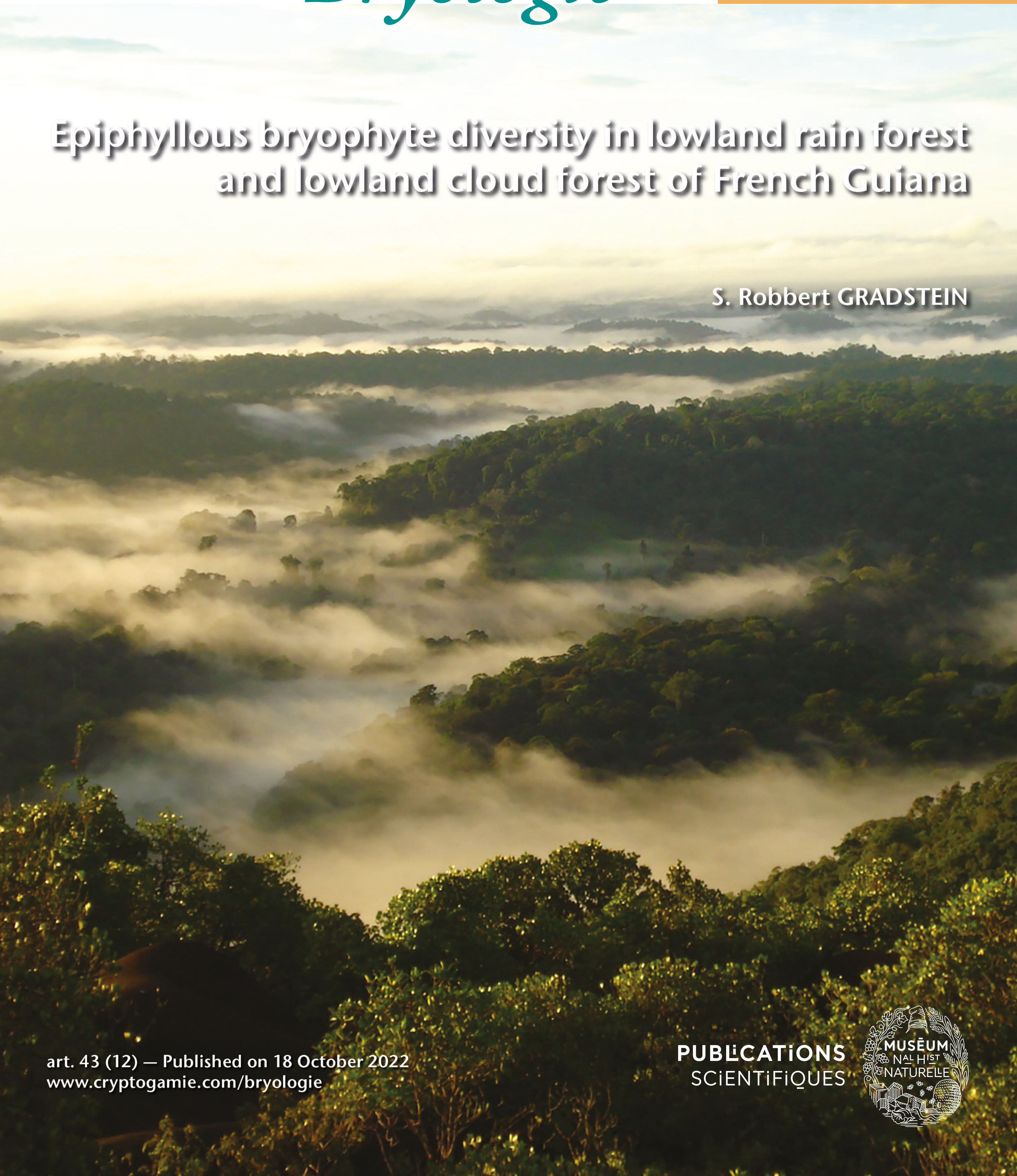
cryptogamie
Bryologie
2022 • 43 • 12



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art. 43 (12) — Published on 18 October 2022
www.cryptogamie.com/bryologie

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Couverture / *Cover*:
Photographie de LCF et LRF prise par Christine Gehrig en 2009 / Photograph of LCF and LRF taken by Christine Gehrig in 2009

Cryptogamie, Bryologie est indexé dans / Cryptogamie, Bryologie *is indexed in:*
- Biological Abstracts
- Current Contents
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal).

Cryptogamie, Bryologie est distribué en version électronique par / Cryptogamie, Bryologie *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Cryptogamie, Bryologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Bryologie *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia, Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae, Comptes Rendus Palevol,*** **Cryptogamie sous-sections *Algologie, Mycologie.***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*): 1290-0796 / ISSN (électronique / *electronic*): 1776-0992

Epiphyllous bryophyte diversity in lowland rain forest and lowland cloud forest of French Guiana

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Submitted on 7 February 2022 | Accepted on 8 June 2022 | Published on 18 October 2022

Gradstein S. R. 2022. — Epiphyllous bryophyte diversity in lowland rain forest and lowland cloud forest of French Guiana. *Cryptogamie, Bryologie* 43 (12): 187-193. https://doi.org/10.5252/cryptogamie-bryologie2022v43a12. http://cryptogamie.com/bryologie/43/12

ABSTRACT
Tropical lowland cloud forests (LCF) are only reported from French Guiana but may be widespread in the tropics. They are botanically distinguished from lowland rain forest (LRF) based on the diversity and composition of epiphyte communities in the forest canopy. To facilitate the detection of LCF, reliable ground-level indicators are needed. A first comparison of epiphyllous bryophyte diversity in the understory of LRF and LCF of French Guiana revealed a five times higher species richness in LCF. Species abundancy was also much higher in LCF. Sampling efficiency was about 80% in each forest type. Six species (11%) were found in both forest types, 43 species (80%) were found only in LCF and five species (9%) only in LRF. Species exclusive to LCF were not unique to cloud forest at a larger scale, however. Lejeuneaceae Rostovzev contributed 100% to epiphyll diversity in LRF and 70% in LCF. The lower representation of Lejeuneaceae in LCF agrees with the notion that epiphyte species diversity in LCF is similar to that of montane forests. Epiphyllous bryophyte diversity, more than species composition, may be a suitable tool for recognition of lowland cloud forest at ground level, without application of tree climbing.

KEY WORDS
Epiphyllous community, epiphylls, liverworts, Lejeuneaceae, species diversity, species richness, lowland rain forest, lowland cloud forest.

RÉSUMÉ
Diversité des bryophytes épiphylles dans une forêt pluviale de plaine et une forêt nuageuse de plaine de Guyane française.
La forêt tropicale nuageuse de plaine (LCF) est seulement connue en Guyane française mais pourrait être plus répandue dans les tropiques. Elle se distingue botaniquement de la forêt pluviale de plaine (LRF) par la diversité et la composition des groupements d'épiphytes présents dans la canopée. Pour faciliter la détection de la LCF, des indicateurs fiables au niveau du sol sont nécessaires. Une première comparaison de la diversité des bryophytes épiphylles dans le sous-bois de la LRF et de la LCF de Guyane française a révélé une richesse en espèces cinq fois plus élevée dans la LCF. L'abondance des espèces était également beaucoup plus élevée dans la LCF. L'efficacité de l'échantillonnage était d'environ 80 % dans chaque type de forêt. Six espèces (11 %) ont été trouvées dans les deux types de forêt, 43 espèces (80 %) ont été trouvées uniquement dans la LCF et cinq espèces (9 %) uniquement dans la LRF. Les espèces exclusives à la LCF n'étaient cependant pas uniques à la forêt nuageuse à une plus grande échelle. Les Lejeuneaceae Rostovzev ont contribué à 100 % de la diversité épiphylle dans la LRF et à 70 % dans la LCF. La plus faible représentation des Lejeuneaceae dans la LCF concorde avec le fait que la diversité des espèces épiphytes dans la LCF est similaire à celle des forêts montagnardes. La diversité des bryophytes épiphylles, plus que la composition des espèces, peut être un outil approprié pour la reconnaissance de la forêt nuageuse de plaine au niveau du sol, sans implication de l'escalade des arbres.

MOTS CLÉS
Communauté épiphylle, épiphylles, hépatiques, Lejeuneaceae, diversité des espèces, richesse des espèces, forêt pluvieuse de plaine, forêt nuageuse de plaine.

INTRODUCTION

Epiphyllous bryophytes are delicate organisms growing on the surfaces of living leaves (synonym: phyllospere) and commonly occur in moist tropical forests (e.g. Pócs 1978, 1982; Richards 1984; Zartman & Ilkiu-Borges 2007; Glime & Pócs 2018). They are the main contributors to biomass in the phyllosphere of tropical rain forests and play important ecological roles in the forest ecosystem, ranging from nitrogen fixation (Bentley 1987), nutrient cycling (Coxson 1990) to fitness of the host plant (Mueller & Wolf-Mueller 1991). Epiphyllous bryophytes are sensitive indicators of humidity and air pollution (Pócs 1996). They are most abundant and speciose in undisturbed humid forests under conditions of constantly high atmospheric humidity (Sonnleitner *et al.* 2009). Pronounced daily fluctuations in air humidity result in a decrease of epiphyllous bryophyte diversity. Because of their preference for constantly high humidity, epiphyllous bryophytes are more diverse in the forest understory than in the canopy and are highly vulnerable to forest alteration (Pócs 1996; Zartman 2003; Pereira-Alvarenga & Pôrto 2007; Malombe *et al.* 2016).

Most epiphyllous bryophytes are liverworts and members of the family Lejeuneaceae Rostovzev. In wet lowland rain forests of Costa Rica and Colombia, Lejeuneaceae accounted for more than 85% of epiphyllous bryophyte diversity (Lücking 1997; Zartman & Ilkiu-Borges 2007; Sonnleitner *et al.* 2009; Benavides & Sastre-de Jesús 2011). Slightly lower figures are found in montane forests; in a Costa Rican montane cloud forest Lejeuneaceae contributed 75% to epiphyllous bryophyte diversity (Gradstein *et al.* 2001) and in African montane cloud forests 73% (Malombe *et al.* 2016). The lower percentage in montane forests reflect the decreased diversity of Lejeuneaceae towards higher elevation and the increase of members of other families in the phyllosphere of the montane forest (Pócs 1978; Gradstein 1995).

Although hundreds of bryophyte species have been recorded from the phyllosphere, few grow exclusively on leaf surfaces; many epiphyllous bryophyte species may occur also on bark. Based on their habitat preference, a distinction is made between "typical epiphylls" and "facultative epiphylls" (Gradstein 1997). Typical epiphylls occur mostly, or exclusively, on living leaves, rarely on other substrates. Characteristic is their flat, appressed growth and the possession of adhesive rhizoid discs, allowing the plants to firmly adhere to the substrate (Winkler 1967). In addition, typical epiphylls are characterized by shortened life-cycles via asexual reproduction or heterochrony. Facultative epiphylls (also called "accidental epiphylls"), in contrast, occur commonly on other substrates as well, such as bark, rotten wood or rock. These plants may grow flat or upright, lack adhesive rhizoid discs and may not have shortened life cycles. Species occurring exclusively on living leaves are also called "obligate epiphylls" (Richards 1984), but obligate epiphylly is difficult to prove and requires numerous habitat observations from the whole range of the species.

This paper deals with the diversity of epiphyllous bryophytes in two types of evergreen lowland forest, tropical lowland rain forest (LRF) and tropical lowland cloud forest (LCF). Tropical cloud forests stand out by their high diversity of epiphytic plants, including bryophytes, and are usually found in montane environments, above 500 m elevation (Bruijnzeel *et al.* 2010). The high richness of epiphytes in cloud forests is due to the frequent cloud immersion, as these plants maintain no direct connection to ground water and are highly dependent on atmospheric water (Hamilton 1995). Because of their predominance in mountain areas, tropical cloud forests are usually described as "montane cloud forests" (Bruijnzeel *et al.* 2010). However, recent evidence is emerging that tropical cloud forests may also be found in lowland areas, well below 500 m (Gradstein *et al.* 2010; Gehrig-Downie *et al.* 2013). Meteorological observations in humid lowland areas of French Guiana showed almost daily occurrence of morning fog in deep valleys and a clear diurnal course of fog frequency (Obregon *et al.* 2011). In contrast, fog events were largely absent on hill sites. Fog development in the valleys was apparently triggered by nocturnal cold air drainage flow from the hills bordering the valleys, causing saturation of air humidity during night and early morning in situations of low air turbulence. The frequent occurrence of fog correlated with significantly higher epiphyte diversities in the valley forest (LCF) as compared to the hill forest (LRF), and supported the occurrence of the hitherto undescribed tropical lowland cloud forest. LCF had significantly greater epiphytic biomass than LRF, and higher species richness of filmy ferns, bryophytes and cyanolichens (Normann *et al.* 2010; Gehrig-Downie *et al.* 2011, 2012, 2013; Obregon *et al.* 2011).

Whereas LRFs occur widely throughout the humid Tropics (Whitmore 1990), LCF has thus far only been described from French Guiana. A recent study on fog distribution in neotropical lowlands, however, indicated that LCF may be widely distributed in tropical America (Pohl *et al.* 2021). The reason why this forest type has not previously been noticed may lie in the lack of biodiversity studies in the forest canopy where the differences between rain and cloud forest are most apparent. To facilitate the detection of LCF, development of reliable ground-level indicators are needed.

The aim of the present investigation was to compare the species diversity and composition of epiphyllous bryophytes in the understory of LRF an LCF. This is the first study comparing epiphyllous diversity in cloud forest and rain forest. Because of their preference for high humidity, we expected to find higher diversity of epiphyllous bryophytes in LCF.

MATERIAL AND METHODS

Study area

Field work was conducted in Nouragues Natural Reserve (4°2'30"N, 52°40'30"W), French Guiana, *c.* 100 km inland from the Atlantic coast. Annual rainfall is *c.* 3000 mm, with a dry season from late July to November. Average temperature is 27°C with little annual variation (Grimaldi & Riéra 2001). LCF occurs in deep valleys and LRF on slopes and ridges (Obregon *et al.* 2011; Gehrig-Downie *et al.* 2012, 2013).

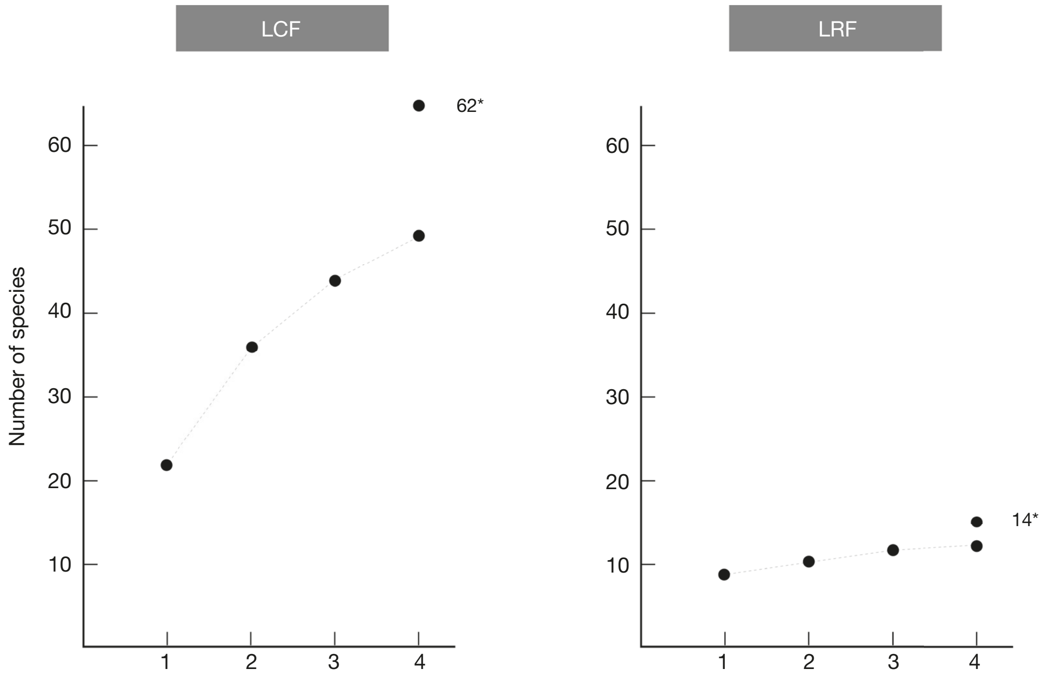

Fig. 1. — Species accumulation curves and estimated total number of species (*) of epiphyllous bryophytes in the understory of lowland cloud forest (**LCF**) and lowland rain forest (**LRF**) at Nouragues, French Guiana.

Sampling

The sampling approach followed Lücking & Lücking (1996). Epiphyllous bryophytes were collected at ground level in eight plots of 5 × 5 m, four in LRF and four in LCF. The plots were laid out well apart from each other in about one hectare of each forest type. LCF plots were located in a deep valley at about 100 m elevation and LRF plots on an adjacent slope at about 220 m. The distance between the LCF and LRF plot areas was about 250 m. In each plot about forty evergreen dicot leaves and ten palm leaves were randomly collected at 0.5-2 m height and transported to the laboratory for identification of epiphylls. The surface area of palm leaves varied between 50-400 cm^2, that of dicot leaves between 30-200 cm^2. Dicot leaves included smooth and hairy leaves. Total leaf surface sampled per plot was about 50 dm^2 and well exceeded the 100 cm^2 recommended for epiphyllous diversity inventories (Lücking & Lücking 1996).

Species identification was done using Gradstein & Ilkiu-Borges (2009). Vouchers were deposited in the bryophyte herbarium of the Muséum national d'Histoire naturelle, Paris (PC).

Species accumulation curves were prepared and the estimated total number of epiphyllous bryophyte species in each forest type was calculated using the Chao2 estimator (Magurran 2013). Frequency of epiphyllous species in each plot was estimated as follows:

1) abundant (+++): occurring on more than ten leaves and usually in large amount, often dominating over other species;

2) frequent (++): occurring on about five to ten leaves and usually with several to many plants per leaf, but never dominating over other species;

3) scarce (+): occurring on less than five leaves and usually with only one or two plants per leaf, rarely in larger amount.

RESULTS AND DISCUSSION

In total 54 species of epiphyllous bryophytes were collected, including 49 in LCF (102 plot records) and 11 in LRF (24 plot records) (Tables 1; 2). Species accumulation curves indicated that sampling efficiency was about 80% in each forest type; the estimated total number of species was 62 in LCF and 14 in LRF (Fig. 1). Average number of species per plot was 25 in LCF (ranging from 21-32) and six in LRF (ranging from 3-9). The number of species per leaf varied from 0-10. Epiphylls were scarcer in LRF than in LCF and many leaves in LRF were without epiphylls. Palm leaves in LCF were particularly rich in epiphylls, being often completely covered by epiphyllous bryophytes and harbouring up to ten different species on a single leaf.

Six species (11%) were found in both forest types, 43 species (80%) were found only in LCF and five species (9%) were found only in LRF (Tables 1; 2). The most common species exclusive to LCF, occurring in more than half of the LCF plots and often in frequent or abundant amount, were *Ceratolejeunea coarina* (Gottsche) Schiffn., *Crossomitrium patrisiae* (Brid.) Müll.Hal., *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans, *C. peruviana* (Lehm. & Lindenb.) A.Evans, *Lejeunea adpressa* Nees, *Odontolejeunea lunulata* (F.Weber) Schiffn. and *O. rhomalea* (Spruce) Steph. All are common and widespread epiphylls in tropical America and are characteristic of habitats with high humidity (e.g. Lücking 1997; Gradstein & Ilkiu-Borges 2009; Sonnleitner *et al.* 2009; Benavides & Sastre-de Jesús 2011; Florschütz-de Waard 2011; Gradstein 2021). Their commonness in LCF was therefore to be expected. None of the species found in

Table 1. — Diversity of epiphyllous bryophytes in four plots in the understory of a lowland cloud forest (**LCF**) and a lowland rain forest (**LRF**) at Nouragues, French Guiana.

	LCF	LRF
Total number of species (number of plot records of species)	49 (102)	11 (24)
Average number of species per plot	25	6
Exclusive species	43	5
Number of abundant species records	9 (9%)	–
Number of frequent species records	25 (25%)	6 (25%)
Number of rare species records	66 (66%)	18 (75%)
Percentage of species of Lejeuneaceae Rostovzev	70%	100%
Typically epiphyllous species	14 (30%)	5 (50%)

LCF are restricted to cloud forest at a larger scale, however (Churchill & Linares 1995; Gradstein 2021).

Exclusive species of LRF included *Cololejeunea cremersii* Tixier, *Drepanolejeunea mosenii* (Steph.) Bischl., *Lejeunea laetevirens* Nees & Mont., *Microlejeunea epiphylla* Bischl. and *Rectolejeunea versifolia* (Schiffn.) L.Söderstr. & A.Hagborg. *Cololejeunea cremersii* is a rare species known from a few localities in French Guiana, Suriname, Costa Rica and Guadeloupe (Pócs *et al.* 2014). The other species are common neotropical taxa and two of them, *L. laetevirens* and *R. versifolia*, are highly drought-tolerant species characteristic of open locations (Gradstein *et al.* 2001; Gradstein 2021). Their presence in LRF correlated with the dryer conditions in this forest type as compared with LCF. The lack of abundant species in LRF (Table 2) also reflects the drier conditions here (Richards 1984; Sonnleitner *et al.* 2009).

Liverworts included 47 species (87%) and mosses seven species (13%). Mosses were found only in LCF and one of them, *Crossomitrium patrisiae*, was a frequent species (Table 2). This is a widespread species of tropical America and a typical epiphyll, growing mainly on leaf surfaces, occasionally on twigs (Florschütz-de Waard 1996). As expected, liverworts of the family Lejeuneaceae were the dominant group; in LRF all epiphyllous species were Lejeuneaceae and in LCF 70% of the species were members of this family (Tables 1; 2). The high contribution of Lejeuneaceae to epiphyllous diversity in LRF agrees with previous studies (e.g. Lücking 1997; Sonnleitner *et al.* 2009; Benavides & Sastre-de Jesús 2011; Mežaka *et al.* 2020). The reduced representation of Lejeuneaceae in LCF is similar to that in humid montane forests (e.g. Gradstein 1995; Malombe *et al.* 2016) and this supports the observations of Gehrig-Downie *et al.* (2011, 2013) who found that lowland cloud forests are similar to montane forests in terms of epiphyte species diversity.

About 30% of the epiphyllous bryophyte species in LCF were typical epiphylls and the remaining species (70%) were facultative epiphylls. In LRF typical epiphylls were more prominent and accounted for half of the species. The higher percentage of facultative epiphylls in LCF may be explained by the moister and more favourable conditions in LCF for bryophyte growth, allowing for non-specialist species to establish in the hazardous phyllosphere.

The results of this study support the hypothesis that epiphyllous diversity is higher in lowland cloud forest than in lowland rain forest. Total species richness of epiphyllous bryophytes was 4.5 times higher in LCF than in LRF at forest level, and four times higher at plot level. Species abundancy was also significantly higher in LCF; the number of plot records was four times higher in LCF and abundant epiphyllous species only occurred in LCF. The results may be compared with those of Sonnleitner *et al.* (2009), who compared epiphyllous bryophyte diversity in three lowland rain forest habitats in Costa Rica differing in relative humidity: ravine forest with rather constantly high humidity, slope forest with minor daily fluctuations in relative air humidity, and ridge forest with major fluctuations in air humidity. The humidity fluctuations in slope and ridge forest were explained by the occurrence of local air flows; formation of fog, however, was not mentioned. Of 60 epiphyllous species recorded, almost all occurred in the ravine forest, and species richness in the ravine forest was about 1.7× higher than in the slope forest and almost five times higher than in the ridge forest. *Odontolejeunea lunulata* was abundant in the ravine forest and *Diplasiolejeunea pellucida* (Spreng.) Schiffn. was most common in the ridge forest.

The differences between ravine and ridge forest at the Costa Rican study site in terms of epiphyll richness are strikingly similar to those between cloud forest and rain forest at Nouragues. This shows the importance of air humidity as driver of epiphyll diversity. The abundance of *O. lunulata* in ravine forest and the preference of *D. pellucida* for the drier ridge forest also agree with the observations in this study. The total number of species and the representation of Lejeuneaceae (90%) were higher in the Costa Rican site than at Nouragues, however. The greater species richness at the Costa Rican site may be explained by the very high annual precipitation at this site, which was almost twice higher than at Nouragues. The higher representation of Lejeuneaceae might be due to the somewhat lower elevation of the Costa Rican study site; in addition, it could reflect the absence of fog at this site.

The botanical distinction of lowland cloud forest and lowland rain forest is based on differences in epiphytic diversity in the forest canopy (Gehrig-Downie *et al.* 2011, 2012, 2013). Analysis of this diversity is usually not possible from ground level and requires tree climbing for access of the canopy. An exception are functional epiphyte groups, which may be assessed from ground level (Pardow *et al.* 2012). The latter authors found that LCF in French Guiana had a richer bryo-

Table 2. — Epiphyllous bryophyte species in a lowland cloud forest (**LCF**) and a lowland rainforest (**LRF**) at Nouragues, French Guiana. *****, typically epiphyllous (Gradstein 1997; Gradstein & Ilkiu-Borges 2009); **+++**, abundant; **++**, frequent; **+**, rare; **–**, no record.

	LCF1	LCF2	LCF3	LCF4	LRF1	LRF2	LRF3	LRF4
Number of species	21	27	22	32	9	3	6	6
LCF only								
Archilejeunea juliformis (Nees) Gradst.	+	–	+	–	–	–	–	–
**Ceratolejeunea coarina* (Gottsche) Schiffn.	+++	+++	++	++	–	–	–	–
Ceratolejeunea cornuta (Lindenb.) Steph.	–	–	+	–	–	–	–	–
Cololejeunea obliqua (Nees & Mont.) Schiffn.	+	–	+	++	–	–	–	–
**Cololejeunea papillosa* (K.I.Goebel) Mizut.	–	++	–	+	–	–	–	–
**Cololejeunea platyneura* (Spruce) A.Evans	–	++	–	++	–	–	–	–
Cololejeunea sicifolia (A.Evans) Pócs & Bernecker	+	–	–	+	–	–	–	–
Colura tenuicornis (A.Evans) Steph.	–	–	–	+	–	–	–	–
**Crossomitrium patrisiae* (Brid.) Müll.Hal.	+	++	+	++	–	–	–	–
**Cyclolejeunea chitonia* (Taylor) A.Evans	–	++	–	–	–	–	–	–
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	+++	+++	+++	+++	–	–	–	–
Cyclolejeunea luteola (Spruce) Grolle	–	+	–	–	–	–	–	–
**Cyclolejeunea peruviana* (Lehm. & Lindenb.) A.Evans	+++	+++	–	+	–	–	–	–
Dibrachiella parviflora (Nees) X.Q.Shi, R.L.Zhu & Gradst.	–	–	–	+	–	–	–	–
Diplasiolejeunea brunnea Steph.	+	–	–	++	–	–	–	–
Drepanolejeunea inchoata (C.F.W.Meissn.) Steph.	+	+	–	+	–	–	–	–
**Drepanolejeunea polyrhiza* (Nees) Grolle & R.L.Zhu	+	+	–	+	–	–	–	–
Frullania brasiliensis Raddi	–	–	+	–	–	–	–	–
Frullania nodulosa (Reinw., Blume & Nees) Nees	–	–	+	–	–	–	–	–
Frullania sp. (subg. Diastaloba)	+	–	–	–	–	–	–	–
Harpalejeunea oxyphylla (Nees & Mont.) Steph.	–	+	–	–	–	–	–	–
Lejeunea adpressa Nees	+	++	+	++	–	–	–	–
Lejeunea cerina (Lehm. & Lindenb.) Lehm. & Lindenb.	–	–	–	+	–	–	–	–
**Leptolejeunea moniliata* Steph.	+	–	–	++	–	–	–	–
Leucobryum martianum (Hornsch.) Hampe	–	+	–	–	–	–	–	–
Lopholejeunea nigricans (Lindenb.) Schiffn.	–	–	+	–	–	–	–	–
Metzgeria ciliata Raddi	–	–	–	+	–	–	–	–
Microlejeunea acutifolia Steph.	–	++	+	+	–	–	–	–
Neurolejeunea breutelii (Gottsche) A.Evans	–	+	+	–	–	–	–	–
Octoblepharum albidum Hedw.	–	+	–	+	–	–	–	–
**Odontolejeunea lunulata* (F.Weber) Schiffn.	++	++	–	+++	–	–	–	–
**Odontolejeunea rhomalea* (Spruce) Steph.	–	++	++	++	–	–	–	–
Pilotrichum bipinnatum (Schwägr.) Brid.	–	–	+	–	–	–	–	–
Pilotrichum evanescens (Müll.Hal.) Crosby	–	+	–	–	–	–	–	–
Plagiochila montagnei Nees	–	+	+	+	–	–	–	–
Plagiochila simplex (Sw.) Lindenb.	–	–	–	+	–	–	–	–
Plagiochila subplana Lindenb.	–	–	–	+	–	–	–	–
**Radula flaccida* Lindenb. & Gottsche	+	++	+	+	–	–	–	–
Radula stenocalyx Mont.	–	–	++	+	–	–	–	–
Stictolejeunea squamata (Willd.) Schiffn.	–	++	+	+	–	–	–	–
Symbiezidium transversale (Sw.) Trevis.	+	+	–	–	–	–	–	–
Syrrhopodon sp.	+	+	–	+	–	–	–	–
Zeleometeorium patulum (Hedw.) Manuel	–	+	+	+	–	–	–	–
LCF and LRF								
Ceratolejeunea cubescens (Mont.) Schiffn.	–	–	+	–	+	–	–	–
**Cololejeunea diaphana* A.Evans	–	+	+	–	–	–	+	–
**Diplasiolejeunea pellucida* (Spreng.) Schiffn.	+	–	–	+	++	+	+	+
Drepanolejeunea crucianella (Taylor) A.Evans	++	++	–	+	+	–	–	++
Lejeunea aphanes Spruce	+	–	–	–	+	–	–	–
**Leptolejeunea elliptica* (Lehm. & Lindenb.) Besch.	+	–	+	+	+	–	+	–
LRF only								
**Cololejeunea cremersii* Tixier	–	–	–	–	–	+	+	+
**Drepanolejeunea mosenii* (Steph.) Bischl.	–	–	–	–	++	–	++	++
Lejeunea laetevirens Nees & Mont.	–	–	–	–	+	–	–	–
Microlejeunea epiphylla Bischl.	–	–	–	–	+	–	–	+
Rectolejeunea versifolia (Schiffn.) L.Söderstr. & A.Hagborg	–	–	–	–	++	+	+	+

phyte life-form composition than LRF, with diffuse growth forms such as tail, weft and pendants being frequent in LCF and largely absent in LRF. As it can be estimated from the ground, life-form diversity is considered a useful approach for identifying lowland cloud forest without application of tree climbing. The present study indicates that species richness and abundance of epiphyllous bryophytes, and representation of epiphyllous Lejeuneaceae, may be a further suitable tools for recognition of lowland cloud forest at ground level, and may serve to distinguish lowland cloud forest from lowland rain forest. It is recommended that epiphyll cover, which was not measured in this study, be included in future work.

Acknowledgements
I thank Christine Gehrig-Downie and Monica Hoffstädter for collecting the samples, Sven Bellanger for help with the illustrations, and Maaike Bader for constructive comments and corrections on the manuscript which have led to considerable improvement of the paper. This project was funded by the German Research Foundation (DFG grant GR 1588/13-1). I also thank Tamás Pócs and an anonymous reviewer for comments.

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Submitted on 7 February 2022;
accepted on 8 June 2022;
published on 18 October 2022.