Article

Species Composition and Distribution of Terrestrial Herbs in a High Montane Forest in Ecuador

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Abstract: In mountain tropical forests, understory herbs have received little attention compared to trees, and their commonness and rarity are virtually unknown. We studied ground herbs to explore how they are assembled in a full one-hectare plot and to test the influence of light intensity (LI) and topographic habitats in species composition. The plot is a humid montane forest located in the Pasochoa Volcano, at 3300 m. We found 43 genera and 50 perennial species (30 angiosperms in 17 families, and 20 ferns). Interestingly, herbs are 64% richer in species than trees in the same study plot (50 vs. 32). Herbs were mostly obligately terrestrial (70% of the species), while 30% were fallen climbers and epiphytes rooted in the ground. Across the forest, there were 31,119 individuals that covered 8.5% of the ground. We concluded that both LI and topography shaped the species distribution, the floristic composition, and the community structure of ground herbs. For instance, 12% of the species were exclusively found in places with high LI; the rest of species grew in medium- to low-LI environments. Concerning rarity, we found that 39% of the species are rare (judging by botanical collections; <100), which stresses the need of conservation strategies for this group of plants.

Keywords: life forms; Andes; microhabitats; rare species; topography; light availability

1. Introduction

The richest plant community on Earth is the understory of the tropical rain forest [1–3]; however, only few ecological studies have focused on terrestrial herbs. Concerning neotropical rain forests, most of the information about structure, composition, and diversity deals with trees [4–7]. Few quantitative studies include all life forms or other life forms besides trees [1,2,8–19]. These studies have shown that the herbaceous flora is very important for the forest structure, emphasizing the fact that forests are not built just by trees, and that the herbs growing in the forest increased the forest's species richness.

Researchers have included non-woody plants, such as pteridophytes, in ecological studies of tropical forest structure [19–21]. At scales of one hectare or less, the floristic composition of herbs is correlated with topography, soil, biological factors, biogeography, and chance [9,10,13,16,18]. At continental and global scales, the ecological importance of non woody plants like herbs and their high beta diversity have been documented in different regions and forest types [8,11,22].

In the tropical Andean region, ecological, taxonomical, and floristic studies of herbs have been concentrated in the páramos [23–32]. These studies were focused on alpha and beta diversity patterns, growth form composition, plant community structure, regeneration of páramo vegetation after burning and grazing, environmental factors shaping diversity patterns, ecosystem function, changes, and tolerance to climate change [17,33,34]. There are no quantitative studies of herbs in the high montane forest of the Andes >1000 m. Most studies of herbs in the Andes are concentrated on the lower slopes. The major source of information about herbs are botanical collections and flora inventories carried out at

these elevations. At the scale of one hectare, to our knowledge, there are only two studies both carried out in tropical lowland forests, one in Southeast Asia, in Borneo [15], and in the Amazon lowlands, in Ecuador [13]. In these studies, a complete enumeration of herbs allowed us to understand species associations with microhabitats and detect patterns of floristic composition. However, worldwide studies of herbs are usually carried out in smaller areas (<5 ha) [9,19,35–38].

The drivers that trigger herb species composition are mostly related to light, topography, water, and soil. Mostly, these studies were carried out in lowland tropical forests of Borneo, the Ecuadorian Amazon, and India [15,20,39]. The drivers shaping species composition of Andean herbs are unknown; therefore, this study will shed light on this topic to understand species composition in Ecuadorian high Andes.

Because of the historical deforestation of and pressure placed on open agricultural lands, the high montane forests in Ecuador are scarce, covering less than 5% in Ecuador [40], and they are confined to less accessible areas. It is crucial to understand the little-known ecology of herbs in this endangered ecosystem and offer science-based information to take conservation actions.

The conservation status of endemic herbs will give some us some information for directing scarce conservation resources to the species most in need. Unfortunately, the conservation status of most Ecuadorian herbs is unknown, except for endemic species. How rare and endangered a species is needs to be traced urgently.

We chose to study herbs in a tree study plot that was previously established in a high montane forest [41]. The present study describes the floristic composition of herbs in this one-hectare plot located at high elevation and immediately below the timberline of the Pasochoa volcano (3300 m). We carried out a detailed quantification of the herbs and explored their ecological importance (based on species density and cover) and their habitat associations; in particular, we ask to which extent the species composition, density, and cover is associated with topography and light availability on the forest floor. As part of this survey, we evaluated the conservation status of all the species recorded in the study plot.

2. Materials and Methods

2.1. Study Area

The Pasochoa volcano (0°28 S, 78°28 W) is a dormant volcano covered by volcanic ashes, heavily eroded by Pleistocene glaciations, that created a collapsed volcanic cone [42]. This volcano is situated 35 km south of Ecuador's capital Quito, in the inter-Andean valleys with an altitudinal range from 2400 to 4200 m, where humid montane forests and paramos are present. The inter-Andean valleys have fertile soils that have been strongly affected for centuries by agriculture. The Pasochoa shelters a unique refuge of 500 ha of protected forest, declared in 1996 by the Ecuadorian National System of Protected Areas (SNAP) (http://areasprotegidas.ambiente.gob.ec/ (accessed on 13 April 2024)) [43]. This refuge is the best-preserved Ecuadorian inter-Andean forest. The most intact forest grows in the collapsed cone due to its inaccessibility. Besides the collapsed cone, there are several erosion gullies that shelter the well-preserved forest surrounding the external slopes of the Pasochoa volcano. The mid and lower slopes of the volcano are bordered by extensive pastures, planted pine forests, and croplands with potatoes, corn, and wheat. Provoked fires and cattle entering the forest areas are the major factors having an impact on the forest. According to the closest meteorological station at Uyumbicho, the mean temperature is 13.8 °C, and the mean annual precipitation is 1489.5 mm [41]. There are only three dry months (i.e., months with <100 mm precipitation): July, August (precipitation range 35–50 mm), and September (<100 mm). All other months are wet [41]. Even in the dry months, the humidity remained high enough to keep epiphytes like orchids and ferns alive. There were no annual herbs recorded in the study site during the fieldwork period (1996). Throughout the year, including the dry months, it was possible to find all the species reported in this study. Our field data collection took place during both the less rainy and the rainy seasons, yet discernible changes in species density or cover were not apparent.

The one ha plot is located at 3300 m elevation in one of the well-preserved erosion gulleys. The area has little accessibility and belongs to a private property (El Olimpo Farm), where the owners control and limit the accessibility to the land for furtive visitors and cattle. The plot area is on steep terrain with branched erosion gullies with slopes that can reach >100% (>45°), which shelter a mature forest [41,44]. The forest reaches 6–8 m in height and is dominated by trees that branch basally and have inclined or horizontal trunks. In the same one-hectare plot, Valencia and Jørgensen (1992) [41] found 32 species of trees > 5 cm dbh. The most species-rich tree families were Melastomataceae and Asteraceae. *Miconia thaezans* is the most abundant tree species, followed by *Piper andreanum* and *Miconia pustulata*. The forest floor is covered by mosses and hepatics, and the litter layer varies in thickness from 2 to 30 cm.

We choose the study plot for several reasons that make it representative of the forest: (1) the forest structure has trees of different sizes, including big trees (>30 cm dbh) that are seldom seen in less-preserved forests, lianas (some of them >10 cm of diameter), epiphytes, and underground herbs; (2) there has been limited human impact there, and it has remained excluded from cattle for more than 40 years [44]; (3) the plot was established in 1988 to study the forest structure and tree species richness, with both structure and species richness being comparable to other well-preserved Andean forests studied in Ecuador (Jorgensen et al. 1995) [45]; and (4) according to fieldwork observations and revision of herbarium specimens, the plot had a good representation of the understory herbaceous flora, which is different in composition of that found in the open paramos located over 3400 m, just above the tree line at the Pasochoa volcano.

2.2. Species Data

The one-hectare plot was divided into 400 subunits of 5 × 5 m, 100 subunits of 10 × 10 m, and 10 subunits of 10 × 100 m. The latter were oriented from east to west and were used for comparisons purposes. All herb species rooted in the ground were documented with voucher specimens and were identified. This included obligate terrestrial species, which are species that are always rooted in the ground, and facultatively terrestrial species, which are sometimes epiphytic or climbing and not rooted in the ground. The obligate terrestrial species were further divided into prototerrestrials with self-supporting stems and scandents, which depend on others for support. The facultative terrestrials were divided into fallen epiphytes and fallen climbers. The following data were collected for each species in each 5 × 5 m subunit: (1) number of individuals and (2) cover in cm^2. For species with vegetative reproductive habits, each stem was counted as one individual. To describe the species importance in the forest community, we modified the Importance Value Index (IVI) used for trees [46] in our herb study. IVI = relative density + relative cover + relative frequency per hectare. We replaced the relative dominance (relative basal area) used for trees with cover (the area projected on the ground that covers a given species, expressed in m^2). The sum of the three percentages conforms the index and allows to know and visualize which of these parameters are more relevant in the herb community for a given species.
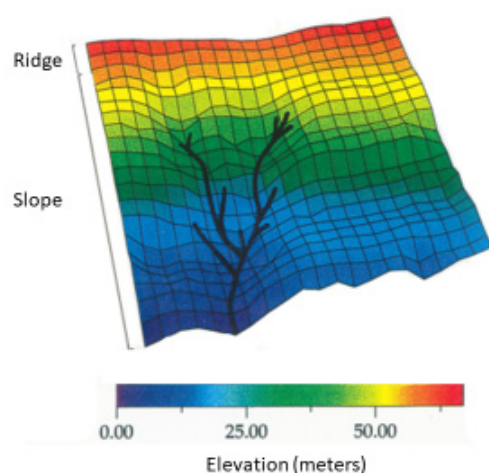
2.3. Species Endemism and Conservation Status

Information about the endemism and conservation status of the species was searched for all the species. The risk of extinction of most species has not been previously evaluated, and we propose here such an evaluation based on historical collection records, the distribution of the species in Ecuador, and the number of collections recorded in the data bases of Missouri Botanical Garden (MBG; https://www.tropicos.org/home (accessed on 13 April 2024)), QCA Herbarium (Bioweb; https://bioweb.bio/portal/ (accessed on 13 April 2024)), and AAU Herbarium, Denmark (https://www.aubot.dk/search_form.php accessed on (13 April 2024)). The number of collections is a good proxy of the species commonness or rarity in nature. A species was designated as well collected (WC) if it had >100 collections all over Ecuador, medium collected (MC) if it had <100–>30, and scarcely collected (SC)

with <30 collections all over Ecuador. To assign the risk of extinction categories, we used the IUCN criteria [47], and, in the case of the endemic species, we used the status reported by León-Yánez et al. (2011) [48].

2.4. Topographic Microhabitats

Each 5 × 5 m subunit was classified as belonging to one of three topographic microhabitats: ridge, erosion gully, or slope (Figure 1). The ridge microhabitat is the least steep terrain of the study plot, with relative altitudes of 59–67 m from the lowest point; it is limited to the first four rows of 5 × 100 m. The extension of this microhabitat is 1775 m^2 (18% of the plot). The slope microhabitat is the rough part of the plot area, located at altitudes of 0–58.9 m. The extension of this zone is 7025 m^2 (70% of the plot). The erosion gully bed is the only microhabitat that has bare rocks as part of the soil structure with rivulets running through it. The extension of this microhabitat is 1200 m^2 (12% of the plot) at altitudes of 0–54 m.

Figure 1. Topographic map of the one-hectare forest plot at 3300 m on the Pasochoa volcano, Ecuador, showing the subdivision into 5 × 5 m units. The relative height varies from 0 to 67 m. Each subunit was classified as one of the three topographic microhabitats. The ridge covered 18% of the study area, the gully bed covered 12% of the study area (black lines in the map), and the slope covered 70% of the study area. Each subunit was classified as one of three light intensity microhabitats.

2.5. Light Microhabitats

Each 5 × 5 m subunit was classified in one of the following three light microhabitats: low, medium, and high light intensity. The light microhabitats depended on both the woody vegetation structure (closed canopy or open canopy) and the relative cover of the woody scandent bamboo *Chusquea scandens*, (estimated as: 1 = presence, 2 = ≤50% cover, and 3 = >50% cover); a combination of both was used to determine the accessibility of light to the forest floor. The low light intensity microhabitat (thicket) had groups of stems of *Chusquea scandens*, tree branches, and lianas that twisted and formed a dense tangle, restricting the access of light to the bottom of the forest. This tangle was found 40–50 cm from the floor and was so compact that it produced an extreme shadow to the forest floor where only few herbs species could survive. The low light microhabitat covers 18% of the plot, and it is mostly (91% of its area) located at the lower part of the plot (0–10 m). The medium light intensity microhabitat has less than 50% cover of *Chusquea scandens*. This microhabitat was found in all three topographic microhabitats. It covered 60% of the plot. The high light intensity microhabitat had trees that produced little shadow to the forest floor. This microhabitat had limited presence of *Chusquea scandens* and lianas, no thicket, and was found in all topographic microhabitats covering 22% of the plot area.
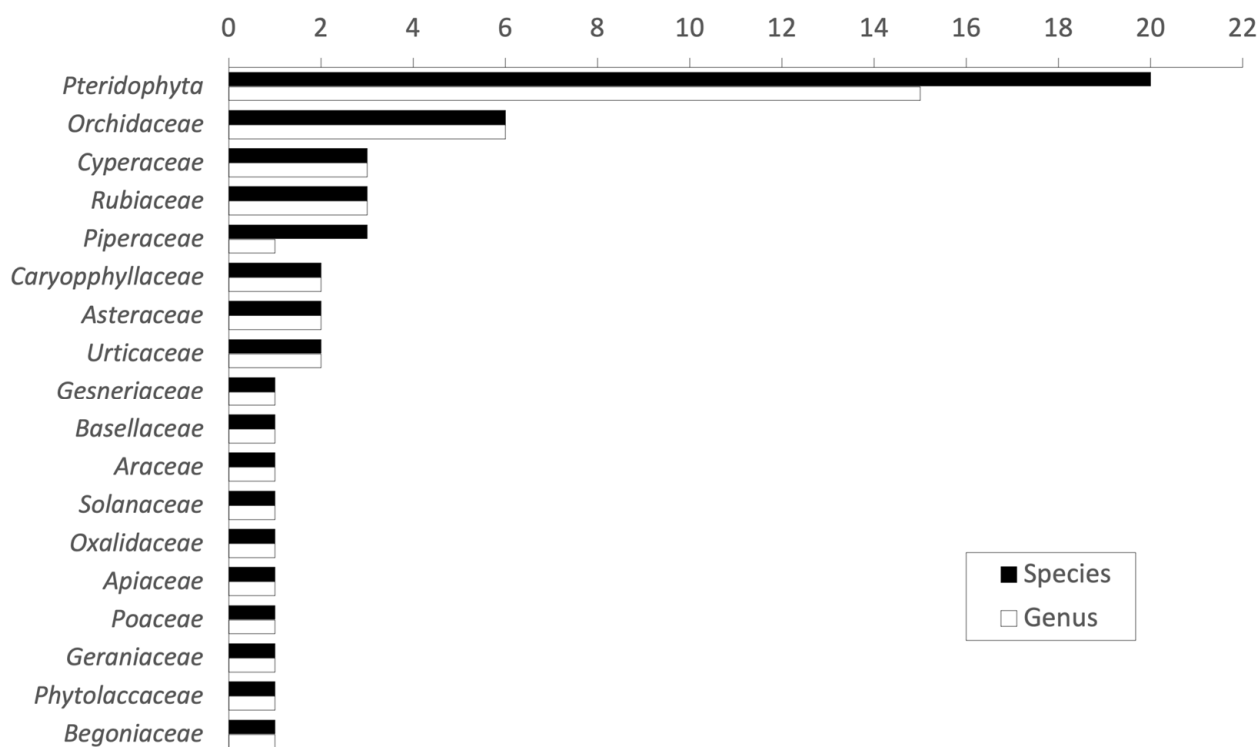
2.6. Statistical Analysis

For the statistical analyses, we used the Mantel and Partial Mantel tests [49] to find out the association of different microhabitats with the species composition in the plot. We tested the correlations of the floristic matrix with the space matrix for the topographic habitats. For the floristic matrix, we used 80 units of 5 × 5 m (25 m^2). We selected 20 units of each of the three main topographical habitats (ridge top, slope, and erosion gulley) and 20 units of light intensity habitats, 10 for high light intensity and 10 for low light intensity (thicket). Light intensity units were located in all topographical habitats. We built (1) a floristic matrix, (2) a topographic matrix, (3) a space (geographical distance) matrix, and (4) a presence/absence matrix of thicket for light intensity (excluding medium light intensity units).

For the floristic matrices, we used Sørensen and Steinhouse indices, but the results are presented with the Sørensen index alone because there were no differences between these two similarity matrices. We used Euclidean distances between centers of pairwise units for the space matrix. The statistical significance was estimated using the Montecarlo permutation test, allowing 999 permutations in each comparison.

3. Results

3.1. Species Composition and Richness

We found 50 herb species (Table 1) in 43 genera and 18 families (ferns were treated as one group). All ground herbs registered in the plot were perennials. Orchidaceae was the most species-rich family for the study area with six species, followed by Cyperaceae, Piperaceae, Rubiaceae, Caryophyllaceae, Urticaceae, and Asteraceae. The remaining 10 families were all represented by a single species (Table 1, Figure 2). Among the ferns (15 gen./20 spp.), *Asplenium* (6 spp.) was the only genus with more than one species (Table 1).

Figure 2. Genus and species richness for the 18 herb families found in the one-hectare plot in the Pasochoa volcano. The pteridophytes are represented by one group.

Table 1. Terrestrial herbs found in the 1 ha plot in a montane rain forest at 3300 m on the Pasochoa volcano, Ecuador. The 50 herb species are grouped into obligate terrestrial (O-P = prototerrestrial, O-S = scandent) and facultative terrestrial (F-C = climber F-E = epiphyte). N = individuals number/ha. C = coverage in m^2/ha. Microhabitat in which the species were found, as follows: r = ridge, s = slope, g = gully bed, h = high light intensity, m = medium light intensity, and l = low light intensity. Conservation status according to the IUCN categories [50]: NT = near threatened, LC = least concern, CA II = CITES Appendix II [51]. Proposed conservation status over Ecuador: WC = well collected >100 collections all over Ecuador, MC = medium collected <100–>30, SC = scarcely collected <30 collections. The collection number for the vouchers is between parentheses, CQ = Catalina Quintana et al. The vouchers are deposited in the QCA and QCNE herbaria.

	Family	Species	Life Form	N	C	Topographic Micro Habitat	Light Micro Habitat	Iucn Conservation Status	Proposed Conservation Status
1	ARALIACEAE	*Hydrocotyle alchemilloides* A. Rich. (CQ 60)	O-P	260	1.3	s,r	h	-	SC
2	ARACEAE	Anthurium pulchrum Engl. (CQ 217)	F-C	276	18.9	s,r	h	-	WC
3	ASTERACEAE	Asteraceae sp. (CQ 126)	O-S	41	1.5	s	m	-	-
4		*Ageratum* sp. (CQ 233)	F-C	16	0.7	s,r,g	m,l	-	-
5	BASELLACEAE	*Tournonia hookeriana* Moq. (CQ 211)	F-C	189	7.8	s	m,l	-	SC
6	BEGONIACEAE	*Begonia sodiroi* C. DC. (CQ 206)	F-C	428	39.2	s,r,g	h,m	NT	SC
7	CARYOPHYLLACEAE	*Arenaria lanuginosa* (Michx.) Rohrb. (CQ 110)	O-S	35	1.5	s,r	h,m,l	-	MC
8		*Stellaria recurvata* Willd. ex D.F.K. Schltdl. (CQ 143)	O-S	59	3.1	s,r,g	h,m,l	LC	WC
9	CYPERACEAE	*Carex hamata* Sw. (CQ 213)	O-P	7116	175	s,r,g	h,m,l	-	WC
10		*Carex muricata* L. (CQ 191)	O-P	2099	28.9	s,r,g	h,m,l	-	MC
11		*Rhynchospora macrochaeta* Steudel ex Boeckeler (CQ 209)	O-P	1702	90	s,r,g	h,m	-	WC
12	FERNS	*Adiantum concinnum* Humb. and Bonpl. ex Willd. (CQ 245)	O-P	6	0.7	r,g	m	-	MC
13		*Asplenium pteropus* Kaulf (CQ 150)	O-P	347	19.8	s,r,g	h,m	-	WC
14		*Asplenium sessilifolium* Desv. (CQ 190)	O-P	1466	46.7	s,r,g	h,m,l	-	MC
15		*Asplenium monanthes* L. (CQ 153)	O-P	187	7.5	s,r,g	h,m	-	WC
16		*Asplenium castaneum* Schltdl. and Cham. (CQ 132)	O-P	475	8.1	s,r,g	h,m	-	SC
17		*Asplenium peruvianum* Desv. (CQ 124)	O-P	110	1.9	s,r,g	h,m	-	SC
18		*Asplenium squamosum* L. (CQ 247)	O-P	10	0.8	g	h,m	-	SC

Table 1. *Cont.*

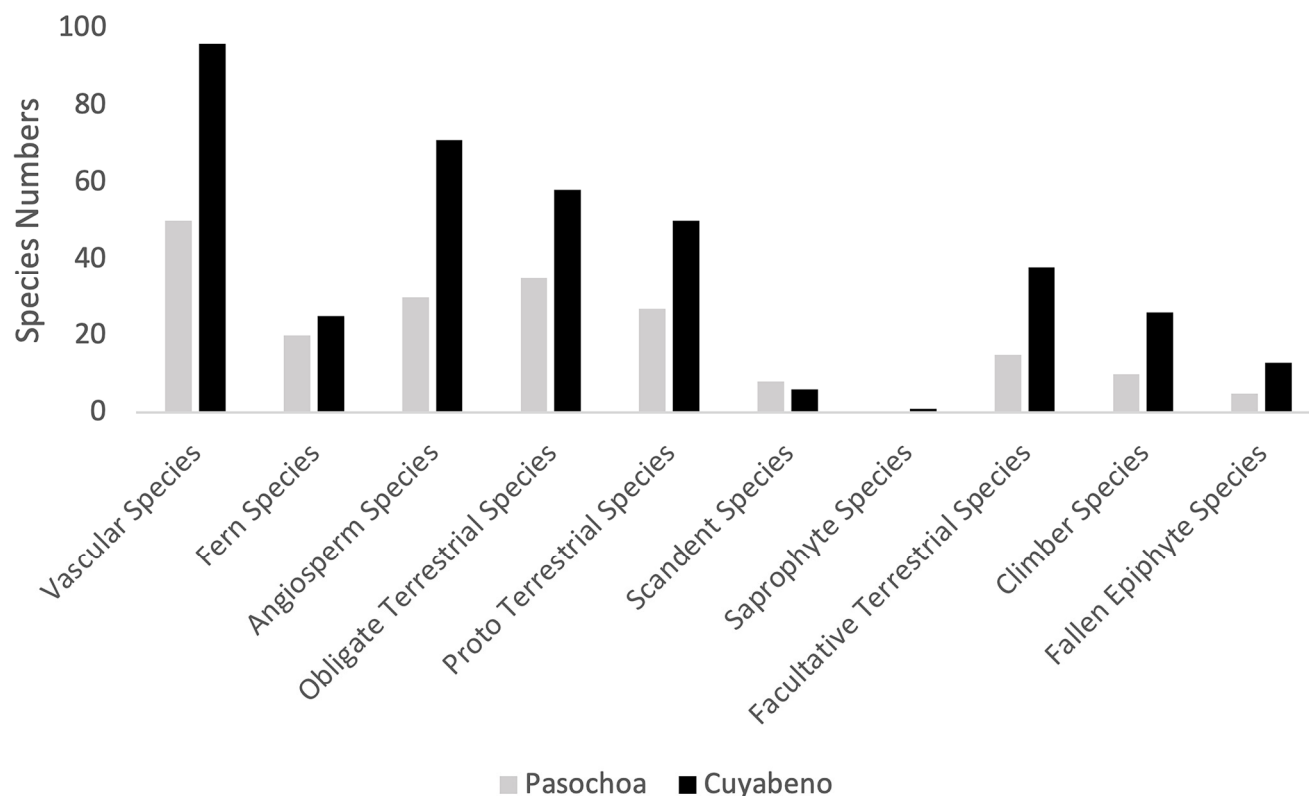|	Family	Species	Life Form	N	C	Topographic Micro Habitat	Light Micro Habitat	Iucn Conservation Status	Proposed Conservation Status
19		*Athyrium dombeyi* Desv. (CQ 116)	O-P	86	9.3	s,r,g	h,m	-	SC
20		*Blechnum fragile* (Liebm.) C.V. Morton and Lellinger (CQ 255)	O-S	23	1.5	g	m	-	MC
21		*Botrychium virginianum* (L.) Sw. (CQ 144)	O-P	41	1.4	s	h,m	-	SC
22		*Campyloneurum amphostenon* (Klotzch) Fée (CQ 155)	F-E	31	0.9	s,r,g	m	-	MC
23		*Dryopteris paleacea* (Sw.) Hand.-Mazz. (CQ 112)	O-P	72	40.5	s,r,g	h,m	-	SC
24		*Elaphoglossum papillosum* (Baker) Christ (CQ 100)	F-E	2	0.1	s	h,m	-	WC
25		*Equisetum bogotense* Kunth (CQ 231)	O-P	48	0.7	s	h,m	-	WC
26		*Hypolepis bogotensis* H. Karst. (CQ 258)	O-P	260	0.9	s	h,m	-	MC
27		*Pecluma divaricata* (E. Fourn.) Mickel and Beitel (CQ 229)	O-P	8	1	s,g	h,m	-	MC
28		*Polypodium subandinum* Sodiro (CQ 193)	F-C	4620	43.7	s,r,g	h,m,l	-	WC
29		*Polystichum muricatum* (L.) Fée (CQ 67)	O-P	737	50.6	s,r,g	h,m	-	SC
30		*Pteris muricata* Hook. (CQ 196)	O-P	35	4.5	g	h,m	-	MC
31		*Thelypteris rigescens* (Sodiro) A.R. Sm. (CQ 23)	O-P	102	68	s,r,g	h,m,l	-	SC
32	GERANIACEAE	*Geranium laxicaule* R. Knuth (CQ21)	O-S	27	0.5	s,r	h,m	-	SC
33	GESNERIACEAE	*Alloplectus dielsii* (Mansf.) Wiehler (CQ 197)	O-S	451	19.3	s,r,g	h,m	-	WC
34	ORCHIDACEAE	*Baskervilla auriculata* Garay (CQ 113)	O-P	30	0.9	s,r	h	NT	SC
35		*Cranichis ciliata* Kunth (CQ 135)	O-P	208	6.2	s,r	h	CA II	MC
36		*Malaxis hoppii* (Schltr.)Løjtnant (CQ 119)	O-P	406	6.8	s,r,g	h	CA II	SC
37		*Stelis pusilla* Kunth (CQ 111)	F-E	59	3.1	s,g	h,m	CA II	WC
38		*Odontoglossum pardinum* (Lindl.)Lindl.(CQ 223)	F-E	10	0.1	s,r	h,m	CA II	MC
39		*Pleurothallis* sp. (CQ 240)	F-E	2	0.01	s	h,m	-	-

Table 1. *Cont.*

	Family	Species	Life Form	N	C	Topographic Micro Habitat	Light Micro Habitat	Iucn Conservation Status	Proposed Conservation Status
40	OXALIDACEAE	*Oxalis lotoides* Kunth (CQ 75)	O-S	115	7.5	s,r,g	h,m,l	-	WC
41	PHYTOLACCACEAE	*Phytolacca bogotensis* Kunth (CQ 270)	O-P	14	0.6	s,r	h,m	-	MC
42	PIPERACEAE	*Peperomia rotundata* Kunth (CQ 33)	F-C	4860	58.1	s,r,g	h,m,l	-	WC
43		*Peperomia* sp. 1 (CQ 224)	F-C	102	1.5	s,g	h,m	-	-
44		*Peperomia* sp. 2 (CQ 243)	F-C	24	0.6	g	m	-	-
45	POACEAE	*Poa aequatoriensis* Hack. (CQ 114)	O-P	130	3.7	s,r	h,m	-	SC
46	RUBIACEAE	*Galium obovatum* Kunth (CQ 133)	O-S	39	0.5	s,r	h,m	-	SC
47		*Leptostigma pilosum* (Benth.) Fosberg (CQ 106)	O-P	1159	19.9	s,r	h	-	SC
48	SOLANACEAE	*Solanum dalibardiforme* Bitter (CQ 138)	F-C	97	3.6	s,r,g	m,l	-	SC
49	URTICACEAE	*Pilea pubescens* Liebm. (CQ 117)	F-C	1883	7	s,r	h,m	-	MC
50		*Urtica leptophylla* Kunth (CQ 249)	O-P	8	0.9	s	m	-	MC

3.2. Life Forms

Obligate terrestrial herbs was the group with more species (70%), prototerrestrials represented 54% of the group, while ferns contributed 60%. Facultatively, terrestrials represent 30% of the species found in the study site (Table 1, Figure 3).

Figure 3. Comparison of the species herb number according to the life forms in a montane forest (3300 m) in this study and a tropical rain forest plot 265 m in Cuyabeno [13].

3.3. Species Endemism and Conservation Status

The Pasochoa herb flora presented just three endemic species, two of them being orchids, *Stellaria recurvata* and *Baskervilla auriculata*, and the third species being a Begoniaceae, *Begonia sodiroi*. All the statuses of the orchids are presented in the CITES Appendix II [51], which includes species not necessarily threatened with extinction, but in which trade must be controlled in order to avoid utilization incompatible with their survival [51]. Regarding rarity and commonness, 39% of the non-endemic species were scarcely collected, 32% were medium collected, and 29% were well collected (Table 1). Just one third of the non-endemic species had more than 100 collections in our survey.

3.4. Density

The entire plot had 31,119 individuals, i.e., three individuals/m^2. Most of the 50 species formed dense groups, and it was sometimes difficult to count individual plants. The three species with the highest densities in our study area were *Carex hamata* (N = 7116), *Polypodium subandino* (N = 4620), and *Peperomia rotundata* (N = 4860). These three species contributed 53% of the total number of individual herbs. Five species had densities of 1000–2100 individuals and contributed 26% of the total number. There were 16 species with densities of 100–1000 individuals. In the other extreme, 26 species had <100 individuals and contributed only 2.5% of the total numbers of individuals (14 of these species had densities < to 30 individuals) (Table 1).
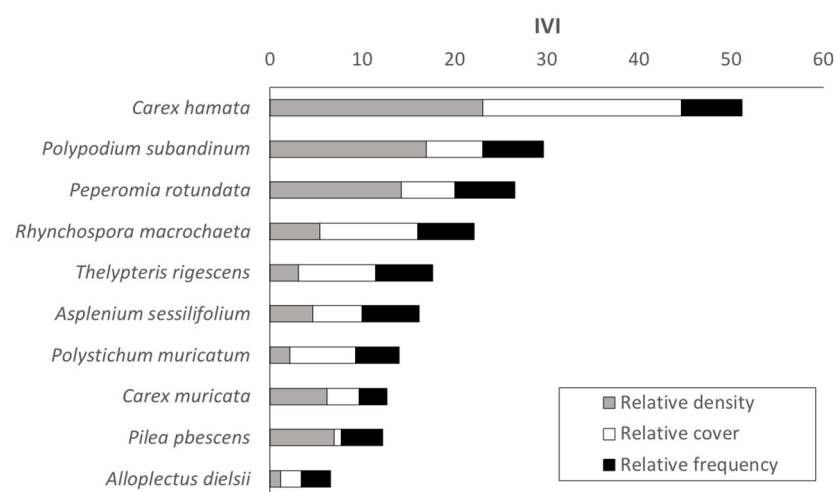
3.5. Cover

The total cover of herbs in the study site was 815 m^2 (8.15%). In units of 25 m^2, 100 m^2, and 1000 m^2 (10 × 100 m), the cover averaged 2, 8, and 81.5 m^2, respectively (Table 2). *Carex hamata* (175 m^2), *Rhynchospora macrochaeta* (90 m^2), *Thelypteris rigescens* (68 m^2), *Peperomia rotundata* (58 m^2), and *Polystichum muricatum* (50 m^2) contributed 52% to the total cover (Table 1). Most of the species in this list have relatively big leaves, except *Carex hamata* and *Peperomia rotundata*, whose high cover is due to their high number of individuals.

Table 2. Species richness of herbs in different studies and altitudes. Plot area varies in most studies. All studies conducted in Ecuador to date are listed, including the present study (in bold). (-) Studies where the number of individuals per species is not reported and (*) studies where obligate terrestrial herbs are not distinguished.

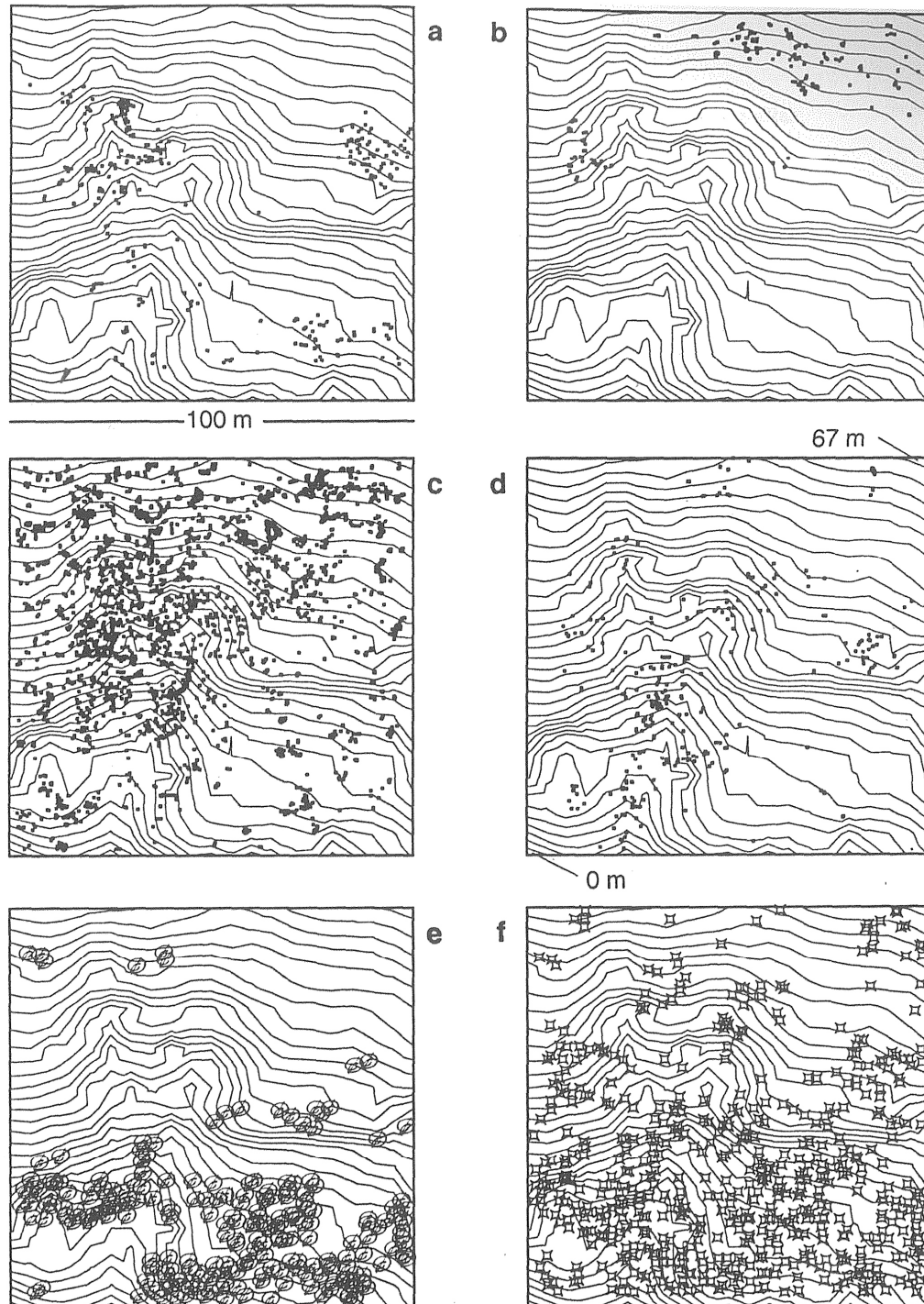| Herbs Species/Individuals	Obligate Terrestrial Herbs Species/Individuals	Density (Number Individuals/m^2)	Plot Area m^2	Altitude m	Study Area	Reference
0.046	*	1.54	464	1710	Ecuador (Borja)	[17]
0.087	*	1.53	464	520	Ecuador (Shinguipino)	[17]
-	0.134	1.19	100	100	Costa Rica	[12]
0.04	**0.03**	**0.03**	**100**	**3300**	**Ecuador (Pasochoa)**	**This study**
-	0.018	2.85	1000	220	Ecuador (Capeira)	[1]
-	0.019	0.94	1000	220	Ecuador (Jauneche)	[1]
-	0.041	1.22	1000	220	Ecuador (Palenque)	[1]
0.009	0.005	1.1	10,000	250	Ecuador (Cuyabeno)	[13]
0.015	*	0.63	10,000	250	Borneo (Brunei)	[15]
0.027	*	0.24	10,000	250	Borneo (Brunei)	[15]
0.014	0.008	0.31	1000	3300	Ecuador (Pasochoa)	This study
0.008	*	2.67	30,000	900–1100	Bolivia (Los Volcanes Reserve)	[19]
0.002	**0.011**	**3.11**	**10,000**	**3300**	**Ecuador (Pasochoa)**	**This study**

3.6. Indices of Importance Value

The Importance Value Index (IVI) for the 10 most important species (Figure 4) varies from 50 for *Carex hamata* to 8 for *Alloplectus dielsii*. Of these 10 species, 8 are prototerrestrials and 2 are climbers.

Figure 4. Species with the highest Importance Value Index of the one-hectare plot at Pasochoa volcano. (IVI) = relative frequency + relative cover + relative density.

3.7. Microhabitats and Species Preferences

The spatial distribution maps (Figure 5a–d) show that only 8 species were restricted to specific topographic microhabitats, while the 42 remaining species were found in more than 1 microhabitat.

Figure 5. Examples of the topographic distribution of four species of herbs found in the study area: (**a**) *Begonia sodiroi*, climber, N = 428; (**b**) *Hydrocotyle alchemilloides*, prototerrestrial, N = 260; (**c**) *Carex hamata*, prototerrestrial, N = 7116; (**d**) *Asplenium pteroporus*, prototerrestrial, N = 347. (**e**) Low light microhabitats (thicket) and (**f**) medium light intensity microhabitats. Level curves each 2 m.

The species that were most associated with the ridge were *Hydrocotyle alchemilloides* (N = 260, Figure 5b), *Galium obovatum* Kunth (N = 39), and *Leptostigma pilosum* (N = 1159). These species were also found in other microhabitats, but they were denser in the ridge. Almost all the species that occurred in the slope were generalists that were also found in the other three topographic microhabitats (Table 1). The species that occurred exclusively on the slope all had very low densities (N < 10)—*Hypolepis bogotensis* (N = 8), *Elaphoglossum papilosum* (N = 2), and *Pleurothalis* sp. (N = 2), with the last two being facultative epiphytes. There were five species that occurred exclusively in the *erosion gully*—*Asplenium squamosum* (N = 10), *Pteris muricata* (N = 35), *Equisetum bogotense* (N = 48), *Urtica leptophylla*. (N = 8), and *Peperomia* sp. 2 (N = 24). These species were found in soils with high humidity, especially in water sources. *Begonia sodiroi* (N = 428) and *Asplenium pteropus* (N = 347) occurred especially in the erosion gully but also in the other two sites (ridge and slope).

The low light microhabitat (Figure 5e) had 12 species, none of which were exclusive to it. The most frequent species were *Thelypteris rigescens*, *Polypodium subandino*, *Peperomia rotundata*, *Solanum dalibardiforme*, *Oxalis lotoides*, *Tournonia hookeriana*, *Arenaria lanuginose*, and *Stellaria recurvata*. The density and cover of *Thelypteris rigescens* was lower in this microhabitat. Five species were exclusive to the *middle light microhabitat* (Figure 5f): *Urtica leptophylla*. (N = 8), *Campyloneurum amphostenon* (N = 31), Lomaria fragilis (N = 23), *Adiantum concinnum* (N = 6), and *Peperomia* sp. 2 (N = 24). In the *high light microhabitat*, we encountered species such as *Baskervilla auriculata* (N = 30), *Cranichis ciliata* (N = 208), *Malaxis hoppii* (N = 406), *Hydrocotyle alchemilloides* (N = 260), *Anthurium pulchrum* (N = 276), and *Leptostigma pilosum* (N = 1159), which were all exclusive to the microhabitat.

3.8. Statistical Analysis

There were positive Mantel correlations between the floristic composition of the herb flora in the montane forest plot that we studied at Pasochoa with the topographic, the light (presence/absence of thicket), and the spatial matrices (Table 3). The strongest correlations were seen with topography and light. The correlation with space was very weak and not significant.

Table 3. Mantel and partial Mantel correlations of the herb composition similarity matrix with space and microhabitat matrices. Matrix B is the matrix correlated with the herb flora composition similarity matrix. Matrix C is the matrix whose effect is removed when calculating the partial correlations.

Matrix B		*r*	*P*
Topography		0.2	0.01
Space		0.09	0.04
Light (presence/absence thicket)		0.21	0.001
Matrix B	Matrix C	*Partial r*	*P*
Topography	Space	0.187	0.0001
Space	Topography	0.02	0.33
Topography	Light (presence/absence thicket)	0.183	0.001
Light (presence/absence thicket)	Topography	0.193	0.007

4. Discussion

The high number of genera of terrestrial herbs (43) in the Pasochoa one-hectare plot stands out. The largest genus comprised six species. This is hard to understand unless the situation is focused on a large scale. In the entire Andean region of Ecuador above a 2400 m elevation, it is common to find families represented by a single genus (46%)

and genera represented by a single species (21%) [52]. This overall pattern of the high Andean flora is reflected in the Pasochoa plot. The pattern is different from that found in Amazonian Ecuador, where most families are represented by more than one genus and more than one species [53]. Even in small plots (e.g., one hectare), such as the plot in the Amazon lowlands at Cuyabeno (250 m), where 96 herb species were found, the richest family, Araceae, had 28 species, followed by ferns (24) and Marantaceae (7) [13]. Pasochoa had 1.11 species/genus, while Cuyabeno had 2.08 species/genus. The most species-rich genera in Cuyabeno had >10 species compared with only 6 species found in the largest genus in Pasochoa.

The high number of rare species (71%) (Table 1), or not easily found within their geographical distribution range [54], should have high priority in conservation programs. Botanical exploration, collections [55–57], and quantitative inventories focused on Andean forest herbs can help to evaluate their conservation status and take action to preserve these groups that are frequently overlooked life forms in forest surveys. These findings showed how poor our knowledge of the Andean herbs is and raised a concern of the urgent need of a conservation plan.

In the Cuyabeno plot, 33% of the prototerrestrials were pteridophytes [14] (vs. 60% in our study site). This finding emphasizes the fact that even areas as small as one hectare have a relatively high number of fern species due to mountain-covered habitats that enable fern coexistence [58]. The high humidity encountered here is mostly due to fog; moreover, the low temperatures of the Andean mountains create appropriate conditions for the development of many pteridophyte species. The highest pteridophyte species richness is found in Ecuador as well as in other neotropical areas are between 1500 and 3000 m [58]. Other studies carried out at a large scale also showed that mountains are richer than lowlands in pteridophyte species [18,19,58–60]. If the fern flora of the entire Andes (2000 species) is compared with that of the entire Amazonian Brazil (300 species), it is obvious that ferns in the lowlands have a poor representation in the Neotropics [58].

Concerning the entire group of herb species, botanical accounts document that species richness increases with increasing altitude, reaching a maximum at 2400–3000 m [52]. However, in small areas like the one-hectare study at Cuyabeno, this pattern is the opposite: Cuyabeno included nearly twice as many species in comparison to Pasochoa at this scale (Figure 3). Whitmore and collaborators (1985) [12] used a category of free-standing herbs, which is equivalent to obligate terrestrials in the present study (Table 2). Gentry and Dodson (1987) [1] as well as Linares-Palomino and collaborators (2009) [19] used the classification of "terrestrial herbs", which is the same as our obligate terrestrials, as the authors had separate categories for climbers and for epiphytes. Comparing the species richness of these studies with the Pasochoa plot (Figure 3, Table 2), we conclude that the Pasochoa plot had the lowest species richness, except if it would be compared with the dry forest of Jauneche located on the coast of Ecuador. This make sense, considering that most herb species, especially ferns, thrive in humid habitats.

4.1. Density

The density of herbs at the Pasochoa plot is three times as high as the density found at the Cuyabeno plot in the Amazon lowlands (Table 2). The density of herbs found at Pasochoa is higher than the densities found in most other study sites [1,12,15], but the density reported by Gentry and Dodson (1987) [1] for a 0.5 ha in a low mountain forest is comparable to our findings (Table 2).

In other tropical forests, such as the Barro Colorado Forest, trees had low densities because of the scarcity of habitats and because of unfavorable regeneration conditions. Therefore, the rare species do not have reproductive advantages over the common species [61]. We believe this also happens in herbs. The low densities of 26 species (<100 individuals/ha) reported in our study might be explained by the low ability of those species to grow in unstable soils, especially on the slopes (Table 1). For a comparison, species tend to be rarer

in the lowland Amazon forest at Cuyabeno [13], where 50% of herb species contribute 7% of the total number of individuals.

In temperate and dry forests, alterations in seasonality can impact the density and cover of the species [39]. At our study site, even in the drier months of July and August, all the species, including the rare ones, were consistently present throughout the year. The lack of annual herbs is a characteristic of tropical humid forests [13,62]. Any potential fluctuation in density and cover between seasons likely did not substantially affect the patterns reported in our study.

4.2. Cover

The Amazonian forest plot at Cuyabeno and the plots in Borneo had lower covers compared to the Pasochoa forest: 2.50% and 0.72% vs. 8.15% (in this study) [13,15]. The vegetative growth (clones) of certain species found in the Pasochoa plot can explain this high cover. In contrast, in the Cuyabeno plot, only two species formed dense groups, *Geophila* and Araceae [13]; therefore, in the montane forests at Pasochoa, more species produce dense groups, constituting to larger covers.

4.3. Importance Value of Species and Microhabitat Associations

The high importance value of Orchidaceae (Figure 2) coincides with the fact that this family is the richest in species in Andean forests over 2400 m [52,63]. The high number of herb genera (Figure 2) represent a great phylogenetic richness in the study area, showing that diversification in the Andes is a continuous and actual process [64]. Certain species like *Carex hamata*, *Polypodium subandinum*, and *Peperomia rotundata* provide high density values, but lower values of frequency can be explained by the fact that vegetative spread gives herbs on the ground the mobility to find suitable edaphic and climatic microhabitats (Figure 4).

The 12 species thriving in the low-light microhabitat were primarily climbers facing challenges in finding exposed areas to reach sunlight. The Andean bamboo, *Chusquea scandens*, not only created shade but facilitated a framework for climbers (*Oxalis lotoides*, *Arenaria lanuginose*, and *Stellaria recurvata*) to eventually access light. In contrast, the prototerrestrial *Thelypteris rigescens* could survive in this challenging microhabitat due to its preference for shade, as described by Richards [65].

In terms of the floristic association with habitats (Mantel correlations), the composition of herbs exhibited a strong correlation with light availability (presence/absence of thicket) and topography. Although thicket units are concentrated in the steep slopes at the lower half of the plot (Figure 1; ~90% of the thicket/presence units are located here), light intensity is independently associated with species composition. The thicket structure had a significant effect on the species composition of ground herbs. Thicket creates low light intensity microhabitats where the species distribution and community structure is distinct. The impact of light availability in the understory herbs aligns with documented findings in Singapore [66] and in seasonally dry tropical forests of India, at local and landscape scales [39].

5. Conclusions

The species composition of the Pasochoa herb community appeared to be structured by topographic and light intensity microhabitat variables. Lack of understory light seems to shape the herb ground cover. Light intensity was more important than topographic microhabitats. Both light and topography influenced the distribution of species and the community structure of herbs. Other variables, such as soil nutrients and tree biomass, which were not measured, could be important drivers of the floristic composition of herbs. Herbs had more species than trees in the present study site (50 vs. 32); at the same time, the herb genera represent a great phylogenetic richness, which illustrates that the Andean herbs deserve to be focused on strongly in conservation strategies as most of them are poorly collected and underestimated in botanical surveys. There is an urgent need to improve

the knowledge of the composition of tropical plant herbs, which is limited to floristic inventories, without ecological information. In the future, new studies with information on epiphytes and ferns will shed some light on the floristic composition of Andean forests and will predict changes in plant communities under rapid climate change conditions in order to design strategies for tropical Andean ecosystems.

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