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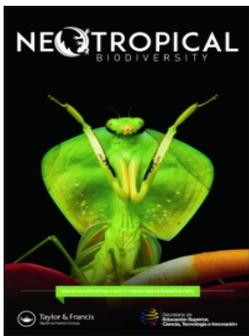
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Liverwort diversity in *Polylepis pauta* forests of Ecuador under different climatic conditions

S. Robbert Gradstein^a and Susana León-Yáñez^b

^aAlbrecht von Haller Institute, University of Göttingen, Göttingen, Germany; ^bHerbario QCA, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador

ABSTRACT

Polylepis forests are the world's highest forests in terms of elevation and host a unique biodiversity of plants and animals. Unfortunately, these forests are rapidly disappearing due to human impact and are one of the most threatened ecosystems of South America. This paper deals with liverwort diversity in *Polylepis* forests of Ecuador. Liverworts are very diverse in tropical forests and are sensitive indicators of changes in humidity conditions. By comparing species richness, species composition and composition of functional groups of liverworts in dry and humid *Polylepis* forest, we explore how liverwort diversity of *Polylepis* forests is affected by climatic conditions differing in humidity. We inventoried liverwort diversity in *Polylepis pauta* forest of Lagunas de Mojanda reserve characterized by a relatively dry climate and in the páramo of Papallacta with a humid climate. In each site, we sampled liverworts on 10 *P. pauta* trees and surrounding soil. Species richness was highest in the humid forest and species composition in the two sites differed significantly. The two sites also had very different patterns of functional groups, with smooth mats dominating the liverwort flora of Mojanda while rough mats prevailed at Papallacta. This underscores the importance of bryophyte life forms as climate indicators in tropical forests. A phytogeographic comparison of the two sites showed a higher number of northern Andean taxa in the humid forest. The greater representation of species with restricted ranges in humid *Polylepis* forest shows the importance of these forests for conservation.

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Introduction

Liverworts (Marchantiophyta) are the second largest group of the bryophytes, after the mosses, and contain more than 5000 species worldwide [1]. They abound as epiphytes in moist tropical forests where they diversified during the late Cretaceous and early Cenozoic with the rise and spread of angiosperm-dominated forests [2–4]. In tropical lowland forests, liverworts are 3–4 times more speciose than mosses and their diversity peaks in lowland cloud forests [5–7]. Along elevational gradients, the contribution of liverworts to overall bryophyte diversity increases with humidity, much more strongly so than of mosses [8–11]. Liverworts play an important role in the hydrology and nutrient cycles of montane cloud forests by intercepting precipitation and diversifying and changing nutrient pathways, both spatially and temporally [12–15]. Due to the lack of a protective cuticle, they are sensitive indicators of changes in humidity, and disturbance of the microclimatic gradient in tropical forests may result in rapid composition changes of the liverwort assemblages [16–18]. Several studies have shown the strong correlation between

environmental factors and specific morphological traits of liverworts, such as life form, life strategy and leaf characters [19–22].

This paper deals with the diversity of liverworts in high-Andean forests dominated by species of *Polylepis* (Rosaceae). *Polylepis* forests are the world's highest forests in terms of elevation, reaching up to almost 5000 m, and are distributed throughout the Andes, from Venezuela to northern Argentina and Chile, where they occur as arboreal islands in a matrix of grassland and scrub [23]. These forests host a unique biodiversity of plants and animals [24–26] and several undescribed species of liverworts were recently detected in *Polylepis* forests [27–29]. *Polylepis* forests are also of great importance to the local communities by supplying building material, firewood, etc. [30]. Unfortunately, these forests are rapidly disappearing due to fire and cattle grazing and have become one of South America's most threatened ecosystem [31,32].

Polylepis trees stand out by their gnarled shape and twisted trunks and branches, considered adaptations to growth in harsh environments. The bark of the trees is typically reddish in color and strongly exfoliating. Thickness and length of the shredded bark segments differs somewhat among species [28]. In spite of their

CONTACT S. Robbert Gradstein  sgradst@gwdg.de  Department of Systematics, Biodiversity and Evolution of Plants, Albrecht von Haller Institute, University of Göttingen, 37073 Göttingen, Germany

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exfoliating bark, *Polylepis* trees may host a rich epiphytic flora including numerous species of bryophytes and lichens and a considerable number of vascular plant species. As shown by Sylvester et al. [33], many epiphyte species reach their highest elevational limits in *Polylepis* forests. Several recent studies have dealt with bryophyte diversity of *Polylepis* forests (see Delgado & León-Vargas [34] and Gradstein & León-Yáñez [27] for reviews). Aldana [35] and Delgado & León-Vargas [34] recorded high diversity of mosses in *Polylepis* forests of Bolivia and Venezuela and Gradstein & León-Yáñez [27] reported a rich liverwort flora in *Polylepis* forest of Ecuador. The results showed the importance of *Polylepis* forests as bryophyte habitats. Moreover, they indicated that liverworts are more diverse in humid forests whereas mosses predominate in drier forests. These data are in agreement with Parolly & Kürschner [20] who reported the occurrence of different cryptogamic epiphyte communities in dry and humid *Polylepis* forests.

The present paper focuses on liverwort diversity in *Polylepis* forests under different climatic conditions, especially humidity. By comparing species richness, species composition and life forms of liverworts in seasonal and everwet *P. pauta* forests, we explore the importance of the climate in enhancing liverwort diversity in these forests.

Materials and methods

Study sites

We conducted fieldwork in *Polylepis pauta* forests (Figure 1) in the páramo of Papallacta and reserve “Lagunas de Mojanda” in Central Ecuador. The studied forests of Papallacta are located on the border

of the provinces of Pichincha and Napo along the road from Quito to Baeza, just before the pass ($0^{\circ} 20' S$, $78^{\circ} 12' W$), at an elevation of about 4000 m a. s.l. The area has a humid, everwet climate due to its location on the windward slope of the Eastern Cordillera of the Andes, where the trade winds from the Amazon basin cause high rainfall and frequent cloudiness [36,37] (Table 1). Annual rainfall in 2017 was about 1800 mm and a distinct dry season is absent. Cloud frequency is high and dense fog events occur during ca. 120 days per year [38]. The *P. pauta*-dominated forests (Polylepetum pautae Lauer et al.) [38] consist of small, remnant patches within a bunchgrass páramo landscape. A description of the forest vegetation was given by Lauer et al. [38], the cryptogamic epiphyte vegetation was described by Parolly & Kürschner [20]. Liverworts are more abundant than mosses and cover the forest floor and the trunks of the *Polylepis* trees [27]. Higher up on branches of the trees, liverworts are less conspicuous and are replaced, in part, by robust acrocarpous mosses (e.g., *Campylopus* spp., *Chorisodontium* spp., *Dicranum frigidum*, *Leptodontium* spp., *Zygodon* spp.) and foliose lichens (e.g., *Hypotrachyna* spp., *Everniastrum* spp., *Sticta* spp.).

Lagunas de Mojanda is a municipal nature reserve on the border of the provinces of Pichincha and Imbabura ($0^{\circ}7'N$, $78^{\circ}15' W$), situated at an elevation of 3700–4350 m a.s.l. The area is volcanic and mainly composed of a large caldera of Late Pleistocene age [39]. The caldera is occupied by three lakes: a large lake, “Caricocha”, in the west, a smaller lake, “Huarmicocha”, in the east and a tiny third lake, “Yanacocha”, uphill. The area has a seasonal, relatively dry climate due to its position in the inter-Andean valley, on the leeward



Figure 1. Interior of *Polylepis* dry forest (a) and humid forest (b), showing bryophyte cover.

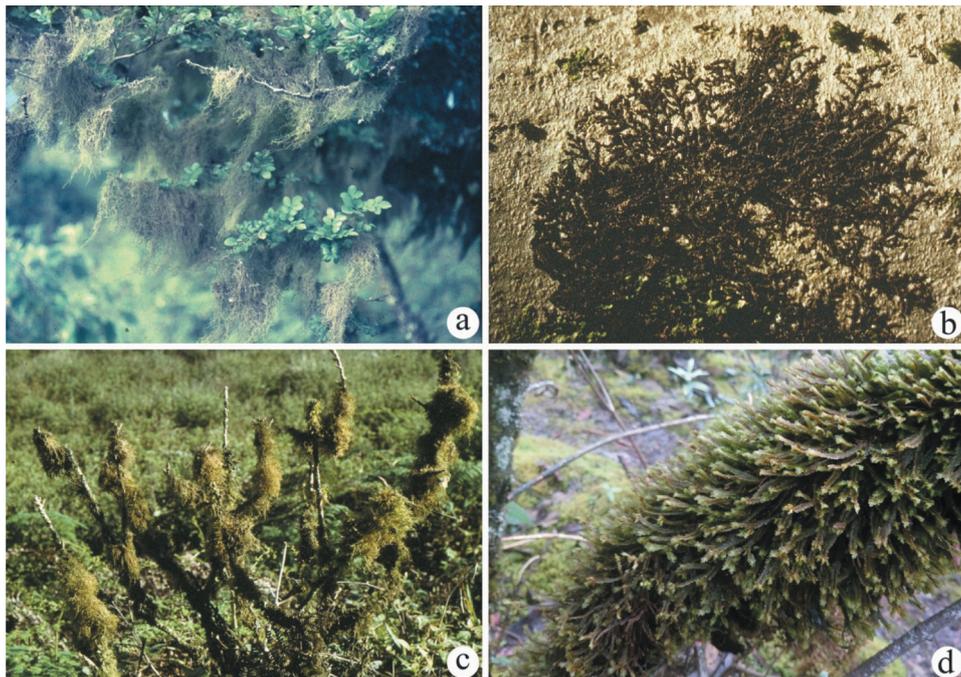
Table 1. Climate and habitat of Lagunas de Mojanda and páramo of Papallacta [37–42].

	Mojanda	Papallacta
Elevation (m)	3725–3850	4000
Slope	leeward	windward
Soil	peaty	peaty
Climate	seasonal	everwet
Annual precipitation (mm)	1000–1300	ca. 1800
Average length of the dry season	4 months	0 months
Cloud frequency	low	high

side of the Western Cordillera. Average annual precipitation is 1000–1300 mm, with a prolonged dry season during May–September [40], and cloud frequency is low [41]. Annual precipitation is significantly lower than in the páramo of Papallacta (Table 1). The *Polylepis* forests of Lagunas de Mojanda are situated between 3725 and 3850 m a.s.l. within a bunchgrass páramo landscape and cover relatively large surface areas. They are dominated by *Polylepis pauta*¹ and *P. incana*, accompanied by *Hedyosmum angustifolium*, *Gynoxys acostae*, *Miconia* spp., *Oreopanax andreanus*, *Gynoxys acostae*, *Buddleja pinchinensis* and other woody species. Introduced *P. racemosa* occurs in the open páramo and putative *Polylepis* hybrids are seen at the forest margins. Bryophytes are rather abundant on the *P. pauta* trees with robust mosses, such as *Neckera* spp., *Macromitrium* spp., *Thuidium peruvianum* and *Porotrichum* spp. dominating the epiphytic vegetation. Liverworts are much less conspicuous than mosses. The peaty forest soil is only sparsely covered by bryophytes with the mosses *Leptodontium luteum* and *Plagiomnium rhynchophorum* being the most common terrestrial bryophyte species.

Data collection and analysis

We collected liverworts in three *P. pauta* forests at Papallacta and in two forests at Mojanda. In each locality we haphazardly collected liverworts on the trunks and branches of *P. pauta* trees (11 trees in total at Mojanda, nine trees at Papallacta) up to about 2.5 m height. Distance between sampled trees was minimally 10 m. Because of the close similarity of the bryophyte communities of trunk bases and the forest floor in terms of species composition [43] we also collected terrestrial liverworts growing near the sampled trees, to up to 1 m away from trunk base. We made 57 liverwort collections in *Polylepis* forest at Papallacta and 75 at Mojanda; the majority of the collections were from bark. A few additional species records from the *P. pauta* forests of the study sites (collections in QCA) were also taken into account. These included *Bazzania placophylla*, *Cheilolejeunea oncophylla*, *Frullania intumescens* *Leiomitra sprucei*, *Lepicolea pruinosa* and *Metzgeria dorsipara* from Papallacta (various collectors) and *Anoplolejeunea conferta*, *Leiomitra flaccida* and *Porella leiboldii* (leg. P. Ramsay) from Mojanda. For analysis of functional diversity of liverworts, we recognized three broad functional groups [44,45]: 1) smooth mats (including tight mats and loose mats), 2) rough mats (including tails and wefts), 3) pendant species (Figure 2). All collections were identified or verified using “The Liverworts and Hornworts of Colombia and Ecuador” [29] and vouchers were deposited in herbarium QCA with selected duplicates in PC.

**Figure 2.** Life forms of liverworts: pendant species (a), smooth mat (b), rough mat (c, d).

Results and discussion

Species richness

A total of 35 liverwort species (in 11 families) were recorded on *P. pauta* trees and soil in Lagunas de Mojanda and 47 species (18 families) in the páramo of Papallacta (Table 2). The great majority of the species occurred on bark; seven species were recorded from soil at Papallacta and two at Mojanda. The terrestrial species also occurred on bark (tree bases) with two exceptions: *Jensensia spinosa* was only found on soil at Papallacta and *Plagiochila ovata* was exclusively terrestrial at Mojanda (but also epiphytic at Papallacta). A species accumulation curve (not shown) of 10 *P. pauta* trees at Lagunas de Mojanda indicated that liverwort sampling was representative. Five trees yielded 90% of the species and an asymptote was reached by sampling 8 trees. The data support the notion that the minimum area of epiphytic bryophytes in tropical forests is rather small and that sampling of few trees may be sufficient for representative sampling [46,47].

Liverwort species richness was 30% higher in Papallacta than in Mojanda, in spite of the fact that we observed more samples from Mojanda. At the family level, the difference was even more pronounced, being 60% higher in Papallacta (Table 2). At the lifestyle level (epiphytic, terrestrial), richness of epiphytic liverworts was similar to total liverwort richness but richness of terrestrial species was about three times higher at Papallacta. The higher richness in the *Polylepis* forests of Papallacta coincides with the humid climate at this site and is in agreement with Gareca et al. [23] who found that plant and bird diversity in Bolivian *Polylepis* forests increased with precipitation. The latter authors also found that length of the growing season and elevation play a role, with species richness increasing under longer growing season regimes while decreasing towards higher elevation. The higher richness of terrestrial species at Papallacta may also be due to the greater abundance of humus on the forest floor at this site (field observation).

A comparison of liverwort diversity in eight different *Polylepis* forest sites across the Andes shows considerable variation in species richness (Table 3). Richness was lowest in *P. sericea* forests of Colombia and Venezuela and on *P. incana* forest of Ecuador, with only 12 species recorded at each site. In contrast, much higher species numbers (>30) were found in the *P. pauta* forests of Ecuador, with richness peaking in the forests of Papallacta, and in *P. racemosa* forests of Peru (Chachapoyas). Somewhat lower numbers (20–25 spp.) were recorded in *P. reticulata* forests of Ecuador and *P. pepeii* forests of Peru. In spite of different sampling intensities and methods at the eight sites, a few trends may be observed in the data. The relatively low liverwort diversity in the *P. sericea*,

P. incana and *P. reticulata* forests (sites 1, 2, 5, 6) should reflect the rather dry climatic conditions in these forests [20] (Y. León-Vargas pers. comm.). The high richness at Papallacta and in *P. racemosa* forests of northern Peru, on the other hand, clearly coincides with humid climatic conditions in these sites. Both are located on the windward eastern slope of the Andes under conditions of high precipitation and cloudiness. The rather low elevation of the *P. racemosa* forests – located in the “Amotape-Huancabamba depression” of northern Peru – may in addition have influenced the high richness of this site [23]. Altitude may also explain the lesser species richness in the *P. pepeii* forests of Central Peru, which were located at very high elevation (4300–4700 m) [33]. The relatively high species richness in the *P. pauta* forests of Mojanda is unexpected in view of the prolonged dry season at this site. An explanation might be the presence of large water bodies, viz. crater lakes, in the vicinity of the studied *P. pauta* forests, which could have caused an increase of air humidity in the forests (not measured).

The question remains whether bark characteristics of the different *Polylepis* species played a role in shaping liverwort species richness. Kessler [24] observed differences in thickness and length of the shredded bark segments among the Bolivian species of *Polylepis*. The possible impact of these or other bark features on the diversity of epiphytic bryophytes has not been studied and needs work.

Species composition

We found very significant differences in the composition of the liverwort floras of the two study sites. Of 72 species recorded in the two sites, only 10 were shared by the two localities, accounting for a low 13% of total diversity. All shared species were epiphytes; two of them, *Plagiochila ensiformis* and *P. ovata*, additionally occurred on soil. The most common species in the forests of Mojanda, occurring on almost every *P. pauta* tree, were *Lophocolea bidentata*, *Metzgeria albinea*, *Plagiochila exigua* and *Radula voluta* (Table 2). Only one of them, *R. voluta*, was found in the forests of Papallacta, albeit much less commonly; the other three species were not seen at Papallacta. The *Polylepis* forests of Lagunas de Mojanda were furthermore much richer in tiny Lejeuneaceae, which included *Cololejeunea microscopica*, *Microlejeunea capillarisa*, *Harpalejeunea cinchonae*, *Lejeunea catinulata*, *L. deplanata* and *L. mojandae* (Table 2). Only one of these, *L. catinulata*, was found at Papallacta. *Lejeunea mojandae* was new to science [29] and is thus far only known from Lagunas de Mojanda, where it was not rare and was collected on four *P. pauta* trees.

The liverwort flora at Papallacta, in contrast, was much more luxuriant than Lagunas de Mojanda and was particularly rich in robust members of the genera

Table 2. Liverwort species diversity on *P. pauta* trees and surrounding soil in Lagunas de Mojanda and Páramo of Papallacta. + = presence. 1 = smooth mat; 2 = rough mat; 3 = pendant (brackets: life form not present in the area); E = endemic to Ecuador; A = Andean; nA = northern Andean; N = neotropical; W = wide-ranging (intercontinental). Bold face: species newly described based on this study [27–29]. Species recorded from rock [27] omitted. Names used in previous papers [20,27] that are no longer accepted are cited in brackets.

	Mojanda (n = 35)	Papallacta (n = 47)	Life form	Geogr. range
ADELANTHACEAE				
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.		+	2	W
<i>Pseudomarsupidium decipiens</i> (Hook.) Grolle (= <i>Adelanthus decipiens</i> (Hook.) Mitt.)		+	2	W
ANEURACEAE				
<i>Aneura pinguis</i> (L.) Dumort.		+	1	W
<i>Riccardia hans-meyeri</i> (Steph.) Meenks & C.De Jong	+		1	A
<i>R. poeppigiana</i> (Lehm. & Lindenb.) Meenks & C.De Jong (= <i>R. cervicornis</i> (Spruce) Gradst. & Hekking)		+	2	N
<i>R. wallisii</i> (Steph.) Gradst. (= <i>R. smaragdina</i> Meenks & C.De Jong)		+	2	A
CALYPOGEIACEAE				
<i>Calypogeia peruviana</i> Nees & Mont.		+	1	N
CEPHALOZOIACEAE				
<i>Cephalozia crossii</i> Spruce		+	1	N
FRULLANIACEAE				
<i>Frullania cuencensis</i> Taylor		+	1	N
<i>F. intumescens</i> (Lehm. & Lindenb.) Lehm. & Lindenb.		+	2	N
<i>F. paradoxa</i> Lehm. & Lindenb.		+	2	A
<i>F. peruviana</i> Gottsche		+	3	N
<i>F. tetraptera</i> Nees & Mont.	+		1	N
<i>F. tungurahuaana</i> Clark & Frye	+		1	A
HERBERTACEAE				
<i>Herbertus acanthelium</i> Spruce		+	2	A
<i>H. pensilis</i> Spruce		+	2	N
<i>H. sendtneri</i> (Nees) Nees (= <i>H. grossispinus</i> (Steph.) Fulford)		+	2	W
JAMESONIACEAE				
<i>Syzygiella rubricaulis</i> (Nees) Steph.		+	2	N
LEJEUNEACEAE				
<i>Anoplolejeunea conferta</i> (Meissn.) A.Evans	+		1	N
<i>Blepharolejeunea incongrua</i> (Lindenb. & Gottsche) van Slageren & Kruijt		+	1	N
<i>Brachiolejeunea laxifolia</i> (Taylor) Schiffn.	+		1	N
<i>Cheilelejeunea oncophylla</i> (ngstr.) Grolle & E.Reiner		+	1	N
<i>Cololejeunea microscopica</i> (Taylor) Schiffn.	+		1	W
<i>Drepanolejeunea andina</i> Herzog		+	1	A
<i>Harpalejeunea cinchonae</i> (Nees) Schiffn.	+	+	1	N
<i>Lejeunea aphanes</i> Spruce	+		1	W
<i>L. catinulifera</i> Spruce	+	+	1	A
<i>L. deplanata</i> Nees	+		1	N
<i>L. mojandae</i> Gradst.	+		1	nA (E)
<i>L. pallescens</i> Mitt.	+		1 (3)	A
<i>Microlejeunea capillarum</i> (Gottsche) Steph.	+	+	1	N
LEPICOLEACEAE				
<i>Lepicolea pruinosa</i> (Taylor) Spruce		+	2	A
LEPIDOZIACEAE				
<i>Bazzania placophylla</i> (Taylor) Grolle		+	2	nA
<i>Lepidozia auriculata</i> Steph.		+	2	A

(Continued)

Table 2. (Continued).

	Mojanda (n = 35)	Papallacta (n = 47)	Life form	Geogr. range
<i>L. cupressina</i> (Sw.) Lindenb.		+	2	W
LOPHOCOLEACEAE				
<i>Cryptolophocolea connata</i> (Sw.) L. Söderstr. & Våña	+	+	1	N
<i>Leptoscyphus amphibolius</i> (Nees) Grolle	+		1	N
<i>L. gibbosus</i> (Taylor) Mitt.	+		1	N
<i>L. hexagonus</i> (Nees) Grolle		+	2	A
<i>L. leoniae</i> Gradst.		+	1	nA (E)
<i>Lophocolea bidentata</i> (L.) Dumort.	+		1	W
<i>L. fragmentissima</i> R.M.Schust.		+	1	A
<i>L. muricata</i> (Lehm.) Nees	+		1	W
METZGERIACEAE				
<i>Metgeria albinea</i> Spruce	+		1	W
<i>M. consanguinea</i> Schiffn.	+	+	1	W
<i>M. dorsipara</i> (Herzog.) Kuwah.		+	1	A
<i>M. filicina</i> Spruce	+			A
<i>M. leptoneura</i> Spruce		+	3 (1)	W
<i>M. liebmanniana</i> Lindenb. & Gottsche	+	+	1	A
PALLAVICINIACEAE				
<i>Jensenia spinosa</i> (Lindenb. & Gottsche) Grolle		+	2	W
<i>Symphyogyna brasiliensis</i> Nees	+		1	W
PLAGIOCHILACEAE				
<i>Plagiochila bicuspidata</i> Steph.	+		1	A
<i>P. bifaria</i> (Sw.) Lindenb.	+	+	2	W
<i>P. buchtiniana</i> Steph.	+		2	A
<i>P. cleefii</i> Inoue		+	2	nA
<i>P. dependula</i> Taylor		+	2	nA
<i>P. ensiformis</i> Taylor	+	+	2	A
<i>P. exigua</i> (Taylor) Taylor	+		1	W
<i>P. fuscolutea</i> Taylor		+	2	A
<i>P. ovata</i> Lindenb. & Gottsche	+	+	2	A
<i>P. pachyloma</i> Taylor	+		2	A
<i>P. pautaphila</i> Gradst. & León-Yáñez		+	2	nA (E)
<i>P. punctata</i> (Taylor) Taylor		+	2	W
<i>P. raddiana</i> Lindenb.	+		2	N
<i>P. stricta</i> Lindenb.		+	1	N
PORELLACEAE				
<i>Porella leiboldii</i> (Lehm.) Trevis.	+		2	N
RADULACEAE				
<i>Radula subinflata</i> Lindenb.	+		1	N
<i>R. voluta</i> Taylor	+	+	1	W
SCAPANACEAE				
<i>Anastrophyllum auritum</i> (Lehm.) Steph.		+	1	W
TRICHOCOLEACEAE				
<i>Leiomitria flaccida</i> Spruce	+		2	A
<i>L. sprucei</i> (Steph.) T.Katagiri (= <i>Trichocolea sprucei</i> Steph.)		+	2	N
<i>L. tomentosa</i> (Sw.) Lindb. (= <i>T. tomentosa</i> (Sw.) Gottsche)		+	2	N

Frullania (*F. intumescens*, *F. paradoxa*, *F. peruviana*), *Riccardia* (*R. poeppigiana*, *R. wallisii*), *Herbertus* (*H. acanthelium*, *H. pensilis*, *H. sendtneri*), *Plagiochila* (*P. bifaria*, *P. dependula*, *P. ensiformis*, *P. fuscolutea*, *P. ovata*, *P. pautaphila*), *Bazzania* (*B. placophylla*), *Lepidozia* (*L. auriculata*) *Leptoscyphus* (*L. hexagonus*) and *Lepicolea* (*L. pruinosa*). None of these species were seen in the forests of Mojanda with exception of three members of *Plagiochila*, *P. bifaria*, *P. ensiformis*, *P. ovata*. The very different liverwort diversities of the two sites are also evident from the numerous liverwort families of the Papallacta forests that are absent in Mojanda (see Table 2) and the make-up of the *Plagiochila* and *Lejeuneaceae* floras, the most important groups in terms of species richness, of the two

Table 3. Liverwort species richness in eight *Polylepis* forest sites across the Andes. +: less than 5 trees sampled, in 1–2 forests. ++: more than 5 trees sampled, in at least 2 forests. *: identification preliminary (M. Kessler pers. comm.). Areas with an everwet climate, without distinct dry season, are scored as “humid”, those with a prolonged dry season as “dry”.

Reference	1	2	3	4	5	6	7	8
country	Ven	Col	Ecu	Ecu	Ecu	Ecu	Peru	Peru
elevation (m)	4000	4130	3725–3850	4000	3800	3900	2900–3300	4300–4700
humidity	dry	dry	dry	humid	dry	dry	humid	dry/humid
main <i>Polylepis</i> species	<i>sericea</i>	<i>sericea</i>	<i>pauta</i>	<i>pauta</i>	<i>incana</i>	<i>reticulata</i>	* <i>racemosa</i>	<i>pepei</i>
sampling intensity	++	+	++	++	+	+	++	++
nr. of liverwort species	12	12	35	47	12	20	32	25

1: Delgado & León-Vargas [34]. 2: Wolf [10]. 3: this study. 4: this study. 5: Parolly & Kürschner [20]. 6: Parolly & Kürschner [20], Gradstein & León-Yáñez (unpubl.). 7: Gradstein & Frahm [48], Kürschner & Parolly [51]. 8: Sylvester et al. [29,33]. Results of a Bolivian inventory [35] are omitted as liverwort species identifications were incomplete. Sampling at localities 5 and 8 included only epiphytic species, in all other localities epiphytic and terrestrial species. Sampling was plot-based in loc. 5, plot-based and haphazard in localities 6 and 7, and haphazard only in all other localities.

sites. Only three species in each group were shared by the two sites, whereas a total of 21 species (75%) were found in only one of the two sites. *Plagiochila dependula* and *P. fuscolutea* and the newly described *P. pautaphila* [27] were common in Papallacta while being absent in Mojanda, whereas *P. exigua* and *P. pachyloma* were common in Mojanda and were not recorded in Papallacta. The latter species was represented by an unusual phenotype characterized by very small trigones and an unpigmented, rather inconspicuous leaf border. Normally, *P. pachyloma* has large trigones and the leaf border is conspicuously brownish-pigmented. Possibly, the phenotype of *P. pachyloma* in the forests of Mojanda belongs to a new species.

The highly different liverwort floras of the two *P. pauta* forest sites may reflect, on the one hand, the island-like distribution of *Polylepis* forests [23], on the other hand the very different climatic conditions in the two sites should play an important role. Numerous studies have shown that differences in species composition are triggered by abiotic factors [17,49,50]. Because of the major role of water availability in shaping the diversity of liverworts, we assume that the different humidity conditions in the two sites (Table 1) largely accounted for the very different compositions of the liverwort assemblages of the two sites. Interestingly, a high species turnover (over 80%) was also recorded in the moss flora of the rather dry *P. sericea* forests of Venezuela [30]. Since the climatic conditions in the latter forests were rather uniform, we assume that other environmental factors (maybe edaphic) played a role here.

Table 4. Proportion of functional groups of liverworts in *Polylepis pauta* forests of Lagunas de Mojanda and páramo of Papallacta. Number of species in brackets.

	Mojanda	Papallacta
smooth mat	80% (29)	40% (19)
rough mat	20% (8)	56% (26)
pendent	-	4% (2)

Functional groups

The very different make-up of the liverwort floras of Mojanda and Papallacta correlated with significant differences in life form composition of liverworts (Table 4). In Mojanda, the great majority of the species were smooth mats, accounting for 80% of the liverwort flora. The remaining species were rough mats (20%), defined here in a broad sense and including tails and wefts. In Papallacta, in contrast, rough mats were the most common life form and included 56% of the species while smooth mats accounted for only 40% of the flora. Two pendant liverworts, *Frullania peruviana* and *Metzgeria leptoneura*, were common in the forest of Papallacta while being fully absent at Mojanda.

The significantly higher proportion of rough mats and the presence of pendant taxa in the liverwort flora of Papallacta should reflect the wetter climatic conditions at this site. Strong correlation of these life forms with high moisture availability has repeatedly been demonstrated [16,20,21,51]. Under increased humidity conditions liverwort species may grow less tightly associated with the substrate. Although appressed-growing smooth mats occurred in both study sites, their contribution to total diversity was two times higher in Mojanda than in Papallacta (Table 4). The greater contribution of smooth mats to overall liverwort diversity in the latter site clearly reflects the drier climatic conditions there. These results underline the importance of bryophyte life forms as robust climate indicators in tropical forests and show the usefulness of functional groups for the characterization of *Polylepis* forests under different climatic conditions.

Table 5. Geographical ranges in the liverwort flora of *Polylepis pauta* forests of Mojanda and Papallacta.

	Mojanda n = 36	Papallacta n = 46
northern Andean species (nA)	1	5
tropical Andean species (A)	13	14
neotropical species (N)	11	16
wide-ranging species (W)	11	11

Phytogeography

A comparison of the geographical ranges of the liverwort species reveals similar biogeographic patterns in the two study sites (Table 5). Species with neotropical and wide, intercontinental ranges account for the majority (60%) of the taxa in each site while about 40% of the species have more restricted, Andean distributions. These results agree with a phytogeographic study in the Colombian Andes [8], which showed that Andean species account for 30%–45% of the bryophyte flora above 3000 m a.s.l. The remaining species were wide-ranging, neotropical and wide-tropical taxa. A lower proportion of Andean species (18%) was seen in the moss flora of *P. sericea* forests of Venezuela. Most of the Andean species recorded in the present study are distributed throughout the cordillera and some of them may extend to Central America and Mexico or southeastern Brazil. Six species are restricted to the northern Andes (*Bazzania placophylla*, *Lejeunea mojanda*, *Leptoscyphus leoniae*, *Plagiochila cleefii*, *P. dependula*, *P. pautaphila*), with three of them (*Lejeunea mojandae*, *Leptoscyphus leoniae*, *P. pautaphila*) being (sub)endemic to *P. pauta* forests of Ecuador. Interestingly, all of them except *Lejeunea mojandae* occurred in the humid forests of Papallacta. The higher number of liverwort species with restricted, northern Andean ranges in the humid, fog-exposed *Polylepis pauta* forests of Papallacta supports the notion that cloud forests are hotspots of liverwort diversity [6,8,17], and underscores the importance of these humid forests for conservation.

Conclusions

Climatic conditions may be key to understanding diversity patterns of bryophytes in different habitats. We show that species richness, species composition and composition of functional groups of liverworts in *Polylepis* forests are affected by climatic conditions differing in humidity. Species richness of liverworts is higher in humid forests than in seasonal, dry forests and their species composition is very different in the two types of forest. Humid and dry forests also have significantly different patterns of functional diversity of liverworts. The strong coupling of liverwort diversity of *Polylepis* forests to climatic conditions suggests a high sensitivity of these organisms to climate change [52]. The greater representation of species with restricted ranges in humid *Polylepis* forest shows the importance of these forests for conservation.

Note

1. *Polylepis pauta* is here defined following Romoleroux [53] and Romoleroux et al. [26]. According to M. Kessler (pers. comm.), the populations of *P. pauta* of Mojanda and Papallacta may belong to different species.

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