was used for the analysis (Table 4). Note that this pattern is strong enough as to be unaffected by the Bonferroni correction (Table 4). Also, in contrast to tracheophytes, for bryophyte communities there was not a significant difference between the two types of wetlands, again independently of the Bonferroni correction. However, given that the *P*-value that supports this conclusion is very close to the significance level of 0.05 (P=0.059; Table 4), it would be advisable to keep sampling these two types of wetlands in the search for a significant result, as recommended by Lane et al. (2020). This advice is supported by the argument that it can never be concluded, just from the *P*-values, that a null hypothesis is true when it is not rejected—indeed, it would be a serious error to do so (Lane et al. 2020). Wetland habitats may look homogenous on the surface, but their floristic composition can actually be very sensitive to minimum changes in flooding regime, or other factors such as pH, organic matter content and water temperature—all of which can influence not only plants but also animals (Da Silva et al., 2010; Hashemi et al., 2015). In fact, Moscoso-Estrella (2019) found, in a boggy paramo located in the Chiles volcano (close to my study area), that it is possible to distinguish different plant community assemblages within the same wetland.

SPATIAL RELATIONS

At the plot level, dominance (vegetation cover) of bryophytes and tracheophytes were not correlated— Because different areas were sampled for tracheophytes and bryophytes, absolute cover (in cm^2) had to be expressed as % cover in order to make a valid comparison among these two plant lineages. The correlation analysis showed that bryophytes and tracheophytes were not correlated (Spearman's ρ [rho]=−0.02, P>0.857; Figure 12). A plausible explanation is that high cover of tracheophytes could either favor or displace bryophytes, as both situations seem possible depending on the growth form and species identity of tracheophytes and how they interact along environmental gradients (see During & Van Tooren, 1990; Corrales et al., 2010; Chantanaorrapint & Frahm, 2011). If, for example, an area is dominated by a very common tracheophyte, the resulting homogenized habitat could either favor only those bryophyte species adapted to such habitat, or the tracheophyte could simply displace many bryophytes through competition for space. Using a similar logic, an area with very few tracheophytes could either have many pioneering bryophytes, or very few bryophytes if there is a lack of proper microenvironmental conditions. Interactions like these seem varied enough in nature as to guarantee that any pattern between tracheophyte cover and bryophyte cover remains elusive. However, analyzing the effect of certain dominant growth forms of tracheophytes on the distribution of bryophytes could provide insight on this issue, as shown below.

At the plot level, the dominance of bryophytes and the dominance of tussocks and basal rosettes did not correlate—Hypothesis 1 stated that there is a negative correlation between vegetation cover of bryophytes and vegetation cover of the dominant species of tussocks, basal rosettes and prostrate shrubs, which are common tracheophyte growth forms in páramos. The dominant species used in this analysis were (Table 1): *Calamagrostis intermedia* and *Cortaderia nitida*, the two most dominant tussocks; *Puya hamata*, the most dominant basal rosette; and *Disterigma empetrifolium*, the most common prostrate shrub. After the correlation analysis, Hypothesis 1 however was not supported by the data (Spearman's ρ [rho]=−0.21, *P*=0.144; Table 5). This can be explained by considering that the bryophyte perception of the tracheophyte presence probably depends a lot on the growth form and species involved. A correlation was expected considering that tracheophyte species that grow relatively close to the soil provide a dense cover of live and dead leaves (Ramsay & Oxley 1997), which should promote the availability of light and moisture for the bryophyte species that grow near or on them. In order to complement this analysis and control for the variation that different growth forms may have on the distribution of bryophytes, I also decided to analyze them separately, as discussed next.

The % cover of the most dominant tussocks (*Calamagrostis intermedia* and *Cortaderia nitida)* did not show a correlation with % bryophyte cover (Spearman's ρ [rho]=−0.20, *P*=0.185; Table 5). I expected a correlation because tussocks occupy large areas, have dense cover and reduce soil moisture, and thus should represent a strong competitor for bryophytes for space, light and water (Herben, 1987; Hellquist & Crow, 1999; BGCI, 2017). When the two species of tussocks were analyzed independently, neither the % cover of *Calamagrostis intermedia* (Spearman's ρ [rho]=−0.29, *P*=0.111; Table 5) nor the % cover of *Cortaderia nitida* (Spearman's ρ [rho]=−0.08, *P*=0.672; Table 5) showed any correlation with % bryophyte cover. All these non-significant results provide evidence that bryophytes are not necessarily sensible to competition by tussocks—by logic of hypothesis testing, however, these non-significant results are not meant to signify that competition does not exist (as we cannot "accept the null hypothesis"). The effect of *Calamagrostis intermedia* and *Cortaderia nitida* on local bryophyte dominance should be further analyzed by conducting experiments under controlled enviromental conditions. For example, in the context of ecological restoration, it is important to assess the effect of using *Calamagrostis* spp., or other Poaceae tussocks, on the long term establishment of bryophytes.

Regarding the % cover of *Puya hamata*, the most dominant basal rosette, it was not correlated with % bryophyte cover (Spearman's ρ [rho]=−0.05, *P*=0.840; Table 5). This is evidence that *Puya*, with its succulent numerous leaves, which reduce light and space, do not seem to influence the bryophyte community under it. In any case, *Puya* should be studied in detail due to its high high resistance to fires (Miller, 1989) and because it could become a strong water and nutrient competitor for other plants, including bryophytes, during the regeneration process of the páramo.

With respect to *Disterigma empetrifolium*, the most dominant prostrate shrub species, and indeed the most dominant woody species, it did not show any correlation with % bryophyte cover (Spearman's ρ [rho]=+0.28, *P*=0.125; Table 5). Thus, the dense ground cover of this species, with their thick leaves and horizontally extending branches (Ramsay & Oxley, 1997), apparently does not have much influence on local bryophyte dominance. This means that bryophytes could either grow abundantly, or not at all, along or near this plant. In fact, I observed in the field that the moss *Breutelia tomentosa*, the most abundant moss species, often used to grow amidst *Disterigma empetrifolium* leaves (pers. obs).

At the plot level, the dominance of bryophytes and dominance of Espeletia pycnopylla did not correlate—Based on previous work that argued that *Espeletia* species create favorable microenvironments for other páramo plants (e.g., Pérez, 1989; Mora et al., 2019), Hypothesis 2 stated that there is a positive correlation between bryophyte cover and the dominant presence of the giant rosette *Espeletia pycnophylla*, commonly known as "frailejón". However, the results of this study do not support this hypothesis (Spearman's ρ [rho]=−0.12, *P*=0.437; Table 5). Bryophytes seem not to be favored by the microenvironmental conditions that *Espeletia pycnophylla* plants create around them, at least under the macroclimatic conditions of El Ángel páramo. If this hypothesis is to be pursued in the future, experiments or observations should focus on the soil conditions under mature *Espeletia pycnophylla* plants and the community of tracheophytes and bryophytes that coexist at or near the base of their stems.

CONCLUSION

In conclusion, this study reports the community structure patterns of tracheophytes and bryophytes and their spatial relations in El Ángel páramo, “Lagunas del Voladero” area, Carchi, Ecuador. In this area, I established *N*=60 small plots (2 m × 2 m) to sample both tracheophytes and bryophytes. These two evolutionary lineages were sampled using a nested design in which bryophytes were only sampled in the center 1 m × 1 m. Plots (*N*) were established in the following habitats: forest (*N*=10), hilltop with *Espeletia pycnophylla* (*N*=16), slope with *E. pycnophylla* (*N*=14), wetland valley with *E. pycnophylla* (*N*=10) and wetland valley with almost no *E. pycnophylla* (*N*=10). For each species, dominance, measured as vegetation cover (cm^2), was estimated using a metallic grid. I found 111 tracheophyte species and 94 bryophyte species. The most speciose tracheophyte family was Asteraceae (19 spp.), whereas the most speciose bryophyte family was Plagiochilaceae (10 spp.). The most dominant families (in terms of vegetation cover) were Asteraceae and Poaceae for tracheophytes, and Bartramiaceae and Dicranaceae for bryophytes. At the species level, the most dominant tracheophytes were *Calamagrostis intermedia* and *Espeletia pycnophylla*, while the most dominant bryophytes were *Breutelia tomentosa* and *Riccardia amazonica*. According to species-area rarefaction curves, tracheophytes had higher species density than bryophytes, and both evolutionary lineages showed higher species density in upland habitats than in wetlands. NMDS analyses for both tracheophytes and bryophytes showed a community structure different for each habitat, except hilltop and slope, which had the same structure. At the plot level, I found that bryophyte species density correlated positively with tracheophyte species density. On the other hand, dominance of bryophytes vs. dominance of tracheophytes did not show any correlation. Further, at plot level, there was no correlation between bryophyte dominance and the dominance of common tussocks, basal rosettes, prostrate shrubs, or *Espeletia pycnophylla*.

To my knowledge, this is the first study in Ecuador that has explored in detail the floristics and community structure of vascular plants (tracheophytes) and non-vascular plants (bryophytes) in páramos. Indeed, it is one of the few studies that has used the same sampling units (plots) to inventory these two evolutionary groups. Furthermore, in contrast to other research initiatives, here I explicitly included in the sampling design different habitats defined by topography and associated soil drainage. This comprehensive approach has made possible not only to determine community structure patterns, but also to assess spatial relations between tracheophytes and bryophytes. For El Ángel páramo, where not many scientific studies focused on vegetation exist, especially on bryophytes, this study represents a (humble) milestone. Even though, in its very nature, this study is basically descriptive, I still decided to propose and statistically test two hypotheses regarding spatial relations between tracheophytes and bryophytes. The framing of these hypotheses, supported by basic ecological theory and findings from other studies, helped me to understand plant ecological processes in páramos—independently if at the end they were not supported. I am sure that the study of the coexistence of these two evolutionary groups can provide tools for the long-term preservation of micro-and macro-habitats in páramos and the ecosystem services they generously provide.

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TABLES

TABLE 1

Total cover (cm^2) and frequency (*N*=number of plots, in parentheses) of the ten most dominant TRACHEOPHYTE species, in the habitats studied at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. Dominance was defined as vegetation cover (cm^2). Habitat codes: Forest (F), Hilltop with *Espeletia pycnophylla* (HE), Slope with *E. pycnophylla* (SE), Wetland Valley with *E. pycnophylla* (WVE) and Wetland Valley with almost no *E. pycnophylla* (WV).

Species (incl. morphospecies)	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total (*N*=60)**
Calamagrostis intermedia (Poaceae)	0 (0)	96613 (15)	119110 (13)	0 (0)	3840 (3)	219563 (3)
Espeletia pycnophylla (Asteraceae)	0 (0)	56184 (16)	52242 (14)	62160 (10)	2190 (3)	172776 (43)
Cortaderia nitida (Poaceae)	120 (1)	32244 (8)	4290 (4)	26340 (8)	13182 (9)	76176 (30)
Disterigma empetrifolium (Ericaceae)	60 (1)	19536 (7)	3846 (4)	16590 (10)	20782 (9)	60814 (31)
Puya hamata (Bromeliaceae)	120 (1)	19902 (8)	14310 (8)	1950 (4)	0 (0)	36282 (21)
Festuca sodiroana (Poaceae)	0 (0)	24847 (15)	6702 (10)	4380 (2)	0 (0)	35929 (27)
Miconia nodosa (Melastomataceae)	30960 (10)	1908 (3)	840 (2)	0 (0)	0 (0)	33708 (15)
Gynoxys pendula (Asteraceae)	30562 (6)	0 (0)	0 (0)	0 (0)	0 (0)	30562 (6)
Diplostephium rhododendroides (Asteraceae)	5766 (2)	1459 (4)	5183 (6)	14670 (8)	1530 (3)	28608 (23)
Oreobolus ecuadorensis (Cyperaceae)	0 (0)	0 (0)	0 (0)	10026 (4)	18540 (9)	28566 (13)

TABLE 2

Total cover (cm^2) and frequency (*N*=number of plots, in parentheses) of the ten most dominant BRYOPHYTE species, in the habitats studied at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. Dominance was defined as vegetation cover (cm^2). Habitat codes: Forest (F), Hilltop with *Espeletia pycnophylla* (HE), Slope with *E. pycnophylla* (SE), Wetland Valley with *E. pycnophylla* (WVE) and Wetland Valley with almost no *E. pycnophylla* (WV).

Species (incl. morphospecies)	F (*N*=10)	HE (*N*=16)	SE (*N*=14)	WVE (*N*=10)	WV (*N*=10)	Total (*N*=60)
Breutelia tomentosa (Bartramiaceae)	720 (3)	14183 (13)	9168 (14)	12708 (10)	19332 (10)	56111 (50)
Riccardia amazonica (Aneuraceae)	8070 (6)	2294 (11)	2548 (11)	4270 (10)	4416 (9)	21598 (47)
Campylopus “puitas1” (Dicranaceae)	2172 (4)	4716 (13)	3624 (9)	6945.6 (8)	3120 (3)	20578 (37)
Pleurozium schreberi (Hylocomiaceae)	13236 (7)	540 (2)	1830 (2)	1222.8 (2)	444 (2)	17273 (15)
Lepidozia “gema” (Lepidoziaceae)	1650 (3)	3348 (5)	900 (3)	240 (1)	4520.4 (5)	10658 (17)
Metzgeria leptoneura (Metzgeriaceae)	6522 (5)	420 (3)	648 (3)	0 (0)	0 (0)	7590 (11)
Rhacocarpus purpurascens (Rhacocarpaceae)	0 (0)	0 (0)	0 (0)	4500 (5)	1374 (3)	5874 (8)
Sematophyllum “setaslargas” (Sematophyllaceae)	0 (0)	4555 (11)	1236 (2)	0 (0)	0 (0)	5791 (13)
Prionodon “puercoespin” (Prionodontaceae)	0 (0)	0 (0)	0 (0)	1764 (4)	3486 (3)	5250 (7)
Plagiomnium rhynchophorum (Mniaceae)	4560 (2)	402 (3)	187 (3)	0	0	5149 (8)

TABLE 3

Stress values from Non-Metric Multidimensional Scaling (NMDS), and *R* and *P*-values from Analysis of Similarities (ANOSIM). Note that the inclusion of uniques (a species occurring in one plot only) does not affect much the stress and R values.

		TRACHEOPHYTES	**BRYOPHYTES**
		NMDS Stress (ANOSIM *R*, *P*-value)	**NMDS Stress (ANOSIM *R*, *P*-value)**
DATA NOT TRANSFORMED	Cover (cm^2) with uniques	0.1567 (0.7053, 0.0001)	0.283 (0.4725, 0.0001)
	Cover (cm^2) without uniques	0.1561 (0.7111, 0.0001) (**Fig. 10A**)	0.2578 (0.3332, 0.0001) (**Fig. 11A**)
DATA TRANSFORMED	Percentage (%) transformation with uniques	0.1569 (0.7054, 0.0001)	0.2574 (0.3299, 0.0001)
	Percentage (%) transformation without uniques	0.1560 (0.7112, 0.0001) (**Fig. 10B**)	0.2578 (0.3332, 0.0001) (**Fig. 11B**)
	Presence/absence transformation with uniques	0.1698 (0.7532, 0.0001)	0.2573 (0.3299, 0.0001)
	Presence/absence transformation without uniques	0.1701 (0.6822, 0.0001) (**Fig. 10C**)	0.2856 (0.4914, 0.0001) (**Fig. 11C**)

TABLE 4

Probability matrices of ANOSIM´s post-hoc pairwise multiple comparisons, using different data transformations of vegetation cover (in cm^2). Only those analyses made without uniques are shown here (i.e., 60 plots × 83 tracheophyte species, and 60 plots × 60 bryophyte species). Habitat codes: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10). Highlighted cells indicate NON-significant pairwise differences between two habitats. Both triangles show uncorrected *P*-values, but in the upper triangle the highlighted cells correspond to a Bonferroni-corrected family-wise α (significance level) of 0.005 (calculate by: original α / No. comparisons = 0.05/10 = 0.005).

Tracheophytes cover (cm^2) without uniques

	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		**0.099**	0.0001	0.0001
SE	0.0001	**0.099**		0.0001	0.0001
WVE	0.0001	0.0001	0.0001		0.0001
WV	0.0001	0.0001	0.0001	0.0001	

Bryophytes cover (cm^2) without uniques

	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		**0.1187**	0.0043	**0.0169**
SE	0.0001	**0.1187**		0.0001	0.0017
WVE	0.0001	0.0043	0.0001		**0.059**
WV	0.0001	0.0169	0.0017	**0.059**	

Tracheophytes percentage (%) transformation without uniques

	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		**0.0984**	0.0001	0.0001
SE	0.0001	**0.0984**		0.0001	0.0001
WVE	0.0001	0.0001	0.0001		0.0001
WV	0.0001	0.0001	0.0001	0.0001	

Bryophytes percentage (%) transformation without uniques

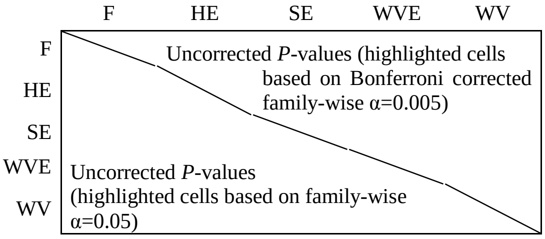
	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		**0.1187**	0.0043	**0.0169**
SE	0.0001	**0.1187**		0.0001	0.0018
WVE	0.0001	0.0043	0.0001		**0.059**
WV	0.0001	0.0169	0.0018	**0.059**	

Tracheophytes presence/absence transformation without uniques

	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		**0.1443**	0.0001	0.0001
SE	0.0001	**0.1443**		0.0001	0.0001
WVE	0.0001	0.0001	0.0001		0.0001
WV	0.0001	0.0001	0.0001	0.0001	

Bryophytes presence/absence transformation without uniques

	F	HE	SE	WVE	WV
F		0.0001	0.0001	0.0001	0.0001
HE	0.0001		0.0021	0.0001	0.0001
SE	0.0001	0.0021		0.0001	0.0002
WVE	0.0001	0.0001	0.0001		**0.0078**
WV	0.0001	0.0001	0.0002	0.0078	



Uncorrected *P*-values (highlighted cells based on Bonferroni corrected family-wise α=0.005)

Uncorrected *P*-values (highlighted cells based on family-wise α=0.05)

TABLE 5

Spearman´s rank correlation between % cover of BRYOPHYTES and % cover of different growth forms of the most dominant TRACHEOPHYTE species, at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. ρ (rho)=Spearman´s correlation coefficient. *P*=probability value.

	Bryophytes (%) vs. …	**ρ (rho)**	***P***
HYPOTHESIS 1	TOTAL TUSSOCKS + BASAL ROSETTE + PROSTRATE SHRUB	−0.21	0.144
	TOTAL TUSSOCKS: *Calamagrostis intermedia* + *Cortaderia nitida*	−0.20	0.185
	TUSSOCK 1: *Calamagrostis intermedia*	−0.29	0.111
	TUSSOCK 2: *Cortaderia nitida*	−0.08	0.672
	BASAL ROSETTE: *Puya hamata*	−0.05	0.840
	PROSTRATE SHRUB: *Disterigma empetrifolium*	+0.28	0.125
HYPOTHESIS 2	CAULESCENTE ROSETTE: *Espeletia pycnophylla*	−0.12	0.437

FIGURES

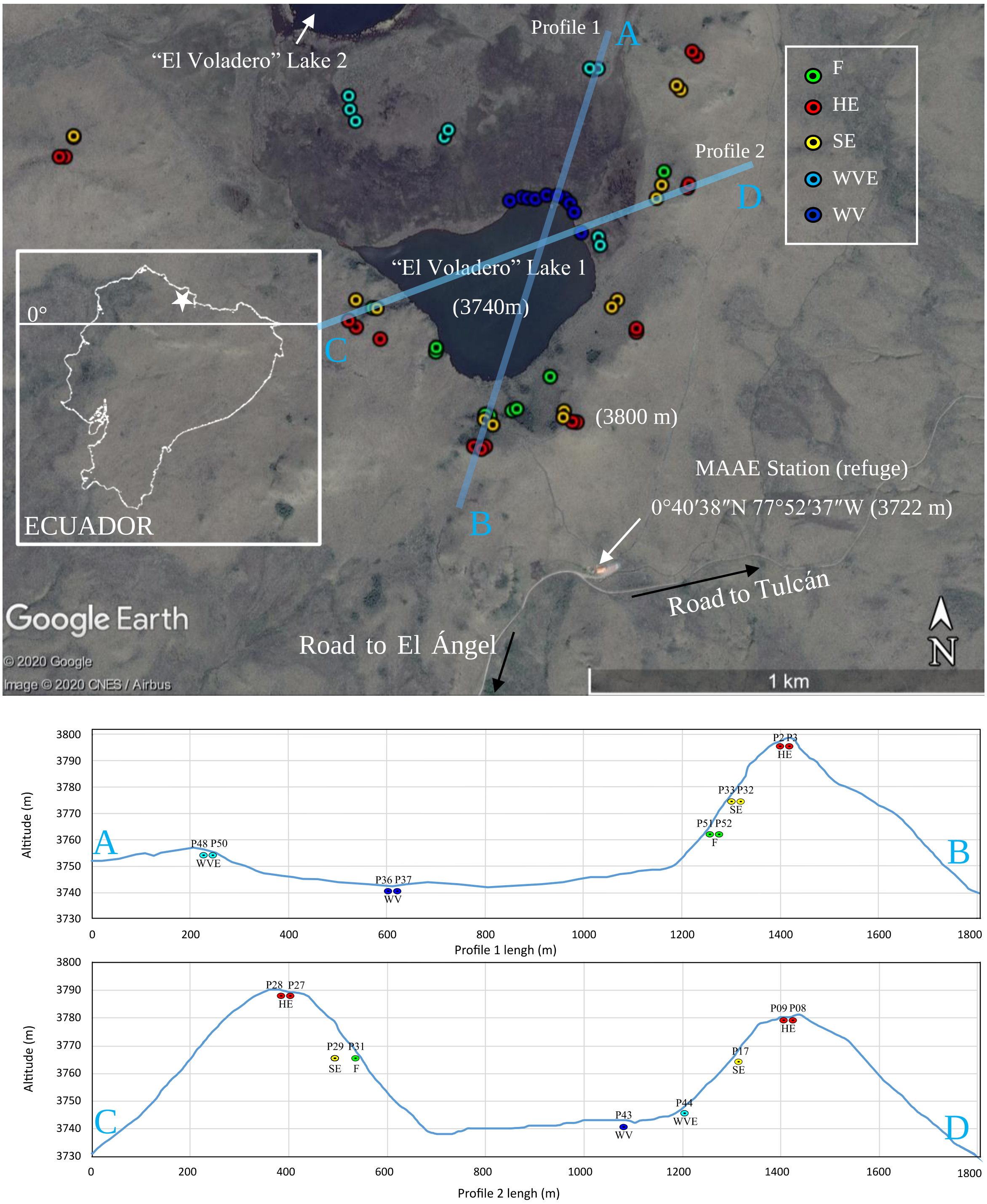


FIGURE 1

The "Lagunas del Voladero" study area in El Ángel páramo (white star in Ecuador´s map). The following habitats were studied: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10). The two light blue lines depict elevation profiles crisscrossing the study area, along which different plots are indicated as a reference.

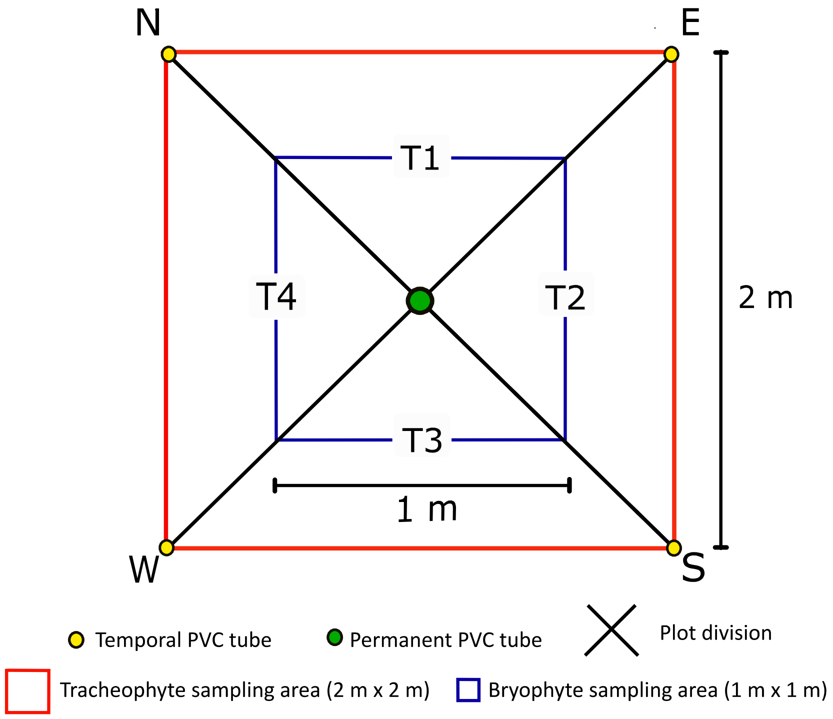


FIGURE 2

Plot sampling design for TRACHEOPHYTES and BRYOPHYTES at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. Vertices of the plot correspond to the cardinal points. Tracheophytes were sampled in the whole area (2 m × 2 m), while bryophytes were sampled in the 1 m × 1 m area at the center of the plot. Sampling always started at the northestern triangular plot division (T1) and continued in clockwise direction.

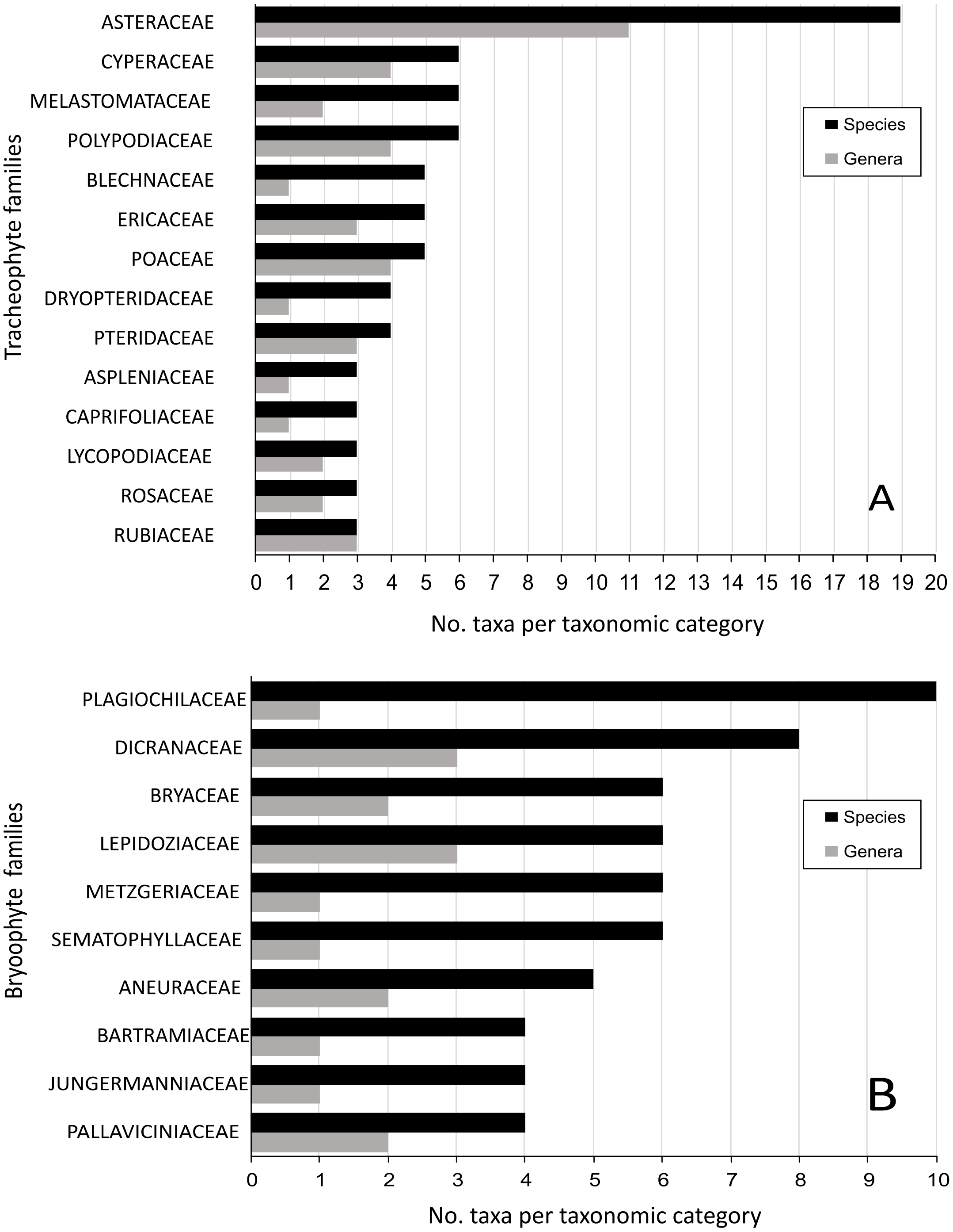


FIGURE 3

Number (No.) of species and genera in the most speciose botanical families at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. **(A)** TRACHEOPHYTE families with three or more species. **(B)** BRYOPHYTE families with four or more species.

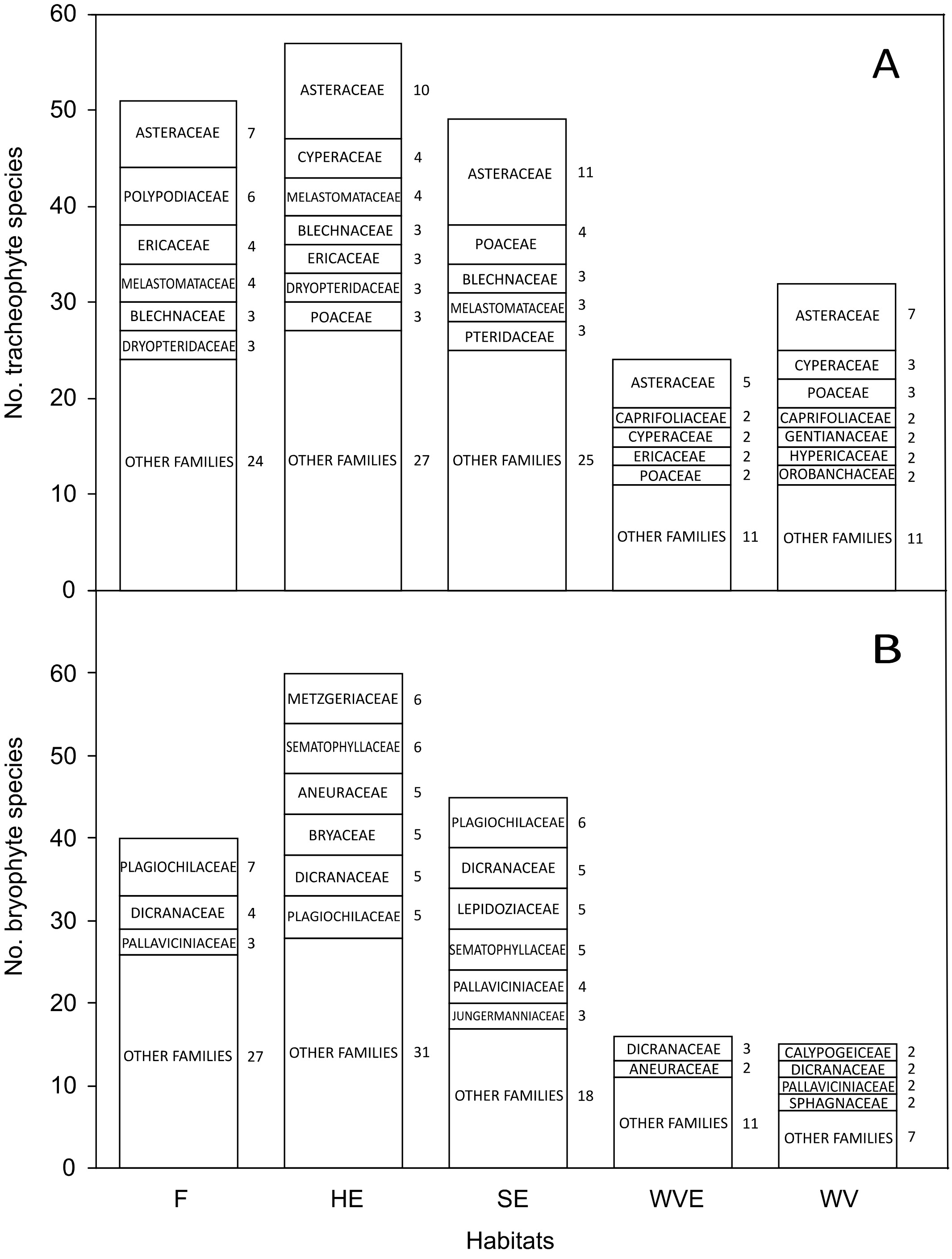


FIGURE 4

Number (No.) of species per family in the habitats studied at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. **(A)** Number of species among TRACHEOPHYTE families. **(B)** Number of species among BRYOPHYTE families. Habitat codes: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10).

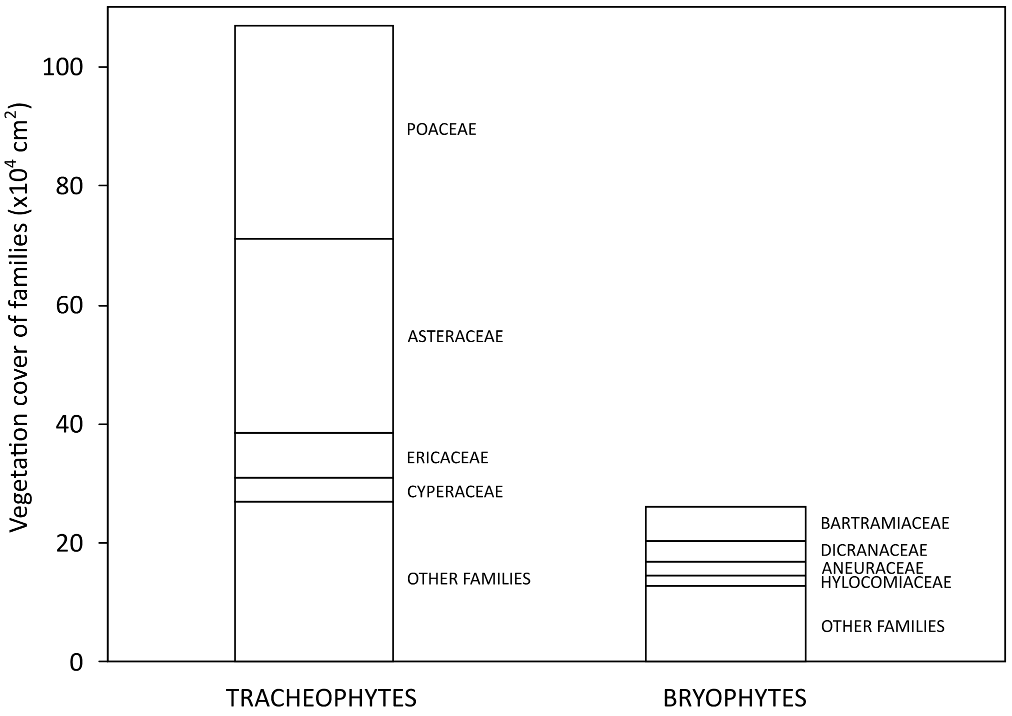


FIGURE 5

Vegetation cover (cm^2) of TRACHEOPHYTE and BRYOPHYTE families for all habitats combined (N=60 plots) at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador.

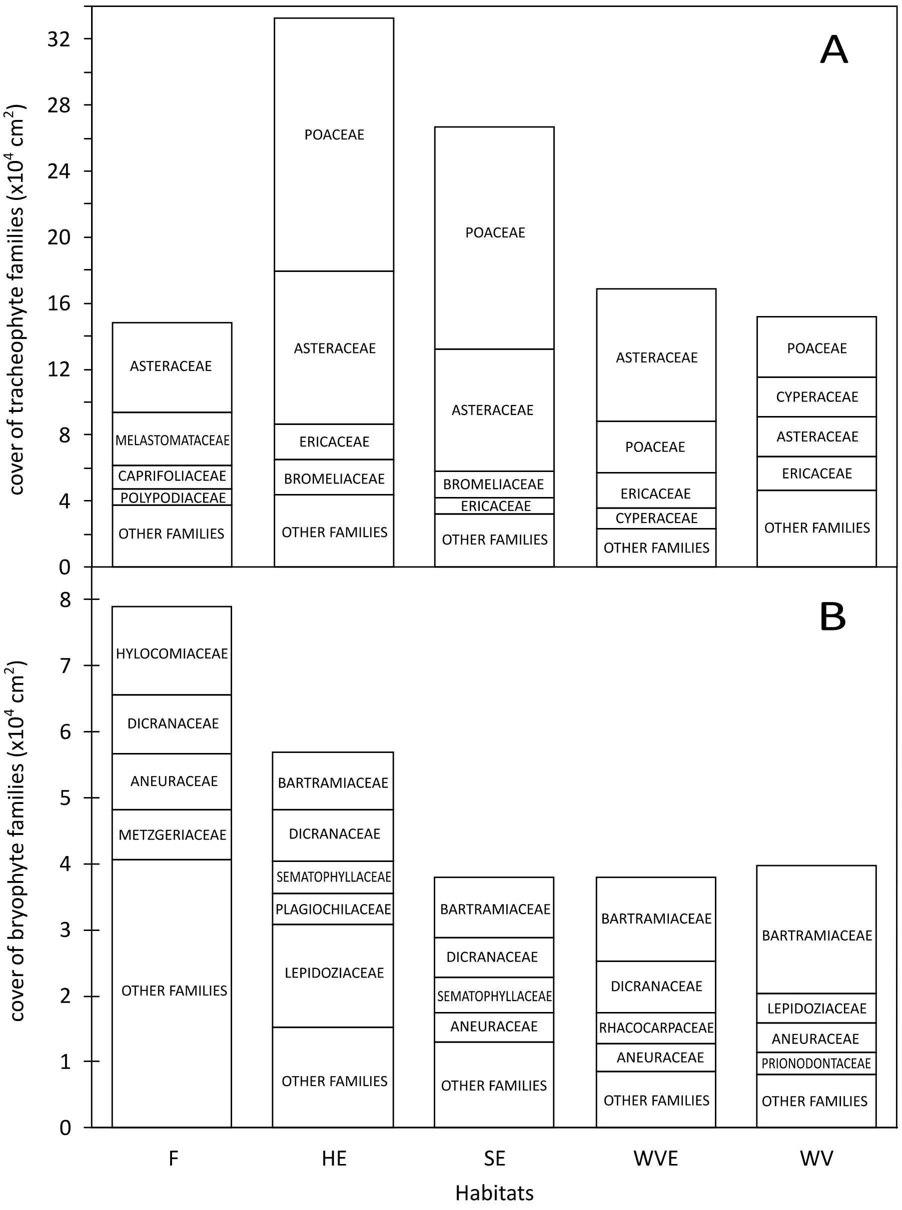


FIGURE 6

Vegetation cover (cm^2) per family in the different habitats studied at the "Lagunas del Voladero" area, El Ángel páramo. **(A)** Cover (m^2) of TRACHEOPHYTE families in different habitats. **(B)** Cover (m^2) of BRYOPHYTE families Habitat codes: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10).

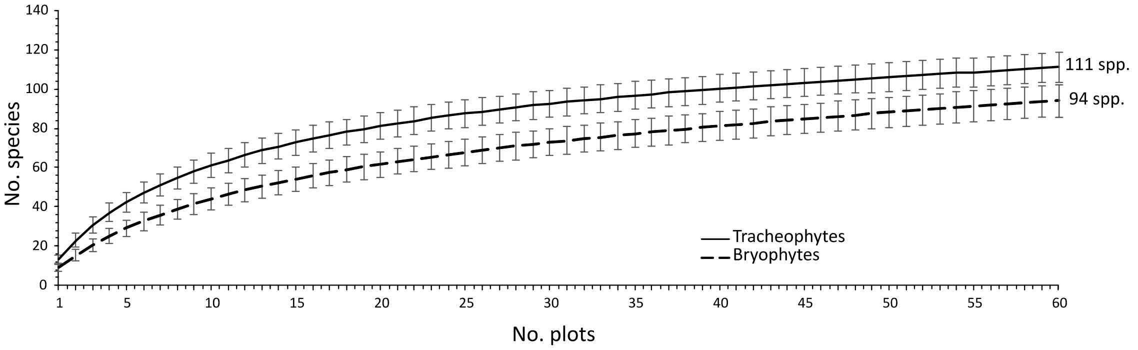


FIGURE 7

Species-area rarefaction curves for TRACHEOPHYTE and BRYOPHYTE plant communities for all habitats combined (*N*=60 plots) at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. The 84% confidence intervals make it possible to statistically compare the two curves at a significance level of 0.05 (Colwell et al., 2012).

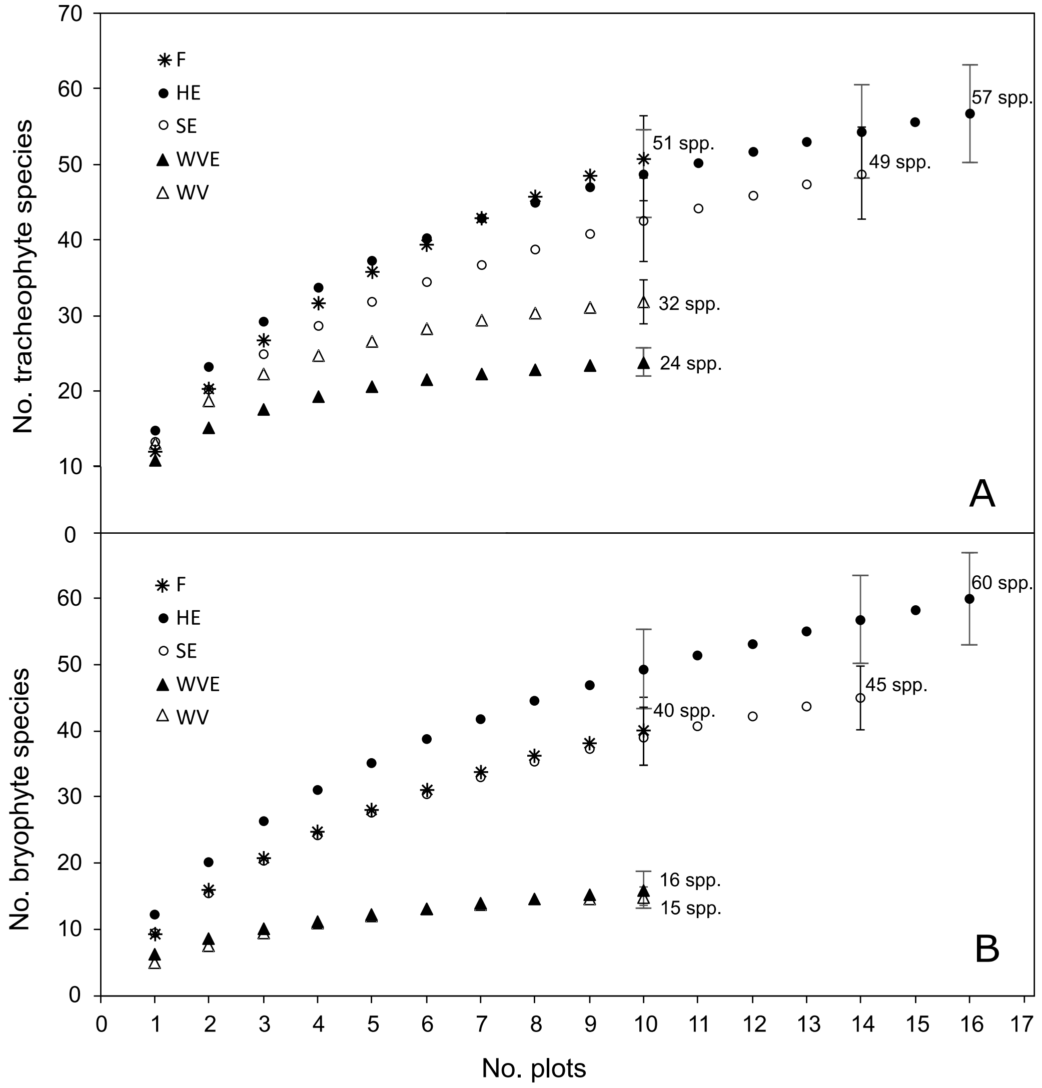


FIGURE 8

Species-area rarefaction curves for **(A)** TRACHEOPHYTE and **(B)** BRYOPHYTE species in the habitats studied at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. For the sake of clarity, 84% confidence intervals are only shown where a comparison is viable (i.e. for the same No. plots sampled). The 84% confidence intervals make it possible to statistically compare the two curves at a significance level of 0.05 (Colwell et al., 2012). Habitat codes: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10).

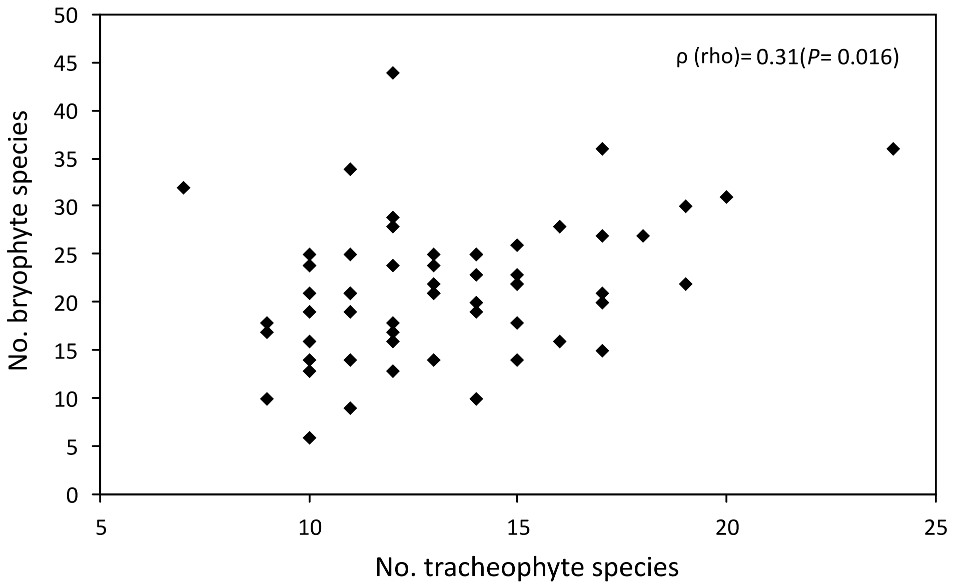


FIGURE 9

Correlation between the number (No.) of BRYOPHYTE and the number of TRACHEOPHYTE species, at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. Each symbol represents one plot (*N*=60 plots).

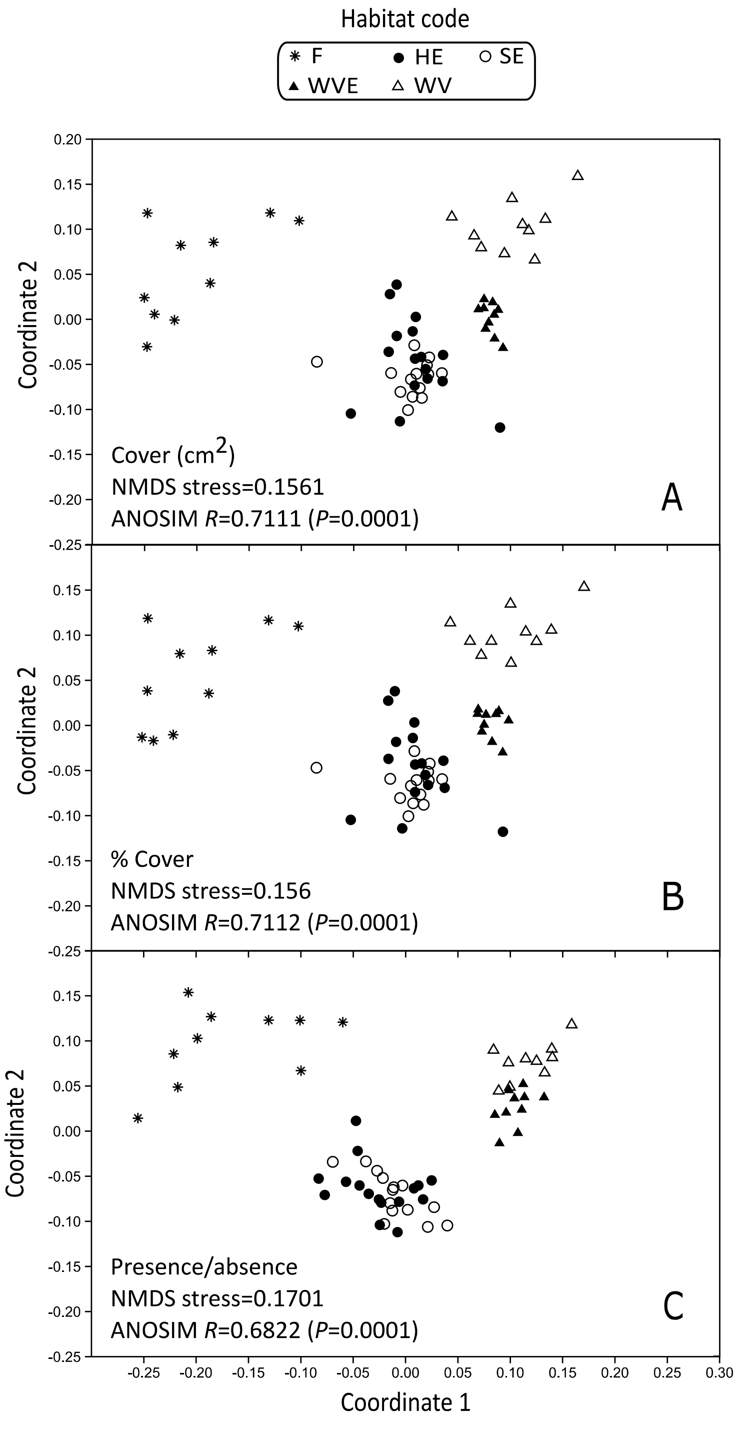


FIGURE 10

Non-metric multidimensional scaling (NMDS) for the TRACHEOPHYTE plant community, excluding uniques, in different habitats at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. **(A)** NMDS based on vegetation cover (cm^2). **(B)** NMDS based on % cover. **(C)** NMDS based on presence/absence (incidence) data. Stress values from NMDS and *R* values from ANOSIM are also shown. Habitat codes: Forest (F, *N*=10 plots), Hilltop with *Espeletia pycnophylla* (HE, *N*=16), Slope with *E. pycnophylla* (SE, *N*=14), Wetland Valley with *E. pycnophylla* (WVE, *N*=10) and Wetland Valley with almost no *E. pycnophylla* (WV, *N*=10).

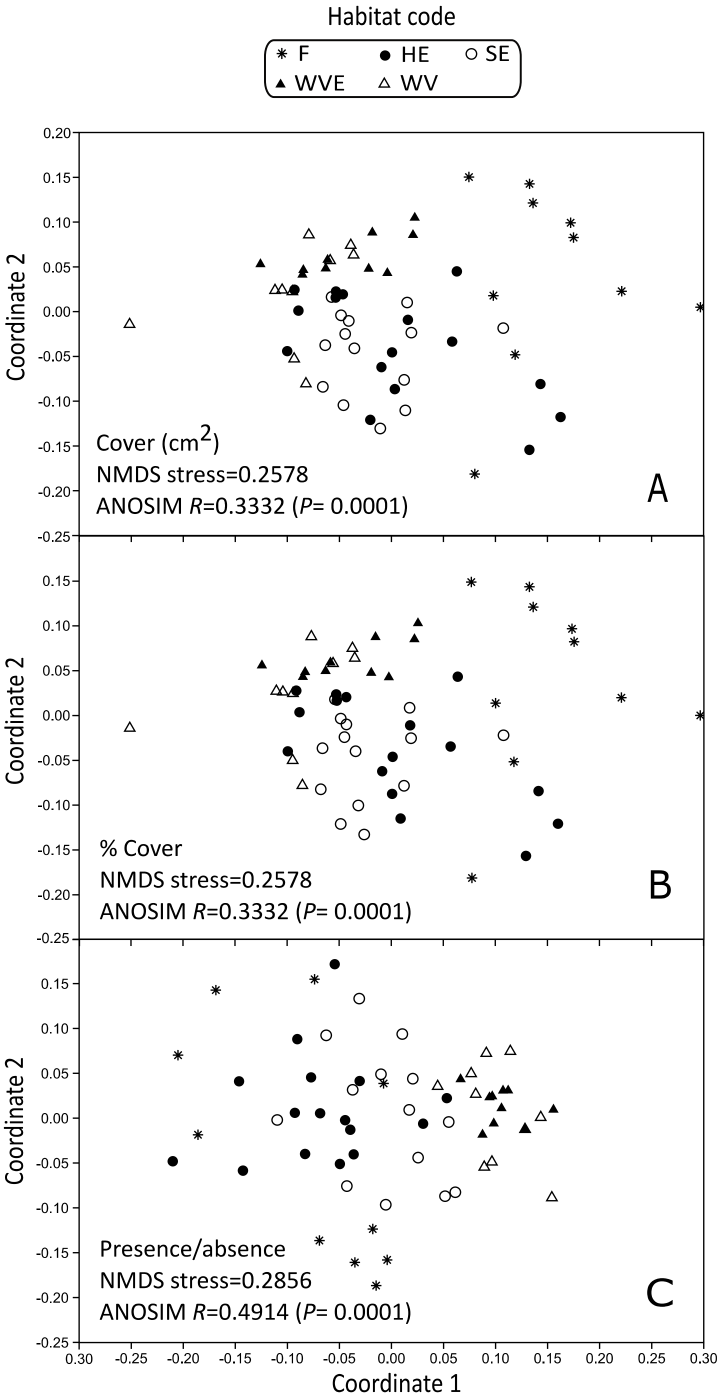


FIGURE 11

Non-metric multidimensional scaling (NMDS) for the BRYOPHYTE plant community, excluding uniques, in different habitats at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. **(A)** NMDS based on vegetation cover (cm^2). **(B)** NMDS based on % cover. **(C)** NMDS based on presence/absence (incidence) data. Stress values from NMDS and R values from ANOSIM are also shown. Habitat codes: Forest (F, N=10 plots), Hilltop with *Espeletia pycnophylla* (HE, N=16), Slope with *E. pycnophylla* (SE, N=14), Wetland Valley with *E. pycnophylla* (WVE, N=10) and Wetland Valley with almost no *E. pycnophylla* (WV, N=10).

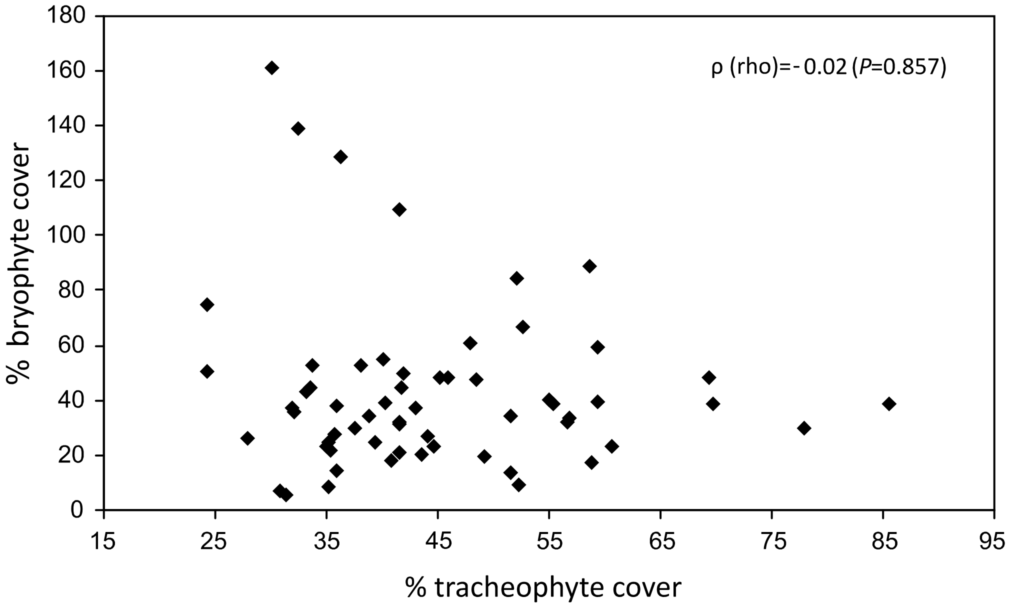


FIGURE 12

Relation between the percentage (%) of BRYOPHYTE cover vs. the percentage of TRACHEOPHYTE cover, at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. Each symbol represents one plot (*N*=60 plots).

APPENDICES

APPENDIX 1

Checklist of vascular species (TRACHEOPHYTES), with total vegetation cover (cm^2) and total frequency (# plots) of each species in each habitat studied, at the "Lagunas del Voladero" area, El Ángel páramo, Ecuador. Habitats are coded as: Forest (F), Hilltop with *Espeletia* (HE), Slope with *Espeletia* (SE), Wetland Valley with *Espeletia* (WVE) and Wetland Valley with almost no *Espeletia* (WV). *N*=number of plots.

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F** **(*N*=10)**	**HE** **(*N*=16)**	**SE** **(*N*=14)**	**WVE** **(*N*=10)**	**WV** **(*N*=10)**	**Total**
APIACEAE						
Azorella crenata (Ruiz & Pav.) Pers.	-	89 (3)	180 (1)	-	-	269 (4)
Eryngium humile Cav.	-	-	-	-	4476 (5)	4476 (5)
ARALIACEAE						
Hydrocotyle bonplandii A.Rich	186 (1)	862 (10)	790 (8)	-	-	1838 (19)
ASPLENIACEAE						
Asplenium castaneum Schltdl. & Cham.	-	48 (1)	-	-	-	48 (1)
Asplenium uniseriale Raddi	60 (1)	-	-	-	-	60 (1)
Asplenium "zzz1"	480 (1)	-	-	-	-	480 (1)
ASTERACEAE						
Baccharis latifolia (Ruiz & Pav.) Pers.	1380 (2)	-	-	-	-	1380 (2)
Diplostephium glandulosum Hieron.	-	15468 (11)	7512 (12)	-	-	22980 (23)
Diplostephium hartwegii Hieron.	8520 (4)	-	66 (1)	-	-	8586 (5)
Diplostephium rhododendroides Hieron.	5766 (2)	1459 (4)	5183 (6)	14670 (8)	1530 (3)	28608 (23)
Escallonia myrtilloides L.f.	7200 (1)	-	12 (1)	-	-	7212 (2)
Espeletia pycnophylla Cuatrec.	-	56184 (16)	52242 (14)	62160 (10)	2190 (3)	172776 (43)
Gynoxys parvifolia Cuatrec.	-	8862 (6)	1290 (1)	-	-	10152 (7)
Gynoxys pendula Sch.Bip. ex Wedd.	30562 (6)	-	-	-	-	30562 (6)
Gynoxys tolimensis Cuatrec.	-	2945 (4)	180 (3)	-	-	3125 (7)
Gynoxys "zzz1"	-	262 (7)	270 (7)	-	-	532 (14)

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F** **(*N*=10)**	**HE** **(*N*=16)**	**SE** **(*N*=14)**	**WVE** **(*N*=10)**	**WV** **(*N*=10)**	**Total**
Hypochaeris sessiliflora Kunth	-	-	-	-	5778 (5)	5778 (5)
Loricaria thuyoides (Lam.) Sch.Bip.	-	-	-	1237 (6)	9428 (10)	10665 (16)
Oritrophium peruvianum (Lam.) Cuatrec.	-	-	-	-	4650 (5)	4650 (5)
Pentacalia andicola (Turcz.) Cuatrec.	1080 (1)	5810 (6)	185 (3)	-	108 (2)	7183 (12)
Pentacalia arbutifolia (Kunth) C.Jeffrey	18 (2)	-	-	-	-	18 (2)
Pentacalia vaccinoides (Kunth) Cuatrec.	-	1020 (1)	-	6 (1)	346 (2)	1372 (4)
Senecio chionogeton Wedd.		72 (1)	-	1926 (4)	-	1998 (5)
Senecio wedglacialis Cuatrec.		582 (4)	60 (1)	-	-	642 (5)
Xenophyllum humile (Kunth) V.A.Funk		-	7320 (2)	-	-	7320 (2)
BLECHNACEAE						
Blechnum auratum (Fée) R.M. Tryon & Stolze	-	5910 (4)	-	-	-	5910 (4)
Blechnum lineatum (Sw.) C. Chr.	1530 (2)	-	1320 (2)	-	-	2850 (4)
Blechnum loxense (Kunth) Hook. ex Salomon	480 (1)	1656 (4)	3696 (8)	-	-	5832 (4) (13)
Blechnum schonburgkii (Klotzsch) C. Chr.	1440 (1)	-	-	-	-	1440 (1)
Blechnum stipitellatum (Sodiro) C. Chr.	-	480 (1)	360 (1)	-	-	840 (2)
BRASSICACEAE						
Cardamine speciosa Britton	-	24 (1)	18 (1)	-	-	42 (2)
BROMELIACEAE						
Puya aequatorialis André (E; LC)	480 (2)	1362 (4)	1278 (3)	-	-	3120 (9)
Puya hamata L.B.Sm.	120 (1)	19902 (8)	14310 (8)	1950 (4)	-	36282 (21)
CALCEOLARIACEAE						
Calceolaria penlandii Pennell	600 (1)	-	-	-	-	600 (1)
CAPRIFOLIACEAE						

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F** **(*N*=10)**	**HE** **(*N*=16)**	**SE** **(*N*=14)**	**WVE** **(*N*=10)**	**WV** **(*N*=10)**	**Total**
Valeriana bracteata Benth.	-	-	-	1470 (3)	1320 (2)	2790 (5)
Valeriana microphylla Kunth	1476 (5)	240 (2)	5336 (4)	3 (1)	180 (1)	7235 (13)
Valeriana plantaginea Kunth	12630 (5)	-	240 (1)	-	-	12870 (6)
CARYOPHYLLACEAE						
Cerastium danguyi J.F.Macbr.	-	12 (1)	-	-	-	12 (1)
Stellaria recurvata Willd. ex Schltdl.	738 (6)	300 (1)	-	-	-	1038 (7)
CYPERACEAE						
Carex lemanniana Boott	-	216 (1)	-	-	-	216 (1)
Carex pichinchensis Kunth	1860 (2)	60 (1)	-	-	-	1920 (3)
Oreobolus ecuadorensis T.Koyama	-	-	-	10026 (4)	18540 (9)	28566 (13)
Oreobolus goeppingeri Suess.	-	1054 (3)	300 (3)	1980 (2)	5310 (2)	8644 (10)
Rhynchospora hieronymi Boeckeler	-	3000 (1)	-	-	-	3000 (1)
Scirpus rigidus Griseb.	-	-	-	-	240 (1)	240 (1)
DENNSTAEDTIACEAE						
*Hypolepis obtusat*a (C. Presl) Kuhn	2730 (3)	-	-	-	-	2730 (3)
DRYOPTERIDACEAE						
Elaphoglossum cuspidatum (Willd.) T. Moore	6600 (2)	2790 (2)	1504 (3)	-	-	10894 (7)
Elaphoglossum notatum (Fée) T. Moore	1200 (1)	-	-	-	-	1200 (1)
Elaphoglossum rupestre (H. Karst.) Christ	-	2090 (1)	-	-	-	2090 (1)
Elaphoglossum vulcanicum Christ	1200 (2)	228 (2)	-	-	-	1428 (4)
ERICACEAE						
Cavendishia engleriana Hoerold	36 (1)	-	-	-	-	36 (1)
Disterigma empetrifolium (Kunth) Nied.	60 (1)	19536 (7)	3846 (4)	16590 (10)	20782 (9)	60814 (31)

Scientific name (with author) (E = endemic; IUCN threat category)	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total**
Gaultheria glomerata (Cav.) Sleumer	-	10 (1)	-	-	-	10 (1)
Gaultheria myrsinoides Kunth	240 (1)	1950 (5)	5678 (10)	5292 (5)	-	13160 (21)
Gaultheria sclerophylla Cuatrec.	1538 (5)	-	-	-	-	1538 (5)
ERIOCAULACEAE						
Paepalanthus muscosus Körn	-	-	-	6840 (7)	780 (1)	7620 (8)
GENTIANACEAE						
Halenia pulchella Gilg (E; LC)	-	-	-	2813 (4)	282 (2)	3095 (6)
Halenia weddelliana Gilg	-	24 (1)	-	-	659 (3)	683 (4)
GERANIACEAE						
Geranium azorelloides Sandwith	-	-	-	2760 (7)	4290 (6)	7050 (13)
Geranium sibbaldioides Benth.	-	210 (3)	978 (5)	-	-	1188 (8)
GROSSULARIACEAE						
Ribes hirtum Willd. ex Roem. & Schult.	1769 (5)	-	2 (1)	-	-	1771 (6)
GUNNERACEAE						
Gunnera magellanica Lam.	-	1146 (4)	1392 (2)	-	-	2538 (6)
HYMENOPHYLLACEAE						
Hymenophyllum polyanthos Sw.	2700 (3)	-	-	-	-	2700 (3)
HYPERICACEAE						
Hypericum brathys Sm.	-	-	-	2980 (6)	4986 (10)	7966 (16)
Hypericum laricifolium Juss.	-	-	-	-	2700 (1)	2700 (1)
JUNCACEAE						
Distichia muscoides Nees & Meyen	-	-	-	-	7050 (2)	7050 (2)
Luzula gigantea Desv.	-	132 (1)	-	-		132 (1)

Scientific name (with author) (E = endemic; IUCN threat category)	F (*N*=10)	HE (*N*=16)	SE (*N*=14)	WVE (*N*=10)	WV (*N*=10)	Total
LENTIBULARIACEAE						
Pinguicula calyptrata Kunth	-	-	60 (1)	-	-	60 (1)
LYCOPODIACEAE						
Huperzia crassa (Humb. & Bonpl. ex Willd.) Rothm.	-	-	-	-	19 (2)	19 (2)
Huperzia sellifolia B. Øllg.	-	-	1740 (1)	-	-	1740 (1)
Lycopodium clavatum L.	-	10434 (5)	6720 (5)	-	-	17154 (10)
MELASTOMATACEAE						
Brachyotum alpinum Cogn. (E; LC)	540 (1)	-	-	-	-	540 (1)
Brachyotum jamesonii Triana (E; VU B1ab(iii))	180 (2)	120 (1)	420 (2)	-	-	720 (5)
Brachyotum lindenii Cogn.	-	-	300 (1)	-	-	300 (1)
Miconia chionophila Naudin	120 (1)	61 (1)	-	360 (1)	-	541 (3)
Miconia nodosa Cogn.	30960 (10)	1908 (3)	840 (2)	-	-	33708 (15)
Miconia salicifolia (Bonpl. ex Naudin) Naudin	-	1734 (3)	-	-	-	1734 (3)
MYRTACEAE						
Myrteola nummularia (Lam.) O.Berg	210 (1)	-	120 (1)	3131 (10)	2482 (8)	5943 (20)
ORCHIDACEAE						
Brachionidium tetrapetalum (F. Lehm. & Kraenzl.) Schltr.	-	-	5 (1)	-	-	5 (1)
OROBANCHACEAE						
Bartsia stricta (Kunth) Benth.	-	-	-	-	883 (3)	883 (3)
Castilleja fissifolia L.f.	-	-	-	-	1082 (3)	1082 (3)
PLANTAGINACEAE						
Plantago rigida Kunth	-	-	-	990 (1)	13380 (7)	14370 (8)
Sibthorpia repens (Mutis ex L.) Kuntze	9450 (5)	252 (4)	10 (1)	-	-	9712 (10)

Scientific name (with author) (E = endemic; IUCN threat category)	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total**
POACEAE						
Calamagrostis effusa (Kunth) Steud.	-	-	4800 (1)	-	-	4800 (1)
Calamagrostis intermedia (J.Presl) Steud.	-	96613 (15)	119110 (13)	-	3840 (3)	219563 (31)
Cortaderia nitida (Kunth) Pilg.	120 (1)	32244 (8)	4290 (4)	26340 (8)	13182 (9)	76176 (30)
Festuca sodiroana Hack. ex E.B.Alekseev (E; LC)	-	24847 (15)	6702 (10)	4380 (2)	-	35929 (27)
Poa paramoensis Laegaard (E; LC)	-	-	-	-	19638 (7)	19638 (7)
POLYGALACEAE						
Monnina crassifolia (Bonpl.) Kunth	-	480 (1)	-	-	-	480 (1)
Monnina obtusifolia Kunth	-	240 (1)	-	-	-	240 (1)
POLYPODIACEAE						
Alansmia elastica (Bory ex Willd.) Moguel & M. Kessler	606 (3)	852 (2)	360 (1)	-	-	1818 (6)
Campyloneurum solutum (Klotzsch) Fée	3120 (3)	-	-	-	-	3120 (3)
Polypodium monosorun Desv.	4740 (5)	-	-	-	480 (1)	5220 (6)
Polypodium murorum Hook.	600 (1)	-	-	-	-	600 (1)
Polypodium “zzz1”	240 (1)	1 (1)	960 (1)	-	-	1201 (3)
Serpocaulon funckii (Mett.) A.R. Sm.	420 (1)	-	-	-	-	420 (1)
PTERIDACEAE						
Cheilanthes bonariensis (Willd.) Proctor	258 (1)	702 (3)	-	-	-	960 (4)
Eriosorus rufescens (Fée) A.F. Tryon	-	-	240 (1)	-	-	240 (1)
Jamesonia pulchra Hook. & Grev	-	-	66 (2)	23 (2)	-	89 (4)
Jamesonia scammaniae A.F. Tryon	60 (2)	1444 (8)	2482 (9)	-	-	3986 (19)
RANUNCULACEAE						

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F** **(*N*=10)**	**HE** **(*N*=16)**	**SE** **(*N*=14)**	**WVE** **(*N*=10)**	**WV** **(*N*=10)**	**Total**
Ranunculus flagelliformis Sm.	300 (1)	-	-	-	-	300 (1)
Ranunculus limoselloides Turcz.	-	6 (1)	-	-	12 (1)	18 (2)
ROSACEAE						
Lachemilla nivalis (Kunth) Rothm.	-	-	-	41 (2)	-	41 (2)
Lachemilla uniflora Maguire	-	1645 (7)	822 (6)	-	-	2467 (13)
Rubus lippaianus Borb s & Holuby	822 (5)	-	-	-	-	822 (5)
RUBIACEAE						
Arcytophyllum aristatum Standl.	-	372 (3)	-	-	-	372 (3)
Galium pseudotriflorum Dempster & Ehrend.	372 (3)	-	-	-	-	372 (3)
Nertera granadensis (Mutis ex L.f.) Druce	180 (1)	1771 (11)	1132 (8)	354 (3)	1144 (6)	4581 (29)
SOLANACEAE						
Solanum carchiense Correll (E; CR)	132 (2)	912 (7)	-	-	-	1044 (9)
ZZZ						
Zzz “helechopartido”	-	372 (5)	240 (1)	-	-	612 (6)
Zzz “hojaovalada”	4.8 (1)	-	-	-	-	4.8 (1)

APPENDIX 2

Checklist of non-vascular species (BRYOPHYTES), with total vegetation cover (cm^2) and total frequency (# plots) of each species in each habitat studied, at the “Lagunas del Voladero” area, El Ángel páramo, Ecuador. Habitats are coded as: Forest (F), Hilltop with *Espeletia* (HE), Slope with *Espeletia* (SE), Wetland Valley with *Espeletia* (WVE) and Wetland Valley with almost no *Espeletia* (WV). *N*=number of plots.

Scientific name (with author) (E = endemic; IUCN threat category)	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total**
ACROBOLBACEAE (Marchantiophyta)						
Acrobolbus laxus (Lehm. & Lindenb.)	240 (1)	-	-	-	-	240 (1)
Lethocolea “doble1”	-	-	216 (1)	-	-	216 (1)
Lethocolea “doble2”	-	-	150 (1)	120 (1)	-	270 (2)
ADELANTHACEAE (Marchantiophyta)						
Pseudomarsupidium decipiens (Hook.) Grolle	240 (1)	-	-	-	-	240 (1)
ANASTROPHYLLACEAE (Marchantiophyta)						
Anastrophyllum auritum (Lehm.)	-	240 (1)	150 (2)	-	-	390 (3)
ANEURACEAE (Marchantiophyta)						
Aneura pinguis (L.) Dumort.	-	48 (1)	2040 (2)	30 (1)	-	2118 (4)
Riccardia “lechugusanito1”	-	373 (2)	-	-	-	373 (2)
Riccardia “lechugusanito2”	-	12 (1)	-	-	-	12 (1)
Riccardia amazonica (Spruce) Schiffner ex Gradst. & Hekking	8070 (6)	2294 (11)	2548 (11)	4270 (10)	4416 (9)	21598 (47)
Riccardia ciliolata (Spruce) Gradst.	480 (1)	96 (1)	-	-	-	576 (2)
BALANTIOPSACEAE (Marchantiophyta)						
Isotachis “cachitos”	-	-	-	90 (2)	-	90 (2)
Isotachis multiceps (Lindenb. & Gottsche) Gottsche	-	-	792 (7)	-	342 (3)	1134 (10)
BARTRAMIACEAE (Bryophyta)						
Breutelia “flaquilarga”	-	720 (1)	-	-	-	720 (1)
Breutelia “maiz”	2 (1)	416 (3)	-	-	-	419 (4)

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total**
Breutelia “tubo”	-	120 (1)	-	-	-	120 (1)
Breutelia tomentosa (Sw. ex Brid.) A. Jaeger	720 (3)	14183 (13)	9168 (14)	12708 (10)	19332 (10)	56111 (50)
BRYACEAE (Bryophyta)						
Bryum “megacapsula”	-	-	366 (4)	-	-	366 (4)
Bryum argenteum Hedw.	-	360 (1)	-	-	-	360 (1)
Rhodobryum “commelina2”	-	4 (1)	-	-	-	4 (1)
Rhodobryum “commelina4”	-	240 (1)	-	-	-	240 (1)
Rhodobryum “commelina5”	-	360 (1)	-	-	-	360 (1)
Rhodobryum “commelina6”	-	30 (1)	-	-	-	30 (1)
CALYMPERACEAE (Bryophyta)						
Syrrhopodon “caripoaceae2”	2124 (7)	-	-	-	-	2124 (7)
CALYPOGEICEAE (Marchantiophyta)						
Calypogeia “malefica”	-	252 (2)	60 (1)	-	120 (1)	432 (4)
Calypogeia peruviana Nees	426 (2)	368 (6)	1188 (4)	96 (1)	22 (2)	2100 (15)
DICRANACEAE (Bryophyta)						
Campylopus “enredados”	2070 (1)	708 (3)	-	-	-	2778 (4)
Campylopus “espantapajaros”	-	-	-	894 (2)	-	894 (2)
Campylopus “estrella”	-	-	300 (1)	-	-	300 (1)
Campylopus “plumero”	1548 (4)	1350 (9)	1320 (6)	30 (1)	90 (1)	4338 (21)
Campylopus “puitas1”	2172 (4)	4716 (13)	3624 (9)	6946 (8)	3120 (3)	20578 (37)
Campylopus richardii Brid.	3120 (1)	1458 (4)	108 (1)	-	-	4686 (6)
Dicranum “caritillandsia1”	-	299 (2)	-	-	-	299 (2)
Leucobryum “punktrue1”	-	-	480 (1)	-	-	480 (1)

Scientific name (with author) (E = endemic; IUCN threat category)	F (*N*=10)	HE (*N*=16)	SE (*N*=14)	WVE (*N*=10)	WV (*N*=10)	Total
FABRONIACEAE (Bryophyta)						
Fabronia “bambu1”	-	270 (2)	-	-	-	270 (2)
Fabronia “bambu1.1”	-	96 (1)	-	-	-	96 (1)
Fabronia “minihojitas”	-	324 (3)	-	-	-	324 (3)
HERBERTACEAE (Marchantiophyta)						
Herbertus acanthelius Spruce	360 (1)	-	-	-	-	360 (1)
HYLOCOMIACEAE (Bryophyta)						
Pleurozium schreberi (Willd. ex Brid.) Mitt.	13236 (7)	540 (2)	1830 (2)	1223 (2)	444 (2)	17273 (15)
JUBULACEAE (Marchantiophyta)						
Frullania “lentejuelahoja”	1470 (3)	120 (1)	-	-	-	1590 (4)
Frullania brasiliensis Raddi	3660 (1)	144 (1)	-	-	-	3804 (2)
JUNGERMANNIACEAE (Marchantiophyta)						
Syzygiella “hojaredonda”	-	-	480 (1)	-	-	480 (1)
Syzygiella “micky1”	-	-	480 (1)	-	-	480 (1)
Syzygiella “micky3”	1260 (1)	-	-	-	-	1260 (1)
Syzygiella “trenza”	1109 (2)	60 (1)	1548 (4)	-	-	2717 (7)
LEJEUNEACEAE (Marchantiophyta)						
Lejeunea “torrechina”	-	96 (1)	-	-	-	96 (1)
LEPICOLEACEAE (Marchantiophyta)						
Lepicolea pruinosa (Taylor) Spruce	510 (1)	-	-	-	-	510 (1)
LEPIDOZIACEAE (Marchantiophyta)						
Bazzania longistipula (Lindenb.) Trevis.	66 (1)	-	-	-	-	66 (1)
Lepidozia “gema”	1650 (3)	3348 (5)	900 (3)	240 (1)	4520 (5)	10658 (17)

Scientific name (with author) (E = endemic; IUCN threat category)	F (*N*=10)	HE (*N*=16)	SE (*N*=14)	WVE (*N*=10)	WV (*N*=10)	Total
Lepidozia “lombrices”	-	-	60 (1)	-	-	60 (1)
Telaranea “alfombra”	-	48 (1)	36 (1)	-	-	84 (2)
Telaranea “pataarañas”	-	732 (3)	744 (2)	-	-	1476 (5)
Telaranea nematodes (Austin) M. Howe LC	-	708 (5)	270 (2)	-	-	978 (7)
LOPHOCOLEACEAE (Marchantiophyta)						
Lophocolea bidentata (L.) Dumort.	-	96 (1)	-	-	-	96 (1)
METZGERIACEAE (Marchantiophyta)						
Metzgeria “bifurcadoglabro”	-	671 (3)	-	-	-	671 (3)
Metzgeria albinea Spruce	-	6 (1)	-	-	-	6 (1)
Metzgeria auriculata Grolle & Kuwah.	1188 (2)	30 (1)	-	-	-	1218 (3)
Metzgeria cylindra Kuwah.	-	2940 (5)	-	-	-	2940 (5)
Metzgeria holzii Gradst. & Benítez	-	72 (1)	-	-	-	72 (1)
Metzgeria leptoneura Spruce	6522 (5)	420 (3)	648 (3)	-	-	7590 (11)
MNIACEAE (Bryophyta)						
Plagiomnium “hojalanza”	6 (1)	24 (2)	504 (1)	-	-	534 (4)
Plagiomnium rhynchophorum (Harv.) T.J. Kop.	4560 (2)	402 (3)	187 (3)	-	-	5149 (8)
NECKERACEAE (Bryophyta)						
Porotrychum “hojas”	2400 (1)	-	-	-	-	2400 (1)
Zzz “pequelaurel2”	4218 (3)	324 (2)	180 (1)	-	-	4722 (6)
ORTHOTRICHACEAE (Bryophyta)						
Orthotrichum “rosa”	-	96 (1)	-	-	-	96 (1)
PALLAVICINIACEAE (Marchantiophyta)						
Jensenia spinosa (Lindenb. & Gottsche) Grolle	-	-	32 (3)	1066 (8)	142 (3)	1240 (14)

Scientific name (with author) (E = endemic; IUCN threat category)	**F (*N*=10)**	**HE (*N*=16)**	**SE (*N*=14)**	**WVE (*N*=10)**	**WV (*N*=10)**	**Total**
Symphyogyna “luz2”	402 (1)	-	90 (2)	-	-	492 (3)
Symphyogyna brasiliensis Nees	570 (1)	1262 (7)	29 (3)	-	228 (2)	2089 (13)
Symphyogyna brongniartii Mont.	4620 (5)	-	12 (1)	-	-	4632 (6)
PELLIACEAE (Marchantiophyta)						
Noteroclada confluens Taylor ex Hook. f. & Wilson	-	-	60 (1)	-	-	60 (1)
PILOTRICHACEAE (Bryophyta)						
Callicostella “laurelnervado”	168 (2)	1512 (6)	-	-	-	1680 (8)
PLAGIOCHILACEAE (Marchantiophyta)						
Plagiochila “concavaespinasmegahojas”	90 (1)	-	-	-	-	90 (1)
Plagiochila “espinastren”	-	958 (5)	354 (3)	-	-	1312 (8)
Plagiochila “messy1”	96 (1)	667 (3)	192 (3)	-	-	955 (7)
Plagiochila “messy2”	-	-	60 (1)	-	-	60 (1)
Plagiochila “mixtultwin”	216 (1)	-	-	-	-	216 (1)
Plagiochila “tricoma”	-	-	24 (1)	-	-	24 (1)
Plagiochila aerea Taylor	1254 (3)	1506 (4)	414 (2)	-	-	3174 (9)
Plagiochila dependula Taylor	1620 (2)	-	-	22 (1)	-	1642 (3)
Plagiochila diversifolia Lindenb. & Gottsche	660 (2)	1716 (3)	660 (1)	-	-	3036 (6)
Plagiochila ovata Lindenb.	2130 (1)	6 (1)	-	-	-	2136 (2)
PRIONODONTACEAE (Bryophyta)						
Prionodon “puercoespin”	-	-	-	1764 (4)	3486 (3)	5250 (7)
RACOPILACEAE (Bryophyta)						
Racopilum tomentosum (Hedw.) Brid.	-	504 (4)	-	-	-	504 (4)
RADULACEAE (Marchantiophyta)						

Scientific name (with author) **(E = endemic; IUCN threat category)**	**F** **(*N*=10)**	**HE** **(*N*=16)**	**SE** **(*N*=14)**	**WVE** **(*N*=10)**	**WV** **(*N*=10)**	**Total**
Radula voluta Taylor	-	-	180 (2)	-	-	180 (2)
RHACOCARPACEAE (Bryophyta)						
Rhacocarpus purpurascens (Brid.) Paris	-	-	-	4500 (5)	1374 (3)	5874 (8)
SEMATOPHYLLACEAE (Bryophyta)						
Sematophyllum “hoja”	456 (2)	2165 (9)	1740 (6)	-	-	4361 (17)
Sematophyllum “hojaancha”	-	276 (5)	1294 (5)	-	-	1570 (10)
Sematophyllum “laurel”	-	564 (4)	12 (1)	-	-	576 (5)
Sematophyllum “pequelaurel1”	-	180 (1)	1104 (6)	-	-	1284 (7)
Sematophyllum “selagdelgada2”	-	156 (2)	-	-	-	156 (2)
Sematophyllum “setaslargas”	-	4555 (11)	1236 (2)	-	-	5791 (13)
SPHAGNACEAE (Bryophyta)						
Sphagnum “spha”	-	-	-	3912 (7)	642 (2)	4554 (9)
Sphagnum magellanicum Brid.	-	-	-	-	1446 (1)	1446 (1)
THUIDIACEAE (Bryophyta)						
Thuidium peruvianum Mitt.	-	600 (1)	-	-	-	600 (1)
TRICHOCOLEACEAE (Marchantiophyta)						
Leiomitra tomentosa (Sw.) Lindb.	3216 (5)	-	-	-	-	3216 (5)