

Floristic overview of the epiphytic bryophytes of *terra firme* forests across the Amazon basin

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ABSTRACT

Epiphytic bryophyte communities in *terra firme* forests of the Amazon region were investigated for the first time through standardized sampling across the Amazon basin. The sampling was carried out at nine localities, where bryophytes were collected in five height zones, from the forest floor to the canopy of eight canopy trees per locality. The sampling generated 3104 records, identifying 222 species and 39 morphospecies, within 29 families. The most common families were Lejeuneaceae (in 55%), Calymperaceae (in 8%), Leucobryaceae (in 4%) and Sematophyllaceae (in 4%). Richness and species composition did not show any geographical gradient. The bryoflora was significantly richer in the localities of Saül, in French Guiana, and Tiputini, in Ecuador, than in the other localities, probably due to differences in local climatic conditions. Among the 155 species recorded for more than one locality, 57 were classified as specialists. A total of 29 species (among which 3 were unidentified) were sampled only in the canopy, which reinforces the importance of canopy sampling for the study of epiphytic bryophytes in the Amazon.

Key words: Epiphyte, diversity, liverworts, mosses, rain forest, vertical gradient

Introduction

It is estimated that approximately 800 bryophyte species (mosses, liverworts and hornworts) occur in the Amazon region (Gradstein *et al.* 2001). In the Brazilian Amazon, the most updated species count indicates a total of 561 taxa (Costa & Luiz-Ponzo 2010). Only in the last decade, several known species have been cited as new records for the region (Moraes & Lisboa 2006; Alvarenga *et al.* 2007; Reiner-Drehwald & Schäfer-Verwimp 2008). In addition, species new to science have been collected and described in the region (Zartman & Ackerman 2002).

The present knowledge of the Amazonian bryoflora is primarily disseminated in publications of local inventories. Most of the bryophyte sampling has been carried out in the eastern Amazon, more specifically in the areas surrounding the Brazilian localities of Belém, Caxiuanã and Ilha do Marajó (Lisboa 1984, 1985; Lisboa & Maciel 1994; Lisboa & Ilkiu-Borges 1997; Lisboa *et al.* 1999). Inventories conducted in scattered localities in the south of the state of Pará and the Serra dos Carajás have summarized the information available for the southeastern Amazon (Ilkiu-Borges *et al.* 2004; Moraes & Lisboa 2006). In central Amazonia, studies have mostly been concentrated in *terra firme* (non-flooded) forest and *campinarana* (white-sand forest) sites, within approximately 100 km of the city of Manaus (Lisboa 1976;

Griffin III 1979; Zartman & Ilkiu-Borges 2007). Further sampling has been conducted across the states of Roraima (Yano 1992; Santiago 1997), Rondônia (Lisboa 1993) and Acre (Costa 2003).

The Amazon occupies an area of approximately 6 million km² and is subject to a range of climatic conditions. Total annual rainfall ranges from 1500 mm (in northern Bolivia) to over 3000 mm (in the Upper Rio Negro region, the Colombian Amazon and northern Peru), the lowest monthly rainfall (in the three driest months) ranging from 0 mm to 447 mm, respectively, in those same regions. Moreover, environmental characteristics such as soil type, topography and catchment drainage vary at local scale, producing a mosaic of habitats and landscapes. Locally and across the region, different sources of variation are associated with diversity and compositional patterns in several plant groups (Londoño & Alvarez 1997; Costa *et al.* 2005; ter Steege *et al.* 2006; Drucker *et al.* 2008; Zuquim *et al.* 2009).

Recently, standardized and robust scientific data from extensive regions such as the Amazon have become a valuable requisite for conservation and governance policies. Large scale biological projects, funded either by the Brazilian government or by non-governmental organizations, have been establishing sampling protocols, a necessary step towards the primary biodiversity data needed to inform policy-makers. Despite the large amount of information

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on bryophytes in the literature reviewed above, there is a need for a pre-established experimental or sampling design. In addition, few studies of bryophytes have explored the canopy, despite the fact that the importance of canopy sampling has previously been made clear by authors such as Cornelissen and Gradstein (1990), who observed that 50% of the listed species in a forest in Guyana were restricted to the canopy.

In order to provide an ecological, as well as a floristic, overview of the epiphytic bryophytes in *terra firme* forests of the Amazon, we sampled bryophyte communities at nine localities across the Amazon basin, using a standard protocol, from the forest floor to the canopy of eight trees per locality. In this paper, we provide a floristic overview of these communities, in which our major questions are as follows: What are the most abundant families and species of epiphytic bryophytes occurring in *terra firme* forests of the Amazon? What are the family and species rankings across the basin and along the vertical gradient on the host trees? Do these rankings change according to the geographical locality or to the height zone on the host tree? Are there species with a statistically significant preference for a given height zone on the host trees? In short, this is the first quantitative description of the epiphytic bryoflora across the Amazon region, conducted with the objective of providing the necessary background information for future large scale research on the ecology and biogeography of the group.

Material and methods

Sampling procedure and composition assessment

In order to sample communities of epiphytic bryophytes, we selected nine localities across the Amazon basin, along an east-west transect (Fig. 1). At each locality, epiphytic bryophyte communities were sampled from the bottom to the top of eight selected canopy trees growing on non-flooded plateaus (*terra firme* forest). The trees were divided into height zones, used as a surrogate for the microclimatic

gradient found from the forest floor to the canopy. The height zones were established as follows (Mota de Oliveira *et al.* 2009): from the base of the tree up to 1.5 m (zone 1); the lower and upper trunk spaces (zones 2 and 3); between the upper trunk and the base of the crown (zone 4); and finally the outer sun-lit twigs (zone 6). The bryophyte communities were pooled samples of 4 patches of approximately 10 × 10 cm² each, per height zone. The collections from the sites Saül (French Guiana), Mabura Mora (Guyana) and Mabura Wallaba (Guyana) were taken from more than ten trees and included bryophyte samples taken from the middle canopy of the host trees (zone 5). In order to balance the sampling strategy, we used a sub-set of the data of these three sites, which consisted of samples from eight randomly chosen trees per locality and five height zones (zones 1-4 and zone 6).

The specimens present in the samples were identified using keys, monographs (Reese 1993; Gradstein 1994; Dauphin 2003) and available floras (Gradstein *et al.* 2001; Gradstein & Costa 2003). Material was deposited at the Herbaria of the Museu Paraense Emilio Goeldi (acronym, MG; Brazil), Instituto Nacional de Pesquisas da Amazônia (acronym, INPA; Brazil) and Nationaal Herbarium Nederland, Leiden University branch (acronym, L; the Netherlands). Material from the Guianas (sites 2-4) was re-identified to ensure synchrony in the taxonomy among the plots. Specimens that could not be identified down to the species level were classified as morphospecies, which allowed the analysis to run at species level. We called species “restricted” when, in our dataset, they were found in only one locality; we call species “typically epiphyllous” when their main habit is epiphyllous, based on its description in current literature (Gradstein & Costa 2003; Zartman & Ilkiu-Borges 2007).

Data analysis

Each pooled sample (40 cm²) was considered a “plot” and generated a species list. We considered the use of an abundance measure inappropriate, due to the impossibility of separating individuals for most of the species and to the

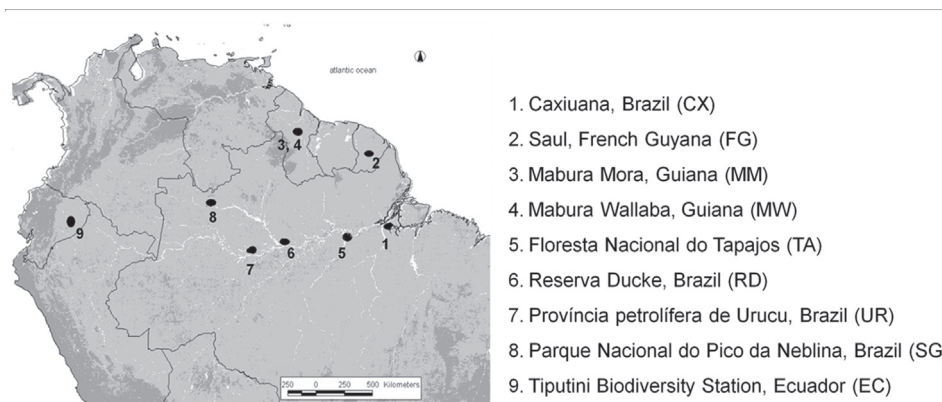


Figure 1. Map of the study area, showing the sampling localities from east to west in the Amazon basin.

intrinsic variation in plant size. To quantify community structure—species abundance distribution for the complete dataset and accumulation curves per locality—we used frequency as a surrogate for abundance, summing the number of plots per locality in which each species was recorded. This value ranged from 1 to 40, the maximum possible number of plots. In order to classify species as specialists (those with a tendency to occur in a given height zone) or generalists (those without such a tendency), we performed indicator species analysis (McCune & Grace 2002), with the software PCORD 5, for species recorded in at least three localities. This analysis also provides an indicator value for those species that show a significant preference for a given height zone. The indicator value ranges from 0 to 100, according to the strength of the preference. We calculated the weighted average height zone for the specialists, as additional and more straightforward information on species occurrence.

Results

A total of 351 plots, sampled from 72 trees, yielded 3104 occurrences of bryophytes, representing 29 families, 97 genera and 261 species or morphospecies (Appendix 1). As shown in Tab. 1, species richness of the localities varied from 51 for Reserva Ducke, Brazil (central Amazon), to 127 for Tiputini, Ecuador (western Amazon). Species richness was significantly higher for two of the nine localities: Tiputini; and Saül (in French Guiana) (Fig. 2). In terms of species richness, there were no significant differences between or among the other seven localities, which had an average of 64 species in eight host trees. On average, nine species were recorded per plot, ranging from 5–6 species in the eastern and central Amazon to a peak of 17 species per plot in Tiputini, Ecuador. Tiputini was also the locality where we found the

highest proportion of restricted species—37.8% (sampled exclusively at one locality)—and the highest proportion of facultative epiphylls—16.5%—the latter ranging from 5.7% to 10.8% among the other localities.

Of the 261 species identified, 155 were recorded in at least two localities. All localities investigated showed at least one locally abundant species that was not among the top 10% of abundant species in the complete dataset (Tab. 1).

The most common families in number of records were Lejeuneaceae (1700 records; 55% of the total), Calymperaceae (265; 9%), Leucobryaceae (197; 6%), Plagiochilaceae (149; 5%) and Sematophyllaceae (147; 5%). The average number of families recorded per locality was 14, being highest for Saül and Tiputini, each of which had 23 families. When the assemblages of the localities were analysed separately, these families still corresponded to the four highest ranked everywhere (Tab. 2), with a few exceptions, such as Jubulaceae in Mabura Wallaba; Lepidoziaceae in São Gabriel da Cachoeira (Brazil); and Geocalycaceae and Neckeraceae in Tiputini. The most common species were *Cheilolejeunea rigidula*, *Ceratolejeunea cornuta*, *Octoblepharum pulvinatum*, *Octoblepharum albidum*, *Archilejeunea fuscescens*, *Sematophyllum subsimplex*, *Lopholejeunea subfusca* and *Symbiezidium barbiflorum*. These eight species alone accounted for 21% of the records, as shown by the species abundance distribution of the complete dataset (Fig. 3).

The family ranking over height zones 1–4 was rather consistent with the general ranking described above for the localities. It differed, however, in height zone 6, where Lejeuneaceae, again the most abundant family, was followed by Jubulaceae, Pterobryaceae, Macromitriaceae and Calymperaceae.

Species richness and the number of records were comparable across the different height zones (Tab. 3). Species composition, however, was partially related to height zone.

Table 1. Species data, by locality.

Site	S	N	P	Rt	El	Locally abundant species*
				(%)	(%)	
CX	61	236	6	13.1	8.2	<i>Ceratolejeunea minuta</i> , <i>Cheilolejeunea neblinensis</i>
FG	102	514	14	14.7	9.8	<i>Radula javanica</i> , <i>Zelometeorium patulum</i>
MM	63	434	12	1.6	7.9	<i>Ceratolejeunea guianensis</i> , <i>Plagiochila laetevirens</i>
MW	74	335	9	6.8	9.5	<i>Frullania caulisequa</i> , <i>Plagiochila subplana</i>
TA	63	234	6	9.5	7.9	<i>Caudalejeunea lehmanniana</i> , <i>Syrrhopodon incompletus</i>
RD	51	199	5	13.7	7.8	<i>Ceratolejeunea minuta</i>
UR	70	229	6	14.3	5.7	<i>Syrrhopodon cryptocarpus</i> , <i>Cheilolejeunea neblinensis</i>
SG	65	183	5	16.9	10.8	<i>Archilejeunea crispistipula</i> , <i>Bazzania hookeri</i>
EC	127	700	17	37.8	16.5	<i>Lophocolea bidentata</i> , <i>Zelometeorium patulum</i>
Total	263	3064	9	14.2	9.4	-

S – (total number of) species; N – (total number of) records; P – (mean number of species per) plot; Rt – (proportion of species) restricted to the locality; El – (proportion of typical) epiphylls; CX – Caxiuana (Brazil); FG – Saül (French Guiana); MM – Mabura Mora (Guyana); MW – Mabura Wallaba (Guyana); TA – Tapajós (Brazil); RD – Reserva Ducke (Brazil); UR – Urucu (Brazil); SG – São Gabriel (Brazil); EC – Tiputini (Ecuador).

*Among the 10 most abundant in a locality but low-ranked in the metacommunity and recorded for less than 5 localities.

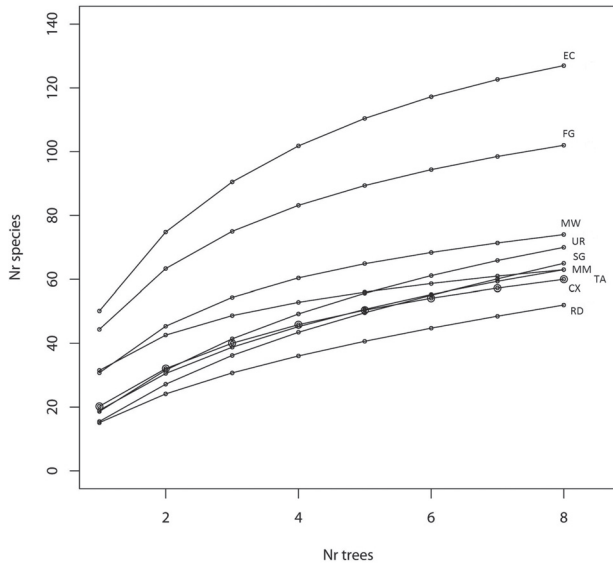


Figure 2. Species accumulation curves of epiphytic bryophytes measured on eight host trees, in each of the localities sampled. Axis x: number of host trees; axis y: number of species recorded.

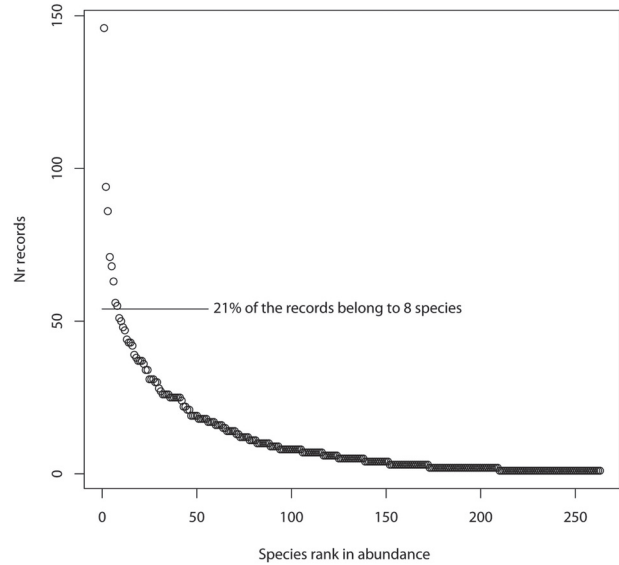


Figure 3. Species abundance distribution based on the complete dataset. Axis x: species ranked by abundance (number of records); axis y: number of records.

Table 2. The 11 most abundant families in the dataset and the proportional distribution of records among the nine sampled localities.

Family	CX	FG	MM	MW	TA	RD	UR	SG	EC
Lejeuneaceae	70.3	47.8	56.4	51.1	56.0	66.8	58.8	64.5	54.6
Calymperaceae	13.1	5.5	4.5	8.4	15.0	11.6	16.4	7.1	5.7
Leucobryaceae	8.9	4.7	5.6	5.9	12.0	10.1	11.9	10.4	0.9
Plagiochilaceae	0.8	5.0	8.4	2.7	1.3	1.5	0.9	1.1	7.7
Sematophyllaceae	3.8	3.0	8.6	6.9	9.0	4.5	4.4	2.7	1.7
Jubulaceae	2.1	4.7	3.9	9.8*	0.4	2.5	0.0	0.5	0.3
Lepidoziaceae	0.0	0.4	0.0	2.0	0.0	1.0	2.7	9.3*	0.3
Fissidentaceae	0.4	1.6	0.2	0.0	1.3	0.0	0.9	0.5	2.1
Geocalyceae	0.0	0.7	0.2	0.2	0.0	1.0	0.0	0.0	5.1*
Macromitriaceae	0.0	3.7	2.2	5.9	0.0	0.0	0.0	0.0	0.6
Neckeraceae	0.0	2.5	2.0	0.0	0.0	0.0	0.0	0.0	5.3*
Other	0.4	20.2	8.1	7.1	5.1	1.0	4.0	3.8	15.7

CX – Caxiuana (Brazil); FG – Saül (French Guiana); MM – Mabura Mora (Guyana); MW – Mabura Wallaba (Guyana); TA – Tapajós (Brazil); RD – Reserva Ducke (Brazil); UR – Urucu (Brazil); SG – São Gabriel (Brazil); EC – Tiputini (Ecuador).

*Correspond to observations in the text.

Out of 155 species recorded in at least two localities, 57 were significant indicator species for a particular zone. Zone 6 had the highest number of indicator species (30), followed by zone 1 (19), zone 4 (7) and zone 2 (1) (Tabs. 3 and 4). Some species, although widespread across the basin, were completely restricted to zone 6, which was the case for *Vitalianthus urubuensis*, *Colura greig-smithii* and *Caudalejeunea lehmanniana*, as well as for all five *Diplasiolejeunea* species recorded (with the exception of 1 record of the 46, for *D. cavifolia* in zone 4). The two most abundant indicator species of zone 6, however, were found in at least three other

height zones. Accordingly, the five most abundant indicator species of zone 1 were also found in other height zones, as were other zone 1 indicator species. Indicator species of zone 1 belonged to 11 different families and only 7 of the 26 species belonged to Lejeuneaceae. In zone 6, however, the indicator species belonged mainly to Lejeuneaceae, followed by Pterobryaceae and Jubulaceae. Accordingly, when we performed the same indicator analysis at the family level, we found that the number of families classified as specialists was higher in the understory—zones 1 and 2—than in the canopy—zones 4 and 6 (Tab. 5).

Table 3. Data related to indicator species, extracted from the complete dataset, per height zone (Z): total number of species (S), total number of records (N), average number of species per plot (P), number of indicator species calculated for species occurring in at least two localities (155 sp) according to ISA (p<0.05) (IndS), most abundant indicator species calculated for the complete dataset according to ISA (p<0.05).

Z	S	N	P	IndS*	Most abundant indicator species**
1	144	598	8.4	19	<i>Sematophyllum subsimplex</i> , <i>Pictolejeunea picta</i> , <i>Taxithelium planum</i> , <i>Plagiochila laetevirens</i>
2	135	569	8.0	1	<i>Cheilolejeunea neblinensis</i> , <i>Calymperes lonchophyllum</i>
3	122	533	7.5	0	<i>Acroporium pungens</i> ***
4	138	679	9.6	7	<i>Cheilolejeunea rigidula</i> , <i>Ceratolejeunea cornuta</i> , <i>Octoblepharum albidum</i> , <i>Cheilolejeunea holostipa</i>
6	136	685	9.6	30	<i>Lopholejeunea subfusca</i> , <i>Pycnolejeunea contigua</i> , <i>Frullania caulisequa</i> , <i>Diplasiolejeunea rudolphiana</i>

Z – (height) zone; S – (total number of) species; N – (total number of) records; P – (mean number of species per) plot; IndS – (number of) indicator species.
 *Calculated for the species occurring in at least two localities (n=155), according to the indicator species analysis, (p<0.05); **calculated for the entire dataset (p<0.05); ***non-indicator.

Table 4. Species classified as specialists.*

Species	HZ	WA**	IV	IVR	IVR _{SD}
Understory specialists (height zones 1 and 2)					
<i>Callicostella pallida</i> (Hornsch.) Angström	1	1.3	5	1.8	0.92
<i>Cyclolejeunea luteola</i> (Spruce) Grolle	1	1	6.9	1.6	0.87
<i>Fissidens guianensis</i> Mont.	1	1.5	14.3	2.9	1.03
<i>Haplolejeunea cucullata</i> (Steph.) Grolle	1	1.4	14.2	2.5	0.98
<i>Leucobryum martianum</i> (Hornsch.) Hampe ex Müll. Hal.	1	1.4	9.9	2.7	1.01
<i>Leucomium strumosum</i> (Hornsch.) Mitt.	1	1.4	7.4	2.3	0.98
<i>Leucophanes molleri</i> Müll. Hal.	1	1	6.9	1.6	0.87
<i>Micropterygium leiophyllum</i> Spruce	1	1.8	5.7	1.7	0.9
<i>Mnioloma parallelogrammum</i> (Spruce) R. M Schust	1	1	5.6	1.4	0.84
<i>Ochrobryum gardneri</i> (C. Müll.) Mitt	1	1.3	5	1.8	0.92
<i>Pictolejeunea picta</i> (Gottsche ex Steph.) Grolle	1	1.1	22.7	3	1.08
<i>Pilosium chlorophyllum</i> (Hornsch.) C. Mull.	1	1.1	14.1	2.3	0.98
<i>Plagiochila laetevirens</i> Lindenb.	1	1.4	9.4	2.9	1.09
<i>Prionolejeunea microdonta</i> (Gottsche) Steph.	1	1	5.6	1.5	0.88
<i>Prionolejeunea muricatoserrulata</i> (Spruce) Steph.	1	1.1	7.1	1.8	0.91
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	1	2.3	10.2	6.2	1.32
<i>Taxithelium planum</i> (Brid.) Mitt.	1	1.3	17.2	3.2	1.1
<i>Vesicularia vesicularis</i> (Schwägr.) Broth.	1	1	5.6	1.5	0.88
<i>Xylolejeunea crenata</i> (Spruce) Steph.	1	1	6.9	1.6	0.88
<i>Radula flaccida</i> Lindenb. & Gott.	2	2.1	5.5	2	0.93
Inner canopy specialists (height zone 4)					
<i>Ceratolejeunea cornuta</i> (Spruce) Steph.	4	3.7	16.5	8.3	1.4
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.L. Zhu	4	3.9	13.4	5.1	1.25
<i>Cheilolejeunea rigidula</i> (Mont.) R.M.Schust.	4	3.8	19.8	11.5	1.45
<i>Cheilolejeunea trifaria</i> (Reinw., Blume & Nees) Mizut.	4	4	9.7	4.5	1.22
<i>Neurolejeunea seminervis</i> (Spruce) Schiffn.	4	4.5	6.2	1.9	0.93
<i>Octoblepharum albidum</i> Hedw.	4	3	10.4	6.7	1.34
<i>Pycnolejeunea macroloba</i> (Mont.) Schiffn.	4	3.6	10.7	5.3	1.27
Outer canopy specialists (height zone 6)					
<i>Caudalejeunea lehmanniana</i> (Gottsche) A.Evans	6	6	23.9	2.7	1.04
<i>Diplasiolejeunea brunnea</i> Steph.	6	6	14.9	2.1	0.95

Continues

Table 4. Continuation.

Species	HZ	WA**	IV	IVR	IVR _{SD}
<i>Diplasiolejeunea cavifolia</i> Steph.	6	5.6	6.3	1.7	0.91
<i>Diplasiolejeunea cobrensis</i> Gottsche ex Steph.	6	6	7.5	1.6	0.87
<i>Diplasiolejeunea pellucida</i> (C.F.W. Meissn. ex Spreng.) Schiffn.	6	6	11.9	1.9	0.95
<i>Diplasiolejeunea rudolphiana</i> Steph.	6	6	26.9	2.8	1.04
<i>Drepanolejeunea fragilis</i> Bischl.	6	4.5	13.1	3.8	1.13
<i>Frullania apiculata</i> (Reinw., Blume & Nees) Nees	6	5	10.2	2.8	1.04
<i>Frullania caulisequa</i> (Nees) Nees	6	5.2	19.8	4.1	1.16
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	6	5.6	12.6	2.3	0.98
<i>Frullania nodulosa</i> (Reinw., Nees & Blume) Gottsche et al.	6	5.8	12.2	2.1	0.94
<i>Frullania riojaneirensis</i> (Raddi) Spruce	6	6	7.5	1.6	0.85
<i>Groutiella tomentosa</i> (Hornsch.) Wijk. & Marg.	6	5.7	6.3	1.7	0.9
<i>Henicodium geniculatum</i> (Mitt.) W.R. Buck	6	5.6	14.5	2.6	1.04
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn.	6	5.2	16.3	3.1	1.04
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	6	4.2	14.6	5.7	1.3
<i>Macromitrium punctatum</i> (Hook & Grev.) Brid.	6	5.2	4.8	1.9	0.91
<i>Microlejeunea bullata</i> (Taylor) Steph.	6	4.5	12.3	4.3	1.17
<i>Microlejeunea epiphylla</i> Bischl.	6	4.5	9.2	3.3	1.11
<i>Pycnolejeunea contigua</i> (Nees) Grolle	6	5.3	20.3	3.5	1.09
<i>Pycnolejeunea papillosa</i> X.-L. He	6	3.6	6.2	2.3	0.99
<i>Rectolejeunea berteroana</i> (Gottsche ex Steph.) A. Evans	6	5	6.8	2.2	0.97
<i>Rectolejeunea emarginuliflora</i> (Gottsche ex Schiffn) Evans	6	5.4	13	2.5	0.98
<i>Rectolejeunea flagelliformis</i> A. Evans	6	4.8	13.2	3.4	1.11
<i>Sematophyllum subpinnatum</i> (Brid.) Britt.	6	5.3	5.4	1.8	0.95
<i>Symbiezidium transversale</i> var. <i>hookerianum</i> (Gottsche) Gradst. & van Beek	6	5.1	15.6	3.4	1.11
<i>Syrhodon parasiticus</i> Brid.	6	4.6	12	3.4	1.08
<i>Thysananthus amazonicus</i> (Spruce) Schiffn.	6	5.2	10.8	2.7	1.04
<i>Verdoornianthus griffinii</i> Gradst.	6	5.8	12.2	2.1	0.93
<i>Vitalianthus urubuensis</i> Zartman & I. L. Ackerman	6	6	9	1.7	0.91

HZ – height zone; WA – weighted average (height zone, from all records); IV – indicator value; IVR – indicator value for randomized groups; IVRSD – standard deviation of the indicator value for randomized groups.

*p<0.05, by indicator species analysis, for all; **where the WA is a natural number, the species occurred only in that height zone.

Discussion

Floristics

Is there a general Amazonian bryoflora? We found that the most abundant families (Lejeuneaceae, Calymperaceae, Sematophyllaceae, Leucobryaceae and Plagiochilaceae) kept their rank, in terms of abundance, across the basin. This result supports a general description of the Amazonian bryoflora (Gradstein *et al.* 2001). The family rank of epiphytic bryophytes only changed when the assemblages of the different height zones on the host tree were analyzed separately: the family composition of the outer canopy was distinct, Lejeuneaceae being followed by Jubulaceae, Pterobryaceae, Macromitriaceae and Calymperaceae.

It has long been known that bryophyte species composition differs between the understory and the canopy, both in terms of species composition and in terms of life forms (Richards 1984; Cornelissen & ter Steege 1989; Mota de Oliveira *et al.* 2009; Sporn *et al.* 2010). The restriction of some bryophyte species to the canopy has also previously been observed in the Amazon rain forest (Gradstein *et al.* 1990), as has the shift of the occurrence of some bryophyte species to lower height zones in a tree, as a result of opening of the canopy (Acebey *et al.* 2003). Based on such observations, epiphytic species were traditionally classified as “shade epiphytes” when restricted to the bottom part of the host tree, “generalists” when occurring in many height zones, and “sun epiphytes” when restricted to the canopy (Richards 1984). We suggest that the mechanisms leading

Table 5. Families to which the species classified as specialists belong.*

Family	HZ	WA	IV	IVR	IVR _{SD}
Calypogeiaceae	1	1.0	6.9	1.6	0.84
Fissidentaceae	1	1.0	20.3	3.8	1.16
Hookeriaceae	1	1.1	5.0	1.8	0.92
Lepidoziaceae	1	1.3	7.4	3.8	1.16
Leucobryaceae	1	1.4	17.4	12.5	1.43
Leucomiaceae	1	1.5	7.4	2.3	0.96
Leucophanaceae	1	1.6	6.9	1.6	0.86
Plagiochilaceae	1	2.1	12.6	9.2	1.49
Sematophyllaceae	1	2.5	21.3	10.0	1.52
Stereophyllaceae	1	2.5	14.1	2.3	0.97
Thuidiaceae	1	2.6	9.9	2.5	1.00
Calymperaceae	3	3.7	17.6	14.8	1.38
Macromitriaceae	4	4.3	8.6	3.3	1.10
Jubulaceae	6	4.9	29.3	5.4	1.39
Pterobryaceae	6	5.3	9.4	4.6	1.23

HZ – height zone; WA – weighted average (height zone, from all records); IV – indicator value; IVR – indicator value for randomized groups; IVRSD – standard deviation of the indicator value for randomized groups.

* $p < 0.05$, by indicator species analysis, for all.

to the restriction/preference of a given species to one of the habitats are not only related to light intensity, as suggested by the denomination, but also to population dynamics. While the occurrence of some species in the canopy is clearly related to the requirement of high light levels for development, such as reported for *Frullania* species (Romero *et al.* 2006), we hypothesize that our observations of typical epiphylls in the canopy branches, such as *Colura greig-smithii*, *Odontolejeunea rhomalea* and *Leptolejeunea elliptica*, are more related to their ability to rapidly colonize recent substrates than to light availability. This working hypothesis certainly deserves further testing with a proper experimental design.

Species richness

Is bryophyte species richness across the Amazon comparable to tree species diversity? According to our results, species richness was highest in two localities. The high richness in geographically separate localities such as Tiputini and Saül, as well as the unchanged family ranking across the basin, clearly differed from the gradients in diversity and composition of canopy trees in the Amazon (ter Steege *et al.* 2003; ter Steege *et al.* 2006). In canopy trees, alpha diversity increases along the east-west axis and the composition shows a clear change in family ranking along the axis running from the Guiana Shield, in the northeast part of the basin, to Bolivia, in the southwest. In the epiphytic bryophytes of the region, however, the sharpest compositional gradient is apparently established locally, rather than across geographic distances, at least in the Guianas region

(Mota de Oliveira *et al.* 2009). We therefore believe that Tiputini (Ecuador) and Saül (French Guiana) showed high species richness due to specific microclimatic conditions. In biomes adjacent to the Amazon, such as the Andes and the Atlantic Forest of Brazil (Wolf 1993; Kessler 2000; Costa & Lima 2005), the richness gradient in bryophyte assemblages is set by altitude and is usually attributed to the correlated gradient in relative humidity and temperature. Saül and Tiputini are also at higher elevations than are the other localities studied. Elements of sub-montane and mid-montane forest, such as the genus *Porotrichum*, occurred in these two localities and nowhere else. The high species richness of Saül has been related to the high and constant levels of relative humidity and regular fog in comparison with other Amazonian *terra firme* sites (Gradstein 2006). Tiputini may offer similar conditions. In our data, the percentage of typically epiphyllous species growing on bark in Tiputini was significantly higher than in any other locality, which may again indicate favorable conditions of relative humidity. For instance, *Odontolejeunea rhomalea* and *O. lunulata*, *Colura greig-smithii*, *Radula mammosa*, found on the bark of the host trees only in Tiputini, are typical epiphylls. Published records of those same species indicate their presence in Central and Eastern Amazonia (so there is no dispersal barrier), albeit growing on leaves (Zartman & Ilkiu-Borges 2007). Apparently, the more favorable microclimatic conditions in Tiputini and Saül simply allow the establishment of a greater number of species. In Tiputini, the proximity with the Andes may also play a role as an extra source of species. The greater relative importance

of the family Neckeraceae, for instance, can be related to the fact that this is an important Andean family in terms of abundance (Churchill 2009); and the higher number of *Plagiochila* species, a well known feature of sub-montane and montane forests, is probably caused by the abundance of *Plagiochila* in the Andes.

Understory specialists and canopy specialists

The indicator species of zone 1 belonged to 11 different families, whereas those of zone 6 belonged to only three families: Lejeuneaceae, Pterobryaceae and Jubulaceae. This result suggests that the canopy habitat may be a recent “acquisition” in evolutionary time, as has been demonstrated for an epiphyllous habitat (Wilson *et al.* 2007) and for ferns (Schneider *et al.* 2004; Schuettpelz & Pryer 2009). However, the attempt to verify habitat specialization at the family level, as we have shown in our results, should be carefully discussed. The fact that Lejeuneaceae, Calymperaceae, Sematophyllaceae and Leucobryaceae presented a statistically significant preference for a given zone is not entirely consistent, because these families have indicator species in both the understory zones and the canopy zones along the gradient. On the basis of our results, the families that can be consistently classified as indicators are Calypogeiaceae, Leucophanaceae, Hookeriaceae, Leucomiaceae, Thuidiaceae and Fissidentaceae for the lower (understory) height zones; and Jubulaceae, Pterobryaceae and Macromitriaceae for the upper (canopy) height zones. These can be designated indicator families because most of their species are “restricted” to their respective height zones.

Sampling considerations and future research

The results of our study clearly indicate the need to include the canopy of trees in standard protocols for bryophyte inventories in the Amazon, which has not been the case. Interestingly, species recently described, such as *Vitalianthus urubuensis* (Zartman & Ackerman 2002) and *Cheilolejeunea neblinensis* (Ilkiu-Borges & Gradstein 2008) were recorded in several of our localities and thus proved not to be rare. That means that we can still expect to find even common new bryophyte species in the Amazon. After describing *Vitalianthus urubuensis*, Zartman and Ackerman (2002) posed the question of whether the new species was restricted to Manaus region or was undersampled. The answer is now clear: the canopy was undersampled. That species was first collected by the authors exactly in a secondary forest, where canopy opening allows some canopy specialists to occur in lower height zones.

Regarding the geographic distribution of bryophytes in the Amazon, we propose the investigation of the local conditions at Tiputini and Saül, followed by the identification and analysis of climatically comparable areas in order to test whether bryophyte species richness is climate related.

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Appendix 1. List of species (and unidentified material) and their occurrence in the nine Amazon basin localities investigated in the present study.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
Calymperaceae									
<i>Calymperes afzelli</i> Sw.		X	X			X			
<i>Calymperes erosum</i> Müll. Hal.	X		X	X	X			X	X
<i>Calymperes guildingii</i> Hooker & Greville		X							
<i>Calymperes lonchophyllum</i> Schwaegr.		X	X	X	X			X	
<i>Calymperes mitrafugax</i> Florschütz		X							
<i>Calymperes othmeri</i> Herzog						X			
<i>Calymperes palisotii</i> Schwaegr.		X							
<i>Calymperes platyloma</i> Mitt.	X					X		X	X
<i>Calymperes rubiginosum</i> (Mitten) Reese								X	
<i>Calymperes smithii</i> Bartram								X	
<i>Calymperes</i> species 01 INPA 217763							X		X
<i>Calymperes</i> species 02 INPA 217755									X
<i>Syrrhopodon africanus</i> (Mitt.) Paris		X							
<i>Syrrhopodon cymbifolius</i> C. Muller		X							
<i>Syrrhopodon cryptocarpus</i> Dozy & Molk.	X		X				X	X	X
<i>Syrrhopodon elatus</i> Montagne		X							X
<i>Syrrhopodon flexifolius</i> Mitten					X	X			
<i>Syrrhopodon graminicola</i> Williams	X								
<i>Syrrhopodon incompletus</i> Schwaegr. var. <i>incompletus</i>		X	X		X	X		X	
<i>Syrrhopodon leprieuri</i> Mont.							X		X
<i>Syrrhopodon ligulatus</i> Mont.	X	X	X		X	X		X	X
<i>Syrrhopodon</i> species 01 MPEG 186275	X								
<i>Syrrhopodon</i> species 02 INPA 217501							X		
<i>Syrrhopodon parasiticus</i> Brid.	X	X	X		X			X	
<i>Syrrhopodon simmondsii</i> Steere	X	X			X		X		
Calypogeiaceae									
<i>Calypogeia laxa</i> Gottsche & Lindenb.									X
<i>Mnioloma parallelogrammum</i> (Spruce) R. M Schust							X		X
Cephaloziaceae									
<i>Odontoschisma falcifolium</i> Steph.				X	X			X	
Cephaloziellaceae									
<i>Cylindrocolea planifolia</i> (Steph.) R.M. Schust.						X			
Daltoniaceae									
<i>Crossomitrium patrisiae</i> (Brid.) Müll. Hal.		X	X	X	X				
<i>Lepidopilum affine</i> Müll. Hal.		X							
<i>Lepidopilum radicale</i> Müll. Hal.		X							
<i>Lepidopilum scabrisetum</i> (Schwaegr.) Steere			X	X					
<i>Lepidopilum surinamense</i> Müll. Hal.			X						

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Pilotrichum evanescens</i> (Müll. Hal.) Crosby		X	X						
Dicranaceae									
<i>Holomitrium arboreum</i> Mitt.			X	X	X				
<i>Leucoloma cruegerianum</i> (Müll. Hal.) A. Jaeger				X	X				
Fissidentaceae									
<i>Fissidens diplopus</i> Mitt.								X	X
<i>Fissidens guianensis</i> Mont.		X	X	X					
<i>Fissidens prionodes</i> Mont.									X
<i>Fissidens radicans</i> Mont.			X						
<i>Fissidens steerei</i> Grout	X						X	X	
<i>Fissidens weirii</i> Mitt.		X	X						
<i>Fissidens zollingeri</i> Mont.		X							
Geocalycaceae									
<i>Leptoscyphus porphyrius</i> (Nees) Grolle					X	X			
<i>Leptoscyphus species</i> 01						X			
<i>Lophocolea bidentata</i> (L.) Dumort.		X	X						
<i>Lophocolea liebmanniana</i> Gottsche		X	X						
Hookeriaceae									
<i>Callicostella pallida</i> (Hornsch.) Angström		X	X	X					
Hypnaceae									
<i>Chryso-hypnum diminutivum</i> (Hampe) W.R. Buck		X							
<i>Isopterygium tenerum</i> (Sw.) Mitt.		X	X	X					
<i>Phyllocladon truncatulus</i> (Müll. Hal.) W.R. Buck		X							
<i>Rhacopilopsis trinitensis</i> (Müll. Hal.) E. Britton & Dixon		X	X					X	
<i>Vesicularia vesicularis</i> (Schwägr.) Broth.		X	X						
Jubulaceae									
<i>Frullania apiculata</i> (Reinw., Blume & Nees) Nees	X		X	X	X	X			
<i>Frullania caulisequa</i> (Nees) Nees	X		X	X	X				
<i>Frullania gibbosa</i> Nees							X		
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.			X	X	X	X			
<i>Frullania nodulosa</i> (Reinw., Nees & Blume) Gottsche et al.		X	X		X				
<i>Frullania patens</i> Lindenb.					X				
<i>Frullania riojaneirensis</i> (Raddi) Spruce		X	X						
<i>Frullania</i> subg. <i>Chonanthelia</i>								X	
Lejeuneaceae									
<i>Acrolejeunea emergens</i> (Mitt.) Steph.									X
<i>Acrolejeunea torulosa</i> (Lehm. & Lindenb.) Schiff.			X		X		X	X	
<i>Aphanolejeunea camillii</i> (Lehman) R.M.Schuster		X							
<i>Aphanolejeunea contractiloba</i> (A.Evans) R.M.Schuster		X				X			

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Aphanolejeunea kunertiana</i> Steph.							X		
<i>Aphanolejeunea microscopia</i> var. <i>africanus</i> (Taylor) A.Evans		X							
<i>Aphanolejeunea</i> species 01 INPA 217693									X
<i>Archilejeunea auberiana</i> (Mont.) A. Evans			X						
<i>Archilejeunea crispistipula</i> (Spruce) Steph.						X	X		
<i>Archilejeunea fuscescens</i> (Hampe & Lehm.) Fulford	X		X	X	X	X	X	X	X
<i>Archilejeunea parviflora</i> (Nees.) Schiffn.	X	X	X			X	X	X	X
<i>Archilejeunea</i> species 01 INPA 217802							X	X	
<i>Brachiolejeunea conduplicata</i> (Steph.) Gradstein						X			
<i>Caudalejeunea lehmanniana</i> (Gottsche) A.Evans	X	X					X	X	
<i>Ceratolejeunea cerathanta</i> (Nees & Mont.) Schiffn.						X			
<i>Ceratolejeunea coarina</i> (Gottsche) Schiff.			X	X				X	
<i>Ceratolejeunea confusa</i> R.M.Schust.	X		X		X		X		
<i>Ceratolejeunea cornuta</i> (Spruce) Steph.	X	X	X	X	X	X	X	X	X
<i>Ceratolejeunea cubensis</i> (Mont.) Schiff.	X	X	X	X		X	X	X	X
<i>Ceratolejeunea desciscens</i> (Sande-Lac) Schiff.						X	X		
<i>Ceratolejeunea guianensis</i> (Nees & Mont.) Steph.			X	X		X			
<i>Ceratolejeunea laetefusca</i> (Aust) Schust.	X	X				X		X	X
<i>Ceratolejeunea malleigera</i> (Spruce) Steph.						X		X	
<i>Ceratolejeunea minuta</i> G. Dauphin	X					X			X
<i>Ceratolejeunea</i> species 01								X	
<i>Cheilolejeunea acutangula</i> (Nees) Grolle							X		X
<i>Cheilolejeunea adnata</i> (Kunze ex Lehm.) Grolle		X	X	X	X	X			
<i>Cheilolejeunea clausa</i> (Nees & Mont.) R.M.Schust.		X						X	
<i>Cheilolejeunea discoidea</i> (Lehm. & Lindenb) Kachroo & R M. Schust							X		
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.L. Zhu	X	X	X	X	X	X	X		X
<i>Cheilolejeunea neblinensis</i> Ilkiu-Borges & Gradstein	X						X	X	X
<i>Cheilolejeunea oncophylla</i> (Angstr.) Grolle & E. Reiner									X
<i>Cheilolejeunea rigidula</i> (Mont.) R.M.Schust.	X	X	X	X	X	X	X	X	X
<i>Cheilolejeunea trifaria</i> (Reinw., Blume & Nees) Mizut.		X	X	X	X	X	X		X
<i>Cololejeunea cardiocarpa</i> (Mont.) Steph.		X							
<i>Cololejeunea</i> species 01 http://hanstersteege.jalburn.net		X							
<i>Colura cylindrica</i> Herz.			X						
<i>Colura greig-smithii</i> Jovet-Ast		X							
<i>Colura tortifolia</i> (Nees & Mont.) Steph.			X						
<i>Cyclolejeunea convexistipa</i> (Lehm. & Lindenb.) Evans	X		X	X					X
<i>Cyclolejeunea luteola</i> (Spruce) Grolle						X	X		X
<i>Cyclolejeunea peruviana</i> (Lehm. & Lindenb.) A. Evans							X		
<i>Diplasiolejeunea brunnea</i> Steph.		X					X		X

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Diplasiolejeunea cavifolia</i> Steph.			X	X	X				
<i>Diplasiolejeunea cobrensis</i> Gottsche ex Steph.	X				X				
<i>Diplasiolejeunea pellucida</i> (C.F.W. Meissn. ex Spreng.) Schiffn.			X	X	X				
<i>Diplasiolejeunea rudolphiana</i> Steph.	X	X	X	X	X				X
<i>Drepanolejeunea crucianella</i> (Taylor) A. Evans		X							
<i>Drepanolejeunea fragilis</i> Bischl.	X	X	X	X	X	X		X	
<i>Drepanolejeunea lichenicola</i> (Spruce) Steph.		X							
<i>Drepanolejeunea orthophylla</i> Bischl.		X							
<i>Drepanolejeunea</i> species 01 MPEG 186262	X								
<i>Echinocolea asperrima</i> (Spruce) R.M. Schust.		X							
<i>Frullanoides liebmanniana</i> (Lindenb. & Gottsche) Slageren				X					
<i>Haplolejeunea cucullata</i> (Steph.) Grolle	X				X	X		X	
<i>Harpalejeunea oxyphylla</i> (Nees & Mont.) Steph.	X	X	X					X	
<i>Harpalejeunea stricta</i> (Lindenb. & Gottsche) Steph.		X	X		X				X
<i>Harpalejeunea tridens</i> (Besch. & Spruce) Steph.		X							
<i>Lejeunea boryana</i> Mont.	X	X							
<i>Lejeunea caespitosa</i> Steph.		X						X	
<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gottsche et al.			X						
<i>Lejeunea controversa</i> Gottsche		X							
<i>Lejeunea flava</i> (Sw.) Nees		X	X					X	X
<i>Lejeunea laetevirens</i> Nees & Mont.	X	X	X		X	X	X	X	X
<i>Lejeunea longifissa</i> Steph.			X						
<i>Lejeunea magnoliae</i> Lindenb. & Gott.								X	
<i>Lejeunea maxonii</i> (A. Evans) X.-L. He		X							
<i>Lejeunea monimiae</i> (Steph.) Steph.		X							
<i>Lejeunea phyllobola</i> Nees & Mont.	X		X				X		X
<i>Lejeunea reflexistipula</i> (Lehm. & Lindenb.) Gottsche et al.		X	X				X		
<i>Lepidolejeunea involuta</i> (Gottsche) Grolle		X	X		X				
<i>Lepidolejeunea ornata</i> (H. Rob.) R.M. Schust		X							
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn.	X	X	X	X	X		X		X
<i>Leptolejeunea obfuscata</i> (Spruce) Steph.		X							
<i>Leucolejeunea unciloba</i> (Lindenb.) A. Evans			X						
<i>Lopholejeunea nigricans</i> (Lindenb.) Schiffn.				X	X				
<i>Lopholejeunea quelchii</i> Steph.		X							
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.		X	X	X	X		X	X	X
<i>Macrocolura sagittispula</i> (Spruce) R.M. Schust.			X	X					
<i>Mastigolejeunea auriculata</i> (Wils.) Schiffn.	X	X	X	X	X			X	X
<i>Metalejeunea cucullata</i> (Reinw. et. al) Grolle			X						
<i>Microlejeunea acutifolia</i> Steph.		X	X					X	X

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Microlejeunea aphanella</i> (Spruce) Steph.									X
<i>Microlejeunea bullata</i> (Taylor) Steph.	X	X				X	X	X	X
<i>Microlejeunea epiphylla</i> Bischl.	X	X	X		X	X	X	X	X
<i>Microlejeunea globosa</i> (Spruce) Steph.	X	X					X		
<i>Neurolejeunea breutelii</i> (Gott.) Evans		X	X						
<i>Neurolejeunea seminervis</i> (Spruce) Schiffn.				X	X				
<i>Odontolejeunea lunulata</i> (Weber) Schiffn.		X							
<i>Odontolejeunea rhomalea</i> (Spruce) Steph.		X							
<i>Oryzolejeunea saccatiloba</i> (Steph.) Gradstein	X								X
<i>Oryzolejeunea</i> species 01		X							
<i>Pictolejeunea picta</i> (Gottsche ex Steph.) Grolle	X		X	X		X		X	
<i>Prionolejeunea aemula</i> (Gottsche) A. Evans		X							
<i>Prionolejeunea denticulata</i> (Web.) Schiff.		X							
<i>Prionolejeunea microdonta</i> (Gottsche) Steph.							X	X	
<i>Prionolejeunea muricatoserrulata</i> (Spruce) Steph.	X	X						X	
<i>Pycnolejeunea contigua</i> (Nees) Grolle	X	X	X		X	X	X	X	X
<i>Pycnolejeunea macroloba</i> (Mont.) Schiffn.	X	X	X	X	X	X	X		X
<i>Pycnolejeunea papillosa</i> X.-L. He	X					X			
<i>Pycnolejeunea</i> species 01 INPA 186240	X				X		X	X	X
<i>Rectolejeunea berteriana</i> (Gottsche ex Steph.) A. Evans	X	X						X	X
<i>Rectolejeunea emarginuliflora</i> (Gottsche ex Schiffn) Evans	X	X						X	X
<i>Rectolejeunea flagelliformis</i> A. Evans			X	X	X				
<i>Stictolejeunea squamata</i> (Willd.) Schiffner		X	X	X				X	
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gott.) Evans		X	X	X			X		X
<i>Symbiezidium</i> species 01 INPA 217504							X		
<i>Symbiezidium transversale</i> var. <i>hookerianum</i> (Gottsche) Gradst. & van Beek		X		X	X				
<i>Taxilejeunea asthenica</i> Spruce (Steph.)		X							
<i>Taxilejeunea obtusangula</i> (Spruce) A. Evans		X							
<i>Thysananthus amazonicus</i> (Spruce) Schiffn.	X			X	X				
<i>Trachylejeunea aneogyna</i> (Spruce) Grolle	X						X	X	X
<i>Trachylejeunea</i> species 02 MPEG 186234	X								
<i>Lejeuneaceae</i> species 01 INPA 217817, http://hanstersteege.jalbum.net/	X					X	X	X	X
<i>Lejeuneaceae</i> species 02 INPA 217594					X	X	X		
<i>Lejeuneaceae</i> species 03 Mota de Oliveira pers. coll. ECT02Z4		X							
<i>Lejeuneaceae</i> species 04 INPA 217625									X
<i>Lejeuneaceae</i> species 05 Mota de Oliveira pers. coll. ECT02Z1		X							
<i>Lejeuneaceae</i> species 07 MPEG 186263	X								
<i>Lejeuneaceae</i> species 08 INPA 217800								X	
<i>Lejeuneaceae</i> species B MPEG 186234	X								

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Verdoornianthus griffinii</i> Gradst.	X	X				X	X		X
<i>Vitalianthus urubuensis</i> Zartman & I. L. Ackerman	X					X	X	X	
<i>Xylolejeunea crenata</i> (Spruce) Steph.					X	X	X		
Lepidoziaceae									
<i>Arachniopsis</i> species 01 INPA 217507						X			
<i>Bazzania aurescens</i> Spruce		X							
<i>Bazzania cuneistipula</i> (Gottsche, Lindenb. & Nees) Trevis.					X		X		
<i>Bazzania hookeri</i> (Lindenb.) Trevis.			X		X		X		X
<i>Bazzania</i> species 01 INPA 217566						X			
<i>Bazzania</i> species 02 INPA 217501							X		
<i>Micropterygium leiophyllum</i> Spruce							X		X
<i>Micropterygium parvistipulum</i> Spruce							X		X
<i>Micropterygium trachyphyllum</i> Reimers							X		
<i>Zoopsidella macella</i> (Steph.) R.M. Schuster									X
Lepidoziaceae species 01 INPA 217624							X		X
Leucobryaceae									
<i>Leucobryum martianum</i> (Hornsch.) Hampe ex Müll. Hal.					X	X	X		X
<i>Ochrobryum gardneri</i> (C. Müll.) Mitt							X	X	X
<i>Octoblepharum albidum</i> Hedw.	X	X	X	X	X	X	X	X	X
<i>Octoblepharum cocuiense</i> Mitt.							X		
<i>Octoblepharum cylindricum</i> Schimp. ex Mont.				X	X				
<i>Octoblepharum pulvinatum</i> (Dozy & Molck.) Mitt.	X		X	X			X	X	X
<i>Octoblepharum stramineum</i> Mitt.			X		X			X	X
Leucomiaceae									
<i>Leucomium strumosum</i> (Hornsch.) Mitt.		X	X	X				X	
Leucophanaceae									
<i>Leucophanes molleri</i> Müll. Hal.		X	X						X
Macromitriaceae									
<i>Groutiella apiculata</i> (Hook.) Crum & Steere			X	X					
<i>Groutiella obtusa</i> (Mitt.) Florsch.		X		X	X				
<i>Groutiella tomentosa</i> (Hornsch.) Wijk. & Marg.		X	X						
<i>Macromitrium cirrosum</i> (Hedw.) Brid.				X	X				
<i>Macromitrium pellucidum</i> Mitt.				X	X				
<i>Macromitrium podocarpi</i> Müll. Hal.			X						
<i>Macromitrium punctatum</i> (Hook & Grev.) Brid.			X	X	X				
<i>Schlotheimia rugifolia</i> (Hook.) Schwaegr.					X				
<i>Schlotheimia torquata</i> (Hedw.) Brid.					X				
Meteoriaceae									
<i>Zelometeorium patulum</i> (Hedw.) Manuel		X	X		X				

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
Metzgeriaceae									
<i>Metzgeria decipiens</i> Schiff.		X	X						
Metzgeriaceae species 01 INPA 217647							X		X
Neckeraceae									
<i>Neckeropsis disticha</i> (Hedw.) Kindb.		X							
<i>Neckeropsis undulata</i> (Hedw.) Reichdt.		X	X						
<i>Porotrichum substriatum</i> (Hampe) Mitt.		X	X	X					
Phylloprepariaceae									
<i>Mniomalia viridis</i> (Mitt.) Müll. Hal.		X		X					
Plagiochilaceae									
<i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lindenb.		X	X	X				X	X
<i>Plagiochila laetevirens</i> Lindenb.			X	X					
<i>Plagiochila montagnei</i> Nees			X		X		X		
<i>Plagiochila simplex</i> (Sw.) Lindenb.	X								
<i>Plagiochila</i> species 00					X				
<i>Plagiochila</i> species 01 http://hanstersteege.jalburn.net		X				X			
<i>Plagiochila</i> species 02 http://hanstersteege.jalburn.net						X			
<i>Plagiochila</i> species 05 http://hanstersteege.jalburn.net		X							
<i>Plagiochila</i> species 06 http://hanstersteege.jalburn.net		X							X
<i>Plagiochila</i> species 09 http://hanstersteege.jalburn.net		X							
<i>Plagiochila subplana</i> Lindenb.			X	X	X			X	
Pterobryaceae									
<i>Henicodium geniculatum</i> (Mitt.) W.R. Buck		X	X		X				
<i>Jaegerina scariosa</i> (Lorentz) Arzeni			X						
<i>Orthostichopsis tetragona</i> (Sw. ex Hedw.) Broth.			X	X	X				
<i>Pirella cymbifolia</i> (Sull.) Cardot		X							
<i>Pirella pohlii</i> (Schwaegr.) Card.		X	X	X					
Racopilaceae									
<i>Racopilum tomentosum</i> (Hedw.) Brid.			X						
Radulaceae									
<i>Radula flaccida</i> Lindenb. & Gott.		X	X		X				
<i>Radula husnotii</i> Castle		X	X						
<i>Radula javanica</i> Steph.		X	X		X			X	
<i>Radula mammosa</i> Spruce		X							
<i>Radula</i> species 01 Mota de Oliveira pers. collection ECT03Z2		X							
Sematophyllaceae									
<i>Acroporium pungens</i> (Hedw.) Broth.			X	X	X				
<i>Meiothecium boryanum</i> (Müll. Hal.) Mitt.		X							
<i>Meiothecium urceolatum</i> (Schwaegr.) Mitt.			X						

Continue

Appendix 1. Continuation.

Family	CX	EC	FG	MM	MW	RD	SG	TA	UR
<i>Sematophyllum subpinnatum</i> (Brid.) Britt.		X	X	X	X				
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	X	X		X	X	X	X	X	X
<i>Taxithelium planum</i> (Brid.) Mitt.		X	X	X	X				
<i>Taxithelium pluripunctatum</i> (Renauld & Cardot) W.R.Buck			X						
<i>Trichosteleum papillosum</i> (Hornsch.) A. Jaeger	X			X	X	X		X	X
Stereophyllaceae									
<i>Pilosium chlorophyllum</i> (Hornsch.) C. Mull.	X			X		X		X	X
Thamnobryaceae									
<i>Homaliodendron piniforme</i> (Brid.) Enroth		X							
Thuidiaceae									
<i>Cyrtohypnum involvens</i> (Hedw.) W.R.Buck & H.A. Crum			X						
<i>Cyrtohypnum scabrosulum</i> (Mitten) W.R. Buck et Crum		X							
<i>Cyrtohypnum schistocalyx</i> (Müller Hal.) W.R. Buck & Crum		X							