

Species richness and phytogeography of the Bryophyte flora of the Guianas, with special reference to the lowland forest*

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*Studies on the flora of the Guianas 46. Dedicated to Jeanne Florschütz-de Waard on the occasion of her 65th birthday.

Abstract. The Guianas (French Guiana, Suriname, Guyana) are probably one of the last areas of the world covered largely by virgin lowland rain forest. Species diversity of epiphytic bryophytes was investigated in dry evergreen forest and mixed forest using mountaineering techniques to ascend into the canopy. The results indicate that the lowland rain forest is richer in species than previously believed due to neglect of the canopy flora, which may hold more than 50% of the local species. The mixed forest holds the richest flora and on one single forest tree up to 67 bryophyte species were found (50 on average); 28 trees yielded 154 species. A species/area curve indicates that epiphytic bryophyte species are usually commonly distributed in the forest and a few trees may yield much of the local flora.

A recent checklist of the Guianas includes over 600 species of bryophytes: 375 Hepaticae and 234 Musci. As the region lacks in altitude (except on Mt. Roraima) the general character of the bryophyte flora of the Guianas is typically lowland neotropical. Over 80% of the species are rather widespread in tropical America (Amazonian species included), and the remaining are Guayana Highlands, northern Amazonian or Caribbean elements. Endemism is very low: 2.5 %.

Introduction

The Guianas are situated between 1°-9° North and 51°-62° West, and comprise the countries French Guiana (an overseas French Department), Suriname (formerly Dutch Guiana) and Guyana (formerly British Guiana). The latter two are now independent countries. The total area of the Guianas is about 470,000 square kilometers.

The Guianas are one of the last areas of the world covered largely by virgin rain forest. A reason for the presence of vast areas of untouched rain forest is the very thin

population of the region, which totals ca. 1.3 million people. Rainfall varies between about 2000-4000 mm annually (values may be higher in the mountains) and there are one or two dry seasons which last 1-3 month each (Lindeman and Mori 1989).

Most of the population is concentrated in the coastal region, where the forest gives way to swamps, savannas and cultivated land. The interior of the Guianas is rather hilly, with numerous small mountain ranges not exceeding 1000 m. in altitude. The highest mountains of the Guianas are the sandstone table mountains or tepuis of the Guayana Highlands, which extend



Fig. 1. Map of the Guianas, showing the main areas where bryophyte inventories of the rainforest were carried out recently. 1. Saül, French Guiana (Montfoort and Ek pers. comm.) 2. Kabalebo, western Suriname (Florschütz-de Waard and Bekker 1987). 3. Mabura Hill, Guyana (Cornelissen and Ter Steege 1989; Biesmeijer and Bleij pers. comm.) 4. Upper Mazaruni District (incl. Mount Roraima), Guyana (Gradstein and Florschütz-de Waard 1989).

in the east. In Venezuela the tepuis reach up to 3000 m. but in the Guianas they are much lower and usually about 1000- 1200 m. high. The highest peak of the Guianas is Mount Roraima (2750 m.) at the border of Venezuela, Guyana and Brazil. This is the only mountain in the Guianas which harbours a well-developed montane flora.

The bryophyte flora of the Guianas became known in the 19th century by the important collections of F.R.M. Leprieur from French Guiana (Montagne 1835, 1851) and H.A.H. Kegel from Suriname (Müller 1848, Lindenberg and Gottsche 1851), which hold many

types. Later, Richards (e.g. 1952, 1954) did his pioneering work on tropical rainforest ecology and the bryophyte communities of lowland rain forest at Moraballi Creek in Guyana. Florschütz (1964) and Florschütz-de Waard (1986) produced an important treatment of the mosses of the Guianas in the 'Flora of Suriname'. The liverworts of the Guianas remained poorly known, however.

In recent years the senior author, together with his research associates, carried out investigations on the bryophyte flora of the Guianas in the framework of the 'Flora of the Guianas' project (Florschütz-de Waard and Bekker

with his research associates, carried out investigations on the bryophyte flora of the Guianas in the framework of the 'Flora of the Guianas' project (Florschütz-de Waard and Bekker 1987, Frahm and Gradstein 1987, Inoue & Gradstein 1988, Grolle and Gradstein 1988, Cornelissen and Ter Steege 1989, Gradstein and Hekking 1989, Gradstein & Florschütz-de Waard 1989). Main goals of the program were to inventory selected areas (Fig. 1) with the purpose of obtaining more insight in the bryophyte richness and diversity of the various habitats within the Guianas, in particular the rain forest, and to produce a checklist for the region as a basis for future Flora treatments and phytogeographic studies. The present paper briefly reviews some of the results.

Species Richness of the Lowland Rain Forest

The Guianan rain forest has been described by Richards (1952) and De Granville (1988). Richards (1934, 1954, 1984), moreover, was the first to study the species richness of the rain forest bryophytes. At Moraballi Creek, Guyana, in an area of a few square kilometers entirely covered with lowland rain forest, he found 48 species of mosses in four months of collecting. About 48 species of liverworts were identified, but as about half of the liverwort collection was lost before identification, the number of liverworts is uncertain and is estimated by the author to be as much as 100. The author concluded that the lowland rain forest is rather poor in species and that there are more liverwort species than mosses.

Florschütz-de Waard and Bekker (1987) compared species richness and diversity in the understory of three different lowland rainforest types (dry-evergreen or savanna forest, marsh or inundated forest, mixed or mesophytic forest) in West Suriname, in an area of about 200 square kilometers. Although epiphyllous liverworts were

not taken into account, the authors could confirm that liverworts are more numerous than mosses in the rain forest. Species richness proved highest in periodically flooded marsh forest: 41 mosses and 70 liverworts. Fewer species were found in the mixed forest (34 mosses, 47 liverworts) and the dry evergreen forest (26 mosses, 44 liverworts). The authors suggested that the higher air humidity, better illumination and somewhat lower average temperature in the understory of the marsh forest, as compared to the other forest types, were responsible for the higher species richness in the former. They also found significant floristic differences among the three forest types, especially among the mosses. These results are in general agreement with data from other areas (see Richards 1984).

Although Florschütz-de Waard and Bekker inventoried a much larger area than Richards, they found fewer species of bryophytes. Presumably this is due to the fact that their study was restricted to the understory of the forest. The bryophyte flora of the canopy of the rain forest is very poorly known. Until recently, information about its composition has been obtained mainly from felled trees and fallen branches. Richards (1984) found that the tree crowns have fewer species than the understory and only about half of the species in the former are also found in the latter. Presumably many canopy species may occur outside the forest in relatively exposed locations at low levels, for instance in scrub, orchards, on roadside trees and on rock. The available data are fragmentary, however, and do not allow for firm conclusions.

In order to obtain more detailed information on the bryophyte flora of the rainforest canopy, inventories were recently carried out in the different rainforest types of the Guianas by graduate students from the University of Utrecht. Whole standing trees were sampled by means of a modified mountaineering technique (Ter Steege and

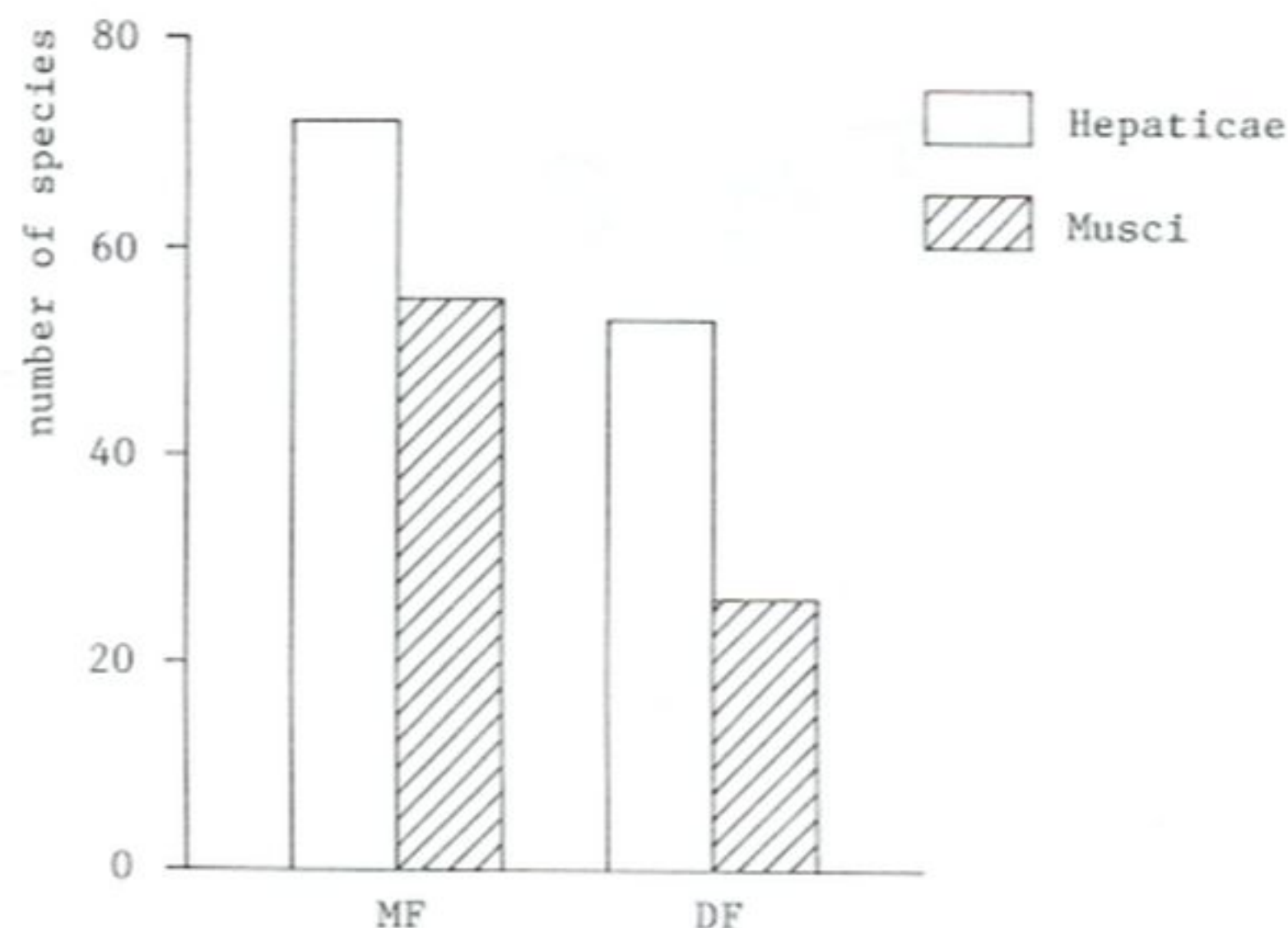


Fig. 2. Species richness of bryophytes in the mixed forest (MF) of Saül, French Guiana and the dry evergreen forest (DF) of Mabura Hill, Guyana.

forest. Presumably the higher humidity in the mixed forest, the greater richness in tree species and the larger diversity in microhabitats of the latter account for the larger number of species found in the mixed forest. While most of the sampled trees in the mixed forest are different species, those sampled in the dry evergreen belong to only two species of 'wallaba' (*Eperua falcata*, *E. grandiflora*).

As expected, our figures on species richness of the different forest types are much higher than those given by Florschütz-de Waard and Bekker (1987) for the understory of the forest. It appears that in the dry evergreen forest more than half of the species are restricted to the tree crowns and the upper portions of the trunks (Table 1). In the mixed forest this percentage is somewhat lower and more species from the tree crowns are also found lower down on the trunks. On one single tree in the mixed forest of French Guiana (Saül) up to 67 bryophyte species were found; the minimum number per tree

was 29, the average number 50. In comparison, these figures were 54, 12 and 32 respectively for lichens and 64, 25 and 46 respectively for vascular epiphytes (Ek & Montfoort, pers. comm.) Nine species of trees carried more than 90 species of cryptogamic epiphytes (bryophytes and lichens) on single host individuals and the highest number of cryptogamic species recorded on one single tree (*Protium* sp.) was 106. The number of epiphytic species found in the mixed forest of French Guiana are the highest thus far recorded for lowland rainforest.

Previous authors have suggested that bryophyte species richness in the tropical lowland rain forest is much lower than in tropical montane rain forest and may also be lower than in temperate forests (Richards 1984, Schuster 1988, Gradstein & Pócs 1989). None of these studies took full account of the canopy flora, however. Our data from the Guianan rain forest indicate that species richness of epiphytic bryophytes in tropical lowland rainforest is usually higher

	Mosses	Liverworts	Total
exclusively above 10 m.	16 (55%)	22 (47%)	38 (50%)
exclusively below 10 m.	2 (7%)	6 (13%)	8 (11%)
both above and below 10 m.	11 (38%)	19 (40%)	30 (39%)

Table 1. Occurrence of epiphytic bryophyte species above and below 10 m. height on eleven trees (*Eperua falcata*, *E. grandiflora*) in the dry evergreen forest ("wallaba forest") of Mabura Hill, Guyana. Numbers of species are given.

than in temperate forests; it is lower than in tropical montane rainforests, although less than previously assumed. Barkman (1959) found on average 20-30 species of cryptogamic epiphytes (bryophytes and lichens) per tree in The Netherlands, with a maximum of 45. Individual trees in a montane rainforest of Colombia at 2500 m., however, carry 70 species of bryophytes on average and on four trees 112 bryophyte species were found (Wolf pers. comm.); three fourth of them are liverworts.

Vertical distribution patterns on the tree differ greatly among individual epiphytic species, and usually a distinction can be made between 'specialists', which have a narrow vertical amplitude and 'generalists', which show little height preference (Cornelissen and Ter Steege 1989). A difference in vertical distribution was also observed between corticolous and epiphyllous species in the mixed forest (Fig. 3). Whereas the number of corticolous species per tree increases towards the outer canopy, epiphyllous

species decrease in number. Epiphylls require more shade and higher humidity than many other epiphytes and are thus largely confined to the understory and the shaded lower part of the canopy (Richards 1984).

A species/area curve for epiphytic bryophytes of the mixed forest of French Guiana indicates that most bryophyte species are common in the forest and a few trees may yield much of the local bryophyte flora (Fig. 4). An inventory of twenty eight trees, belonging to twenty two different species, yielded 154 species of bryophytes (Montfoort & Ek pers. comm.) About 75% of the species were collected on five trees only and each additional tree sampled yielded only few (1-3) new species. Species area curves for tree base and tree crown separately are rather similar, but with 75% limits reached at slightly larger numbers of trees (ca. 10-13 trees). Apparently the minimum area for epiphytic bryophytes in this forest is very small, as opposed to tree species (Mori 1987). The results

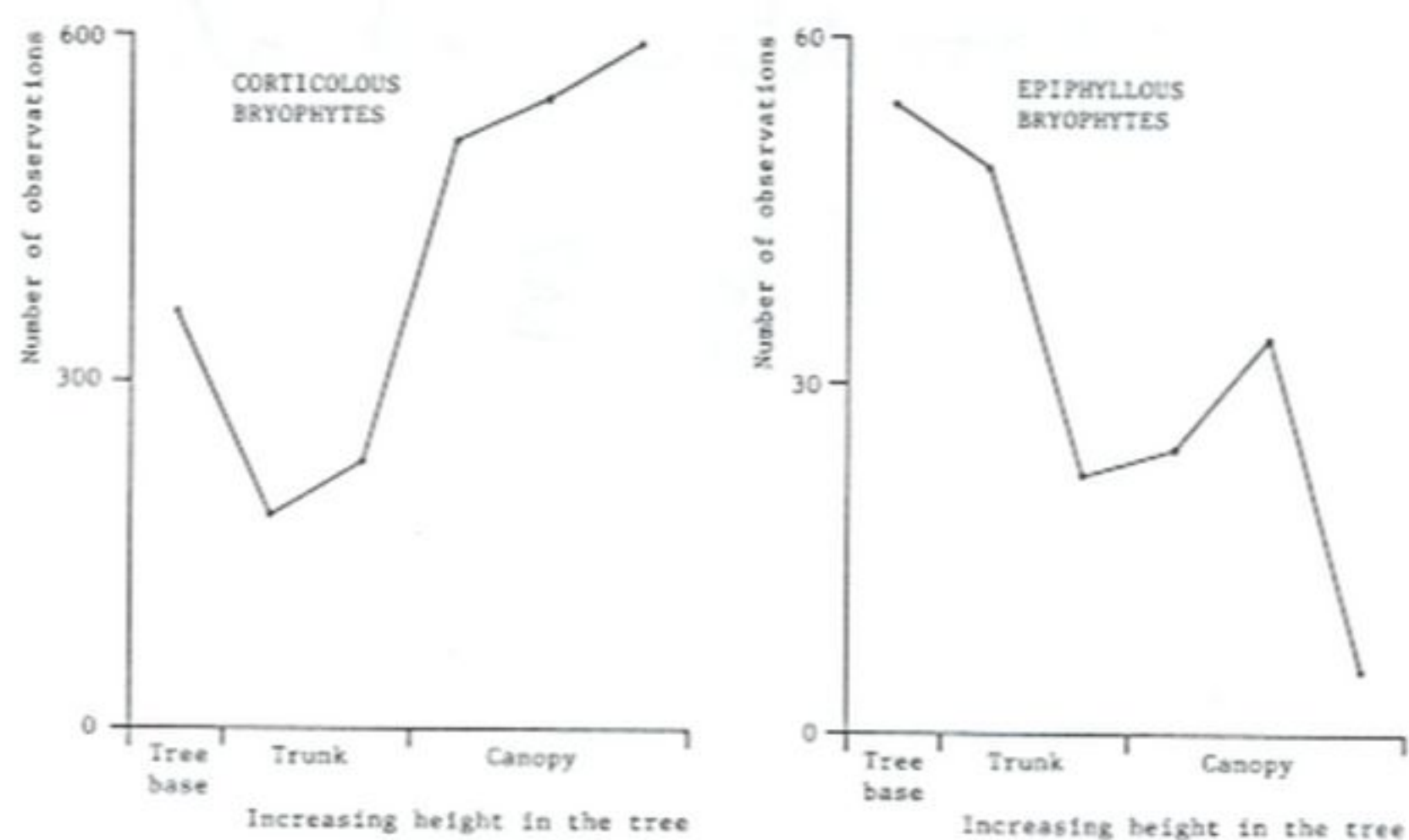


Fig. 3. Vertical distribution of corticolous and epiphyllous bryophytes on trees in the mixed forest of Saül, French Guiana.

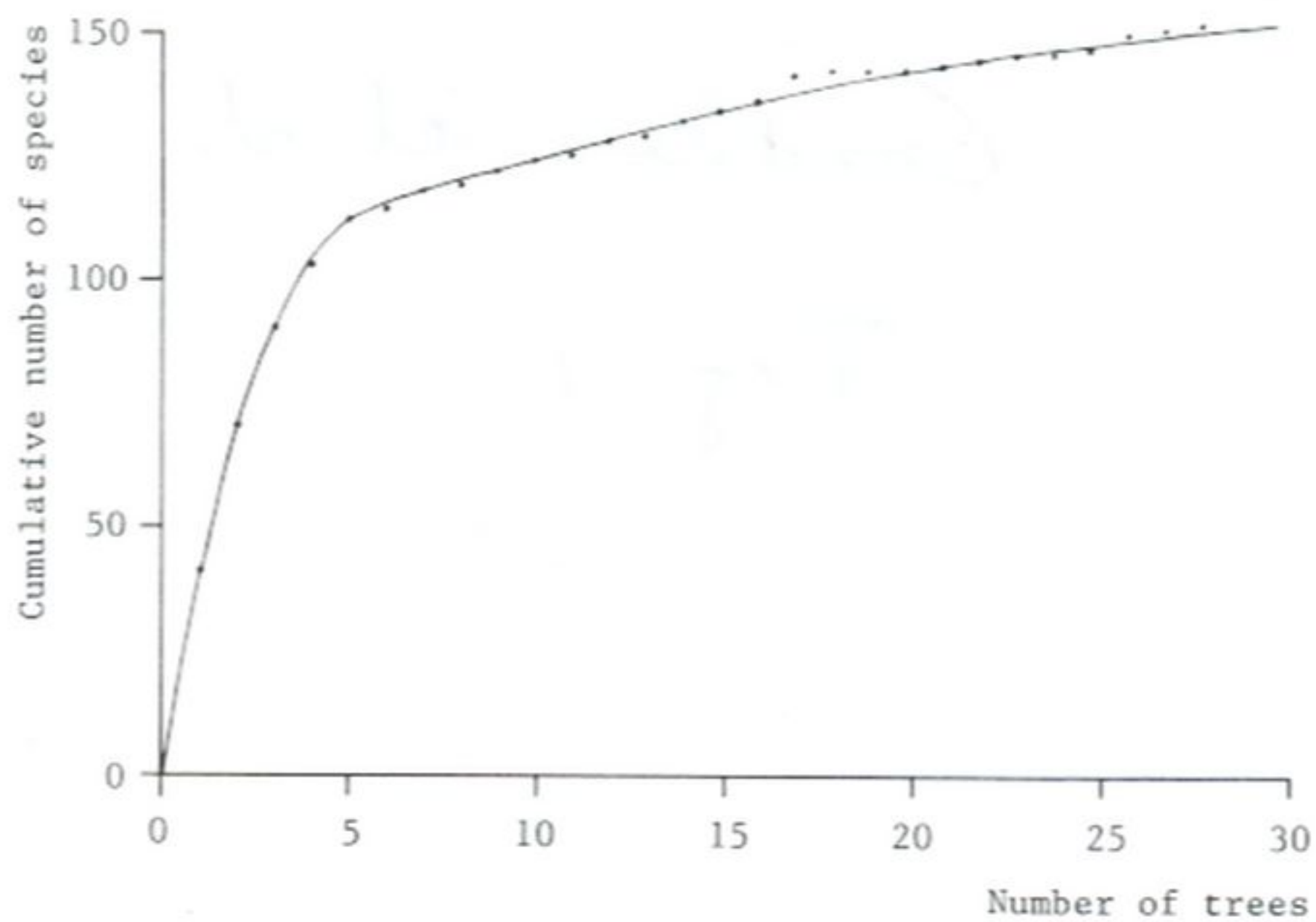


Fig. 4. Species/area curve of epiphytic bryophytes in the mixed forest of Saül, French Guiana. Area is expressed by number of trees sampled.

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Phytogeography

The recent checklists of the bryophytes of the Guianas include 234 species of mosses (Florschütz-de Waard pers. comm.) and 375 species of liverworts (Gradstein and Hekking 1989). Some further liverworts not included in the checklist are reported by Gradstein and Florschütz-de Waard (1989). The actual bryophyte flora of the region may be estimated at about 250 species of mosses and 400 liverworts, taking into account revisions of old names and new discoveries.

The majority of the bryophyte species seem to be rather widespread in Tropical America. Guianan species with more

limited distributions fall in one of the following five categories:

1. Guayana Highlands element (17 spp.). This category includes (sub)montane species which are largely restricted to the tepuis of the Guayana Highlands. In the Guianas most of these species are only known from the North slope of Mount Roraima (see Gradstein and Florschütz-de Waard 1989). Many of them are restricted to the eastern portion of the Guayana Highlands, which seems to be a speciation center for bryophytes: the 'Gran Sabana' element (Robinson 1986). Species that belong to the latter element are marked "(GS)".

Mosses: *Brachymenium sipapoense*, *Dicranoloma brittonae* (also Panama), *Leucomium steerei* (GS), *Trichostomum duidense*.

Liverworts: *Adelanthus squarrosus* (GS), *Calypogeia venezuelana*, *Echinocolea sp. nov.* (GS), *Haesselia acuminata* (GS), *H. roraimensis* (GS), *Micropterygium grandistipulum* (GS), *M. tenax*, *M. tumidulum* (GS), *Mytilopsis albifrons*, *Pleurozia heterophylla* (GS), *Radula gradsteinii* (GS), *Trabacellula tumidula* (GS), *Vanaea plagiophiloides* (GS).

2. Northern Amazonian element (20 spp.). This category includes species restricted to the lowland rain forests and savannas at the northern outskirts of the Amazon basin and the Upper Orinoco. Their range extends maximally from eastern Colombia to the state of Para, Brasil. Some of them go up the lower slopes of the Guayana Highlands, up to ca. 1000 m. Lowland taxa endemic to the Guianas (marked 'E') are included in this category, as well as species from the rich upper Rio Negro flora (Spruce 1884-85). Mosses: *Calymperes mitrafugax* (E), *Fissidens geyskesii* (E), *Hydropogon fontinaloides*, *Micromitrium telephorotheicum* (also northeastern Brazil), *Sphagnum negrense*, *Syrrhopodon*

helicophyllus, *S. hornschuchii*.

Liverworts: *Arachniopsis pecten*, *Drepanolejeunea integribracteata* (E), *Frullania* sp. nov., *Haplolejeunea cremersii* (E), *Marsupidium gradsteinii*, *Plagiochila gymnocalyx*, *Pteropsiella serrulata*, *Radula guyanensis* (E), *R. mazarunensis* (E), *Schusterolejeunea inundata*, *Stenorrhypis grollei* (E), *Stictolejeunea balfourii* var. *bekkeri* (E), *Zoopsis macella*.

3. Amazonian element. This category includes species occurring throughout the Amazon basin and in the Guianas, but not elsewhere. A full list of the Amazonian species cannot yet be given, however, and needs further work. Examples are the mosses *Calymperes platyloma*, *C. rubiginosum*, *Octoblepharum cocuiense* and *Syrrophodon simmondsii* and the liverworts *Archilejeunea juliformis*, *Archilejeunea crispistipula*, *Calypogeia miquelii*, *Lepidolejeunea ornata*, *Neurolejeunea seminervis*, *Pycnolejeunea callosa* and *Verdoornianthus griffinii*. In view of the great floristic similarity of the Guianan and Amazonian rainforests (Prance 1989), the Amazonian element could be expected to be a significant component of the Guianan bryophyte flora. However, we estimate that the total percentage will not exceed 5-10%, as many bryophyte species of these lowland forests occur elsewhere in the neotropics as well.

4. Caribbean element (31 spp.). These are oceanic species which are largely restricted to the West Indian islands but in addition occur in adjacent (coastal) continental regions. Some are quite rare in the Guianas and are known there by only one or two collections (e.g. *Calymperes guildingii*, *Plagiochila dussiana*, *Cystolejeunea lineata*), others are rather common in the Guianas such as *Groutiella obtusa* and *Campylopus cubensis*. A few are restricted to the coastal plain of the Guianas (*Frullanoides corticalis*), but the majority of the Caribbean species occur in the interior, in particular on the table

mountains. Pócs (1988) recognized Caribbean-Guayana links in his phyto-geographical analysis of the Cuban bryophyte flora.

Mosses: *Brachymenium wrightii*, *Calymperes guildingii*, *C. smithii*, *C. venezuelanum*, *Campylopus cubensis*, *Eucamptodontopsis pilifera*, *Groutiella obtusa*, *Lepidopilidium portoricense*, *Leskeodon cubensis*, *Macromitrium leprieurii*, *M. trinitensis*, *Octoblepharum erectifolium*.

Liverworts: *Alobiella husnotii*, *Bazzania longa*, *Calypogeia cellulosa*, *Colura clavigera*, *C. greig-smithii*, *C. rhynchophora*, *Cystolejeunea lineata*, *Frullanoides corticalis*, *Drepanolejeunea pinnatiloba*, *Micropterygium carinatum*, *Leptoscyphus ovatus*, *Lopholejeunea quelchii*, *Metzgeria innovans*, *Microlejeunea crenulifolia*, *M. epiphylla*, *Nowellia evansii*, *Plagiochila dussiana*, *Riccardia schwaneckeii*, *Symphyogyna marginata*.

5. Disjunct element (8 spp.). This category includes Guianan species with disjunct ranges, which are difficult to explain. Examples are the Andean *Campylopus luteus*, *Omphalanthus paramicola* and *Rhacocarpus purpurascens*, which in the Guayana Highlands have been recorded only from Mt. Roraima. Presumably they occur on other tepuis further westwards as well. *Campylopus surinamensis* and *C. trachyblepharon* represent a 'savanna element' which is disjunct in southeastern Brazil, the Guianas and southeastern North America (Frahm & Gradstein 1987). Finally, at least three species are Guianas-Central America disjuncts: *Renauldia paradoxica*, which is only known from western Panama and Mt. Roraima (Gradstein and Florschütz-de Waard 1989); *Leptolejeunea mexicana*, known from Mexico, the Guianas and S.E. Brazil (Bischler 1969); and *Leptolejeunea foraminulosa* from Mexico and the Guianas (Bischler 1969). The Guianas-Central America disjunction is also known

from forest tree species (Prance 1989) and may be relictual, resulting from extinction in parts of a former continuous range due to past climatic changes.

In conclusion, it appears that the bryophyte flora of the Guianas is largely (80-85%) made up of widespread neotropical or pantropical species. Many of them may have originated in the Amazon basin, but the number of species actually restricted to that area (Amazonian element) may not exceed 5-10% of the Guianan bryophyte flora. About 5% of the species are restricted to the Guayana Highlands or to the northern portion of the Amazon basin, and may have originated there. Another 5% are Caribbean species which presumably colonized the Guianas from the West Indian islands. Two mosses and twelve liverworts are endemic to the Guianas, totalling no more than about 2.5% of the total flora. The majority of them occur on the North slope of Mount Roraima, which is indeed by far the richest locality for bryophytes in the Guianas (Gradstein & Florschütz-de Waard 1989). The very low endemism in the bryophyte flora of the Guianas is probably due to the lack of high mountain ranges and the proximity of the region to Amazonia, allowing the species to distribute freely beyond the borders of the territory.

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