

# DIVERSITY AND HABITAT DIFFERENTIATION OF MOSESSES AND LIVERWORTS IN THE CLOUD FOREST OF MONTEVERDE, COSTA RICA

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## ABSTRACT

An inventory of the understory and canopy of 4 ha of lower montane cloud forest at Monteverde, Costa Rica, yielded 190 bryophyte species: 133 hepatics, 56 mosses and 1 hornwort. Thick branches of the lower canopy were by far the richest habitat in terms of number of species (99), trunks from 1 m upwards had 65 species, lianas, shrubs, saplings, or living leaves in the understory had about 36-46 species each, and 16 species were found on rotten logs. The figures are illustrative of the great diversification of microhabitats of bryophytes in a tropical montane cloud forest. About 36% of the species, including more than half of the corticolous ones, occurred exclusively in the canopy. It appeared that the percentage of bryophyte species restricted to the canopy may be the same in lowland and montane rain forests, in spite of the great differences in species abundance and composition in the two kinds of forest.

**Key words.** Bryophytes, Cloud forest, Biodiversity, Costa Rica.

## RESUMEN

Ciento noventa especies de briofitas (133 hepáticas, 56 musgos, 1 antocerote) fueron encontradas en un inventario hecho en 4 hectáreas del sotobosque y el dosel en el bosque nublado (1500 m) de Monteverde, Costa Rica. Las ramas gruesas del dosel fueron la porción más rica en termino de numero de especies (99), en troncos había 65 especies, lianas, arbustos, árboles juveniles o hojas vivas en el sotobosque tenían entre 36-46 especies cada una, y 16 especies fueron encontradas en troncos en descomposición. Las cifras ilustran la gran diversidad de microhabitats de briofitas en el bosque nublado. Cerca de 36% de las especies, incluyendo mas de la mitad de los corticolos, se presentaron exclusivamente en el dosel. Parece que el porcentaje de especies de briofitas restringidas al dosel podría ser el mismo en bosques de tierras bajas y en bosques nublados, a pesar de la gran diferencia en abundancia y composición taxonómica de las briofitas en las dos clases de bosque.

**Palabras clave.** Briofitas, Bosque nublado, Biodiversidad, Costa Rica.

## INTRODUCTION

Tropical rain forests, including montane cloud forests, harbour a large diversity of bryophytes, probably due to the great variety of microhabitats in these forests. Of an estimated 4000 species (2650 mosses, 1350 hepatics) occurring in tropical America, about 80% of the hepatics and 50 % of the mosses are confined to these forests (Gradstein et al., in press). Most of the bryophytes in tropical rain forest are epiphytes and their abundance varies considerably with elevation. In lowland rain forests, below 500 m, bryophyte cover is poor and mostly restricted to the canopy. In montane rain forests, especially in the very moist cloud forests, growth of epiphytic bryophytes is usually much more luxuriant. Moreover, the forest floor may be covered with dense bryophyte carpets. The lower temperatures and higher light levels in the cloud forest and the availability of plentiful water due to impact of fog favour the accumulation of dead organic material on the ground and the abundant growth of the epiphytic and terrestrial bryophytes (Richards, 1984; Gradstein & Pócs, 1989).

Our understanding of bryophyte diversity of tropical rain forests is still fragmentary. Complete inventories are very scarce. Most studies only deal with part of the flora, leaving "difficult" groups such as the tiny *Lejeuneaceae* (Hepaticae) unidentified. Moreover, attention is usually restricted to the lower part of the forest, whilst the higher portions of the trunks and the canopy branches are neglected due to their inaccessibility (Wolf, 1993). Cornelissen and Gradstein (1990) found that in lowland rain forest of Guyana about 50 % of the bryophyte species occurred only in the tree crowns and on the upper portions of the trunks, over 10 m above ground level. In contrast, only 14 % of the species were exclusive to the understory. The number of species restricted to the canopy in cloud forests is still unknown. Another important finding of recent work is that species density

of epiphytic bryophytes in rain forests is high and minimum areas for sampling therefore relatively small. Complete sampling of 4-5 trees (from base to outer canopy) may yield over 75% of the flora of a homogeneous forest stand (Cornelissen & ter Steege, 1989; Wolf, 1993; Gradstein et al., 1996). Costa Rica's Monteverde Cloud Forest Reserve is one the best studied montane moist forests worldwide. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (Nadkarni & Wheelwright, 1999) incorporates contributions of 140 authors and over 1800 references. Vascular epiphytes have been studied in detail by Nadkarni and associates (e.g., Nadkarni, 1986; Nadkarni & Matelson, 1992; Ingram & Nadkarni, 1993). In contrast, very little work has been done on the bryophytes of Monteverde. Reed & Robinson (1971) published a first list of 164 species (90 mosses, 73 hepatics, 1 hornwort) based on random collecting in the forests and in pasture areas. Additional species were reported by Gradstein et al. (1994) and Sillet et al. (1995). The latter authors analysed the epiphytic bryophyte flora in the canopy of six *Ficus tuerckheimii* trees, three in the dense primary forest and three isolated ones in adjacent pasture land, and could demonstrate that the two sets of trees had very different species assemblages.

This paper deals with the bryophyte diversity in the cloud forest of Monteverde. The main purpose of this study was to describe the composition and habitat differentiation of the flora and to determine floristic differences between the canopy and understory of the forest.

## MATERIAL AND METHODS

We conducted an inventory of bryophytes within a 4 ha study site, consisting of four plots of one hectare each, in Monteverde Cloud Forest Reserve during November 1992 and January 1994. The Monteverde Cloud

Forest Reserve is situated in northcentral Costa Rica (10°18'N, 84°48'W) along the crest of the continental divide in the Cordillera de Tilarán. The forest is subject to cloud-bearing trade winds that move across the Cordillera from the northeast. The trade winds occur throughout the year, but most frequently deliver mist between November and May. Total annual rainfall is 2000-2500 mm, most of which falls during May to October, but fog and mist may contribute an additional 500-2000 mm of annual precipitation (Ingram & Nadkarni, 1993).

The 4 ha study site is in the lower montane rain forest (1550 m elevation) about 1 km southwest of the headquarters of the reserve, on the leeward, Pacific side of the Cordillera. The primary forest is 20-30 m high with a few emergents to 35 m tall. *Ocotea tonduzii* (Lauraceae), *Ficus tuerckheimii* (Moraceae) and *Meliosma ideapoda* (Sabiaceae) are the principal canopy tree species, making up ca. 40% of total basal area of trees.

About 350 collections of bryophytes were gathered randomly in the four hectare plots. An average of 2-3 trees per plot were climbed and samples were taken from branches of the lower canopy. Sampling of the outer canopy was done from recently fallen trees. In general, canopy sampling was less detailed than the inventory of the understory, however. The collections were deposited in FLAS, U and USJ.

## RESULTS AND DISCUSSION

### 1. *Distribution of species in the cloud forest.*

Bryophytes were abundant on treelets, shrubs, lianas and rather exposed trunks in the forest understory and, particularly, on thick branches of the inner forest canopy. On trunks in deep shade, bryophyte cover was usually rather scanty. Hepatics were more abundant than mosses, both in terms of biomass and in number of species.

*Understory.* The bryophyte flora of the forest understory was very different from that

of the canopy. The most frequent bryophytes on trunks, shrubs, lianas etc. in the understory were *Plagiochila* spp., *Porotrichum korthalsianum* and *Radula antillana*. Other common taxa included *Metzgeria leptoneura*, *Lepidopilum muelleri*, *Omphalanthus filiformis*, *Taxilejeunea pterigonia* and *Trichocolea tomentosa*. In well-lit sites the pendent mosses *Phyllogonium fulgens* and various *Meteroriaceae* were frequently seen together with the robust hepatics *Porella swartziana*, *Bryopteris filicina*, *Radula gottscheana* and *Plagiochila* spp.

On trunk bases *Cephalozia crassifolia*, *Fissidens* spp., *Hookeriopsis falcata*, *Hypopterygium tamariscinum*, *Lophocolea connata*, *Telaranea nematodes* and various unidentified species of *Lejeunea* were quite common. Other taxa characteristic of this habitat included *Calypogeia* spp., *Pallavicinia lyellii*, *Cyrtohypnum schistocalyx* (= *Thuidium schistocalyx*), *Leskeodon andicola*, *Octoblepharum erectifolium* and *Syrrhopodon* spp. Species of *Bazzania* occurred here and there on trunk bases but were much more common in the forest canopy.

The forest floor had much rotten wood (logs, fallen branches) and this was also an important habitat for bryophytes, e.g., the thalloid hepatics *Monoclea gottschei* and *Riccardia* spp. and the mosses *Hookeriopsis falcata*, *Mittenothamnium reptans*, *Plagiomnium rhynchophorum* and *Pyrrhobryum spiniforme*. The single hornwort encountered in the study site, *Megaceros vincentianus*, was also a species of rotten logs. The majority of the species of rotten logs also occurred on the trunk bases, especially on rotten, humose ones.

*Canopy.* The lower, ± horizontal branches of the canopy were thickly covered by bryophyte mats. Species of *Bazzania*, *Lepidozia*, *Macromitrium*, *Plagiochila*, *Herbertus* and *Frullania convoluta* were the most prominent elements. *Macromitrium* and *Herbertus* were restricted to the canopy but

species of *Bazzania* and *Lepidozia* also occurred lower down in the understory. Plants of *Frullania convoluta* fallen from the canopy sometimes continued growth on branches in the understory.

Other bryophytes characteristic of thick canopy branches and lacking in the understory included the hepatic genera *Frullania*, *Adelanthus* and *Ceratolejeunea* (the latter sometimes forming extensive dark mats), furthermore *Kurzia capillaris*, *Leptoscyphus porphyrius*, *Syzygiella pectiniformis*, *Tylimanthus laxus*, and the mosses *Acroporium pungens*, *Bryum capillare*, *Campylopus arctocarpus*, *Leucobryum giganteum*, *Leucoloma cruegerianum*, *Pilotrichella flexilis*, *Squamidium nigricans*, and *Syrrhopodon lycopodiodes*. Light-green mats of *Papillaria imponderosa* and the pendent *Phyllogoniums* and *Omphalanthus filiformis* were common both in the canopy and in the understory, behaving as ecological "generalists".

Fine twigs of the outer canopy harboured a rich ramicolous bryophyte community characterized by *Daltonia gracilis* and many small species of *Lejeuneaceae*. Some of these also grew on living leaves. Foliicolous bryophytes, most of them *Lejeuneaceae*, were abundant especially in the forest understory.

The most common ones included *Odontolejeunea lunulata* and species of *Cyclolejeunea* (*C. convexistipa*, *C. peruviana*), *Drepanolejeunea* and *Aphanolejeunea*.

**2. Species richness.** Our inventory yielded 190 bryophyte species (Table 1): 133 hepatics, 56 mosses, and 1 hornwort (*Megaceros vincentianus*). The average number per hectare was 88 species, with highest number in plot 2 (118) and lowest number in plot 4 (74). In comparison, a very detailed analysis of the canopy by Sillet et al (1995) found 109 bryophyte species on three *Ficus tuerckheimii* trees in the Monteverde cloud forest. This suggests that our canopy species list is still incomplete.

Species-area curves showed that one plot yielded 45 % of total diversity, and two plots yielded 75% (Fig. 1). In comparison, when bryophyte diversity on trees only is studied (excluding shrubs, logs etc.), the 75% level is usually obtained by analysis of just four trees (Wolf, 1993).

The absolute dominance of hepatics over mosses at the study site in terms of species number is characteristic of these neotropical moist forests. In palaeotropical forest, mosses tend to be more abundant (Gradstein & Pócs, 1989). *Plagiochila* was by far the most

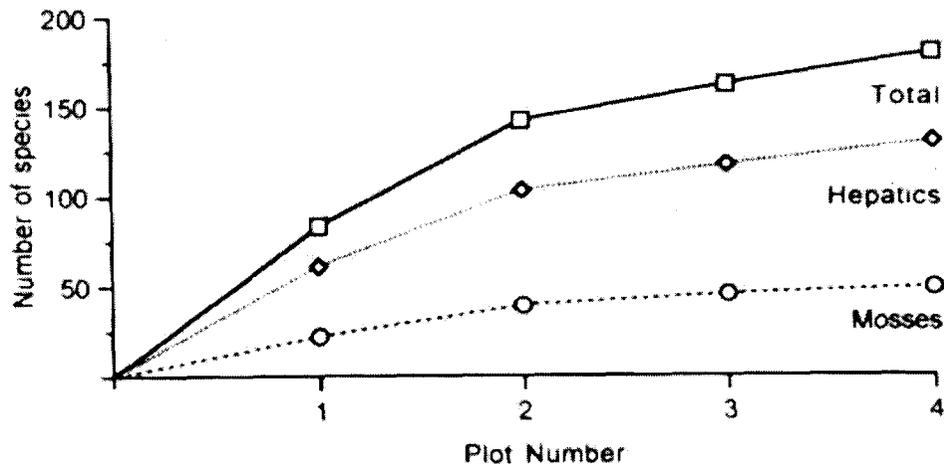


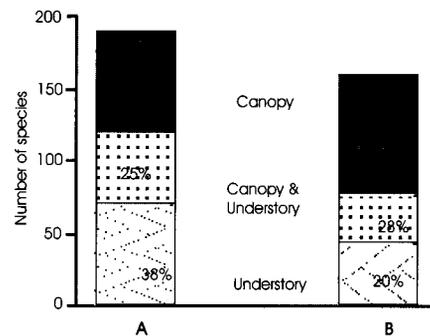
Fig. 1. Species-plot relationships.

speciose genus (18 spp.), followed by the hepatic genera *Lejeunea* and *Bazzania* (7 spp. each), and *Frullania* and *Radula* (6 spp.). Among the mosses, *Lepidopilum* and *Macromitrium* (4 spp.) were the most speciose genera, the former mainly in the understory, the latter very abundant in the canopy.

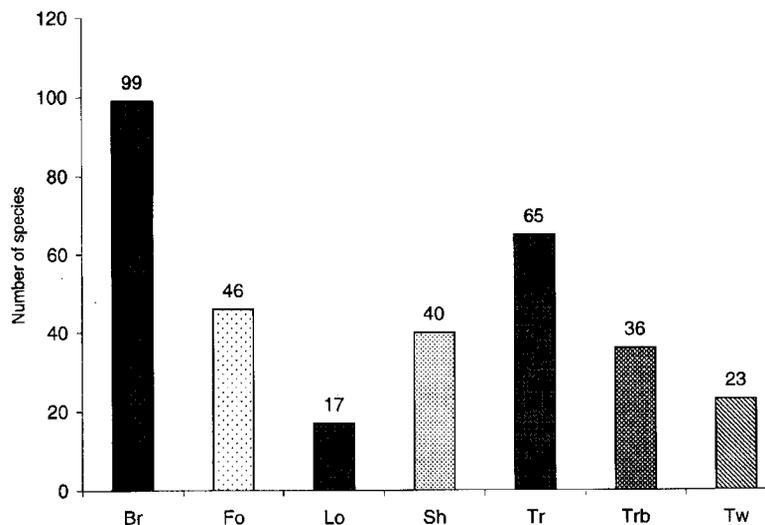
**3. Habitat diversification.** The distribution of the species of the species over the various microhabitats is shown in Fig. 2. Thick branches of the lower canopy were by far the richest habitat for bryophytes and yielded about 100 species. Trunks (from 1 m upwards) had 65 species, living leaves 46 species and trunk bases 36 species. Fourty species were found on lianas, poles and small branches on shrubs, sapling etc. in the forest understory. The lowest number of species (17) was found on rotten logs; however, half of these were exclusive to rotten logs and not found elsewhere. A similar percentage was obtained for epiphylls: about half of the foliicolous species (23) were only found on living leaves, others occurred also on other substrates. The

figures are illustrative of the great diversification of microhabitats of bryophytes in a tropical montane forest.

Species richness in the canopy compared to the understory was 117 vs. 121. Of these, 48 (25%) occurred both in the canopy and the understory, 38% were exclusive to the understory, and 36% to the canopy (Fig. 3A).



**Fig. 3.** Comparison of bryophyte species richness in understory and canopy. A. Total species diversity. B. Corticolous species diversity (species of rotten logs and epiphylls excluded).



**Fig. 2.** Distribution of bryophyte species over different microhabitats. For abbreviations see Table 1.

**Table 1.** Bryophyte species collected in the 4 ha study site (hectare plots 1-4) in the Monteverde Cloud Forest Reserve.

	PLOT	CANOPY	UNDERSTORY		PLOT	CANOPY	UNDERSTORY
<b>HEPATICAE</b>				<i>Aphanolejeunea exigua</i>	2, 4		Fo
<b>Acrobolbaceae</b>				Evans			
<i>Tylimanthus laxus</i> Spruce	1, 2, 4	Br	-	<i>A. gracilis</i> Jov.-Ast	1, 2, 3, 4		Fo
<b>Adelanthaceae</b>				<i>A. subdiaphana</i> var.	1, 2, 3, 4		Fo
<i>Adelanthus carabayensis</i> (Mont.) Grolle	1	Br	-	<i>crutulata</i> (Schust.) Pöcs	4		
<i>A. decipiens</i> (Hook.) Mitt.	2	Br	-	<i>Brachiolejeunea laxifolia</i> (Tayl.) Schiffn.	2	Tw	-
<i>A. pittieri</i> (Steph.) Grolle	4	Br	-	<i>Bryopteris filicina</i> (Sw.) Nees	1, 2, 4	Br	Sh, Tr
<b>Aneuraceae</b>				<i>Ceratolejeunea cornuta</i> (Lindenb.) Steph.	2	Br	-
<i>Riccardia fuceoides</i> (Sw.) Schiffn.	4	Br	Lo	<i>C. maritima</i> (Spruce) Steph.	1, 2, 4	Br	Fo
<i>R. sp.</i>	1, 2, 3, 4	Br	Lo	<i>C. sp.</i>	1, 2	Br	-
<b>Calypogeiaceae</b>				<i>Cheilojeunea rigidula</i> (Mont.) Schust.	1, 2	Br	-
<i>Calypogeia crenulata</i> Bischler	1	-	Trb	<i>Cololejeunea cf. standleyi</i> Herz.	1, 2, 3, 4		Fo
<i>C. peruviana</i> (Nees & Mont.) Steph.	3	-	Trb	<i>Colura ulei</i> Jov.-Ast	2	Tw	-
<i>C. rhombifolia</i> (Spruce) Steph.	3	-	Trb	<i>Cyclolejeunea accedens</i> (Gott.) Evans	2, 3, 4	-	Fo
<i>C. rhynchophylla</i> (Herz.) Bischler	2	-	Trb	<i>C. convexistipa</i> (Lehm. & Lindenb.) Evans	1, 2, 3, 4	Fo	Fo
<b>Cephaloziaceae</b>				<i>C. luteola</i> (Spruce) Grolle	4		Fo
<i>Cephalozia crassifolia</i> (Lindenb. & Gott.) Fulf.	1, 2, 3, 4	Br	Lo, Sh, Trb	<i>C. peruviana</i> (Lehm. & Lindenb.) Evans	1, 2, 3, 4	Fo, Tw	Fo
<i>Odontoschisma longiflorum</i> (Tayl.) Steph.	4	Br	-	<i>Dicranolejeunea axillaris</i> (Nees & Mont.) Schiffn.	2	Tw	-
<b>Geocalyceae</b>				<i>Diplasiolejeunea alata</i> Jov.-Ast	2	Tw	-
<i>Leptoscyphus porphyrius</i> (Nees) Grolle	2	Br	-	<i>D. brunnea</i> Steph.	3		Fo
<i>Lophocolea connata</i> (Sw.) Nees	1, 2, 3, 4	-	Lo, Trb	<i>D. cavifolia</i> Steph.	2, 3	Tw	Fo
<i>L. muricata</i> (Lehm.) Nees	2, 3, 4	-	Fo, Sh, Tr, Trb	<i>D. johnsonii</i> Evans	1, 4	Br	Fo
<i>L. trapezoidea</i> Mont.	2	Br	-	<i>D. montecristensis</i> Winkler	3		Fo
<b>Herbertaceae</b>				<i>D. pellucida</i> (Meissn. ex Spreng.) Schiffn.	1, 2, 3, 4	Tw	Fo
<i>Herbertus divergens</i> Steph.	1	Br	-	<i>Drepanolejeunea campanulata</i> (Spruce) Steph.	1		Fo
<i>H. juniperoides</i> (Sw.) Grolle	?	Br	-	<i>D. inchoata</i> (Meissn.) Evans	1, 2, 3	Br, Tw	Fo
<i>H. pensilis</i> Tayl.	1, 2, 4	Br	-	<i>D. lichenicola</i> (Spruce) Steph.	2	Tw	-
<b>Jubulaceae</b>				<i>Echinocolea dilatata</i> (Evans) Schust.	3, 4		Fo
<i>Frullania arecae</i> (Spreng.) Gott.	2	Br	-	<i>Harpalejeunea aspera</i> Grolle	3		Fo
<i>F. brasiliensis</i> Raddi	2, 4	Br	-	<i>H. oxyphylla</i> (Nees & Mont.) Steph.	4		Fo
<i>F. convoluta</i> Lindenb. & Hampe	1, 2, 3, 4	Br	Sh (fallen from canopy?)	<i>Lejeunea cephalandra</i> Spruce	2	Br	
<i>F. exilis</i> Tayl.	1, 2, 4	Br, Tw	-	<i>L. controversa</i> Gott.	1, 2, 4		Lo, Sh, Tr, Trb
<i>F. laxiflora</i> Spruce	2	Br	-	<i>L. aff. filipes</i> Spruce	1, 2	Tw	-
<i>F. riojaneirensis</i> (Raddi) Aongstr.	2	Br	-	<i>L. flava</i> (Sw.) Nees	1, 2	Br	Tr
<i>Jubula bogotensis</i> Gott.	3	-	Tr	<i>L. phyllobola</i> Nees & Mont.	2	Tw	-
<b>Jungermanniaceae</b>							
<i>Syzygiella pectiniformis</i> Spruce (det. Vána)	2	Br	-				
<b>Lejeuneaceae</b>							
<i>Anoplolejeunea conferta</i> (Meissn.) Schiffn.	?	Br	-				

**Conventions**

Br = thick, ± horizontal branches of the inner forest canopy

Fo = living leaves (foliicolous)

Lo = rotten logs

Sh = lianas, poles and small branches (of shrubs, treelets and saplings) in the forest understory

Tr = tree trunks (from 1 m upwards)

Trb = bases of tree trunks (0-1 m) and roots

Tw = twigs of the outer forest canopy

Cont. Table 1

	PLOT	CANOPY	UNDERSTORY		PLOT	CANOPY	UNDERSTORY
L. (subgen. Otigoniolejeunea) sp.	2, 3	-	Sh, Trb	Telaranea nematodes (Gott. ex Aust.) Howe	1, 2, 3, 4	-	Lo, Trb
L. sp. A	2, 3	-	Sh	<b>Metzgeriaceae</b>			
L. sp. B	1, 3	-	Tr, Trb	Metzgeria albinea Spruce	2	Br	-
Lepidolejeunea involuta (Gott.) Grolle	1, 2	Br	Fo, Tr	Metzgeria decipiens (Mass.) Schiffn.	1, 2, 3	-	Fo, Sh, Tr
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	2, 3		Fo	M. leptoneura Spruce	2, 3, 4	-	Sh
L. serratifolia Schiffn.	1, 2		Fo	M. liebmanniana Lindenb. & Gott.	2	Tw	-
Macrolejeunea lancifolia (Steph.) Herz.	1, 2, 3, 4	-	Fo, Sh	<b>Monocleaceae</b>			
Marchesinia robusta (Mitt.) Schiffn.	4	Br	-	Monoclea gottschei Lindb.	1, 2, 3, 4	-	Lo, Trb
Microlejeunea acutifolia Steph.	3		Fo	<b>Pallaviciniaceae</b>			
M. bullata (Tayl.) Evans	1, 2, 3	Tw	Fo	Pallavicinia lyellii Hook.	1, 2	Br	Trb
M. stricta (Gott. et al.) Steph.	1, 4		Fo	Symphogyna brogniartii Mont.	4	-	Lo
Neurolejeunea breutelii (Gott.) Evans	2	Br	-	<b>Plagiochilaceae</b>			
Odontolejeunea decedentata (Spruce) Steph.	2, 3		Fo	Plagiochila adiantoides (Sw.) Lindenb.	2, 3, 4	Br	Sh
O. lunulata (Web.) Schiffn.	1, 2, 3, 4	Fo, Tw	Fo	P. aerea Tayl.	1, 2, 4	Br	-
Omphalanthus filiformis (Sw.) Nees	1, 2, 3, 4	Br, Tw	Fo, Sh	P. breuteliana Lindenb.	1, 2, 3, 4	-	Trb
O. grandistipulus Steph.	2, 4	Br	-	P. crispabilis Lindenb.	3	-	Sh
O. ovalis (Lindenb. & Gott.) Gradst.	1, 2, 4	Br	Fo, Sh	P. cristata (Sw.) Lindenb.	1, 4	Br	-
Prionolejeunea schlimiana (Gott.) Steph. (det. Grolle)	1, 3	-	Fo, Sh	P. diversifolia Lindenb. & Gott.	2, 3	-	Sh, Tr
P. sp.	1, 2	-	Fo, Sh	P. gymnocalycina (Lehm. & Lindenb.) Mont.	2	Br	Sh
Rectolejeunea berteroaana (Gott.) Evans	2, 3, 4	Tw	Fo	P. laxa Lehm. & Lindenb.	1, 2, 3	Br	Sh, Tr, Trb
Stictolejeunea squamata (Willd. ex Web.) Schiffn.	1, 2		Fo	P. martiana Nees	2	-	Sh
Symbiezidium transversale (Sw.) Trevis. var. hookerianum (Gott. et al.) Gradst. & van Beek	3	Br	-	P. miqueliana Lehm. & Lindenb.	2, 4	Br	-
Taxilejeunea sulphurea (Lehm. & Lindenb.) Schiffn.	3	-	Fo, Sh	P. raddiana Lindenb. (= P. guilleminiana Nees & Mont.)	4	Br	Tr
T. pterigonia (Lehm. & Lindenb.) Schiffn.	2, 3, 4	Br	Sh	P. rudischusteri Robins.	4	-	Sh
T. sp.	4	-	Lo	P. stolonifera Lindenb. & Gott.	2	Br	-
<b>Lepidoziaceae</b>				P. stricta Lindenb.	1, 2	Br	Trb
Bazzania affinis (Lindenb. & Gott.) Trevis.	1, 2, 3, 4	Br	Tr, Trb	P. subplana Lindenb.	1, 2	Br	-
B. breuteliana (Lindenb. & Gott.) Trevis.	2	Br	Trb	P. tenuis Lindenb.	2, 3, 4	Tw	Tw, Sh (rare)
B. denticulata (Lindenb. & Gott.) Trevis.	4	Br	-	P. sp. A	1, 2	Br	-
B. gracilis (Hampe & Gott.) Steph.	1, 4	Br	Trb	P. sp. B	1, 2	Br	-
B. hookeri (Lindenb.) Trevis.	2, 3, 4	Br	Trb (rare)	<b>Porellaceae</b>			
B. longa (Nees) Trevis.	1	Br, Tr	Tr	Porella swartziana (Web.) Trevis.	1, 2, 3	Br	Sh, Tr
B. stolonifera (Sw.) Trevis.	?	Br	-	<b>Radulaceae</b>			
Kurzia capillaris (Sw.) Grolle	1	Br	Fo	Radula antilleana Castle	1, 2, 3, 4	Br, Tr	Sh, Tr
Lepidozia armata Steph.	4	Br	-	R. frondescens Steph.	1, 2, 3, 4	Br, Tr	Sh, Tr
L. cupressina (Sw.) Lindenb.	1, 2	Br, Tr	TRb	R. gottscheana Tayl.	1, 2, 4	Tr	Sh, Tr
L. squarrosa Steph.	4	Br	-	R. javanica Gott. (= R. macrostachya Lindenb. & Gott.)	1	-	Tr
				R. stenocalyx Mont.	3	-	Fo
				R. tenera Mitt. ex Steph.	2	Br	-
				<b>Scapaniaceae</b>			
				Scapania portoricensis Gott.	4	Br (rare)	-
				<b>Trichocoleaceae</b>			
				Trichocolea flaccida (Spruce) Jack & Steph.	3		Fo
				Trichocolea tomentosa (Sw.) Gott.	1, 2, 3, 4	Br	Sh, Tr

Cont. Table 1

	PLOT	CANOPY	UNDERSTORY		PLOT	CANOPY	UNDERSTORY
<b>ANTHOCEROTAE</b>				<b>Leucobryaceae</b>			
<b>Anthocerotaceae</b>				<b>Leucobryum crispum</b> C.M.			
<i>Megaceros vincentianus</i> (Lehm. & Lindenb.) Steph.	4	-	Lo	3	-	Trb	
<b>MUSCI</b>				<b>L. giganteum</b> C.M.			
<b>Bartramiaceae</b>				1, 2	Br	-	
<i>Leiomelea bartramioides</i> (Hook.) Par.	4	-	Tr	<b>Octoblepharum erectifolium</b> Mitt.			
<b>Brachytheciaceae</b>				4	-	Trb	
<i>Rhynchostegium serrulatum</i> (Hedw.) Jaeg.	2	Br	-	<b>Meteoriaceae</b>			
<b>Bryaceae</b>				<b>Meteorium remotifolium</b> (C.M.) Manuel			
<i>Bryum capillare</i> Hedw.	2	Br	-	2, 3	Br	Sh	
<i>Orthodontium pellucens</i> (Hook.) B.S.G.	1	Br, Tr	-	<b>Papillaria imponderosa</b> (Tayl.) Broth.			
<b>Calymperaceae</b>				2, 3	Br, Tw	Sh, Tr	
<i>Syrhropodon incompletus</i> Schwaegr. var. <i>berteroanus</i> (Brid.) Reese	1, 2, 3, 4	Br (rare)	Trb	<b>Pilotrichella flexilis</b> (Hedw.) Aongstr.			
<i>S. lycopodioides</i> (Brid.) C.M.	4	Br	-	2	Br, Tw	-	
<i>S. prolifer</i> Schwaegr. var. <i>tenuifolius</i> (Sull.) Reese	4	-	Trb	<b>P. pentasticha</b> (Brid.) Wijk & Marg.			
<b>Dicranaceae</b>				3	-	Tr	
<i>Campylopus arctocarpus</i> (Hornsch.) Mitt.	1	Br	-	<b>Squamidium nigricans</b> (Hook.) Broth.			
<i>Holomitrium arboreum</i> Mitt.	?	Br	-	2	Br	-	
<i>Leucoloma cruegerianum</i> (C.M.) Jaeg.	1, 2, 3	Br, Tw	-	<b>Mniaceae</b>			
<i>L. serrulatum</i> Brid.	1	-	Sh	<b>Plagiomnium</b>			
<b>Fissidentaceae</b>				2, 3	-	Lo	
<i>Fissidens elegans</i> Brid.	3	-	Trb	<b>rhynchophorum</b> (Hook.) T. Kop.			
<i>F. minutus</i> Thwaites	1	-	Trb	<b>Neckeraceae</b>			
<i>F. steerei</i> Grout	1	-	Trb	<b>Isodrepanium lentulum</b> (Wils.) Britt.			
<b>Hookeriaceae s.l.</b>				1	-	Trb	
<i>Callicostella pallida</i> (Hornsch.) Aongstr.	1, 2	-	Lo	<b>Neckeropsis disticha</b> (Hedw.) Reichenardt			
<i>Crossomitrium patrisiae</i> (Brid.) C. M.	2, 3	-	Fo	<b>Porotrichum korthalsianum</b> (Dozy & Molk.) Mitt.			
<i>Daltonia gracilis</i> Mitt.	1	Tw	-	1, 2, 3, 4	-	Sh, Tr, Trb	
<i>Hookeriopsis falcata</i> (Hook.) Jaeg.	1, 2, 3, 4	-	Lo, Trb	<b>P. longirostre</b> (Hook.) Mitt.			
<i>Hypnella cymbifolia</i> (Hampe) Jaeg.	1, 2, 3, 4	-	Trb	2, 3	-	Sh	
<i>H. diversifolia</i> (Mitt.) Jaeg.	2	Br	-	<b>Porotrichum mutabile</b> ?			
<i>Lepidopilum falcatum</i> C.M.	3	-	Sh	?	Br	-	
<i>L. muelleri</i> (Hampe) Mitt.	1, 2, 3, 4	-	Fo, Sh	<b>Hampe</b>			
<i>L. scabrisetum</i> (Schwaegr.) Steere	?	Br	-	<b>Orthotrichaceae</b>			
<i>Leskeodon andicola</i> (Mitt.) Broth.	1, 3	-	Trb	<b>Macromitrium cirrosum</b> (Hedw.) Brid.			
<i>L. cnbensis</i> (Mitt.) Thér.	3	-	Fo	2	Br	-	
<i>Rhynchostegiopsis flexuosa</i> (Sull.) C.M.	2	-	Lo	<b>M. mamillosum</b> Bartr. ?			
<b>Hypnaceae</b>				<b>M. cf. parvirete</b> Bartr. ?			
<i>Ectropothecium leptochaeton</i> (Schwaegr.) Buck	2	Br	-	1, 2	Br	-	
<i>Mittenothamnium reptans</i> (Hedw.) Card.	1, 4	Br	Lo	<b>M. cf. tonduzii</b> Ren. & Card.			
<b>Hypopterygiaceae</b>				<b>Phyllogoniaceae</b>			
<i>Hypopterygium tamariscinum</i> (Hedw.) Brid.	2, 3	-	Trb	<b>Phyllogonium fulgens</b> (Hedw.) Brid.			

## Conventions

Br = thick, ± horizontal branches of the inner forest canopy

Fo = living leaves (foliicolous)

Lo = rotten logs

Sh = lianas, poles and small branches (of shrubs, treelets and saplings) in the forest understory

Tr = tree trunks (from 1 m upwards)

Trb = bases of tree trunks (0-1 m) and roots

Tw = twigs of the outer forest canopy

In a lowland rain forest of Guyana, Cornelissen and Gradstein (1990) found that about 50% of the bryophyte species were restricted to the canopy and 14% to the understory. The latter figures, however, were restricted to corticolous species and did not include species of rotten logs and living leaves. When calculations for the Monteverde study site are restricted to corticolous taxa, 52% of the species are exclusive to the canopy and 20% to the forest understory (Fig. 3B). It thus appears that the percentage of species restricted to the canopy may be the same in lowland and montane rain forests, in spite of the great differences in species abundance and composition in the two kinds of forest (see also Gradstein, 1995).

4. **Floristics.** At least 19 species appeared to be previously unreported from Costa Rica (Gradstein *et al.*, 1994): the hepatics *Adelanthus carabayensis*, *Bazzania affinis*, *Calypogeia crenulata*, *C. rhombifolia*, *Colura ulei*, *Cyclolejeunea accedens*, *Frullania exilis*, *F. laxiflora*, *Kurzia capillaris*, *Lophocolea connata*, *Marchesinia robusta*, *Metzgeria albinea*, *M. decipiens*, *Plagiochila rudischusteri*, *Prionolejeunea schlimiana*, *Radula antillana*, *R. frondescens*, *R. tenera*, and *Syzygiella pectiniformis*. Three of these, *Bazzania affinis*, *Lophocolea connata* and *Radula antillana*, were surprisingly common in the forest. Among the mosses and hornworts, none were new to the country.

The list includes several rare bryophyte species, known otherwise from only very few localities. *Plagiochila rudischusteri* is known from a few localities in northern Venezuela, Panama and Pacific Colombia, *Syzygiella pectiniformis* is a rare northern Andean species, and *Calypogeia rhynchophylla* is endemic to Costa Rican cloud forests with three known localities on the mainland and occurring also on Cocos Island, where it is very common (Dauphin, 1999). The rare endemic *Nowellia reedii* Robins., described from Monteverde (exact locality unknown) and not

recorded anywhere else, was not found during this study.

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