doi: http://dx.doi.org/10.15446/caldasia.v37n1.50980
http://ciencias.bogota.unal.edu.co/icn/publicaciones/ Caldasia 37(1):47-59. 2015

THE EPIPHYTIC BRYOPHYTE FLORA OF THE COLOMBIAN AMAZON

Los briófitos epífitos de la región amazónica de Colombia

Laura V. Campos
Instituto de Ciencias Naturales. Universidad Nacional de Colombia. Apartado 7495, Bogotá D.C. Colombia. Correspondence author: lvcamposs@unal.edu.co

Hans ter Steege
Naturalis Biodiversity Center, Einsteinweg 2, P.O. Box 9514, 2300 RA Leiden, The Netherlands. hans.tersteege@naturalis.nl

Jaime Uribe
Instituto de Ciencias Naturales. Universidad Nacional de Colombia. Apartado 7495, Bogotá D.C. Colombia. juribem@unal.edu.co

ABSTRACT
An inventory of 384 plots on 64 trees, in four localities across the Colombian Amazon region (Amazonas, Caquetá, Putumayo, Vaupés), yielded 160 species of epiphytic bryophytes (116 of liverworts, 44 of mosses), in 64 genera and 26 families. Sampling was carried out in four non-seasonally flooded forests (*Terra Firme)*, where bryophytes where collected from the base to the outer canopy, of 16 trees per locality. The flora is characterized by dominance of liverworts, especially Lejeuneaceae. The families with the highest number of records were Lejeuneaceae (55%), Calymperaceae (10%), Lepidoziaceae (8%), Octoblepharaceae (6%) and Sematophyllaceae (5%). The most common genera in number of records were *Cheilolejeunea* (11%), *Pycnolejeunea* (8%), *Archilejeunea* (8%) *Ceratolejeunea* (8%) and *Syrrhopodon* (7%). *Syrropodon* and *Lejeunea* were the most species-rich genera, followed by *Ceratolejeunea* and *Cheilolejeunea.* In average, the localities had 102 species in sixteen phorophytes. In terms of species richness and composition there were no significant differences between the four localities.

Key words. Epiphyte, inventory, liverworts, mosses, Colombia, Amazonia.

RESUMEN
El inventario de 384 parcelas sobre 64 árboles, en cuatro localidades de la región amazónica de Colombia (Amazonas, Caquetá, Putumayo, Vaupés), produjo 160 especies de briófitos epífitos (116 hepáticas, 44 musgos), distribuidas en 64 géneros y 26 familias. El muestreo se llevó a cabo en cuatro bosques no inundables de la selva tropical (*Terra Firme*). Los briofitos epífitos fueron recolectados desde la base hasta el dosel exterior de 16 árboles, en cada una de las localidades. La flora se caracterizó por la dominancia de hepáticas, particularmente de la familia Lejeuneaceae. Las familias con mayor número de registros fueron Lejeuneaceae (55%), Calymperaceae (10%), Lepidoziaceae (8%), Octoblepharaceae (6%) y Sematophyllaceae (5%). Los géneros con mayor número de registros fueron *Cheilolejeunea* (11%), *Pycnolejeunea* (8%), *Archilejeunea* (8%) *Ceratolejeunea* (8%) y *Syrrhopodon* (7%). *Syrropodon* y *Lejeunea*

fueron los géneros más diversos, seguidos por *Ceratolejeunea* y *Cheilolejeunea*. El promedio de especies por localidad fue de 102. En términos de riqueza y composición de especies, no hubo diferencias significativas entre las cuatro localidades.

Palabras clave. Epífitos, inventario, hepáticas, musgos, Colombia, Amazonia.

INTRODUCTION

Bryophytes are important in terms of species richness and cover in many habitats, as well as for ecosystem functioning (Goffinet & Shaw, 2009). Bryophytes are the first colonizers of various different types of substrates, and in several landscapes produce a major part of the biomass. In addition, epiphytic bryophytes are an integral component of forest ecosystems and represent a significant part of the plant species diversity (Lesica *et al*., 1991). They have important ecosystem functions as they increase structural complexity, influence nutrient cycles and moisture retention, and provide habitats for plants and animals (Rhoades, 1995).

Tropical forests harbor a rich diversity of bryophytes, because of their complexity and variety of microhabitats (Gradstein, 1992). In the Colombian Amazon nearly of 221 species of bryophytes have been recorded, including 114 liverworts distributed in eleven families and 44 genera, and 107 mosses, distributed among 23 families and 49 genera (Churchill, *in press*; Gradstein & Uribe, *in press*). For the Amazon region an estimated 188 genera and 700 species of mosses and liverworts have been reported (Gradstein *et al.,* 2001). In Colombia, inventories and floristic studies on bryophytes in Colombia have principally focused on the Andean area. There are very few studies on bryophyte diversity patterns in the Colombian Amazon, only one of these (Ruiz & Aguirre, 2004) sampled the trees, and studied the vertical distribution of bryophyte diversity on different types of phorophytes in several landscapes of Tarapacá (Amazonas). Other studies in the Colombian Amazon (Benavides *et al*., 2004; Benavides *et al*., 2006) have focused on the bryophyte diversity in flooded and non-flooded forests along the Caquetá river, and two areas of the Chiribiquete and Araracuara regions.

Here we provide the most updated inventory of the epiphytic bryophyte flora along of 64 trees distributed in four localities across the Colombian Amazon. Epiphytic bryophytes were sampled on mature rainforest trees, from the base to the outer canopy. All the species were collected in the framework of the project "Diversity of epiphytic bryophytes in the Colombian Amazon".

MATERIAL AND METHODS

Study area. Fieldwork was carried out in four non-flooded forests in the Colombian Amazon. This forest is the dominant forest type in the region and covers ca. 80% of the total area of the Amazon basin (ter Steege *et al*., 2000), occupies fairly well drained and non-flooded clayey soils. The forests have an average annual rainfall of ca. 3.300 millimeters. December - January has the lowest monthly means whereas the maximum monthly means are from May to June. The average temperature in the region is 25.3°C, with a minimum level of 21°C and a maximum level of 30.2°C. June and August have the lowest minimum values while the maximum values are in December and January. Some dominant Angiosperm families in the forest are Fabaceae, Rubiaceae, Melastomataceae, Moraceae, Annonaceae, Araceae, Euphorbiaceae, Clusiaceae, Lauraceae, Arecaceae (SINCHI 2007). Canopy height of upland forest in the study sites varied from 30 to 40 m. Four study sites were selected; their location and characteristics are showed in Tab. 1

Table 1. Site location and characteristics for the four study sites, Amazonas: AM, Caquetá: CA, Putumayo: PU, and Vaupés: VA

Site	Localities	Alt.	Lat.	Long.	AT	MaxT	MinT	AP
AM	"Reserve El Zafire"	123	-3,99	-69,892	25.9	31.3	20.1	2832
CA	"La Gamitana"	134	-0,244	-72,413	26.3	32.0	20.8	2891
PU	"Puerto Colombia"	230	-0,608	-74,345	25.2	31.8	20.6	2893
VA	"Macaquiño"	190	1,275	-70,1	25.6	31.6	20.6	3384

Alt: Altitude, AT: Annual Temperature, MaxT: Max. Temperature, MinT: Min. Temperature, AP: Annual Precipitation. Data from Bioclim (Hijmans *et al.,* 2005).

Data collection. Epiphytic bryophytes were sampled on mature trees, from the base to the outer canopy. Epiphylls were not included. To climb trees a static rope technique was used as described by Perry (1978), ter Steege & Cornelissen (1988) and ter Steege (1998). The communities of bryophytes were sampled on 64 trees (16 trees in each site study), using six plots of 40 cm^2 per tree, as described by Mota de Oliveira *et al*., (2009). Thus, there were 96 plots per study site and a total of 384 for the Colombian Amazon.

Samples of all species were collected for identification in the laboratory and subsequently deposited in the Herbario Nacional Colombiano (COL) with some duplicated in the Herbario Amazonico Colombiano (COAH). Nomenclature of bryophytes was based on Gradstein & Uribe (*in press*), and Churchill (*in press*).

Data analysis. Species presence-absence matrices were prepared for all localities per tree as well as per plot. Species abundance was not measured due to the difficulty of separating the small individuals and to the variations in plant size. To quantify community structure (species accumulation curves per locality and abundance distribution for the complete dataset) we used frequency, viz. number of plots per site in which each species was present, as a surrogate for abundance. Frequency values ranged from 1 to 96, being the maximum number of plots per locality. Species richness per tree in each locality was compared using the Shannon Index and by calculating evenness (Magurran, 2004; Chao *et al*., 2005). The floristic similarity of epiphytic bryophytes in each study site was tested with the Jaccard Similarity Coefficient (Magurran, 2004).

RESULTS

Eighteen liverworts species new to Colombia were collected (Campos *et al.,* 2014): seventeen species of Lejeuneaceae and one of Lepidoziaceae. The species in Lejeuneaeaceae include *Ceratolejeunea ceratantha* (Nees & Mont.) Steph., *Ceratolejeunea confusa* R.M. Schust., *Ceratolejeunea desciscens* (Sande Lac.) Schiffn., *Ceratolejeunea laetefusca* (Austin) R.M. Schust., *Cheilolejeunea aneogyna* (Spruce) A. Evans., *Cheilolejeunea clausa* (Nees & Mont.) R.M. Schust., *Cheilolejeunea neblinensis* Ilk.-Borg. & Gradst., *Cheilolejeunea urubuensis* (Zartman & I.L.Ackerman) R.L.Zhu & Y.M.Wei, *Cololejeunea cardiocarpa* (Mont.) A. Evans., *Cololejeunea diaphana* A. Evans, *Diplasiolejeunea buckii* Grolle, *Drepanolejeunea anoplantha* (Spruce) Steph., *Leptolejeunea exocellata* (Spruce) A. Evans., *Microlejeunea aphanella* (Spruce) Steph., *Schiffneriolejeunea amazonica* Gradst., *Verdoornianthus griffinii* Gradst., *Verdoornianthus marsupifolius* (Spruce) Gradst. and *Telaranea pecten* (Spruce) J.J. Engel & G.L. Merr., in Lepidoziaceae.

The 384 plots on 64 sampled trees yielded 2827 records of bryophytes. The inventory contained 160 (morpho-)species (116

liverworts, 44 mosses), in 26 families and 64 genera; 95% of the species could be identified. The epiphytic bryophyte flora was dominated by liverworts, which included 72% of all bryophyte species. Most of them were leafy liverworts of the family Lejeuneaceae, only two thallose species were recorded, *Riccardia amazonica* (Spruce) Gradst and *Symphyogyna brasiliensis* (Nees) Nees & Mont.

The richness distributions showed a high proportion of families with few genera and species, as well as a high proportion of genera with few species. Eleven families (42%) and 32 genera (50%) were represented by one species; and twelve families (46%) were represented by one genus. Twelve families (46%) and 27 genera (42%) were represented by two to five species; and 13 families (50%) were represented by one genus (Tab. 2). The average number of species per locality was 102. Species richness was highest in the Putumayo site with 122 species (23 families, 57 genera), followed by Amazonas with 99 species (20 families, 48 genera), Vaupés with 98 species (15 families, 45 genera), and Caquetá with 92 species (16 families, 41 genera) (Tab. 3, Fig. 1).

Table 2. Distribution of species richness at family and genera level, and genera richness at family level in Colombian Amazon.

Number of species	Families		Genera		Number of genera	Families	
	#	%	#	%		#	%
1	11	42	32	50	1	12	46
2 – 5	12	46	27	42	2 – 5	13	50
6 – 10	0	0	4	6	6 – 10	0	0
10 – 15	1	4	1	2	10 – 15	0	0
>15	2	8	0	0	>15	1	4

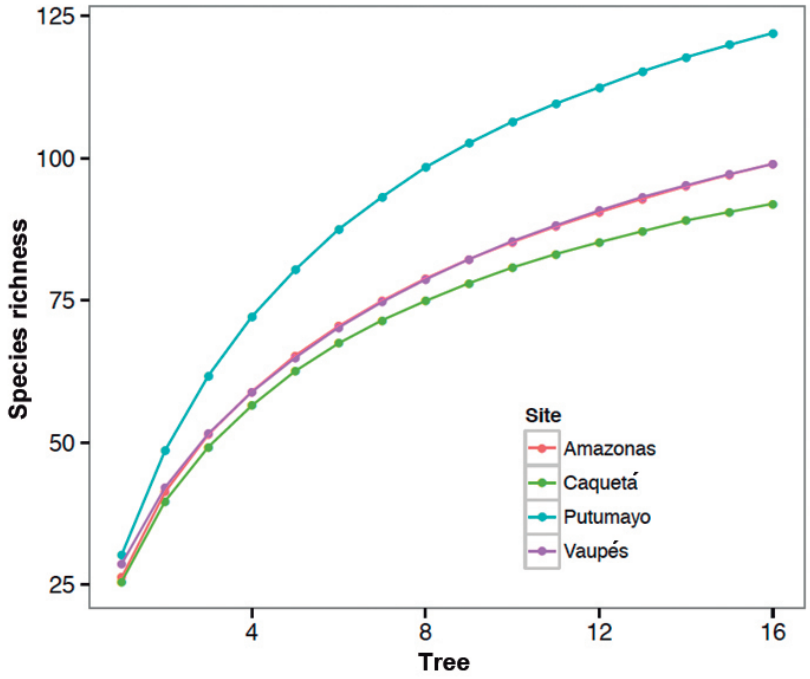

Figure 1. Species-accumulation curves for epiphytic bryophytes measured on sixteen host trees, in each site sampled.

Table 3. Species diversity by locality.

Locality	S	R	SP	SR
Amazonas	99	675	8	5
Caquetá	92	668	7	2.5
Putumayo	122	763	8	15.6
Vaupés	98	721	8	6.2
Total	160	2827	8	7.3

S (total number of species), R (total number of records), SP (average species per plot), SR (percentage of species restricted to each locality).

From 160 species identified, 51 (32%) occur in all sites, 35 (22%) in three localities, 28 (18%) in two localities and 46 (28%) were restricted to one locality (Appendix). The highest proportion of species recorded from only one locality was found in Putumayo (15.6%). The number of bryophytes species per tree varied from 18 to 42 and the average number of species per plot (40 cm^2) was eight. The mean number of species per tree was highest in the Putumayo site with 30.4±4.66, followed by Vaupes with 28.3±5.8, Amazonas 26.5±4.0 and Caquetá with 25.8±4.72 ($P<0.01$). The Shannon index was slightly higher in Putumayo ($H' = 4.2$) than in Amazonas ($H' = 4.0$), Caquetá ($H' = 3.9$) and Vaupes ($H' = 3.9$), but evenness was similar in all localities ($E = 0.5$). In terms of species richness there were no significant differences between the localities (AMOVA; $F = 2.52$; $p = 0.066$).

The percentage of floristic similarity between the four sites in the Colombian Amazon was 53%, with a coefficient correlation of 0,69. The highest floristic similarity was found between Caquetá – Vaupés and between Putumayo - Amazonas (59% and 57% each one), and Putumayo-Vaupes was the lower similarity with 49%.

Families, genera and species recorded are listed in Tab. 4 and 5, and in Appendix. The families with the highest number of records were Lejeuneaceae with 1556 (=55% of the total), followed by Calymperaceae (294, 10%), Lepidoziaceae (224, 8%), Octoblepharaceae (157, 6%) and Sematophyllaceae (138, 5%). These five families also attained the highest abundance in each locality with few exceptions, viz. Leucobryaceae in Caquetá and Cephaloziaceae in Vaupes (Tab. 6). Lejeuneaceae, Calymperaceae and Lepidoziaceae were the most species-rich families, with 85, 19 and 12 species, respectively. The most frequent genera in terms of number of records were *Cheilolejeunea* (308 records), *Pycnolejeunea* (235), *Archilejeunea* (230) *Ceratolejeunea* (214), *Syrrhopodon* (184), *Octoblepharum* (157), *Bazzania* (143), *Leucobryum* (128), *Sematophyllum* (126) and *Drepanolejeunea* (114). These ten genera accounted for the 65% of the total genera records. *Syrropodon* and *Lejeunea* were the most species-rich genera, with 14 and 10 respectively, followed by *Ceratolejeunea* and *Cheilolejeunea* with 9 species. The most frequent moss species in number of records were *Leucobryum martianum* (128 records), *Sematophyllum subsimplex* (120), *Octoblepharum albidum* (90) and *Leucophanes molleri* (89). These species included 33% of the total moss records. The most frequent liverworts were *Archilejeunea fuscescens* (162 records), *Pycnolejeunea macroloba* (119), *Pycnolejeunea contigua* (116), *Ceratolejeunea cornuta* (103), *Cheilolejeunea aneogyna* (101), *Cheilolejeunea rigidula* (71) that accounted for the 54% of the liverwort records. As shown in Fig. 2 (SAD - species abundance distribution) these nine species included the 36% of the records in the complete data set.

Lejeuneaceae had the highest species richness by far in all four localities. In each site this family included more than 50% of all bryophyte species (Amazonas and Caquetá 51%, Putumayo 54%, Vaupés 57%). The next-highest species richness was seen in Calymperaceae, Lepidoziaceae, Plagiochilaceae and Calypogeiaceae, at all four localities (Fig. 3). The Amazonas site has the largest proportion of families represented by one species (65%), followed by Putumayo (52%), Caquetá (50%) and Vaupes (40%).

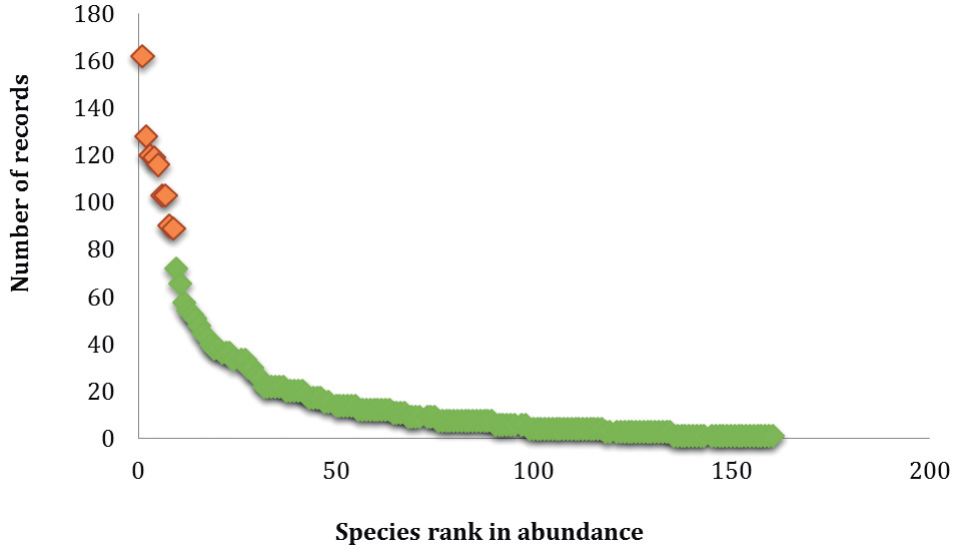

Figure 2. SAD - Species abundance distribution based on the complete dataset. (Orange points are representing the nine species that recorded the 36% of the records in the data set).

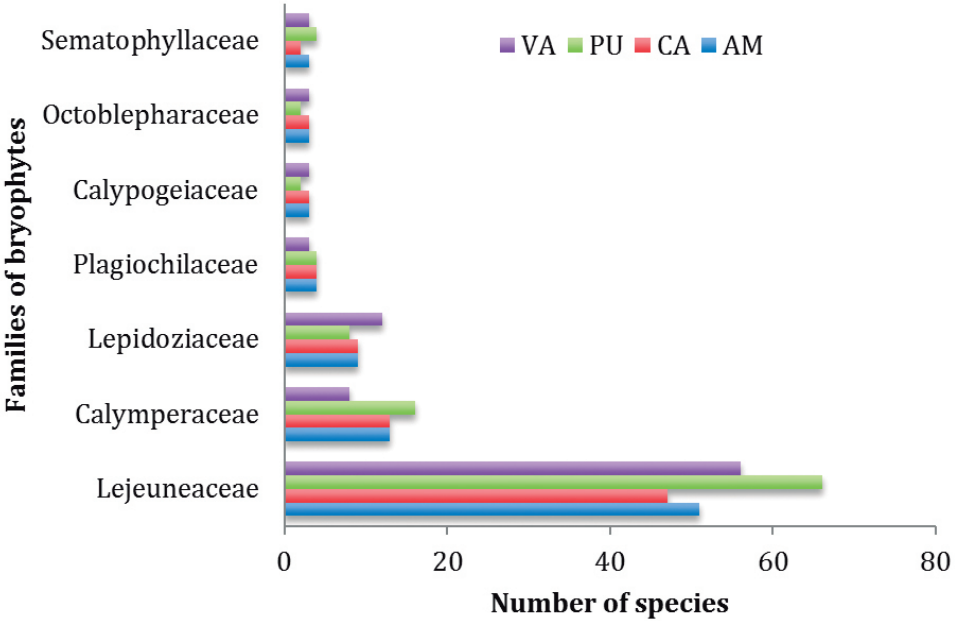

Figure 3. Summary of the species richness per family in four localities of the Colombian Amazon: Amazonas AM, Caquetá CA, Putumayo PU, and Vaupés VA

Table 4. Family richness in the four sites in the Colombian Amazon.

Families	Genera	Species
Lejeuneaceae	27	85
Calymperaceae	3	19
Lepidoziaceae	4	12
Plagiochilaceae	1	5
Sematophyllaceae	3	5
Calypogeiaceae	2	3
Frullaniaceae	1	3
Octoblepharaceae	1	3
Cephaloziaceae	1	2
Fissidentaceae	1	2
Hypnaceae	2	2
Lophocoleaceae	2	2
Macromitriaceae	2	2
Pilotrichaceae	2	2
Subtotal	52 (81,2%)	147 (92 %)
Σ families with only one genera recorded	12 (18,8%)	13 (8%)
Total	64	160

Table 5. Number of species per genus in the 4 sites of the Colombian Amazon.

Genera	Species
Syrrohopodon	14
Lejeunea	10
Ceratolejeunea	9
Cheilolejeunea	9
Drepanolejeunea	8
Plagiochila	5
Archilejeunea	4
Bazzania	4
Calymperes	4
Cololejeunea	4
Colura	4
Micropterygium	4
Prionolejeunea	4
Diplasiolejeunea	3
Frullania	3
Harpalejeunea	3
Lopholejeunea	3
Microlejeunea	3
Octoblepharum	3
Telaranea	3
Acroporium	2
Calypogeia	2
Cyclolejeunea	2
Fissidens	2
Leptolejeunea	2
Odontoschisma	2
Pycnolejeunea	2
Radula	2
Rectolejeunea	2
Sematophyllum	2
Symbiezidium	2
Verdoornianthus	2
Subtotal	128 (80 %)
Σ families with only one species recorded	32 (20%)
Total	160

Table 6. The most abundant families in the four localities and the proportional distribution of records (in percent).

Family	Amazonas	Caquetá	Putumayo	Vaupes
Lejeuneaceae	53.0	56.4	56.7	53.8
Calymperaceae	14.0	10.4	9.8	6.6
Lepidoziaceae	7.4	7.9	4.4	12.0
Octoblepharaceae	6.8	4.0	5.4	6.4
Sematophyllaceae	5.5	4.6	6.5	2.8
Leucobryaceae	5.2	4.8	3.9	4.3
Plagiochilaceae	1.8	3.0	3.3	1.6
Calypogeiaceae	1.6	1.6	0.6	2.3
Frullaniaceae	0.0	1.3	0.0	1.7
Cephaloziaceae	0.7	1.5	1.0	6.1
Stereophyllaceae	1.0	0.4	1.6	0.4
Lophocoleaceae	0.7	2.5	1.8	0.5
Other	1.6	1.2	4.7	1.2

DISCUSSION

With 160 species recorded from 64 trees sampled from the base to the canopy, this study is the first inventory of epiphytic bryophytes across the entire Colombian Amazon. Most of the species recorded are widespread in the Amazon basin and also occur in Brazil, Colombia, French Guiana, Guyana, and Ecuador (e.g., Benavides *et al*., 2004; Benavides *et al*., 2006; Churchill, 1994; Churchill, *in press*; Gradstein & Uribe, *in press*; Mota de Oliveira *et al*., 2009; Mota de Oliveira & ter Steege, 2013; Zartman & Ilkiu-Borges, 2007). Nevertheless, there is also a high number of new records for the Colombian Amazon, especially in the Lejeuneaceae (Campos *et al*., 2014). Many of these new records are from the forest canopy. Since the canopy of the Amazonian forests of Colombia had been little studied, the high number of new records found was to be expected.

Our results are consistent with the recent bryophyte inventory of the Amazon region by Mota de Oliveira & ter Steege (2013),

which focused on sites in eastern Ecuador, Brazil, French Guiana, Guyana and used the same sampling method. In that recent study 72 trees were sampled and 261 species of epiphytic bryophytes distributed in 97 genera and 29 families were identified. The average number of species per locality was 75, and the average per plot was 9 species. In both studies Lejeuneaceae, Calymperaceae, Plagiochilaceae and Sematophyllaceae were the most species-rich families. *Archilejeunea fuscescens, Ceratolejeunea cornuta*, *Cheilolejeunea rigidula, Sematophyllum subsimplex* and *Octoblepharum albidum* were the most common species. The results of this study are also in agreement with the general description of the bryophyte flora of the Amazon region by Gradstein *et al*. (2001).

The Lejeuneaceae family was clearly the most dominant in the Colombian Amazon with more than 50% of all species. Dominance of this family has also been reported in other studies on lowland rain forest areas, e.g. by Mota de Oliveira & ter Steege (2013) with 47%, Gradstein (1995) with 70%, and Gradstein (2006) with 75%. These results and our data show the importance of this family in the flora of tropical lowland forests (Schuster, 1983; Richards, 1984). It can be related with the consideration that Lejeuneaceae is the most advanced and most highly specialized family among the leafy liverworts (e.g., Heinrichs *et al*., 2007; Wilson *et al*., 2007).

There were floristic similarities between localities in the Colombian Amazon. The localities share a high percentage of species, 72% presents in more than one site (32% in all sites, 22% in three sites and 18% in two sites) and 28% of species restricted to one site. Species richness (number of species per site) was rather similar among sites, except for Putumayo where the number of species was slightly higher. This could be related to the influence of the northern Andes. Putumayo is the site with the highest elevation in the study (230 m). This condition may favor the presence of Andean species. Surprisingly, most of the species found only in Putumayo (80%) have a predominant Andean distribution (Churchill, *in press*; Gradstein & Uribe, *in press*). The northern Andes has a highly diverse vegetation and flora, due to the variation in climate and elevation (Gradstein *et al*., 2001). Mota de Oliveira & ter Steege (2013), in their study, of nine localities, also reported a higher number of species in the locality with the highest elevation, which was also adjacent to the Andes.

ACKNOWLEDGMENTS

We thank Rob Gradstein for help with the identification of some specimens. The first author would like to express her gratitude to COLCIENCIAS for sponsoring her doctoral study, to IDEA WILD for climbing equipment, to Dairon Cárdenas, Fernando Jaramillo (SINCHI), Cristina Peñuela (Reserve El Zafire) and Jorge Contreras (UNAL) for help with the logistics of field work, to Maklin Muñoz for invaluable field assistance and safe climbing of the trees and to Rob Gradstein, Juan Carlos Benavides, Mary Lou Price, Orlando Rangel and an anonymous reviewer for useful comments and improvements to the manuscript.

LITERATURE CITED

Benavides, J.C., A. Idarraga & E. Alvarez. 2004. Bryophyte diversity patterns in flooded and tierra firme forest in the Araracuara region, Colombian Amazonia. Tropical Bryology 25: 117-126.

Benavides, J.C., A.J. Duque, J.F. Duivenvoorden & A.M. Cleef. 2006. Species richness and distribution of understory bryophytes in different forest types of Colombian Amazonian. Journal of Bryology 28: 182-189.

Campos, L.V., S.R. Gradstein, J. Uribe & H. ter Steege. 2014. Additions to the Catalogue of Hepaticae of Colombia II. Cryptogamie, Bryologie 35(1): 77-92.

Chao, A., R.L. Chazdon, R.C. Colell & T.J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8: 148-159.

Churchill, S.P. 1994. The mosses of Amazonian Ecuador. AAU Rep. 35:1-211.

Churchill, S.P. in press. Bryophyta (mosses). In: R. Bernal, S.R. Gradstein and M. Celis (eds.), *Catalogue of the Plants of Colombia*. Universidad Nacional de Colombia, Bogotá.

Goffinet, B. & J. Shaw. 2009. *Bryophyte Biology*. Cambridge University Press, Oxford, 565pp.

Gradstein, S.R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: J.W. Bates & A.M. Farmer (eds.), *Bryophytes and lichens in a changing environment*, 232-256. Clarendon Press, Oxford, Great Britain.

Gradstein, S.R. 1995. Diversity of Hepaticae and Anthocerotae in montane forest of the tropical Andes. In: S.P. Churchill, H. Balslev, E. Forero & J.L. Luteyn (eds.), *Biodiversity and conservation of neotropical montane forest*, 321-334. New York Botanical Garden, New York.

Gradstein, S.R. 2006. The lowland cloud forest of French Guiana: a liverwort hotspot. Cryptogamie, Bryologie Lichénologie 27: 141-152.

Gradstein, S.R. & Uribe, J. in press. Marchantiophyta (liverworts). In: R. Bernal, S.R. Gradstein and M. Celis (eds). *Catalogue of the Plants of Colombia*. Universidad Nacional de Colombia, Bogotá D.C.

Gradstein, S.R., S.P. Churchill & N. Salazar-Allen. 2001. *Guide to the bryophytes of the tropical America*. Memoirs of the New York Botanical Garden 86: 577pp.

Heinrichs, J., J. Hentschel, R. Wilson, K. Feldberg & H. Schneider. 2007. Evolution of leafy liverworts (Jungermanniidae, Marchantiophyta): estimating divergence times from chloroplast DNA sequences using penalized likelihood with integrated fossil evidence. Taxon 56(1): 31-44.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Lesica, P., B. Mccune, S.V. Cooper & W.S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Canadian Journal of Botany 69: 1745–1755.

Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, Great Britain, 215pp.

Mota de Oliveira, S., H. ter Steege, J.H.C. Cornelissen & S.R. Gradstein. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. Journal of Biogeography 36(11): 2076-2084.

Mota de Oliveira, S. & H. ter Steege. 2013. Floristic overview of the epiphytic bryophytes of *terra firme* forests across the Amazon basin. Acta Botanica Brasilica 27: 347-363.

Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155-157.

Rhoades, F.M. 1995. Nonvascular epiphytes in forest canopies: worldwide distribution, abundance and ecological roles. In: M.D. Lowman & N.M. Nadkarni (eds.), *Forest Canopies*. 353-408. Elsevier Inc., San Diego, California, USA.

Schuster, R.M. 1983. Phytogeography of bryophyte. In: R.M. Schuster (ed.), *New Manual of bryology*. Vol. 1. Hattori Botanical Laboratory, Nichinan. 463–626.

Ruiz, C. & J. Aguirre. 2004. Distribución de la brioflora en el gradiente vertical y la selectividad de hábitats en Tarapacá (Amazonas – Colombia). Tropical Bryology 25: 81-96.

Sinchi, 2007. Balance anual sobre el estado de los ecosistemas y el ambiente de la Amazonia colombiana. Instituto Amazónico de Investigaciones Científicas, Bogotá D.C.

Ter Steege, H. 1998. Single rope techniques in tropical rain forest trees: Going down safe and sound. Biotropica 30(3): 496-497.

Ter Steege, H. & J.H.C. Cornelissen. 1988. Collecting and studying bryophytes in the canopy of standing rain forest trees. In: J.M. Glime (ed.), *Methods in Bryology*, 285-290. Proceeding of Bryological Methods Workshop, Mainz, Germany.

Ter Steege, H., D. Sabatier, H. Castellanos, T. van Andel, J.F. Duivenvoorden, A.A. De Oliveira, R. Ek, R. Lilwah, P. Maas & S.A. Mori. 2000. An analysis of the floristic composition and diversity of Amazonian forest including those of the Guiana Shield. Journal of Tropical Ecology 16: 801-828.

Wilson, R., S. R. Gradstein, H. Schneider & J. Heinrichs. 2007. Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): Evidence for four main lineages. Molecular Phylogenetics and Evolution 43: 270–282.

Zartman, C. & A.L. Ilkiu-Borges. 2007. *Guia para as Briófitas Epífilas da Amazônia Central*. Editora INPA, Manaus, Brasil, 140pp.

Recibido: 29/10/2014
Aceptado: 30/05/2015

Appendix. Species of bryophytes recorded in the four localities of the Colombian Amazon showing the distribution, Amazonas: AM, Caquetá: CA, Putumayo: PU and Vaupés: VA

Species	AM	CA	PU	VA
Archilejeunea crispistipula (Spruce) Steph.	X	X	X	X
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	X	X	X	X
Archilejeunea parviflora (Ness) Schiffn.	X	X	X	X
Bazzania aurescens Spruce	X	X	X	X
Bazzania diversicuspis Spruce	X	X	X	X
Bazzania hookeri (Lindenb.) Trevis.	X	X	X	X
Calypogeia laxa Gottsche & Lindenb.	X	X	X	X
Calypogeia tenax (Spruce) Steph.	X	X	X	X
Ceratolejeunea cornuta (Lindenb.) Schiffn.	X	X	X	X
Ceratolejeunea cubensis (Mont.) Schiffn.	X	X	X	X
Cheilolejeunea aneogyna (Spruce) A. Evans	X	X	X	X
Cheilolejeunea neblinenesis Ilk.-Borg. & Gradst.	X	X	X	X
Cheilolejeunea rigidula (Mont.) R.M. Schust.	X	X	X	X
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	X	X	X	X
C. urubuensis (Zartman & Ackerman) R.L.Zhu & Y.M.Wei	X	X	X	X
Cololejeunea cardiocarpa (Mont.) A. Evans	X	X	X	X
Cololejeunea contractiloba A. Evans	X	X	X	X
Colura greig - smithii Jovet-Ast	X	X	X	X
Colura sagittistipula (Spruce) Grolle	X	X	X	X
Cyclolejeunea luteola (Spruce) Grolle	X	X	X	X
Drepanolejeunea anoplantha (Spruce) Steph.	X	X	X	X
Fissidens steerei Grout	X	X	X	X
Harpalejeunea oxyphylla (Nees & Mont.) Steph.	X	X	X	X
Lejeunea boryana Mont.	X	X	X	X
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	X	X	X	X
Leptoscyphus porphyrius (Nees) Grolle	X	X	X	X
Leucobryum martianum (Hornsch.) Müll. Hal.	X	X	X	X
Leucophanes molleri Müll. Hal.	X	X	X	X

Species	AM	CA	PU	VA
Metalejeunea cucullata (Reinw. et al.) Grolle	X	X	X	X
Microlejeunea bullata (Tayl.) Steph.	X	X	X	X
Micropterygium leiophyllum Spruce	X	X	X	X
Micropterygium parvistipulum Spruce	X	X	X	X
Monodactylopsis monodactyla (Spruce) R.M. Schust.	X	X	X	X
Octoblepharum albidum Hedw.	X	X	X	X
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.	X	X	X	X
Odontoschisma variabile (Lindenb. & Gottsche) Trev.	X	X	X	X
Pilosium chlorophyllum (Hornsch.) Broth.	X	X	X	X
Plagiochila montagnei Ness	X	X	X	X
Plagiochila simplex (Sw.) Lindenb.	X	X	X	X
Pycnolejeunea contigua (Ness) Grolle.	X	X	X	X
Pycnolejeunea macroloba (Ness & Mont.) Schiffn.	X	X	X	X
Rectolejeunea emarginuliflora (Gottsche) A. Evans	X	X	X	X
Sematophyllum subsimplex (Hedw.) Mitt.	X	X	X	X
*Syrrhopo*don cryptocarpus Dozy & Molk.	X	X	X	X
Syrrhopodon fimbriatus Mitt.	X	X	X	X
Syrrhopodon leprieurii Mont.	X	X	X	X
Syrrhopodon simmondsii Steere	X	X	X	X
Verdoornianthus griffinii Gradst.	X	X	X	X
Verdoornianthus marsupiifolius (Spruce) Gradst.	X	X	X	X
Xylolejeunea crenata (Nees & Mont.) X.L. He & Grolle	X	X	X	X
	AM	**CA**	**PU**	
Calymperes erosum Müll. Hal.	X	X	X	
Calymperes othmeri Herzog	X	X	X	
Cheilolejeunea holostipa (Spruce) Grolle & R.-L. Zhu	X	X	X	
Cheilolejeunea oncophylla (Ångstr.) Grolle & M.E. Reiner	X	X	X	
Drepanolejeunea bidens (Steph.) A. Evans	X	X	X	
Hyophila involuta A. Jaeger	X	X	X	
Lejeunea flava (Sw.) Ness	X	X	X	
Lejeunea species 01	X	X	X	
Plagiochila species 02	X	X	X	
Prionolejeunea denticulata (Weber) Schiffn.	X	X	X	
Sematophyllum subpinnatum (Brid.) E. Britton	X	X	X	
Syrrhopodon hornschuchii Mart.	X	X	X	
Syrrhopodon incompletus Schwägr.	X	X	X	
Syrrhopodon ligulatus Mont.	X	X	X	
	AM	**CA**		**VA**
Lejeunea phyllobola Nees & Mont.	X	X		X
Micropterygium trachyphyllum Reimers	X	X		X
Mnioloma parallelogramum (Spruce) R.M. Schust.	X	X		X
Octoblepharum stramineum Mitt.	X	X		X
	AM		**PU**	**VA**
Drepanolejeunea araucariae Steph.	X		X	X
Lopholejeunea eulopha (Tayl.) Schiffn.	X		X	X
Lopholejeunea subfusca (Nees) Schiffn.	X		X	X
Symbiezidium dentatum Herzog	X		X	X
Syrrhopodon flexifolius Mitt.	X		X	X
Telaranea diacantha (Mont.) J.J. Engel & Merrill	X		X	X
Thysananthus amazonicus (Spruce) Schiffn.	X		X	X
		CA	**PU**	**VA**
Anoplolejeunea conferta (Meissn.) A. Evans		X	X	X
Ceratolejeunea confusa R.M. Schust.		X	X	X
Ceratolejeunea desciscens (Sande Lac.) Steph.		X	X	X
Ceratolejeunea guianensis (Ness & Mont.) Steph.		X	X	X

		CA	PU	VA
Colura tenuicornis (A. Evans) Steph.		X	X	X
Drepanolejeunea lichenicola (Spruce) Steph.		X	X	X
Lepidolejeunea involuta (Gottsche) Grolle		X	X	X
Micropterygium pterygophyllum (Nees) Trevis.		X	X	X
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.		X	X	X
Symphyogyna brasiliensis (Nees) Nees & Mont.		X	X	X
Syrrhopodon xanthophyllus Mitt.		X	X	X
	AM	**CA**		
Ceratolejeunea coarina (Gottsche) Steph.	X	X		
Syrrhopodon rigidus Hook. & Grev.	X	X		
	AM		**PU**	
Ceratolejeunea laetefusca (Austin) R.M. Schust.	X		X	
Ceratolejeunea species 01	X		X	
Cheilolejeunea clausa (Nees & Mont.) R.M. Schust.	X		X	
Groutiella obtusa (Mitt.) Florsch.	X		X	
Microlejeunea epiphylla Bischl.	X		X	
Mniomalia viridis (Mitt.) Müll. Hal.	X		X	
Neckeropsis undulata (Hedw.) Reichardt	X		X	
Rhacopilopsis trinitensis (Müll. Hal.) E. Britton & Dixon	X		X	
Symbiezidium *barbiflorum* (Lindenb. & Gottsche) A. Evans	X		X	
Syrrhopodon lanceolatus (Hampe) W.D. Reese	X		X	
	AM			**VA**
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	X			X
Acroporium guianense (Mitt.) Broth.	X			X
Bazzania cuneistipula (Gottsche & Lindenb.) Trevis.	X			X
Ceratolejeunea ceratantha (Nees & Mont.) Steph.	X			X
Drepanolejeunea species 01	X			X
		CA	**PU**	
Diplasiolejeunea brunnea Steph.		X	X	
		CA		**VA**
Diplasiolejeunea buckii Grolle		X		X
Drepanolejeunea palmifolia (Nees) Steph.		X		X
Frullania caulisequa (Nees) Nees		X		X
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.		X		X
Riccardia amazonica (Spruce) Gradst.		X		X
Telaranea pecten (Spruce) J.J Engel & G.L. Merr.		X		X
			PU	**VA**
Diplasiolejeunea cavifolia Steph.			X	X
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.			X	X
Lejeunea laetevirens Nees & Mont.			X	X
Schiffneriolejeunea amazonica Gradst.			X	X
Trichosteleum papillosum (Hornsch.) A. Jaeger			X	X
	AM			
Amblystegium species 01	X			
Callicostella pallida (Hornsch.) Ångstr.	X			
Cheilolejeunea adnata (Kunze) Grolle	X			
Harpalejeunea tridens (Besch. & Spruce) Steph.	X			
Pictolejeunea picta (Gottsche ex Steph.) Grolle	X			
Plagiochila species 01	X			
Radula mammosa Spruce	X			
		CA		
Calymperes rubiginosum (Mitt.) W.D. Reese		X		
Drepanolejeunea orthophylla (Nees & Mont.) Bischl.		X		
Frullania apiculata (Reinw. et al.) Nees		X		
Lejeunea species 03		X		

	PU	
Acroporium pungens (Hedw.) Broth.	X	
Calymperes lonchophyllum Schwägr.	X	
Cololejeunea gracilis (Jovet-Ast) Pócs & Bernecker	X	
Cryphaea species 01	X	
Fissidens prionodes Mont.	X	
Frullanoides liebmanniana (Lindenb. & Gottsche) van Slag	X	
Holomitrium arboreum Mitt.	X	
Lejeunea adpressa Nees	X	
Lejeunea caespitosa Lindenb.	X	
Lejeunea reflexistipula (Lehm. & Lindenb.) Gottsche	X	
Lejeunea species 02	X	
Leptolejeunea exocellata (Spruce) A. Evans	X	
Lophocolea bidentata (L.) Dumort	X	
Lopholejeunea nigricans (Lindenb.) Schiffn.	X	
Pelekium schistocalix (Müll. Hal.) Touw	X	
Pilotrichum bippinatum (Schwägr.) Brid.	X	
Prionolejeunea aemula (Gottsche) A. Evans	X	
Prionolejeunea mucronata (Sande Lac.) Steph.	X	
Prionolejeunea scaberula (Spruce) Steph.	X	
Radula javanica Gottsche	X	
Schlotheimia torquata (Hedw.) Brid.	X	
Syrrhopodon parasiticus Paris	X	
Syrrhopodon prolifer Schwägr.	X	
Vesicularia vesicularis (Schwägr.) Broth.	X	
		VA
Archilejeunea ludoviciana (Lehm.) Geissler & Gradst.		X
Cololejeunea diaphana A. Evans		X
Colura cylindrica Herzog		X
Cyclolejeunea peruviana (Lehm. & Lindenb.) A. Evans		X
Drepanolejeunea crucianella (Tayl.) A. Evans		X
Microlejeunea aphanella (Spruce) Steph.		X
Odontoschisma portoricensis (Hampe & Gottsche) Steph.		X
Rectolejeunea berteroana (Gottsche ex Steph.) A. Evans		X
Syrrhopodon africanus (Mitt.) Paris		X
Telaranea nematodes (Gottsche ex Austin) M.A Howe		X